

The Population Dynamics and Migration Patterns of Alpine Butterfly *Colias behrii*

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Abstract Climate change has affected numerous ecosystems by modifying the phenology of plants and animals. Insect distribution is exceptionally sensitive to temperature change because many insect life cycles are dependent on established seasonal temperatures and water availability. Alpine butterfly populations are at a particular risk because their life cycles are regulated by a short seasonal growth cycle that is dependent on snow melt and involves the formation of diffuse metapopulations. Examining migration between butterfly populations illustrates their dynamic population structure in a topographically complex habitat that is sensitive to change. Migration is often dependent on climate, population size, and natural barriers and I aim to determine which barriers will limit migration in this study area. I hypothesize that butterfly dispersal varies randomly across all sites despite population size, topographic, vegetative, or constructed barriers. My alternative hypothesis is that dispersal is reduced between those sites with small population sizes and geographic barriers such as roads and ridges. I used a mark-recapture study to estimate population parameters and dispersal of *Colias behrii*, a butterfly endemic to the Sierra Nevada mountains of California. The insects were marked so that they were successfully identified to number and site location in subsequent recaptures. No migration was observed among the *C. behrii* populations. Butterfly dispersal is likely limited by intrinsic species differences and varies widely with habitat and seasonal variation.

Introduction

Anthropogenic induced climate change is the primary factor contributing to the current loss in biodiversity, with extinction rate projections increasing tenfold in the next 50 years (Millennium Ecosystem Assessment 2005). Climate change is particularly important because it can lead to irreversible transformations in distributions of plants and animals as well as alter the phenology of host plants and insect life cycles (McLaughlin *et al.* 2002). In many regions, low overwintering temperatures directly limit the distribution and survival of many insect species. These overwintering temperatures may modify the corresponding areas where insect species occupy which can have large economic consequences, especially if the insect in question is an agricultural pest (Cammell and Knight 1992, Stephens *et al.* 2007). Although scientists have proven that many insects are affected by climate change (Cammell and Knight 1992, Roland *et al.* 2000, Stephens *et al.* 2007, McLaughlin *et al.* 2007), butterflies are especially vulnerable because they have a complicated life cycle, unique migration strategies, and intimate relationships with their host plants (McLaughlin *et al.* 2002). Small endemic butterfly populations are at risk of decline and possible extinction due to anthropogenic changes in habitats and environment (Ehrlich and Murphy 1987, McLaughlin *et al.* 2002). In particular, temperature and precipitation play a central role in determining butterfly distribution and abundance because they directly affect the growth of the butterflies' host plants. One study concluded that temperature and butterfly abundance were negatively correlated; this was most likely due to a decrease in plant growth during the hotter and drier years (Woods *et al.* 2008). Climate change can also affect butterfly phenology, as a recent study determined that sixteen butterfly species in California have advanced their migration flight date within the last 30 years by an average of 24 days (Parmesan 2006). In the San Francisco Bay Area in California, two extinctions of checkerspot butterfly *Euphydryas editha bayensis* populations were caused by increased habitat loss and precipitation variability as a result of climate change (McLaughlin *et al.* 2002).

Habitat loss is an important factor influencing the population size of butterflies because of the complex spatial relationships they develop with their environment. Butterflies often form metapopulations wherein small colonies occupy patchy meadow and grassland habitats (Watt *et al.* 1977, Roland *et al.* 2000, Schneider *et al.* 2003) although this can vary as some species live in harsh mountainous environments (Matsumoto 1985). Butterflies tend to favor meadow

environments and the largest populations will form in this habitat (Woods *et al.* 2008). Habitat succession from meadows to forests has been occurring in many alpine habitats as the tree line is rising and diffusing into the meadow. This has occurred as a result of fire suppression and global warming effects, both of which promote the development of smaller and increasingly isolated alpine meadows (Roland and Matter 2007). In one Canadian alpine region, the rising tree line resulted in limited individual butterfly movement due to a 78% loss of meadow (Roland *et al.* 2000). The persistence of these small colonies depends on a dynamic cycle of dispersal, extinction, and recolonization (Roland *et al.* 2000). Any reduction in the connectivity of suitable habitat patches or an increase in the distance between patches can put local populations at risk to decline and extinction, or even genetic isolation. Indeed, dispersal allows for colonization of uninhabited areas or rescue of declining populations and helps maintain genetic variation. When applied to vulnerable endemic species, these concepts become increasingly important for conservation plans (Casula 2006). A landmark study conducted in Jasper Ridge, California on checkerspot butterflies detailed the importance and difficulty of protecting metapopulations and highlighted the significance of environmental stochasticity on long-term population trends. Even these large populations are at risk because of habitat loss due to ecosystem changeover (Ehrlich and Murphy 1987).

Habitat and climate are consequently equally important in determining butterfly distribution and abundance. Alpine butterflies are particularly vulnerable to changes in environmental and climate shifts because their brief life cycle is highly correlated with the melting of snow and increasing summer temperature (Garth and Tilden 1963, McLaughlin, *et al.* 2002). I propose to study an endemic alpine species in the Sierra Nevada, the Sierra Green Sulfur butterfly, *Colias behrii* (Pieridae). This light green butterfly is active only in July and August when it mates and lays eggs. The eggs hatch and the caterpillars feed in the fall, pupate during the winter, and emerge from their pupal stage into butterflies in the summer once again. Their host plant is the dwarf bilberry *Vaccinium caespitosum*, a small shrub which the butterfly noticeably resembles (Scott 2001). This butterfly is relatively abundant in the Sierras Nevada mountains of California and many large populations exist in several locations in Yosemite National Park. However, it has a very small overall geographic range throughout a topographically complex habitat (Schoville, unpublished data). *C. behrii* presence in the Yosemite area was documented in the late 1800s and was recorded to have its largest populations in Tuolumne Meadows (Garth and

Tilden 1963). Currently, no *C. behrii* has been found in this location for the last 5 years (Schoville, unpublished data). Tuolumne Meadows is located at 2500 meters, and the *C. behrii* populations are now located at higher elevations. Many other alpine butterfly species prefer to inhabit open meadows similar to Tuolumne (Watt *et al.* 1977, Roland *et al.* 2000). Open meadows are perhaps even vital to maintaining butterfly metapopulations because they maintain the source populations from which butterflies disperse to surrounding habitats (Ockinger and Smith 2007).

Although there are recognized metapopulations of *C. behrii* in Yosemite, the causes of migration between the metapopulations facilitates understanding of the butterflies' population structure in this topographically complex habitat vulnerable to climate change. Do barriers influence migration of endemic butterflies? This migration may be based on the size and longevity of the populations (Matsumoto 2000, Roland *et al.* 2000), but also may be due to geographic barriers (Roland *et al.* 2000). This can include cross-road, cross-ridge, cross-treeline, and open meadow movements. Of the sites chosen in Yosemite to study *C. behrii*, highways, rocky mountain ridges, forests, and large open meadows constitute geographic barriers that separate the populations. Roland *et al.* (2000) found that butterflies disperse along ridgetops more slowly than through open meadows and in some instances, did not even cross through forests. Butterfly movement is determined by the permeability of these varying types of ecosystems. Less permeable ecosystems like forests present high-risk situations which butterflies will typically avoid whereas more permeable ecosystems may facilitate migration. However, this was shown to vary by species related to body size and agility (Stasek *et al.* 2008).

In addition to natural barriers, it is predicted that anthropogenic barriers also influence dynamics of butterfly populations. Highway 120 is the only road through Yosemite National Park and provides transportation for an estimated three and a half million people who visit the park each year (Yosemite National Park 2008). Other park systems have implemented bus transportation through parks in order to minimize disturbance from cars, but this has not been introduced in Yosemite. The effects of Hwy 120 through Tuolumne Meadows are unknown, and it is hypothesized that the high rates of traffic is having some effect on the survival of populations adjacent to the road.

The survivorship data of *C. behrii* is also unclear. Although other estimates have been made about how long butterflies live ranging from days to months, it is unknown how long these

insects live. One study of a butterfly species living in a similar alpine habitat, the butterfly *Parnassius glacialis* (Papilionidae) showed an average life of 4.7-6.6 days for males with females living approximately 1-2 days less. These averages were found in similar studies of other Papilionidae species conducted in Japan and Colorado. The populations of these butterflies lived no longer than a month and a half and varied in size from year to year based on annual climate patterns (Watt 1977, Matsumoto 1985). Roland *et al.* (2000) found that within the metapopulations, abundance of butterflies affected emigration and immigration, as more butterflies departed from sites with small populations. Population size might be regulated by larval plant preference (Knight *et al.* 1999) or adult resource density (Schneider *et al.* 2003) and although I am testing the hypothesis that the distribution and abundance of *C. behrii* is correlated with geographic barriers, it is notable that these factors may influence the distribution as well.

The main objective of this study is to examine migration among the metapopulations of *C. behrii* in the alpine meadow habitats sensitive to climate change. I aim to find whether these butterflies disperse amongst their seemingly isolated populations and whether this dispersion is affected by the geographic barriers between each population in addition to metapopulation size and longevity. Do barriers influence migration of these endemic butterflies? I hypothesize that butterflies will not move as easily across roads and ridges as they do across meadows. My null hypothesis is that dispersal varies randomly across all sites, with dispersal occurring between adjacent sites despite topographic, vegetative, or constructed barriers. My alternative hypothesis is that dispersal is reduced between sites with barrier interference. In addition, I hypothesize that survivorship will vary between sites in relation to habitat quality (host plant abundance, distance from road). Mark-recapture will be used to estimate population parameters and dispersal of *C. behrii*. The insects will be marked so that they can be successfully identified by number and site location in subsequent recaptures.

Methods

A mark-recapture is a well-used method in biology to estimate the number of individuals in a population. In this method, subsamples are used to estimate population size by marking a certain number of individuals where the number recaptured represents a percentage of the total population. It was also an efficient way to mark butterflies to determine if individuals disperse among populations. Before a mark recapture study can be undertaken, a few assumptions are

necessary. First, it is assumed that no individuals enter or leave the population. This means that the system under study is a closed population (Cooch and White 2008). In some ways this assumption was fulfilled because we marked all known populations in the area. However, we cannot account for the fact that individuals should have lived throughout the entire marking and capture period. Second, recaptures cannot be affected by the initial capture and marking. These effects were minimized as much as possible. Other studies have shown that the size and location of the mark do not affect predation (Morton 1982), and this was also minimized by the fact that we marked individuals on the underside of their wing. When butterflies rest on flowers they spread out their wings to absorb sunlight and warmth, so the mark could not be seen. Also, we reduced selection bias because the marks could not be seen until the butterfly was already captured.

The mark recapture organism, *Colias behrii*, (Garth and Tilden 1963) is also known as the green sulfur butterfly (Family Pieridae). It is endemic to the Sierra Nevada mountain range of California. *C. behrii* uses its host plant, dwarf bilberry (*Vaccinium caespitosum*) for mating and camouflage. In the field, identification of the butterfly was simple and quick as males have a yellow outline to their wings, whereas females have a pink wing outline and pink fuzz on their heads (Scott 2001).

The study was conducted in the upper alpine meadows of Yosemite National Park. The elevation of the meadows ranged from 2400 to 2700 meters. Seven site locations were selected based on *C. behrii*'s presence in these meadows from first hand observations: Mono Pass, Gaylor Lake, Vogelsang, Dana Meadows, Lee Vining, Dog Lake, and Elizabeth Lake. (Schoville, unpublished data). The meadows varied in size and quality, but were generally near a water source (lake or river) and contained typical alpine species of wild flowers, grasses, and sedges native to the region. To determine whether geographic barriers impact migration, the seven sites were chosen based on the varying degrees of barriers between them. Two of the locations were separated by only a meadow whereas the other locations were separated by tree lines, mountain ridges, and roads. Four of the sites were separated by varying degrees of mountainous ridges and three of the sites were separated by thick forests. Two of the sites were within thirty feet of a highway.

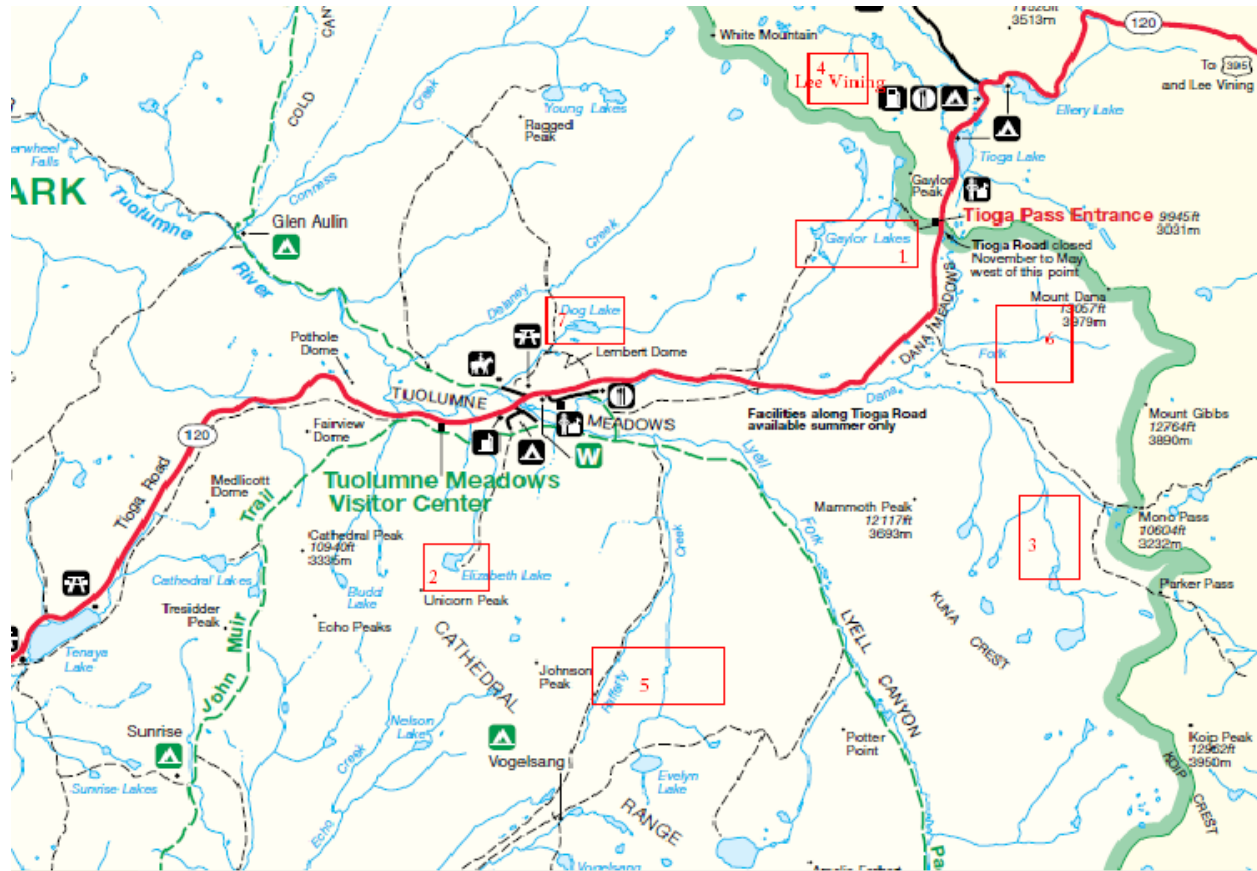


Figure 1: Map of Tuolumne Meadows. The 7 capture sites are marked with red flags. These include locations at 1) Gaylor Lakes, 2) Elizabeth Lake, 3) Mono Pass, 4) Lee Vining 5) Vogelsang 6) Dana Meadows and 7) Dog Lake.

The mark-recapture study took place from July 16th through August 10th, 2008. Every sampling day was a sunny day ideal for capturing butterflies as butterflies are inactive on rainy or cloudy days. Each site was visited every 6 days for a total of four trips to each site (an additional fifth trip was taken to Elizabeth Lake, Dana Meadows and Lee Vining.) Two sites were sampled each collecting day, one in the morning and one in the afternoon for approximately 2-3 hours each. The locations were visited in the same order and at the same time of day to avoid sampling bias. In each meadow, individual butterflies were caught with a hand net and marked with a letter (location A-G) and a number (1-150) on the ventral side of the forewing with a fine-tipped permanent marker. The sampling size is 150 individuals because it was the maximum number of individuals that could be captured per the Yosemite park permit. An additional seventh site, designated at site D, is not subject to park permits and 226 individuals were marked at this location.

Sex, weight (decigrams), length of wing (cm), and wing wear were all recorded. Wing wear was taken on a scale of 1-4, which was formulated using examples from other butterfly mark-recapture studies (Ockinger and Smith, 2007 Roland *et al.* 2000). This helped us to roughly estimate the number of fresh and old individuals on each recapture day in order to track the progress of the population's survival for personal reference during the 4 weeks. Upon net capture, butterflies were placed into glassine envelopes used to hold the butterflies until they could be marked. Wing movement was restricted in the envelopes to avoid loss of wing scales. This technique was mostly employed to avoid wasting time catching the same individuals. No "marking effects" or abnormal behavior were observed.

Results

Population sizes varied from small to large. This was assessed qualitatively from field observations because the recapture numbers were too small in relation to the sampling size to yield results without large errors (Cooch and White 2008). My study did not find any migration among the metapopulations, as recaptures were restricted to sites (i.e. only B marked butterflies were found at site B) (Table 1). No mark-recapture analysis or population estimation was performed.

Table 1. Summary of recapture data among nine sites in Yosemite. Data was collected in a 4 week mark-recapture period (Jul-Aug 2008). Each site was visited four times, and sites B, D, and F were visited five times.

Site	Individuals Marked	Recaptures	Percent recaptured	Populations Recaptured
A- Gaylor Lake	150	3	2%	A
B- Elizabeth Lake	141	21	15%	B
C- Mono Pass	150	8	5%	C
D- Lee Vining	226	33	15%	D
E- Vogelsang	150	6	4%	E
F- Dana Meadows	150	4	3%	F
G- Dog Lake	10	3	30%	G

Discussion

My study did not find any migration among the metapopulations, an assumption behind the study design and questions. My study was devised to test what factors were affecting migration but these could not be considered because no migration was found. I was unable to identify whether barriers reduced migration. Each site was unique in terms of quantitative factors such as

population size, density, longevity, as well as the varying degrees of barriers between them (Fig. 1). Although unique, the sites are comparable in that they were all alpine meadows and contain viable populations of *Colias behrii*. There is a large range of population sizes, from the smallest with 10 individuals at Dog Lake to those with thousands at Gaylor Lakes and Mono Pass (Fig. 1). These population sizes may have an effect on the results of the study, particularly as explanations as to why no migrating butterflies were recaptured.

Some of the populations were very large, and in some cases, much larger than anticipated. Due to collection and time restrictions, we were only able to get a few recaptures in the very large populations (3 or 4 recaptures for the Gaylor Lakes and Dana Meadow populations) (Table 1). This cannot be the sole explanation of why migration was not found because some sites had smaller population sizes such as Elizabeth Lake and Dog Lake, and we were able to record a large number of recapture data at these sites. Perhaps there was migration to Gaylor Lakes and Dana Meadows, but since the populations were too large, locating recaptures at these sites was not feasible. The methodology may not have allowed for accurate assessment of migration.

As discussed, migration may be due to a number of factors such as oviposition sites, food availability, and even distance to other butterflies (Knight *et al.* 1999, Schneider *et al.* 2003). However, the influence of any of these factors affecting migration may be family or even species specific. We can conclude that although migrations may occur between sites, they seem to be rare events in the *C. behrii* populations. Many studies show butterfly migration as a normal and regular occurrence, and there is an insufficient number of studies highlighting lack of migration in alpine habitats. Studies of butterflies in tropical environments do highlight a lack of migration, (Shahabuddin *et al.* 2000, Jiggins *et al.* 2001) but rainforest habitats are very climatically stable as they do not have changing of seasons including frost and snow melt. Therefore, a comparison of alpine butterflies to tropical butterflies will involve examining different life cycle adaptations and is not practical. A lack of butterfly migration has also been found as a result of insufficient habitat to migrate to as a result of urban development (Hill *et al.* 2001).

Previous studies of butterflies in similar habitats (Roland *et al.* 2000, Matsumoto 1985, and Morton 1982) all suggest that migration does occur regularly in alpine habitats, although varying in degrees on a temporal basis (Watt *et al.* 1977). Many of the studies researched larger and more robust butterflies than *C. behrii*. These studies examined the swallowtail butterflies from

the family Papilionidae (Roland *et al.* 2000 and Matsumoto 1985) as well as the famously studied monarch butterfly (family Nymphalidae), notorious for its complex migration patterns (Knight *et al.* 1999). However, Pierid butterflies have been examined as a model system for the study of genetics and ecology of population structure and evolutionary mechanisms. In this study, three species of Pierids were examined in an alpine meadow habitat in Colorado and recapture data was collected on their population structure and migration (Watt *et al.* 1977). So although butterfly migration has been studied in a variety of families, it may be a species specific phenomenon and cannot be extrapolated to all alpine butterfly species.

As discussed, other reasons for butterfly migration include suitable habitat and climate. Alpine butterflies live in a vulnerable environment that is sensitive to small changes in temperature and precipitation. Changes in meadow size and habitat due to anthropogenic impacts such as fire suppression or climate change can impact the phenology of butterfly behaviors. These characteristics define habitat quality and are especially essential because it has been shown that alpine butterflies prefer to inhabit open meadow habitats (Watt *et al.* 1977). They have been known to cross tree lines (Roland *et al.* 2000); however, I observed in some of the Yosemite habitats that, when chased, many *C. behrii* flew into the trees to escape my net, but shortly after circled around and came back out into the meadow. *C. behrii* lives in a protected national park, and this sheltered habitat could have some effect on the lack of migration patterns. On the landscape, fire is suppressed and recreational use, habitat quality and resource management are all heavily monitored and studied by the National Park Service. Rising tree lines due to fire suppression has been documented to limit migration (Roland *et al.* 2000).

Migration behavior can have genetic implications. When species populations become too isolated, sink populations can form which leads to a metapopulation becoming genetically uniform. This can put the populations at risk for extinction, or even lead to speciation (Watt *et al.* 1977 and Ockinger and Smith 2007). Migration was not detected among the *C. behrii* populations in Yosemite, so this knowledge about their population dynamics may be vital for determining their potential for genetic isolation. However, these mechanisms of evolutionary genetics occur on time scales that span many generations. Patterns of migratory behavior have critical importance for the population's genetic variability, evolutionary potential, structure, and ecology (Watt *et al.* 1977). It is important to note however, that only seven sites were selected for this study based on the known information of *C. behrii* populations. There may in fact be

more unsampled populations of *C. behrii*, one of which we located near the Mono Pass location at Helen Lake.

Although many confounding factors have arisen that could explain the lack of migration among *Colias behrii* populations in Yosemite, if the observed pattern is consistent, my results have many far-reaching implications. An examination of the pressures that promote migratory behavior in any species is significant for understanding its biology, relationships with other species, and the habitat in which it lives. A study of butterflies in California found that environmental stochasticity is the major cause of extinction, particularly in small populations. Populations that become isolated are at risk to extinction based on environmental events, such as droughts (Ehrlich and Murphy 1987). Further knowledge into the population structure of these butterflies is significant for drawing conclusions on how they can best be protected and preserved, especially with recent global warming trends. Habitat loss is a central issue for butterflies because they form complex spatial relationships with their habitat. Although Yosemite National Park is protected wilderness and cannot be affected by any type of development or natural resources use, roads and campsites continue to be constructed and revised in the park and effective research management is important for these areas.

Migration was not observed among the seven *C. behrii* metapopulations in Yosemite National Park in July 2008. Migration may still occur between unsampled populations or vary on a temporal basis, and perhaps another study with larger sample sizes at more locations would complement my findings. Given that passing on genetic traits is the fundamental objective of each butterfly (Ockinger and Smith 2007) and *C. behrii* live no longer than a month, it is likely that mate availability is sufficient in these habitats to sustain populations and migration is not a necessity for producing offspring. Further research for a more complete picture of alpine butterfly migration habits can be suggested to examine migration behavior among other alpine butterfly species that co-inhabit all of the same meadows including *Parnassius clodius*, *Lycaena heteronea*, and *Pyrgus communis*. It appears that butterfly dispersal behavior varies widely from place to place, year to year, and is strongly overlaid with intrinsic species differences. Whether these differences are internal, environment specific, and more likely, a combination of both, awaits further research.

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References

- Cammell, M.E. and J.D. Knight. 1992. Effects of climatic change on the population dynamics of crop pests. *Advances in Ecological Research* 22: 117-62.
- Casula, P. 2006. Evaluating hypotheses about dispersal in a vulnerable butterfly. *Ecological Restoration* 21: 263-270.
- Cooch, Evan and Gary C. White. Eds. 2008. Program MARK: a gentle introduction. EGC, New York. 750 pp.
- Ehrlich, P.R. and D.D. Murphy. 1987. Conservation lessons from long-term studies of checkerspot butterflies. *Conservation Biology* 1: 122-131.
- Garth, J.S. and J.W. Tilden. 1963. An ecological survey of the butterflies of the Yosemite sector of the Sierra Nevada, California. *Journal of Research on the Lepidoptera* 2: 1-96.
- Hill, J.K. Y.C. Collingham, C.D. Thomas, D.S. Blakeley, R. Fox, D. Moss and B. Huntley. 2001. Impacts of landscape structure on butterfly range expansion. *Ecology Letters* 4(4): 313-321.
- Jiggins, C. D., R.E. Naisbit, R.L. Coe and J. Mallet. 2001. Reproductive isolation caused by color pattern mimicry. *Nature* 411: 302-305.
- Knight, A., L.P. Brower and E.H. Williams. 1999. Spring remigration of the monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae) in north-central Florida: estimating population parameters using mark-recapture. *Biological Journal of the Linnean Society* 68: 531-556.
- Konvicka, M. and T. Kuras. 1999. Population structure, behavior, and selection of oviposition sites of an endangered butterfly, *Parnassius mnemosyne*, in Litovelske Pomoravi, Czech Republic. *Journal of Insect Conservation* 3: 211-223.
- Matsumoto, K. 1985. Population dynamics of the Japanese clouded apollo *Parnassius Glacialis* Butler (Lepidoptera: Papilionidae). I. Changes in population size and related population parameters for three successive generations. *Restoration Population Ecology* 27: 301-312.

- McLaughlin, J.F., J.J. Hellman, C.L. Boggs and P.R. Ehrlich. 2002. Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences* 99: 6070-6074.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, DC.
- Morton, A.C. 1982. The effects of marking and capture on recapture frequencies of butterflies. *Oecologia* 53: 105-110.
- Ockinger, E. and H.G. Smith. 2007. Asymmetric dispersal and survival indicate population sources for grassland butterflies in agricultural landscapes. *Ecography* 30: 288-298.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637-669.
- Roland, J. and S.F. Matter. 2007. Encroaching forests decouple alpine butterfly population dynamics. *Proceedings of the National Academy of Sciences* 104: 13702-13704.
- Roland, J., N. Keyghobadi and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* 81: 1642-1653.
- Schneider, C., J. Dover and G.L.A. Fry. 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. *Ecological Entomology* 28: 219-227.
- Schoville, Sean. Graduate Student, University of California, Berkeley, Berkeley, California. 2008, personal communication.
- Scott, J.A. 2001. *The butterflies of North America: a natural history and field guide*. Stanford University Press, Stanford, CA.
- Shahabuddin G., G. A. Herzner, C. Aponte and M.D. Gomez. 2000. Persistence of a frugivorous butterfly species in Venezuelan forest fragments: the role of movement and habitat quality. *Biodiversity and Conservation* 9(12): 1623-1641.
- Stasek, D.J., C. Bean and T.O. Crist. 2008. Butterfly abundance and movements among prairie patches: the roles of habitat quality, edge, and forest matrix permeability. *Environmental Entomology* 37: 897-906.
- Stephens, A.E.A., D.J. Kriticos and A. Leriche. 2007. The current and future potential geographical distribution of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Bulletin of Entomological Research* 97: 369-378.
- Watt, B.W. and F. S. Chew and L.R.G. Snyder and A.G. Watt and D. E. Rothschild. 1977. Population Structure of Pierid Butterflies. *Oecologia* 27: 1-22.

Woods, J.N., J. Wilson and J.R. Runkle. 2008. Influence of climate on butterfly community and population dynamics in western Ohio. *Environmental Entomology* 37: 696-706.

Yosemite National Park. 2008. National Park Service homepage.

<http://www.nps.gov/yose/historyculture/index.htm>. Accessed 2008 Apr 19.