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Habitat variables, mammal interactions, and recovery approaches important to a rare, New Mexican butterfly, *Euphydryas anicia cloudcrofti* (Lepidoptera: Nymphalidae)

Julie McIntyre

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**HABITAT VARIABLES, MAMMAL INTERACTIONS, AND RECOVERY
APPROACHES IMPORTANT TO A RARE, NEW MEXICAN
BUTTERFLY, *EUPHYDRYAS ANICIA CLOUDCROFTI*
(LEPIDOPTERA: NYMPHALIDAE)**

BY

JULIE LINCOLN MCINTYRE

B.A., Environmental Science, University of Virginia, 1989
B.A., Religious Studies, University of Virginia, 1989

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

**Doctor of Philosophy
Biology**

The University of New Mexico
Albuquerque, New Mexico

May, 2010

DEDICATION

In memory of my father, William Reynolds McIntyre, who gracefully imparted his sense of curiosity and wonder of the natural world.

This work is dedicated to my children, Eva Lillian Lowry and Shayden Liam Lowry, with the hope that they continue to experience the magic of nature and believe in their own abilities to seek solutions for planetary healing.

And to the Sacramento Mountains checkerspot butterfly and all wild beings across the globe, to engender deeper understanding and respect for all life forms and wild places.

ACKNOWLEDGMENTS

I am incredibly grateful to my co-advisors, Astrid Kodric-Brown and Dave Lightfoot, for their willingness to work with me, interest in my research, natural openness about all ideas, and mentoring both as excellent ecologists and as human beings. Astrid's ready smile along with her unique angles and questions gave me fresh perspectives on approaching complex ecological interactions, which continue to guide me. Dave's passion for insects and conservation and amazing abilities as a field naturalist set a model for bridging academia and nature to which I will continually aspire. Sandy Brantley, always enthusiastic, supportive, and quick to provide great feedback, shared kindness and laughs woven with scientific expertise at the precise moments when most needed, and for this I am most thankful. Tim Lowrey and Julie Coonrod offered guidance and, at all times, good humor, and I appreciate their cheerful involvement with my committee. Collectively, all committee members exhibited great patience and generosity with their time and advice throughout the entire process of creating this dissertation.

I appreciate the great generosity of the Albuquerque Botanical Gardens and Las Lunas Plant Materials Center in donating *Penstemon neomexicanus* plants to transplant for the experimental field study. Providing larvae with additional host plants would not have been possible without their willingness to donate these carefully cultivated plants. The staff was kind, efficient, and willing to entrust their plants to me, and I thank the staff of these important and beneficial organizations.

Field helpers, Mark Cedar Love-Williamson, Ben Zimmerman, Josh Jones, Isabel Constable, Angela England, Alicia Paz, and Charlie Jackson, collected valuable data, appreciated the beauty of the study area, and brought a spirit of devoted work ethic and fun while working and camping in the Sacramento Mountains; I very much appreciate their efforts and companionship.

Insect experts Steve Cary, Dick Fagerlund, and Dick Holland, along with Dave Lightfoot and Sandy Brantley, taught me how to identify insects in the lab and field and freely shared the wide range of their expertise for which I am grateful. At UNM, Ana Davidson's energetic approach to ecology was contagious, and I thank you, Ana, for demonstrating how to accomplish feats with joy, applicability, and interesting science. I

thank Phil Tonne for his gentle, humorous encouragement and solutions to random GIS questions and map finessing. Annette Evangelisti and Chuck Hayes were instrumental in maintaining daily sanity during the final throes of “dissing” and their refreshing energy will be remembered. The help of Geoff Carpenter, Alea Trafton, and Kina Murphy in reviewing documents was greatly appreciated, and I’m happy to repay the favors any time. I have been tremendously fortunate in having an excellent selection of considerate and interesting office mates at UNM, and to you all, I thank you for your sharing and tolerance while we have traversed this grad school journey together.

My work associates, Wendy Brown, Brady McGee, Susan Jacobsen, Eric Hein, Sarah Rinkevich, Catherine Liller, Steve Chambers, Nancy Riley, and Stuart Leon, offered wisdom, flexibility, and good company with polished professionalism. I have learned much from each of these individuals, and am honored to work with such dedicated, hopeful, and intelligent folks. I continue to profoundly admire their efforts to conserve endangered species.

I am most grateful to my family, Marc, Eva, Shayden, and Helen Lowry, along with Targ Matteucci, Mary Lee McIntyre, Andy McIntyre, Elise Athens, and Terry Lowry, for their support of my endeavors in so many forms. Marc, Helen, Targ, Mary Lee, Terry, and my inspiring community of visionary friends, I thank you for your help in taking care of my children so that I could accomplish tasks relating to this degree.

To Eva and Shayden, thank you for seeing things I would have missed in the field and in life. To Marc, I am indebted for your endurance and love to see this through to the end where new beginnings are forming. Finally, I send gratitude to the butterflies, pollinators, and plants, the Spirit of the Sacramento Mountains, and the stars above Zinker Canyon.

**HABITAT VARIABLES, MAMMAL INTERACTIONS, AND RECOVERY
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ABSTRACT

Impacts of habitat features, local mammals, and experimental host plant transplants on the Sacramento Mountains checkerspot butterfly (*Euphydryas anicia cloudcrofti*) were addressed in this research. Comprised of three separate studies, this work investigated the butterfly's ecology from different angles designed to contribute to more effective conservation for this rare species. In the first study, abiotic and biotic habitat variables examined at four spatial scales, were found to be different between occupied and unoccupied habitat. Each scale reflected similar patterns, with connectivity, host plant resource concentration, and plant structural diversity preferred by the butterfly at the scale of the landscape, meadow, host plant patch, and natal host plants. High habitat quality, low isolation, broad hostplant patch area, and high host plant patch density were associated with occupied habitats. Despite being far more vagile than larvae, adults were tightly associated with the distribution of the preferred nectar source within a meadow, *Helenium hoopesii*, suggesting their specialized use of this one plant species, in time and space.

The second study investigated interactions of the Sacramento Mountains checkerspot butterfly (*Euphydryas anicia cloudcrofti*) and its primary host plant *Penstemon neomexicanus*, with two other common factors in their environment: soil

disturbance by the pocket gopher (*Thomomys talpoides*) and grazing by Rocky Mountain elk (*Cervus elaphus nelsoni*). These interactions appeared to be impacting the abundance of egg masses and larval tents of the butterfly over a range of spatial scales and probably temporal scales as well. Associations between the butterfly, gopher soil disturbance, and elk grazing were significant during one year, but not the next, revealing the dynamic nature of this system. The strongest and most consistent relationship discovered was between elk grazing on *P. neomexicanus* plants growing on gopher mounds.

To accommodate low population numbers and buffer the butterfly against changes in climate or habitat connectivity on a scale meaningful to highly sensitive pre-diapause larvae, the third study tested effects of transplanting additional host plants, adjacent to occupied host plants in the field over one pre-diapause season. Results showed that pre-diapause butterfly larvae can benefit from an increase in nearby host plants. Larval abundance and length responded most favorably to large penstemon host plants with broad plant and stem diameters, many leaves, and tall heights, and those growing in a patch. If such rare butterfly species are to persist, novel strategies to conserve them, and pollinators in general, must be adopted to restore and maintain landscape heterogeneity and connectivity and at different scales, without harming individual butterflies during implementation. Overall findings demonstrate that the butterfly responds to connectivity and abundance of required resources at all spatial scales and that disturbance processes that maintain early successional, open conditions may be important in sustaining this butterfly into the future.

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The Sacramento Mountains checkerspot butterfly, *Euphydryas anicia cloudcrofti* (Ferris and Holland 1980), visiting its preferred nectar source, orange sneezeweed, *Helenium hoopseii* A. Gray, in the Lincoln National Forest in southeast New Mexico.

INTRODUCTION

In a world of changing climate and increasing human population pressures on ecosystems, endemic species with specific habitat needs are likely to require conservation management to meet conditions that will maintain local diversity. As habitats suitable for specialist species become more fragmented, primarily from anthropogenic impacts, the status of bioindicator species, such as butterflies, could convey information about what will sustain their populations and those of other sympatric species through their responses to a shifting world. Montane species, with ranges at the highest available elevations, are particularly indicative of how species and ecosystems may respond to future climate change (Parmesan 2006, Seager et al. 2007). To understand how to address these issues before vulnerable species become extinct, studies investigating habitat requirements and recovery strategies are needed to provide the most effective response for not only a species of focus, but with the continued functioning of the entire ecosystem in mind. This task involves taking the rich background of theoretical biology a step further into the challenging realm of offering practical and applicable conservation measures on the ground to benefit the most species possible, including humans. In addressing needed field work and applied solutions, this research attempts to explore habitat characteristics, biotic interactions, and recovery approaches of a rare, mountain-top butterfly found only in an 85km² area in the Sacramento Mountains of southern New Mexico.

Discovered in 1964 and described in 1980, the Sacramento Mountains checkerspot butterfly, *Euphydryas anicia cloudcrofti*, (Ferris and Holland) belongs to the subtribe Euphydryina Higgins 1978, the tribe Melitaeni Tutt 1896, subfamily Nymphalinae, family Nymphalidae, and superfamily Papilionoidea (Murphy et al. 2004). Currently, the closest sister taxa are located in the Chuska Mountains (*E. a. chuskae* (Ferris and Holland 1980)) in San Juan County and in the Sangre de Cristo Mountains (undescribed taxon) in Mora County, New Mexico (Ferris and Holland 1980, Steve Cary, pers. comm. 2009). The butterfly is one of the ‘variable checkerspots,’ within the *chalcona* complex (including *anicia* and *colon*), a taxonomically difficult group known to exhibit phenotypic plasticity and collectively comprised of 38 subspecies (Howe 1975, Wahlberg and Zimmermann 2000; Austin et al. 2003, Wahlberg et al. 2005). The well-

researched *Euphydryas* genus has six recognized species in North America and a holarctic distributional range. Some species are now isolated into constricted areas that likely reflect Pleistocene rearrangements and refugia. The species *anicia* appears to be one of the more derived of the *Euphydryas* lineages, although *cloudcrofti* is the southernmost member of its genus and may have been the first to become isolated from other *anicia* (Ryan 2007). As climate warmed and ice retreated northward, the more cold resistant species could have been forced into high altitude zones and become separate species as a result of genetic drift, lack of gene flow, and natural selection within a unique habitat.

Euphydryas anicia cloudcrofti is geographically distinct, exhibits morphological differences at both the adult and larval stages, uses a unique, endemic penstemon species as its main hostplant, and displays behavioral differences, such as drainage-following as opposed to “hill topping” found in other *Euphydryas* and *anicia* species (Cullenward et al. 1979). Recent genetic analysis has determined that *E. a. cloudcrofti* should be considered a species (Ryan 2007). At present, *E. a. cloudcrofti* is considered a species of concern by the U.S. Fish and Wildlife Service. At the state level, it is a “species of greatest conservation need.” The butterfly is managed under *The Conservation Plan for the Sacramento Mountains Checkerspot Butterfly* (USFWS et al. 2005) by the U.S. Forest Service in the Lincoln National Forest. It has been petitioned for listing twice, but both times has not warranted federal listing (USFWS 2009), primarily due to proactive efforts of the Cloudcroft community and to a lack of knowledge concerning the butterfly’s ecology and population numbers.

The Conservation Plan provides a list of research needs for *E. a. cloudcrofti*, including more specific habitat information. This is especially important for habitat restoration or butterfly reintroduction efforts designed to boost population numbers or establish populations in currently unoccupied areas. The species occurs only in areas exhibiting the following characteristics: elevations between 2400 and 2750 m (7800-9000 ft); drainages, meadows, or grasslands; less than 5% tree canopy cover; plant communities supporting New Mexico penstemon, sneezeweed, valerian, arrowleaf groundsel, figwort, skyrocket, milkweed, Arizona cliff rose, and wallflower; or proximity

to areas with some or all of these features (USFWS 2001). Within these parameters, *E. a. cloudcrofti* forms small, disjunct populations that fluctuate in size, experience little migration, and exhibit a metapopulation structure (USFWS 2001). The butterfly tends to fly close to the ground and has limited dispersal abilities (USFWS et al. 2005). Dispersed subpopulations inhabit approximately 13 major montane meadow drainages. Divided by forests, development, and roadways, the butterfly's suitable, open meadow habitat is fragmented primarily by a mixed-conifer forest matrix and spans an elevational gradient between 2377 and 2743m (7800 and 9000 ft). Within *E. a. cloudcrofti*'s range, seemingly suitable meadows have remained unoccupied since 1999 when surveys were originally conducted for this recently discovered subspecies. Given that 88.6% of adult *E. a. cloudcrofti* movements remained within a discrete, small area in their native meadow, and that the longest dispersal distance recorded for adult *E. a. cloudcrofti* is 890 meters after a 14 day period (Pittenger and Yori 2003), migration to new meadows may be uncommon for this relatively sedentary taxon. Aside from habitat elements mentioned above, little is known about this butterfly and field research is needed.

The butterfly is a univoltine habitat specialist that over-winters as a larva. Its flight period starts in June and generally lasts through mid July, with the peak flight around July 4th. Adults exhibit nectaring preference for orange sneezeweed (*Helenium hoopseii* A. Gray) that flowers during six week flight time. Adult females deposit eggs in masses of 20-100 eggs on the underside of an endemic forb, the New Mexico penstemon (*Penstemon neomexicanus* Woot. & Standl), and rarely on mountain valerian, also known as tobacco root (*Valeriana edulis* Nutt. ex Torr. & Gray). The penstemon is an early successional perennial that is capable of reproducing via seed and through rhizomes, often forming patches. Eggs hatch within two weeks of oviposition and gregarious early instar larvae weave silken tents and feed by skeletonizing *P. neomexicanus* leaves. Larvae remain on the hostplant from one to two months, depending on the hostplant's size and availability of neighboring *P. neomexicanus* if all leaves are consumed on the natal hostplant. Larvae will eat leaves of *V. edulis*, but it is less common than *P. neomexicanus* within the butterfly's habitat. Pre-diapause larvae pass through about 4 instars, diapause in litter or under bark, and emerge in April to finish their larval

development. Post-diapause larvae grow to be about 2.5 cm in length and then pupate until late May or mid-June when eclosion occurs. Thus adults and immature stages use different microhabitats through the seasons where each butterfly must find resources for egg placement, larval use, pupation protection, and adult feeding, breeding, and cover. Assessing habitat variables therefore must include conditions that promote both larval and adult sustenance and survival.

The butterfly's narrow distribution on a confined "mountain island," coupled with the lack of natural history and long-term population data, warrant the exploration of preferred habitat variables and their mechanisms to assist in conservation strategies. With this information, the goal is not only to contribute to the conservation of this rare butterfly, but also to understand what abiotic, biotic, and spatial patterns potentially are important to similar butterflies and other members of the globally declining pollinator community (Buchmann and Nabhan 1996, Allen-Wardell et al. 1998, Kearns et al. 1998, Withgott 1999).

Research on *E. a. cloudcrofti* comprising this dissertation is compiled into three subprojects corresponding to three chapters. Chapter 1 reports on findings regarding the abiotic and biotic habitat variables in occupied and unoccupied areas at four spatial scales: landscape, meadow, patch, and hostplant. Given that the butterfly expands from the egg into each of these scales as it progresses through its life cycle to culminate as a flying adult, each parameter may reveal a unique portion of what the butterfly prefers within potentially suitable habitat. Furthermore, as a species exhibiting a fragmented distribution and low population numbers, this butterfly may be particularly selective of biotic and abiotic resources defining habitat quality where the species does occur. This information was compared to the same variables in vacant meadows to elucidate why this butterfly uses certain meadows but not others.

Chapter 2 reports on the effects of pocket gopher soil disturbance and wild ungulate herbivory upon the hostplant, and the egg and larval stages of the butterfly. As representatives of ecosystem engineers and dominant species, respectively, pocket gophers and elk have strong and potentially interactive influences on their environment (Jones et al. 1994, Wilby et al. 2001, Soule 2003, Wright and Jones 2006). At a landscape

scale, disturbances associated with herbivory, trampling, or excavating modify successional processes by curbing the encroachment of trees and other potentially dominant vegetation (Cantor and Whitham 1989). These processes keep meadows open and allow a blend of early- and late-successional plants to coexist. Within the community where the butterfly is found, these mammal activities can change suitable habitat by altering the composition, phenology, growth rates, chemical characteristics, cover, and structure of the plant community. Furthermore, local mammals can exert consistent physical effects upon soil properties important to hostplants and butterflies by soil compaction, soil movement, and nutrient additions (Crawley 1983, Collins 1987, Huntley and Inouye 1988, Denyer et al. 2007). Incidental consumption of eggs or larvae also can occur, as both gophers and elk are known to forage on either above- or below-ground portions of *P. neomexicanus* plants. *Penstemon neomexicanus*, often seen growing in soils disturbed by gophers, is a stress-tolerant hostplant favoring early successional stages, and responds to disturbance in open habitats. Information about impacts of native wild ungulates on butterflies is virtually nonexistent, and at present, the effects of elk versus cattle or other livestock on *E. a. cloudcrofti* butterfly are not understood.

Chapter 3 reports on an experimental study testing pre-diapause larval survival in response to *P. neomexicanus* transplants in the field. As a method for habitat enhancement in meadows both occupied and unoccupied by the butterfly, growing and transplanting *P. neomexicanus* host plants is considered one of the simpler methods of reducing larval mortality without disrupting or handling individual butterflies or larvae. The pre-diapause larval stage is considered the most vulnerable in a butterfly's lifetime, with the greatest chance of mortality. For larvae, a hostplant is not only food, but also offers structure on which to develop and form communal tents, provides shelter and protection from the elements, gives a place to sleep and rest, and is a locus for congregating with other con-specifics for safety and chemical information. The size and density of hostplants are known to influence insect community diversity (Strong et al. 1984) and provide a concentrated resource for specialist insects (Root 1973). For this system, previous field observations revealed a high occurrence of larval starvation due to defoliation of the entire natal hostplant near which few other hostplants were located.

Based on this finding, this experiment tests the hypothesis that larvae exposed to extra penstemon hostplants will demonstrate increased survival compared to adjacent control, measured by abundance and size of pre-diapause larvae over time.

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CHAPTER 1:
HABITAT VARIABLES IMPORTANT TO A RARE, NEW MEXICAN BUTTERFLY
Euphydryas anicia cloudcrofti (Lepidoptera: Nymphalidae)

Introduction

Environmental conditions such as microclimate and plant associations are key factors affecting the distribution and abundance of butterflies (Erhardt and Thomas 1991, Kevan 1999, Thomas and Clark 2004, van Swaay et al. 2006, Parmesan 2009). Non-migratory, habitat and host plant specialist species are especially sensitive to variation in environmental factors because these butterflies must find all of their specific resources within their immediate surroundings in order to persist. Butterflies are not evenly distributed across the landscape; even within suitable habitat, conditions can vary with climate, season, or succession following disturbance due to the resource patchiness and dynamics of natural systems. Furthermore, natural habitats can become degraded, primarily from human disturbance, invasive plants, the lack of natural disturbance regimes, or natural disasters, which can lead to fewer resources for butterflies (Schultz and Dlugosch 1999, Stefanescue et al. 2004). However, even areas within the range of a species that appear to meet necessary habitat parameters can remain unoccupied, suggesting that differences among these specialized habitats can be subtle or complex and in need of further study.

As butterflies develop through their life cycle, morphological and physiological transformations often accompany changes in habitat preference. Life stages for butterflies can be so dissimilar that, based on the size and mobility of each phase, entirely different habitat features are used. To view a system from the temporal and spatial perspective of a species, one must attempt to examine butterfly ecology by addressing several scales at once (Levine 1992, Grand and Mello 2004). For example, larvae of many species tend to remain on the original host plant for up to two months while developing through the first several instars. Early instar larval habitat quality consists of host plant structural and chemical features, ground surface cover variables, and microclimates, along with possible biological interactions of disease and predation, all at the scale of the host plant (Williams et al. 1983, Weiss et al. 1987, Clarke et al. 1997). The immature stages of

butterflies exhibit a narrower, species-specific niche that typically is far more limiting than adult resource requirements (Thomas 1991). Adults depend on broader spatial extents, since they maneuver through a more expansive aerial landscape during their flight period. Patch quality may be more important at smaller spatial scales (Dennis and Eales 1997, WallisDeVries 2004, Krauss et al. 2005), whereas the overall area of suitable habitat and its connectivity may be more significant over larger spatial and temporal scales (Hanski 1994, Moilanen and Hanski 1998, Wahlberg et al. 2002). Thus, both habitat quality and spatial arrangement are important predictors of where butterfly populations are likely to persist (Thomas et al. 2001). Studies focused on a single scale or perspective may omit a portion of the butterfly-habitat system or lead to management decisions that fail to promote long term conservation (Bergman et al. 2004).

Local ecological conditions are shaped by structural features of the landscape, such as elevation, aspect, and slope, which govern the heat, water, light, and nutrients available for a plant community (Parker 1982). Within a climatic zone, terrain features form landscape patterns that determine how vegetation is arranged, which in turn, shapes where butterflies will be found. Although climate is a primary driver of all biotic distributions, long-term research on butterflies has found that butterfly survival is mediated more by the indirect impacts of temperature and precipitation on the phenology and distribution of food plants across the landscape than on direct climatic effects upon butterfly physiology (Parmesan 2009). Topographically heterogeneous habitats are important for sustaining butterfly species and communities over time by creating a variety of microhabitats that moderate the extreme effects of weather or stochastic events (Weiss et al. 1988, Kocher and Williams 2000, McLaughlin et al. 2002).

Open-habitat specialist butterflies often are sensitive to physical characteristics of boundaries, such as shading from canopy cover or increased foliar density, which can impede movement between habitats (Kuefler and Haddad 2006). A stable metapopulation of butterflies strictly dependent on open areas requires a permeable matrix between habitats for adequate gene flow among a set of dynamic subpopulations. Within this framework, corridors or vacant areas of suitable habitat can be interspersed with occupied areas, and may represent extirpated habitats or new colonizing opportunities,

depending on how a butterfly moves through the landscape (Gutierrez 2005). However, increased isolation of subpopulations, due to inhospitable matrix elements or habitat fragmentation, decreases the chances of emigration from a native habitat or successful immigration to new areas (Hanski and Thomas 1994, Hanski 1999). Furthermore, for habitat and food plant specialists with limited dispersal abilities, confined geographic ranges, and low and fluctuating population numbers, reduced habitat connectivity is linked with increased chances of endangerment (Lawton 1995, Thomas 2000).

Increased habitat area has been positively correlated with greater population numbers and long-term viability of butterfly populations and species (Steffan-Dewenter and Tschardt 2000, Krauss et al. 2003). Larger areas provide not only more chances of habitat heterogeneity (Connor and McCoy 1979), but also are more likely to support a source subpopulation for smaller, less self-sustaining groups of a butterfly species, and increased cover of the host plant (Thomas and Hanski 1997, Hanski 1998, Hanski 1999, Moilanen 1999, Krauss et al. 2004, Yamaura 2008). However, some studies have found area to have little effect on the presence of butterfly species (Fleishman et al. 2002, Betzholtz et al. 2007), so this factor may be species-specific. Overall, how the usable habitat is arranged in terms of size, fragmentation, connectivity, and the intervening matrix is therefore related to butterfly abundance, distribution, and long-term persistence (Clarke et al. 1997, Hanski 1999, Dover and Settele 2009).

Plant community composition and configuration provide a variety of microclimates, food sources, and structures which dictate the distribution of butterflies at finer scales such as that of a meadow or a plant patch. In most habitats, plant communities serve as a measure of the local diversity of seral stages, collectively shape the physical structure of the environment, and consequently, strongly influence the distributions and interactions of local fauna (Feber et al. 1996, Collinge et al. 2002, Tews et al. 2004). Habitat quality for butterflies has been measured in terms of plant richness, plant architecture, ground surface conditions, and overall heterogeneity of all of these factors (Singer 1972, Feber et al. 1996, Wettstein and Schmid 1999, Collinge et al. 2002, Dennis et al. 2006). Measures of plant diversity and structure (tree canopy, shrub layer, and ground cover) along with abiotic ground surface cover variables can quantify

resources directly related to ecological functions yielding greater butterfly survival (food plants, shelter, microclimate) (Dover et al. 1997, Cook 2002, Tews et al. 2004, Dennis et al. 2006).

In addition to larval host plants, nectar sources are critical to maintaining adult butterfly presence, providing water, sugar, and amino acids, as well as ‘utility’ resources for basking, roosting, sheltering, or courting mates (Murphy et al. 1983, Dennis 2004, Dennis et al. 2006, Vanreusel et al. 2006). Plant community data are useful indicators of insect and butterfly biodiversity (Panzer and Schwartz 1998, Collinge et al. 2003). Floristic diversity has been associated with higher densities of endangered butterflies (Britten and Riley 1994, Williams 1988, Freese et al. 2006). Egg distribution for the bay checkerspot, *Euphydryas editha*, has been linked to greater nectar availability, as have increased life span, higher egg production, and consistent presence in an area over time for other butterfly species (Murphy 1982, Murphy et al. 1983, Hill and Pierce 1989, Hill 1992, Boggs and Ross 1993). Higher ratios of native to exotic plant species have been correlated with increased habitat quality, butterfly species richness, and overall butterfly densities (Collinge et al. 2003). As host-specialist butterflies often exhibit selectivity for a favorite nectar-providing species, these butterflies may be more sensitive to the availability of native nectar sources and to the distribution and abundance their preferred nectar plants (Schultz and Dlugosch 1999, Tudor et al. 2004, Hardy et al. 2007).

Host plant abundance and density have been used as a measurement for habitat quality in butterfly studies, mainly because its use has produced the closest correlation to butterfly species’ presence (Ehrlich and Raven 1965, Quinn et al. 1998, Schultz and Dlugosch 1999, Anthes et al. 2003, Auckland et al. 2004). Moreover, habitat specialist butterflies display a higher response to host plant cover than generalist butterflies (Kuefler and Haddad 2006). Use of host plants is determined originally by oviposition, but once larvae are mobile they can disperse to accessible host plants themselves. Host plants are selected based on the size of the plant (Anthes et al 2003), quantity of leaves (Schultz and Dlugosch 1999), nutritional quality (Williams et al. 1983), allelochemicals (Williams et al. 1983), phenology (Williams et al. 1983, Weiss et al. 1988) microclimate conditions (Weiss et al. 1988, Albanese et al. 2007), degree of conspecific presence

(Denno et al. 1997), and the quality and density of a host plant patch (Stanton 1982, Dennis and Eales 1997, Hanski 1999, Thomas et al. 2001). Patch quality depends upon the composition, architecture, and accessibility of resources in the patch (Dennis et al. 2006). Butterflies occupying larger, connected patches of host plants generally have access to a greater pool of conspecifics and resources, and, as such, are more buffered from environmental, demographic, or genetic stochastic events that can leave butterflies associated with small patches increasingly vulnerable to extirpation (Hilty et al. 2006, Dover and Settele 2009). While a few studies have failed to reveal statistically significant associations between adult butterfly microdistribution and the occurrence of their larval food plants (Sharp et al. 1974), most studies have determined that butterfly species and their host plants are positively correlated and represent a measure of habitat quality (Ehrlich and Raven 1965, Turchin 1991, Schultz and Dlugosch 1999, Cowley et al. 2001, Auckland et al. 2004, Krauss et al. 2004, Kuussaari et al. 2004, Kuefler and Haddad 2006).

Representing the extent of parental care for butterflies, a female's search behavior for an oviposition site can be highly selective and this choice strongly influences the individual fitness of larvae (Mackay 1985, Floater and Zalucki 2000). Oviposition cues range across scales and are visual and olfactory from a distance, then comprised of combined sensory stimulants after landing (Hirota and Kato 2001). Female butterflies respond to host plant chemicals, variations in the nutritional quality of a host plant, physiological differences of size or display, host plant density, and surrounding habitat heterogeneity (Rausher 1981, Rausher 1983, Thompson and Pellmyr 1991, Floater and Zalucki 2000, Nieminen et al. 2003, Prudic et al 2005, Rabasa et al. 2005, Talsma et al. 2008; but see Albanese et al. 2007). Females of the cabbage white butterfly (*Pieris rapae*) select large host plants with an enhanced green color, which is related to increased transpiration, higher leaf water content, and higher nitrogen and phosphorus levels (Myers 1985). Other *Euphydryas* species oviposit on leaves with higher concentrations of iridoid glycosides, the secondary compound in host plants that is sequestered by larvae as a predator deterrent and is believed to be an oviposition cue for specialists (Nieminen et al. 2003, Penuelas et al. 2006). Because the first few instars are considered the most

vulnerable and experience the highest mortality (White 1974), oviposition and subsequent larval performance play a huge role in dictating population numbers, making oviposition preference a significant force in the evolution of Lepidopteran behavior (Soberon 1986, Ehrlich and Hanski 2004).

The Sacramento Mountains checkerspot butterfly, *Euphydryas anicia cloudcrofti* (Ferris and Holland 1980), is a regional endemic species that appears to have specialized habitat and host plant requirements. The butterfly has a small global population, limited flight and colonizing capability, and a correspondingly restricted range (USFWS 2005). It is found only within a 55 mi² (85 km²) area, located in the Sacramento Mountains of Otero County, in southern NM. The butterfly is associated with sunny, alpine meadow drainages and is dependent upon its primary host plant (as a larva), New Mexico penstemon (*Penstemon neomexicanus* Woot. & Standl.), and preferred nectar source (as an adult), orange sneezeweed (*Helenium hoopesii* A. Gray). Rarely, oviposition occurs on mountain valerian (*Valeriana edulis* Nutt. ex Torr. & A. Gray), and larvae will consume *V. edulis* if available. Although *P. neomexicanus* is a regional endemic plant, the butterfly's distribution is far more restricted than that of the penstemon's. Endemism of *P. neomexicanus* is likely a result of local speciation (Sivinski and Knight 1996), whereas the butterfly is believed to be a relictual paleoendemic (Ferris and Holland 1980). The butterfly's nearest conspecifics, *E. a. chuskae* and *E. a. capella*, inhabit montane areas in northern New Mexico, but genetic relationships among subspecies are unclear (Ferris and Holland 1980).

Euphydryas a. cloudcrofti forms small, separated groups that fluctuate in size, experience little migration, and exhibit a metapopulation structure (USFWS 2001). The butterfly tends to fly close to the ground and exhibits limited dispersal abilities (USFWS 2005). Dispersed subpopulations inhabit approximately 13 major montane meadow drainages. Divided by forests, development, and roadways, the butterfly's suitable, open meadow habitat is fragmented primarily by a mixed-conifer forest. Within *E. a. cloudcrofti*'s range, seemingly suitable meadows have remained unoccupied since 1999, and migration to new meadows may be uncommon for this relatively sedentary taxon. The butterfly is a univoltine species, with eggs laid in masses after mid-summer, and a

gregarious, tent-forming larva that feeds until winter diapause. Diapause is broken in April, and larvae feed until pupation in May or June. Adults fly for approximately 6 weeks, although each individual likely survives for no more than 2 weeks. Thus in its localized area, each butterfly must find resources for egg placement, larval use, pupation protection, and adult feeding, breeding, and cover. As a species exhibiting a fragmented distribution and low population numbers, this butterfly may be particularly selective of biotic and abiotic resources defining habitat quality where the species does occur.

To understand the relative importance of habitat characteristics for this butterfly, this study investigated habitat variables in occupied and unoccupied areas at four spatial scales: landscape, meadow, patch, and host plant. Why this butterfly uses certain meadows but not others is not understood, hence a broad scale investigation was needed. This study was designed to answer three questions concerning *E. a. euphydryas*'s habitat preferences. First, is the butterfly's occurrence correlated with abiotic, environmental variables such as elevation, slope, aspect, and ground surface cover type? Second, is the presence of the butterfly related to overall plant community composition, including the structure, form, and abundance of food plants in meadows, as tested by comparing occupied and unoccupied habitats? Third, are there differences between the environmental features of occupied and unoccupied apparently suitable habitats at a range of spatial scales, and do those scales interact? I predict that *E. a. cloudcrofti* will demonstrate preferences for different host plant, patch, plant community, surface type, and environmental conditions at all spatial scales. The aim of this study is to contribute to the conservation of this rare butterfly, but also to understand what abiotic, biotic, and spatial patterns may be important to similar butterflies of the globally declining pollinator community (Buchmann and Nabhan 1996, Kearns et al. 1998, Withgott 1999, Thomas and Clarke 2004).

Methods

This study was conducted in the Sacramento Ranger District of the Lincoln National Forest in southern New Mexico within the formerly proposed critical habitat area (USFWS 2001) for *E. a. cloudcrofti* (Figure 1). Long-term (1931-2008) mean annual precipitation is 59.1 centimeters (23.26 inches), about 40% of which occurs during July

and August. Long-term mean monthly temperatures for January and July are -1.1°C (30°F) and 15.6°C (60°F), respectively. The Sacramento Mountains represent the southernmost portion of the Rocky Mountain Conifer Forests ecoregion in the U.S. (EPA Ecoregions map 2009). Existing as an isolated high elevation range immediately surrounded by Madrean Lower Montane Woodlands and then Chihuahuan desert grasslands, the Sacramento Mountains are approximately 260 km from other mountains to the west, and 120 km from similar mountains to the north (EPA Ecoregions map 2009). Geologically, the area is comprised of the Rio Bonito Member of the Lower and Middle Permian San Andres Formation, as well as the Yeso Formation (Rawling et al. 2008). Drainage bottoms contain Quaternary alluvium and most soils are derived from limestone (Rawling et al. 2008).

The butterfly's habitat use at four spatial scales (host plant, penstemon patch, meadow, and landscape) was investigated to accommodate the butterfly's expanding use of space during development from an egg to a flying adult. The occupied or unoccupied status of meadows prior to 2004 was determined from U.S. Forest Service field data and maps obtained from the Sacramento Ranger District Field Office (USFS 2000, 2004). Adult counts for 1999 were derived from U.S. Forest Service data and sampled using the Pollard Walk method (Pollard 1997). Meadows in the northern section of the butterfly's range were selected because they had not been exposed to livestock grazing since 1995 and exhibited similar environmental conditions. Meadow centers were defined by the lowest point in the drainage that remained relatively level and generally formed a linear transect from three to eight meters wide. Meadow sides began as slopes formed on either side of the drainage and continued until approximately three-five meters from tree-line, which became the edge zone. Thus each habitat zone comprised roughly one-third of the habitat area, although the meadows varied in aspect, size, and shape.

Adult surveys - During 2004 and 2005, field surveys of adults were initiated just after the onset of the flight period in early June, and continued weekly throughout the flight season until late July. Equal survey areas and field time for adults were allotted in 2004 and 2005. Specific seasonal and daily times of counts were dependent on climatic conditions and phenology for a particular year, as these factors determine the flight

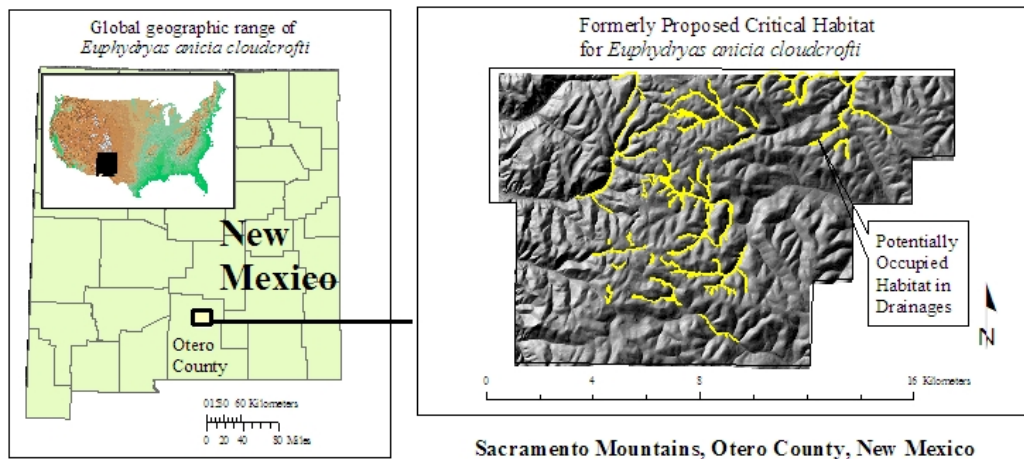


Figure 1. Global range of the Sacramento Mountains checkerspot butterfly, *Euphydryas anicia cloudcrofti*, in the Sacramento Mountains of New Mexico. The area at the right represents the formerly proposed critical habitat (USFWS 2001) and encompasses the known range of the butterfly. Meadow drainages that could potentially support the butterfly are highlighted.

phase of the butterfly, but efforts were made to establish consistency, such as counting in meadows in the same day, at the same times on subsequent days, or during similar weather conditions. Butterflies were counted “on the wing” using a zigzag modified Pollard walk method: the counter slowly paces back and forth within the 10 20m x 100m contiguous grids, forming an continuous “z” pattern over a period of 1.5 hours/meadow (Pollard 1977). While pacing, counts and location of each butterfly were recorded within a five meter distance from the counter’s path, including affiliations with nectar plants. Using this method, all areas within the 1 km x 20 m grid plots were visually covered.

Larval surveys - Surveys of pre-diapause larvae were performed in occupied meadows from August through October in 2004, 2005, 2007, and 2008. The Lincoln National Forest was closed for most of the 2006 summer due to fire danger, prohibiting proper surveying. During larval surveys, each *P. neomexicanus* (penstemon) plant encountered within the five sampling grids was closely examined for immature *E. a. cloudcrofti* in the meadows. Host plant and patch features were noted, including the abundance and proximity of *V. edulis* (valerian), and *H. hoopseii* (Helenium), the other primary food plants. In addition to the six meadows examined for plant and ground surface cover data (Figure 2), larval counts from 2007 included three additional occupied

meadows (Deerhead, Pines Campground, and Bailey Meadow) but these data were used only in the patch and plant analyses to boost the number of occupied samples.

**Occupied and Unoccupied Study Meadows in the Formerly Proposed
Critical Habitat for *Euphydryas anicia cloudcrofti***

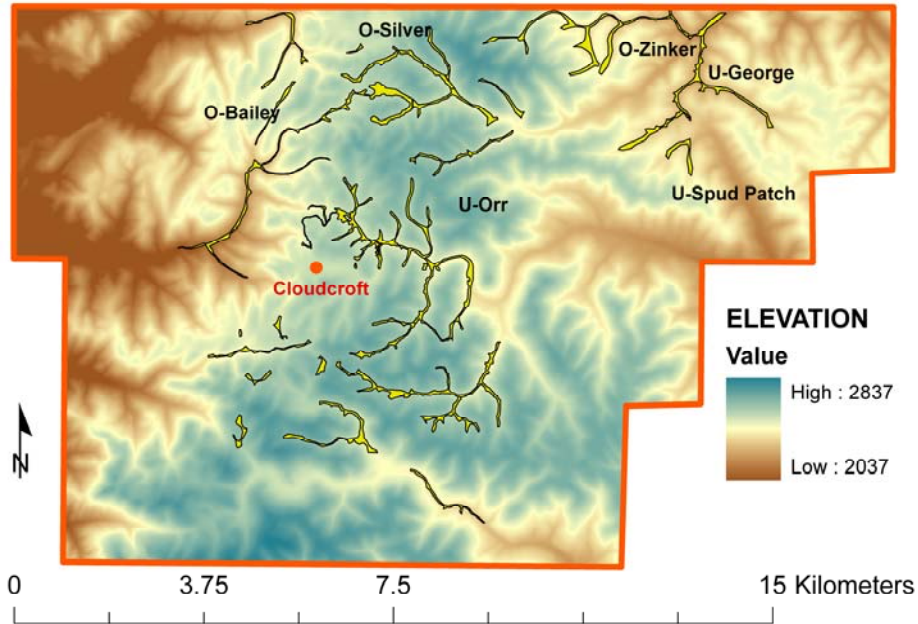


Figure 2. Map of formerly proposed critical habitat boundary for *Euphydryas anicia cloudcrofti* showing occupied drainage habitats outlined in black. The three meadows labeled with an **O** were occupied and three meadows labeled with a **U** were unoccupied at the time of this study and comprise the six meadows analyzed for plant and ground surface variables for this research. Map depicts landscape contours, with blue associated with higher elevations and brown with lower elevations, ranging from 2315-2745m.

Landscape scale - Landscape features within the study area were assessed using digital GIS data. Shapefile and coverage data from the US Forest Service and the US Fish & Wildlife Service outlining the occupied habitat and formerly proposed critical habitat, were projected into 30 meter and later 10 meter resolution DEM raster data, NAD 83, UTM Zone 13. The ArcView (v. 9.1 and 9.3 - ESRI) environment was used to extract information from attribute tables, plot patterns, and statistically analyze data pertaining to habitat preferences of *E. a. cloudcrofti*. Topography (elevation, slope, aspect) and landscape configurations (area, connectivity) were examined for 62 meadows in 13 drainages with suitable habitat for the butterfly on federal lands. Raster data of elevation, slope, and aspect were analyzed by comparing cells in the areas occupied by the butterfly to the rest of the surrounding area enclosed by the formerly proposed critical habitat

boundary. Linear regression was performed on the area and adult population data. Isolation was ranked into five categories to use as a gradient of comparison. Although the abundance of the butterfly in occupied meadows changed from year to year, the presence and absence status of the butterfly within these meadows and the meadows' physical features have remained the same except for one meadow, covered in the discussion.

Meadow scale - Field data were collected in six meadows (Figure 2) between June and October in 2004, 2005, and 2007. The three occupied meadows were surveyed each year for penstemon, eggs, larvae, and adults. All plant community and ground surface cover data were obtained during the summer of 2005 in three randomly selected meadows occupied by the butterfly (Lower Bailey Canyon, Silver Springs Canyon, and Zinker Canyon) and three randomly selected vacant meadows (George Canyon, Orr Canyon, and Upper Spud Patch) (Figure 2). Over a two month period, occupied meadows were surveyed first, followed by the unoccupied meadows. These 6 meadows were located from 4 to 8 km apart in an area that has been withdrawn from cattle grazing since 1995. The elevation of the 6 meadows ranged within 2375-2650 m (7800-8700 ft) and each meadow was situated in an open drainage area surrounded by a dense matrix of aspen and mixed conifer woodland. A 1 km x 20 meter m plot was delineated in each meadow, capturing the meadow's edge, side, and center (Figure 3).

Within each of these 6 meadow plots, plant composition, cover of surface types, and availability of food plants was measured every 40 m along the 1000 m axis using a 1 m x 1 m sampling quadrat placed in three locations representing the center, side, and edge, totaling 75 quadrats per meadow (Figure 3). The direction on either side of the center quadrat for the placement of side and edge quadrats was selected randomly at each 40 m interval, but quadrats are depicted in an alternating pattern below for illustrative clarity.

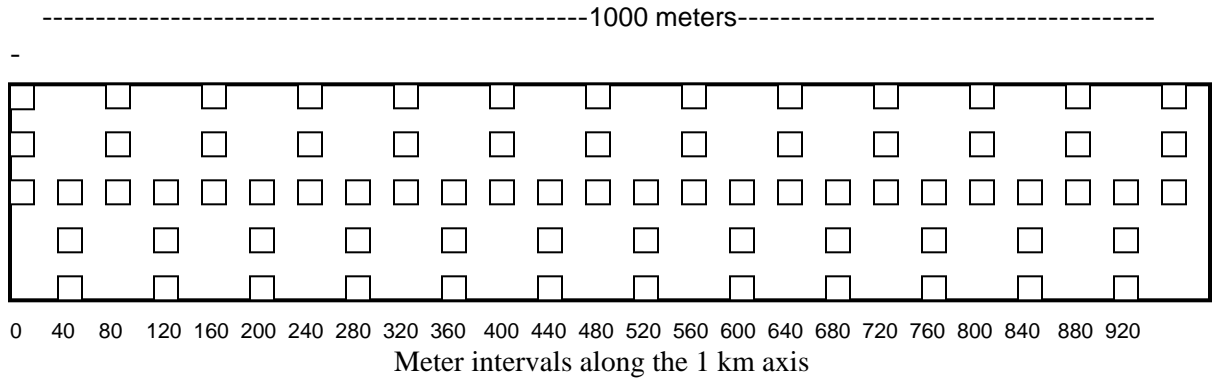


Figure 3. Plant community and ground surface sampling design within 1000 m x 20 m plot in each meadow. Three sets of data were taken every 40 m representing center, side, and edge using 1m x 1m quadrats.

Patch scale - Occupied and unoccupied patches of the primary host plant, *Penstemon neomexicanus*, were compared within the three occupied meadows during 2004, 2005, 2007, and 2008. At the onset of the prediapause larval period, each penstemon plant within five 100 x 20 m grid plots was examined for eggs, hatched larvae, or tents, and penstemon plant and patch features were recorded. These plots spanned 20 m in width to capture at least one edge, side, and center as above, covering alternating 100 x 20 m grid plots in 2005 (in 2004, only the first 20 m area was included) starting at 0, 200, 400, 600, and 800 m locations. As *P. neomexicanus* reproduces both from seed and from rhizomes, clusters of plants often occur within the same location. Patches were defined by groups of *P. neomexicanus* formed by individuals that were not more than three meters apart from another nearest individual in the patch. For each patch, the area, number of *P. neomexicanus* individuals in the patch, density of individuals, distance to the nearest *P. neomexicanus* patch, and average distance between patches was noted. The position of *P. neomexicanus* patches within meadows was recorded with a GPS unit. Analysis of patch distances was performed using ArcGIS (v. 9.3) mapping and an Arc Catalog model to calculate distances from each patch to every other patch within its 100m x 20m plot. Comparisons were made among patch features with and without larvae using Wilcoxon-Mann-Whitney tests, along with natural log-transformed, stepwise regressions in SAS. Logistic regression models using the exact procedure were applied to explain site occupancy by rating variables describing patch characteristics mentioned above.

Plant scale - Due to the scarcity of finding occupied host plants during 2004 and 2005, three additional occupied meadows (Deerhead, Pines Campground, and Bailey Meadow) were sampled in 2007. For each *P. neomexicanus* plant within the sampling grid, an array of morphological features (height, diameter, stem diameter, number of stems, number of leaves, number of stems grazed), reproductive stages (buds, flowers, capsules), and microsite (association with gopher or soil disturbance, insolation, location in the meadow, distance to nearest penstemon plant and patch) data was recorded, including the locations and numbers of eggs, larvae, and tents. The proximity of other food plants (*V. edulis* and *H. hoopseii*) to each *P. neomexicanus* was measured. Data comparisons using Wilcoxon Mann-Whitney tests were conducted for *P. neomexicanus* individuals occupied by larvae and those not occupied, which were the vast majority. Logistic stepwise regressions were used to explore plant variables for the butterfly, with exact logistic regression employed to compare categorical responses and to accommodate uneven, skewed, and heavily tied statistical conditions (Derr 1996).

Results

Butterfly surveys – adults and larvae

During surveys in 1999, the USFS counted a total of 1643 *E. a. cloudcrofti* adults over the peak flight period in late June to early July throughout 13 major meadow drainages (USFS 2000). In 2004, I counted a total of 812 adult butterflies within the three occupied meadows. In 2005, I tallied only 265 adults, over a similar time period in the same locations, representing a 67% drop in the population. For both years, Bailey Canyon had the greatest number of adults, followed by Silver Springs Canyon, and lastly Zinker Canyon. Given the presumed 11-14 day maximum lifespan of each adult butterfly, weekly counts may represent double countings of individual butterflies if their life-spans exceeded one week. Total numbers of tents were 88 in 2004, 75 in 2005, 59 in 2007, and 7 in 2008. The number of individual larvae counted was 2457 in 2005, 1862 in 2007, and 151 in 2008. Butterfly data were analyzed by individual host plant, even if a plant harbored multiple tents or masses, in order to directly compare plant features to those that were not selected by the butterfly. The number of penstemon host plants occupied by

immature stages of the butterfly was: 31 for 2004, 25 for 2005, 59 for 2007 (with data from 3 additional occupied meadows included as explained above), and 7 in 2008.

Landscape scale

Topographic and connectivity elements were dissimilar between potentially occupied habitat and vacant areas within the formerly proposed critical habitat boundary. Habitat occupied by the butterfly had a higher mean elevation and a lower slope than unoccupied habitat. Occupied habitat (OH) had a mean elevation of 2532 m (8307 ft), with a range covering 446 m (1436 ft) from 2314 to 2760 m (7600 to 9055 ft). The surrounding habitat within the critical habitat boundary (CH) had a lower mean of 2436 m (7992 ft) and a broader range of altitudinal values spanning 799 m (2564 ft), ranging from 2036 to 2853 m (6680 to 9301 ft). The mean slope for the OH was 18.46%, with a peak at 10.5% and a range from 0 to 50% slope. The CH exhibited a higher mean slope of 31.48%, a steeper peak at 21.8%, and a broader range of optional slopes from 0 to 72%. The collective aspects of the OH displayed a mean of 148°, with the frequency peaking unimodally in the southeast direction. For the CH, the aspects of each cell had a mean of exactly 180°, with a frequency exhibiting a horizontal, linear distribution conveying that all 360 degrees were equally possible.

The mean area of occupied meadows was 308,123 m², with a minimum area of 1441 m², a maximum area of 3,847,434 m², and a peak in the butterfly's abundance of 312 adults at 1,181,369 m² in Zinker Canyon during 1999 (Figure 4). Although the regression line continues linearly, a parabolic relationship that ascends and then drops when meadows are over 2,700,000 m² may be more accurate. Ranked from most to least isolated, 1999 adult butterfly counts corresponded directly through the five isolation rankings, with the most isolated meadows supporting the fewest number of *E. a. cloudcrofti* and the least isolated meadows maintaining the greatest numbers of adults (Figures 5, 6). Although both area and isolation appeared to influence *E. a. cloudcrofti* distributions for 1999, compared area and isolation effects suggested that for meadows with areas greater than approximately 2,000,000m², connectivity may be more important to *E. a. cloudcrofti* than size (Figure 6). A small, centrally located and well-connected meadow may be more likely to support this species than a large, isolated meadow.

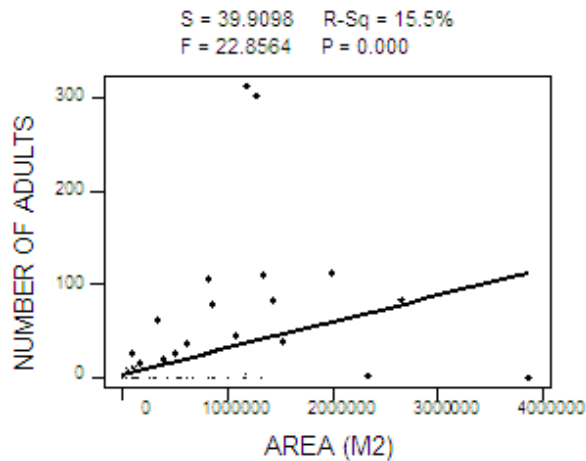


Figure 4. Area of meadows occupied by *E. a. cloudcrofti* during 1999 surveys, with adults more common in meadows of intermediate size. Linear regression revealed that meadow area explained 15.5% of the variation in adult butterfly abundance.

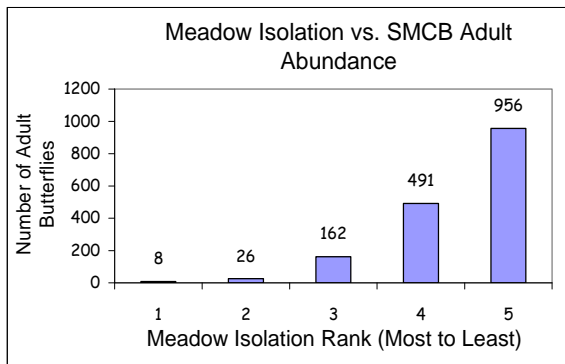


Figure 5. Adults were more abundant in meadows with increased connectivity and reduced isolation (SMCB is Sacramento Mountains checkerspot butterfly).

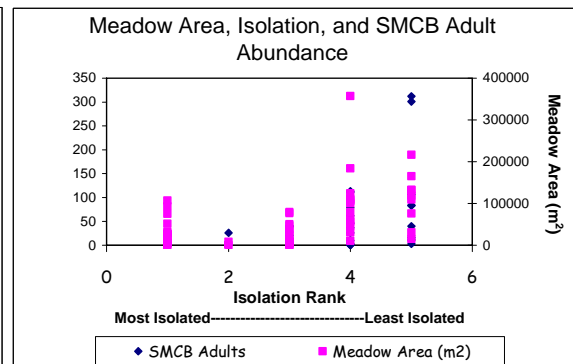


Figure 6. The interaction of meadow area, isolation, and butterfly abundance showed that increased connectivity may be more important than larger area.

Meadow scale

Plant community – Plant community composition measured by percent cover, plant height, and number of inflorescences of species collectively, was not significantly different between occupied and unoccupied meadows using the MRPP analysis (Table 1- all Tables in Appendix). In occupied habitat, 107 species were counted compared to 97 plant species in unoccupied meadows. Altogether, 121 plant species in 47 families were sampled in the 6 meadows. The most common taxa were grasses in the *Poa* L. (native) and *Bromus* L. (exotic) genera, and the forbs *Achillea millefolium* L., *Artemisia carruthii* Alph. Wood ex Carruth., *Lathyrus eucosmus* Butters & H. St. John, and *Geranium richardsonii* Fisch. & Trautv. Although occupied meadows supported 27 unique plant species and unoccupied meadows contained 19 unique plants species, results indicated

that the plant community at the whole meadow scale may not have a predictable effect on the presence of *E. a. cloudcrofti*.

Plant classes - Occupied meadows differed from unoccupied meadows when the plant community was divided into plant classes of forbs, grasses, shrubs, trees, and vines (Table 2). Trees had the greatest proportion of canopy cover (Figure 7) when present in sampling quadrats; however, overall, grasses and forbs were most abundant throughout the meadows (Figure 8). Forbs (herbaceous flowering plants containing the vast majority of nectar species) covered a significantly larger area in occupied meadows than in unoccupied meadows ($W = 1553793$, $P = 0.0290$) (Figures 7, 8; Table 3). Grass cover was significantly greater in unoccupied meadows ($W = 128006$, $P = 0.0001$; Figures 7, 8). Forbs and shrubs were significantly taller and grass height lower in occupied meadows compared to unoccupied meadows (Figure 9, Table 2). Among all plants with floral nectar, composed of forbs and shrubs, occupied meadows held four more species of forbs and one more species of shrub than unoccupied meadows. In sum, 89 species of forbs, 8 species of shrubs, 12 species of grasses, 9 species of trees, and 3 species of vines were counted in study plots.

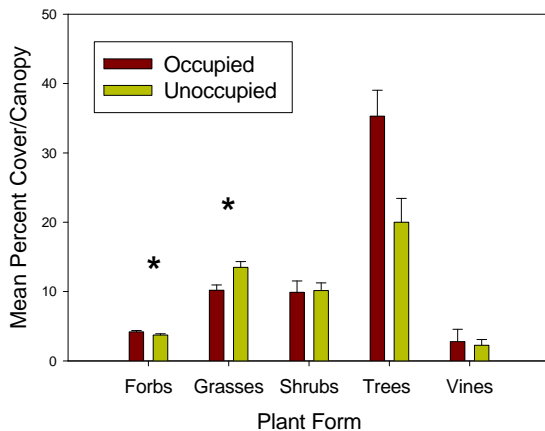


Figure 7. Forb cover was significantly greater ($W=$, 1553793, $P=$ 0.0291) and grass cover significantly reduced ($W=$ 128006, $P=$ 0.0001) in occupied meadows.

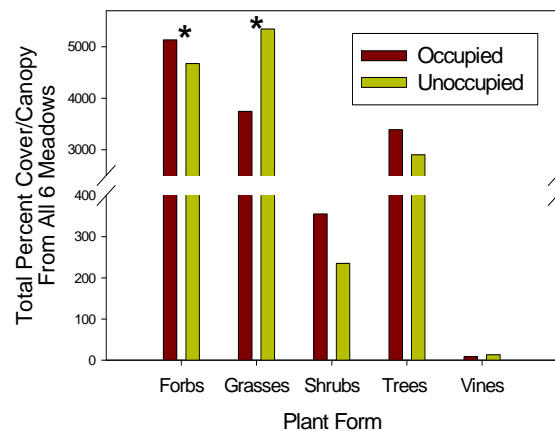


Figure 8. Total percent cover or canopy (for trees) of plant forms in occupied and unoccupied habitats. Forbs covered more area and grasses covered less area in occupied meadows.

Native-Exotic Plants - Exotic forbs and grasses covered significantly more area in unoccupied meadows than in occupied meadows (% cover of all plant species

combined: $W = 103010.5$, $P = 0.0245$) (Figure 10, Table 4). Tree, shrub, and vine species encountered were all native, thus the presence of exotic plants was represented by grasses and forbs (Figure 10). Both native and exotic grass cover occurred with greater frequency in unoccupied meadows than in occupied meadows (Exotic $W = 22046.5$, $P = 0.0070$; Native $W = 1037837$, $P = 0.0066$). Correspondingly, native plants collectively covered a significantly greater area in occupied meadows (84%) than in vacant meadows (79%) ($W = 32208.5$, $P = 0.0036$). Native forbs were spatially dominant in occupied meadows compared to unoccupied meadows ($W = 1037837$, $P = 0.0067$) (Figure 10), and represented 86.4% of the collective forb cover overall, with exotic forbs covering 13.6%.

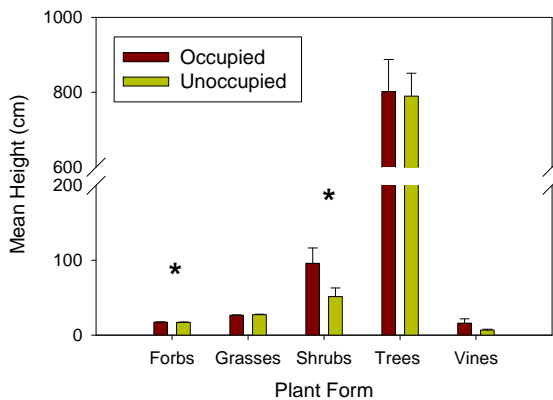


Figure 9. Mean height of plant forms in occupied and unoccupied habitat. Forbs and shrubs were significantly taller in occupied meadows.

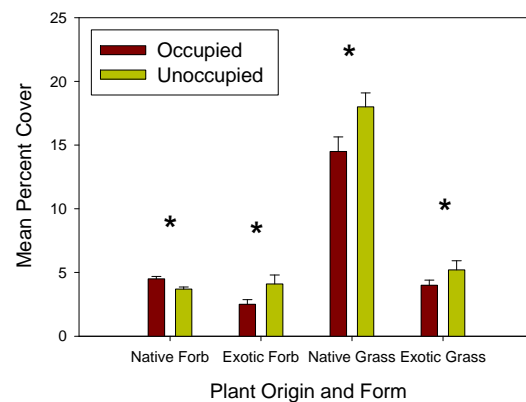


Figure 10. Mean percent cover of native and exotic plants. In all categories, cover was significantly different between occupied and unoccupied habitat.

Mean heights of both exotic and native plants together were greater in occupied vs. unoccupied meadows (Exotic $W = 114720$, $P = 0.0201$; Native $W = 203711$, $P = 0.0492$). Although the number of flowers counted (forbs + shrubs) in occupied meadows (1388 flowers, 49% of all counted) was close to that tallied in unoccupied meadows (1444 flowers, 51% of all counted), unoccupied meadows had significantly more native and exotic inflorescences at the time of sampling than did occupied meadows (Exotic $W = 31298.5$, $P = 0.0014$; Native $W = 1152169$, $P = 0.0124$) (Figure 11). Inflorescences on both native and exotic forbs alone were more profuse in unoccupied meadows compared to occupied meadows (Exotic $W = 31299$, $P = 0.0014$; Native $W = 1099056$, $P = 0.0097$).

Food plants – Differences in percent cover of the larval food plants of *E. a. cloudcrofti*, *P. neomexicanus* and *V. edulis*, were not statistically apparent, although each grew more plentifully in occupied meadows. *Penstemon neomexicanus* was significantly taller ($W = 547.5$, $P = 0.0276$) and manifested significantly more blooming inflorescences ($W = 522.5$, $P = 0.0137$) in occupied meadows compared to unoccupied meadows. *Helenium hoopesii* growing in unoccupied meadows supported a greater number of blooming flowers per plant than those growing in occupied meadows ($W = 9449.5$, $P = 0.0098$) (Table 5).

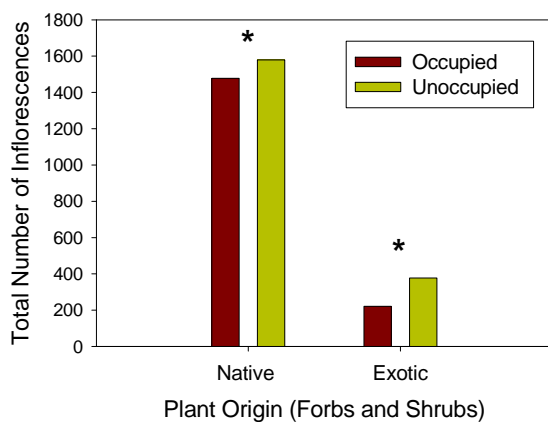


Figure 11. Differences between the total number of inflorescences on native and exotic plants were significant between occupied and unoccupied meadows.

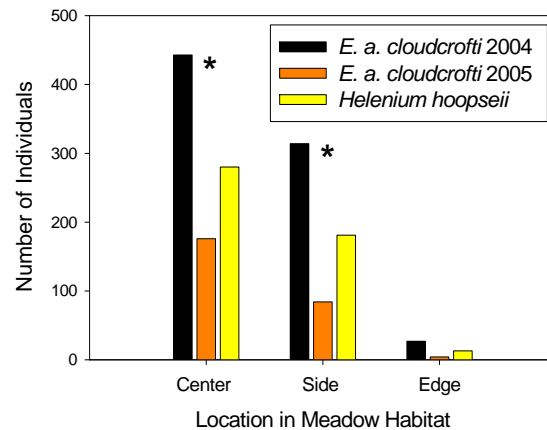


Figure 12. Adult butterfly abundance and distribution in relation to *Helenium hoopesii*, the preferred nectar source. Significant correlations were found with adults and *H. hoopesii* in the center and side meadow habitats.

During flight seasons, distributions of adult *E. a. cloudcrofti* within each meadow concentrated in the center area of the meadows (56.5% in 2004, 66.7% in 2005), with presence at the sides the next most common (40.1% in 2004, 31.8% in 2005). Use of the meadow edges occurred far less frequently, with only 3.4% of individuals noted there in 2004 and 1.5% in 2005. Adult *E. a. cloudcrofti* were associated with the preferred nectar plant, *Helenium hoopesii*, in terms of abundance and location within meadows (Figure 12). Adults were significantly associated with *H. hoopesii* in the center and side areas of meadows, but not the edges (Center: $X^2 = 24.5877$, $P < 0.0001$; Side: $X^2 = 6.4694$, $P = 0.0110$). Adults were highly associated with alighting, nectaring, or resting on *H. hoopesii* significantly more than any plant or ground surface (Off *H. hoopesii* = 263; On

H. hoopseii = 602 observations; $X^2 = 30.2107$, $P < 0.0001$). Adult use amounted to being on *H. hoopseii* for 70% of all surface interactions, and 85% of all floral visits.

Surface – Ground surface cover types were similar throughout the six meadows, exhibiting no differences in overall cover between occupied and unoccupied meadows with MRPP tests (Table 6). As a result of this high degree of similarity, only litter and exposed soil cover were found to be significantly greater in unoccupied meadows in a more thorough investigation of each surface type separately (Figure 13; Table 7). The presence of gopher soil disturbance, which may have positive effects on *P. neomexicanus* germination and growth (McIntyre 2010), was strongly associated with exposed soil in both occupied and unoccupied meadows (Occupied: $W = 2917$, $P = < 0.0001$; Unoccupied: $W = 954.4$, $P = < 0.0001$) (Table 8).

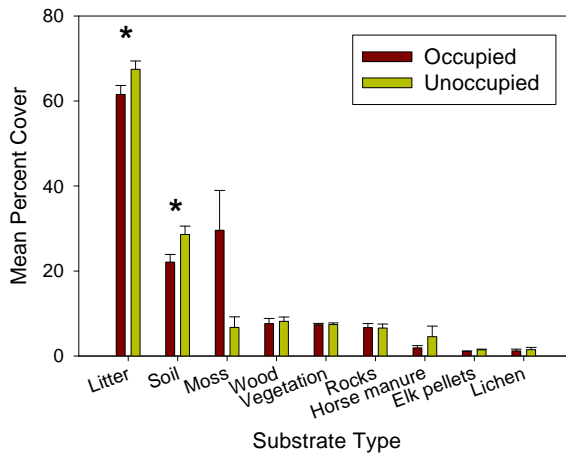


Figure 13. Mean cover of substrate types in occupied and unoccupied meadows. Unoccupied meadows had significantly more litter and bare soil than occupied meadows.

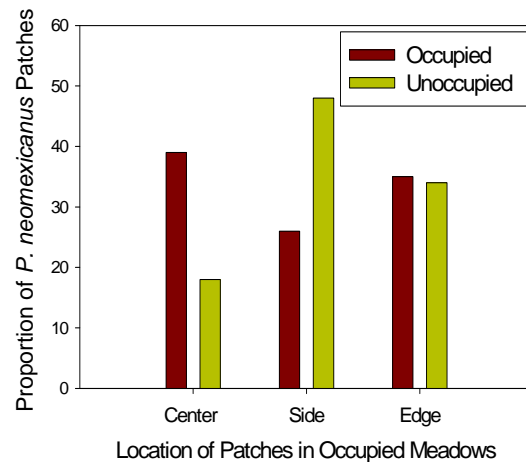


Figure 14. *Penstemon neomexicanus* patch location in occupied meadows.

Collectively, by summed totals, and some overlap due to plants growing over ground surface type, the proportion of meadow coverage was:

Occupied: 23% forbs + 17% grasses + 1.6% shrubs + 0.04% vines + 0.01% lichen + 40% litter + 1.7% moss + 0.2% elk pellets + 0.06% horse manure + 2.7% rocks + 13.6% soil + 2.3% wood (+ 15% tree canopy cover)

Unoccupied: 21% forbs + 24% grasses + 1% shrubs + 0.04% vines + 0.01% lichen + 41% litter + 0.3% moss + 0.3% elk pellets + 2.7% horse manure + 2.7% rocks + 16.4% soil + 2.3% wood (+ 13% tree canopy cover)

Occupied: 0.31% *Penstemon* + 0.36% *Valerian* + 2.3% *Helenium*

Unoccupied: 0.18% *Penstemon* + 0.076% *Valerian* + 2.5% *Helenium*

Patch scale

Proportionately, about half of the *P. neomexicanus* patches were located in the side parts of meadows (48%), however, patches growing in the centers and edges of meadows had a greater chance of being occupied by *E. a. cloudcrofti* larvae or eggs (Figure 14). Approximately 18% of *P. neomexicanus* individuals grew alone as solo plants not associated with patches. Occupied solo penstemon plants were most often located in the center of meadows and were significantly farther from other penstemon individuals and patches. Penstemon growing alone hosted significantly more eggs, tents, and larvae than penstemon host plants affiliated with a patch (Table 9). Moreover, solo penstemon had significantly more buds and seed pods than did patch penstemon and were less likely to be grazed.

Almost twice the number of penstemon individuals grew in occupied patches (42) compared to 23 penstemon individuals found in unoccupied patches ($W = 14409.5$, $P = 0.0034$), verified by the significantly greater patch density in occupied meadows ($W = 67731$, $P = 00002$). Although statistical differences in patch size were not significant (2004, 2005, 2008 data; Table 10), occupied patches were larger, ranging in size from 3600 m² to 1 m², and had a mean area of 78 m², whereas unoccupied patches ranged from 2000 m² and 1 m² and had a mean size of 39 m². Collectively these results indicated that unoccupied penstemon patches were less dense, contained fewer penstemon individuals per patch, and were likely to be smaller (Tables 11, 12).

Multiple logistic regression models analyzing the dependence of eggs and larvae on occupied and unoccupied patch variables showed that the number of penstemon in each patch had the greatest influence on the presence or absence of larvae ($R = 0.0227$, $P = 0.0335$). Adding environmental variables and a plant-scale measure of host plant diameter in the patch added two more significant variables, including the slope and plant density of a patch, yet the predictive capability of the butterfly's occupancy remained under 10% (Table 13). Stepwise regression analysis found no other measured variables to meet the 0.05 significance level, suggesting that other factors perhaps at different scales were impacting this species (Table 14).

Plant scale

Penstemon host plants occupied by eggs or larvae were located mostly on the sides of meadows, whereas most unoccupied penstemon plants were found along the meadow edges (Table 15). The average slope exhibited no statistically significant differences between occupied and unoccupied plants. Eggs were laid on host plants with more southward aspects whereas plants not selected grew on surfaces with more eastward aspects (mean occupied aspect = 162°, median = 140°; mean unoccupied aspect = 119°, median = 110°). The difference in aspect preference ($W = 167158$, $P < 0.0001$) supported the findings of a preference for the southeast-facing direction as found using the coarser-scaled landscape results above quantified using ArcGIS. Penstemon plants with larvae were located in larger patches ($W = 11691$, $P = 0.0445$) with higher patch densities ($W = 16252$, $P < 0.0001$) than unoccupied plants (2004, 2005 data). Contrary to expectations derived from other studies (Pittenger and Yori 2003, McIntyre 2010), gopher soil disturbance was more prevalent with unoccupied penstemon plants ($W = 178055$, $P < 0.0001$).

Plants selected by adult female *E. a. cloudcrofti* for oviposition, as evidenced by the presence of eggs, tents, and early instar larvae, were significantly larger than plants not selected (Tables 15, 16). The mean plant diameter for *P. neomexicanus* with eggs or larvae was 21.03 cm, but was just 14.78 cm for plants without larvae ($W = 132478$, $P < 0.0001$). Stems on occupied host plants grew over twice as high ($W = 135677$, $P < 0.0001$) and were doubly as numerous as stems on unoccupied host plants ($W = 152085$, $P = 0.0022$). The largest stem diameter was over twice as thick on plants with eggs and larvae compared to those plants without evidence of *E. a. cloudcrofti* ($W = 112866$, $P < 0.0001$). Occupied *P. neomexicanus* had a greater display of reproductive effort, as evidenced by more buds, flowers, and seed capsules, than vacant plants, with statistically significant results displayed only with number of seed capsules ($W = 85719$, $P = 0.0395$) (Figure 17). Despite the potentially more alluring plant size and floral display of occupied host plants, elk grazing was equally present on both occupied and unoccupied *P. neomexicanus* plants.

The mean distance to *Valeriana edulis* was over twice as far from unoccupied *P. neomexicanus* plants (15.2 m) compared to occupied plants (7.08 m) ($W = 14425$, $P = 0.0309$) (Figure 18). The average distance to *H. hoopseii* was significantly closer to unoccupied *P. neomexicanus* plants for plants with and without blooms, however occupied plants were within a maximum of 20 m apart from *H. hoopseii* compared to up to 30 m for unoccupied plants (Table 11). Results suggest that *P. neomexicanus* plants within close proximity to *V. edulis* are preferred but proximity to *H. hoopseii* is less important as long as it is within a range of 20 m.

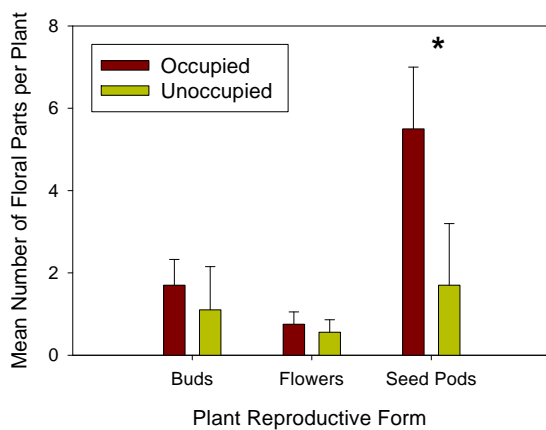


Figure 17. Number of floral parts per *Penstemon neomexicanus* host plant. Reproductive effort was significantly greater in occupied meadows.

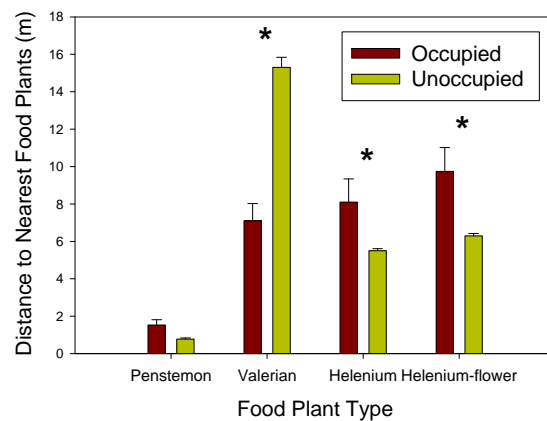


Figure 18. Distance from *Penstemon neomexicanus* plants to nearest food plants. Distance to *Valeriana edulis* was closer and to *Helenium hoopseii* was farther in occupied meadows.

Logistic regression models using a logit binary system to represent presence or absence of larvae or eggs found that only the number of capsules, tallest stem height, and maximum stem diameter were influential. No other plant effects met the 0.05 significance level of the model.

Discussion

This study demonstrated that certain features of landscape topography, plant community composition, host plant patch structure, and host plant morphology were selected above other available conditions by the Sacramento Mountains checkerspot butterfly. Given that the spatial dynamics and patterns of local colonizations and extinctions are unknown for this species, these results were based on presence or absence data. Findings at the four different scales reflected similar patterns, with connectivity,

resource concentration, and plant structural diversity preferred by the butterfly at the scales of landscape, meadow, host plant patch, and native host plant. These mutually supportive themes across scales suggest that the ovipositing female is assessing habitat quality from the level of the meadow and its surroundings to the interplay of resources at the patch, plant and possibly the leaf level. Although some studies have found no evidence for a learned oviposition preference for checkerspot butterfly species (Thomas and Singer 1987, Parmesan et al. 1995), other studies have linked emigration from areas with low host plant density and immigration to patches with higher host plant density by ovipositing females, which could indicate oviposition selectivity (Singer and Thomas 1996, Boughton 2000, Hanski and Singer 2001). Once larvae become sufficiently mobile and leave the original host plant, they, too, select available host plants, but their accessibility to *Penstemon neomexicanus* or *Valeriana edulis* is determined by options set by the mother and depends upon the distribution of resources in space.

At the scale of the landscape, the butterfly appeared to have distinctive habitat associations with higher elevational ranges, gentler slope angles, and more south to south-east aspect orientations than those available in the surrounding habitat. The apparent selection for higher elevations relates to the possible historic adaptation of this species to a cool and relatively moist climate and vegetative zone that remains toward the tops of the Sacramento Mountains. Although the immediately surrounding peaks attain heights over 2740 m, the 3 unoccupied meadows examined in this study had elevational ranges within those of the occupied meadows, with all 6 meadows occurring within a gradient of 2400 to 2630 m (7900 to 8600 ft). In contrast to other *Euphydryas* species using high points as congregating locations, or “hilltopping”, *E. a. cloudcrofti* adults fly close to the ground and appear to be drainage specialists. The presence of *E. a. cloudcrofti* in open, flatter drainages compared to the far more plentiful, steeper terrain may be related to the avoidance of flight over tall objects, such as trees or forested areas on steeper slopes, as found with other *Euphydryas* species (USFWS 2005). Additionally, open canopies enhance the reception of sunlight, a factor correlated with boosted metabolic rates in insects and copious nectar production (Schultz 2001). Meadows

oriented to the south may maximize solar gain needed for enhanced growth, fecundity, and persistence in this montane region.

Connected, centrally-located, proximal meadow drainages of an intermediate size exhibited a 100-fold increase in butterfly abundance compared to isolated, distant meadows that were very small or very large. As a butterfly with a maximum flight of 890 meters based on a solitary record, along with several other records of flights under 500 meters (Pittenger and Yori 2003), *E. a. cloudcrofti* appears to be relatively sedentary and its colonizing capability is unknown. Two recent studies out of Europe also found connectivity of resources to be a main driver in conserving two species of rare butterflies, the endangered violet copper (*Lycaena helle*) and another checkerspot, Nickerl's fritillary (*Melitaea aurelia*) (Eichel and Fartmann 2008, Bauerfeind et al. 2009). For the endangered Fender's blue (*Icaricia icarioides fenderi*), large (>2ha), connected (<1km) areas were found to have high restoration value, but small, connected patches were far more important to butterfly presence than large isolated patches (Schultz and Crone 2004). Connectivity appears to be critical for species with limited dispersal abilities to provide conditions for population establishment into new areas or to replenish locations with dwindling or extirpated subpopulations.

Meadow area is important for *E. a. cloudcrofti* to a certain degree, with adults peaking in numbers at meadows of intermediate size. Increased area can provide the diversity and quality of food plants and utility resources butterflies require, such as physical sites or conditions for roosting, diapause, pupation, or mate location (Dennis et al. 2006). For this species, the assumption that larger areas have an increased chance of providing high quality resources is not supported beyond a meadow size of 200,000m². Habitat quality can vary independently of area, as found with Britain's butterflies (Dennis et al. 2006). A meadow's area must be large enough so that shade cover does not impede upon the butterfly's thermoregulatory needs related to flight and physiological development (Bryant et al. 2002). At the same time, a meadow's area must provide for *E. a. cloudcrofti*'s dependence upon nearby edge habitat for cover from predators or protection from environmental extremes, particularly wind, as has been found with other open-habitat butterflies (Dover et al. 1997, Luoto et al. 2001). Meadow area must balance

immediate edge accessibility, yet contain enough specialized food plant and microclimate resources.

Meadows occupied by *E. a. cloudcrofti* exhibited higher habitat quality than unoccupied meadows, as measured by greater plant species diversity, a significantly broader range in height of forbs and shrubs, a significantly greater area of forb cover, and more native plant cover, as identified by other studies (Luoto et al. 2001, Collinge et al. 2003, Krauss et al. 2004, Schultz and Crone 2004, Betzholtz et al. 2007). More plentiful forbs and native plants in occupied meadows, representative of nectar resources, may be better suited to the nectar nutrients, quantities, and phenology to which *E. a. cloudcrofti* has adapted over time. The dominance of exotic and native grass growth in unoccupied meadows may have crowded out either native or exotic forbs potentially useful as nectar sources. However, increased grass cover in unoccupied meadows also could have been an artifact of surveying later in the season than occupied meadows, as warm weather grasses exhibit peak cover in autumn.

Despite being far more vagile than larvae, adults exhibited specialized use of *Helenium hoopesii* as a nectar source and tightly followed its distribution within meadow centers, perhaps due to adult preference for nectar sources favoring moister conditions at the bottom of mountain drainages. Adults are not known to be dependent on surface water, as found with many other butterfly species, and as such may obtain most of their water needs from nectar, or possibly dew. The butterfly used *H. hoopesii* 85% of the time as a nectar source and visited other available floral species only 15% of the time, quantifying the degree of nectar source specialism. For larvae, and possibly ovipositing females, the food plant, *V. edulis*, may be more important than this analysis has revealed. Co-occurrence of both larval host plants used by *Euphydryas editha* was believed to improve habitat quality and survival by expanding the food resource base and phenological availability before the dry season ensued (Murphy et al. 2004). For *E. a. cloudcrofti*, the almost five-fold greater percent cover of *V. edulis* and almost doubled cover of *P. neomexicanus* in occupied meadows compared to unoccupied meadows, may simply provide a greater range of available food plants through space and time.

Patches of *P. neomexicanus* with larvae were greater in area and density compared to patches without larvae, suggesting that increased access to host plants is important to the butterfly's survival. *Penstemon neomexicanus* reproduces via seed and vegetatively through rhizomes. Plants connected by rhizomes are clumped whereas individuals germinating from seed may be more randomly distributed, accounting for different patch configurations. Greater patch density offers more connectivity among individual penstemon for larval use. Spatial compaction of host plants may enhance pre-diapause larval survival by providing more food and possible structural support for tent formation if accessed early in a pre-diapause stage. In contrast, sparsely dispersed patches with low average plant densities may act as sinks to early instar larvae. Patch isolation has been negatively correlated with the presence of other *Euphydryas* species (Betzholtz et al. 2007), whereas enhanced networks of adjacent patches have been positively associated with increased butterfly presence (Bauerfeind et al. 2009). Thus the number of host plants may be the most important factor determining butterfly presence, as suggested by other studies (Dennis et al. 2005, Bauerfeind et al. 2009), but how these plants are arranged at a finer spatial scale for local dispersal of larvae may hold the key for the butterfly's persistence.

Host plants selected by the butterfly were larger in overall size than those without larvae, and displayed more prolific numbers of stems, buds, flowers, and seed capsules than those penstemon plants without larvae. This trend has been noted with other studies of *Euphydryas* species, where large-sized host plant individuals in open areas have been favored for oviposition (Anthes et al. 2003, Liu et al. 2006). In Colorado, *Euphydryas editha* chose food plants based more on phenologies than on biochemical qualities, exhibiting a preference for host plants that were most available to developing larvae throughout the prediapause period without going into early senescence (Holdren and Ehrlich 1982). Overall growth and inflorescence phenology may have been more optimal where selected host plants were growing, due to microclimates formed by aspect, slope, elevation, and neighboring shade-forming vegetation. During these years, the blooming phenology of *P. neomexicanus* may have been more synchronized with that of the butterfly in the zones where eggs were laid, as tracked by other butterfly species

(Peterson 1997). Occupied natal plants also grew in larger patches with significantly greater plant density than unoccupied plants. Given the responsiveness of *E. a. cloudcrofti* to connectivity at all scales analyzed, a stepping stone approach to linking plants to patches to meadows could hold promise if situated in areas with other supporting abiotic conditions, as attempted with other endangered butterflies in Europe (Maes et al. 2004).

Overall, very low numbers of individual larvae and adults in these meadows and within the entire range of *E. a. cloudcrofti* (USFS 2004) limit the number of potential migrants to unoccupied yet suitable meadows. Few egg masses or tents were found each year, with the most found in 2007 (59) and the least in 2005 (25). During the period of this study, counts of larvae and adults in an occupied canyon (Zinker Canyon) went from 0 larvae and 7 adults in 2005 to 0 larvae or adults in 2006, 2007, and 2008. This canyon was the one where the butterfly exhibited the peak recorded abundance within the entire occupied habitat in 1999 (the point with over 300 adults counted at the fourth ranking, Figure 6) (USFS 2000). It is unknown if the population in this meadow has become extirpated within these three years. Difficulties in locating egg masses or tent webs with low population levels may have been due to encountering the observation threshold, where tents are so scarce that they become overlooked, as experienced with the rapidly declining *Euphydryas aurinia* in Wales (Fowles and Smith 2006). High mortality, primarily during the pre-diapause larval stage, and the trait of laying eggs in masses contribute to dramatic oscillations in population abundance for this and similar species (Labine 1968). Thus the butterfly could reappear in Zinker Canyon or a newly colonized canyon as a natural phenomenon. However, strong population fluctuations decrease the genetically effective population size and enhance the risk of stochastic extinctions making it crucial to track these patterns to employ conservation practices (Traill et al. 2009).

At this time, the butterfly appears to occupy the highest open meadows available within its known range, although a handful of unoccupied meadows above 2743 m (9000 ft) exist to the south of the formerly proposed critical habitat boundary (USFWS 2009). It is unknown whether the butterfly could naturally become established in these meadows

to the south that do contain the food plants. The fact that the butterfly has not already migrated into these potentially usable meadows leaves the future fate of this species in question, particularly in light of global climate change interacting with a spatially limiting mountain-island system. Localized and rare butterfly species may be less inclined toward habitat exploration than more widely distributed species (Norberg et al. 2002). Meadows may remain unoccupied as a result of this lack of exploratory behavior, as well as physical limits of dispersal abilities, or nonexistent connectivity. Another high-alpine, relict species, the Uncompahgre fritillary (*Botoria acrocneuma*), lives atop mountains in Colorado (Britten et al. 1994). This fritillary has endured a history of severe sheep grazing and over-collection, but now is faced with very low numbers that are genetically depauperate; its plight is uncertain in light of future environmental impacts wrought by climate change. Because *E. a. cloudcrofti* lives nowhere else on the planet, we lack the models of what a more thriving population scenario would be – we have a single remnant population possibly pushed into suboptimal habitat. This might account for the low numbers of individuals in occupied areas; without a second population for comparison, our conclusions must be drawn within this narrow area of endemism.

Once habitat variables supporting *E. a. cloudcrofti* are better understood through research, habitat within the dispersal limits or along corridors could be enhanced to promote natural colonization of the species with the target of increased resource connectivity. Creating pathways of *P. neomexicanus*, *V. edulis*, and *H. hoopseii*, connecting meadows with suitable habitat, could extend the butterfly's range and abundance. These corridors should be embedded in a diversity of microtopography with adequate insolation and edge components and south-southeast aspect exposure for optimum value. As the rarity of this species does not offer the luxury of repeated trials of management experiments, the outcomes of each action to enhance the habitat require monitoring and swift adaptation to new ecological findings. Freshly colonized meadows could be supplemented with captive reared larvae or relocated from donor source populations that would not be vulnerable to a loss of individuals (if any exist). Captive reared or translocated larvae could then be introduced into currently uninhabited meadows, where favorable patch and plant conditions are found or perhaps developed.

Modifying patch traits is one of the simpler solutions for rare species management (Fleishman et al 2002). To this end, the results of this study may assist projects in the field.

In sum, for this habitat specialist butterfly, which exhibits high home-meadow fidelity, spatially contiguous resources appear to be crucial regardless of scale. High habitat quality, low isolation, broad host plant patch area, and high host plant patch density were associated with occupied habitats. To match resource requirements, understanding the condition and spatial organization of habitat at the scales of the landscape, meadow, patch, and host plant and how these scales inter-relate is necessary for long-term conservation of this species. Even within a spatial level, larvae exhibit scalar expansion – initially operating at the finest scale at the beginning of the prediapause season and then crossing a spatial threshold to a courser exploration of surrounding habitat a few meters away just before going into winter diapause. How habitat quality and networked resources interact with the butterfly's different life phases annually and with the successional requirements of open habitat over the long-term, are important conservation parameters for this butterfly. Distinctions among the plant community and ground surface type vary over time and were noted here over only the course of a few years, offering a glimpse into a dynamic system. Understanding resource requirements spatially and temporally opens the door to adjusting land management practices or restoring habitats with potential for supporting the species.

Defining a species' habitat is a common challenge in ecology, yet is crucial for successful management and conservation of rare species and supporting natural communities (Dennis et al. 2006, New 2007). Determining the precise ecology and the spatial dynamics of resources and how these interact with a species' behavior involves much effort which explains why so little is known about rare insects in their natural settings (New 2007). Even when a species' ecological needs are clear, these needs may temporarily conflict, as when disturbance provides open soil that facilitates the germination of the host plant, but immature and adult butterfly stages perform best with a high amount of host plants and low disturbance density (Eichel and Fartmann 2008). A vision that encompasses short- and long-term recovery from the perspective of the

species being studied, along with the multifaceted desires of humans, is worth cultivating in order to maintain and restore rare species in native habitats. Because globally threatened butterfly species serve as bioindicators of overall ecosystem function, these butterflies have inspired “research-based approaches to insect conservation” that can serve as models for modern conservation approaches (Thomas et al. 2009). Given that the Sacramento Mountain checkerspot’s needs may encapsulate those of other butterfly species, this research may provide insight into spatial characteristics preferred not only by the checkerspot, but also by similar, valuable members of the pollinator community.

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Appendix

Tables and figures referenced in above text:

To discern differences in plant communities and ground surface characteristics, the multi response permutation procedure (MRPP) nonparametric analysis (McCune and Grace 2002) was used to compare percent cover, height, and number of inflorescences for each species between occupied and unoccupied meadows. A test of group differences, the MRPP generated the T value and the A statistic in addition to a P, which describe relationships among and between groups. The T value describes the separation among groups, with more negative T values indicating a greater difference among groups. A, the agreement statistic, describes within group heterogeneity. A can be negative if you have less agreement within groups than expected by chance. Ideally, the A statistic should be close to 0.3 for ecological data. The MRPP test was generated using the PC-Ord statistical package.

Table 1. Results of plant diversity by habitat location (center, side, edge) and by meadow occurrence in meadows occupied or unoccupied by *Euphydryas anicia cloudcrofti*. Data measuring plant cover, height, and number of inflorescences within meadows were not significantly different between occupied and unoccupied meadows within the butterfly's habitat. The T value, which identified the separation among groups, was not extremely negative, indicating that there was not a high degree of difference among groups. The A statistic, a measure of heterogeneity within groups, remained below 0.2, as a result of similarity within groups.

MRPP test	N down	N across	T value	A statistic	P-value
All tests compared occupied vs unoccupied meadow groups					
Plant Species					
Percent Cover – by Habitat	6	118	-0.2384	0.03174	0.3634
Mean Height – by Habitat	6	118	-0.9393	0.09524	0.1731
Number of Inflorescences – by Habitat	6	118	0.2288	-0.03175	0.5470
Percent Cover – by Meadow	6	118	1.1918	-0.15873	0.9024
Mean Height – by Meadow	6	118	1.2524	-0.12698	0.8969
Number of Inflorescences – by Meadow	6	118	1.0297	-0.14286	0.8570
Percent Cover – by Habitat Meadow	18	118	0.5980	-0.02063	0.6699
Mean Height – by Habitat Meadow	18	118	-0.3842	0.01088	0.2567
Number of Inflorescences – by Habitat Meadow	18	118	0.1383	-0.00357	0.4831

Table 2. Results of plant species divided into classes and analyzed by meadow habitat (center, side, edge) and occupied or unoccupied status using the MRPP test.

MRPP test	N down	N across	T value	A statistic	P
All tests defined by grouping occupied vs unoccupied meadows (Status)					
Plant Species by Class					
		Species			
Forb Sum Cover - Habitat Status	6	89	-2.09660	0.31746	0.03148
Forb Mean Cover – Habitat Status	6	89	-1.81956	0.11111	0.04011
Forb Mean Height - Habitat Status	6	89	-2.24942	0.20635	0.02956
Forb Sum Inflorescence - Habitat Status	6	89	0.24253	-0.03175	0.54878
Shrub Sum Cover – Habitat Status	6	8	-1.39443	0.11111	0.08159

Shrub Mean Cover – Habitat Status	6	8	0.55048	-0.03175	0.69410
Shrub Mean Height - Habitat Status	6	8	-1.90847	0.20634	0.04147
Shrub Sum Inflorescence - Habitat Status	6	8	0.28006	-0.02041	0.57883
Forb+Shrub Sum Cover – Habitat Status	6	95	-1.98956	0.30159	0.03440
Forb+Shrub Mean Cover – Habitat Status	6	95	0.30715	-0.01587	0.63649
Forb+Shrub Mean Height – Habitat Status	6	95	-2.02920	0.22222	0.03562
Forb+Shrub Sum Inflorescence – Habitat Status	6	95	0.22881	-0.03175	0.54703
Grass Sum Cover - Habitat Status	6	12	-0.30555	0.04762	0.28569
Grass Mean Cover – Habitat Status	6	12	-1.37931	0.17460	0.09547
Grass Mean Height - Habitat Status	6	12	-2.95298	0.42857	0.02174
Tree Sum Cover - Habitat Status	6	9	0.14586	-0.01587	0.53918
Tree Mean Cover – Habitat Status	6	9	-0.10220	0.00000	0.45111
Tree Mean Height – Habitat Status	6	9	-0.94632	0.09524	0.16905
Vine Mean Cover – Habitat Status	6	3	-1.15311	0.08730	0.12625
Vine Mean Height – Habitat Status	6	3	0.51912	-0.03741	0.64272

Table 3. Results of plant classes for percent cover, mean height, and number of inflorescences between occupied vs. unoccupied meadows using the Wilcoxon Mann-Whitney test.

Wilcoxon Mann-Whitney Results

Variable	Plant Form	Occ	Uno	Occ	Uno	Occ	Uno	Uno	Uno	Wilcoxon M-W 2 sample test		Ties Adj
		f	f	Mean	Mean	Median	Median	Std Err	Std Err	W stat	P	P
% Cover	Forb	1224	1252	4.199	3.744	2	2	0.1725	0.1792	1553793	0.0291	0.0290
	Grass	366	396	10.24	13.5	5	7	0.7521	0.8166	128006	0.0001	0.0001
	Shrub	35	22	9.943	10.14	4	3	1.9562	4.4309	558.5	0.1982	0.1929
	Tree	96	100	35.32	29.03	20	15	3.6413	3.369	10132.5	0.0896	0.0880
	Vine	3	6	2.83	2.25	2.25	1.5	1.1667	0.8342	16.5	0.8003	0.7937
Mean Height (cm)	Forb	1223	1255	17.27	17.01	15.24	12.7	0.3956	0.4418	1575840	0.0007	0.0007
	Grass	370	397	26.48	28.6	25.4	25.4	0.635	0.7107	141331	0.2587	0.2538
	Shrub	35	22	100.66	69.02	45.72	38.1	21.318	15.366	568	0.0167	0.0141
	Tree	96	100	801.5	789.5	548.64	853.44	85.857	61.186	9433.5	0.9558	0.9558
	Vine	3	6	16.09	6.77	12.7	7.62	5.552	1.071	19.5	0.3222	0.2914
Number Inflorescences	Forb	540	543	1.314	1.451	0	0	0.1609	0.1498	1473076	<0.0001	<0.0001
	Shrub	6	2	7	0	1.5	0	1.834	4.744	622	0.6576	0.6559
	Tree	2	1	0.021	0.000	1	35	0.0147	0	1.0000	0.1515	0.1499

Table 4. Results of native and exotic plants in occupied vs. unoccupied meadows divided into plant classes.

Plant Form	Variable Percent Cover	Native				WMW W statistic	P	Exotic				WMW W statistic	P
		Occ Mean	Uno Mean	Occ Median	Uno Median			Occ Mean	Uno Mean	Occ Median	Uno Median		
All Plants		1405	1415	1433.2	1388	2013595.5	0.1362	319	361	322.9	356.0	103010.5	0.0245
Forb		4.48	3.69	2	2	1037837	0.0067	2.49	4.12	1	1	32209	0.1126
Grass	Mean Height	14.45	18.04	8	10	47916.5	0.0049	3.96	5.23	3	3	22047	0.007

	Number Flowers											
All Plants	1408	1418	1443.7	1383.5	2032711	0.0492	319	362	359.6	324.6	114720	0.0201
Forb	17.78	17.66	15.24	12.7	1046306	0.0252	14.17	14.22	7.62	7.62	37057	0.0054
Grass	27.13	27.56	25.4	25.4	54614	0.5061	25.49	26.54	20.32	24.13	20622	0.5077
All Plants	1.4	1.5	0	0	1152169	0.0124	1.3	1.7	0	0	31298.5	0.0014
Forb	2.8	3.27	0	0	1099056	0.0097	4.8	3.7	1	2	31299	0.0014

Table 5. Results of food plant cover, height, and inflorescence number in occupied and unoccupied meadows.

Wilcoxon Mann-Whitney Results of Food Plants

Variable	Foodplant	Occ f	Uno f	Occ Mean	Uno Mean	Occ Median	Uno Median	Occ Std Err	Uno Std Err	W stat	P	One-sided P
Percent Cover	<i>Helenium</i>	100	106	5.2	5.35	3	3	0.5892	0.5262	10214	0.7494	0.7491
Height (cm)	<i>Helenium</i>	100	106	27.6	30.4	25.4	25.4	1.6098	1.646	9797	0.1957	0.1942
Number of Inflorescences	<i>Helenium</i>	100	106	1.26	1.94	0	0	0.457	0.3707	9449.5	0.0098	0.0091
Percent Cover	<i>Penstemon</i>	30	24	2.35	1.67	2	1	0.3918	0.2285	606	0.3387	0.3343
Height (cm)	<i>Penstemon</i>	30	24	23.1	16.7	25.4	15.24	2.2795	1.9395	547.5	0.0555	0.0276
Number of Inflorescences	<i>Penstemon</i>	30	24	9.67	2.83	4	0	2.4725	1.6393	522.5	0.0137	0.0108
Percent Cover	<i>Valerian</i>	27	10	2.96	1.7	2	1.5	0.6044	0.3	163.5	0.3624	0.3562
Height (cm)	<i>Valerian</i>	27	10	15.5	11.9	15.24	7.62	2.3845	2.7335	165	0.4038	0.3982
Number of Inflorescences	<i>Valerian</i>	27	10	0.11	1	0	0	0.1111	1	199	0.4631	0.4583

Table 6. Results of MRPP tests for ground surface variables collectively between occupied and unoccupied meadows.

MRPP	N down	N across	T	A	P	
All tests defined by grouping occupied vs unoccupied meadows (status)						
Ground Surface Variables						
Mean Cover by Canyon		6	8	0.3627	-0.0159	0.5678
Mean Cover by Habitat		6	8	-0.6367	0.04762	0.2539
Sum Habitat Gopher		12	8	-0.3012	0.00171	0.3663
Sum Habitat Meadow		18	8	-1.1953	0.03428	0.1193

Table 7.

Surface Type %	Occ f	Uno f	Occ Mean	Uno Mean	Occ Median	Uno Median	Occ Std Err	Uno Std Err	W Stat	P
Litter	213	219	61.545	67.456	71	79	2.1046	1.9605	42898	0.0197
Moss	19	17	29.579	6.7059	3	2	9.3539	2.5143	302.5	0.7132
Lichen	3	2	1.1667	1.5	1	1.5	0.441	0.5	7	0.7609
Soil	199	207	22.098	28.585	10	16	1.7924	1.9782	37778	0.0316
Elk pellets	62	72	1.0887	1.4514	1	1	0.0972	0.1513	3886	0.1572
Horse manure	11	15	1.9091	4.5333	1	2	0.5301	2.4859	135	0.4659

Rocks	132	146	6.6818	6.5655	2	2.5	0.9317	0.9484	18181	0.7973
Vegetation	1724	1776	7.3283	7.4175	3	3	0.3364	0.3354	3038678.5	0.4800
Wood	98	103	7.648	8.1569	4	4	1.1976	1.0298	9543.5	0.4523

Table 8. Results of gopher associations with types of ground surface cover

Gopher Effects on Ground Surface Cover

All combined				Occupied				Unoccupied			
Gopher Presence	Surface Type	N	Mean	Gopher Presence	Surface Type	N	Mean	Gopher Presence	Surface Type	N	Mean
N	Lichen	2	1	N	Lichen	1	1	N	Lichen	1	1
Y	Lichen	3	1.5	Y	Lichen	2	1.25	Y	Lichen	1	2
N	Litter	126	74	N*	Litter	78	67.5	N	Litter	48	84.7
Y	Litter	306	60.7	Y	Litter	135	58.1	Y	Litter	171	62.8
N	Moss	14	30	N	Moss	8	46.7	N	Moss	6	7.83
Y	Moss	22	11.6	Y	Moss	11	17.1	Y	Moss	11	6.09
N	Elk pellets	29	1.16	N	Elk pellets	19	1.24	N	Elk pellets	10	1
Y	Elk pellets	105	1.31	Y*	Elk pellets	43	1.02	Y	Elk pellets	62	1.52
N	Horse manure	4	2.25	N	Horse manure	0	0	N	Horse manure	4	2.25
Y	Horse manure	22	3.64	Y	Horse manure	11	1.91	Y	Horse manure	11	5.36
N	Rocks	64	8.36	N	Rocks	39	7.82	N	Rocks	25	9.2
Y	Rocks	214	6.07	Y	Rocks	93	6.2	Y	Rocks	121	5.98
N	Soil	80	8.04	N	Soil	55	8.33	N	Soil	25	7.4
Y	Soil	326	29.6	Y	Soil	144	27.4	Y	Soil	182	31.4
N	Wood	71	10.2	N	Wood	40	11.8	N	Wood	31	8.1
Y	Wood	130	6.63	Y	Wood	58	4.78	Y	Wood	72	8.11

Table 9. Results *E. a. cloudcrofti* response, plant variables, and patch features of solo *P. neomexicanus* plants compared to patch *P. neomexicanus* plants in occupied meadows.

Wilcoxon Mann-Whitney Tests of Solo Penstemon vs. Patch Penstemon Characteristics

Variable	Solo		Patch		Solo		Patch		W stat	P	Ties adjust P
	N	Median	N	Median	N	Mean	N	Mean			
Egg Mass	51	2127	0	0	0.098	0.0047	57542	0.656	0		
Tent	51	2127	0	0	0.216	0.031	65535.5	0.0247	0		
Eggs	51	2127	0	0	6.667	0.306	57541	0.6562	0		
Larvae	51	2127	0	0	3.541	0.85	65502	0.0252	0		
Mass+Tent	51	2127	0	0	0.314	0.0353	65514.5	0.025	0		
Egg+Larvae	51	2117	0	0	10.21	1.155	65189.5	0.0253	0		
Tent Height	10	31	3.18	5	8.509	6.047	240	0.3705	0.234		
Stem Diameter	44	1971	2	2	1.805	1.536	50061.5	0.1347	0.1179		
Stem Height	50	1971	4	3	6.537	5.103	45001	0.3105	0.2921		
Stem Flowers	41	1971	0	0	0.317	0.353	39277	0.6263	0.422		
Stem Buds	41	1971	0	0	0.707	0.66	37900.5	0.3607	0.1521		
Stem Seeds	41	1971	0	0	1.341	0.802	41856	0.8729	0.7913		
Plant Flowers	41	1971	0	0	0.902	0.573	45969.5	0.2015	0.0594		
Plant Seeds	41	1971	0	0	4.512	1.728	48160.5	0.0612	0.008		
Plant Buds	41	1971	0	0	1.78	1.087	46908.5	0.1239	0.034		
Stems Grazed	41	1971	0	0	0.561	0.857	36544.5	0.1997	0.1342		
Total Stems	41	1971	1	1	1.122	1.373	41477.5	0.9544	0.9519		
Plants Grazed	41	1971	1	4	0.268	0.369	3649	0.0006	0.0005		

Patch Average Density	11	2121	0.4	0.8768	0.792	1.115	8100.5	0.0746	0.0746
Distance to Penstemon Patch	33	1909	4	0.5	6.015	0.703	63121.5	0	0
Average Plant Diameter	28	1988	9.25	6	10.27	7.068	40352	0.0001	0.0001
Distance Helenium	41	2127	12.7	11.43	15.33	14.629	49228	0.2303	0.2294
Distance Helenium Flowers	41	1971	5	4	6.546	5.565	44619	0.3626	0.361
Distance Valerian	41	1971	8	5	8.439	6.305	47802.5	0.0759	0.0752
Disease Gopher	35	1471	10	9	14.24	15.09	25755	0.8083	0.8078
Disturbance Soil	41	1930	0	0	0.293	0.328	39554	0.809	0.7591
Disturbance Solar Exposure	41	1971	2	2	1.512	1.615	37075	0.255	0.1771
Slope	41	1971	2	2	1.805	1.95	35494	0.117	0.0001
Aspect	41	1971	2	2	1.634	1.627	41497	0.9501	0.9404
	41	1971	5	7	9.463	12.503	33399	0.0326	0.0319
	41	2107	100	110	96.71	109.84	39876	0.2881	0.2869

Table 10. Results of occupied and unoccupied patch variables in occupied meadows using WMW tests.

PATCH VARIABLES - WILCOXON MANN WHITNEY TEST RESULTS

Data Combined

2004, 2005, 2007, 2008	Occ	Occ	Occ	Occ	Occ	Occ	Occ		2-sided	Ties	1-sided
Variable	N	Mean	Median	Std Err	Std Dev	Min	Max	W stat	P	P	P
Elevation	26	8470	8454	31.40	451	8305	8756	1119	0.9366		
Slope	26	14.1	10	3.20	33	2	35	1393	0.044		
Aspect	26	126.9	120	12.10	180	30	210	1239	0.3118		
Patch Area	92	77.9	12	44.40	425.7	1	3600	15013.5	0.2488	0.2484	
Number Pen In Patch	51	42.3	22	26.82	107.8	2	707	14409.5	0.0034	0.0034	
Patch Density	79	1.589	1.25	0.13	1.164	0.2	6.67	67731	0.0002	0.0001	
Distance Next Patch GPS	26	10	10.5	1.20	15.1	3.2	18.4	1402.5	0.0797		
Distance Helenium 05	25	8.086	4.81	1.24	4.81	0.15	19	31198.5	0.0365	0.0364	
Distance Helenium Flower 05	25	9.74	4.97	1.28	4.97	1	20	33162	0.0056		
Distance Valerian 05	25	7.08	3.55	0.92	3.55	1	16	14824	0.0617	0.0615	0.0309
Penstemon Disease Rating	58	0.733	0.727	0.10	0.727	0	1	76252.5	<.0001	<.0001	

Table 11. Results of patch variables for 2005 only compared between occupied and unoccupied patches in occupied meadows.

	Uno	Uno	Uno	Uno	Uno	Uno	Uno
Variable	N	Mean	Median	Std Err	Std Dev	Min	Max
Elevation	312	8398	8490	22.5	924	7866	8790
Slope	312	9.2	5	0.99	50	0	50
Aspect	312	107.3	110	7.3	350	0	380
Patch Area	254	38.67	12	9.03	143.9	0.07	2000
Number Pen In Patch	410	23.33	10	2.42	48.9	2	382
Patch Density	340	1.338	0.895	0.12	2.215	0.03	28.6

Distance Next Patch GPS	312	8.39	7.3	0.48	43.1	0.65	43.8
Distance Helenium 05	1988	5.551	5.025	0.116	5.025	0.1	30
Distance Helenium Flower 05	1988	6.324	5.286	0.122	5.286	0.1	30
Distance Valerian 05	1482	15.23	19.88	0.535	19.88	0.1	100
Penstemon Disease Rating	1948	0.325	0.559	0.013	0.559	0	3

Table 12. Patch variables for 2005 data alone.

PATCH VARIABLES - WILCOXON MANN WHITNEY TEST RESULTS
2005 Data Only

Variable	Occ		Occ		Uno		Uno		Wilcoxon Mann-Whitney Two-Sample		Ties Adj	One-sided
	N	Mean	St Dev	St Err	N	Mean	St Dev	St Err	W stat	P	P	P
PatchAreaAveraged05	25	65.8	198.4	39.7	188	34.5	90.45	6.6	3258	0.0442	0.0442	
PatchAreaStacked05	38	78.9	321.5	52.2	254	38.7	1434	9.03	6648.5	0.026	0.0258	
PatchAreaAveraged05 OutlierNo	24	26.3	22.2	2.76	188	34.5	90.45	6.6	3045	0.0843	0.0842	
PatchAreaStacked05 OutlierNo	37	27	31.3	5.15	254	38.7	1434	9.03	6357	0.0459	0.0457	
DistancePenstemon05	23	0.63	0.65	0.177	1920	0.78	2.696	0.064	17973.5	0.0984	0.0983	0.0491
DistancePatch05	15	7	2.52	0.9	1982	7.05	4.49	0.532	15672	0.7566		
AveragePatchDensity05	38	1.28	0.709	0.142	253	1.45	2.184	0.149	5968.5	0.3856	0.3849	

Table 13. Ranking of transformed patch variables resulting from stepwise regression procedures

TENT OR MASS PRESENCE/ABSENCE AND DESCRIPTIVE PATCH VARIABLES						
	Logistic Stepwise Regression Patch Variables			Logistic Stepwise Regression Patch Variables with Plant Diameter and Environmental Variables		
Ranking	Variable	R2	P	Variable	R ²	P
1	Log number Penstemon per patch	0.0227	0.0335	Log number Penstemon per patch	0.0285	0.0207
2	Log patch area	0.0355	0.1976	Log slope	0.0437	0.0341
3	Log patch density	0.0512	0.0814	Log patch density	0.0739	0.0303
4	Log distance to nearest patch	0.0589	0.2251	Log patch size	0.0771	0.0886
5	Log number Penstemon in nearest patch	0.0599	0.6724	Log distance to nearest patch	0.0909	0.1242

Table 14. Results of stepwise regression procedures using different sets of *P. neomexicanus* plant and patch data.

LTentMass05 no envi vars					LTentMass05 w envi vars				
Rank	Variable	R2	Entering P	Model P	Rank	Variable	R2	Entering P	Model P
1	LAvDen	0.0181	0.0769	0.0617	1	LAvDen	0.0197	0.0743	0.0335
2	LMinDisM	0.0282	0.184	0.3909	2	LMinDisM	0.0304	0.1857	0.3247
3	LNoPen05	0.0329	0.3655	0.3734	3	LAspect1	0.0397	0.2166	0.1543
4	LAveDisM	0.0356	0.4919	0.4294	4	LElevation	0.044	0.3962	0.3220
5	LNoBigNext	0.0365	0.6911	0.6911	5	LAveDisM	0.0481	0.4116	0.4116

LTentMass08 no envi vars					LTentMass08 w envi vars				
Rank	Variable	R2	Entering P	Model P	Rank	Variable	R2	Entering P	Model P

1	LNoPen08	0.0689	0.0005	0.0009	1	LNopen08	0.0756	0.0004	0.0010		
2	LMinDisM	0.0793	0.1669	0.1947	2	LMinDisM	0.0871	0.1571	0.1563		
3	LxBdiam	0.0874	0.3143	0.1000	3	LAspect1	0.0973	0.1832	0.2001		
4	LNoBigNext	0.0891	0.3697	0.2970	4	LxBdiam	0.1015	0.3903	0.1934		
5	Lavden	0.095	0.297	0.2970	5	LNoBigNext	0.1072	0.3183	0.3183		
LTentMass0508 no envi vars					Entering	Model	LTentMass0508 w envi vars			Entering	Model
Rank	Variable	R2	P	P	Rank	Variable	R2	P	P		
1	Lnopen0508	0.0227	0.0473	0.0335	1	Lnopen0508	0.0285	0.0313	0.0207		
2	LxBdiam	0.0355	0.1333	0.1976	2	Lslope1	0.0437	0.1119	0.0341		
3	Lavden	0.0512	0.096	0.0814	3	Lavden	0.0739	0.1055	0.0303		
4	LMinDisM	0.0589	0.2396	0.2251	4	LxBdiam	0.0771	0.0538	0.0886		
5	LNoBigNext	0.0599	0.6724	0.6724	5	LMinDisM	0.0909	0.1242	0.1242		
LTentMass0508 w no envi vars w pldi					Entering	Model	LTentMass0508 envi vars w pldi			Entering	Model
Rank	Variable	R2	P	P	Rank	Variable	R2	P	P		
1	LAvPIDicm	0.0293	0.0238	0.0147	1	LNopen0508	0.0285	0.0313	0.0158		
2	LNopen0508	0.059	0.0214	0.0050	2	LAvPIDicm	0.0569	0.0296	0.0419		
3	LAvDen	0.0767	0.2269	0.0748	3	Lavden	0.0804	0.1503	0.0360		
4	LxBdiam	0.0841	0.0616	0.0964	4	LxBdiam	0.0823	0.0729	0.0585		
5	LMinDisM	0.0918	0.2345	0.2345	5	LSlope1	0.1012	0.0712	0.0712		
LTentMass05 w no envi vars w pldi					Entering	Model	LTentMass05 envi vars w pldi			Entering	Model
Rank	Variable	R2	P	P	Rank	Variable	R2	P	P		
1	LAvPIDicm	0.0656	0.0006	0.0004	1	Lavpldiam	0.0711	0.0006	0.0007		
2	LAvDen	0.0874	0.0448	0.0225	2	Lavden	0.0947	0.0427	0.0207		
3	LMinDisM	0.0966	0.1899	0.1875	3	LMinDisM	0.102	0.2558	0.3971		
4	LNoBigNext	0.101	0.6138	0.3677	4	LSlope1	0.1054	0.4396	0.4454		
5	LxBdiam	0.1014	0.3519	0.3519	5	LAveDisM	0.108	0.5065	0.5065		

Table 15. Results of plant variables using combined data from 2004, 2005, and 2007 between occupied and unoccupied plants in occupied meadows.

PLANT VARIABLES - WILCOXON MANN WHITNEY TEST RESULTS

Variable	Data Combined										Wilcoxon Mann-		Ties Adj	1-sided P
	2004, 2005, 2007 N	Occ Mean	Occ Me d	Occ St Dev	Occ St Err	Uno N	Uno Mean	Uno Me d	Uno St Dev	Uno St Err	Whitney 2-Sample W stat	P		
Slope	109	11.94	5	11.16	1.211	2323	12.68	8	12.63	0.2696	124516	0.2576	0.2575	
Aspect	102	161.8	140	72.35	8.165	2459	119	110	82.99	1.72	167158	<.0001		
Gopher	180	1.88	2	0.584	0.048	2309	2.16	2	0.604	0.013	178055	<.0001		
Soil Disturbance	180	1.728	2	0.446	0.033	2309	1.875	2	0.331	0.0069	193450	<.0001	0	
Stem Diameter	65	4	4	1.08	0.158	1988	1.71	2	1.56	0.0361	112866	<.0001		
Stem Height	83	30.36	28	14.06	1.783	1988	12.74	7.6	14.69	0.34	135677	<.0001		
Flowers	76	0.75	0	2.27	0.303	1988	0.563	0	1.706	0.3027	74950	0.3055	0.3054	
Buds	75	1.737	0	4.69	0.625	1987	1.068	0	2.937	1.054	77802	0.8638		
Pods	76	5.487	0	11.16	1.487	1984	1.656	0	4.733	1.4868	85719	0.0395	0.0394	
Number of Stems	108	2.306	2	2.44	0.267	2320	1.453	1	1.844	0.0394	152085	0.0022		
Number of Stems No Rosettes	69	3.609	2	2.31	0.326	1420	2.373	2	1.855	0.051	68964	<.0001		
Plant Diameter	82	21.03	20	7.2	0.919	2144	14.78	13	8.156	0.1814	132478	<.0001		
Plants Grazed	110	0.316	0	0.436	0.047	2323	0.363	0	0.436	0.0471	139828	0.321	0.3209	

Grazing Height 04	19	49.38	46	23	7.046	109	45.41	38	27.7	3.0107	1339.5	0.446	0.4446
Patch Area (m ²)	79	40.5		224.6	25.3	254	38.67		1434	9.03	11691	0.0445	0.0443
Average Patch Density	78	1.799	1.5	1.009	0.133	253	1.447	1	2.184	0.1494	16252	<.0001	
Distance Penstemon	81	1.529	0.6	2.184	0.281	1920	0.778	0.5	2.696	0.0635	90725	0.0563	0.028
Distance Patch	35	5.466	5	2.53	0.532	1982	7.048	6	4.49	0.5319	27820	0.0225	
Distance Helenium 05	25	8.086		4.81	1.242	1988	5.551		5.025	0.1162	31199	0.0365	0.0364
Distance Helenium in Flower 05	25	9.74		4.97	1.283	1988	6.324		5.286	0.1223	33162	0.0056	
Distance Valerian 05	25	7.08	1	3.55	0.916	1482	15.23		19.88	0.5351	14824	0.0617	0.0615
Penstemon Disease	58	0.733		0.727	0.095	1948	0.325	0	0.559	0.0127	76253	<.0001	<.0001

Table 16. Results of plant variables for 2005 data only.

PLANT VARIABLES - WILCOXON MANN WHITNEY TEST RESULTS

2005 Data Only

Variable	Occ		Occ		Uno		Uno		Wilcoxon Mann-Whitney Two-Sample		Ties Adj	One-sided
	N	Mean	St Dev	St Err	N	Mean	St Dev	St Err	W stat	P	P	P
Stem Diameter 05	25	4.28	1.29	0.334	1988	1.71	1.56	0.036	43175.5	<.0001		
Stem Height 05	25	39	14.77	3.81	1988	12.7	14.69	0.34	42962	<.0001		
Flowers 05	25	2	3.33	0.86	1988	0.56	1.706	0.303	28050.5	0.1423	0.1421	
Buds 05	25	3.72	4.85	1.054	1987	1.07	2.937	1.054	33520.5	<.0001		
Pods 05	25	12.5	14.43	3.719	1984	1.66	4.733	1.487	34392.5	<.0001		
Stem Total 05	25	2.76	1.767	0.456	1988	1.35	1.852	0.043	35908	<.0001		
Stem Total No Rosettes 05	21	3.29	1.59	0.459	1097	2.44	1.907	0.06	15321	0.0108	0.0107	
Plant Diameter 05	25	23.2	8.76	2.259	2144	14.8	8.156	0.181	40048	<.0001		
Plants Grazed 05	25	0.28	0.355	0.092	1988	0.37	0.468	0.092	22983	0.3635	0.3634	
Stems Grazed 05	25	0.88	1.606	0.414	1988	0.85	1.55	0.036	23412.5	0.4763	0.4762	
Distance Penstemon 05	23	0.63	0.65	0.177	1920	0.78	2.696	0.064	17973.5	0.0984	0.0983	0.0491
Distance Patch Average Patch Density 05	15	7	2.52	0.9	1982	7.05	4.49	0.532	15672	0.7566		
	38	1.28	0.709	0.142	253	1.45	2.184	0.149	5968.5	0.3856	0.3849	

CHAPTER 2:
EFFECTS OF MAMMAL HABITAT DISTURBANCE UPON A RARE, NEW
MEXICAN BUTTERFLY

Euphydryas anicia cloudcrofti (Lepidoptera: Nymphalidae)

Introduction

Effective conservation of rare species requires not only the maintenance of appropriate habitat, but also the preservation of community interactions that form those habitat conditions. For rare species with patchy distributions, such as specialist butterflies, suitable habitat is defined by a habitat's climatic conditions, size, connectivity, and availability and quality of resources (Thomas et al. 2001, Ovaskanen and Hanski 2004, Dennis et al. 2006). Resources needed by butterflies are determined by a butterfly's life cycle, which ties butterflies intimately to the landscape through their foodplants (Thomas et al. 2001, Krauss et al. 2004, Dennis et al. 2006). However, habitat requirements extend beyond vegetation alone into the function of habitats for activities such as basking, roosting, courting, mating, pupating, and diapausing (Luoto et al. 2001, Dennis 2004, Krauss et al. 2005, Vanreusel et al. 2006). Changes to the physical and ecological features of a habitat by other animals such as dominant mammals may redirect a butterfly's use of a favorable patch temporally and spatially. Animal activities can modify suitable habitat by altering the vegetation composition, phenology, growth rates, chemical characteristics, cover, and structure of the plant community, and exert consistent physical effects upon soil properties important to host plants and butterflies (Holdren and Ehrlich 1982, Wooten 1994, Krauss et al. 2004, Strauss and Irwin 2004).

For many butterflies, life history traits and use of resources reflect the strategies of their host plants, with rare butterflies depending primarily on stress-tolerating host plants that respond to open habitats and disturbance (Dennis et al. 2004, 2005). Butterflies also depend on an array of nectar sources and can become nectar-limited in the absence of floral abundance and diversity (Schultz and Duglosch 1999, Hardy et al. 2007). Processes promoting increased foodplant availability and other utility resources frequently result from natural disturbance regimes that form new swaths of exposed lands. Areas recently disturbed and devoid of trees offer direct sunlight and associated

early-colonizing forbs and grasses that are necessary for open-habitat specialist butterflies (Steffan-Dewenter and Tschardt 1997, Balmer and Erhardt 2000, Bergman et al. 2004). Thus, community interactions that establish necessary plants, structures, and microclimates to perform essential functions, help support the habitat needs of butterflies.

Mammal interactions known to influence the presence of local flora and fauna include consumption and trampling, as well as soil disturbance and nutrient additions (Crawley 1983, Collins 1987, Huntley and Inouye 1988, Denyer et al. 2007). Moreover, continued burrowing and herbivory have been linked with generating and maintaining open habitats and forb diversity (Huntly and Inouye 1988, Cantor and Whitham 1989, Huenneke et al. 1990). Although these processes modify suitable habitat and availability of host plants, which direct distributions of specialist butterflies, interactive impacts of dominant native vertebrates upon butterflies and their food plants remain unexplored. Functional interactions between butterflies and other species often are unknown, yet it is essential that these ecological processes are preserved along with the habitat and species to maintain community structure (Fisher 1998). Given that the deterioration of habitat suitability may lead to local butterfly extinctions, understanding how mammal activities shape habitat features over a range of spatial scales and consequently impact butterfly densities could hold keys to a species' survival and aid in conservation management.

One such rare, specialist butterfly of open habitats is the Sacramento Mountain checkerspot, *Euphydryas anicia cloudcrofti* (Ferris and Holland 1980) of southern New Mexico. This endemic, univoltine, gregarious subspecies lives within an 85km² (33 mi²) area in some of the highest meadows of the Sacramento Mountains and overwinters as a larva. Females oviposit on the New Mexico penstemon, *Penstemon neomexicanus* (Plantaginaceae – formerly Scrophulariaceae), and rarely on mountain valerian, *Valeriana edulis* (Valerianaceae). Larvae mainly consume *P. neomexicanus*, but will also eat *V. edulis* (USFWS 2001). The common sneezeweed, *Helenium hoopesii* (Asteraceae), appears to be a preferred nectar source (McIntyre 2010). The butterfly is dependent primarily upon the local abundance and connected patches of *P. neomexicanus*, which often are found growing in disturbed, bare soil associated with pocket gopher burrows, wildlife paths, or road verges (USFWS 2005, McIntyre 2010).

Specific host plant characteristics that are known to modify butterfly presence in general include host plant density, phenology, nutrient quality, secondary compounds, size, number of flowers, patch size, and proximity to nectar plants and protective cover (Ehrlich and Raven 1965, Stanton 1982, Britten and Riley 1994, Rodriguez et al. 1994, Schultz and Dlugosch 1999, Leon-Cortez et al. 2003, Krauss et al. 2004, McIntyre 2010). Large host plants have been correlated with oviposition preference of *E. a. cloudcrofti*, and plants in the *Penstemon* genus have exhibited enhanced growth in disturbed soils associated with gopher mounds (Davis et al 1991, 1995; Dolek et al. 1998; McIntyre 2010). Elk grazing may change the quality of the butterfly's host plants for oviposition or larval use by altering a plant's biomass, architecture, phenology, and chemistry, depending on when and where a plant is pruned (Rausher 1981, Huntley 1991, Crawley 1983, Ehrlen 1997, Strauss 1997, Strauss 1991, Shiojiri et al. 2001). Because oviposition and larval development are dependent upon host plant availability, location, and condition (Rausher 1981, Murphy 1983, Dempster 1997, Hellmann 2002, Krauss et al. 2004), factors that affect plant community and its spatial structure most likely impact the butterfly.

As representatives of ecosystem engineers, keystone species, dominant species, or highly interactive species, mammals such as pocket gophers (*Thomomys talpoides*) and elk, have strong influences on their environment (Jones et al. 1994, Soule 2003). Disturbances associated with herbivory, trampling, or excavating modify successional processes by curbing the encroachment of trees and other potentially dominant vegetation (Cantor and Whitham 1989). These processes allow a blend of early- and late-successional plants and different microhabitats to coexist at a landscape scale, which encourage greater plant diversity over time (Huntley and Inouye 1988, Huntley and Reichman 1994, Badano and Cavieres 2006). Pocket gopher disturbance in the forms of burrowing, mound building, and above- and below-ground herbivory alters soil texture and microtopography, redistributes nutrients, and modifies plant demography, productivity, and composition at local scales (Mielke 1977, Huntly and Inouye 1988, Inouye et al. 1997, Ostrow et al. 2002).). In the western U.S., Rocky Mountain elk (*Cervus elaphus nelsoni*) are large, generalist herbivores that consume approximately

40% of available forbs and 24% of available grasses in mountain meadows, including *Penstemon* species (Wright 2000, USFWS 2001, Ross and Wikeem 2002). Such disturbance may impact butterfly populations, primarily through the quality or phenology of butterfly food plants, particularly if a host plant is stress-tolerant or disturbance-dependent (Dennis et al. 2004). As a result, indirect impacts on the plant community by mammals may rival direct impacts to butterflies, such as incidental consumption or destruction, in overall importance.

Multi-species interactions appear to be affecting the Sacramento Mountains checkerspot butterfly and its host plant. Ecosystem engineering (by gophers) and herbivory by a dominant, large herbivore (elk) can be closely associated, depending on the scope of each activity by each animal (Wilby et al. 2001, Wright and Jones 2006). Information about effects of native wild ungulates on butterflies is virtually nonexistent, and effects of elk, cattle, or other livestock on *E. a. cloudcrofti* are not understood (USFS 2000, 2004). Results of this study will form a baseline of elk impacts within butterfly meadows, upon which the impacts of cattle may be factored in. As butterflies are known to be responsive to changes in resource management (Thomas et al. 2001, Wallis de Vries 2004), the objective here is to capture these bottom-up and top-down relationships in the field and translate a partial quantitative habitat assessment into practical conservation measures for the butterfly's long-term persistence. The following questions are addressed: 1) Are *P. neomexicanus* and immature stages of *E. a. cloudcrofti* associated with soil disturbance from gopher activities or other sources? 2) What proportion of the *P. neomexicanus* population is grazed by ungulates, and is consumption of *P. neomexicanus* by ungulates related to the distribution or abundance of immature butterflies? 3) Are elk or deer more likely to forage on *P. neomexicanus* plants associated with gopher mounds or plants on mounds with *E. a. cloudcrofti*, rather than *P. neomexicanus* plants found independently in the meadow clearings (Figure 1)?

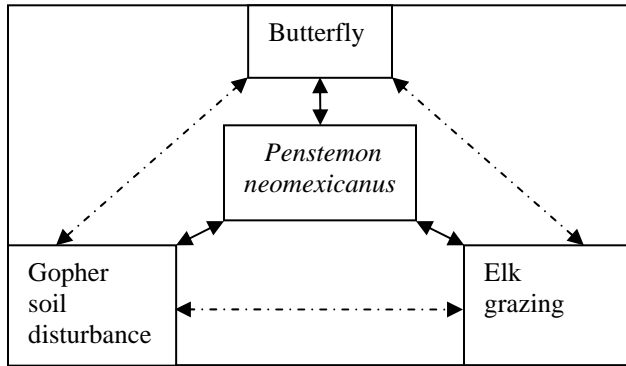


Figure 1. Diagram of explored interactions among the butterfly, host plant, gopher, and elk. Dashed lines indicate possible indirect interactions, while solid lines represent possible direct interactions.

Methods

This study was conducted in the Sacramento Ranger District of the Lincoln National Forest in southern New Mexico over the summers of 2004 and 2005. Long-term (1931-2008) mean annual precipitation was 59.1 centimeters (23.26 inches), about 40% of which occurred during July and August. Long-term mean monthly temperatures for January and July were -1.1°C (30°F) and 15.6°C (60°F), respectively. The Sacramento Mountains represent the southernmost portion of the Rocky Mountain Conifer Forests ecoregion in the U.S.A (Griffith et al. 2006). Existing as an isolated high elevation range immediately surrounded by Madrean Lower Montane Woodlands and then Chihuahuan desert grasslands, the Sacramento Mountains are approximately 260 km from other mountains to the west, and 120 km from similar mountains to the north (EPA Ecoregions map 2009). Geologically, the area is comprised of the Rio Bonito Member of the Lower and Middle Permian San Andres Formation, as well as the Yeso Formation (Rawling et al. 2008). Drainage bottoms contain Quaternary alluvium and most soils are derived from limestone (Rawling et al. 2008).

Maps prepared by the U.S. Forest Service (USFS 2000) of butterfly habitat were used to select recently occupied meadows within the Sacramento Ranger District. Field data were gathered in three meadow canyons within a single 1 km x 20 m grid plot in each meadow, capturing the meadow's edge, side, and center. Meadow centers were defined by the lowest point in the drainage that remained relatively level and generally formed a linear transect from three to eight meters wide. Meadow sides began as slopes

formed on either side of the drainage which then continued until approximately three-five meters from tree-line, which became the edge zone. Thus each habitat zone comprised roughly one-third of the habitat area, although the meadows varied in aspect, size, and shape.

The three study meadows consisted of Lower Bailey Canyon (Bailey), Silver Springs Canyon (Silver), and Zinker Canyon (Zinker). Bailey ran north to south, was approximately 1.5 km long, ranged from 20 m to 80 m wide, and had the narrowest width for the most extended portion. Silver was roughly 2.5 km long and ran from southeast to northwest with an extended wide stretch that relegated the side and edge to only one side for about a 200 m portion. Zinker was approximately two km long and was L-shaped, with the lower part oriented from north to south and the upper part oriented from east to west. Zinker had a width ranging from 60 m to 20 m. Each meadow had a dirt road situated between the side and edge habitats running parallel to the meadow's length. The three meadows were each located from 4 to 8 km apart (Figure 2). Meadow elevations ranged within 8200-8700 feet (each meadow had a gradient of elevation within the 1000 m transect). Meadows were situated in a naturally open drainage area surrounded by a dense matrix of aspen and mixed conifer woodland.

After the oviposition period, the 1000 x 20 m grid transect established in each meadow was divided into five 100 x 20 m grid plots starting at 0, 200, 400, 600, and 800 m locations. Within each 100 x 20 m grid plot, every *P. neomexicanus* plant was examined for eggs, hatched larvae, or tents, and plant and patch features, as well as evidence of disturbance, were recorded. The five grid plots per meadow captured at least one edge, side, and center meadow region. For 2004, the size of the subgrid sampled was 20 m x 20 m, at the beginning of each grid plot. In 2005, the plot size was increased to 20 m wide x 100 m long. The probability of detecting *P. neomexicanus* plants, gopher mounds, and *E.a. cloudcrofti* eggs, larvae, and adults was consistent across sites, with equal amounts of observer time and spatial coverage of meadows.

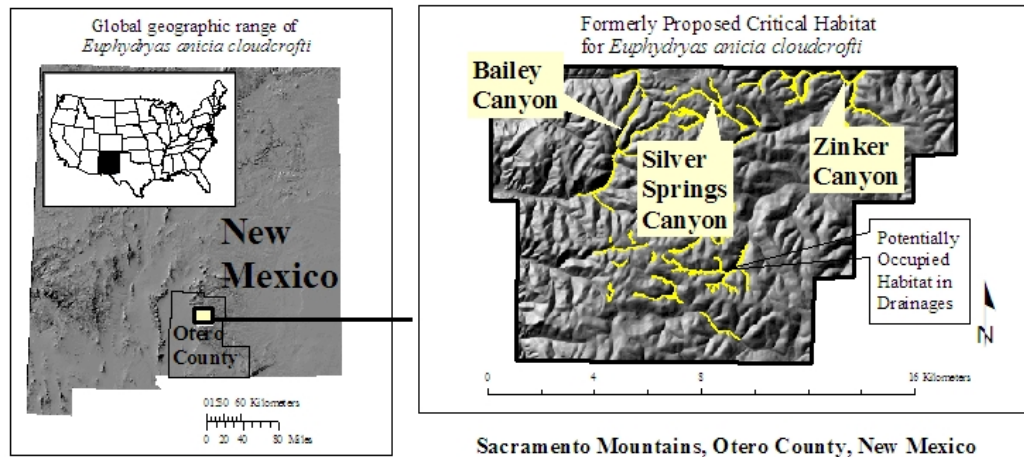


Figure 2. Global range of *Euphydryas anicia cloudcrofti*. Closest conspecifics inhabit mountainous areas in northern New Mexico. *Euphydryas a. chuskae* inhabits San Juan County, and an un-named subspecies is found in Mora County, but the genetic relationships among these subspecies and *cloudcrofti* to other *anicia* are unclear.

Larval and ungulate herbivory had distinctively different patterns of herbivory. Ungulate herbivory was distinguished by an even clip of a *P. neomexicanus* stem, whereas larval herbivory skeletonized the leaves and was typically found with frass or silken material. The Sacramento Mountains support a large population of Rocky Mountain elk (*Cervus elephus nelsoni*) that was several thousand elk higher than the optimal management goal (for Unit 34) of the New Mexico Department of Game and Fish (NMDGF) during 2005. While evidence of ungulate grazing could not be attributed to elk with total certainty, elk were continually seen over the course of the study in each meadow, while not a single deer or deer fecal pellet was detected.

Field data collected in 2004 comprised a pilot study and covered the same habitat areas but with 1/5 of the sampling intensity for *P. neomexicanus* as the data for 2005. Nevertheless, 2004 data were useful for supporting broader trends and were analyzed separately and together with 2005 data (2004+2005) when similar types of data collection were employed. Because larvae and tents develop from eggs and masses within two weeks, egg masses and the resulting communal larval tents were lumped together (tent+mass) during 2004 and 2005, and the number of larvae per host plant and the number of eggs per mass were also pooled (larvae+eggs) for 2005 to simplify the

statistical analyses. Analyses were performed using each *P. neomexicanus* plant as an independent sample based on the perspective of the ovipositing female *E. a. cloudcrofti* as she assessed potential host plants. Non-parametric Spearman rank correlation coefficients were used to investigate relationships among abundances of *E. a. cloudcrofti*, *P. neomexicanus*, gopher mounds and other soil disturbance, and elk grazing within three meadow canyons of the Sacramento Mountains. Categorical count data were analyzed by use of Chi Square contingency tables to assess the probabilities of interactions between certain features for 2004 and 2005 data. Both tests were performed at the 0.05 level using SAS (2001).

Results

Host plant/butterfly relationships

The distribution of *P. neomexicanus* plants varied among canyons, dominating the edge habitats in Bailey Canyon, while favoring the side habitats in Silver Springs and Zinker Canyons (Table 1- Appendix). For both 2004 and 2005, most *P. neomexicanus* plants and immature *E. a. cloudcrofti* were found in Bailey Canyon. The distribution of tents+masses and larvae+eggs with *P. neomexicanus* across all three meadows and the three habitats (center, side, edge) was not significantly correlated. However, at a finer level of meadow division throughout the three meadows, significant correlations were apparent (for tents+masses: $N = 41$, $R = 0.43448$, $P = 0.0045$; for larvae+eggs: $N = 41$, $R = 0.40035$, $P = 0.0095$). The maximum number of tents counted on a single *P. neomexicanus* was 11 in 2004 and 13 in 2005. Although tents were most abundant on *P. neomexicanus* host plants growing along meadow edges in 2005, edge host plants had the lowest mean density of larvae (21 larvae/tent) compared to the center (98 larvae/tent) and side habitats (mean = 73 larvae/tent). Strong differences in *P. neomexicanus* distribution with and without *E. a. cloudcrofti* were apparent among center, side, and edge habitat zones (for 2004: $X^2 = 5.8058$, $P = 0.0549$; for 2005: $X^2 = 12.8141$, $P = 0.0016$; for 2004+2005: $X^2 = 12.8633$, $P = 0.0016$) (Figure 3). In 2004, notably fewer tents or masses were located in the edge habitat compared to the center or side. In 2005, significant differences were due to more tents+masses found in the edge habitat (15 tents+masses) than at the sides (3 tents+masses) or centers (7 tents+masses). With 2004+2005 data,

statistical significance is more likely a result of the most tents+masses found in the center (22) where the fewest *P. neomexicanus* overall were growing (465) (Table 2 – Appendix).

Host plant/gopher relationships

Penstemon neomexicanus abundance and distribution on gopher mounds matched gopher mound availability and remained consistent from 2004 to 2005 in the three meadows. The side habitats had both the greatest number of *P. neomexicanus* growing with mounds and most *P. neomexicanus* growing in any type of disturbed soil. Association with other types of soil disturbance, such as erosion and road disturbance, occurred mainly at the edges of the meadows. In the center, most *P. neomexicanus* associated with disturbed soil were growing with gopher mounds. Among the canyons, gopher soil disturbance was most prevalent in Silver Springs, and least common in Bailey. *Penstemon neomexicanus* plants found on soils disturbed by roads, erosion, or paths were over 9 times as prevalent in Bailey (64%) than in Zinker (7%) and 3 times more common than in Silver Springs (18%). Overall, collective soil disturbance occurred with 70% of *P. neomexicanus* in Zinker, 95% in Bailey, and 98% in Silver Springs. Significant correlations occurred between *P. neomexicanus* and gopher soil disturbance only at finer-grained divisions of sampling during 2004 (N = 14, R = 0.86329, P <0.0001), 2005 (N = 41, R = 0.65519, P <0.0001), and 2004+2005 (N = 41, R = 0.66713, P <0.0001), but also with overall soil disturbance in 2004 (N = 14, R = 1.000, P <0.0001), 2005 (N = 40, R = 0.99225, P <0.0001), and 2004+2005 (N = 41, R = 0.95891, P <0.0001) (Figure 3).

Butterfly/gopher relationships

Significant differences between the presence or absence of gopher soil disturbance and the butterfly in 2004 were driven by the greater proportion of tents+masses on gopher mounds than on non-mounds. Overall, over twice as many tents were found on disturbed soils as on undisturbed soils during 2004. In 2005, differences between the presence of non-gopher soil disturbance and tents+masses were highly significant, owing to the greater proportion of tents on *P. neomexicanus* associated with road and erosion disturbance than with other soil types (Figure 4, Table 2). From

combined 2004+2005 data, non-gopher soil disturbance revealed differences with tent+mass presence (Table 2), but effects of gopher disturbance were likely swamped by road effects from the larger 2005 data set and were not significant with tent+mass interactions.

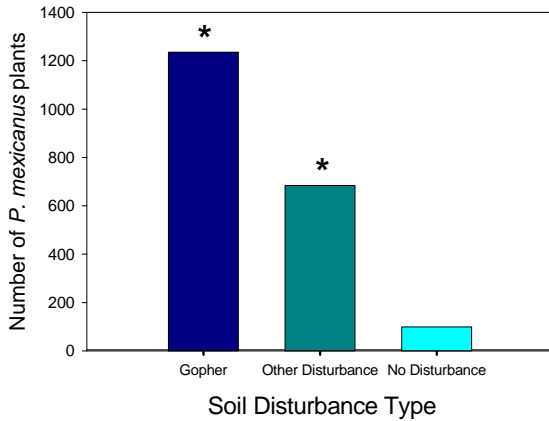


Figure 3. Number of *Penstemon neomexicanus* growing in different soil disturbance types, with significant correlations between gopher and other disturbance.

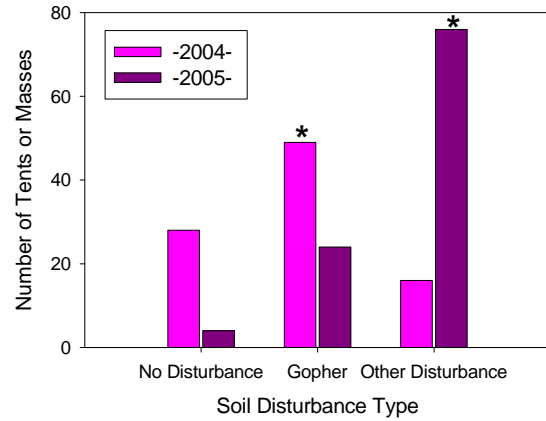


Figure 4. Number of larval tents and egg masses on disturbed soils during 2004 and 2005. Significant correlations were found with gopher and other

The density of larvae and eggs was lowest on *P. neomexicanus* in non-gopher disturbed soil along edges, and highest in gopher disturbed soil in the center of meadows (Figures 5, 6). Eggs and larvae together were significantly correlated only with non-gopher soil disturbance ($N = 41$, $R = 0.37466$, $P = 0.0158$) (Figure 6). *Penstemon neomexicanus* growing in non-gopher disturbed soil averaged 19 individuals/mass or tent at the edge, 70/mass or tent at the sides, and 61/mass or tent in the center. *Penstemon neomexicanus* growing on gopher mounds supported 114 eggs/mass or larvae/tent in the center compared to 27 eggs/mass or larvae/tent at the sides and 40 eggs/mass or larvae/tent at the edge. The side habitats had greater densities of eggs and larvae on non-gopher disturbed soil than on gopher mounds, with an average of 47 eggs/mass or larvae/tent.

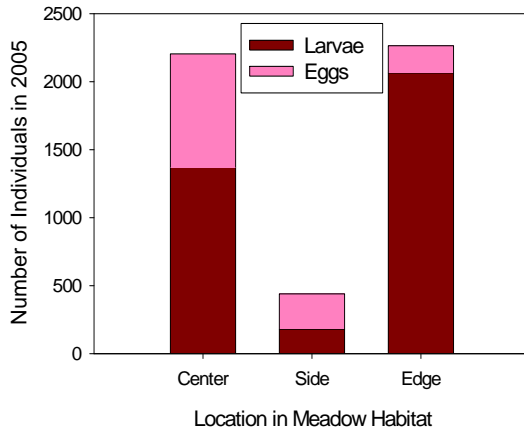


Figure 5. 2005 larvae and eggs by location in meadow habitat. Meadow centers had more eggs than sides or edges.

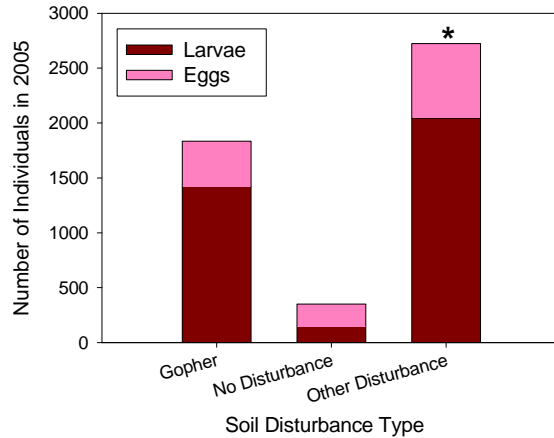


Figure 6. 2005 larvae and eggs on soil disturbance type. Although more larvae and eggs were associated with non-gopher soil disturbance than with gopher disturbance in 2005, the density of eggs/mass and larvae/tent was highest on gopher soil disturbance compared to other substrates.

Host plant/elk relationships

Approximately 36% of all *P. neomexicanus* plants encountered during 2004, and 37% of those in 2005 within the three study meadows, showed signs of herbivory. Of a total of 2014 *P. neomexicanus* plants with elk grazing data in 2005, 1275 were ungrazed and 739 were grazed. During both years, *P. neomexicanus* plants were consumed preferentially at the sides of meadows, followed by the center, and lastly the edge (Figure 7).

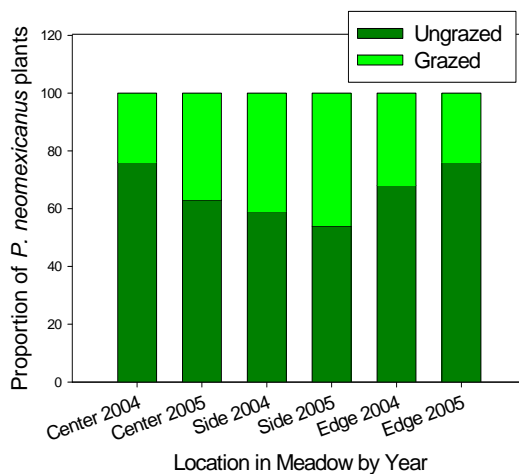


Figure 7. Number of *P. neomexicanus* plants grazed in center, side, and edge meadow habitats.

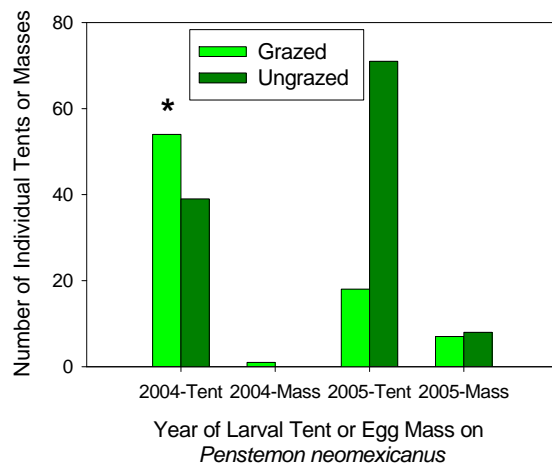


Figure 8. Immature *Euphydryas anicia cloudcrofti* and grazing by year.

Even after grazing occurred, an average of 19% of a grazed penstemon's number of stems remained on a plant. Of *P. neomexicanus* plants still in the rosette stage, 31 of 854 rosettes recorded in 2005 were grazed (amounting to <4% of all rosettes grazed). Given that the relatively flat rosettes seldom experienced grazing, subtracting rosettes showed that 60% of all *P. neomexicanus* plants with stems experienced some elk grazing. On average, *P. neomexicanus* in Bailey had 0.7 stems/plant, in Zinker had 1.3 stems/plant, and in Silver Springs had 1.9 stems/plant. Bailey, the meadow with the greatest number of tents+masses, had the fewest stems grazed per plant, the most rosettes, and the lowest levels of grazing. *P. neomexicanus* found in Silver Springs and Zinker averaged a larger size, in terms of stem number, suggesting more mature plants to select from during oviposition, but experienced higher levels of grazing.

Butterfly/host plant/elk relationships

Consumption of *P. neomexicanus* by ungulates revealed significant associations with tents+masses in 2004, but not in 2005 or in 2004+2005 (Figure 8, Table 2). During 2004 alone, the numbers of tents+ masses were positively correlated with grazing at the side (N = 206, R = 0.14738, P = 0.0345) and edge (N = 69, R = 0.30142, P = 0.0118) habitats, but not the meadow centers. Although not correlated with plants or stems grazed in 2005, the number of tents+masses was positively correlated with the number of stems per *P. neomexicanus* plant for the centers (N = 392, R = 0.10522, P = 0.0373) and edges (N = 703, R = 0.15322, P <0.0001), but was not significantly correlated for the sides (N = 920, R = 0.00879, P = 0.7900) of meadows. Differences among meadow habitat types were due to far more *P. neomexicanus* being grazed in the side habitats than the center, with the lowest levels of grazing on the edge for 2004+2005 data combined.

Host plant/elk/gopher relationships

Wild ungulates consumed *P. neomexicanus* growing on disturbed soils in greater quantity than *P. neomexicanus* growing in undisturbed soils (Figure 9). Most *P. neomexicanus* consumption took place in association with gopher mound disturbance, quantified by both number of plants grazed and number of stems grazed. In 2004, 2005, and 2004+2005 combined, highly significant differences occurred between grazing and gopher mounds, with elk consuming *P. neomexicanus* growing on soil disturbed by

gopher activities at greater proportions than on other substrates measured (Table 2). By year, grazing was positively correlated with gopher mounds in 2004, 2005, 2004+2005 throughout the range of the three meadows (2004: N = 355, R = 0.19846, P = 0.0002; 2005: N = 2011, R = 0.13878, P <0.0001; 2004+2005: N = 2367, R = 0.15155, P <0.0001). In 2004, 2005, and 2004+2005, grazing was also positively correlated with all soil disturbance over all meadows (2004: N = 355, R = 0.20954, P <0.0001; 2005: N = 2011, R = 0.04526, P = 0.0337; 2004+2005: N = 2367, R = 0.06241, P = 0.0024) and negatively correlated with non-gopher soil disturbance in 2005 (N = 2011, R = -0.12556, P <0.00010) and in 2004+2005 (N = 2367, R = -0.11892, P <0.0001). Mound age, ranked in three categories (new, medium, old), was not a statistically significant factor in terms of *P. neomexicanus* selected for grazing (P = 0.1926) However, *P. neomexicanus* was found most often on medium-aged mounds (50%), followed by old (36%), and then new mounds (14%), with new mounds having the highest proportion of grazed to ungrazed plants.

The total number of stems grazed on each *P. neomexicanus* plant, measured solely in 2005, was positively correlated only with gopher mounds (N = 2015, R = 0.14259, P <0.0001) and was negatively correlated with non-gopher soil disturbance (N = 2015, R = -0.12256, P <0.0001) over all canyons. Gopher mounds supported the greatest amount of total stems per *P. neomexicanus* plant, providing habitat for an average of 1.5 stems/plant, compared with 1.2 for *P. neomexicanus* growing with no soil disturbance, 1.1 for disturbance from roads, paths, or erosion, and 1.4 for all soil disturbance types collectively. Grazed stems per *P. neomexicanus* plant were also correlated with all soil disturbance combined (N = 2015, R = 0.06487, P = 0.0036). Correlations between the total number of stems per *P. neomexicanus* plant and gopher soil disturbance (N = 2015, R = 0.14259, P <0.0001) and all soil disturbance (N = 2015, R = 0.04526, P = 0.0422) were positively significant, while stem total was negatively correlated with non-gopher disturbed soil (N = 2015, R = -0.15450, P <0.0001), suggesting that *P. neomexicanus* plants growing in soil disturbed by gophers have more stems per plant.

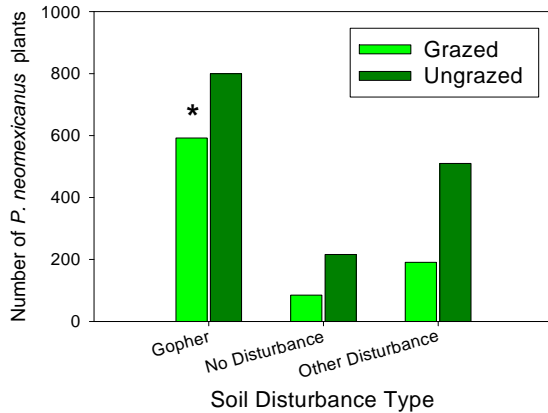


Figure 9. Number of *P. neomexicanus* grazed while growing in different soil disturbance types during 2004 and 2005. Elk grazed on *P. neomexicanus* growing on gopher disturbance significantly more than on *P. neomexicanus* associated with non-gopher disturbance types.

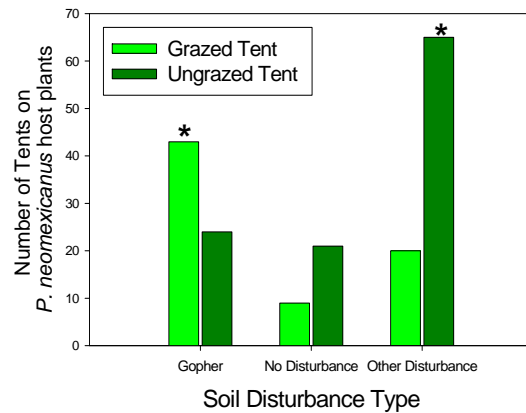


Figure 10. Number of *E. a. cloudcrofti* larval tents on *P. neomexicanus* grazed by elk while growing in different types of soil during 2004 and 2005. Tents on gopher mounds received more grazing than tents in other soil types.

Butterfly/host plant/elk/gopher relationships

The interaction among the butterfly, gopher soil disturbance, and elk herbivory via *P. neomexicanus* host plant was significant for 2004+2005 data, but not for 2004 or 2005 (Table 2). Although relationships were not statistically significant, 2004 counts had the largest proportion of host plants with eggs or larvae growing in gopher disturbed soil and grazed upon by wild ungulates. Patterns for 2004+2005 showed the butterfly more likely to occur on host plants that were either not on gopher mounds and ungrazed or on gopher mounds and grazed (Figure 10). Omitting larval and egg locations not on gopher soil disturbance and not grazed for 2004+2005, when grazing did occur, elk selected for *P. neomexicanus* growing on gopher-disturbed substrates rather than non-gopher disturbed soils. Measured by ranked age of gopher soil disturbance, 61% of eggs and larvae were found on *P. neomexicanus* in intermediate degrees of soil disturbance, followed by 22% on new soil disturbance, and 18% on old soil disturbance.

Discussion

This study captured the strong associations of *Euphydryas anicia cloudcrofti* with soil disturbance and the occasional affiliation with gopher soil disturbance and elk grazing. Statistically significant associations were apparent when both gopher soil disturbance and elk grazing occurred with a *Penstemon neomexicanus* plant hosting

larvae or eggs, based on stronger presence with both ungrazed/non-gopher soils and grazed/gopher mounds. The most dominant relationship uncovered in this study, however, was between elk and gopher, via preferential grazing on *P. neomexicanus* plants growing on gopher mounds. Given the small sample size of host plants with larvae and the scope of three meadows in two years, interactions that were not statistically significant might prove to be significant in a larger study with more spatial and temporal data, and provide more insight into this system.

Host plants and gopher soil disturbance

At all scales examined, *P. neomexicanus* was strongly associated with all types of soil disturbance, with over 95% of all *P. neomexicanus* sampled occurring in disturbed soils. Although gopher disturbance was the most prevalent type of soil disturbance, comprising 64% of disturbed soil associations over 2004 and 2005, significant relationships between *P. neomexicanus* and gopher soil disturbance were detected only at tightly partitioned, localized scales. Recent road disturbance, with associated steep embankments, open strips of soil disturbance, and erosion, may have slanted the impacts of soil disturbance toward road edges in 2005. The matched spatial distribution of *P. neomexicanus* and gopher soil disturbance within meadows suggests that the plant and mammal may seek similar conditions, dictated by soil texture and drainage properties, presence of roots, rocks, and litter, and preference for sunlight (Hansen and Beck 1968, Davis et al. 1995). Other *Penstemon* species growing in bare soils associated with pocket gophers have had higher rates of *Penstemon* survivorship, growth, and reproduction compared to *Penstemon* growing in crowded situations (Davis et al. 1991, Davis et al. 1995). *Penstemon neomexicanus* has a broader range distribution than the butterfly, possibly a result of a wider spectrum of adaptive conditions, such as mechanisms of soil disturbance. Although *P. neomexicanus* exhibited patterns shared by gopher mound availability, the lack of statistical correlation with gopher soil disturbance at larger scales, across meadows and habitats, suggests that the effects of gopher disturbance in particular, may not be as important as the overall availability of disturbed soil throughout the habitat for *P. neomexicanus*.

Butterfly and gopher soil disturbance

Soil disturbance strongly influenced the location of *E. a. cloudcrofti* eggs and larvae throughout the meadows during both years, but an association with gopher mounds in particular was detected only in the first year of this study. A more accurate portrayal of natural meadow interactions may have occurred in 2004, before road maintenance effects were detectable, which likely swamped out more natural, long-term interactions with gopher soil disturbance in 2005. The lack of association with specific types of soil disturbance may reflect the butterfly's adaptation to an array of soil disturbance mechanisms.

Of the soil types, gopher mounds appeared to sustain the highest density of individuals in both tents and egg masses. Gopher digging may extend more deeply into the soil layers, functioning to mix deeper nutrient-rich soils with surface soils containing organic material and enhance infiltration (Grant et al. 1980). Furthermore, egg and larval density was highest on gopher mounds in meadow centers, where the deepest and possibly most fertile soils likely have accumulated. This suggests there may be other benefits offered by gopher foraging trails, mound excavations, and herbivory, such as higher nutrient content or enhanced microclimate properties selected by ovipositing females. Contrastingly, egg and larval density was lowest on non-gopher soil at meadow edges, suggesting a safer or more nurturing environment with gopher mounds and away from edges. The slightly cooler temperatures and increased moisture of drainages may have provided more available soil moisture for host plants and altered plant phenology, or facilitated milder temperature and moisture ranges than edge areas, with greater survival of eggs and larvae, as found with studies of *Euphydryas editha* (Murphy et al. 2004). Soil structure itself may be more evenly distributed and stable once created by gopher activity compared to a more constantly dynamic soil arrangement formed by active erosion or animal trails that could be disruptive to eggs or larvae. Overall, *E. a. cloudcrofti* may be more dependent on gopher disturbance than these data suggest, but eggs or larvae may experience mortality from incidental gopher consumption or mechanical disruption of host *P. neomexicanus* before this is observed.

Host plants and elk grazing

The impact of elk grazing on the *P. neomexicanus* was far greater when measured in terms of number of stems grazed (60% overall) than when measured by percent of overall *P. neomexicanus* plants grazed (37%). In a separate calculation, the proportion of *P. neomexicanus* grazed rose substantially, from 37% to 60%, when rosettes were subtracted from available forage. The 60% of stems and 60% of *P. neomexicanus* plants consumed exceeds the 30-40% forage utilization range, associated with moderate-intensity grazing, which is the management goal for grazing levels in butterfly habitat (USFWS 2009). As *P. neomexicanus* phenology begins in the rosette stage and generally bolts after a year or more (average time spent as a rosette in the butterfly's range is unknown), the larger proportion of rosettes in Bailey Canyon signified a system more recently disturbed or one maintained at earlier seral stages than *P. neomexicanus* in Silver and Zinker Canyons. The statistically significant relationships between *P. neomexicanus* and elk grazing detected within habitats and across meadows suggest that *P. neomexicanus* may be selected as a preferred forage species wherever it is growing.

Butterfly and elk grazing

Obtaining an accurate assessment of the butterfly in relation to grazing was tricky, due to the uncertainty of knowing how many larvae might have been consumed along with evidence of *P. neomexicanus* grazing. Thus this resource-mediated interaction between immature *E. a. cloudcrofti* and grazing as measured by plant and stem consumption may not be the best way to capture grazing effects. But significant herbivory upon *P. neomexicanus* with larvae in 2004 suggested that plants selected for oviposition also may be selected for grazing. Cues enticing to females for oviposition could be perceived by elk grazers as well, including a plant's nutritional value, water content, plant size, leaf color, chemical composition, and surrounding habitat placement (Rausher 1981, Thompson and Pellmyr 1991, Floater and Zalucki 2000, Nieminen et al. 2003, Prudic et al 2005, Talsma et al. 2008). Lack of an association between grazing and immature forms of the butterfly in 2005 could have been the result of the penstemon's phenological stage, other morphological or environmental cues, or a glimpse into the changing or random nature of elk herbivory from year to year.

The dominance of grazing at the sides, then centers, and lastly edges, could have implications within Bailey Canyon, where the vast majority of immature *E. a. cloudcrofti* were located in edge habitats. Along these edges, eggs and larvae may have survived and been more plentiful as a result of less elk grazing. Meadow sides experienced the most grazing and harbored the fewest immature *E. a. cloudcrofti*, possibly the aftermath of twice the level of elk grazing compared to grazing along the edge. Elk grazing prior to oviposition by female *E. a. cloudcrofti*, could have modified consumed *P. neomexicanus* plants in a way that influenced oviposition, possibly corroborating the lack of correlation between eggs and larvae on grazed plants during 2005. Of the meadows, Bailey Canyon exhibited the least amount of *P. neomexicanus* grazing, the greatest proportion of rosettes, and the smallest average *P. neomexicanus* plant size. Bailey Canyon is the closest to a major highway, and its high degree of human presence may decrease its appeal to wild grazers and ultimately benefit the butterfly. Evidence of heavier grazing pressure in Silver Springs and Zinker Canyons may have been due to their more remote locations. Moreover, grazed *P. neomexicanus* appeared to have more stems, with a greater proportion of those stems consumed in Silver Springs and Zinker Canyons. Higher levels of grazing in these two canyons could account for the very few eggs and larvae located in these canyons, but this study lacks direct evidence of this relationship.

Three possible scenarios of elk grazing and butterfly interactions are apparent based on the conflicting results of 2004 and 2005. These are: 1) elk are randomly grazing among all grasses and forbs within the meadows; 2) elk are selecting for *P. neomexicanus*, but not for those particular host plants used by the butterfly; and 3) elk prefer *P. neomexicanus* plants with eggs or larvae. The first scenario would directly impact the butterfly the least, but would depend on overall grazing intensity and climate. The second scenario could have negative effects on the butterfly if *P. neomexicanus* abundance was low and elk grazing levels were high. Elk selecting specifically to consume plants hosting eggs or larvae would be detrimental to the butterfly both in terms of incidentally eaten individuals and lost host plant biomass for food and shelter for the remaining butterfly individuals. Relatively few studies have investigated effects of native wild ungulates on butterflies, as most grazing-butterfly studies have been conducted with

livestock, and may not be directly applicable to natural, montane systems. Reduction of egg-laying sites due to wild ungulate herbivory, as documented by muntjac deer selectively browsing on the honeysuckle host plant, has been associated with the decline of the white admiral butterfly (*Ladoga camilla*) of western Europe (Pollard and Cooke 1994). Grazing exclosure studies of red deer in Scotland and of wild ungulates (using elk exclosures) in mountains of the Southwestern U.S. have found reduced grazing to promote greater overall lepidopteran abundance, based on the increased availability of forb biomass or vegetative structural complexity over the short term (Baines et al. 1994, Rambo and Faeth 1999, Kleintjes et al. 2007).

Immediate impacts of larval abundance on grazed host plants must be balanced with more long-term, landscape-level effects of wild ungulate grazing that help maintain open meadows and early successional conditions. Most butterfly species of temperate regions, particularly endemic species, are dependent on successional stages sustained by natural disturbance regimes (Bergman 2001). Up to 75% of resident butterfly species in Great Britain depend on these open areas that provide optimal states for greatest species richness and structural diversity (Feber et al. 2001). Because some natural disturbance events, such as fire or insect outbreak, are actively minimized in many butterfly habitats, host plants dependent on early successional stages may rely on wild ungulate grazing to perform the function of reducing vegetative biomass and preventing tree encroachment into open areas (Bergman 2001). Deer grazing in Scotland was found to be important in supporting the threatened pearl-bordered fritillary (*Pteridium aquilinum*) because deer controlled advancement of trees and maintained open areas and varied edge habitats (Feber et al. 2001). For *E. a. cloudcrofti*, the mixed effects of elk grazing between years show a dynamic picture of interaction temporally and spatially. At scales of the natal host plant and surrounding *P. neomexicanus* patch during the year of a butterfly's lifetime, herbivory may be detrimental by consuming eggs or larvae or by removing needed host plant biomass. Yet at scales across landscapes and decades, wild ungulate grazing may be a key mechanism for slowing down natural regeneration and meadow take-over by alpine forest. In either case, this analysis is not capable of quantifying these effects, and more work is needed over the long term to address the influence of grazing on the butterfly.

Host plants, gopher soil disturbance, and elk grazing

Elk were more likely to graze on *P. neomexicanus* associated with gopher mounds as opposed to non-mound areas, including other soil disturbance. This significant trend was evident using both *P. neomexicanus* plants and stems as gauges of grazing intensity, for gopher mounds also supported the greatest amount of total stems per *P. neomexicanus* plant. As mounds appeared to produce larger *P. neomexicanus* plants, perhaps this was an invitation for more grazing. Soil textures, nutrients, and microhabitats on mounds may offer conditions that enhance *P. neomexicanus* growth, and that possibly promote higher nutritional value, fewer alkaloids, and more flowers. Mammalian herbivores (bison, cattle, rabbits) select for plants growing in nutrient-rich spots compared to surrounding plants, due to greater inputs of nitrogen in small soil patches (Day and Detling 1990, Jaramillo and Detling 1992, Steinauer and Collins 1995, Denyer et al. 2007). In a partially water-limited system, increased infiltration in gopher-tilled soils could make a notable difference in *P. neomexicanus* growth to elk grazers in the Sacramento Mountains. The surrounding exposed soil may diminish competition with other adjacent plants for water or nutrients as well as make the presence and condition of individual *P. neomexicanus* plants more visible to both butterflies looking to oviposit and elk. The invasion of an exotic grass decreased host plant apparency for the endangered Fender's blue butterfly, *Icaricia icarioides fenderi*, and may have been responsible for the overloading of eggs on host plants that were more conspicuous (Severns 2008). Positive correlations across and within meadows were found between *P. neomexicanus* grazing and gopher disturbance, but not between grazed plants and other types of disturbance excluding gopher disturbance, which indicates that *P. neomexicanus* may be more edible on mounds compared to other substrates.

Gopher mounds provided the disturbance habitat for the greatest number of ungrazed *P. neomexicanus*, confounding the positive relationship between mounds and increased grazing, and possibly relating the grazing preference of gopher mounds to an outcome of overall availability. The age of gopher mounds, although not statistically associated with grazing, can affect plant recolonization (Forbis et al. 2004), and may have been a source of variation in grazing due to the different soil properties and time lag

for vegetative response after disturbance. Within new, intermediate, and old rankings of time elapsed since gopher disturbance, the middle level of time ascribed to mounds supported the greatest number of *P. neomexicanus* noted and grazed. This intermediate mound age, not freshly disturbed but not older with a flattened surface and plant encroachment, appeared to represent the most ideal conditions for *P. neomexicanus* growth. Thus, both gopher soil disturbance and elk herbivory may have long-lasting effects on perennial plants, including *P. neomexicanus*.

In a similar interaction between bison and prairie dog colonies, bison spent proportionally more time on the far smaller areas associated with disturbed prairie dog colonies than in surrounding grasslands (Coppock et al. 1983). Consumption rates by prairie dogs, bison, pronghorn antelope, and elk have been over twice as high on vegetation associated with prairie dog colonies than in uncolonized, native grasslands (Whicker and Detling 1988). Prairie dogs foraged more in areas where bison had been, suggestive of a mutualistic relationship in prairie grasslands (Krueger 1986). Enhanced grazing of vegetation on prairie dog colonies has been attributed to greater nitrogen content than found in off-colony vegetation related to available nitrogen content in the soil (Coppock et al. 1983, Reichman 1988). Biotic disturbance by gophers changes the water content and organic matter in soils, and disperses minerals more evenly within the disturbed areas, supporting a succession of plants through time (Grant et al. 1980, Huntley and Inouye 1988, Huntley 1991, Reichman and Seabloom 2002). Despite biological differences in prairie dog sociality versus the solitary, territorial nature of gophers, their engineering impacts are similar, as is the capacity for feedback systems of creating habitat that promotes plants preferred by gophers or other herbivores (Seabloom and Richards 2003). At a smaller scale, altered plant chemistry, instigated by gopher consumption of roots or even larval consumption of *P. neomexicanus* leaves, could improve plant palatability to wild grazers (Louda and Collinge 1992). As there has been little work on the response of wild mammalian herbivores to effects of gopher soil disturbance on plant palatability, the result of elk preference for *P. neomexicanus* associated with gopher soil disturbance unveils yet another facet of this complex, interactive environment in which the butterfly persists.

Butterfly, host plants, gopher soil disturbance, and elk grazing

The multitrophic interaction among three herbivores centered on *P. neomexicanus* and two forms of disturbance potentially impacting the butterfly (Figure 1) was significant in 2004+2005 data, but more pronounced in 2004 than in 2005. Eggs and larvae were associated with gopher-disturbed soils and subjected to elk herbivory more than any other condition in 2004. In 2005, however, this multilayered interaction was the least likely situation for eggs and larvae due to most larvae being located in non-gopher disturbed soils on ungrazed host plants along the edge of Bailey Canyon (Table 2). Eggs and larvae were predominantly associated with both ungrazed and non-gopher disturbed *P. neomexicanus* opposed by grazed and gopher-disturbed *P. neomexicanus*, indicating that a diversity of conditions may occur and even provide optimal survival opportunities for this butterfly species.

Conclusions

Interactions involving *Penstemon neomexicanus*, wild herbivores, and soil disturbance processes were impacting this butterfly at a range of spatial and most likely temporal scales. Within the butterfly's natural community, suitable habitat conditions can be influenced by local mammal species via the physical creation of habitat zones, direct interaction with a species, or mediation of interactions with other species. Differences in associations with the variety of soil disturbance processes and grazing levels over two years of field work elucidate the dynamic nature of this system and make future work of exploring long-term trends even more important. Precise effects of gophers, elk, and *P. neomexicanus* upon the butterfly's abundance and distribution are challenging to unravel, however a more detailed investigation of finer dissections of the habitat at a scale potentially meaningful to *E. a. cloudcrofti*, may illuminate processes driving this butterfly's fate.

Effects of interacting disturbances examined may conflict with the welfare of the butterfly, depending on the time frame considered. Short term detriments to the butterfly and its host plant via consumption or destruction by elk or gophers may be balanced by the benefits of providing habitat heterogeneity for plant establishment, and maintaining open meadows and corridors between suitable habitats necessary for the butterfly's

persistence. Overall, the butterfly's habitat should be large enough to permit natural disturbance regimes in a mosaic of different stages of successional responses (Hobbs and Huenneke 1992). As this study has noted, an increase in ungulate grazing may not be beneficial for immature phases, but cumulative moderate to low grazing levels may be sustainable. A reduced or alternated grazing regime, but not gopher soil disturbance, may prove effective for management purposes. Given that non-adult phases of *E. a. cloudcrofti* comprise over 95% of each individual's lifespan, a sustainable habitat must consider ecological processes along with habitat features that promote site occupancy for all life stages to best conserve the species.

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Appendix

Table 1. 2004 and 2005 field data of *E. a. cloudcrofti* and *P. neomexicanus* host plant counts

2004 Number of Individuals								
		CANYONS			HABITATS			TOTAL
Butterfly Stage	Bailey	Silver	Zinker	Center	Side	Edge	Total	
Tent	91	1	0	27	56	9	92	
Egg Mass	1	0	0	1	0	0	1	
Tent+Mass	92	1	0	28	49	10	93	
Penstemon Total	284	85	63	110	247	75	432	
Penstemon Host plants	33	1	0	14	17	3	34	

2005 Number of Individuals								
		CANYONS			HABITATS			TOTAL
Butterfly Stage	Bailey	Silver	Zinker	Center	Side	Edge	Total	
Tent	58	2	0	7	3	50	60	
Egg Mass	8	0	0	5	2	1	8	
Tent+Mass	66	2	0	12	5	51	68	
Egg	650	0	0	420	130	100	650	
Larva	1727	80	0	685	90	1032	1807	
Egg+Larva	2377	80	0	1105	220	1132	2457	
Penstemon Total	800	725	647	391	1029	753	2173	
Penstemon Host plants	23	2	0	7	3	15	25	

Table 2. Results of X² contingency table analysis.

Variables Tested		Chi Square 2-Way Contingency Table Results					
Variable 1	Variable 2	absent - absent	absent - present	present - absent	present - present	X² value	Probability
2004							
Tents+masses	Gopher soil disturbance	194	127	14	20	4.7003	0.0302*
Tents+masses	Non-gopher soil disturbance	321	0	31	3	28.5649	<0.0001*
Tents+masses	All soil disturbance	194	127	11	23	9.9371	0.0016*
Tents+masses	Grazing	225	110	14	20	9.1358	0.0025*
Grazing	Gopher soil disturbance	153	80	55	67	11.4658	0.0002*
Grazing	Non-gopher soil disturbance	232	1	120	2	1.3995	0.2368
Grazing	All soil disturbance	152	81	53	69	15.5866	<0.0001*
Grazing	Gopher with butterfly only	8	6	6	14	2.5049	0.1135
2005		absent - absent	absent - present	present - absent	present - present	X² value	Probability
Tents+masses	Gopher soil disturbance	918	1228	16	9	4.5406	0.0331*
Tents+masses	Non-gopher soil disturbance	1455	691	10	15	8.7035	<0.0032*
Tents+masses	All soil disturbance	59	1935	1	25	0.0928	0.7606
Tents+masses	Grazing	1255	731	18	7	0.8245	0.3639
Grazing	Gopher soil disturbance	558	715	220	518	38.7299	<0.0001*
Grazing	Non-gopher soil disturbance	768	505	537	201	31.7047	<0.0001*
Grazing	All soil disturbance	43	1230	13	725	4.5084	0.0337
Grazing	Gopher with butterfly only	12	4	6	3	0.1984	0.6560
2004+2005		absent - absent	absent - present	present - absent	present - present	X² value	Probability
Tents+masses	Gopher soil disturbance	1112	1355	30	30	0.5738	0.4488
Tents+masses	Non-gopher soil disturbance	1799	688	42	18	0.253	0.6150
Tents+masses	All soil disturbance	292	2023	12	48	2.8589	0.0909
Tents+masses	Grazing	1483	838	33	27	2.0006	0.1572
Grazing	Gopher soil disturbance	714	796	272	585	33.4748	<0.0001*
Grazing	Non-gopher soil disturbance	1011	499	670	187	34.0697	<0.0001*
Grazing	All soil disturbance	215	1295	85	772	9.2189	0.0024*
Grazing	Gopher with butterfly only	20	10	11	17	4.3639	0.0367*

CHAPTER 3:
HOSTPLANT AUGMENTATION AS A RECOVERY STRATEGY FOR THE
SACRAMENTO MOUNTAINS CHECKERSPOT BUTTERFLY

Euphydryas anicia cloudcrofti (Lepidoptera: Nymphalidae)

Introduction

Endemic butterflies with restricted geographic ranges are vulnerable to extinction because they tend to be relatively sedentary and low in numbers, and generally are food and habitat specialists (Ehrlich et al. 1980, Thomas 1988, Gaston 1994). These species breed and fly only in localized zones or suitable habitat patches where their favored climatic conditions and food plants are found (Murphy 1983, Hardy et al. 2007). They persist in classic metapopulations, or dispersed populations, that depend on the size, quality, and connectivity of the habitat to prevent extinction (Ehrlich 1988). Isolated habitats restrict a species' movement by presenting unfavorable conditions between suitable locations, which reduce migration and gene flow among each small, separated colony (Saccheri et al. 1998, Hanski 1999, Krauss et al. 2003), and can lead to population declines (Eichel and Fartmann 2008, Bauerfeind et al. 2009). Without large, connected areas offering diverse successional stages, such butterflies are highly sensitive to habitat loss and fragmentation, human disturbance, environmental change, and, possibly, extinction.

Access to suitable habitat is further restricted when an entire butterfly species is confined to an isolated mountaintop surrounded by inhospitable biomes at lower elevations. This 'mountain island' effect typically limits species that are biological relicts of past climatic conditions or landscape connectivity (Brown 1971). Butterfly natural history traits that likely developed with formerly cooler conditions may further control dispersal, such as having one generation per year (univoltine); a long, overwintering larval period; and a short, dispersing adult phase. These species tend to lay eggs in masses so that populations are clustered and mates are not available outside of the natal area (Stamp 1980), or males may use genital plugs that limit further mating opportunities for females (Ehrlich and Ehrlich 1978). To persist, butterflies on mountaintops must find cooler, moister zones in response to the extrinsic rise in global temperatures or decreased

precipitation, and at the same time they can be restricted by intrinsic biological mechanisms (Boggs and Murphy 1997, Wilson et al. 2007, Merrill et al. 2008).

Climate change is predicted to have serious impacts on mountain island butterfly populations that synchronize their life phases with the phenology, abundance, and distribution of their food plants (McLaughlin et al. 2002, Parmesan 2007). Temperature and moisture affect butterflies directly through their ectothermic physiology, but more strongly indirectly, via the phenology and location of the host and nectar plants (Parmesan 2005). Phenological shifts in plants, such as earlier flowering or senescence, can alter the phase relationship between food plants and butterfly developmental stages, resulting in local butterfly extinctions, as documented with Edith's checkerspot (*Euphydryas editha*) (Parmesan 2005). Numerous plant species have shifted their geographic distributions higher in elevation on mountain slopes at rates ranging from 1 to 29 meters per decade since the early 1900s, and butterflies dependent on those plants also must shift uphill in order to persist (Grabherr et al. 1994, Konvicka et al. 2003, Wilson et al. 2007, Lenoir et al. 2008). Latitudinal shifts have extirpated butterfly species from the southern, warmer parts of their range, decreasing butterfly diversity in these areas (Parmesan 1996, Parmesan 1999, Hill et al. 2002, Parmesan and Yohe 2003, Franco et al. 2006, Merrill et al. 2008). Furthermore, climate-induced species shifts can effectively fragment and shrink suitable habitat and also interact with encroaching human development, producing losses in butterfly resources and individuals, and possibly leading to increased specialization by butterflies of remaining, limited resources (Boggs and Murphy 1997, Hardy et al. 2007, Preston et al. 2008).

Although climate affects all butterfly species, specialist butterflies exhibit a greater sensitivity to hostplant availability and habitat diversity than do generalist butterflies (Ehrlich and Dennis 1987, Menendez et al. 2008). Butterfly species that are larval hostplant specialists tend to be nectar specialists as adults (Tudor et al. 2004, Hardy et al. 2007, McIntyre 2010), so these species need areas that support both larval and adult food plants. Generalist butterfly species, typically more geographically widespread and polyphagous, can exploit broadly distributed hostplants and move with plant shifts and climate change (Braschler and Hill 2007). Continued warming trends are

expected to decrease butterfly species richness, with a disproportionate loss of specialists compared to widespread species (Wilson et al. 2007). Consequently, specialist butterfly species, along with other sensitive pollinators, are declining around the world, partially in response to habitat alteration and climate change (Parmesan 1996, Kearns et al. 1998, Kerr 2001, Hill et al. 2002, New 2008), more so than losses within other wildlife groups recorded during the 20th century (Thomas 1991, Thomas et al. 2004).

Two approaches have been developed to conserve butterfly species believed to be heading toward extinction: population augmentation and habitat or plant community restoration. Butterfly augmentation has involved the relocation of wild-caught or captive reared adults, larvae, or pupae into unoccupied areas containing food plants, with many of these attempts not succeeding (Duffey 1968, Pullin et al. 1995, Pullin 1996). Habitat management or restoration has been employed to enhance declining butterfly populations *in situ* (Thomas 1991, Schultz 2001). Successful projects have included two principal conditions: 1) enough individuals, so that the population can be maintained over time, and 2) available suitable habitat with the combination of characteristics and functions the species depends upon, whether it is within the original locale or a restored landscape (Asher et al. 2004, Vanreusel and Van Dyck 2007). For rare or reintroduced butterflies to survive once released, butterfly population dynamics and necessary environmental features must be integrated, yet little is known about specific habitat requirements for wild butterflies at all life stages.

Early larval stages are the most vulnerable phase of a butterfly's life cycle, often with more specialized or complex habitat needs for eggs and larvae than those of adults (Thomas 1991). Pre-diapause larvae, occurring just after hatching in late summer yet before winter dormancy in the larval stage (diapause), are quite small and relatively immobile. Thus, pre-diapause larvae are highly dependent on the maternal oviposition site and tend to remain on the hostplant for the first few instars. During the first larval instar alone, the chance of mortality ranges from 25 to 75% (Zalucki et al. 2002). Other univoltine butterflies (Pullin et al. 1995; Nicholls and Pullin 2000), as well as *Euphydryas* species (Singer 1972, White 1974), tend to experience the highest levels of mortality during the pre-diapause phase of their life cycle which typically covers the first

four instars. *Euphydryas editha* (Bay checkerspot) studies found 80 – 97% of eggs and pre-diapause larvae to die (Singer 1972, Moore 1989) primarily due to early senescence of their hostplant (Singer 1972). High levels of hostplant defoliation were found to be correlated with high prediapause starvation rates of up to 99% in *Euphydryas editha* populations (White 1974).

In North America, only 5% of butterfly species have larvae that aggregate into groups of at least 10 caterpillars, often formed as a result of eggs laid in clusters (Stamp 1980). Living in groups may be advantageous in terms of facilitating feeding, hastening larval growth (Denno and Benrey 1997), improving thermoregulation, particularly by forming silk tents (Knapp and Casey 1986), and enhancing defensive strategies behaviorally, visually, or chemically (Reavey 1993). For gregarious larvae with restricted mobility, the size and density of hostplants provide a concentrated resource for specialist insects (Root 1973, Dennis et al. 2004). Hostplant resource limitation, however, is based on the availability of nearby hostplants rather than the number of hostplants within an entire meadow (Hanski 1999). Greater hostplant defoliation, leading to intraspecific competition and starvation among prediapause larvae, has been positively associated with increased distance to other hostplants (White 1974). Numerous studies have affirmed the tight relationship between the presence of butterfly species and the spatial availability of their hostplants, based on successful larval development (Ehrlich and Raven 1965, Turchin 1991, Schultz and Dlugosch 1999, Auckland et al. 2004, Krauss et al. 2004, Kuussaari et al. 2004, Kuefler and Haddad 2006, McIntyre 2010, among others). Establishing larval food plants at a scale significant to life stage use may create connectivity and reduce the effects of host plant isolation, particularly for the smaller and more sessile pre-diapause larvae.

The Sacramento Mountains checkerspot butterfly, *Euphydryas anicia cloudcrofti* (Ferris and Holland), is a univoltine, host and nectar plant specialist in the butterfly family Nymphalidae (McIntyre 2010). The butterfly is endemic to an 85km² (33 mi²) area at the top of the Sacramento Mountains of southern New Mexico. Egg-laying and larval feeding occur on primarily on *Penstemon neomexicanus* Woot. & Standl. (Plantaginaceae), which is also a narrow endemic, and less commonly on *Valeriana*

edulis Nutt. ex Torr. & A. Gray (Valerianaceae). Although the butterfly has been petitioned twice for emergency federal listing, it is currently considered a subspecies of concern by the U.S. Fish and Wildlife Service (USFWS 2009). This butterfly is an ideal taxon with which to study the effects of host plant supplementation because it is specific to primarily one host in the early instars of larval development, and its aposematic coloration and limited range and mobility make it easy to identify in the field. Also, *E. a. cloudcrofti* warrants significant conservation interest because of its beneficial function as a pollinator, its high sensitivity to habitat changes, and its status as a Pleistocene relict and globally rare subspecies (USFWS 2005). As such, this subspecies may offer cues to evolutionary conditions of the past along with being a bioindicator of the future in response to a shift in climate and the status of biodiversity.

The purpose of this study was to evaluate the effects of hostplant augmentations as a method for enhancing *E. a. cloudcrofti* to increase its population in occupied habitats or to colonize unoccupied areas without destructive effects (Harrison et al. 1991). In field observations, I noted that a large proportion of the larvae died as a result of starvation on isolated penstemon hostplants, presenting a need for an increased number of adjacent *P. neomexicanus* plants. For the larvae, a hostplant not only provides food, but also offers structure or habitat on which to develop and form communal tents, provides shelter and protection from the elements, and is a locus for congregating with other con-specifics for safety from predators and parasitoids. Growing and transplanting *P. neomexicanus* hostplants could be an effective and practical method of reducing larval mortality without disrupting or handling individual butterflies or larvae. This experiment was designed to test the hypothesis of whether host plant augmentation in the field would result in increased survival of *E. a. cloudcrofti* larvae compared to adjacent controls. Hostplant characteristics and growth positions were measured in relation to larval number and length. Penstemon plants with greater plant volume as well as host plants growing closer to greater numbers of penstemon were predicted to support greater numbers of larvae and larger larvae until diapause. The following questions were specifically addressed:

1. What were the effects of control vs. treatment hostplants on larval number and larval length?

2. What were the effects of isolated (solo) vs. patch hostplants on larval number and length?
3. What were effects of interactions among treatment (T), control (C), patch (P), and solo (S) hostplant conditions on larval number and length?
4. Which plant and patch characteristics were most influential on larval number and length?

Methods

This research was conducted on the Lincoln National Forest in the Sacramento Mountains of Otero County in south-central New Mexico (Figure 1). Long-term (1931-2008) mean annual precipitation is 59.1 centimeters (23.26 inches), about 40% of which occurs during July and August. Long-term mean monthly temperatures for January and July are -1.1°C (30°F) and 15.6°C (60°F), respectively. The Sacramento Mountains represent the southernmost portion of the Rocky Mountain Conifer Forests ecoregion in the U.S. (EPA Ecoregions map 2009). Existing as an isolated high elevation range immediately surrounded by Madrean Lower Montane Woodlands skirted by Chihuahuan desert grasslands, the Sacramento Mountains are approximately 260 km from other mountains to the west, and 120 km from similar mountains to the north (EPA Ecoregions map 2009). Geologically, the area is comprised of the Rio Bonito Member of the Lower and Middle Permian San Andres Formation, as well as the Yeso Formation (Rawling et al. 2008). Drainage bottoms contain Quaternary alluvium, and most soils are derived from limestone (Rawling et al. 2008). Habitat selected by *E. a. cloudcrofti* is characterized by open meadows situated in natural drainages in a landscape of mixed conifer, aspen forest between altitudes of 2375 to 2750 m (7800 to 9000 ft) (USFWS 2004). At any point in time, the butterfly occupies a fraction of the approximately 2,500 acres considered to be potential habitat.

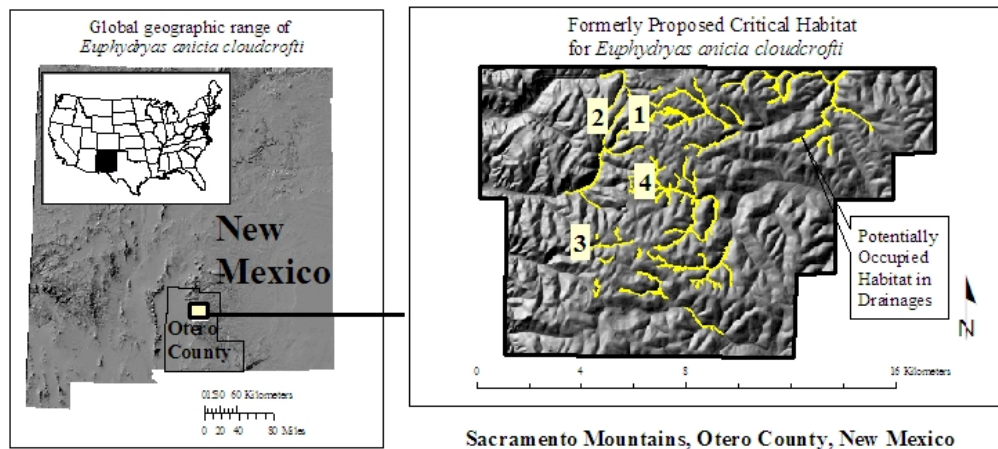


Figure 1. Map of the global range of *Euphydryas anicia cloudcrofti* and the four meadows in this study.

To investigate effects of transplants and penstemon patches on larval number and length, I established study plots in four meadows occupied by *E. a. cloudcrofti* in the Lincoln National Forest. Larval number and length were selected as measurements of a larva's ability to survive, obtain food, and prepare for approaching winter diapause. During August, 2006, a total of 60 naturally occurring penstemon host plants with early instar larvae were located among the 4 meadows (or canyons) and divided into 30 nearby pairs with field conditions as similar as possible. The 4 meadows, numbered in the map above (Figure 1), had the following number of naturally occurring pairs of hostplants: 1) Bailey Meadow = 7 pairs; 2) Bailey Road Canyon = 9 pairs; 3) Deerhead Canyon = 9 pairs; and 4) Pines Campground = 5 pairs.

Within pairs, one penstemon was randomly selected as the treatment hostplant, receiving two transplanted penstemon plants, and the other became the control (Figure 2). The 60 transplanted penstemon plants were placed at 180° apart at a distance of 20 cm from each treatment hostplant when larvae were approximately 5mm long. Isolated penstemon hostplants with larvae, or 'solos,' were defined as those with no other penstemon plants growing within a 3 meter radius. There were fewer penstemon plants with larvae growing as solos than there were growing in natural patches, and this produced an uneven number of patch and solo plants. At each of the 30 paired sites, 4

penstemon plants were sampled: control hostplant, treatment hostplant, and 2 transplants (Figure 2).

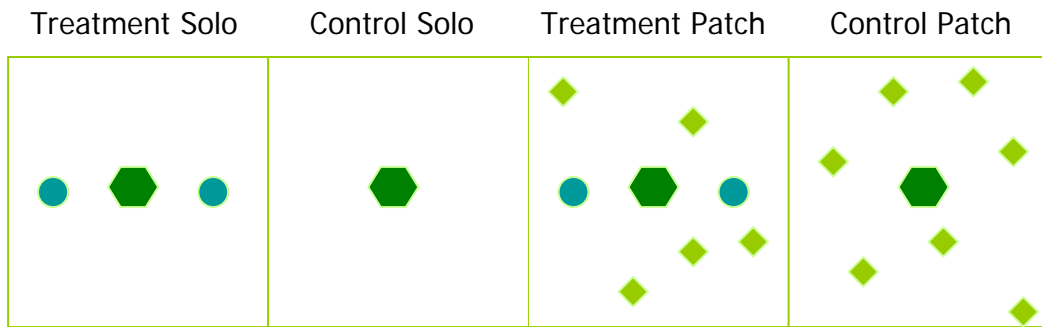


Figure 2. Study design and the four possible field conditions. Hexagons represent the original, natal hostplant with larvae found naturally occurring in the field. Circles represent the two transplanted *P. neomexicanus* plants, and squares represent other *P. neomexicanus* plants naturally occurring as a patch.

On the penstemon, the number of *E. a. cloudcrofti* larvae, average larval length, and larval activities were monitored once every one to two weeks at seven intervals from late August until diapause began at the end of October. In the few cases where larvae were found on the ground between hostplants later in the season and could have been affiliated with either hostplant, larvae were spatially divided using the midpoint between each original hostplant and counted with the closer hostplant. As the season progressed and the larvae grew in size and mobility, larvae up to 3 meters away from the original hostplant for both treatment and control plants were counted. A 3 meter distance was designated because larvae seldom were observed past 3 meters from a study hostplant and larvae at that distance, in a few cases, could have been affiliated with another natal hostplant in the study.

Penstemon transplants were grown from seed collected in the Cloudcroft area and were either rosettes or had flowered for one year. Thirty of the penstemon transplants were transported in pots from the Plant Materials Center in Los Lunas, New Mexico, under the USFWS Partners program, and the other 30 plants were dug up, potted, and replanted from the rare species support garden at Albuquerque Botanical Gardens. Self-contained, temporary, metal cages were placed around each penstemon to protect the host plants, transplants, and controls from deer, elk, and wild horse herbivory, as well as to deter inadvertent human damage from forest visitors. Transplants were watered once per week to help with their establishment. During the following spring, transplanted

penstemon emergence was monitored to determine the success of transplanting penstemon, and any post-diapause larvae in the vicinity were recorded.

Statistical analysis - Analyses were performed using SAS version 9.1 (SAS Institute 2001) and Minitab Statistical Software version 13.1 (Minitab Inc. 2000). Data were tested for normality in SAS univariate using the Shapiro-Wilk test but even after transformation, the majority of the data remained nonparametric, resulting in the use of nonparametric Wilcoxon tests to look at changes throughout the study period and prohibiting use of repeated measures analysis of variance (RMANOVA) tests. Larval abundance and size were compared for treatment and control penstemon and for penstemon occurring as solos or in patches using Wilcoxon-Mann-Whitney tests for the same plants at each of the seven time periods. Paired data of the 30 treatment host plants and the associated controls were analyzed using Wilcoxon Signed Rank tests to determine differences in larval number and size.

Relationships among hostplant variables, involving plant and patch characteristics and larval number and size, were analyzed using stepwise multiple regressions. Pearson and Spearman-rank correlations were used to determine colinearity of penstemon plant and patch variables to ensure independence for regression analysis. Stepwise multiple regressions were performed using SAS, and non-parametric data were \log_{10} transformed for the stepwise procedure. Statistical significance of all analyses was determined using a 95% confidence interval.

Results

Of the 60 penstemon transplants planted in the field adjacent to the 30 treatment hostplants, 59 transplants survived until the hard frost; thus statistical results are based on 58 individuals or 29 pairs (Table 1). All of the transplanted penstemon plants were at least partly consumed if the treatment hostplant was entirely consumed, indicating that larvae were willing to consume adjacent penstemon plants whether the plants were transplanted or naturally present.

Table 1. Totals and means of larvae, hostplants, and hostplant leaves over entire study period, August 26 - October 21.

Larval and Penstemon Data								
	All Treatment	All Control	All Patch	All Solo	Treatment Patch	Treatment Solo	Control Patch	Control Solo
Number of Hostplants	29	9	44	14	22	7	22	7
Mean Number of Larvae / Hostplant	12.55	10.36	12.64	9.81	12.88	12.09	12.81	6.75
Total Larval Count Over All 7 Periods	2297	1824	3079	1042	1378	919	1345	479
Mean Larval Length (mm) / Hostplant	9.05	8.42	8.8	8.6	9.1	9.0	8.8	7.6
Mean Number of Leaves / Hostplant	20.76	22.4	25.43	15.63	22.2	18.58	27.57	14.2
Total Leaf Count Over All 7 Periods	3446	3763	5162	2047	2220	1226	2840	923

Treatment effects

Over all locations and time periods combined, the mean number of larvae was significantly greater for hostplants that received 2 transplants (*treatment*) than on hostplants with no planted transplants (*control*) (treatment mean = 12.55, control mean = 10.35; $W = 6866.5$, $p\text{-value} = 0.015$) (Table 2). However, temporal patterns of larval abundance and larval length in response to additional hostplants were only detected during a few time periods over the continuum of this study. One of the seven time periods, Period 3, exhibited significantly more larvae on the hostplants that received treatments.

Table 2. Larval abundance in response to treatment and control effects.

TREATMENT V. CONTROL						
Variable tested: Larval number (paired)						
Period	Time	Mean for Control	Mean for Treatment	Wilcoxon Rank Sum Statistic (W)	Paired Wilcoxon P-value	
	Period 1	13.20	14.00	126.0	0.502	
	Period 2	16.63	15.11	121.5	0.276	
	Period 3	6.95	15.52	31.5	0.004*	
	Period 4	23.61	22.48	184.5	0.563	
	Period 5	5.79	12.93	103.0	0.067	
	Period 6	3.62	3.22	28.5	0.959	
	Period 7	2.96	3.00	57.0	0.223	
		10.35	12.55	6866.5	0.015*	

* = significant at 0.05 level

In the four meadows combined, both the treatment and control larval numbers increased until 24 September (observation period 4), just before the time of the first hard frost, and then decreased until diapause set in, during mid-late October (Figure 3).

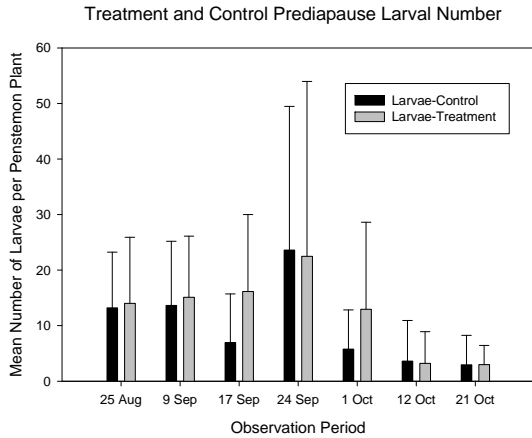


Figure 3. Transplant effect for mean larval abundance from August to October for 4 meadows. Transplants had significant effect when paired control and treatment larvae considered collectively and during the 3rd observation.

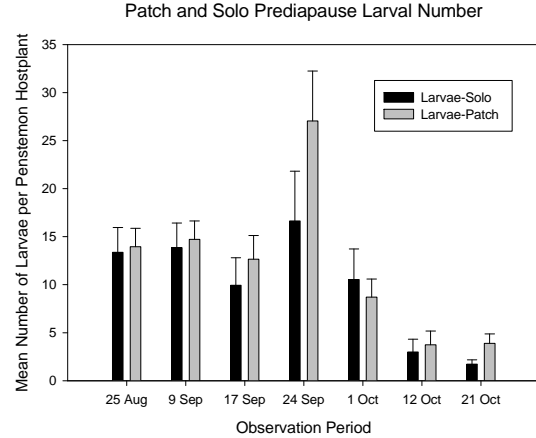


Figure 4. Mean number of larvae counted on each penstemon host plant growing alone and within a patch. A significant difference was found only during the 4th were observation period, dated September 24th (p-value 0.0378, Mann-Whitney Test).

Although penstemon transplants were planted August 26, larvae were not observed using transplant hostplants until the third observation date, September 17 (Figures 5, 6). Use of transplants peaked on October 1 for total larval numbers (Figure 5), but peaked on September 24 in terms of mean larval abundance among all transplants (Figure 6). The mean number of larvae using transplants exceeded that of original treatment and control hostplants after September 24, however the total number of larvae continued to be greater on original treatment and control hostplants until diapause (Figure 6).

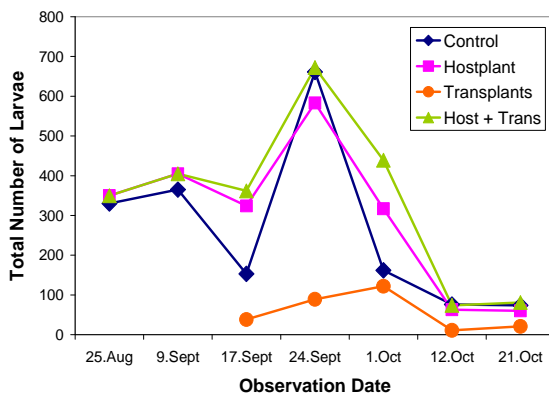


Figure 5. Total number of larvae counted on control hostplants, treatment hostplants, both transplants, and combined treatment hostplants together with the two transplants.

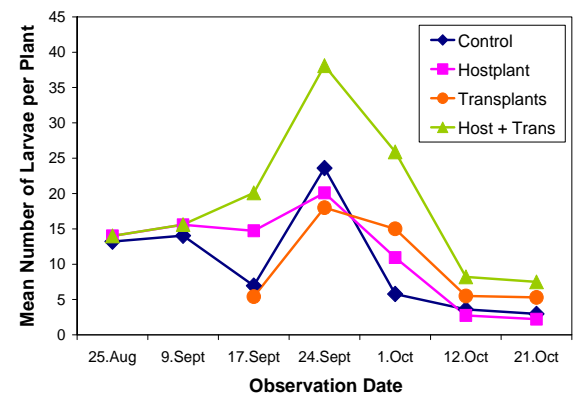


Figure 6. Mean number of larvae counted on control hostplants, treatment hostplants, both transplants, and combined treatment hostplants with the two transplants.

Larval length increased steadily, starting at a mean length of 5.13 mm in late August, and concluding at a mean length of 12.78 mm in mid-late October. The largest

larvae were found in Bailey Meadow, reaching a mean length of 15 mm by October 1. Although larvae associated with treatment penstemon were larger than control larvae during every time period except that of the sixth observation, dated October 12, no significant differences in larval length between treatment and control hostplants were observed over the study period.

Patch effects

Larval abundance over all time periods for all meadows (Figure 4) was greater for patch than solo hostplants collectively, during the biological peak just before frost (Period 4), and when entering into diapause (Period 7) (Table 3). Larvae found on penstemon growing in patches or on solo penstemon were approximately the same size during the course of this study over all meadows. There were uneven numbers of patch and solo hostplants because this was a random variable in the field, so paired data could not be accurately analyzed.

Table 3. Larval number in response to penstemon patch and solo effects.

PATCH V. SOLO				
Variable tested: Larval number (unpaired)				
Time Period	Median for Solo	Median for Patch	Wilcoxon Mann-Whitney Statistic	Wilcoxon Mann-Whitney P-value
Period 1	8.50	7.00	396.0	0.2004
Period 2	8.00	9.00	489.5	0.5489
Period 3	3.00	16.00	333.0	0.1732
Period 4	5.00	7.50	428.0	0.0371*
Period 5	0.00	11.00	491.5	0.3082
Period 6	0.00	4.50	343.0	0.2689
Period 7	0.00	17.50	429.0	0.0474*
Overall collectively	5.00	8.00	20283.5	0.0019*

* = significant at 0.05 level

Treatment and patch interactions

Patch effects were more distinct than treatment effects in the field for the number of larvae (Figure 7). Larval abundance was greatest when hostplants occurred in a patch and was lowest when hostplants were not associated with a patch (Figures 7, 8). Treatment and patch effects were graphed both individually (Figure 7) and as interacting variables (Figure 8). There were more hostplants affiliated with patches (44 plants) than there were as solos occurring naturally in the landscape (14 plants).

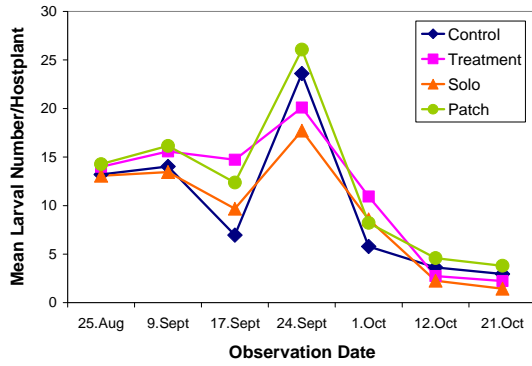


Figure 7. Larval abundance in response to all four conditions, peaking just before the hard frost. Control and Treatment were significantly different ($P = 0.015$) as were Solo vs. Patch ($P = 0.0019$) over all time periods combined.

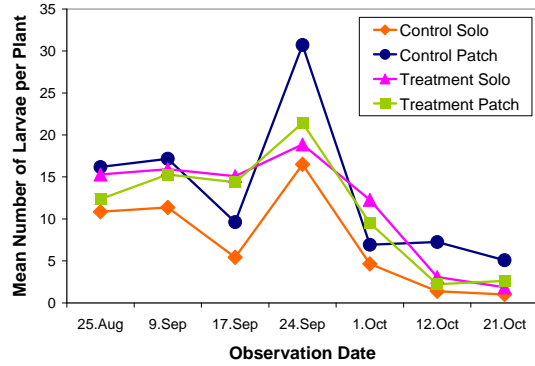


Figure 8. Larval abundance response to interacting conditions. Control Solo and Control Patch were significantly different ($P = 0.0379$), as were Control Solo vs. Treatment Solo ($P = 0.0071$) over all time periods combined.

At a more detailed scale, larvae were more than twice as abundant on control hostplants located in patches ($N_{\text{controlpatch}} = 12.4$ larvae/hostplant) than on control hostplants growing as solos ($N_{\text{controlsolo}} = 5.52$ larvae/hostplant), showing significant statistical differences (Figure 8, Table 4). Control solo hostplants ($N_{\text{controlsolo}} = 5.52$ larvae/hostplant) versus treatment solo hostplants ($N_{\text{treatmentsolo}} = 8.42$ larvae/hostplant) also exhibited a significant difference in larval abundance. However, the other comparisons, including control and treatment both in patches ($N_{\text{controlpatch}} = 12.4$ larvae/hostplant, $N_{\text{treatmentpatch}} = 14.4$ larvae/hostplant) and treatment plants as solos and in patches ($N_{\text{treatmentsolo}} = 8.42$ larvae/hostplant, $N_{\text{treatmentpatch}} = 14.4$ larvae/hostplant) did not show significant differences (Table 4). In sum, significant relationships were found when comparisons involved control solo hostplants (between control patch and between treatment solo).

Table 4. Larval abundance responded negatively to associations with control solo penstemon hostplants, but was not significantly affected by other combinations of treatments.

LARVAL ABUNDANCE		
Effects Tested	Wilcoxon Mann-Whitney Statistic	P-value
Control Solo v Control Patch	3123.5	0.0379 *
Control Solo v Treatment Solo	2425.5	0.0071 *
Control Patch v Treatment Patch	15415.0	0.7960
Treatment Solo v Treatment Patch	4653.0	0.0739

* = statistical significance

Analysis of larval length among the combinations above revealed no significant differences within any of the combinations of treatment or patch effects.

Plant and patch characteristics

Leaf quantity and plant diameter were the dominant hostplant characteristics correlated with larval abundance. Hostplant morphological features were more influential than spatial patch aspects in promoting larval survival, although both were important. Plant characteristics tested for effects on larvae were: number of penstemon leaves per hostplant; hostplant diameter; and plant height. The number of leaves per hostplant and transplant was the only variable that significantly changed over the 2-month study period, as leaves were consumed by larvae over time while the other plant and patch variables remained relatively constant during the study. Patch features included: number of penstemon plants within a 1-meter radius; distance to the closest penstemon plant; number of penstemon in the surrounding patch (if a patch existed); and area of the penstemon patch.

Greater numbers of leaves were most strongly correlated to larval abundance of the 5 most influential factors for all periods combined ($R^2 = 0.1162$, p -value < 0.0001). The additive effect of hostplant diameter as the second most important variable affecting larval number ($R^2 = 0.1406$, p -value < 0.0001), followed by the patch's area ($R^2 = 0.1462$, p -value < 0.0001), hostplant height (\log_{10} hostplant height $R^2 = 0.1480$, p -value < 0.0001), and lastly the distance to the nearest penstemon plant (\log_{10} distance $R^2 = -0.1501$, p -value < 0.0001), all served to support the model, but the model was not a strong predictor of larval abundance, explaining only 15% of the variation as the larvae grew to approximately their fourth instar (Table 5). However, the importance of these plant variables changed as the season progressed from August through October. Analysis within solely period four showed that larger penstemon hostplants led to more larval use ($R^2 = 0.3016$, p -value = 0.0002). Proximity of surrounding penstemon had the next most significant effect on larval number ($R^2 = -0.3319$, p -value = 0.0006), followed by the density of penstemon within a 1 meter radius ($R^2 = 0.3372$; p -value = 0.0018), hostplant leaf number ($R^2 = 0.3418$, p -value = 0.0046), and finally the area of the penstemon patch ($R^2 = 0.3434$, p -value = 0.0108). Cumulatively, these variables accounted for 34% of the model's variation for the fourth period (Table 5).

Table 5. Results of mixed model and stepwise regression. Hostplant diameter was the most significant variable related to number of larvae in two of three methods except the stepwise regression where it was also significant.

LARVAL NUMBER AND DESCRIPTIVE PLANT AND PATCH VARIABLES						
	Stepwise Regression All Periods			Stepwise Regression Period 4 Only		
Ranking	Variable	R²	P-value	Variable	R²	P-value
1	Leaf number	0.1162	<0.0001	Hostplant diameter	0.3016	0.0002
2	Hostplant diameter	0.1406	<0.0001	Distance nearest pen	-0.3319	0.0006
3	Patch area	0.1462	<0.0001	Penstemon 1 meter radius	0.3372	0.0018
4	Hostplant height	0.1480	<0.0001	Leaf number	0.3418	0.0046
5	Distance nearest penstemon	-0.1501	<0.0001	Patch area	0.3434	0.0108

Similar to the results from larval number, leaf number of penstemon hostplants played an important role in larval length ($R^2 = 0.2282$, p -value < 0.0001) in a cumulative model over the entire study. The diameter of hostplants ranked as second most influential ($R^2 = 0.2397$, p -value < 0.0001) in addition to the number of penstemon in a patch ($R^2 = 0.2450$, p -value < 0.0001), hostplant height ($R^2 = 0.2463$, p -value < 0.0001), and lastly, patch density within a 1 meter radius ($R^2 = 0.2474$, p -value < 0.0001). Results from analysis for the 4th period alone showed plant diameter emerging as the most significant variable in the model ($R^2 = 0.2698$, p -value = 0.0010). The regression model continued to be shaped by hostplant height (\log_{10} hostplant height $R^2 = 0.3429$, p -value = 0.0008), leaf number (\log_{10} leaf number $R^2 = 0.3499$, p -value = 0.0024), penstemon density (\log_{10} number of penstemon within a 1 meter radius $R^2 = 0.3529$, p -value = 0.0063), and finally the number of penstemon in a patch (\log_{10} number of penstemon in patch $R^2 = 0.3552$, p -value = 0.0142). The final stepwise model, which best described significant plant and patch effects on larval number, accounted for approximately 36% of the variation in the data.

Discussion

Treatment effects of transplanted *Penstemon neomexicanus*

This research demonstrated that pre-diapause butterfly larvae can benefit from an increase in nearby hostplants. Results suggested that larval abundance and larval size are greater when hostplants are larger in diameter, as well as more numerous and accessible at finer scales of temporal and spatial analysis. Although a statistical interaction with

time over each of the seven sequential study periods was not detected in this study, both larval abundance and larval length did significantly respond to treatment effects of two additional transplanted penstemon when treatment and control were analyzed as collective groups. As time elapsed, the treatments became more differentiated and distinct up until the hard frost, just after the fourth time period, and the peak of larval abundance. After the hard frost, climate effects may have dominated any detectable hostplant effects, although use of transplants remained important, as shown by higher mean numbers of larvae on transplants than on either control or treatment original hostplants (Figure 6).

Interpreted spatially or in terms of increased food resource, the lack of treatment effects between time periods could have been a result of too few transplants or use of transplants that were too small to significantly affect larval number and growth. Several transplanted penstemon were eaten thoroughly, leaving skeletonized stalks, indicating that additional nearby penstemon could have provided more food and contributed positively to larval survival. Transplanting only two penstemon plants may not have been enough to make a difference, particularly if the original hostplant was a solo with many larvae. Alternatively, two hostplants also may not have been detectable if the hostplant was large enough to support all the larvae or if other penstemon plants naturally occurred nearby. Planting more penstemon could produce significant differences in larval use or provide a selection of more palatable hostplant individuals.

The large flux in larval abundance at the fourth time period, just before the first significant frost, suggested that hostplant use changed over time. However, comparing over all time periods may have been too broad a temporal scale, capturing variation in the data over different developmental phases that did not permit detection of subtle differences in larval behavior. The increase likely was not due to immigration, given that occupied host plants were rare and not noted in the immediate surroundings, but instead possibly due to enhanced detectability. The peak in larval abundance at the fourth period was biologically notable because larvae were still gregarious yet at their largest size before beginning to disperse and hide for winter diapause. At this phase, larvae were the most readily observable. Aggregating behavior, particularly of aposematic species which

are warningly colored and unpalatable, benefits sedentary larvae by advertising their distastefulness (Bowers 1993). Studies of other gregarious lepidopteran species with aposematic larvae have found that large groups of larvae experience lower levels of insect predation than larvae in smaller groups by conspicuously displaying their unpalatability (Stamp 1993, Reader et al. 2003). Dark, aposematic larvae clustered together in sunshine can increase growth rates by raising body temperature and digestion rates (Stamp and Bowers 1990). This helps to understand potential benefits of this aggregating behavior that often results in intraspecific competition and ultimately starvation if other hostplants are not accessible. Abundance data could have been biased because larger, aggregating, aposematic larvae were more detectable to the human eye than smaller, individual larvae. Larger larvae also were more mobile and ate greater quantities of leaf material than smaller larvae, reducing foliar cover and leaving larvae more obvious. By this time, much of the foodplant leaf material was consumed and some penstemon had senesced from dehydration or defoliation, leaving fewer edible leaves and plants, which in turn experienced more concentrated use by larvae. Hostplant chemistry could have stimulated larval aggregation if a plant was particularly nutritious or releasing appealing concentrations of iridoid glycosides (Bowers 1983).

Patch effects

Larval abundance was greater on hostplants situated in natural patches compared with hostplants growing in solitude. The patch effect may have been important primarily at times when the larvae were large and numerous (i.e. Period 4), or later in the season when penstemon leaves were consumed or less available due to the onset of senescence (i.e. Period 7), and not a factor in the early observation times of this study. Furthermore, patch impacts could have swamped out the addition of only two penstemon transplants, as the influence of patch was more significant than the treatment to larval abundance. Greater numbers of accessible penstemon plants provided more food, locations for resting, and opportunities for protection from predators or parasitoids, as well as an increase in space and structural diversity for tent formation. In turn, more penstemon plants decreased the amount of competition among sibling or unrelated, conspecific larvae, which increases chances of survival, as found with the congeneric butterfly,

Euphydryas editha (Moore 1989). Although this effect was not documented in this study, enhanced larval survival could have been partly due to more favorable microclimate conditions in the immediate vicinity formed by having more penstemon plants nearby, as exhibited by increased hostplant abundance of *Euphydryas editha quino*, the federally endangered Quino checkerspot butterfly (Osborne and Redak 2000).

Combined treatment and patch effects

Larvae appeared to detect interactions at a finer scale, which served to isolate combined treatment and patch effects. Dividing specific conditions into treatment solo, treatment patch, control solo, and control patch defined a gradient of scenarios from only one possible hostplant (control solo), to two or more (control patch and treatment solo), to at least 4 accessible penstemon (treatment patch). In all cases involving control solo (compared with control patch, treatment solo, and treatment patch), larval abundance on control solo hostplants was significantly reduced. An increase of merely one or two additional penstemon plants provided the larvae with several times the amount of their critical resource and suggested that location within a patch was more important to larvae than their position in the overall landscape for the pre-diapause stage. Similar results have been found with other butterfly species and member of this genus, where spatial scale at the level of larval use is paramount to immediate larval survival (Weiss et al. 1987, Dennis et al. 2003, Bauerfeind et al. 2009).

Use of transplanted penstemon hostplants by larvae was not immediate; larvae were not observed using the transplants until two time periods after planting. The lag in larval response to the transplants was likely due to the small size and related immobility of earlier instars and the still plentiful supply of leaves on their original hostplant. As larvae grew, they were able to function at broader scales in their environment, beyond only the natal hostplant. Increased mouthpart size, leg size, and body size with larval development facilitates access to more of their hostplant and then other plants in the patch, if available. Larval use of transplants appeared to increase as the original hostplant became increasingly defoliated and the leaves became skeletonized. All transplanted penstemon plants were at least partly consumed if the treatment hostplant was entirely consumed, indicating that larvae were willing to eat adjacent penstemon plants whether

the plants were transplanted or naturally present. To larvae of *E. a. cloudcrofti*, foodplant availability, or proximity in terms of accessible distances based on larval body size, may be more important than foodplant quality or chemistry. Larval foraging behavior of a different nymphalid species was found to lack selectivity for feeding, whereby larvae fed on the closest leaves both just after hatching, and later when they were significantly more mobile (Stamp 1984). From other studies, it is known that the number of plants needed depends on larval number, size, and growth rate (Moore 1989). Growth rate is determined partly by genetics, food quantity and quality, and by temperature and direct exposure to sunlight (Stamp 1993, Kelly and Debinski 1999). Knowledge of larval tolerance for transplanted penstemon has useful applications for future colonization or augmentation studies with this species.

Effects of plant and patch variables

Plant variables, such as plant diameter, height, largest stem diameter, and leaf number, were more important than patch variables to larval abundance and length, as reflected by the mixed model and stepwise regressions. Of the four hostplant variables, plant diameter impacted larval abundance and larval length most strongly (Tables 7, 8). Plant diameter was related to the number of leaves and occasionally to plant height which also played a role in supporting larvae. However, approximately 2/5 of the penstemon hostplants measured in the field were rosettes, with no developed stems, and were fairly short in stature, indicating that plant diameter was not consistently correlated with height. Leaf number, which varied through the time of this study as leaves were being produced by the plant but also consumed by larvae, was most strongly associated with plant height, illustrating that greater leaf numbers per penstemon were found with greater penstemon height. Patch variables exhibited the same ranking order of influence for both larval abundance and length. Larval abundance and growth were more dependent upon penstemon density within close proximity to the hostplant than on the area of the patch. Although patch variables were not as strongly correlated with larval abundance and length as plant variables, association with patches appeared to enhance larval survival.

Conservation applications

These findings have implications for assisting any threatened or endangered butterfly limited by hostplant resources on a small scale and are directly applicable to the intimate spatial scale delineated by larval selectivity and mobility exhibited by narrow range endemics. Information gained here is relevant for supplementing butterfly hostplants holding eggs or larvae, or for relocating or reintroducing gregarious larvae in the field. To enhance chances of pre-diapause larval survival within an occupied meadow, transplanting several penstemon plants around a hostplant provides additional food and shelter later into the season and mimics the resources of a natural patch. For larval relocation projects, taking larvae to relocate from a smaller, solo hostplant would be preferable to taking larvae from a large, healthy penstemon growing in a natural patch, based on the lower chances of survival for larvae on solo hostplants. Specifically, moving larvae relocated (from one field position to another) or reintroduced (from captive rearing into formerly occupied habitat) to a large hostplant only if it is growing in a patch and avoiding hostplant situations where no other penstemon are within a meter away could improve larval survival. These procedures likely would apply to other rare butterfly species with low vagility, high host- and nectar plant specialization, and a dispersed metapopulation structure.

As bioindicators, butterflies inform us of the condition of native habitats (Pearson and Carroll 1997, Boggs et al. 2003, Thomas et al. 2004, Thomas 2005). The resident Sacramento Mountains checkerspot butterfly offers a unique opportunity to manage for conditions important to its conservation, measure the status of upland meadows in southern New Mexico, and monitor effects of global climate change on sky island systems. As the Sacramento Mountains contain several known endemic species, this environment merits the preservation of these communities and maintenance of the interdependent and largely unknown relationships among plants and animals. To alleviate high mortality associated with competition for larval food resources in meadows presently occupied by the butterfly and to promote successful reintroduction into unoccupied meadows, findings of this study can be used to guide future habitat restoration or augmentation of the butterfly population. Combined results suggest that

larval abundance and length respond most favorably to large penstemon hostplants with broad plant and stem diameters, many leaves, and tall heights, and those growing in a patch. Optimal conditions further involve greater numbers of penstemon hostplants occurring either naturally in dense clusters or using at least two transplants planted as densely as possible within a one meter radius of a central hostplant. In summary, results of this experiment indicate that larvae will achieve greater numbers and length if affiliated with large penstemon plants in dense patches. Supporting pre-diapause larvae with conditions that maximize survival during this sensitive life phase will help to ensure the long-term persistence of the Sacramento Mountains checkerspot butterfly.

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CONCLUSION

This research addressed the impacts of habitat features, local mammals, and experimental hostplant transplants on the Sacramento Mountains checkerspot butterfly (*Euphydryas anicia cloudcrofti*) to contribute to more effective conservation for this rare species. Overall findings demonstrate that the butterfly responds to connectivity and abundance of required resources at all spatial scales and that disturbance processes that maintain early successional, open conditions may be important in sustaining the butterfly into the future.

Abiotic and biotic variables at the four examined scales reflected similar patterns, with connectivity, resource concentration, and plant structural diversity preferred by the butterfly at the scale of the landscape, meadow, hostplant patch, and natal hostplants. This research demonstrated that pre-diapause butterfly larvae can benefit from the food source addition of just two host plants adjacent to the natal host plant. This may be applicable to other gregarious butterflies that consume their entire natal host plant before completing development prior to diapause. Larval abundance and length responded most favorably to large penstemon hostplants with broad plant and stem diameters, many leaves, and tall heights, and those growing in a patch. High habitat quality, low isolation, broad hostplant patch area, and high hostplant patch density were associated with occupied habitats. Despite being far more vagile than larvae, adults were tightly associated with the distribution of the preferred nectar source within a meadow, suggesting their specialized use of one plant species in time and space. Distinctions among the plant community and ground surface type vary over time and were noted here over only the course of a few years, offering a glimpse into a dynamic system. How habitat quality and networked resources interact with the butterfly's different life phases annually and with the successional requirements and mammal facilitation of open habitats over the long-term, are important conservation parameters for this butterfly.

As with much original field research, results from this study hinted at answers to investigated questions but also led to more questions. Some important aspects of the Sacramento Mountains checkerspot butterfly ecology that were not resolved from this research include specific reasons why the butterfly population numbers remain low and

why its global range is so small. The genus *Euphydryas* is one of the more thoroughly researched wild insect genera, inspired by early studies in the 1960s that paved the way for other plant-insect interaction work (Ehrlich and Raven 1965). Still, within the genus there is enough variation in natural history, species' population size, and habitat selection that many assumptions cannot be transferred from one species to another. Thus research focused on each species is needed, especially for those taxa meeting conditions for global rarity.

Recommendations

If butterfly species are to persist, novel strategies to conserve butterflies and pollinators in general must be adopted to restore and maintain varied landscape types at different scales. Some degree of disturbance appears to be necessary, to mimic pulses of ungulate presence or fire regimes of the past, and to encourage annuals and increase the range of flowering forbs and shrubs. Gopher soil disturbance and elk herbivory appear to be interacting with *P. neomexicanus*, the primary host plant. Gopher activities should remain as prevalent as they are in butterfly meadows, but baseline elk grazing is already impacting over 35% of all penstemon plants, and 60% of all stems, making the addition of livestock to meadows occupied by the butterfly less desirable for *E. a. cloudcrofti* conservation. A reduction in the numbers of elk, at least by managing for more natural top predators, should be considered in areas with the butterfly. Overall, the butterfly's habitat should be large enough to permit natural disturbance regimes in a mosaic of different stages of successional responses. If the goal is to increase the butterfly's population, a sustainable, high quality, and connected habitat must be maintained for both the adults and the non-adult phases, which comprise over 95% of the species' life span.

For this habitat specialist butterfly, which exhibits high home-meadow fidelity, spatially contiguous resources appear to be crucial to regardless of scale. Habitat within the dispersal limits or along corridors could be enhanced to promote natural colonization of the species with the target of increased resource connectivity. Augmenting penstemon could help to form vegetation corridors for larvae with limited mobility that could be duplicated more intensively or at larger scales. Creating pathways of *P. neomexicanus*, *V.*

edulis, and *H. hoopseii*, which connect meadows with suitable habitat, could extend the butterfly's range and abundance. These corridors should be embedded in a diversity of microtopography with adequate insolation and edge components and south-southeast aspect exposure for optimum value.

As the rarity of this species does not offer the luxury of repeated trials of management experiments, the outcomes of each action to enhance the habitat require monitoring and swift adaptation to new ecological findings. Freshly colonized meadows could be supplemented with captive reared larvae or relocated from donor source populations (if any exist) that would not be vulnerable to a loss of individuals. Captive reared or translocated larvae could then be introduced into currently uninhabited meadows, including the high meadows to the south, where favorable patch and plant conditions are found or perhaps developed by supplementing with additional host plants. Larvae were willing to eat adjacent penstemon plants whether the plants were transplanted or naturally present, offering a practical approach to enhancing butterfly numbers and habitat. To this end, the results of this study may assist projects in the field.

Determining the precise ecology and the spatial dynamics of resources and how these interact with a species' behavior and conservation involves much effort, which explains why so little is known about rare insects in their natural settings. A vision that encompasses short- and long-term recovery from the perspective of the species being studied, along with the multifaceted desires of humans, is worth cultivating in order to maintain and restore rare species in native habitats. Given that the Sacramento Mountain checkerspot's needs may encapsulate those of other butterfly species, and that globally threatened butterfly species serve as bioindicators of overall ecosystem health and function, this research may provide insight into managing for not only by the checkerspot's conservation, but also other for other pollinators and their natural communities.