

Draft Report to Placer County

Butterfly Community Change in Response to Rural Residential Development

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ABSTRACT

This study examined changes in butterfly community structure in response to rural residential development in the oak-woodlands of central California. Rural residential development is associated with the replacement of native habitat with new habitat types and alteration of hydrologic and disturbance regimes. Small parcel size was positively correlated with the diversity of habitat and negatively related to the percent area of native habitat at sites across the range of parcel sizes observed; this suggests that parcel size may be a useful management tool for influencing native habitat conservation. Species richness at sites was negatively related to parcel size, positively related to habitat diversity, and peaked at intermediate levels of percentage native habitat area at a site. However, the loss of native habitat associated with smaller parcel sizes resulted in the loss of native habitat-limited species. The ability of a species to exploit or persist in human-altered environments depends on its life history characteristics. While vagility did not influence the distribution of butterfly species, the numbers of hostplant specialists and univoltine species were positively correlated with the percent area of native habitat at a site. Further, the numbers of multivoltine species and hostplant generalists were higher at sites with smaller parcels and higher percent area of modified habitat. These trends represent a shift in butterfly species composition from specialist to generalist species with increasing urbanization. This study provides evidence for the importance of parcel size in butterfly conservation, but maintaining native habitat, even on small parcels, helps retain native habitat-limited butterfly species.

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INTRODUCTION

Habitat loss and fragmentation affect biodiversity by causing both expansions and constrictions of species' ranges, resulting in changes in species composition and overall diversity (McKinney and Lockwood 1999). Most conservation efforts have long been concentrated on public lands and nature reserves. This trend, however, overlooks the extreme importance of biodiversity conservation on private lands, particularly for ecosystems in which most of the land is privately owned. For conservation on private lands to be successful it is critical to understand how biodiversity is affected by habitat changes resulting from different intensities of urban development.

The oak-woodlands of central California represent an ecosystem under considerable threat from increasing fragmentation and habitat modification due to urbanization. The western foothills of the Sierra Nevada are characterized by hardwood forest dominated habitats comprised of fairly continuous oak-woodland, grassland, and chaparral that extend approximately 400 miles from Lassen to Kern counties (1500-4000 ft) in California. Human population in this region is rising rapidly, and Placer County's is the fastest growing in California with a growth rate of 3.5 percent in 2000 (California Department of Finance 2001). This growth is resulting in increased residential development and associated habitat degradation. Thus far, habitat loss and degradation in the region has not resulted in the listing of species as threatened or endangered under the Endangered Species Act of 1973, but with increasing pressure for reductions in parcel size and continual development, anticipatory planning at this juncture may be important to prevent future listings. More than eighty percent of blue oak-woodlands in California (Davis et al. 1998), and 93 percent of such woodlands in Placer County, California, are in private ownership (Placer County Planning Department 2000). Thus, private lands are critical for maintaining oak-woodland biodiversity.

County planning departments tend to have limited regulatory control over private land use. However, they do control parcel size zoning, which may prove to be a useful tool for implementing private land conservation efforts. This study examines the effects of zoning on habitat and butterfly diversity.

Butterflies were selected as the focal taxon for this study for several reasons. Butterflies have been shown to respond both to changes in vegetation and alteration of disturbance and hydrologic regimes that result from rural residential development. Butterflies have been suggested as indicators of ecological change because they are closely dependent on specific species of plants during several stages of their life cycles, and they are sensitive to environmental changes including local weather, climate, and light levels that are affected by habitat disturbance (Watt et al. 1968, Ehrlich et al. 1972, Weiss et al. 1987, 1988, Hill et al. 1995, Blair and Launer 1997, Wood and Gilman 1998, Kitahara and Sei 2001).

Further, the butterfly fauna associated with the Sierra Nevada foothills is well documented and has been characterized to some extent with respect to habitat associations. Some butterfly species are specialists limited in distribution by specific habitat such as oak-woodland, while others are weedy generalists that can use a wide variety of often highly modified habitats including widespread or weedy plant species that have characterized the central valley since its conversion to agriculture (Shapiro). This diversity in host plant and habitat specificity among butterfly species provides an unique perspective in which to view the changes in butterfly community composition associated with rural residential development. A shift towards increased numbers of generalist species and decreased numbers of specialist species in human modified environments has been documented for a variety of taxa including butterflies in several ecological systems (Kitahara and Fujii 1994, Kitahara et al. 2000, Kitahara and Sei 2001).

Understanding the consequences of parcel size reduction and its attendant modification and fragmentation of habitats can be important to developing policy and educational programs that will minimize the loss of biodiversity. This study examines the relationship between parcel size and habitat characteristics, determines how these habitat characteristics influence butterfly community composition, and identifies patterns of community change with respect to specialist and generalist species.

METHODS

Study Area and Site Selection:

Study sites were located in the western foothills of the Sierra Nevada in Placer County, California, along the route 49 corridor extending north of Auburn, California. This area was historically dominated by blue oak-woodland. Currently this area is a mosaic of second growth oak-woodland, pastureland, and habitat associated with rural residential development such as lawns, gardens, and cultivated shrubs. The intensity of development in this study ranges from sites with 0.4 hectare (one acre) parcels and highly modified vegetation to greater than 81 hectare (200 acre) parcels characterized by undeveloped oak-woodland.

Twenty-six study sites were chosen based on parcel size and elevation using a G.I.S. database of Placer County parcel information. Areas of similarly sized, contiguous parcels were identified, and study sites were established within these regions. Sites were selected to have a surrounding buffer of land with levels of urbanization similar to that of the site to minimize edge effects. Sites were chosen systematically with respect to parcel size to encompass the full gradient of urbanization, but sites were selected at random with respect to other characteristics including land-use and area of remaining oak-woodland. All sites were between 250 and 450 meters in elevation and were located within an area 20 kilometers north to south and 6 kilometers east to west in Placer County, California. Permission to access each site was obtained from land-owners.

Butterfly Sampling:

Each site was sampled for day-flying Papilionoidea and Hesperioidea, henceforth referred to as butterflies, a total of nine times between May 25 and August 20, 2000, and between April 16 and May 18, 2001. Sites were sampled about once every two weeks for one to 1.5 hours each using the visual encounter survey technique described by Crump and Scott (1994). Although sampling time varied across sampling periods, all sites were surveyed for the same amount of time within a given sampling round. Sampling was limited to days when weather was conducive

to butterfly flight. For each visit to a site, all species observed were recorded; species that were difficult to identify in the field were collected for later identification.

Sites were sampled so that at least one site representing high density development (0.4 to 1.2 hectare (one to three acre) parcels), medium density development (1.8 to 8.1 ha (4.5 to twenty acre) parcels), and low density development (greater than 8.1 ha (twenty acre) parcels) were sampled each day to minimize effects of daily variation. In addition, each site was sampled alternately in the afternoon and morning in consecutive visits.

Landscape Variables:

Because butterflies could disperse into a site from adjacent areas, site characteristics were analyzed for an area that included both the sampling site and a 100 meter buffer surrounding it.

Color aerial photographs were used to identify habitat types within study sites and were digitized and attributed using G.I.S. (ESRI ArcView GIS 3.2). Field surveys were used to corroborate habitat type identification. Habitat was classified into five habitat categories. 'Native habitat' included all uncultivated areas characterized by oak-woodland. 'Mowed oak-woodland' was oak-woodland with an uncultivated, but periodically mowed, understory. 'Grassland' was uncultivated grassland, characterized primarily by annual grasses. 'Cultivated areas' included all irrigated land, ornamental vegetation, mowed grasslands, and other non-native or cultivated vegetation. The final habitat category was 'non-habitat' and included all non-vegetated areas, including buildings, roads, and pavement. All variables were measured as the percent of land in that habitat type at a site.

Parcel size was measured as the weighted average of the log transformation of parcel size for all parcels within each site and buffer. Habitat diversity was calculated using the Shannon-Weaver diversity index (Magurran 1998). This index was calculated using proportion of total habitat, excluding 'non-habitat', that was represented by each habitat type.

Data analysis:

We calculated species richness as the total number of species observed at a site across all sampling periods. Species occurrences were defined as the number of visits to a site during which the species was observed (i.e. species occurrences could range from 0 to 9, the total number of visits to each site). Migratory species, including *Nymphalis* spp., *Danaus plexippus*, and *Vanessa* spp., were excluded from the analyses in this study. In addition, *Erynnis tristis* and *E. funeralis* and *Satyrrium californica* and *S. sylvinus* were not differentiated in the field. Thus *Erynnis* sp. and *Satyrrium* sp. were included in analyses of total species richness but were omitted from all other analyses. Species that occurred at only a single site (i.e. *Lycaena helloides*, *Celastrina ladon*, *Glaucopsyche lygdamus*, *Pieris napi*, and *Pontia protodice*) were also excluded from all analyses except total species richness.

Site characteristics:

Site characteristics, including habitat diversity and percent area of non-habitat, cultivated area, mowed oak-woodland, native habitat, and grassland, were fit as linear functions of the natural log of parcel size (Table 1). Percent areas of each habitat type were converted to proportions and transformed using an arcsine square-root transformation prior to fitting each model.

In addition, habitat diversity was modeled as a quadratic function of the percent area of native habitat at each site.

Species richness:

Species richness was fit as five separate functions of site characteristics to compare the explanatory value of each variable (Table 2). Site characteristics included in these models were habitat diversity, the natural log of parcel size, and the percent area of native habitat at each site.

Influence of Site Characteristics on Species' Distributions:

Canonical Correspondence Analysis (CCA) was used to determine the influence of the habitat variables and parcel size on the distribution and occurrences of individual butterfly species. Analyses were conducted using the program PC-ORD (Version 4, MJM Software). A Monte Carlo test with 499 iterations was used to test the null hypothesis that no relationship exists between the environmental variables and species distributions.

CCA is a constrained ordination gradient analysis technique that incorporates unimodal responses of species to environmental variables. This technique performs well with skewed species distributions and intercorrelated variables (Palmer 1993). CCA maximally separates species and sites along axes, but, unlike indirect gradient analyses, the axes are constrained to be linear combinations of the environmental variables. The eigenvalues produced by CCA measure the separation of species along ordination axes (Ter Braak 1987).

Classification of species as oak-woodland specific and disturbance tolerant:

To classify species as native habitat-limited or disturbance tolerant, a logit model was constructed for each butterfly species to examine its probability of occurrence with respect to the percent area of native habitat at a site (Table 3). Species were categorized as native habitat-limited if the coefficient on 'native habitat' was positive and the probability of the slope coefficient equaling zero was less than five percent, according to the G statistic calculated from the log-likelihood value. Similarly, species were classified as disturbance tolerant if the coefficient on 'native habitat' was negative and the slope coefficient was significant at the five percent probability level.

We modeled the percentage of native habitat-limited species present at a site as separate linear functions of the percent area of native habitat and the natural log of parcel size (Table 4). To determine the suitability of mowed oak-woodland and grassland for supporting these habitat-

specific species, we alternately added these habitat variables to the model that included percent area of native habitat (Table 4).

Species' life history characteristics and responses to habitat change:

Logistic regression was used to assess the influence of species' life history characteristics on the probability of species occurring at sites that differed in their percent area of native habitat. Specifically, the importance of interactions between percent area of native habitat and species' larval hostplant breadth, vagility, and voltinism in predicting species occurrences, was examined. This analysis was conducted using the program Mini-tab (Release 12, Microsoft Corp). Variables included in this analysis were percent area of native habitat, hostplant breadth, voltinism, vagility, and interactions between percent area of native habitat and hostplant breadth, voltinism, and vagility, respectively (Table 5). Interaction terms were calculated by centering both variables (subtracting the mean) and taking their product.

Hostplant specificity and voltinism data for each butterfly species were taken from Garth and Tilden (1986). Species hostplant specificity scores ranged from 1 to 4 depending on the taxonomic breadth of their larval feeding (Appendix 1). Species which feed only on one plant species were scored as 1; butterflies that feed on plants from only one genus were scored as 2; butterflies that feed on species limited to one family were scored as 3; and butterflies that feed on species from more than one family were scored as 4. Voltinism scores equaled the typical number of broods for the species (Appendix 1). If a range was provided for the number of broods, the average of that range was used for the score. Likewise, "multiple" and "many" broods were scored as three broods.

Vagility estimates were provided by George Austin (pers. communication.) and scored as in Fleishman et al. (1997) (Appendix 1). Species that disperse tens of meters were scored as 1, hundreds of meters were scored as 2, thousands of meters were scored as 3, and ten thousands of meters and higher were scored as 4.

A second set of analyses was conducted to determine whether the patterns of voltinism and hostplant breadth across the habitat gradient identified by the logit model were the result of species additions, deletions, or both. Species were categorized as specialists and generalists with respect to both voltinism and hostplant breadth. Species were categorized as seasonal generalists if they have greater than two broods per year and as seasonal specialists if they are univoltine. Likewise, species were categorized as feeding specialists if they feed on species from a single genus and as feeding generalists if they feed on species across several plant families.

The richnesses of seasonal specialists and univoltine species were modeled as quadratic functions of the percent area of native habitat at sites to allow for a non-linear response to habitat change (Table 6). Models were reduced if the quadratic term was found to be non-significant ($p > 0.05$). The richnesses of feeding and seasonal generalists were modeled as functions of the percent of native habitat area at sites, habitat diversity, and the natural log of parcel size to examine the explanatory value of these aspects of urbanization (Table 6).

Seasonality:

To understand how species with different seasonal characteristics utilized habitat between seasons, we modeled species richness and richnesses of univoltine and multivoltine species as functions of percent area of native habitat, season, and habitat/season interactions (Table 7). Site visits were categorized as spring or summer and richnesses were calculated for each site and season. Spring included all visits during which at least some understory in native habitat remained green (unsenesced). These included the first two visits in 2000 (May 25 to June 18) and the three visits in spring 2001 (April 16 to May 18). Summer included those visits during which the understory of the native habitat was completely dried, which were the last four visits in 2000 (June 21 to August 20).

RESULTS

Site Characteristics:

The 26 sites in this study ranged in average parcel size from approximately 0.4 to 81 hectares (one to 200 acres). A linear function of the natural log of parcel size explained 57.2, 78.1, 46.8, 55.2, and 36.5 percent of the variation in habitat diversity and percent area of non-habitat, cultivated habitat, mowed oak-woodland, and native habitat, respectively (all habitat characteristics were arcsine square root transformed) (Figure 1 a-e; Table 1). There was no linear relationship between parcel size and percent area of grassland (Figure 1 f; Table 1).

Habitat diversity was related to percent area of native habitat as a quadratic function (F-test; d.f. = 2, 23; $p < 0.001$; $r^2 = 91.3$ %; Figure 2).

Species Richness:

Including migrants and rare species, fifty species of butterflies were observed during nine visits to each of 26 sites. Species richness reached a maximum at intermediate levels of remaining native habitat and was significantly related to the percent area of native habitat at a site as a quadratic function (F-test; d.f. = 2,23; $p = 0.014$; $r^2 = 31.1$ %; Figure 3a; Table 2). Species richness was negatively, linearly correlated with the natural log of parcel size (F-test; d.f. = 1,24; $p = 0.005$; $r^2 = 28.5$ %; Figure 3b; Table 2) and positively linearly related to habitat diversity (F-test; d.f. = 1,24; $p = 0.020$; $r^2 = 20.4$ %; Figure 3c; Table 2). No additional variance in species richness was explained by including habitat diversity into the models that included native habitat or parcel size (Table 2). However, a function including a linear response to the natural log of parcel size and a quadratic function of the percent area of native habitat explained 43.8 % of the variance in species richness (F-test; d.f. 3,22; $p = 0.005$; Table 2) with correlation between characteristics maintaining the same sign.

Influence of Site Characteristics on Species' Distributions:

The Canonical Correspondence Analysis showed that landscape-level habitat characteristics did influence the distribution of butterfly species ($p < 0.01$) and that percent areas of native habitat and cultivated habitat were the land cover variables most important in determining the distribution of species (Figure 4). The first ordination axis was significant ($p = 0.002$) and explained 23.8 percent of the total variance in species. This axis was most correlated with the percent area of native habitat at sites (intra-set corr: 0.971; inter-set corr: 0.926). The percent area of cultivated habitat was also highly, but negatively, correlated with the first ordination axis (intra-set corr: -0.834; inter-set corr: -0.795). A significant relationship existed along the first ordination axis between the environmental variables and species distributions and occurrences ($p = 0.002$). The second and third ordination axes were not significant ($p > 0.05$) and explained little additional variance in the data (5.4 and 3.7 percent, respectively). The relationship between species distributions and area of native habitat is further illustrated in Figure 5.

Classification of species as oak-woodland specific and disturbance tolerant:

Nine species were identified as limited to native habitat based on the results of the logistic regressions (Table 3). These were *Anthocaris sara*, *Zerene eurydice*, *Adelpha bredowii*, *Cercyonis sthenele*, *Euphydryas chalcedona*, *Erynnis propertius*, *Hesperia colorado*, *Ochloides agricola*, and *Satyrium auretteum*. Ten species were identified as being limited to modified habitat (Table 3). These species were *Pieris rapae*, *Polites sabuleti*, *Pyrgus communis*, *Pholisora catullus*, *Hylephila phyleus*, *Junonia coenia*, *Phyciodes mylitta*, *Everes comyntas*, *Limentis lorquini*, and *Strymon melinus*. All other species showed no significant response to the percent area of native habitat at sites ($p > 0.05$; Table 3).

The percent of native habitat-limited species occurring at a site declined linearly with decreasing percent area of native habitat (F-test; d.f. = 1,24; $p < 0.001$; $r^2 = 66.7\%$; Figure 6a; Table 4) and with decreasing parcel size (natural log transformed) (F-test; d.f. = 1,24; $p = 0.007$;