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# 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, 1988; 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

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has investigated decisions regarding hilltop preference and its consequences for connectivity and population structure (but see Brussard, Ehrilich, & 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 on or near 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 $21.1 \pm 7.4$ days (mean $\pm$ 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, Crutsinger, & 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