Testing predictions of movement behaviour in a hilltopping moth

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‘Hilltopping’ is a common mate-locating behaviour exhibited by numerous insect taxa; individuals aggregate on summits, ridges and other topographic features, and thereby increase their likelihood of mating. Recently, hilltopping has gained interest as a model system to study nonrandom dispersal. We tested four predictions from the hilltopping literature regarding individual movement behaviour and the resulting spatial distribution of summit aggregations. Through observations and capture–mark–recapture studies using the day-flying tiger moth, Arctia (formerly Platyprepia) virginalis, we found evidence for all predictions. The highest densities of moths were associated with a few, high-elevation summits and were recaptured over multiple days. No individuals were found to move between summit aggregations and mated females had shorter residency times than males. We discuss our results in the context of the predictions, the behaviour of other hilltopping species, implications for population structure and spatial population dynamics.

A substantial literature has accumulated regarding the dynamics of spatially structured populations (Hanski & Thomas, 1994; Levins, 1969; Opdam, 1990; Pulliam, 1988). Through this body of work, we have learned that connectivity and dispersal are critical for the persistence of such populations. This is especially important for those populations that are small and isolated due to human-induced habitat loss and fragmentation (Thomas, 2000). Consequently, identifying dispersal barriers and landscape features or other factors that influence dispersal is crucial in predicting the dynamics of spatially structured populations (Ricketts, 2001; Wiens, Stenseth, Van Horne, & Ims, 1993).

Models that attempt to predict the dynamics of spatially structured populations generally assume that dispersal between habitat patches is random (Hanski & Thomas, 1994; Kuussaari, Nieminen, & Hanski, 1996; Moilanen & Hanski, 1998). However, numerous studies have demonstrated that this assumption is often violated. Behavioural decisions affect many aspects of dispersal, including departure, flight path and settlement (Reed & Levine, 2005). Consequently, dispersing individuals locate high-quality resource patches or avoid those that are suboptimal at higher frequencies than what would be expected by random chance (Conradt, Bodsworth, Roper, & Thomas, 2000; Matter & Roland, 2002). Because most spatial population models ignore individual behaviour for the sake of simplicity (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009), the prevalence of nonrandom, behaviourally based dispersal and its consequences on population dynamics of spatially structured populations is not well understood (but see Reed & Levine, 2005).

Recently, hilltopping has gained interest as a model system to study nonrandom dispersal (Painter, 2013; Pe’er, Heinz, & Frank, 2006; Pe’er, Saltz, & Münkemüller, 2013; Pe’er, Saltz, Thulke, & Motro, 2004; Pe’er, Saltz, & Frank, 2005). Like lekking, ‘hilltopping’ is a mate-locating strategy, where flying insects aggregate on topographic features such as hills, summits or ridges and thereby increase their likelihood of mating (Alcock, 1987; Baughman & Murphy, 1986; Ehrlich & Wheye, 1988; Scott, 1975; Shields, 1967). Males typically occupy summits first and await the arrival of females. After mating, females descend and disperse in search of oviposition sites. Hilltopping behaviour is especially common in one of the most specious taxonomic groups, the Lepidoptera. In one survey, 48% of butterfly species were found to hilltop (Shields, 1967).

A primary focus within the hilltopping literature has been testing the hypothesis that hilltopping lek-mating systems optimize mating success (Courtney & Anderson, 1986; Ehrlich & Wheye, 1986; Painter, 2013; Singer & Thomas, 1992). Less work...
has investigated decisions regarding hilltop preference and its consequences for connectivity and population structure (but see Brussard, Ehrlich, & Singer, 1974). More recent work found that released Melitaea trivia butterflies moved to continually increase elevation, indicating that topography greatly influenced movement (Pe’er et al., 2004). Simulations based on this empirical study demonstrated that simple movement rules in response to elevation changes can lead to spatial distribution patterns like the clustering of individuals on summits, a distributional pattern seen in hilltopping species (Painter, 2013; Pe’er et al., 2013). These simulations suggested that the choice of particular summits on which aggregations form is a function of the spatial distribution of topographic features in relation to larval patches: individuals move from simulated release points towards, and aggregate on, the tallest topographical features. Demonstrating a preference for summits with particular characteristics (e.g. highest relative elevation) versus randomly aggregating on the nearest summits from a larval patch would likely affect the size of summit aggregations and in turn the likelihood of encountering mates. Moreover, larval food patches farther away from preferred summits may receive less ovipositing females compared to a model that assumes unconstrained, random dispersal from eclosion sites, which are often found near or larval food plants (Courtney & Parker, 1985; Rutowski, 1991).

The location or abundance of larval food plants and adult nectar plants are known to affect insect movement (Dover & Settele, 2008; Ehrlich & Hanski, 2004). Indeed, Ehrlich and Wheye (1984) suggested that the hilltopping butterfly Euphydryas editha may select aggregation sites based on the density of flowers. However, it is also common for hilltopping species to aggregate on summits devoid of vegetation (Shields, 1967). Melitaea trivia was used to study movement behaviour because it hilltops on barren summits, and thus is not thought to select aggregation sites based on nectar resources (Pe’er et al., 2004). A general approach in ecological modelling is to start with a simplistic model and build complexity. Melitaea trivia provides a hilltop-lek system that is reduced in complexity compared to other hilltopping species whose movements are likely to be influenced by the spatial distribution of nectar plants.

Motivated by the novel use of hilltopping behaviour to understand decisions leading to nonrandom dispersal and its broader population implications, we combined previous interpretations of empirical findings with those from recent simulations based on the behaviour of M. trivia to generate a list of testable hypotheses. Specifically, we made the following four predictions based on the assumption that the location of summit aggregations is determined by the response of hilltopping individuals to topography rather than nectar resources.

1. Aggregations will occur on a subset of all possible summits.
2. Individuals will exhibit high summit fidelity.
3. Female summit residency time will be less than that of males.
4. Summit elevation will predict aggregation density better than summit proximity to larval patches.

We restricted our predictions to those pertaining to movement to and between summit aggregations and did not consider predictions regarding movement within aggregations (e.g. patrolling and perching). To test these predictions, we employed capture–mark–recapture at multiple hilltop aggregations of a day-flying moth Arctia (formerly Platyprepia) virginalis (Lepidoptera: Erebidae, formerly Arctiidae) that is not known to nectar. Arctia virginalis is comparable to M. trivia in that its selection of aggregation summits is probably not influenced by nectar resources, making it an appropriate study organism to test the model presented by Pe’er et al., 2004. Our intent was to provide a baseline to compare more complex hilltop lek-mating systems, such as those that might use vegetation cues to navigate through the landscape to locate aggregation sites.

METHODS

Study System

This study was conducted within the Bodega Marine Reserve (BMR), Sonoma County, California (38.3184°N, 123.0718°W). Arctia virginalis is a univoltine, day-flying moth that exhibits hilltopping behaviour (Grof-Tisza, Steel, & Karban, 2017). Males engage in both perching and patrolling behaviour. Upon detecting movement of a conspecific, males exhibit investigative flights. Females entering aggregations quickly perch and await males. Caterpillars are polyphagous but are tightly associated with patches of Lupinus arboreus at our study site. Consistent with predictions in Rutowski (1991) regarding correlates of encounter-site locations, caterpillars leave L. arboreus and pupate on nonfood plants in late spring (April–June; Grof-Tisza, Antell, Holyoak, & Karban, 2015). Adult moths emerge in summer (June–August) and live for 21.1 ± 7.4 days (mean ± SD) in the laboratory and do not appear to nectar (Grof-Tisza et al., 2017). Oviposition occurs across multiple plant species and eggs hatch within 1 week (Grof-Tisza et al., 2017). Neonates disperse into leaf litter and become conspicuous in the landscape the following spring (Karban, Tawny, Grof-Tisza, Crut-singer, & Holyoak, 2013). An ongoing annual census programme has surveyed caterpillars in larval patches of L. arboreus within BMR since 1983. Observed patch extinction and recolonization are typical of spatially structured butterfly populations (Karban, Grof-Tisza, Maron, & Holyoak, 2012).

Aggregations Will Occur on a Subset of All Possible Summits (Prediction 1)

Using movement rules based on empirical studies demonstrating that males and virgin female butterflies move upward in response to an elevational gradient (Pe’er et al., 2004; Shields, 1967; Wickman, 1988), Pe’er et al. (2013) found that the degree of responsiveness to elevation of simulated butterflies caused different spatial distributional patterns of butterfly aggregations. A strong response to elevation caused simulated individuals to move towards and remain on summits close to release points. A weaker response enabled individuals to move past these local summits and aggregate on a few, high-elevation summits. Large aggregations on a subset of summits likely optimize the likelihood of mating in low-density populations (Painter, 2013). Consequently, we expected a few large aggregations across the landscape as opposed to several smaller aggregations.

Survey transects for A. virginalis were established across BMR including on the highest elevation summits and all major dune ridge systems (i.e. greater than 100 m in length). For the purposes of this paper, we do not distinguish between summits and ridges and hereafter refer to them collectively as summits. Transects were walked weekly at a constant pace (10 m/min) between 1000 and 1500 hours during the 2010 and 2011 flight seasons (a more detailed description of survey methodology can be found in Grof-Tisza et al., 2017). Data from this study was used to estimate the proportion of area occupied by moths previously classified as a summit. Because moths were observed in flight, their exact location could not be obtained. Consequently, occupancy was assigned to a 20 m radius around the recorded GPS coordinates of where the
Individuals Will Exhibit High Summit Fidelity (Prediction 2) and Female Summit Residency Time Will Be Less Than That of Males (Prediction 3)

Based on empirical studies (Shields, 1967) and simulated hilltopping behaviour of hilltopping butterflies (Painter, 2013; Pe’er et al., 2013), individuals in aggregations that do not nectar-feed should not move between summit aggregations (i.e. exhibit high summit fidelity). Furthermore, females should remain at summits until they mate, and males should stay until death. Male departure could also be a result of being chased out by competing males, but previous observations of A. virginalis suggest that males are fairly tolerant of other males within aggregations (P. Grof-Tisza, personal observation). The divergent behaviour of postmating males and females leads to prediction 3: the time between the first and last recapture (residency time) should be less for females than for males.

To test these predictions, we used capture–mark–recapture methods at the five summits that were found to have consistently high moth densities (Fig. 1). At each site, we restricted our capture efforts to a 1 ha plot to access the majority of perching sites and stay consistent between summits. Capture events occurred daily for 30 min (not including handling time) at each site between 1000 and 1700 hours during 6–23 June 2011. The order in which sites were visited on each day was randomized. In addition to recording GPS coordinates, we determined the sex and uniquely marked each individual with an indelible marker according to the technique described by Ehrlich and Davidson (1960) prior to release.

Anticipating that moth movement between summits might be rare based on preliminary surveys, we conducted a second set of capture–mark–recapture observations. We walked parallel transects daily on a ridge connecting the two highest-density summit sites assuming that individuals would be more likely to transition across this ridge than through low-lying habitat (Overlooks 1 and 2, Fig. 1). Capture events occurred daily between 1000 and 1700 hours during 11–25 July 2011. Relative search effort (time/area) within these transects was equivalent to that at the summit sites to ensure comparability. We calculated average maximum distance moved (i.e. the farthest distance between capture events) and the interval between the first and last recapture events as well as the interval between the first recapture found in copula and the last recaptures to determine residency time postmating. Average maximum distance was calculated as opposed to average distance because we were interested in movement ability that could influence landscape connectivity and provide a better dispersal ability estimate needed for prediction 4. We log transformed distances moved and used a linear model in R (R Development Core Team, 2013) to compare differences between the sexes. Similarly we used a Poisson generalized linear model to compare residency time between males and females.

To estimate apparent daily survival, we used Cormack–Jolly–Seber (CJS) models in the program MARK (White & Burnham, 2009). CJS models use capture–recapture histories to develop maximum likelihood estimates of the probability of apparent survival ($\Phi$) and capture ($p$). The probability of apparent survival is the likelihood that an individual survived and did not permanently emigrate out of the monitoring area between sampling periods. We used Akaike’s information criterion (AIC) to compare CJS models and evaluate whether apparent daily survival ($\Phi$) of A. virginalis adults varied with sex or sampling day (Table 1). We estimated density and its associated variance using Chapman’s unbiased version of the Lincoln–Peterson estimator (Seber, 1982). Because of the complexity of the Huggins closed capture model, small sample

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**Figure 1.** Topographic map of the Bodega Marine Reserve. Plots where we conducted capture–mark–recapture are represented by squares. Labels within the plots represent site names (M: Mussel Point; A: Artemisia; F: Front Dune; 1: Overlook 1; 2: Overlook 2; S: South Dune; N: North Dune). Transect capture–mark–recapture occurred between Overlooks 1 and 2. Circles represent temporally stable larval patches and their size represents relative caterpillar densities, the letter ‘L’ representing the highest density larval patch. Shading intensity is directly proportional to moth density and arrows represent high-density aggregations that were present in 2011 (Front Dune and South Dune) but not in 2012. Shading overlay was generated using the Point Density tool in ArcGIS (v.10.2, Environmental Systems Research Institute (ESRI), Redlands, CA, U.S.A.). To enhance readability, transects are not shown.
similar to connectivity indices used in metapopulation studies (e.g. function of Euclidean distance. We modelled summit connectivity unequal caterpillar densities across larval patches in our system as larval patches. Our connectivity index (equation 1) accounts for tations sites should negatively correlate with the natural log of relation between moth density and elevation. elevation summits in the process, we would expect a positive cor- tance. In contrast, if moths continually oriented towards the highest sites and summit elevation as well as connectivity to larval patches. examined the relationship between moth density at aggregation sites and summit elevation as well as connectivity to larval patches. If, upon emergence, moths moved randomly until encountering an elevation gradient and continually oriented to a local summit regardless of elevation! we would expect to find a positive corre- a function of distance. In contrast, if moths continually oriented towards the highest summit residency time will be less than that of males (Prediction 3)

Connectivity Index and Statistical Analysis

The probability of butterflies reaching a habitat patch decrease exponentially with increasing distance to that patch (Stevens, Turlure, & Baguette, 2010). Based on this well-established relationship, we assumed that the density of moths at summit aggregation sites should negatively correlate with the natural log of distances to larval patches, if caterpillar densities were equal across larval patches. Our connectivity index (equation 1) accounts for unequal caterpillar densities across larval patches in our system as determined in previous surveys (Karban et al., 2012) and is a function of Euclidean distance. We modelled summit connectivity similar to connectivity indices used in metapopulation studies (e.g. Hanski & Thomas, 1994; Winfree, Dushoff, & Crone, 2005).

\[
C_h = \sum_{i \neq h} D_i e^{-d_i/D}
\]  

Our model assumes a fragmented landscape with discrete adult aggregation sites (summits) and larval patches. \(D_i\) is the density of caterpillars in larval patch \(i\), \(d_i\) is the distance between the focal summit \(h\) and larval patch \(i\) considered over all larval patches in the system, and \(D\) is the average dispersal ability of adult moths. We used \(D = 1\) km, as commonly used in lepidopteran metapopulation studies (Hanski, Moilanen, Pakkala, & Kuussaari, 1996; Schultz, 1998). Considering that the actual distances that \(A.\ virginalis\) was found to move (see Results), this value conservatively over-estimates dispersal ability. The index can be interpreted as sum- ming predicted movement to hilltops from the surrounding larval patches assuming that the propensity of movement to hilltop decreases with distance from larval patches and dispersal capacity. We fitted all models using maximum likelihood with the ‘glm’ function in the MASS package (Venables & Ripley, 2002). Models used the negative binomial error structure to account for over-dispersion in the count data (Ver Hoef & Boveng, 2007). We compared all possible models using AIC, and likelihood ratio tests were used to determine the significance of factors within the best performing model (Crawley, 2013).

Ethical Note

All applicable institutional and/or national guidelines for the care and use of animals were followed. Moth handlers were trained by the primary investigator and all moths were released within minutes of capture.

RESULTS

Aggregations Will Occur on a Subset of All Possible Summits (Prediction 1)

Roughly 78% (44 101/56 540 m²) of the area classified as a summit was occupied by at least one moth during transect surveys. An estimated 26% of the total area (14 700/56 560 m²) contained over 90% of all moth observations (Fig. 1). The area associated with these high densities of moths consisted of three summits (Muscle Point, Overlook 1, Overlook 2) and four dune ridges (Front Dune, Artemisia Dune, North Dune, South Dune) with the highest densities on the highest summit in both 2010 and 2011. In 2011, two of these areas (Front Dune and South Dune) had markedly lower moth densities than the previous year and consequently were not included in our capture—mark—recapture study in 2011.

Individuals Will Exhibit High Summit Fidelity (Prediction 2) and Female Summit Residency Time Will Be Less Than That of Males (Prediction 3)

We marked a total of 1021 individual moths. Two aggregations contained greater than 70% of all total captures during the first recapture period (Table 2). Consistent with the second prediction, no movement between hilltop aggregations was detected in either capture—mark—recapture period. Using the transect data from the second capture—mark—recapture period, we found that both males and females remained at summits for multiple days, with no detectable difference in residency time between the sexes (GLM: \(Z = 14.32, P = 0.87\)) and on average males moved farther than fe- males (GLM: \(Z = 4.79, P < 0.001\); Table 3). During this same period, we observed 104 mating pairs. Consistent with the third prediction, mated females on average stayed 1.1 day less than mated males (GLM: \(Z = 1.96, P = 0.05\); Table 3).

We estimated male and female population sizes for the first and second week of the second recapture period, which corresponded with the peak of flight seasons for males and females, respectively. (mean ± SE: first week: 799.6 ± 166.6 males, 218.2 ± 33.8 females; second week: 526 ± 64.2 males, 310.1 ± 72.9 females). During this period, the male:female ratio decreased from 3.67 to 1.70, with a
received the lowest AIC score and showed a significant relationship between elevation and moth density (LRT: χ² = 11.87, P < 0.001; Fig. 2). The maximal model (i.e. elevation + connectivity) and the model with connectivity as the sole predictor contributed no additional explanatory power (LRT: χ² = 0.37, P = 0.54). Although these results indicate elevation is a superior predictor to connectivity, we cannot completely rule out connectivity as a partial driver of moth aggregation. A relatively weak relationship between moth density and connectivity would only become apparent with increased sample size.

DISCUSSION

We found evidence that supported all four predictions regarding the movement and spatial distribution of a nonfeeding, hilltopping moth using elevation as an orientation cue. With regard to the first prediction, we found that moths were not evenly distributed across all summits. Although a high proportion of areas classified as summits were occupied, the high densities of moths were located at just a few summits (Fig. 1). As discussed by Painter (2013), if individuals existing in a low-density population aggregate at just a few summits as opposed to many, it increases the density of individuals at each aggregation, thereby increasing the likelihood of encountering a mate. However, the opposite may be true for individuals within high-density populations (Baughman & Murphy, 1988; Ehrlich & Wheye, 1988; Painter, 2013). Our capture–mark–recapture study at five of these summit aggregations found that moths remained at these sites for multiple days (Tables 2, 3), indicating their likely importance. Moreover, 11% of total captures at these sites were of mating pairs. Pe’er et al. (2013) found that with a weak response to elevation, simulated individuals would move towards the nearest summit from release points but would continue to move onto the higher summits and not become trapped at lower local summits. Because we did not conduct capture–mark–recapture at summits associated with low densities of moths, we could not determine whether individuals remained at these sites or moved to other summits with larger aggregations. Studies have shown that lower-elevation hills are also used as aggregation sites by some hilltopping species (Baughman & Murphy, 1988). However, while lower elevations are used, the highest densities are often associated with the highest elevations (Alcock, 1983; 2000). If some hilltop characteristics are linked to fitness benefits such as the increased likelihood of successful mating events (Ehrlich & Wheye, 1984), then the pattern of hilltop occupancy may reflect the heterogeneity of hilltop quality. For territorial hilltopping species that exist in a topographically heterogeneous landscape, less dominant males may be forced to establish territories on lower-quality (i.e. lower elevation) summits.

Evaluating the second prediction, we found evidence that individuals exhibit summit fidelity. Specifically, we did not detect any movement between aggregations during the two capture–mark–recapture studies despite their likely capability; maximum movement distances observed suggest that at least males are capable of moving between the closest aggregations but choose not to, or do so rarely (Table 3). This is consistent with other studies showing that butterflies removed and released kilometres away from hilltop aggregations returned to the same summits from which they were taken (Shields, 1967). While others have shown that species that use landmarks as mate encounter sites often exhibit high site tenacity (time spent at an encounter site; reviewed in Rutowski, 1991), most of these investigations were conducted at just one summit, so aggregation fidelity could not be determined. Despite not testing this question explicitly, some of these studies are suggestive of summit fidelity. For example, Lederhouse (1982) demonstrated that Papilio polyxenes spent upwards of 8 h per day at a particular site and returned to it over multiple days.

With regard to our third prediction, we found that mated males on average stayed approximately 1.1 day longer than females (Table 2). Considering that the average residency time for all moths

### Table 2
Summary of *A. virginalis* adult capture data from the first capture–mark–recapture study conducted at five summit aggregation sites

<table>
<thead>
<tr>
<th>Sites</th>
<th>Artemisia</th>
<th>North Dune</th>
<th>Mussel Point</th>
<th>Overlook 1</th>
<th>Overlook 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Captured males</td>
<td>14</td>
<td>15</td>
<td>30</td>
<td>79</td>
<td>126</td>
</tr>
<tr>
<td>Captured females</td>
<td>4</td>
<td>3</td>
<td>16</td>
<td>24</td>
<td>44</td>
</tr>
<tr>
<td>Total captures</td>
<td>18</td>
<td>18</td>
<td>46</td>
<td>103</td>
<td>170</td>
</tr>
<tr>
<td>Recaptured males</td>
<td>0</td>
<td>2</td>
<td>8</td>
<td>12</td>
<td>22</td>
</tr>
<tr>
<td>Recaptured females</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Total recaptures</td>
<td>0</td>
<td>2</td>
<td>9</td>
<td>15</td>
<td>28</td>
</tr>
<tr>
<td>% Male recaptures</td>
<td>0.0</td>
<td>13.3</td>
<td>26.7</td>
<td>15.2</td>
<td>17.5</td>
</tr>
<tr>
<td>% Female recaptures</td>
<td>0.0</td>
<td>0.0</td>
<td>6.3</td>
<td>12.5</td>
<td>13.6</td>
</tr>
<tr>
<td>% Total recaptured</td>
<td>0.0</td>
<td>11.1</td>
<td>19.6</td>
<td>14.6</td>
<td>16.5</td>
</tr>
</tbody>
</table>

42% increase in the estimated female population size. The model that best explained the capture–recapture history assumed apparent survival to be constant over time, with sex and recapture rates varying over time (Table 1). The likelihood of survival from one capture session to the next (i.e. daily survival rate) was 0.71 (95% CI: 0.66, 0.74).

#### Summit Elevation Will Predict Aggregation Density Better Than Summit Proximity to Larval Patches (Prediction 4)

Elevation was a better predictor of moth density than connectivity (a function of proximity) to larval patches. Of the four models tested (Table 4), the model with elevation as the sole predictor received the lowest AIC score and showed a significant correlation between elevation and moth density (LRT: χ² = 11.87, P < 0.001; Fig. 2). The maximal model (i.e. elevation + connectivity) assumed a weak response to elevation, simulated individuals would move towards the nearest summit from release points but would continue to move onto the higher summits and not become trapped at lower local summits. Because we did not conduct capture–mark–recapture at summits associated with low densities of moths, we could not determine whether individuals remained at these sites or moved to other summits with larger aggregations. Studies have shown that lower-elevation hills are also used as aggregation sites by some hilltopping species (Baughman & Murphy, 1988). However, while lower elevations are used, the highest densities are often associated with the highest elevations (Alcock, 1983; 2000). If some hilltop characteristics are linked to fitness benefits such as the increased likelihood of successful mating events (Ehrlich & Wheye, 1984), then the pattern of hilltop occupancy may reflect the heterogeneity of hilltop quality. For territorial hilltopping species that exist in a topographically heterogeneous landscape, less dominant males may be forced to establish territories on lower-quality (i.e. lower elevation) summits.

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With regard to our third prediction, we found that mated males on average stayed approximately 1.1 day longer than females (Table 2). Considering that the average residency time for all moths

### Table 4
Model comparison for determinants of hilltop selection explaining moth density (response variable)

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>df</th>
<th>AICwt</th>
</tr>
</thead>
<tbody>
<tr>
<td>-Elevation</td>
<td>42.7</td>
<td>0</td>
<td>3</td>
<td>0.69</td>
</tr>
<tr>
<td>-Elevation + connectivity</td>
<td>44.3</td>
<td>4</td>
<td>4</td>
<td>0.31</td>
</tr>
<tr>
<td>-Intercept only</td>
<td>53.3</td>
<td>10.7</td>
<td>2</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>-Connectivity</td>
<td>54.2</td>
<td>11.5</td>
<td>3</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

AIC: Akaike’s information criterion; ΔAIC: difference between the model of interest and the top-ranked model; AICwt: model weight.

### Table 3
Summary of *A. virginalis* adult capture data from the second period of capture–mark–recapture within and between Overlook sites 1 and 2, where residency time is the interval between the first and last recapture or between the first recapture found in copula and the last recapture for mated individuals

<table>
<thead>
<tr>
<th>Sites</th>
<th>Captured males (NM)</th>
<th>Recaptures</th>
<th>% Recapture</th>
<th>Recapture distance (m)</th>
<th>Residency time (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Minimum</td>
<td>Mean ± SE</td>
<td>Maximum</td>
<td>Minimum</td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>Males</td>
<td>623</td>
<td>129</td>
<td>20.4</td>
<td>0.41</td>
<td>41.22±5.0</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2.81±0.2</td>
<td>11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>316</td>
<td>71</td>
<td>22.0</td>
<td>0.19</td>
<td>21.39±5.5</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2.77±0.3</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mated males</td>
<td>67</td>
<td>15</td>
<td>22.39</td>
<td>0</td>
<td>2.53±0.8</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>1.46±0.4</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mated females</td>
<td>37</td>
<td>13</td>
<td>35.1</td>
<td>0</td>
<td>1.13±0.4</td>
</tr>
</tbody>
</table>
was 2.8 days, 1 extra day represents a considerable amount of additional time (36% more) spent on summits. Although our sample size for this analysis was low in comparison to the analysis for individuals not previously found in copula, finding mating individuals at summit aggregations is rare (Ehrlich & Wheye, 1986; Singer & Thomas, 1992), and tracking residency time of naturally mated individuals has proven challenging. In an attempt to deal with this common sample size problem, others have attempted to assess the behaviour of mated butterflies using translocated individuals (Shields, 1967; Wickman, 1988). However, a study by Rutowski, Alcock, and Carey (1989) suggested that translocated individuals exhibit different behaviour compared to their wild counterparts.

Consistent with other hilltopping studies (Brussard et al., 1974; Ehrlich & Wheye, 1986; Shields, 1967), we captured more males within aggregations than females (Tables 2, 3). As posited by others, this finding could be explained by females encountering males prior to reaching the summit (Ehrlich & Wheye, 1986). An alternative hypothesis is protandry: the selective pressure for males to eclose before females. Consistent with protandry-based mating systems, we found that the sex ratio within aggregations became less male skewed over the flight season (Morley & Ydenberg, 2001), and males generally eclosed before females when reared under laboratory conditions (Grof-Tisza, 2017 n.d.).

Regarding our fourth prediction, we found evidence suggesting that moths aggregate on high-elevation summits and not simply those that are most connected (i.e. nearest) to larval patches (i.e. assumed source locations for adults). Summit elevation was the best predictor of moth density, with summit connectivity to larval patches showing little explanatory power (Table 4, Fig. 2). Although this result was consistent across multiple statistical tests (e.g. ANOVA, data not shown), finding an effect of elevation and not connectivity must be viewed with caution given our small sample size and low statistical power to find statistical significance (using an alpha of 0.05), if actually present (i.e. type II error). However, if connectivity were an important factor in summit selection, we would expect the aggregation at North Dune to have the highest densities of moths due its close proximity to larval patch, which contained the highest densities of caterpillars (i.e. highest connectivity; Fig. 1). Instead, we observed the highest densities of moths (20× higher) at the two most isolated (i.e. least connected) but tallest summit aggregation sites, Overlooks 1 and 2.

Despite the numerous publications on hilltopping, no studies have rigorously examined the determinants of summits associated with aggregations. Baughman and Murphy (1988) found that a population of E. editha appeared to select summits on the basis of topography alone. Others found that rock outcroppings (Gradish & Otis, 2015) and nectar plants (Ehrlich & Wheye, 1984) were often associated with aggregation sites. We purposely chose A. virginalis to address these predictions because of its similarities to M. trivia, namely because the movements of both species are likely not influenced by vegetation (Pe’er et al., 2004). The importance of nectar resources for species that feed as adults and other potential drivers of hilltopping behaviour other than elevation remain unexplored.

It is generally assumed that animal movement between patches is random (Hanski & Thomas, 1994; Moilanen & Hanski, 1998). Consistent with other studies (Baughman & Murphy, 1988; Pe’er et al., 2004; Wickman, 1988), we found that dispersal-like movements in A. virginalis are likely influenced by topography. Consequently, the likelihood of an adult female reaching a patch containing host plants (i.e. larval patch) after mating might involve more than the sizes and the distance between patches, factors included in most metapopulation models (i.e. isolation; Hanski, 1998; Hanski & Thomas, 1994). The distance of larval patches to high-elevation summits might also be important. For example, larval patches farther away from hilltop aggregations might have a lower likelihood of colonization by postmating females. At a broader spatial scale, high-elevation summits could act as local attractors and prevent the mixing of neighbouring populations, thereby imposing population structure. We only studied hilltopping behaviour within BMR, so we could not address these hypotheses in this study. However, the closest A. virginalis population outside of BMR is located 8 km away within Point Reyes National Seashore (PRNS). Interestingly, despite the presence of host plant patches in between BMR and PRNS, we have never documented occupancy by A. virginalis caterpillars (P. Grof-Tisza, personal observation). Attraction to regional high-elevation summits could potentially explain this occupancy pattern.

Figure 2. The relationship of A. virginalis density on the five hilltop congregation sites (M: Mussel Point; A: Artemisia; 1: Overlook 1; 2: Overlook2; N: North Dune) and their connectivity to larval patches (upper graph) and their elevation (lower graph). Line represents the best fit from a negative binomial generalized linear model using hilltop elevation as a predictor of moth density, with dotted lines representing the 95% confidence intervals.
Despite the commonness of hilltopping and fragmented insect populations in topographically heterogeneous landscapes and the importance of dispersal as a driver of spatial population dynamics (Wu, Vankat, & Barlas, 1993), hilltopping behaviour has yet to be incorporated into spatially explicit population models. Modelling organismal movement as diffusing particles is a useful null model to start understanding landscape-scale, long-term population dynamics. However, neglecting to incorporate behaviour-based dispersal decisions will likely generate poor predictions and potentially underestimate extinction potential of spatially structured populations (Reed & Levine, 2005). Our work presented here demonstrates the predictive utility of the simple movement rules for hilltopping species developed by others. Such movement rules could be incorporated into established spatial population models (e.g. incidence function model: Hanski, 1994) to determine the importance of hilltopping behaviour on species persistence. This work extends to analogous mating systems such as lek polygyny in vertebrates, where males move to and defend areas devoid of resources, and await receptive females (Alcock, 1983; Bradbury & Vehrencamp, 1977) thereby constraining subsequent female dispersal.

Our study was limited in two ways. First, for prediction 3, we were limited by the number of aggregation sites available to test the relationship between moth density and our two predictors of interest, elevation and connectivity. However, combining our observational and capture—mark—recapture data, the highest-elevation summits over multiple generations were consistently associated with the highest densities of observed moths, while summits nearest to the largest larval patches generally had lower densities of moths. Together, this evidence supports the prediction that moths move towards and aggregate on the highest-elevation summits as expected if they use topography as an orientation cue. Second, we inferred movement of individuals from larval patches to summit aggregations rather than measuring movement directly. One strategy to deal with this issue is to use translocated individuals. However, as previously stated, some evidence suggests that results from studies using translocated individuals may provide spurious results in the context of hilltopping (Rutowski et al., 1989).

**Conclusion**

Through observations and capture—mark—recapture studies with a hilltopping diurnal moth, we found evidence supporting four predictions regarding the response of hilltopping species to elevation changes and its influence on movement behaviour and the resulting spatial distribution of summit aggregations. The highest densities of A. virginalis moths were associated with a few, high-elevation summits. Both males and females were recaptured over multiple days at the same aggregation sites. Mated females were found to have shorter residency times than males and no individuals moved between hilltop aggregations. A fundamental goal in ecology is to understand the factors that determine the abundance and distribution of organisms in the environment. Our work demonstrated that the predictions based largely on simulations of one hilltopping species in virtual landscapes predicted movement behaviours and consequently the abundance and spatial distribution of another hilltopping species in a real topographically heterogeneous landscape.

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**References**


