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ORIGINAL PAPER

A first step towards successful conservation: understanding local oviposition site selection of an imperiled butterfly, mardon skipper

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Abstract Lack of basic biological information is a key limiting factor in conservation of at-risk butterflies. In the Puget prairies of Washington State little is known about the habitat requirements of mardon skipper (*Polites mardon*, federal candidate, WA endangered). We investigated oviposition site selection and used our results to assess oviposition habitat quality at a restored site with reintroduction potential. During the 2009 flight season we marked eighty-eight eggs and sampled vegetation at oviposition and random locations, measuring habitat variables with respect to the oviposition plant, vegetation structure, and vegetation cover. Eighty-six of the eighty-eight eggs were laid on *Festuca roemeri*, a native, perennial bunchgrass. Discriminant function analysis revealed selection of oviposition sites based on habitat structure; females laid eggs in small *F. roemeri* tufts in sparsely vegetated areas of the prairie. These results are contrary to results from a previous study in the Cascade Mountains of WA where females are generalists and selected densely vegetated areas, suggesting that the species has geographically specific habitat requirements. To assess oviposition habitat at a potential reintroduction site we measured the six variables most important for oviposition at the occupied site and a proposed reintroduction site. Results revealed differences in habitat quality between locations and suggest a need for further habitat management at the reintroduction site. Our results highlight the importance of understanding the local habitat use of a rare species where restoration activities occur and increase our ability to target habitat management where it is most needed for the persistence of the species.

Keywords Butterfly · Endangered species · Habitat requirements · Hesperiinae · Prairie management · Restoration

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Introduction

Habitat restoration and reintroduction strategies are essential elements of recovery plans for rare and endangered species. These efforts often fail, however, because the ecology of focal species is unknown (Griffith et al. 1989; Miller and Hobbs 2007; Morrison 2009; Settele and Kuhn 2009). In the absence of detailed knowledge of a species' ecology, land managers are limited in what they can do to conserve and restore rare species populations. Often, ecosystems known to contain target species are protected. This strategy can fail, however, when protected areas are too small and/or isolated to sustain populations or do not maintain crucial habitat elements for target organisms (Barinaga 1990; Hanski 1991; New et al. 1995; Newmark 1996; Panzer and Schwartz 1998; Wenzel et al. 2006; Settele and Kuhn 2009). This is particularly true for animals with specialized habitat requirements such as butterflies (Thomas 1984).

The needs of each butterfly life stage (egg, larva, pupa, adult) are distinct and often occur at different scales (Dennis 2010). The resource based view of butterfly habitat defines suitable habitat as an area where adult and larval resources co-occur within the exploratory range of individual butterflies (Dennis et al. 2003, 2006; Shreeve et al.

2004; Dennis 2010). A suitable habitat patch therefore must contain the full complement of resources, and optimally supplemental resources to buffer for stochastic events (Dennis 2010). The loss of the habitat important for any critical resource such as adult food sources, basking locations, and specific microclimatic conditions for larvae, reduces fecundity and/or survivorship (Boggs and Ross 1993; Nylin and Gotthard 1998; Karlsson and Wiklund 2005). In addition to local resources, butterfly populations rely on appropriate landscape conditions such as patch size (Crone and Schultz 2003), and for some species the proper spatial arrangement of habitat patches is vital to maintain metapopulations (Crone and Schultz 2003; Hanski 2003).

The specific nature of butterfly habitat requirements has led to the use of single species and single population conservation approaches (New et al. 1995; Dennis et al. 2008). The most successful of these endeavors come from systems where detailed knowledge of the ecology of target species exists, specifically the preferred larval habitat and optimum larval resource (Thomas et al. 2011), and is incorporated into conservation strategies (Schultz and Crone 2008; Thomas 1983; Warren 1991; Thomas et al. 2009; Longcore et al. 2010). Within the relatively well-studied group of temperate butterflies and skippers critical information gaps still exist, particularly for rare species (New et al. 1995; Garcia-Barros and Fartmann 2009).

The mardon skipper (*Polites mardon*, Washington State endangered) is a candidate for listing under the United States Endangered Species Act whose survival depends on habitat restoration (USFWS 2011). Mardon skipper populations in the glacial outwash prairies of the Puget lowland, Washington, USA (hereafter referred to as Puget prairies) have declined precipitously in recent decades (Potter et al. 1999). Because of these declines, prairie restoration in the region often aims to improve mardon skipper habitat. However, restoration planning is limited because little is known about the butterfly (but see Beyer and Schultz 2010). Important nectar species have been identified (Hays et al. 2000), but the host plant, life history, and specific habitat requirements of the butterfly in the Puget prairies remain unknown.

Mardon skippers are confined to two isolated Puget prairies. As a result, reintroduction has been proposed to return mardon skippers to previously occupied sites where habitat restoration has occurred (A. Potter, personal communication). The World Conservation Union guidelines for reintroductions state that habitat quality at target sites must be evaluated, and reintroduction should occur only where high quality habitat exists (IUCN 1998). It is impossible, however, to restore habitat or assess habitat quality without knowledge of the target species' requirements. In this paper, we aim to (1) identify hostplants used by mardon skippers in the Puget prairies, (2) identify habitat characteristics that influence oviposition site selection, and (3) use this information to develop a method to evaluate the suitability of habitat restored for the mardon skipper.

Methods

Study species

The mardon skipper is a member of the grass skipper subfamily Hesperiinae of which at least 35 species are at-risk worldwide (Beyer and Schultz 2010). Mardon skippers are endemic to the Pacific Northwest of the United States and occur in four disjunct locations: the Puget prairies, montane meadows in both the Cascade Mountains of southern Washington and the Siskiyou Mountains of southern Oregon, and serpentine grasslands in northern California (Fig. 1). The Siskiyou Mountain population has been described as the distinct sub-species *P. mardon klamathensis* (Mattoon et al. 1998). The taxonomic status of the other three populations has not been evaluated; given the highly disjunct nature of the species' distribution each regional population may be taxonomically unique.

Mardon skipper populations range-wide are isolated and small. The largest populations support 1,000–4,000 butterflies, but most range from 50–200 individuals (Potter et al. 1999; Beyer and Black 2006; Jepsen et al. 2008). Mardon skippers are univoltine with adults in the Puget prairies flying from mid-May to mid-June. Females drop eggs into the grass singly without affixing them to a particular location. The eggs hatch 7–10 days later and larvae feed until late fall when they diapause in dried grass shelters at the base of the grass (Henry unpublished data). In spring, larvae feed again before pupating in April (Henry unpublished data).

Study sites

Lack of historic disturbance and subsequent succession of grasslands have dramatically reduced mardon skipper habitat throughout its range (Noss et al. 1995; Crawford and Hall 1997). Additionally, development and conversion to agriculture have shrunk the Puget prairies to 3 % of their previous distribution (Crawford and Hall 1997). Amerindians historically maintained these prairies by setting frequent, low intensity fires (Storm and Shebitz 2006). In the absence of frequent disturbance, remaining prairie habitat has been degraded by the invasion of non-native species such as Scotch broom (*Cytisus scoparius*) and tall oatgrass (*Arrhenatherum elatius*). These species greatly alter the vegetation structure and outcompete native plants (Dennehy et al. 2011). To combat invasive species, prairie management in the region involves a combination of techniques including

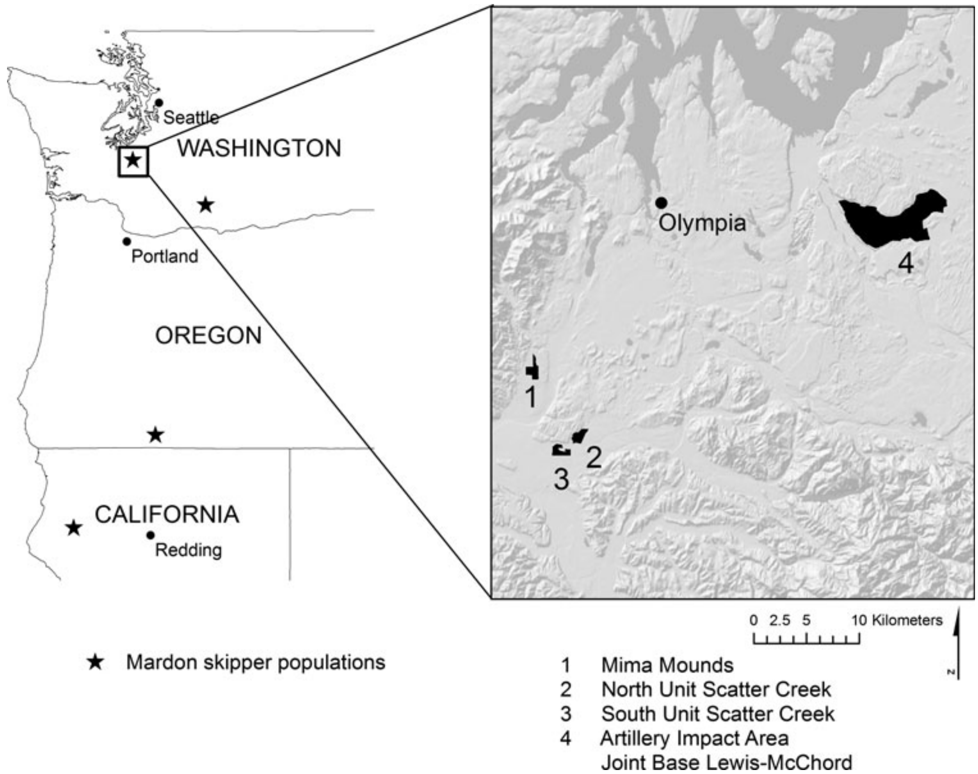

Fig. 1 Mardon skipper range. West coast distribution (*left*) and detail of Puget lowland sites (*right*)

prescribed burning, mowing, native species planting and invasive species removal through herbicide application and hand pulling (Dennehy et al. 2011). In the 1980's mardon skippers occurred in at least eight Puget prairies and now persist at only two, Scatter Creek Wildlife Area and a few locations on the edge of the Artillery Impact Area at Joint Base Lewis-McChord (Fig. 1) (Potter et al. 1999). Because of active military training, the Artillery Impact Area was not included in this study.

Scatter Creek Wildlife Area (46°50′14″ N, 122°59′42″ W) includes 250 ha of glacial outwash prairie, and is managed by the Washington Department of Fish and Wildlife (WDFW). In 2009 the north (120 ha of prairie) and south unit (130 ha of prairie) of Scatter Creek supported populations of 100–300 and approximately 1,000 mardon skippers respectively (G. Olson, unpublished data). Prairie quality and species composition varies dramatically across the wildlife area (Olson 2010).

Mima Mounds (46°53′40″ N, 123°3′12″ W; Fig. 1) is a Washington Department of Natural Resources Natural Area Preserve located 8 km northwest of Scatter Creek with 160 ha of prairie. Mardon skippers were last recorded at Mima Mounds in 1994 (Potter et al 1999). State biologists have proposed that a series of large (20–80 ha) prescribed burns in the early 1990s was the primary driver of their extirpation, although other factors including nectar limitation, invasive species, and/or climate may have contributed as well (D. Wilderman, personal communication).

Both Scatter Creek and Mima Mounds are part of a Prairie Quality Monitoring project (Olson 2010). This project involves mapping vegetation across the entire site at a 25 m × 25 m resolution. Roemer's fescue (*Festuca roemeri*, a native perennial bunchgrass), tall oatgrass, and scotch broom are three of the species for which percent cover is estimated within each grid cell. The abundance of a variety of forb species, including early blue violet (*Viola adunca*), is also measured (Olson 2010). WDFW collected these data at Mima Mounds in the summer of 2008 and at Scatter Creek in the summer of 2009 (Olson 2010).

Oviposition habitat selection

Oviposition surveys

We coordinated our oviposition surveys with WDFW biologists conducting mardon skipper distribution and abundance surveys (Potter and Olson 2009) during the 2009 flight season (May 15–June 15). WDFW surveyors walked east-west transects spaced 100 m apart and dropped a flag at all mardon skipper detection locations (Fig. 2). After each of their three surveys, WDFW sent us the locations of all flagged mardon skipper detections. We then searched for females by starting at a randomly selected detection location and haphazardly searching the surrounding hectare for 20 min or until the first female was located. If no female was detected within 20 min the

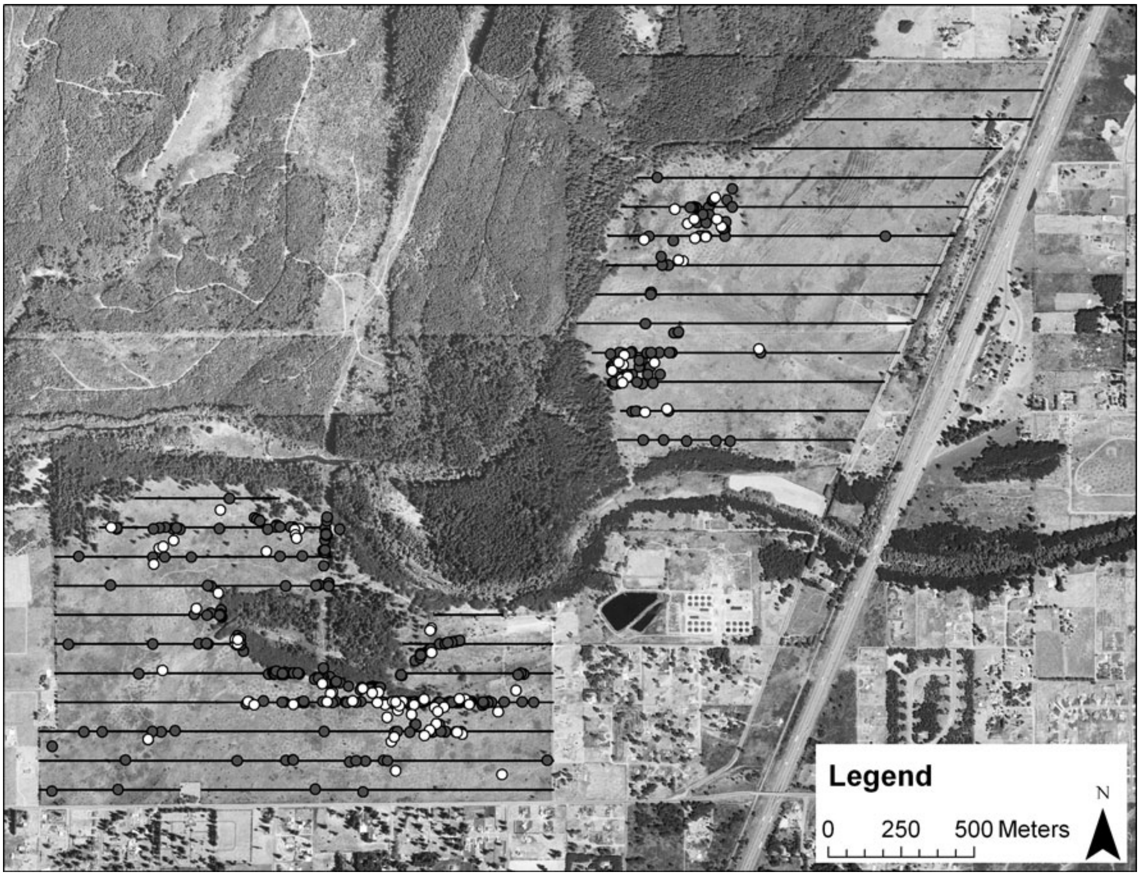

Fig. 2 Mardon skipper detections and ovipositions. Locations of Washington Department of Fish and Wildlife (*WDFW*) mardon skipper survey detections (*black circles*) and our observed oviposition locations (*white circles*) in 2009 at the north and south units of Scatter Creek Wildlife Area, WA. *Black lines* are transects walked by WDFW surveyors

observer proceeded to the next random detection location. Once located, the observer followed the female until she oviposited, was lost, or 30 min had passed. If a female was lost or exhibited no oviposition behavior in 30 min, the observer continued to search for additional females at the same location. Once the observer saw oviposition, s/he marked the egg location by placing a flagged wooden skewer as close to the egg as possible without disturbing it, identified the selected grass species, and recorded the GPS coordinates. During observations of female mardon skippers in 2008 we witnessed no ovipositions before 11:00 h; instead, female butterflies spent the morning hours nectaring (Henry, unpublished data). Therefore, we conducted oviposition surveys between 11:00–16:00 h on all days during the flight season when mardon skippers were observed flying.

Vegetation sampling

To effectively assess the vegetation community and structure experienced by mardon skipper females, we sampled vegetation within 2 weeks of oviposition. We sampled vegetation at oviposition locations and a paired random location 30–45 m away in a random direction. We chose this distance to capture the variability within the landscape while remaining within the exploratory range of female butterflies. During pilot observations in 2008 we watched mardon skippers routinely fly up to 50 m (Henry, unpublished data). We centered meter-square plots on the oviposition plant and the plant of the same species closest to the random location. Within each plot we measured habitat variables with respect to the oviposition plant, the structure of the vegetation, and vegetation cover, all of which influenced mardon skipper oviposition site selection in the Washington Cascades (Beyer and Schultz 2010). Oviposition plant variables included the footprint (maximum width × length), and height of the tallest leaf in the grass tuft (multiplied to get an index of tuft size), number of culms (flowering stalks), maximum culm height, percent dead leaves (category 1 = 0–25 % dead, 2 = 26–50 % dead, 3 = 51–100 % dead), distance to nearest plant of the same species as selected oviposition plant, and ground-cover (ie. thatch, moss) depth immediately adjacent to base of the oviposition plant. Vegetation structure attributes included tallest vegetation species and height, distance to nearest tree, number of individual fescue tufts, number of nectar flowers, and vertical vegetation density. We measured vertical vegetation density with one observer holding a meter stick parallel to the ground at 20 cm off the ground along the north edge of the plot, and a second observer lying on the ground on the south edge of the plot estimating the % of the meter stick obscured by vegetation.

Because visual percent cover estimates can vary greatly between observers (Sykes et al. 1983), we used the point intercept method (Goodall 1952) to collect vegetation cover data. Based on power analysis of data collected in 2008 we used 33 pins/m^2 to estimate vegetation cover (Henry 2010). Our pin frame contained eleven pins along a meter, one every 10 cm starting at zero. We placed the frame at three randomly selected locations within the quadrat (either at 10, 30, 50, 70, or 90 cm along the perimeter) and recorded every species that contacted each pin as well as the ground cover at the base of the pin.

Statistical analysis

We ran discriminant function analysis (DFA) to determine if oviposition and random plots formed independent groups (Williams 1983). Before running DFA we identified highly correlated variables (Pearson correlation > |0.7|) and randomly selected one of each pair to eliminate (McGarigal et al. 2000). Only two pairs of our measured variables were highly correlated: moss cover and thatch cover (0.82), and maximum culm height and number of culms (0.81). Moss and thatch are both prevalent prairie ground covers and, as the negative correlation suggests, where one is present, the other is absent; maximum culm height and the number of culms are both measures of plant vigor. The resulting twenty-two variables were included in the DFA (Table 1). Only samples with complete data sets were entered in the analysis, which left us with 74 oviposition locations and 82 random locations. Prior to analysis we $\log_{10}(x + 1)$ transformed continuous data and arcsine square-root transformed percent cover data; all variables had homoscedastic variances and we subjectively assessed the variance among groups with the ordination plot (Quinn and Keough 2002). To determine which variables contributed most to the separation of groups along the canonical axis we used total structure coefficients, which measure correlations between individual variables and the canonical function, and interpreted variables with the highest absolute value coefficients to be most important. We conducted DFA in SAS 9.2 statistical package using the CANDISC procedure.

In addition to identifying differentiating factors between oviposition and random locations, we used one-way ANOVAs

Table 1 Discriminant function analysis variables and results

Variables (units)	Total structure coefficient	Oviposition locations	Random locations	*F*	*p* value
Tuft size (cm^3)[1]	**0.733**	**6,873 ± 7,017**	**21,136 ± 21,167**	**55.23**	**<0.001**
Number of tufts (count)[2]	**−0.662**	**11.0 ± 4.4**	**6.5 ± 3.9**	**47.99**	**<0.001**
Percent dead (category 1–3)[1]	**0.610**	**1.4 ± 0.6**	**2.049 ± 0.780**	**32.54**	**<0.001**
Vertical vegetation density (%)[2]	**0.606**	**14.9 ± 19.5**	**36.3 ± 30.1**	**31.65**	**<0.001**
Tall oatgrass cover (%)[3]	**0.488**	**2.8 ± 5.3**	**10.3 ± 13.0**	**21.25**	**<0.001**
Moss cover (%)[3]	**−0.474**	**56.1 ± 23.0**	**39.0 ± 24.8**	**19.79**	**<0.001**
Distance to nearest Fescue (cm)[1]	**0.442**	**17.7 ± 8.3**	**31.1 ± 33.4**	**11.3**	**0.001**
Scotch broom cover (%)[3]	0.356	2.9 ± 5.9	8.9 ± 14.8	10.61	0.001
Fescue cover (%)[3]	−0.343	51.6 ± 20.1	39.9 ± 24.4	9.57	0.002
Thatch depth @ ovp plant (cm)[1]	0.328	3.4 ± 1.9	4.4 ± 2.2	10.6	0.001
Carex sp. cover (%)[3]	0.316	25.3 ± 16.3	34.8 ± 21.1	8.19	0.005
Height of tallest vegetation (cm)[2]	0.288	63.1 ± 15.5	71.2 ± 18.7	8.61	0.004
Total vegetation cover (%)[3]	0.272	92.9 ± 12.4	97.0 ± 2.9	6.02	0.014
Number of culms (count)[1]	0.254	1.6 ± 3.4	3.3 ± 6.6	3.74	0.055
Hypochaeris sp. cover (%)[3]	−0.244	6.2 ± 6.5	4.0 ± 4.9	4.25	0.041
Bare ground cover (%)[3]	0.139	6.6 ± 10.7	7.9 ± 11.1	0.6	0.439
Dry vegetation cover (%)[3]	0.130	60.6 ± 23.9	65.1 ± 23.6	1.58	0.210
Nectar flowers (count)[2]	−0.098	1.5 ± 5.0	0.7 ± 1.3	1.17	0.282
Distance to nearest tree (m)[2]	−0.082	39.8 ± 30.8	34.8 ± 26.9	1.16	0.283
Danthonia sp. cover (%)[3]	−0.063	4.8 ± 6.2	4.2 ± 5.4	0.33	0.564
Agrostis sp. cover (%)[3]	0.023	10.4 ± 12.6	11.1 ± 12.7	0.13	0.721

Variables included in the DFA. Variables are ranked by the absolute value of their total structure coefficients. Top discriminating variables are bold. *p* values are significant at $p < 0.002$. Superscripts refer to the type of variable: *1* oviposition plant, *2* vegetation structure, *3* vegetation cover. Variable values are mean ± 1 SD. Corresponds with Fig. 4

to examine differences in individual variables between oviposition and random locations. After transformations, all variables met the assumption of homoscedasticity and we ran ANOVAs regardless of normality (Scheffe 1959) ($\alpha = 0.002$, Bonferroni multiple comparison).

Developing an oviposition habitat quality assessment method

Habitat assessment

The effects of habitat management in Puget prairies are often measured by comparing native and/or invasive species abundance before and after treatment (Stanley et al. 2011). We were interested in developing an easy to implement method for use by land managers to assess how management activities impact mardon skipper oviposition habitat quality. Washington State biologists have proposed Mima Mounds as a candidate site for mardon skipper reintroduction (A. Potter, personal communication) so we chose to collect data there for use in developing our method. Our method involved a two-step approach. We first used vegetation data from the Prairie Quality Monitoring dataset to find suitable locations within Mima Mounds for potential reintroduction. We conducted GIS analysis (ArcGIS 9.3) to locate areas of Mima Mounds with moderate fescue cover (potential host plant), high violet abundance (important nectar source), and no scotch broom or tall oatgrass cover to limit the need for additional weed control efforts in potential reintroduction sites. We then chose two locations that contained areas that met these criteria in which to sample fine scale habitat elements based on recommendations from the Program Ecologist at Mima Mounds (Fig. 3) (D. Wilderman, personal communication). During the 2010 mardon skipper flight season we measured variables from the 2009 oviposition versus random DFA analysis with total structure coefficients > |0.4| except for tall oatgrass cover which was excluded a priori through the aforementioned GIS analysis (hereafter referred to as the top discriminating variables). We chose the 0.4 cutoff based on results from similar analyses of mardon skipper oviposition and random locations performed by Beyer and Schultz (2010). At all but one of the nine meadows they surveyed in the Washington Cascades the top 5 discriminating variables had structure coefficients > |0.4| (Table 3 in Beyer and Schultz 2010). In our analysis, Scotch broom and fescue cover are the two variables immediately below the 0.4 cut-off (Table 1) both of which we accounted for a priori in the GIS analysis. We measured the top discriminating variables in eight, meter-square plots, randomly placed along each of five 50 m transects. All transects were contained within a half-hectare polygon (50 m × 100 m). Each plot was centered on the potential oviposition plant (of the oviposition species observed in 2009) nearest to each randomly selected transect meter mark. In 2010 we also sampled vegetation at the south unit of Scatter Creek using the same method in two half-hectare polygons that encompassed as many 2009 oviposition locations as possible Fig. 3. This sampling allowed us to compare the habitat quality in the locations sampled at Mima Mounds to that of an area at Scatter Creek that supports a relatively high density of mardon skippers.

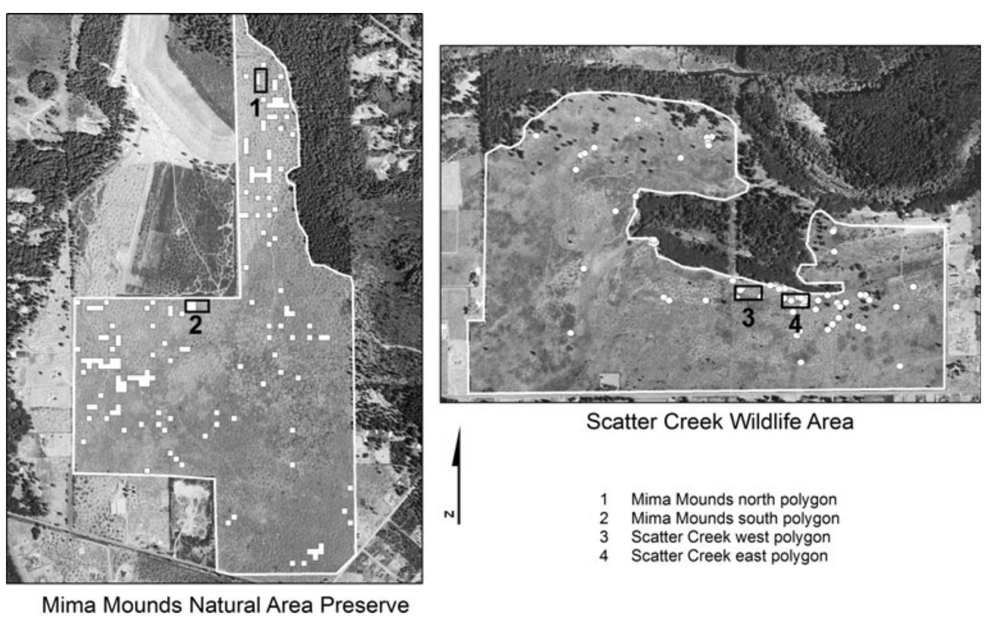

Fig. 3 Polygons sampled for habitat assessment analysis. Locations of ½ ha polygons sampled at Mima Mounds and Scatter Creek (*black rectangles*). Prairie habitat at both locations is outlined in grey. *White boxes* on Mima Mounds map are results from GIS calculation to locate areas with moderate fescue cover, high violet abundance, and no scotch broom or tall oatgrass cover, individual *squares* are 25 m × 25 m. 2009 oviposition locations at Scatter Creek are indicated with *white circles*

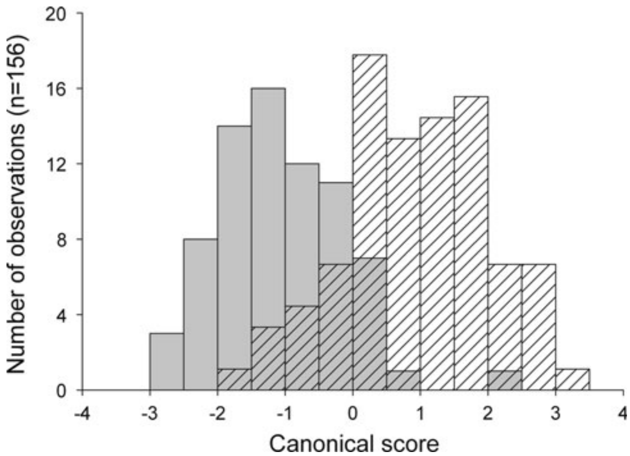

Fig. 4 Discriminant function analysis results. Oviposition locations are grey, random locations are hatched. Oviposition and random locations form two different groups along the canonical axis. Percent of canonical variation explained by group differences (r^2) = 0.50. Variables corresponding to the canonical axis are given in Table 1

Statistical analysis

As multiple variables influence oviposition selection, we were interested in quantifying where appropriate values of the measured variables co-occurred, not just how mean values compared across locations. To do this, we ran DFA with our oviposition and random plot data from 2009 using only the top six discriminating variables. This created a discriminant function that we then used to calculate the probability of oviposition occurring within each 2010 meter-square plot based on all six of the sampled variables (DISCRIM procedure, SAS 9.2). By using the average probability of oviposition in each half-hectare polygon as a measure of habitat quality, we compared oviposition habitat quality in the four polygons using a one-way ANOVA and post hoc Tukey tests (Minitab 15).

Results

Oviposition surveys

During the 2009 flight season weather conditions were conducive for mardon skipper activity on 13 days during which we searched for females at 105 of the 217 WDFW mardon skipper detection locations. We found females at 98 of the detection sites and witnessed oviposition at 88 locations. While patchy in distribution, oviposition locations are widespread thus confirming that butterflies are ovipositing across the prairie (Fig. 2). All but two of the 88 observed ovipositions were on Roemer's fescue, a native perennial bunchgrass. The remaining two eggs were laid on yellow hairgrass (*Aira praecox*) a non-native annual grass. Roemer's fescue cover accounts for only fifty percent of the total grass cover in all plots sampled suggesting female butterflies are actively selecting to oviposit on fescue over other available grasses.

Vegetation sampling

Discriminant function analysis revealed that oviposition and random locations were different from each other (MANOVA: Wilks' Lambda = 0.499, $F = 6.01$, $df = 22$, $p < 0.0001$; r^2 (proportion of total variation explained by function) = 0.50; Fig. 4). The variables that contributed most to discrimination between groups were related to the structure of both the selected fescue tufts and vegetation within the plot. Females laid eggs in small, relatively green fescue tufts. In the square-meter surrounding oviposition locations there was little tall oatgrass cover and vertical vegetation density, and moss is the predominant ground cover (Table 1). All of these variables differ between oviposition and random plots ($p \leq 0.001$; Table 1). Fescue cover is greater in oviposition plots than in random plots, however, its structure coefficient of -0.343 ranks 9th out of the 22 variables in the analysis indicating that host plant cover is not a primary driver of oviposition site selection (Table 1). The discriminant function classifies samples better than random with a classification success of 80 %.

Oviposition habitat assessment method

The average probability of oviposition in the two polygons sampled in the high-density area of Scatter Creek is the same (Table 2). The south polygon at Mima Mounds has a probability of oviposition similar to the polygons at Scatter Creek but the probability of oviposition in the north polygon of Mima Mounds is lower than that of the Scatter Creek polygons (one-way ANOVA ($\alpha = 0.05$): $F = 3.52$, $df = 163$, $p = 0.017$; Table 2). The discriminant function derived from the top discriminating variables from 2009 had an error rate of 16 % thereby classifying plots better than a random classification scheme.

Discussion

Mardon skippers are host specialist butterflies in the Puget prairies. Our observations of 86 of 88 eggs laid on Roemer's fescue confirm prior speculation of fescue specialization in Puget populations. This is contrary to results from Beyer and Schultz (2010) who found females to be generalists, laying eggs on 23 graminoid species across nine meadows in the Washington Cascades. However, in meadows where Idaho fescue (*Fescue idahoensis*; closely

Table 2 Classification analysis results

Polygon	Number of plots classified as oviposition	Average probability of oviposition	Tuft size (cm^3)	# of fescue tufts	% dead (category 1–3)	Vertical vegetation density (%)	Moss cover (%)	Dist. To nearest fescue tuft (cm)
Scatter Creek E	26	0.66[a]	8,889 ± 8,837	14 ± 5	2.0 ± 0.8	13 ± 14	58 ± 16	16 ± 8
Scatter Creek W	28	0.66[a]	8,908 ± 7,909	14 ± 7	1.9 ± 0.8	19 ± 20	52 ± 26	18 ± 11
Mima Mounds N	14	0.47[b]	13,131 ± 14,451	11 ± 5	2.4 ± 0.7	19 ± 21	62 ± 13	19 ± 12
Mima Mounds S	25	0.58[ab]	12,096 ± 12,663	11 ± 5	2.1 ± 0.8	6 ± 7	59 ± 24	19 ± 8

Results from discriminant function classification analysis of polygons sampled at Mima Mounds, WA and Scatter Creek, WA based. We sampled six habitat variables in 40 1-m^2 plots in each of four ½ ha (100 m × 50 m) polygons. The number of plots per polygon classified as oviposition and the average probability of oviposition within each polygon are given. Locations with different superscripts have significantly different oviposition probabilities (ANOVA: $df = 163$, $f = 3.52$, $p = 0.017$). Variable values are mean ± 1 SD

related to Roemer's fescue) was present, it was overwhelmingly preferred for oviposition indicating that some montane populations exhibit oviposition specificity similar to prairie populations. Local populations of other generalist butterfly species exhibit specialist tendencies (Singer 2004; Wiklund and Friberg 2008; Garcia-Barros and Fartmann 2009). Localized host specialization can result from host availability, host nutritional quality, parasitoid and or predator communities supported by a particular host, ability of an herbivore to exploit a host's chemical defenses, or host architecture which can influence microclimate and predator abundance (Lill et al. 2002; Reudler Talsma et al. 2008; Garcia-Barros and Fartmann 2009).

For mardon skippers, simple presence of the hostplant, Roemer's fescue, is not adequate for oviposition. When selecting oviposition locations, mardon skippers choose small fescue tufts, at least half of the leaves of which are green. Selected tufts are surrounded by moss, and neighboring tall oatgrass cover and density of vertical vegetation are low. The sparse, open vegetation structure of oviposition locations is similar to that of historic glacial outwash prairies (Chappell and Crawford 1997). Invasion of the Puget prairies has dramatically altered their shortgrass structure as both scotch broom and tall oatgrass can reach heights of over 2 m. During oviposition surveys we often lost females when they encountered large swaths of tall oatgrass primarily due to behavioral changes—mainly increased velocity. We did, however, follow one female in fast, straight, flight across 70 m of tall oatgrass to a mossy, open fescue patch where she promptly laid an egg. Although anecdotal, this observation suggests that even when fescue is hiding below a canopy of tall oatgrass females avoid ovipositing in heavily invaded areas, as has been observed in other butterfly species (Severns 2008). WDFW biologists hypothesize that changes from the open vegetation structure of historic plant communities to the complex structure of invaded areas has led to mardon skipper population declines in Puget prairies (A. Potter, personal communication). We did not explicitly test this hypothesis; however, our findings of females selecting to lay eggs in areas with low vertical vegetation density and little tall oatgrass cover (Table 1) are consistent with the hypothesis. The short, open vegetation structure of mardon oviposition habitat in the Puget prairies is similar to that of other rare, temperate butterfly populations for which changes in vegetation structure have contributed to population declines (Thomas 1983; Thomas et al. 1986, 2009; Gutierrez et al. 1999; Möllenbeck et al. 2009).

Changes of both host plant architecture and local vegetation structure at oviposition sites can impact larval survival in a number of ways including altering the microclimate and predator community. Butterfly populations are constrained by temperature (Crozier 2003, 2004) and are restricted to especially warm macro- and microhabitats in temperate climates (Thomas et al. 2001). The small tufts and open habitat structure selected by ovipositing females are likely to correspond to the warmest locations in the prairie (Forsberg 1987; Stoutjesdijk and Barkman 1992). Weather in the Puget lowlands is cool and cloudy with intermittent sun breaks for much of the year, particularly in spring when overwintering larvae complete development and pupate (February–April average max temp: 12.1 °C, average min temp: 1.2 °C; Western Regional Climate Center 2010). In these conditions, locations where ectothermic larvae can take advantage of solar heating may result in increased foraging and faster development time, potentially increasing individual survival (Bonebrake et al. 2010).

Another explanation for selection of oviposition locations is predator avoidance. Larger, more structurally complex grass tufts support a greater density of invertebrate predators (Reid and Hochuli 2007) that may play an important role in early instar larval predation (Wiklund and Friberg 2008). Additionally, larval predation rates are influenced by vegetation density; with predation being lowest in isolated host plants and greatest where there is a high density of vegetation surrounding the host plant (Wiklund and Friberg 2008). Mardon skipper larvae developing in large fescue tufts or tufts surrounded by vegetation may be more likely to encounter predators than those in small, isolated tufts.

The selection of oviposition sites with 56 % moss cover reinforces the need for open space at oviposition locations. Bare ground and lichen crusts occupied the interstitial areas of historic prairies (Chappell and Kagan 2001). In modern prairie environments, bare ground is quickly invaded, most often by non-native species. The mat-like carpet of moss (primarily *Racomitrium canescens*) that has developed in the absence of fire inhibits plant germination and establishment (Morgan 2006; Stanley et al. 2011), effectively maintaining weed-free open spaces. We observed mardon skippers actively using the moss spaces between fescue tufts for basking. Males used the moss space when perching and chasing potential mates, and searched for females in these open mossy spots when patrolling (E. Henry personal observation). These observations suggest that adults use moss for thermoregulation and mate finding much in the way other species use bare ground and open areas (Clench 1966; Wickman 2009).

Maintaining the vegetation structure characteristic of mardon skipper oviposition habitat in Puget prairies requires continued invasive species management. Although scotch broom cover was not one of the primary discriminating variables it is still significantly lower at oviposition locations than at random locations and its management is not unimportant. Intense, ongoing scotch broom control at Scatter Creek has reduced and prevented the expansion of scotch broom across the site, especially in areas occupied by the butterflies. Without such control, it is likely that scotch broom cover would have a greater influence on oviposition site selection because of the dramatic structural changes associated with its invasion.

Removal of invasive species alone, however, will not be sufficient when restoring mardon skipper habitat. Despite the near absence of tall oatgrass and scotch broom, our habitat assessment analysis showed that the north polygon at Mima Mounds does not have the same probability of oviposition as high quality areas at Scatter Creek. Fescue tufts in both polygons at Mima Mounds are on average 50 % larger than those in the high-density area of Scatter Creek, and twice as big as selected oviposition tufts (Tables 1, 2). This pattern illustrates the potential need for tuft size management in areas of prairie where tall oatgrass and scotch broom are presently under control.

Maintenance of small host plants and short sward heights for butterflies in Europe has primarily been achieved through grazing (WallisDeVries and Raemakers 2001; Eichel and Fartmann 2008; Thomas et al. 2009). In Puget prairies, grazing was not instrumental in maintaining historic vegetation structure and is unlikely to be implemented in prairie restoration. Instead, common butterfly habitat management techniques in the region include grass specific and broad-spectrum herbicide application, mowing, and prescribed burning (Schultz et al. 2011). Of these techniques only fire has the ability to reduce the basal area of individual fescue plants (Conrad and Poulton 1966; Tveten and Fonda 1999). Prescribed burning is commonly used in grassland restoration projects with goals of creating habitat for rare species (Warren 1991; Schultz and Crone 1998; Möllenbeck et al. 2009). One challenge of using fire to improve habitat for endangered butterflies is that larvae rarely survive burning (Swengel 2001). However, when patchy burning strategies are employed that allow re-colonization of burned areas by adults, the benefits of prescribed burning may potentially outweigh the costs (Dana 1991; Schultz and Crone 1998; Relf and New 2009). A well-planned burn relies on understanding the life history, habitat requirements, and distribution within a site of species that will be impacted (Dana 1991; Schultz and Crone 1998). Without sufficient species specific information, burning, or any intensive management, can be catastrophic for small populations (Warren 1991; Konvicka et al. 2008).

Conclusion

Oviposition habitat requirements of mardon skippers in the Puget prairies are distinct from those in the southern Washington Cascades. In the Cascades, female mardon skippers oviposit on larger (greater cover) graminoids where there is more vegetation cover and less bare ground (Beyer and Schultz 2010). These divergent results, in part, reflect differences in climate between the two regions. In the mountains, larvae are buried by snow from November to June. When not under the snow, mountain larvae are exposed to greater daily temperature swings and perhaps greater graminoid cover buffers these extreme temperatures, keeping caterpillars from both freezing and overheating (Stoutjesdijk and Barkman 1992). Additionally, mountain larvae may be exposed to higher levels of solar radiation than prairie larvae thus causing females to target different host structure for oviposition in the two populations (Anthes et al. 2008).

Given the contrasting structural habitat requirements between the two regions, application of results from Beyer and Schultz's (2010) work in the mountains to mardon skipper habitat restoration projects in the Puget prairies could result in the enhancement of structural attributes away from those that promote mardon skipper oviposition in these prairies. Results from both of these studies emphasize the importance of understanding local behavior and habitat use of rare species populations where restoration activities occur (Dennis 2004, 2010).

Butterfly habitat quality at a site is often evaluated by hostplant abundance alone (Lipman et al. 1999; Fartmann 2006; Relf and New 2009; Bartel et al. 2010) even though all potential hosts in a site may not be suitable for oviposition and larval development (Thomas 1984; Eichel and Fartmann 2008; Bonebrake et al. 2010; Dennis 2010). Results of our habitat assessment analysis confirm that our method works to pick up important differences in oviposition habitat quality in multiple locations, and can be useful to land managers when selecting target areas for habitat management and measuring effects of those activities. It is important to note that another aspect of habitat suitability not accounted for herein is the area of suitable habitat (patch size) necessary for mardon skipper persistence. In a large prairie site such as Mima mounds it is unlikely that the entire site must contain suitable mardon skipper oviposition habitat, but rather that a large enough patch, or series of patches, within the site does. Prior to reintroduction this must be assessed. Currently the data needed to determine appropriate patch size and distribution—such as dispersal behavior and demography (Schultz and Crone 2005)—are not available; this would be a logical next-step toward the conservation of the species.

The need for restoration and conservation of specific habitat attributes is not unique to rare butterflies. Microhabitat attributes such as vegetation structure and microclimate are also critical to the survival of rare insects such as a flightless bush-cricket (*Methoptera brachyptera*), a long-horned beetle (*Rosalia alpina*), and a dung beetle (*Onthophagus gibbulus*) (Roslin et al. 2009; Poniatowski and Fartmann 2010; Russo et al. 2010). The research needed to elucidate these fine-scale habitat requirements is often seen as time consuming and expensive; however, truly understanding the ecology of a rare species is fundamental to successful conservation (Miller and Hobbs 2007; Schultz and Crone 2008; Morrison 2009). Without the kind of detailed information gleaned by scrutinizing individuals' behaviors and habitat, habitat conservation and restoration projects run the risk of missing the mark, or wasting resources on activities that turn out to be detrimental to the target species (Dennis 2010). Our approach of translating individual habitat use, to specific structural habitat requirements, to a habitat evaluation technique advances the understanding of an understudied butterfly family, and greatly increases our ability to target habitat restoration where it is most needed and useful for the persistence of the species.

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