

Evidence for Mate Guarding Behavior in the Taylor's Checkerspot Butterfly

Victoria J. Bennett · Winston P. Smith ·
Matthew G. Betts

Revised: 29 July 2011 / Accepted: 9 August 2011 /
Published online: 19 August 2011
© Springer Science+Business Media, LLC 2011

Abstract Discerning the intricacies of mating systems in butterflies can be difficult, particularly when multiple mating strategies are employed and are cryptic and not exclusive. We observed the behavior and habitat use of 113 male Taylor's checkerspot butterflies (*Euphydryas editha taylori*). We confirmed that two distinct mating strategies were exhibited; patrolling and perching. These strategies varied temporally in relation to the protandrous mating system employed. Among perching males, we recorded high site fidelity and aggressive defense of small (<5 m²) territories. This territoriality was not clearly a function of classic or non-classic resource defense (i.e., host plants or landscape), but rather appeared to constitute guarding of female pupae (virgin females). This discrete behavior is previously undocumented for this species and has rarely been observed in butterflies.

Keywords *Euphydryas editha taylori* · mating systems · pre-copulatory mate guarding · protandry · sexual selection

Introduction

Intrasexual selection is the most commonly observed and well-documented sexual selection process exhibited by butterfly species (Andersson 1994; Rutowski 1997; Wiklund 2003). Competition between males for sexually receptive females has led to the evolution of a large variety of mating systems in this taxon (Rutowski 1991). Among these mating systems, mate acquisition strategies, such as mate locating,

V. J. Bennett (✉) · M. G. Betts

Department of Forest Ecosystems and Society, Oregon State University, Richardson Hall, Corvallis,
OR 97331, USA
e-mail: tory.bennett@oregonstate.edu

W. P. Smith

USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory,
3625 93rd Avenue, SW, Olympia, WA 98512, USA

resource defense, and mate guarding, have been identified (Rutowski 1984; Wiklund 2003). However, in many instances there is no clear distinction between various strategies. Nor are they exclusive, as more than one can be subsumed within a mating system (Ide 2004; Bergman and Wiklund 2009; Takeuchi 2010). Butterfly mating systems are often plastic and dependent upon a variety of ecological variables, such as temperature and landscape composition (Merckx and van Dyck 2005; Ide 2010; Tiple et al. 2010). Therefore, discerning the structure of a mating system can be challenging. Despite the fact that mating systems are multifarious and complex, efforts have been made to identify the principal ecological correlates that shape butterfly mating systems (Dennis and Shreeve 1988). The mate locating strategies employed by males are correlated with the availability of ‘receptive’ females (Rutowski 1991). When receptive females are widely distributed over a large area, males tend to seek females actively (Magnus 1963; Scott 1974). Generally, this involves males constantly in flight in the search of females. For example, they may be seen 1) flying long distances across relatively extensive areas (Campbell et al. 2007), 2) patrolling a local area or series of habitat patches, or 3) concentrating their efforts on specific (potentially small) areas with resources (such as patches of host plants). Males may also employ a strategy known as ‘hilltopping’ or lekking (Prieto and Dahners 2009). Hilltopping involves males congregating in areas with few or no classic resources (i.e. consumer resources, such as host or nectaring plants). These congregations are associated with specific landscape features, such as hill-tops and ridges (which represent non-classic or utility resources). Receptive females visit such areas only to mate (Wickman and Jansson 1997; Jiggins 2002; Chaves et al. 2006).

When receptive female densities exceed those of males, males tend to adopt less active strategies, such as ‘waiting’ or perching with the intent to intercept receptive females as they approach (Jones et al. 1998; Fischer and Fiedler 2001). Males perching on or near to key resources waiting for females to approach, whether it be a host plant, patch of nectar flowers, or sunspot, can readily be observed establishing and defending territories from other males (Lederhouse et al. 1992; Takeuchi and Imafuku 2005).

Mate guarding represents a non-classic resource-based perching strategy in which the resource being defended is the female (Deinert 2003). Pre-copulatory behaviors, such as pupal or immature female mate guarding, are not uncommon among invertebrates (Johansson et al. 2009; Parker and Vahed 2010; Takeshita and Henmi 2010) but have rarely been observed among butterflies (Deinert 2003; Sourakov 2008; Estrada et al. 2010). These behaviors involve males seeking out female pupae and guarding them from other males. Without actually observing males on or in very close proximity to immature females, mate guarding is difficult to identify. This is especially true for butterfly species that have cryptic or concealed pupae, such as the Taylor’s checkerspot (*Euphydryas editha taylori*).

The Taylor’s checkerspot is a candidate for listing under the U.S. Endangered Species Act and a species of concern in Washington State (Vaughn and Black 2002; Stinson 2005). This Pacific Northwest subspecies of the Edith’s checkerspot (*Euphydryas editha*) is restricted to a handful of small isolated prairie habitats in Oregon, Washington and British Columbia (Stinson 2005; Ross 2009). To manage these remnant populations successfully, a thorough understanding of all aspects of the butterfly’s ecology is required. To date, few studies have been undertaken to

explore the mating system of this sub-species. Though all populations of Edith's checkerspot appear to exhibit 1:1 sex ratios, that males usually emerge 2 weeks prior to the females' eclosing (as a form of protandry), and that males exhibit both mate patrolling and mate intercept perching (Brussard et al. 1973; Scott 1986; Boggs and Nieminen 2004).

In 2010 we conducted a series of detailed behavioral surveys that explored the mating system of Taylor's checkerspot butterfly populations at sites in Oregon and Washington, USA. In these surveys, we were able to visibly distinguish both patrolling and perching behaviors among males. Males primarily exhibited perching behaviors in the 2 weeks prior to females emerging, thus when no receptive females were apparently available. Further observations of a subset of individuals indicated that perching was likely a form of pre-copulatory mate guarding, however the prevalence of this behavior in the population was unknown. Under the hypothesis that Taylor's checkerspots at our study sites mate guard, we would expect: (1) agonistic territorial behaviors that cannot be readily explained by defense of any classic or other non-classic resources, (2) high site fidelity, (3) the presence of teneral females on territories, and (4) cessation of territorial defense on conclusion of copulation.

Material and Methods

Study Site

We conducted surveys at two sites within Fitton Green Natural Area (FGNA) in Benton County, Oregon, USA and three sites located within the Olympic National Forest (ONF) in Washington (Bear Mountain, Upper Dungeness and 3 O'Clock Ridge). Topographically, FGNA and ONF appear diverse. FGNA represents an area of relatively low elevation (300 m) within a former Douglas-fir (*Pseudotsuga menziesii*) managed forest containing a meadow system that provided habitat for the Taylor's checkerspot butterfly. We surveyed the two meadows with the highest concentrations of Taylor's checkerspots. Both sites comprise small short-grass meadows almost entirely surrounded by Douglas-fir trees (Ross 2009). Site 1, the larger of the two meadows, is about 7,200 m² with a southwest facing aspect (see Fig. 1), whereas Site 2 is about 2,770 m² on a gentle south-facing slope. In comparison, the ONF sites represent high- elevation (900 m) rocky, shallow-soiled openings in forests clear-cut logged in the 1960s (Olympic National Forest records; see Fig. 2). ONF sites are much larger than the FGNA sites, ranging from 16,000 m² to 32,400 m². All ONF sites occur on very steep rocky, southwest to southeast facing slopes. Consequently, a high proportion of each site's composition is bare ground, exposed rock, and tree stumps. The fact that the two sets of sites encompassed a large range of variation in size, elevation, and vegetation types allowed us to explore whether the mating strategies exhibited by males were restricted to landscapes with particular characteristics.

Field Study

We conducted observational tracking surveys to collect detailed information on the mating behavior of males, including territorial behavior and habitat use in relation to



Fig. 1 Photograph of site 1 in Fitton Green natural area. Picture taken by Shalynn Pack



Fig. 2 Photograph of Bear Mountain in Olympic national forest

resource availability across the survey sites. At the FGNA sites, surveys took place between April 10th and May 8th 2010 during the adult flight period, whereas ONF adults emerged around May 6th and were surveyed until June 14th 2010. From a distance that did not apparently disturb the butterfly's behavior (>3 m), we selected an individual and made continuous observations using a Brunton single macro-lens spotting scope. To identify the characteristics that defined different mating strategies, we mapped the movement of individuals onto site-specific high-resolution aerial photographs. For each individual tracked, we plotted flight paths detailing movement patterns, extents and turning angles, along with all stationary locations, including basking, nectaring, and mating sites. We tracked an individual for as long as it remained in sight or until it displayed repetitive patterns of space use. For example, we ceased to follow an individual once it returned to the same structure three times. Using digital voice recorders, we detailed all observed activities such as basking, nectaring, in flight, and interactions with conspecifics and heterospecifics, along with the duration of each activity. We transferred all the individual flight paths collected onto a projected aerial photograph of each site in ArcGIS (ESRI, Redlands CA). Attribute tables associated with each butterfly flight path were populated with details of behavior and durations at each recorded position.

To determine site fidelity, we marked 76 and 60 butterflies over the survey period at FGNA sites 1 and 2 respectively. We tracked marked individuals as a priority (>24 h post marking) and these individuals were only followed once during the survey season. By marking individuals with a unique alpha-numeric code, we were able to monitor site usage and fidelity of individual butterflies over a longer timeframe. At the beginning of every survey day we recorded the presence and positions of all marked individuals still on a site. In addition, by marking all adults within the first week of the flight period we were able to confirm that individual turnover at the sites was high. Based on this initial information, we conducted observational tracking surveys once a week thereafter, and selected individuals from different locations across each site within a survey day. This minimized the likelihood of following individuals more than once. We also employed this protocol at the ONF sites.

In addition, to aid tracking surveys, we placed 38-cm tall metal pin flags in a 5 by 5 m cell grid covering an area of 40 m by 20 m at each FGNA site. To determine if mating strategies were correlated with the presence of classic resources, we used the grid to collect vegetation abundance data. Of the 32 cells at each site, 16 cells were randomly selected and within each of these a corner was randomly chosen. From this corner, we sampled a 2 m by 2 m quadrat recording the presence of host and nectar plant species. We used logistic regression in SAS (PROC LOGISTIC; SAS 1988) to assess whether the distribution of perching behaviors exhibited by the Taylor's checkerspot butterfly across our study sites was associated with the presence of their host or nectar plants (as the categorical predictor variables). We also recorded weather conditions across the sites. We used a luxmeter and a Kestrel 3000 pocket weather meter to collect light levels (candles) temperature ($^{\circ}\text{C}$) and wind speeds (km/hr) at both FGNA and ONF sites, and temperature data logging stations to collect fine-scale temperature readings at FGNA sites. Each station contains 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 at

1-min intervals. Six stations were placed out at Site 1 and 14 out at Site 2. We used logistic regression to assess whether the presence or absence of perching males near temperature stations was associated with the thermal conditions.

To discern the movement characteristics that differentiated the various behaviors we observed, such as dispersing, we used a custom built program in Python 2.5.1 (2007) to calculate the tortuosity (the mean vector length of successive turning angles) and speed (m/sec) of the flight paths recorded. Tortuosity was measured using techniques described in Batschelet (1965) to calculate an *r* value ranging from 0 to 1, in which '1' represented a straight line and '0' represented a circle. By distinguishing separate behaviors, determining the temporal and spatial patterns of these behaviors across the adult flight period, and comparing characteristics associated with each behavior, such as resources, level of site fidelity, and occurrence of aggression, we can establish whether mate guarding is occurring.

Results

We tracked 62 male Taylor's checkerspot butterflies over the course of the adult flight period at FGNA; 31 in each of the two sites. This represented approximately 28 h of recorded activities and 3,223 individual butterfly positions. In ONF, we tracked 51 male butterflies; 8 at Bear Mountain, 16 at 3 O'Clock Ridge, and 27 at Upper Dungeness. This represented approximately 12 h of recorded activities and 2,109 positions.

Among the males tracked, we identified two general behaviors that were equivalent to patrolling and perching. Across all sites, 47% of tracked individuals undertook a patrolling behavior. As part of this behavior, male Taylor's checkerspots exhibited a distinct flight pattern (a constant low slow zig-zagging searching flight) compared to other forms of flight we observed (such as dispersing flight, discussed below). In comparison, 42% of male Taylor's checkerspot butterflies exhibited a perching behavior. Among all survey sites, males were observed perching consistently within areas approximately 5 m². We also tracked 5% of males exhibiting both patrolling and perching behavior. On these occasions, we initially recorded males exhibiting a patrolling behavior in which they moved continuously across a site. We then observed them switching to a perching behavior in which they remained within that area. Of the remaining 6% of individuals we tracked, six males were only observed nectaring and two males dispersed from the site.

Patrolling

We found that patrolling males across all sites travelled at average speeds of 1.6 m/sec (SD=0.42 m/sec). We also calculated an *r* value (tortuosity) of 0.21 with an angular deviation of 72, thus revealing that patrolling males change their direction regularly. This corroborated our observations that males exhibit a slow zigzagging searching flight.

We recorded 223 conspecific interactions among males exhibiting patrolling behavior (100 at the FGNA sites and 123 in ONF); 95% of these interactions involved conflicts initiated by perching males, i.e. the focal individual was

approached and chased away by a perching male. The other 5% of interactions involved tracked individuals joining a multi-male interaction. This involved three or more males engaged in 1) a spiraling flight either rising from the ground up to 2 m in height or flying parallel to the ground no more than 0.5 m high, or 2) a procession of males following a female. Across all conspecific interactions recorded among patrolling males, 82% involved one other male, 11.6% involved two other, 5.8% comprised other three males and 0.4% included 4 or more additional males. In addition, none of the patrolling individuals we tracked engaged in a heterospecific interaction. Thus patrolling males exhibited very little antagonistic behavior in comparison to perching males (see below).

Perching

Among the male Taylor's checkerspot butterflies exhibiting perching behavior, we found evidence to support territoriality. At all sites, tracking surveys revealed that individual males perched consistently in specific locations. At these locations, we recorded males repeatedly using the same perching structures (ranging from 1 to 5) throughout the survey. In comparison, no patrolling males returned to a previously used perching structure. Based on the perching locations, the average area in which male Taylor's checkerspot were found perching (hereafter referred to as a territory) was 3.6 m² in FGNA (ranging from 2.19 m² to 4.87 m²) and 0.6 m² in ONF sites (ranging from 0.16 m² to 1.57 m²). At ONF, males were only observed perching on vegetation-covered steps formed in the slopes. Often, these steps were no more than 1 m in width. Across all sites, the territories represented areas of short vegetation often containing both nectaring and host plants.

We recorded on 364 of occasions, individuals moving from perching positions only to initiate an interaction with an approaching male(s) or heterospecifics. After each interaction, all tracked males directly returned to their original location to perch. We recorded 8 events in which 'perching' males engaged in a heterospecific interaction with Sara orangetip (*Anthocharis sara*) or Propertius duskywing (*Erynnis propertius*). We also noted interactions with silvery blue (*Glaucopsyche lygdamus*), echo azure (*Celastrina ladon echo*), various moth species, various bee species, and wild turkeys (*Meleagris gallopavo*). We recorded 356 conspecific interactions among the perching males tracked (103 at the FGNA sites and 256 at ONF) and all of them involved conflicts initiated by the tracked males. Overall, 83% of interactions involved conflicts with one other male, 12% with two males, 4% with three males and 1% included 4 or more males. Perching males therefore demonstrated antagonistic behavior, a characteristic of territory defense. Furthermore, no perching males were displaced from their territories as a result of an interaction.

We found perching males in areas both with and without host and/or nectar plant opportunities. We did not detect an influence of classic resources on the distribution of territories; we found no significant influence of either host plant ($\chi^2=0.03$, $P=0.84$, $df=43$) or nectar plants ($\chi^2=1.72$, $P=0.18$, $df=43$) on the distribution of perching males, nor was there a significant interaction between variables ($\chi^2=0.02$, $P=0.88$, $df=43$). The only areas we consistently did not record perching behavior were those areas 1) with tall grass, 2) with encroaching shrubs and trees, and 3) that

were shaded for part of the day. At the ONF sites, no males were observed perching in areas consisting primarily of bare ground or rock. We also noted that across the majority of the sites at FGNA (primarily the core area that was not subject to the above three criteria) light levels, wind speeds, and temperature remained consistent. Twelve temperature stations were located in these core areas, six with perching males holding territories within a 2 m radius of the station and six stations without perching males. We found no significant difference between the thermal conditions recorded at stations with and without perching males ($\chi^2=0.51$, $P=1.00$, $df=59$).

Perching structures commonly included tall blades of grass, flower heads, wood, twigs and branches, mounds of dirt, rocks, and our pin flags (occasionally placed out to aid mapping). Among the short-grass meadows surveyed in FGNA, the majority (99%) of perching structures were blades of grass. In comparison, 80% of perching structures among ONF's rocky clear-cut sites were grass; 11% were mounds of dirt, 6% were rocks, and 3% consisted of wood, twigs and branches. We found that typical perching structures provided males with a clear view of their territory or approaching individuals. We noted that males consistently used the tallest structures available. For example, in many instances males demonstrated a preference to using our 38 cm tall pin flags if present. Moreover, of the 48 males tracked exhibiting perching behavior, only 5 males were recorded nectaring (ranging from 10 s to 4 min).

A teneral (newly emerged) female appeared within the defended territory of 7 of the 48 males (i.e. 15% of those exhibiting perching behavior). On no occasion was the female observed crawling into the male's territory from beyond its limits. This was particularly evident at the ONF sites as most territories were surrounded by unstable bare ground and rocks. As such, a female crawling on these substrates would clearly be visible. In each instance, the perching male at the territory immediately approached the teneral female and mated with her. Copulation lasted an average of 40 min (ranging from 18 min to 1 h 30 min). Once separated from the mated female, the male (hereafter the 'attending male') positioned himself directly behind the female. For an average of 11 min (ranging from 7 min to 14 min), attending males maintained this position. On all occasions, we recorded up to 4 additional males joining the pair (ranging from 2 to 4 males). This appeared as a procession of males chasing after a crawling or hopping (i.e., short bursts of flight) female. The position of the attending male prevented the other males from getting close to the female's abdomen and none of the females we observed were mated again during this time. Following this activity, the attending male flew from the female and his territory. In five of the seven instances we observed attending males leaving mated females; these males were recorded dispersing from the survey site entirely. Three of these males were marked and they were not observed again on the survey site. In all instances, dispersing males flew more directly than individuals conducting patrolling with an r value of 0.66 and an angular deviation of 47 across all sites. The average speed of dispersing males was also greater at 2.7 m/sec (SD= 1.5 m/sec). After the departure of the attending male, little or no attention was directed toward the mated females by other males. These females crawled into vegetation close to the ground, where they remained for at least ½ hour to 3 h post copulation, and possibly longer as we did not monitor them further.

Of the 48 males we recorded exhibiting perching behavior, 13 were marked. Although we tracked these individuals only once, transect surveys revealed that

males remained within their defended territories from 1 to 10 days (Table 1). This demonstrates that perching males have high site fidelity. Perching duration also varied across the adult flight period. Males that were marked in the first week remained on their territories for longer (an average of 6 days) compared with males marked in the second week (averaging 2 days). In addition, we did not record any males on territories marked during the 3rd and 4th weeks of the adult flight period. This corresponded to the variation we observed in the proportions of perching versus patrolling males across the flight period (see Fig. 3).

Discussion

Our observations of territorial defense and high site fidelity in the absence of any classic or other non-classic resources, along with direct observations of teneral females on territories and nearly immediate cessation of territorial defense on conclusion of copulation, all support the hypothesis that mate guarding occurs in Taylor's checkerspot butterfly.

As is the case with many other butterfly species, the mating system of the Taylor's checkerspot butterfly comprises alternative behaviors and the specific behavior adopted by the males corresponds temporally to the density of receptive females (Kemp 2001; Merckx and van Dyck 2005). For example, protandry in this subspecies results in a high male-biased adult sex ratio in the early adult flight period (e.g., 1:13 at FGNA; Wiklund et al. 1996). In this early period, males adopt a perching strategy, establishing territories within which receptive females might visit and potentially solicit mating (Fig. 3). However, given the low abundance of adult females on the wing at this time and the even lower number of receptive

Table 1 Length of time (in days) marked male Taylor's checkerspots were recorded continuously maintaining a specific territory at sites in Fitton Green Natural Area, Oregon, USA, during the adult flight period in 2010

Marked butterfly ID	Site	Date marked	Adult flight period	Date 1st recorded on territory	Date last recorded on territory	Total number of days at territory
A1	2	13-Apr-10	Week 1	14-Apr-10	23-Apr-10	10
A2	2	13-Apr-10		14-Apr-10	18-Apr-10	5
A3	1	12-Apr-10		13-Apr-10	20-Apr-10	8
A8	2	13-Apr-10		14-Apr-10	20-Apr-10	7
A9	1	12-Apr-10		13-Apr-10	16-Apr-10	4
B2	1	12-Apr-10		13-Apr-10	17-Apr-10	5
B3	1	12-Apr-10		15-Apr-10	17-Apr-10	2
B7	2	13-Apr-10		14-Apr-10	20-Apr-10	7
B9	2	13-Apr-10		14-Apr-10	16-Apr-10	3
N3	1	18-Apr-10	Week 2	19-Apr-10	21-Apr-10	2
P4	1	18-Apr-10		19-Apr-10	20-Apr-10	1
O4	1	18-Apr-10		19-Apr-10	22-Apr-10	4
R3	1	18-Apr-10		20-Apr-10	21-Apr-10	1

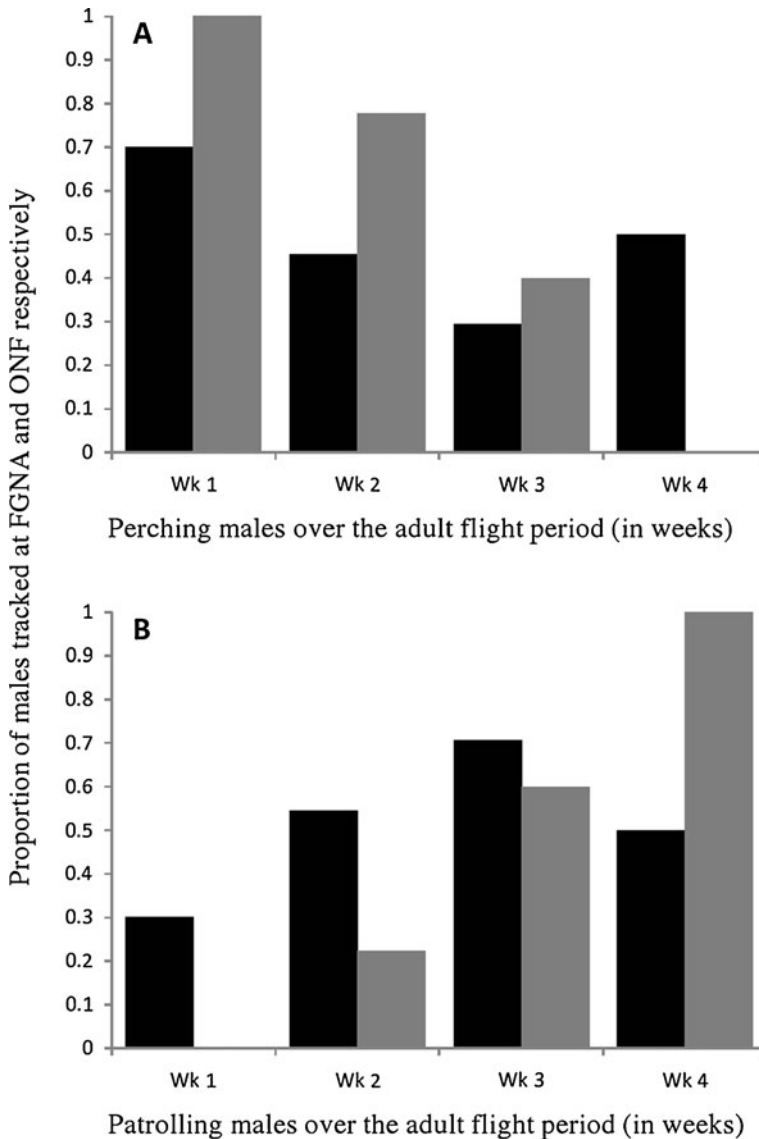


Fig. 3 The proportion of males exhibiting perching behavior (**a**) compared to those males exhibiting patrolling behavior (**b**) across the adult flight period. Dark colored segments represent the proportion of males tracked in Fitton Green Natural Area (FGNA) and lighter shading represents males tracked in Olympic National Forest (ONF)

females, male mating opportunities appear minimal. Early male emergence therefore does not appear to be an effective mating strategy for males. The occurrence of pre-copulatory mate guarding provides a rational explanation for such a counterintuitive mating system.

Males engage in a war of attrition with all conspecifics and heterospecifics approaching their territory and operate from vantage points within or near to their selected territories (Lederhouse et al. 1992; Takeuchi and Imafuku 2005). Such

aggressive behavior recorded in perching males suggests that an aspect of their territory is worth defending, and most likely relates to reproduction. From our surveys and observations, we did not detect any classic resource-based differences between the defended territories and the surrounding habitat (Lederhouse et al. 1992). This was particularly evident in FGNA sites in which vegetation composition appeared consistent across the site, including host and nectar plant distribution. We found established territories with and without host and/or nectar plants present, suggesting these classic resources are not driving the territorial behavior we observed. We also noted that areas with patches of wild strawberry (*Fragaria virginiana*), which is a primary nectar plant, were not defended. Nor did we observe perching males aggregated within specific areas, such as hilltops, in any of our study sites. We found perching males to be randomly distributed across our sites further indicating that landscape features (non-classic resources) are not driving the territorial behavior we observed in the Taylor's checkerspot (Dennis and Sparks 2005; Merckx and van Dyck 2005). In addition, we did not find the positions of territorial males to be influenced by fine-scale thermal conditions. However, we did observe teneral females at some of the defended territories. For this to have occurred, a female pupa must have been within the male's territory. This suggests that, with females yet to eclose, male Taylor's checkerspot butterflies at both FGNA and ONF sites are exhibiting pre-copulatory mate guarding behavior, in which they locate and defend immature females. With individual males holding territories for up to 10 days, the probability of observing teneral females at the defended territories during our surveys was inevitably low. This demonstrates that the use of mate guarding strategies in butterfly mating systems can easily have gone unnoticed. We suggest that further investigations include experimental testing, in which female pupae are placed in the field to see if males form territories at these locations.

By remaining in close proximity to female pupae and waiting for them to emerge, the defending male greatly increases the likelihood that he will mate with a virgin female. This strategy therefore has high reproductive value (Boggs and Nieminen 2004; Ide 2004) and is certainly cost effective in a protandrous mating system (Rutowski 1991; Wiklund et al. 1996; Wiklund 2003; Ferkau and Fischer 2006). However, we can only speculate about how males locate immature females. Taylor's checkerspot butterfly pupae are well-concealed, often attached to the underside of vegetation close to the ground. As such, it is unlikely that males use visual cues (Rutowski 2003; Stinson 2005). Chemical cues, such as the pheromones commonly used among butterflies, would be more plausible (Estrada et al. 2010). Alternatively, female pupae may be using acoustic signals to reveal their locations (Travassos and Pierce 2000).

During our study we also were able to identify post-copulatory mate guarding. This involves males preventing females they have just mated from re-mating (Wiklund 2003). Among the 7 mating events we observed, in all instances males remained for a short time (<15 min) in close proximity to that female appearing to prevent other males from mating her. This behavior may ensure that the sperm plug or sphragis is in place and hardened in the female copulatory duct (i.e. sperm-guarding) preventing the female from immediately copulating again (Orr and Rutowski 1991; Orr 2002; Vlasanek and Konvicka 2009). Alternatively, this mate guarding behavior may be driven by chemical cues, as newly emerged females release pheromones to indicate

they are receptive (Dennis and Williams 1987; Deinert 2003; Raguso and Willis 2003). Our observations of processions of males following newly emerged females, along with very few observations of patrolling males interacting with mature females, indicates that males having mated a female remain in proximity to physically prevent that female from re-mating while she is still receptive.

Finally, in contrast to perching males, we noted that in the third and fourth weeks of the adult flight period patrolling males gravitated more towards specific areas within the ONF sites. For example, at 3 O’Clock Ridge, males moved laterally to a rocky outcrop traversing the length of the site’s slope. This supports previous investigations that male checkerspots appear to hilltop (Ehrlich and Wheye 1986, 1988; Baughman et al. 1990). In contrast, we found no evidence of this behavior among FGNA sites. This supports Singer and Thomas’s (1992) studies in which they found no evidence to support hilltopping behavior in this same subspecies. Based on these findings, we hypothesize that it is the topographic structure of the sites that drives this behavior among different populations of checkerspot butterflies.

Our investigation demonstrates that discerning the specific mating strategies that comprise a mating system can be difficult. This is particularly true when 1) multiple strategies are employed, 2) they may be plastic - as individuals can switch between strategies, 3) they are influenced by spatial and temporal variables, such as topographic structure, and 4) they are cryptic, as in the case of pupal mate guarding. We determined the mating system of Taylor’s checkerspot butterfly to be more complex than previously described and there likely remains much to be learned (Boggs and Nieminen 2004). However, as a species of concern, understanding Taylor’s checkerspot behavior, habitat use and movement dynamics within a site is critical to conservation efforts. One significant advantage of identifying pre-copulatory mate guarding behavior among the Taylor’s checkerspot butterfly is that we can more effectively identify within-site habitat that is suitable for pupation (Pratt and Emmel 2010). Thus, the more we know about the Taylor’s checkerspot and similar sub-species, the more effectively we will be able to manage existing populations and inform reintroduction efforts (Stinson 2005; Miller and Hammond 2007; Ross 2009).

Acknowledgments We thank Oregon State University’s General Research Fund for supporting this project and the National Geographic/Waitt Fund for supporting and funding additional data collection. 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, USDA Forest Service in Washington for providing the opportunity, supporting and encouraging our research on the Taylor’s checkerspot carried out at their sites. Many thanks to Shalynn Pack, Maria Rocco, Diana Raper, Katelynn Karch, Aaron McAlexander, James Lafferty, Susan Shirley, and Yvon Han for providing much needed assistance in data collection. Additional thanks to Ann Potter, Diana Raper, and Karen Holtrop for providing feedback on manuscript drafts.

References

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Batschelet E (1965) Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. *Am Instit Biol Sci Monogr*, p 57

- Baughman JF, Murphy DD, Ehrlich PR (1990) A re-examination of hilltopping in *Euphydryas editha*. *Oecologia* 83:259–260
- Bergman M, Wiklund C (2009) Differences in mate location behaviours between residents and non-residents in a territorial butterfly. *Anim Behav* 78:1161–1167
- Boggs CL, Nieminen M (2004) Checkerspot reproductive biology. In: Ehrlich PR, Hanski I (eds) *On the wings of checkerspots: a model system for population biology*. Oxford University Press, New York, pp 92–111
- Brussard PF, Ehrlich PR, Singer MC (1973) Adult movements and population structure in *Euphydryas editha*. *Evolution* 28:408–415
- Campbell JW, Hanula JL, Waldrop TL (2007) Observations of *Speyeria diana* (Diana fritillary) utilizing forested areas in North Carolina that have been mechanically thinned and burned. *SE Nat* 6:179–182
- Chaves GW, Patto CEG, Benson WW (2006) Complex non-aerial contests in the lekking butterfly *Charis cadytis* (Riodinidae). *J Insect Behav* 19:179–196
- Deinert EI (2003) Mate location and competition for mates in a pupal mating butterfly. In: Boggs CL, Watt WB, Ehrlich PR (eds) *Ecology and evolution taking flight: butterflies as model systems*. The University of Chicago Press, Chicago, pp 91–108
- Dennis RLH, Shreeve TG (1988) Hostplant-habitat structure and the evolution of butterfly mate-location behaviour. *Zool J Linn Soc* 94:301–318
- Dennis RLH, Sparks TH (2005) Landscape resources for the territorial Nymphalid butterfly *Inachis io*: microsite landform selection and behavioural responses to environmental conditions. *J Insect Behav* 18:725–742
- Dennis RLH, Williams WR (1987) Mate-location behaviour in the butterfly *Ochlodes venata* (Br. and Grey) (Hesperiidae). Flexible strategies and spatial components. *J Lepid Soc* 41:45–64
- Ehrlich PR, Wheye D (1986) “Non-adaptive” hilltopping behavior in male checkerspot butterflies (*Euphydryas editha*). *Am Nat* 127:477–483
- Ehrlich PR, Wheye D (1988) Hilltopping checkerspot butterflies revisited. *Am Nat* 132:460–461
- Estrada C, Yildizhan S, Schulz SA, Gilbert LE (2010) Sex-specific chemical cues from immatures facilitate that evolution of mate guarding in *Heliconius anynana* and *Pieris napi* butterflies: effects of mating history and food limitation. *Ethology* 112:1117–1127
- Fischer K, Fischer K (2006) Costs of reproduction in male *Bicyclus anynana* and *Pieris napi* butterflies: effects of mating history and food limitation. *Ethology* 112:1117–1127
- Fischer K, Fiedler K (2001) Resource-based territoriality in the butterfly *Lycaena hippothoe* and environmentally induced behavioural shifts. *Anim Behav* 61:723–732
- Ide J-Y (2004) Diurnal and seasonal changes in the mate-locating behavior of the satyrine butterfly *Lethe Diana*. *Ecol Res* 19:189–196
- Ide J-Y (2010) Weather factors affecting the male mate-locating tactics of the small copper butterfly (Lepidoptera: Lycaenidae). *Eur J Entomol* 107:369–376
- Jiggins FM (2002) Widespread ‘hilltopping’ in *Acraea* butterflies and the origin of sex-role-reversed swarming in *Acraea encedon* and *A. encedana*. *Afr J Ecol* 40:228–231
- Johansson F, Soderquist M, Bokma F (2009) Insect wing shape evolution: independent effects of migratory and mate guarding flight on dragonfly wings. *Biol J Linn Soc* 97:362–372
- Jones MJ, Lace LA, Harrison EC, Stevens-Wood B (1998) Territorial behaviour in the speckled wood butterflies *Pararge xiphia* and *P. aegeria* of Madeira: a mechanism for interspecific competition. *Ecography* 21:297–305
- Kemp DJ (2001) Investigating the consistency of mate-locating behavior in the territorial butterfly *Hypolimnas bolina* (Lepidoptera: Nymphalidae). *J Insect Behav* 14:129–147
- Lederhouse RC, Codella SG, Grossmueller DW, Maccarone AD (1992) Host plant-based territoriality in the white peacock butterfly, *Anartia jatrophae* (Lepidoptera, Nymphalidae). *J Insect Behav* 5:721–728
- Magnus DBE (1963) Sex-limited mimicry. II. Visual selection in the mate choice of butterflies. *Proc Inter Congr Zool* 4:179–183
- Merckx T, van Dyck H (2005) Mate location behaviour of the butterfly *Pararge aegeria* in woodland and fragmented landscapes. *Anim Behav* 70:411–416
- Miller JC, Hammond PC (2007) Butterflies and moths of Pacific Northwest forest and woodlands: Rare, endangered and management-sensitive species. Forest Health Technology Enterprise Team, Technology transfer species identification report
- Orr AG (2002) The sphragis of *Heteronympha penelope* Waterhouse (Lepidoptera: Satyridae): its structure, formation and role in sperm guarding. *J Nat Hist* 36:185–196
- Orr AG, Rutowski RL (1991) The function of the sphragis in *Cressida-cressida* (Fab) (Lepidoptera, Papilionidae): a visual deterrent to copulation attempts. *J Nat Hist* 25:703–710

- Parker DJ, Vahed K (2010) The intensity of pre- and post-copulatory mate guarding in relation to spermatophore transfer in the cricket *Gryllus bimaculatus*. *J Ethol* 28:245–249
- Pratt GF, Emmel JF (2010) Sites chosen by diapausing or quiescent stage quino checkerspot butterfly, *Euphydryas editha quino*, (Lepidoptera: Nymphalidae) larvae. *J Insect Conservat* 14:107–114
- Prieto C, Dahners HW (2009) Resource utilization and environmental and spatio-temporal overlap of a hilltopping Lycaenid butterfly community in the Colombian Andes. *J Insect Sci* 9:Article 16
- Raguso RA, Willis MA (2003) Hawkmoth pollination in Arizona's Sonoran Desert: behavioral responses to floral traits. In: Boggs CL, Watt WB, Ehrlich PR (eds) *Ecology and evolution taking flight: butterflies as model systems*. The University of Chicago Press, Chicago, pp 43–65
- Ross D (2009). Draft Benton County Taylor's Checkerspot butterfly management plan. Benton County Natural Areas and Parks Department
- Rutowski RL (1984) Sexual selection and the evolution of butterfly mating behavior. *J Res Lepid* 23:125–142
- Rutowski RL (1991) The evolution of male mate-locating behavior in butterflies. *Am Nat* 138:1121–1139
- Rutowski RL (1997) Sexual dimorphism, mating systems and ecology in butterflies. In: Chloe JC, Crespi BJ (eds) *The evolution of mating systems insects and arachnids*. Cambridge University Press, Cambridge, pp 257–272
- Rutowski RL (2003) Visual ecology of adult butterflies. In: Boggs CL, Watt WB, Ehrlich PR (eds) *Ecology and evolution taking flight: butterflies as model systems*. The University of Chicago Press, Chicago, pp 67–90
- Scott JA (1974) Mate-locating behaviour in butterflies. *Am Midl Nat* 91:103–117
- Scott JA (1986) *The butterflies of North America*. Stanford University Press, Stanford, p 583
- Singer MC, Thomas CD (1992) The difficulty of deducing behaviour from resource use: an example from hilltopping in checkerspot butterflies. *Am Nat* 140:654–664
- Sourakov A (2008) Pupal mating in Zebra longwing (*Heliconius charithonia*): photographic evidence. *News Lep Soc* 50:26–32
- 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. 138+ xii pp
- Takeshita FA, Henmi Y (2010) The effects of body size, ownership and sex-ratio on the precopulatory mate guarding of *Caprella penantis* (Crustacea: Amphipoda). *J Mar Biol Assoc UK* 90:275–279
- Takeuchi T (2010) Mate-locating behavior of the butterfly *Lethe Diana* (Lepidoptera: Satyridae): do males diurnally or seasonally change their mating strategy? *Zool Sci* 27:821–825
- Takeuchi T, Imafuku M (2005) Territorial behavior of a green hairstreak *Chrysozephyrus smaragdinus* (Lepidoptera: Lycaenidae): site tenacity and wars of attrition. *Zool Sci* 22:989–994
- Tiple AD, Padwad SV, Dapporto L, Dennis RLH (2010) Male mate location behaviour and encounter sites in a community of tropical butterflies: taxonomic and site associations and distinctions. *J Biosci* 35:629–646
- Travassos MA, Pierce NE (2000) Acoustics, context and function of vibrational signalling in a lycaenid butterfly-ant mutualism. *Anim Behav* 60:13–26
- 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. Xerces Society, Portland
- Vlasanek P, Konvicka M (2009) Spragis in *Parnassius mnemosyne* (Lepidoptera: Papilionidae): male-derived insemination plugs loose efficiency with progress of female flight. *Biologia* 64:1206–1211
- Wickman P-O, Jansson P (1997) An estimate of female mate searching costs in the lekking butterfly *coenonympha pamphilus*. *Behav Ecol Sociobiol* 40:321–328
- Wiklund C (2003) Sexual selection and the evolution of butterfly mating systems. In: Boggs CL, Watt WB, Ehrlich PR (eds) *Ecology and evolution taking flight: butterflies as model systems*. The University of Chicago Press, Chicago, pp 67–90
- Wiklund C, Lindfors V, Forsberg J (1996) Early male emergence and reproductive phenology of the adult overwintering butterfly *Gonepteryx rhamni* in Sweden. *Oikos* 75:227–240