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

Mark D. Preston,^a Matthew L. Forister,^b Jonathan W. Pitchford^c
and Paul R. Armsworth^d

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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.

^aCorresponding author, National Institute for Biological Standards and Control, South Mimms, EN6 3QG, UK. mark.preston@nibsc.org

^bDepartment of Biology, University of Nevada, Reno, Nevada USA. mforister@unr.edu

^cYork Centre for Complex Systems Analysis and Departments of Biology and Mathematics, University of York, UK. jon.pitchford@york.ac.uk

^dDepartment of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, USA. p.armsworth@utk.edu

From these data we created and parameterized 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 maximizing 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.

Keywords: Melissa blue butterfly, sex-biased, Allee effect, host range, host shift, population model

1 Introduction

Behaviours that enable individuals to find mates are integral to their fitness and to the persistence of populations and species [1]. Limitations on individuals' abilities to find mates can lead to reproductive failure of populations and Allee effects [2, 3, 4]. 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 [5, 6, 7]. 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 [8, 9, 10, 11]. This close association with resource use suggests that the success of mate-finding strategies could be affected by changes in resource availability and distribution [12]. Changes 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 [13, 14, 15, 16, 17]. Implications of changes in resource use and availability for growth and fecundity of herbivores have been well-studied [18, 19, 20], but possible implications for mate-finding appear to have received less attention (although see [21, 22, 23] 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 behavioral 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 [1]; 2) in species characterized by scramble competition polygyny (*sensu* [24]), male-male competition is ex-

pressed 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 [25, 26]. 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 butterfly species, the Melissa blue (*Lycaeides melissa*), a close relative of the United States-federally endangered Karner blue (*L. samuelis*; formerly *L. melissa samuelis* [27]). 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.* [28, 29, 30], and, with the exception of studies on hill-topping behaviour [31, 32], 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 [33], 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 [34]. During the initial approach, males can discriminate against heterospecific females based on visual assessment of wing patterns [35] and can choose females based on overall size [22].

81 *L. melissa* has been the subject of a number of studies focused on the ecology of host plant
82 use [36, 37, 38, 39, 40], as well as the evolutionary consequences of hybridization [41, 42].
83 In our study area, western Nevada, USA, the host range of *L. melissa* includes one plant
84 that has been recently colonized, exotic alfalfa (*Medicago sativa*), as well as native hosts,
85 commonly *Astragalus canadensis* and *Lupinus argenteus*. The spatial distribution of these
86 host plant species differs. *M. sativa* is found both as isolated (feral) patches distributed
87 across the landscape, often along roadsides, and also in large monocultured stands; while
88 *A. canadensis* and *L. argenteus* are components of native Great Basin plant communities.
89 Alfalfa was introduced to North America within the last 200 years [43], and is grown largely as
90 a forage crop in Nevada. Previous studies have investigated the consequences of native versus
91 exotic host use by *L. melissa*. For example, larval consumption of the exotic host *M. sativa*
92 results in adults that are smaller and less fecund than individuals that consume a juvenile
93 diet of a native host [38]. The choice of the suboptimal host plant by females appears to be
94 mediated at least in part by the phenology of flowering of native and exotic hosts: female *L.*
95 *melissa* can extract nectar from the flowers of alfalfa, while they are less likely to lay eggs
96 on one native (*A. canadensis*) when that host is flowering. The relative availability of nectar
97 on different hosts highlights the complexity of resource use, many aspects of which have yet
98 to be studied in any detail [44]. In particular, none of these studies have investigated the
99 implications of differences in the abundance and spatial distribution of the different host
100 plant species for the success of mate-finding strategies [45].

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 (Figure 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*.

Figure 1: The butterfly tracks collected at the three collection sites: (a) Crystal Peak Park (CP); (b) Silver Lake (SL); and (c) Washoe Lake (WL). Regions of host plants are shaded and 10m scale is included (a)-(c). The three sites are located on the western edge of the Great Basin (d) near the border of Nevada and California (both highlighted in gray in the inset map of the United States).

Individual butterflies were tracked using a hand-held Trimble GeoXT GPS unit that

records latitude and longitude at 1 second intervals. Individuals were acquired for tracking “on the wing”, *i.e.* they were acquired whilst flying. 84 individuals (37 female, 47 male) were followed for a maximum of 500 seconds, or until they could no longer be followed. The data comprise over 23000 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 analyzing movement data, we compared parameter estimates obtained when treating the data as individual steps (1 sec intervals), individual flights separating each alighting event and as whole tracks, thereby testing for any sensitivity due to the particular discretisation used [46]. Details on how track level data were analyzed 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 either landing on a plant or flying in the immediate vicinity of a plant; for example, males and females will both land on foliage and fly around individual stems of a plant while looking for nectar, oviposition sites, mates or a place to bask. We then define an “interaction” as any period of time in which a male and a female are alighting on the same host plant. While butterflies, as mentioned, pursue a range of activities on plants, cohabitation of a host plant is a useful and necessary indication of the

potential for courtship and mating. We do not consider alighting behaviour that does not involve host plants, such as basking on bare ground or visiting non-host nectar sources. Our focus on encounters on host plants is a simplifying approach and justifiable for the study system where the majority of mating activity is indeed associated with hosts [34, 35].

The stochastic movements of each virtual butterfly are characterised by four parameters extracted from the data: the time spent alighting on a host plant; the time spent in each flight between plants; the speed in each flight; and the diffusivity of each flight. The times spent alighting on each plant and flying are randomly generated from distributions fitted to the track data observed in the field (Appendix A.2). The speed and diffusivity are also derived from the observed data (Table A.6).

Upon leaving a host plant, the next host plant on which a butterfly alights is determined according to the algorithm in Figure 2.

Figure 2: A flowchart representation of the simulator algorithm, see the main text and Appendix A.3.

The time in flight is determined from a log series distribution, parameterised by the field data (Figure A.2) and the maximum range of a flight is calculated by multiplying the flight speed by the duration of the flight. If no plants fall within this disc (with radius of the maximum flight range) then at the conclusion of the flight the butterfly is deemed to have performed a looped flight and returned to the plant it took off from. Otherwise, each plant within this disc is assigned a probability, based on its distance from the starting plant, taken

from a Rayleigh distribution. This distribution describes the distance from the origin when the orthogonal coordinates of the final position are described by two independent normal distributions of zero mean and equal variance as has been used in other dispersal models [47] but not for an individual based model. The destination plant is selected according to these weighted probabilities. The butterfly alights on this plant for a number of seconds taken, again, from a log-series distribution parametrised from the data and then the algorithm repeats for the butterfly’s next flight.

The simulator records all flight and alight events from which the frequency and duration of every interaction between each male and each female is calculated. In many mate limitation models, encounter rates have been assumed to be directly proportional to mating success (reviewed in [48, 49]). However, as mechanisms governing female mate choice are not well-understood, we use the detailed simulation data to explore an alternative time-threshold model. In this model, we assume a precondition for mating is that a male and female first spend a sufficiently long time period interacting (*e.g.* long enough to potentially allow courtship behaviour). To implement this assumption, we sum the duration of all interactions over all plants, for each male-female pair and only score interactions that exceed this threshold when assessing the performance of different mate-finding strategies. We call a set of interactions that exceed the female selection threshold an “encounter”. We varied the required threshold from one second (recovering the more typical assumption that mating success is directly proportional to unadjusted encounter rates) to 30 seconds, over 4 times the average period for which a female alights on a host plant as observed in the empirical data. We also assumed that after the threshold is exceeded there is no further reproductive value from more interactions, as would be appropriate if, for example, there were no further fitness gain from repeat copulation with the same partner. This threshold model allows us

to characterise an important nonlinear trade-off for males between meeting many females when patrolling over a large range, but with only a low percentage of interactions reaching the threshold time to allow courtship behaviour and copulation, versus meeting fewer females when patrolling a smaller range but with a larger percentage of encounters potentially leading to mating.

The full set of parameter combinations that we considered is listed in Table A.6. In the main text and figures, we use particular parameter combinations that illustrate the key results that we observed across many parameter combinations. The basic simulation consisted of 200 host plants uniformly randomly distributed in a 25m x 25m environment with 200 females, giving an equal host plant and female butterfly density of 0.32 per m^2 . Simulations ran for 1000 seconds. Butterflies move with parameters based on observed values when partitioning tracks into flight and alight segments (Table A.1). For each movement parameter we use the average across all three locations as the base case for comparison. Specifically, for females we used log-series parameters 0.830 and 0.964 for flight and alight times with a mean speed of 0.476m/s and α diffusivity of 1.071. Here α diffusivity is defined following Nouvellet *et al.* (2009) [50]; values for α diffusivity that are closer to 1 indicate movement that is relatively more diffusive and α diffusivities that are greater than 1 indicate more ballistic, less diffusive movements (Appendix A.2 for further details). For males, we used fitted log-series parameters 0.939 and 0.866 for flight and alight times. For males we also used the observed mean speed of 0.487m/s and α diffusivity of 1.238. In addition, we compared the predictions about encounters with potential mates with a movement scenario in which males move more diffusively than we observed in the field ($\alpha=1.1$), and with ones in which males move more ballistically ($\alpha=1.4$). Further sensitivity testing, including independently varying both speed and diffusivity, showed that this range of scenarios was adequate to reveal

200 the key contrasts in predictions. For each set of movement parameters, we simulated 1000
201 different male movement paths and repeated each experiment 1000 times, giving one million
202 males in each scenario.

203 We applied the simulator to examine how the success of different male mate-finding
204 strategies could be affected by changes to female mate selection criteria and the spatial dis-
205 tribution of host plants. To mimic differing female receptivity to male attention we varied
206 the cumulative time (potentially over many interactions/host plants as this threshold in-
207 creases) a male and female are required to interact before an encounter that may lead to
208 mating can occur. We varied the abundance of the host plants from 25% to 200% of its
209 baseline value (50 to 400 plants in 25m x 25m plot) while maintaining a uniform spatial
210 distribution of plants. To ensure that we were measuring only the effect of changes in host
211 plant abundance we kept the number of female butterflies constant *i.e.* 200 per simulated
212 environment. Then we considered the spatial patchiness of the underlying host plant distri-
213 bution, while controlling for overall host plant abundance. We compared simulations with
214 200 uniformly distributed host plants with environments that had the same number of host
215 plants overall but distributed in clumps. These patchier environments were created using a
216 Lévy-type random walk to locate plants [25]; see Figure A.4 for an example and Appendix
217 A.3 for further details.

3 Results

The results are divided into three sections: analysis of the empirical movement data; synthesis of these movement data within spatially explicit simulations; and an extension to explore the consequences of changes in resource density and spatial structure.

3.1 Field Data

The movement tracks reveal consistent quantitative and qualitative differences between males and females. Males move more ballistically than do females: mean $\alpha=1.45$ (IQR:1.33-1.56) for males compared with $\alpha=1.21$ (1.06-1.30) for females. Males also have a higher mean speed of movement when averaged over whole tracks: mean speed 0.46m/s (IQR:0.32-0.56) for males compared with 0.22m/s (0.10-0.26) for females, (Table A.1). The track data shows significantly differing behaviours between genders and between the three sites in both speed and α diffusivity (Table 1 and Figure 3). Examining the movement data at the step level (1 second segments) reveals that tracks comprise two distinct movement behaviours as expected: perching/alighting (including slow movements on and around host plants as discussed above); and patrolling/flying (faster movement between plants). The density distribution for observed speeds in the step data determines a threshold speed between these two behaviours of 0.101m/s (Figure A.1).

Speed	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Locations	2	9.60	4.80	30.38	<0.0001
Gender	1	10.98	10.98	69.48	<0.0001
Location:Gender	2	1.07	0.53	3.38	0.0391
Residuals	78	12.33	0.16		

α diffusivity	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Locations	2	0.22	0.11	7.70	0.0009
Gender	1	0.62	0.62	43.63	<0.0001
Location:Gender	2	0.02	0.01	0.73	0.4868
Residuals	78	1.11	0.01		

Table 1: A two way ANOVA for the mean speed (m/s) and α diffusivity of each track with interaction between gender and location. The data show that there is a strong dependence on both location and gender. A Box-Cox transformation was applied to the speed and α data (with parameters 0.0925 and -0.0287, respectively).

Figure 3: Track level speed (m/s, (a)) and α diffusivity (b) box plots by gender and the three locations: Crystal Peak (CP); Silver Lake (SL); and Wahoe Lake (WL).

We constructed an intermediate discretization of the step data by amalgamating consecutive steps above the 0.101m/s threshold, which we label ‘flights’. The periods between flights are referred to as ‘alights’. When aggregating the step data into flights and alights in this way, we find that there is little gender differentiation in the movement when in flight or in/around host plants: both males and females move at a mean flight speed of 0.48m/s and exhibit a large overlap in diffusivity (IQR: 1-1.69 for males and 1-1.44 for females, Table A.1). Rather the differences we observe between genders are caused by males taking longer

duration flights while females spend more time alighting on and around host plants (Table A.1). Furthermore we find that the durations of flights and alights are best fit by log series (logarithmic) distributions and use this to create a key component of our simulator (Figure A.2).

The overlap between the two modes and log-series flight and alight times (Figures A.1 and A.2) we observe hinders more advanced techniques, such as the multiphasic MCMC of Morales *et al.* [51] and Beyer *et al.* [52], to separate the fast and slow (flight and alight) movement types (Appendix A.2).

3.2 Simulations

In the simulations, the performance of a male movement strategy is scored as the mean number of different females encountered, *i.e.* females with whom the male interacts for longer than the minimum interaction time threshold required for any courtship behaviour prior to possible mating. The male mate finding success decreases with increasing female mate selection threshold for the three male movement strategies considered (Figure 4). Simulated male butterflies move according to the movement parameters observed in the field data ($\alpha = 1.238$, solid line), more diffusively ($\alpha = 1.1$, dashed) or more ballistically ($\alpha = 1.4$, dotted). Figure A.5 illustrates simulated movement tracks for females and for the three different male strategies.

More ballistic males have a larger range (Figure A.5) and therefore interact with more females. If every interaction is equally likely to lead to an encounter (threshold time to mate acceptance is one second) then these individuals will have the greatest mating success (Figure 4(a)). In contrast, more diffusive male butterflies tend to remain in a small area and interact for a longer total time with a smaller set of females. If threshold times for

mate acceptance are long then this strategy leads to more encounters and therefore greater mating success. At very short or very long female selection thresholds, males encounter up to 30% more females using the optimal strategy compared to those employing suboptimal strategies (Figure 4(b)). The male movement strategies we observe in the field would be optimal (*i.e.* outperforming the more diffusive and more ballistic strategies) if females had a mate selection threshold of ~ 12 seconds in the model.

Figure 4: (a) The mean number of female encounters for simulated male butterflies moving more diffusely (dotted) and more ballistically (dashed) than those moving with the observed parameters (solid) as the female encounter threshold varies from 1 to 30 seconds. (b) Data is presented relative to the butterflies moving with the observed parameter (solid line = 1). Male butterflies moving with the observed empirical parameters outperform the other two male movement strategies when females employ a ~ 12 second selection threshold.

Figure 5: (a) The mean number of female encounters for simulated male butterflies moving more diffusely and more ballistically than those moving with the observed parameters as the number of plants varies from 50 to 400 with a female selection threshold of 12 seconds. As the plant abundance decreases there are more male-female encounters registered with males moving more ballistically having an advantage. (b) When accounting for the female density, *i.e.* normalising by butterflies per plant then the mean number of male-female encounters decreases as plant abundance moves to either extreme.

3.3 Simulating changing spatial resource distributions

As mate-finding happens on or around host plants, then the underlying host plant distribution has the potential to influence the success of different mate-finding strategies. To quantify this possibility, we varied both the abundance of the host plants and the patchiness of the host plant distribution in the simulations. We utilised the result of Figure 4 and fixed females to have a mate selection threshold of 12 seconds, for which the male movement strategies we observed in the field would have greatest success.

As plant abundance increases there is a reduction in the number of male-female pairs repeatedly interacting, leading to fewer male-female encounters (Figure 5(a)). If host plants

are scarce then more ballistic males with their larger ranges have greater mating success, even with this female selection threshold. On the other hand, if host plants are more abundant then the more diffusive males have more successful mate encounters.

A key reason for the decline in encounters with abundance in Figure 5(a) is the reduction in females per host plant as these simulations hold the female butterfly population constant at 200. The result of renormalising the encounter rates of Figure 5(a) by the mean number of female butterflies per plant is given in Figure 5(b) and the effect of male search strategies is emphasised.

Environments containing the same number of host plants have the same large scale (simulation-wide) plant density irrespective of the resource distribution but differ in the small scale density (within the locality of any given host plant) dependent on whether the plants are patchily or uniformly randomly distributed. This increase in local density in the patchily distributed environments accentuates the male mate finding performance under certain conditions (Figure 6). In low encounter simulations, such as those with high plant abundance or longer female selection thresholds, the change of resource distribution decreases further the number of male-female encounters. Conversely, in high encounter environments, patchy environments increase the mean number of encounters. In the extremes, there is up to a 40% change in male mate-finding success due to the change in local host plant density.

The results for male movement strategies are qualitatively the same for both uniform random and patchily distributed resources (*c.f.* Figures 4, 5, A.6 and A.7): increased plant abundance reduces the success of male mate-finding strategies; more ballistic males enjoy greater success at low female selection thresholds and when plants are scarcer; and more diffusive males enjoy the greater success at high female selection thresholds and when plants are more abundant. In patchy environments, the male movement using the observed param-

eters is optimal at the lower female selection threshold of ~ 6 seconds (Figure A.6). This lower bound means that more diffusive males encounter more mates over a larger range of female selection thresholds. When varying the abundance of host plants within the patchy distribution (Figure A.7) diffusive male strategies are more successful over a wider range of increased plant abundance.

Figure 6: The mean encounter rates for male movement parameterised by the observed data in 25mx25m environments with uniformly randomly (solid) and patchily distributed (dashed) host plants. The effect of the change in plant distribution is shown for (a) female encounter threshold between 1 and 30 seconds and (b) host plant abundance. The 12 second threshold is marked on (dotted). When plants are patchily distributed then the mean number of male-female encounters increases as females employ a lower selection threshold and as plants become scarcer. Conversely patchily distributed plants decrease the mean number of encounters as females employ longer selection thresholds and as plant become more abundant, compared to the same number of plant uniformly randomly distributed.

4 Discussion

Ongoing and projected changes in resource distributions due both to anthropogenic (*e.g.* climate change, habitat change) and natural processes (*e.g.* niche shifts) will have fitness consequences for many species. While the implications of changing resource use and availability for some demographic processes (*e.g.* growth and fecundity) have been well-studied, implications for other processes, like mate-finding, have received less attention. We examine possible implications of distributional changes to host plants for mate-finding success in herbivorous insects. We present a mechanistic, spatially explicit, individual based movement model that allows us to simulate interactions between male and female butterflies. The simulator design and parameterization is heavily influenced by the *L. melissa* field data; including the gender behavioural differences and log-series flight and alight duration distributions. We used our models to explore the consequences of changes to the spatial distribution of key resources (host plants) for the success of different mate-finding strategies. We also explored how the effectiveness of different male mate-finding strategies would be affected if the probability of mating success depended on the interaction duration between males and females.

The movement tracks recorded from the field reveal clear sex differences in male and female movement behaviour in *L. melissa*. Males move faster and more ballistically than females over entire tracks. This is seen to be the consequence of two behaviours apparent in the high resolution data: high speed flights and low speed alights around host plants. Males spend more time in the high speed flights leading to track level faster mean speeds. Diffusivity, jointly with speed, determines the spatial spread of individuals, and the sex differences we find are such that males will spread over a greater area than females in a fixed time period

due to more ballistic movement *i.e.* higher Nouvellet α . It is assumed here that females are
 primarily responding to the distribution of host plants as they search for oviposition sites
 and that males, in contrast, are searching for females. In our analyses, we focus on the impli-
 cations of these differences for mate-finding within host plant patches. Studies on the spatial
 dynamics of butterfly movement have focused more commonly on probabilities of individuals
 leaving host plants patches [53, 54, 55, 56, 57] and possible consequences of this for patch
 residency and inter-patch dispersal [55, 58, 59]. For example, in their studies on Fender's
 blue (*Icaricia icarioides fender*), [55, 57] report sex differences in movement behaviour at
 patch edges potentially due to the change in local density. It would be interesting to extend
 our results to test whether we would also find sex differences in movement at and outside of
 patch boundaries in *L. melissa*.

Males that move more ballistically cover a greater area and encounter a greater number of
 females. However, we explored the possibility that not all encounters are of equal value [60].
 Specifically, we examined how our results would be affected if females preferentially mated
 with males with whom they interacted for longer periods of time. With this mate acceptance
 model, a male faces a trade-off between the increasing time invested in interactions with each
 unmated female within an area and the decreasing density of females nearby with whom it
 has not previously mated. Two game theoretic extensions of our work present themselves:
 the inclusion of female behavioural strategies; and the potential impact of horizontal disease
 or parasite transmission [61, 62]. The movement strategies of females may be constrained
 by the need to locate suitable oviposition sites, but females could vary the number of dif-
 ferent mates they encounter and the frequency of single or repeat matings by altering their
 acceptance threshold. The negative population implications of the horizontal transmission
 of an infectious disease through a different butterfly interaction threshold model could be

measured against the benefits of maximizing mate finding.

We applied our model to consider the possible implications of changing spatial patterns of resources, here host plants, which are critical to mate-finding. *L. melissa* recently colonized a novel, non-native host plant, *M. sativa*, one that grows in some cases with very different local spatial distribution than native hosts. The spatial distributions of the native hosts and the novel host may also shift with ongoing climatic and land use changes in the study region [63, 64, 65]. For increasing host plant abundance, we found that the optimal male movement strategy, one that maximized the number of sufficiently long encounters with females, corresponded to a more diffuse strategy. When undergoing a host shift or when confronting changes to the spatial distribution of its current host plants, the question then becomes one of how quickly mate-finding behaviours can adjust to match the new spatial configuration of host plants. Indeed, the track data themselves reveal differences in butterfly movements between populations, including those associated with the novel and native host plants, although we would require much greater replication to assess whether this could be evidence of some kind of adaptive response. That we predict a decrease in mating success at very high densities of host plants (even while maintaining a constant female to host plant ratio) also offers an intriguing suggestion for resolving a particular conundrum for *L. melissa*. While we often find *L. melissa* occupying low-density patches of feral alfalfa, or on the margins of large, managed fields, we rarely find butterflies utilizing the interior of dense fields of cultivated alfalfa located nearby. Previously, we assumed this might be because of spraying or other management practices in commercial stands, or because of a lack of mutualistic ants that might prefer the edges of fields affecting the persistence of *L. melissa* populations [39]. However, the simulations suggest an alternative hypothesis; namely that a break-down of mate-finding could lead to reproductive failure in high density stands.

In addition to the effects of large-scale host plant density, we find a separate effect of small-scale host plant density. In particular, when the underlying host plant distribution patchiness was increased, the male movement strategies become more successful for mate-finding in the resource rich environments and less successful in resource scarce environments. Of course, in many situations we would expect the patchiness and abundance of host plants to covary inversely, *i.e.* as plant abundance increases patchiness would decrease. Our results suggest, for example, that when considering the break-down of mate-finding at geographic range edges [66] or the leading edge of invasions [67] then it would be worth looking for any increases in the patchiness of resources towards the range edge or invasion front.

Arguably, the most important assumptions underpinning our analyses concern the design of the simulator and the mate acceptance threshold model. In designing the simulator, we placed the emphasis on exploiting the measured movement datasets to model co-occurrence of individual males and females on host plants during alighting events. One consequence of those choices, for example, is that our simulator did not allow us to explore the consequences of males cueing in on females while both are flying or when females have alighted on a non-host substrate. However, most courtship that we have observed in our focal populations has involved males finding females that are perched on or in the close vicinity of hosts, as in our simulators (MLF pers. obs.). The use of simulations to exploit detailed, but necessarily limited, movement data so as to make ecologically relevant predictions is an important and emerging area of research, see for example [68].

The challenge of changing patterns of resource availability, due, for example to habitat alterations, species invasions and climate change, is one faced by many species. Most studies focusing on the impacts of changing resource availability have emphasized direct demographic consequences, *e.g.* through changes to mortality or to growth and fecundity. Here we explore

404 how changing spatial patterns of resources can also influence male and female encounter rates,
405 perhaps triggering mate limitation and associated Allee effects. We also show the importance
406 of teasing apart the details of individual movement strategies when seeking to predict how
407 changing resource availability could impact reproductive success of populations.

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A Appendix

A.1 Experimental Design

At each of the three sites, butterfly tracks were recorded at the height of the summer flight season, when adults are abundant, and only in good “butterfly weather” which in this case means when the air temperature was above 26 C, with little or no wind or cloud cover. The butterflies were found on the wing and their movements mimicked at a distance of one meter to reduce the observer effect. They were followed for 500 seconds, or whenever they were lost (because they disappeared into vegetation or were indistinguishable from other individuals). During following, the observer held the GPS unit at approximately 1 meter from the butterfly and moved in concert with the butterfly, keeping the GPS unit at a fixed distance and angle from the butterfly. If the butterfly was at rest, the observer remained at rest until the butterfly moved again. When the 500 seconds were complete or the butterfly had been lost, the next individual that passed within the observer’s field of vision was followed in the same manner.

A.2 Data Processing and Analysis

The raw longitude and latitude data for each tracked butterfly from the GPS device was saved in CSV format. For each track the gender and site was recorded. The geopotential data was transformed into data on a square grid with positions in metre offsets. As the time between each measurement was 1s then the distance (in m) between successive points also gave an instantaneous speed (m/s). The mean speed per track and the Nouvellet α diffusion metric were calculated for each track. We measure particle diffusion by mean squared displacement over time ($\sigma^2(\tau)$). If a particle is diffusing with parameter α then $\sigma^2(\tau) \approx \tau^\alpha$, where α

601 less than 1 represents sub diffusive, α equal 1 is purely diffusive, α greater than 1 is super
602 diffusive and α equals 2 is ballistic movement [46]. This is related to the (mean of the cosine
603 of the) turning angles measured in a path by [50] through two formulae:

$$\zeta = \frac{1}{2} \frac{\sigma^2(2\tau)}{\sigma^2(\tau)} - 1 \quad \text{and} \quad E(\cos(\theta)) = \frac{\pi}{4}\zeta + \frac{\pi}{32}\zeta^3 + O(\zeta^5).$$

604 For each track or flight we solve the cubic equation for ζ and then calculate α via the
605 following:

$$\zeta = \frac{1}{2} \frac{(2\tau)^\alpha}{\tau^\alpha} - 1 = \frac{1}{2} 2^\alpha - 1 \quad \Rightarrow \quad \alpha = \frac{\log(2\zeta + 2)}{\log(2)}$$

606 The data was initially analysed at the three discretisation levels (track, flight/alight and
607 step).

Discretisation	Metric	All		Male		Female	
		N	Mean, Median (IQR)	N	Mean, Median (IQR)	N	Mean, Median (IQR)
Track	Speed (m/s)	84	0.36, 0.31 (0.19 - 0.47)	47	0.46, 0.43 (0.32 - 0.56)	37	0.22, 0.18 (0.10 - 0.26)
	α	84	1.34, 1.34 (1.20 - 1.48)	47	1.45, 1.44 (1.33 - 1.56)	37	1.21, 1.16 (1.06 - 1.30)
Alight	Speed (m/s)	2082	0.04, 0.03 (0.02 - 0.06)	933	0.04, 0.04 (0.02 - 0.06)	1149	0.04, 0.03 (0.02 - 0.05)
	α	2082	1.04, 1.00 (0.93 - 1.33)	933	1.03, 1.00 (1.00 - 1.25)	1149	1.05, 1.00 (0.89 - 1.37)
	Duration (s)	2082	6.39, 2.00 (1.00 - 7.00)	933	4.14, 2.00 (1.00 - 4.00)	1149	8.21, 3.00 (1.00 - 9.00)
	Speed (m/s)	2061	0.48, 0.38 (0.22 - 0.62)	918	0.48, 0.40 (0.24 - 0.62)	1143	0.48, 0.35 (0.21 - 0.62)
Flight	α	2061	1.15, 1.00 (1.00 - 1.61)	918	1.24, 1.07 (1.00 - 1.69)	1143	1.07, 1.00 (1.00 - 1.44)
	Duration (s)	2061	4.12, 2.00 (1.00 - 4.00)	918	5.66, 2.00 (1.00 - 7.00)	1143	2.88, 2.00 (1.00 - 3.00)
	Speed (m/s)	23525	0.27, 0.05 (0.01 - 0.35)	10070	0.40, 0.22 (0.03 - 0.58)	13455	0.17, 0.02 (0.01 - 0.13)
	Speed (m/s) > 0.101	9799	0.61, 0.45 (0.24 - 0.81)	6120	0.64, 0.48 (0.26 - 0.84)	3679	0.56, 0.40 (0.21 - 0.76)
Speed	Angle (cos)	23441	0.70, 0.80 (0.48 - 0.96)	10023	0.71, 0.83 (0.50 - 0.96)	13418	0.68, 0.78 (0.46 - 0.95)
	Angle (degree)	23441	39.58, 36.46 (16.42 - 61.40)	10023	38.19, 34.17 (15.57 - 59.92)	13418	40.61, 38.41 (17.33 - 62.62)

Table A.1: The summary statistics of the movement data at three discretisation levels and by gender. The flight level analyses are shown split into flights and alights, as defined in the text by amalgamating steps above and below the threshold of 0.101m/s. IQR = interquartile range.

Two-way ANOVAs were applied to the track level data, see Table 1 and main text.

The step data (speed) is bimodal representing the two main behaviours: in flight and on host plants. We define the threshold between flying and alighting at the local minimum of the density of the step speed data at 0.101m/s (Figure A.1).

Figure A.1: The bi-modal density of the logarithm of the step data (m/s). The density has maxima at -4.1 and -0.66 (dashed) as well as a minimum at -2.29 (dotted), equating to speeds of 0.016m/s 0.519m/s and 0.101m/s, respectively. These data mirror the two states that the butterfly may be in, either alighting on an host plant or flying between them. We use the minimum (0.101m/s) as a threshold when further analysing the data to parametrise the simulator. These data have been smoothed by convolving the empirical density with a discrete Gaussian kernel (bandwidth = 0.2358), for further details please refer to the *density* function in R.

We further analyse the flight and alight duration by finding the probability distribution with the best fit. For male and female butterflies separately, the flight and alight durations were fitted to geometric, exponential, Poisson and log-series distributions (Figure A.2). The best fit (by examining the parameter space and any MLE) were compared and the log series distribution provided the best fit for all four data sets.

Figure A.2: The flight and alight times histograms (solid), best fitted log-series (dashed) and best fitted exponential/geometric/Poisson distributions (dotted). The flight histograms are on the left and the male histograms are on the top row.

A complementary multiphasic MCMC method [52] was also applied to these data to identify the properties of the fast/flight and slow/alight phases. We analysed our male, female and combined movement data with the code supplied with Beyer *et al.* [52] (Table A.2). The MCMC schemes, applied to our data, identify slow ($\approx 0.02\text{m/s}$ average speed) and fast ($\approx 0.5\text{m/s}$) phases (Table A.2, combined) that closely match our data (*cf.* Table A.1). The male slow phase speed is calculated to be 0.358m/s that is much larger than the female MCMC, combined MCMC or results from our analyses (0.02 , 0.02 and 0.04m/s , respectively). The proximity between the MCMC calculated slow and fast speeds (under 0.10m/s difference) indicates that the MCMC method may be misidentifying the slow phase

as its peak for males is lower, see the logarithm of the instantaneous speeds in Figure A.3(a). Additionally the MCMC method shows increase in time spent in the slow phase for female butterflies (54% >50%) that qualitatively reinforce our results, but not quantitatively as we observe greater differentiation in the phase durations. Importantly the MCMC method provides no information on the duration distributions spent in each phase.

Group	Slow (mean(sd), IQR, m/s)	Fast (mean(sd),IQR,m/s)	Slow Time (mean(sd))	Fast Time (mean)
Females	0.018 (0.0002), 0.018-0.018	0.427 (0.006), 0.423-0.431	0.542 (0.285)	0.458
Males	0.358 (0.022), 0.342-0.373	0.444 (0.022), 0.428-0.460	0.500 (0.288)	0.500
Combined	0.021 (0.0002), 0.021-0.021	0.539 (0.004), 0.536-0.542	0.507 (0.288)	0.483

Table A.2: The mean speed and proportion of time in the slow and fast states of the multi-phasic MCMC model.

Figure A.3: The bi-modal density of the logarithm of the step data for (a) males and (b) females (*cf.* Figure A.1). The male peaks are at 0.020m/s and 0.533m/s whereas the females are at 0.015m/s and 0.328m/s, for the alighting/slow and flying/fast phases. The males spend much less time at the slower speeds, reinforcing the duration bias seen in the flight/alight data (Table A.1. The bandwidths for these density plots are: 0.246 and 0.232.

To confirm that the measurement error is minimal, we have repeated our analyses by adding random perturbations to our data. Explicitly, we add a uniform random error in the original longitude and latitude data of upto $\pm 1\text{cm}$, $\pm 5\text{cm}$ and $\pm 10\text{cm}$, independently at each observed time step. On the tracking level analyses, the summary statistics for these data fall within the confidence intervals of our original results. Due to the uncorrelated nature of the artificial perturbations to the data, the subsequent flight and alight analyses change, but in ways which are consistent and which do not alter the logic of our research. The flights

defined from the perturbed data are shorter and tend more towards Brownian motion, as
 expected due to the influence of the noise (see Tables A.3, A.4 and A.5). This gives us
 confidence that the strong signal of directed flights in our original analysis is robust.

0.01	Title	N	Stats	M	Stats	F	Stats
Track	Speed	84	0.36 (0.19 - 0.47)	47	0.46 (0.32 - 0.56)	37	0.22 (0.10 - 0.26)
	α	84	1.25 (1.03 - 1.45)	47	1.40 (1.28 - 1.54)	37	1.05 (0.89 - 1.16)
Alight	Speed	2085	0.04 (0.02 - 0.06)	925	0.04 (0.03 - 0.06)	1160	0.04 (0.02 - 0.05)
	α	2085	0.95 (0.67 - 1.17)	925	0.97 (0.83 - 1.09)	1160	0.93 (0.58 - 1.21)
	Time	2085	6.36 (1.00 - 7.00)	925	4.15 (1.00 - 4.00)	1160	8.13 (1.00 - 9.00)
Flight	Speed	2064	0.48 (0.22 - 0.62)	910	0.48 (0.24 - 0.61)	1154	0.47 (0.21 - 0.62)
	α	2064	1.15 (1.00 - 1.62)	910	1.24 (1.00 - 1.70)	1154	1.08 (1.00 - 1.45)
	Duration	2064	4.13 (1.00 - 4.00)	910	5.71 (1.00 - 7.00)	1154	2.87 (1.00 - 3.00)
Speed	Speed	23525	0.27 (0.02 - 0.35)	10070	0.40 (0.03 - 0.58)	13455	0.17 (0.01 - 0.13)
	Speed >0.101	9808	0.61 (0.24 - 0.81)	6132	0.64 (0.26 - 0.84)	3676	0.56 (0.21 - 0.76)
	Angle (cos)	23441	0.69 (0.47 - 0.96)	10023	0.71 (0.50 - 0.96)	13418	0.68 (0.44 - 0.95)
	Angle (degree)	23441	40.07 (16.89 - 62.27)	10023	38.52 (15.57 - 59.96)	13418	41.23 (17.97 - 63.58)

Table A.3: Movement analysis of GPS positional data perturbed by a uniformly random amount up to $\pm 1\text{cm}$.

0.05	Title	N	Stats	M	Stats	F	Stats
Track	Speed	84	0.37 (0.21 - 0.49)	47	0.47 (0.34 - 0.56)	37	0.25 (0.13 - 0.28)
	α	84	1.03 (0.64 - 1.33)	47	1.27 (1.12 - 1.43)	37	0.73 (0.50 - 0.86)
Alight	Speed	2524	0.06 (0.05 - 0.07)	1032	0.06 (0.04 - 0.07)	1492	0.06 (0.05 - 0.07)
	α	2524	0.71 (0.07 - 1.00)	1032	0.79 (0.25 - 1.00)	1492	0.66 (0.00 - 1.00)
	Time	2524	4.99 (1.00 - 6.00)	1032	3.44 (1.00 - 4.00)	1492	6.06 (1.00 - 7.00)
Flight	Speed	2499	0.39 (0.14 - 0.52)	1015	0.42 (0.17 - 0.55)	1484	0.38 (0.13 - 0.50)
	α	2499	1.06 (1.00 - 1.43)	1015	1.17 (1.00 - 1.62)	1484	0.99 (1.00 - 1.03)
	Duration	2499	3.78 (1.00 - 3.00)	1015	5.39 (1.00 - 6.00)	1484	2.69 (1.00 - 3.00)
Speed	Speed	23525	0.29 (0.05 - 0.36)	10070	0.41 (0.07 - 0.59)	13455	0.20 (0.04 - 0.14)
	Speed >0.101	10719	0.57 (0.20 - 0.77)	6426	0.62 (0.24 - 0.82)	4293	0.50 (0.16 - 0.68)
	Angle (cos)	23441	0.69 (0.46 - 0.95)	10023	0.70 (0.49 - 0.96)	13418	0.68 (0.44 - 0.95)
	Angle (degree)	23441	40.37 (17.31 - 62.36)	10023	39.02 (16.26 - 60.54)	13418	41.39 (18.30 - 63.61)

Table A.4: Movement analysis of GPS positional data perturbed by a uniformly random amount up to $\pm 5\text{cm}$.

0.10	Title	N	Stats	M	Stats	F	Stats
Track	Speed	84	0.40 (0.25 - 0.51)	47	0.49 (0.37 - 0.58)	37	0.28 (0.17 - 0.32)
	α	84	0.92 (0.53 - 1.23)	47	1.18 (1.03 - 1.38)	37	0.59 (0.36 - 0.79)
Alight	Speed	3895	0.06 (0.05 - 0.08)	1282	0.06 (0.05 - 0.08)	2613	0.06 (0.05 - 0.08)
	α	3895	0.93 (1.00 - 1.00)	1282	0.94 (1.00 - 1.00)	2613	0.92 (1.00 - 1.00)
	Time	3895	1.73 (1.00 - 2.00)	1282	1.59 (1.00 - 2.00)	2613	1.79 (1.00 - 2.00)
Flight	Speed	3847	0.26 (0.14 - 0.29)	1253	0.31 (0.14 - 0.42)	2594	0.23 (0.13 - 0.23)
	α	3847	0.67 (0.00 - 1.00)	1253	0.82 (0.00 - 1.18)	2594	0.60 (0.00 - 1.00)
	Duration	3847	3.91 (1.00 - 4.00)	1253	5.35 (1.00 - 5.00)	2594	3.21 (1.00 - 4.00)
Speed	Speed	23525	0.32 (0.09 - 0.37)	10070	0.44 (0.12 - 0.59)	13455	0.24 (0.08 - 0.20)
	Speed >0.101	16758	0.43 (0.14 - 0.54)	8005	0.53 (0.17 - 0.71)	8753	0.33 (0.13 - 0.33)
	Angle (cos)	23441	0.69 (0.46 - 0.95)	10023	0.70 (0.48 - 0.96)	13418	0.68 (0.45 - 0.95)
	Angle (degree)	23441	40.57 (17.74 - 62.34)	10023	39.46 (16.28 - 61.27)	13418	41.39 (18.77 - 63.08)

Table A.5: Movement analysis of GPS positional data perturbed by a uniformly random amount up to $\pm 10\text{cm}$.

A.3 Simulator Design

The simulator is based on that described in Preston et al. (2010). The parameters for each of its three components, environment, flight characteristics, and alight time, are derived from the observed data. For the environment, it takes a spatial size, the number of plants (equivalently: the density), and the placement algorithm (uniform and Lévy-like). Both male and female butterflies are described by four parameters: time on plants, time in flight, speed in flight and diffusivity in flight. The distributions for the male time alighting/in flight, and four female movement parameters, are fixed according to the data summarised in Appendix A.2, leaving the male speed and diffusivity free to be varied in the simulations. See Table A.6 for the parameters used.

The simulator either places plants in an independently and uniformly **random** pattern throughout the environment or for patchy environments it places plants at the end of each step of a Lévy random walk with exponent 2.1. The Lévy walk mimics a patchy environment and is also constrained to remain in the given area and is centred. After the host plants have been positioned, 1000 male and 200 female butterflies are independently moved through the environment, using the algorithm described in the main text, for 1000s. All individuals are treated independently. The interactions for each male with the female population are recorded. This process is repeated independently 1000 times for each set of environment and movement parameters.

	Metric	Female	Male
Flight	Speed	0.476m/s	0.485
	α	1.071	1.1 - 1.4 (1.238)
	Log series	0.830	0.939
Alight	Log series	0.964	0.866

Table A.6: The parameters used in the simulator, all derived from the data analysis in Appendix A.2. These determine how long butterflies spend alighting on plants and in flight, and whilst in flight how fast and ballistic/diffuse to move. The range of parameters investigated for the male movement are given with the 'default' values in brackets.

Figure A.4: Example plant distributions used in the simulations: (a-d) uniformly distributed plants and (e-f) patchily distributed plants with 50 ((a) and (e)), 100 ((b) and (f)), 200 ((c) and (g)) and 400 ((d) and (h)) plants. The patchy distributed plants are placed at each turning point in a Lévy random walk (Appendix A.3).

Figure A.5: Example movements in the standard simulated 25x25m environment containing 200 uniformly distributed plants: (a) illustrates females moving in the simulations ($\alpha=1.07$), and Figure (b)-(d) illustrates three different male movement strategies: (b) more diffusive than observed in the track data ($\alpha=1.1$); (c); the observed diffusivity ($\alpha=1.238$) and (d) more ballistic movements than we observed ($\alpha=1.4$).

Figure A.6: The mean number of encounters for males moving in patchy environments, with the observed parameters (solid), more diffusely (dotted) and more ballistically (dashed) as the female selection threshold varies (a), the plant abundance varies (b) and the normalised plant abundance varies. For a full description see Figure 4 for results in uniformly randomly distributed environments.

Figure A.7: The mean number of encounters for males moving in patchy environments, with the observed parameters (solid), more diffusely (dotted) and more ballistically (dashed) as the plant abundance varies (a), the plant abundance varies (b) and the normalised plant abundance varies. For a full description see Figure 5 for results in uniformly randomly distributed environments.