Journal of Theoretical Biology 395 (2016) 115–125

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

On the evolution of patch-type dependent immigration

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HIGHLIGHTS

- We analyse the evolution of immigration into two types of patches.
- Generalists settle in any patch, specialists settle only in good patches.
- A high death rate during the dispersal season in rewarding patches favours branching.
- Evolutionary branching may lead to a stable coexistence of a generalist & specialist.

ARTICLE INFO

Article history:
Received 8 September 2015
Received in revised form
21 January 2016
Accepted 23 January 2016
Available online 6 February 2016

Keywords:
Dispersal
Kin competition
Generalist-specialist
Adaptive dynamics
Settlement

ABSTRACT

Empirical studies of dispersal indicate that decisions to immigrate are patch-type dependent; yet theoretical models usually ignore this fact. Here, we investigate the evolution of patch-type dependent immigration of a population inhabiting and dispersing in a heterogeneous landscape, which is structured by patches of low and high reward. We model the decision to immigrate in detail from a mechanistic underpinning. With the methods of adaptive dynamics, we derive both analytical and numerical results for the evolution of immigration when life-history traits are patch-type dependent. The model exhibits evolutionary branching in a wide parameter range and the subsequent coevolution can lead to a stable coexistence of a generalist, settling in patches of any type, and a specialist that only immigrates into patches of high reward. We find that individuals always settle in the patches of high reward, in which survival until maturation, relative fecundity and emigration probability are high. We investigate how the probability to immigrate into patches of low reward changes with model parameters. For example, we show that immigration into patches of low reward increases when the emigration probability in these patches increases. Further, immigration into patches of low reward decreases when the patches of high reward become less safe during the dispersal season.

1. Introduction

Dispersal is the key ecological process of individuals moving between and breeding in different habitats. Dispersal enables populations to thrive in a heterogeneous environment in which habitats differ in size, the geography and location in the landscape, quality, food availability, conspecific presence (Bowler and Benton, 2005; Travis et al., 2012) or the social environment (Cote and Clobert, 2007). Such environmental variations trigger dispersal decisions to be based on local circumstances and individuals come equipped with sophisticated receptors and cognitive or sensory abilities (Doyle, 1975; Ehlinger, 1990; Garant et al., 2005) to smell, detect or sample the environment (Zollner and Lima, 1999; Matter and Roland, 2002; Schooley and Wiens, 2003). Ultimately, individuals may base emigration and immigration decisions only on a specific cue inferred from the habitat type (Rees, 1969; Mitchell, 1977). Examples include scarce coppers which favour flower-rich patches (Schneider et al., 2003), or the butterfly species *Parnassius smintheus* which settles in habitats with high abundance of host plants and nectar flowers (Matter and Roland, 2002).

The number of theoretical studies on dispersal is staggering. Although the immigration decision is an important part of dispersal (Edelaar et al., 2008; Travis et al., 2012; Bonte et al., 2012), the greater body of literature focuses on emigration and avoids an explicit description of immigration. Most models assume that dispersers are evenly distributed over space (e.g. Hamilton and May, 1977) or travel to a certain distance (e.g. Rousset and Gandon, 2002). Models of habitat choice may treat the probability of entering a certain habitat directly as an evolving parameter, suppressing details of locating habitats during dispersal and making a decision on settlement (e.g. Ravigné et al., 2009). In models of

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http://dx.doi.org/10.1016/j.jtbi.2016.01.042
0022-5193/

structured populations, dispersers are often assumed to settle in the first patch they encounter (e.g. Parvinen, 2002). Some studies, however, have made immigration dependent on local population density (Saether et al., 1999; Metz and Gyllenberg, 2001; Poethke et al., 2011; Parvinen et al., 2012), also in combination with mate abundance (Shaw and Kokko, 2015), or preferred distance (Delgado et al., 2014), dependent on patch size (Hanski and Gyllenberg, 1993), or on expected fitness (Ruxton and Rohani, 1998). In this paper, we focus on immigration depending on the physical characteristics (but not on population density) of the target patch.

When dispersal is modelled, one has to consider the processes explicitly and model survival during the dispersal season, patch encounter and the decision on settlement in a mechanistic way, since it should be clear that it is the individual's behaviour that shapes the dynamics of the population as a whole. With a mechanistic underpinning of patch-type dependent immigration, it is possible to incorporate the individual's decision to settle more realistically. In this latter respect, our model is conceptually similar to the studies of Doyle (1975), Ward (1987), Baker and Rao (2004) and Stamps et al. (2005). These authors determined the optimal patch-dependent immigration behaviour when habitats differ in abundance and suitability, but (except for an attempt by Ward, 1987) neglected eco-evolutionary feedbacks from the immigration behaviour of individuals to the strength of competition experienced in different habitats.

Here, we derive a mechanistic underpinning for immigration of dispersing individuals, where we explicitly incorporate a continuous time dispersal season during which individuals randomly encounter patches. Upon encounter individuals settle in a patch with a patch-type dependent settlement probability (we follow the terminology of Clobert et al., 2009; Travis et al., 2012; Bonte et al., 2012). Habitat type affects survival during the dispersal season, survival from establishment to reproduction, fecundity and the probability of emigration of the offspring. We call individuals that settle in any patch generalists, whereas individuals that settle in patches of a specific type are called specialists. In this work, we study the eco-evolutionary dynamics of patch-type dependent immigration, i.e., the settlement strategy.

In Section 2 we derive the ecological model that incorporates the mechanistic derivation of the dispersal process of a population. In Section 3 we use the adaptive dynamics framework to study the long-term evolutionary behaviour of settlement strategies. In Section 3.1 we derive the monomorphic singularities and in Section 3.2 we investigate the stability conditions of the singular strategy. We give conditions when patch-type dependent settlement is prone to undergo evolutionary branching. We show an example where, after evolutionary branching, the coevolution of the two strategies leads to a stable coexistence of a specialist and a generalist strategy. In Section 3.3 we investigate the change (increase or decrease) of the settlement probability as we vary the model parameters. In Section 3.4 we focus on the effects of the parameters on the stability of evolutionary singularities of the different evolutionary outcomes. In Section 4 we discuss our results.

2. The model

We consider an asexual, annual, semelparous organism inhabiting a heterogeneous landscape of M patches of different types $i=1,2$ and frequencies ϕ_1 and $\phi_2=1-\phi_1$. Patches differ in death rates during the dispersal season once settled in the patch (patch safety or pre-competitive death), survival until reproduction (post-competitive survival), in relative fecundity, and the probability to emigrate (disperse). Individuals are characterised by their patch-type dependent settlement probability, the trait vector $f=(f_1,f_2)$, which is under natural selection. In the beginning of the year every patch is occupied by one individual. Each individual survives with a patch-type dependent survival probability s_i and gives birth to $B\beta_i$ offspring, where β_i is the relative fecundity in a patch of type i. We assume that the number of offspring B and the number of patches M are infinitely large, such that the model remains deterministic. Offspring disperse from a patch of type i with probability p_i and stay in the natal patch (of type i) with probability $1-p_i$. Every disperser joins the dispersal pool and may settle during a continuous-time dispersal season of length T. During the dispersal season dispersers encounter patches of type i at a rate $\phi_i\rho$ and settle in a patch of type i with probability f_i. Throughout the dispersal season every individual faces a risk of death (during dispersal and in the patches). We denote the death rate of individuals during transfer by ν and the death rate in a patch of type i by μ_i. We assume that the death rate in the dispersal pool is higher than the death rate in any of the patches during the dispersal season, i.e., $\nu>\mu_i$ for $i=1,2$. Dispersers who have not settled by the end of the dispersal season die. After the dispersal season the remaining individuals compete for one site per patch. All model parameters are summarised in Table 1.

To keep track of the dynamics of the model, we construct a disperser generation expansion (Diekmann et al., 1990, 1998). It follows the expected total offspring and their descendants of a single mother in the dispersal pool. The mother and her descendants are called a *family*. Let $\mathcal{G}$ be the next generation operator that maps the number of dispersers N of strategy f in one generation to the next during the lifetime of the disperser's family:

$$\mathcal{G}(N)=F(n,f^1,\ldots,f^l,f)N, \tag{1}$$

when the number of different settlement strategies present is l. The unit vector $n\in\mathbb{R}^l$, with entries n_j, describes the frequency of individuals characterised by the settlement trait vector f^j in the dispersal pool, where $f^j=(f_1^j,f_2^j)$ and $j=1,\ldots,l$. We assume that the population is either monomorphic, where all patches are occupied by individuals of a single settlement strategy ($n_1=1$), or in the polymorphic case it has reached its positive equilibrium. The function $F(n,f^1,\ldots,f^l,f)$ can be written as

$$F(n,f^1,\ldots,f^l,f)=Q^\top(n,f^1,\ldots,f^l)\mathbf{V}(n,f^1,\ldots,f^l)\Pi(f). \tag{2}$$

The entries $Q_i(n,f^1,\ldots,f^l)$ of the two-dimensional vector $Q(n,f^1,\ldots,f^l)$ describe the expected number of offspring that a family occupying a patch of type i contributes to the dispersal pool. The elements $V_i(n,f^1,\ldots,f^l)$ of the two-dimensional diagonal matrix $\mathbf{V}(n,f^1,\ldots,f^l)$ describe the probability of an individual winning a patch of type i. The two-dimensional vector $\Pi(f)$ has entries $\Pi_i(f)$ that describe the probability of a disperser settling in any of the patches of type i and surviving until the end of the dispersal season.

Table 1
Notation.

Variable	Definition
B	Number of offspring
β_i	Relative fecundity in patch of type i
$f=(f_1,f_2)$	Settlement trait vector
f_i	Settlement probability into patch of type i
$k_i=s_i\beta_i p_i$	Reward in patch of type i
M	Number of patches
μ_i	Death rate in patch of type i (patch safety)
ν	Death rate of dispersers
p_i	Emigration probability from patch of type i
ϕ_i	Frequency of patch of type i
ρ	Encounter rate
s_i	Survival until reproduction in patch of type i
T	Length of the dispersal season