University of Alberta

Beyond the host plant: Multi-scale habitat models for a northern peripheral population of the butterfly, *Apodemia mormo* (Lepidoptera: Riodinidae)

by

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ABSTRACT

The Mormon metalmark (*Apodemia mormo*) butterfly is widely distributed throughout western North America. It is listed as threatened, however, in Saskatchewan, Canada because of a small population size within a restricted habitat. To most effectively manage for this species, land managers and conservationists require a more thorough understanding of its ecology and habitat. I completed three studies that advance the understanding of this threatened butterfly. First, in a microhabitat study I showed that host plant abundance, soil chemistry, and microtopography are important in determining whether a butterfly habitat is occupied. Second, I developed and evaluated the prediction accuracy of species distribution models using two modeling techniques, the results of which increased the known *A. mormo* colonies in Saskatchewan from 37 to 88. Finally, I document the oviposition of *A. mormo* in Canada, showing that northern peripheral populations of this butterfly exhibit reproductive strategies divergent from those in its central range.

Keywords: *Apodemia mormo*, *Eriogonum pauciflorum*, species distribution modeling, microhabitat, Grasslands National Park, Saskatchewan, Conservation

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I.

The ecology and natural history of the Mormon metalmark

Introduction

Butterflies (Lepidoptera) are taxonomically well known, relatively easy to find, have short life cycles that are easy to work with, and, are charismatic. It is therefore no surprise that, for modern-day research, butterflies are the insect group most frequently modeled for development and testing of ecological theory (Thomas 2005).

Life history and basic ecology of a species can sometimes be overlooked, especially in the case of outlier, or peripheral, populations. In this introductory chapter I first present an overview of the biology and ecology of my study subject, the Mormon metalmark (Lepidoptera: Riodinidae *Apodemia mormo* Felder & Felder 1859), a butterfly listed as threatened in the far reaches of its northern range in Saskatchewan, Canada (COSEWIC 2003). Second, I describe the study sites, Grasslands National Park (GNP) and the neighboring Val Marie Community Pasture (VMCP), both located in extreme southwestern Saskatchewan. Next, I summarize previous studies on *A. mormo* and related species. Lastly, I present my objectives for the following chapters of this thesis and describe how they relate to the current conservation needs of the species.

Natural history of A. mormo

Apodemia mormo is a small-bodied (wing span 25-32 mm) butterfly of the family Riodinidae (Layberry *et al.* 1998; COSEWIC 2003). The metalmarks belong to the superfamily Papilionidea, or the true butterflies. Riodinids, or the metalmarks, are so-named because of metallic marks on the wings of many species. The name “Mormon metalmark” occasionally elicits curiosity as to its etymology. In fact, Felder & Felder were mistaken when they gave the butterfly its “Mormon” moniker. The

Felders were stay-at-home taxonomists who would receive specimens from others on field expeditions. When they gave the species name to this *Apodemia* they thought that the type specimens had come from Utah, when in fact they were mistaken and the specimens were from Nevada. In the end, this butterfly was left with a name, albeit inaccurate, that endures in naturalists' memories.

Worldwide there are over 1400 species of metalmarks, only 24 of which are found in North America (Scott 1986; Layberry *et al.* 1998; Pelham 2008). According to Opler & Powell (1962), *A. mormo* was originally 5 allopatric species, but these have all been reduced to subspecies in taxonomic revisions. *Apodemia mormo* is the most widespread riodinid in North America, with a range that extends from northwest Mexico throughout the western United States and up into southern Canada (Scott 1986; Layberry *et al.* 1998). It is the only riodinid found in Canada (Layberry *et al.* 1998) with a distribution that becomes more isolated and disjunct in its northern range (COSEWIC 2003). It is polytypic with respect to the array of *Eriogonum* host species it uses, and in the diversity of adult size and color across its range (Opler & Powell 1962; Powell 1975).

The Canadian populations represent less than 1% of *A. mormo*'s total population and global range (Cannings *et al.* 1998). Two *A. mormo* populations have been documented in Canada: an endangered population in the Similkameen River Valley of British Columbia and a threatened population in the mixed grass prairies of southern Saskatchewan (COSEWIC 2003). The two listings were given originally by the Committee on the Status of Endangered Wildlife in Canada under the Federal Species At Risk Act (SARA; COSEWIC 2003). The prairie population in Saskatchewan is part of a northern outlier population that continues into the United States along the Milk and Missouri Rivers and their tributaries, but is disjunct (or spatially separate) from the main part of the distribution in the southwestern USA (Opler 1999; Pruss *et al.* 2008). The listing in Saskatchewan is based on the extreme fluctuations of populations from year to year and its occurrence in a highly restricted habitat (COSEWIC 2003; Pruss *et al.* 2008). Habitat loss and fragmentation, exotic species, pollution from agrochemicals, and climate change could pose additional threats to the already rare butterfly in Saskatchewan (Pruss *et* *al.* 2008). *Apodemia mormo* (including subspecies) remains the only member of its family in the world to be listed, although this may be attributed to a lack of information about many riodinids that reside in the hyper-biodiverse and loosely regulated neotropical forests.

Apodemia mormo utilizes various species of *Eriogonum*, a buckwheat of the family Polygonaceae, as its larval food plant throughout its range. The Saskatchewan population uses the branched umbrella plant (Polygonaceae: *Eriogonum pauciflorum*) as its host plant and nectar source (Pruss *et al.* 2008). Although *E. pauciflorum* is abundant in and around GNP, it appears that *A. mormo* does not occupy many of the seemingly suitable host plant habitat patches. It is possible that there may be other biotic and/or abiotic variables affecting whether or not a given patch of habitat to be suitable *A. mormo*. The adult butterfly uses rubber rabbitbrush (Asteraceae: *Ericameria nauseosa*) as a secondary nectar source particularly during the latter part of the flight season when *Eriogonum* spp. may be deteriorating (Hooper 2002). The butterfly also tends to perch on other substrates found in badland habitat where *Eriogonum* spp. is plentiful, such as rocks and bare soil, creeping juniper (*Juniperus horizontalis* Moench), sagebrush (*Artemisia cana* Pursh), wolf-willow (*Elaeagnus commutate* Bernh. Ex Rydb) and buffalo berry shrubs (*Sheperdia argentea* Nutt.; Hooper 2002; Wick pers. obs.).

The Saskatchewan population is markedly univoltine with a staggered emergence of adults at the beginning of August that diminishes towards the end of the month. However, depending on weather, it may fly from mid-July into September (Henderson *et al.* 2008; Wick pers. obs.). Its flight and breeding are mostly synchronized with the flowering of *E. pauciflorum*. Within its lifespan, which is about 10 days, the butterfly emerges, mates, and females oviposit their eggs (Pruss *et al.* 2008; Wick pers. obs.). The peak adult population in Saskatchewan is reached in the second and third weeks of the flight period in mid-August, but may vary depending on temperature and drought conditions. According to Howe (1975), in other parts of its range the butterfly overwinters as young larvae in the stems of *Eriogonum* spp. or under litter. It is currently unverified at what stage the butterfly overwinters in Saskatchewan.

Study sites

In this research I attempt to examine and define the occupied habitat conditions of *A. mormo* in its northern peripheral range in Saskatchewan. I conducted these studies in Grasslands National Park (GNP; 49° 15’ N, 107° 0’ W), which is located in extreme southern Saskatchewan, in May and June of 2011. Long, cold, dry winters and short, hot, humid summers characterize its sub-humid climate. Mean daily temperatures for Val Marie, Saskatchewan range from -12.4° C in January to 18.3° C in July with temperature extremes in January of -49.4 C and July 41.1C (Environment Canada 2012). There are 170 days between killing frosts (Frid & Wilmhurst 2009).

Of the 52,700 ha that comprise GNP, approximately 29,000 ha are sparsely vegetated badland habitat, also referred to as eroded communities, and the remaining is classified as upland and lowland grasslands (Michalsky & Ellis 1994). Based on data from field surveys summarized in this thesis, I estimate that there are approximately 4017 ha with significant *E. paciflorum* coverage within GNP (Wick unpublished data). The park is divided into two main areas, the East Block and the West Block, separated by approximately 40 km of pasture and farmland. The East Block, surrounded by the Wood Mountain plateau, includes much of Rock Creek; the West Block surrounds the Frenchman River valley southeast of the village of Val Marie (Saskatchewan Institute of Pedology 1992). The West Block of the Park is home to a herd of plains bison (*Bison bison*) which are stocked at a rate of 1 bison per 55 ha (W. Olson pers. com. 2012), as well as many SARA listed species, such as the greater sage grouse (*Centrocercus urophasianus*), greater short horned lizard (*Phynosoma hernandesi*), and Sprague’s pippet (*Anthus spragueii*). A variety of wildlife unique to Canada, GNP is ecologically valuable. Threats to wildlife within the Park include invasion by exotic species such as yellow sweet clover (*Melilotus officinalis*), crested wheatgrass (*Agropyron cristatum*), and smooth brome (*Bromus inermis*) (Pruss et al. 2003).

Because several *A. mormo* colonies have been documented there, I included the Val Marie Community Pasture (VMCP; 49° 41' N, 107 °92' W), which is located several kilometers northwest of GNP. The VMCP was originally created as part of the Prairie Farm Rehabilitation Administration but has since been integrated into the Agri-Environment Services Branch. The pasture is made of up 40,649 ha of varied topography much like GNP, and is grazed by at a rate of 1 cow per 35 hectares (T. Dyck pers. com. 2012). The VMCP is communally grazed by cattle from around the 1st of May until the end of October and patrons are charged 43 cents per day per cow plus $20/year fee for each calf.

Previous studies on Apodemia mormo

Apodemia mormo consists of a complex of allopatrically separated populations in North America, with 17 recognized subspecies, 15 of which are found in California (Pelham 2008; USFWS 2001). One subspecies, Lange's metalmark (*Apodemia mormo langei*), was described in 1938 and is noteworthy because it has been closely studied after being one of the first insects to be listed as endangered under the Endangered Species Act of the United States (ESA; Arnold & Powell 1983; Morse 2009; Johnson *et al.* 2011). Lange's metalmark is endemic to the Antioch Dunes of Contra Costa County, California (USFWS 2001). In 1983, Arnold & Powell (1983) reported densities of 28.7 males/acre and 41.8 females/acre and found that adults of both sexes lived about one week. There are two populations within the dunes with only minimal gene flow between them, even though less than a mile separates them. According to Arnold & Powell (1983), only one marked individual (a male) traversed the gap in several years of study. Lange's metalmark employs naked stem buckwheat (*Eriognoum nudum ssp. auriculatum*) as a host plant. In 2006, the peak count of Lange's metalmark was just 45 (USFWS 2001).

The 2002 designation of *A. mormo* as endangered in British Columbia has prompted further research in Canada. Surveys in British Columbia have shown that the adult population, once thought to be limited to a few hundred individuals, may actually be upwards of 2000 (S. Desjardins pers. com. 2011). A recent investigation found that the British Columbia and Saskatchewan populations are not closely related genetically, suggesting that they have arrived as a separate northerly colonization and have not moved west to east (Proshek *et al.* 2013). Proshek *et al.* (2013) also revealed that the Saskatchewan population is more genetically diverse than the British Columbia population, and concluded that the conservation listings as threatened and endangered are accurate.

All documented *A. mormo* sightings in Saskatchewan have occurred in the current or proposed boundaries of GNP or the VMCP (COSEWIC 2003). Ronald Hooper was the first to document *A. mormo* in Saskatchewan in the Killdeer Badlands of what is now the East Block of GNP in 1974, and made repeated trips to new locations in GNP in 1983 and then again in 2002, in which he discovered several more colonies (Hooper 2002). By 2002 there were 8 known colonies of the butterfly in Saskatchewan but Hooper claims that more had not been documented because lepidopterists were not looking at the right time, in the right places (Hooper 2002). Searches after the species was listed in 2002 yielded additional colonies so that, when I began this research in 2011, there were 37 known colonies of *A. mormo* in Saskatchewan.

The listing of *A. mormo* in Canada led to additional studies on the butterfly in its northern range. For instance, in 2010 Peterson et al. recorded the first caterpillar observations of the metalmark in Canada, in GNP. This study provided novel information on the behavior and phenology of the species' caterpillar stages in the metalmark's northern range. They observed caterpillars in June and July in the West Block of GNP and found that the caterpillars are crepuscular and feed for short periods in the evenings around dusk, and longer in the early pre-dawn hours. The authors did not observe the caterpillars feeding when the temperature was lower than 8°C. *Apodemia mormo* is a solitary forager, but one may sometimes observe several individuals on the same plant (Peterson et al. 2010).

Apodemia mormo has never been reported in Alberta even though there is suitable habitat where the host plant occurs. In 2007, a survey conducted for the butterfly in suitable host plant habitat in Alberta failed to yield any evidence of *A. mormo* (Anweiler 2007). Repeated surveys are needed to confirm the absence of the butterfly in Alberta.

Recent research shows that *A. mormo* oviposition in Saskatchewan differs from that in other parts of the range; this work is presented in Chapter IV of this thesis. This study showed that females oviposited on soil and under rocks, not on the host plant, and that the females laid their eggs singly, not in clusters. Wick et al. (2012) suggested that the Saskatchewan population is likely under different adaptive pressures that have potentially prompted this change in reproductive strategy.

Thesis overview

In this thesis I present my work on *A. mormo*, and the autecology of this elusive butterfly in its northern range. Combining tools and theory from landscape ecology, population and community ecology, and observational studies of natural history, I have defined and characterized habitat for *A. mormo* at the micro and landscape level. Aside from the primary research goals of this project, it is my hope that these results will help Parks Canada to better protect habitat that is critical for all life stages of the butterfly. My results for metalmark populations in the Agri-Environment Services Branch (formerly the PFRA) community pastures presented in this thesis have already been used in the inter-jurisdictional South of the Divide Multi-Species Action Plan (in press) in which species distribution models for at-risk species were combined to develop regional goals for conservation in southern Saskatchewan. *Apodemia mormo* is the only insect included in this Action Plan, which has been used to identify biodiversity host spots for at risk species in southern Saskatchewan. Additionally, data from my results is being incorporated into a multi-species management plan for GNP.

To identify new colonies of *A. mormo,* in Chapter II I constructed a landscape-level habitat suability model across the study area based on spatial environmental variables. I used two contrasting modeling techniques, a resource selection function, which is based on a generalized linear model, and Random Forests, which is an algorithmic machine-learning technique. While the resulting models predicted different butterfly localities within the study area, field assessments in potential habitats showed that both models performed moderately well in predicting butterfly presence with independent samples (verified with ground-validation). Prediction success was 76% for Random Forests and 64% for the Resource Selection Function. Overall prediction success was higher when I removed data from the VMCP, as success was only 19% in the habitat grazed by cattle. Application and field verification of these models increased the known locations of *A. mormo* colonies in Saskatchewan from 37 to 88.

To determine potential microhabitat requirements of *A. mormo* in Chapter III, I asked: “Is host plant habitat occupied by the butterfly fundamentally different from habitat that is unoccupied?” I answered the question by measuring habitat variables on soil, vegetation, and microtopography in 102 quadrats, roughly half of which were unoccupied and the other half occupied by the butterfly. The results indicated that butterflies selected host plants growing in habitat with greater % host plant cover, greater % bare ground cover, a steeper slope, a south-westerly aspect, lower soil nitrogen, and higher soil acidity than in unoccupied *Eriogonum* colonies. Thus, unoccupied habitat differs different from habitat currently occupied by the butterfly. Conservation efforts should focus on those areas where the butterfly is currently found.

In Chapter IV, is a version of a paper published in *The Canadian Field Naturalist* in 2012. This paper provides the first documentation of the oviposition of *A. mormo* in Canada and shows that this behavior diverges from that seen in other parts of the butterfly’s range.

Finally, in Chapter V, the thesis discussion, I summarize the main findings of the research I conducted, revisit key issues that relate to the natural history and conservation of *A. mormo* in Saskatchewan, and conclude by presenting management and conservation recommendations.

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CHAPTER II.

Species distribution models reveal new colonies of a threatened butterfly, *Apodemia mormo* (Lepidoptera: Riodinidae)

Introduction

Developing models to effectively predict habitat conditions required by rare species is a central pursuit of conservation biology and essential to conservation planning (Thompson 2004; Guisan et al. 2006; Turlure et al. 2009; Lawson et al. 2012; Oliver et al. 2012). For rare species, and particularly peripheral populations, understanding ecological requirements is especially important for defining habitat or distribution. Species distribution models (SDMs) support conservation initiatives by relating a species' distribution to the distribution of environmental factors that predict habitat use (Guisan & Zimmermann 2000; Soberón & Peterson 2005; Araujo & Guisan 2006; Oliver et al. 2012). Such tools are particularly important to maximize effective use of limited resources for habitat protection and conservation (Cabeza & Moilanen 2001; Araujo et al. 2002; Wilsey et al. 2012). Predictions from SDMs can assist conservationists in prioritizing and facilitating habitat protection for threatened species by identifying where success is most likely to occur (Manel et al. 1999; Jaberg & Guisan 2001; Araujo et al. 2002; Cabeza & Moilanen 2003; Wilson et al. 2011).

Popularity of SDMs has increased in recent years in part because of the development of a variety of mapping and statistical techniques that effectively correlate species distributions to environmental characteristics (Pulliam 2000; Soberón & Peterson 2005; Araujo & Guisan 2006). Such models offer a useful alternative to monitoring species on the ground, while aiding conservationists in efficiently assessing and projecting impacts of land-use changes or climate change on the distribution of organisms, as well as facilitating habitat protection for threatened species (Kienast et al. 1996; Lischke et al. 1998; Manel et al. 1999; Jaberg & Guisan 2001; Rebelo & Jones 2010).

Northern peripheral populations of a wide variety of species reside in Canada, including that of the Mormon metalmark (Lepidoptera: Riodinidae, *Apodemia mormo* Felder & Felder 1859). The range of this butterfly extends from northwest Mexico through much of the western US and into extreme southern Canada (Scott 1986; Layberry et al. 1998). *Apodemia mormo* is of particular ecological interest because its Canadian range is disjunct from central parts of its range and populations of the species residing in Saskatchewan have disparate reproductive adaptations (Wick et al. 2012).

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recently assessed the two populations of *A. mormo* in Canada. The mixed-grass "prairie population" in southern Saskatchewan was designated as 'threatened,' and a small population located in the Similkameen River Valley of southern British Columbia was listed as 'endangered' (COSEWIC 2003).

In this study I used SDMs to define the butterfly's habitat by identifying environmental factors associated with habitat occupancy at the landscape level. In particular, I was interested in why the butterfly does not occupy many areas in which its host plant, *Eriogonum pauciflorum* Pursh, is abundant. I hypothesized that landscape-level environmental features influence the suitability of habitat for *A. mormo* and account for its absence in some host plant patches. I used these environmental features to model habitat occupancy for the badlands of southern Saskatchewan through the use of two modeling approaches: a resource selection function (RSF; Manly et al. 2002); and Random Forests (Breiman 2001). I then tested model predictions with ground validation by searching for butterflies in previously unsurveyed areas during the butterfly's brief adult flight period.

Materials & methods

Study species: Apodemia mormo

The prairie population of *A. mormo* in Saskatchewan is strictly univoltine, with adults emerging in early August and flying for 2-3 weeks (Henderson et al. 2008;

Peterson et al. 2010). Although this butterfly species uses several species of *Eriogonum* throughout its range, the prairie population relies solely on *E. pauciflorum* as its obligatory larval food plant and primary nectar source (Scott 1986; Pruss et al. 2008). In Saskatchewan, *A. mormo* also uses rabbitbrush (*Ericameria nauseosa* Pall. Ex Pursh) as a secondary nectar source. The butterfly and its host plants are associated with eroded hillsides and embankments in the badlands of southern Saskatchewan (Pruss et al*.* 2008).

Study area

This work was conducted in Grasslands National Park (GNP; Figure 2-1; 49° 06' N, 107° 25' W) is located in extreme southern Saskatchewan and comprises 52,700 ha in the mixed grass ecoregion (Thorpe & Nicolichuk 2009). The Park contains 29,000 ha of badlands, terrain too rugged and unproductive for human cultivation (Saskatchewan Institute of Pedology 1992; Pruss et al. 2008). Much of the badlands area remains unaffected by human activity, apart from some historical cattle grazing. The butterfly's primary host plant, *E. pauciflorum,* occurs only in the badlands. I estimate that there are approximately 4017 ha of *E. pauciflorum* in the badlands of GNP based on calculations from vegetation transects completed in 2011 (Wick unpublished data). The Park is made up of two parcels separated by about 40 km: 1) the West Block, in the Frenchman River Valley, which contains a herd of *Bison bison* and 2) the East Block, located around Rock Creek (Figure 2-1). The West Block is grazed at a rate of one bison per 55 ha (Olson pers. com. 2012) and the East Block is ungrazed with the exception of a small experimental area that does not include badlands which is grazed by cattle.

Located several kilometers northwest of GNP, the Val Marie Community Pasture (VMCP; Figure 2-1; 49° 41' N, 107° 92' W) comprises 40,629 ha that was set aside during the Dust Bowl under the Prairie Farm Rehabilitation Administration, which was recently changed to the Agri- Environmental Services Branch. The VMCP is grazed at a rate of one cow per 35 ha (T. Dyck pers. com. 2012).

All known *A. mormo* colonies in Saskatchewan are located within GNP and the VMCP.

Butterfly presence

Multiple *A. mormo* surveys conducted in GNP and the VMCP from 1974 until 2011 provided 301 geo-referenced locations where the butterfly had been documented. Using a 222 m buffer radius to define colonies these records suggest a total of 37 known colonies. The 222 m buffer was calculated by walking the perimeters of known colonies and averaging the size of these colonies (S. Pruss pers. com. 2012). These known butterfly locations were treated as "used" points during the modeling described below. Absence data were not systematically documented prior to this study so I generated a set of unused, or available habitat locations where the host plant occurred but *A. mormo* presence was unknown (Manly et al. 2002). I generated this list of available habitat areas as a random sample of landscape locations by in Geographic Information System (GIS; Boyce et al. 2002; ArcMap 10; ESRI 2011). These presence/available locations comprised the response variable for subsequent *A. mormo* models.

Predictor variables

All variables used to model and predict butterfly habitat (for a full list see Table 2-1) were geospatial and available in GIS (ArcMap 10; ESRI 2011). I employed a 20 x 20 m cell size to characterize *A. mormo* habitat in the study area. This resolution is compatible with the biology of the rather sessile butterfly and all predictor variables were available at this scale (or smaller). Because of the *a priori* knowledge that *A. mormo*'s host plant is restricted to badlands, I also restricted the study area to badlands habitat. Other habitats, such as river valley bottoms or hilltop prairies, do not support populations of the host plant, and thus were considered to be matrix habitat.

I derived six variables as environmental predictors (Table 2-1) from a digital elevation model (DEM) of the study area, and developed a normalized difference vegetation index (NDVI) in GIS from SPOT-5 (2007) satellite imagery. The NDVI is a measure of 'greenness', or density of plant growth, in a given area using remotely sensed data. I used a correlation matrix within the Program R (R Development Core Team 2009) to determine whether predictor variables were highly correlated ($r > 0.70$; see Manly et al. 2002) for further analyses I identified the more parsimonious model in relation to Akaike's Information Criterion (AIC) which increases when including a variable adds more variance than it explains (Burnham & Anderson 2002; Manly et al. 2002). Topographic Ruggedness Index (TRI) was removed from further analyses because it was correlated with slope (SLOPE). Aspect (ASPECT) was strongly correlated with solar radiation (SOL202) and hillshade (HLSHD), a measurement of shaded relief, so I did not include ASPECT in the modeling efforts (Table 2-1). HLSHD was not shown to be significant in the RSF, but excluding it increased the models AIC, so I included it.

Models

I used two models to study the relationship between *A. mormo* presence and the environmental predictors. In the first approach, I constructed a resource selection function (RSF) using an exponential generalized linear model with the logit function (Guisan & Zimmermann 2000; Manly et al. 2002). A RSF is any function that gives a result proportional to the probability that a resource unit will be selected by an animal (Manly et al. 2002). Resource selection functions are based on the premise that individuals of a given species behaviorally select particular resources, and these functions have been used to develop predictive models in conservation planning for a variety of mammal and avian species, including mountain caribou, northern goshawks and northern flying squirrels (Johnson et al. 2004; Carroll et al. 2006; Hough & Dieter 2009). This 'use/availability' design is the most commonly used method when dealing with data collected in wildlife studies (Johnson et al. 2006). I used the Package lme4 (Bates et al. 2011) in the Program R to provide GLM-based logistic regression RSF to input into the GIS.

As a second modeling approach, I employed Random Forests, a bootstrapped regression tree analysis in the machine-learning family of modeling techniques

(Breiman 2001; Breiman & Cutler 2005). Random Forests has several advantages over other modeling methods. For instance, it can include many correlated variables, it is thought not to overfit, it assumes nonlinear interactions among predictor variables, and it delivers an output of 'variable importance' by ranking predictor variables with respect to how often they correctly predict an outcome of presence or absence (Prasad et al. 2006; Cutler et al. 2007; Roberts & Hamann 2011). Because Random Forests is an algorithmic model, it has no assumptions of normality or co-linearity. Instead, the model learns the relationship among variables starting from an uniformed state, and goes on to elucidate complex relationships among variables (Breiman 2001). I used the package "RandomForests" in the Program R to build this model (Liaw & Wiener 2002; Breiman & Cutler 2005; R Development Core Team 2009).

I constructed a predictive map of *A. mormo* habitat in both GNP and the VMCP using each model. In August 2012 I validated model performance by methodically searching for host plants and butterflies in the sites that each model predicted would have butterfly presence (>0.60 relative probability of presence). Additionally, I searched for host plant habitat, in lieu of butterflies because the flight season had ended, where Random Forests predicted habitat would be absent (<0.40 relative probability of presence). I validated predictions of absence for only Random Forests because it performed better than the RSF in the first portion of the study.

Results

The final models included the following five variables: normalized difference vegetation index (NDVI), compound topographic index (CTI), slope (SLOPE), hillshade (HLSHD), and area solar radiation (SOL202). Although HLSHD did not contribute significantly to the RSF model, excluding it resulted in a less parsimonious model, so it was included. The following RSF coefficients are shown in Table 2-2 and the equation was used in the GIS to predict *A. mormo* habitat across the study area:

y = exp [4.390 - CTI(0.391) + HLSHD(0.012) - SOL202 (0.006) - SLOPE(0.043) - NDVI(62.4)]

Although Random Forests relaxes many assumptions about predictor variables required by GLMs, I used the same set of predictor variables for both models to support the best possible comparison between models. The Random Forests model is based on a machine-learning algorithm and therefore cannot be represented by an equation, but instead gives output in terms of the relative importance of variables (Figure 2-2). Outputs show that the variable importance measured by the increase in % mean square error (Inc%MSE). Greater Inc%MSE indicates higher variable importance; in other words, importance values are assigned in relation to the number of times that a variable is included in an iteration of the model and correctly predicts presence in a known area. In the final model, NDVI was the most important predictor according to the variable importance plot (Figure 2-2). In decreasing order of importance the predictors included in the Random Forests model were: NDVI, SLOPE, SOL202, HLSHD, CTI.

Overall, findings indicated that butterfly presence was associated with moderately sloped, dry habitat with little vegetation, low solar radiation with higher shaded relief values. I used each model to predict probability of butterfly presence based on environmental characteristics of each 20 x 20 m cell within the study area (Figure 2-3). The RSF predicted a much higher proportion of unsuitable habitat in the VMCP (Figure 2-4d) than in GNP (Figure 2-4b,f) in comparison to the results from Random Forests (Figures 2-4a,b,c).

In 2012, I searched previously unsurveyed areas in the VMCP and GNP where the models predicted *A. mormo* presence or absence. To select search sites, I divided the 20 x 20 pixels into the following two categories based on the output of each model: 1) areas predicted to have butterflies (>0.6 probability) and 2) areas with low probability (<0.4) of occurrence. With these binary high/low maps I randomly selected 200 points from the output of each model for each category in GIS. I searched for *A. mormo* in these sites during the peak flight season in August 2012. It appeared that the flight period ended early, due to 2012 being a drought year;

therefore, I did not include data collected after 27 August, in order to avoid detection errors. No butterflies were seen after this date, even in several areas with known *A. mormo* colonies.

I visited 168 sites that were predicted to have butterflies (Figure 2-4), and 76 sites that were predicted not to have butterflies (Figure 2-5). Regarding prediction of presence, RSF was accurate 64% of the time, while Random Forests was correct 76% of the time (Figure 2-4). Since Random Forests consistently outperformed the RSF model with respect to butterfly and host plant presence, I used Random Forests to randomly select sites predicted to have no butterflies. Random Forests was accurate at 92% in predictions of no habitat suitable for *A. mormo* (Figure 2-5).

The model results apportioned by the type of grazing are shown in Figure 2-6. The models were only accurate in correctly predicting *A. mormo* presence 19% (N = 31) of the time in the VMCP, which is grazed by cattle at a rate of one cow per 35 ha. The models were more accurate 73% (N=106) in the West Block of GNP, which is grazed by bison at a rate of one bison per 55 ha. The models were most accurate in the East Block of GNP (85%, N=27)where there is no grazing by cattle or bison in any areas studied that were occupied by *A. mormo*.

Discussion

Species distribution models have been developed for many species, but their application in conservation biology has been compromised by the lack of independent assessments of model performance (Greaves et al. 2006). There are several studies that have validated such models in the field. For example, Newbold et al. (2010) used SDMs to model the distribution of butterflies, mammals, reptiles, and amphibians and then tested the accuracy of their models using ground validation. Ground validation uncovered 15 new localities of the rare bat, *Barbastella barbastellus,* in Portugal, extending its known range by 100 km (Rebelo & Jones 2010). In the present study, I developed alternative SDMs to predict *A. mormo* presence and absence, and then used ground validation to test the ability of the models, to correctly predict presence and absence and to document new colonies of the butterfly, as well as compare two modeling methods.

The SDMs I used here successfully predicted suitable and unsuitable habitat for *A. mormo* and provide an improved understanding of what constitutes habitat for this species. Given these successes, these models can be applied in the conservation of *A. mormo* and these approaches may have general utility for modeling populations of threatened species that use patchy habitats.

Environmental variables that predict butterfly presence

Prior to this investigation, knowledge of the habitat of the *A. mormo* prairie population was limited to the presence of its host plant, *E. pauciflorum,* in badlands. In this study, I demonstrated that five environmental variables can be used to improve predictions of butterfly presence and absence within these constraints. The NDVI was the most important predictor of butterfly presence in both models. NDVI had a negative relationship with probability of butterfly occurrence; *A. mormo* is most likely to occur in sparsely vegetated areas where host plants occur in the badlands. I could not identify host plant at the scale of SPOT satellite images (10 m). However, I suspect that low NDVI values indicate the presence of *E. pauciflorum* and *E. nauseosa* because these plants are likely favored by the low levels of competition in highly eroded habitat. In a related study (Chapter III of this thesis), I demonstrated that *A. mormo* occurs in areas with little vegetation cover as long as its host plants are abundant; in fact, scarcity of other plant species may encourage butterfly presence. In general, *A. mormo* habitat can be characterized as sites with *E. pauciflorum* that are not steeply sloped, with little vegetation, low solar radiation, and drier with higher shaded relief with host plant densities.

Ground validation & model comparison

Validation against new data is essential to test if SDMs effectively predict occurrences of species. In general, model performance is best tested against new presence/absence data from the study area, but that have not been used to develop the model (Manel et al. 2001; Wintle et al. 2005). Validation of model usefulness is best achieved by searching for the target species in areas predicted by the model (Boyce et al. 2002). Therefore, I searched for *A. mormo* during the August 2012 flight period at sites where they were predicted to be either present or absent. Ground validation confirmed the usefulness of both models, and increased the number of known *A. mormo* colonies from 37 to 88 in a single flight season.

In addition to better predicting new sites for *A. mormo*, Random Forests more accurately predicted the absence of butterfly habitat. Although the evaluation of models is inextricably related to their intended purpose (Araujo & Guisan 2006), my results corroborate the earlier suggestion that Random Forests is suitable for uncovering patterns and relationships in highly complex, non-linear ecological data (Cutler et al. 2007). This approach is well suited for use with threatened, endangered, or peripheral species (Marmion et al. 2009).

Grazing and A. mormo

Within the VMCP, in which cattle were grazed, the models were correct only 19% of the time. Model predictions were substantially more accurate in areas ungrazed (85%) or grazed by bison (73%) in the East and West Blocks of GNP, respectively. These results suggest that cattle grazing has a differential impact on the ability of *A. mormo* to use available host plant patches, or at least on the ability of either modeling approach to predict butterfly presence in areas grazed by cattle. However, further work is required to ascertain if grazing types (cattle or bison) differentially affect *A. mormo*, but also the stocking rates, as these are higher in the VMCP.

Many of the sites in the VMCP that were predicted to have butterflies had abundant host plants, but no butterflies, even during the peak of the flight season. Neither cattle nor bison appeared to target *E. pauciflorum* as a food source. Recent research demonstrated that ovipositing females of *A. mormo* place eggs directly on soil or rocks, not on the host plant, as was previously thought (Wick et al. 2012). There is limited peer-reviewed data to compare life history and the ecological effects of managed or unmanaged grazing both in (Fuhlendorf et al. 2010).

However, the effect that livestock grazing may have on butterfly populations is complex and the nature of the relationship depends on many factors, such as butterfly life history traits, plant community succession, grazing regimes, and invasive plant dynamics (Swengel 2001; Vogel et al. 2007; Preston et al. 2012). Further work, such as a comparative study on the ecosystem interactions of cattle and bison in badlands habitat on the Saskatchewan population of *A. mormo* would likely clarify these issues.

Implications for the conservation & management of A. mormo

Resource limitation is a pressing problem for conservation and land management planning. This study resulted in an additional 106 observations of individual *A. mormo* localities in GNP and VMCP, simply by using widely available spatial data to predict butterfly distributions. While the number of known colonies in Saskatchewan increased by 237% (i.e. from 37 to 88 colonies), this study also confirmed the observation that *A. mormo* is not found in many areas of host plant habitat (Pruss et al*.* 2008).

The results I have presented here have significant implications for the conservation of *A. mormo* in its northern peripheral range. First, it appears that new colonies of the species can be predicted with remotely sensed data. The habitat of *A. mormo* was reasonably well characterized using widely available predictor environmental variables derived from a digital elevation model (DEM) and satellite imagery (SPOT 2007). Second, using the same environmental predictors, the possible presence of *A. mormo* may be investigated in other areas of southern Saskatchewan. The model could also be applied to search areas of Alberta with similar badlands but where no *A. mormo* colonies have been previously uncovered (Anweiler 2007).

This study was focused on the prairie population of *A. mormo* in Saskatchewan; however, greater knowledge of this population will likely contribute to conservation efforts across the species' northern range, including populations in British Columbia, Montana, Washington and Utah. Our understanding of the conservation of most invertebrate species often depends on an intimate understanding of habitat associations. Tools such as SDMs may help conservationists and land managers predict and understand distributions, assist in making decisions regarding reintroduction, restoration, and measures to reduce probability of local extirpation (Manel et al. 2001; Bartel & Sexton 2009). In the face of the pernicious effects of climate change and habitat alteration, habitat modeling methods may save valuable time and energy in documenting species' distributions as well as uncovering unknown populations.

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Tables & Figures

Table 2-1. Predictor variables used to build the resource selection function and Random Forests models predicting new colonies of *Apodemia mormo* in southern Saskatchewan. Candidate variables were tested for assumptions prior to the final models.

Source	**Process**	**Outcome Variable**	**Units**	**Resolution**
Digital elevation model (DEM)	NA*	Elevation	Meters	20 m
DEM	Surface Analyst (Spatial Analyst, ArcGIS 10)	Topographic Ruggedness Index (TRI)	Index	20 m
DEM	Surface Analyst (Spatial Analyst, ArcGIS 10)	Slope (SLOPE)	Degrees	20 m
DEM	Surface Analyst (Spatial Analyst, ArcGIS 10)	Aspect (ASPECT)	Categorial (N, NE, E, etc.)	20 m
DEM	Surface Analyst (Spatial Analyst, ArcGIS 10)	Hillshade (HLSHD)	NA*	20 m
DEM	Surface Analyst (Spatial Analyst, ArcGIS 10)	Area Solar Radiation (SOLAR202)	NA*	20 m
SRC Predictive vegetation model	NA*	Vegetation (SRCE2)	Index	1:20,000 polygon
DEM	Raster calculator	Compound Topographic Index (CTI)	Index	20 m
SPOT5 (2007) Satellite Imagery	Raster calculator	Normalized Difference Vegetation Index	Index	10 m

*NA = Not applicable

Table 2-2. Generalized linear model coefficients of *Apodemia mormo* occurrences for the variables using a resource selection function. P-values illustrate significance for each variable. AIC model selection was used to rank model support and find the most parsimonious model. Residual deviance and null deviance are also shown, showing that deviance decreased from the null model.

Resource Selection Function model creation		
Null deviance:	1391.6	
Residual deviance:	1044.8	
Variable[1]	**RSF Coefficient**	**RSF P-value**[2]
Intercept	10.49	0.1077
CTI	-0.391	1.36e-08*
HLSHD	0.012	0.1396
SOL202	-0.006	0.0074 *
SLOPE	-0.043	0.000122*
NDVI	-62.372	< 2e-16 *

[1] Variables were explained in Table 1.

[2] *Indicates significance at 0.01 = alpha

Figure 2-1. The study are consisting of the Val Marie Community Pasture and Grasslands National Park's East and West Blocks, in southern Saskatchewan, Canada.

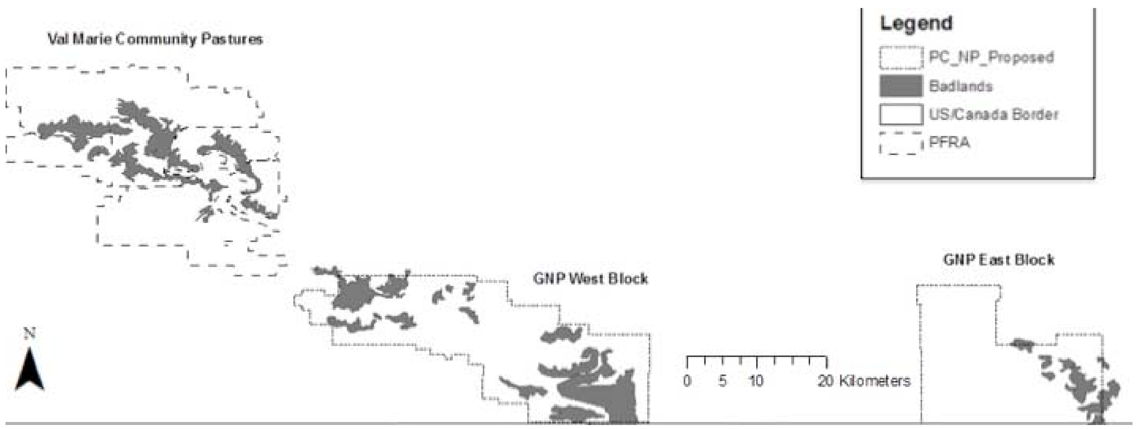


Figure 2-2. Variable importance plot generated by the Random Forests algorithm. The plot shows the variable importance measured as increased node purity (IncNodePurity) and the increase of mean square error (%IncMSE), which represents the deterioration of the predictive ability of the model when each prediction is replaced in turn by random noise. A higher value of %IncMSE indicates a higher variable importance. The full variable names are shown in Table 1.

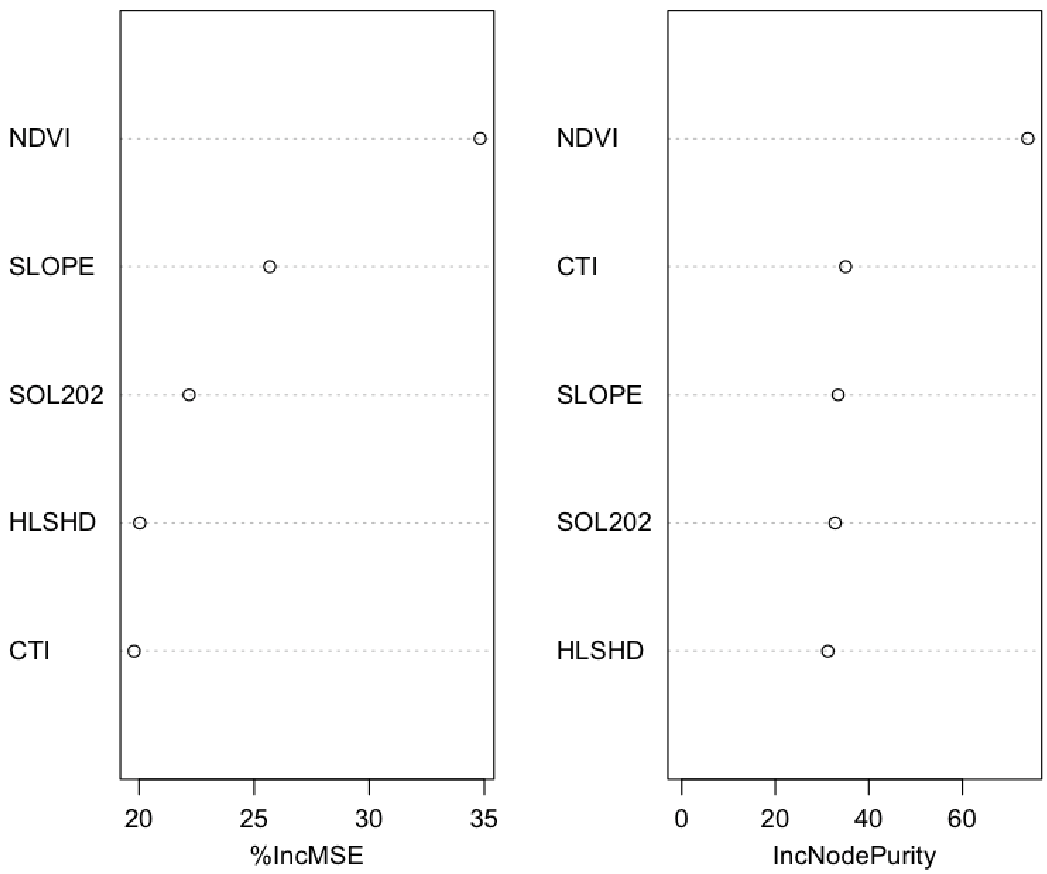


Figure 2-3. Probability of finding *Apodemia mormo* in Grasslands National Park. Maps are divided up by section, the East Block (a, b) the VMCP (c, d), and the West Block of GNP (e, f). The resource selection function is shown on the right (b, d, f) and Random Forests on the left (a, c, e). The model was only targeted for areas that have previously been delineated as badland habitat prior to this study.

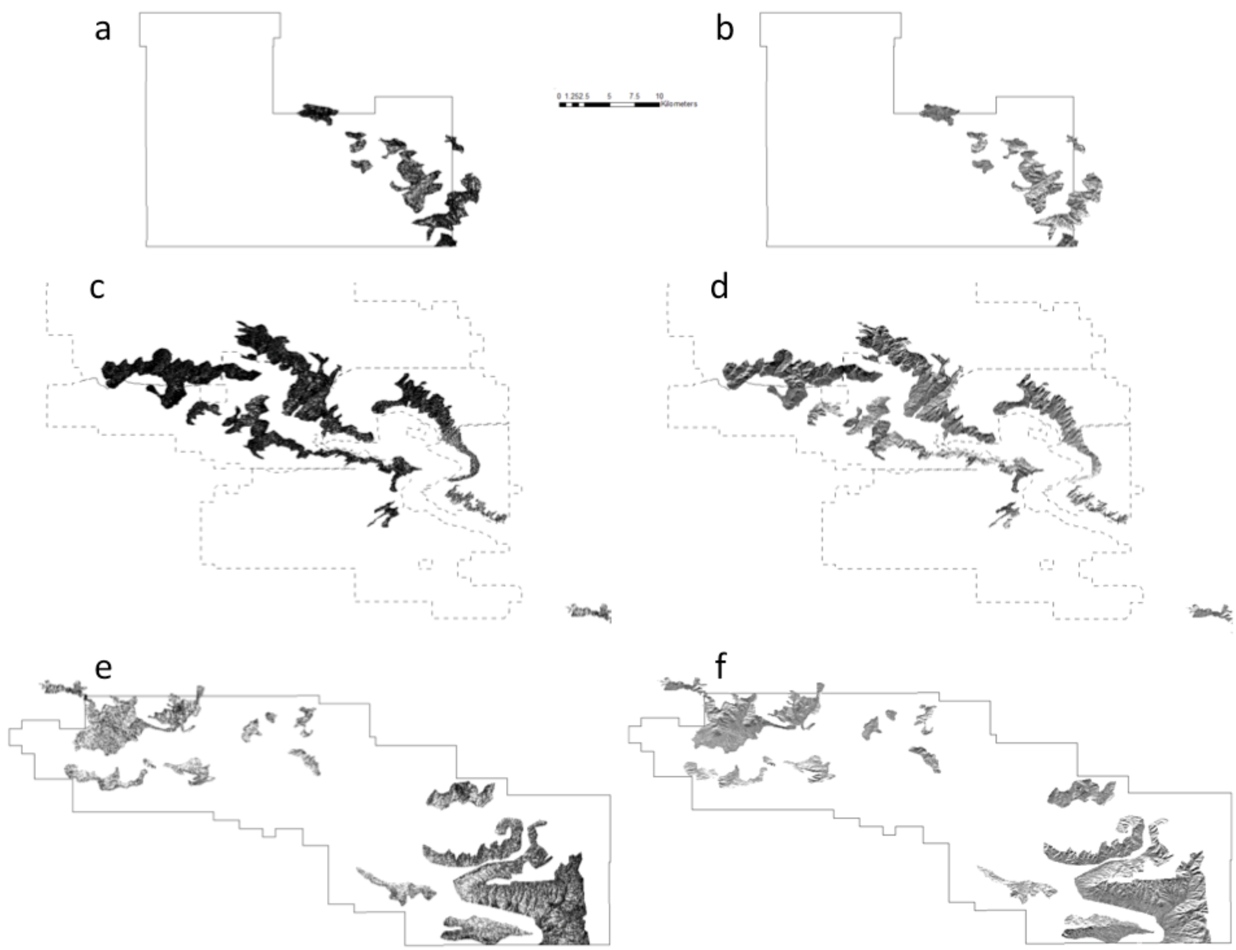


Figure 2-4. Number of observed (sites where *Apodemia mormo* was actually found) versus expected (sites predicted to have *Apodemia mormo* presences) by each model (probability of 0.60 or higher) were searched in Grasslands National Park and the neighboring Val Marie Community Pasture in southern Saskatchewan, Canada.

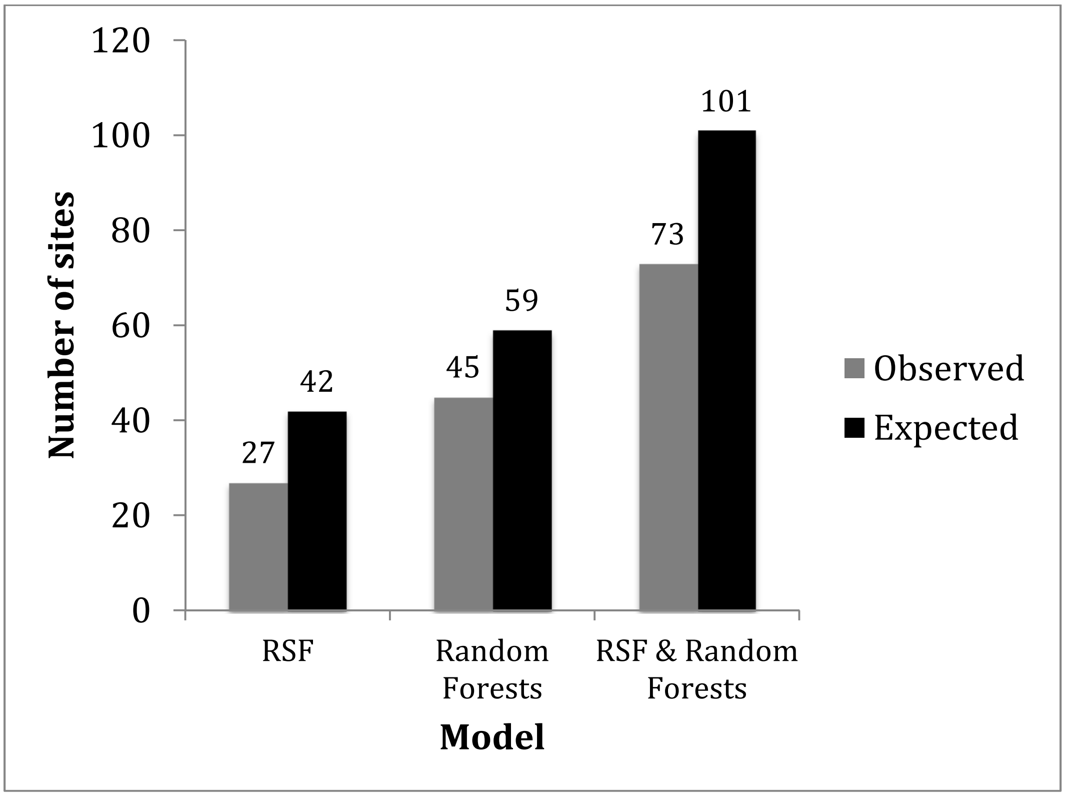


Figure 2-5. Number of observed (sites where *Apodemia mormo* was not found) versus expected (sites predicted to not have *Apodemia mormo*) by the Random Forests model for both the Val Marie Community Pasture (VMCP) and Grasslands National Park (GNP) in southern Saskatchewan, Canada.

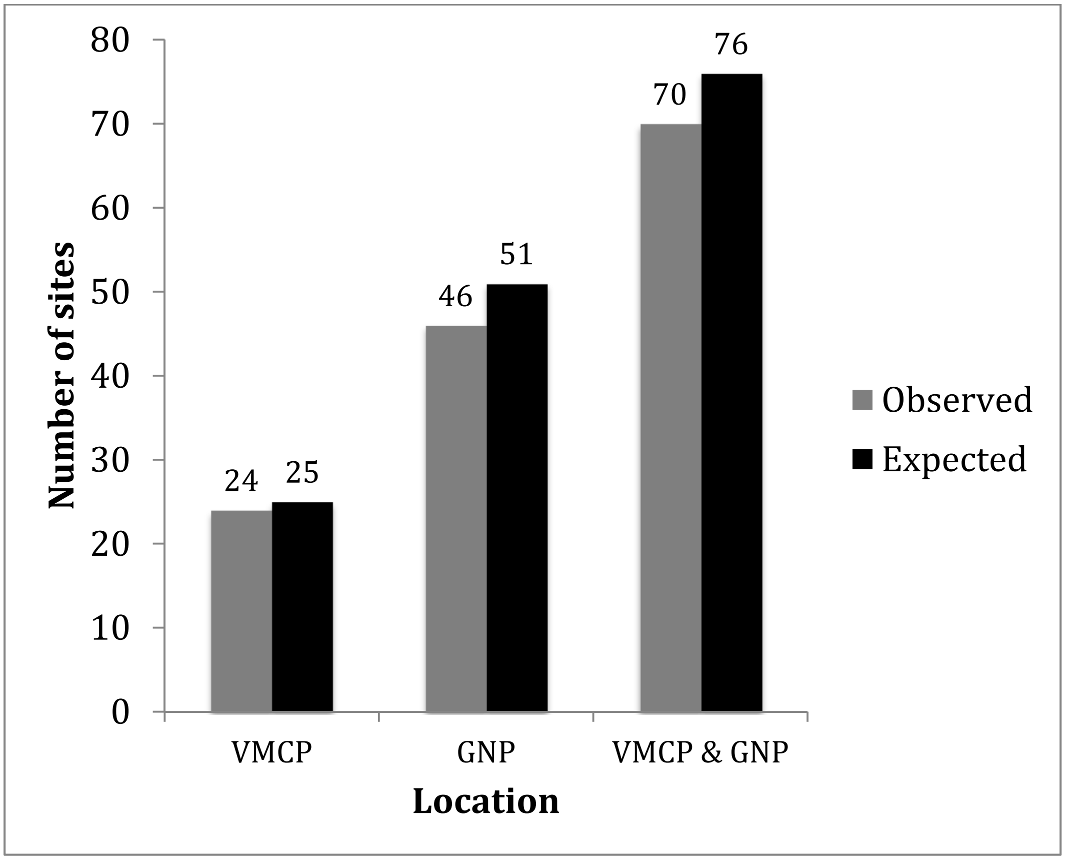
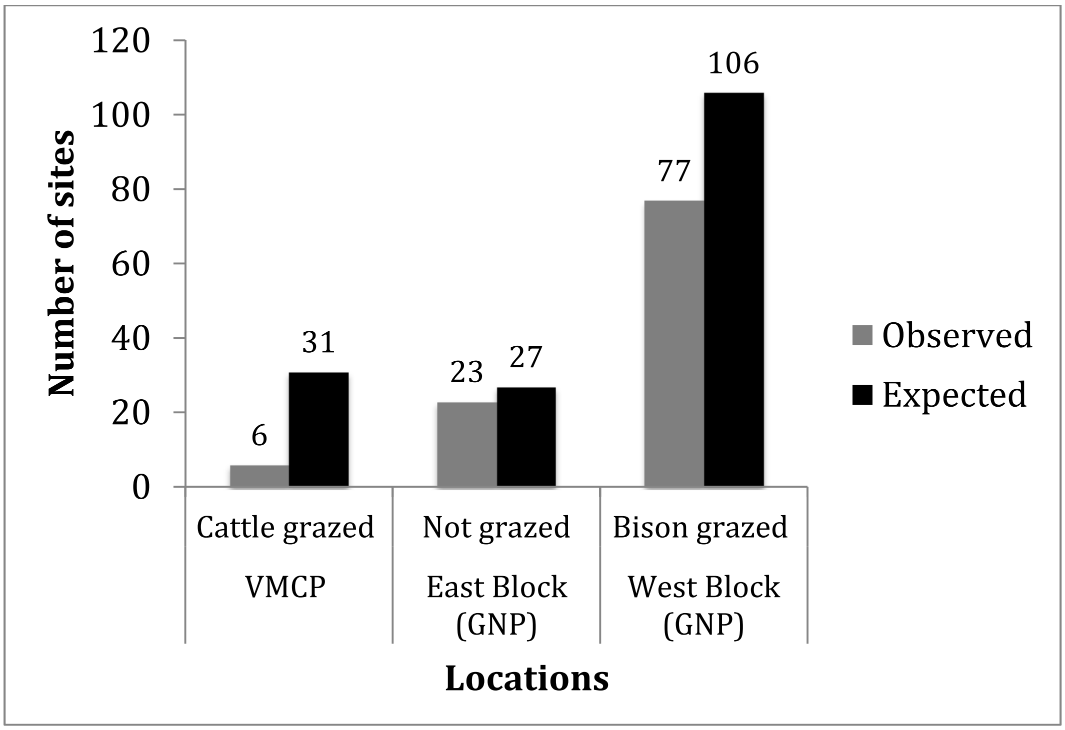


Figure 2-6. Number of observed (sites where *Apodemia mormo* was actually found) versus expected (sites predicted to have *Apodemia mormo* presences) model results separated based on whether or not an area was ungrazed, grazed by bison, or grazed by cattle. The Val Marie Community Pasture (VMCP) is grazed by cattle, the East Block of Grasslands National Park (GNP) is not grazed, and the West Block of GNP is grazed by bison, all sites are located in southern Saskatchewan, Canada.



CHAPTER III.

Beyond the host plant: Additional factors explaining microhabitat associations in a northern peripheral population of *Apodemia mormo* (Riodinidae)

Introduction

Understanding relationships between species and their habitats is a central aspect of ecology (Grinnell 1917; Elton 1927). Defining and understanding habitat is of particular significance for species at risk and those at the extreme periphery of their ranges (Fraser 2000). According to evolutionary theory, individuals should be more concentrated at the center of their range than the periphery and thus one can expect gradual declines in abundance at range edges (Brown 1984). However, these features are dynamic and some species are presently shifting their distributions to higher latitudes in response to climate warming (Root et al. 2003; Parmesan & Yohe 2003). Under such conditions, northern peripheral populations will likely become increasingly important for persistence of such taxa.

Peripheral populations are of evolutionary significance as they are thought to be freer to evolve and thus may be premier sites for evolutionary change, and ultimately, speciation (Mayr 1940). Although many peripheral populations are more genetically impoverished than central populations, they also may be more genetically distinct and therefore of interest to students of evolution and ecology (Noss 1994). Environmental changes such as global warming can affect the distribution, phenology, abundance, and diversity of species (Crick & Sparks 1999; Roy & Sparks 2000; Parmesan & Yohe 2003; Root et al. 2003), particularly at latitudinal and altitudinal range limits and thus peripheral populations may be important to long-term persistence of many species (Hunter 1991; Fraser 2000; Davies et al. 2006). Furthermore, phenological mismatches between insects and their host plants, which may be most common at range limits, can have dire consequences in peripheral populations (Hunter 1992; Quiring 1993; Peterson 1997). In a landmark paper Rosenzweig (1991) suggested that it is crucial to investigate microhabitat characteristics of populations at range peripheries, where natural selection may drive them to select the most advantageous microhabitats.

Lepidoptera have long been used as a model species for studies in ecology and evolutionary biology and recent literature suggests that Lepidoptera discriminate among habitats based on environmental variables beyond simple presence of their host plants (Papaj & Rausher 1987; Lastra et al. 2006; Ashton et al. 2009). For example, several studies suggest that soil nutrients affect habitat preferences of butterfly species (Ehrlich 1965; Ravenscroft 1994; Prudic et al. 2005). Grassland habitats that vary in exposure to solar radiation because of slope and aspect create a variety of thermal microenvironments that dramatically affect larval growth and development, especially in the cooler, northern range of the bay checkerspot butterfly (Murphy & Weiss 1988).

In this chapter I investigate microhabitat characteristics for the disjunct northern peripheral population of the Mormon metalmark (*Apodemia mormo*) in southern Saskatchewan, Canada. The conservation status of this population is listed as threatened (COSEWIC 2003). My objective was to define possible butterfly microhabitat use by examining soils, vegetation, and topography for host plant habitats where the butterfly is present (occupied habitat) and that where it is absent (unoccupied habitat).

Materials & methods

Study sites

Grasslands National Park (GNP; 49° 15’ N, 107° 09’ W) was established in 1984 and is located in the mixed grass prairie region of southern Saskatchewan, Canada. With long, cold, dry winters and short, hot, humid summers, GNP comprises upland and lowland grasslands that are interspersed with sparsely vegetated badland habitat. The 52,700 ha that comprise GNP include approximately 29,000 ha of badlands, which are eroded communities characterized by sparse vegetation (Michalsky & Ellis 1994).

Grasslands National Park is apportioned into two main areas: the East Block and the West Block. These parcels are separated by approximately 40 km of privately owned pasture and farmland. The East Block includes much of Rock Creek and is surrounded by the Wood Mountain plateau; the West Block surrounds the Frenchman River valley southeast of the village of Val Marie, SK (Saskatchewan Institute of Pedology 1992). The West Block contains a herd of bison (*Bison bison*) that graze the area at a density of one bison per 55 ha (W. Olson pers. com. 2012).

In addition to GNP, I also studied butterfly habitats in the Val Marie Community Pasture (VMCP; 49° 41' N, 107° 92' W), which is located several kilometers northwest of the park. The VMCP was originally created as part of the Prairie Farm Rehabilitation Act but is now managed by the Agri- Environment Services Branch. It is made up of 40,649 ha and is stocked at a density of one cow per 35 ha and cattle graze from April until the end of October (T. Dyck pers. com. 2012). The VMCP contains several colonies of *A. mormo* as well as large areas of host plant habitat where repeated surveys have not uncovered the presence of the butterfly.

Apodemia mormo and host plant

Apodemia mormo is a small butterfly of the principally neotropical family Riodinidae. The most wide-ranging riodinid in North America, it occurs from Mexico to Canada, throughout the western United States. Only two populations are found in southern Canada and these comprise the extreme northern range of the species (Scott 1986; Layberry et al. 1998): the "prairie population" in Saskatchewan and the "mountain population" in the Similkameen River Valley in British Columbia (COSEWIC 2003; Pruss et al. 2008). The subject of this study is the prairie population, located in the northern mixed grass prairie ecoregion in Saskatchewan.

While *A. mormo* populations in the southern part of its range may have multiple flight periods, the prairie population is strictly univoltine with adults generally emerging at the beginning of August and waning towards the end of the month (Arnold 1980; Peterson et al. 2010). However, depending on weather, the flight period of *A. mormo* can range from mid-July into September (Henderson et al. 2008). The adult population density typically peaks during mid-August.

The butterfly uses branched umbrella plant (*Eriogonum pauciflorum*) as its sole larval host plant and primary nectar source. Rabbitbrush (*Ericamerica nauseosa*) is used as a secondary nectar source, although it is not always present the area where butterfly colonies occur. Adults use both plants, as well as creeping juniper (*Juniperus horizontalis*), bare soil, and rocks, for perching and mating (Wick pers. obs.). Females in the prairie population oviposit in small crevices in the soil and on rocks near *E. pauciflorum*, not directly on the host plant as previously thought from studies of other populations (Wick et al. 2012).

Study design

Historically, presence of *A. mormo* has been documented through field surveys by Parks Canada, the University of Alberta, and Fish and Wildlife staff. Locations of *E. pauciflorum* patches unoccupied by the butterfly have also been recorded (Parks Canada, unpublished data 2011). Using this information, I established 102 5 m x 5 m quadrats in areas where *E. pauciflorum* was present in the badlands of GNP and VMCP in 2011. Roughly half (n=50) of these quadrats were located in areas where *A. mormo* had previously been documented; these are hereafter referred to as "occupied habitat". The remaining quadrats (n=52) in "unoccupied habitat" were chosen according to a random stratified design and located in known *E. pauciflorum* locations. These quadrats were visited from May to June of 2011 and a series of microhabitat measurements were taken in each quadrat.

After verifying that host plants were indeed present, I recorded the elevation as measured at the center of each quadrat and noted if the habitat was grazed (by bison in GNP or cattle in VMCP). I collected a soil core from the center of each quadrat using an open-faced auger. The soil samples were dried and subsequently analyzed for total nitrogen content (TKN, mgL; an indicator of soil fertility status), acidity (pH) and soil electrical conductivity (EC; a measurement of soil salinity) in the High Volume Lab at the University of Alberta. On site I also measured soil penetrability using a pentrometer (g/cm; E280 Dayton Pocket Pentrometer).

At the center of each quadrat I measured slope and aspect. To characterize the biotic community I estimated % bare ground, % host plant cover and % cover of all vascular plant species to the nearest 5%. Grasses and sedges were difficult to reliably identify to species, so I estimated sedges and grasses as a total grass cover to characterize the relationships between this vegetation type and the host plant.

Data Analysis

In order to use the data to discriminate between occupied and unoccupied habitats I ran a linear discriminant analysis (LDA) using the R package MASS (Venables & Ripley 2002; R Development Core Team 2009). Linear discriminant analysis is a classic parametric method of classification used with a categorical response variable (Sherrod 2012). An LDA aims to minimize within group variance by explaining the variance among groups using a set of predictor variables and maximizes the ratio of between-class variance to within-class variance by finding a linear transformation or a "discriminant function" (Sherrod 2012). The LDA results yield two distributions: one each for occupied and unoccupied habitat. I used a Welch two sample t-test to test whether the two distributions statistically differed from one another.

Results

As summarized in Table 3-1, average measurements for the independent variables differed between unoccupied and occupied habitat. Soil penetrability, available soil nitrogen, % bare ground cover, and elevation were all lower in occupied habitats, while unoccupied habitats had lower soil salinity and higher soil pH. Occupied patches were on steeper slopes and more generally had a south-westerly aspect.

The vegetation composition and structure surveys (Table 3-2) were done in the early part of summer (May/June), and therefore, aside from the host plant and primary nectar plant (*E. nauseosa*), the most common plants were spring flowers. Some plants were plentiful in the plots surveyed early in the season and all but absent from plots by the late summer, and because of this obvious phenological effect, these plants were excluded from further analyses. However, yellow umbrella plant, saltbush, prickly pear cactus and sage were all present throughout the summer. Table 3-3 shows the abundances of plants that were surveyed in the plots.

Since I was interested in whether the overall communities differed between occupied and unoccupied habitat, I present the results of the LDA (Figure 3-1), instead of presenting results for each individual variable. The LDA suggests distinct distributions for occupied and unoccupied habitats. A Welch Two Sample T-test showed a significant difference (df: 133.9, T=2.347, P=0.02) between the distributions, indicating that *E. pauciflorum* patches that are occupied or unoccupied by *A. mormo* differ based on a combination of the following seven variables: % *E. pauciflorum* cover, elevation, aspect, available soil nitrogen, slope, % bare ground cover, and soil pH (Table 3-3).

Discussion

Presence of *A. mormo* in *E. pauciflorum* habitat patches reflects a combination of topographic, soil and biotic variables. Although host plant presence is a key predictor of butterfly presence, it is insufficient to fully characterize habitat occupancy by the butterfly. *Apodemia mormo* was found disproportionately in patches of *E. pauciflorum* that had lower elevation than average, greater slope, and a south-westerly aspect, lower soil nitrogen, higher acidity, and higher % bare ground cover.

Clearly, the extent of local *E. pauciflorum* cover increases the probability of *A. mormo* presence. It is likely that high host plant densities are important for developing larvae as they undertake short distance migration from one host plant to another during their late instar development, as adult *A. mormo* females do not oviposit on host plants (Peterson et al. 2010; Wick et al. 2012). In another study, density of host plant flowerheads was the most important factor in determining presence and abundance of the endangered large blue butterfly, *Maculinea teleius* (Batary et al. 2007).

Other studies have shown that microhabitat factors affect which plants insects choose as their hosts. Yamatoto et al. (2007), for example demonstrated that the biomass of particular host plant species positively affected the abundance of butterfly species. This aligns with my findings: although host plant presence is insufficient to predict *A. mormo* presence, although probability of occupancy increases with abundance of the host plant. In a study of the vulnerable British silver spotted skipper butterfly (*Hesperia comma)* the butterfly's ideal habitat consisted of broken south-facing terrain with 45% host plant cover and 40% bare ground (Thomas et al. 1986). Interestingly, the butterfly had apparently disappeared from sites after these habitat characteristics had changed.

My results are also consistent with findings about the Quino checkerspot butterfly (*Euphydryas editha quino*), for which presence was positively associated with microhabitat features such as host plant presence, vegetation structure, and areas with high solar insolation (Osborne & Redak 2000). These authors also found that high shade was associated with delayed emergence from diapause whereas low shade was associated with early emergence and accelerated development. Furthermore, Dobkin et al. (1987) and Weiss et al. (1988) both found that topographic heterogeneity with respect to slope exposure in serpentine grasslands, contributed to the long term persistence of populations of *E. editha*. This is likely because microclimate, which depends on microtopography, affects the phenology of host plants of larvae and nectar sources (Weiss et al. 1988). Shading and microclimate effects on *A. mormo* could be investigated to identify potential mechanisms that explain habitat preferences determined in this study.

Similar microhabitat features are important to habitat use in other species of conservation concern. For example, a study on the microhabitat selection of five-lined skinks (*Eumeces fasciatus*; listed as special concern under SARA) in their northern peripheral populations in Canada found that site preferences were driven primarily by thermoregulation and protection from predators (Quirt et al. 2006).

Similar to the current study, the findings of Quirt et al. (2006) increased the understanding of habitat selection in the northern range of a northern peripheral population.

Presence of exotic plants influences habitat use in many butterfly species, mainly through competitive exclusion of host plants (Proctor & Woodwell 1975; Murphy & Ehrlich 1988; Murphy & Weiss 1988; Mattoni et al. 1997; Osborne & Redak 2000). However, the only exotic species I documented in *E. pauciflorum* habitat was *Melilotus officinalis*. Although the occurrence of this species in host plant habitat was very low at an average of 0.1% cover in occupied habitat and 0.9% cover in unoccupied habitat, it may have influenced habitat selection by *A. mormo*. In fact, in GNP there are large tracts of land that have been densely occupied by this exotic plant, some of them bordering small *E. pauciflorum* patches, which may influence *A. mormo* movement between larger habitat patches. Additionally, dispersal was not a parameter that we examined in this study, but could likely influence whether or not the butterfly can reach a given *E. pauciflorum* habitat.

Conservation implications

In the face of global warming and other major environmental and land use changes, peripheral populations will likely be important for the long-term persistence of many species (Hunter 1991; Fraser 2000). It is vital to understand the ecology and habitat requirements of these populations in order to effectively manage habitats for persistence of such peripheral populations. The distribution of *A. mormo* in the prairie population is restricted in two ways: butterflies only occur in badland habitat and in proximity of the larval host plant, *E. pauciflorum*. Beyond these previously understood habitat restrictions, I have shown that other environmental characteristics influence butterfly occupancy in *E. pauciflorum* patches. I suggest that the primary concern for conservation of the prairie population of *A. mormo* is to preserve and maintain the quality of habitat that the butterfly currently occupies because it appears that *A. mormo* is selecting for a subset of host plant habitat.

Most importantly, the results presented here improve understanding of habitat requirements for *A. mormo* in its northern range, and can be used by land managers to identify and conserve habitat for the butterfly. The following criteria should be helpful for defining and designating critical habitat for *A. mormo*: patches with high % of *E. pauciflorum* cover, growing on soils with higher pH and low available nitrogen, on steep slopes that are south-west to south facing at lower than average elevation, in badland habitat with bare ground cover, and particularly, areas that are currently or have been recently occupied by the butterfly.

Acknowledgements

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Tables & Figures

Table 3-1. Summary statistics averages (standard error of the mean) of habitat predictors at 102 microhabitat plots representing occupied or unoccupied sites by *Apodemia mormo* in southern Saskatchewan, Canada.

Variable	Unoccupied	Occupied
Penetrability [a]	3.234 (0.199)	2.95 (0.188)
TKN mgL [b]	0.099 (0.07)	0.089 (0.005)
Soil acidity (pH)	5.858 (1.49)	5.962 (0.190)
Soil salinity (EC) [c]	1055.263 (169)	1159.043 (198.081)
Bare ground % cover	50.980 (3.0)	51.270 (3.101)
Elevation	841.10 (5.905)	831.532 (6.337)
Aspect	171.62 (13.62)	201.04 (15.12)
Slope	12.58 (1.22)	17.766 (1.754)

[a] Penetrability is a measure of the penetrability of the soil.

[b] TKN is available soil nitrogen, an indicator of soil fertility status.

[c] Soil electrical conductivity (EC) is a measurement of soil salinity.

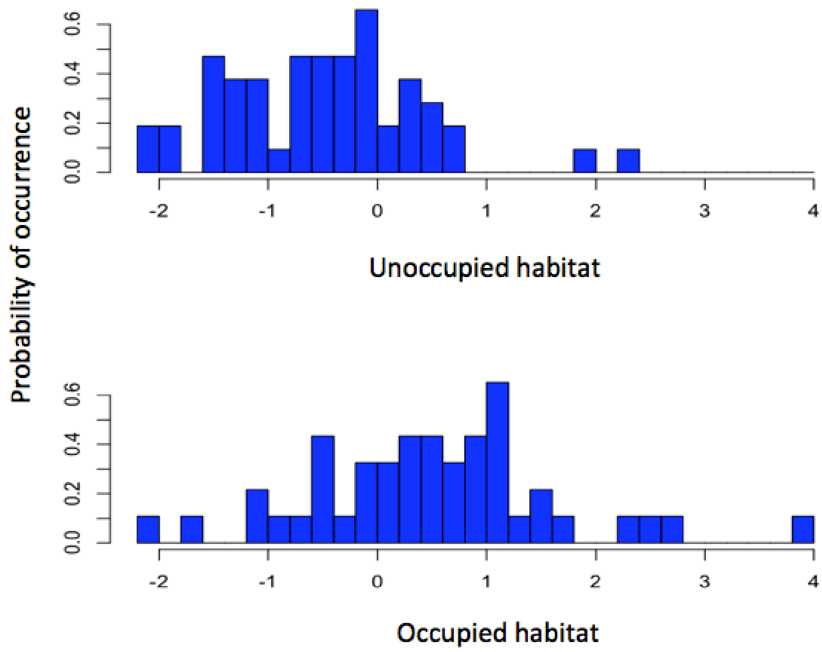
Table 3-2. Plant survey results expressed as the average % cover for each species in occupied and unoccupied sites, in southern Saskatchewan, Canada

Latin name	**Common Name**	**Occupied %**	**Unoccupied %**
Eriogonum pauciflorum	Branched umbrella plant	21.5	16.0
Ericamerica nauseosa	Rabbitbrush	6.4	5.1
Juniperus horizontalis	Creeping juniper	3.7	2.8
Opuntia polyacantha	Prickly Pear Cactus	0.46	0.92
Poaceae & Cyperaceae	Grasses and sedges	5.4	7.4
Hymenoxys richardsonii	Colorado Rubberweed	0.1	1.1
Eriogonum flavum	Yellow Umbrella plant	0.7	0.6
Artemisia sp.	Sage (prairie and pasture)	4.5	5.0
Atriplex nuttallii	Saltbush	2.3	0.9
Melilotus officinalis	Yellow sweet clover	0.1	0.6
Rosa sp.	Wild rose	1.6	2.6

Table 3-3. Coefficients of linear discriminants (Scores) included in the model. Explaining the relationship of each variable with butterfly presence in host plant habitat.

Variable	**Scores**	**Relationship**
Elevation	-0.0139	-
Aspect	0.0042	+
TKN	-4.1195	-
Slope	0.0665	+
% Bare ground cover	0.0248	+
pH	0.2216	+
% Eriogonum cover	0.0627	+

Figure 3-1. Linear discriminant analysis shows the distribution "discriminants" of the two distributions, the first of which is "unoccupied" habitat and the second, which is "occupied" habitat.



CHAPTER IV.

First Observations of Mormon Metalmark (*Apodemia mormo*) Oviposition Behaviour in Canada

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Wick, A.A., Jannelle, J., Pruss, S. & Erbilgin, N. 2012. First observations of oviposition behaviour of the Mormon metalmark (*Apodemia mormo*) in Saskatchewan. The Canadian Field Naturalist. 126: 34-37.

Introduction

The Mormon Metalmark, *Apodemia mormo* (Felder and Felder 1859) is a butterfly of the primarily neotropical family Riodinidae. Its range extends from northwestern Mexico through much of the western United States, but its distribution becomes patchy in the northwestern U.S. and southern Canada (Scott 1986; Layberry et al. 1998). The Canadian prairie populations of the Mormon Metalmark comprise the most northerly documented extent of the species' range.

The species was first observed in Canada in August 1974, when lepidopterist Ronald Hooper documented the Mormon Metalmark in what is now the east block of Grasslands National Park of Canada (GNP) in southern Saskatchewan (Hooper 2002*). Surveys were sporadic, but in 1983 search efforts yielded two new colonies, in the west block of Grasslands National Park. In 2002, six additional colonies were discovered (Hooper 2002*). The species was assessed as threatened in Saskatchewan (Hooper 2002*), and the Prairie population of the Mormon Metalmark was assessed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2003*). With these assessments, increased search efforts have led to the documentation of 40 colonies in GNP, as well as the federal Val Marie Community Pasture managed by Agriculture and Agri-Food Canada, which is located northwest of the park.

There is a second population in Canada located in the Similkameen River valley in southern British Columbia (the Southern Mountain population); this population was assessed as endangered by COSEWIC (COSEWIC 2003*). Both populations are on the List of Wildlife Species at Risk of the federal Species at Risk Act, the Prairie population as threatened and the Southern Mountain population as endangered.

Recent work on the population genetics of the Mormon Metalmark in the northern part of its range has reinforced the listings of endangered and threatened under the Species at Risk Act and has uncovered new information that the British Columbia and Saskatchewan populations are only distantly related (Proshek et al. 2012). This suggests that further research should investigate whether these populations may warrant a separate taxonomic status (Proshek et al. 2012). Little is known about the biology and population dynamics of the northern prairie populations, and much of the information currently available refers to observations in the U.S. southwest.

Mormon Metalmark larvae in Saskatchewan are known to feed on the Branched Umbrella Plant (also known as Few-flowered Buckwheat) (*Eriogonum pauciflorum* Pursh), which grows almost exclusively on eroded or heavy clay soils, found on hillsides, slopes, and embankments (COSEWIC 2003*). The Branched Umbrella Plant is common under these conditions in badlands habitat, of which there are roughly 290 km^2 within the current and proposed boundaries of Grasslands National Park (Pruss et al. 2008*). Rubber Rabbitbrush, *Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & Baird, is also used by Mormon Metalmark adults, which feed on the nectar and perch on the plants. In 2010, the first observations of Mormon Metalmark caterpillars in Grasslands National Park provided valuable information about the early life history of this butterfly in Canada (Peterson et al. 2010). However, there was no documented evidence of oviposition behavior of the Mormon Metalmark in Canada. Given the importance of Grasslands National Park in this species' Canadian range and the lack of biological information specific to northern populations, further understanding of the life history and behaviour of this species is vital for effective conservation planning.

Observations

On several occasions in August 2011, we observed Mormon Metalmark females ovipositing in Timmons coulee in the west block of Grasslands National Park, near the town of Val Marie. On August 21, between noon and 5:00 P.M., we followed several females that would find an area of exposed soil or rock within the host plant's habitat. One in particular began curling her abdomen underneath her and walking forward until she located a suitable spot under a rock (Figure 1). All the individuals we observed laid a single amber-coloured egg approximately the size of a pinhead, either in cracks in the soil or under small rocks. In the instances where the eggs were laid in soil cracks, more than one egg may have been laid, but we did not observe this. While these locations were all near (<2 m) Branched Umbrella Plants, we did not observe any eggs being laid on the lower leaves of the host plant in groups of 2–4, as previously described (Arnold and Powell 1983; Scott 1986; Pyle 2002). The entire oviposition process took anywhere from 5 to 30 seconds.

Discussion

Evidence that this oviposition behaviour differs from that which has been documented in the southern portion of the species' range suggests that different ecological adaptations may be at work at the northern periphery of its range. These adaptations may be the result of alternate reproductive strategies. The physiology of ectotherms such as butterflies and other arthropods is largely dependent on optimal temperature ranges, and natural and experimental manipulations reveal that these organisms are capable of phenotypic plasticity in response to temperature differences (Fischer et al. 2003a, 2003b, 2004; Steigenga and Fischer 2007; Berger et al. 2008). Specifically, in certain species of butterfly, females raised in cooler temperatures tend to produce a smaller number of larger eggs than conspecifics raised under warmer conditions (Fischer et al. 2003b; Geister et al. 2009). Atypical Mormon Metalmark egg deposition numbers and sites may also reflect the colder temperatures found in northern parts of its range. In studying other butterfly species, Berger et al. (2008) suggest that both egg placement and maturation are limited by temperature; egg development times are also influenced by direct solar radiation (Bryant et al. 2002). Eggs laid in open habitat developed more quickly (Bryant et al. 2002), and those eggs with an orientation to morning sun had higher survivorship in the coldest years (Bonebrake et al. 2010). In cooler climates, where development time is limited, the position of an egg can have a profound influence on survival and maturation (Bonebrake et al. 2010).

Experiments with other butterfly species also indicate significant temperature effects on egg and larval development as well as on mortality rates (Fischer et al. 2004; Koda & Nakamura 2010). Thus, Mormon Metalmark eggs laid in the ground and covered with snow may be subject to more moderate temperature ranges as well as lower rates of desiccation than eggs laid above ground on the host plant. However, at this point, it is unclear whether eggs or early instar caterpillars overwinter in the Saskatchewan population.

Other studies have shown that eggs placed away from the host plant on alternate substrates may also benefit from decreased predation. For example, in a study of the neotropical buttterfly *Oleria onega,* significant increases in survival were found when the eggs were transferred to alternate substrates (De-Silva et al. 2011). However, De-Silva et al. (2011) state that this anti-predation strategy must outweigh the cost to the larvae of finding the host plant. Additionally, the Mormon Metalmark may not suffer from extremely high predation from ants, as it does in the southern parts of its range, such as California, where the endangered subspecies Lange's Metalmark (*Apodemia mormo langei*) resides (Johnson et al. 2011*).
The differences in oviposition behaviour reported here add important biological information for this species of conservation concern and may affect the residence description under the Species at Risk Act and the way in which critical habitat is designated and protected under that legislation. This reproductive strategy diverges from what we currently know about the species in other parts of its range. Further investigation will elucidate the mechanisms driving this behavioral difference across the species' range.

Acknowledgements

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Tables & Figures

Figure 4-1. Female Mormon Metalmark, *Apodemia mormo,* ovipositing in cracks in the soil in Timmons coulee, Grasslands National Park of Canada (west block), near Val Marie on August 21, 2011. Photo: Johane Janelle.

CHAPTER V.

General Discussion

Summary of new information about the habitat and ecology of *Apodemia mormo*

Introduction

The aim of this thesis was to improve understanding of the biology of the Mormon metalmark (Lepidoptera: *Apodemia mormo*), as well as the ecological requirements of this threatened species its northern range in Saskatchewan, Canada. I presented an up-to-date review of information about the butterfly in both Canada and the United States in Chapter I. In Chapter II I compared two landscape-level predictive species distribution models for *A. mormo*. I developed these models with geospatial environmental data and records of *A. mormo* occupancy using two contrasting modeling techniques: the GLM-based resource selection function, and Random Forests, which is a nonparametric bootstrapped regression tree analysis rooted in a machine-learning algorithm. I then ground-validated these models by conducting searches for new butterfly localities within the known range. Through these efforts I increased the number of known colonies in Saskatchewan from 37 to 88 in only three weeks of search effort. In Chapter III I investigated the microhabitat characteristics that were associated with the presence/absence of the butterfly. In that study I demonstrated that microhabitat attributes are related to *A. mormo* occupancy. More specifically, butterflies selected habitat with higher % host plant cover, higher % bare ground cover, a steeper slope, a south-westerly aspect, lower soil nitrogen, and higher soil pH.

A 2012 paper published in *The Canadian Field Naturalist* and included in this thesis as Chapter IV reports the first observations of the oviposition behavior of *A. mormo* in Canada, presenting new information specific to the species' northern range (Wick *et al.* 2012). This paper demonstrated that the butterfly oviposits directly on soil and rocks, not just on the host plant, *Eriogonum pauciflorum*, as was previously thought from studies of the species elsewhere. In this final chapter I further discuss several topics touched on in the body of the thesis, including the butterfly's conservation status in Canada, grazing and its relationship to the butterfly, and the potential interaction of *A. mormo* with exotic species. Finally, I outline potential future directions for work on this species in its northern peripheral populations.

Conservation status of Apodemia mormo

Butterflies continue to be a crucial conservation target, not just for their key role in food webs or as pollinators in many terrestrial ecosystems, but also because we can use them as model species to effectively answer ecological and evolutionary questions. As many have pointed out, (e.g., New *et al.* 1995) habitat security must continue to be the main general strategy for butterfly conservation, and the case of *A. mormo* is no exception to this principle. As I reflect on the studies I conducted as part of my Master's thesis at the University of Alberta, it is my opinion that the conservation status of *A. mormo* in Saskatchewan is accurate, and that the continued persistence of the butterfly will be assured given certain circumstances. Primarily, land managers of GNP must continue to be mindful of the butterfly's presence and its habitat requirements. Trails, campgrounds, and tourist facilities should not be placed in areas where the host plant*, Eriogonum pauciflorum*, occurs, even if the butterfly does not currently occupy this habitat. Fortunately, the host plant, *E. pauciflorum*, occurs in badlands habitat, which is not often used for other purposes such as recreation or agriculture.

Permanent protection of GNP is key to the continued survival of *A. mormo* in Canada. The "mountain population" of *A. mormo* in British Columbia is not located in a protected area, and is thus correctly listed as "endangered." Unfortunately, the third location in Canada that houses *A. mormo* is in the Val Marie Community Pasture, part of the Prairie Farm Rehabilitation Administration, which has since been integrated into the Agri- Environment Services Branch. Canada's community pasture program has recently been dissolved and the future of this land, and the wildlife that uses it, remain uncertain.

Inadequate knowledge of this butterfly's ecology and habitat requirements in its northern range has impeded critical habitat designation for the prairie population in southern Saskatchewan. Prior to this study, habitat requirements for the prairie population were unclear and the Recovery Strategy for the species stressed the importance of defining such habitat for the long-term persistence of *A. mormo*'s prairie population (Pruss et al. 2008). The information I gathered as part of this thesis has already been contributed to the South of the Divide multi-species action plan for southwest Saskatchewan. In the following sections I discuss two key interactions that may impact the continued persistence of *A. mormo* in Saskatchewan: grazing and invasive species.

Grazing

Livestock are ubiquitous throughout western North America. Although presence of livestock can be effectively integrated with habitat management and used as a management tool, even for butterfly communities, applications tend to be limited (Severson 1990; Cushman 2009). Livestock are heavier, more abundant, and more concentrated than native mammals and moreover, trampling by livestock can compact soil, reducing its capacity for water infiltration. One study on Smith's blue butterfly (*Euphilotes enoptes smithi*) investigated the use of grazing to help restore native communities that had been invaded by Eurasian exotics (Cushman 2009). While Cushman found that grazing reduced the overall cover of exotic grasses, it increased the cover of exotic forbs. Further, *Eriogonum parvifolium*, which is a relative of the host plant of *A. mormo*, was reduced both in size and volume by grazing (Cushman 2009). Grazing practices, along with industry and recreation, are to blame for the extensive habitat loss of the dune habitat needed by the endangered *Apodemia mormo langei* in California (USFWS 2001).

The study area of my investigation consisted of Grasslands National Park (GNP), which is comprised of a West Block and East Block, as well as the Val Marie Community Pasture (VMCP). The VMCP is grazed by at a rate of one cow per 35 hectares (T. Dyck pers. com. 2012). The West Block of GNP is grazed by one bison per 55 ha (W. Olson pers. com. 2012) and the East Block is ungrazed, except for a small experimental area that does not include *A. mormo* habitat. The species distribution models I developed in Chapter II correctly predicted 19%, 73% and 85% of butterfly presence in the VMCP, the West Block of GNP and the East Block, respectively.

I suspect that differences in accuracy of the predictive models between the VMCP and GNP may be in part explained by differences in grazing type (cattle, bison, or ungrazed). My results suggested that cattle grazing is associated with reduced ability of either modeling approach to correctly predict butterfly presence in badlands habitat and raises the possibility that cattle grazing or its intensity is a negative factor in the conservation of *A. mormo*.

Many of the sites in the VMCP that were predicted to have butterflies had abundant host plant habitat, but no butterflies, even during the peak of the flight season. This may be due to the fact that the requirements of many insect species are determined by larvae, not adults ovipositing females of *A. mormo* place eggs directly on soil or rocks, not on the host plant, as was previously thought (Thomas et al. 1992; Wick et al. 2012). One hypothesis is that cattle grazing diminishes the quality of egg and larval habitats by compacting soil, and therefore ovipositing female butterflies might avoid habitats that have been degraded by grazing.

The federal government is currently divesting the Prairie Farm Rehabilitation Administration (PFRA) community pastures (such as the VMCP) from federal to provincial control, a process that began in 2012. The PFRA has been heralded by some as one of Canada's greatest success stories, as its creation in 1935 helped quell the effect of the Dust Bowl (Monk 2012). Nowhere is the loss of this program felt more strongly than in southern Saskatchewan – 62 out of the program's 80 community pastures are located in Saskatchewan, covering 720,340 hectares, and they have been managed by the federal government for ecological purposes for 65 years (Herriot 2012; Wark 2012). The effects of the dissolution of this program are already being seen in loss of jobs in Saskatchewan, where some school districts are a quarter-filled with children of PFRA employees (Monk 2012). It currently remains uncertain as to what will happen to these large tracts of land, much of which contains threatened and endangered species, in addition to several colonies of *A. mormo*.

Exotic species

Other studies have found that non-host plants, especially Eurasian exotics, can indirectly affect butterfly distribution through competitive exclusion of host plants (Proctor & Woodwell 1975; Murphy & Ehrlich 1988; Murphy & Weiss 1988; Mattoni et al. 1997; Osborne & Redak 2000). In a recent report on the status of *A. mormo langei*, invasive plants were listed as one of the primary threats. The host plant of *A. mormo langei*, *Eriogonum parviifolium*, like *E. pauciflorum*, relies on natural disturbance. In the case of *E. parviifolium* the constant erosion, reformation and destabilization of the sand dunes in California is needed for it to thrive. The invasive species documented in the Antioch Dunes, where *A. mormo lanegi* resides, stabilize the sand dune system, eliminating the disturbance regime on which *E. parviifolium* relies.

The only exotic species that I documented in coexistence with *A. mormo*'s host plant in this study was yellow sweet clover (*Melilotus officinalis*). However, the occurrence of this species in host plant habitat is presently low at an average cover of less than 1% in habitat occupied by the butterfly. Although the degree of invasion of *M. officinalis* in *E. pauciflorum* habitat was marginal, there is reason for land managers to be cautious of this exotic species. In GNP there are substantial tracts of land that have been engulfed by this plant, some of them bordering small *E. pauciflorum* habitat patches. Many of these *E. pauciflorum* patches have the potential to be used as stepping stone habitat by individual butterflies as they move from one colony to another, movements that are likely to be critical in the maintenance of a metapopulation of *A. mormo* in GNP.

Future directions

Although the work presented in this thesis has made substantial strides in advancing understanding of the ecology of northern peripheral populations of *A. mormo*, like most research, it also highlights the need for additional investigation. Although work on other populations reveals that caterpillars are typically solitary foragers and use litter at the base of host plants as shelter, little is known about caterpillar foraging and movement in the northern population (Peterson et al. 2010). Thus, future work to better understand the movement and dispersal of the caterpillar would be valuable. In our paper in the *Canadian Field Naturalist* we documented that *A. mormo* exhibits divergent oviposition choice in northern populations and thus other life history modifications may exist (Chapter IV of this thesis; Wick et al. 2012). This new knowledge of the butterfly in its northern range leads one to ask how else this butterfly may have changed its life history strategy to adapt to the frigid, blustery winters and hot, dry summers in southern Saskatchewan?

My species distribution models and associated maps (Chapter II) successfully predicted locations of many new colonies of *A. mormo* in GNP and the VMCP. Data used to develop these models are widely available as digital elevation models (DEMs) and SPOT satellite imagery, both of which have coverage that extends across the entirety of the butterfly's known and potential northern range. I chose to use only these data to enhance potential transferability of these models to other areas where the butterfly is not known to occur, such as those in the other prairie regions in southern Saskatchewan, Manitoba, or Alberta. Previous searches in Alberta have not yielded *A. mormo* (Anweiler 2007), however, with the help of my models, areas worthy of focus could be identified and specific sites could be searched. In the future, I would recommend that model parameterization include soils data, as I showed that soil salinity and acidity are related to butterfly presence on host plant habitat at the microhabitat level in Chapter III, and such data are commonly available.

It was not within the scope of my studies to investigate relationships between plant chemistry and host plant selection or larval survival. However, investigation of this relationship may help answer the question of why the butterfly occupies some host plants and not others. Butterfly oviposition choice and larval feeding have been directly linked to plant quality, particularly in terms of primary and secondary chemistry (Carter & Feeney 1999).

Thus, there are myriad veins for future work on *A. mormo* in its Canadian range, and it is my hope that the ideas presented in this thesis will promote and provide baseline data for future investigations.

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Personal communications

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Olson, Wes. 2012. Warden, Grasslands National Park.

APPENDIX I.

Mark release recapture of the Mormon metalmark

Table. Appendix-1. Mark release recapture results from August 2011. G6-BH1 are plots established in Grasslands National Park, VM10-VM14 represent plots established in the Val Marie Community Pasture. A total of 885 butterflies were caught with 142 recaptures.

	N*HAT	Lower 95% CI	Upper 95% CI	SE	Ha	N*HAT/ m^2	N*HAT /Ha
G6	1097.49	887.08	1307.90	107.35	2.54	0.04	431.59
G5	534.23	397.17	671.29	69.93	0.18	0.29	2918.01
G4	359.94	183.86	536.03	89.84	0.49	0.07	730.54
BH1	417.56	286.12	548.99	67.06	0.82	0.05	510.09
VM10	99.14	26.45	171.82	37.08	0.27	0.04	361.38
VM12	88.29	48.87	127.72	20.12	0.41	0.02	215.86
VM14	56.26	9.68	102.85	23.77	0.32	0.02	177.47

Table. Appendix-2. An explanation of the terms shown in Table 6-1. All results were based on analyses from the Program MARK (White 2012; www.phidot.org).

Term in Table 6-1	**Explanation of Term**
N*HAT	Population estimation from Jolly-Seber Method
Lower 95% CI	Confident interval for N*HAT
Upper 95% CI	Confident interval for N*HAT
SE	Standard error for N*HAT
Ha	Hectare of each plot
N*HAT/m2	Population estimation (N*HAT) per m^2
N*HAT/Ha	Population estimation (N*HAT) per hectare