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Oviposition selection by a rare grass skipper *Polites mardon* in montane habitats: Advancing ecological understanding to develop conservation strategies

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ABSTRACT

The Grass skipper subfamily (Hesperiinae) includes many at risk species across the globe. Conservation efforts for these skippers are hindered by insufficient information about their basic biology. Mardon skipper (*Polites mardon*) is declining throughout its range. We surveyed mardon oviposition across nine study meadows in the Gifford Pinchot National Forest of Washington State. We conducted habitat surveys with respect to oviposition ($n = 269$) and random ($n = 270$) locations, recording data on over 50 variables. Mardon oviposited on 23 different graminoid species, yet are selective for specific graminoids within meadows. Most frequent ovipositions across meadows occurred on *Festuca idahoensis* and *Poa pratensis* (accounting for 112 of 269 total oviposition observations). Discriminant Function Analyses revealed that mardon habitat was too variable to detect oviposition selection across study meadows, yet there was strong selection occurring within meadows (r^2 ranging from 0.82 to 0.99). Variables important to within meadow selection were graminoid cover, height, and community; oviposition plant structure (leaf density, height, area); insolation factors (tree abundance and canopy shading); and litter layer factors (cover and depth). With few exceptions the primary variables discriminating between oviposition and random locations were significantly different ($p < 0.001$). Conservation implications include maintaining native meadow ecosystems with sensitivity to local habitat preferences.

1. Introduction

Lepidoptera are one of the largest, most diverse, and most endangered taxonomic groups (Thomas et al., 1994; Smallidge and Leopold, 1997; Liu et al., 2006). Habitat loss and degradation has led to declines in butterfly populations across many parts of the world; including Europe, Africa, Asia, Australia, and North America (Thomas et al., 1994; Smallidge and Leopold, 1997; Bergman, 1999; Eastwood and Hughes, 2003; Fox et al., 2006; Freese et al., 2006; Liu et al., 2006; Albanese et al., 2007b; Edge et al., 2008). Successful recovery of at risk species largely depends on a sufficient understanding of their basic biology, yet this knowledge is often lacking for rare butterflies (Schultz and Crone, 2008).

Butterfly declines often signal the degradation of the habitats with which they are associated (Oostermeijer and van Swaay, 1998). Lepidoptera have a polymorphic life history, including a larval and pupal form in the juvenile state and a winged form in the adult state, making them dependent on a variety of resources within their environment. Adult life stages require sufficient food resources, most commonly nectar flowers, access to host plants, and large scale structural components; such as habitat connectivity, refuge from adverse weather, and adequate insolation (Dennis et al., 2006). Larval stages may require specific plant species for forage as well as particular microhabitat conditions (Grundel et al., 1998; Awmack and Leather, 2002; Albanese et al., 2007a). Resources for adults may be spatially segregated with adults requiring adequate daily access to multiple resources across an area. The dependence on so many habitat variables creates sensitivity to even small changes within the ecosystem, and many species are considered environmental indicators (Oostermeijer and van Swaay, 1998; Brown and Freitas, 2000; Eastwood and Hughes, 2003). Rare butterflies are especially useful for monitoring unique ecosystems and are often associated with other threatened fauna (Brown and Freitas, 2000).

An understanding of what factors determine essential habitat for rare butterflies is imperative to their conservation. Important habitat characteristics are commonly determined by investigating larval habitat use (Ellis, 2003; Anthes et al., 2008). The susceptibility of butterflies to environmental changes is pronounced in the larval state due to their limited mobility and restricted habitat requirements (Thomas et al., 2001; Anthes et al., 2003). Larval survivorship is significantly influenced by ovipositing females, as larvae generally do not travel far, if at all, from their natal locations (Awmack and Leather, 2002; Bergman 1999; Doak et al., 2006).

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Female butterflies are selective during oviposition, depositing eggs in locations that are favorable to larval development and survival will increase their fecundity (Awmack and Leather, 2002). Correspondingly, female butterflies may increase the number of eggs deposited in high quality habitats and host plants (Fownes and Roland, 2002; Chen et al., 2004; Mizumoto and Nakasuji, 2007). Habitat factors that a female butterfly may cue-in on when selecting a suitable oviposition location include host plant species (e.g. Apollo butterfly, *Parnassius apollo,* Fred et al., 2006), host plant nutritional and chemical content (e.g. cabbage white butterfly, *Pieris rapae*, Chen et al., 2004), host plant size and structure (e.g. marsh fritillary, *Euphydryas aurina*, Anthes et al., 2003), and oviposition location microclimate (e.g. Karner blue butterfly, *Lycaeides melissa samuelis*, Grundel et al., 1998; Grundel and Pavlovic, 2007).

The skipper butterfly family, Hesperiidae, harbors approximately 4000 species (Warren et al., 2008). There are at least 55 at risk skippers world wide, including a minimum of 35 grass skippers (subfamily Hesperiinae, Supplementary Data A). Mardon skipper (*Polites mardon*, US federal candidate, Washington State endangered) is a rare and declining butterfly endemic to the Pacific Northwest of the United States (Mattoon et al., 1998). The biology of this species is poorly understood (Potter et al., 2002; Black and Vaughan, 2005; Beyer and Black, 2006). In the US there are three federally listed skippers, including Carson wandering (*Pseudocopaeodes eunus obscurus*, endangered) Laguna Mountains (*Pyrgus ruralis lagunae*, endangered), and Pawnee montane (*Hesperia leonardus montana*, threatened). There are two US federal candidate species, Dakota skipper (*Hesperia dacotae*, Canada endangered) and mardon skipper (*P. mardon*, Washington State endangered), as well as several other state-listed skippers. To date, limited information on habitat requirements inhibits management efforts for these butterflies (US Fish and Wildlife Service, 1997, 1998, 2005; Potter et al., 2002; Beyer and Black, 2006; Warren et al., 2008). Grass-feeding butterflies, in general, have highly complex resource requirements and very little is known about how they utilize habitats. In 2006 we conducted an exploratory study of mardon skipper with the Xerces Society for Invertebrate Conservation. Eleven species of grasses and sedges were observed as oviposition plants (Beyer and Black, 2006). Formerly mardon were believed to deposit eggs only on *Festuca* species, however *Festuca* was absent in many of the sites. This result completely changed former perceptions about mardon habitat (Black and Vaughan, 2005), and further stimulated inquiry as to what makes this butterfly rare.

In this study we investigate mardon skipper site utilization to determine what aspects are critical to conservation. The primary goal of this study is to determine what influences mardon skipper oviposition location selection, thereby understanding larval habitat needs. We aim to determine (1) what graminoid species are utilized for oviposition, (2) what landscape and local factors influence oviposition selection, and (3) to what extent these factors vary between sites. This information is the first step in developing mardon skipper conservation plans and serves as baseline ecological information for future research. In addition, the information contributes to conservation of other rare skippers by advancing knowledge of this understudied family.

2. Methods

2.1. Study species and habitat

Mardon skipper belongs to the grass skipper subfamily, *Hesperiinae* and are dependent on meadow-grassland habitats. Female mardon drop eggs singly while perched; eggs do not affix to host plant. Distributions of extant mardon skipper populations are disjunct; ranging from the grasslands of northwest California to the Puget Trough including the Cascade Mountain Range in both Oregon and Washington State. All known mardon skipper sites are small; most support populations of less than 50 individuals and are isolated from neighboring populations (Potter et al., 2002; Black and Vaughan, 2005).

Existing mardon habitat has undergone major reductions and several populations have been extirpated (Black and Vaughan, 2005). Threats to its existing habitat are a consequence of urban development, resource management (logging, grazing, and fire suppression), and increased recreational use of public lands (Black and Vaughan, 2005). Montane meadow habitats have drastically declined (Coop and Givnish, 2007; Roland and Matter, 2007). Fire suppression has led to tree and shrub encroachment in forest meadows (Norman and Taylor, 2005). Grazing, recreation, increased logging roads, and agriculture have aided the spread of invasive weeds (Leung and Marion, 2000; Trombulak and Frissell, 2000). As a result, meadows and grasslands are disappearing (Griffiths et al., 2005) or undergoing drastic habitat changes (Crawford and Hall, 1997; Noss et al., 1995).

2.2. Meadows

Since 2000, 39 mardon skipper meadows have been documented in the Gifford Pinchot National Forest (Fig. 1). These meadows range from 800 to 1700 m in elevation, and have various management histories. This provided a great opportunity to study several distinct populations, each persisting within different habitat types, and allowing us to investigate the commonality between them. In 2007, 21 of the 39 documented mardon skipper meadows had historically recorded populations where counts exceeded 10 butterflies and were scouted as potential research sites. Of these 21 meadows, three were excluded because they were not logistically feasible, five of the populations never produced adults during our research season, and four were excluded due to small population sizes (under 15 individuals). The nine remaining meadows were included in this study (Fig. 1): Cave Creek, Peterson, Lost, Flog Salvage, Midway, Smith Butte, Muddy, 7A, and Grapefern.

Dominant vegetation at all study meadows consisted of a mix of grasses and sedges. Rushes were only noted present at Cave Creek, Muddy, and 7A meadows which are a mix of moist wetland and dry grassland. Cave Creek is particularly impacted by noxious weeds including houndstounge (*Cynoglossum officinale*) and Canada thistle (*Circium arvense*). Approximately 80% of the Cave Creek meadow has been fenced to reduce grazing and spread of invasive weeds. Historically, Peterson Prairie had heavy livestock grazing impacts. In recent years all grazing on Peterson Prairie has ceased. Flog Salvage was heavily logged, and reseeded with Lodgepole pine (*Pinus contorta*). Approximately 80% of the original meadow is now densely overgrown with saplings, and graminoid diversity there includes only a few species. Lost Meadow, bordered by an open second generation forest, is exposed to short periods of heavy grazing. Midway is an open meadow connected to other open areas of potential mardon habitat. The area surveyed was chosen based on *a priori* knowledge of high mardon use areas.

2.3. Oviposition surveys

Within each meadow we surveyed mardon skipper oviposition selectivity. Surveys were conducted on calm (<5 on Beauford wind scale), sunny days with temperatures above 15 °C. Oviposition observations began when any female was observed flying. A random point and direction within the meadow was located, using random number tables, from which a transect line (~10 m wide) was walked until a female was encountered. Observations were made with the aid of 8 × 42 binoculars. If the female was not indicating oviposition behavior after 10 min, the surveyor terminated

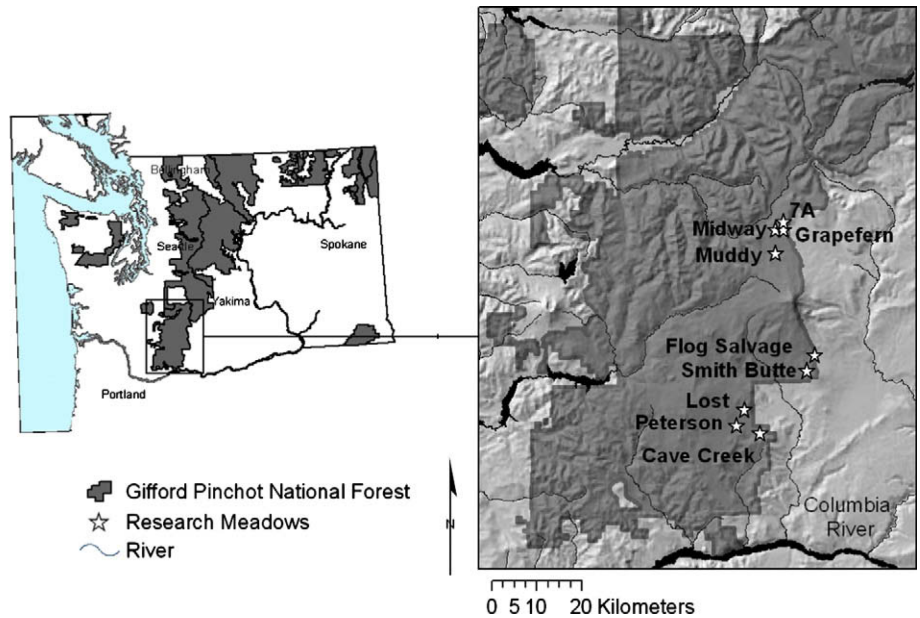

Fig. 1. Research meadows. Nine research meadows located in the Gifford Pinchot National Forest in Washington State, USA.

the observation. If oviposition behavior was observed, the observation continued for an additional 10 min. If no oviposition had occurred at the end of 20 min, the observation was terminated and another female was located from a new random transect. Females engaged in oviposition were watched for up to five individual egg depositions. Often the female was lost after exhibiting oviposition as the observer prioritized marking the oviposition location over continuing observation on the individual.

All precise physical locations where oviposition occurred, hereafter referred to as "oviposition locations", were marked with metal stakes. The number of days spent surveying oviposition behavior at a single meadow ranged from 1 to 6 days, occasionally spanning a few weeks. We targeted marking a minimum of 30 oviposition locations per study meadow. The duration of time surveying each meadow was subject to how long it took to meet that target, which was highly dependent on weather conditions and population size. Thirty random-haphazard locations were also selected from each meadow. We would determine a starting point and pacing distance by use of random number tables. Pacing direction was determined by indiscriminately selecting a compass bearing. Random "host plants" were determined by blindly throwing a pin flag from the random-haphazard locations, hereafter called "random locations". All variables were recorded in the same way for both random and oviposition locations.

2.4. Population counts

Population counts were conducted every 5–7 days, between 10 AM and 5 PM on sunny days with low wind speeds (<5 on Beauford wind scale) and temperatures above 15 °C. We walked transect lines (~10 m apart) using a modified Pollard approach to walk the area actively used by mardon at each site. When mardon were observed, the number of butterflies was recorded and their spatial locations were recorded on a map or with GPS. Butterflies that entered from behind the surveyor were ignored. In meadows where there was overlap in the flight periods of mardon and closely related Sonora skippers (*Polites sonora*), an individual of both species was caught and viewed to acclimate the observer's eye. Thereafter, mardon skipper identification was made without capture and with the aid of 8 × 42 binoculars. We assume that the population size at each size is at least as great as the highest survey count during the 2007 season. We refer to this count as an index of minimum population size.

2.5. Habitat surveys

To capture the environmental conditions at the time of oviposition all habitat surveys were conducted within 7 days of the observed oviposition for oviposition locations, and during the meadow-specific adult flight period for the random locations. Both local and landscape variables influence butterfly oviposition behavior and larval survivorship (Schweiger et al., 2006; Davis et al., 2007; Kuussaari et al., 2007). We measured over 50 variables at each random and each oviposition location to capture possible factors that contribute to mardon reproductive ecology (Supplementary Data B). These variables included characterization of graminoid communities, oviposition plant, fine scale microhabitat, and meadow landscape.

A 1 m^2 quadrat, centered at each oviposition and random location, was utilized to capture local habitat. Each graminoid species was recorded along with its corresponding percent cover and maximum height. Litter depth, soil pH and soil moisture potential were measured as near to the oviposition location as possible without disturbing the egg. Soil variables were measured with a Kelway Soil Tester Model HB-2 (Kel Instruments Co., Inc. Wyckoff, NJ, USA). Total percent cover of vascular plants, forbs, graminoids, litter, rocks, shrubs, trees, bare ground, and cryptograms was estimated. Percent cover was estimated in 5% intervals for features with 5–100% cover. For features with less than 5% cover, we estimated cover to the nearest 1%. The tallest plant was measured and identified to species. Horizontal vegetation thickness was measured by recording the percent cover, on a meter stick position parallel with the ground, at 0.3, 0.6, and 0.9 m heights.

A 0.1 m^2 sub-plot was used to characterize the vegetation community in the immediate vicinity of oviposition or random locations. Percent cover of total graminoid and total forbs, as well as percent cover of each species of graminoid and their corresponding maximum heights were measured within the sub-plot. Graminoid species richness was included as a variable within both the quadrat and sub-plot, as well as graminoid heterogeneity and evenness indices (abundance weighted by percent cover).

Table 1
Description of 9 mardon skipper research meadows in the Gifford Pinchot National.

Meadow	Elevation (m)	Aspect	Habitat size (ha)		Total Days surveys were conducted			Minimum population size	Minimum flight period		
			Available area	Min use area	Oviposition	Habitat	Population		From	To	Impacts/management
Cave Creek	850	Flat	2	1	6	10	4	56	May 31	June 23	Past and current partial grazing, fenced, road, noxious weeds removal management
Peterson	915	Flat	4.3	1.3	3	5	3	34	June 8	June 28	Past grazing, fenced, road
Lost	975	Flat	1.5	1.1	1	5	3	15	June 18	June 29	Grazing
Flog Salvage	1190	Flat	<0.8	<0.8	3	4	3	23	June 21	June 30	Logged and seeded historically, road
Midway	1280	North	2	1.3	2	3	3	54	July 8	Aug 1	Recreation, horse watering and grazing, road, campground
Smith Butte	1295	South	0.5	0.3	1	3	2	38	July 1	July 3	Light grazing
Muddy	1340	Mixed	1.5	0.9	2	5	3	91	July 12	August 2	Hiking trail, horse back riding and grazing
7A	1430	West	0.9	0.6	2	3	3	50	July 8	August 1	Hiking trail, horse back riding and grazing, conifer encroachment management
Grapefern	1430	West	0.6	0.6	1	3	3	313	July 9	August 1	Hiking trail, horse back riding and grazing, conifer sapling removal

Oviposition plants and random “host plants” were identified to species. Graminoids often grow in bunches of several leaf blades, and occasionally more than one species is present in those bunches. If it was not clear which species was being selected by the female skipper, then the other species present in the bunch were recorded and noted as “mixed”. Oviposition plant (or bunch) length, width, maximum basal leaf height, and maximum culm height were measured. The plant density was categorized from 1 to 4 as a solitary blade, a loose structure (approximately 2–50 blades), a dense structure (50 + blades), or matted (forming a carpet like coverage) respectively. The percent of the oviposition plant that was dead (brown) was estimated. Finally, the distance to the nearest neighboring plant of the oviposition plant of the same species was measured.

Potential nectar resources were defined as any forb in bloom at the time of the survey. The number of blooms per species were counted within the 1 m^2 quadrat as well as sampled from eight 1×0.25 m plots in a 5 m radius of the survey quadrat. Number of shrubs, trees, tree saplings, and tree seedlings were counted within 10 m of the quadrat. Tree and shrub species present within 20 m of the quadrat were recorded. Nearest distance from the quadrat to the nearest forest edge and visible water source as well as distance to the nearest tree and nearest shrub were measured. Visible water source was categorized as “none”, “seasonal standing water”, “intermittent stream”, “small creek”, or “river”. Finally, the slope and aspect were recorded with regard to a 20 m radius of the oviposition and random locations.

2.6. Data analysis

We delineated available meadow habitat and mardon use areas by overlaying our spatial population data on orthophotos in ArcMap GIS. We established if oviposition and random locations form independent groups among and within meadows by conducting Discriminant Function Analyses (DFA). We first conducted a single DFA assessing the differences between both meadow and location factors (forming 18 groups – nine meadows with two location-types). We then conducted individual DFAs on a meadow by meadow basis (location-types forming two groups per meadow analysis). In the meadow specific DFAs, the percent cover and maximum heights of the respective oviposition plant species were included. Total structure coefficients, here after referred to as “loadings”, were used to determine which habitat variables contributed to discrimination between groups. Variables with the highest absolute loading values were considered the primary descriptors for each canonical axis. As we included over 50 variables per meadow in the DFAs, we considered the first five primary descriptors as the “most important” variables. We then investigated the next five primary descriptors to determine if any other variables surfaced more than once across meadows.

Discriminant Function Analyses were run with SAS statistical software using the PROC CANDISC procedure (SAS 9.1). Data were natural-log and arcsine-square root transformed (for continuous and percent cover data respectively) to achieve multivariate normality and homogeneous variances. Some of the variables were not normal, even after appropriate transformations, so we used nonparametric Mann Whitney U tests to determine significant differences between oviposition and random locations with regard to the descriptor variables. Bonferroni multiple comparisons calculated a minimum P-value of $P = 0.001$ (0.05 divided by an average of 50 variables per site).

3. Results

Oviposition, habitat, and population surveys were conducted from 31 May to 1 August, 2007. Survey meadows ranged in size from 0.6 ha to 4.3 ha, and mardon use areas ranged from 0.3 ha to 1.3 ha. Except for Grapefern and Flog Salvage, use areas were smaller than the available open meadow habitat. Minimum population sizes ranged from 15 to 313 individuals (Table 1, Supplementary Data C).

We identified nineteen oviposition plant species, including seven sedges and 12 grasses during the 2007 research season. Including *Carex multicostata, Danthonia californica, Deschampsia cespitosa, and Festuca roemeri* which were observed only in the 2006 pilot season (at meadows located in Southern Oregon), there were a total of 23 documented mardon skipper oviposition plants (Table 2). All observed oviposition species were native perennials with the exceptions of non-native perennial *Poa pratensis*, and native annual *Muhlenbergia filiformis*. The frequency of ovipositions on *M. filiformis* was low (two observations). Oviposition species *P. pratensis* and *Festuca idahoensis* were most frequently used, both with 56 oviposition observations each (Table 2). However, *F. idahoensis* was only present in the two meadows where it was used. *P. pratensis* was used for oviposition across seven meadows, and was present in all meadows except for Smith Butte (Table 2). Over

Table 2
Frequency of ovipositions per graminoid species at each of the nine research meadows in 2007[a] Species are native perennials unless otherwise noted. A = annual, NI = non-native invasive.

Oviposition plant species	Common name	7A	Cave Creek	Flog Salvage	Grape-fern	Lost	Midway	Muddy	Peterson Prairie	Smith Butte	Total
Festuca idahoensis	Idaho fescue	–	–	27	–	–	–	–	–	29	56
Poa pratensis (NI)	Kentucky bluegrass	3	8	0	2	5	23	4	11	–	56
Danthonia intermedia	Timber oatgrass	10	–	0	1	–	1	15	–	–	27
Carex inops	Long-stolen sedge	2	–	3	14	–	–	0	0	0	19
Festuca rubra	Red fescue	1	17	–	–	–	–	–	–	1	19
Carex deflexa	Short term sedge	1	–	–	–	13	2	–	–	–	16
Carex fracta	Fragile sheathed sedge	7	0	–	3	1	1	0	0	–	12
Carex praticola	Meadow sedge	0	0	–	–	0	–	–	11	–	11
Carex hoodii	Hood's sedge	–	3	–	1	2	1	–	3	–	10
Danthonia unispicata	One-spiked oatgrass	–	0	–	–	8	–	0	1	–	9
Agrostis thurberiana	Thurber bent	3	–	–	–	–	–	5	–	–	8
Stipa occidentalis	Western needlegrass	1	–	0	2	0	–	4	1	0	8
Carex halliana	Hall's sedge	0	–	–	2	–	–	–	2	–	4
Carex species					3						3
Bromus carinatus	California brome	0	–	–	1	–	1	0	0	0	2
Muhlenbergia filiformis (A)	Pullup muhly	1	–	–	–	–	–	1	–	–	2
Unknown Grass			1						1		2
Calamagrostis canadensis	Bluejoint	–	–	–	–	–	–	1	–	–	1
Carex luzulina	Woodrush sedge	1	–	–	–	–	–	–	–	–	1
Elymus elymoides	Squirreltail	0	0	0	1					0	1
Hordeum brachyantherum	Meadow barley	0	–	–	–	–	1	0	–	–	1
Unknown Sedge						1					1

0 = species present at site but not used; – = species not present at the site.
[a] In addition, ovipositions were observed on the following species in 2006 (*Carex multicostata*, manyrib sedge, *Dechampsia cespitosa*, tufted hairgrass, *Danthonia californica*, California oatgrass, and *Festuca roemeri*, Roemer's fescue).

75% of ovipositions occurred on a single species at Flog Salvage, Smith Butte, and Midway meadows, indicating graminoid preferences there. We followed 24 individual female skippers for multiple ovipositions (Supplementary Data D). Seven of these females clearly switched plant species during consecutive ovipositions; the remaining 17 selected a single species.

There was no significant separation between oviposition and random locations when the data were analyzed for discrimination between meadows and location-type collectively (18 groups including nine meadows, each with two locations), Fig. 2a. However, data grouped distinctly by meadow factors (Fig. 2b), indicating that the differences among individual meadow habitats overshadowed differences occurring within meadows. Squared canonical correlation (r^2) was 88% and 79% for the first and second discriminating axes respectively. Tree abundance was the dominant contributing variable to variation on the first axis (variable loading = −0.883), and percent slope was the dominant contributing variable on the second axis (variable loading = 0.807).

Meadow by meadow DFAs revealed strong separation between oviposition and random locations (Fig. 3). Squared canonical correlation was over 90% at all meadows except for Smith Butte (r^2 = 84%). Primary descriptors were different at each meadow (Table 3). With regard to the first five primary descriptors, variables related to graminoid cover and structure were important across all meadows. Tree variables were important at four meadows. In Flog Salvage, Muddy, Midway, and Smith Butte specific graminoid species (*F. idahoensis, D. intermedia, and P. pratensis*) were important. In these cases the respective species were the primary oviposition plants. The oviposition plant was the most dominant species in terms of ground cover in the sub-plot (77% of observations), and in the quadrat (65% of observations). Litter cover and depth at Grapefern, and soil pH and graminoid richness at Muddy were the first primary descriptors within those meadows. When we investigated the next five primary descriptors, higher graminoid species richness, relative to random locations, were important at four meadows; greater litter cover and depth appeared important at four meadows; greater vascular plant cover, lower vegetation

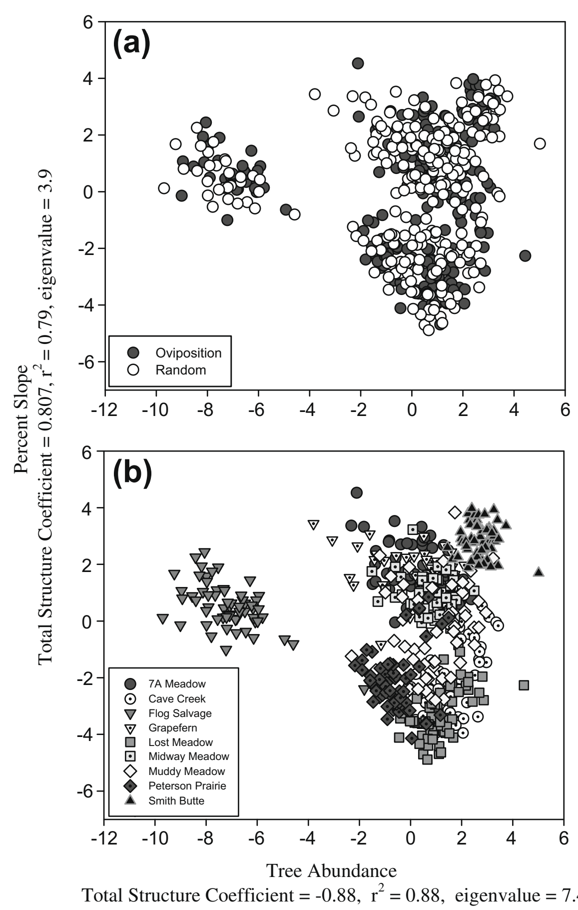

Fig. 2. Among meadow Discriminate Analysis. DFA results on n = 539 observations by meadow and location collectively, 18 groups (nine meadows two location-types each). Data symbolized by location-type (a) and by meadow (b). Squared canonical correlation = r^2.

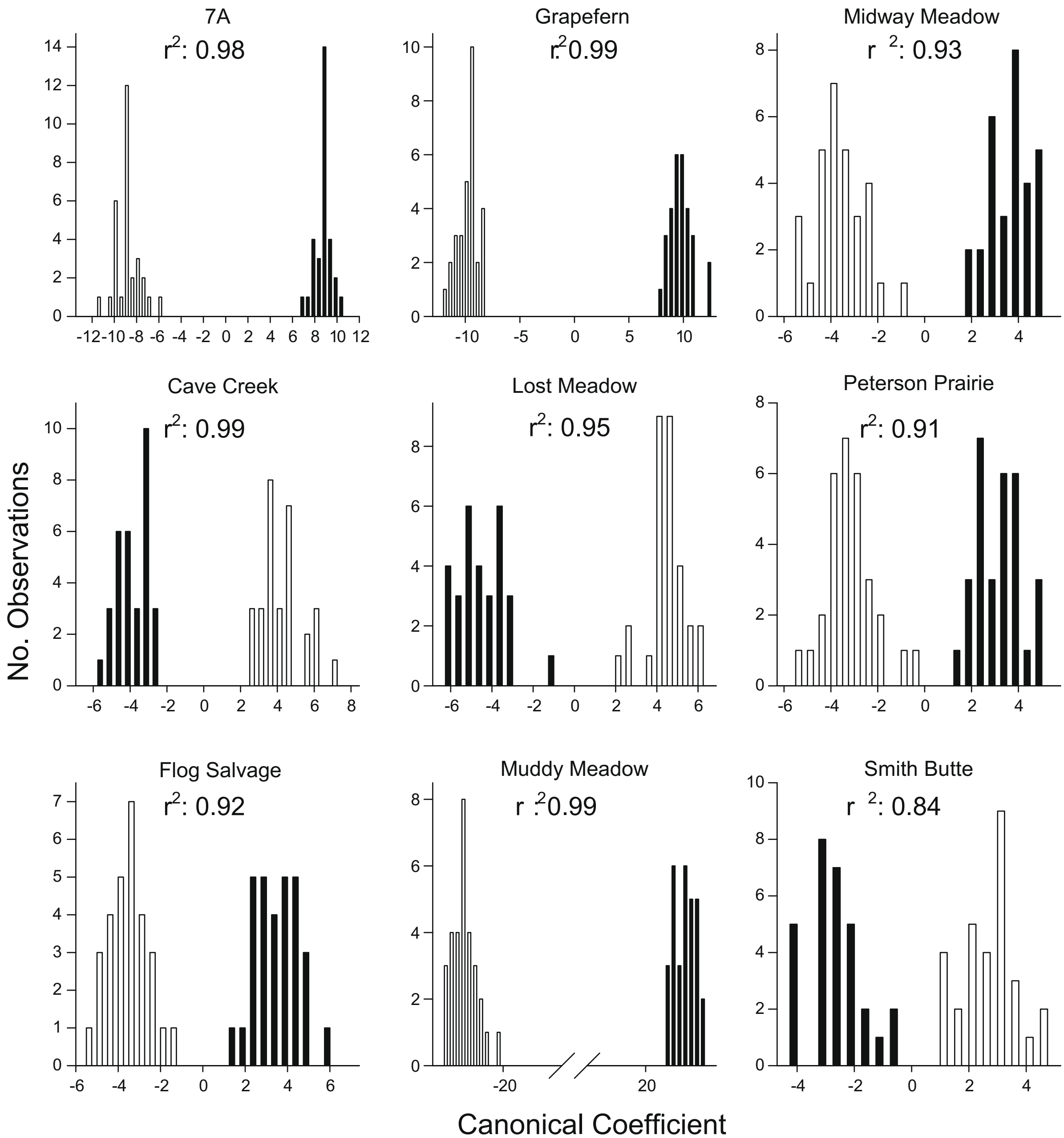

Fig. 3. Within meadow Discriminant Function Analyses. Meadow by meadow DFA grouped by location. Oviposition locations represented in black random locations in white. Percent of discriminant variation explained by variables = r^2. Variables corresponding to *X*-axes given in Table 3.

height and bare ground cover were each important at three meadows (Fig. 4, Supplementary Data E and F).

Oviposition and random locations were significantly different for all primary discriminating variables (Mann Whitney U tests $P < 0.001$). With few exceptions, all of the first five discriminating variables were significantly different (Table 3). *Poa. pratensis* cover in the quadrat was not significant at the $p = 0.05$ level in Midway meadow.

4. Discussion

Our records of 23 species of oviposition plants, in conjunction with our observations on individuals alternating host species during consecutive ovipositions, indicate that mardon skippers are generalists in terms of oviposition selection. Other generalist skippers include the Dun (*Euphyes vestries*), US federal candidate Dakota (*Hesperia dacotae*), and Illinois state threatened Ottoe (*H. ottoe*) skippers of which female oviposition and larval feeding on several graminoid species has been documented (Dana, 1997; Shephard, 2000).

There are advantages to a generalist life history strategy (Singer et al., 2004; Wee and Singer, 2007). Host plant nutrients, microclimate, parasitism and predation influence whether or not a particular plant species is used for oviposition and successfully occupied by larvae (Smallidge and Leopold, 1997; Lill et al., 2002; Singer and Bernays, 2003; Chen et al., 2004; Singer et al., 2004; Agosta, 2006; Fartmann, 2006). The ability of larvae to utilize multiple species as host plants reduces restrictions on oviposition selection allowing females to respond to multi-trophic factors (Singer and Bernays, 2003; Doak et al., 2006; Freese et al., 2006). Additionally, larvae may compensate for a poor natal habitat by switching to more favorable host plants (Hellmann, 2002; Albanese et al., 2007a).

Table 3
Top five primary discriminating variables in meadow by meadow Discriminant Function Analysis.

Meadow	Discriminatory axis variable	Variable loadings	*Location*		Unit of measure
			Oviposition	Random	
7A	Tree abundance	−0.486	8.5 ± 7.3	18 ± 10.1	count
	Graminoid cover (egg vicinity)	0.460	34.8 ± 14.0	20.5 ± 16.2	%
	Distance to visible water source[a]	0.440	89.1 ± 19.6	64.9 ± 30.0	Meters
	Oviposition plant leaf density[a]	0.439	2.2 ± 7.0	1.5 ± 0.6	Category (1–4)
	Tree canopy cover[a]	−0.433	5.5 ± 4.6	13.3 ± 11.4	%
Cave Creek[c]	Maximum plant height	0.657	38.4 ± 6.2	52.8 ± 10.8	cm
	Oviposition plant leaf density	−0.588	2.7 ± 0.7	1.8 ± 0.7	Category (1–4)
	Distance to nearest tree	0.539	1.5 ± 1.6	4.7 ± 4.5	Meters
	Festuca rubra cover (egg vicinity)	−0.474	32.2 ± 12.6	19.1 ± 18.4	%
	Tree Canopy Cover	0.455	5.4 ± 7.4	16.4 ± 17.2	%
Flog Salvage	*Festuca idahoensis cover (egg vicinity)*	0.783	34.3 ± 20.6	12.2 ± 12.2	%
	Oviposition plant footprint	0.772	212.3 ± 168.1	30.7 ± 29.1	cm^2
	Oviposition plant leaf density	0.709	2.8 ± 0.5	1.6 ± 0.7	Category (1–4)
	Graminoid cover (egg vicinity)	0.679	42.6 ± 20.1	16.5 ± 10.1	%
	Graminoid cover (quadrat)	0.614	34.7 ± 11.9	20.3 ± 8.0	%
Grapefern	Litter depth	0.670	2.1 ± 0.9	0.8 ± 0.8	cm
	Graminoid cover (quadrat)	0.608	48.9 ± 12.8	27 ± 15.5	%
	Litter cover	0.568	82.5 ± 10.9	53.8 ± 28.0	%
	Graminoid cover (egg vicinity)	0.541	50.8 ± 17.1	27.5 ± 19.2	%
	Tree abundance	−0.486	3.0 ± 3.9	16.3 ± 20.9	Count
Lost[c]	Graminoid cover (egg vicinity)	−0.600	54.7 ± 18.2	29.1 ± 19.2	%
	Graminoid cover (quadrat)	−0.540	53.2 ± 18.3	32.3 ± 16.3	%
	Vascular plant cover (quadrat)	−0.479	68.5 ± 16.7	51.3 ± 16.9	%
	Poa pratensis cover (quadrat)	−0.476	16.0 ± 9.9	8.4 ± 5.4	%
	Bare ground cover[a]	0.471	10.3 ± 6.5	28.3 ± 22.9	%
Muddy	Soil pH	−0.477	6.1 ± 0.3	6.4 ± 0.3	Scale
	Graminoid Species Richness (quadrat)[a]	0.474	6.4 ± 1.4	4.9 ± 1.5	Count
	Danthonia intermedia height (quadrat)[a]	0.467	34.5 ± 7.0	33.9 ± 8.5	cm
	Danthonia intermedia cover (quadrat)	0.441	23.7 ± 11.9	23.0 ± 21.1	%
	Agrostis thurberiana cover (quadrat)[a]	0.429	22.4 ± 26.1	11.7 ± 5.6	%
Midway	*Poa pratensis* height (quadrat)	−0.456	31.3 ± 9.1	41.1 ± 11.2	cm
	Poa pratensis cover (quadrat)[b]	0.364	28.8 ± 24.1	15.1 ± 10.8	%
	Graminoid cover (quadrat)[a]	0.354	49 ± 20.5	36.2 ± 14.6	%
	Bare ground cover[a]	−0.351	5.4 ± 6.7	15.8 ± 20.0	%
	Flower abundance (5 m radius)[a]	0.318	12.3 ± 8.9	7.7 ± 6.1	Count
Peterson Prairie	Distance To forest edge	0.520	54.2 ± 11.8	37.7 ± 17.0	Meters
	Distance To Nearest Tree	0.509	39.1 ± 12.5	23.5 ± 15.8	Meters
	Tree Canopy cover	−0.501	0.4 ± 1.1	7.3 ± 10.9	%
	Poa pratensis Cover (quadrat)	0.494	17 ± 8.8	9.8 ± 5.3	%
	Graminoid cover (quadrat)[a]	0.461	2.1 ± 0.03	2.0 ± 0.04	Scale
Smith Butte[c]	Oviposition plant leaf density	−0.694	2.2 ± 0.4	1.5 ± 0.5	Category (1–4)
	Festuca idahoensis Cover (egg vicinity)	−0.686	24.0 ± 13.9	12.2 ± 9.6	%
	Festuca idahoensis height (egg vicinity)	−0.649	25.2 ± 31.4	14.8 ± 3.3	cm
	Festuca idahoensis cover (quadrat) 1	−0.505	24.3 ± 13.7	16.4 ± 9.8	%
	Oviposition plant footprint	−0.503	76.4 ± 61.3	40.9 ± 116.0	cm^2

Total structure coefficients, means ± standard deviations for oviposition and random locations, and unit of measure given. Corresponds with Fig. 4.
[a] Mann–Whitney U test not significant after correcting for multiple comparisons.
[b] Mann–Whitney U test not significant at the 0.05 level.
[c] Class means indicate that oviposition locations are negatively correlated with the canonical function.

Pinpointing essential habitat across meadows for the mardon skipper was confounded by vast differences between meadows. The generalist nature of mardon likely enables it to persist in a variety of habitat types (Singer et al., 2004; Wee and Singer, 2007). Within meadow analyses revealed that mardon were selective with respect to meadow specific habitat components, and allowed us to generalize for patterns of habitat use across meadows (Singer and Thomas, 1996; Kuussaari et al., 2000). The variability in primary discriminators between meadows reflected the response of each mardon population to their respective habitats.

Graminoid cover was important at all meadows. Mardon oviposited on larger graminoids (greater cover) relative to random locations. A higher cover of a host plant is indicative of a larger larval food resource as well as additional structure which influences larval microhabitat (Awmack and Leather, 2002; O'Brien et al., 2004). Mardon also selected for greater amounts of total vascular plant cover and lower amounts of bare ground (at three meadows). Bare ground restricts movement of larvae and exposes them to predation, where a greater amount of vegetative cover may provide protection (Doak, 2000).

Percent cover of specific graminoid species was important at seven of nine meadows; *F. idahoensis, F. rubra, P. pratensis, A. thurberiana, and D. intermedia*. Additionally, 77% of oviposition plant species had the most amount of cover relative to other species present in the egg vicinity (sub-plot), and 65% in the local vicinity (quadrat). These results indicate that mardon may prefer some graminoid species over others. However, every plant species has an inherent structure and distinct invertebrate community (Reid and Hochuli, 2007). Strong within meadow preferences for specific species may reflect a selection for host plant architecture, chemistry, or nutrient value (Reid and Hochuli, 2007; Wee and

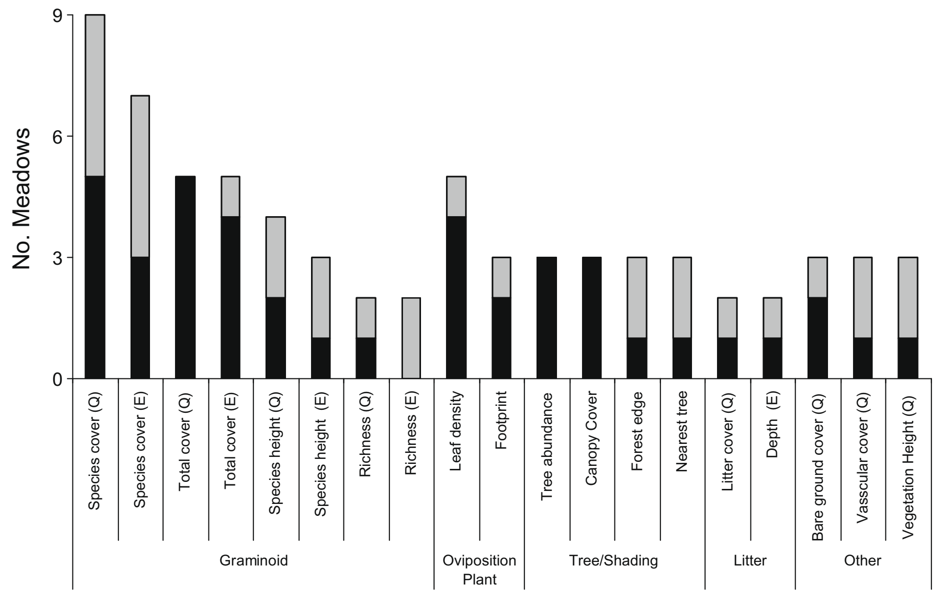

Fig. 4. Across meadow trends. Across meadow trends showing variables important to discriminating axes in Fig. 4. First five primary descriptors in black, next five primary descriptors in gray. Q = 1 m^2 quadrat and E = egg vicinity (0.1 m^2 sub-plot).

Singer, 2007; Talsma et al., 2008) rather than a species specific dependency.

Oviposition plant leaf density was important at four sites. Additionally, graminoid height was important at four meadows and maximum vegetation height is important at three meadows. This result indicates that vegetation height and graminoid structure (height, leaf size, and density) is important in the local area (quadrat), and egg vicinity (sub-plot), and is an important characteristic of the oviposition plant. Structure of the host plant and surrounding vegetation directly influences the microclimate (humidity, temperature, solar exposure) important for egg and larval development; and affords protection from predation and parasitism (Awmack and Leather, 2002; Freese et al., 2006). The silver spotted skipper (*Hesperia comma*), and Duke of Burgundy butterfly (*Hamearis lucina*), have specific structural requirements for their larval host plants (Thomas and Jones, 1993; New, 1997; Davies et al., 2005; Agosta, 2008).

At four sites graminoid species richness and litter factors appeared in the first ten primary discriminating variables. Species richness was higher in oviposition locations relative to random locations at all but one site. Insect herbivore species richness increases with plant species richness (Panzer and Schwartz,1998; Haddad et al., 2001; Reid and Hochuli, 2007) as there is a greater availability of alternate vegetative resources and structure (Haddad et al., 2001). Plant species richness may stem from greater soil nutrients, which in turn affect the diets of insect herbivores (Haddad et al., 2001; Ockinger et al., 2006).

Greater litter cover and depth likely offer protection during egg and larval life stages. The fungal pathogen (*Entomophaga maimaiga*), specific to Lepidopteran species, rarely occurs in species that inhabit litter layers during the larval state (Hajek et al., 2000). Additionally, forest dwelling Lepidoptera often pupate under litter layers on the ground (Dugdale, 1996), where they are less exposed to extreme weather conditions. During our 2006 pilot season we found mardon larvae to be active just prior to the first snow fall, which is an indication that they overwinter in this state (Beyer and Black, 2006). Therefore, litter may have an insolation benefit to skippers, protecting them from extreme temperatures during early life stages.

Data from five of nine meadows indicated that tree factors were important to oviposition selection. At these meadows tree canopy cover and tree abundance were negatively associated with oviposition locations indicating a preference for low cover and low tree abundance. Distance to forest edge and distance to nearest tree were positively associated with oviposition locations, indicating a preference for larger distances from trees. A high amount of tree and shrub cover reduces solar insolation and shading of habitat creates a cooler environment. Butterflies are physiologically limited to daylight hours when temperatures are high enough to enable butterfly mobility (Davies et al., 2005; Doak et al., 2006; Freese et al., 2006). Additionally, oviposition rates are temperature dependent (Davies et al., 2006). The fact that mardon skipper lays eggs singly places further time restrictions for selecting suitable host plants, as there is a greater time investment per egg (Courtney, 1984).

Graminoid communities change in response to forest proximity due to shading effects. Encroaching conifers alter the composition of soil creating favorable conditions for tree seedling establishment while making soils unsuitable for meadow-specific vegetation (Griffiths et al., 2005). Forest encroachment also reduces the soil microbial communities important to nitrogen fixation of meadow grasses and forbs (Griffiths et al., 2005), and likely reduces the nutrient content of larval food plants. It is likely that mardon skipper selects for more exposed oviposition locations because it is selecting for exposed open meadow habitat, and the graminoid communities that are associated with it.

5. Conservation implications

Anthropogenic land use has shaped meadow and grassland habitats globally (Crawford and Hall, 1997; Davies et al., 2005; Ockinger et al., 2006; Louy et al., 2007). Relative to other butterfly families, knowledge of the basic life history requirements of grass skippers is poor (Wahlberg et al., 2005). Our research has taken a critical step in understanding what influences oviposition behavior in mardon skipper. The most prominent finding herein is that successful conservation measures need to consider meadow specific habitat selection. Mardon are not regionally selective for specific grass species, however they do exhibit oviposition plant specificity within localities. It is clear from our work that mardon skipper selects for open habitats, high graminoid cover, and meadow-specific vegetative structure. Graminoid communities should be enhanced with regard to local preferences regarding vegetative structure and oviposition plant species. The vast differences between mardon meadows, and the variation in selectivity among meadows, indicate that there are no simple solutions to conserving this butterfly.

Our results suggest that preserving mardon skipper in montane meadow habitats will require active management to control forest encroachment as well as maintain meadow specific graminoid communities and structure important to their respective mardon populations. The removal and alteration of natural disturbance regimes (such as fire suppression) that once maintained low conifer seedling establishment rates, has led to the loss and degradation of forest-meadow ecosystems (Norman and Taylor, 2005; Coop and Givnish 2007). Mardon populations in this study are isolated by thick forest barriers, and exist in low numbers. Forest encroachment not only reduces the amount of open habitat but closes off corridors between meadows isolating remnant populations (Roland and Matter, 2007).

Conserving mardon will require striking a balance between incorporating enough disturbance to maintain meadow ecosystems and too much disturbance which can cause habitat degradation and butterfly mortality (Schultz et al., 2008). Livestock grazing adversely impacts butterfly populations by altering plant community composition (Stoner and Joern, 2004) and trampling during immobile life stages (egg, larvae, pupae) or during cool temperatures when adult movement is restricted (Warren, 1993a,b). Over-grazing can be detrimental by stripping habitat of vegetation, removing adult nectar resources, and introducing invasive weeds (Hayes and Holl, 2003). However, light-rotational grazing, mowing, and burning can maintain vegetation heights and habitat heterogeneity favorable to butterflies (Ravenscroft, 1994; Vogel et al., 2007). The silver spotted skipper has not only shown a positive response to moderate grazing, but depends on it to maintain the structure of its host plant (Thomas and Jones, 1993; Davies et al., 2005). Similarly, to achieve the benefits of restorative burning, fire treatments must be carefully prescribed to prevent local extinction (Schultz and Crone, 1998; Vogel et al., 2007).

Understanding the effects of non-native invasive species on mardon skipper is critical. All oviposition plants in this study are native species, except for *P. pratensis*, and all but one species are perennials. *Poa. pratensis* is widely used as an oviposition plant across meadows, but is generally not heavily selected for within meadows. *Poa. pratensis* has been correlated with increased abundances and invertebrate species richness in other studies (Reid and Hochuli, 2007), and may be selected for by mardon skipper because it is structurally similar to other native oviposition plants at our research meadows. Non-native grasses that do not fit the structural requirements of mardon may, however, be detrimental to populations. Invasive plants tend to out-compete native plant communities, and negatively impact grassland ecosystems by homogenizing the habitat (Kolb et al., 2002; Possley and Maschinski, 2006).

Finally, there has been considerable discussion in the butterfly conservation literature on the influence of resources and habitat quality on the persistence of rare butterfly populations (e.g. Dennis et al., 2003; Baguette and Mennechez, 2004; Turlure et al., 2009). We echo the need to focus on resource needs, in addition to structural landscape factors, to capture habitat components critical to all life stages of rare species. The method we present here, using the linkages from behavior to resource use to conservation recommendations, has broad application across multiple taxa.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.12.031.

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