JOURNAL OF APPLIED ENTOMOLOGY

J. Appl. Entomol.

ORIGINAL CONTRIBUTION

Influence of thermal conditions on habitat use by a rare spring-emerging butterfly *Euphydryas editha taylori*

V. J. Bennett[1,2], M. G. Betts[2] & W. P. Smith[3]

1 School of Geology, Energy and the Environment, Texas Christian University, Fort Worth, TX, USA
2 Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA
3 USDA Forest Service Pacific Northwest Research Station Forestry Sciences Laboratory, Olympia, WA, USA

Keywords
adult flight period, habitat quality indicator, *in situ* habitat use, larval distribution, Taylor's checkerspot butterfly, thermal thresholds

Correspondence
V. J. Bennett (corresponding author), School of Geology, Energy and the Environment, Texas Christian University, Fort Worth, TX 76129, USA. E-mail: v.bennett@tcu.edu

Received: September 2, 2013; accepted: April 11, 2014

doi: 10.1111/jen.12137

Abstract

We may expect butterflies as ectotherms to have particularly active life-history stages that occur in the warmest and lightest times of the year; however, there are temperate species that are active when climatic conditions seem unfavourable and photoperiod short, such as the Taylor's checkerspot (*Euphydryas editha taylori*). For such species, studies suggest that even subtle changes to microclimate can potentially impact populations. Thus, understanding how *in situ* variations in microclimate influence the Taylor's checkerspot butterfly could provide much needed insights into more effective management. We conducted a series of surveys that explored (i) adult habitat use, (ii) final instar larval distribution and (iii) adult movement up to and across site boundaries at two sites in Oregon, USA, in 2010 and 2011. We found that *in situ* habitat use by the Taylor's checkerspot butterfly was strongly influenced by microclimate. Both adult activities and final instar larvae distribution were clustered within the warmest areas of the sites. Moreover, adults did not use up to 59% and larva up to 90% of their sites, despite vegetation structure and composition being uniform. More specifically, butterfly habitat use increased with increasing ground temperatures, and we found that areas with the highest ground temperatures were more exposed to direct sunlight. Similarly, we found that butterflies tended to only move through sunlit site boundaries. We conclude that the Taylor's checkerspot is sensitive to changes in its thermal environment at fine spatial scales. Our results highlight the importance of microclimate as an indicator of habitat quality, and establishing the thermal criteria in which species of concern exists may provide valuable insights into the implications of climate change.

Introduction

As ectotherms, many butterflies control their body temperature passively via environmental heat sources (Berwaerts et al. 2001; Bryant et al. 2002; Kemp and Krockenberger 2004). Thus, to effectively and efficiently undertake activities that require higher levels of heat energy, such as flight, we would expect such activities to occur during the warmest and lightest times of the year (Berwaerts and Van Dyck 2004; Bonebrake et al. 2010; Singer and Parmesan 2010). However, there are several temperate species that have adopted an alternative life-history approach in which peak activity occurs when climatic conditions seem unfavourable and photoperiod short (i.e. in late winter and spring; Porter 1982; Sparks and Yates 1997; Pratt and Emmel 2010).

The Taylor's checkerspot butterfly (*Euphydryas editha taylori*), a candidate for listing under the US Endangered Species Act, is one such species (Vaughn and Black 2002; Stinson 2005). Across its current range, which is restricted to Oregon, Washington and British Columbia, the Taylor's checkerspot conducts active life-history stages (including final-stage instars,

pupation and adult flight) when temperatures and light intensity are relatively low. For example, the fourth and fifth instar larvae of this butterfly enter diapause towards the beginning of the summer and become active (post-diapause) again as early as January in Oregon (Stinson 2005) and at higher elevations in Washington, larvae are seen moving when snow is on the ground (K. Holtrop, pers comm). Adult butterflies then emerge and fly for approximately 2–5 weeks in early April in Oregon and early May in Washington (Stinson 2005). As a univoltine species, population growth of the Taylor's checkerspot is therefore dependent on this one breeding period (Cushman et al. 1994; Stinson 2005).

Consequently, there is a higher risk that climatic perturbations could threaten the survival of existing populations of the Taylor's checkerspot, which currently persist in a handful of small isolated habitat patches (Stinson 2005). Furthermore, a number of studies have suggested that even subtle changes to microclimate can potentially influence this butterfly's populations (Dobkin et al. 1987; Weiss et al. 1988; Suggitt et al. 2011). For example, among a number of different butterfly species, including subspecies of the investigated butterfly, microclimate changes have led to variations in larval occupancy, behavioural mating strategies employed by males and activity patterns across a site (Weiss et al. 1988; Fischer and Fiedler 2001; Albanese et al. 2008). Consequently, if the microclimate was to change across one of the habitat patches in which this butterfly currently exists, it could render that site unsuitable for the butterfly. Understanding how microclimate influences the Taylor's checkerspot could therefore provide much needed insights into the effective management of this butterfly, equivalent subspecies and other spring flying butterflies (Vaughn and Black 2002). Thus, we conducted a series of surveys that explored adult habitat use and final instar larval distribution of the Taylor's checkerspot at two sites in Oregon in 2010 and 2011. We then compared the spatial distribution of these activities to variations in microclimate that occurred across the sites. In addition, we investigated microclimate variation along the site boundaries at each site and hypothesized that any changes in microclimate at these habitat edges could affect the butterfly's dispersal propensity (Ries and Debinski 2001; Ross et al. 2005; Dover and Settele 2009). Such restrictions in emigration could isolate Taylor's checkerspot populations further and subsequently put them at greater risk of extinction (Hanski 1998). Finally, we discuss whether establishing a thermal criteria for this butterfly would contribute significantly towards conservation efforts, both in terms of site management and in the selection of sites for reintroduction initiatives.

Material and Methods

Study sites

We conducted surveys at Fitton Green Natural Area in Benton County, Oregon, USA. This area contains one of two remaining populations of Taylor's checkerspot butterfly known in Oregon. The population occurs in a system of connected meadows (forest glades) within a former Douglas-fir managed forest situated in the Willamette Valley at an elevation of approximately 300 m. We conducted our observations in two meadows that contained known breeding populations of Taylor's checkerspots; these were both small short-grass-covered sites almost entirely surrounded by a Douglas-fir forest and the occasional Oregon white oak (*Quercus garryana*). The larger of the two meadows (hereafter known as 'Site 1') was narrow with an oblong shape, approximately 220 × 50 m, with a gentle south-west-facing slope. 'Site 2' was much smaller, approximately 75 × 65 m on a south-facing slope. The two sites were approximately 100 m apart.

At these sites, the primary host plant for the Taylor's checkerspot butterfly is the English plantain (*Plantago lanceolata*) and the primary nectar plant is wild strawberry (*Fragaria virginiana*). English plantain is the only potential host plant at our sites that appears to be available when the fourth and fifth instar larvae emerge from diapause and throughout the adult flight period. In preliminary vegetation surveys, we recorded the number of individual host and nectar plants present and their percentage cover in randomly selected 1-m^2 plots across each site. These surveys revealed that nectar and host plants were found throughout both sites and the density and condition of these plants did not vary within each site or between sites (i.e. there were no patches or concentrations of plants identified; Bennett et al. 2013).

Adult *in situ* distribution and activity surveys

We conducted tracking surveys during the adult flight period of the Taylor's checkerspot butterfly between April 10th and May 8th of 2010 and between May 1st and June 9th of 2011. In these surveys, we collected detailed information on the movement dynamics and behaviour of individuals (both males and females) across the survey sites.

From preliminary observations, we noted that Taylor's checkerspots carried out all non-flight activities (i.e. basking, nectaring, mating, crawling, ovipositing, perching and resting) in or on the short-grass and low-lying vegetation comprising our sites. To avoid trampling and disturbance to the butterfly's natural behaviour, we conducted all tracking surveys from the margins of the sites. Thus, prior to adult emergence, we placed 38-cm-tall metal pin flags in a 5 × 5 m cell grid across each site. On a high-resolution aerial photograph with an equivalent 5 × 5 m cell grid we then mapped the flight path of each observed individual. For this, we recorded each turn made in flight and when crawling, and the location of each alighting event (e.g. the location a butterfly landed to bask) or change in behaviour. Each position (point) mapped on the aerial photograph was numbered and given a code that defined the behaviour (e.g. B represented basking). To confirm behaviour, particularly those that could be cryptic (such as ovipositing), we used a Brunton single macro-lens spotting scope. As the study sites were small, we were able to effectively track a single butterfly across the entire site from static locations along the site margins.

We selected individual butterflies opportunistically from different grid cells and never selected an individual from the same cell or neighbouring cell on the same day. Once selected, we observed an individual continuously for as long as it remained in sight. Tracking was therefore terminated when (i) an individual left the study site, (ii) an individual engaged in a conspecific interaction and could not be confidently distinguished for another butterfly, and (iii) weather conditions deteriorated and all butterfly activity across the sites ceased for periods exceeding 30 min.

To avoid surveying individuals multiple times, we marked 76 and 60 butterflies over the survey period at Sites 1 and 2, respectively. Each butterfly was marked with a self-adhesive coloured foam disc with a unique alpha-numeric code placed on the dorsal surface of the butterfly's thorax. Priority was given to following marked individuals (a minimum of 24 h post-marking), and each individual was followed once. In addition, preliminary mark–release–resight surveys revealed the turnover of individuals at the sites was high (e.g. individuals were recorded no more than 5 days on average at a site). Thus, by conducting observational tracking surveys every 5 days at each site and selecting individuals from different locations across each site within a survey day, we minimized the likelihood of following the same individuals. In total, we conducted tracking surveys for 11 days in 2010 and 15 days in 2011.

Larval *in situ* distribution

We conducted final instar larvae surveys between March 17th and April 11th of 2011. We systematically walked the 5 m lateral grid lines set out at each site as transects between 12 pm and 2 pm every 3 days; thus, we surveyed larvae a total of 8 days. Within a 2.5-m field of view either side of each transect, we recorded the positions of visible larvae across both sites onto a high-resolution aerial photograph with an equivalent 1 × 1 m cell grid. To control for decreasing larvae detectability with distance from the transect lines, we used a Brunton single macro-lens spotting scope to do a second larvae count in each grid cell.

Boundary surveys

In preliminary observations, we noted that butterfly activity varied along the site boundaries with direct sunlight exposure; thus, we conducted boundary surveys during the adult flight period in 2010 at boundaries with different directional aspects. For Site 1, we identified four Douglas-fir woodland edge boundaries: (i) north-eastern, (ii) north-western, (iii) south-eastern and (iv) south-western. For Site 2, we selected four woodland edge boundaries with (i) northern, (ii) eastern, (iii) southern and (iv) western aspects. Along a 10-m stretch of each selected boundary, we surveyed a zone extending 3 m from that boundary into the site. We divided the 3-m boundary zone into seven distance categories (i.e. 0, 0.5, 1, 1.5, 2, 2.5 and 3 m). As butterflies entered the boundary zone, we recorded how close each butterfly came to boundary edge (i.e. the nearest distance category to the boundary edge crossed by the butterfly) along with the behaviour it was exhibiting within that distance category and whether a boundary crossing attempt was made by that butterfly. For a boundary crossing attempt, we also recorded the height at which the butterfly flew, the characteristics of their flight (e.g. searching behaviour and direct flight) and their responses to the boundary on approach, such as turning distance from boundary or whether the butterfly crossed through or over the boundary. Additional data collected at the start of the surveys and cloud cover, wind speed, light levels, and temperature, and data collected during the surveys included sex and mark (if present), respectively. We conducted 1-h surveys at each boundary between 10 am–12 pm, 12 pm–2 pm and 2 pm–4 pm to discern any variation in daily activity patterns associated with these boundaries. A total of 10 boundary surveys were undertaken per week across the adult flight period. Each

boundary in each session was surveyed on two separate occasions, and we always surveyed two different boundaries simultaneously.

Microclimate measurements

During our surveys, we distributed 20 temperature data logging stations among our sites; six at Site 1 (four at selected boundaries; detailed below, and two within the centre of the site) and 14 at Site 2 (spaced 10 m apart across the entire site) during our survey periods. These stations were set out to record data from the start of the larva survey period to the end of the adult flight survey period. Each station comprised three thermochron temperature DS1921G *i*buttons: one at ground level, one 1 m from the ground and one 2 m above ground. All *i*buttons were set to record temperatures (within 0.5°C) at 1-min intervals. These data allowed us to explore temperature gradients in relation to the spatial and temporal habitat use of adults and final instar larvae. We also used these data to determine whether variation in temperature between boundaries influenced the movement of adults across them (i.e. a temperature data logging station was centred in each of the eight boundaries surveyed).

Analysis

We transferred all adult flight paths and larvae locations onto a projected aerial photograph of each site in ArcGIS (ESRI, Redlands, CA) to create a set of point.shp files. We then used a spatial statistical approach in ArcGIS to analyse and visualize the data, respectively. For the latter, we used an ArcGIS tool known as 'point statistics analysis'. This application summed the number of point locations recorded in 0.2 m^2 cells across each site from which a raster map delineating a gradient of habitat use was built. We therefore used this application to build four raster maps, one for adult butterflies and one for final instar larvae at each of the two study sites.

We then explored the spatial distribution of habitat use by adults and larvae across study sites using the Average Nearest Neighbor tool in ArcGIS. For this analysis, the average distance from each point to its nearest neighbour was calculated and used to determine whether the pattern of distribution (even, random and clustered) across the site was significant. We used *Z*-scores to determine statistical significance as a measure of the standard deviation associated with a normal distribution and P-values to determine the probability of falsely rejecting the null hypothesis that the pattern of distribution is random. Small P-values (<0.05) and either very high or very low (negative) *Z*-scores indicated that the spatial pattern of adults and larva was not random. We also calculated the percentage of the site not used by adults and larvae.

We used a GLMM procedure (PROC GLIMMIX in SAS v.9.4, Cary, NC, USA) to explore whether variations in temperature across our study sites influenced where adults were active and larva were recorded. We identified the predictor variables to be (i) study site (Site 1 and 2) and (ii) temperature (°C) at each temperature logging station. For this procedure, the site variable was included as a random effect. For the temperature variable, we used average temperatures recorded at *i*buttons at ground level only as the majority of adult and larval activities occurred there. For adults, the average temperatures recorded at each *i*button per session (i.e. session 1 = 10 am–12 pm, session 2 = 12 pm–2 pm and session 3 = 2 pm–4 pm) during the adult flight period were used. For larvae, the average temperature at each *i*button between 12 pm and 2 pm during the larvae survey period was used. The response variables applied included the number of individual adults per session recorded within 5 m radius of each temperature logging station and the number of larvae recorded within 5 m radius of each temperature logging station. Using a Pearson correlation coefficient in Minitab (v. 16.2.4; Minitab Inc., State College, PA, USA), we also determined whether there was a relationship between average temperature at data loggers with temperature gradient (°C) between *i*buttons on the ground and those 2 m above ground level (i.e. the area in which adult butterflies may be actively flying).

For boundary surveys, we used a GLMM procedure to explore whether temperature at the site edges influenced proximity of adult butterflies to boundary edges. The response variable was identified as the number of butterflies recorded in each 1-h boundary survey. Predictor variables included boundary type, temperature at boundary at the time of survey, session (i.e. session 1 = 10 am–12 pm, session 2 = 12 pm–2 pm and session 3 = 2 pm–4 pm) and distance from boundary edge (i.e. 0–3 m in 0.5-m intervals). For this procedure, the boundary type and session variables were included as hierarchical random factors (i.e. session was nested within boundary types). In addition, we explored whether the types and frequency of behaviours exhibited by adults at different boundaries varied with their temperature regimes. For this procedure, we included boundary type, average temperature at each boundary and session as predictor variables and the number of

butterflies exhibiting each behaviour recorded within the boundary zone as the response variable (i.e. searching flight, basking, nectaring, dispersing flight, conspecific interaction, mating and ovipositing). Again, the boundary type and session variables were included as hierarchical random factors (i.e. session was nested within boundary types).

Results

We tracked a total of 174 individual butterflies over the adult flight period at Fitton Green Natural Area; 105 at Site 1 (36 female and 69 males) and 69 at Site 2 (38 females and 31 males). During this period, we found adult butterflies to be active at temperatures ranging from 15 to 27.2°C, wind speeds below 4.8 km/h and light levels ranging from 503 to 698 candles. Overall, conditions at both sites ranged in temperature from 7 to 37°C (for more details, see table 1), wind speed from 0 to 18 km/h and light levels from 333 to 700 candles. Precipitation was common during the adult flight period and sporadic showers occurred on 67% of our survey days. Nevertheless, we found that adults were active between rain showers. For final instar larval surveys, we recorded a total of 143 larvae: 62 at Site 1 and 71 at Site 2. Temperatures at both sites during the larval survey period ranged from 2.5 to 34°C (for more details, see table 2).

Maps delineating the distribution and density of points at each site revealed that site usage by adults and larvae was not uniform (figs 1 and 2). Adults demonstrated a significant clustering in their habitat use at both of our two study sites (Site 1: Z-score = −28.73, $P < 0.001$; Site 2: Z-score = −21.02, $P < 0.001$). Moreover, adults did not appear to use 59% of Site 1 and 33% of Site 2. In comparison, we found larvae evenly distributed within the areas they were found at both sites (Site 1: Z-score = 3.47, $P < 0.001$; Site 2: Z-score = 4.64, $P < 0.001$), but we did not find them in 88% of Site 1 and 79% of Site 2.

The GLMM analysis revealed that the number of adults recorded within 5 m of each temperature logging station demonstrated a significant level of

Table 1 Average temperatures recorded at temperature logging stations (comprising three *i*buttons positioned at different heights from the ground) during the adult flight period

	Site 1			Site 2		
*i*button position	2 m > ground	1 m > ground	Ground level	2 m > ground	1 m > ground	Ground level
Average temperature (°C)	15.6	15.7	19.5	15.5	15.7	19.5
±SE	0.24	0.25	0.67	0.45	0.43	1.06
Range of temperatures among *i*buttons (°C)						
Minimum	11.7	12.1	11.1	11.3	12.2	12.5
Maximum	20.8	21.1	27.9	21.0	20.8	27.5
Average temperature within sessions (°C)						
10 am–12 pm	14.2	14.5	17.0	14.0	14.4	17.0
±SE	0.27	0.27	0.59	0.57	0.52	1.24
12 pm–2 pm	15.9	15.9	20.0	15.9	16.0	20.2
±SE	0.3	0.3	0.8	0.47	0.49	1.15
2 pm–4 pm	14.0	14.2	16.5	14.4	14.3	16.7
±SE	0.16	0.22	0.5	0.26	0.36	0.5

Table 2 Average temperatures recorded at temperature logging stations (comprising three *i*buttons positioned at different heights from the ground) during the larval survey period

	Site 1			Site 2		
*i*button position	2 m > ground	1 m > ground	Ground level	2 m > ground	1 m > ground	Ground level
Average temperature (°C)	11.0	10.8	13.0	10.3	10.4	12.5
±SE	0.25	0.32	0.60	0.16	0.20	0.45
Range of temperatures among *i*buttons (°C)						
Minimum	8.5	7.9	8.1	6.9	6.9	7.7
Maximum	14.9	15.3	18.2	14.7	15.3	18.5

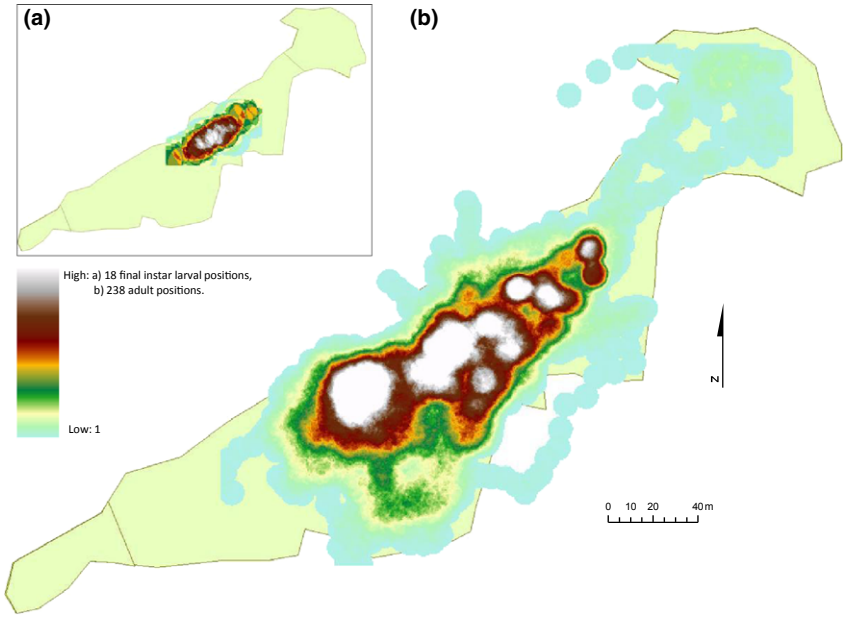

Fig. 1 Map of Site 1 delineating the distribution of habitat use by Taylor's checkerspot (a) final instar larvae and (b) adult butterflies. This is based on the sum of butterfly positions in 0.2 m^2 sections across the site in Fitton Green Natural Area, Oregon, USA.

variation (for temperature, the fixed effect parameter, $F_{57} = 21.97$, $P < 0.0001$). Primarily, we found that the number of individuals increased near temperature logging stations with higher temperatures (gradient of the slope = 7.11E−15; fig. 3a) and those stations with higher temperatures also had higher temperature gradients. We also found that activity varied between sessions, with adults more active at temperature logging stations on the western and central portions of our study sites in session 1. In contrast, during sessions 2 and 3, adults tended to avoid the western portions of ours study site and concentrate their activities in the north and east. Finally, we found that there was a positive correlation between average temperature at the temperature logging stations and temperature gradient between ground level and 2 m above ground level ($r = 0.60$, $P < 0.001$). Note that study site, as a random effect, explained 5.4% of the total variance (estimate = 0.812; residual 14.234).

The GLMM analysis for larvae occupancy of the study sites revealed that the number of larvae recorded within 5 m of each temperature logging station demonstrated no significant variation (for temperature, the fixed effect parameter, $F_{17} = 0.63$, $P = 0.4381$). We found that although there was an increase in larvae numbers recorded at temperature logging stations with temperatures up to 15°C at both sites, at temperatures >15°C, larvae numbers decreased again (slope of the gradient = 1.78E−15; fig. 3b). Note that study site, as a random effect, explained 9.9% of the total variance (estimate = 1.189; residual 10.837).

Among boundary surveys, we recorded 1165 butterflies (655 at Site 1 and 510 at Site 2) entering boundary zones. Only two of these butterflies were females. We found that butterflies were not equally active across our eight boundaries. Boundaries with northern, north-eastern, north-western and eastern aspects (ranging from 160 to 281 individuals) had greater numbers of individuals entering the boundary zone compared to boundaries with southern, south-eastern, south-western and western aspects (ranging from 16 to 60 individuals). The GLMM analysis revealed that the interaction between distance and temperature significantly influenced how often and close adult butterflies came to boundary edges ($F_{229} = 2.81$, $P = 0.0112$). The temperature at a selected boundary depended on boundary type (fig. 4), session and how close butterflies go to each boundary edge (fig. 5). Note that boundary type and session, as a hierarchical random effect, explained 62% of the total variance (estimate = 1.629; residual 2.644). Butterflies were less likely to fly within 2 m of the southern, south-eastern, south-western and western boundary edges. Furthermore, we observed that butterflies tended to only enter boundary zones that were sunlit; hence, we found that boundaries with western aspects were more active than eastern aspects, between 10 am and 12 pm, and eastern aspects were more active than western in our latter survey session between 2 pm and 4 pm.

The GLMM analysis revealed that the frequency of behaviours exhibited by adults at boundaries significantly varied with temperature and type of behaviour

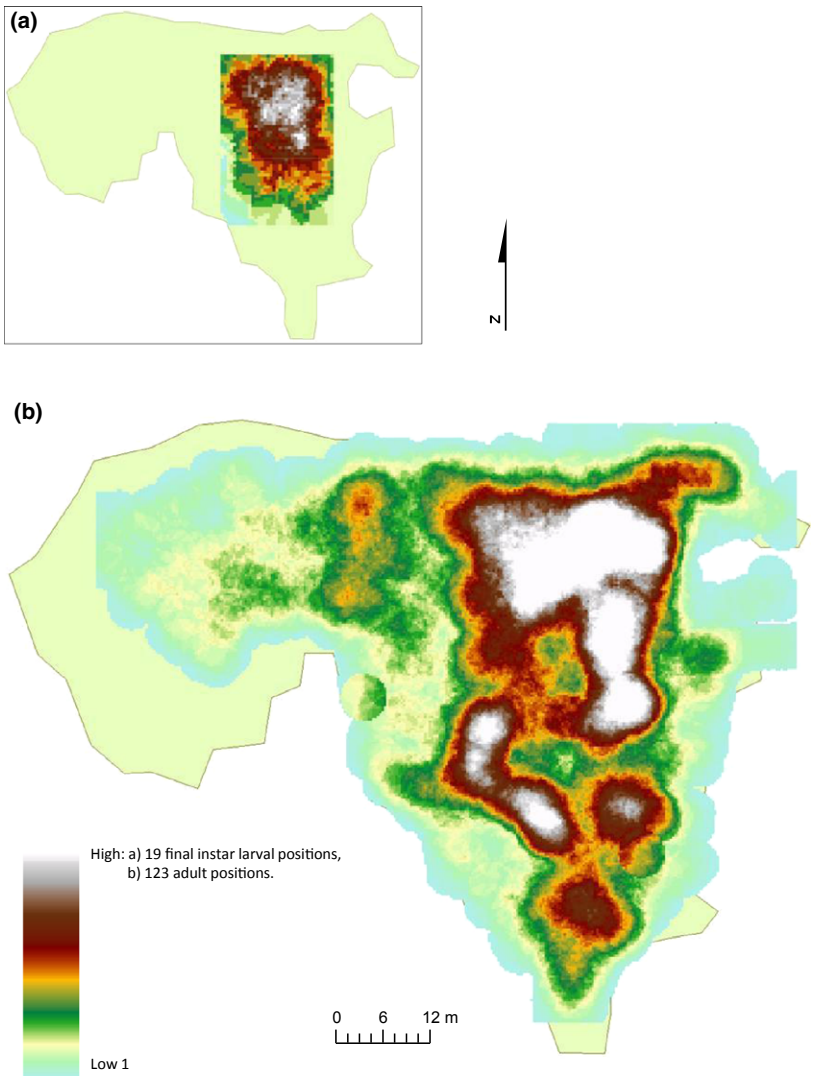

Fig. 2 Map of Site 2 delineating the distribution of habitat use by Taylor's checkerspot (a) final instar larvae and (b) adult butterflies. This is based on the sum of butterfly positions in 0.2 m^2 sections across the site in Fitton Green Natural Area, Oregon, USA.

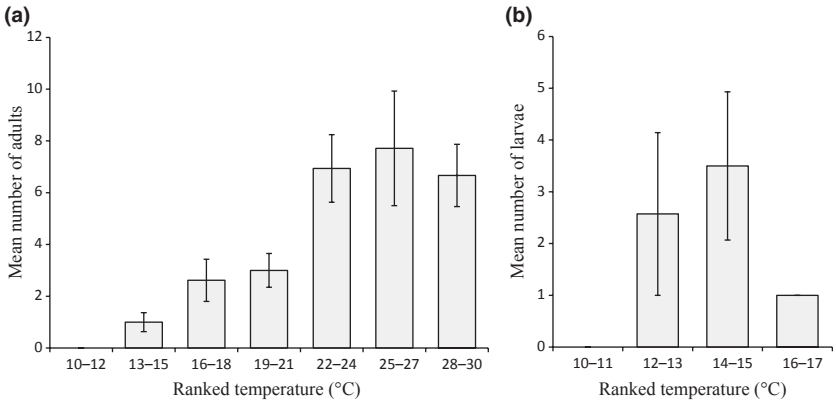

Fig. 3 Barplot for (a) temperature (°C) and mean number of Taylor's checkerspot butterfly adults active within 5 m of temperature logging stations, including ±SE and (b) temperature (°C) and mean number of larvae with ±SE recorded within 5 m of temperature logging stations.

exhibited (F_{297} = 7.81, P < 0.0001). Note that boundary type and session, as a hierarchical random effect, explained 33% of the total variance (estimate = 1.558; residual 4.695). Primarily, we found that some behaviours (such as searching flight and basking) were more common overall than others (such as nectaring and dispersing; table 3). Nevertheless, the frequency of behaviours at boundaries,

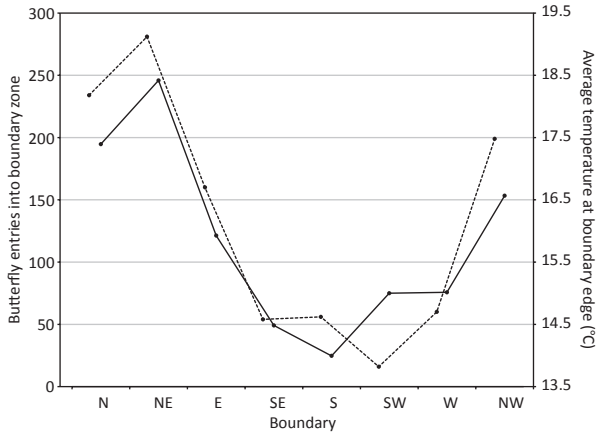

Fig. 4 Graph to compare temperature (continuous line) at eight boundary edges and Taylor's checkerspot butterfly activity (dotted line) recorded within each of the boundary zones surveyed.

particularly those uncommon behaviours, was significantly influenced by temperatures at each boundary. For example, we recorded very few boundary crossing attempts (dispersing) at southern, south-eastern, south-western and western boundary edges (table 3).

Interestingly, the heights at which butterflies entered the boundary zones, indicated that Taylor's checkerspot butterflies rarely flew higher than 0.5 m from the ground (table 4). Butterflies were only recorded flying above 0.5 m when they were either engaging in a conspecific interaction or they crossed a boundary edge into the surrounding habitat. The majority of conspecific interactions involved one male chasing another male, often resulting in the males becoming entwined in an upward spiralling flight. We noted that following this type of interaction both males would immediately return to the interior of their site. Similarly, we recorded individuals attempting to cross through boundary edge by flying directly up to the edge and then fly vertically until they could fly over the tree canopy (>10 m height).

Discussion

In our investigation to explore the thermal requirements of the Taylor's checkerspot butterfly, we found that *in situ* habitat use by adults, distribution of final instar larva and potential dispersal of adults from the site were influenced by microclimate or more specifically variations in temperature that occurred within each site (see also Weiss et al. 1993). We found that adult activities were concentrated within the warmest areas of the butterfly's sites (see also Daily et al. 1991). Thus, despite vegetation structure and composition being consistent across the site, the majority of activities undertaken by Taylor's checkerspot butterflies were clustered either towards the centre of a site or slightly offset to the north-east of the site, that is, those areas exposed to the most direct sunlight. The avoidance or limited use of areas with average temperatures <15.5°C by adults and <12°C by final instar larvae reveals that the Taylor's checkerspot butterfly has a thermal threshold for each life-history stage. In other words, areas within a site that have temperatures below such thermal thresholds would render habitat unsuitable for the butterfly. As a result, the amount of suitable habitat available to the Taylor's checkerspot populations, and thus the effective size of each site, may very well be less than the actual size of the site (Dennis and Eales 1997).

The question is 'How much of a site is thermally suitable?' Across our sites, we found that the temperature gradient between the ground surface and 1 m above the ground varied considerably. Those areas with little or no usage by the butterfly had small temperature gradients (with 1°C difference), whereas areas in which butterfly activities were clustered had much larger gradients, with ground temperatures up to 5°C higher than those temperatures 1 m above ground. We found that the areas with smaller gradients comprised areas adjacent to the southern and western edges of the study sites. These areas were shaded for the majority of the daily activity period by the surrounding Douglas-fir trees (>10 m in height) and received the least direct sunlight when the butterflies were most active between 12 pm and 4 pm. Such areas also had little or no adult activity, final instar larva observations and attempts by adults to cross in surrounding habitat (i.e. potentially disperse). Thus, those areas that are shaded for a large proportion of the butterfly's daily activity period are potentially thermally unsuitable.

The overall shape of a site therefore likely influences the proportion of thermally suitable habitat. For example, Site 1, a thin oblong site, had more areas shaded than Site 2, a more square-shaped site, and corresponded to our findings that 59% and 33% of the sites, respectively, were not used by adults. Similarly, we only recorded adult butterflies attempting to cross through site boundaries with northern and eastern aspects into the surrounding environment, and only when these boundaries were sunlit. These observations suggest that the edges of site boundaries need to be above thermal thresholds for butterflies to successfully disperse through them. Thus, the shape of a site will dictate where butterflies can disperse from their sites.

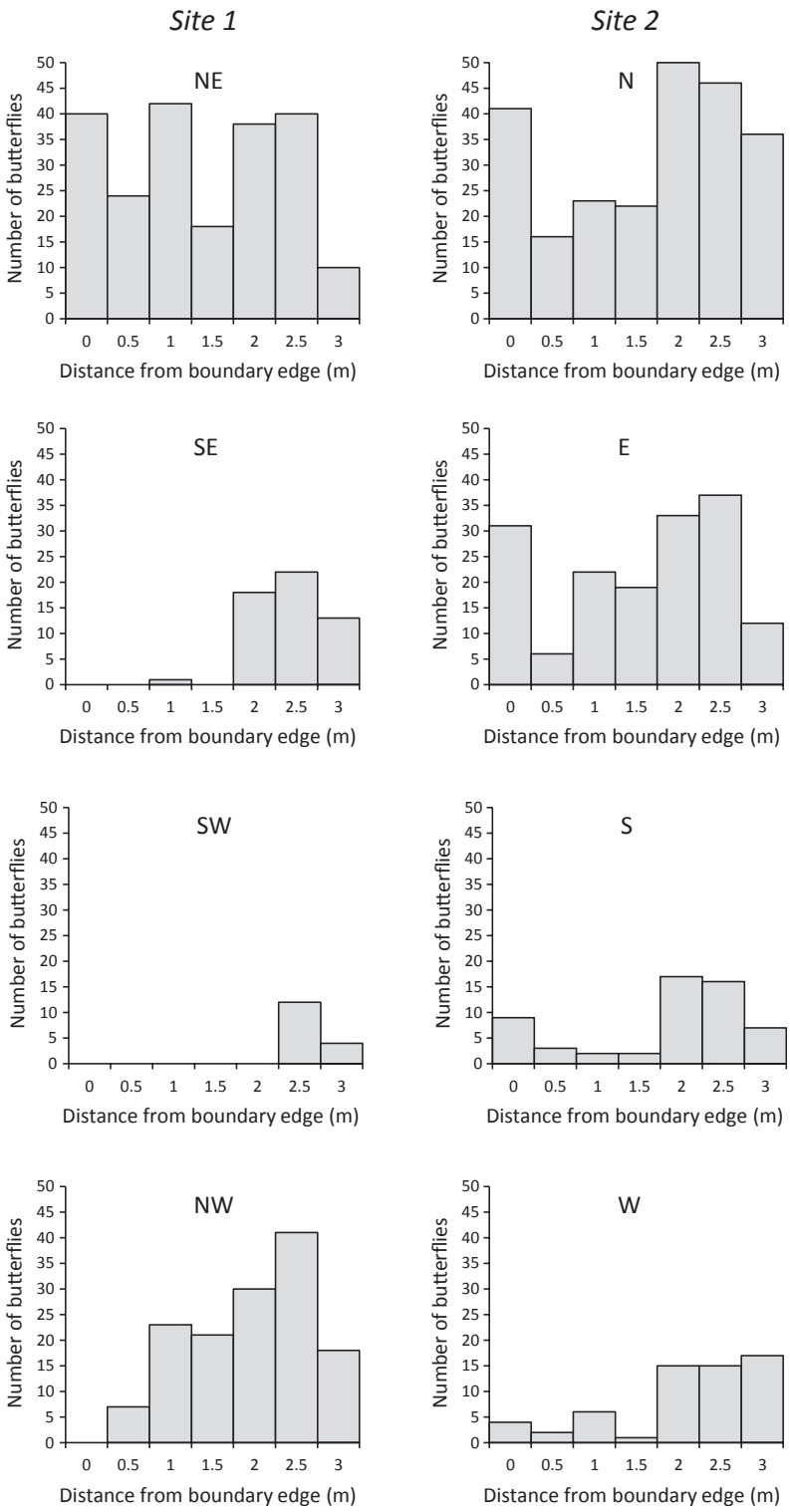

Fig. 5 Histograms showing the distance distributions of adult Taylor's checkerspot butterflies at eight selected boundary edges.

Overall, our findings show that microclimate is an important indicator of habitat quality (see also Eilers et al. 2013). Without knowing the sensitivity of a species or sub-species to microclimate, or more specifically, to individual environmental variables (such as temperature, light levels, wind speeds.; Ehrlich et al. 1980; Murphy and White 1984; Wikström et al. 2009), we run the risk of (i) over-estimating

Table 3 Proportion of each type of activity conducted by butterflies entering boundary zones at eight different boundary edges

Type of activity								
Site	Boundary	Searching	Basking	Nectaring	Conspecific interaction	Boundary crossing	Ovipositing	Mating
2	S	0.64	0.18	0	0.07	0.11	0	0
1	SE	0.57	0.31	0	0.11	0	0	0
1	SW	0.81	0.19	0	0	0	0	0
2	W	0.62	0.25	0	0.12	0.02	0	0
2	E	0.52	0.26	0	0.10	0.13	0	0
1	NW	0.47	0.28	0	0.25	0	0	0
2	N	0.38	0.35	0.01	0.18	0.07	0	0
1	NE	0.50	0.20	0.03	0.16	0.12	0	0

Table 4 Proportion of butterflies entering boundary zones at various heights at eight different boundary edges

		Height at which butterflies entered boundary zone			
Site	Boundary	<0.5 m	>0.5 m < 1 m	>1 m < 1.5 m	>1.5 m to 2 m
2	S	0.82	0.05	0.07	0.05
1	SE	0.95	0.05	0	0
1	SW	1	0	0	0
2	W	0.9	0	0.1	0
2	E	0.79	0.11	0.09	0.01
1	NW	0.77	0.09	0	0.04
2	N	0.79	0.09	0.09	0.03
1	NE	0.83	0.06	0.10	0.01

effective site sizes and (ii) undertaking standard management practices, such as opening up habitat and removing encroaching vegetation, that could have negative repercussions for microsite quality. For example, wind traversing a site can not only hinder a butterfly's ability to fly, but also may reduce ground temperature (i.e. wind chill; Ries and Debinski 2001; Berwaerts and Van Dyck 2004). Thus, wind chill, which itself is determined by exposure, may significantly reduce the habitat suitability of a site. In short, management that alters the thermal dynamics of a site reduces the suitability of that site for an existing butterfly population. Understanding how microclimate influences the butterfly species has therefore substantial implications for its conservation (Smee et al. 2011).

By understanding the range of thermal conditions within which butterflies are active, we can identify specific areas within a site that can support the butterfly (Albanese et al. 2008; Kuefler et al. 2010). More importantly, with this information, managers can more effectively direct available resources towards effective restoration efforts in areas with existing populations, such as planting host and nectar plants. Furthermore, using thermal criteria to select potentially suitable sites for reintroduction and introduction initiatives may significantly improve success rates and thus more effectively contribute to the establishment of stable metapopulations (Thomas and Jones 1993).

In summary, site suitability for temperate species, such as the Taylor's checkerspot butterfly, may be strongly dependent on fine-scale environmental variables, such as ground temperature (Wikström et al. 2009). Thus, to support and effectively inform conservation efforts for such species, we recommend that the range of environmental variables favoured by a species be determined for all aspects of their life-history cycles. As an additional habitat quality indicator, management strategies can be implemented that will more effectively contribute to (i) maintenance and enhancement of existing populations, (ii) restoration and reintroduction of populations into sites previously supporting populations, (iii) development and introduction of butterflies to new sites and (iv) establishment of a stable metapopulation (Hanski and Thomas 1994; Bergman 2001). Finally, by determining the range of environmental variables in which any species of concern thrives, we can better predict, prepare and implement appropriate management strategies that specifically address the implications of climate change (McLaughlin et al. 2002; Preston et al. 2008; Kharouba and Kerr 2010; Westward and Blair 2010).

Acknowledgements

Thanks to Oregon State University's General Research Fund for funding this project. Special thanks to Al Kitzman, superintendent of Benton County Natural Areas and Parks in Oregon and Karen Holtrop and Susan Piper of the Olympic National Forest, Forest Service in Washington for providing the opportunity, supporting and encouraging our research on the Taylor's to be carried out at their sites. Many thanks to Shalynn Pack, Maria Rocco, Diana Raper, Katelynn Karch, Aaron McAlexander, James Lafferty, Susan Shirley and Yuon Han for providing much needed assistance in data collection. Additional thanks to Diana Raper, Karen Holtrop and Ann Potter of the Washington Department of Fish and Wildlife for providing feedback on manuscript drafts.

References

Albanese G, Vickery PD, Sievert PR, 2008. Microhabitat use by larvae and females of a rare barrens butterfly, frosted elfin (*Callophrys irus*). J. Insect Conserv. 12, 603–615.

Bennett VJ, Pack SM, Smith WP, Betts MG, 2013. Sex-biased dispersal in a rare butterfly and the implications for its conservation. J. Insect Conserv. 17, 949–958.

Bergman K-F, 2001. Population dynamics and the importance of habitat management for conservation of the butterfly *Lopinga achine*. J. Appl. Ecol. 38, 1303–1313.

Berwaerts K, Van Dyck H, 2004. Take-off performance under optimal and suboptimal thermal conditions in the butterfly *Pararge aegeria*. Oecologia 141, 536–545.

Berwaerts K, Van Dyck H, Matthysen E, 2001. Effect of manipulated wing characteristics and basking posture on thermal properties of the butterfly *Pararge aegeria* (L.). J. Zool. (Lond.) 255, 261–267.

Bonebrake TC, Boggs CL, McNally JM, Ranganathan J, Ehrlich PR, 2010. Oviposition behaviour and offspring performance in herbivorous insects: consequences of climatic and habitat heterogeneity. Oikos 119, 927–934.

Bryant SR, Thomas CD, Bale JS, 2002. The influence of thermal ecology on the distribution of three nymphalid butterflies. J. Appl. Ecol. 39, 43–55.

Cushman JH, Boggs CL, Weiss SB, Murphy DD, Harvey AW, Ehrlich PR, 1994. Estimating female reproductive success of a threatened butterfly: influence of emergence time and hostplant phenology. Oecologia 99, 194–200.

Daily GC, Enrlich PR, Wheye D, 1991. Determinants of spatial distribution in a population of the subalpine butterfly *Oeneis chryxus*. Oecologia 88, 587–596.

Dennis RLH, Eales HT, 1997. Patch occupancy in *Coenonympha tullia* (Muller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. J. Insect Conserv. 1, 167–176.

Dobkin DS, Olivieri I, Ehrlich PR, 1987. Rainfall and the interaction of microclimate with larval resources in the population-dynamics of checkerspot butterflies (*Euphydryas-editha*) inhabiting serpentine grassland. Oecologia 71, 161–166.

Dover J, Settele J, 2009. The influences of landscape structure on butterfly distribution and movement: a review. J. Insect Conserv. 13, 3–27.

Ehrlich PR, Murphy DD, Singer MC, Sherwood CB, White RR, Brown IL, 1980. Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. Oecologia 46, 101–105.

Eilers S, Pettersson LB, Öckinger E, 2013. Micro-climate determines oviposition site selection and abundance in the butterfly *Pyrgus armoricanus* at its northern range margin. Ecol. Entomol. 38, 183–192.

Fischer K, Fiedler K, 2001. Resource-based territoriality in the butterfly *Lycaena hippothoe* and environmentally induced behavioural shifts. Anim. Behav. 61, 723–732.

Hanski I, 1998. Metapopulation dynamics. Nature 396, 41–49.

Hanski I, Thomas CD, 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biol. Conserv. 68, 167–180.

Kemp DJ, Krockenberger AK, 2004. Behavioural thermoregulation in butterflies: the interacting effects of body size and basking posture in *Hypolimnas bolina* (L.) (Lepidoptera: Nymphalidae). Aust. J. Zool. 52, 229–239.

Kharouba HM, Kerr JT, 2010. Just passing through: global change and the conservation of biodiversity in protected areas. Biol. Conserv. 143, 1094–1101.

Kuefler D, Hudgens B, Haddad NM, Morris WF, Thurgate N, 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology 91, 944–950.

McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR, 2002. Climate change hastens population extinctions. Proc. Natl. Acad. Sci. U.S.A. 99, 6070–6074.

Murphy DD, White RR, 1984. Rainfall, resources and dispersal in southern populations of *Euphydryas editha* (Lepidoptera: Nymphalidae). Pan-Pac. Entomol. 60, 350–354.

Porter K, 1982. Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. Oikos 38, 308–312.

Pratt GF, Emmel JF, 2010. Sites chosen by diapausing or quiescent checkerspot butterfly, *Euphydryas editha quino*, (Lepidoptera: Nymphalidae) larvae. J. Insect Conserv. 14, 107–114.

Preston KL, Rotenberry JT, Redak RA, Allen MF, 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. Glob. Chang. Biol. 14, 2501–2515.

Ries L, Debinski DM, 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. J. Anim. Ecol. 70, 840–852.

Ross JA, Matterm SF, Roland J, 2005. Edge avoidance and movement of the butterfly *Parnassius smintheus* in matrix and non-matrix habitat. Landscape Ecol. 20, 127–135.

Singer MC, Parmesan C, 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? Philos. Trans. R. Soc. Lond. B Biol. Sci. 365, 3161–3176.

Smee M, Smyth W, Tunmore M, Ffrench-Constant R, Hodgson D, 2011. Butterflies on the brink: habitat requirements for declining populations of marsh fritillary (*Euphydryas aurina*) in SW England. J. Insect Conserv. 15, 153–163.

Sparks TH, Yates TJ, 1997. The effect of spring temperature on the appearance dates of British butterflies 1883–1993. Ecography 20, 368–374.

Stinson DW, 2005. Washington State status report for the Mazama pocket gopher, streaked horned lark, and Taylor's checkerspot. Washington Department of Fish and Wildlife, Olympia, WA, 129 pp.

Suggitt AJ, Gillingham PK, Hill JK, Huntley B, Kunin WE, Roy DB, Thomas CD, 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos 120, 1–8.

Thomas CD, Jones TM, 1993. Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. J. Appl. Ecol. 62, 472–481.

Vaughn M, Black SH, 2002. Petition to emergency list Taylor's (whulge) checkerspot butterfly (*Euphydryas editha taylori*) as an endangered species under the U.S. Endangered species act. The Xerces Society, Center for Biological Diversity, Oregon Natural Resources Council, Friends of the San Juans, and Northwest Ecosystem Alliance, 26 pp.

Weiss SB, Murphy DD, White RR, 1988. Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69, 1486–1496.

Weiss SB, Murphy DD, Ehrlich PR, Metzler CF, 1993. Adult emergence phenology in checkerspot butterflies: the effects of macroclimate, topoclimate, and population history. Oecologia 96, 261–270.

Westward AR, Blair D, 2010. Effect of regional climate warming on the phenology of butterflies in boreal forests in Manitoba, Canada. Environ. Entomol. 39, 1122–1133.

Wikström L, Milberg P, Bergman K-O, 2009. Monitoring of butterflies in semi-natural grasslands: diurnal variation and weather effects. J. Insect Conserv. 13, 203–211.