

Sex-biased dispersal in a rare butterfly and the implications for its conservation

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Abstract The survival of many species may be dependent on their ability to exist in human-altered landscapes within metapopulations; in turn, metapopulation persistence is dictated by the ability of individuals to move effectively among patches to promote recolonization. The Taylor's checkerspot butterfly (*Euphydryas editha taylori*) is a species that does not naturally occur in fragmented landscapes, yet it is now restricted to a handful of small isolated prairie habitats. Current recovery plans aim to establish a stable metapopulation; however, to date little is known about the species' ability to move across the landscape. In 2010 and 2011, we conducted marking, tracking and boundary surveys to explore the movement dynamics of adults within two sites in Oregon, USA. Over the survey period, we marked 136 male butterflies, tracked 174 individuals and observed the behavior of 1,576 individual butterflies at site boundaries. Our study revealed a significant sex-bias in the movement dynamics of the Taylor's checkerspot in both suitable habitat and surrounding matrix. Males were highly motile, whereas females appeared sedentary, rarely moving from their natal site. The limited dispersal behavior of females indicates that populations cannot persist naturally in a metapopulation

and thus are at high risk of extinction. Based on our findings, we recommend that managers take proactive measures to increase or enable dispersal (including translocation) to existing and/or restored sites.

Keywords Connectivity · *Euphydryas editha taylori* · Human-altered landscape · Metapopulations · Movement dynamics

Introduction

In human-fragmented landscapes, the survival of many species can be dependent on their ability to exist in metapopulations (Schultz 1998; Bergman 2001; Wood and Pullin 2002). Whereas some species persist naturally in metapopulations, land-use change has forced other species adapted to continuous habitats to subsist within habitat fragments (Hanski 1998; Marini and Martins 2010; Fronhofer et al. 2012). If these species are unable to move effectively between fragments, their populations can become isolated (Bruckmann et al. 2010; Leidner and Haddad 2011). Without an influx of emigrants, they are less likely to recover from stochastic events, such as disease and climate change (Hanski 2011). Such populations are therefore at a greater risk of extinction (Saccheri et al. 1998). Thus, many recovery plan objectives for species of concern, particularly invertebrate species, aim to establish stable metapopulations (Bergman 2001; Wahlberg et al. 2002; Smeed et al. 2011). Currently, habitat restoration of existing patches and the surrounding matrix represents an essential strategy used by managers to improve the stability of existing metapopulations and establish new ones (Schtickzelle et al. 2005; Shreeve and Dennis 2011). The success of this strategy, however, is dependent on the ability of

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the focal species to disperse from their natal habitat patch to a new suitable habitat patch (Stevens et al. 2010). Regardless of the density and distribution of suitable patches in the landscape, individuals cannot disperse if physiological, behavioral, or physical constraints impede their movement (Doak 2000; Wood and Pullin 2002; Cassel-Lundhagen and Sjogren-Gulve 2007). Understanding how these constraints influence the movement abilities of a species or sub-species is therefore fundamental to designing effective conservation strategies.

To date, a number of studies have established the dynamics of existing metapopulations and dispersal rates through mark-release-recapture experiments (Boughton 1999; Hovestadt et al. 2011; Zimmermann et al. 2011). From these studies, it has been possible to identify features in the landscape that potentially act as barriers or filters to movement. In most instances, however, no direct data exist to explain mechanisms for movement limitation (Ranius et al. 2011). A few studies have focused on the implications of behavior on dispersal (Schultz 1998; Bergman and Landin 2002; Turlure et al. 2011) and explored why individuals may be physically constrained by certain features in the landscape (Bélisle 2005; Dover and Settele 2009; Stevens et al. 2012). From these studies, it has been suggested that the behavioral responses of individuals within a population provide valuable insights into the mechanisms that drive dispersal, which in turn influences metapopulation stability (Shreeve and Dennis 2011; Turlure et al. 2011; Stevens et al. 2012). Thus, understanding how both behavioral and physical characteristics drive or inhibit dispersal will help managers devise strategies that effectively enhance metapopulation structure (Wang et al. 2004; Buchholz 2007; Delattre et al. 2010).

In this paper, we assess the behavioral and physical factors that influence the dispersal behavior of the Taylor's checkerspot butterfly (*E. editha taylori*). This Pacific Northwest subspecies of the Edith's checkerspot (*E. editha*) is a candidate for listing under the U.S. Endangered Species Act, listed as endangered under the 'Species at Risk Act' in Canada, and a species of concern in Washington State, USA (Black and Vaughan 2005). Petition for its listing came as a result of the butterfly's extirpation in all but a handful of small isolated prairie habitats in the states of Oregon (2 sites) and Washington (10 sites), and in British Columbia, Canada (1 site; Vaughn and Black 2002; Stinson 2005; Ross 2009). Because these existing populations are vulnerable to stochastic events, primarily weather (Stinson 2005), it is essential that (1) these remnant sites are effectively managed, (2) areas of suitable habitat are restored, and (3) stable metapopulations are created. For the latter to be successful, management plans must be based on the abilities of individual butterflies to move between habitat patches, colonizing newly restored habitat,

and recolonizing existing patches when necessary. To date, however, no studies have been undertaken to explore the dispersal ability of the Taylor's checkerspot. To address this need, we conducted field surveys that assessed the dispersal ability and movement dynamics of adult butterflies at two sites in Oregon. We discuss our findings and consider their implications for the conservation and future management of the Taylor's checkerspot butterfly and other species whose persistence is dependent on their ability to exist in a human-altered landscape.

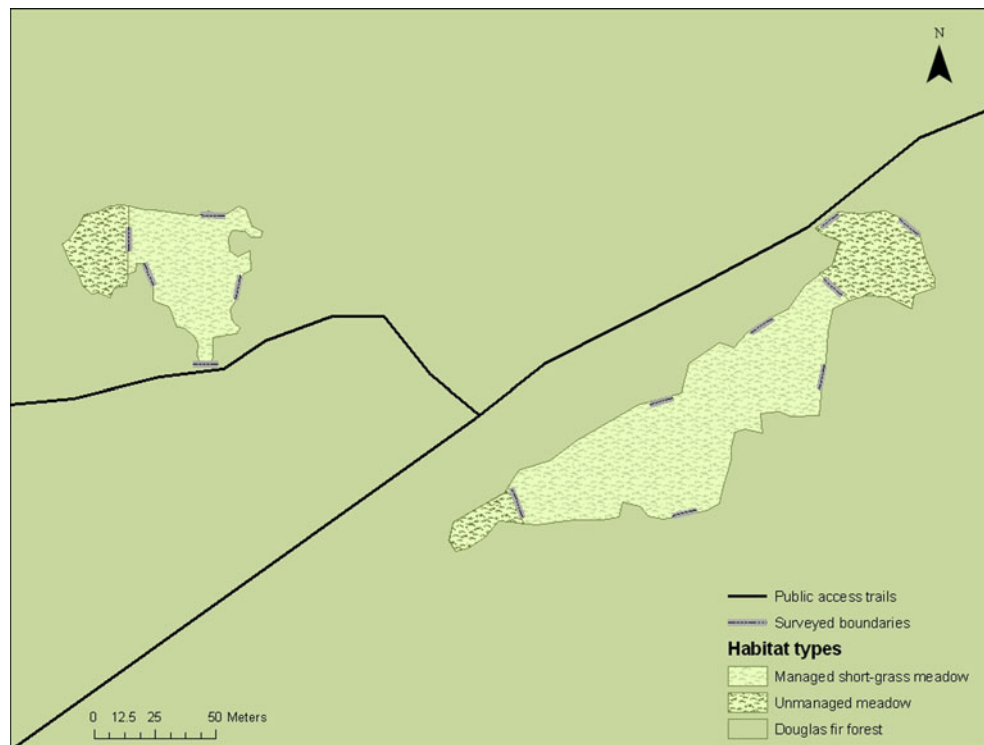
Materials and methods

Study site

We conducted all surveys within Fitton Green Natural Area in Benton County, Oregon, USA. This area supports one of two remaining populations of Taylor's checkerspot butterfly currently known in Oregon. Both populations occur within a system of connected meadows (forest glades) surrounded by former Douglas-fir (*Pseudotsuga menziesii*) managed forests. Mark-release-resight experiments have yet to provide evidence of dispersal between the two populations (unpublished data), which are approximately 7.5 km apart. Within the meadow system in Fitton Green, we surveyed two meadows with annual population numbers ranging from 300 to 1,200 (Ross 2009). These short-grass meadows, comprising primarily native fescues, such as *Festuca roemerii* (Stinson 2005), were surrounded by Douglas-fir forest and the occasional Oregon white oak (*Quercus garryana*). The larger of the two meadows (hereafter known as 'Site 1') was a narrow, oblong grassland with a gentle southwest-facing slope, approximately 220 m by 50 m. 'Site 2', the smaller of the two, was approximately 75 m by 65 m and located on a south-facing slope, approximately 100 m northwest of site 1.

We conducted preliminary vegetation surveys at both our sites. Each site was divided into a grid of 5 m² plots. Using Hawth's Analysis Tools for ArcGIS (Beyer 2004), we then randomly selected three 1 m² plots within these 5 m² plots to survey. In each selected plot, we recorded the number of individual host and nectar plants present, and their percentage cover. These surveys revealed that nectar plants, including wild strawberry (*Fragaria virginiana*), and host plants, English plantain (*Plantago lanceolata*), were found throughout both sites. We found that the density, quality, and distribution of these plants did not vary across the majority of each site or between sites. However, patches of unmanaged habitat containing non-native tall species, including false brome (*Brachypodium sylvaticum*), were present at both sites; two at either end of site 1 and one in the northeast corner of site 2 (Fig. 1).

Fig. 1 Site map of sites 1 and 2 located in Oregon, USA and identification of boundaries surveyed to assess the crossing probability of male and female Taylor's checkerspot butterflies from their natal sites into the surrounding landscape matrix



Field study

We conducted all surveys during the entire adult flight period of the Taylor's checkerspot butterfly between April 10 and May 8, 2010, and between May 1 and June 9, 2011. We collected detailed information on the movement patterns of individuals (both males and females) across the study sites in a series of marking, tracking, and boundary surveys. Over the survey period, we marked 136 male butterflies with an alpha-numeric code on a foam disc attached to the dorsal surface of the thorax. To minimize disruption to breeding, female butterflies were not marked. We were able to discern males and females using sexually dimorphic characteristics, such as the female's larger and distinctively rounded abdomen.

Note that the following surveys were designed to minimize anthropogenic disturbance to the study sites and therefore the butterfly. For example, all data was collected by observers positioned along site perimeters, thus we avoided trampling core habitat. As our survey sites were small (refer back to study site), this made it possible to observe an individual butterfly moving across the entire site from perimeters using a Brunto single marco-lens spotting scope. In observational surveys (hereafter referred to as tracking surveys), we plotted individual flight paths, detailing the spatial and temporal movement patterns and extents and turning angles of each tracked butterfly onto a 5 m by 5 m gridded aerial photograph of the survey sites and surrounding area. We also plotted the locations of all

stationary behaviors, including basking, nectaring, mating and ovipositing sites. Using Olympus WS-510M digital voice recorders, we detailed all observed activities and behaviors, including interactions with conspecifics and heterospecifics, and the duration of each activity. We transferred all the individual flight paths onto site-equivalent GIS maps in ArcGIS (ESRI, Redlands CA). Attribute tables associated with each projected flight path were populated with details of behavior and durations at each recorded position (data point). For each tracking survey, we selected an individual butterfly opportunistically, although individuals marked with an alpha-numeric identification code (at a minimum of 24 h post-marking) had priority over unmarked males. To minimize the likelihood of duplicate observations, marked individuals (47 males of 174 individuals tracked) were followed only once during a survey season and unmarked individuals were tracked 1 day a week at each site. The latter tracking interval was selected as preliminary observations of marked individuals indicated a high male turnover of <6 days. In addition, unmarked individuals (53 males and 74 females) were selected from different locations across each site within a survey day by multiple observers and tracked simultaneously to avoid replication. Once an individual was selected, we made continuous observations of the butterfly for as long as the surveyor had visual contact and the butterfly remained active (e.g., butterflies were not active when it rained). Furthermore, as Taylor's checkerspot butterflies were only active within small range of weather

conditions (unpublished data), we only tracked individuals when conditions were suitable and butterflies were observed flying.

In addition to tracking, we conducted boundary surveys to establish the dispersal/off-site movement and boundary crossing probabilities of males and females. We define ‘crossing probability’ as the probability that once an individual entered a boundary zone, it would permanently move from the current site to a new site. We identified and surveyed 13 different types of boundary at our sites (Fig. 1). These included 8 boundaries at site 1: 5 Douglas-fir woodland edge boundaries with varying directional aspects (north, south, northeast, northwest and southeast), 2 tall grass habitat edges (northeast and southwest) and a 3 m wide dirt trail paralleling site 1’s northern edge. At site 2, 5 boundaries were selected, including a former logging road (skid road) running along the southern edge of site 2, 3 woodland edges (north, east and southwest) and a tall grass habitat with a western aspect. Note that preliminary observations indicated that butterfly activity varied within our sites with direct sunlight exposure. Thus, we deemed boundaries with the same habitat type, but different directional aspects to be separate boundary types as their levels of sunlight exposure varied. Along a 10 m strip of each selected boundary, we surveyed a zone extending 3 m from that boundary into the site. We recorded all behavioral activities and boundary crossing attempts (successful and unsuccessful) made by individual butterflies entering the survey zone. This included recording the height at which the butterfly flew, characteristics of their flight (e.g., searching behavior and direct flight), and their responses to boundaries on approach, such as avoidance or changes in flight pattern. A successful boundary crossing occurred when a butterfly crossed the boundary into the surrounding habitat. Whereas an unsuccessful crossing was recorded when a butterfly attempted to go through a boundary, but was hindered in the process and subsequently returned to the site. We also recorded the direction butterflies crossed the boundary, i.e., from the site into the surrounding area or from the surrounding area into the site. Surveyors used digital recorders to verbally record all observational data, including sex and the presence of a mark.

Analysis

To discern the density of space use by males and females (hereafter referred to as the utilization distribution, or UD), we created local convex hulls (LoCoH) for each individual flight path using OpenJUMP (version 1.4.0.1) within the home range analysis and estimation (HoRAE) toolbox, an open source GIS software. This non-parametric kernel estimation combines a series of convex hulls (subsets of the data) associated with each spatial data point and its $k - 1$

nearest neighbors (Getz and Wilmers 2004; Getz and Saltz 2008). We selected this method over the standard minimum convex polygon (MCP) algorithm, as it more effectively accounted for unused areas due to boundaries and other features within and surrounding our survey sites (Moorcroft and Lewis 2006; Getz et al. 2007; Liu et al. 2010). The ‘ k ’ values were set as the square root of the total number of data points recorded for each track and we used the 100 % isopleth to create LoCoH and establish the area of each hull (m^2). Using a custom built program in Python 2.5.1 (2007), we also calculated (1) tortuosity, the mean vector length of successive turning angles, where 1 indicates a straight line (Batschelet 1965), and (2) speed (m/s) of the specific behaviors we observed, such as dispersing and searching (for mate, host plant or nectar plant).

To determine the extent to which movement and habitat use varied between males and females, we used a general linear model (GLM) in Minitab version 16. We considered two response variables, (1) length of each track (m), and (2) UD (the area of the LoCoHs), and three independent variables as (1) sex, (2) site, and (3) behavior. As weather conditions in which butterflies were active were invariant within and between years, we do not include them in our analysis. Prior to the GLM analysis, we checked that all variables met the appropriate assumptions. If they did not follow a normal distribution, we used a rank transformation (Conover and Iman 1981). We then used a Spearman’s rank correlation to determine whether there was a correlation between the two aforementioned response variables and the duration that each butterfly was tracked. Finally, to compare male and female activity within boundary zones and determine whether successful and unsuccessful crossing attempts varied between boundary types between the sexes, we used a χ^2 goodness-of-fit test ($P < 0.05$).

Results

Marking and tracking surveys

We marked 76 males on site 1 and 60 males on site 2 over the survey period. No marked individuals from site 1 were observed on site 2, or visa versa during our surveys. We tracked a total of 174 individual butterflies during the adult flight period at Fitton Green Natural Area; 105 at Site 1 (36 females and 69 males) and 69 at Site 2 (38 females and 31 males). We tracked individuals for a total of approximately 72 h and recorded 8,953 point locations. Track durations averaged 22 min for males (ranging from 40 s to 1 h 50 min) and 29 min for females (ranging from 2 min to 2 h 48 min). See Table 1 for the descriptive statistics on male and female track lengths and LoCoH, as well as Fig. 2

Table 1 Descriptive statistics for male and female track lengths and LoCoH

	Male		Female	
	Track length (m)	LoCoH (m ²)	Track length (m)	LoCoH (m ²)
Mean	124	681	69	309
Standard error	9	101	6	39
Median	108	530	57	210
SD	63	714	54	334
Sample variance	12,765	1,637,149	9,532	358,190
Kurtosis	0.47	2.13	1.66	1.59
Skewness	0.38	0.77	0.60	0.66
Range	288	3,537	288	1,595
Minimum	46	22	0	0
Maximum	334	3,558	288	1,595
Sum	6,218	34,044	5,130	22,851
Count	16	16	23	23
Largest	334	3,558	288	1,595
Smallest	46	22	0	0
Confidence level (95.0 %)	18	203	13	77

delineating the distribution of male and female LoCoHs across the study sites.

Among the males tracked, we identified four general behaviors: nectaring, dispersing, and two separate mating strategies, perching and patrolling (Bennett et al. 2012). We recorded 30 % of males (n = 30) perching consistently within areas <5 m², regularly engaging in conspecific interactions with other passing males. Another 60 % of tracked males (n = 60) undertook a patrolling behavior, in which individuals exhibited a constant low, slow, zigzagging, searching flight. We found that patrolling males travelled at average speeds of 1.6 m/s (SD = 0.42 m/s). We calculated tortuosity (r value) as 0.21, with an angular deviation (AD) of 72, indicating that patrolling individuals change their direction regularly. We also tracked 6 % of males (n = 6) switching from patrolling behavior to perching behavior. Of the remaining individuals tracked, 4 % of males (n = 4) were only observed nectaring. Among the patrolling males, 42 % (n = 25) suddenly stopped patrolling and flew directly out of the site. We concluded that these latter males had dispersed (defined as the permanent emigration of an individual from the site), as all marked males exhibiting this behavior (7 of 25) were not observed again in

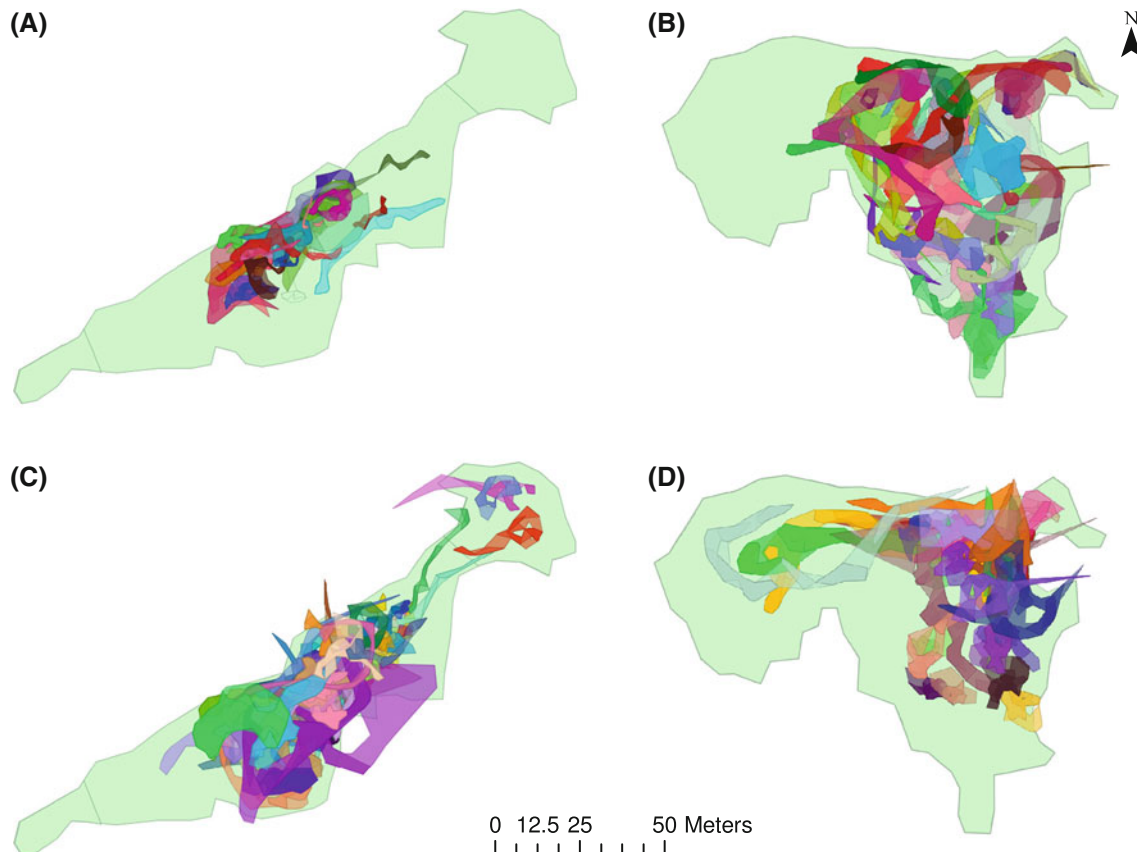


Fig. 2 Local convex hulls for Taylor’s checkerspot butterflies at two study sites in Oregon, USA. Females at site 1 and site 2 are shown in (A) and (B), respectively, and males at site 1 and site 2 are shown in (C) and (D), respectively

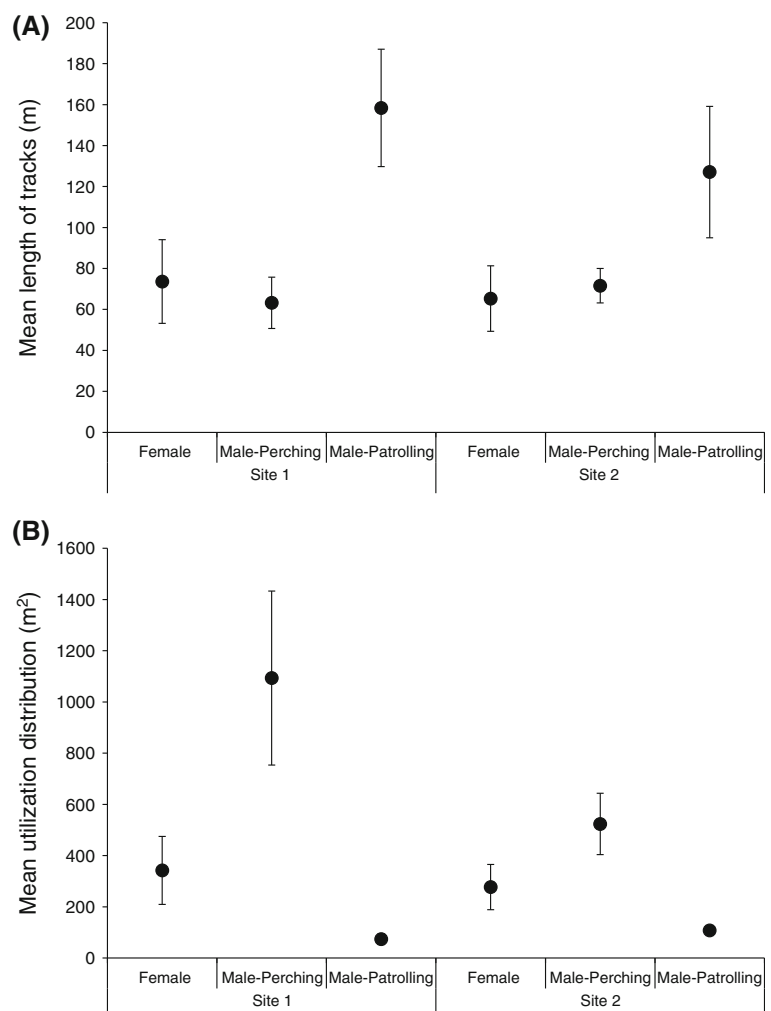
the site during the survey season. In addition, we did not observe any of the 136 marked males returning to their release sites after a period of absence, further indicating that once a male leaves a site he does not return. We noted that when males switched from patrolling to dispersing flight, they moved in a straight path from wherever they were in the site towards the nearest boundary edge, with a tortuosity of 0.66 ($AD = 47$). In all cases, males that exhibited this flight would fly either through or over the boundary, and continue to fly in this manner across the surrounding habitat. The average speed of dispersing males was also greater than patrolling flight at 2.7 m/s ($SD = 1.5$ m/s).

In contrast, we rarely observed females in continuous flight. When females were observed flying, they either displayed short bursts of shallow flight moving from one host or nectar plant to another, or a ‘hopping’ style flight when harassed by males. During these flights, we found speeds and tortuosity averaged 0.7 m/s ($SD = 0.1$ m/s) and 0.6 ($AD = 53$), respectively, indicating relatively slow movement rates with straight trajectories. Typically, we observed females crawling through the vegetation at speeds

of 0.4 m/s ($SD = 0.1$ m/s) with a tortuosity of 0.4 ($AD = 63$). We observed five general behaviors among females: nectaring, ovipositing (searching for host plants and laying eggs), mating (27 mating events were recorded), avoiding males, and dispersing. During our surveys the majority of females (45 of 74) were recorded either nectaring (23 %), or ovipositing (38 %) within the bounds of our survey sites. In fact, over the adult flight period we only tracked two females (3 %) that moved from the survey site. In both instances, the females crawled less than 10 m from the site boundary before they ceased to move. After 30 min we terminated these two tracking surveys, but returned to find both females in the same locations at the end of the survey day (approximately 3 and 2 h later, respectively) when butterfly activity had ceased at the sites.

For the GLM analysis, we found that our response variables did not follow a normal distribution and therefore conducted a rank transformation on the data. In addition, as patrolling and perching strategies exhibited by males influenced site use, we considered these strategies as two separate behaviors in our analysis. We found that the length of tracks

Fig. 3 Interval plot showing **A** the mean length (m) of Taylor’s checkerspot butterfly tracks and **B** the mean utilization distribution (m^2) at both sites 1 and 2 for females, perching males and patrolling males, respectively



significantly varied between females, perching males and patrolling males ($F_2 = 17.76, P < 0.001$; Fig. 3A). However, we found no significant difference between the length of tracks recorded at site 1 and site 2 ($F_1 = 0.88, P = 0.349$). Similarly, we found that UD varied significantly between females, perching males and patrolling males ($F_2 = 12.20, P < 0.001$; Fig. 3B), but UD did not vary between site 1 and site 2 ($F_1 = 2.17, P = 0.142$). The Spearman rank correlation revealed that among patrolling males track length and UD increased with track duration ($r_s = 0.972, n = 60, P < 0.001$ and $r_s = 0.577, n = 60, P < 0.001$, respectively). However, among females track length and UD did not increase with track duration ($r_s = -0.140, n = 74, P = 0.234$ and $r_s = -0.233, n = 74, P = 0.045$, respectively). Similarly, with perching males there was no correlation in track length and UD with track duration ($r_s = 0.168, n = 30, P = 0.372$ and $r_s = -0.140, n = 30, P = 0.458$, respectively).

Boundary surveys

A total of 148 h of boundary surveys were conducted, constituting 6 h at each boundary. Among the boundary surveys, we recorded 1,576 individual butterflies (889 at site 1 and 687 at site 2) entering the boundary zones of which 99 % were male (Table 2). Furthermore, no females attempted to cross any of our boundaries exiting the survey sites during the boundary surveys, thus their crossing probability was 0. In contrast, 14 % of males ($n = 216$) entering the boundary zone attempted to cross through the boundaries into the surrounding area (male crossing probability = 0.14). Of these boundary crossings, 91 % were successful and 9 % of the attempts were unsuccessful as males were hindered during their crossing attempt (i.e., by a gust of wind, the sun going behind clouds, or conspecific interaction), resulting in the individual returning to the site. Chi square revealed that successful crossing attempts by males varied significantly by boundary ($\chi^2 = 203.647, df = 10, P < 0.001$). The physical structure of the boundaries did not appear to restrict the movement of males beyond the site within a 30 s period. For example, we

recorded 29 % of males ($n = 62$) flying up and over 10 m high woodland edges and 33 % of males ($n = 72$) flying underneath the canopy ($\chi^2 = 0.746, df = 1, P = 0.3877$). However, the position of the boundary within the site significantly influenced whether males attempted to cross a particular boundary (site 1: $\chi^2 = 59.409, df = 4, P < 0.001$; site 2: $\chi^2 = 41.2, df = 3, P < 0.001$). We found that the majority of crossing attempts occurred at boundaries with a north to east aspect (Fig. 4). A two-sample *t* test revealed no significant difference in the number of crossing attempts made by males between sites (*t* value = $-1.13, df = 11, P = 0.283$). Finally, we only recorded one individual coming from the surrounding habitat into our site. This male was recorded shortly after a successful crossing attempt. In this instance the individual was exhibiting searching flight not dispersing flight. All other males that successfully or unsuccessfully crossed a boundary zone exhibited dispersing flight.

Discussion

Our study revealed a significant sex-bias in the movement and dispersal behaviors of the Taylor’s checkerspot butterfly. We found distinct differences in the movement dynamics of males and females in both suitable habitat and surrounding matrix. Overall, males were highly motile, whereas females appeared sedentary, rarely moving from their natal site. Within both survey sites, we found that males tended to move longer distances at faster speeds over larger areas than females; a pattern that has been reported in other butterfly species (Konvicka and Kuras 1999; Cassel-Lundhagen and Sjogren-Gulve 2007; Korosi et al. 2008). In contrast, we found females were significantly less motile, moving smaller overall distances at much slower speeds.

These differences in movement dynamics and area utilization appear to be strongly associated with sex-specific behaviors. We recorded four distinct male flight behaviors, including nectaring, dispersing and two mating strategies: perching and patrolling. In the latter, males exhibited a

Table 2 Number of male and female Taylor’s checkerspot butterflies to enter the 3 m boundary zone (*in zone*), number of individuals that attempted to cross each boundary type (*crossing event*) and number of those attempts that failed (*failed crossing events*)

Site	Boundary type	Male			Female		
		In zone	Crossing event	Failed crossing event	In zone	Crossing event	Failed crossing event
Site 1	Woodland	655	45	8	0	0	0
	Tall grass	132	26	0	0	0	0
	Fence/trail edge	102	17	0	0	0	0
Site 2	Woodland	454	69	4	3	0	0
	Skid road	56	8	0	0	0	0
	Tall grass	177	36	0	0	0	0
Total		1,576	201	12	3	0	0

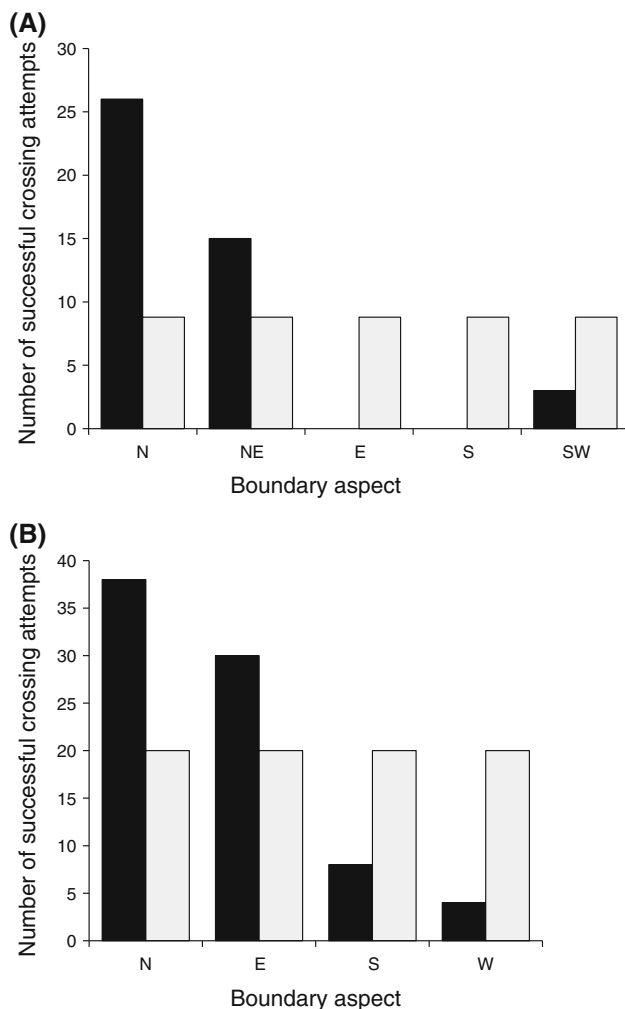


Fig. 4 Graph to compare the observed (*black bars*) and expected (*grey bars*) number of successful crossing attempts by male Taylor's checkerspot butterflies at site boundaries with different aspects at **A** site 1 and **B** site 2

quick continuous zigzagging flight to find receptive females (Bennett et al. 2012). Such patrolling strategies are common among many butterfly species and it is only the extent of area patrolled that varies. For example, the males of some species patrol patches of habitat, whereas others patrol whole sites or even a series of habitat patches (Scott 1974; Campbell et al. 2007). Thus, males that employ patrolling strategies will tend to have larger UD than females, which supports our findings. In contrast, perching involves males remaining within a specific area waiting for receptive females (Scott 1974). At both our study sites, we found that male Taylor's checkerspots perched consistently within areas $<5 \text{ m}^2$ (Bennett et al. 2012). By associating themselves with such small areas, perching males are likely to have a smaller UD than females, and this supports our findings. We also observed dispersing flight (a fast straight flight) in which males moved from our study sites into the surrounding landscape matrix and they did not return.

In comparison, females could have exhibited four potential flight behaviors; (1) searching for mates, (2) searching host plants on which to oviposit, (3) searching for nectaring opportunities and (4) dispersing (Bergman and Landin 2002). As the Taylor's checkerspot mating system involves males seeking receptive females, it is unlikely females would exhibit mate searching behaviors as well (Scott 1974). This is supported by our findings that no tracked females were recorded seeking males at our study sites. Furthermore, we did not record any females exhibiting dispersing behavior equivalent to those observed among males, and only two tracked females attempted to move (crawling) into the surrounding matrix. Thus, the majority of female Taylor's checkerspots were observed searching for nectar and host plants. Across our study sites, both nectar and host plants commonly occurred $<1 \text{ m}$ from each other. Under these conditions, females could find sufficient host and nectar plants within a small area. This may have minimized their need to move greater distances, which led to the small UD we recorded.

We also found that despite being a small to medium-sized butterfly (ca. 60 mm wingspan, Stinson 2005), males were able to (1) move across all of our boundaries unhindered, (2) fly up to heights above 10 m, allowing them to fly over tree canopies, (3) utilize both natural and non-natural corridors (such as public access trails), and (4) 1 in 7 male butterflies that approached site boundaries dispersed from the site. Our study, therefore, shows that male Taylor's checkerspots are strong fliers able to move effectively out of their natal sites into the surrounding matrix. This, in turn, suggests that males have the potential to migrate between sites (depending on distance) and thus contribute to maintenance of a stable metapopulation (Perrin and Mazalov 2000).

In contrast, physical factors seem to limit female movement (Korosi et al. 2008; Niitepold et al. 2011). Females did not appear to be strong fliers, opting to crawl or restrict their flight time to short bursts (Konvicka and Kuras 1999). As females tended to be mated shortly after enclosing, their movement may have been limited by physical constraints, such as the weight of the eggs in their abdomen (Bergman and Landin 2002; Korosi et al. 2008; Delattre et al. 2010). In support of this, we noted that 81 % of the females that crawled were ovipositing. In contrast, nectaring females flew more frequently, at longer distances and faster speeds than ovipositing females. Many of these nectaring females were observed towards the end of the adult flight period, potentially when the majority of their eggs had been laid. Thus, it is possible that females at this time are less physically restricted and could potentially disperse, but we did not observe any dispersing flight among females during our tracking surveys. Overall, females were unable to fly effectively in or near the

forested matrix surrounding the open meadows of sites 1 and 2, suggesting that they would not be able to migrate and thus could not contribute to maintenance of a stable metapopulation.

Our study reveals that it is important that we identify the extent to which movement differs between sexes and raises awareness that sex-biased dispersal may go unnoticed unless specifically assessed. Without identifying Taylor's checkerspot butterflies to sex, the species appears to be quite motile, as individuals (males) can move efficiently across their habitat and into the surrounding landscape. Thus, it would be quite easy to overestimate species mobility from such observations and underscores the need to thoroughly understand the movement dynamics of both males and females to successfully manage fragmented subpopulations.

Implications for conservation

Although studies have shown sex-biased dispersal in other butterfly species, female dispersal was still generally more common than observed in our study (Konvicka and Kuras 1999; Perrin and Mazalov 2000; Bergman and Landin 2002). As the viability of a metapopulation is dictated by the ability of individuals of both sexes to disperse and move from one habitat patch or population to another (Boughton 1999; Cassel-Lundhagen and Sjogren-Gulve 2007; Marini and Martins 2010), our study demonstrates that the Taylor's checkerspot butterfly does not appear to have this ability. This suggests that this butterfly subspecies will not be able to re-colonize existing habitat patches or colonize restored patches. Thus, standard management practices, such as habitat restoration, may not be successful unless combined with other strategies, such as interlinking habitat corridors (Bergman 2001; Schultz 1998; Wood and Pullin 2002).

However, even the creation of corridors between habitat patches might not be as effective for this and similar species (Dover and Settele 2009). Although corridors are designed to increase functional habitat connectivity and link fragmented subpopulations (Cassel-Lundhagen and Sjogren-Gulve 2007; Hanski 1998; Öckinger and Smith 2008), they can only be effective if individuals have the physical and behavioral capability to move through them (Öckinger and Smith 2008; Wood and Pullin 2002). As female Taylor's checkerspots do not tend to move far and are easily hindered by unfavorable conditions, such as limited sunlight, corridors may only be useful if they link habitat patches that are very close to each other (potentially <100 m). The most effective distance may be one that allows females to crawl between sites, if necessary, over a number of days. This strategy is plausible between our two study sites (100 m apart) and potentially other sites within

Fitton Green Natural Area, but not between Oregon's remaining two populations (7.5 km apart). Thus, for species such as the Taylor's checkerspot, there may be a need for more proactive forms of management to be included in recovery plans. The translocation of females from existing populations to unoccupied sites within the same area may help create and maintain a stable metapopulation (Schultz et al. 2008, 2009; Shreeve and Dennis 2011; Smee et al. 2011). As a potentially crucial conservation strategy for species of concern, we recommend further studies into the effectiveness of translocation exercises in conjunction with continuing habitat restoration. Furthermore, given the challenges of restoring landscape connectivity, it may be easier to increase habitat patch size and thus the size of a local population in the short term than restore the landscape. For this the fundamental question is "What is the minimum size an isolated population needs to be to persist?" To answer this further demographic studies are needed (e.g. Smith and Person 2007).

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