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The evolution of site-selection strategy during dispersal

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ABSTRACT

We propose a mathematical model that enables the evolutionary analysis of site-selection process of dispersing individuals that encounter sites of high or low quality. Since each site can be inhabited by at most one individual, all dispersers are not able to obtain a high-quality site. We study the evolutionary dynamics of the low-quality-site acceptance as a function of the time during the dispersal season using adaptive dynamics. We show that environmental changes affect the evolutionary dynamics in two ways: directly and indirectly via density-dependent factors. Direct evolutionary effects usually follow intuition, whereas indirect effects are often counter-intuitive and hence difficult to predict without mechanistic modeling. Therefore, the mechanistic derivation of the fitness function, with careful attention on density- and frequency dependence, is essential for predicting the consequences of environmental changes to site selection. For example, increasing fecundity in high-quality sites makes them more tempting for dispersers and hence the direct effect of this ecological change delays the acceptance of low-quality sites. However, increasing fecundity in high-quality sites also increases the population size, which makes the competition for sites more severe and thus, as an indirect effect, forces evolution to favor less picky individuals. Our results indicate that the indirect effects often dominate the intuitive effects, which emphasizes the need for mechanistic models of the immigration process.

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1. Introduction

The fate of a dispersing individual is greatly affected by its ability to choose the target patch (Clobert et al., 2012, 2001; Greene, 2003; Johnson and Gaines, 1990; Morris, 2003, 2011; Ronce, 2007). However, the evolution of prospecting and site-selection strategies remains poorly understood due to complex eco-evolutionary interactions (Travis et al., 2012). These interactions have gained little mathematical modeling attention, and models focusing on the site-selection process of dispersing organisms have usually utilized game-theoretical tools or optimization techniques (Baker and Rao, 2004; Brown, 1990; McGill and Brown, 2007; Rosenzweig, 1981; 1987; 1991).

In the studies focusing on the evolution of dispersal process, eco-evolutionary interactions have usually been taken into account only in computational, individual-based models (Poethke et al., 2011; Shaw and Kokko, 2014, 2015), whereas mathematical models involving the eco-evolutionary feedback-loop, have usually focused on the emigration rates assuming some rather simple immigration process. For example, dispersal may be assumed global such that the probability that the disperser arrives in a specific patch is the same independent of the natal patch (Gyllenberg et al., 2002; Parvinen, 2002, 2006; Ronce et al., 2000). Alternatively, dispersal is assumed to occur only between neighboring patches (Travis and Dytham, 1998, 1999; Travis et al., 1999), or the number of habitat patches is assumed small such that the natal patch affects the probability distribution of the target patches, but the disperser is not able to make decisions considering immigration (Doebeli and Ruxton, 1997; McPeek and Holt, 1992; Olivieri et al., 1995; Parvinen, 1999). The eco-evolutionary dynamics of dispersal have also been studied in the context of invasive species, where the evolution of dispersal often affects, e.g., the speed at which invasion proceeds (Perkins et al., 2016, 2013; Travis and Dytham, 2002).

Previously, only a couple of mathematical models have included the evolution of patch selection in the eco-evolutionary setting: the evolution of dispersal strategies in a setting where immigration decisions may depend on the local population size was studied by Parvinen et al. (2012), Nonaka et al. (2013) and Parvinen and Brännström (2016), whereas Gyllenberg et al. (2016) studied the evolution of immigration strategies that depend on the quality of the target patch but remain constant during the dispersal season.

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In this paper, we propose a mathematical model that enables the evolutionary analysis of immigration behavior in the case with two site types: high- and low-quality sites. We assume that a disperser always immigrates into a high-quality site when possible, but immigrates into a low-quality site only with a certain probability that may depend on the time during the dispersal season. In the evolutionary analysis, we utilize the adaptive dynamics approach (Geritz et al., 1998; Metz et al., 1992).

The ecological setting and the assumed life-history of the dispersing species are inspired by the dispersal ecology of Siberian flying squirrels (*Pteromys volans*) analyzed by Hanski and Selonen (2009) and Selonen and Hanski (2010). However, the assumed life-history also applies to the dispersal process of any species that makes decisions about whether to settle in a low-quality patch or risk extended searching for a high-quality patch (Dale et al., 2006; Mabry and Stamps, 2008; Reed et al., 1999; Stamps, 2001).

The dispersal behavior of flying squirrels has two levels. Flying squirrels are born in spring or early summer. Nearly all the juvenile female flying squirrels leave their natal site during a dispersal season that begins in mid-July and ends in late-August. Typically, individual dispersal events last between one day and two weeks (Hanski and Selonen, 2009). The behavior of the juvenile squirrels can be classified roughly into two basic types: some dispersers foray the surroundings of their natal site and search for potential new home ranges while still returning to the natal site for rest between dispersal nights (centrally-based prospecting), whereas some long-distance dispersers start the dispersal season by leaving the natal site on a straight-lined path during several consecutive nights without returning to natal site (sequential dispersal, Selonen and Hanski (2010)). Other animal species vary in the degree to which they use centrally-based or sequential dispersal (Danchin et al., 2001; Reed et al., 1999; Schtickzelle et al., 2007). For example, some species use only centrally-based prospecting strategy (Conradt and Roper, 2006; Danchin et al., 2001; Harrison et al., 1991; Mabry and Stamps, 2008; Vangen et al., 2001). In this paper, we focus on the site-selection process of the centrally-based dispersers.

Living organisms affect the environment in which they live. This environment, in turn, affects the ecological and evolutionary dynamics of the organism (Diekmann et al., 2001, 2003, 1998; Pelletier et al., 2007, 2009; Post and Palkovacs, 2009; Schoener, 2011). Due to this environmental feedback loop, ecological changes may affect the evolutionary dynamics of the site-selection process in two ways: directly and indirectly via population size, availability of free sites and the severeness of competition for sites. Below, we show that the indirect effects are often counter-intuitive, and moreover, in many cases dominate the direct ones. This underlines the need for mechanistically underpinned ecological models when predicting the evolutionary responses to environmental changes.

2. Model and methods

2.1. Ecological assumptions

We assume that the environment consists of a large (mathematically speaking infinite) number of nest sites. Each site can be occupied by at most one individual at a time. The sites are equally connected by dispersal, i.e., dispersal takes place globally via a dispersal pool independent of the site locations. There are two different types of sites: high-quality sites preferred by dispersers whenever available (large aspen trees with cavities in the case of flying squirrels) and low-quality sites less optimal for winter survival and reproduction (twig dreys in the case of flying squirrels).

In order to enable reasonable evolutionary analysis, we base our model on individual level processes (Rueffler et al., 2006). We assume the following life-history of the animal (e.g., flying squirrel):

1. In the spring, adult individuals reproduce with fecundity depending on the site quality.
2. All juveniles disperse. Adults don't disperse. Natal dispersal takes place during dispersal season that is divided into several separate, consecutive dispersal periods. In the case of flying squirrels, dispersal season takes place around August and lasts about two weeks. One dispersal period corresponds to a single night during this fortnight.
3. During each dispersal period, an individual encounters and assesses the quality of at most one site. By exploring the site during one period, the individual is able to deduce its quality (high/low).
4. If a disperser finds a free high-quality site, it immigrates into this site immediately. If a disperser encounters a low-quality site, it immigrates into it with a probability that depends on the time during the dispersal season (how many dispersal periods have passed and how many remain). The vector of these probabilities is the individual's strategy, the evolution of which we study. A disperser that does not immigrate during a certain dispersal period continues the search for sites during the next period, or dies, if the dispersal season is over.
5. Immigration means that the disperser stops the search for high-quality sites and starts to defend its new territory (site). Once a disperser has immigrated, it can no longer be displaced by other incoming immigrants. Thus, a site becomes unoccupied only by the death of the holder, which may take place only during winter.
6. If two or more dispersers are willing to foray the same unoccupied site during the same dispersal period, there is a contest competition, i.e., only one of the dispersers will be able to assess the quality of the site. The winner of this site-competition is a randomly picked contestant. For a low-quality site, it is even possible that the winner of the competition decides to abandon the site and continues the search during the next dispersal period.
7. Mortality occurs only during winter, not during the reproduction and dispersal seasons. Therefore, no site will become vacant during the dispersal season. The model does not involve cost of dispersal in the form of increased mortality during site-search. This is, in the case of flying squirrels, in line with the observations of Selonen and Hanski (2006). However, the cost of dispersal is still indirectly involved, since all dispersers face the risk of being left without a site, and this risk is higher for picky dispersers.
8. When the dispersal season is over, all individuals without a site perish. Those holding a site survive the next winter with a probability that depends on the site quality.

Based on these assumptions, we assemble a discrete-time population model for the ecological dynamics and analyze its evolutionary dynamics using an adaptive dynamics approach.

2.2. Adaptive dynamics

Adaptive dynamics (Dieckmann and Law, 1996; Durinx et al., 2008; Geritz et al., 1998; Geritz et al., 1997; Metz et al., 1996; 1992) is a tool for studying the course of frequency- and density-dependent evolution of continuous traits in ecological models. In adaptive dynamics, evolutionary analyses are based on the invasion fitness function $r(S^{\text{mut}}, E^{\text{res}})$ of a strategy S^{mut} mutant in the environment E^{res} set by the residents. This invasion fitness function is deduced mechanistically from the ecological dynamics whereas most of the other approaches of evolutionary modeling are based on phenomenologically built fitness functions. The evolutionary analysis based on the invasion fitness function involves the following three basic assumptions:

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