POST-FIRE ASSOCIATIONS OF BUTTERFLY BEHAVIOR, OCCUPANCY, AND ABUNDANCE WITH ENVIRONMENTAL VARIABLES AND NECTAR SOURCES IN THE SIERRA NEVADA, CALIFORNIA

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Abstract

Fire can change the quality of habitat for many taxonomic groups, including butterflies. The abundance of nectar-producing plants, and the volume and concentration of the nectar in those plants, peaks in the initial years following a fire. Laboratory and controlled experiments have demonstrated that butterflies may have preferences for different sugars in those nectar sources, especially sucrose. However, sugar preferences have not been quantified for an assemblage of butterflies in a field setting. In 2014 and 2015, we conducted butterfly and vegetation surveys within the Rim Fire boundary on the Stanislaus National Forest (Tuolumne County, California). We surveyed eight sites throughout the butterfly flight season in both years and four additional sites in 2015. We analyzed the sugar and sucrose masses, and relative proportion of sucrose, in 20 known nectar sources. We found no evidence that intensity of butterfly use was associated with sugar mass or concentration, mass of sucrose, or the relative proportion of sucrose. Instead, butterflies appeared to use any sources that were available to them indiscriminately.

Fire also affects environmental attributes associated with the distribution, abundance, and reproduction of butterflies. Studies have demonstrated that species richness and abundance of butterflies respond to fire. However, the effects of fire on butterfly occupancy, and on environmental attributes that are associated with butterfly occupancy, are largely unknown. Abundance estimates are generally more-informative measures of population status than occupancy, but collecting data for abundance estimates is more time consuming than for estimating occupancy. We examined the extent to which butterfly occupancy and abundance in the first two years following the

Rim Fire were associated with environmental attributes that were affected by fire. We also tested whether fire severity explained variation in the environmental attributes that we included in models of butterfly occupancy and abundance. We found that environmental attributes associated with occupancy of some species were also associated with the abundances of those species, although the consistency of associations varied. Burn severity affected environmental attributes that were associated with butterfly occupancy and abundance. Understanding how fire affects environmental attributes that are associated with occupancy and abundance can inform use of prescribed fire or management following wildfire.

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CHAPTER 1

Sugars in nectar sources and their use by butterflies in the Sierra

Nevada, California

INTRODUCTION

The spatial and temporal distribution of plants that produce nectar affects the survival and reproduction of nectivorous invertebrates. For example, adults of many species of butterflies feed exclusively on nectar, and lack of nectar may limit the population sizes of certain species (Schultz and Dlugosch 1999). Moreover, the amount and composition of sugars in nectar can affect the survival and fecundity of some butterfly species; for example, sucrose was incorporated into the eggs of four butterfly species (O'Brien et al. 2004), and the volume of nectar consumed was correlated with female fecundity in *Speyeria mormonia* and *Euphydryas editha* (Murphy et al. 1983, Boggs and Ross 1993).

The abundance of plants that produce nectar, and the volume and concentration of nectar, peaks in the initial years following a fire. In some cases, prescribed fire can be used to promote regeneration of nectar-bearing forbs (King 2003, Potts et al. 2003). For example, nectar volume and sugar concentration were greatest in the first two years following fires in a Mediterranean ecosystem in Israel (Potts et al. 2003), and prescribed fire increased the abundance of plants that serve as nectar sources for *Lycaeides melissa samuelis*, a subspecies listed as endangered under the US Endangered Species Act, in Wisconsin, USA (King 2003). Furthermore, the abundance of nectar-containing flowers has been associated with the abundance and species richness of nectivorous insects. For example, in forests in eastern Texas, USA, the abundance of butterflies and their nectar sources was greatest in areas maintained by prescribed fire (Rudolph and Ely 2000). Similarly, the abundance of bees, species richness of bees, cover of flowers, and species richness of flowers were greatest in the first two years after a fire in the Mount Carmel

National Reserve, Israel (Potts et al. 2003). Additionally, butterfly abundance increased as the cover of nectar sources increased in grasslands of southern England (Curtis et al. 2015), and the density of the butterfly *Icaricia icarioides fenderi*, and other subspecies listed as endangered, was positively correlated with the amount of sugar in its native sources of nectar in Oregon, USA (Schultz and Dlugosch 1999). However, despite these investigations, little is known about nectar use in relation to the concentration and composition of sugar in individual flowers.

The three primary sugars in nectar are the disaccharide sucrose and the hexose monosaccharides fructose and glucose (Baker and Baker 1983). Some species of butterflies distinguished among these sugars in laboratory and controlled experiments. For example, *Battus philenor* preferred sucrose to fructose, and fructose to glucose (Erhardt 1991). *Ornithoptera priamus* preferred both sucrose and fructose to glucose (Erhardt 1992), and *Inachis io* preferred sucrose to fructose or glucose (Rusterholz and Erhardt 1997). In each of these experiments, captive butterflies were offered pure solutions of each sugar. In only one study (Rusterholz and Erhardt 1997) were butterflies offered mixtures of sugars (sucrose dominated; equal concentrations of sucrose, glucose, and fructose; and hexose dominated). One study concluded that *Colias alexandra* and *C. meadii* preferred nectar sources high in monosaccharide sugars to sucrose in a natural setting (Watt et al. 1974). These studies evaluated sugar preferences of individual species. To our knowledge, relations between nectar use by an assemblage of butterflies and the total amount and composition of sugars have not been studied in the field. Because most studies conducted in the laboratory or controlled environments found

single-species preferences for sucrose, it is possible that assemblages of butterflies may show similar preferences in a natural setting.

Optimal foraging theory posits that an animal's fitness is a function of its foraging efficiency, and that natural selection has resulted in foraging behaviors that maximize fitness (Pyke et. al. 1977). Therefore, one might expect butterflies to use nectar sources that maximize foraging efficiency. In laboratory and controlled experiments, the rate of nectar intake by several species of butterflies peaked at sucrose concentrations from 30-50% (weight : weight) (May 1985, Pivnick and McNeil 1985). Sucrose ingestion by *S. mormonia* was greatest at sucrose concentrations from 30-40 mg/ml (weight : volume) (Boggs 1988).

Nectar produced by different plants has different absolute and relative amounts of sucrose, glucose, and fructose. Baker and Baker (1983) proposed four sugar-ratio classes: sucrose dominant [sucrose/(fructose + glucose) (i.e., sugar ratio) > 0.99], sucrose rich (sugar ratio 0.50–0.99), hexose rich (sugar ratio 0.10–0.49), and hexose dominant (sugar ratio < 0.10). In some cases, butterflies may have access only to hexose-rich or hexose-dominant nectar sources, which are believed to be of lower quality than sucrose-rich or sucrose-dominant sources. The extent to which butterflies will use hexose-rich or hexose-dominant nectar sources in the absence of sucrose-rich or sucrose-dominant sources is unknown. Furthermore, the mass of sugar in hexose-dominated nectar may be greater than in sucrose-dominated nectar. Nectivorous animals, especially those with high energy requirements, may require nectar sources with a high concentration or volume of sugar, regardless of the composition of the sugar, whereas animals with low energy requirements may be able to use nectar sources with dilute sugar (Heinrich and Raven

1972). For example, Watt et al. (1974) concluded that *C. alexandra* and *C. meadii* preferred dilute nectar and nectar with a high concentration of monosaccharides to nectar that was rich in sucrose.

We tested whether use (not preference) of nectar sources by butterfly species in the Sierra Nevada (California, USA) in the first two growing seasons after a major fire was associated with the amount or composition of sugars. On the basis of the studies described above, we anticipated that use would be positively correlated with the mass of sugar and of sucrose, and with the relative proportion of sucrose. We also expected that use of nectar sources with sugar concentrations from 30-50 mg/ml would be greater than use of nectar sources with other sugar concentrations. However, because the majority of these hypotheses were based on studies conducted in controlled or laboratory environments, it was uncertain whether similar behavior would be observed in natural, uncontrolled environments.

METHODS

Field Methods

We collected data within the Rim Fire boundary on the Groveland Ranger District of the Stanislaus National Forest (Tuolumne County, California). The Rim Fire, one of the largest fires in California since accurate fire records have been maintained in this region (1932-present), occurred from August through October 2013 and burned more than 1040 km^2 (257,000 acres) of public and private land (USFS 2014). The vegetation on transects we surveyed is classified as Sierran yellow pine forest and Sierran montane forest (Miksicek et al. 1996). These forests are dominated by ponderosa pine (*Pinus*

ponderosa), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), and black oak (*Quercus kelloggii*). Understory species include manzanita (*Arctostaphylos* spp.), buckbrush (*Ceanothus* spp.), mountain misery (*Chamaebatia foliolosa*), chinquapin (*Castanopsis sempervirens*), and various berries (Miksicek et al. 1996).

Random selection of sampling locations was not possible due to steep topography, the lack of roads, and limited time available for travel. In 2014, we established eight 300-500 m transects. We established an additional four transects of the same length in 2015. Transects were placed along established two tracks and roads. Pre-fire vegetation composition and structure along each transect appeared to have been homogenous. Transect length varied because in some cases we could not locate 500 m with apparently homogenous vegetation composition and structure. The elevation of each transect ranged from approximately 1350 to 1450 m. In all but one case, the endpoints of different transects were separated by ≥ 100 m. In that case, the endpoints of two transects were separated by approximately 30 m, but the transects had opposing orientations, which minimized the probability of double-counting individual butterflies. The maximum distance between transects was approximately 24 linear km. We sampled each transect five times during June and July 2014 and five times from May through July 2015, which encompassed the majority of the butterfly flight seasons in these years. During each survey, an observer walked along the transect and identified each butterfly observed within 10 m on either side (Pollard and Yates 1993). We noted whether each butterfly was taking nectar, and, if so, the species on which it was feeding. We considered a

butterfly to be taking nectar if we observed the proboscis probing a floret. In some cases, we observed the same individual taking nectar from more than one plant species.

For each plant species on which we observed butterflies feeding, we collected from multiple plants a total of five florets that showed no signs of senescence. We covered each floret overnight with a fine-mesh cloth bag to prevent feeding by insects and to allow nectar to regenerate following any previous feeding (Bentley and Ellas 1983, Morrant et al. 2009). We secured the bag to the floret with a rubber band. We collected the floret during the following afternoon. We placed each floret in a 30 ml plastic vial with 2 ml of distilled water and shook the vial for 60 sec to wash the nectar from the floret (Grunfeld et al. 1989, Morrant et al. 2009). We maintained the samples on ice (typically for less than a week) and then transferred them to a -80ºC freezer.

Analysis Methods

We used high performance liquid chromatography-mass spectrometry (LC-MS) to quantify the masses of glucose, fructose, and sucrose for all plant species on which we observed butterflies feeding. We used an Agilent Technologies (Santa Clara, CA) 1290 high performance liquid chromatograph equipped with a 1290 Infinity column oven, a 1200 series auto-sampler, and a 6150B single quadrupole mass spectrometer.

The chromatography column was an Acquity BEH Amide column (2.1 × 100 mm, 1.7 µm particle size) (Waters, Milford, Massachusetts). Mobile phase A was acetonitrile and water (90:10) with 0.1% ammonium hydroxide. Mobile phase B was acetonitrile and water (50:50) with 0.1% ammonium hydroxide. The gradient was 100:0 to 30:70 (mobile phase A:B) with a flow rate of 0.40 ml/min. We set the column

temperature to 60˚C. We used OpenLAB CDS software (C.01.05) to analyze sugars. We analyzed five samples from each nectar source and reported the average and standard deviation. In a small number of cases ($n = 2$), we analyzed four rather than five samples due to improper handling or storage of one sample. For each sample analysis, we injected 1 µl of the nectar solution into the LC-MS without any pre-treatment.

To quantify the amount of sugars in each nectar sample, we prepared standard solutions of glucose, fructose, and sucrose at concentrations from 0.0005 to 0.30 mg/ml, which encompassed the anticipated range of sugar concentrations in our samples, and generated a calibration curve based on their peak area in the LC-MS. We then used the external calibration curve to quantify each sugar in the nectar solutions. In rare cases, we had to extrapolate the calibration curve to lower sugar concentrations. Because the volume of nectar we collected was unknown, we expressed concentrations as mg/ml of nectar solution (Grunfeld et al. 1989). To calculate sugar mass, we multiplied the sugar concentration by two because we used 2 ml of distilled water to wash nectar from the florets. The volume of nectar in each floret was negligible compared to the 2 ml of distilled water. To ensure accuracy of the measurements over the entire time the nectar samples were analyzed, the calibration curve was recollected after every 10 samples were processed.

We did not analyze nectar use by butterfly species or year due to small sample sizes. With the exception of *Eriodictyon californicum*, all plant species used as nectar sources in 2014 also were used in 2015. With the exception of *Pyrgus communis*, which was not observed in 2015, all butterfly species observed taking nectar in 2014 also were observed taking nectar in 2015. Before running regression models, we examined whether

covariates were correlated. No pair of covariates had a correlation coefficient >0.60, and therefore we did not remove any of the covariates from our analyses (Neter et al. 1996). We used linear regression to test whether intensity of use of each nectar source (the number of butterflies observed taking nectar from each source across both seasons) was associated with the total sugar mass, mass of sucrose, or relative proportion of sucrose. Additionally, we used multiple regression to examine the contributions of total sugar mass, mass of sucrose, and relative proportion of sucrose to intensity of use. We did not test for differences between intensity of use and nectar source abundance because not all nectar sources were available to all individuals across our sampling sites (Northrup et al. 2013).

RESULTS

In 2014, we observed 1–198 individuals of each of 29 species of butterflies (Table 1). During surveys, we recorded 11 nectar sources (i.e., plant species on which we observed one or more butterflies feeding) and observed 78 butterflies of 16 species taking nectar from one or more species of plants (Table 2). In 2015, we observed 1–974 individuals of each of 44 species of butterflies (Table 1). We recorded 19 nectar sources and observed 234 butterflies of 28 species taking nectar (Table 2). Across both years, we recorded a total of 45 species of butterflies and 20 nectar sources (Table 2). *Icaricia lupini* accounted for 104 of the 312 observations of butterflies taking nectar. We observed 31 *Vanessa cardui*, 29 *Colias eurytheme*, and 25 *Phyciodes mylitta* taking nectar, and observed ≤ 20 individuals of each of the 42 other butterfly species feeding on nectar.

The total mass of sugars from each nectar source (mean ± SD) ranged from 0.004 ± 0.002 mg (*Ceanothus* sp.) to 0.913 ± 0.599 mg (*Arnica* sp.) (Table 2). Thus, the

minimum and maximum mean concentrations of sugar from each nectar solution were 0.002 and 0.457 mg/ml, respectively. Average fructose mass ranged from 0.007 ± 0.015 mg (*Erysimum capitatum*) to 0.463 ± 0.324 mg (*Arnica* sp.), average glucose mass from 0.003 ± 0.003 mg (*Trifolium pratense*) to 0.448 ± 0.276 mg (*Arnica* sp.), and average sucrose mass from < 0.001 (*Dichelostemma* sp.) to 0.289 ± 0.179 mg (*E. californicum*) (Table 2). The average proportion of sucrose to total sugar mass ranged from < 0.001 (*Dichelostemma* sp.) to 0.414 ± 0.09 (*Collomia grandiflora*) (Table 2).

The correlation between the relative proportion of sucrose and the total mass or concentration of sugar was -0.20. The correlation between the mass or concentration and relative proportion of sucrose was 0.51, and the correlation between the mass or concentration of sucrose and all sugars was 0.49.

Intensity of use was not associated with the total mass or concentration of sugar ($R^2 < 0.01$, $p = 0.92$) (Figure 1), the total amount of sucrose ($R^2 < 0.01$, $p = 0.96$) (Figure 2), or the relative proportion of sucrose ($R^2 < 0.01$, $p = 0.76$) (Figure 3). Nor was intensity of use explained by a combination of total sugar mass, mass of sucrose, and proportion of sucrose ($R^2 = 0.02$, $p = 0.95$).

DISCUSSION

On the basis of the results of controlled or laboratory experiments, we anticipated that as the mass of sugar, mass of sucrose, or relative proportion of sucrose in a given nectar source increased, intensity of use by butterflies would increase. However, we found no evidence that intensity of use was associated with sugar mass or concentration, mass of sucrose, or the relative proportion of sucrose. The lack of correlation between

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intensity of use and the sugar properties we measured may be attributed to several factors.

Even if butterflies have preferences related to concentration or composition of sugar, nectar sources with those attributes may not be available in some locations or time periods. Different nectar sources are present throughout the flight season. Because survival or reproduction of many species of butterflies is associated with nectar, a majority of taxa may be relative generalists with respect to this resource (Scott 1986). Most of the butterfly species we observed used diverse nectar sources throughout the season (Table 1). We only analyzed sugar amount in our samples, but other nectar constituents exist.

Not only sugars but amino acids and water in nectar may affect survival and reproduction of butterflies (Boggs 1987). Provision of amino acids increased reproduction in male and female *Cenonympha pamphilus* and female *Araschnia levana* (Mevi-Schutz and Erhardt 2005, Cahenzli and Erhardt 2012, 2013). In controlled experiments, *Pieris rapae* preferred solutions with both sugar and amino acids to sugar-only solutions (Alm et al. 1990). However, male *B. philenor* preferred solutions with sugar only to those with both sugar and amino acids (Erhardt 1991). Additionally, although sucrose, fructose, and glucose are the three main sugars in nectar, other sugars can be present. It is possible that, when present, these other sugars are used by or attract butterflies. We recommend that future studies of nectar-source preferences of butterflies, especially those at the assemblage level, examine amino acid composition and the full range of sugars.

We estimated the amount of sugar in a given floret for each nectar source. Many factors affect the amount of sugar produced by a floret, including ambient temperature, time of collection, microclimate, and soil chemistry (Jakobsen and Kristjansson 1994, Farkas et al. 2012). However, the ratio of sucrose to glucose and fructose in the florets of a given plant species is relatively constant (Baker and Baker 1982, 1983). We collected samples at roughly the same time each day, but we could not control for environmental attributes such as microclimate and soil chemistry, and we did not sample each nectar source in both years. Additionally, drought may have negative effects on the volume of nectar produced (Carroll et al. 2001), and our study areas experienced drought conditions in 2014 and 2015. In non-drought years, the volume of nectar produced may be higher, although the concentrations of sugars in nectar should remain constant (Carroll et al. 2001). We expected that intensity of use would be greater between sugar concentrations of 30-50 mg/ml. However, the concentrations in our sugar solutions never exceeded 50 mg/ml, and we found no relation between intensity of use and concentration.

Our response variable was related to use, not preference. In part because we surveyed transects over a relatively large area, not all nectar sources were available to all species of butterflies in all locations. Moreover, the period of our observations was brief relative to the flight period of an individual or species. We observed the greatest number of individuals feeding on the nectar source for which we recorded the greatest number of florets, *Acmispon nevadensis*, which was present on eight of our 12 transects. However, the species on which we observed the second-greatest number of individuals feeding, *Calyptridium umbellatum*, was present on two transects. A few small patches of the nectar source *Apocynum androsaemifolium* were present on one transect, but the number

of individuals we observed feeding on *A. androsaemifolium* was greater than the number we observed feeding on 50% of the nectar sources. By contrast, nectar sources such as *Chamerion angustifolium* and *C. grandiflora* were present and abundant on most transects, but we observed one individual feeding on each.

Some plant species have many small and dense florets, whereas other species have one large floret. When florets are dense, insects can take nectar from many florets without expending much energy on flight, even if the amount of sugar or nectar in each floret is relatively low (Heinrich and Raven 1972). Some nectar sources in our study area, such as *C. foliolosa* and *A. nevadensis*, were present in patches that included hundreds or thousands of florets. The density of other nectar sources, such as *Drymocallis glandulosa* and *Lathyrus nevadensis*, was comparatively low.

All of the nectar sources in our study area were native except *T. pratense*. Butterflies may prefer native nectar sources or sugars. For example, in upland prairies in western Oregon, *I. icarioides fenderi* densities were not associated with the densities of native flowering plants, but were strongly associated with the mass of sugars from native sources (Schultz and Dlugosch 1999). Female *I. icarioides fenderi* preferred native nectar sources to non-native nectar sources (Thomas and Schultz 2015). It is possible that butterflies in our study area selected native nectar sources. However, we noted few non-native species of flowering plants in the areas that we surveyed. Therefore, butterflies may have had access only to native species, and their use of these native sources may be attributable to availability rather than preference. Species richness and abundance of bumblebees, solitary bees, and lepidoptera were greater in plots in which an invasive

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non-native source of nectar and pollen (the thistle *Carduus acanthoides*) was present than in identical plots in which it was absent (Russo et al. 2015).

Previous studies of butterfly preferences for different sugars or nectar sources in controlled or laboratory settings do not represent what is available to species in an uncontrolled environment. Our field data were inconsistent with expectations based on data from laboratory and controlled experiments. Butterflies appeared to use any sources that were available to them, regardless of nectar or sugar mass or composition. Individual butterfly species may have sugar preferences, but we found no evidence of assemblage-level patterns. The difference between intensity of sugar use or sugar preferences in the laboratory and in the field may be explained by individual species' preferences, competition for resources, resource availability, or energy requirements. Moreover, the abundance of nectar-producing plants, and the volume and concentration of nectar, is thought to peak in the initial years after a fire. Therefore, as time since fire increases, and as succession progresses, the composition of plants from which butterflies will take nectar and the attributes of that nectar will change. Longer-term studies of nectar use from a more-extensive area may reveal species-specific or temporal patterns.

Table 1. Number of butterflies observed during surveys in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015. Taxonomy and nomenclature follow Pelham (2015).

	Number of individuals observed		Number of observations of feeding
Species	2014	2015	
Parnassius clodius	3	3	1
Papilio rutulus	0	5	2
Papilio eurymedon	3	31	3
Papilio multicaudatus	0	1	0
Colias eurytheme	79	482	29
Anthocharis sara	0	3	0
Pieris rapae	0	1	0
Pontia protodice	1	5	1
Pontia occidentalis	0	1	0
Lycaena cupreus	4	1	2
Satyrium californica	0	3	2
Satyrium saepium	0	3	0
Callophrys gryneus	1	14	16
Callophrys augustinus	6	3	6
Strymon melinus	15	10	13
Celastrina ladon	2	16	11
Glaucopsyche piasus	2	23	4
Leptotes marina	0	1	1
Cupido amyntula	2	14	0
Icaricia saepiolus	5	4	0
Icaricia icarioides	17	71	3
Icaricia lupini	198	974	104
Danaus plexippus	5	11	0
Bolora epithore	6	4	0
Speyeria hydaspe	11	28	3
Limenitis lorquini	1	32	1
Adelpha californica	37	23	1
Vanessa virginiensis	0	18	8
Vanessa cardui	90	22	31
Vanessa atalanta	0	1	1
Nymphalis californica	0	1	1
Polygonia gracilis	3	2	0
Junonia coenia	1	189	18
Euphydryas chalcedona	1	1	1
Chlosyne palla	0	1	0

Phyciodes mylitta	15	181	25
Coenonympha tullia	2	12	1
Epargyreus clarus	3	4	1
Thorybes pylades	0	1	3
Erynnis propertius	0	1	0
Erynnis persius	6	207	16
Pyrgus communis	2	0	1
Hesperia juba	0	1	0
Polites sonora	0	5	1
Poanes melane	1	1	0
Total	522	2415	312

Table 2. Nectar sources, number of butterflies that were observed feeding on those sources in 2014 and 2015, masses (mg) of constituent sugars, and relative proportion of sucrose. Masses and proportions are averages (± SD) from 5 florets.

Species	Number of observations of use (2014)	Number of observations of use (2015)	Fructose mass	Glucose mass	Sucrose mass	Total sugar mass	Proportion sucrose
Acmispon nevadensis	33	90	0.071 ± 0.040	0.057 ± 0.032	0.083 ± 0.060	0.210 ± 0.127	0.355 ± 0.125
Calyptridium umbellatum	20	25	0.012 ± 0.009	0.008 ± 0.007	0.002 ± 0.002	0.022 ± 0.017	0.031 ± 0.013
Arnica sp.	0	31	0.463 ± 0.324	0.448 ± 0.276	0.001 ± 0.002	0.913 ± 0.599	0.002 ± 0.003
Ceanothus sp.	1	15	0.002 ± 0.001	0.002 ± 0.001	0.000 ± 0.000	0.004 ± 0.002	0.013 ± 0.025
Chamaebatia foliolosa	1	14	0.395 ± 0.097	0.382 ± 0.125	0.049 ± 0.008	0.825 ± 0.226	0.061 ± 0.012
Monardella odoratissima	4	10	0.059 ± 0.042	0.035 ± 0.030	0.037 ± 0.023	0.131 ± 0.089	0.291 ± 0.079
Gilia capitata	3	10	0.110 ± 0.018	0.125 ± 0.011	0.057 ± 0.021	0.292 ± 0.030	0.196 ± 0.065
Dichelostemma sp.	3	10	0.113 ± 0.049	0.085 ± 0.044	< 0.001	0.198 ± 0.093	< 0.001
Apocynum androsaemifolium	10	3	0.137 ± 0.149	0.037 ± 0.021	0.092 ± 0.060	0.267 ± 0.217	0365 ± 0.084

Trifolium pratense	1	7	0.008 ± 0.008	0.003 ± 0.003	0.002 ± 0.002	0.014 ± 0.012	0.310 ± 0.387
Drymocallis glandulosa	1	4	0.270 ± 0.118	0.190 ± 0.083	0.002 ± 0.005	0.463 ± 0.197	0.004 ± 0.007
Anaphalis margaritacea	0	4	0.012 ± 0.009	0.008 ± 0.007	0.002 ± 0.002	0.022 ± 0.017	0.133 ± 0.066
Erysimum capitatum	0	4	0.007 ± 0.015	0.004 ± 0.009	0.003 ± 0.007	0.014 ± 0.031	0.248 ± 0.433
Wyethia angustifolia	0	2	0.145 ± 0.076	0.115 ± 0.061	0.134 ± 0.076	0.394 ± 0.200	0.333 ± 0.088
Eriodictyon californicum	1	0	0.226 ± 0.060	0.210 ± 0.055	0.289 ± 0.179	0.725 ± 0.275	0.365 ± 0.127
Chamerion angustifolium	0	1	0.421 ± 0.054	0.276 ± 0.059	0.127 ± 0.043	0.824 ± 0.074	0.157 ± 0.059
Prunella vulgaris	0	1	0.029 ± 0.011	0.021 ± 0.012	0.014 ± 0.002	0.063 ± 0.024	0.241 ± 0.102
Lathyrus nevadensis	0	1	0.070 ± 0.097	0.035 ± 0.047	0.033 ± 0.066	0.139 ± 0.180	0.114 ± 0.190
Achillea millefolium	0	1	0.017 ± 0.007	0.010 ± 0.005	0.003 ± 0.002	0.029 ± 0.013	0.094 ± 0.042
Collomia grandiflora	0	1	0.016 ± 0.009	0.016 ± 0.011	0.027 ± 0.023	0.059 ± 0.043	0.414 ± 0.091
Total	78	234					

Figure 1: Relation between intensity of use (number of times each nectar source was used) and total sugar mass in each nectar source used by butterflies in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015. The dotted line is the correlation trend line ($R^2 < 0.01$, $p = 0.92$).
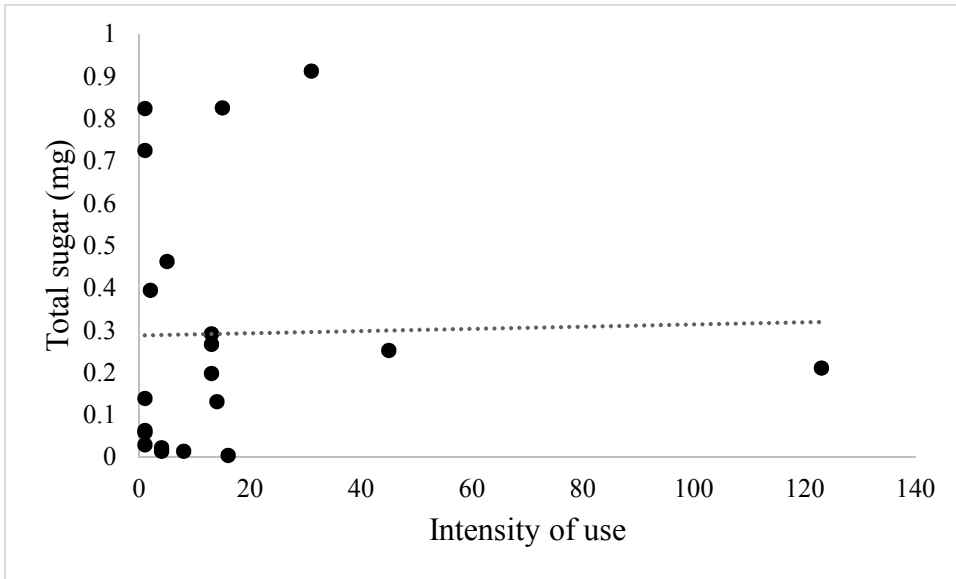
Figure 2: Relation between intensity of use (number of times each nectar source was used) and the total sucrose mass in each nectar source used by butterflies in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015. The dotted line is the correlation trend line ($R^2 < 0.01$, $p = 0.96$).
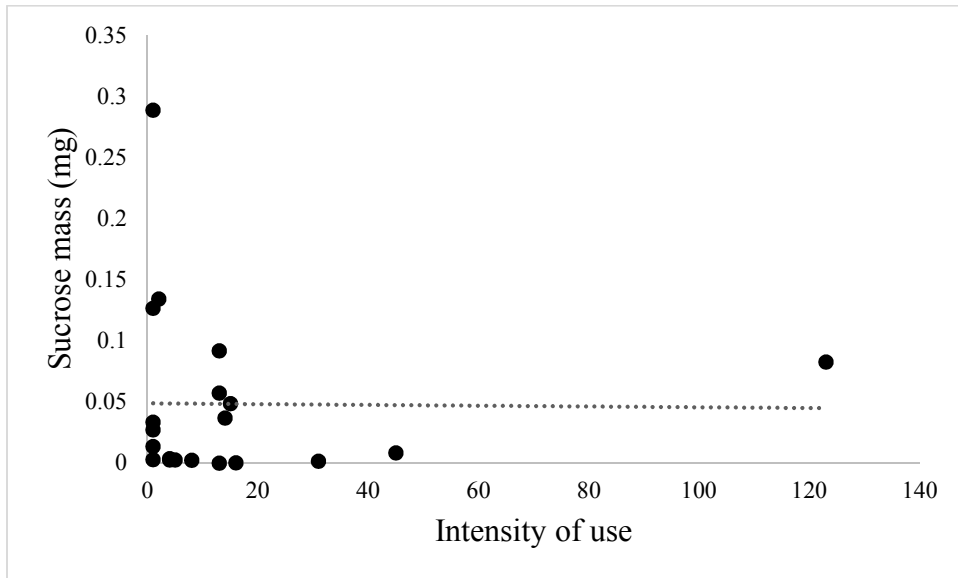
Figure 3: Relation between intensity of use (number of times each nectar source was used) and proportion of sucrose to total sugar amount in each nectar source used by butterflies in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015. The dotted line is the correlation trend line ($R^2 < 0.01$, $p = 0.76$).
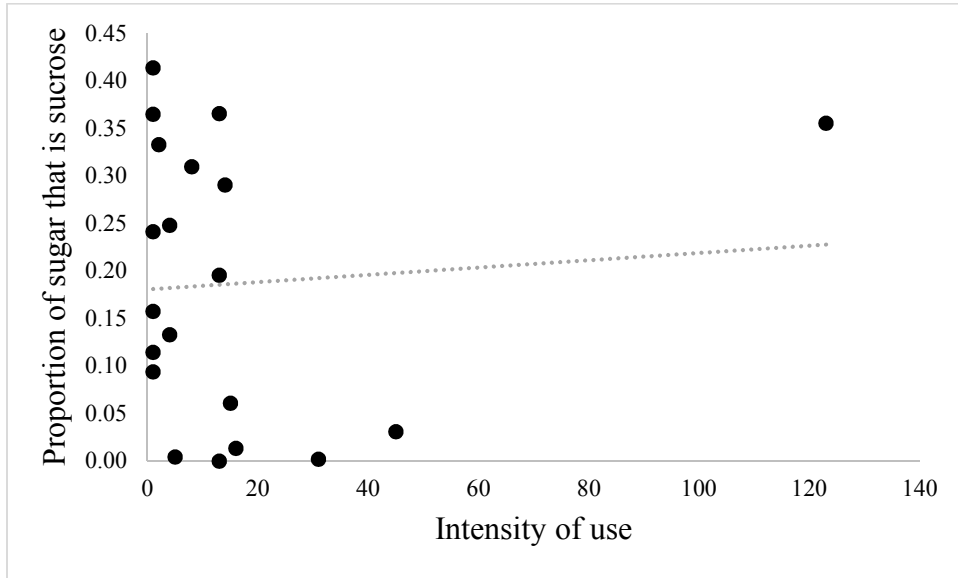
CHAPTER 2

Environmental associations with post-fire butterfly occupancy in

the Sierra Nevada, California

INTRODUCTION

Fire affects environmental attributes associated with the distribution, abundance, and reproduction of butterflies, including nectar availability and quality. Adults of many species of butterflies feed exclusively on nectar, and availability of nectar affects the population sizes or fecundity of certain species (Murphy et al. 1983, Boggs and Ross 1993, Schultz and Dlugosch 1999). Prescribed fire has been used to increase the abundance of nectar sources used by butterflies. For example, the abundance of nectar sources for *Lycaeides melissa samuelis*, a subspecies listed as endangered under the US Endangered Species Act, increased after a prescribed fire in Wisconsin, USA (King 2003). In forests of eastern Texas, USA, the abundances of nectar sources used by butterflies were greatest in areas maintained by prescribed fire (Rudolph and Ely 2000). Abundance and species richness of butterflies also respond to fire. For example, following fires in riparian areas within coniferous forests in Oregon and California, USA, the number of butterflies in burned areas was two to three times greater than the number in comparable areas that were not burned (Huntzinger 2003). However, the effects of fire on butterfly occupancy (the probability that a given site is occupied by a given species; MacKenzie et al. 2002), and on environmental attributes that are associated with butterfly occupancy, are largely unknown.

Occupancy is relevant to both population monitoring and assessment of habitat associations. Although estimates of abundance are more-informative measures of population status than estimates of occupancy, collection of the data necessary to estimate abundance generally requires more time and money than collection of occurrence data (MacKenzie et al 2004). Therefore, estimation of abundance may not be

feasible for many studies. Because models of occupancy do not require individuals to be marked or recaptured, they can be applied to animals that occur at low densities, or when capturing animals is not practical. It is possible that environmental factors that are associated with occupancy of a species also could be associated with that species' abundance.

Effective modeling of occupancy depends on whether five assumptions are met or, if violated, overcome: occupancy probability remains constant, or changes in probability of occupancy are accurately modeled; probability of detection remains constant, or changes in probability of detection are accurately modeled; detections of individuals at each site are independent; species are not falsely detected; and occupancy status does not change among surveys (closure) (MacKenzie et al. 2002). Application of occupancy models to multiple species of butterflies that were sampled simultaneously is complicated by movements of butterflies between surveys (Hayes et al. 2015) and by taxonomic, temporal, and spatial variation in phenology. In these cases, individual species often do not meet the assumption of closure. Previous authors have addressed violations of this assumption by modeling individual broods of multivoltine species (Pellet 2007) or by limiting analyses to known flight periods (van Strien et al. 2011). More recently, butterfly occupancy has been estimated with models that relax the assumption of closure by allowing for a single entry and exit of the species from each sampling location (Kendall et al. 2013, Roth et al. 2014, Fleishman et al. in review). Environmental covariates can be added to these models to explore whether they are associated with probabilities of detection and occupancy.

We examined the extent to which butterfly occupancy and abundance in the first two years following the Rim Fire, one of the largest fires in California since accurate fire records for that region have been maintained (1932–present), were associated with environmental attributes that were known or hypothesized to be affected strongly by the fire. The Rim Fire burned on the west slope of the Sierra Nevada from August through October 2013 and encompassed more than 1040 km^2 (257,000 acres) of public and private land (USFS 2014). We also tested whether variation in the environmental attributes that we included in models of butterfly occupancy and abundance was explained by local differences in fire severity. To our knowledge, this is the first study of post-fire butterfly occupancy, and the first to compare the effects of environmental attributes on both butterfly occupancy and abundance.

METHODS

Field Methods

We collected data within the Rim Fire boundary on the Groveland Ranger District of the Stanislaus National Forest (Tuolumne County, California). The vegetation in the areas in which we worked is classified as Sierran yellow pine forest and Sierran montane forest (Miksicek et al. 1996). These forests are dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), and black oak (*Quercus kelloggii*). Understory species include manzanita (*Arctostaphylos* spp.), buckbrush (*Ceanothus* spp.), mountain misery (*Chamaebatia foliolosa*), chinquapin (*Castanopsis sempervirens*), and various berries (Miksicek et al. 1996).

Random selection of sampling locations was not possible due to steep topography, the lack of roads, and limited time available for travel. In 2014, we established eight 300-500 m transects along which pre-fire vegetation composition and structure appeared to have been homogenous. We established an additional four transects within the same range of lengths in 2015. Transect length varied because in some cases we could not locate 500 m with apparently homogenous pre-fire vegetation composition and structure. Transects were placed along established two tracks and roads. The elevation of each transect ranged from approximately 1350 to 1450 m. In all but one case, the endpoints of different transects were separated by ≥ 100 m. The maximum linear distance between transects was approximately 24 km. We sampled each transect that was established in 2014 five times during June and July 2014 and we sampled all transects five times from May through July 2015, which encompassed the majority of the butterfly flight seasons in those years. We divided each transect into 20-m segments, which were the sample units for analysis. During each survey, an observer walked along the transect and identified each butterfly observed within 10 m on either side (Pollard and Yates 1993). We noted whether each butterfly was taking nectar, and, if so, the species on which it was feeding. In some cases, the same individual was observed taking nectar from more than one plant species. We estimated abundance as the total number of individuals of each species that we observed during the season. It is possible that a small number of individuals were recorded on more than one survey, but we considered this situation unlikely given the lag time between surveys.

We surveyed vegetation along each transect within one day of each butterfly survey, except in one case, when we conducted vegetation surveys 9 days after butterfly

surveys for a subset of the transects due to inclement weather. During each survey, we used a random number generator to select 1 m^2 in each 20-m segment for fine-resolution vegetation sampling. Within that 1-m^2, we used a concave spherical densiometer to measure the percentage of canopy cover, visually estimated the percentage of live ground cover, identified all known or potential nectar sources, and counted the number of florets of each nectar source.

For each plant species on which we observed adult butterflies feeding, we collected from multiple plants a total of five florets that showed no signs of senescence. We covered each floret overnight with a fine-mesh cloth bag, secured with a rubber band, to prevent feeding by insects and to allow nectar to regenerate following any previous feeding (Bentley and Ellas 1983, Morrant et al. 2009). We collected the florets during the following afternoon. We placed each floret in a 30 ml plastic vial with 2 ml of distilled water and shook the vial for 60 sec to wash the nectar from the floret (Grünfeld et al. 1989, Morrant et al. 2009). We maintained the samples on ice (typically for less than a week) and then transferred the samples to a -80ºC freezer.

We used high performance liquid chromatography-mass spectrometry to quantify the masses (mg) of glucose, fructose, and sucrose for all plant species from which we collected florets. In most cases, we analyzed each of the five samples (florets) from each nectar source. In a small number of cases, we analyzed four rather than five samples due to improper handling or storage of one sample. We multiplied the mean mass of sugar (sum of glucose, fructose, and sucrose) for each nectar source by the number of florets in each 20-m segment to estimate the mass of sugar available to butterflies in that segment. Full methods for extraction and estimation of sugar mass are in Chapter 1 (Methods).

From the vegetation surveys, we derived six environmental covariates for each segment. We calculated the survey-specific number of florets and also summed the number of florets across each season. For each season, we calculated the average canopy cover, live ground cover, sugar mass, and categorical abundance of florets that serve as nectar sources. Researchers previously found that detection probabilities and occupancy of a considerable proportion of butterflies in three ecosystems increased as the categorical abundance of nectar sources increased (Fleishman et al. in review). Those categorical estimates were intended to classify abundance along an approximately logarithmic or semi-logarithmic scale. The estimates were comparable among observers in a given geographic area (Fleishman and Pavlik unpublished data), but might vary among years and likely would vary among regions. In this study, we measured abundance of nectar sources quantitatively, as a continuous variable. Nevertheless, to explore whether inferences about the strength of associations between occupancy and nectar abundance depended on the precision with which the latter was assessed, we created post-hoc categories of abundance of nectar sources (none, low, moderate, and high) on the basis of our previous field experience. In 2014, we classified segment-level abundances of 1-49, 50-399, and > 399 florets as low, moderate, and high, respectively. In 2015, the abundance of florets was greater than in 2014, and we classified segment-level abundances of 1-99, 100-499, and > 499 florets as low, moderate, and high, respectively. We acknowledge that it would have been preferable to conduct a categorical assessment in the field, but felt the rough comparison was worthwhile regardless.

Analysis Methods

We used single-season occupancy models with relaxed closure assumptions in Program MARK (White and Burnham 1999) to estimate occupancy and detection probabilities (Kendall et al. 2013). The original occupancy model includes two parameters: ψ_i, the probability that a given species is present at site i; and $p_{i,t}$, the probability that the species is detected at site i at time t, conditional on its presence (MacKenzie et al. 2002). The occupancy model with relaxed closure assumptions adds two parameters: β_{ij}, the probability that the species enters the site between visits (surveys) j and $j + 1$, given that the site is occupied; and d_{ij}, the probability that the species exits the site (and therefore cannot be detected) before visit $j + 1$, given that the species is present on visit j (Kendall et al. 2013). We standardized all continuous covariates. We limited analyses to species with naïve occupancy (i.e., the proportion of sites in which the species was observed, not accounting for detection probability) ≥ 0.28 and ≤ 0.70 in each year, and to those that we observed using the transects (e.g., taking nectar, mating, perching).

We used forward model selection to add covariates to models one at a time, and implemented model selection in two stages: modeling probability of detection and modeling probability of occupancy. In both stages, we used Akaike's Information Criterion adjusted for small sample sizes (AICc) to compare models (Burnham and Anderson 2002). In the first stage, we evaluated associations between covariates and probabilities of detection (p_{ij}), entry (β_{ij}), and departure (d_{ij}). We estimated p_{ij} as a fixed effect of visit (i.e., we estimated p_{ij} for each of the 5 surveys). We also tested whether the survey-specific number of florets affected p_{ij} estimates. We used survey five as the intercept in our models. We estimated β_{ij}, and d_{ij} as linear functions of time. If univariate models were ranked lower than the null models, the covariates in the univariate models

were not retained for further modeling. We fit multivariate models that contained every possible combination of covariates from the univariate models that were ranked higher than the null model. We included the highest-ranked model (or, if the AICc value of a competing model was within two units of our highest-ranked model, the most parsimonious model) in the second stage of modeling.

In the second stage, we modeled occupancy as a function of five covariates: number of florets across the season, categorical abundance of nectar, sugar mass, canopy cover, and live ground cover. We included ground cover in our models because as the cover of understory vegetation increases, the distribution and abundance of host plants also may increase. Additionally, ground cover affects microclimatic factors, such as temperature, that may affect butterflies (Calvert et al. 1986). We included categorical abundance of nectar in addition to number of florets and sugar mass because the former was associated with detection and occupancy of many butterfly species in the Chesapeake Bay Lowlands of eastern Virginia and in the Great Basin of Nevada and California (Fleishman et al. in review). Moreover, estimation of categorical abundance of nectar generally requires less time than estimation of abundance as a continuous variable.

Initially, we fit univariate models of occupancy. Because we fit models with three different measures of nectar abundance (number of florets, categorical abundance, and sugar mass), we included only the covariate from the highest-ranked univariate model (or, if the AICc value of a competing model was within two units of our highest-ranked model, from the most parsimonious model) in our multivariate models. If the null model had a higher rank than the univariate models, we did not retain the covariates from the

univariate models. If multiple univariate models had higher ranks than the null model, we fit models with every combination of those covariates.

If the 95% confidence interval of the regression coefficient for a given covariate in the most highly ranked model did not overlap zero, we considered the covariate to be associated strongly with the response variable. We report occupancy and detection probabilities from the highest-ranked model for each species. If the AICc value of a competing model was within two units of our highest-ranked model, we report occupancy and detection probabilities from the most parsimonious model.

We used univariate, negative binomial generalized linear models to examine the effects of canopy cover, live ground cover, number of florets, sugar mass, and categorical abundance of nectar sources on the abundances of the species for which we modeled occupancy.

We used single-factor, one-way analysis of variance (ANOVA) to examine relations between soil and vegetation burn severity and canopy cover, live ground cover, number of florets, and sugar mass in 2014 and 2015. We excluded transects that had been logged after the 2014 field season from our analysis of canopy cover in 2015 ($n = 2$). We used Tukey's post-hoc tests to quantify pairwise differences between fire severity classes. During the first survey in 2014, we qualitatively classified the proportion of each segment that burned (none, some, or all). We used ArcGIS v. 10.3 (ESRI, Redlands, California) to compare these data with remotely sensed measures of vegetation burn severity from the US Forest Service's Rapid Assessment of Vegetation Condition after Wildfire (RAVG) process (http://www.fs.fed.us/postfirevegcondition/index.shtml). The RAVG classification generally matched our classification. The RAVG process derives vegetation

burn severity by applying a Relative Differenced Normalized Burn Ratio (RdNBR) to pre-fire and post-fire images from the Landsat Thematic Mapper. Vegetation burn severity was classified by RAVG as unchanged, low, moderate, or high. We obtained estimates of soil burn severity from the US Forest Service's Burned Area Emergency Response (BAER) team (http://activefiremaps.fs.fed.us/baer/download.php?year=2013). The BAER team derives soil burn severity by measuring the difference in spectral reflectivity in pre-fire and post-fire satellite images. Soil burn severity was classified as unburned or very low, low, moderate, or high. If any of our segments overlapped multiple severity classes, we assigned the segment to the severity class that covered the majority of that segment. If multiple severity classes appeared to be equally represented in a segment, we assigned the segment to the lower severity class.

RESULTS

In 2014, we recorded 1-198 individuals of 29 species of butterflies (Table 1). One species, *Icaricia lupini*, met our criteria for modeling occupancy. In 2015, we observed 1-974 individuals of 44 species of butterflies (Table 1). Five species—*Colias eurytheme*, *Icaricia lupini*, *Junonia coenia*, *Phyciodes mylitta*, and *Erynnis persius*—met our criteria for modeling occupancy. Naïve estimates of occupancy were 0.63 for *C. eurytheme*, 0.38 and 0.66 for *I. lupini* in 2014 and 2015, respectively, 0.52 for *J. coenia*, 0.44 for *P. mylitta*, and 0.28 for *E. persius*. The number of florets of nectar sources per segment was 83.8 ± 322.6 (mean ± SD) in 2014 and 143.0 ± 341.6 in 2015.

Maximum detection probabilities on a given survey ranged from 0.35 for *J. coenia* to 0.81 for *I. lupini* (2015) and *E. persius* (Table 2). Time was associated with the probability of detection of *J. coenia*, *P. mylitta*, and *E. persius* (effect sizes varied among

surveys). Survey-specific number of florets was associated with the probability of detection of *I. lupini* (0.95) in 2015. No covariates were associated with the probability of detecting *I. lupini* in 2014 or *C. eurytheme* in 2015.

Occupancy ranged from 0.22 (*E. persius*) to 0.88 (*C. eurytheme*) (Table 2). Occupancy of each species was associated with at least one covariate (Table 3). Canopy cover was negatively associated with occupancy of *C. eurytheme*, *I. lupini*, *P. mylitta*, and *E. persius*. Regression coefficients ranged from -1.20 for *P. mylitta* to -1.81 for *C. eurytheme*. Live ground cover was positively associated with occupancy of *I. lupini*, *J. coenia*, and *P. mylitta*. Regression coefficients ranged from 0.47 (2014) for *I. lupini* (2014) to 1.75 for *P. mylitta*. Number of florets was positively associated with occupancy of *I. lupini* (2014; regression coefficient 4.04) and *E. persius* (1.18). Sugar mass was positively associated with occupancy of *C. eurytheme* (regression coefficient 2.23). Categorical abundance of nectar was not associated with occupancy of any species. The highest-ranked or most parsimonious models for all species except *J. coenia* included multiple covariates (Table 3).

Occupancy models for *C. eurytheme* and *I. lupini* (2015) that included sugar mass were supported more strongly than models that included number of florets or categorical abundance of nectar. Models for *I. lupini* (2014), *P. mylitta*, and *E. persius* that included number of florets were supported more strongly than models that included sugar mass or categorical abundance of nectar. The null model for *J. coenia* was supported more strongly than models that included nectar covariates.

Canopy cover was significantly associated with the abundances of *C. eurytheme*, *I. lupini* (2015), *P. mylitta,* and *E. persius* (Table 4). Live ground cover was significantly

associated with the abundances of all five species (Table 4). Categorical nectar abundance was significantly associated with the abundances of *C. eurytheme*, *I. lupini* (2015), *P. mylitta*, and *E. persius* (Table 4). Number of florets and sugar mass were significantly associated with the abundances of *C. eurytheme*, *I. lupini* (2015), and *E. persius* (Table 4).

In 2014, canopy cover and sugar mass were significantly associated with vegetation burn severity (Table 5). Average canopy cover in areas with low, moderate, and high vegetation burn severity was significantly lower than in unchanged areas (Tables 6, 8). In 2015, all environmental covariates were significantly associated with vegetation burn severity (Table 5). Canopy cover decreased significantly as vegetation burn severity increased (Tables 6, 8). Live ground cover was significantly greater in areas with moderate or high vegetation burn severity than in unchanged areas or areas with low vegetation burn severity. Number of florets and sugar mass were significantly greater in areas with high vegetation burn severity than in unchanged areas or areas with low vegetation burn severity.

In 2014, no covariates were significantly associated with soil burn severity (Table 5). In 2015, however, all environmental covariates were significantly associated with soil burn severity. Canopy cover was significantly greater in areas that were unburned or had very low or low soil burn severity than in areas with moderate soil burn severity (Tables 7, 8). Live ground cover was significantly greater in areas with moderate soil burn severity than in areas with any other severity level. Number of florets and sugar mass were significantly greater in areas with moderate soil burn severity than in areas that were unburned or had very low or low soil burn severity.

DISCUSSION

By fitting occupancy models that accounted for lack of closure, we identified environmental covariates associated with probabilities of detection and occupancy of five species of butterflies at fine spatial resolution. As time since fire increases, environmental associations with detection and occupancy probabilities of butterflies likely change. For example, different covariates were included in the highest-ranked models of occupancy of *I. lupini* in 2014 and 2015.

In 2015, survey-specific number of florets was strongly associated with the detection probability of *I. lupini*. The number of *I. lupini* that we observed taking nectar in 2015 was greater than that of any other butterfly species. Butterflies generally are easier to detect when they are feeding on nectar than when they are hidden in vegetation or flying. Observers also may spend more time searching for butterflies near known nectar sources. However, the number of florets of nectar sources did not appear to be associated with detection probabilities of species that rarely if ever took nectar within our study area. For example, we observed relatively few *P. mylitta* and *E. persius* taking nectar, and the null models of detection for these species were ranked higher than univariate models that included survey-specific number of florets.

Time was associated with detection probabilities of three species. Because we used survey five, the last survey of the season, as the intercept in our models, the phenology of a given species affected whether time was positively or negatively associated with its detection probability. In temperate ecosystems, the average lifespan of an adult butterfly is about one week (Scott 1986). Flight periods differ among species and among years. If surveys are conducted outside of the flight period for a species, or when

few individuals are present, detection probabilities will be lower than if surveys are

conducted during peak flight periods or when many individuals are present. However, if

the flight period is sufficiently long (e.g., if the species has multiple broods) and

individuals are available for detection throughout the sampling period, the probability of

detection may not change over time. *I. lupini* and *C. eurytheme* were present during all

surveys, and probabilities of detection of these species were not associated with time. We

noted temporal changes in the presence and abundance of the three species for which

time was associated with probability of detection.

Live ground cover was positively associated with occupancy of three species. We

observed each of the five species that we modeled laying eggs on plants in the

understory. As noted above, ground cover may be correlated with the distribution and

abundance of host plants and microclimate. Additionally, ground cover may be positively

correlated with the number of florets of nectar sources, although we found a negative

correlation between these two covariates in our study ($r = -0.31$).

Canopy cover was strongly and negatively associated with occupancy of four

species. Some species of butterflies bask to increase or maintain body temperatures

(Clench 1966). As canopy cover decreases, solar insolation in the understory increases.

Solar insolation may affect butterflies either physiologically (Weiss et al. 1988, 1991) or

indirectly, via responses of host plants, nectar sources, and other plants that provide

shelter or perches in the understory.

We previously included categorical abundance of nectar in occupancy models for

butterflies (Fleishman et al. in review). Our results suggest that continuous measures of

nectar abundance may explain a greater proportion of the variance in probabilities of

detection and occupancy than categorical measures. The number of florets often was more strongly associated with occupancy than abundance classes or sugar mass. Additionally, the time and cost necessary to estimate sugar mass with high performance liquid chromatography-mass spectrometry is considerably higher than that necessary to estimate the number of florets.

Abundances of butterflies increased substantially between the first and second growing seasons after the Rim Fire. For example, we detected 198 *I. lupini* in 2014 and 974 in 2015. Canopy cover was associated with both abundance and occupancy of all species except *J. coenia*. Live ground cover was associated with the abundances of all five species and with occupancy of all species except *E. persius*. Categorical nectar abundance was not associated with occupancy of any species, but was significantly associated with the abundances of four species. Number of florets and sugar mass generally were more strongly associated with abundance than with occupancy of butterflies.

Fire severity affected values of environmental variables associated with butterfly occupancy, such as canopy cover and live ground cover. Many plant species that are used by butterflies are early successional species, and high levels of soil nutrients after the fire may have supported growth of understory plants (Rice 1993). Our results suggest that fires of high and moderate severity, or patches in which severity was relatively high, may stimulate regrowth of understory plants and increase nectar source abundance more than low-severity fires, while decreasing canopy cover. Butterfly occupancy and abundance ultimately may be greater in areas in which fire severity was moderate or high than in areas with low severity fires.

Life history traits of butterflies also may affect their spatial distribution or colonization rates after a fire. *J. coenia* and *C. eurytheme* typically travel long distances as adults (Scott 1986, Fleishman et al. 1997), and species with high vagility may be able to colonize severely burned areas more quickly than species with low vagility. However, we recorded numerous species with low vagility in areas with high burn severity in the first growing season after the Rim Fire. *I. lupini*, the only species with sufficiently high naïve occupancy in 2014 to facilitate occupancy analysis, typically does not move large distances as an adult (Scott 1986, Fleishman et al. 1997). The distance from our transects to the nearest unburned patches was greater than the reported vagility of this species. Our data and observations suggest that some adults or larvae can survive high-severity fire, are capable of moving longer distances than reported, or move in association with smoke plumes. For example, some species of beetles can detect smoke from fires and use these signals as cues for dispersal (Schütz et al. 1999). However, this behavior has not been observed in butterflies.

Environmental attributes other than the abundance of host plants and nectar sources were associated with occupancy of butterflies after a major fire in the Sierra Nevada, California. Some of these environmental attributes also were associated with abundances of butterflies, although the consistency of associations varied among species. Vegetation and soil burn severity, in turn, affected the environmental attributes that were associated with occupancy and abundance. Understanding how vegetation and soil burn severity affects environmental attributes that are associated with butterfly occupancy and abundance may inform strategies for managing these species with prescribed fire or following wildfire.

Table 1. Number of butterflies observed during surveys in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015. Taxonomy and nomenclature follow Pelham (2015).

Species	Number of individuals observed	
	2014	2015
Parnassius clodius	3	3
Papilio rutulus	0	5
Papilio eurymedon	3	31
Papilio multicaudatus	0	1
Colias eurytheme	79	482
Anthocharis sara	0	3
Pieris rapae	0	1
Pontia protodice	1	5
Pontia occidentalis	0	1
Lycaena cupreus	4	1
Satyrium californica	0	3
Satyrium saepium	0	3
Callophrys gryneus	1	14
Callophrys augustinus	6	3
Strymon melinus	15	10
Celastrina ladon	2	16
Glaucopsyche piasus	2	23
Leptotes marina	0	1
Cupido amyntula	2	14
Icaricia saepiolus	5	4
Icaricia icarioides	17	71
Icaricia lupini	198	974
Danaus plexippus	5	11
Bolora epithore	6	4
Speyeria hydaspe	11	28
Limenitis lorquini	1	32
Adelpha californica	37	23
Vanessa virginiensis	0	18
Vanessa cardui	90	22
Vanessa atalanta	0	1
Nymphalis californica	0	1
Polygonia gracilis	3	2
Junonia coenia	1	189
Euphydryas chalcedona	1	1
Chlosyne palla	0	1
Phyciodes mylitta	15	181

Coenonympha tullia	2	12
Epargyreus clarus	3	4
Thorybes pylades	0	1
Erynnis propertius	0	1
Erynnis persius	6	207
Pyrgus communis	2	0
Hesperia juba	0	1
Polites sonora	0	5
Poanes melane	1	1
Total	522	2415

Table 2. Probabilities of detection and occupancy for butterflies in the Stanislaus National Forest, Sierra Nevada, California in 2014 and 2015. 95% confidence intervals are shown in parentheses.

Species and year	Detection	Occupancy
Colias eurytheme (2015)	0.71 (0.63–0.78)	0.88 (0.73–0.95)
Icaricia lupini (2014)	0.78 (0.53–0.91)	0.58 (0.41–0.73)
Icaricia lupini (2015)	0.81 (0.73–0.87)	0.78 (0.69–0.85)
Junonia coenia (2015)	0.35 (0.27–0.45)	0.85 (0.46–0.97)
Phyciodes mylitta (2015)	0.67 (0.33–0.90)	0.83 (0.45–0.96)
Erynnis persius (2015)	0.73 (0.54–0.86)	0.22 (0.15–0.32)

Table 3. Estimates of regression coefficients in the highest ranked or most parsimonious models of occupancy of butterflies in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015. 95% confidence intervals are shown in parentheses.

Species and year	Canopy cover	Live ground cover	Categorical abundance of nectar	Number of florets	Sugar mass
Colias eurytheme (2015)	-1.81 (-2.57 – -1.05)				2.23 (0.32–4.14)
Icaricia lupini (2014)		0.47 (0.07–0.86)		4.04 (1.34–6.74)	
Icaricia lupini (2015)	-1.30 (-1.83 – -0.78)	0.72 (0.28–1.16)			
Junonia coenia (2015)		1.62 (0.21–3.04)			
Phyciodes mylitta (2015)	-1.20 (-2.12 – -0.28)	1.75 (0.27–3.23)			
Erynnis persius (2015)	-1.76 (-2.26 – -1.25)			1.18 (0.20–2.16)	

Table 4. Relations between environmental covariates and abundances of butterflies in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015. *p*-values derived from negative binomial generalized linear models.

Species and year	Canopy cover	Live ground cover	Categorical abundance of nectar	Number of florets	Sugar mass
Colias eurytheme (2015)	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Icaricia lupini (2014)	0.20	< 0.01	0.06	0.48	0.60
Icaricia lupini (2015)	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Junonia coenia (2015)	0.17	< 0.01	0.40	0.22	0.97
Phyciodes mylitta (2015)	< 0.01	< 0.01	< 0.01	0.13	0.14
Erynnis persius (2015)	< 0.01	0.01	0.01	< 0.01	< 0.01

Table 5. Results of analyses of variance (ANOVA) assessing the responses of covariates included in occupancy models and abundance analyses to vegetation burn severity and soil burn severity in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015.

2014	Treatment	F	p
Canopy cover	Vegetation burn severity	6.40	<0.01
Live ground cover	Vegetation burn severity	2.23	0.09
Number of florets	Vegetation burn severity	2.51	0.06
Sugar mass	Vegetation burn severity	2.90	0.04
Canopy cover	Soil burn severity	0.46	0.71
Live ground cover	Soil burn severity	2.37	0.07
Number of florets	Soil burn severity	2.04	0.11
Sugar mass	Soil burn severity	2.22	0.09
2015			
Canopy cover	Vegetation burn severity	22.44	<0.01
Live ground cover	Vegetation burn severity	17.40	<0.01
Number of florets	Vegetation burn severity	5.65	<0.01
Sugar mass	Vegetation burn severity	8.90	<0.01
Canopy cover	Soil burn severity	12.97	<0.01
Live ground cover	Soil burn severity	15.79	<0.01
Number of florets	Soil burn severity	7.68	<0.01
Sugar mass	Soil burn severity	10.42	<0.01

Table 6. *p*-values derived from Tukey's pairwise comparisons between vegetation burn severity classes and environmental covariates in the Stanislaus National Forest, Sierra Nevada, California during 2014 and 2015.

Vegetation burn severity classes	2014		2015			
	Canopy cover	Sugar mass	Canopy cover	Live ground cover	Number of florets	Sugar mass
Unchanged : Low	0.01	~1.00	0.02	0.52	0.83	0.80
Unchanged : Moderate	<0.01	0.27	0.00	0.01	0.27	0.13
Unchanged : High	0.01	0.38	0.00	0.00	0.01	0.00
Low : Moderate	0.32	0.10	0.00	0.04	0.45	0.21
Low : High	0.99	0.12	0.00	0.00	0.00	0.00
Moderate : High	0.21	0.99	0.14	0.09	0.53	0.34

Table 7. *p*-values derived from Tukey's pairwise comparisons between soil burn severity classes and environmental covariates in the Stanislaus National Forest, Sierra Nevada, California during 2015.

Soil burn severity classes	Canopy cover	Live ground cover	Number of florets	Sugar mass
Unburned / very low : Low	0.90	0.99	0.99	~1.00
Unburned / very low : Moderate	0.00	0.00	0.02	0.00
Unburned / very low : High	0.65	0.99	0.52	0.17
Low : Moderate	0.00	0.00	0.00	0.00
Low : High	0.49	0.99	0.31	0.13
Moderate : High	0.97	0.01	0.93	0.97

Table 8. Average values (± SE) of environmental covariates associated with different vegetation and soil burn severity classes for statistically significant ANOVAs in 2014 and 2015 (see Table 5).

| Covariate | Treatment | Severity class | | | |
		Unchanged (vegetation) or Unburned / very low (soil)	Low	Moderate	High
2014					
Canopy cover (percent)	Vegetation burn severity	88.51 ± 2.52	69.60 ± 2.96	61.86 ± 3.95	70.97 ± 2.80
Sugar mass (mg)	Vegetation burn severity	0.57 ± 0.52	2.97 ± 1.07	37.23 ± 22.90	32.15 ± 8.29
2015					
Canopy cover (percent)	Vegetation burn severity	87.57 ± 1.90	71.91 ± 2.16	56.82 ± 3.78	46.46 ± 4.17
Live ground cover (percent)	Vegetation burn severity	28.24 ± 3.56	33.99 ± 1.57	42.79 ± 2.61	50.73 ± 2.23
Number of florets	Vegetation burn severity	6.22 ± 2.14	71.31 ± 17.28	162.26 ± 61.56	245.72 ± 47.50
Sugar mass (mg)	Vegetation burn severity	3.71 ± 1.48	18.85 ± 3.07	44.74 ± 13.03	67.06 ± 10.64
Canopy cover (percent)	Soil burn severity	68.01 ± 4.42	71.18 ± 1.93	45.20 ± 4.26	51.39 ± 20.74
Live ground cover (percent)	Soil burn severity	36.47 ± 2.87	35.37 ± 1.54	52.89 ± 2.35	36.9 ± 4.39
Number of florets	Soil burn severity	82.76 ± 27.89	65.22 ± 18.18	283.92 ± 57.76	225.21 ± 89.85
Sugar mass (mg)	Soil burn severity	18.11 ± 5.22	20.74 ± 3.81	74.15 ± 12.73	65.53 ± 20.19

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APPENDIX A: Occupancy models for butterflies in the Stanislaus National Forest,

Sierra Nevada, California during 2014 and 2015. Covariates included in models of

occupancy (ψ), entry (β), departure (d), and detection (p) were time (survey number; T),

survey-specific number of florets (florS), live ground cover (live), canopy cover

(canopy), seasonal number of florets (flor), sugar mass (sugar), and categorical

abundance of nectar (nectar).

Table A1.1. Associations between covariates and probabilities of detection, entry, and

departure of *Junonia coenia* in the Stanislaus National Forest, Sierra Nevada, California

during 2015. Occupancy was held constant.

Model	AICc	ΔAICc	Number of parameters
ψ (.) β (T) d (T) p (florS+T)	1009.76	0.00	11
ψ (.) β (T) d (T) p (T)	1010.88	1.12	10
ψ (.) β (.) d (.) p (T)	1012.32	2.56	8
ψ (.) β (.) d (.) p (florS+T)	1012.82	3.06	9
ψ (.) β (T) d (T) p (florS)	1025.41	15.65	7
ψ (.) β (T) d (T) p (.)	1027.13	17.37	6
ψ (.) β (.) d (.) p (florS)	1050.03	40.27	5
ψ (.) β (.) d (.) p (.)	1054.13	44.37	4

Table A1.2. Associations between covariates and occupancy of *Junonia coenia* in the Stanislaus National Forest, Sierra Nevada, California during 2015. We used the highest-ranked model, or, if the AICc value of a competing model was within two units of our highest-ranked model, the most parsimonious model, from the first model section step in this step of model selection.

Model	AICc	ΔAICc	Number of parameters
ψ (live) β (T) d (T) p (T)	987.66	0.00	10
ψ (canopy+live) β (T) d (T) p (T)	990.74	3.08	12
ψ (flor+live) β (T) d (T) p (T)	991.99	4.33	12
ψ (canopy+live+flor) β (T) d (T) p (T)	992.89	5.23	13
ψ (canopy) β (T) d (T) p (T)	995.74	8.08	9
ψ (canopy+flor) β (T) d (T) p (T)	1002.17	14.51	12
ψ (flor) β (T) d (T) p (T)	1010.87	23.21	11
ψ (.) β (T) d (T) p (T)	1010.88	23.22	10
ψ (sugar) β (T) d (T) p (T)	1012.48	24.82	11
ψ (nectar) β (T) d (T) p (T)	1015.29	27.63	13

Table A2.1. Associations between covariates and probabilities of detection, entry, and departure of *Colias eurytheme* in the Stanislaus National Forest, Sierra Nevada, California during 2015. Occupancy was held constant.

Model	AICc	ΔAICc	Number of parameters
ψ (.) β (T) d (T) p (florS)	1331.63	0.00	7
ψ (.) β (T) d (T) p (florS+T)	1332.42	0.79	11
ψ (.) β (T) d (T) p (.)	1333.31	1.68	6
ψ (.) β (T) d (T) p (T)	1334.64	3.01	10
ψ (.) β (.) d (.) p (florS+T)	1383.81	52.18	9
ψ (.) β (.) d (.) p (T)	1385.77	54.14	8
ψ (.) β (.) d (.) p (florS)	1437.72	106.09	5
ψ (.) β (.) d (.) p (.)	1438.35	106.72	4

Table A2.2. Associations between covariates and occupancy of *Colias eurytheme* in the Stanislaus National Forest, Sierra Nevada, California during 2015. We used the highest-ranked model, or, if the AICc value of a competing model was within two units of our highest-ranked model, the most parsimonious model, from the first model section step in this step of model selection.

Model	AICc	ΔAICc	Number of parameters
ψ (canopy+sugar+live) β (T) d (T) p (.)	1252.13	0.00	9
ψ (canopy+sugar) β (T) d (T) p (.)	1253.74	1.61	8
ψ (canopy+live) β (T) d (T) p (.)	1258.54	6.41	8
ψ (canopy) β (T) d (T) p (.)	1262.92	10.79	7
ψ (sugar+live) β (T) d (T) p (.)	1297.04	44.91	8
ψ (sugar) β (T) d (T) p (.)	1305.23	53.10	7
ψ (flor) β (T) d (T) p (.)	1307.94	55.81	7
ψ (live) β (T) d (T) p (.)	1312.61	60.48	7
ψ (nectar) β (T) d (T) p (.)	1317.47	65.34	9
ψ (.) β (T) d (T) p (.)	1333.31	81.18	6

Table A3.1. Associations between covariates and probabilities of detection, entry, and departure of *Icaricia lupini* in the Stanislaus National Forest, Sierra Nevada, California during 2014. Occupancy was held constant.

Model	AICc	ΔAICc	Number of parameters
ψ (.) β (.) d (.) p (T)	467.33	0.00	8
ψ (.) β (T) d (T) p (.)	468.54	1.21	6
ψ (.) β (T) d (T) p (T)	471.82	4.49	10
ψ (.) β (.) d (.) p (.)	498.43	31.10	4
ψ (.) β (.) d (.) p (florS)	500.23	32.90	5

Table A3.2. Associations between covariates and occupancy of *Icaricia lupini* in the Stanislaus National Forest, Sierra Nevada, California during 2014. We used the highest-ranked model, or, if the AICc value of a competing model was within two units of our highest-ranked model, the most parsimonious model, from the first model section step in this step of model selection.

Model	AICc	ΔAICc	Number of parameters
ψ (flor+live) β (T) d (T) p (.)	451.90	0.00	8
ψ (flor+live+canopy) β (T) d (T) p (.)	453.85	1.95	9
ψ (flor) β (T) d (T) p (.)	455.29	3.39	7
ψ (nectar) β (T) d (T) p (.)	456.22	4.32	9
ψ (flor+canopy) β (T) d (T) p (.)	456.64	4.74	8
ψ (sugar) β (T) d (T) p (.)	459.55	7.65	7
ψ (live) β (T) d (T) p (.)	459.82	7.92	7
ψ (canopy+live) β (T) d (T) p (.)	462.01	10.11	8
ψ (canopy) β (T) d (T) p (.)	467.03	15.13	7
ψ (.) β (T) d (T) p (.)	468.54	16.64	6

Table A4.1. Associations between covariates and probabilities of detection, entry, and departure of *Icaricia lupini* in the Stanislaus National Forest, Sierra Nevada, California during 2015. Occupancy was held constant.

Model	AICc	ΔAICc	Number of parameters
ψ (.) β (T) d (T) p (florS)	1295.63	0.00	7
ψ (.) β (.) d (.) p (florS+T)	1301.69	6.06	9
ψ (.) β (T) d (T) p (.)	1303.26	7.63	6
ψ (.) β (T) d (T) p (florS+T)	1303.68	8.05	11
ψ (.) β (.) d (.) p (florS)	1304.62	8.99	5
ψ (.) β (T) d (T) p (T)	1309.93	14.30	10
ψ (.) β (.) d (.) p (T)	1311.09	15.46	8
ψ (.) β (.) d (.) p (.)	1318.37	22.74	4

Table A4.2. Associations between covariates and occupancy of *Icaricia lupini* in the Stanislaus National Forest, Sierra Nevada, California during 2015. We used the highest-ranked model, or, if the AICc value of a competing model was within two units of our highest-ranked model, the most parsimonious model, from the first model section step in this step of model selection.

Model	AICc	ΔAICc	Number of parameters
ψ (canopy+live) β (T) d (T) p (florS)	1225.70	0.00	9
ψ (canopy+live+sugar) β (T) d (T) p (florS)	1227.87	2.17	10
ψ (canopy) β (T) d (T) p (florS)	1236.14	10.44	8
ψ (canopy+sugar) β (T) d (T) p (florS)	1237.83	12.13	9
ψ (live+sugar) β (T) d (T) p (florS)	1264.45	38.75	9
ψ (live) β (T) d (T) p (florS)	1266.17	40.47	8
ψ (sugar) β (T) d (T) p (florS)	1284.63	58.93	8
ψ (flor) β (T) d (T) p (florS)	1287.31	61.61	8
ψ (nectar) β (T) d (T) p (florS)	1293.02	67.32	10
ψ (.) β (T) d (T) p (florS)	1295.64	69.94	7

Table A5.1. Associations between covariates and probabilities of detection, entry, and departure of *Phyciodes mylitta* in the Stanislaus National Forest, Sierra Nevada, California during 2015. Occupancy was held constant.

Model	AICc	ΔAICc	Number of parameters
ψ (.) β (T) d (T) p (T)	863.82	0.00	10
ψ (.) β (.) d (.) p (T)	866.13	2.31	8
ψ (.) β (T) d (T) p (.)	867.17	3.35	6
ψ (.) β (.) d (.) p (.)	936.36	72.54	4
ψ (.) β (T) d (T) p (florS)	938.40	74.58	5

Table A5.2. Associations between covariates and occupancy of *Phyciodes mylitta* in the Stanislaus National Forest, Sierra Nevada, California during 2015. We used the highest-ranked model, or, if the AICc value of a competing model was within two units of our highest-ranked model, the most parsimonious model, from the first model section step in this step of model selection.

Model	AICc	ΔAICc	Number of parameters
ψ (canopy+live) β (T) d (T) p (T)	822.09	0.00	12
ψ (canopy+live+flor) β (T) d (T) p (T)	823.55	1.46	13
ψ (live) β (T) d (T) p (T)	834.60	12.51	11
ψ (live+flor) β (T) d (T) p (T)	835.05	12.96	12
ψ (canopy) β (T) d (T) p (T)	836.57	14.48	11
ψ (canopy+flor) β (T) d (T) p (T)	837.96	15.87	12
ψ (flor) β (T) d (T) p (T)	854.91	32.82	11
ψ (sugar) β (T) d (T) p (T)	858.88	36.79	11
ψ (nectar) β (T) d (T) p (T)	860.95	38.86	13
ψ (.) β (T) d (T) p (T)	863.82	41.73	10

Table A6.1. Associations between covariates and probabilities of detection, entry, and departure of *Erynnis persius* in the Stanislaus National Forest, Sierra Nevada, California during 2015. Occupancy was held constant.

Model	AICc	ΔAICc	Number of parameters
ψ (.) β (.) d (.) p (T)	712.35	0.00	8
ψ (.) β (.) d (.) p (.)	715.71	3.36	4
ψ (.) β (T) d (T) p (.)	716.39	4.04	6
ψ (.) β (.) d (.) p (florS)	716.60	4.25	5

Table A6.2. Associations between covariates and occupancy of *Erynnis persius* in the Stanislaus National Forest, Sierra Nevada, California during 2015. We used the highest-ranked model, or, if the AICc value of a competing model was within two units of our highest-ranked model, the most parsimonious model, from the first model section step in this step of model selection.

Model	AICc	ΔAICc	Number of parameters
ψ (canopy+flor) β (.) d (.) p (T)	600.26	0.00	10
ψ (canopy+live+flor) β (.) d (.) p (T)	601.31	1.05	11
ψ (canopy+live) β (.) d (.) p (T)	609.76	9.50	10
ψ (canopy) β (.) d (.) p (T)	611.89	11.63	9
ψ (live+flor) β (.) d (.) p (T)	673.32	73.06	10
ψ (flor) β (.) d (.) p (T)	673.37	73.11	9
ψ (nectar) β (.) d (.) p (T)	682.88	82.62	11
ψ (sugar) β (.) d (.) p (T)	688.84	88.58	9
ψ (live) β (.) d (.) p (T)	702.47	102.21	9
ψ (.) β (.) d (.) p (T)	712.35	112.09	8