Research Paper

Unsuccessful dispersal affects life history characteristics of natal populations: The role of dispersal related variation in vital rates

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ABSTRACT

Individuals that disperse from one habitat to another has consequences for individual fitness, population dynamics and gene flow. The fitness benefits accrued in the new habitat are traded off against costs associated with dispersal. Most studies focus on costs at settlement and effects on settlement populations; the influence of dispersal to natal populations is assessed by monitoring change in numbers due to emigration. However, the extent to which natal populations are affected when individuals that invest in dispersal fail to disperse/emigrate is unclear. Here, we use an Integral Projection Model (IPM) to assess how developing into a disperser affects natal population structure and growth. We do so using the bulb mite (*Rhizoglyphus robini*) as a study system. Bulb mites, in unfavourable environments, develop into a dispersal (deutonymph) stage during ontogeny; these individuals are called dispersers with individuals not developing into this stage called non-dispersers. We varied disperser expression and parameterised IPMs to describe three simulations of successful and unsuccessful dispersal: (i) 'no dispersal' - dispersal stage is excluded and demographic data are from non-disperser individuals; (ii) 'false dispersal' - dispersal stage included and demographic data from non-disperser individuals are used; (iii) 'true dispersal' - dispersal stage included and demographic data are from individuals that go through the dispersal stage and from non-disperser individuals. We found that the type of dispersal simulation (no dispersal < false dispersal < true dispersal) and disperser expression increases generation time and reduces lifetime reproductive success and population growth rate. Our findings show that disperser individuals that fail to leave, can change the structure and growth of natal populations.

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1. Introduction

The importance of dispersal on the ecology of populations can be substantial (see Clobert et al., 2001). The role of dispersal into and out of populations impacts numbers, sex ratios, age structure, social dynamics and genetic structure of the population and so, as with reproduction and mortality, can be a crucial demographic process (Stenseth and Lidicker, 1992). With the dispersal process come associated costs that are traded off against (potential) fitness benefits that are accrued in the new habitat at both the individual and (meta-) population level (see review by Bowler and Benton 2005; Bonte et al., 2012). Dispersal is therefore a strat-

egy that increases individual fitness in a heterogeneous (spatial and temporal) landscape by the process of moving the organism into a new environment, whereby variability in expected fitness between different habitat patches drives the evolution of dispersal (Bowler and Benton, 2005). Although there is some support for a purely genetic control of dispersal, there is widespread evidence that dispersal can be conditional upon a variety of traits (e.g. state-dependent, behavioural) and environmental conditions (McPeek and Holt, 1992; Clobert et al., 2004; Bowler and Benton, 2005).

Dispersal is a multi-phase life-history process that typically first entails energy investment into dispersal through increased reserves or into the expression of dispersal morphology (pre-departure), followed by the actual departure (initiating the eventual movement), transfer (the movement itself) and settlement (completion of the movement phase) (Bonte et al., 2012). Dispersal may fail during any of these stages, as individuals might not have sufficient reserves to invest into dispersal morphology, may be unable to find a host when dispersing through phoresy, could die during transfer or upon arriving at the settlement pop-

ulation, could fail to locate suitable habitat or disperse to suitable habitat and fail to find a mate (Bonte et al., 2012). Such unsuccessful dispersal could have important consequences for natal population and meta-population dynamics that can in turn feedback to influence dispersal expression and even its evolutionary trajectory. The study of unsuccessful dispersal has largely focused on the consequences of failure to disperse during the transfer stage and failing to establish during the settlement stage (Hanski 1999; Bowler and Benton 2005; Clobert et al., 2009; Burgess et al., 2012). To what extent pre-departure unsuccessful dispersal, where individuals have invested into dispersal but fail to leave their natal patch, affects natal populations in terms of population growth and structure is still unclear. Here, we examine the demographic consequences of the presence of unsuccessful dispersers, defined as individuals that have invested into dispersal morphology prior to intended departure but are not successful in leaving the natal population, on the size and structure of the natal population as well as key quantities that characterise population demography including population growth rate, mean lifetime reproductive success and generation time.

Expression of dispersal morphology prior to departure is often related to other individual characteristics such as energy reserves, mass or body size (Bonte et al., 2012; Deere et al., 2015). Different approaches exist to relate such characteristics of individuals to the dynamics of populations including Physiologically Structured Population Models (PSPMs) (Metz and Dieckmann, 1986), Matrix Population Models (MPMs) (Caswell 2001), Individual Based Models (IBMs) (Grimm and Railsback, 2005), and Integral Projection Models (IPMs) (Easterling et al., 2000). Of these, IPMs are useful for investigating simultaneous ecological and rapid evolutionary change in quantitative characters, life-history evolution and population dynamics (Easterling et al., 2000; Coulson, 2012; Merow et al., 2014). They are closely and easily linked to field and experimental data, can be applied to species with complex demography, and require relatively straightforward mathematical techniques from matrix calculus (Easterling et al., 2000; Ellner and Rees, 2006). Here we use IPMs to assess the consequences of unsuccessful dispersal by individuals during the pre-departure phase on natal population demography. As a study system we use the bulb mite (*Rhizoglyphus robini*, Acaridae). The bulb mite is an ideal study system for this research as its life-cycle contains a facultative, juvenile dispersal morph (deutonymph) (Fig. 1). Our IPM is density-independent, structured by life stage and body size (Fig. 1) and built from character-demography functions, which describe, for each life stage, the association between body size and female survival, growth and reproduction. We parameterise the IPM to describe three simulations of successful and unsuccessful dispersal: (i) 'no dispersal' - the dispersal stage is excluded and functions are parameterised using demographic data on non-disperser mites; (ii) 'false dispersal' - dispersal stage is included but functions are parameterised using demographic data on non-disperser mites; (iii) 'true dispersal' - dispersal stage is included and functions are parameterised using 'true dispersal' demographic data for those individuals that go through the dispersal stage and demographic data from non-disperser individuals. Comparing simulation (i) and (ii) allows us to assess the consequences for the natal population of adding a life stage to the life cycle, whereas the more interesting comparison between simulations (ii) and (iii) allows us to assess whether there are further demographic consequences of the dispersal stage, additional to that of adding an extra life stage. In our comparisons we analyse mean and variance in body size of each life stage, population growth rate (λ_0), lifetime reproductive success (R_0), and generation time. These results provide information on which demographic rates are most influential in natal population persistence under the different dispersal simulations.

2. Materials and methods

2.1. Study system and data collection

Bulb mites live in the soil and feed on bulbs and tubers and are pests of many crops and ornamentals (Diaz et al., 2000). Bulb mites are small (0.1–1.0 mm) and live for up to a few months (Diaz et al., 2000). From egg to adult, they go through a larval and two to three nymph stages, which take between 11 and 40 days depending on food quality (Smallegange 2011). Additionally, bulb mites have male dimorphism and males are either fighters, which kill other mites with their thickened third pair of legs, or scramblers, which do not have this modification and are defenceless (Radwan et al., 2000). Male morph is determined by the final instar (tritonymph) size, with larger tritonymphs developing into fighters. Dispersal occurs in both sexes via phoretic association with an arthropod host; attachment to the host is through the use of a sucker plate that is unique to the deutonymph stage (Diaz et al., 2000). Deutonymph expression is induced by unfavourable environmental conditions (e.g. low temperature, humidity, food quality) and is a non-feeding stage within the life-cycle (Diaz et al., 2000).

Data from Deere et al. (2015) were used to parameterise the IPMs. Briefly, in these experiments, first, females were isolated from stock cultures and allowed to lay eggs. The eggs were then reared individually to the adult stage and their life-history trajectory documented. Survival was scored on a daily basis for each individual. Surviving individuals were photographed daily, until maturation, using a Lumenera Infinity 3.1 camera (Lumenera Corporation, Ottawa, 22 Ontario, Canada) connected to a Meiji 20 EMZ-8TRD (10–45×) stereomicroscope and its length (body size) without mouthparts measured to the nearest 0.001 mm using Infinity Analyze Imaging Software (Lumenera Corp.). Mature females were mated with randomly chosen virgin males and eggs were counted and measured (measurements were limited to max. 10 eggs) on a daily basis until the female's death. However, this initial dataset contained a very small proportion of individuals that expressed the deutonymph. We therefore isolated individual deutonymphs and protonymphs from the stock population to supplemented our dataset. By doing so we make two assumptions: (1) development during the egg to protonymph stages did not differ between individuals that did not develop into the deutonymph stage and those that did, and (ii) any differences in life-history traits between dispersers and non-dispersers are due to deutonymph expression and occur after this point in development. We were able to test the first assumption only. We compared the demographic trajectories of non-dispersing individuals (i.e. individuals that do not express the deutonymph stage) that were either isolated as eggs (initial dataset) or as protonymphs (supplemented data) and found no significant difference in growth and survival between non-dispersing individuals isolated from the stock culture as eggs or as protonymphs (see Deere et al., 2015). Given this we combined the initial and supplemented data.

2.2. Model construction and analyses

A number of steps were involved in model construction and analysis. First, we parameterised the character-demography functions that comprise each IPM for the three dispersal simulations (no dispersal, false dispersal, true dispersal) using bulb mite life-history data (see *2.2.1 Integral projection model* and Supplementary material) and, second, built an IPM for each dispersal simulation (see *2.2.1 Integral projection model*). Third, we varied the probability of transition into the dispersal stage for the false and true dispersal simulation to assess the effect of changes in dispersal expression on natal population demography (see *2.2.2 Dispersal expression*).