OVIPOSITION SELECTION BY A RARE GRASS SKIPPER, POLITES MARDON, IN MONTANE HABITATS: ADVANCING ECOLOGICAL UNDERSTANDING FOR DEVELOPING CONSERVATION STRATEGIES

By

LONI JEAN BEYER

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE IN ENVIRONMENTAL SCIENCE

WASHINGTON STATE UNIVERSITY VANCOUVER
School of Earth and Environmental Science

MAY 2009

To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of LONI JEAN BEYER find it satisfactory and recommend that it be accepted.

____
Chair

____

____

ACKNOWLEDGEMENTS

In addition to my committee members Cheryl Schultz, Scott Black and Brian Tissot, I would like to thank my fellow lab mates Aldina Franco, Dina Roberts, Caitlin LaBar, Erica Henry, Leslie Rossmell, Cheryl Russel, Alexa Carelton for constant feedback and support. A special thanks to John Scott, Barbara Wilson, and Wayne Rolle who were integral to the identification of over sixty graminoid species. I am grateful for the dedication and diligence of field assistants Luke Frishkoff, Mike Lumio, and Betsy Scott as our team succeeded in covering expansive territory and collecting a fantastic amount of data. I am thankful for the support of Tom Kogut, Mitch Wainwright, Dave Nunnalee, and Ann Potter for sharing their knowledge of the Gifford Pinchot National Forest and expertise on *Polites mardon*. Finally, I would like to thank Kelly Van Norman, Marianne Turley, Wayne Rolle, Jim Algeria, Norm Barrett, Bruce Marcot, Darci Rivers-Pankratz, and Dana Ross, for their feedback on protocols and statistics; and the support of the Xerces Society for Invertebrate Conservation.

This project was funded by the United States Forest Service, the United States Bureau of Land Management, Washington State University Vancouver, and a WSU Robert Lane Fellowship in Environmental Studies to Loni J. Beyer.

OVIPOSITION SELECTION BY A RARE GRASS SKIPPER, POLITES MARDON, IN MONTANE HABITATS: ADVANCING ECOLOGICAL UNDERSTANDING FOR DEVELOPING CONSERVATION STRATEGIES

Abstract

by Loni Jean Beyer
Washington State University Vancouver
May 2009

Chair: Cheryl B. Schultz

The Grass skipper subfamily (Hesperiidae) includes many at risk species across the globe. Conservation efforts for these skippers are hindered by insufficient information about their basic biology. The rare Washington State endangered Mardon skipper (*Polites mardon*) is declining throughout its range. We surveyed Mardon oviposition across 9 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 0.82-0.99). 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 discriminating variables were significantly different ($p<0.001$). Conservation implications include maintaining native meadow ecosystems with sensitivity to local habitat preferences.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

Dedication

This thesis is dedicated to the Mardon skippers (*Polites mardon*), all those who have worked toward Mardon skipper conservation, and the friends who have supported them during this endeavor. Together we can accomplish great things.

1. Introduction

Lepidoptera are one of the largest, most diverse, and most endangered taxonomic groups (Liu et al. 2006; Smallidge & Leopold 1997; Thomas et al. 1994). Habitat loss and degradation has led to declines in butterfly populations across many parts of the world; including Europe, Japan, Asia, Australia, and North America (Albanese et al. 2007; Bergman 1999; Eastwood & Hughes 2003; Fox et al. 2006; Freese et al. 2006; Liu et al. 2006; Smallidge & Leopold 1997; Thomas et al. 1994). 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 & Crone 2008).

Butterfly declines often signal the degradation of the habitats with which they are associated (Oostermeijer & van Swaay 1998). Lepidoptera have a polymorphic life history, including a larval 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, or adequate insolation (Dennis et al. 2006). Larval stages may require specific plant species for forage as well as particular micro-habitat conditions (Albanese et al. 2007; Awmack & Leather 2002; Grundel et al. 1998). The dependence on so many habitat variables creates sensitivity to even small changes within the ecosystem, and many species are considered environmental indicators (Brown & Freitas 2000; Eastwood & Hughes 2003; Oostermeijer & van Swaay 1998). Rare butterflies are especially useful for monitoring unique ecosystems and are often associated with other threatened fauna (Brown & 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 (Anthes et al. 2008; Ellis 2003). The susceptibility of butterflies to environmental changes is pronounced in the larval state due to their limited mobility and restricted habitat requirements (Anthes et al. 2003; Thomas et al. 2001). Larval survivorship is largely determined by ovipositing females, as larvae generally do not travel far, if at all, from their natal locations (Awmack & Leather 2002; Bergman et al. 2004; Doak et al. 2006).

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

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, Appendix A). The Mardon skipper (*Polites mardon*, U.S. federal candidate, Washington State endangered) is a rare and declining butterfly in the Pacific Northwest of the United States of America. The basic biology of this species is poorly understood (Beyer & Black 2006; Black & Vaughan 2005; Potter et al. 2002). In the U.S. there are three federally listed skippers, including the Carson wandering (*Pseudocopaeodes eunus obscurus*, endangered) Laguna Mountains (*Pyrgus ruralis lagunae*, endangered), and Pawnee Montane (*Hesperia leonardus montana*, threatened). There are two U.S. federal candidate species the Dakota skipper (*Hesperia dacotae*, Canada endangered) and the Mardon skipper (*Polites mardon*, Washington State endangered), as well as several other state-listed skippers. To date, limited information on the habitat requirements inhibits management efforts for all of these butterflies (Beyer & Black 2006; Potter et al. 2002; USFWS 1997, 1998, 2005; Warren et al. 2008). Grass-feeding butterflies, in general, have highly complex resource requirements and very little is known about how they utilize their habitats (Dennis et al. 2006).

Mardon skippers occur across a range of habitat types which vary from expansive 5,000 ha of low elevation prairies to isolated high elevation forested meadows that ranging in size from 0.5 to 5 ha (Beyer & Black 2006; Potter et al. 2002). However, the aspects of these habitats critical to Mardon persistence are entirely unknown. In 2006 we conducted an exploratory study with the Xerces

Society for Invertebrate Conservation. In this study we investigated oviposition behavior of the Mardon skipper. Eleven species of grasses and sedges were observed as oviposition plants (Beyer & Black 2006; Potter et al. 2002). What was once considered the primary larval host plant, *Festuca* species, was absent in many of the known sites. This result completely changed former perceptions about Mardon habitat (Black & Vaughan 2005), and further stimulated inquiry as to what makes this butterfly rare.

In this study we investigate Mardon skipper site utilization across a variety of montane habitat types to determine what aspects are critical to population recovery. The primary goal of this study is to determine what influences Mardon skipper oviposition location selection, thereby understanding larval habitat requirements. 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. The answers to these questions are essential to understanding Mardon habitat requirements. This information is the first step in developing a Mardon skipper conservation plan and serves as baseline ecological information from which future research can be founded. Additionally, the information herein contributes to the conservation of other rare and endangered skippers by advancing knowledge of the understudied grass skipper family.

2. Methods

2.1 Study Species & Habitat

The Mardon skipper belongs to the grass skipper subfamily, *Hesperiinae*. Skippers of this family forage exclusively on graminoids as larvae, and are dependent on meadow-grassland habitats. Female Mardon deposit eggs singly while perched. Distributions of extant Mardon skipper populations are disjunct; ranging from the grasslands of northwest California to the Puget Tough 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 (Black & Vaughan 2005; Potter et al. 2002).

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

2.2 Meadows

Since 2000, thirty-nine Mardon skipper meadows have been documented in the Gifford Pinchot National Forest. These meadows range from 800 to 1700 meters 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 determine the commonality between them. Twenty-one 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) during the 2007 season. The nine remaining meadows were included in this study (Figure 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; various strategies to control houndstounge (*Cynoglossum officinale*) and Canada thistle (*Circium arvense*) have been implemented since 2004, including weed-whacking and hand removal. Approximately 80% of the Cave Creek meadow has been fenced to reduce cattle grazing impacts and the spread of invasive weeds. Historically, Peterson Prairie was fenced to contain livestock, and grazing impacts were heavy. In recent years all grazing and storing of livestock on Peterson Prairie has ceased. Flog Salvage was heavily logged historically, 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.

Microhabitat temperature and humidity affect larval survivorship, and may influence oviposition behaviors (Kuhrt et al. 2006; Schweiger et al. 2006). We distributed four to five iButton data-loggers, model DS1923-F5, throughout six of the study meadows to capture ground level temperature and relative humidity. Loggers recorded data every four hours for one year (Appendix G).

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° Celsius. Oviposition observations began when any individual female butterflies were observed flying. A random point within the meadow was located, using random number tables, from which a transect line was walked until a female was encountered. Observations were made with the aid of 8x42 binoculars. If the female being observed was not indicating oviposition behavior after 10 minutes the surveyor terminated the observation. If oviposition was still suspected to occur then the observation continued for an additional 10 minutes. If no oviposition had occurred at the end of 20 minutes 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 laying behaviors. 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 one to six 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 dependant 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 would be 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° Celsius. We walked transect lines spaced approximately 10 meters apart. 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 observers eye. Thereafter, Mardon skipper identification was made without capture and with the aid of 8x42 binoculars.

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 (Davis et al. 2007; Kuussaari et al. 2007; Schweiger et al. 2006). We measured over 50 variables at each random and each oviposition location to capture as many possible factors that may contribute to Mardon reproductive ecology (Appendix B). These variables included characterization of graminoid communities, the oviposition plant, the fine scale microhabitat, and the meadow landscape.

A one m^2 quadrat, centered at each oviposition and random location, was utilized to capture the 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. Total percent cover of vascular plants, forbs, graminoids, litter, rocks, shrubs, trees, bare ground, and cryptograms was estimated. 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 meter heights.

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

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 x ¼ m plots in a 5m radius of the survey quadrat. The 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. The nearest distance from the quadrat to the nearest forest edge and visible water source as well as the distance to the nearest tree and nearest shrub were measured. The type of 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. 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 range in size from 0.6 ha to 4.3 ha, and Mardon use areas range from 0.3 ha to 1.3 ha. Except for Grapefern and Flog Salvage, use areas are smaller than the available open meadow habitat. Minimum population sizes range from 15 to 313 individuals (Table 1, Appendix C).

We identified nineteen oviposition plant species, including seven sedges and 12 grasses during the 2007 research season. When including *Carex multicostata, Danthonia californica, Deschampsia cespitosa, and Festuca roemeri* observed only in the 2006 pilot season (at meadows located in Southern Oregon), there is a total of 23 documented Mardon skipper oviposition plants (Table 2). All observed oviposition species are native perennials with the exceptions of nonnative perennial *Poa pratensis*, and native annual *Muhlenbergia filiformis*. The frequency of ovipositions on *M. filiformis* is low (two observations). Oviposition species *P. pratensis* and *Festuca idahoensis* are most frequently used, both with 56 oviposition observations each (Table 3). However, *F. idahoensis* was only present in the two meadows where it was used. *Poa pratensis* is used for oviposition across seven meadows, and was present in all meadows except for Smith Butte (Table 3). Over 75% of ovipositions occur 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 (Appendix D). Seven of these females clearly switched plant species during consecutive ovipositions; the remaining seventeen selected a single species.

There is no significant separation between oviposition and random locations when the data are analyzed for discrimination between meadows and location-type collectively (18 groups including nine meadows, each with two locations), Figure 3a. However, data group distinctly by meadow factors (Figure 3b), indicating that the differences among individual meadow habitats overshadow differences occurring within meadows. Squared canonical correlation (r^2) is 88% and 79% for the first and second discriminating axes respectively. Tree abundance is the dominant contributing variable to variation on the first axis (variable loading = -0.883), and percent slope is the dominant contributing variable on the second axis (variable loading = 0.807).

The meadow by meadow DFAs reveal strong separation between oviposition and random locations (Figure 4). Squared canonical correlation is over 90% at all meadows except for Smith Butte (r^2 = 84%). Primary descriptors are different at each meadow (Table 4). With regard to the first five primary descriptors, variables related to graminoid cover and structure are important across all meadows. Tree variables are important at four meadows. In Flog Salvage, Muddy, Midway, and Smith Butte specific graminoid species (*F. idahoensis, D. intermedia, and P. pratensis*) are important. In these cases the respective species are the primary oviposition plants (Table 3). The oviposition plant is 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 are the first primary descriptors within those meadows. When we investigate the next five primary descriptors higher graminoid species richness, relative to random locations, are important at four meadows; greater litter cover and depth appear important at four meadows; greater vascular plant cover, lower vegetation height and bare ground cover are each important at three meadows (Figure 5, Appendix E and F).

Oviposition and random locations are significantly different for all primary discriminating variables (Mann Whitney U tests $P<0.001$). With few exceptions, all of the first 5 discriminating variables are significantly different (Table 5). *Poa pratensis* cover in the quadrat is 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*), U.S. federal candidate Dakota (*Hesperia dacotae*), and Illinois state threatened Ottoe (*Hesperia 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 & Singer 2007). Host plant nutrients, microclimate, parasitism and predation all influence whether or not a particular plant species is used for oviposition and successfully occupied by larvae (Agosta 2006; Chen et al. 2004; Fartmann 2006; Lill et al. 2002; Singer & Bernays 2003; Singer et al. 2004; Smallidge & Leopold 1997). The ability of larvae to utilize multiple species as host plants reduces restrictions on oviposition selection allowing females to respond to multi-trophic factors (Doak et al. 2006; Freese et al. 2006; Singer & Bernays 2003). Additionally, larvae may compensate for a poor natal habitat by switching to more favorable host plants (Albanese et al. 2007; Hellmann 2002).

Pinpointing essential habitat across meadows for the Mardon skipper is confounded by the vast differences between meadows. The generalist nature of Mardon likely enables the species to persist in a variety habitat types (Singer et al. 2004; Wee & Singer 2007). Within-meadow analyses reveal that Mardon are selective with respect to meadow specific habitat components, and allow us to generalize for patterns of habitat use across meadows (Kuussaari et al. 2000; Singer & Thomas 1996). The variability in primary discriminators between meadows reflects the response of each Mardon population to their respective habitats.

Graminoid cover is 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 (Awmack & Leather 2002; O'Brien et al. 2004). Mardon also select for a greater amount of total vascular plant cover and a lower amount 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).

The percent cover of specific graminoid species is important at seven of the 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 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 & Hochuli 2007). Strong within meadow preferences for specific species may reflect a selection for host plant architecture, chemistry, or nutrient value (Reid & Hochuli 2007; Talsma et al. 2008; Wee & Singer 2007) rather than a species specific dependency.

Oviposition plant leaf density is important at 7A, Cave Creek, Flog Salvage and Smith Butte meadows. Additionally, graminoid height is important at four meadows and maximum vegetation height is important at three meadows. This result enforces that vegetation height and graminoid structure (height, leaf size, & density) is important in the local area (quadrat), and egg vicinity (sub-plot), and is an important characteristic of the oviposition plant. The structure of the host plant and the surrounding vegetation directly influences the microclimate (humidity, temperature, solar exposure) important for egg and larval development; and affords protection from predation and parasitism (Awmack & 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 (Agosta 2008; Davies et al. 2005; New 1997; Thomas & Jones 1993).

At four sites graminoid species richness and litter factors appear in the first ten primary discriminating variables. Species richness is higher in oviposition locations relative to random locations at all sites except Peterson Prairie. Insect herbivore species richness increases with plant species richness (Haddad et al. 2001; Panzer & Schwartz 1998; Reid & Hochuli 2007) as there is a greater availability of alternate vegetative resources and structure (Haddad et al. 2001). Plant species richness is also indicative of 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 & Black 2006). Therefore, litter may have an insolation benefit to skippers, protecting them from extreme temperatures during early life stages.

The data from five of nine meadows indicate that tree factors are important to oviposition selection. At these meadows tree canopy cover and tree abundance are negatively associated with oviposition locations indicating a preference for low cover and low tree abundance. Distance to forest edge and distance to nearest tree are 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. As butterflies are ectotherms, they 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, egg-laying rates are temperature dependent (Davies et al. 2006). The fact that Mardon skippers lay 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 skippers select for more exposed oviposition locations because they are selecting for exposed open meadow habitat, and the graminoid communities that are associated with it.

4.1 Conservation implications

Our results suggest that preserving Mardon skippers 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 the 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 (Coop & Givnish 2007; Norman & Taylor 2005). Forest encroachment not only reduces the amount of open habitat but closes off corridors between meadows reducing butterfly dispersal (Roland & Matter 2007).

All of the Mardon populations in this study are isolated by thick forest barriers, and exist in low numbers. A better understanding of the feasibility and the effects of reconnecting neighboring Mardon populations that have been isolated by forest encroachment is warranted (Bergman 1999; Dennis et al. 2006). Careful consideration should be given to the genetic and behavioral implications of local habitat preferences (Kuussaari et al. 2000; Moreau et al. 2008) as Mardon have displayed meadow specific selectivity in our research.

There is a fine balance between incorporating enough disturbance to maintain meadow ecosystems and too much disturbance causing habitat degradation and butterfly mortality (Schultz et al. 2008). Livestock grazing adversely impacts butterfly populations by altering plant community composition (Stoner & 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 & 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 (Davies et al. 2005; Thomas & Jones 1993). Similarly, to achieve the benefits of restorative burning, fire treatments must be carefully prescribed to prevent local extinction (Schultz & Crone 1998; Vogel et al. 2007).

Understanding the effects of non-native invasive species on Mardon skippers is critical. All oviposition plants in this study are native species, except for *P. pratensis*, and all but one species are perennials. When present in meadows *F. idahoensis* is clearly preferred over other species, which supports former conceptions about the importance of *Festuca* grasses to this species (Black & Vaughan 2005; Potter et al. 2002). *Poa pratensis* is the most widely used oviposition plant across meadows, but is generally not heavily selected for within meadows (Table 4). *Poa pratensis* has been correlated with increased abundances and invertebrate species richness in other studies (Reid & Hochuli 2007), and may be selected for by skippers because it is structurally similar to other native oviposition plants at our research meadows. Non-native grasses that do not fit the structural and nutritive requirements of Mardon may, however, be detrimental to populations. Invasive plants tend to out-compete native communities, and negatively impact grassland ecosystems by homogenizing the habitat (Kolb et al. 2002; Possley & Maschinski 2006).

Continued research into larval preference and larval survivorship is essential to understand host plant characteristics vital to larval Mardon skippers. Our results indicate that graminoid abundance and architecture are key discriminators for oviposition selection. A more extensive and refined look into the characteristics of oviposition plants and surrounding vegetation is warranted. Understanding adult habitat use, movement within and dispersal from habitat patches is also essential to developing effective conservation strategies (Kuefler & Haddad 2006; Ries & Debinski 2001; Schtickzelle et al. 2007; Schultz & Crone 2008; Turchin et al. 1991).

Anthropogenic land use has shaped meadow and grassland habitats globally (Crawford & Hall 1997; Davies et al. 2005; Louy et al. 2007; Ockinger et al. 2006). Relative to all other butterfly families, knowledge of the basic life history requirements of grass skippers is poor (Wahlberg et al. 2005). To curb skipper declines, knowledge about their biology must be expanded. Our research has taken the first step in understanding what influences oviposition behavior of the Mardon skipper. It is clear from our work that Mardon skippers select for open habitats, and specific vegetative structure. Though Mardon are not regionally selective for specific grass species, they do exhibit oviposition plant specificity within localities. The vast differences between Mardon meadows, and the variation in selectivity among meadows, indicate that there are no simple solutions to conserving this butterfly. A more complete understanding of Mardon biology and resource use across the habitats of extant populations is necessary before broad and regional generalizations can be reliably made.

REFERENCES

Agosta, S. J. 2006. On ecological fitting, plant-insect associations, herbivore host shifts, and host plant selection. Oikos **114**:556-564.

Agosta, S. J. 2008. Fitness consequences of host use in the field: temporal variation in performance and a life history tradeoff in the moth *Rothschildia lebeau* (Saturniidae). Oecologia **157**:69-82.

Albanese, G., P. Vickery, and P. Sievert. 2007a. Microhabitat use by larvae and females of a rare barrens butterfly, frosted elfin (*Callophrys irus*). Journal of Insect Conservation.

Albanese, G., P. D. Vickery, and P. R. Sievert. 2007b. Habitat characteristics of adult frosted elfins (*Callophrys irus*) in sandplain communities of southeastern Massachusetts, USA. Biological Conservation **136**:53-64.

Anthes, N., T. Fartmann, and G. Hermann. 2008. The Duke of Burgundy butterfly and its dukedom: larval niche variation in *Hamearis lucina* across Central Europe. Journal of Insect Conservation **12**:3-14.

Anthes, N., T. Fartmann, G. Hermann, and G. Kaule. 2003. Combining larval habitat quality and metapopulation structure-the key for successful management of pre-alpine *Euphydryas aurina* colonies. Journal of Insect Conservation **7**:175-185.

Awmack, C. S., and S. R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. Annual Review of Entomology **47**:817-844.

Bergman, K. O. 1999. Habitat utilization by *Lopinga achine* (Nymphalidae : Satyrinae) larvae and ovipositing females: implications for conservation. Biological Conservation **88**:69-74.

Bergman, K. O., J. Askling, O. Ekberg, H. Ignell, H. Wahlman, and P. Milberg. 2004. Landscape effects on butterfly assemblages in an agricultural region. Ecography **27**:619-628.

Brown, K. S., and A. V. L. Freitas. 2000. Atlantic forest butterflies: Indicators for landscape conservation. Biotropica **32**:934-956.

Calabrese, J. M., L. Ries, S. F. Matter, D. M. Debinski, J. N. Auckland, J. Roland, and W. F. Fagan. 2008. Reproductive asynchrony in natural butterfly populations and its consequences for female matelessness. Journal of Animal Ecology **77**:746-756.

Chen, L. L., and Z. S. Lin. 2008. The effect of habitat destruction on metapopulations with the Allee-like effect: A study case of Yancheng in Jiangsu Province, China. Ecological Modelling **213**:356-364.

Chen, Y. Z., L. Lin, C. W. Wang, C. C. Yeh, and S. Y. Hwang. 2004. Response of two *Pieris* (Lepidoptera : Pieridae) species to fertilization of a host plant. Zoological Studies **43**:778-786.

Courtney, S. P. 1984. The evolution of egg elustering by butterflies and other insects. The American Naturalist **123**:276-281.

Davies, Z. G., R. J. Wilson, T. M. Brereton, and C. D. Thomas. 2005. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. Biological Conservation **124**:189-198.

Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. Journal of Animal Ecology **75**:247-256.

Davis, J. D., D. M. Debinski, and B. J. Danielson. 2007. Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. Landscape Ecology **22**:1341-1354.

Dennis, R. L. H., T. G. Shreeve, and H. Van Dyck. 2006. Habitats and resources: The need for a resource-based definition to conserve butterflies. Biodiversity and Conservation **15**:1943-1966.

Doak, P. 2000. Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. Ecology **81**:1828-1841.

Doak, P., P. Kareiva, and J. Kingsolver. 2006. Fitness consequences of choosy oviposition for a time-limited butterfly. Ecology **87**:395-408.

Dugdale, J. S. 1996. Natural history and identification of litter-feeding Lepidoptera larvae (Insecta) in beech forests, Orongorongo Valley, New Zealand, with especial reference to the diet of mice (*Mus musculus*). Journal of the Royal Society of New Zealand **26**:251-274.

Eastwood, R., and J. M. Hughes. 2003. Molecular phylogeny and evolutionary biology of *Acrodipsas* (Lepidoptera : Lycaenidae). Molecular Phylogenetics and Evolution **27**:93-102.

Ellis, S. 2003. Habitat quality and management for the northern brown argus butterfly *Aricia artaxerxes* (Lepidoptera : Lycaenidae) in North East England. Biological Conservation **113**:285-294.

Fartmann, T. 2006. Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany. Annales Zoologici Fennici **43**:335-347.

Fownes, S., and J. Roland. 2002. Effects of meadow suitability on female behaviour in the alpine butterfly *Parnassius smintheus*. Ecological Entomology **27**:457-466.

Fox, R., T. B. Asher, D. Roy, and M. Warren. 2006. The state of butterflies in Britain and Ireland. J Insect Conserv.

Fred, M. S., R. B. O'Hara, and J. E. Brommer. 2006. Consequences of the spatial configuration of resources for the distribution and dynamics of the endangered *Parnassius apollo* butterfly. Biological Conservation **130**:183-192.

Freese, A., J. Benes, R. Boz, O. Cizek, M. Dolek, A. Geyer, P. Gros, M. Konvicka, A. Liegl, and C. Stettmer. 2006. Habitat use of the endangered butterfly *Euphydryas maturna* and forestry in Central Europe. Animal Conservation **9**:388-397.

Griffiths, R., M. Madritch, and A. Swanson. 2005. Conifer invasion of forest meadows transforms soil characteristics in the Pacific Northwest. Forest Ecology and Management **208**:347-358.

Grundel, R., and N. B. Pavlovic. 2007. Resource availability, matrix quality, microclimate, and spatial pattern as predictors of patch use by the Karner blue butterfly. Biological Conservation **135**:135-144.
Grundel, R., N. B. Pavlovic, and C. L. Sulzman. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation **85**:47-53.
Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. H. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: A field experiment. American Naturalist **158**:17-35.
Hajek, A. E., L. Butler, J. K. Liebherr, and M. H. Wheeler. 2000. Risk of infection by the fungal pathogen *Entomophaga maimaiga* among Lepidoptera on the forest floor. Environmental Entomology **29**:645-650.
Hayes, G. F., and K. D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. Conservation Biology **17**:1694-1702.
Hellmann, J. 2002. The effect of an environmental change on mobile butterfly larvae and nutritional quality of their hosts. Journal of Animal Ecology **71**:925-936.
Kolb, A., P. Alpert, D. Enters, and C. Holzapfel. 2002. Patterns of invasion within a grassland community. Journal of Ecology **90**:871-881.
Kuefler, D., and N. M. Haddad. 2006. Local versus landscape determinants of butterfly movement behaviors. Ecography **29**:549-560.
Kuhrt, U., J. Samietz, and S. Dorn. 2006. Thermal response in adult codling moth. Physiological Entomology **31**:80-88.
Kuussaari, M., I. Saccheri, M. Camara, and I. Hanski. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. OIKOS **82**:384-392.
Kuussaari, M., M. Singer, and I. Hanski. 2000. Local specialization and landscape-level influence on host use in an herbivorous insect. Ecology **81**:2177-2187.
Leung, Y., and J. L. Marion. 2000. Recreation impacts and management in wilderness: a state of-knowledge review. . USDA Forest Service Proceedings 25.
Lill, J. T., R. J. Marquis, and R. E. Ricklefs. 2002. Host plants influence parasitism of forest caterpillars. Nature **417**:170-173.
Liu, W. H., Y. F. Wang, and R. M. Xu. 2006. Habitat utilization by ovipositing females and larvae of the Marsh fritillary (*Euphydryas aurinia*) in a mosaic of meadows and croplands. Journal of Insect Conservation **10**:351-360.
Mizumoto, M., and F. Nakasuji. 2007. Egg size manipulation in the migrant skipper, *Parnara guttata guttata* (Lepidoptera : Hesperiidae), in response to different host plants. Population Ecology **49**:135-140.
Moreau, J., J. Rahme, B. Benrey, and D. Thiery. 2008. Larval host plant origin modifies the adult oviposition preference of the female European grapevine moth *Lobesia botrana*. Naturwissenschaften **95**:317-324.
Myers, J. H. 1985. Effect of physiological condition of the host plant on the ovipositional choice of the Cabbage white butterfly, *Pieris rapae*. Journal of Animal Ecology **54**:193-204.

New, T. R., editor. 1997. Butterfly Conservation. Oxford University Press Australia, Melbourne.
Norman, S. P., and A. H. Taylor. 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. Forest Ecology and Management **215**:51-68.
Noss, R. F., E. T. L. III, and J. M. Scott 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. National Biological Service, Washington, D. C.
O'Brien, D. M., C. L. Boggs, and M. L. Fogel. 2004. Making eggs from nectar: the role of life history and dietary carbon turnover in butterfly reproductive resource allocation. Oikos **105**:279-291.
Ockinger, E., O. Hammarstedt, S. G. Nilsson, and H. K. Smith. 2006. The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. Biological Conservation **128**:564-573.
Oostermeijer, J. G. B., and C. A. M. van Swaay. 1998. The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. Biological Conservation **86**:271-280.
Panzer, R., and M. W. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. Conservation Biology **12**:693-702.
Portugal, A. H. A., and J. R. Trigo. 2005. Similarity of cuticular lipids between a caterpillar and its host plant: A way to make prey undetectable for predatory ants? Journal of Chemical Ecology **31**:2551-2561.
Possley, J., and J. Maschinski. 2006. Competitive effects of the invasive grass *Rhynchelytrum repens* (Willd.) CE Hubb. on pine rockland vegetation. Natural Areas Journal **26**:391-395.
Ravenscroft, N. O. M. 1994. The Ecology of the Chequered skipper butterfly *Carterocephalus palaemon* in Scotland .1. Microhabitat. Journal of Applied Ecology **31**:613-622.
Reid, A. M., and D. F. Hochuli. 2007. Grassland invertebrate assemblages in managed landscapes: Effect of host plant and microhabitat architecture. Austral Ecology **32**:708-718.
Ries, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. Journal of Animal Ecology **70**:840-852.
Roland, J., and S. F. Matter. 2007. Encroaching forests decouple alpine butterfly population dynamics. Proceedings of the National Academy of Sciences **104**:13702-13704.
Schtickzelle, N., C. Turlure, and M. Baguette. 2007. Grazing management impacts on the viability of the threatened bog fritillary butterfly *Proclossiana eunomia*. Biological Conservation **136**:651-660.
Schultz, C. B., and E. E. Crone. 1998. Burning prairie to restore butterfly habitat: A modeling approach to management tradeoffs for the Fender's blue. Restoration Ecology **6**:244-252.
Schultz, C. B., and E. E. Crone. 2008. Note: Using ecological theory to advance butterfly conservation. Israel Journal of Ecology & Evolution **54**:63-68.

Schweiger, O., C. F. Dormann, D. Bailey, and M. Frenzel. 2006. Occurrence pattern of *Pararge aegeria* (Lepidoptera : Nymphalidae) with respect to local habitat suitability, climate and landscape structure. Landscape Ecology **21**:989-1001.

Singer, M. C., and C. D. Thomas. 1996. Evolutionary responses of a butterfly metapopulation to human- and climate-caused environmental variation. American Naturalist **148**:S9-S39.

Singer, M. S., and E. A. Bernays. 2003. Understanding omnivory needs a behavioral perspective. Ecology **84**:2532-2537.

Singer, M. S., D. Rodrigues, J. O. Stireman, and Y. Carriere. 2004. Roles of food quality and enemy-free space in host use by a generalist insect herbivore. Ecology **85**:2747-2753.

Smallidge, P. J., and D. J. Leopold. 1997. Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated landscapes. Landscape and Urban Planning **38**:259-280.

Stoner, K. J. L., and A. Joern. 2004. Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. Ecological Applications **14**:1306-1320.

Stuart, B. W. 1999. Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conservation Biology **13**:1476-1486.

Talsma, J. H. R., A. Biere, J. A. Harvey, and S. van Nouhuys. 2008. Oviposition cues for a specialist butterfly-plant chemistry and size. Journal of Chemical Ecology **34**:1202-1212.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. Nature **411**:577-581.

Thomas, C. D., and T. M. Jones. 1993. Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges- lessons for conservation in a fragmented landscape. Journal of Animal Ecology **62**:472-481.

Thomas, J. A., M. G. Morris, and C. Hambler. 1994. Patterns, mechanisms, and rates of extinction among invertebrates in the United-Kingdom. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **344**:47-54.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14**:18-30.

Turchin, P., F. J. Odendaal, and M. D. Rausher. 1991. Quantifying insect movement in the field. Environmental Entomology **20**:955-963.

Vogel, J. A., D. M. Debinski, R. R. Koford, and J. R. Miller. 2007. Butterfly responses to prairie restoration through fire and grazing. Biological Conservation **140**:78-90.

Wallisdevries, M. F., and C. A. M. Van Swaay. 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. Global Change Biology **12**:1620-1626.

Warren, M. S. 1993a. A review of butterfly conservation in Central Southern Britain .1. Protection, evaluation and extinction on prime sites. Biological Conservation **64**:25-35.

Warren, M. S. 1993b. A review of butterfly conservation in Central Southern Britain .2. Site management and habitat selection of key species. Biological Conservation **64**:37-49.

Wee, B., and M. C. Singer. 2007. Variation among individual butterflies along a generalist-specialist axis: no support for the 'neural constraint' hypothesis. Ecological Entomology **32**:257-261.

Table 1: Meadow Descriptions

Description of 9 Mardon skipper research meadows in the Gifford Pinchot National Forest, Washington State. All meadows may be exposed to elk grazing.

			Habitat Size (ha)		Total Days Surveys were Conducted				Minimum Flight Period		
Meadow	Elevation (m)	Aspect	Available Area	Min Use Area	Oviposition	Habitat	Population	Population Size	From	To	Impacts/Management
Cave Creek	850	Flat	2	1	6	10	4	56	May 31	June 23	Past & 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 & 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	Aug 2	Hiking trail, Horse back riding & grazing
7A	1430	West	0.9	0.6	2	3	3	50	July 8	Aug 1	Hiking trail, Horse back riding & grazing, Conifer encroachment management
Grapefern	1430	West	0.6	0.6	1	3	3	313	July 9	Aug 1	Hiking trail, Horse back riding & grazing, Conifer sapling removal

Table 2: Oviposition Plant Species

Observed oviposition plant species in the 2007 research and 2006 pilot seasons. Species are native perennials unless otherwise noted. A=annual, NI=non-native invasive, 2006 = only observed in the pilot study.

Species	Common Name	Alternate names
Sedges		
Carex inops	Long-stolon Sedge	*C. pensylvanica*
Carex deflexa	Short Stem Sedge	*C. brevicaulis, C. rossii*
Carex luzulina	Woodrush Sedge	
Carex halliana	Hall's Sedge	
Carex hoodii	Hood's Sedge	
Carex fracta	Fragile Sheathed Sedge	
Carex multicostata 2006	Manyrib Sedge	
Carex praticola	Meadow Sedge	
Grasses		
Agrostis thurberiana	Thurber Bent	*A. humilis, Podagrostis thurberiana*
Bromus carinatus	California Brome	*B. marginatus*
Calamagrostis canadensis	Bluejoint	
Deschampsia cespitosa 2006	Tufted Hairgrass	
Danthonia intermedia	Timber Oatgrass	*Danthonia canadensis*
Danthonia californica 2006	California Oatgrass	*D. americana*
Danthonia unispicata	One-spike Oatgrass	
Festuca idahoensis	Idaho Fescue	
Festuca rubra	Red Fescue	
Festuca roemeri 2006	Roemer's Fescue	
Hordeum brachyantherum	Meadow Barley	
Muhlenbergia filiformis A	Pullup Muhly	*M. idahoensis, M. simplex*
Poa pratensis NI	Kentucky Bluegrass	
Elymus elymoides	Squirreltail	*Sitanion hystrix*
Stipa occidentalis	Western Needlegrass	*Achnatherum occidentalis*

Table 3: Oviposition Frequency By Plant Species

The frequency of ovipositions per graminoid species at each of the 9 research meadows in 2007.

Oviposition Plant Species	7A	Cave Creek	Flog Salvage	Grapefern	Lost	Midway	Muddy	Peterson Prairie	Smith Butte	Total
Festuca idahoensis			27						29	56
Poa pratensis	3	8	-	2	5	23	4	11		56
Danthonia intermedia	10		-	1		1	15			27
Carex inops	2		3	14			-	-	-	19
Festuca rubra	1	17							1	19
Carex deflexa	1				13	2				16
Carex fracta	7	-		3	1	1	-	-		12
Carex praticola	-	-			-			11		11
Carex hoodii		3		1	2	1		3		10
Danthonia unispicata		-			8		-	1		9
Agrostis thurberiana	3						5			8
Stipa occidentalis	1		-	2	-		4	1	-	8
Carex halliana	-			2			-	2		4
Carex species				3						3
Bromus carinatus	-			1		1	-	-	-	2
Muhlenbergia filiformis	1						1			2
Unknown Grass		1					-	1		2
Calamagrostis canadensis							1			1
Carex luzulina	1									1
Elymus elymoides	-	-	-	1					-	1
Hordeum brachyantherum	-					1	-			1
Unknown Sedge					1					1

\- Species present at site but not used for oviposition

Table 4: Within Meadow Primary Descriptors

Top 5 primary discriminating variables in meadow by meadow Discriminant Function Analysis. Total structure coefficients, means ± standard deviations for oviposition and random locations, and unit of measure given. Corresponds with Figure 4.

Meadow	Discriminatory Axis Variable	Variable Loadings	Location: Oviposition	Location: Random	Unit of Measure
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[1]	0.440	89.1 ± 19.6	64.9 ± 30.0	meters
	Oviposition Plant Leaf Density[1]	0.439	2.2 ± 7.0	1.5 ± 0.6	category (1-4)
	Tree Canopy Cover [1]	-0.433	5.5 ± 4.6	13.3 ± 11.4	%
Cave Creek[3]	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 [3]	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 [1]	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)[1]	0.474	6.4 ± 1.4	4.9 ± 1.5	count
	Danthonia intermedia Height (Quadrat)[1]	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)[1]	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) [2]	0.364	28.8 ± 24.1	15.1 ± 10.8	%
	Graminoid Cover (Quadrat) [1]	0.354	49 ± 20.5	36.2 ± 14.6	%
	Bare Ground Cover [1]	-0.351	5.4 ± 6.7	15.8 ± 20.0	%
	Flower Abundance (5m radius) [1]	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)[1]	0.461	2.1 ± 0.03	2.0 ± 0.04	scale
Smith Butte[3]	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

1 Mann-Whitney U test not significant after correcting for multiple comparisons

2 Mann-Whitney U test not significant at the 0.05 level

3 Class means indicate that oviposition locations are negatively correlated with the canonical function

Figure 1: Research Meadows
Nine research meadows located in the Gifford Pinchot National Forest in Washington State, USA

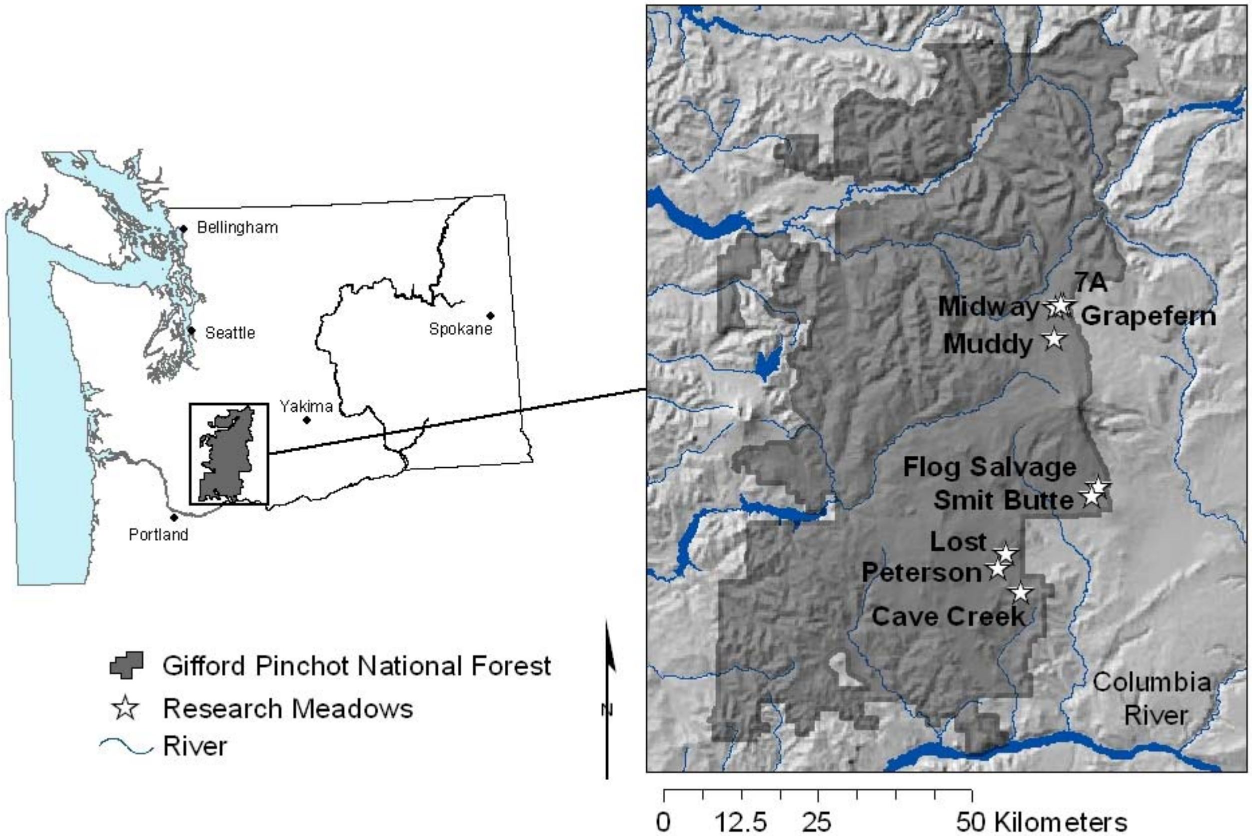


Figure 2: Quadrat and Sub-plot Diagram

1 m^2 quadrat and 0.1 m^2 sub-plot (egg vicinity)

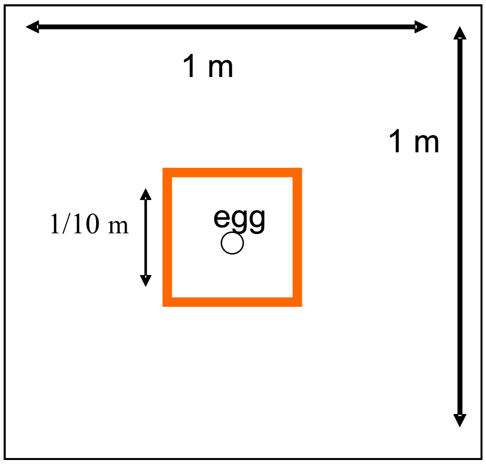


Figure 3: Among Meadow Discriminate Analysis
DFA results on n=540 observations by meadow and location collectively, 18 groups (9 meadows two location-types each). Data symbolized by Location-type (a) and by meadow (b). Squared canonical correlation = r^2.

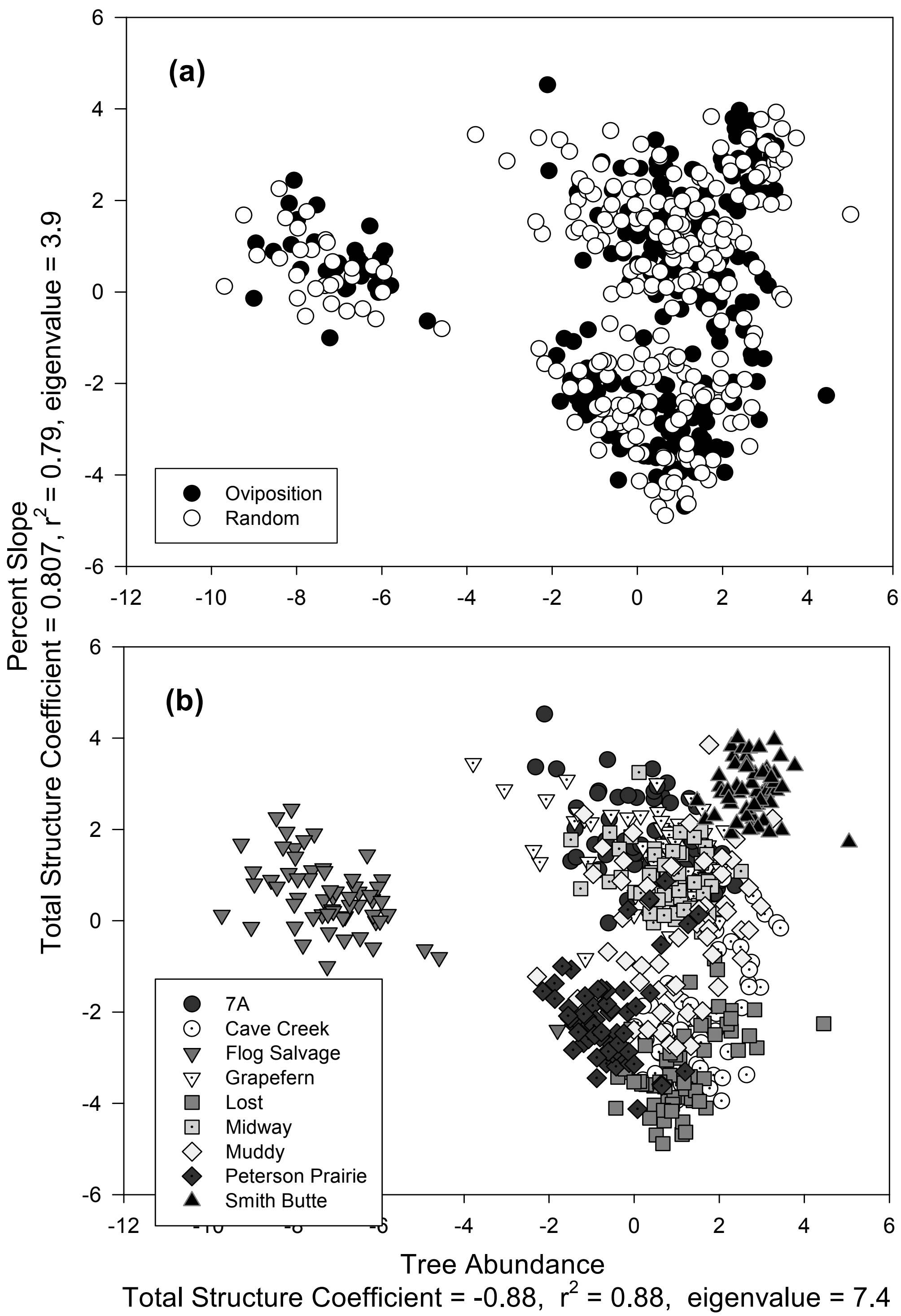


Figure 4: Within Meadow Discriminant Function Analyses
Meadow by meadow DFA grouped by location. Oviposition locations represented in black random locations in white. Percent of discriminant variation explained by variables = r^2. Variables corresponding to X-axes given in Table 4.

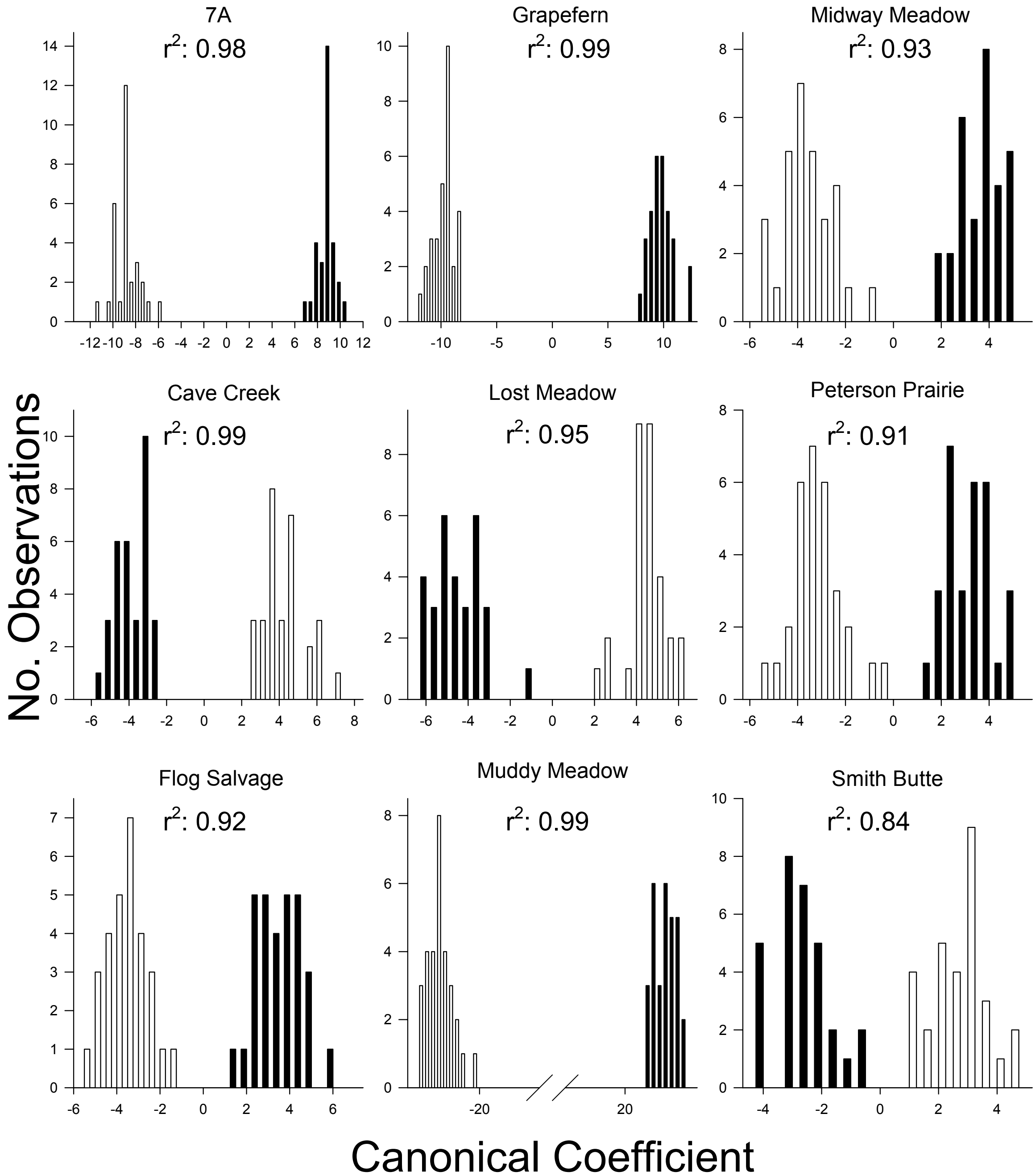
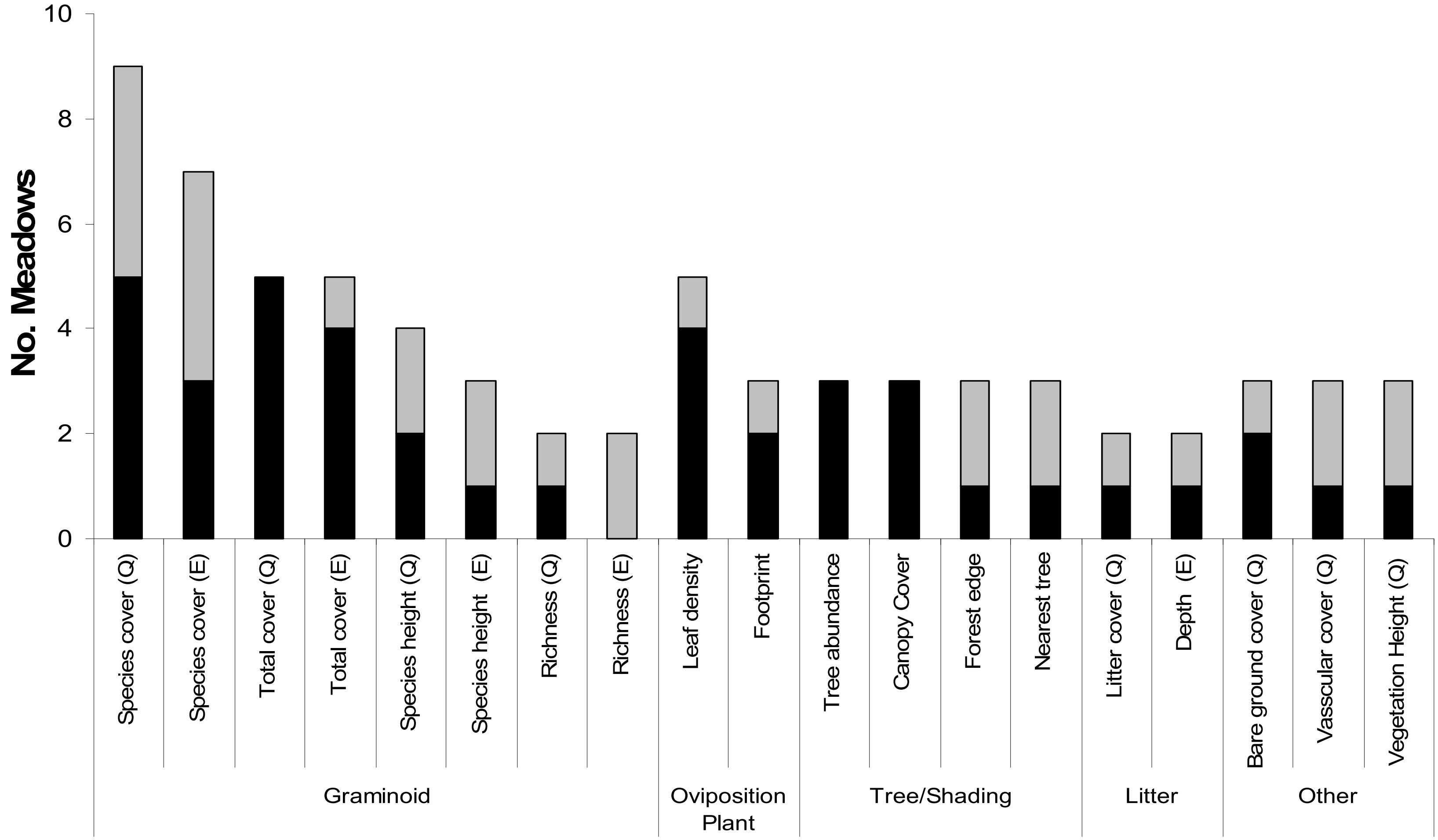


Figure 5: Across Meadow Trends
Across meadow trends showing variables important to discriminating axes in Figure 4. First five primary descriptors in black, next five primary descriptors in gray. Q = 1 m^2 quadrat and E = egg vicinity (0.1 m^2 subplot).



APPENDICES

Appendix A: Examples of Global At-Risk Skippers

In the grass skipper subfamily (Hesperiinae) Y= yes, N=no. Generalist larval diets include more than one plant species

Species	Common Name	Status	Larval Diet	Hesperiinae?	Reference
Europe					
Carterocephalus palaemon palaemon	Chequered	Priority (Scotland), Endangered (Japan)	Specialist	N	(3)
Erynnis tages	Dingy	Priority species (UK, Ireland)	Generalist	N	(3)
Hesperia comma comma	Silver spotted	Rare, Protected (UK)	Specialist	Y	(3)
Pyrgus cirsii	Cinquefoil	Threatened, Vulnerable, Declining (Throughout Europe)	Specialist	N	(6)
Pyrgus malvae	Grizzled	Priority species (UK, Ireland)	Generalist	N	(3)
Thymelicus acteon	Lulworth	Protected (UK)	Specialist	Y	(7)
Austrailia					
Anisynta cynone cynone	Cynone grass	Vulnerable	Generalist	N	(4)
Herimosa albovenata albovenata	White veined grass	Vulnerable	Generalist	N	(4)
Hesperilla chrysotricha cyclospila	Chrysotricha sedge	Vulnerable	Generalist	N	(4)
Hesperilla donnysa donnysa	Yellowish sedge	Endangered	Generalist	N	(4)
Hesperilla idothea clara	Flame sedge	Vulnerable	Generalist	N	(4)
Taractrocera anisomorpha	Orange grass dart	Rare	Generalist	Y	(4)
Taractrocera papyria papyria	White banded grass dart	Rare	Generalist	Y	(4)
Trapezites eliena	Eliena rush	Vulnerable	Generalist	N	(4)
Trapezites luteus luteus	Rare White spot rush	Vulnerable	Generalist	N	(4)
Trapezites phigalia	Phigalia rush	Vulnerable	Generalist	N	(4)
Trapezites symmomus soma	Symmomus rush	Vulnerable	Specialist	N	(4)
North America					
Atrytone arogos	Arogos	Endangered (USA states IL, NJ, NY), Threatened (USA state MN), Species of Concern (USA state IA)	Generalist?	Y	(10, 16)
Dalla octomaculata	Light spotted	Data Deficient, rare (Costa Rica,	-	-	(6)

Species	Common Name	Status	Larval Diet	Hesperiinae?	Reference
		Panama)			
Euphyes dukesi	Dukes'	Threatened (US state (MI)	Generalist	Y	(15, 16)
Hesperia dacotae	Dakota	Threatened (Canada), Endangered (Canada province MB), Federal Candidate (USA), Vulnerable (ICUN)	Generalist	Y	(6, 14)
Hesperia leonardus montana	Pawnee montane	Threatened (USA Federal listing)	Generalist	Y	(6, 12)
Hesperia ottoe	Otto	Endangered (Canada), Threatened (Canada province MB), Threatened (USA states (IL, MI, MN)	Generalist	Y	(10, 16)
Oarisma poweshiek	Poweshiek ling	Threatened (Canada), Endangered (USA state WI), Threatened (USA state IA, MI), Species of Concern (USA state MN)	Generalist	Y	(2, 13, 16)
Panoquina errans	Wandering	Threatened (Mexico, USA)	Specialist	Y	(6)
Polites mardon	Mardon	Endangered (USA state WA & Federal Candidate USA)	Generalist	Y	(1, 8)
Problema bulenta	Rare	Endangered (US state DE)	?	Y	(10, 16)
Problema byssus	Byssus	Threatened (US state IA)	?	Y	(10, 16)
Pseudocopaeodes eunus obscurus	Carson wandering	Endangered (USA Federal listing)	Specialist	Y	(13, 16)
Pyrgus ruralis lagunae	Laguna mountains	Endangered (USA Federal listing)	-	N	(1, 11)
Taiwan/Japan					
Caltoris bromus yanuca Fruhstorfer		Extremely Rare, Taiwan	Specialist	-	(5)
Carterocephalus palaemon palaemon	Chequered	Priority (Scotland), Endangered (Japan)	Specialist	N	(3)

Appendix A References

1. Black, S. H., and D. M. Vaughan. 2005. In Shepherd, M. D., D. M. Vaughan, and S. H. Black (Eds). Red List of Pollinator Insects of North America. CD-ROM Version 1 (May 2005). Portland, OR: The Xerces Society for Invertebrate Conservation.

2. COSEWIC. 2003. COSEWIC assessment and status report on the Powesheik skipperling *Oarisma poweshiek* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vi + 25 pp.

3. Eeles, P. 2002. "U.K. Butterflies". Last updated 2008. Date of access November 28, 2008. http://www.ukbutterflies.co.uk/species.php?

4. GRUND R., 1998. "South Australian Butterflies". Last update 4 October 2004. Date of access November 21, 2008. http://users.sa.chariot.net.au/~rgrund/checklist.htm

5. Hsu, Y. F., Wang, S. M. 2004. Notes on immature biology of a rare skipper *Caltoris bromus yanuca Fruhstorfer* (Lepidoptera : Hesperiidae), with a discussion on the systematic status of *Parnara ranrunna Sonan*. Pan-Pacific Entomologist. **80**: 69-80.

6. ICUN 2008. "International Union for Conservation of Nature and Natural Resources" Date of access December 1, 2008. http://www.iucnredlist.org/

7. Opler et al 2008. "The butterflies and skippers of North America". Date of access December 1, 2008. http://www.nearctica.com/butter/bylist/lhesp.htm

8. Potter, A., J. Fleckenstein, S. Richardson, and D. Hays. 1999. Washington State Status Report for the Mardon Skipper. Washington Department of Fish and Wildlife, Olympia 39 pp.

9. Shepard, J.H. 2000. Status of five butterflies and skippers in British Columbia. B.C. Minist. Environ., Lands and Parks, Wildl. Branch and Resour. Inv. Branch, Victoria, BC. 27pp.

10. Shepherd, M. D. 2005. In Shepherd, M. D., D. M. Vaughan, and S. H. Black (Eds). Red List of Pollinator Insects of North America. CD-ROM Version 1 (May 2005). Portland, OR: The Xerces Society for Invertebrate Conservation.

11. USFWS. 1997. Endangered and threatened wildlife and plants; determination of endangered status for the Laguna Mountains skipper and Quino Checkerspot Butterfly. Federal Register.62,2313-2322

12. USFWS. 1998. Pawnee montane skipper butterfly (*Hesperia leonoardus montana*) recovery plan. Denver, Colorado. . Page 16 pp.

13. USFWS. 2005. Draft recovery plan for the Carson wandering skipper (*Pseudocopaedes eunus obscurus*).U.S. Fish and Wildlife Service, Portland, Oregon. viii:71 pp.

14. USFWS 2008."Endangered Species Program" Last updated December 3, 2008. Date of access December 7, 2008. http://www.fws.gov/northdakotafieldoffice/endspecies/species/dakota_skipper.htm

15. Vaughan, D. M., and M. D. Shepherd. 2005. Species Profile: Euphyes dukesi. In Shepherd, M. D., D. M. Vaughan, and S. H. Black (Eds). Red List of Pollinator Insects of North America. CD-ROM Version 1 (May 2005). Portland, OR: The Xerces Society for Invertebrate Conservation.

16. Xerces 2008. "The Xerces Society for Invertebrate Conservation; Red List of Butterflies and moths". Date of access December 7, 2008. http://www.xerces.org/red-list-of-butterflies-and-moths/

Appendix B: Measured Habitat Variables

Scale	Variable
Oviposition Plant	
	Maximum Culm height (cm)
	Basal leaf height (cm)
	Percent brown or dead
	Foot print area (cm^2)
	Distance to nearest neighboring plant of the same species (cm)
	Structure (Category 1-solitary, 2-loose, 3-dense, 4-matted)
Quadrat ($1m^2$)	
	Percent cover of bare ground
	Percent cover over story canopy
	Percent cover of cryptograms
	Percent cover of graminoids combined
	Percent cover of each species of graminoid
	Percent cover of forbs combined
	Percent cover of litter
	Percent cover of rocks/pebbles
	Horizontal Vegetation thickness (0.3, 0.6, & 0.9 meter increments)
	Maximum plant height (cm)
	Maximum height of each species of graminoid (cm)
	Number of blooming forbs (potential nectar resources)
	Graminoid species richness (Count of species present)
	Graminoid Heterogeneity (Shannon-diversity calculation)
	Graminoid Evenness (Shannon-diversity calculation)
Sub-plot (1/10th m^2)	
	Soil Ph
	Soil Moisture retention capacity
	Litter Depth (cm)
	Percent cover of graminoids combined
	Percent cover of each species of graminoid
	Percent cover of forbs combined
	Maximum height of each species of graminoid (cm)
	Graminoid species richness (Count of species present)
	Graminoid Heterogeneity (Shannon-diversity calculation)
	Graminoid Evenness (Shannon-diversity calculation)
Landscape	
	Number of blooming forbs (potential nectar resources) sampled from 5 m radius
	Distance to nearest visible water source (m)
	Distance to nearest tree (m)
	Distance to nearest shrub (m)
	Sapling abundance within 10m of quadrat
	Seedling abundance within 10m of quadrat
	Tree abundance within 10m of quadrat
	Distance to forest edge (m)
	Percent slope with regards to 20 m radius of quadrat

Appendix C: 2007 Population Counts

Meadow	Date	Count
7A	8-Jul	49
	25-Jul	32
	1-Aug	7
Cave Creek	31-May	31
	8-Jun	56
	18-Jun	39
	23-Jun	0
Flog Salvage	17-Jun	23
	22-Jun	23
Grapefern	9-Jul	313
	26-Jul	37
	1-Aug	2
Lost	12-Jun	15
	18-Jun	14
	26-Jun	9
Midway	8-Jul	54
	25-Jul	5
	1-Aug	0
Muddy	12-Jul	91
	26-Jul	31
	2-Aug	10
Peterson	8-Jun	23
	18-Jun	34
	23-Jun	17
Smith Butte	1-Jul	15
	3-Jul	37

Appendix D: Multiple Consecutive Ovipositions

Meadow	Individual	Oviposition Plant Species	No. Consecutive Ovipositions
7A	1	*Carex fracta, C. fracta/Dantonia intermedia* mix	2
	2	***Carex deflex, C. fracta***	2
	3	***Danthonia intermedia, Muhlenbergia filiformis***	2
Cave Creek	4	*Festuca rubra*	2
	5	*F. rubra*	3
	6	*Poa pratensis, P. pratensis/F. rubra* mix	2
	7	***Carex hoodii, P. pratensis***	2
	8	*F.rubra*	2
Flog Salvage	9	*Festuca roemeri*	2
	10	*F.roemeri*	2
	11	*F. roemeri*	2
Grapefern	12	*Carex inops*	2
Lost	13	*C. deflex, C.deflexa/P. pratensis* mix	2
	14	***C. deflexa, P. pratensis***	2
	15	*P. pratensis*	2
	16	***D. intermedia, C. deflexa***	2
	17	***C.deflexa, P. pratensis***	2
Midway	18	*P. pratensis, P. pratensis/Bromus carinatus* mix	2
Muddy	19	*Agrostis thurberiana*	2
	20	*D. intermedia, D. intermedia/Deschampsia cespitosa* mix	2
Peterson	**21**	***Carex hallinana, P. pratensis***	3
Smith Butte	22	*F. roemeri*	3
	23	*F. roemeri*	2
	24	*F. roemeri*	5

Appendix E: Within Meadow DFA Variable Descriptions

DFA Total Structure Coefficients, level of significance, mean and standard deviations for each variable in oviposition and random locations, and unit of measurement.

7A Meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Tree abundance within 10 m of quadrat	-0.486	<0.0001	8.5 ± 7.3	18.0 ± 10.0	count
Total graminoid cover (Egg vicinity)	0.460	<0.0001	34.8 ± 24.6	20.5 ± 27.1	%
Distance to nearest visible water source	0.440	<0.01	89.1 ± 0.9	64.9 ± 1.1	meters
Oviposition plant leaf density	0.439	<0.01	2.2 ± 0.3	1.5 ± 0.2	category (1-4)
Canopy cover	-0.433	<0.05	5.5 ± 109.9	13.3 ± 93.2	%
Poa pratensis cover (Quadrat)	0.315	<0.05	5.0 ± 3.3	3.2 ± 2.9	%
Distance to nearest tree	0.312	<0.05	6.9 ± 2.7	5.2 ± 2.8	meters
Percent slope relative to 20 m radius of quadrat	0.312	<0.05	11.0 ± 6.0	8.3 ± 6.7	%
Litter depth (Egg vicinity)	0.307	<0.05	1.6 ± 0.7	1.2 ± 0.8	cm
Carex fracta cover (Egg vicinity)	0.280	-	6.8 ± 12.7	1.2 ± 3.9	%
Oviposition plant footprint	0.277	<0.05	78.9 ± 11.3	43.3 ± 8.4	cm^2
Carex fracta height (Quadrat)	0.272	-	20.3 ± 12.1	13.3 ± 13.3	cm
Carex fracta cover (Quadrat)	0.263	<0.05	5.9 ± 6.1	3.3 ± 4.6	%
Graminoid species richness (Egg vicinity)	0.255	-	3.6 ± 1.2	3.0 ± 0.9	count
Poa pratensis height (Quadrat)	0.248	-	25.4 ± 13.5	18.5 ± 14.2	cm
Muhlenbergia filiformis height (Egg vicinity)	0.247	-	3.0 ± 11.9	0.2 ± 1.3	cm
Litter cover (Quadrat)	0.246	<0.05	68.3 ± 10.3	55.4 ± 7.7	%
Oviposition plant nearest neighbor	-0.241	<0.05	6.5 ± 20.2	8.2 ± 14.5	cm
Danthonia intermedia height (Egg vicinity)	0.236	<0.05	17.2 ± 9.5	12.5 ± 10.4	cm
Poa pratensis cover (Egg vicinity)	0.229	-	3.5 ± 3.3	2.0 ± 2.6	%
Number of blooming forbs within 5 m radius	0.223	-	14.2 ± 7.6	11.1 ± 6.3	count
Total graminoid cover (Quadrat)	0.221	<0.05	37.8 ± 4.6	31.5 ± 11.4	%
Oviposition plant maximum culm height	0.220	-	6.7 ± 0.7	3.0 ± 0.6	cm
Oviposition plant dead basal leaves	0.220	-	2.8 ± 4.0	1.4 ± 2.8	%
Bare ground cover (Quadrat)	-0.214	-	14.2 ± 21.8	20.9 ± 20.0	%
Muhlenbergia filiformis cover (Egg vicinity)	0.210	-	3.4 ± 9.7	0.7 ± 3.7	%
Carex fracta height (Egg vicinity)	0.208	-	6.5 ± 11.1	2.0 ± 5.2	cm
Soil Ph (Egg vicinity)	-0.188	-	6.5 ± 9.1	6.6 ± 7.4	scale
Stipa occidentalis cover (Egg vicinity)	0.185	-	1.6 ± 4.6	0.3 ± 1.0	%
Danthonia intermedia cover (Egg vicinity)	0.179	-	11.2 ± 8.5	0.7 ± 3.7	%
Cryptogram cover (Quadrat)	-0.177	-	12.1 ± 17.0	14.2 ± 18.0	%
Soil moisture (Egg vicinity)	0.171	-	33.3 ± 19.6	26.1 ± 30.0	%
Graminoid heterogeneity (Egg vicinity)	0.158	-	0.4 ± 0.1	0.4 ± 0.1	index
Muhlenbergia filiformis cover (Quadrat)	0.146	-	4.9 ± 11.9	2.0 ± 4.8	%
Agrostis thurberiana cover (Quadrat)	0.142	-	4.1 ± 7.0	2.1 ± 3.6	%
Shrub abundance within 10 m	0.124	-	8.3 ± 10.4	5.3 ± 6.2	count
Rock/pebble cover (Quadrat)	0.115	-	0.6 ± 16.9	0.5 ± 20.2	%
Danthonia intermedia cover (Quadrat)	0.114	-	15.5 ± 10.2	14.1 ± 14.9	%
Stipa occidentalis cover (Quadrat)	0.111	-	0.8 ± 1.8	0.5 ± 1.3	%
Forb cover (Quadrat)	0.108	-	37.2 ± 4.6	39.0 ± 3.6	%
Number of blooming forbs (Quadrat)	0.108	-	5.2 ± 4.1	4.8 ± 5.5	count
Poa pratensis height (Egg vicinity)	0.098	-	12.2 ± 10.5	10.3 ± 9.2	cm
Stipa occidentalis height (Quadrat)	0.097	-	5.1 ± 11.2	3.2 ± 9.3	cm
Stipa occidentalis height (Egg vicinity)	0.091	-	2.5 ± 6.4	1.9 ± 7.4	cm
Agrostis thurberiana cover (Egg vicinity)	0.090	-	4.0 ± 8.0	2.8 ± 7.6	%
Horizontal vegetation thickness at 0.3 m height	-0.076	-	1.5 ± 1.4	1.9 ± 2.6	%
Maximum plant height (Quadrat)	-0.069	-	40.3 ± 9.5	42.3 ± 11.9	cm
Agrostis thurberiana height (Egg vicinity)	0.052	-	20.3 ± 3.9	19.3 ± 7.5	cm
Danthonia intermedia height (Quadrat)	-0.041	-	30.6 ± 10.0	31.4 ± 11.7	cm
Agrostis thurberiana height (Quadrat)	0.037	-	11.6 ± 14.1	10.7 ± 12.9	cm
Graminoid species richness (Quadrat)	0.032	-	6.3 ± 1.7	6.2 ± 1.4	count
Oviposition plant basal leaf height	-0.032	-	11.7 ± 11.5	12.1 ± 8.7	cm
Graminoid species evenness (Egg vicinity)	-0.031	-	0.8 ± 0.2	0.8 ± 0.2	index
Muhlenbergia filiformis height (Quadrat)	0.029	-	1.8 ± 3.0	2.6 ± 5.8	cm
Graminoid species evenness (Quadrat)	0.017	-	0.8 ± 0.1	0.8 ± 0.1	index
Forb cover (Egg vicinity)	0.016	-	40.8 ± 23.2	40.2 ± 19.9	%
Distance to forest edge	0.008	-	17.5 ± 14.0	16.9 ± 16.2	meters
Graminoid heterogeneity (Quadrat)	0.007	-	0.7 ± 0.1	0.7 ± 0.1	index
Vasscular plant cover (Quadrat)	-	-	64.5 ± 17.4	59.7 ± 15.5	%
Horizontal vegetation thickness at 0.6 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	0.1 ± 0.3	%
Sapling abundance within 10 m of quadrat	-	-	3.1 ± 4.0	4.4 ± 3.7	count
Seedling abundance within 10 m of quadrat	-	-	2.6 ± 2.7	5.7 ± 4.5	count

Cave Creek Meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Maximum plant height (Quadrat)	0.656944	<0.0001	38.4 ± 6.2	52.8 ± 10.8	cm
Oviposition plant leaf density	-0.588236	<0.0001	2.7 ± 0.4	1.8 ± 0.3	category (1-4)
Tree abundance within 10 m of quadrat	0.539355	<0.0001	1.5 ± 1.6	4.7 ± 4.5	count
Festuca rubra cover (Egg vicinity)	-0.473703	<0.0001	28.9 ± 22.0	10.9 ± 16.7	%
Canopy cover	0.455402	<0.0001	5.4 ± 80.3	16.4 ± 68.9	%
Distance to nearest tree	-0.452389	<0.001	9.2 ± 4.8	5.1 ± 3.3	meters
Oviposition plant basal leaf height	0.407111	<0.0001	10.8 ± 16.9	18.7 ± 3.4	cm
Number of blooming forbs within 5 m radius	-0.359243	<0.01	47.0 ± 35.6	29.5 ± 28.9	count
Shrub abundance within 10 m	0.32858	-	0.4 ± 0.8	4.3 ± 10.1	count
Sapling abundance within 10 m of quadrat	0.325884	<0.05	0.1 ± 0.4	0.7 ± 1.3	count
Bare ground cover (Quadrat)	-0.315773	<0.05	14.3 ± 15.8	9.4 ± 14.4	%
Graminoid species richness (Quadrat)	0.312784	<0.05	3.1 ± 0.5	3.5 ± 0.9	index
Festuca rubra cover (Quadrat)	-0.311138	<0.05	21.4 ± 17.5	12.9 ± 15.0	%
Vasscular plant cover (Quadrat)	0.308497	<0.05	72.8 ± 17.1	81.2 ± 20.9	%
Poa pratensis height (Quadrat)	0.287832	<0.05	30.5 ± 11.8	39.1 ± 17.6	cm
Carex hoodii height (Quadrat)	-0.279337	<0.05	25.6 ± 14.9	15.9 ± 19.7	cm
Oviposition plant footprint	-0.271652	<0.05	85.1 ± 11.5	47.8 ± 16.5	cm^2
Rock/pebble cover (Quadrat)	-0.260067	<0.05	0.6 ± 10.4	0.1 ± 11.1	%
Horizontal vegetation thickness at 0.3 m height	0.258576	-	9.6 ± 17.3	26.6 ± 35.0	%
Distance to nearest visible water source	0.254345	-	80.5 ± 1.1	94.0 ± 0.5	meters
Carex hoodii cover (Quadrat)	-0.253685	<0.05	11.7 ± 11.0	8.3 ± 13.5	%
Total graminoid cover (Egg vicinity)	-0.238895	-	46.4 ± 23.2	36.7 ± 28.6	%
Graminoid species evenness (Egg vicinity)	0.233471	<0.01	0.7 ± 0.3	0.8 ± 0.3	index
Festuca rubra height (Egg vicinity)	-0.206937	-	17.6 ± 10.3	12.7 ± 13.5	cm
Graminoid heterogeneity (Egg vicinity)	0.206375	-	0.3 ± 0.1	0.3 ± 0.1	index
Forb cover (Quadrat)	0.206001	-	34.5 ± 2.1	43.0 ± 2.5	%
Litter cover (Quadrat)	0.201905	-	52.6 ± 16.7	62.1 ± 8.5	%
Horizontal vegetation thickness at 0.6 m height	0.197964	<0.05	0.2 ± 0.9	1.6 ± 7.3	%
Oviposition plant maximum culm height	-0.187409	-	12.5 ± 0.7	10.8 ± 0.8	cm
Poa pratensis cover (Egg vicinity)	-0.169455	-	14.0 ± 14.4	10.6 ± 12.7	%
Cryptogram cover (Quadrat)	-0.166846	-	7.5 ± 17.7	3.1 ± 19.6	%
Percent slope relative to 20 m radius of quadrat	0.16112	-	1.1 ± 5.4	1.8 ± 8.1	%
Poa pratensis height (Egg vicinity)	0.154348	-	20.4 ± 9.3	24.0 ± 14.6	cm
Number of blooming forbs (Quadrat)	-0.153629	-	17.0 ± 21.3	9.6 ± 9.8	count
Forb cover (Egg vicinity)	0.146338	-	27.9 ± 22.0	33.7 ± 22.6	%
Distance to forest edge	0.121675	-	20.5 ± 20.2	25.1 ± 22.8	meters
Soil moisture (Egg vicinity)	-0.094334	-	68.9 ± 24.9	65.3 ± 18.9	%
Oviposition plant dead basal leaves	-0.087642	-	3.7 ± 3.3	3.3 ± 4.3	%
Poa pratensis cover (Quadrat)	-0.087043	-	15.1 ± 10.7	14.7 ± 13.9	%
Soil Ph (Egg vicinity)	0.071653	-	6.2 ± 9.7	6.2 ± 14.0	scale
Litter depth (Egg vicinity)	0.064973	-	1.4 ± 0.7	2.1 ± 3.4	cm
Carex hoodii cover (Egg vicinity)	-0.064289	-	5.2 ± 10.7	4.9 ± 10.3	%
Total graminoid cover (Quadrat)	0.060235	-	50.0 ± 7.4	52.3 ± 17.1	%
Oviposition plant nearest neighbor	0.052678	-	6.8 ± 22.3	4.4 ± 18.1	cm
Carex hoodii height (Egg vicinity)	0.048411	-	6.7 ± 8.7	7.7 ± 13.9	cm
Festuca rubra height (Quadrat)	0.04409	-	23.6 ± 11.4	25.0 ± 20.7	cm
Graminoid species richness (Egg vicinity)	0.011476	-	2.6 ± 0.6	2.6 ± 0.7	index
Graminoid species evenness (Quadrat)	-	-	0.8 ± 0.1	0.8 ± 0.1	index
Graminoid heterogeneity (Quadrat)	-	-	0.4 ± 0.1	0.4 ± 0.1	index
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	1.0 ± 5.5	%
Seedling abundance within 10 m of quadrat	-	-	0.0 ± 0.0	0.1 ± 0.6	count

Flog Salvage meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Festuca idahoensis cover (Egg vicinity)	0.783	<0.0001	30.8 ± 22.1	2.0 ± 6.5	%
Oviposition plant footprint	0.772	<0.0001	212.3 ± 9.8	30.7 ± 5.9	cm^2
Oviposition plant leaf density	0.709	<0.0001	2.8 ± 0.2	1.6 ± 0.2	category (1-4)
Total graminoid cover (Egg vicinity)	0.679	<0.0001	42.3 ± 24.0	16.5 ± 28.6	%
Total graminoid cover (Quadrat)	0.614	<0.0001	34.5 ± 6.4	20.3 ± 9.4	%
Graminoid species richness (Egg vicinity)	0.609	<0.0001	2.3 ± 0.6	1.4 ± 0.6	count
Festuca idahoensis height (Egg vicinity)	0.591	<0.0001	12.8 ± 7.0	2.8 ± 7.9	cm
Oviposition plant nearest neighbor	0.568	<0.0001	18.8 ± 20.9	3.9 ± 12.5	cm
Festuca idahoensis cover (Quadrat)	0.565	<0.0001	11.0 ± 6.5	3.7 ± 6.0	%
Forb cover (Quadrat)	0.480	<0.01	12.3 ± 0.4	6.7 ± 0.3	%
Graminoid heterogeneity (Egg vicinity)	0.453	<0.01	0.2 ± 0.1	0.1 ± 0.1	index
Festuca idahoensis height (Quadrat)	0.437	<0.0001	20.7 ± 13.8	8.5 ± 13.1	cm
Graminoid species richness (Quadrat)	0.435	<0.01	3.0 ± 0.7	2.2 ± 1.0	count
Graminoid species evenness (Egg vicinity)	0.434	<0.01	0.6 ± 0.3	0.3 ± 0.4	index
Forb cover (Egg vicinity)	0.430	<0.01	7.6 ± 6.3	3.1 ± 4.5	%
Graminoid heterogeneity (Quadrat)	0.385	<0.01	0.4 ± 0.1	0.2 ± 0.2	index
Vasscular plant cover (Quadrat)	0.378	<0.01	44.3 ± 7.0	33.5 ± 4.7	%
Tree abundance within 10 m of quadrat	-0.301	-	85.3 ± 31.3	105.8 ± 37.3	count
Sapling abundance within 10 m of quadrat	-0.298	<0.05	56.2 ± 22.4	71.7 ± 29.6	count
Graminoid species evenness (Quadrat)	0.294	-	0.7 ± 0.2	0.6 ± 0.4	index
Carex inops cover (Quadrat)	0.275	<0.05	19.6 ± 12.4	13.0 ± 8.0	%
Oviposition plant basal leaf height	0.262	-	13.5 ± 19.8	11.6 ± 3.5	cm
Horizontal vegetation thickness at 0.6 m height	-0.261	-	0.8 ± 3.0	11.1 ± 26.6	%
Carex inops height (Quadrat)	-0.244	-	17.4 ± 4.5	20.3 ± 7.1	cm
Horizontal vegetation thickness at 0.9 m height	-0.218	<0.05	0.5 ± 2.7	7.9 ± 24.6	%
Oviposition plant dead basal leaves	-0.194	-	3.5 ± 2.7	6.2 ± 9.1	%
Horizontal vegetation thickness at 0.3 m height	-0.182	-	2.4 ± 6.2	9.6 ± 21.3	%
Maximum plant height (Quadrat)	-0.180	-	31.6 ± 12.9	55.9 ± 71.5	cm
Seedling abundance within 10 m of quadrat	0.162	-	21.5 ± 12.5	18.3 ± 7.3	count
Litter cover (Quadrat)	-0.155	-	67.6 ± 3.2	75.4 ± 5.1	%
Distance to nearest tree	0.142	-	7.9 ± 8.2	5.1 ± 3.8	meters
Rock/pebble cover (Quadrat)	0.115	-	0.9 ± 14.6	0.7 ± 17.5	%
Soil moisture (Egg vicinity)	0.112	-	21.2 ± 20.9	17.2 ± 12.5	%
Canopy cover	-0.110	-	6.4 ± 168.1	8.4 ± 29.1	%
Cryptogram cover (Quadrat)	0.105	-	1.9 ± 11.8	1.7 ± 8.0	%
Bare ground cover (Quadrat)	0.101	-	15.3 ± 13.2	12.6 ± 15.7	%
Litter depth (Egg vicinity)	0.097	-	3.2 ± 1.4	3.3 ± 2.8	%
Shrub abundance within 10 m	-0.062	-	11.3 ± 7.2	12.5 ± 9.6	count
Soil Ph (Egg vicinity)	0.054	-	6.8 ± 30.4	6.8 ± 28.7	scale
Carex inops cover (Egg vicinity)	-0.052	-	12.2 ± 11.6	12.4 ± 8.6	%
Percent slope relative to 20 m radius of quadrat	0.035	-	0.1 ± 4.2	0.1 ± 4.5	%
Number of blooming forbs (Quadrat)	0.032	-	0.7 ± 1.2	0.9 ± 2.0	count
Oviposition plant maximum culm height	0.030	-	2.6 ± 0.5	1.4 ± 0.7	cm
Carex inops height (Egg vicinity)	-0.019	-	14.2 ± 7.4	14.4 ± 5.3	cm
Distance to forest edge	-0.015	-	43.1 ± 19.8	43.4 ± 10.6	meters
Number of blooming forbs within 5 m radius	0.012	-	3.0 ± 3.6	2.7 ± 3.0	count

Grapefern Meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Litter depth (Egg vicinity)	0.667	<0.0001	2.1 ± 0.7	0.8 ± 0.9	cm
Total graminoid cover (Quadrat)	0.605	<0.0001	48.8 ± 15.5	27.0 ± 12.8	%
Litter cover (Quadrat)	0.565	<0.0001	82.5 ± 28.0	53.8 ± 10.9	%
Total graminoid cover (Egg vicinity)	0.538	<0.0001	50.8 ± 19.2	27.5 ± 17.1	%
Tree abundance within 10 m of quadrat	-0.484	<0.0001	3.0 ± 20.9	16.3 ± 3.9	count
Seedling abundance within 10 m of quadrat	-0.476	<0.0001	2.3 ± 10.7	9.5 ± 3.3	count
Vasscular plant cover (Quadrat)	0.467	<0.0001	65.8 ± 16.3	50.2 ± 13.1	%
Carex inops cover (Quadrat)	0.452	<0.01	20.5 ± 15.6	6.9 ± 12.1	%
Bare ground cover (Quadrat)	-0.435	<0.01	6.9 ± 24.4	25.8 ± 6.7	%
Distance to forest edge	0.412	-	27.5 ± 9.5	18.5 ± 10.7	meters
Canopy cover	-0.386	<0.05	1.0 ± 10.6	7.2 ± 1.3	%
Oviposition plant basal leaf height	0.367	<0.01	17.4 ± 5.7	12.7 ± 6.3	cm
Carex inops height (Egg vicinity)	0.365	<0.01	13.7 ± 10.2	6.5 ± 8.5	cm
Oviposition plant leaf density	0.352	<0.01	2.2 ± 0.8	1.7 ± 0.8	category (1-4)
Carex inops height (Quadrat)	0.343	<0.01	19.3 ± 12.7	10.9 ± 10.6	cm
Shrub abundance within 10 m	-0.342	<0.05	7.4 ± 31.2	23.2 ± 17.2	count
Carex inops cover (Egg vicinity)	0.335	<0.01	23.8 ± 20.3	10.2 ± 18.8	%
Soil Ph (Egg vicinity)	-0.321	<0.01	6.4 ± 0.3	6.6 ± 0.3	Scale
Distance to nearest tree	0.316	<0.01	15.1 ± 6.6	11.3 ± 4.6	meters
Poa pratensis height (Quadrat)	0.303	<0.05	22.3 ± 17.7	11.8 ± 15.8	cm
Horizontal vegetation thickness at 0.3 m height	0.278	<0.05	6.7 ± 5.9	3.9 ± 8.1	%
Sapling abundance within 10 m of quadrat	-0.255	<0.05	0.6 ± 11.8	4.9 ± 1.6	count
Bromus carinatus cover (Quadrat)	0.249	-	5.1 ± 4.6	3.0 ± 3.6	%
Oviposition plant footprint	0.245	<0.05	108.2 ± 59.2	46.3 ± 186.5	cm2
Bromus carinatus cover (Egg vicinity)	0.236	<0.05	8.1 ± 11.6	3.3 ± 8.4	%
Number of blooming forbs within 5 m radius	0.233	-	7.8 ± 4.3	5.6 ± 6.1	count
Cryptogram cover (Quadrat)	-0.225	-	8.5 ± 10.6	12.7 ± 7.2	%
Graminoid heterogeneity (Egg vicinity)	0.218	-	0.3 ± 0.2	0.2 ± 0.1	Index
Graminoid species richness (Egg vicinity)	0.213	-	2.8 ± 1.1	2.4 ± 0.7	Index
Danthonia intermedia height (Egg vicinity)	-0.209	-	2.0 ± 7.1	3.6 ± 6.6	cm
Soil moisture (Egg vicinity)	0.205	-	26.7 ± 8.0	23.0 ± 9.9	%
Graminoid species evenness (Egg vicinity)	0.202	-	0.7 ± 0.4	0.6 ± 0.2	Index
Poa pratensis cover (Quadrat)	0.179	-	4.0 ± 4.3	2.9 ± 4.0	%
Carex fracta cover (Quadrat)	0.169	-	10.1 ± 12.3	6.4 ± 7.6	%
Carex fracta cover (Egg vicinity)	0.153	-	6.5 ± 15.1	2.3 ± 6.5	%
Carex fracta height (Quadrat)	0.147	-	19.2 ± 14.8	14.8 ± 15.3	cm
Maximum plant height (Quadrat)	0.137	-	45.7 ± 15.9	44.3 ± 8.7	cm
Graminoid species evenness (Quadrat)	-0.132	-	0.8 ± 0.1	0.8 ± 0.1	Index
Danthonia intermedia cover (Egg vicinity)	-0.127	-	1.3 ± 4.3	2.0 ± 4.0	%
Graminoid species richness (Quadrat)	0.121	-	4.6 ± 1.5	4.3 ± 1.3	Index
Stipa occidentalis cover (Egg vicinity)	0.118	-	3.7 ± 13.2	1.4 ± 4.9	%
Oviposition plant dead basal leaves	-0.117	-	2.9 ± 4.1	4.1 ± 2.9	%
Bromus carinatus height (Quadrat)	0.114	-	29.4 ± 19.4	29.0 ± 26.4	cm
Stipa occidentalis height (Egg vicinity)	0.113	-	5.2 ± 13.5	2.8 ± 7.3	cm
Elymus elymoides cover (Egg vicinity)	0.100	-	1.5 ± 5.8	0.5 ± 2.0	%
Forb cover (Quadrat)	0.086	-	28.0 ± 17.6	26.5 ± 12.2	%
Poa pratensis height (Egg vicinity)	0.086	-	9.1 ± 11.9	7.2 ± 10.4	cm
Number of blooming forbs (Quadrat)	0.085	-	2.3 ± 2.7	1.9 ± 3.3	count
Carex fracta height (Egg vicinity)	0.073	-	5.8 ± 11.0	4.0 ± 9.3	cm
Oviposition plant nearest neighbor	-0.070	-	4.8 ± 4.4	5.5 ± 4.2	cm
Danthonia intermedia cover (Quadrat)	-0.069	-	3.2 ± 6.6	3.3 ± 4.5	%
Percent slope relative to 20 m radius of quadrat	-0.068	-	6.3 ± 2.4	6.7 ± 2.6	%
Stipa occidentalis cover (Quadrat)	0.056	-	2.8 ± 6.4	1.8 ± 3.7	%
Graminoid heterogeneity (Quadrat)	0.054	-	0.5 ± 0.2	0.5 ± 0.1	Index
Poa pratensis cover (Egg vicinity)	0.053	-	3.6 ± 6.9	3.0 ± 5.1	%
Danthonia intermedia height (Quadrat)	-0.046	-	10.4 ± 15.2	11.7 ± 13.7	cm
Elymus elymoides height (Egg vicinity)	0.030	-	2.1 ± 7.0	1.7 ± 6.5	cm
Forb cover (Egg vicinity)	0.024	-	23.1 ± 15.9	24.0 ± 10.3	%
Oviposition plant maximum culm height	-0.022	-	5.4 ± 14.4	6.5 ± 11.9	cm
Stipa occidentalis height (Quadrat)	0.009	-	12.0 ± 22.7	11.6 ± 21.3	cm
Bromus carinatus height (Egg vicinity)	0.009	-	12.7 ± 12.1	9.3 ± 17.5	cm
Elymus elymoides cover (Quadrat)	-0.008	-	2.2 ± 4.4	2.3 ± 5.7	%
Elymus elymoides height (Quadrat)	0.002	-	9.8 ± 16.2	9.7 ± 15.0	cm
Horizontal vegetation thickness at 0.6 m height	-	-	0.1 ± 1.0	0.3 ± 0.4	%
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Rock/pebble cover (Quadrat)	-	-	0.0 ± 0.3	0.1 ± 0.0	%
Carex hoodii cover (Egg vicinity)	-	-	1.83 ± 10	0 ± 0	%
Carex hoodii cover (Quadrat)	-	-	0.67 ± 3.7	0 ± 0	%
Carex hoodii height (Egg vicinity)	-	-	0.67 ± 3.7	0 ± 0	cm
Carex hoodii height (Quadrat)	-	-	1.33 ± 7.3	0 ± 0	cm

Lost Meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Total graminoid cover (Egg vicinity)	-0.592	<0.0001	54.7 ± 18.2	29.1 ± 19.2	%
Total graminoid cover (Quadrat)	-0.540	<0.0001	53.2 ± 18.3	32.3 ± 16.3	%
Vasscular plant cover (Quadrat)	-0.479	<0.0001	68.5 ± 16.7	51.3 ± 16.9	%
Poa pratensis cover (Quadrat)	-0.476	<0.0001	15.9 ± 9.9	8.1 ± 5.5	%
Bare ground cover (Quadrat)	0.471	<0.01	10.3 ± 6.5	28.3 ± 22.9	%
Graminoid species richness (Quadrat)	-0.470	0.01	3.0 ± 0.0	3.0 ± 0.0	count
Oviposition plant footprint	-0.448	<0.01	65.1 ± 59.7	28.5 ± 42.0	cm^2
Graminoid species richness (Egg vicinity)	-0.442	-	2.0 ± 0.0	2.0 ± 0.0	count
Graminoid heterogeneity (Egg vicinity)	-0.410	<0.01	0.2 ± 0.0	0.2 ± 0.0	index
Danthonia unispicata cover (Quadrat)	-0.366	<0.01	21.5 ± 20.6	10.3 ± 14.9	%
Poa pratensis cover (Egg vicinity)	-0.355	-	12.5 ± 11.4	6.3 ± 6.0	%
Litter depth (Egg vicinity)	-0.352	<0.01	0.7 ± 0.3	0.5 ± 0.5	cm2
Carex fracta cover (Quadrat)	-0.341	<0.05	4.2 ± 6.7	0.7 ± 2.2	%
Carex deflexa cover (Egg vicinity)	-0.333	<0.05	11.5 ± 12.3	4.3 ± 6.6	%
Soil moisture (Egg vicinity)	0.333	<0.01	59.7 ± 11.5	68.6 ± 13.8	%
Oviposition plant leaf density	-0.329	<0.05	2.3 ± 0.6	1.9 ± 0.6	category (1-4)
Number of blooming forbs within 5 m radius	0.325	<0.05	27.0 ± 21.4	42.6 ± 29.4	count
Graminoid heterogeneity (Quadrat)	-0.319	<0.05	0.4 ± 0.0	0.4 ± 0.0	index
Graminoid species evenness (Egg vicinity)	-0.311	-	0.5 ± 0.0	0.5 ± 0.0	index
Rock/pebble cover (Quadrat)	0.298	-	0.2 ± 0.4	1.1 ± 2.2	%
Danthonia unispicata cover (Egg vicinity)	-0.285	<0.05	19.4 ± 22.8	9.2 ± 14.8	%
Danthonia unispicata height (Quadrat)	-0.281	-	13.1 ± 5.7	8.9 ± 9.0	cm
Soil Ph (Egg vicinity)	-0.280	<0.05	6.3 ± 0.4	6.1 ± 0.4	scale
Carex deflexa cover (Quadrat)	-0.278	-	12.0 ± 12.0	6.0 ± 6.0	%
Danthonia unispicata height (Egg vicinity)	-0.274	<0.01	7.4 ± 5.7	3.5 ± 5.1	cm
Carex deflexa height (Egg vicinity)	-0.273	<0.05	6.1 ± 7.2	3.0 ± 4.2	cm
Poa pratensis height (Egg vicinity)	-0.234	-	12.0 ± 6.2	9.1 ± 6.6	cm
Oviposition plant maximum culm height	-0.211	-	4.1 ± 5.9	2.3 ± 5.4	cm
Number of blooming forbs (Quadrat)	0.195	-	7.5 ± 7.4	10.4 ± 11.0	count
Forb cover (Quadrat)	0.194	-	22.0 ± 8.2	25.7 ± 10.6	%
Shrub abundance within 10 m	0.189	-	0.6 ± 2.1	1.7 ± 3.5	count
Oviposition plant basal leaf height	-0.177	-	7.7 ± 3.2	7.1 ± 4.5	cm
Oviposition plant dead basal leaves	0.142	-	2.5 ± 2.8	4.4 ± 9.2	%
Forb cover (Egg vicinity)	-0.142	-	17.2 ± 11.6	14.6 ± 12.0	%
Carex hoodii cover (Quadrat)	-0.137	-	9.4 ± 7.5	7.6 ± 6.0	%
Distance to forest edge	0.130	-	17.4 ± 7.8	19.6 ± 8.1	meters
Carex hoodii height (Quadrat)	-0.124	-	20.1 ± 9.8	17.5 ± 11.4	cm
Distance to nearest tree	-0.124	-	16.4 ± 7.0	14.7 ± 7.0	meters
Percent slope relative to 20 m radius of quadrat	-0.108	-	0.9 ± 1.6	0.7 ± 0.9	%
Canopy cover	-0.096	-	7.9 ± 15.1	6.1 ± 7.6	%
Maximum plant height (Quadrat)	-0.091	-	26.0 ± 5.5	25.1 ± 6.3	cm
Poa pratensis height (Quadrat)	-0.088	-	20.5 ± 6.9	19.1 ± 9.5	cm
Carex deflexa height (Quadrat)	-0.084	-	5.9 ± 4.8	5.3 ± 4.9	cm
Oviposition plant nearest neighbor	0.067	-	2.8 ± 1.6	3.9 ± 5.4	cm
Litter cover (Quadrat)	-0.042	-	42.5 ± 23.7	40.9 ± 29.3	%
Cryptogram cover (Quadrat)	-0.041	-	8.8 ± 8.9	9.9 ± 15.6	%
Carex hoodii height (Egg vicinity)	-0.038	-	7.9 ± 10.3	7.2 ± 8.9	cm
Graminoid species evenness (Quadrat)	-0.025	-	0.9 ± 0.0	0.9 ± 0.0	index
Carex hoodii cover (Egg vicinity)	-0.023	-	6.9 ± 11.4	5.8 ± 8.5	%
Tree abundance within 10 m of quadrat	-0.021	-	1.1 ± 2.2	1.2 ± 2.8	count
Horizontal vegetation thickness at 0.3 m height	-	-	0.1 ± 0.2	0.1 ± 0.3	%
Horizontal vegetation thickness at 0.6 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Sapling abundance within 10 m of quadrat	-	-	0.2 ± 0.8	0.3 ± 1.3	count
Seedling abundance within 10 m of quadrat	-	-	0.0 ± 0.0	0.0 ± 0.0	count
Carex fracta cover (Egg vicinity)	-	-	1.9 ± 5.9	1.0 ± 3.8	%
Carex fracta height (Egg vicinity)	-	-	1.7 ± 4.8	0.7 ± 2.9	cm
Carex fracta height (Quadrat)	-	-	7.2 ± 9.9	2.2 ± 5.9	cm

Muddy Meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Soil Ph (Egg vicinity)	-0.477	<0.0001	6.1 ± 0.3	6.4 ± 0.3	Scale
Graminoid species richness (Quadrat)	0.474	<0.0001	6.4 ± 1.4	4.9 ± 1.5	Index
Danthonia intermedia height (Quadrat)	0.467	<0.01	29.9 ± 13.6	13.6 ± 17.7	cm
Danthonia intermedia cover (Quadrat)	0.441	<0.0001	20.5 ± 13.7	9.2 ± 17.3	%
Agrostis thurberiana cover (Quadrat)	0.429	<0.01	17.1 ± 24.7	3.5 ± 6.2	%
Vasscular plant cover (Quadrat)	0.422	<0.01	92.4 ± 12.9	79.8 ± 17.5	%
Danthonia intermedia height (Egg vicinity)	0.409	<0.01	17.4 ± 12.0	6.8 ± 12.1	cm
Forb cover (Quadrat)	0.407	<0.01	59.7 ± 19.1	41.0 ± 23.8	%
Horizontal vegetation thickness at 0.3 m height	-0.397	<0.01	4.2 ± 4.6	15.0 ± 17.6	%
Danthonia intermedia cover (Egg vicinity)	0.374	<0.01	12.3 ± 13.6	5.1 ± 13.5	%
Graminoid species richness (Egg vicinity)	0.368	<0.01	3.9 ± 1.1	3.0 ± 1.0	index
Agrostis thurberiana height (Quadrat)	0.358	<0.01	19.2 ± 12.1	9.0 ± 14.9	cm
Muhlenbergia filiformis cover (Quadrat)	0.349	<0.05	20.2 ± 22.6	7.5 ± 12.2	%
Forb cover (Egg vicinity)	0.348	<0.05	56.7 ± 20.7	39.6 ± 27.6	%
Stipa occidentalis cover (Quadrat)	-0.347	<0.05	3.2 ± 6.7	12.0 ± 15.3	%
Soil moisture (Egg vicinity)	0.323	<0.05	51.4 ± 11.5	42.3 ± 15.2	%
Horizontal vegetation thickness at 0.6 m height	-0.319	<0.05	0.1 ± 0.3	0.7 ± 1.4	%
Graminoid heterogeneity (Quadrat)	0.314	<0.01	0.6 ± 0.1	0.5 ± 0.1	index
Oviposition plant maximum culm height	0.304	<0.05	10.8 ± 14.5	3.8 ± 10.6	cm
Stipa occidentalis height (Quadrat)	-0.300	<0.05	11.8 ± 22.1	31.1 ± 33.1	cm
Oviposition plant basal leaf height	-0.295	<0.05	11.4 ± 6.4	16.4 ± 9.1	cm
Stipa occidentalis height (Egg vicinity)	-0.280	<0.05	4.8 ± 10.9	15.8 ± 22.2	cm
Maximum plant height (Quadrat)	-0.279	<0.05	47.3 ± 11.1	56.5 ± 16.7	cm
Oviposition plant dead basal leaves	-0.277	-	1.0 ± 2.2	3.1 ± 4.2	%
Agrostis thurberiana cover (Egg vicinity)	0.255	-	12.9 ± 26.6	2.3 ± 4.9	%
Oviposition plant nearest neighbor	-0.220	<0.05	4.0 ± 6.6	6.1 ± 7.9	cm
Oviposition plant leaf density	0.213	-	2.3 ± 0.9	1.9 ± 0.8	category (1-4)
Muhlenbergia filiformis height (Quadrat)	0.204	-	5.5 ± 4.7	3.5 ± 5.1	cm
Poa pratensis cover (Quadrat)	0.202	-	6.0 ± 6.6	3.6 ± 3.7	%
Distance to nearest visible water source	-0.196	-	29.7 ± 8.7	38.1 ± 17.4	meters
Stipa occidentalis cover (Egg vicinity)	-0.191	-	6.6 ± 19.5	12.5 ± 20.8	%
Number of blooming forbs within 5 m radius	0.175	-	28.2 ± 27.8	21.9 ± 26.8	count
Muhlenbergia filiformis cover (Egg vicinity)	0.174	-	12.8 ± 21.8	6.8 ± 12.7	%
Graminoid heterogeneity (Egg vicinity)	0.167	-	0.4 ± 0.2	0.4 ± 0.2	index
Total graminoid cover (Quadrat)	0.163	-	59.2 ± 23.8	52.5 ± 19.2	%
Calamagrostis canadensis height (Quadrat)	0.160	-	3.9 ± 10.7	1.9 ± 10.4	cm
Cryptogram cover (Quadrat)	0.158	-	14.0 ± 23.5	7.5 ± 10.8	%
Total graminoid cover (Egg vicinity)	0.153	-	52.8 ± 24.5	46.5 ± 20.4	%
Agrostis thurberiana height (Egg vicinity)	0.139	-	7.6 ± 10.7	4.8 ± 9.4	cm
Tree abundance within 10 m of quadrat	-0.135	-	4.7 ± 8.5	6.7 ± 12.0	count
Distance to nearest tree	0.134	-	11.9 ± 5.8	10.1 ± 4.5	meters
Bare ground cover (Quadrat)	-0.133	-	2.7 ± 10.2	5.5 ± 15.5	%
Percent slope relative to 20 m radius of quadrat	0.133	-	4.3 ± 4.1	3.5 ± 4.8	%
Sapling abundance within 10 m of quadrat	-0.117	-	1.4 ± 3.3	2.6 ± 5.2	count
Calamagrostis canadensis height (Egg vicinity)	0.113	-	1.0 ± 5.3	1.9 ± 10.4	cm
Canopy cover	-0.108	-	5.3 ± 6.0	6.6 ± 6.8	%
Seedling abundance within 10 m of quadrat	-0.075	-	1.4 ± 2.4	2.1 ± 4.3	count
Graminoid species evenness (Egg vicinity)	-0.074	-	0.7 ± 0.3	0.7 ± 0.3	index
Poa pratensis cover (Egg vicinity)	0.070	-	3.1 ± 4.7	2.7 ± 4.0	%
Graminoid species evenness (Quadrat)	-0.059	-	0.8 ± 0.1	0.8 ± 0.1	index
Litter cover (Quadrat)	-0.054	-	80.2 ± 24.8	83.1 ± 23.2	%
Muhlenbergia filiformis height (Egg vicinity)	0.053	-	3.1 ± 3.7	2.6 ± 4.6	cm
Number of blooming forbs (Quadrat)	-0.037	-	7.4 ± 14.7	6.9 ± 9.3	count
Poa pratensis height (Quadrat)	0.035	-	24.6 ± 16.5	23.4 ± 19.4	cm
Oviposition plant footprint	-0.019	-	78.6 ± 113.6	87.4 ± 133.5	cm^2
Litter depth (Egg vicinity)	-0.019	-	1.8 ± 1.1	1.9 ± 1.3	cm
Distance to forest edge	0.014	-	36.1 ± 16.6	35.7 ± 16.2	meters
Poa pratensis height (Egg vicinity)	-0.014	-	9.8 ± 11.0	10.2 ± 15.8	cm
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Rock/pebble cover (Quadrat)	-	-	0.1 ± 0.4	0.2 ± 0.7	%
Shrub abundance within 10 m	-	-	0.3 ± 1.8	0.9 ± 3.8	count
Calamagrostis canadensis cover (Egg vicinity)	-	-	0.8 ± 4.6	0.3 ± 1.8	%
Calamagrostis canadensis cover (Quadrat)	-	-	2.0 ± 6.5	1.2 ± 6.4	%

Midway Meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Poa pratensis height (Quadrat)	-0.456	-	31.3 ± 9.1	41.1 ± 11.2	cm
Poa pratensis cover (Quadrat)	0.364	-	28.8 ± 24.1	15.1 ± 10.8	%
Total graminoid cover (Quadrat)	0.354	<0.05	49.0 ± 20.5	36.2 ± 14.6	%
Bare ground cover (Quadrat)	-0.351	<0.05	5.4 ± 6.7	15.8 ± 20.0	%
Number of blooming forbs (Quadrat)	0.318	<0.05	3.5 ± 3.2	2.3 ± 2.3	count
Poa pratensis cover (Egg vicinity)	0.305	-	23.4 ± 21.7	12.7 ± 11.1	%
Soil moisture (Egg vicinity)	0.305	<0.05	32.1 ± 9.6	25.4 ± 12.4	%
Oviposition plant leaf density	0.293	<0.05	2.0 ± 0.6	1.7 ± 0.5	category (1-4)
Maximum plant height (Quadrat)	-0.289	<0.05	39.6 ± 10.6	45.5 ± 11.4	cm
Litter cover (Quadrat)	0.287	-	86.6 ± 11.1	74.9 ± 24.4	%
Litter depth (Egg vicinity)	0.280	-	1.1 ± 0.7	0.8 ± 0.6	cm
Rock/pebble cover (Quadrat)	-0.269	-	0.1 ± 0.3	0.3 ± 0.5	%
Total graminoid cover (Egg vicinity)	0.253	-	38.8 ± 22.5	29.4 ± 13.8	%
Carex hoodii cover (Egg vicinity)	0.232	-	3.0 ± 8.9	0.2 ± 0.9	%
Poa pratensis height (Egg vicinity)	-0.226	-	14.3 ± 4.9	20.5 ± 10.6	cm
Carex fracta height (Egg vicinity)	-0.224	-	10.6 ± 12.0	16.1 ± 13.2	cm
Vasscular plant cover (Quadrat)	0.218	-	70.5 ± 17.3	62.2 ± 20.1	%
Graminoid species evenness (Quadrat)	-0.199	-	0.8 ± 0.2	0.8 ± 0.2	Index
Carex hoodii height (Quadrat)	0.194	-	7.5 ± 15.4	2.6 ± 10.1	cm
Oviposition plant footprint	0.189	-	33.6 ± 45.4	30.9 ± 61.3	cm2
Carex hoodii cover (Quadrat)	0.187	-	3.0 ± 7.5	1.0 ± 4.0	%
Forb cover (Quadrat)	-0.184	-	29.0 ± 16.6	35.7 ± 21.2	%
Number of blooming forbs within 5 m radius	0.176	-	12.3 ± 8.9	7.7 ± 6.1	count
Graminoid species evenness (Egg vicinity)	-0.173	-	0.7 ± 0.3	0.8 ± 0.2	Index
Carex hoodii height (Egg vicinity)	0.158	-	2.9 ± 7.5	0.9 ± 5.1	cm
Bromus carinatus height (Egg vicinity)	0.147	-	10.3 ± 10.7	7.7 ± 8.1	cm
Seedling abundance within 10 m of quadrat	0.136	-	0.9 ± 2.4	0.4 ± 1.0	count
Stipa occidentalis height (Quadrat)	-0.135	-	7.3 ± 17.1	10.6 ± 17.5	cm
Graminoid heterogeneity (Quadrat)	-0.122	-	0.5 ± 0.2	0.5 ± 0.2	Index
Cryptogram cover (Quadrat)	0.109	-	4.9 ± 7.8	3.5 ± 5.5	%
Hordeum brachyantherum cover (Quadrat)	-0.099	-	0.5 ± 1.2	1.1 ± 3.3	%
Sapling abundance within 10 m of quadrat	-0.090	-	0.4 ± 1.0	0.5 ± 0.9	count
Oviposition plant dead basal leaves	0.087	-	1.5 ± 1.9	1.6 ± 5.5	%
Horizontal vegetation thickness at 0.3 m height	-0.085	-	1.6 ± 2.2	2.3 ± 3.9	%
Carex fracta cover (Quadrat)	-0.084	-	11.8 ± 8.5	13.7 ± 10.2	%
Distance to forest edge	0.084	-	57.0 ± 14.1	55.2 ± 15.4	meters
Oviposition plant basal leaf height	-0.083	-	9.5 ± 3.5	10.2 ± 4.9	cm
Forb cover (Egg vicinity)	0.070	-	27.4 ± 18.0	25.2 ± 18.3	%
Graminoid heterogeneity (Egg vicinity)	-0.069	-	0.3 ± 0.2	0.4 ± 0.1	Index
Bromus carinatus cover (Quadrat)	0.068	-	6.1 ± 5.0	5.6 ± 4.4	%
Distance to nearest tree	0.062	-	21.9 ± 10.2	20.7 ± 10.4	meters
Distance to nearest visible water source (m)	-0.060	-	44.9 ± 21.2	46.7 ± 18.8	meters
Bromus carinatus cover (Egg vicinity)	0.058	-	5.1 ± 6.7	4.4 ± 6.0	%
Stipa occidentalis cover (Quadrat)	-0.051	-	1.8 ± 4.0	2.1 ± 4.2	%
Hordeum brachyantherum height (Quadrat)	-0.044	-	2.7 ± 7.0	5.3 ± 13.4	cm
Graminoid species richness (Quadrat)	0.039	-	4.3 ± 1.2	4.2 ± 1.5	Index
Graminoid species richness (Egg vicinity)	-0.032	-	2.8 ± 1.1	2.9 ± 1.1	Index
Oviposition plant nearest neighbor	0.031	-	3.5 ± 5.3	2.7 ± 2.0	cm
Bromus carinatus height (Quadrat)	0.028	-	28.6 ± 15.5	27.7 ± 19.1	cm
Carex fracta height (Quadrat)	-0.021	-	25.6 ± 12.5	26.1 ± 13.2	cm
Canopy cover	-0.019	-	0.6 ± 1.9	0.6 ± 1.5	%
Oviposition plant maximum culm height	-0.002	-	2.1 ± 5.2	3.4 ± 9.0	cm
Soil Ph (Egg vicinity)	-	-	6.6 ± 0.2	6.6 ± 0.2	Scale
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Horizontal vegetation thickness at 0.6 m height	-	-	0.0 ± 0.0	0.1 ± 0.3	%
Tree abundance within 10 m of quadrat	-	-	1.5 ± 3.0	1.6 ± 3.6	count
Shrub abundance within 10 m	-	-	0.0 ± 0.2	0.3 ± 1.8	count
Percent slope relative to 20 m radius of quadrat	-	-	5.0 ± 0.0	5.0 ± 0.0	%
Carex fracta cover (Egg vicinity)	-	-	6.4 ± 8.8	11.6 ± 14.1	%
Hordeum brachyantherum cover (Egg vicinity)	-	-	0.3 ± 1.8	0.2 ± 0.9	%
Hordeum brachyantherum height (Egg vicinity)	-	-	0.3 ± 1.8	0.5 ± 2.9	cm
Stipa occidentalis cover (Egg vicinity)	-	-	0.4 ± 1.3	1.9 ± 4.8	%
Stipa occidentalis height (Egg vicinity)	-	-	2.3 ± 7.7	4.0 ± 8.3	cm

Peterson Prairie Meadow			Location		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Distance to forest edge	0.521	<0.0001	54.2 ± 11.8	37.7 ± 17.0	meters
Distance to nearest tree	0.509	<0.0001	39.1 ± 12.5	23.5 ± 15.8	meters
Canopy cover	-0.501	-	0.4 ± 1.1	7.3 ± 10.9	%
Poa pratensis cover (Quadrat)	0.494	<0.0001	17.0 ± 8.8	9.5 ± 5.5	%
Total graminoid cover (Quadrat)	0.461	<0.01	36.2 ± 11.9	25.5 ± 10.7	%
Soil Ph (Egg vicinity)	0.390	-	6.8 ± 0.2	6.6 ± 0.3	Scale
Poa pratensis cover (Egg vicinity)	0.390	-	8.2 ± 6.0	4.6 ± 4.3	%
Maximum plant height (Quadrat)	-0.367	<0.01	28.5 ± 7.5	34.1 ± 8.1	cm
Total graminoid cover (Egg vicinity)	0.347	<0.01	24.3 ± 10.8	17.7 ± 10.0	%
Carex hoodii height (Quadrat)	0.335	<0.05	7.4 ± 11.7	1.4 ± 5.3	cm
Oviposition plant dead basal leaves	-0.331	<0.05	1.6 ± 3.7	4.8 ± 6.8	%
Tree abundance within 10 m of quadrat	-0.324	<0.01	0.1 ± 0.3	2.9 ± 6.1	count
Litter cover (Quadrat)	0.318	<0.05	82.9 ± 16.3	67.6 ± 27.8	%
Percent slope relative to 20 m radius of quadrat	0.295	-	0.8 ± 1.9	0.0 ± 0.2	%
Carex praticola cover (Quadrat)	0.279	<0.05	12.3 ± 8.7	7.8 ± 5.8	%
Soil moisture (Egg vicinity)	-0.274	-	28.9 ± 11.8	35.8 ± 16.2	%
Seedling abundance within 10 m of quadrat	-0.273	-	0.1 ± 0.3	1.4 ± 3.2	count
Oviposition plant footprint	0.271	<0.05	50.2 ± 47.7	25.0 ± 35.1	cm^2
Carex hoodii cover (Quadrat)	0.265	<0.05	2.5 ± 4.5	0.6 ± 2.8	%
Oviposition plant leaf density	0.257	-	1.8 ± 0.4	1.5 ± 0.5	category (1-4)
Carex hoodii height (Egg vicinity)	0.255	-	3.8 ± 8.7	0.8 ± 4.6	cm
Forb cover (Egg vicinity)	-0.248	-	26.0 ± 12.3	33.0 ± 16.6	%
Horizontal vegetation thickness at 0.3 m height	-0.245	<0.01	0.2 ± 0.9	2.3 ± 8.3	%
Cryptogram cover (Quadrat)	-0.225	-	5.7 ± 8.7	12.0 ± 17.7	%
Rock/pebble cover (Quadrat)	-0.220	-	0.0 ± 0.2	0.2 ± 0.6	%
Forb cover (Quadrat)	-0.217	-	31.2 ± 16.4	38.7 ± 19.3	%
Graminoid species evenness (Quadrat)	-0.213	-	0.8 ± 0.1	0.9 ± 0.1	Index
Carex hoodii cover (Egg vicinity)	0.197	-	1.6 ± 4.5	0.3 ± 1.8	%
Carex praticola height (Egg vicinity)	-0.190	-	9.4 ± 6.9	11.9 ± 7.3	cm
Shrub abundance within 10 m	-0.186	<0.05	0.1 ± 0.4	2.4 ± 9.2	count
Oviposition plant maximum culm height	0.183	-	3.1 ± 8.5	0.8 ± 4.6	cm
Carex praticola cover (Egg vicinity)	0.181	-	9.6 ± 8.8	6.9 ± 6.6	%
Bare ground cover (Quadrat)	-0.173	-	3.1 ± 4.1	6.6 ± 11.6	%
Oviposition plant basal leaf height	-0.171	-	12.8 ± 4.2	14.6 ± 5.9	cm
Stipa occidentalis cover (Quadrat)	0.162	<0.05	5.5 ± 3.1	4.8 ± 4.7	%
Graminoid heterogeneity (Quadrat)	-0.152	-	0.5 ± 0.1	0.5 ± 0.1	Index
Poa pratensis height (Quadrat)	-0.142	-	23.0 ± 8.7	25.9 ± 12.3	cm
Oviposition plant nearest neighbor	-0.129	-	5.5 ± 10.1	4.8 ± 3.0	cm
Carex halliana cover (Egg vicinity)	-0.107	-	0.6 ± 2.0	1.1 ± 2.7	%
Carex halliana height (Egg vicinity)	-0.092	-	2.3 ± 5.3	3.3 ± 6.6	cm
Carex halliana cover (Quadrat)	0.082	-	1.5 ± 1.6	1.3 ± 2.1	%
Graminoid species richness (Egg vicinity)	-0.078	-	2.3 ± 0.6	2.4 ± 0.7	Index
Carex praticola height (Quadrat)	-0.069	-	14.7 ± 6.4	15.7 ± 8.3	cm
Graminoid species richness (Quadrat)	-0.061	-	4.2 ± 0.8	4.3 ± 0.9	Index
Stipa occidentalis height (Quadrat)	-0.061	-	21.8 ± 6.4	24.5 ± 10.1	cm
Graminoid heterogeneity (Egg vicinity)	-0.060	-	0.3 ± 0.1	0.3 ± 0.1	Index
Number of blooming forbs within 5 m radius	0.043	-	52.5 ± 35.8	47.5 ± 26.6	count
Carex halliana height (Quadrat)	0.036	-	8.3 ± 8.0	7.7 ± 8.8	cm
Litter depth (Egg vicinity)	0.028	-	1.2 ± 0.9	1.2 ± 1.0	cm
Graminoid species evenness (Egg vicinity)	0.021	-	0.8 ± 0.3	0.8 ± 0.3	Index
Poa pratensis height (Egg vicinity)	-0.016	-	15.5 ± 5.4	15.7 ± 8.0	cm
Vasscular plant cover (Quadrat)	-0.007	-	56.5 ± 16.8	56.7 ± 20.7	%
Number of blooming forbs (Quadrat)	0.002	-	22.0 ± 22.7	16.8 ± 13.4	count
Horizontal vegetation thickness at 0.6 m height	-	-	0.0 ± 0.0	0.0 ± 0.2	%
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Sapling abundance within 10 m of quadrat	-	-	0.0 ± 0.0	0.6 ± 1.9	count
Stipa occidentalis cover (Egg vicinity)	-	-	2.2 ± 2.8	2.9 ± 5.3	%
Stipa occidentalis height (Egg vicinity)	-	-	9.9 ± 9.7	8.4 ± 9.9	cm
Danthonia unispicata cover (Egg vicinity)	-	-	0.7 ± 0.9	0.0 ± 0.0	%
Danthonia unispicata cover (Quadrate)	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Danthonia unispicata height (Egg vicinity)	-	-	0.2 ± 1.3	0.0 ± 0.0	cm
Danthonia unispicata height (Quadrat)	-	-	0.0 ± 0.0	0.0 ± 0.0	cm

Smith Butte Meadow			*Location*		
Variable	Total Structure Coefficient	Significance	Oviposition	Random	Unit
Oviposition plant leaf density	-0.694	<0.0001	2.2 ± 0.4	1.5 ± 0.5	category (1-4)
Festuca idahoensis cover (Egg vicinity)	-0.686	<0.0001	23.2 ± 14.3	6.5 ± 9.3	%
Festuca idahoensis height (Egg vicinity)	-0.649	<0.0001	18.8 ± 7.1	7.9 ± 7.9	cm
Festuca idahoensis cover (Quadrat)	-0.505	<0.001	23.5 ± 14.2	11.5 ± 11.2	%
Oviposition plant footprint	-0.503	<0.0001	76.4 ± 61.3	40.9 ± 116.0	cm2
Distance to forest edge	-0.459	<0.001	16.2 ± 3.9	12.4 ± 4.3	meters
Festuca rubra height (Quadrat)	0.418	<0.001	2.1 ± 8.2	13.5 ± 17.8	cm
Festuca rubra cover (Quadrat)	0.416	<0.01	1.0 ± 4.6	5.9 ± 8.2	%
Percent slope relative to 20 m radius of quadrat	-0.404	<0.01	28.0 ± 6.1	22.5 ± 7.7	%
Horizontal vegetation thickness at 0.3 m height	0.402	<0.05	5.3 ± 4.4	26.6 ± 32.9	%
Horizontal vegetation thickness at 0.6 m height	0.377	<0.01	0.0 ± 0.0	0.7 ± 1.4	%
Festuca idahoensis height (Quadrat)	-0.376	<0.01	26.1 ± 11.6	16.4 ± 14.8	cm
Festuca rubra height (Egg vicinity)	0.373	<0.01	0.9 ± 5.1	6.9 ± 11.9	cm
Litter depth (Egg vicinity)	0.364	<0.05	2.5 ± 1.3	4.3 ± 2.8	cm
Maximum plant height (Quadrat)	0.266	-	46.8 ± 8.4	52.4 ± 12.2	cm
Festuca rubra cover (Egg vicinity)	0.263	<0.01	0.3 ± 1.8	3.0 ± 7.4	%
Forb cover (Quadrat)	0.255	-	7.8 ± 4.8	9.4 ± 3.2	%
Soil Ph (Egg vicinity)	-0.206	-	6.8 ± 0.1	6.7 ± 0.2	Scale
Distance to nearest tree	-0.201	-	12.3 ± 5.1	10.5 ± 4.6	meters
Soil moisture (Egg vicinity)	0.182	-	23.7 ± 7.3	27.4 ± 10.8	%
Canopy cover	0.168	-	10.4 ± 3.9	12.7 ± 7.0	%
Graminoid heterogeneity (Egg vicinity)	-0.158	-	0.4 ± 0.1	0.4 ± 0.1	Index
Graminoid heterogeneity (Quadrat)	-0.157	-	0.6 ± 0.1	0.5 ± 0.1	Index
Graminoid species evenness (Egg vicinity)	-0.156	-	0.8 ± 0.1	0.8 ± 0.2	Index
Bare ground cover (Quadrat)	-0.156	-	15.7 ± 18.1	12.1 ± 14.1	%
Total graminoid cover (Quadrat)	0.149	-	53.2 ± 18.1	57.7 ± 16.1	%
Graminoid species richness (Egg vicinity)	-0.145	-	4.5 ± 0.6	4.2 ± 1.1	Index
Litter cover (Quadrat)	0.127	-	77.5 ± 22.4	81.5 ± 20.2	%
Graminoid species richness (Quadrat)	-0.118	-	3.3 ± 0.8	3.1 ± 1.0	Index
Vasscular plant cover (Quadrat)	0.108	-	58.0 ± 19.3	61.5 ± 16.1	%
Tree abundance within 10 m of quadrat	0.108	-	0.7 ± 1.3	1.0 ± 1.9	count
Number of blooming forbs (Quadrat)	0.085	-	0.4 ± 0.7	0.6 ± 1.1	count
Graminoid species evenness (Quadrat)	-0.081	-	0.9 ± 0.1	0.8 ± 0.1	Index
Forb cover (Egg vicinity)	0.080	-	5.9 ± 5.1	6.7 ± 5.4	%
Oviposition plant basal leaf height	0.079	-	16.7 ± 4.7	17.8 ± 9.2	cm
Sapling abundance within 10 m of quadrat	-0.079	-	0.2 ± 0.6	0.2 ± 0.9	count
Rock/pebble cover (Quadrat)	-0.071	-	1.1 ± 1.5	0.9 ± 1.3	%
Shrub abundance within 10 m	0.061	-	1.3 ± 1.7	2.3 ± 4.3	count
Oviposition plant nearest neighbor	-0.045	-	4.0 ± 3.2	3.6 ± 2.2	cm
Number of blooming forbs within 5 m radius	-0.044	-	1.8 ± 1.6	1.7 ± 1.9	count
Total graminoid cover (Egg vicinity)	-0.012	-	42.7 ± 17.5	42.5 ± 22.1	%
Oviposition plant dead basal leaves	-0.003	-	1.3 ± 1.3	1.6 ± 2.8	%
Oviposition plant maximum culm height	-	-	2.6 ± 9.9	0.0 ± 0.0	cm
Cryptogram cover (Quadrat)	-	-	0.0 ± 0.2	0.0 ± 0.0	%
Horizontal vegetation thickness at 0.9 m height	-	-	0.0 ± 0.0	0.0 ± 0.0	%
Seedling abundance within 10 m of quadrat	-	-	0.0 ± 0.0	0.0 ± 0.0	count

Appendix F: Within Meadow DFA λ, r2, and Class Mean Values

			Class Means	
Meadow	λ	r^2	Oviposition	Random
7A	80.2	0.98	8.8	-8.8
Cave Creek	16.2	0.94	-4	3.9
Flog Salvage	11.9	0.92	3.4	-3.4
Grapefern	96.2	0.99	9.6	-9.6
Lost	17.3	0.95	-4.1	4.1
Midway	12.5	0.93	3.5	-3.5
Muddy	554.5	0.99	23.2	-23.2
Peterson Prairie	9.7	0.91	3.1	-3.1
Smith Butte	4.6	0.82	-2.3	2.3

Appendix E: Temperature and Relative Humidity
Data from four iButton data loggers placed in six Mardon skipper Meadows, Standard deviation = SD. Temperature in degrees Celsius.

Meadow	Season		Mean		SD	Minimum	Maximum
7A	Fall	Temp	4.04	±	6.71	-5.99	39.63
		RH	100.44	±	18.70	11.13	113.83
	Winter	Temp	0.00	±	0.30	-0.44	0.60
		RH	112.01	±	1.62	109.42	115.98
	Spring	Temp	-0.17	±	0.27	-0.44	0.60
		RH	112.25	±	2.31	107.93	116.46
	Summer	Temp	11.81	±	10.33	-1.96	46.59
		RH	92.68	±	23.73	14.13	115.50
Bunny Hill	Fall	Temp	10.39	±	11.14	-5.48	50.04
		RH	48.76	±	43.83	-3.93	112.52
	Winter	Temp	0.22	±	0.27	-0.47	0.60
		RH	110.71	±	1.24	106.82	113.98
	Spring	Temp	3.15	±	7.50	-3.42	47.62
		RH	106.59	±	15.41	23.58	114.98
	Summer	Temp	17.18	±	12.24	-0.94	56.03
		RH	38.09	±	34.61	2.61	114.35
Flog	Fall	Temp	6.36	±	11.39	-16.51	44.64
		RH	94.08	±	23.03	15.50	116.39
	Winter	Temp	0.06	±	0.11	-0.43	0.10
		RH	110.96	±	1.73	106.35	115.38
	Spring	Temp	0.77	±	3.70	-5.45	35.67
		RH	111.21	±	6.71	25.12	118.41
	Summer	Temp	0.77	±	12.74	-6.45	41.60
		RH	111.21	±	25.22	20.78	118.91
Grapefern	Fall	Temp	4.53	±	7.09	-6.41	37.20
		RH	98.43	±	19.12	12.54	114.08
	Winter	Temp	4.53	±	0.26	-0.46	0.13
		RH	98.43	±	39.07	29.72	112.43
	Spring	Temp	-0.16	±	0.26	-0.44	0.13
		RH	82.84	±	39.07	-4.22	112.92
	Summer	Temp	-0.16	±	10.54	-3.39	43.61
		RH	82.84	±	29.98	-21.59	111.69
Lost	Fall	Temp	5.87	±	7.77	-5.97	36.13
		RH	95.29	±	21.51	13.58	113.95
	Winter	Temp	14.15	±	0.24	-0.44	0.61
		RH	82.91	±	1.62	105.64	113.88
	Spring	Temp	1.07	±	3.95	-0.94	32.15
		RH	109.71	±	6.70	37.80	114.50

Meadow	Season		Mean		SD	Minimum	Maximum
	Summer	Temp	14.15	±	9.52	-1.44	41.62
		RH	82.91	±	25.78	13.94	111.44
Peterson	Fall	Temp	5.60	±	9.08	-9.46	47.08
		RH	100.87	±	18.92	20.22	116.92
	Winter	Temp	0.13	±	0.16	0.06	1.08
		RH	108.51	±	7.36	89.27	116.40
	Spring	Temp	0.95	±	3.38	-0.90	29.17
		RH	105.13	±	13.40	37.56	115.89
	Summer	Temp	14.62	±	11.10	-4.93	48.12
		RH	89.28	±	23.27	15.16	113.29