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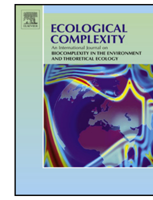

Original Research Article

Impact of individual movement and changing resource availability on male–female encounter rates in an herbivorous insect

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ABSTRACT

Species often confront changing resource distributions that result from natural and anthropogenic processes. For species that reproduce on or in close association with particular resources (*e.g.* host plants), changing resource distributions could affect the success of mate finding. We examine how mate-finding behaviours in an herbivorous insect mediate the impact of changing host plant spatial distribution. We tracked movements of 84 Melissa blue butterflies (*Lycaeides melissa*) in the Great Basin of western North America. Track data revealed sex differences in movement: males spent more time moving fast and females more time moving slowly; males moved more ballistically and females moved more diffusely. These differences vary quantitatively, but not qualitatively, between environments with contrasting resource distributions.

From these data we created and parameterised a computer model of male–female encounters and used it to examine implications of changes to the patchiness and abundance of host plants. We use the cumulative encounter time between each simulated male–female pair as a proxy for mating success, thus allowing for the consideration of different female behaviours. The simulations suggest observed movement parameters exist in a trade-off between individuals maximising the number of potential mates they encounter and the probability that each encounter leads to mating success. Increasing host plant abundance decreases encounter rates thus encouraging males to be more diffuse to compensate. Changing the local resource density, *i.e.* increasing host plant patchiness, accentuated these trade-offs: by decreasing cumulative encounter time in resource rich environments and increasing it in resource sparse ones. Thus we see that both spatial resource geometry at multiple scales and plasticity in male movement strategies are important factors to consider when seeking to understand population reproductive behaviour, for example when assessing ecological impact of development, determining range boundaries and slowing invasions or outbreaks.

1. Introduction

Behaviours that enable individuals to find mates are integral to their fitness and to the persistence of populations and species (Emlen and Oring, 1977). Limitations on individuals' abilities to find mates can lead to reproductive failure of populations and Allee effects (Courchamp et al., 2008; Gascoigne et al., 2009; Kramer et al., 2009). When individuals actively search for mates, variation in speed, directionality and other activity parameters can influence the frequency of male–female encounters and of mate-finding (Berec and Boukal, 2004; Gurarie and Ovaskainen, 2013; Laidre et al., 2013). In many species, mate-finding is also closely associated with patterns of resource use when mating happens on or near key resources. For example, in many herbivorous insects, mating happens on host plants that are also used by females for oviposition (Thornhill and Alcock, 1983; Jaenike, 1990; Landolt and Phillips, 1997; Bruce et al., 2005). This close association with resource use suggests that the success of mate-finding strategies could be affected by changes in resource availability and distribution (Dennis and Shreeve, 1988). Changes

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in resource availability can be driven by anthropogenic processes, such as habitat alterations or climate change, or by natural processes, such as niche shifts and host range expansion (Singer et al., 1993; Singer and Thomas, 1996; Mayhew, 1997; Thomas et al., 2001; Streitberger et al., 2012). Implications of changes in resource use and availability for growth and fecundity of herbivores have been well-studied (Thomas et al., 1996; Carroll et al., 2005; Singer et al., 2008), but possible implications for mate-finding appear to have received less attention (although see Knüttel and Fieldler, 2001; Forister and Scholl, 2012; Anderson et al., 2013 for recent relevant examples).

In this paper, we combine field data and individual-based simulations to explore how individual movement behaviours affect male–female encounter rates and mate-finding in an herbivorous insect. Our approach and focal questions are grounded in three related observations well-established in the relevant behavioural ecology literature: (1) the distribution of nutritional resources can determine the effectiveness of reproductive strategies, which may, as a consequence, vary in their effectiveness across different environments (Emlen and Oring, 1977); (2) in species characterised by scramble competition polygyny (*sensu* Alcock, 1980), male–male competition is expressed through differences in search strategies used to locate potential mates; and (3) the efficacy of different search strategies depends on the spatial distribution of "resources" (Preston et al., 2010; Rutowski, 1991). Specifically, we examine how mate-finding success depends on the distribution of host plants and the search strategies employed by males, and how mate-finding might therefore be affected by changes in the availability and distribution of host plants. In doing so, we also explore the hypothesis that the relationship between search strategy, resource density and mate-finding is mediated by a trade-off between locating many potential mates and interacting with females for long enough to allow courtship and successful copulation.

To do so, we focus on a butterflies species, the Melissa blue (*Lycaeides melissa*), a close relative of the United States-federally endangered Karner blue (*L. samuelis*; formerly *L. melissa samuelis* Forister et al., 2011). Butterflies have often been used in the study of mating behaviour. However, these behavioural studies have tended to focus on comparisons between categorical behaviours, such as "perching" versus "patrolling" strategies (*e.g.* Fischer and Fiedler, 2001; Kemp, 2001; Merckx and Van Dyck, 2005) and, with the exception of studies on hill-topping behaviour (Turchin et al., 1991; Pe'er et al., 2004), have given less consideration to detailed spatial dynamics of mate-finding movements. Mating in *L. melissa* takes place in close association with host plants. Males use a patrolling strategy (Scott, 1974), actively searching for females within and around individual plants or clusters of plants throughout the day, while females move between host plants seeking oviposition sites. Courtship begins with stationary females typically on host foliage in a head-down posture with wings closed, exposing the ventral surface of the hind wings. When a male has located a female, she is approached with a fluttering flight, after which a set of characteristic courtship interactions may lead to copulation (Pellmyr, 1982). During the initial approach, males can discriminate against heterospecific females based on visual assessment of wing patterns (Fordyce et al., 2002) and can choose females based on overall size (Forister and Scholl, 2012).

L. melissa has been the subject of a number of studies focused on the ecology of host plant use (Nice et al., 2002; Fordyce and Nice, 2003; Forister et al., 2009, 2011; Scholl et al., 2012), as well as the evolutionary consequences of hybridisation (Lucas et al., 2008; Gompert et al., 2012). In our study area, western Nevada, USA, the host range of *L. melissa* includes one plant that has been recently colonised, exotic alfalfa (*Medicago sativa*), as well as native hosts, commonly *Astragalus canadensis* and *Lupinus argenteus*. The spatial distribution of these host plant species differs. *M. sativa* is found both as isolated ("feral") patches distributed across the landscape, often along roadsides, and also in large monocultured stands; while *A. canadensis* and *L. argenteus* are components of native Great Basin plant communities. Alfalfa was introduced to North America within the last 200 years (Michaud et al., 1988), and is grown largely as a forage crop in Nevada. Previous studies have investigated the consequences of native versus exotic host use by *L. melissa*. For example, larval consumption of the exotic host *M. sativa* results in adults that are smaller and less fecund than individuals that consume a juvenile diet of a native host (Forister et al., 2009). The choice of the suboptimal host plant by females appears to be mediated at least in part by the phenology of flowering of native and exotic hosts: female *L. melissa* can extract nectar from the flowers of alfalfa, while they are less likely to lay eggs on one native (*A. canadensis*) when that host is flowering. The relative availability of nectar on different hosts highlights the complexity of resource use, many aspects of which have yet to be studied in any detail (Forister and Wilson, 2013). In particular, none of these studies have investigated the implications of differences in the abundance and spatial distribution of the different host plant species for the success of mate-finding strategies (Severns and Breed, 2014).

2. Materials and methods

2.1. Data collection and analysis

We collected movement tracks of individual butterflies throughout repeated visits during the summer of 2010 to three locations in Nevada: (1) Crystal Peak Park, a field near a municipal park in Verdi, NV, with a mix of native and exotic plants including *M. sativa*; (2) Silver Lake just north of Reno, NV, a seasonally dry lake bed with a diversity of native plants; and (3) Washoe Lake, south of Reno, where host plants ring a permanent, terminal desert lake (Fig. 1). *L. melissa* populations at Silver Lake and Washoe Lake are associated with native host plants (*A. canadensis*) and at Crystal Peak Park with the exotic host, *M. sativa*.

Individual butterflies were tracked using a hand-held Trimble GeoXT GPS unit that records latitude and longitude at 1 s intervals. Individuals were acquired for tracking "on the wing", *i.e.* they were acquired while flying. 84 individuals (37 female, 47 male) were followed for a maximum of 500 s, or until they could no longer be followed. The data comprise over 23,000 latitude/longitude measurements, giving the instantaneous speed and direction of each butterfly at each second. For further details on the study design see Appendix A.1. Each track combines periods of movement (flights) interspersed with periods spent on, or closely moving around, host plants (alights). When analysing movement data, we compared parameter estimates obtained when treating the data as individual steps (1 s intervals), individual flights separating each alighting event and as whole tracks, thereby testing for any sensitivity due to the particular discretisation used (Codling and Hill, 2005). Details on how track level data were analysed are given in Appendix A.2.

2.2. Individual-based simulations

We created a simulator that uses the track data and allows us to explore how male and female encounters are affected by differences in movement parameters and in the distribution of host plants. An outline of the simulator is given here; additional details are found in Appendix A.3. An environment of randomly distributed host plants is generated, the movement of each virtual butterfly is determined, and finally interactions between males and females are quantified. We define "alighting" as a butterfly