AN ABSTRACT OF THE THESIS OF

Melissa M. York for the degree of Master of Science in Wildlife Science presented on November 1, 2002.
Title: Relationship Between Plant and Butterfly Community Composition on Upland Prairies of the Willamette Valley, Oregon.

Abstract approved

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Daniel K. Rosenberg

Small remnants of 'natural' habitats exist today throughout much of the world. Upland prairies in the Willamette Valley, Oregon have been nearly eliminated by conversion to agriculture and other uses. As a result, very few prairies remain and at least four butterfly species that require this habitat appear to be locally uncommon. To better understand requirements for conservation and management of upland prairies and the species that depend on them, I investigated plant abundance and species richness, butterfly abundance and species richness, and prairie integrity on 17 prairie remnants. To evaluate the relationship between prairie integrity and butterfly community composition, integrity was defined by abundance and species richness of native, prairie plant species. Because little is known about the habitat requirements of prairie-dwelling organisms, I also investigated juvenile and adult food resource use and spatial patterns associated with resource use by four locally uncommon butterfly species: common checkered-skipper, Fender's blue, Anise swallowtail, and field crescent. Plant species used and not used for nectaring and oviposition and spatial relationships between the two were explored for each butterfly species. My study provides evidence that remnants, including small, degraded sites, serve as refuges for locally uncommon butterfly species. The greatest mean number of butterfly species was detected on sites of high integrity, but total butterfly abundance at all but one

unique site was similar to that of low and medium integrity sites. Butterfly species richness appeared to be positively associated with remnant integrity while factors other than remnant integrity as defined here may be influential on butterfly abundance. Furthermore, I suggest that the locally uncommon butterflies studied here have specific habitat requirements and this likely contributed to their sparse distribution. Although host plant abundance did not appear to limit butterfly distributions within either site, I lacked sufficient sample sizes necessary to make strong inferences. Factors other than, or in combination, with host plant occurrence, such as presence of Composite nectar species and native plant abundance, may be important in determining their distribution within a site. Lack of large areas of habitat and incidence of uncommon species on remnants makes it imperative that we conserve biodiversity by the maintenance, improvement, and protection of some very small areas.

Relationship Between Plant and Butterfly Community Composition on Upland Prairies of the Willamette Valley, Oregon

by
Melissa M. York

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Melissa M. York, Author

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GENERAL INTRODUCTION

> "The balance of nature does not exist and perhaps never existed."
>
> \- C. Elton

WILLAMETTE VALLEY PRAIRIES

Upland prairies once dominated the landscape of the Willamette Valley, Oregon (Johannessen et al. 1971), but have been nearly eliminated by conversion to agriculture and other uses (Habeck 1961). Habitat destruction has threatened global biodiversity (Wilson 1988) but locally rare and endangered animal species maintain populations in remnant habitats (Liston et al. 1995; Wilson et al. 1997; Schultz & Dlugosch 1999). Because virtually all threatened ecosystems now require human intervention to persist (Ehrlich & Murphy 1987), the greatest opportunity for conservation of the diversity of organisms that rely on prairies may be best achieved with protection, restoration, and management efforts focused on remnants. The purpose of my study was to assist in these efforts by providing insight into prairie remnant integrity and patterns of community composition in the Willamette Valley, Oregon.

In Chapter One, I describe the work I performed in 2000 to explore butterflies as indicators of prairie remnant integrity in the Willamette Valley and to investigate the relationship between plant community characteristics used to determine prairie integrity (native plant, native host plant, and native nectar source abundance) and butterfly abundance and species richness. I used principal components analysis to group study sites into prairie integrity levels based on native plant and host plant abundance and host plant and nectar species richness. I used Poisson regression models to explore the relationships between plant community characteristics and butterfly abundance and species richness. The most parsimonious models were selected using Akaike's Information Criterion (Burnham and Anderson 1998).

In Chapter Two, I describe the work I undertook in 2001 to better understand characteristics associated with remnant integrity, focusing on four butterfly species that appear to be locally uncommon on Willamette Valley upland prairies, the common checkered-skipper, Fender's blue, Anise swallowtail, and field crescent. In particular, I describe these species' use of plants that provide nectar and host plants to their larvae and the spatial patterns associated with resource use. To evaluate nectar source selection, I estimated selection ratios by each butterfly species following Manly et al. (1993). To investigate possible spatial factors associated with resource use, I explored distance between nectar sources and host plants using a two-sample t-test, spatial randomness of events (nectaring and oviposition combined) using an index to dispersion, and vegetation patterns associated with used areas and areas with no observed use by using a two-sample t-test.

Information on the relationships between plant and butterfly community characteristics will be important to designing effective conservation and management strategies for upland prairie remnants in the Willamette Valley, Oregon. Information on resource and space use will be important in creating effective strategies for the conservation of locally uncommon butterfly species on Willamette Valley prairies.

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CHAPTER ONE: RELATIONSHIP BETWEEN PLANT AND BUTTERFLY COMMUNITY COMPOSITION OF UPLAND PRAIRIES IN THE WILLAMETTE VALLEY, OREGON

> "Breaking prairie was the most beautiful, the most epochal,
> the most hopeful, and as I look back on it, in one way the most
> pathetic thing man ever did, for in it, one of the loveliest things
> ever created began to come to its predestined end."
>
> -Herbert Quick

INTRODUCTION

Habitat remnants

Habitat destruction has threatened biodiversity on local and global scales (Wilson 1988). Habitat remnants play an important role in conserving biodiversity by providing refuges for locally rare and uncommon species (Grover & Slater 1994; Launer & Murphy 1994; Kirkpatrick & Gilfedder 1995) and by supporting subsets of the original regional biota (Lunt 1997). Small remnants of 'natural' habitats exist today throughout much of the world, particularly lowland temperate grasslands, grassy forests, and woodlands in Australia (Grover & Slater 1994; Lunt 1997) and native prairies in the United States (Launer & Murphy 1994; Samson & Knopf 1994). Habitat loss in the United States alone has been so substantial that prairies, especially those of the Great Plains region, have been reduced to less than 1% of their former area (Swengel & Swengel 1999) and are considered the most endangered ecosystems in North America (Samson & Knopf 1994). Loss of prairie habitat in other regions of North America also appears to be severe, particularly in the Willamette Valley, Oregon.

Upland prairies once dominated the landscape of the Willamette Valley (Johannessen et al. 1971), but have been nearly eliminated by conversion to agriculture, invasion by trees, and other development (Habeck 1961). However, locally rare and endangered species such as the Fender's blue butterfly (*Icaricia icarioides fenderi*) and Kincaid's lupine (*Lupinus sulphureus kincaidii*) maintain populations in remnant habitats (Liston et al. 1995; Wilson et al. 1997; Schultz & Dlugosch 1999). Because virtually all threatened ecosystems now require human intervention to persist (Ehrlich & Murphy 1987), the greatest opportunity for conservation of the diversity of organisms that rely on prairies may be best achieved with protection, restoration, and management efforts focused on remnants. The purpose of my study was to assist in these efforts by evaluating patterns of plant community composition on Willamette Valley prairie remnants and exploring the use of a set of possible indicator species. Butterflies are sensitive indicators of their habitat (Erhardt 1985) because they coevolved with plants and have specific associations with native species (Ehrlich & Raven 1964). Thus, I investigated the relationship between plant community characteristics and butterfly abundance and species richness and evaluated butterflies as indicators of prairie integrity; greater native components indicated higher integrity prairie habitat. By evaluating the relationship between prairie integrity and butterfly community characteristics, I was also able to identify integrity levels necessary to retain butterfly species. Establishment of indicator species and insight into patterns of plant community characteristics on remnant habitats may provide opportunities for conservation of prairie habitats.

Predictions and hypotheses

Butterfly community composition, as measured by abundance and species richness, should respond positively to several plant community characteristics. Plant species diversity may be influential (Murdoch et al. 1972; Southwood et al. 1979; Viejo 1985; Brown & Hyman 1986). However, plants that serve as larval host plants (juvenile resources) and nectar sources (adult resources) define species' distributions (Ehrlich & Raven 1964; Scott 1986; Hill 1992; Feber et al. 1996; Schultz & Dlugosch 1999). Thus, I expected butterfly community composition to be most closely associated with juvenile and adult food resources (Dempster & Pollard 1981; Hill & Pierce 1989; Erhardt 1985), particularly abundance and species richness of native food resources. Butterfly abundance and species richness should be greater on sites of higher integrity, where high integrity sites are defined as having greater abundance and species richness of native plants. Prairie size or area also may be associated with the ability of remnants to maintain populations of native plants and animals. Generally, a greater abundance of organisms and species richness is expected on a site of greater area (Preston 1960). However, only small areas of high integrity prairie exist in the Willamette Valley, while low integrity sites range from small to very large areas (Wilson 1996). Thus, I expected butterfly abundance and species richness to be negatively influenced by patch area. I expected a linear relationship between butterfly and plant community characteristics, such as butterfly and plant species richness, or a non-linear relationship where some upper limit of these factors is achieved, after which, the response remains relatively constant.

METHODS

Study sites

Within the Willamette Valley, Oregon (Figure 1.1), I selected prairie sites to fill an array of sizes, integrity levels, and geographical locations (Table 1.1). A recent survey of native prairies in the Willamette Valley (Wilson 1996) and communication with local conservation groups and government agencies served as the basis for study site selection. Criteria for selection included landowner permission, area $\geq$ 0.2 ha, absence or near absence of woody vegetation, and absence of on-going management, such as mowing.

I placed a 2000 m^2 plot (40 m X 50 m; Figure 1.2) within each site, allowing me to sample an equal area at all sites. Plots were positioned in each site so as to contain plant species composition and structure representative of the entire site. All butterfly and plant surveys were conducted within the study plots.

Within each study site, I defined a 'patch' as the area of plant composition and structure similar to that of the study plot. For most sites, patch area was less than total site area. I collected Universal Transverse Mercator (UTM) coordinates for the perimeter of each patch using a handheld Global Positioning System unit (Garmin, Model 12XL, Olathe, KS). With Geographic Information System software (ArcView 1995), I calculated the area (ha) for each patch.

Plant and butterfly community composition

I placed 15 quadrats, each measuring $0.5m^2$, within each plot at randomly selected locations (Figure 1.2) twice during the butterfly flight season in order to estimate plant abundance and species richness. Percent cover was ocularly estimated by 1% increments

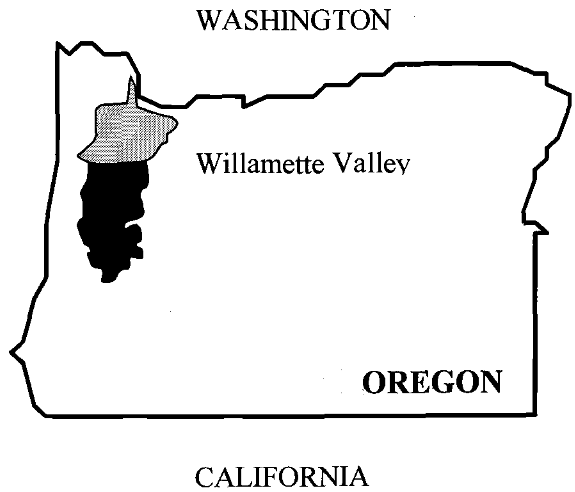

Figure 1.1. Location of Willamette Valley, Oregon; black shaded area indicates extent of sampling effort in 2000.

Table 1.1. Description of study sites in the Willamette Valley, Oregon, 2000.

Prairie integrity group[a]	*Site name*	*Site size (ha)*	*County*	*Township, Range, and, Section*
Low				
	Bald Top	0.4	Benton	T13S R5W S19
	Carson Prairie	0.9	Benton	T10S R5W S23
	E.E. Wilson Wildlife Area	8.9	Benton	T10S R4W S19
	Pigeon Butte	1.8	Benton	T13S R5S S32
	Spires Lane	4.6	Lane	T17S R4W S14
	Wainwright property	10.3	Polk	T7S R5W S2
Medium				
	Bald Hill Low	0.3	Benton	T11S R5W S31
	Blakesley Creek	0.9	Benton	T11S R6W S26
	Forest Peak	0.3	Benton	T10S R5W S22
	Jackson Place	1.6	Benton	T11S R5W S16
	Open Space Park	0.6	Benton	T11S R6W S23
	Willow Creek Nature Preserve	5.6	Lane	T18S R4W S3
High				
	Bald Hill High	0.8	Benton	T11S R5W S22
	Butterfly Meadow	0.5	Benton	T11S R5W S18
	Kingston Prairie Preserve	4.4	Linn	T9S R1E S19
	Philomath Heights	0.4	Benton	T12S R6W S2
	Shoulder-to-Shoulder Farm	0.3	Benton	T11S R6W S26

[a] *Based on principal components analysis of four native vegetation variables.*

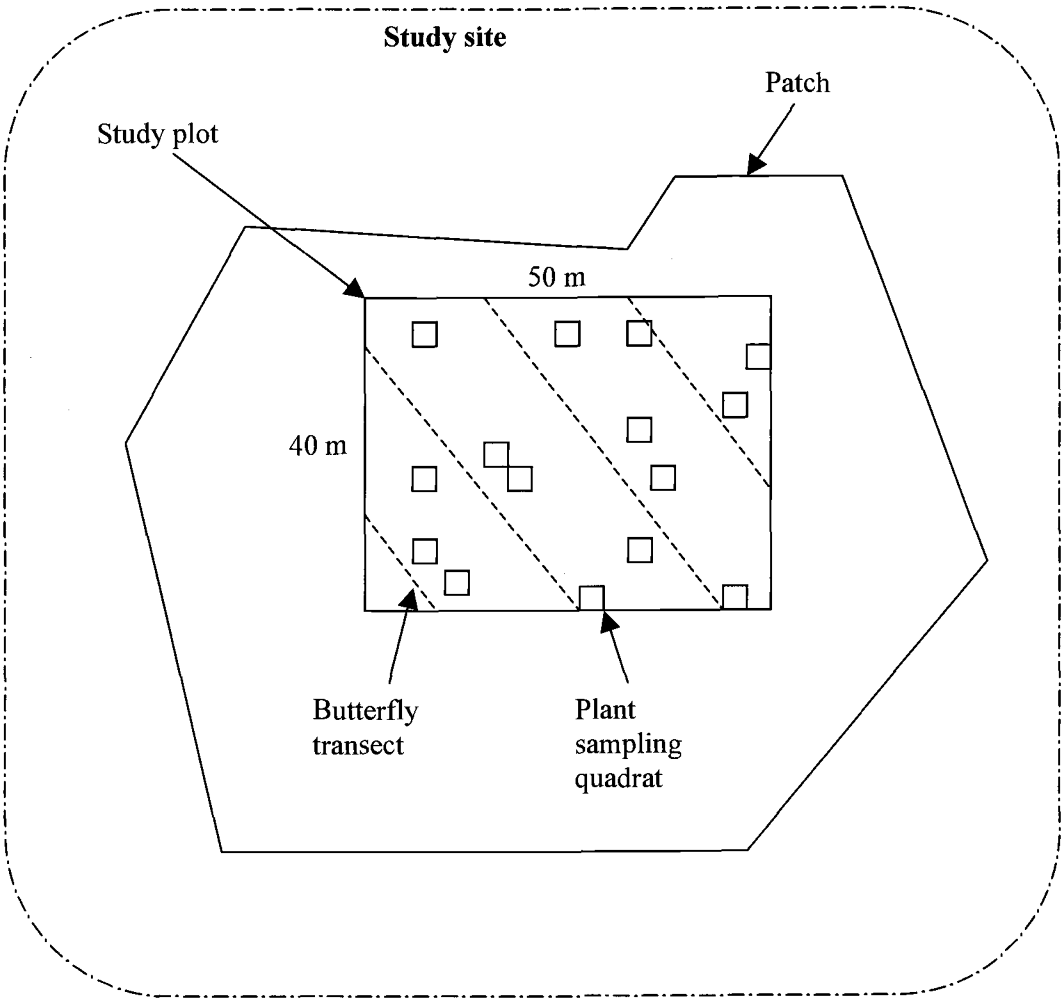

Figure 1.2. Example study site with sampling scheme used to collect data on butterfly and plant community characteristics on prairie sits in the Willamette Valley, Oregon, 2000.

for each species within a quadrat (Bonham 1989). The number of quadrats was based on the coefficient of variation (CV) obtained from past research on native prairies (CV = 0.8; Mark Wilson, Oregon State University, personal communication). I sampled twice based on the assumption that the vegetation would change throughout the butterfly flight season. I estimated plant, nectar source, and host plant abundance as the arithmetic mean of percent cover of each group over all quadrats and both surveys.

I randomly positioned a systematic set of transect lines in each study plot (Figure 1.2) to estimate butterfly abundance. The first transect began at a randomly selected start point and was directed with a randomly selected compass angle. I placed successive lines 10 m apart at the randomly chosen compass angle. Observers recorded number of diurnal butterfly species along transects at each site weekly during June-August 2000. Although adult butterflies are active in the Willamette Valley between March and September (Paul Hammond, Oregon State University, personal communication), surveys were limited to June-August because of site accessibility. Only those species known to feed on prairie plant species as juveniles (Scott 1986) were included in the analysis. The perpendicular distance from the transect line to each detected butterfly was also recorded to account for differences in detection probability among species (Buckland et al. 1993). To avoid systematic effects of time and day, I alternated the order in which I visited each site.

I estimated plant, nectar source, and host plant species richness, as well as butterfly species richness, with the first-order jackknife estimator because it allows for heterogeneity in detection probabilities among species. Although indices are often used to measure abundance and species richness (Askins et al. 1987; Patterson & Best 1995; Sparks & Parish 1995; Kilgo et al. 1997; Sanders & Edge 1998; Gabrey at al. 2001; Rodewald & Yahner 2001), one must assume that equal detectability exists among different species or that all individuals or species are detected, which is generally a false assumption (Boulinier et al. 1998a). I used the jackknife method proposed by Heltshe and Forrester (1983) because it is appropriate for samples in which the number of individuals of each species was recorded; this method is an adaptation of Burnham and Overton's (1979) estimator for population size using capture-recapture data. The jackknife estimate used by Heltshe and Forrester (1983) can be interpreted as being $1/n(n - 1)$ more than the total number of species detected for each unique species found in the sample, where n is the number of quadrats. I also estimated butterfly species richness with an index; I used the number of species detected during weekly counts because the data was unreliable to test whether equal detectability existed among butterfly species in the Willamette Valley. I compared the results obtained for butterfly species richness estimated as the number of species detected and as the estimated number of species detected from the Jackknife estimator. I considered results from both estimation methods when making inferences.

Weekly butterfly counts were summed for each species at each site as a measure of abundance during the sampling period. I placed butterfly species into functional groups based on larval host plant preference and estimated abundance for each of these groups (Table 1.2). Although distance sampling methods (Buckland et al. 1993) are commonly used to account for differences in species detectability when estimating animal abundance, the data were too sparse to use these methods. However, I was able to use the distance data to modify butterfly abundance estimates, and thus comparisons may be more reliable. I pooled the number of individuals detected over all sites and then re-grouped the butterfly species by size, color, and flight characteristics to obtain sufficient sample sizes for

Table 1.2. Prairie-dependent butterfly species detected on 17 upland prairie sites of the Willamette Valley, Oregon, June-August 2000.

Group	*Species*	*Common name*	*Number of sites where detected*	*Integrity of sites where detected* [c]
	Papilio zelicaon [a b]	Anise swallowtail	3	L, M, H
	Polites sonora [a b]	Sonoran skipper	2	M, H
	Pyrgus ruralis [a b]	Two-banded checkered skipper	2	H
	Strymon melinus [a]	Gray hairstreak	2	M
Mallow-feeder				
	Pyrgus communis [b]	Checkered skipper	7	L, M, H
Pea-feeder				
	Colias eurytheme	Western sulfur	1	L
	Everes comyntas [b]	Western tailed-blue	4	M, H
	Glaucopsyche lygdamus	Silvery blue	3	L, H
	Icaricia icarioides fenderi [b]	Fender's blue	1	H
Composite-feeder				
	Phyciodes mylitta	Mylitta crescent	4	L, M
	Phyciodes pratensis [b]	Field crescent	2	M, H
Grass-feeder				
	Cercyonis pegala	Large wood nymph	17	L, M, H
	Coenonympha tullia	Common ringlet	17	L, M, H
	Euphyes vestris [b]	Dun skipper	2	H
	Ochlodes sylvanoides	Woodland skipper	14	L, M, H

[a] *These species were not considered in functional groups because of small sample sizes.*

[b] *These species considered locally uncommon on Willamette Valley prairies (Paul Hammond, Oregon State University, personal communication).*

[c] *L: low; M: medium; H: high.*

modeling in program DISTANCE (Buckland et al. 1993; Laake et al. 1993). Simple detection functions with ≤ 2 adjustment terms were used to model the data for each butterfly group (APPENDIX A). Based on graphical displays of the data and detection functions selected with Akaike's Information Criterion, I truncated the data where the probability of detection fell below 0.25 (APPENDIX A). Although the probability of detection fell below 0.25 at varying distances among species, individuals of any species were not readily detected beyond 1.5m, indicating that detectability of butterfly species on Willamette Valley prairies decreases markedly beyond 1.5m perpendicular distance from the observer. Because I was unable to test whether differences in detection probability existed among butterfly species, I compared results obtained for abundance estimated with the full and truncated data sets. I considered all results when making inferences.

Statistical analysis

Prairie integrity groups

I used principal components analysis (PCA) in S-PLUS (2000) to classify sites according to their similarity in plant species composition (Timm 2002). I included in the PCA four native vegetation variables that remained after I removed highly redundant (correlation coefficient ≥ 0.70) variables from the original list of 11: plant and host plant abundance (percent cover) and host plant and nectar species richness (jackknifed number of species). I designated integrity levels based upon principal component (PC) values relative to the axis of maximum variation (Timm 2002) and confirmed these groupings with a scatterplot of the PC values from the first and second axes of maximum variation (Figure 1.3; Ramsey & Schafer 1997).

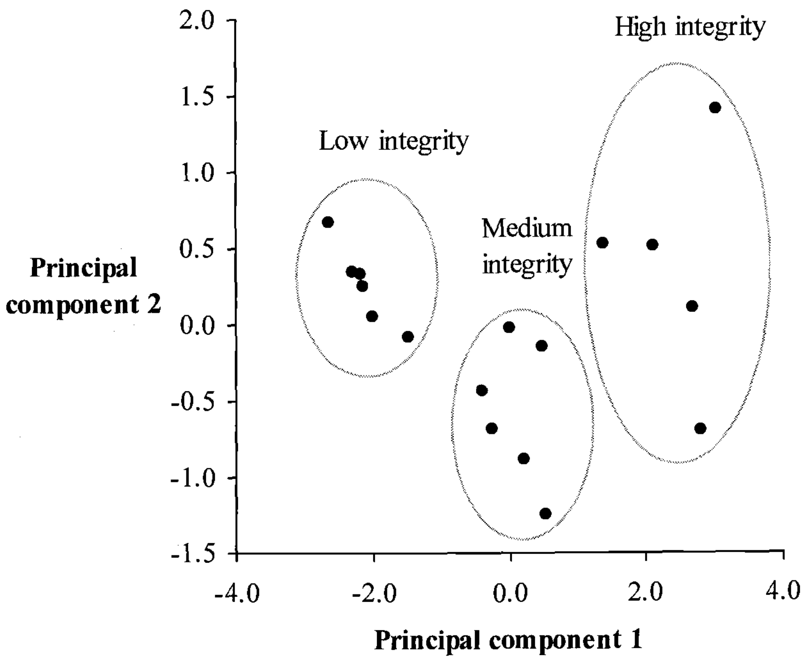

Figure 1.3. Scatterplot of the first two axes from a principal components analysis of native plant and host plant species abundance (% cover) and native host plant and nectar source species richness data to evaluate placement of sites into prairie integrity groups for 17 sites in the Willamette Valley, Oregon, 2000. Principal component 1 (PC 1) was positively associated with all four variables. Principal component 2 was positively related to native plant and host plant cover and negatively associated with species richness of native host plants and nectar sources. Sites with PC 1 values <-1 were designated low integrity, between -1 and 1 medium integrity, and >1 high integrity.

I also used PCA to evaluate similarities among sites based on butterfly community composition (abundance and species richness). I included in the PCA six variables that describe different aspects of the community: butterfly species richness (jackknifed number of species), abundance of butterflies within the group I classified as "locally uncommon" (number of individuals; Table 1.2), and composite-, grass-, pea-, and mallow-feeder abundance (number of feeder-group individuals).

Modeling procedures

Prior to data analysis, I developed hypotheses, relating butterfly abundance and species richness to vegetation variables. I explored plant abundance and species richness, host plant abundance and species richness, nectar source abundance and species richness, and patch area as vegetation variables. I expressed these hypotheses as regression models (APPENDIX B). Logarithmic forms of variables were used to express non-linear relationships.

I fit models to the data using Poisson regression in PROC GENMOD of SAS (2000) because this method is useful for describing responses that consist of integer counts (Ramsey & Schafer 1997). I examined the deviance residuals and deviance divided by its degrees of freedom to test for model lack-of-fit. I examined correlations between explanatory variables using PROC CORR in SAS (2000). Variables that were highly correlated (correlation coefficient > 0.70) were not considered together in the same regression model because these variables contained essentially the same information.

I used Akaike's Information Criterion with small sample bias adjustment (AIC_c) to select the best approximating model from my set of *a priori* models (Burnham & Anderson 1998). I report Akaike weights (w_i), a relative measure of the likelihood of the model from the set of models considered, to show the uncertainty in the ranking of models used for inferences (Burnham & Anderson 1998).

RESULTS

Locating remnant prairies in the Willamette Valley that were of sufficient size for study was difficult. Large variation existed in study site area; all sites (n = 17) were <11 ha with the majority <1 ha (Table 1.1). Some of the sites included in the study were likely upland prairie communities at one time but, because of conversion to agricultural uses, they resembled prairies only in structure. However, some prairie plants were detected on these sites (APPENDIX C) so they were retained in the study.

Plant community composition

I placed the study sites into 3 prairie integrity groups, low, medium, and high, based on the results of PCA. Low integrity sites were designated as those with PC 1 values <-1, medium sites as those with PC 1 values between -1 and 1, and high sites as those with PC 1 values >1. Sites of similarly high native composition were considered high integrity while sites of lesser native composition were considered low and medium integrity. PC 1 accounted for 87% of the variation in the data and was positively related to native plant and host plant abundance and species richness of native host plants and nectar sources (Table 1.3). PC 2 accounted for an additional 10% of the variation and was positively related to native plant and host plant cover but negatively related to species richness of native host plants and nectar sources (Table 1.3). A scatterplot PC 1 and PC 2 confirmed 3 relatively distinct integrity levels (Figure 1.3). High integrity sites were less similar to each other than were sites at other levels; high integrity sites were similar along PC 1 axis but varied widely

Table 1.3. Principal components 1 and 2 loadings based on native vegetation composition of 17 prairie sites in the Willamette Valley, Oregon, 2000.

	Loadings	
Variable	Principal component 1	Principal component 2
Native plant abundance (% cover)	0.52	0.32
Native host plant abundance (% cover)	0.49	0.61
Native host plant species richness	0.51	-0.28
Native nectar species richness	0.48	-0.67
% variance accounted for	0.87	0.10
Total variance	0.87	0.97

along PC 2 axis (Figure 1.3). Analysis of the factor loadings suggests that range in native host plant abundance created a wide spread along PC 2 axis (Table 1.3). As expected, high integrity sites were smallest in area and low integrity sites were greatest in area (Table 1.4). Medium integrity sites were remarkably similar to high integrity sites in mean species richness of most plant groups but differed dramatically in mean abundance of the same groups (Table 1.4, APPENDIX D). Low integrity sites were very similar to each other, mostly lacking native plant species (Figure 1.3, Table 1.4).

Butterfly community composition

The composition of the butterfly community at most sites was very similar based on total butterfly abundance and species richness. Three grass-feeder species were ubiquitous, occurring at a majority of the sites and at all integrity levels (Table 1.2). Seven species were observed at a maximum of 2 sites and three species were observed only on high integrity sites (Table 1.2). Sites were very similar along both PC 1 and 2 axes (Figure 1.4). PC 1 was positively related to species richness and abundance of locally uncommon, mallow-, pea,-, grass-, and composite-feeder species (Table 1.5). PC 2 was positively related to mallow- and grass-feeder abundance but negatively related to pea- and composite-feeder abundance (Table 1.4).

Butterfly species richness

Butterfly species richness differed dramatically among study sites and among prairie integrity levels. I detected a total of 15 species, over half of which were uncommon on Willamette Valley prairies (Table 1.2) and occurred only in small localized populations.

Table 1.4. Mean (±SE) plant and butterfly community characteristics at 17 sites of low, medium, and high integrity in the Willamette Valley, Oregon, 2000.

Community characteristic (units)	*Site integrity*		
	Low	*Medium*	*High*
Area	4.5 ± 1.7	1.6 ± 0.8	1.3 ± 0.8
Plant species abundance (% cover)			
Native plant	2.2 ± 1.6	20.8 ± 2.7	59.4 ± 5.4
Native hostplant	0.3 ± 0.2	12.8 ± 2.2	44.8 ± 5.1
Hostplant	46.7 ± 3.1	50.0 ± 5.3	58.60 ± 6.5
Native nectar	1.5 ± 1.3	8.3 ± 2.1	24.4 ± 6.1
Nectar	14.8 ± 4.0	32.8 ± 4.3	36.6 ± 8.8
Native pea	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2
Pea	8.0 ± 3.7	3.8 ± 0.5	1.6 ± 0.1
Native grass	0.2 ± 0.2	8.7 ± 2.2	27.2 ± 4.3
Grass	35.7 ± 4.2	24.50 ± 3.5	32.0 ± 5.3
Mallow	0.1 ± 0.0	0.5 ± 0.5	0.1 ± 0.1
Plant species richness (# of species)			
Plant	31.2 ± 3.3	65.3 ± 2.7	69.0 ± 4.5
Native plant	9.0 ± 2.1	31.3 ± 3.0	39.0 ± 3.8
Native hostplant	6.8 ± 0.9	17.7 ± 1.3	23.8 ± 1.7
Hostplant	16.5 ± 1.6	35.0 ± 1.9	34.2 ± 2.6
Native nectar	7.2 ± 1.2	22.0 ± 2.1	26.8 ± 2.3
Nectar	14.5 ± 1.3	31.5 ± 2.3	35.4 ± 2.5
Native pea	5.5 ± 0.7	11.8 ± 0.8	11.6 ± 1.2
Pea	9.0 ± 0.7	16.7 ± 1.1	15.2 ± 1.4
Native grass	6.3 ± 0.8	14.8 ± 0.9	16.2 ± 1.7
Grass	10.8 ± 1.5	22.3 ± 1.5	20.8 ± 2.1
Butterfly species abundance (# of individuals observed)			
Mallow-feeder	0.2 ± 0.2	7.2 ± 7.0	2.2 ± 1.0
Pea-feeder	2.3 ± 2.1	0.5 ± 0.1	4.8 ± 3.4
Composite-feeder	3.8 ± 2.9	1.2 ± 2.1	6.2 ± 8.0
Grass-feeder	40.2 ± 10.1	70.0 ± 17.3	57.2 ± 7.5
Butterfly species richness (# of species)	3.8 ± 0.5	4.7 ± 0.8	6.0 ± 1.3

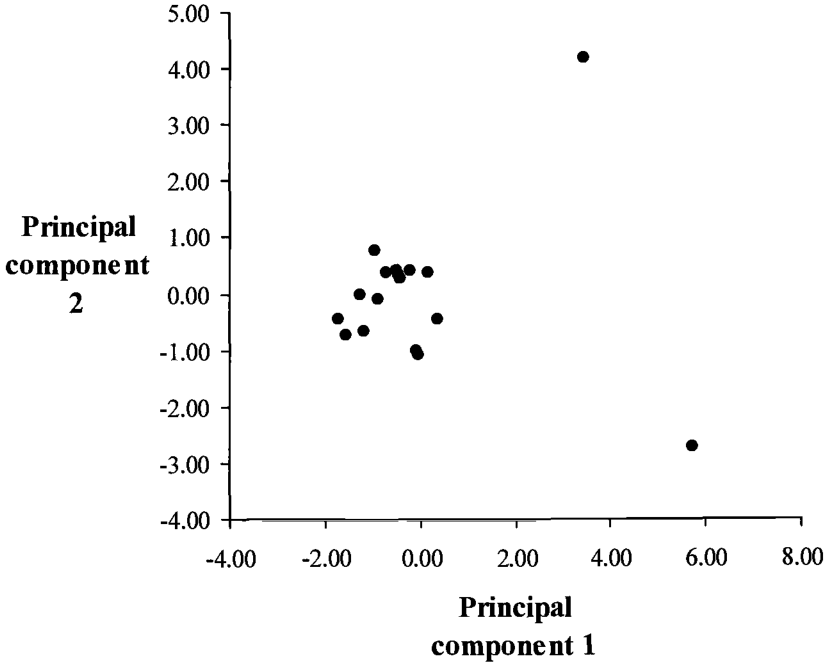

Figure 1.4. Evaluation of similarity in butterfly community composition among 17 prairie sites in the Willamette Valley, Oregon, based on principal components analysis of butterfly species richness (# species) and abundance of locally uncommon, mallow-, pea-, grass-, and composite-feeder butterflies (# individual butterflies per group). Principal component 1 was positively related to species richness and abundance of locally uncommon, mallow-, pea-, grass-, and composite-feeder species. Principal component 2 was positively related to mallow- and grass-feeder abundance but negatively related to pea- and composite-feeder abundance.

Table 1.5. Principal components 1 and 2 loadings based on butterfly community composition of 17 prairie sites in the Willamette Valley, Oregon, 2000.

	Loadings	
Variable	Principal component 1	Principal component 2
Species richness	0.53	
Rare species abundance	0.53	
Mallow-feeder abundance	0.27	0.59
Pea-feeder abundance	0.38	-0.37
Grass-feeder abundance	0.24	0.57
Composite-feeder abundance	0.41	-0.42
% variance accounted for	0.55	0.29
Total variance	0.55	0.84

As prairie integrity increased, butterfly species richness, as well as the number of locally uncommon species, increased dramatically (Figure 1.5). Plant species richness appeared to be the most influential habitat factor associated with butterfly species richness; butterfly species richness increased with plant species richness. However, the AIC weights of several models were relatively close (Table 1.6), indicating that several models may have explained the data equally well. Additionally, the "no effects" model was not heavily weighted ($w < 0.001$). Although slightly different models were selected when butterfly species richness was estimated with an index versus an estimator, most of the models with the greatest weight included positive effects of either plant species richness or native plant species richness. Positive effects of plant abundance or native nectar species richness, or negative effects of patch area were included in the competing models (Table 1.6).

Butterfly abundance

Each feeder group was most abundant at sites of medium or high integrity and each was associated with similar habitat factors. Mean mallow-feeder butterfly abundance appeared to be greatest on sites of medium integrity; however, the standard error was large and probably attributed to a single site of greater abundance (Table 1.4). Mallow-feeder butterfly abundance was most associated with mallow and native nectar abundance; mallow-feeder abundance increased dramatically with the abundance of mallow species but only very slightly with native nectar abundance (Table 1.7). Mallow-feeder butterflies were only abundant at one site ($n = 42$ individuals; APPENDIX E), which contained the greatest abundance of mallow host plants (% cover = 3; APPENDIX D). Mallow-feeders were otherwise uncommon (range among sites = 0-5 individuals) as was their hostplant, rosy checkermallow (range among sites = 0-0.4% cover). All competing models included

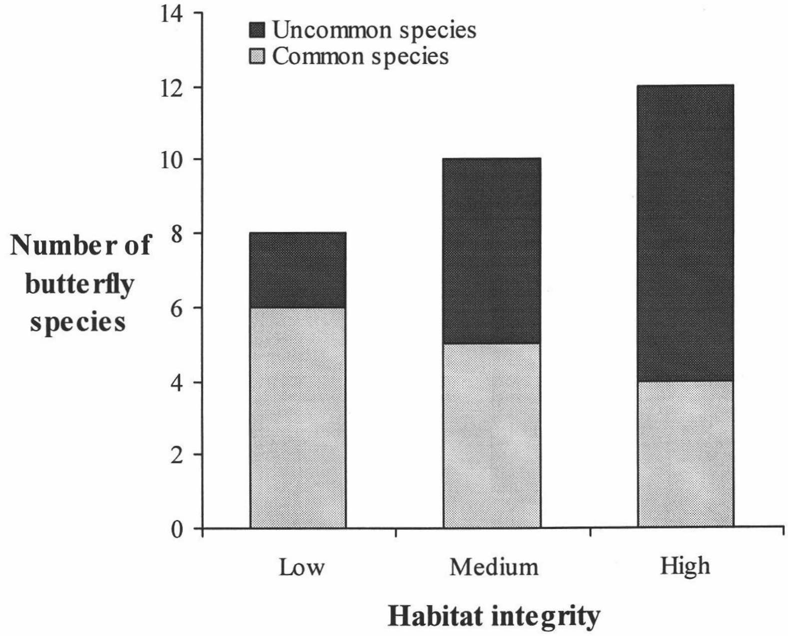

Figure 1.5. Total number of butterfly species detected at all prairie sites of low, medium, and high integrity in the Willamette Valley, Oregon, 2000. Locally uncommon and common species definitions are given in Table 1.2.

Table 1.6. Best approximating and competing Poisson regression models relating butterfly species richness (estimated with counts and jackknife estimator) to plant community characteristics on 17 prairie sites in the Willamette Valley, Oregon, 2000, with coefficient estimates (±SE) only for models with w > 0.10. All models that were considered are shown in Appendix B.

Estimator	*Predictors*	*Model rank*	w^a	*Coefficient ± SE*
Counts				
	(ln) PR[b]	1	0.49	1.01 ± 0.11
	(ln) PC [b]	2	0.11	-0.04 ± 0.36
	(ln) PR[b]			1.02 ± 0.13
	(ln) PR[b]	3	0.11	1.00 ± 0.14
	(ln) A[b]			-0.01 ± 0.04
Jackknife				
	NATPR[b]	1	0.21	0.02 ± 0.01
	NATNECR[b]	2	0.18	0.03 ± 0.01
	NATPR[b]	3	0.11	0.03 ± 0.01
	A[b]			0.06 ± 0.04

[a]*Akaike's weight is a relative measure of the likelihood of the model from the set of models considered (Burnham & Anderson 1998).*

[b]*Predictor variables include PR (plant species richness), NATPR (native plant species richness), PC (plant species abundance), NATNECR (native nectar species richness), and A (patch area).*

Table 1.7. Best approximating and competing Poisson regression models relating butterfly group abundance to plant community characteristics on 17 prairie sites of the Willamette Valley, Oregon in 2000, with regression coefficient estimates (±SE) for heavily weighted models only.

		Model	*w*[a]		*Coefficient ± SE*	
Butterfly group	*Predictors*	*rank*	*Full*[b]	*Truncated*[b]	*Full*[b]	*Truncated*[b]
Mallow-feeder species	MC[c]	1	0.48	0.87	1.48 ± 0.13	1.54 ± 0.20
	NATNECC[c]				0.04 ± 0.02	0.07 ± 0.03
	MC[c]	2	0.28	0.00	1.31 ± 0.13	
	A[c]				-0.43 ± 0.33	
	MC[c]	3	0.15	0.00	1.46 ± 0.12	
	MC[c]	4	0.09	0.00	1.57 ± 0.16	
	NECC[c]				0.03 ± 0.02	
Pea-feeder species	NATNECR[c]	1	0.81	0.67	0.28 ± 0.05	0.22 ± 0.05
	A[c]				0.72 ± 0.11	0.57 ± 0.12
	NATPR[c]	2	0.18	0.30	0.16 ± 0.03	0.13 ± 0.03
	A[c]				0.68 ± 0.11	0.56 ± 0.12

[a]*Akaikie's weight is a relative measure of the likelihood of the model from the set of models considered (Burnham & Anderson 1998).*

[b]*Refers to data set used for analysis; the full data set included all butterfly detections and the truncated data set excluded individuals at a distance from the observer where the probability of detection fell below 0.25.*

[c]*Predictor variables included MC (mallow abundance), NATNECC (native nectar species abundance), NECC (nectar species abundance), NATNECR (native nectar species richness), A (patch area), and NATPR (native plant species richness).*

positive effects of mallow abundance. Competing models also included negative effects of patch area and positive effects of nectar abundance (Table 1.7).

Mean abundance of pea-feeders appeared to be greatest on low and high integrity sites. Standard errors on the means were large because of two unique sites (Table 1.4). At one site, the Fender's blue butterfly, a pea-feeder species listed by the US Fish and Wildlife Service (USFWS, 2000) accounted for the majority of detections because it was active during the surveys; this site was of high integrity and was the only site with the species' known host plant, Kincaid's lupine. The abundance of another pea-feeder species, the silvery blue butterfly (*Glaucopsyche lygdamus*), was relatively high (n = 13; range among sites = 0-18 individuals; APPENDIX E) on a low integrity site where the abundance of pea host plant species was greatest (% cover = 26 $\pm$ 7; range = 1-26 %; APPENDIX D). However, pea-feeder butterfly abundance was most associated with the number of native nectar source species and patch area; pea-feeder abundance increased slightly with native nectar species richness and patch area. The only competing model also included slightly positive effects of patch area as well as slightly positive effects of native plant species richness (Table 1.7).

Composite-feeder butterflies were nearly absent on most study sites. However, they were detected at high abundance at 3 sites, one site each of low, medium, and high integrity (n = 18, 13, 40, respectively; range = 0-40 individuals; APPENDIX E). The locally uncommon field crescent (*Phyciodes pratensis*) was most abundant at high and medium integrity sites. A common species in this group, the mylitta crescent (*Phyciodes mylitta*), was most abundant at low integrity sites. Although the mylitta and field crescents feed within the same plant family (Compositae) as juveniles, they use different species within the family. Because of small sample sizes and lack of host plant species data for the field crescent due to misidentification problems rather than absence, I was not able to model the effects of habitat variables for each species separately nor could I evaluate the influence of host plant abundance. When I attempted to use a modeling approach with the species combined into a single group, the models with the greatest weight did not fit the data well for either the full or truncated sets, even after removing 2 unique sites (deviance/degrees of freedom ≥ 5). Plant and nectar source abundance and species richness, and patch area did not account for the variation in composite-feeder butterfly abundance among sites, providing further evidence that other factors, such as host plant abundance and species richness, may have been most influential. It is also plausible that each species responded to different vegetation characteristics.

Grass-feeders were the most abundant group at all sites. Mean grass-feeder abundance was greatest on medium integrity sites (Table 1.4). The common ringlet (*Coenonympha tullia*) and the large wood nymph (*Cercyonis pegala*) were detected at all 17 sites and the woodland skipper (*Ochlodes sylvanoides*) was detected at most sites ($n = 14$; Table 1.2). Modeling of grass-feeder butterfly abundance did not uncover any patterns, which would be expected for a group of ubiquitous species. I could not achieve an adequate model structure for this group (deviance/degrees of freedom ≥ 11) and concluded that the explanatory variables I measured did not adequately represent the variation in the responses. However, grasses were abundant at all sites and native grasses were only abundant at high integrity sites (Table 1.4). Thus, it is likely that this group of ubiquitous butterflies does not require native grasses to persist.

DISCUSSION

Patterns of prairie integrity

Low integrity sites were highly degraded but appeared to serve as refuges for small populations of a few common butterfly species. Non-native plant species were abundant on sites of low integrity, particularly grasses (e.g. *Arrhenatherum elatius*, *Dactylis glomerata*, *Poa pratensis*, and *Taeniatherum caput-medusae*), peas (e.g. *Vicia spp.*), and thistles (e.g. *Cirsium spp.*) (APPENDIX C). Some of these plants appear to serve as adequate host plants and nectar sources for some ubiquitous grass-feeder butterflies as well as for the silvery blue, a pea-feeder, and the mylitta crescent, a thistle-feeder. Native plants accounted for <2% of the total plant abundance at most sites; these sites cannot be considered prairie remnants. The majority of these sites was at low elevations and previously were farmed or grazed by cattle, disturbances that likely kept these sites in an open state but also contributed to species declines (Erhardt 1995; Lunt 1997). A population of native checkermallow (*Sidalcea virgata*) occurred at one low integrity site and appeared to support at least a small population of locally uncommon mallow-feeder butterflies. Restoration that encourages small populations of native plant species and provides refuges for locally uncommon species may provide benefits to these sites despite their overall degradation.

In contrast to what has been found in other studies on the relationship between species richness and area of habitat remnants (e.g. Daily & Ehrlich 1995), medium and high integrity sites in this study were smaller on average than low integrity sites but maintained greater butterfly species richness. Medium and high integrity sites maintained populations of ubiquitous butterfly species similar to low integrity sites but also maintained populations of locally uncommon butterfly species such as the field crescent and Western tailed-blue (*Everes comyntas*). The majority of these sites occurred at higher elevations than the low integrity sites but, similar to low integrity sites, non-native plants were abundant. Medium and high integrity sites were also being encroached upon by coniferous-deciduous forest because of lack of natural disturbances such as fire. Restoration that encourages native plant populations and natural disturbance regimes may be vital for these sites to maintain populations of locally common and uncommon butterfly species.

Butterflies as indicators of prairie integrity

Butterfly species richness may track prairie integrity in the Willamette Valley. The greatest mean number of butterfly species was detected on sites of high integrity. However, the difference between the number of butterfly species occurring on high integrity sites did not differ remarkably from the number occurring on low integrity sites. Furthermore, the butterfly community as a whole (abundance and species richness combined) at only one site appeared to be indicative of the plant community; a diverse plant community was matched with high abundance and species richness of pea-, composite-, and grass-feeder species, as well as the presence of mallow-feeders and other locally uncommon species. Although butterfly species richness tracked prairie integrity, I suggest that its use as an indicator be with prudence and only in combination with other community descriptors such as presence of each pea-, mallow-, grass-, and composite-feeder species.

Factors other than prairie integrity as measured here may be influential on butterfly abundance. Total abundance was similar among integrity levels, excluding one unique site. Butterfly abundance is thought to be most influenced by the distribution of food resources for both larvae (host plants) and adults (nectar sources) (Ehrlich & Raven 1964;

Scott 1986; Hill 1992; Feber et al. 1996; Schultz & Dlugosch 1999). The abundances of locally uncommon mallow- and composite-feeder butterflies appeared to be most associated with food resources. As predicted, abundance of mallow-feeders increased dramatically with abundance of mallow host plants and slightly with native nectar sources. One locally uncommon composite-feeder, the field crescent, feeds on *Aster spp.* (Scott 1986) that are uncommon in the Willamette Valley. A common composite-feeder, the mylitta crescent, feeds on *Cirsium spp.* (Scott 1986) that were abundant on low integrity sites. Given the observed distribution and abundance of these butterfly species and their host plants in the study, host plant abundance may have been most influential on mallow- and composite-feeder butterfly abundance.

Patterns of butterfly abundance were not always as expected. Although abundance of pea-feeders was most associated with native nectar species richness and area, the Poisson regression coefficients were small, suggesting weak relationships. Pea-feeders were nearly absent at all but two sites; this distribution may have contributed to the weak relationships I found. Late timing of the surveys may have influenced this distribution as I observed pea-feeders while conducting preliminary site analysis earlier in the season at sites where I did not observe them later in the season. Analysis of sampling data collected during peak flight time may provide better insight into factors associated with pea-feeder abundance. The grass-feeder species occurring on Willamette Valley prairies are generalists (Scott 1986) and were abundant on all sites because host plant species were similarly abundant. These species do not seem limited by host plant abundance and may feed minimally as adults (Scott 1986), making most upland grassland sites suitable habitat.

The observation that some species were abundant at only certain locations rather than particular integrity levels suggests that geographical, historical, and other factors may have also influenced present day species communities. The local plant and butterfly communities may be affected by processes acting on larger spatial or temporal scales, such as elevation (Erhardt 1995; Roland et al. 2000), land use changes including farming and livestock grazing (Buffington & Herbel 1965; Thomas 1984; Viejo et al. 1989; Pollard et al. 1995; Lunt 1997), and habitat fragmentation (Lefkovitch & Fahrig 1985; Hanski et al. 1995; Neve et al. 1996; Boulinier et al. 1998b; Mortberg 2001).

Habitat fragmentation may have influenced community composition. Remnant habitats are often geographically fragmented (e.g. Rodrigues et al. 1993; Warren 1993; Mortberg 2001). For a number of species, isolation is thought to be the cause of population declines or local extinctions (Ehrlich & Murphy 1987; Mattoni 1990; Andren 1994; Prendergast & Eversham 1995). In the Willamette Valley, patches of host plants for the endangered Fender's blue butterfly were historically located approximately 0.5 km apart; today the patches are isolated and are 3-30 km apart (Schultz 1998). Since this species is restricted to less than 20 sites in the Willamette Valley and is reported to disperse a maximum of 2.0 km, the probability of dispersal among patches is extremely unlikely (Schultz 1998). The Fender's blue butterfly occurred at only one of the sites surveyed in this study; I did not locate host plant patches or Fender's blue butterfly populations within 2 km of this site, suggesting it may represent an isolated population. Fragmentation of habitat reduces the ability of sedentary species such as the Fender's blue butterfly to move among suitable patches and survival probability of individual populations may be greatly decreased if sufficient habitat with means of connectivity is lacking (Lefkovitch & Fahrig 1985; Hodgson 1993; Andren 1994; Hanski et al. 1995; Neve et al. 1996). Future research in the Willamette Valley focused on issues surrounding fragmentation of upland prairies may help to elucidate the need for habitat connectivity.

Conservation implications

Clearing and disturbance of native vegetation for agriculture and other development has occurred at an unprecedented rate in recent centuries. Lack of large areas of habitat and incidence of rare and uncommon species on remnants makes it imperative that we conserve biodiversity by the maintenance, improvement, and protection of some very small areas. The present study provides some encouragement that even very small and very degraded remnants sustain rare and uncommon species and populations of plants and butterflies.

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CHAPTER TWO: RESOURCE USE AND SELECTION BY LOCALLY UNCOMMON BUTTERFLIES OF UPLAND PRAIRIES IN THE WILLAMETTE VALLEY, OREGON

> "Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?"
>
> -C. Darwin

INTRODUCTION

During recent history, particularly the latter half of the 20th century, butterfly populations around the world have decreased dramatically because of habitat alteration and destruction (e.g. Pyle 1976, Sibatani 1990). Butterfly populations in the United States have severely declined, particularly populations of species occurring in open areas once dominated by native grasses, areas such as prairies and wetlands (New 1997). In Oregon alone, upland prairies of the Willamette Valley (Figure 1.1) have been nearly eliminated in the last century as a result of conversion to agriculture and other uses (Habeck 1961); at least four butterfly species occurring there are restricted geographically or occur at very few sites (Chapter 1). This worldwide trend of declining populations and habitat loss has resulted in an increased awareness of conservation of butterflies and their habitats.

Detailed studies on the habitat requirements of declining butterfly species are necessary to enhance conservation efforts (Warren 1987, Bourn and Thomas 1993, Bergman 1999). Most butterfly species are specialized, relying on a limited set of native, larval host plants (Ehrlich and Raven 1964) and using a limited number of nectar sources, even when a large number of nectar-producing plants are available (Wiklund 1977, Wiklund and Ahrberg 1978, Jennerston 1984). Researchers suggest that blue and violet flowers are visited more often than yellow or white flowers (Wiklund 1977, Jennerston

1984). Butterflies also tend to utilize areas within a site where host plants are in close proximity to nectar sources; the location of host plants receiving eggs can be associated with the locations of nectar sources (Murphy 1983, Murphy et al. 1984, Grossmueller and Lederhouse 1987). Thus, the distance between used host plants and nectar sources should be less than the distance between available host plants and nectar sources. Furthermore, nectaring and oviposition events should be aggregated according to abundance of host plants and nectar sources.

The aim of this work was to study plant species utilization and spatial patterns associated with use by locally uncommon species in order to facilitate efforts to preserve both prairie habitat and organisms that depend on prairies in the Willamette Valley, Oregon. The common checkered-skipper (Hesperiidae: Pyrginae: *Pyrgus communis*), Anise swallowtail (Papilionidae: Papilioninae: *Papilio zelicaon*), and field crescent (Nymphalidae: Nymphalinae: *Phyciodes pratensis =campestris*) occur throughout much of western North America (Scott 1986) but are restricted to relatively small and localized populations in the Willamette Valley (Paul Hammond, Oregon State University, personal communication). The Fender's blue (Lycaenidae: Lycaeninae: *Icaricia icarioides fenderi*) is restricted geographically to the Willamette Valley. Although 'rare' can used to describe species fitting these descriptions, the definition is not well-defined, rarity may vary at different spatial scales, and cut-off points that separate commonness from rarity are inevitably arbitrary (Gaston 1994). Thus, to avoid confusion, I define these four species to be 'locally uncommon'.

METHODS

Study areas

In order to explore habitat utilization by four locally uncommon butterfly species, I selected sites where these species occurred at relatively high abundance within the Willamette Valley. I conducted surveys at Butterfly Meadow, which supported relatively large populations of Fender's blue, Anise swallowtail, and field crescent butterflies, and Forest Peak, where a very large population of common-checkered skippers occurred in the Willamette Valley (personal observation). Butterfly Meadow and Forest Peak are located in the northeast corner of Benton County, Oregon (Figure 2.1). Each site consisted of short-stature upland prairie surrounded by Oregon white oak (*Quercus garryana*) and mixed coniferous-deciduous forest. Elevation of both sites was approximately 450 m (1500 ft) above sea level.

Resource availability and use

Nectar source and host plant use and availability (abundance) data were collected during repeated surveys at the site (population) level for each butterfly species. I assumed that availability and use were equal for all individuals of a given species at a given site (Design I, modified Sampling Protocol A procedure, Manly et al. 1993). I defined resources for each butterfly species separately; host plants were those species they are known to feed on as larvae and nectar sources were those species that I observed each study species feeding on in the field. I estimated nectar source and plant species availability by conducting surveys throughout the study period, May-June 2001. This scheme offered the most effective means of evaluating plant species composition given that the vegetation gradually changed over the

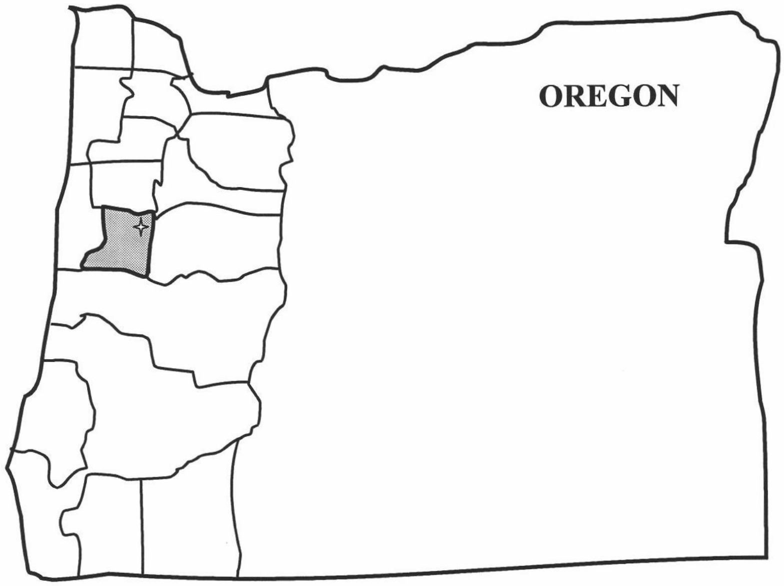

Figure 2.1. Location of Butterfly Meadow and Forest Peak in Benton County, Oregon.

course of the season and a large sample size was needed to assess spatial distribution of plant species. I created a systematic grid within each study site by placing 1 m wooden stakes at equal intervals of 10 m, creating 10 m x 10 m grid cells (Figure 2.2). Within each grid cell, I systematically placed one quadrat at Forest Peak and two quadrats at Butterfly Meadow (0.5 m^2 each). The number of quadrats I sampled differed between the sites; the preferred additional plant sampling at Forest Peak was not possible at Butterfly Meadow because of sensitivity of the vegetation to foot traffic. I identified plants to species and recorded percent cover and number of flowers for each species. I also recorded distance from host plants to the nearest nectar source and nearest host plant. To estimate nectar source and plant species abundance, I calculated the arithmetic mean of flower number and percent cover of each plant species, respectively, over all quadrats at each site.

I estimated nectar source and host plant use for each butterfly species by conducting surveys throughout May and June 2001, using the grid of 10 m X 10 m cells. I conducted surveys of butterfly activity throughout the day (0900-1600 hours) to avoid bias toward activities that occurred only at specific times of the day. Observations were not made on days with rain. Butterfly observations began after plant surveys were completed; thus, my start point for butterfly observations was determined by my location upon completion of plant sampling. I systematically walked from the start point, using the grid to search for the study species (Figure 2.2). This method produced the least amount of trampling to plants and ensured that I surveyed all parts of the meadow equally. When I located an individual butterfly of the study species, I followed it until I lost sight of it, recording information on plant species used for nectaring and oviposition. When I finished an observation, I continued searching for study species from the location where I began the last observation.

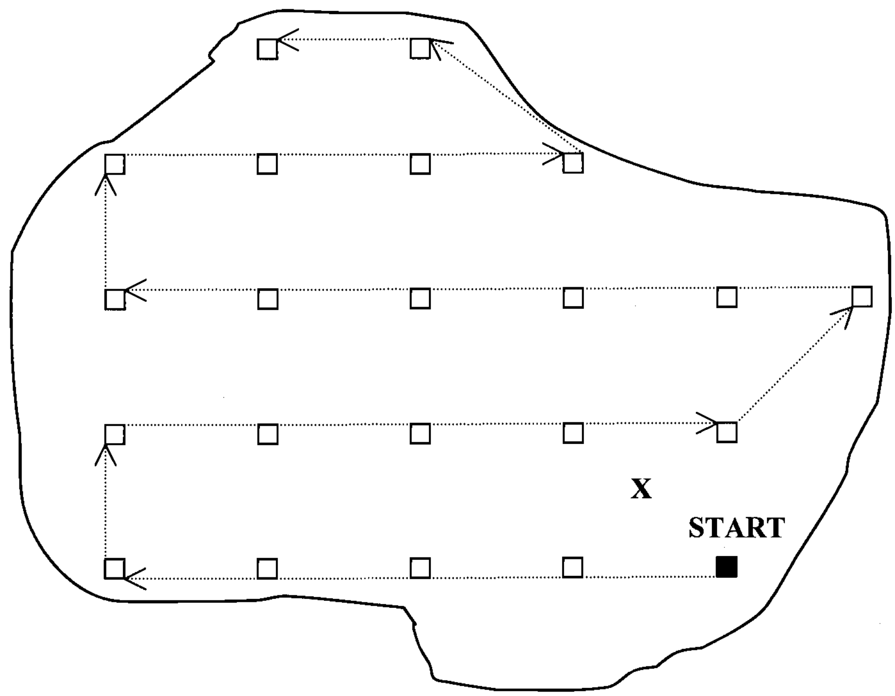

Figure 2.2. Simplified example of systematic scheme for observing butterfly resource use on two upland prairie sites in the Willamette Valley, Oregon, 2001. An open square (□) represents a grid cell corner marked with a wooden stake; each is separated by 10 m vertically and horizontally. Upon completion of plant survey (**X**), observer located corner nearest the edge of the prairie for start point of butterfly observations, represented here with a black box (■). The grid created with wooden stakes served as the butterfly observation route. Specific route through meadow was chosen to reduce trampling of plants.

Resource selection estimation

To evaluate nectar source selection, I estimated selection ratios by each butterfly species. Following Manly et al. (1993), I estimated the selection ratio (w_i) as the proportion used (number of used flowers of the ith species divided by the total number of used flowers) divided by the proportion available (number of available flowers of the ith species divided by the total number of available flowers). I constructed Bonferroni-adjusted confidence intervals (CI) on the selection ratios in order to assess whether the ith species was selected, used in proportion to its availability, or used less than in proportion to its availability. I considered species i to be selected (used more than in proportion to availability) if the lower limit of the CI was >1, used less than in proportion to its availability if the upper limit of the CI was <1, and used in proportion to its availability if the CI included the value 1. To compare selection among nectar sources used by the study species, I ranked the selection ratios from smallest to largest; I made pairwise comparisons with Bonferroni-adjusted confidence intervals. If the confidence interval contained zero, I considered evidence to be lacking for a difference between the selection ratios. However, because the butterfly observations were not independent (i.e., individuals were indistinguishable with the sampling scheme), it is likely that I underestimated the standard errors; as a result, the confidence intervals are narrower than would be expected with independent samples. Thus, for confidence intervals used to assess whether a plant species was selected, used in proportion to its availability, or used less than in proportion to its availability that included an endpoint at or very near (within 1) to a stated criterion, I considered evidence to be weak. For confidence intervals used to make comparisons among nectar sources that included an endpoint near zero (within 1), I considered evidence to be lacking for a difference between the selection ratios.

I did not estimate selection ratios for host plant species because each butterfly species used only one host plant species; I did not observe the butterflies using alternative host plants.

Spatial distribution of resource use

To investigate possible spatial factors associated with resource use, I explored distance between nectar sources and host plants, spatial randomness of events (nectaring and oviposition combined), and vegetation patterns associated with used and usused areas. Because of small sample sizes, I explored the influence of distance between nectar sources and host plants for only one species, the common checkered-skipper. I observed very few oviposition events for the other study species ($n \leq 9$ each); thus, I was not able to evaluate whether distance to nectar sources or other host plants was influential on host plant selection by these species. I used a two-sample t-test to evaluate the difference in mean distance to nearest nectar sources and mean distance to nearest host plants from sampled and used host plants.

I investigated the spatial distribution of nectaring and oviposition for each study species. I could not evaluate spatial distribution of these events separately because I observed very few oviposition events for any single species. Thus, I tallied the number of both events in each grid cell for each butterfly species and evaluated whether the sample of events was random from a Poisson distribution, the distribution most appropriate for count data (Diggle 1983). I used an index to dispersion, $I = \sum(n_i - n)^2/\{(m - 1)n$, where n_i is the number of events in grid cell i, n is the mean number of events over all grid cells, and m is the total number of grid cells (Diggle 1983). This test statistic is appropriate for quadrat counts and has a natural spatial interpretation (Diggle 1983). Aggregated or regular departures from complete spatial randomness are indicated by relatively large or small values, respectively (Diggle 1983).

To investigate whether vegetation composition influenced spatial patterns of butterfly use, I designated used areas and areas in which I did not observe use for each butterfly species. I did not observe any events in the majority of grid cells at either site; thus, all cells with ≥ 1 event were designated as used areas and all cells with no events were designated as areas with no observed use. To evaluate whether differences existed in mean native plant, host plant, and nectar source abundance between used and areas with no observed use, I used a two-sample t-test and constructed 95% confidence intervals. I considered evidence to be lacking for a difference in means for the used areas and areas with no observed use if the confidence interval included zero.

Unless noted otherwise, reported results are mean ± SE. Nomenclature follows Hitchcock and Cronquist (1973) for plants and Opler (1999) for butterflies.

RESULTS

Host plant selection

Species used

Each butterfly species was observed using previously documented host plants. I observed a total of 33 ovipositing events over the sampling period. Similar to available information (Scott 1986), I observed ovipositing by approximately four Fender's blue butterflies on Kincaid's lupine ($n = 9$) on two separate days, by approximately six common checkered-skippers on rose checker-mallow (*Sidalcea virgata,* $n = 20$) on five separate days, and by one field crescent on Hall's aster (*Aster chilensis hallii,* $n = 4$) on one day. I did not observe the Anise swallowtail ovipositing.

Influence of distance to other resources

Neither distance to a nectar source nor to other host plants appeared to influence host plant selection by the common checkered-skipper. Mean distance (m) to nearest nectar source did not differ between used host plants (0.15 $\pm$ 0.26) and available host plants (0.20 $\pm$ 0.37); 95% confidence interval for difference in means: (-0.98, 1.07). Likewise, mean distance (m) to nearest host plant was similar between used host plants (0.35 $\pm$ 1.12) and available host plants (0.36 $\pm$ 0.56); 95% confidence interval for difference in means: (-0.91, 0.93).

Nectar source selection

Collectively, the study species used only a small subset of available nectar sources. I observed 13 of 35 (Butterfly Meadow) and 11 of 24 (Forest Peak) potential nectar sources visited collectively by the study species (Tables 2.1, 2.2, 2.3, 2.4). All of the flowers that I observed visited at both sites were yellow, violet, pink, or white (in the human visual spectrum). I did not observe visits to red or blue flowers. At each site, two Composite species, wooly sunflower (*Eriophyllum lanatum*) and oxeye daisy (*Chrysanthemum leucanthemum*), accounted for ≥62% of all visits and were selected or used in proportion to availability by each of three of the butterfly species (Table 2.1, 2.3).

On an individual basis, each study species selected a very limited set of nectar sources. In particular, the Anise swallowtail used only three species; each of these nectar sources was extremely scarce, especially mountain thistle (*Cirsium callilepis*), and each was used in much greater proportion than availability (Table 2.1). There was no evidence to suggest that any nectar source was used by the Anise swallowtail in greater proportion than any other nectar sources (Table 2.5).

TABLE 2.1. Nectar source availability, use (% visitation), and selection ($w_i \pm$SE; 95% confidence interval) by three locally uncommon butterfly species at Butterfly Meadow in the Willamette Valley, Oregon, during May-June 2001.

Common name (Scientific name)	*Availability* (%)	*Use (%)* *FB*[a]	*AS*[a]	*FC*[a]	*Selection ratio* *FB*[a]	*AS*[a]	*FC*[a]
Wooly sunflower (*Eriophyllum lanatum*)	1	55.3	0.0	55.6	54.2 $\pm$ 7.1 (36.3, 72.1)		53.6 $\pm$ 2.5 (47.2, 60.0)
Oxeye daisy (*Chrysanthemum leucanthemum*)	3	14.9	0.0	43.0	6.1 $\pm$ 2.1 (0.8, 11.4)		17.6 $\pm$ 1.0 (14.9, 20.3)
Puget balsamroot (*Balsamhoriza deltoidea*)	0	0.0	39.0	0.5		1019.5 $\pm$ 127.5 (713.5, 1325.5)	13.5 $\pm$ 6.8 (0, 31.2)[b]
Mountain thistle (*Cirsium callilepis*)	0	0.0	32.0	0.0		2509.4 $\pm$ 365.8 (1631.5, 3387.4)	
Northern saitas (*Brodiaea congesta*)	1	0.0	29.0	0.0		65.0 $\pm$ 10.2 (40.6, 89.4)	
Oregon geranium (*Geranium oreganum*)	0	14.9	0.0	0.0	389.3 $\pm$ 135.8 (51.4, 727.3)		
Kincaid's lupine (*Lupinus sulphureus kincaidii*)	3	10.6	0.0	0.0	3.5 $\pm$ 1.5 (0.0, 7.1)[b]		

TABLE 2.1. Continued

Common name (Scientific name)	Availability (%)	Use (%) FB[a]	AS[a]	FC[a]	Selection ratio FB[a]	AS[a]	FC[a]
Yarrow (*Achillea millefolium*)	1	0.0	0.0	0.8			0.7 ± 0.4 (0.0, 1.7)[b]
American vetch (*Vicia americana*)	0	4.3	0.0	0.0	15.2 ± 10.8 (0.0, 42.3)[b]		
Large-flowered agoseris (*Agoseris grandiflora*)	0	0.0	0.0	0.3			20.2 ± 20.5 (0.0, 73.4)[b]
Common cryptantha (*Cryptantha intermedia*)	0	0.0	0.0	0.3			6.7 ± 6.7 (0, 24.2)[b]
Bigroot (*Marah oreganus*)	0	0.0	0.0	0.3			20.2 ± 149.8 (0.0, 383.7)[b]
Least hop clover (*Trifolium dubium*)	77	0.0	0.0	0.3			0.0 ± 0.0 (0.0, 0.0)

[a] *Butterfly species: FB(Fender's blue butterfly, n* = 47*); AS (Anise swallowtail, n* = 100*); FC (Field crescent, n* = 388*).*

[b] *Negative lower limits are impossible and thus, were replaced with 0.0.*

TABLE 2.2. Availability of nectar sources not utilized by three locally uncommon butterfly species at Butterfly Meadow in the Willamette Valley, Oregon, May-June 2001.

Common name (Scientific name)	*Availability (%)*
Heal-all (*Prunella vulgaris*)	2.8
Dandelion (*Taraxacum officinale*)	2.1
Godetia (*Clarkia sp.*)	1.2
Dovefoot geranium (*Geranium molle*)	0.6
Gum-weed (*Madia gracilis*)	0.4
Harvest brodiaea (*Brodiaea coronaria*)	0.1
Death-camas (*Zigadenus venenosus*)	0.1
Bedstraw (*Galium sp.*)	0.1
Bi-colored flaxflower (*Linanthus bicolor*)	0.1
Hooker's silene (*Silene hookeri*)	0.1
Common centaury (*Centaurium umbellatum*)	<0.1
Grass pea (*Lathyrus sphaericus*)	<0.1
Rose checker-mallow (*Sidalcea virgata*)	<0.1
Flytrap dogbane (*Apocynum androsaemifolium*)	<0.1
Stork's bill (*Erodium cicutarium*)	<0.1
Wild strawberry (*Fragaria virginiana*)	<0.1
Hairy cat's ear (*Hypochaeris radicata*)	<0.1
Hareleaf (*Lagophylla ramosissima*)	<0.1
English plantain (*Plantago lanceolata*)	<0.1
Western buttercup (*Ranunculus occidentalis*)	<0.1
Prickly sow-thistle (*Sonchus asper*)	<0.1
Purslane (*Veronica peregrina*)	<0.1

TABLE 2.3. Nectar source availability, use (n = 166), and selection (w_i±SE; 95% confidence interval) by the common checkered-skipper (*Pyrgus communis*) at Forest Peak in the Willamette Valley, Oregon, during May-June 2001.

Common name (Scientific name)	*Availability (%)*	*Use (%)*	*Selection ratio*
Wooly sunflower (*Eriophyllum lanatum)*	1.7	56.0	33.2 ± 2.3 (28.9, 37.5)
Wooly clover (*Trifolium microcephalum*)	18.0	16.3	0.9 ± 0.2 (0.6, 1.2)
Rose checker-mallow (*Sidalcea virgata*)	1.6	13.9	8.5 ± 1.6 (5.4, 11.6)
Oxeye daisy (*Chrysanthemum leucanthemum*)	1.2	6.0	5.1 ± 1.6 (2.1, 8.0)
Tolmie's mariposa lily (*Calochortus tolmiei*)	0.1	3.6	72.9 ± 0.0 (72.9, 72.9)
Thimble clover (*Trifolium microdon*)	1.5	1.2	0.8 ± 0.6 (0.0, 1.9)[a]
Northern saitas (*Brodiaea congesta*)	0.4	0.6	1.7 ± 1.7 (0.0, 5.0)[a]
Common vetch (*Vicia sativa*)	0.5	0.6	1.2 ± 1.2 (0.0, 3.5)[a]
Common cryptantha (*Cryptantha intermedia*)	4.0	0.6	0.2 ± 0.2 (0.0, 0.4)[a]
Field madder (*Sherardia arvensis*)	5.4	0.6	0.1 ± 0.1 (0.0, 0.3)[a]
Macrae's clover (*Trifolium macraei*)	0.1	0.6	12.2 ± 12.5 (0.0, 35.1)
Total	34.5	100	

[a] *Negative lower limits are impossible and thus, were replaced with 0.00.*

TABLE 2.4. Availability of nectar sources not utilized by the common-checkered skipper (*Pyrgus communis*) at Forest Peak in the Willamette Valley, Oregon, during May-June 2001.

Common name (Scientific name)	*Availability (%)*
Small-flowered lotus (*Lotus micranthus*)	62.9
Menzies' larkspur (*Delphinium menziesii*)	0.8
Grass pea (*Lathyrus sphaericus*)	0.5
Dovefoot geranium (*Geranium molle*)	0.4
Microsteris (*Microsteris gracilis*)	0.2
Hairy vetch (*Vicia hirsuta*)	0.2
Wild strawberry (*Fragaria virginiana*)	0.2
Oregon iris (*Iris tenax*)	0.2
Dandelion (*Taraxacum officinale*)	0.2
Stork's bill (*Erodium cicutarium*)	0.1
Two-color lupine (*Lupinus bicolor*)	0.1
Purslane (*Veronica peregrina*)	0.1
Miner's lettuce (*Montia perfoliata*)	0.1

TABLE 2.5. Bonferroni confidence intervals for the set of possible differences between selection ratios for nectar sources used by the Anise swallowtail (*Papilio zelicaon*, $n = 100$) at Butterfly Meadow in the Willamette Valley, Oregon, 2001. Each confidence interval (lower limit, upper limit) contained zero, providing evidence for no difference between selection ratios.

Species	*CICA*[a]	*BADE*[a]
BADE	-4799.2, 7779.1	
BRCO[a]	-3671.3, 8560.3	-511.7, 2420.7

[a] *CICA:* Cirsium callilepis; *BADE:* Balsamhoriza deltoidea; *BRCO:* Brodiaea congesta.

Although the Fender's blue occurred at the same site as the Anise swallowtail, different nectar sources were selected. The Fender's blue butterfly used only five species for nectaring (Table 2.1). Oregon geranium (*Geranium oreganum*) had the greatest selection ratio and was extremely scarce (Table 2.1). Wooly sunflower had the second greatest selection ratio and accounted for 55% of nectaring visits by the Fender's blue (Table 2.1); wooly sunflower was preferred over two other species (Table 2.6).

Similar to the Fender's blue, the field crescent used eight nectar sources (Table 2.1) and seemed to prefer wooly sunflower. Wooly sunflower accounted for 55% of the nectaring visits by the field crescent (Table 2.1) and was preferred over other selected nectar sources (Table 2.7). I also observed the field crescent imbibing fluid from a small seep in the meadow on a few occasions.

Comparable to the Fender's blue and field crescent, the common checkered-skipper seemed to prefer wooly sunflower out of the 11 species it visited for nectar. Wooly sunflower received >50% of all visits by the skipper and was used in greater proportion than all other selected species with lesser selection ratios (Table 2.3, 2.8). Tolmie's mariposa lily (*Calochortus tolmiei*) and Macrae's clover (*Trifolium macraei*) had the greatest selection ratios but accounted for <5% of all visits by the skipper and were not preferred over any of the other selected species (Table 2.3, 2.8). The selection ratios were probably large because Tolmie's mariposa lily and Macrae's clover were extremely scarce.

TABLE 2.6. Bonferroni confidence intervals for the set of possible differences between selection ratios for nectar sources used by Fender's blue butterfly (*Icaricia icarioides fenderi*, $n = 47$) at Butterfly Meadow in the Willamette Valley, Oregon, 2001. Confidence intervals (lower limit, upper limit) not containing zero provide evidence for a difference between selection ratios.

Species	*GEOR*[a]	*ERLA*[a]	*VIAM*[a]	*CHLE*[a]
ERLA	-417.8, 1088.0			
VIAM	-378.6, 1126.9	-7.3, 85.4		
CHLE	-368.9, 1135.4	13.4, 82.9	-22.9, 41.1	
LUSU[a]	-366.3, 1137.9	16.4, 85.2	-19.9, 43.4	-5.2, 10.5

[a] *GEOR:* Geranium oreganum; *ERLA:* Eriophyllum lanatum; *VIAM:* Vicia americana; *CHLE:* Chrysanthemum leucanthemum; *LUSU:* Lupinus sulphureus kincaidii.

TABLE 2.7. Bonferroni confidence intervals for the set of possible differences between selection ratios for nectar sources used by the field crescent (*Phyciodes pratensis*, $n = 388$) at Butterfly Meadow in the Willamette Valley, Oregon, 2001. Confidence intervals (lower limit, upper limit) not containing zero provide evidence for a difference between selection ratios.

Species	*ERLA*[a]	*AGGR*[a]	*MAOR*[a]	*CHLE*[a]	*BADE*[a]	*CRIN*[a]	*ACMI*[a]
AGGR	-52.0, 118.7						
MAOR	-52.0, 118.7	-117.2, 117.2					
CHLE	15.0, 57.0	-80.4, 85.7	-80.4, 85.7				
BADE	-1.0, 81.1	-83.5, 97.0	-83.5, 97.0	-32.0, 40.2			
CRIN	16.5, 77.2	-72.4, 99.4	10.5, 16.4	-12.4, 34.0	-35.5, 48.9		
ACMI	52.2, 53.6	-6.2, 45.3	-40.5, 79.6	15.2, 18.6	1.7, 23.9	-25.9, 38.0	
TRDU	38.9, 68.2	-11.2, 52.7	-97.0, 137.4	15.6, 19.6	-0.1, 27.0	-40.7, 54.2	-2.9, 4.3

[a] *ERLA:* Eriophyllum lanatum*;* *AGGR:* Agoseris grandiflora*;* *MAOR:* Marah oreganus*;* *CHLE:* Chrysanthemum leucanthemum*;* *BADE:* Balsamhoriza deltoidea*;* *CRIN:* Cryptantha intermedia*;* *ACMI:* Achillea millefolium.

TABLE 2.8. Bonferroni confidence intervals for the set of possible differences between selection ratios for nectar sources used by the common checkered-skipper (*Pyrgus communis*, $n = 166$) at Forest Peak in the Willamette Valley, Oregon, 2001. Confidence intervals (lower limit, upper limit) not containing zero provide evidence for a difference between selection ratios.

Species	*CATO*	*TRMA*	*ERLA*[a]	*SIVI*[a]	*CHLE*[a]	*BRCO*[a]	*VISA*[a]	*TRMM*[a]	*TRMI*[a]	*CRIN*[a]
TRMA	-197.0, 318.5									
ERLA	-213.0, 292.4	-80.0, 37.9								
SIVI	-187.5, 316.4	-51.8, 59.1	2.3, 47.2							
CHLE	-184.0, 319.7	-48.2, 62.2	6.1, 50.2	-6.1, 12.9						
BRCO	-180.7, 323.0	-44.9, 65.7	9.5, 53.4	-2.7, 16.1	-5.2, 11.8					
VISA	-180.1, 323.5	-44.2, 66.0	10.5, 53.5	-1.1, 15.6	-3.5, 11.2	-6.7, 7.7				
TRMM	-179.8, 323.5	-43.7, 66.2	11.2, 53.4	0.2, 14.9	-1.9, 10.2	-5.1, 6.8	-3.8, 4.4			
TRMI	-179.7, 323.8	-43.6, 66.3	11.2, 53.6	0.1, 15.2	-2.1, 10.6	-5.3, 7.1	-4.1, 4.9	-1.9, 2.1		
CRIN	-179.0, 324.5	-42.9, 66.9	11.9, 54.2	1.0, 15.6	-1.2, 11.0	-4.4, 7.5	-3.0, 5.2	0.0, 1.5	-1.3, 2.6	
SHAR[a]	-179.0, 324.6	-42.9, 67.0	12.0, 54.2	1.0, 15.6	-1.1, 11.0	-4.3, 7.6	-3.0, 5.2	0.1, 1.4	-1.2, 2.6	-0.6, 0.6

[a] *CATO:* Calochortus tolmiei; *TRMA:* Trifolium macraei; *ERLA:* Eriophyllum lanatum; *SIVI:* Sidalcea virgata; *CHLE:* Chrysanthemum leucanthemum; *BRCO:* Brodiaea congesta; *VISA:* Vicia sativa; *TRMM:* Trifolium microcephalum; *TRMI:* Trifolium microdon; *CRIN:* Cryptantha intermedia; *SHAR:* Sherardia arvensis.

Spatial patterns of resource use

Each of the study species exhibited an aggregated pattern of nectar source and host plant use. The common checkered-skipper had the greatest index of dispersion (Table 2.9) and was observed using only the edges of the meadow for both nectaring and oviposition (Figure 2.3). However, when I evaluated vegetation composition of nectaring and oviposition areas with use and no observed use for this species, only host plant abundance differed. Mean host plant abundance was greater in used nectar areas than nectar areas with no observed use but did not differ between used oviposition areas used and oviposition areas with no observed use (Table 2.10). The Anise swallowtail used only areas of greatest elevation ("hilltops") at Butterfly Meadow (Figure 2.4). The small portion of the prairie used had greater mean native plant abundance than did the area with no observed use by Anise swallowtails (Table 2.11). Mean nectar source abundance was extremely low and did not differ between used areas and areas with no observed use for this species (Table 2.11). I observed the Fender's blue using only the most westerly sections at Butterfly Meadow (Figure 2.4). These sections generally contained a greater abundance of native plants and possibly host plants than areas with no observed use (Table 2.11). Although events were also aggregated for the field crescent (Table 2.9, Figure 2.4), abundance of nectar sources, host plants, and native plants did not differ between used areas and areas with no observed use (Table 2.11).

DISCUSSION

Each butterfly species used a limited number of nectar sources and was observed using only one host plant species. These results support the observations of Wiklund (1977), Jennerston (1984), Wiklund and Ahrberg (1978), and Schultz and Dlugosch (1999) that

TABLE 2.9. Evaluation of spatial distribution of nectaring and oviposition events by four butterfly species, estimated by the index of dispersion *I* at Forest Peak and Butterfly Meadow in the Willamette Valley, Oregon, 2001. Probability for each species that events are a random sample from a Poisson distribution <0.0005.

Common name (Scientific name)	$I \pm SE$
Common checkered-skipper (*Pyrgus communis*)	37.4 ± 9.8
Field crescent (*Phyciodes pratensis*)	21.8 ± 8.1
Anise swallowtail (*Papilio zelicaon*)	15.1 ± 3.4[a]
Fender's blue butterfly (*Icaricia icarioides fenderi*)	6.1 ± 1.6

[a] *Nectaring events only.*

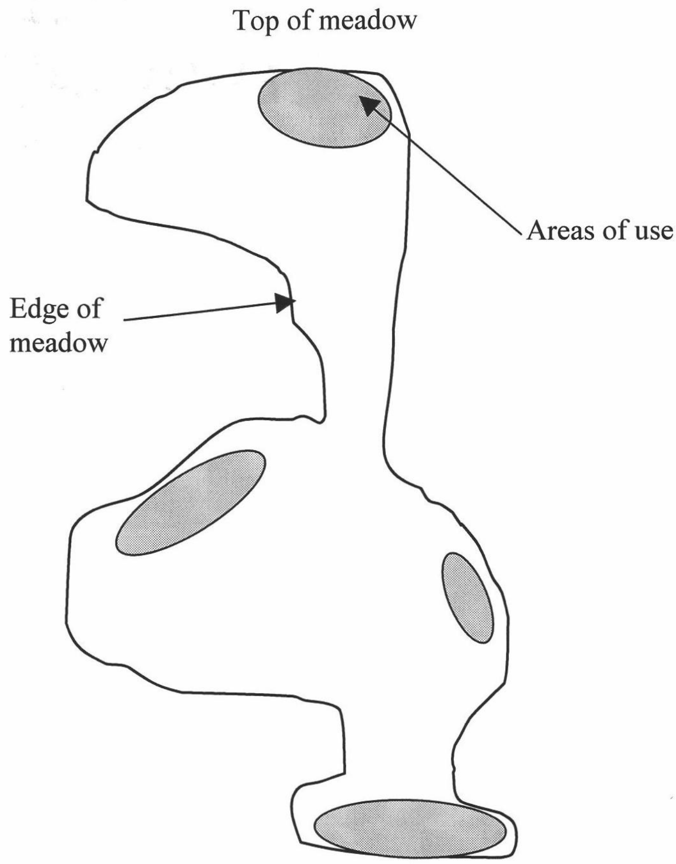

Figure 2.3. Schematic diagram of Forest Peak, with approximate areas of use by the common checkered-skipper shaded and areas with no observed use unshaded. Top of meadow designates area of greatest elevation.

TABLE 2.10. Mean (±SE) abundance of native plants (% cover), hostplants (% cover), and nectar sources (# flowers) for used areas and areas with no observed use (No obs. use) by the common checkered-skipper (*Pyrgus communis*) at Forest Peak in the Willamette Valley, Oregon, 2001, with 95% confidence intervals (CI) for differences between the means.

	Areas used for nectaring		Areas used for oviposition	
	Used (n = 17)	No obs. use (n = 52)	Used (n = 10)	No obs. use (n = 59)
Abundance	(CI)		(CI)	
Native plant	18.5 ± 3.2	15.7 ± 1.9	19.3 ± 4.6	15.9 ± 13.5
	(-4.8, 10.4)		(-5.9, 12.7)	
Hostplant	4.0 ± 1.7	0.9 ± 0.6	3.6 ± 2.3	1.3 ± 0.6
	(0.4, 6.0)		(-1.2, 5.8)	
Nectar source	10.2 ± 16.9	9.9 ± 32.2	3.1 ± 4.0	11.2 ± 31.1
	(-101.2, 119.7)		(-143.5, 159.6)	

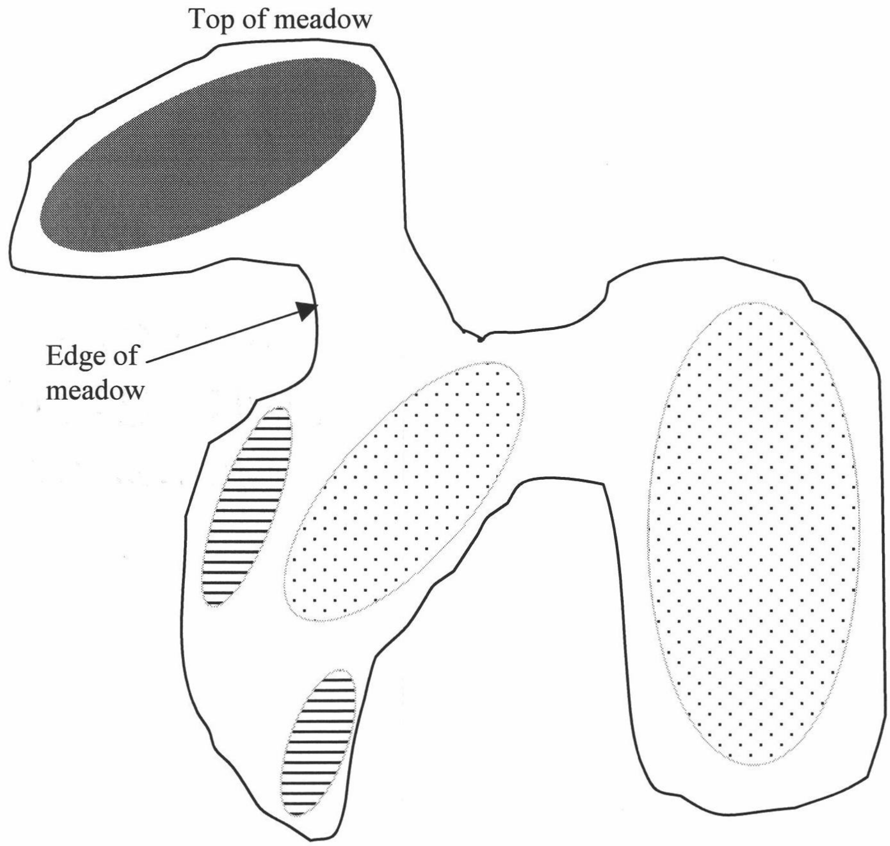

Figure 2.4. Schematic diagram of Butterfly Meadow with approximate areas used by the field crescent designated with dots, approximate areas used by the Fender's blue designated with stripes, and approximate overlapping areas of use by the field crescent, Fender's blue, and Anise swallowtail shaded gray. Top of meadow designates area of greatest elevation.

TABLE 2.11. Mean (±SE) abundance of native plants (% cover), hostplants (% cover), and nectar sources (# flowers) for used and areas with no observed use (No obs. use) by 3 species at Butterfly Meadow in the Willamette Valley, Oregon, 2001, with 95% confidence intervals (CI) for the differences between the means.

	Anise swallowtail[a]		Fender's blue[a]		Field crescent[a]	
	Used (n = 12)	No obs. use (n = 118)	Used (n = 13)	No obs. use (n = 117)	Used (n = 50)	No obs. use (n = 80)
Abundance	(CI)		(CI)		(CI)	
Native plant	48.8 ± 5.2	28.9 ± 1.9	44.7 ± 5.5	29.2 ± 1.9	32.9 ± 2.9	29.4 ± 2.3
	(7.9, 31.9)		(3.7, 27.2)		(-3.9, 11.0)	
Hostplant[b]			4.2 ± 1.8	1.4 ± 0.4	0.1 ± 0.1	0.0 ± 0.0
			(-0.1, 5.5)		(-0.1, 0.3)	
Nectar source	1.0 ± 2.0	0.2 ± 1.0	8.1 ± 17.6	3.7 ± 10.6	5.7 ± 11.1	1.1 ± 4.6
	(-5.4, 7.0)		(-59.8, 68.6)		(-16.3, 25.5)	

[a] *Anise swallowtail:* Papilio zelicaon; *Fender's blue:* Icaricia icarioides fenderi; *Field crescent:* Phyciodes pratensis.

[b] *Host plant data not available for Anise swallowtail.*

butterflies use a limited number of resources among a large number of potential resources. Although each butterfly species appeared to exhibit a monophagic strategy, utilizing only one host plant species, host plant abundance did not appear to limit butterfly distribution within either site. Host plant abundance did not differ between used areas and areas with no observed use by the Fender's blue, field crescent, and common checkered-skipper. However, host plant abundance probably contributes to these butterfly species' limited distributions among Willamette Valley prairies. The Fender's blue butterfly and its host plant, Kincaid's lupine, were not observed on 16 other upland prairie sites in 2000 (Chapter 1). Similarly, the common checkered-skipper was observed at very low abundances where its host plant, rosy checkermallow, was found at very low abundance in 2000 and the skipper was absent from sites that did not contain its host plant (Chapter 1).

Several factors may have influenced the observed similarity in host plant abundance between used areas and areas with no observed use. First, Hall's aster, host plant of the field crescent, existed only in the vegetative state during field sampling, making it difficult to locate and identify. Thus, I may have underestimated its abundance. Second, the microhabitat of host plants within areas of no observed use may have not been suitable for oviposition. Number of ovipositions may be influenced by host plant growing conditions, namely leaf structure and projection of the plants clear of surrounding vegetation (Rauscher 1981, Bourn and Thomas 1993, Warren et al. 1986, Schultz and Dlugosch 1999). Large areas of Butterfly Meadow and Forest Peak have become infested with dense stands of tall, non-native grasses (e.g. *Brachypodium sylvaticum* at Butterfly Meadow and *Dactylis glomerata* at Forest Peak) and a native fern (*Pteridium aquilinum*). Although host plants did survive in these areas, growing conditions may have been unfavorable and surrounding vegetation may have impeded both my ability to observe butterflies and the ability of butterflies to utilize host plants. Third, my study lacks sufficient oviposition sample sizes necessary for strong inferences on actual host plant use. Additional observations of these butterfly species and information on host plant microhabitat are necessary to understand factors associated with host plant selection.

Each butterfly species used a limited number of nectar sources even though a large number of nectar-producing plants was available. These results support the observations of Jennerston (1984) in which many common species were never visited. Color and form of these plants may have played an important role in butterfly foraging. Butterflies see the human-visible spectrum as well as the near ultraviolet (Post and Goldsmith 1969, Scott 1986). Flowers may possess visual patterns in the near ultraviolet (Eisner et al. 1969, Scott 1986); butterflies may use these patterns for resource recognition, namely a "target" pattern whereby yellow, white, or violet petals with bright peripheral reflection in the UV spectrum are radially symmetrical about the nectar target (Watt et al. 1974). This target pattern may signal a desired solution of nectar to all UV-perceiving pollinators who may have formed a "search image" of the most favorable species, thereby maximizing their foraging efficiency (e.g. Levin 1978). The Composite species used by the study species all appear to possess this target pattern. Although it is possible that the study species have formed search images for a target pattern, I was not able to evaluate appearance in the UV of the plant species they used. I also was not able to explore the relationship between target pattern and nectar characteristics. Thus, additional information on visual patterns in the UV spectrum and nectar characteristics of plants used by the study species may provide insight into nectar source selection and requirements.

Although all of the study species exhibited an aggregated pattern of nectaring events, factors other than nectar source abundance may have been influential on the distribution of nectaring events. Nectar source abundance did not differ between used areas and areas with no observed use for any of the four species. However, host plant abundance differed between used areas and areas with no observed use for the common checkered-skipper and native plant abundance differed between used areas and areas of no observed use for the Anise swallowtail and Fender's blue. This suggests that the common checkered-skipper preferred to nectar in close proximity to host plants and in areas with greater native composition. The Anise swallowtail only used areas of higher elevation so it is unclear whether elevation or native plant abundance was most influential on the species distribution. Factors not measured in this study that are related to microhabitat condition of native vegetation (e.g. structure of vegetation surrounding nectar sources) may have been most influential on nectaring habitat utilization by the Fender's blue. Elevation and microhabitat condition deserve additional evaluation in order to understand habitat utilization by these four locally uncommon species.

In conclusion, this study has begun to elucidate plant resources that are potentially important to four butterfly species that appear to be locally uncommon on Willamette Valley prairies. Maintenance of suitable host plant populations, including rose checker-mallow, Kincaid's lupine, and Hall's aster, is clearly important. Maintaining a variety of nectar sources, especially native Composites and particularly wooly sunflower, is also important for these species. Further studies are required to assess why these plant species are selected and the demographic consequences associated with changes in their abundance. Additionally, research on the optimal microhabitat for these butterflies, including elevation and vegetation structure, is needed to provide more effective management guidelines.

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SUMMARY

"Most is likely to be gained when we walk to the
edge of established knowledge and peer over."
- P. A. Keddy

CHAPTER ONE

Clearing and disturbance of native vegetation for agriculture and other development has occurred at an unprecedented rate in recent centuries. Lack of large areas of habitat and incidence of rare and uncommon species on remnants makes it imperative that we conserve biodiversity by the maintenance, improvement, and protection of some very small areas. The present study provides some encouragement that even very small and very degraded remnants sustain rare and uncommon species and populations of plants and butterflies.

Butterfly species richness appeared to track habitat integrity but factors other than habitat integrity as measured here may be influential on butterfly abundance. The butterfly community (abundance and species richness) at only one site appeared to be indicative of the plant community, with high abundance and species richness of pea-, composite-, and grass-feeder species, as well as the presence of mallow-feeders and other locally uncommon species. I suggest that use of butterfly species richness as an indicator of prairie integrity be with prudence and only in combination with other community descriptors such as presence of each pea-, mallow-, grass-, and composite-feeder species.

CHAPTER TWO

The common checkered-skipper, Fender's blue, Anise swallowtail, and field crescent appear to be locally uncommon on upland prairie remnants. My study suggests that these species have specific habitat requirements. Factors other than or in combination with host plant occurrence, such as presence of Composite nectar species and native plant abundance, may be important in determining their distribution. Although each butterfly species appeared to exhibit a monophagic strategy, utilizing only one host plant species, host plant abundance did not appear to limit butterfly distribution within a site. Areas used by the Fender's blue, field crescent, and common checkered-skipper were of similar host plant abundance to avoided areas. Furthermore, distance from selected host plants to nearest host plant or nectar source was similar to distance from available host plants to nearest host plant or nectar source. Each study species used a limited number of nectar sources even though a large number of nectar-producing plants was available. Color and form of these plants may have played an important role in butterfly foraging.

Success of butterfly conservation efforts requires detailed studies that identify environmental variables important to a species of interest. This study has begun to elucidate such variables for four butterfly species that appear to be locally uncommon on Willamette Valley prairies. Maintenance of suitable host plant populations, including rose checker-mallow, Kincaid's lupine, and Hall's aster, is clearly important. It is also important to maintain a variety of nectar sources, especially native Composites and particularly wooly sunflower. Research on the optimal microhabitat for these butterflies, including elevation and vegetation structure, is needed to provide more effective management guidelines.

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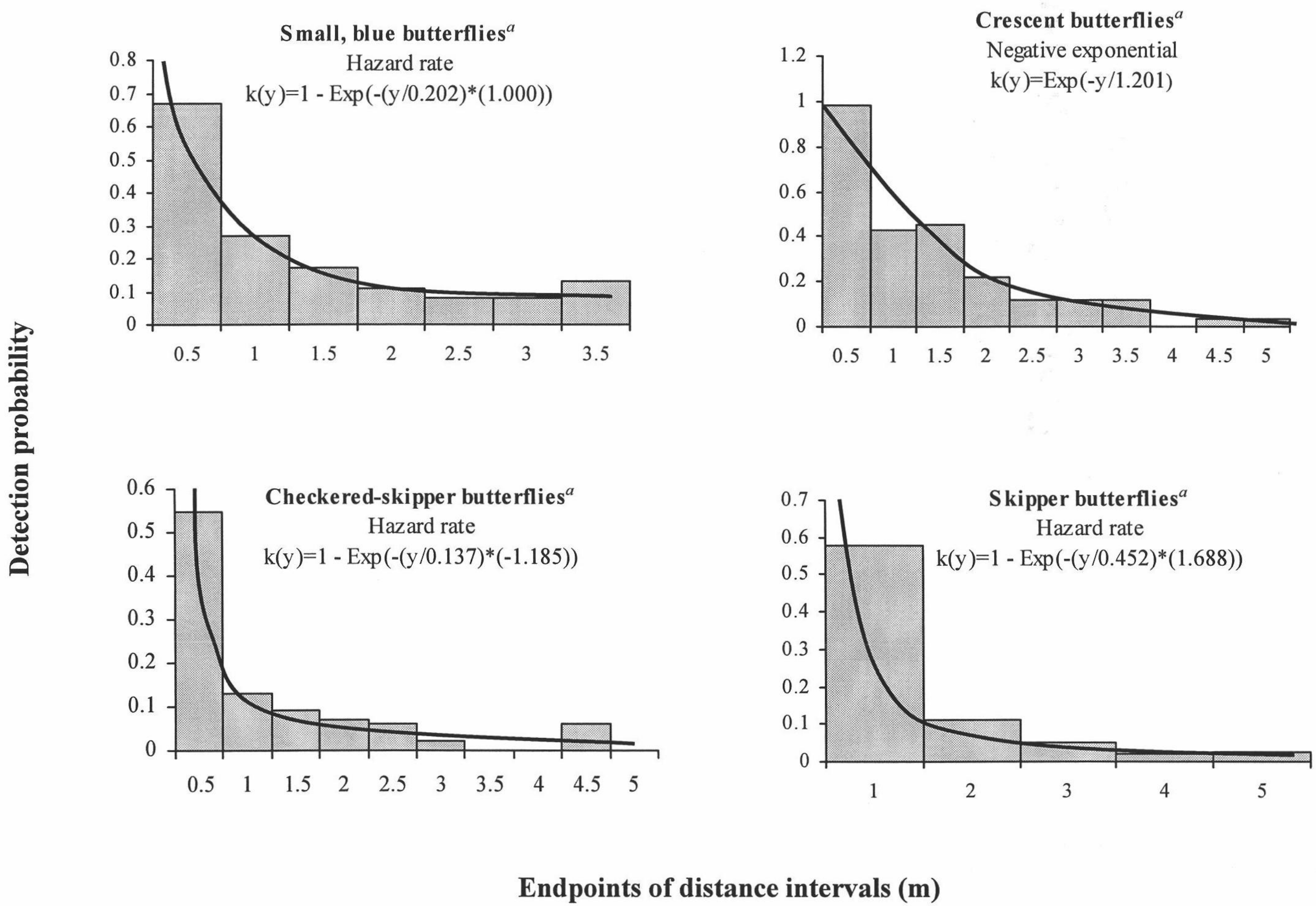
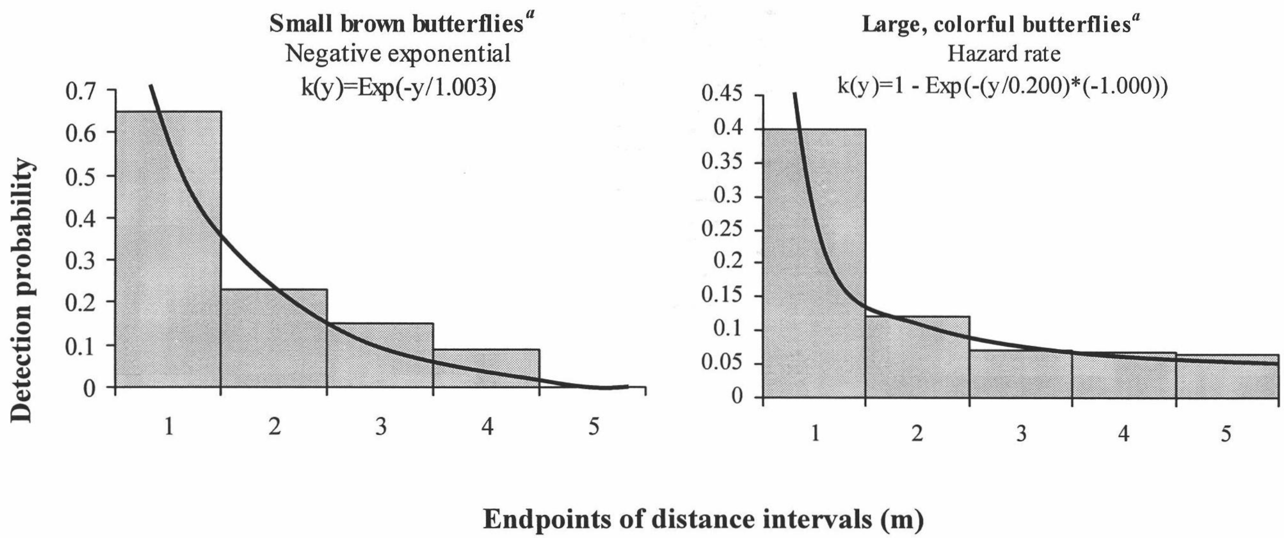
APPENDICES

APPENDIX A. Evaluation of detection functions and detection probabilities with increasing distance to observer for four butterfly groups.



APPENDIX A. Continued



a Small blue butterflies: Icaricia icarioides fenderi, Glaucopsyche lygdamus, Everes comyntas; *Crescent butterflies:* Phyciodes pratensis, P. mylitta; *Checkered-skipper butterflies:* Pyrgus communis, P. ruralis; *Skipper butterflies:* Ochlodes sylvanoides, Polites sonora; *Small brown butterflies:* Coenonympha tullia, Euphyes vestris; *Large colorful butterflies:* Papilio zelicaon, Cercyonis pegala, Colias eurytheme.

APPENDIX B. Regression models considered in analyses of the relationship of butterfly species richness and abundance to host plant, nectar source, and plant species richness and abundance.

Set	*Model*[a b]	*Description of set*
	β_0	No effects
	$\beta_0 + \beta_1$ A	Negative effect of patch area
Host plant species[c]		Positive effects of host plant species abundance and richness, and/or negative effect of patch area
	$\beta_0 + \beta_1$ NATHC	
	$\beta_0 + \beta_1$ NATHR	
	$\beta_0 + \beta_1$ NATHC + β_2 A	
	$\beta_0 + \beta_1$ NATHR + β_2 A	
	$\beta_0 + \beta_1$ NATHC + β_2 NATHR + β_3 A	
	$\beta_0 + \beta_1$ HC	
	$\beta_0 + \beta_1$ HR	
	$\beta_0 + \beta_1$ HC + β_2 A	
	$\beta_0 + \beta_1$ HR + β_2 A	
	$\beta_0 + \beta_1$ HC + β_2 HR + β_3 A	
Nectar source species		Positive effects of native nectar species abundance and richness, and/or negative effect of patch area
	$\beta_0 + \beta_1$ NATNECC	
	$\beta_0 + \beta_1$ NATNECR	
	$\beta_0 + \beta_1$ NATNECC + β_2 A	
	$\beta_0 + \beta_1$ NATNECR + β_2 A	
	$\beta_0 + \beta_1$ NATNECC + β_2 NATNECR	
	$\beta_0 + \beta_1$ NATNECR + β_2 NATNECR + β_3 A	
	$\beta_0 + \beta_1$ NECC	
	$\beta_0 + \beta_1$ NECR	
	$\beta_0 + \beta_1$ NECC + β_2 A	
	$\beta_0 + \beta_1$ NECR + β_2 A	
	$\beta_0 + \beta_1$ NECC + β_2 NECR	
	$\beta_0 + \beta_1$ NECR + β_2 NECR + β_3 A	

Continued

APPENDIX B. Continued

Set	*Model*[a b]	*Description of set*
Plant species		Positive effects of plant species abundance and richness, and/or negative effect of patch area
	$\beta_0 + \beta_1$ NATPC	
	$\beta_0 + \beta_1$ NATPR	
	$\beta_0 + \beta_1$ NATPC + β_2 A	
	$\beta_0 + \beta_1$ NATPR + β_2 A	
	$\beta_0 + \beta_1$ NATPC + β_2 NATPR	
	$\beta_0 + \beta_1$ NATPC + β_2 NATPR + β_2 A	
	$\beta_0 + \beta_1$ PC	
	$\beta_0 + \beta_1$ PR	
	$\beta_0 + \beta_1$ PC + β_2 PR	
	$\beta_0 + \beta_1$ PC + β_2 A	
	$\beta_0 + \beta_1$ PR + β_2 A	
	$\beta_0 + \beta_1$ PC + β_2 PR + β_3 A	

[a]*A: area; NATHC: native host plant species abundance; NATHR: native host plant species richness; HC: host plant species abundance; HR: host plant species richness; NATNECC: native nectar species abundance; NATNECR: native nectar species richness; NECC: nectar species abundance; NECR: nectar species richness; NATPC: native plant species abundance; NATPR: native plant species richness; PC: plant species abundance; PR: plant species richness.*

[b]*Identical models with logarithmic forms of variables were used to express non-linear relationships.*

[c]*All host plant species were used for butterfly species richness analysis; for all butterfly group abundance analyses, specific host plant species groups were used, i.e., pea species abundance was included in host plant species models for pea-feeder butterfly abundance analysis.*

APPENDIX C. Plant and butterfly species observed at 17 sites in the Willamette Valley, Oregon, 2000.

Site	*Plant species*	*Butterfly species*
Bald Hill-High	*Achillea millefolium*	Cercyonis pegala
	Agrostis tenuis	*Coenonympha tullia*
	Aira caryophyllea	*Erynnis propertius*
	Allium amplectens	*Euphyes vestris*
	Amelanchier alnifolia	*Glaucopsyche lygdamus*
	Anthoxanthum odoratum	*Ochlodes sylvanoides*
	Aster chilensis	*Papilio rutulus*
	Boisduvalia densiflora	*Everes comyntas***
	Briza minor	*Limenitis lorquini***
	Brodiaea coronaria	*Phyciodes mylitta***
	Brodiaea hyacinthina	
	Bromus carinatus	
	Bromus mollis	
	Bromus secalinus	
	Calochortus tolmiei	
	Cammassia quamash	
	Carex tumulicola	
	Carex viridula	
	Centaurium umbellatum	
	Cerastium viscosum	
	Chrysanthemum leucanthemum	
	Cirsium vulgare	
	Crataegus monogyna	
	Crepis accuminata	
	Cynosurus cristatus	
	Cynosurus echinatus	
	Dactylis glomerata	
	Danthonia californica	
	Daucus carota	
	Daucus pusillus	
	Deschampsia cespitosa	
	Dianthus armeria	
	Elymus glaucus	
	Epilobium paniculatum	
	Eriophyllum lanatum	
	Euphrasia nemorosa	
	Festuca idahoensis	
	Fragaria virginiana	
	Galium bifolium	
	Galium parisiense	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Bald Hill-High	*Geranium columbinum*	
	Geranium dissectum	
	Grindelia integrifolia	
	Holcus lanatus	
	Hordeum brachyantherum	
	Hypericum perforatum	
	Hypochaeris radicata	
	Juncus tenuis	
	Koeleria cristata	
	Lathyrus sphaericus	
	Linum angustifolium	
	Lolium perenne	
	Lomatium nudicaule	
	Lomatium triternatum	
	Madia gracilis	
	Myosotis discolor	
	Plantago lanceolata	
	Potentilla gracilis	
	Poa pratensis	
	Prunella vulgaris	
	Pyrus malus	
	Ranunculus occidentalis	
	Rhamnus purshiana	
	Rosa eglanteria	
	Rumex acetosella	
	Sidalcea campestris	
	Sisyrinchium angustifolium	
	Taeniatherum caput-medusae	
	Taraxacum officinale	
	Vicia cracca	
	Vicia hirsuta	
	Vicia sativa	
	Vicia tetrasperma	
	Wyethia angustifolia	
	Zigadenus venenosus	
Bald Hill-Low	*Aira caryophyllea*	*Cercyonis pegala*
	Agrostis tenuis	*Coenonympha tullia*
	Alopecurus pratensis	*Ochlodes sylvanoides*
	Brodiaea congesta	*Papilio eurymedon*
	Brodiaea coronaria	*Papilio rutulus*

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Bald Hill-Low	*Bromus commutatus*	*Phyciodes mylitta***
	Bromus inermis	*Pieris rapae***
	Bromus mollis	
	Bromus rigidus	
	Bromus secalinus	
	Carex tumulicola	
	Centaurium umbellatum	
	Cerastium viscosum	
	Chrysanthemum leucanthemum	
	Cirsium vulgare	
	Dactylis glomerata	
	Daucus carota	
	Daucus pusillus	
	Dianthus armeria	
	Dipsacus sylvestris	
	Epilobium paniculatum	
	Festuca arundinacea	
	Fraxinus latifolia	
	Galium aparine	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Hypericum perforatum	
	Lolium perenne	
	Madia gracilis	
	Myosotis discolor	
	Plantago lanceolata	
	Poa pratensis	
	Prunella vulgaris	
	Quercus garryana	
	Ranunculus occidentalis	
	Rosa eglanteria	
	Rumex acetosella	
	Rubus discolor	
	Senecio jacobaea	
	Sherardia arvensis	
	Taraxacum officinale	
	Tragopogon porrifolius	
	Trifolium dubium	
	Valerianella locusta	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Bald Hill-Low	*Vicia hirsuta*	
	Vicia sativa	
	Vicia tetrasperma	
Bald Top	*Agrostis tenuis*	*Cercyonis pegala*
	Aira caryophyllea	*Coenonympha tullia*
	Anthoxanthum odoratum	*Papilio rutulus*
	Arrhenatherum elatius	*Phyciodes mylitta*
	Briza minor	*Pyrgus communis*
	Brodiaea congesta	*Papilio zelicaon***
	Brodiaea coronaria	
	Bromus carinatus	
	Bromus mollis	
	Bromus rigidus	
	Bromus secalinus	
	Cerastium viscosum	
	Cirsium vulgare	
	Cynosurus echinatus	
	Galium bifolium	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Hypericum perforatum	
	Lathyrus sphaericus	
	Lotus micranthus	
	Myosotis discolor	
	Parentucellia viscosa	
	Plantago lanceolata	
	Rumex acetosella	
	Rubus discolor	
	Senecio jacobaea	
	Sherardia arvensis	
	Sidalcea virgata	
	Trifolium dubium	
	Trifolium subterraneum	
	Vicia hirsuta	
	Vicia sativa	
	Vulpia bromoides	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Blakesley Creek	*Aira caryophyllea*	Cercyonis pegala
	Amelanchier alinifolia	*Coenonympha tullia*
	Arrenatherum elatius	*Neophasia menapia*
	Avena fatua	*Ochlodes sylvanoides*
	Brodiaea coronaria	*Papilio rutulus*
	Bromus carinatus	*Limenitis lorquini***
	Bromus mollis	*Plebejus acmon***
	Bromus pacificus	
	Bromus secalinus	
	Calochortus tolmiei	
	Carex tumulicola	
	Centaurium umbellatum	
	Cerastium viscosum	
	Chrysanthemum leucanthemum	
	Clarkia amoena	
	Crataegus monogyna	
	Cynosurus echinatus	
	Cytisus scoparius	
	Danthonia californica	
	Daucus carota	
	Dactylis glomerata	
	Dianthus armeria	
	Elymus glaucus	
	Epilobium panniculatum	
	Eriophyllum lanatum	
	Festuca arundinacea	
	Festuca idahoensis	
	Fragaria virginiana	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Hypericum perforatum	
	Hypochaeris radicata	
	Juncus tenuis	
	Koeleria cristata	
	Lathyrus sphaericus	
	Linum angustifolium	
	Lolium perenne	
	Lotus micranthus	
	Madia gracilis	
	Myosotis discolor	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Blakesley Creek	*Plantago lanceolata*	
	Platanthera dilatata	
	Poa annua	
	Poa pratensis	
	Prunella vulgaris	
	Pseudotsuga menziesii	
	Pyrus communis	
	Rosa eglanteria	
	Sanicula crassicaulis	
	Sherardia arvensis	
	Taeniatherum caput-medusae	
	Vicia cracca	
	Vicia hirsuta	
	Vicia sativa	
	Vulpia bromoides	
Butterfly Meadow	*Achillea millifolium*	*Cercyonis pegala*
	Agoseris grandiflora	*Coenonympha tullia*
	Aira caryophyllea	*Erynnis propertius*
	Allium amplectens	*Euphyes vestris*
	Balsamorhiza deltoidea	*Glaucopsyche lygdamus*
	Bromus carinatus	*Icaricia icarioides ssp. fenderi*
	Bromus commutatus	*Limenitis lorquini*
	Brodiaea congesta	*Neophasia menapia*
	Brodiaea coronaria	*Ochlodes sylvanoides*
	Bromus mollis	*Papilio eurymedon*
	Bromus pacificus	*Papilio rutulus*
	Calochortus tolmiei	*Papilio zelicaon*
	Castilleja hispida	*Parnassius clodius*
	Centaurium umbellatum	*Phyciodes pratensis*
	Cerastium viscosum	*Pyrgus communis*
	Chrysanthemum leucanthemum	*Pyrgus ruralis*
	Cirsium callilepis	*Speyeria hydaspe*
	Clarkia amoena	*Speyeria cybele***
	Clarkia purperea	*Strymon melinus***
	Crepis capillaris	*Vanessa atalanta*
	Cynosurus echinatus	
	Danthonia californica	
	Dactylis glomerata	
	Daucus pusillus	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Butterfly Meadow	*Elymus glaucus* *Epilobium panniculatum* *Erigeron sp.* *Eriophyllum lanatum* *Festuca pratensis* *Festuca rubra* *Fragaria virginiana* *Galium aparine* *Galium bifolium* *Galium parisiense* *Hieracium cynoglossoides* *Hypericum perforatum* *Iris tenax* *Juncus tenuis* *Koeleria cristata* *Lotus micranthus* *Lomatium utriculatum* *Lupinus sulphureus kincaidii* *Myosotis discolor* *Osmorhiza chilensis* *Plantago lanceolata* *Platanthera dilatata* *Prunella vulgaris* *Pseudotsuga menziesii* *Pteridium aquilinum* *Ranunculus occidentalis* *Rhus diversiloba* *Rosa eglanteria* *Rumex acetosella* *Rubus ursinus* *Sanicula bipinnatifida* *Sanicula crassicaulis* *Senecio macounii* *Sherardia arvensis* *Silene hookeri* *Symphoricarpos mollis* *Synthris reniformis* *Tragopogon dubius* *Vicia americana* *Vicia sativa* *Zigadenus venenosus*	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Carson Prairie	*Achillea millifolium*	*Adelpha bredowii*
	Agoseris grandiflora	*Cercyonis pegala*
	Arrhenatherum elatius	*Coenonympha tullia*
	Avena fatua	*Limenitis lorquini*
	Bromus commutatus	*Ochlodes sylvanoides*
	Brodiaea coronaria	*Papilio rutulus*
	Brodiaea hyacinthina	*Erynnis propertius***
	Bromus mollis	*Neophasia menapia***
	Bromus rigidus	
	Bromus secalinus	
	Centaurea cyanus	
	Cirsium vulgare	
	Crepis capillaris	
	Cynosurus echinatus	
	Danthonia californica	
	Daucus carota	
	Dactylis glomerata	
	Daucus pusillus	
	Elymus glaucus	
	Epilobium paniculatum	
	Eriphyllum lanatum	
	Festuca arundinacea	
	Festuca idahoensis	
	Galium parisiense	
	Hypericum perforatum	
	Hypochaeris radicata	
	Juncus tenuis	
	Lathyrus sphaericus	
	Madia gracilis	
	Myosotis discolor	
	Pteridium aquilinum	
	Quercus garryana	
	Rubus discolor	
	Sherardia arvensis	
	Taeniatherum caput-medusae	
	Tragopogon dubius	
	Vicia cracca	
	Vicia sativa	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
EE Wilson	*Agrostis alba*	*Cercyonis pegala*
	Centaurium umbellatum	*Coenonympha tullia*
	Chrysanthemum leucanthemum	*Colias eurytheme*
	Cirsium arvense	*Ochlodes sylvanoides*
	Cirsium vulgare	*Phyciodes mylitta*
	Holcus lanatus	
	Hypericum perforatum	
	Lathyrus sphaericus	
	Lotus micranthus	
	Myosotis discolor	
	Parentucellia viscosa	
	Plantago lanceolata	
	Rumex acetosella	
	Senecio jacobaea	
	Vicia hirsuta	
	Vicia sativa	
	Vicia tetrasperma	
Forest Peak	*Achillea millifolium*	*Cercyonis pegala*
	Adenocaulon bicolor	*Coenonympha tullia*
	Agoseris grandiflora	*Erynnis propertius*
	Allium amplectens	*Everes comyntas*
	Amelanchier alnifolia	*Limenitis lorquini*
	Aster chilensis	*Ochlodes sylvanoides*
	Avena fatua	*Papilio eurymedon*
	Brodiaea congesta	*Papilio rutulus*
	Brodiaea coronaria	*Papilio zelicaon*
	Brodiaea hyacinthina	*Parnassius clodius*
	Bromus carinatus	*Phyciodes mylitta*
	Bromus mollis	*Pyrgus communis*
	Bromus pacificus	*Pyrgus ruralis*
	Bromus rigidus	*Speyeria cybele*
	Bromus secalinus	*Speyeria hydaspe*
	Calochortes tolmiei	*Strymon melinus*
	Carex tumulicola	*Neophasia menapia***
	Centaurea cyanus	*Nymphalis californica***
	Cerastium viscosum	*Plebejus acmon***
	Chrysanthemum leucanthemum	
	Cirsium arvense	
	Cirsium vulgare	
	Convolvulus nyctagineus	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Forest Peak	*Cynosurus echinatus*	
	Daucus carota	
	Dactylis glomerata	
	Daucus pusillus	
	Delphinium menziesii	
	Dianthus armeria	
	Elymus glaucus	
	Epilobium paniculatum	
	Eriophyllum lanatum	
	Fragaria virginiana	
	Galium aparine	
	Galium bifolium	
	Galium parisiense	
	Geranium columbinum	
	Hypericum perforatum	
	Iris tenax	
	Juncus tenuis	
	Lathyrus sphaericus	
	Lomatium utriculatum	
	Lotus micranthus	
	Madia gracilis	
	Marah oreganus	
	Moehringia macrophylla	
	Phleum pratense	
	Poa pratensis	
	Polystichum munitum	
	Pseudotsuga menziesii	
	Quercus garryana	
	Ranunculus occidentalis	
	Rhus diversiloba	
	Rumex acetosella	
	Rubus ursinus	
	Sanicula bipinnatifida	
	Sanicula crassicaulis	
	Sidalcea virgata	
	Silene hookeri	
	Taeniatherum caput-medusae	
	Vicia americana	
	Vicia hirsuta	
	Wyethia angustifolia	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Jackson Prairie	*Achillea millifolium*	*Cercyonis pegala*
	Aira caryophyllea	*Coenonympha tullia*
	Allium vineale	*Ochlodes sylvanoides*
	Arrhenatherum elatius	*Papilio rutulus*
	Avena fatua	*Euphyes vestries***
	Briza minor	*Everes comyntas***
	Brodiaea coronaria	*Nymphalia californica***
	Bromus carinatus	*Papilio eurymedon***
	Bromus mollis	*Phyciodes mylitta***
	Bromus rigidus	*Phyciodes pratensis***
	Bromus secalinus	
	Centaurium umbellatum	
	Chrysanthemum leucanthemum	
	Clarkia amoena	
	Crataegus monogyna	
	Cynosurus echinatus	
	Dactylis glomerata	
	Danthonia californica	
	Daucus carota	
	Daucus pusillus	
	Dianthus armeria	
	Elymus glaucus	
	Epilobium paniculatum	
	Eriophyllum lanatum	
	Fragaria virginiana	
	Galium bifolium	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Hypochaeris radicata	
	Juncus tenuis	
	Lathyrus sphaericus	
	Linum angustifolium	
	Lotus micranthus	
	Madia gracilis	
	Phalaris aquatica	
	Plantago lanceolata	
	Poa pratensis	
	Prunella vulgaris	
	Pseudotsuga menziesii	
	Pyrus communis	

APPENDIX C. Continued

Site	Plant species	Butterfly species
Jackson Prairie	*Quercus garryana*	
	Ranunculus occidentalis	
	Sanicula bipinnatifida	
	Taeniatherum caput-medusae	
	Trifolium dubium	
	Vicia cracca	
	Vicia sativa	
Kingston Prairie Preserve	*Achillea millifolium*	*Cercyonis pegala*
	Agrostis diegoensis	*Coenonympha tullia*
	Aira caryophyllea	*Ochlodes sylvanoides*
	Allium amplectens	*Papilio eurymedon*
	Anthoxanthum odoratum	*Papilio rutulus*
	Aster chilensis	*Pyrgus communis*
	Brodiaea hyacinthine	*Pyrgus ruralis*
	Bromus carinatus	
	Bromus mollis	
	Bromus secalinus	
	Centaurium umbellatum	
	Clarkia amoena	
	Comandra umbellata	
	Crepis capillaris	
	Cytisus scoparius	
	Danthonia californica	
	Daucus carota	
	Delphinium menziesii	
	Erigeron foliosus	
	Eriophyllum lanatum	
	Festuca arundinacea	
	Festuca rubra	
	Fragaria virginiana	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Holcus lanatus	
	Hypericum perforatum	
	Hypochaeris radicata	
	Juncus tenuis	
	Lianthus bicolor	
	Lotus micranthus	
	Lotus purshiana	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Kingston Prairie Preserve	*Myosotis discolor*	
	Parentucellia viscosa	
	Plantago lanceolata	
	Potentilla gracilis	
	Prunella vulgaris	
	Pteridium aquilinum	
	Ranunculus occidentalis	
	Rosa gymnocarpa	
	Saxifraga integrifolia	
	Senecio jacobaea	
	Sherardia arvensis	
	Sidalcea campestris	
	Trifolium dubium	
	Trifolium variegatum	
	Vicia sativa	
	Vulpia bromoides	
Open Space Park	*Acer macrophyllum*	*Cercyonis pegala*
	Achillea millefolium	*Strymon melinus*
	Arrhenatherum elatius	*Coenonympha tullia*
	Avena fatua	*Erynnis propertius*
	Brodiaea congesta	*Everes comyntas*
	Brodiaea coronaria	*Limenitis lorquini*
	Bromus commutatus	*Ochlodes sylvanoides*
	Bromus mollis	*Speyeria hydaspe***
	Bromus rigidus	*Euphyes vestries***
	Bromus secalinus	*Neophasia menapia***
	Carex tumulicola	*Papilio eurymedon***
	Centaurium umbellatum	*Papilio rutulus***
	Cerastium viscosum	*Papilio zelicaon***
	Chrysanthemum leucanthemum	
	Cirsium vulgare	
	Clarkia amoena	
	Crataegus monogyna	
	Cynosurus echinatus	
	Daucus carota	
	Dactylis glomerata	
	Danthonia californica	
	Daucus pusillus	
	Delphinium menziesii	
	Dianthus armeria	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Open Space Park	*Elymus glaucus*	
	Epilobium paniculatum	
	Eriophyllum lanatum	
	Festuca arundinacea	
	Festuca idahoensis	
	Fragaria virginiana	
	Galium bifolium	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Holcus lanatus	
	Hypericum perforatum	
	Hypochaeris radicata	
	Lathyrus sphaericus	
	Madia gracilis	
	Myosotis discolor	
	Plantago lanceolata	
	Potentilla gracilis	
	Poa pratensis	
	Prunalla vulgaris	
	Pteridium aquilinum	
	Rhus diversiloba	
	Rumex acetosella	
	Sanicula crassicaulis	
	Senecio jacobaea	
	Sherardia arvensis	
	Sidalcea virgata	
	Taeniatherum caput-medusae	
	Trifollium dubium	
	Vicia sativa	
	Vulpia bromoides	
Philomath Heights	*Achillea millifolium*	*Cercyonis pegala*
	Agoseris grandiflora	*Coenonympha tullia*
	Aira caryophyllea	*Erynnis persius*
	Allium amplectens	*Everes comyntas*
	Allium vineale	*Ochlodes sylvanoides*
	Amelanchier alnifolia	*Papilio rutulus*
	Arrhenatherum elatius	*Pyrgus communis*
	Aster chilensis	*Danaus plexxipus***
	Brodiaea coronaria	*Erynnis propertius***

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Philomath Heights	*Brodiaea hyacinthina*	
	Bromus carinatus	
	Bromus mollis	
	Calochortus tolmiei	
	Carex tumulicola	
	Centaurium umbellatum	
	Cerastium viscosum	
	Chrysanthemum leucanthemum	
	Cirsium vulgare	
	Comandra umbellata	
	Crepis acuminata	
	Crataegus monogyna	
	Cynosurus echinatus	
	Dactylis glomerata	
	Danthonia californica	
	Daucus carota	
	Daucus pusillus	
	Delphinium menziesii	
	Dianthus armeria	
	Elymus glaucus	
	Epilobium panniculatum	
	Eriophyllum lanatum	
	Festuca idahoensis	
	Fragaria virginiana	
	Galium bifolium	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Hypericum perforatum	
	Hypochaeris radicata	
	Juncus tenuis	
	Koeleria cristata	
	Lathyrus sphaericus	
	Leontodon nudicaulis	
	Lomatium nudicaule	
	Lolium perenne	
	Lotus nevadensis	
	Lotus purshiana	
	Madia gracilis	
	Myosotis discolor	
	Plantago lanceolata	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Philomath Heights	*Potentilla gracilis*	
	Poa pratensis	
	Prunella vulgaris	
	Pseudotsuga menziesii	
	Rhus diversiloba	
	Rosa pisocarpa	
	Senecio jacobaea	
	Sherardia arvensis	
	Sidalcea virgata	
	Taeniatherum caput-medusae	
	Trifolium dubium	
	Vicia cracca	
	Vicia pannonica	
	Vicia sativa	
	Vicia tetrasperma	
	Zigadenus venenosus	
Pigeon Butte	*Agrostis tenuis*	*Papilio zelicaon*
	Bromus secalinus	*Phyciodes mylitta*
	Centaurium umbellatum	*Cercyonis pegala*
	Chrysanthemum leucanthemum	*Coenonympha tullia*
	Cirsium vulgare	*Ochlodes sylvanoides*
	Crepis capillaris	*Papilio rutulus*
	Cynosurus echinatus	*Papilio eurymedon***
	Daucus carota	
	Galium parisiense	
	Holcus lanatus	
	Hypochaeris radicata	
	Lotus micranthus	
	Lolium perenne	
	Parentucellia viscosa	
	Phleum pratense	
	Rubus discolor	
	Senecio jacobaea	
	Sonchus asper	
	Sonchus oleraceus	
	Vicia cracca	
	Vulpia bromoides	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Shoulder-to-Shoulder Farm	*Aira caryophyllea*	*Cercyonis pegala*
	Allium amplectens	*Coenonympha tullia*
	Amelanchier alnifolia	*Ochlodes sylvanoides*
	Anthoxanthum odoratum	*Papilio rutulus*
	Arrhenatherum elatius	*Pieris rapae*
	Aster chilensis	*Pyrgus communis*
	Brodiaea congesta	*Colias eurytheme***
	Brodiaea coronaria	*Nymphalis californica*
	Brodiaea hyacinthia	
	Bromus carinatus	
	Bromus pacificus	
	Bromus rigidus	
	Calochortus tolmiei	
	Carex tumulicola	
	Centaurea cyanus	
	Centaurium umbellatum	
	Chrysanthemum leucanthemum	
	Clarkia amoena	
	Crataegus monogyna	
	Cytisus scoparius	
	Danthonia californica	
	Daucus carota	
	Dactylis glomerata	
	Daucus pusillus	
	Delphinium menziesii	
	Elymus glaucus	
	Eriophyllum lanatum	
	Festuca arundinacea	
	Festuca idahoensis	
	Fragaria virginiana	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Hieracium albiflorum	
	Hypericum perforatum	
	Hypochaeris radicata	
	Juncus tenuis	
	Iris tenax	
	Koeleria cristata	
	Lomatium nudicaule	
	Lolium perenne	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Shoulder-to-Shoulder Farm	*Lomatium utriculatum*	
	Myosotis discolor	
	Plantago lanceolata	
	Potentilla gracilis	
	Poa pratensis	
	Prunella vulgaris	
	Pseudotsuga menziesii	
	Pyrus malus	
	Quercus garryana	
	Ranunculus occidentalis	
	Rosa eglanteria	
	Rosa pisocarpa	
	Sanicula bipinnatifida	
	Sidalcea virgata	
	Symphoricarpos mollis	
	Valerianella locusta	
	Vicia pannonica	
	Vicia sativa	
	Zigadenus venenosus	
Spires Lane	*Agrostis tenuis*	*Cercyonis pegala*
	Aira caryophyllea	*Coenonympha tullia*
	Arrhenatherum elatius	*Papilio rutulus*
	Bromus mollis	*Pieris rapae*
	Bromus secalinus	*Everes comyntas***
	Cerastium viscosum	
	Chrysanthemum leucanthemum	
	Cirsium arvense	
	Cirsium vulgare	
	Crepis capillaris	
	Dactylis glomerata	
	Daucus carota	
	Festuca arundinacea	
	Galium parisiense	
	Holcus lanatus	
	Hypericum perforatum	
	Hypochaeris radicata	
	Koeleria cristata	
	Marah oreganus	
	Myosotis discolor	
	Parentucellia viscosa	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Spires Lane	*Plantago lanceolata*	
	Pteridium aquilinum	
	Rumex acetosella	
	Rubus discolor	
	Senecio jacobaea	
	Sidalcea virgata	
	Vicia hirsuta	
	Vicia sativa	
	Vicia tetrasperma	
	Vulpia bromoides	
Wainwright Property	*Agrostis tenuis*	*Cercyonis pegala*
	Aira caryophyllea	*Coenonympha tullia*
	Allium vineale	*Glaucopsyche lygdamus*
	Alopecurus pratensis	*Ochlodes sylvanoides*
	Brodiaea coronaria	*Colias eurytheme***
	Bromus commutatus	*Pieris rapae***
	Bromus mollis	*Lycaena helloides***
	Bromus secalinus	
	Centaurium umbellatum	
	Cirsium vulgare	
	Crataegus monogyna	
	Daucus carota	
	Epilobium paniculatum	
	Festuca arundinacea	
	Galium bifolium	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Hieracium albiflorum	
	Holcus lanatus	
	Hypericum perforatum	
	Hypochaeris radicata	
	Myosotis discolor	
	Parentucellia viscosa	
	Poa pratensis	
	Rubus discolor	
	Senecio jacobaea	
	Sonchus asper	
	Taeniatherum caput-medusae	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Wainwright Property	*Vicia cracca*	
	Vicia hirsuta	
	Vicia tetrasperma	
	Vulpia bromoides	
Willow Creek	*Achillea millefolium*	*Cercyonis pegala*
Nature Preserve	*Agrostis tenuis*	*Coenonympha tullia*
	Aira caryophyllea	*Papilio rutulus*
	Allium amplectens	*Phyciodes pratensis*
	Briza minor	*Polites sonora*
	Brodiaea congesta	*Danaus plexxipus***
	Brodiaea coronaria	*Euphyes vestries***
	Brodiaea hyacinthine	*Everes amyntula***
	Bromus carinatus	*Everes comyntas***
	Bromus commutatus	*Limenitis lorquini***
	Bromus mollis	*Ochlodes sylvanoides***
	Bromus rigidus	*Papilio eurymedon***
	Bromus secalinus	*Phyciodes mylitta***
	Carex tumulicola	*Plebejus acmon***
	Calochortus tolmiei	*Pyrgus communis***
	Centaurium umbellatum	*Strymon melinus***
	Chrysanthemum leucanthemum	
	Cirsium vulgare	
	Clarkia species	
	Convolvulus nyctagineus	
	Crataegus monogyna	
	Cynosurus cristatus	
	Cynosurus echinatus	
	Daucus carota	
	Danthonia californica	
	Epilobium paniculatum	
	Eriophyllum lanatum	
	Festuca arundinacea	
	Fragaria virginiana	
	Fraxinus latifolia	
	Galium parisiense	
	Geranium columbinum	
	Geranium dissectum	
	Grindelia integrifolia	
	Holcus lanatus	
	Hypericum perforatum	

APPENDIX C. Continued

Site	*Plant species*	*Butterfly species*
Willow Creek Nature Preserve	*Hypochaeris radicata*	
	Juncus tenuis	
	Koeleria cristata	
	Lathyrus sphaericus	
	Linum angustifolium	
	Lotus micranthus	
	Madia gracilis	
	Marah oreganus	
	Myosotis discolor	
	Parentucellia viscosa	
	Phalaris aquatica	
	Plantago lanceolata	
	Poa annua	
	Poa pratensis	
	Prunella vulgaris	
	Pseudotsuga menziesii	
	Pteridium aquilinum	
	Pyrus malus	
	Ranunculus occidentalis	
	Rosa 'hybrid'	
	Rosa nutkana	
	Rubus discolor	
	Senecio jacobaea	
	Solidago canadensis	
	Trifolium dubium	
	Trifolium subterraneum	
	Vicia hirsuta	
	Vicia sativa	
	Vicia tetrasperma	

*** Species observed outside of macroplot or outside of designated sampling time.*

APPENDIX D. Plant community characteristic data collected at 17 sites in the Willamette Valley, Oregon, 2000.

	Prairie integrity group																
	Low							*Medium*					*High*				
Community characteristic	*Bald Top*	*Carson Prairie*	*EE Wilson*	*Pigeon Butte*	*Spires Lane*	*Wainwright*	*Bald Hill Low*	*Blakesley Creek*	*Forest Peak*	*Jackson Place*	*Open Space*	*Willow Creek*	*Bald Hill High*	*Butterfly Meadows*	*Kingston Prairie*	*Philomath Heights*	*Shoulder-to-Shoulder*
Area	0.4	0.9	8.9	1.8	4.6	10	0.3	0.9	0.3	1.6	0.6	5.6	0.8	0.5	4.4	0.4	0.3
Species abundance																	
Native plant	0.6	10	0	0.2	2	0.2	12	24	26	28	14	21	55	65	45	55	77
Native hostplant	0.4	1	0	0	0.1	0	11	22	11	16	8	9	46	31	39	46	62
Hostplant	48	32	47	48	51	54	71	44	37	41	60	47	73	38	50	62	70
Native nectar	0.5	8	0	0.2	0	0.1	2	7	15	14	6	6	41	16	9	20	36
Nectar	9	24	9	6	11	30	43	25	19	37	28	45	66	27	13	34	43
Native pea	0	0	0	0	0	0	0	0	0.2	0	0	0	0	1	0.5	0	0
Pea	5	4	5	0.1	8	26	5	2	4	4	3	5	2	2	1	1	2
Native grass	0.1	1	0	0	0.1	0	9	17	6	12	2	6	12	23	35	33	33
Grass	42	19	38	46	41	28	35	24	26	17	32	13	14	30	47	34	35
Mallow	0.3	0	0	0	0	0	0	0	3	0	0.1	0	0	0	0.1	0.4	0

Continued

APPENDIX D. Continued

	Prairie integrity group																
	Low							*Medium*					*High*				
Community characteristic	*Bald Top*	*Carson Prairie*	*EE Wilson*	*Pigeon Butte*	*Spires Lane*	*Wainwright*	*Bald Hill Low*	*Blakesley Creek*	*Forest Peak*	*Jackson Place*	*Open Space*	*Willow Creek*	*Bald Hill High*	*Butterfly Meadows*	*Kingston Prairie*	*Philomath Heights*	*Shoulder-to-Shoulder*
Species richness																	
Plant	36	36	19	23	36	37	63	63	68	57	64	77	82	75	56	68	64
Native plant	9	18	3	6	8	10	24	30	44	26	29	35	41	53	32	35	34
Native hostplant	7	10	3	6	7	8	17	21	13	16	18	21	28	27	19	21	24
Hostplant	18	21	11	12	18	19	33	36	38	29	32	42	43	34	27	33	34
Native nectar	7	12	3	6	6	9	18	19	29	18	20	28	28	35	22	26	23
Nectar	13	17	9	14	16	18	32	27	36	26	28	40	42	39	29	37	30
Native pea	5	5	3	6	6	8	12	11	13	10	10	15	15	14	10	9	10
Pea	11	8	7	8	9	11	16	16	17	15	14	22	20	16	13	15	12
Native grass	6	8	3	6	7	8	14	17	15	13	12	18	21	19	12	13	16
Grass	10	15	5	9	12	14	23	24	22	18	19	28	27	23	16	16	22

APPENDIX E. Butterfly community characteristic data collected at 17 sites in the Willamette Valley, Oregon, 2000.

	Prairie integrity group																
	Low						*Medium*						*High*				
Community characterisitc	*Bald Top*	*Carson Prairie*	*EE Wilson*	*Pigeon Butte*	*Spires Lane*	*Wainwright*	*Bald Hill Low*	*Blakesley Creek*	*Forest Peak*	*Jackson Place*	*Open Space*	*Willow Creek*	*Butterfly Meadows*	*Bald Hill High*	*Kingston Prairie*	*Philomath Heights*	*Shoulder-to-Shoulder*
Species richness																	
Index (# species)	4	3	5	5	2	4	4	3	8	3	5	5	11	5	5	5	4
Estimator (jackknife)	6	3	6	6	2	5	5	3	12	4	6	6	15	7	9	5	4
Feeder group abundance																	
Mallow (full set)	1	0	0	0	0	0	0	0	42	0	0	1	1	0	1	5	4
Mallow (truncated set)	0	0	0	0	0	0	0	0	23	0	0	0	1	0	1	2	4
Pea (full set)	0	0	1	0	0	13	1	0	1	0	1	0	18	2	0	4	0
Pea (truncated set)	0	0	1	0	0	8	1	0	1	0	1	0	9	1	0	3	0
Composite (full set)	1	0	4	18	0	0	0	0	1	0	0	13	40	0	0	0	0
Composite (truncated set)	1	0	4	15	0	0	0	0	0	0	0	7	31	0	0	0	0
Grass (full set)	11	47	83	34	23	43	72	88	135	8	71	46	52	71	66	67	30
Grass (truncated set)	7	32	52	23	15	34	50	53	106	6	49	30	37	53	50	36	16