ARTHUR M. SHAPIRO
Center for Population Biology
University of California
Davis, California

27

Status of Butterflies

ABSTRACT

The Sierra Nevada has an unusually rich butterfly fauna that, however, is distinguished by little endemism at either species or subspecies levels. This may change soon, as more taxonomic subspecies are named. The fauna is structured altitudinally, latitudinally, and between east and west slopes. Maximum species richness occurs at middle elevations on the west slope and around lower passes. Endemism and relictualism are concentrated at high elevation (subalpine and alpine) and on unusual soils at lower elevations. Some patterns of endemism and relictualism suggest a very dynamic biogeography in the Quaternary period, further supported by phylogeographic (genetic) studies. The historic butterfly record is so poor that the effects of land use and management on the fauna can only be guessed at. Taxa of special concern are mostly relicts, especially on ultramafic soils; one is found in marshes and wet meadows on the east slope *(Speyeria nokomis apacheana).*

INTRODUCTION

The middle-elevation Sierra Nevada has one of the richest butterfly faunas in temperate North America; its only close competitor is the Colorado Front Range (Scott and Epstein 1987). On June 8, 1992, I observed sixty-two species on the wing along four miles of Old Highway 40 (Donner Pass Road). To put this in perspective, only about sixty-five species have ever been recorded in the British Isles, and only fifty-eight occur there today (Dennis 1992). There are few sites outside the tropics where one could see sixty-two butterfly species in one day.

This is especially striking when one considers that butterflies are uncommon in old-growth forests. The Sierran fauna is overwhelmingly adapted to successional and edaphic, nonforest habitats (meadows, barrens, riparian corridors, and alpine fell fields). Most of the Sierra is forested, yet most of its butterfly diversity is not found in the forest—a fact first noted by Emmel and Emmel (1963b).

Butterflies are important for biodiversity and conservation biology because they are diverse enough that patterns in distribution and diversity are demonstrable; their taxonomy is in relatively good shape, at least compared with that of most other invertebrates; they include both ecological generalists and specialists, with some of these specialists tied to unusual and/or endangered habitats; they often have close and potentially coevolved relationships with larval host plants and sometimes with adult nectar sources; they are relatively easy to study and are large enough to be marked individually (and are identifiable as individuals without recapture); and perhaps most importantly they are pretty, often charismatically so. Their appeal thus extends beyond professionals to a larger number of dedicated amateurs and to the public at large (Pollard and Yates 1993).

Not only are people interested in butterflies in an abstract sense, but they also like butterflies and want them as part of their environment, even though butterflies have no perceived economic importance. In the Sierra Nevada, butterflies are often a prominent part of the landscape. I know of no formal studies of public opinion about butterflies, but twenty-four years' experience as a Sierran field naturalist has taught me that people are interested in butterflies and like to talk about them. The most common remark I hear—with or without foundation—is that numbers of butterflies have declined "since [my interlocutor] was a kid."

The existence of so many butterfly enthusiasts has both good and bad aspects. It generates pro- and anticollecting tensions, support and hostility for endangered species regulation and enforcement, reliable and spurious identifications and distribution records, good and bad taxonomy. All of these impinge on both perception and management of the Sierran butterfly fauna.

Given how popular butterflies are, it is remarkable that the

Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. Davis: University of California, Centers for Water and Wildland Resources, 1996.

Back to CD-ROM Table of Contents

Sierran fauna is so poorly documented. Butterfly studies in California date to 1849, when a Frenchman, Pierre Joseph Michel Lorquin, began collecting butterflies for the distinguished Parisian entomologist J. B. A. Boisduval (Emmel and Emmel 1973). Lorquin's notes are lost, but Boisduval records that Lorquin collected in the Sierra between 1850 and 1856 and ascended at least the Sacramento and Feather Rivers. Boisduval published the first faunistic treatment of California butterflies in 1868, with occasional references to the Sierra. In his introductory remarks he praises Lorquin for "braving the tooth of the bear and the fangs of the rattlesnake." Boisduval described many common and a few scarce California butterflies, none of them endemic to the Sierra. The absence of high-altitude taxa (species) indicates that Lorquin never reached the alpine zone.

Although California butterflies continued to be described—eventually by American authors—the next faunistic paper on Sierran butterflies (really the first, because Boisduval attempted to cover the entire state) took twenty-two years to appear (Behr 1890). It was a report of twenty butterfly species from Yosemite, followed closely by two more Yosemite lists (Dyar 1892; Van Dyke 1892). Van Dyke enumerated thirty-eight identified species, with accurate ecological notes. Newcomer (1910) produced an excellent paper, containing a credible sketch of the vegetation, climate, and topography of the Tahoe Basin as well as records of seventy-five taxa. Unsurprisingly, the species-level taxonomy has not fared well in eighty-five years. Nonetheless, the portrait of the Tahoe fauna is recognizable; the biological information (such as host plants) is quite accurate.

Unfortunately, the same cannot be said for the next paper (McGlashan 1914), which was privately published and, perhaps fortunately, has rarely been referenced since. It is misleading and highly inaccurate but of interest as an example of "local color."

It was ostensibly written by Ximena McGlashan, the young daughter of Truckee's most prominent citizen, Charles Fayette McGlashan. Actually the elder McGlashan, an indefatigable promoter, probably wrote it himself—just as he did Ximena's subscription magazine, The Butterfly Farmer. The paper purports to be a list of Truckee butterflies. It also served as a sales list (all the species were said to be available by mail for 5 cents each). The paper included ninety-one species, a reasonable number for Truckee, but explicitly disclaimed completeness and does not define "Truckee" at all. The list contains species of the western foothills, the high desert, and the alpine zone as well as species that might reasonably be expected at Truckee. Clearly the McGlashans had a very broad concept of Truckee boundaries, and the list is useless for any study of faunal turnover—illustrating the pitfalls of taking historical documents at ecological face value (S. Smallwood and A. M. Shapiro in preparation).

It took sixteen years for the next faunistic paper on Sierran butterflies to appear (Martin and Ingham 1930), listing eighty-three taxa for the Huntington Lake area, Fresno County. This paper suffers from some archaic taxonomy and is tainted by appalling "game hog" collecting data, but it is nonetheless useful. It was quickly followed by two papers published by John S. Garth (1935a, 1935b) on Yosemite butterflies, also in the Bulletin of the Southern California Academy of Sciences. In 1959 James W. Tilden published another Yosemite paper, "The Butterfly Associations of Tioga Pass," in the Wasmann Journal of Biology. These three papers set many precedents, which came to fruition in 1963 when the authors combined to publish a ninety-six-page monograph, Yosemite Butterflies, that in turn set the standard for such studies (Garth and Tilden 1963).

Garth and Tilden use the Merriam life-zone concept, which had great currency then—it was also used by Storer and Usinger in Sierra Nevada Natural History in the same year. Using thirty years of records, Garth and Tilden cross-characterize each species' distribution in terms of Merriam's altitudinal zones and Dice's (1943) biotic provinces, which reflect the role of the Sierra as a climatic divide. They also list each species' usual plant community associations.

One year earlier, in 1962, two young brothers, John and Thomas Emmel, published a preliminary fauna for Donner Pass. Though they missed the autumn fauna by leaving too early, they did a sophisticated study of butterfly activity as a function of weather and climate (Emmel and Emmel 1963a) and a study of biodiversity as a function of community and landscape that was decades ahead of its time (Emmel and Emmel 1963b). Also published in 1962 was a minor commentary on the high-altitude fauna (Eriksen 1962). Shields (1966) published a list of seventy-four species from a middle-elevation, west-slope locality in Tuolumne County, embracing diverse habitat types. The next Sierran faunistic paper was my own on Castle Peak, Nevada County, one of the last alpine areas in the northern Sierra (Shapiro 1978). This is, to my knowledge, the last faunistic paper on Sierran butterflies, though my group has published on various components of the northern Californian montane faunas. We have twenty-four years of Sierran faunistic and phenological data, as yet unpublished but constituting one of the largest butterfly data sets of its sort in existence.

These data, however, have nearly all emanated from the Interstate 80 / Highway 20 corridor, where I have maintained a permanent transect. There is a much more extensive data set not only for the Sierra but for all of California. The Emmel brothers and Sterling O. Mattoon have been working on a definitive butterfly fauna of California, which when published will be the most complete and detailed such work ever done in the United States (and perhaps the world). They have assembled most of the data from private and institutional collections, filling gaps by targeted collecting of their own. They have also reared and photographed the early stages of virtually the entire fauna, most of which was previously unreared.

Had their book appeared before the Sierra Nevada Ecosystem Project (SNEP), this chapter would be very different. Because their data set is not yet available for analysis, this chapter is based on a much smaller data set, along with frequent conversations with the Emmels and Mattoon. A by-product of their project is a taxonomic work (Emmel 1995) that will have major repercussions for our perception of the Sierran fauna. I will refer repeatedly to this potential problem/opportunity.

THE SIERRAN FAUNA

Butterfly taxonomy has been singularly unstable recently, which makes it difficult to quantify the Sierran butterfly fauna. Philosophers and biologists may argue over the nature and reality of species, but to discuss faunistics one must have a taxonomic touchstone. Using the 1981 Catalogue/Checklist of the North American butterflies by Miller and Brown (because it is the most copiously documented and widely circulated of the possible lists), I estimate that there are 155 species of butterflies (excluding rare casuals) in the Sierra Nevada. I define the Sierra as extending from Buck's Lake, Plumas County, to Tehachapi Valley, Kern County. Buck's Lake is the approximate northern limit of a number of characteristic Sierran butterflies, for example, Polites sabuleti tecumseh, Phyciodes campestris montana, and Anthocharis stella. To the north are increasing numbers of Cascadian and Klamath taxa, absent from the Sierra proper. The estimate of 155 is conservative. Garth and Tilden (1963) recorded 134 species in Yosemite; I have counted 115 at Donner Pass in twenty-four years. Both counts include strays. I am not appending a taxonomic list to this chapter because imminent nomenclatorial changes are sure to render any such effort obsolete within a year. Table 27.1 gives the distribution among families.

Intuitively, this seems a rich fauna, but proving it is not easy. Faunal richness is related not only to area but also to topographic, climatic, and vegetational diversity—which are not simple functions of area. It is also related to history. It is not self-evident how to make appropriate comparisons, and there are few reliable species lists for well-defined montane areas in western North America. Stanford and Opler (1993) collate distribution data for the western butterflies by county. Interpretation of data arranged in this way is difficult, because counties seldom correspond to physiographic or vegetational units. Arizona has 142.5 species per county versus 103.1 for California; but Arizona has fourteen counties with an average area of 13,065 km^2 (8,120 mi^2), while California has fifty-eight counties with an average area of 4,344 km^2 (2,700 mi^2), plus a much greater variance in county area. On a prorata basis California has the richer fauna, but statewide Arizona has more species per mi^2. Table 27.2 shows the most species-rich California counties. Although the top three are all non-Sierran, the Sierran counties far surpass these southern desert counties in richness. A multivariate analysis of butterfly diversity patterns in California akin to the plant study by Richerson and Lum (1980) is in progress in my lab. It is already evident that butterflies and plants do not respond identically to environmental factors; the best diversity predictors are likely to be different, though topography is important to both.

TABLE 27.1

Taxonomic composition of the Sierra Nevada and North Coast Range butterfly faunas (approximated from Miller and Brown 1981).

	Sierra Nevada		North Coast Range	
Family	**Species**	**Subspecies**	**Species**	**Subspecies**
Hesperiidae	30	31	30	31
Pieridae	20	22	14	16
Papilionidae	7	8	6	6
Lycaenidae	52	57	38	47
Nymphalidae	36	44	31	35
Satyridae	8	9	4	4
Danaidae	2	2	1	1
Totals	155	173	124	140

TABLE 27.2

California counties with more than 135 butterfly species recorded. The two smallest counties are entirely Sierran and are the top-ranking counties in terms of species per area.

County	Land Area (mi^2)	Number of Species[a]	Species per mi^2	Rank in Species per mi^2
San Bernardino	20,119	153	0.0076	8
Inyo[b]	10,130	150	0.0148	7
Tulare[c]	4,844	150	0.0310	4
San Diego	4,262	146	0.0343	3
Riverside	7,176	143	0.0200	5
El Dorado[c]	1,726	140	0.0811	2
Kern[b]	8,152	139	0.0171	6
Nevada[c]	975	138	0.1415	1

[a] According to Ray E. Stanford, phone call, June 1995. Includes strays and casual records.
[b] Counties with significant Sierran area.
[c] Mainly Sierran counties.

Using Miller and Brown (1981) and treating every species as represented by at least one subspecies, the Sierran fauna contains 173 subspecies; Garth and Tilden (1963) recorded 151 subspecies in Yosemite.

Distribution Patterns within the Sierran Fauna

Some butterfly species extend completely across the Sierra, transcending Merriam life zones and Dice biotic provinces. These species usually are seasonal or altitudinal migrants (Colias eurytheme, Vanessa spp., Plebeius acmon) (Shapiro 1980), or they have distinctive ecotypes in different climates (Papilio zelicaon) (Shapiro 1995). Many species, however, are confined to either the west (Californian biotic province) or east (Artemisian) slope. The west-slope species include mixed mesic (characterized by moderate moisture) forest endemics like Pieris napi and Amblyscirtes vialis; the east-slope ones are high plains–high desert–steppe species such as Colias alexandra, Satyrium behrii, and Pontia beckerii. In other cases different subspecies of the same complex replace each other on the two slopes (Anthocharis s. sara and s. thoosa, Euchloe h. hyantis and h. lotta, Coenonympha tullia california and t. ampelos), or the situation is taxonomically ambiguous (species or subspecies?—The Cupressaceae-feeding Mitoura). As with the vegetation, elements of the high-desert fauna penetrate the alpine (Pontia occidentalis, P. sisymbrii, Cercyonis oetus, Lycaena heteronea, etc.). Altitudinal stratification of the fauna overall is much more pronounced on the west than on the east slope.

Many west-slope species have well-defined altitudinal ranges or are confined to particular vegetation belts (or Merriam zones). Not all of these extend the entire length of the range, but those extending over more than a few counties usually show a pronounced north–south altitudinal gradient. Some species listed by Garth and Tilden (1963) as “Hudsonian” or “Arctic-Alpine” at Yosemite dip down to middle elevation in the northern Sierra, often in very un-Hudsonian plant communities. Thus Lycaena cupreus and L. editha, as well as Polites sabuleti tecumseh, occur on mesic meadows at 1,500 m (4,950 ft) north of Interstate 80. Garth and Tilden’s ecological typology thus does not hold for the entire range.

It did, however, characterize the Merriam life-zone spread for every species at Yosemite, permitting a comparison of faunal diversity on a zonal transect across the region. (I treat their “unrestricted” species as occurring in all zones, though this is usually not true.) The distribution (table 27.3) shows a species maximum in the Transition Zone (1,200–2,100 m [3,950–6,900 ft], according to Garth and Tilden), corresponding to mixed mesic forest, which also has the greatest precipitation and the greatest floristic diversity (Barbour and Major 1977). The cumulative faunas for the Sierran stations on my Interstate 80 transect (table 27.4) reach their maximum at Donner Pass (2,100 m [6,900 ft]). The vegetation here is in Merriam’s Canadian Zone, with some Hudsonian elements. The difference is probably an artifact of the topography. Donner Pass is low enough for many east- and west-slope species to pass into the other’s territory in at least some years, partially doubling the fauna. The passes at Yosemite are higher (Tioga Pass, 3,010 m [9,930 ft]) and more difficult to cross. The middle-elevation maximum is consistent with various other insect studies, though the causes of the pattern remain controversial (McCoy 1990).

TABLE 27.3

Distribution of butterfly species by Merriam life zones at Yosemite National Park according to Garth and Tilden 1963. “Unrestricted” species are included in the totals for all zones.

Merriam Zone	Number of Species
Lower Sonoran	19
Upper Sonoran	81
Transition	86
Canadian	72
Hudsonian	53
Arctic-Alpine	35

TABLE 27.4

Distribution of butterfly species on a transect parallel to Interstate 80 across the north-central Sierra, based on 1972–94 data by A. M. Shapiro, unpublished.

Station	Elevation	Number of Species (Breeding Residents)
Washington, Nevada County	803 m	73(55)
Lang Crossing, Nevada County	1,500 m	99(80)
Donner Pass, Nevada-Placer Counties	2,100 m	115(85)
Castle Peak, Nevada County	2,730 m	58(45)
Sierra Valley, Sierra County	1,500 m	72(62)

The most famous of the “unrestricteds” are the mass migrants, the California Tortoiseshell (Nymphalis californica) and the Painted Lady (Vanessa cardui). Both migrate by the millions in favorable years; the Tortoiseshell has often tied up July traffic over the summits. Its larvae cause spotty mass defoliation of foothill Ceanothus in spring and of C. velutinus (tobaccobrush) in the high country in summer.

Anthocharis lanceolata is predominantly a west-slope species (also in the Coast Range and northwestern California) that, however, also occurs locally on the east slope, for example, in the Carson Range, in canyons east of Monitor Pass, and in southern Inyo County, and thence (as subspecies australis) into the desert ranges of southern California. It is associated with rocky canyon walls, feeding on various Arabis, but on the west slope is commonly found in mesic forest openings on the rather weedy Arabis glabra. This may be a nonnative plant in the Sierra, and the presence of A. lanceolata in mesic forest may be a recent phenomenon. It is a mobile species whose disjunctions do not necessarily imply relictualism, as witnessed by its dramatic movement upslope in the Donner Pass area during the late 1980s–early 1990s under drought conditions.

In several cases species pairs occur in which one is a weedy ecological generalist and the other a narrow specialist; the generalist is highly dispersive and regularly transgresses zonal and community boundaries, while the specialist is philopatric (“stay-at-home”). Examples are Plebeius acmon and P. lupini, and Lycaena helloides and L. nivalis. In one case three specialists are stratified altitudinally, from west (foothill) to east (subalpine, alpine): Thorybes pylades, diversus, and mexicana. T. diversus, a rare and poorly known species, seems more common in the Coast Range and Trinities.

The most unusual pattern in the Sierran fauna (Shapiro 1992a) has two species or subspecies altitudinally stratified with a “no-man’s land” between them, occupied permanently by neither. In the pairs Anthocharis sara sara and A. stella, and

Phyciodes c. campestris and P. c. montana, the low-elevation entity is widespread beyond the Sierra, but the high-altitude one is endemic. In the Pontia protodice and P. occidentalis pair both species have immense ranges, but neither is a permanent resident at middle elevation. Some other species (Euchloe ausonides, E. hyantis, Everes amyntula) have unnamed ecological races or ecotypes differing dramatically in altitudinal and ecological distribution and host plants. Papilio zelicaon has already been mentioned.

North of Mount Lola the crest dips below the subalpine zone, and the high-country biota disappears. Of the Sierran, truly alpine butterflies, only Callophrys lemberti jumps to Mount Lassen. Species diversity is lower in the north than in the central and southern Sierra, presumably reflecting the lessened topographic diversity. In the far north the subspecies of Coenonympha tullia, isolated by the crest elsewhere, intergrade (merge into one another) near Portola and again in the Pit River drainage (Porter and Geiger 1988).

Endemism in the Sierran Fauna

How much of the Sierran fauna is endemic, and at what taxonomic levels? The taxonomic level of endemism is significant in that, in general, higher-level endemism indicates greater antiquity. A Sierran endemic is here defined as any taxon found only in the Sierra, as previously defined. Again, the analysis is tied to Miller and Brown (1981). Raw endemism figures are meaningful only in some comparative context; how else can we say if endemism is "high" or "low"? Good data are available for Ball Mountain (Siskiyou County), the Trinity Alps, the Eddies and the Trinity Divide, and the North Coast Ranges. All but the last have strong Cascadian affinities that reduce the usefulness of the comparison unless the Cascades are included. I will restrict my comparisons here to the North Coast Ranges, defined as extending from Marin County to Highway 299 from Eureka to Weaverville, to avoid this problem.

As noted earlier, the Sierran fauna is estimated at 155 species and 173 subspecies, or 1.12 subspecies per species. This figure suggests little differentiation within the Sierra, hence little endemism on a fine scale. At the species level there are only three endemics, and two of them are problematic; to list one, I had to deviate from Miller and Brown (1981) and adhere to more recent biological information. They list Anthocharis stella as a subspecies of A. sara. In 1986 Geiger and I convincingly demonstrated that A. stella was specifically distinct, a conclusion now supported by several localities where the two are sympatric (occur together) with no evidence of hybridization (unpublished findings by Shapiro, T. C. Emmel, J. F. Emmel, S. O. Mattoon, and G. Austin). Oeneis ivallda is treated as a full species both by Miller and Brown and by Stanford and Opler (1993), but its relationship to what has been called Oe. chryxus stanislaus has been in doubt since the latter was discovered. Porter and Shapiro (1991) found no genetic evidence for speciation, and subsequent unpublished work by C. C. Nice and Shapiro supports their conspecificity (condition of belonging to the same biological species). Thus ivallda may have to be demoted to a subspecies-level endemic. Only Colias behrii is transparently both a species and endemic.

This seems like very low endemism. There are many endemics in the Rockies, but it is unclear how that huge montane area should be subdivided for purposes of comparison; the Sierra, we must recall, is one continuous range. Austin and Murphy (1987) conclude that there are no species-level endemics in the entire Great Basin.

The North Coast Ranges, including the high country of the Yolla Bollys, cover roughly 35%–40% the area of the Sierra Nevada. They have no alpine and only tiny amounts of subalpine habitat, but their topography is often very rugged. They have 124 species and 140 subspecies, for a ratio of 1.13 subspecies per species—indistinguishable statistically from the Sierra.

Because the area involved is so much smaller, however, an equal ratio of subspecies per species implies that subspecific differentiation has occurred on a finer geographic scale in the Coast Ranges than in the Sierra (the average ranges of subspecies are smaller). There are two broad sets of explanations for this: either the habitat mosaic is finer in the Coast Ranges (as perceived by butterflies), or the fauna is older. Both may be true. The percentage of endemism at the subspecies level is identical for the two ranges (20%; table 27.5). Again, this equivalence really translates into more endemism in the Coast Ranges relative to area, some of which is surely due to the distinctive climates of the immediate coastal fog belt.

Behr (1890) commented on the apparent lack of Sierran mid-altitude endemism, going so far as to declare that "there is much more affinity between [the California North Coast] and the Sierra Nevada, up to 4000 or 5000 feet, than there is for instance between the insect fauna of the Andalusian Coast and that of the Sierra Nevada of Granada [or] between Marseilles

TABLE 27.5

Taxonomic composition of the endemic Sierra Nevada and North Coast Range butterfly fauna (approximated from Miller and Brown 1981), and frequency of endemics at the species and subspecies levels in both faunas.

	Sierra Nevada		North Coast Range	
Family	Species	Subspecies	Species	Subspecies
Hesperiidae	0	3	0	3
Pieridae	2	0	0	2
Papilionidae	0	3	0	1
Lycaenidae	0	7	0	13
Nymphalidae	0	19	0	9
Satyridae	1	3	0	0
Totals	3	35	0	28

Sierra Nevada: Species 3/155 = 0.019
Subspecies 35/173 = 0.202
North Coast Range: Species 0/124 = 0
Subspecies 28/140 = 0.200

and the upper valley of the Rhône." He also noted the floristic affinities of the North Coast and the Sierra Nevada. (Ironically, a recent paper underscores the lack of endemism in the Sierra de Javalambre, central Spain [Sánchez-Rodríguez and Baz 1995].)

Subjectivity and the Recognition of Endemism

Interpretation of endemism at the subspecies level is complicated by the lack of a "biological" concept of the subspecies; subspecies are inherently subjective. There is neither a phenotypic nor a genomic criterion available to objectify them. There is no particular reason to suspect that taxonomists have been more reluctant to name subspecies in Sierran versus Coast Range butterflies. However, I suspect a statistical investigation would reveal that the California montane butterfly fauna is less "split" at the subspecies level than other western North American montane faunas. Does the relatively low endemism reflected in table 27.5 indicate a genuine lack of differentiation in the fauna, or taxonomic conservatism?

This point is important, because the faunistic work of Emmel, Emmel, and Mattoon has generated a long list of new subspecific taxa to be published in Emmel (1995). With this book, the appearance of a poorly subspeciated California fauna will vanish. About 150 new subspecies are being named statewide (nearly one for every two species). Of these, twenty to twenty-five will be Sierran (J. F. Emmel, personal communication, August 1995). Once the new names are validated we will be able to assess whether the Sierra is still relatively low in endemism, in comparison with the North Coast Ranges, for example. Of course, whatever the answer, nothing will have changed about the biology—only our perception of it. With that change may come both collecting pressure on the newly recognized subspecies and moves to protect some of them under federal or state legislation. Perceptions of endemism are important not only for understanding how faunas evolve but also for their potential economic and political consequences.

Large-Scale Biogeographic Affinities of the Fauna

Although butterfly biogeography was addressed by European and American workers in the nineteenth century, the first major analysis of paleoprocesses on butterfly distributions was done by Kostrowicki (1969) for the Palearctic region. Kurentsov (1986) analyzed the role of Beringia in Northern Hemisphere insect biogeography. A formal biogeographic analysis akin to Kostrowicki's has yet to appear in North America, but some patterns are already evident.

Shapiro, Palm, and Wcislo (1981) discuss the derivation of the Trinity-Eddy faunas, placing them in a phytogeographic context. Because butterfly fossils are very rare (and none is from California), butterfly paleogeography must be inferred from other types of evidence, mainly paleobotanical. We must assume that host relationships have been stable during this time frame and that plant associations, even on a very coarse scale, are useful as butterfly indicators. These are risky assumptions (Dennis 1977, 1992). Ecotypes often transgress perceived ecological associations, threatening our ability to extrapolate butterfly ranges based on vegetation; and some paleocommunities existed in climates without modern analogs, leaving us clueless as to potential butterfly faunas.

The oldest butterfly fossils are mid-Tertiary; some belong to extant genera. The antiquity of the major families is unknown, but clearly butterflies were widely distributed and fairly diverse by the mid-Oligocene. The western montane fauna can be interpreted as derived from Madro-Tertiary and Arcto-Tertiary sources (Raven and Axelrod 1978). Among Arcto-Tertiary elements the most extraordinary is the Golden Oak Hairstreak, Habrodais grunus, which with its recently discovered sister species H. poodyi, restricted to Baja California, clearly represents a relict (persistent remnant) of a stock otherwise confined to the Old World and best developed in East Asia.

The Sierran component of the Gray-Veined White (Pieris napi) complex is indistinguishable from inner Coast Range populations. This is a group with strong indications of multiple invasions across Beringia (and perhaps also across the North Atlantic). The Californian populations may ultimately be found most closely related to warm-temperate East Asian ones, representing one of the older episodes of dispersal. A preliminary outline of the biogeography of this group appears in Geiger and Shapiro (1992).

The rest of the western cordillera has high-altitude taxa with arctic or subarctic affinities. Chabot and Billings (1972) noted that the circumpolar-boreal relict element in the Sierran alpine flora was unusually poor. The same is true in the butterflies. Lycaena phlaeas occurs in Yosemite and in the White Mountains, and then skips to the northern Rockies and northeastern Oregon. Colias behrii is a very localized subalpine endemic in the central Sierra that is obviously derived from either the circumpolar C. palaeno or (less likely) the Nearctic boreal C. pelidne. It is thus presumably of Quaternary origin. A strikingly convergent endemic, probably of similar age, exists in the Andes between Santiago de Chile and Mendoza, Argentina (C. mendozina) (Shapiro 1991).

One of the strangest relictual patterns, currently being studied genetically in our lab, concerns the Greenish Blue, Plebeius saepiolus. Virtually all Californian populations of this cordilleran-boreal species are unique in having only a brown morph in the female. Most Rocky Mountain and boreal populations have only blue females. Fixed blue-female populations occur along the far north coast of California and northward, and in the subalpine and alpine zones of the White Mountains. The Sierran populations across from the Whites have brown females only. This situation hints broadly of a double invasion.

The characteristic arctic and alpine Satyrid genus Erebia does not occur in California at all. Its associate Oeneis is represented by Oe. c. stanislaus and Oe. ivallda in the Sierra, which are discussed later but do not seem to be strandings of tundra species, and by Oe. nevadensis, which barely reaches the Sierra and represents a low-elevation species group found in cool, mesic forest around the Northern Hemisphere. Neominois ridingsii is a subalpine-steppe species in the Sierra, Warners, and Whites, disjunct from the Rockies and Great Basin ranges. Neominois appears to be the sister-genus of the large Central Asian Karanasa and appears to be derivative from Pleistocene steppe-tundra, as may also be Pontia occidentalis, P. beckerii, Euchloe ausonides, Lycaena cupreus, and perhaps others. These distributions are related to that of the Crucifer Stroganowia (Rollins 1982). Rigorous phylogeographic studies (Avise 1994) may strengthen these scenarios.

Relations of the Sierra Fauna to Northern and Northwestern California Faunas

Shapiro (1992b) provided outlines of a biogeographic scenario relating the various montane butterfly faunas in California. It was based on a nested pattern of distributions, interpreted in terms of Holocene climatic change. The broad outlines of this process are now emerging in the light of recent progress in paleoclimatic reconstruction, and the forthcoming Emmel, Emmel, and Mattoon book may provide distributional data that are detailed enough to allow the scenario to be fine-tuned for at least some of the most interesting butterflies. Prospects seem particularly good for the North Coast Range disjunctions and serpentine relicts discussed later.

I identified four components in the nested pattern. Group I species are found in northwestern California and northward but are unknown in the Sierra Nevada (e.g., Colias occidentalis, a species frequently misrecorded from the Sierra—as in Garth and Tilden 1963—based on confusion with female Zerene eurydice). Group II is similar but has at least one known population in the northern Sierra (Oeneis nevadensis, Carterocephalus palaemon). Group III includes many montane species widely distributed in both northwestern California and the Sierra Nevada. Some of these, such as the red fir forest specialist Chlosyne hoffmanni, are subspecifically differentiated between the two ranges. The two subspecies of Parnassius phoebus (sternitzkyi in the northwest, behrii in the Sierra) are phenotypically very different and may not be closely related. Group IV consists of the strict Sierran endemics.

Shapiro, Palm, and Wcislo (1981) attempted to use Trinity Alps butterfly distributions to test competing scenarios for colonization of the high Sierra from the north (Cascades) versus the east (Rockies, across the Great Basin [Major and Bamberg 1963, 1967]). None of the Rocky Mountain–related high Sierran taxa were found in the Trinities, but because the Trinity climate was more severe than the Sierran in the Pleistocene, the result was not definitive. Since then, the newly discovered (as yet undescribed) species of Agriades (Lycaenidae) has been found in both the high Sierra and northwest California, the only such distribution seen to date (J. Emmel and S. O. Mattoon, personal communication). The presence of relict populations of Oeneis nevadensis and Carterocephalus palaemon in the northern Sierra supports the idea that the cool, moist-adapted fauna retreated and mostly disappeared from the low northern Sierra in the Hypsithermal/Xerothermic. The presence of relicts such as Parnassius clodius (in the Yolla Bollys, formerly in Santa Cruz County) and the unnamed Cascade-Trinity subspecies of Polites sabuleti (in Colusa and northern Lake Counties) shows a similar northward retreat in the North Coast Ranges. The Mormon Fritillary, Speyeria mormonia, has relict populations in the Eddies, on Ball Mountain north of Mount Shasta, and in the Warners. These populations seem to suggest its route between the Cascades and the Sierra Nevada, but as a meadow species it might well have been able to cross a cool, pluvial (characterized by abundant rain) Great Basin. Phylogeography offers a concrete hope of resolving its regional history.

Phyciodes orseis is one of the rarest butterflies in northern California. It has a Group III distribution, with different subspecies (P. orseis orseis in northwest California, formerly south to Marin County [although there is some ambiguity about the authenticity of Marin County due to the age of the records]; P. o. herlani in a small area centered on the Lake Tahoe basin). However, both "subspecies" may actually be stabilized hybrid swarms between P. mylitta and the corresponding geographic subspecies of P. campestris (P. c. campestris in the northwest, P. c. montana in the Sierra). If so, they arose independently as epiphenomena of the distribution of the parental species. P. mylitta and P. campestris are widely sympatric at low elevations today, with no apparent hybridization. Scott (1994) ignores the hybrid hypothesis.

The lack of relicts of northern affinity in bogs in the Sierra Nevada is striking, because they are relatively common in the higher North Coast Ranges. At least one North Coast Range butterfly, Lycaena xanthoides, gives hints of ancient hybridization with its close relative L. editha, now confined to the Sierra and south Cascades in California. A probable stabilized hybrid population between these two exists in far northern California, from Dunsmuir to near Yreka, and there is a smaller apparent hybrid zone in canyons in the White Mountains (Shapiro and Geiger in preparation).

At the southeast end of the Sierra a fairly small faunistic element derived from the desert enters on the east side. One of the most spectacular Sierran butterflies, the Nokomis Fritillary (Speyeria nokomis apacheana), belongs to this element; it is confined to wet, east-slope meadows. The species as a whole is in decline, and its presence in the Sierra at all reflects wetter times in the Pleistocene. For its genetics see Britten et al. 1994.

Another pattern of disjunction that we are studying phylogeographically is associated with serpentine soils in the North Coast Range and Sierra. Once again the butterfly ranges are nested, but the pattern is asymmetrical. Mitoura muiri and Hesperia columbia are found mostly on serpentine. M. muiri has never been recorded from the Sierra, while H. columbia was reported from two sites (Mariposa and Kern Counties) by Shields (1978). H. columbia is a bunchgrass feeder with undetermined preferences; M. muiri feeds on Sargent and MacNab cypresses; both thus could occur in the Sierra. Hesperia lindseyi, another bunchgrass feeder, and Erynnis brizo lacustra, which in northern California feeds only on Quercus durata, were formerly thought to be absent from the Sierra. They are now known to occur on a number of ultramafic barrens in Nevada, Placer, and El Dorado Counties (both) and Mariposa County (brizo). Both extend through the Central Coast Ranges and the Transverse Ranges, so that there is a potential dispersal route into the Sierra from the south—perhaps followed by extinction south of El Dorado County as the climate became hotter and drier along the east flanks of the San Joaquin Valley. The strangest component of this pattern is an unnamed subspecies of the Hesperia comma complex. The normal west-slope Sierran entity is H. c. yosemite, which occurs at middle elevations with a single brood in June and July. A phenotypically different entity, but apparently also a member of the comma complex, is known from a serpentine barren in Nevada County, where it flies in the third week of September and into early October. Normal yosemite occurs on nonserpentine soils both above and below this site. Apparently the same entity is widespread in the south Yolla Bollys on nonserpentine soils; it also flies in late September and October. Additional Sierran localities are reported from El Dorado and Mariposa Counties. The biogeography of the comma complex in California is extremely difficult, and many "blend zone" populations are known that mix characteristics of named subspecies (MacNeill 1964). Only phylogeography is likely to clarify this confusion.

Genetics and the Subspecies Problem

The "subspecies problem" has bedeviled lepidopterists for decades. Porter and Geiger (1988) focus on the problem in their revision of the Coenonympha tullia complex, based on electrophoretic genetics (a technique used to make concealed genetic variability in populations visible in the lab). We have traditionally named subspecies based on color and pattern, but molecular-phylogeographic techniques, including both enzyme electrophoresis and various DNA-based methods (Avise 1994), now give us new access to the genetic architecture of populations and species complexes. Baughman et al. (1990) attempted to work out the history of the Euphydryas editha complex in western North America. This species is highly colonial and breaks down into a number of ecotypes associated with particular host plants on a geographic basis, but its genomic architecture was remarkably uninformative, with most populations very similar and a few anomalously, and idiosyncratically, distinct. The result of Baughman et al. is similar to that of Tong and Shapiro (1989) on the physiologically very distinct, but electrophoretically nearly identical, ecotypes of Californian Papilio zelicaon. Porter and Geiger (1988) and Porter and Shapiro (1991) found that the Satyrids Coenonympha tullia ampelos / california and Oeneis ivallda / chryxus stanislaus were less differentiated electrophoretically than phenotypically. Recent unpublished work by C. C. Nice and Shapiro on various Lycaenids (Lycaeides idas and melissa complexes, Mitoura nelsoni / muiri / siva) points in the same direction. If parallelism is common in butterfly ecotypes, discordance with phylogeography is to be expected.

Recently, Ball and Avise (1992) reviewed phylogeographic versus phenotypic differentiation in avian subspecies. Predictably, they found that some taxonomic subspecies corresponded to well-defined genetic entities, while others did not. Their conclusions bear on butterflies perhaps even more than on birds:

> Recognition of deep historical separations may not be the only rationale for subspecies descriptions . . . . Any mutations serving as genetic markers of breeding populations (including those underlying particular morphological or behavioral traits) can be of great utility . . . even if the mutations are of recent origin and do not reflect long-term population separations or genome-wide patterns of differentiation . . . . We have argued that short-term population separation should not be sufficient to justify formal taxonomic recognition of subspecies (in part, because sensitive and refined genetic assays will likely reveal significant structure even at deme and family levels in most species) . . . . Subspecies names should be reserved for the major subdivisions of gene-pool diversity within species . . . concordant subdivisions at multiple independent loci . . . therefore, some other means of cataloging geographic distributions of individual markers should be implemented. Overall, an enlightened perspective on intraspecific differentiation would recognize the great variety of evolutionary breadths and patterns likely to be represented among populations, and the various taxonomic and population applications to which these levels of genetic separation might be applied.

Overall, genetic studies of Sierran butterflies—both published and in progress—point to a predominance of stasis at the genomic level. Yet, in many species, ecotypic differentiation (genetically based ecological races) is obvious; it involves phenology, diapause (developmental arrest; a time of seasonal dormancy), and host-plant use, but seldom color and pattern (which seem to vary in other, nonconcordant ways). These attributes are under genetic control, and to the extent they have been studied in our fauna and others, that control tends to be simple and Mendelian. Presumably we are seeing strong selection on life-history traits, superimposing the resultant variation on an otherwise nearly invariant background. We simply do not see the level of genetic differentiation in butterflies that we would expect in so large and ecologically complex an area as the Sierra, were the fauna old. (The single deviant case, Speyeria nokomis apacheana, involves extremely small effective population size and is consistent with drift

[Britten et al. 1994]). Genetics thus dovetails with geography in suggesting that the existing fauna only quite recently attained its current distribution.

CONSERVATION AND MANAGEMENT ISSUES

Some Basic Natural History

Butterflies are holometabolous (having complete metamorphosis) insects. This fact has tremendous implications for butterfly ecology and management. To succeed, a butterfly population must have access to appropriate resources in all life stages. Butterflies are diverse enough in their life histories that it is difficult to generalize about them. This section is largely abstracted from Dennis 1992 and Scott 1986 and adapted to a Sierran faunal context. Rather than burden this chapter with dozens of references to basic (non-Sierran) butterfly biology, I refer the reader to the bibliographies of these works. In addition, I will not attempt to cite the hundreds of publications touching on the natural history of species found in the Sierra. Emmel, Emmel, and Mattoon will inventory this literature in their forthcoming book. Meanwhile, the Dennis book in particular is extremely useful.

As far as is known, the larvae of all Sierran butterflies are phytophagous (feeding on plants). Host-plant adaptations may be very strict (some Euphilotes ecotypes on single species or even races of Eriogonum) or extremely broad (Vanessa cardui on many unrelated plant families). Most species lie somewhere in between, feeding on a few plants typically sharing their defensive chemistry: Pieris, Euchloe, and their close relatives eat only plants containing glucosinolates (Cruciferae and Capparidaceae), but not those having an additional line of defense, such as Thlaspi and Erysimum; Junonia coenia eats Scrophulariaceae, Plantaginaceae, and the Verbenaceous genus Lippia, which share iridoid glycosides. The more specialized the relationship, in general, the more vulnerable to disruption. Multiple-brooded species may have different host plants in successive generations; Nymphalis californica tracks young foliage of Ceanothus upslope as the season advances. Some species feed on particular parts of the plant or distinct seasonal stages (phenophases): Euchloe and Anthocharis eat only buds, flowers, and fruit of Cruciferae; many blues, such as Everes amyntula, are seed feeders. The plants used as larval hosts by butterflies are a small and very nonrandom selection from the total flora. Certain genera and families are particularly important; these include willows (Salix), oaks (Quercus), wild buckwheats (Eriogonum), Malvaceae, and Papilionaceous legumes (Vicia, Lathyrus, Astragalus, Lupinus, Trifolium). All the Californian Satyrids and Hesperiine skippers feed on grasses or sedges, but their preferences in the wild are largely unknown, largely because few people can identify graminiforms well. These butterflies rarely feed on naturalized annual species. Annuals in general are infrequently used as butterfly hosts. Most associations are with herbaceous perennials and woody plants, but because of the clustered taxonomic preferences noted earlier and because of climatic correlations, species diversity of these plant groups is not a very useful predictor of butterfly diversity. Many Lycaenid and Riodinid larvae have mutualistic relationships with ants, here as elsewhere. These relationships may be obligate or facultative.

Most butterflies are heliotherms (they depend on incoming solar radiation to heat their bodies to temperatures sufficient for flight), and thus are animals of sunny climates. Coastal fog-belt climates have high floristic diversity but few butterflies. Cloudiness is seldom if ever limiting to Sierran butterflies during the flight season, except perhaps in the alpine zone (but compare Emmel and Emmel 1963a).

The number of broods per year may be fixed or variable. Univoltine (single-brooded) species tend to be thus throughout their ranges, while multivoltine species rarely persist where they can produce only one brood per year. There is a predictable seasonal succession of adult butterflies in a given locality. The flight periods of different species tend to have a constant seasonal relationship even though the actual flight dates may vary greatly with the weather. At higher elevations the timing of snowmelt is critical to initiating the flight season. Philotes sonorensis, typically the earliest-flying butterfly in the Sierra that does not hibernate as an adult, has emerged at the same 1,500 m (4,950 ft) site as early as late February (in drought years) and as late as May to mid June (in years of late snowmelt).

All breeding residents in the alpine zone are univoltine, and some, such as Oeneis ivallda, Oe. chryxus stanislaus, and Neominois ridingsii, require two years to complete a generation (diapausing twice as larvae). This phenomenon also occurs in alpine butterflies in Eurasia and in some arctic species. Both alpine species and those of stressful foothill habitats, especially serpentine, often show multiple-year diapause as larvae or pupae. This pattern appears to be a hedge against short-term catastrophe, analogous to a soil seed bank in plants.

Most foothill butterflies are either spring-univoltine or spring-bivoltine, a cycle that allows them to exploit the combination of lush vegetation and sunny days that occurs only then. At middle elevation about half of the fauna is univoltine, increasing to 80% at 2,100 m (6,900 ft). Univoltines may fly at any season, but very few (Apodemia mormo, Neophasia menapia, Ochlodes sylvanoides) fly in the last third of the season. Like crops, butterflies are highly vulnerable to density-independent catastrophes, including unusual or severe weather and fire. Management practices with the potential to produce catastrophic mortality (logging, pesticide use, prescribed burning, grazing) need to figure butterfly life cycles into their scheduling if sensitive species are at risk.

The peak of butterfly adult diversity occurs in the lower foothills in May, moving gradually upslope with the advancing season. There may be striking differences in butterfly seasonality with slope and exposure, especially at high elevations. At Carson Pass, for example, the dry, south-facing slopes of Red Lake Peak and Little Round Top may be three weeks advanced relative to the north-facing slopes of Round Top at the same elevation, just across Highway 88.

Adult butterflies feed on nectar. Some species also or primarily visit sap fluxes or rotting fruit. Although most flower-visiting butterflies have preferences (which typically reflect the geometry of the flower relative to the tongue and leg lengths of the animals), there are apparently no tightly co-evolved pollinator-butterfly systems in the Sierra. Flowers particularly important to butterflies in general include Chrysothamnus, Aster and Solidago (Compositae), Eriogonum (Polygonaceae), Rhamnus (Rhamnaceae), Aesculus (Hippocastanaceae), Agastache and Monardella (Labiatae), Spraguea (Portulacaceae), Apocynum (Apocynaceae), and Asclepias (Asclepiadaceae). The only butterfly that visits turpentine weed and vinegar weed (Trichostema, Labiatae) is the skipper Ochlodes sylvanoides; it is unclear if it is an effective pollinator.

In addition to the vicinity of nectar sources, large butterfly aggregations are observed on mud puddles and on rocky summits. The puddling groups consist almost entirely of young males, with each species tending to cluster separately. Among frequent participants are various Blues (Lycaeides, Celastrina, Everes, Euphilotes, Plebeius), Pieris napi, Papilio zelicaon, indra, eurymedon, and rutulus, Adelpha bredowii, Chlosyne and Euphydryas spp., Erynnis spp., Thorybes spp., and Hesperia nevada. These animals seem to be collecting minerals that may be physiologically necessary for reproductive activity, but the phenomenon is still poorly understood.

Hilltop aggregations are interpreted as an epigamic (mate-locating) strategy for low-density populations spread over difficult terrain. On the summits males may either perch or patrol a territory, and females are only transient visitors, coming to mate and then departing. Among hilltopping species commonly observed in the Sierra are Pontia occidentalis, P. sisymbrii, Euchloe hyantis, Papilio zelicaon, indra, and eurymedon, Parnassius phoebus behrii, Oeneis spp., Vanessa and Nymphalis spp., Speyeria egleis, Thorybes mexicana nevada, and Hesperia nevada.

It is important to remember that hilltop aggregations may draw on a large area and cannot be interpreted as representative of overall population density. Hilltopping species are highly vagile (free-moving) and may cover several kilometers a day in routine upslope and downslope flights between breeding and mating sites. On the other hand, some species (such as many Euphilotes) are intensely philopatric ("stay-at-home") and may spend their entire lives within a few meters of the plant they fed on as larvae. Hilltopping promotes gene flow and may prevent population differentiation. From a genetic standpoint, philopatric butterflies are likely to show much more population substructuring than others; most of the likely candidates are Blues (Lycaenidae).

The adverse season is typically spent in diapause. Each species or lineage has a characteristic phase of the life cycle capable of diapause, and there is usually little or no flexibility in this regard. In subalpine and alpine climates unseasonable snow may make it difficult to complete development in one season. In most species natural selection has made the cycle more conservative than it need be in most years, as "insurance" against unusual weather events. In a few species, such as Papilio zelicaon, normally univoltine populations may produce a partial second brood in unusually favorable years.

Historical Changes in the Sierran Fauna

Because there are no pre–gold rush records and very few precise records before 1930 anywhere in the Sierra, it is almost impossible to say anything about historic change unless we extrapolate from vegetation or community-level change to the probable butterfly fauna. This practice is risky.

Fire suppression in the Sierra Nevada has undoubtedly changed the environment for butterflies. Because butterflies are rare in continuous closed-canopy forest, the more open landscapes maintained by fire may have been more conducive to butterflies than are current ones, but this depends in part on the distribution of understory resources, including larval host plants and adult nectar sources. The middle-elevation forests of the inner North Coast Range may approximate historic Sierran conditions better than Sierran forests do today. In these forests we may travel long distances and see few if any butterflies, only to encounter tremendous concentrations along streams or anywhere such butterfly flowers as Apocynum or Agastache are abundant. Fritillaries (Speyeria spp.), which are strong fliers, tend to be abundant in these forests. The openness of the forest floor also favors their host plants, Viola spp.

Insofar as it opens up the forest, selective logging may mimic the beneficial effects of natural fire for butterfly breeding. In much of the Sierra, bull thistle (Cirsium vulgare) is virtually the signature of logging disturbance, and it is a valuable nectar source in habitats where native flowers are uncommon in late summer.

Because few butterflies occur in mature forest but many species are associated with successional vegetation, both clear-cutting and fire, even in its current form, are likely to enhance the richness of butterfly species in the short to medium term. The butterfly fauna of montane chaparral (Ceanothus velutinus, Arctostaphylos spp., Prunus emarginata, Quercus vacciniifolia, etc.) is small but consistent, including Nymphalis californica, Incisalia iroides, and Celastrina argiolus echo and usually Callophrys (dumetorum or lemberti) and Hesperia (comma complex and juba). The richest butterfly fauna in the Sierra are found in vegetationally diverse successional habitats with many perennial herbs and in canyon bottoms with rock faces in close proximity to riparian vegetation (especially on west- and southwest-facing slopes).

Experience suggests that butterfly species richness may peak in the early stages of tree establishment, when the community is becoming multilayered but is still strongly insolated.

Fire suppression leads to enhanced shade, and a few mesic-adapted species such as Pieris napi, Parnassius clodius, and Amblyscirtes vialis may have expanded their ranges beyond their normal riparian corridors at middle elevation under these conditions.

There is no reason to think that either logging or fire has added to or subtracted from the Sierran butterfly fauna. Undoubtedly there have been local changes in distribution and abundance, but no direct information is available.

Nor is direct information available on grazing effects on Sierran meadow and riparian butterflies. Intuitively, we would expect selective grazing to reduce plant diversity and thus injure butterflies through depletion of host plants and/or nectar resources. We might also expect injury from trampling and the disturbance of wet, peaty soils. In fact, there is no evidence known to me that this has occurred in the Sierra, and many meadow butterflies use disturbed mud and animal tracks as puddling sites, enhancing their apparent abundance.

Climatic Instability in Recent Decades

The climatic instability in the past twenty-five years has been correlated with both conspicuous and subtle changes in Sierran butterfly distribution and abundance as tracked by my Interstate 80 transect. In no case is there solid proof of causal mechanisms, but plausible mechanisms exist in many cases.

The transect study, initiated in 1972, embraces the 1975–77 drought, the 1982/83 "year of the big snow," the December 1990 cold wave, and the 1994/95 snowy winter, as well as less dramatic but in some cases even more significant climatic perturbations in other years. The short but intense 1975–77 drought had few effects, but the less intense but more prolonged drought of the 1980s through early 1990s coincided with many changes in butterfly distribution and abundance. Polites sabuleti tecumseh disappeared from the lower part of its range at 1,450–1,500 m (4,785–4,950 ft), at the same time becoming more abundant at 2,100–2,400 m (6,900–7,920 ft). Its disappearance from Bear Valley (Nevada County) coincided with the removal of grazing, however, and this may also have been a factor. Euchloe ausonides and Thorybes pylades, both resident at my 800 m (2,625 ft) site, colonized and bred repeatedly at 1,500 m (but apparently disappeared over the winter of 1994/95). Anthocharis lanceolata, common at and below 1,500 m, colonized and bred at 2,100 m. Several species declined precipitously at 2,100 m, including Lycaena arota, which had been abundant in the 1970s and early 1980s, and Plebeius shasta, which was widespread at Donner Pass when the Emmels worked there thirty years ago but may now be extinct there below 2,300 m (7,590 ft). The data are not entirely unambiguous, but there are hints that the Castle Peak (2,700 m [8,900 ft]) fauna was systematically enriched from below during the drought years, with previously incidental species beginning to breed at tree line. This coincided with a decline in the resident fauna nearby at 2,100 m.

Although species numbers have fluctuated strikingly at Donner Pass since 1971, the most dramatic and causally explicit changes occurred in 1992. The 1991/92 snowpack was unusually light and melted very early. May 1992 was warmer than a normal June; at Donner (as elsewhere in the Sierra) both species numbers and individual abundances hit record highs, and there was an influx of subtropical strays from the desert (Shapiro 1993). A sudden snowstorm June 10–11 and accompanying cold wave dropped the number of species flying from sixty-two on June 8 to twenty-nine a week later. The fauna has not yet recovered from this event and what followed. Much of the reproduction achieved before June 10 was undoubtedly lost. Stragglers of many species continued to emerge after the cold wave, but in very low numbers. Immatures that survived the storm were then subjected to very severe drought conditions in late summer, with the vegetation senescing (drying up) 4–7 weeks early. Almost the entire fauna at Donner is univoltine, and any given species typically can diapause only in a particular life-history stage. Diapause is usually initiated in summer and continues until late winter. The 1992 diapausers were subjected to about a month more of hot, dry weather than normal, which must have imposed a tremendous physiological burden on them. There may also have been significant losses when hosts senesced before the larvae were done feeding. The snowy winter of 1992/93 seems to have abetted over-winter survival, but in summer 1994 the vegetation again dried early enough to cause larval mortality.

The alpine zone at nearby Castle Peak was not sufficiently advanced at the time of the June 1992 storm to be seriously affected, and diversity there was not harmed. Drought conditions in summer 1994 were very severe above tree line at Kit Carson Pass, but 1995 flights were mostly good after a very snowy winter.

As dramatic as these events have been, they are only moderately unusual on the scale of historic weather records and have been greatly surpassed in both intensity and duration over the Holocene as documented by palynological, dendrochronological, and other proxy climatic records. I return to climatic lability and butterfly faunistics in the conclusions to this chapter.

Weedy Ecotypes and Anthropogenic Range Extensions

Much of the low-elevation California butterfly fauna now eats exotic weeds (Shapiro 1984); one species, Pieris rapae, is itself an animal "weed" introduced from Europe in the nineteenth century. Relatively few montane or alpine butterflies appear to breed on introduced plants at this time, but some of those that do are widespread and common and may owe some of their success to the use of weedy hosts. Table 27.6 lists some examples known to me. Of these, only Lycaena xanthoides currently seems to be expanding its range in the Sierra, and it suffered at least temporary reversals in 1995.

TABLE 27.6

Some native Sierran butterflies now using weedy host plants. (Several other Sierran butterflies use weeds commonly in the Central Valley but not in the mountains.) Species with distinct weed-adapted ecotypes are not included.

Species	Native Hosts	Weedy Hosts
Pontia protodice, P. occidentalis	Cruciferae	Cruciferae: *Cardaria, Lepidium, Descurainia, Sisymbrium,* etc.
Colias eurytheme	*Astragalus?*	Legumes: Alfalfa *(Medicago)*, Sweet Clover *(Melilotus)*, etc.
Plebeius saepiolus	Native *Trifolium*	Naturalized *Trifolium*
Lycaena cupreus	*Oxyria digyna,* Native *Rumex?*	*Rumex acetosella*
Lycaena editha	*Polygonum phytolaccoides,* Native *Rumex*	Weedy *Rumex*, incl. *R. acetosella*
Lycaena xanthoides	Native *Rumex*	Weedy *Rumex*, incl. *R. acetosella*
Phyciodes mylitta	Native thistles	*Cirsium vulgare*, other weedy spp.

A special case is the formation of disturbance-associated ecotypes feeding on weeds. The species in question had not been associated with disturbed or weedy environments in the past. There have been several spectacular instances of this phenomenon in the eastern United States, including the shift of the skipper Poanes viator from aquatic grasses and sedges to common reed (Phragmites communis) in the Philadelphia–New York corridor and of Erynnis baptisiae from its native, scarce, and local host Baptisia to the introduced vetch Coronilla varia, planted for erosion control on highway embankments in Pennsylvania (Shapiro and Shapiro 1973; Shapiro 1979); in both cases an obscure species became very abundant. (See also Thomas et al. 1987.)

In California the Anise Swallowtail, Papilio zelicaon, has evolved a multitude of host-specialist ecotypes with appropriate phenology and diapause, from sea level to tree line (Shapiro 1995). The multivoltine, weedy ecotype that feeds on sweet fennel (Foeniculum vulgare), which was already widespread near sea level, has followed its host along freeway embankments into much of the Gold Country, up to at least 1,300 m (4,250 ft) (1995), and is still expanding. It now ranges above univoltine and partially bivoltine ecotypes on native hosts on serpentine soils and in rocky canyons. We are rearing increasing numbers of wild nondiapausers from populations where we formerly rarely encountered any, suggesting gene exchange and the dilution of the strong diapause strategy.

We do not know when the Silvery Blue (Glaucopsyche lygdamus) discovered weedy annual vetches along freeway embankments. Its native hosts are perennial vetches and lupines. Populations using introduced Vicia (villosa, benghalensis) may have been present on the floor of the Sacramento valley twenty-five years ago (Shapiro 1974), but they, and the vetches, only recently appeared in the Sierran foothills; Vicia-feeding lygdamus first appeared at Colfax, Placer County, in 1991 and by 1994 had moved down to a disturbed site in the American River canyon, where it now flies within 1 km (0.62 mi) of nonweedy, native populations. Curiously, the same phenomenon is occurring simultaneously in the same species in the northeastern United States (Dirig and Cryan 1991). These ecotypes reinforce the apparent climatic trend by carrying the low-elevation fauna higher into the foothills.

Is the Fauna in Danger?

There are no federal or California threatened or endangered butterfly taxa in the Sierran fauna—at least not yet. Endemic taxa, especially those with very small ranges or those with very narrow ecological specializations, are at the highest risk. The low level of observed endemism would suggest little ground for concern, but once many new subspecies are named, perceptions of threats and pressures for protection are likely to follow.

Endemic Sierran taxa are concentrated in the subalpine and alpine zones. High-altitude taxa are most at risk from climatic change, though no data suggest that any are actually in peril. Anecdotally, we know that the numbers of alpine butterflies have fluctuated wildly with the climatic instability of the past two decades. We do not know if that is a problem; nor do we know the capacity of these insects for multiple-year diapause. Dennis (1992) addresses some of these issues (see also Botkin et al. 1991).

Another group of species of special concern is the relicts restricted (as far as we know) to a few edaphic (soil-determined) barrens—Erynnis brizo lacustra and Hesperia lindseyi, in particular, and the unnamed North Coast Range Hesperia comma entity flying in autumn amidst early-summer Sierran races. Some of the best-known edaphic barrens in the Sierra (e.g., the Ione clays) have no special butterflies. A systematic survey of Sierran serpentine and similar sites needs to be done to document the full extent of the distribution of the relict skippers and to assess the need for protection.

There have been recent changes in the butterfly fauna of the Sierra Valley, north of Truckee, that may have been climate mediated. These include the apparent loss of the once-abundant Phyciodes c. campestris–c. montana intergrade (phenotypically intermediate) populations and of Colias philodice and a drastic decline of Cercyonis pegala boopis. There is no basis for assessing whether such phenomena are purely local or reflect regional processes. The Sierra Valley is an area of special interest because of the intimate interdigitation of the Sierran and Great Basin biota. The most dramatic change observed there has been the replacement of Lycaena arota arota by L. a. virginiensis in 1994/95, apparently representing a climate-driven extinction and colonization at the subspecies level. Populations of the Eriogonum-specialist genus Euphilotes in the nearby hills adjoining Dog Valley and Sardine Valley appear to be evolutionarily active. Some of these may have been affected by the August 1994 fires in the area.

Like many other organisms, butterflies are vulnerable to habitat fragmentation, which prevents reinforcement or recolonization of local populations, inhibits gene flow, and decreases species' ability to rebound from climatic or other natural disasters and to track geographically any directional shifts in climate. Although no specific threats can be adduced, it should be self-evident that rapid development of the western foothills may put at least some butterflies at risk in the region.

One specific threat that can be dealt with by prudent planning is the use of microbial insecticides for the suppression of forest-defoliator outbreaks. Bacillus thuringiensis (BT, Dipel®) is a nonselective lepidopteran larvicide. To date, the U.S. Forest Service has been sensitive to this threat and has solicited input from lepidopterists on potential consequences for nontarget species. It is important that this attitude be maintained and that adequate lists of lepidopterists exist.

Recreational and scientific collecting, done in moderation, has not been identified as a potential problem for any Sierran butterfly except perhaps Speyeria nokomis apacheana. Because of their low reproductive capacity, Parnassians could be vulnerable here, as in Europe, where nearly all populations are now legally protected. However, Californian populations have not been finely subdivided taxonomically as have those in Europe, and there seems to be very little pressure on them. Highly specialized Lycaenid populations (Arnold 1983), having low vagility and very exacting environmental requirements, will always be the butterflies most vulnerable to overcollecting or habitat alteration. Few Sierran Lycaenids have been recognized subspecifically to date, however, and none is known to have been lost.

CONCLUSIONS

1. There is no historic record of Sierran butterflies before 1849. Hardly any serious ecological or faunistic work was done before the 1930s. Faunal change can thus be inferred only by the use of risky assumptions or, more reliably, from relatively short-term and local data sets.

2. Changing concepts of subspecific butterfly taxonomy are likely to change our perceptions of the Sierran fauna in the near future.

3. For a charismatic, popular group, the butterflies are remarkably underdocumented. This will change when the Emmel, Emmel, and Mattoon book on California butterflies appears.

4. The Sierran fauna is rich in species. Some of the richest butterfly faunas in temperate North America occur there, and the richest California counties (corrected for area) are Sierran.

5. Although it is difficult to demonstrate rigorously, the Sierran butterfly fauna as currently understood taxonomically has a low degree of endemism. There are only three endemic species and surprisingly few subspecies, given the area of the range. The North Coast Ranges have higher subspecies-level endemism, corrected for area.

6. Butterflies as a group are not adapted to old-growth, closed-canopy forest and are thus irrelevant to conservation decisions about such habitats. Most butterflies in the Sierra occur in successional, or climatically or edaphically treeless, environments, steppe or savanna, or in riparian corridors.

7. Fire suppression has probably altered butterfly ranges and abundance, but there are no hard data. Neither fire nor logging is necessarily inimical to butterflies, and both may even be beneficial. The impact of grazing in the Sierra is not understood.

8. With the possible exception of Speyeria nokomis apacheana, no Sierran butterflies are at serious regional or global risk. Continuing climatic instability or systematic climatic change can be expected to cause (possibly major) faunal changes. Habitat fragmentation and destruction, especially loss of edaphic barrens with disjunct relicts, could become a problem, especially in the western foothills.

9. Both biogeographic and genetic studies suggest that the existing Sierran butterfly fauna is young. Both the geography of the fauna and existing ecotypes probably date only from the Holocene. Although there are few relict butterfly populations in the Sierra, statewide and regional patterns of relictualism point to northward regression of the fauna in the Hypsithermal, consistent with current understanding of the paleovegetational sequences. There is no basis to consider either historic or current butterfly faunas to be in "equilibrium."

ACKNOWLEDGMENTS

This report could not have been prepared without information supplied informally by John F. Emmel, Sterling O. Mattoon, Greg Kareofelas, Carol Whitham, Christopher C. Nice, Adam H. Porter, Ray E. Stanford, and George Austin. Given its preliminary nature, errors and omissions are to be expected, and for these I take full responsibility. Field work since 1972 has been supported in part by several California Agricultural Experiment Station projects and currently by National Science Foundation grant DEB93-06721.

REFERENCES

Arnold, R. A. 1983. Ecological studies of six endangered butterflies: Island biogeography, patch dynamics, and design of habitat preserves. University of California Publications in Entomology 99:1–161.

Austin, G. T., and D. D. Murphy. 1987. Zoogeography of Great Basin butterflies: Pattern of distribution and differentiation. Great Basin Naturalist 47:186–201.

Avise, J. C. 1994. Molecular markers, natural history, and evolution. New York: Chapman and Hall.

Ball, R. M., Jr., and J. C. Avise. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. The Auk 109:626–36.

Barbour, M. G., and J. Major. 1977. Terrestrial vegetation of California. New York: John Wiley.

Baughman, J. F., P. F. Brussard, P. R. Ehrlich, and D. D. Murphy. 1990. History, selection, drift, and gene flow: Complex differentiation in checkerspot butterflies. Canadian Journal of Zoology 68:1967–75.

Behr, H. H. 1890. Yosemite Lepidoptera. Zoe 1:177–79.

Boisduval, J. B. A. de. 1868. Lépidoptères de la Californie. Annales de la Société Entomologique de Belgique 12:5–95.

Botkin, D. B., R. A. Nisbet, S. Bicknell, C. Woodhouse, B. Bentley, and W. Ferren. 1991. Global climate change and California's ecosystems. In Global climate change and California: Potential impacts and responses, edited by J. B. Knox and A. F. Scheuring, 123–49. Berkeley and Los Angeles: University of California Press.

Britten, H. B., P. F. Brussard, D. D. Murphy, and G. T. Austin. 1994. Colony isolation and isozyme variability of the Western Seep Fritillary, Speyeria nokomis apacheana (Nymphalidae) in the western Great Basin. Great Basin Naturalist 54:97–105.

Chabot, B. F., and W. D. Billings. 1972. Origins and ecology of the Sierran alpine flora and vegetation. Ecological Monographs 42:163–99.

Dennis, R. L. H. 1977. The British butterflies: Their origin and establishment. Faringdon, U.K.: E. W. Classey.

———. 1992. Butterflies and climate change. Manchester, U.K.: Manchester University Press.

Dice, L. R. 1943. The biotic provinces of North America. Ann Arbor: University of Michigan Press.

Dirig, R., and J. F. Cryan. 1991. The status of silvery blue subspecies (Glaucopsyche lygdamus lygdamus and G. l. couperi: Lycaenidae) in New York. Journal of the Lepidopterists' Society 45:272–90.

Dyar, H. G. 1892. Collecting butterflies in the Yosemite Valley. Entomological News 3:30–33.

Emmel, T. C., ed. 1995. Systematics of western North American butterflies. Gainesville, FL: Mariposa Press. In press.

Emmel, T. C., and J. F. Emmel. 1962. Ecological studies of Rhopalocera in a high Sierran community—Donner Pass, California. I. Butterfly associations and distributional factors. Journal of the Lepidopterists' Society 16:23–44.

———. 1963a. Ecological studies of Rhopalocera in a high Sierran community—Donner Pass, California. II. Meteorological influences on flight activity. Journal of the Lepidopterists' Society 17:7–20.

———. 1963b. Composition and relative abundance in a temperate zone butterfly fauna. Journal of Research on the Lepidoptera 1:97–108.

———. 1973. The butterflies of southern California. Science Series 26. Los Angeles: Natural History Museum of Los Angeles County.

Eriksen, C. 1962. Further evidence of the distribution of some boreal Lepidoptera in the Sierra Nevada. Journal of Research on the Lepidoptera 1:89–93.

Garth, J. S. 1935a. Butterflies of the Boundary Hill Research Reserve, Yosemite National Park, California. Bulletin of the Southern California Academy of Sciences 33:131–35.

———. 1935b. Butterflies of Yosemite National Park. Bulletin of the Southern California Academy of Sciences 34:37–75.

Garth, J. S., and J. W. Tilden. 1963. Yosemite butterflies. Journal of Research on the Lepidoptera 2:1–96.

Geiger, H. J., and A. M. Shapiro. 1986. Electrophoretic evidence for speciation within the nominal species Anthocharis sara Lucas (Pieridae). Journal of Research on the Lepidoptera 25:15–24.

———. 1992. Genetics, systematics, and evolution of Holarctic Pieris napi species-group populations (Lepidoptera: Pieridae). Zeitschrift für zoologische Systematik und Evolutionsforschung 30:100–122.

Kostrowicki, A. S. 1969. Geography of the Palearctic Papilionoidea (Lepidoptera). Krakow: Panstwowe Wydawnictwo Naukowe.

Kurentsov, A. I. 1986. Significance of Beringian links in Holarctic insect zoogeography. In Beringia in the Cenozoic Era, edited by V. L. Kontrimavichus, 529–54. Rotterdam: A. A. Balkema.

MacNeill, C. D. 1964. The skippers of the genus Hesperia in western North America with special reference to California. University of California Publications in Entomology 35:1–230.

Major, J., and S. A. Bamberg. 1963. Some cordilleran plant species new for the Sierra Nevada of California. Madroño 17:93–109.

———. 1967. Some cordilleran plants disjunct in the Sierra Nevada of California and their bearing on Pleistocene ecological conditions. In Arctic and alpine environments, edited by H. E. Wright and W. H. Osborn, 171–88. Bloomington: Indiana University Press.

Martin, L. M., and C. H. Ingham. 1930. An annotated list of the diurnal Lepidoptera of Huntington Lake region, Fresno County, California. Bulletin of the Southern California Academy of Sciences 29:115–34.

McCoy, E. D. 1990. The distribution of insects along elevational gradients. Oikos 58:313–22.

McGlashan, X. 1914. List of Truckee butterflies. The Butterfly Farmer 1:125–27.

Miller, L. D., and F. M. Brown. 1981. A catalogue / checklist of the butterflies of North America north of Mexico. Memoir 1. Sarasota, FL: Lepidopterists' Society.

Newcomer, E. J. 1910. The butterflies of the Lake Tahoe region. Entomological News 21:274–317.

Pollard, E., and T. J. Yates. 1993. Monitoring butterflies for ecology and conservation. London: Chapman and Hall.

Porter, A. H., and H. J. Geiger. 1988. Genetic and phenotypic population structure of the Coenonympha tullia complex (Lepidoptera: Nymphalidae: Satyrinae) in California: No evidence for species boundaries. Canadian Journal of Zoology 66:2751–65.

Porter, A. H., and A. M. Shapiro. 1991. Genetics and biogeography of the Oeneis chryxus complex (Satyrinae) in California. Journal of Research on the Lepidoptera 28:263–76.

Raven, P. H., and D. I. Axelrod. 1978. Origin and relationships of the California flora. University of California Publications in Botany 72:1–134.

Richerson, P. J., and K.-L. Lum. 1980. Patterns of plant species diversity in California: Relation to weather and topography. American Naturalist 116:504–36.

Rollins, R. C. 1982. A new species of the Asiatic genus Stronganowia (Cruciferae) from North America and its biogeographic implications. Systematic Botany 7:212–20.

Sánchez-Rodríguez, J. F., and A. Baz. 1995. The effects of elevation on the butterfly communities of a Mediterranean mountain, Sierra de Javalambre, central Spain. Journal of the Lepidopterists' Society 49:192–207.

Scott, J. A. 1986. The butterflies of North America. Stanford, CA: Stanford University Press.

———. 1994. Biology and systematics of Phyciodes. Papilio 7:1–120.

Scott, J. A., and M. E. Epstein. 1987. Factors affecting phenology in a temperate insect community. American Midland Naturalist 117:103–18.

Shapiro, A. M. 1974. The butterfly fauna of the Sacramento valley, California. Journal of Research on the Lepidoptera 13:78–82, 115–22, 137–48.

———. 1978. The alpine butterflies of Castle Peak, Nevada Co., California. Great Basin Naturalist 37:443–52.

———. 1979. Erynnis baptisiae (Hesperiidae) on crown vetch (Leguminosae). Journal of the Lepidopterists' Society 33:258.

———. 1980. Mediterranean climate and butterfly migration: An overview of the California fauna. Atalanta 11:181–88.

———. 1984. Geographical ecology of the Sacramento valley riparian butterfly fauna. In California riparian systems: Ecology, conservation, and productive management, edited by R. E. Warner and K. M. Hendricx, 934–41. Berkeley and Los Angeles: University of California Press.

———. 1991. The zoogeography and systematics of the Argentine Andean and Patagonian Pierid fauna. Journal of Research on the Lepidoptera 28:137–238.

———. 1992a. Twenty years of fluctuating parapatry and the question of competitive exclusion in the butterflies Pontia occidentalis and P. protodice (Lepidoptera: Pieridae). Journal of the New York Entomological Society 100:311–19.

———. 1992b. Genetics and the evolution and biogeography of some Klamath butterflies in a regional context. In Proceedings of symposium on biodiversity of northwestern California, Oct. 28–30, 1991, edited by H. M. Kerner, 237–48. Berkeley: Wildland Resources Center, University of California.

———. 1993. Long-range dispersal and faunal responsiveness to climatic change: A note on the importance of extralimital records. Journal of the Lepidopterists' Society 47:242–44.

———. 1995. From the mountains to the prairies to the oceans white with foam: Papilio zelicaon makes itself at home. In Genecology and biogeographic races, edited by A. R. Kruckeberg, R. B. Walker, and A. E. Leviton, 67–99. San Francisco: Pacific Division of the American Association for the Advancement of Science.

Shapiro, A. M., C. A. Palm, and K. L. Wcislo. 1981. The ecology and biogeography of the butterflies of the Trinity Alps and Mount Eddy, northern California. Journal of Research on the Lepidoptera 18:69–152.

Shapiro, A. M., and A. R. Shapiro. 1973. The ecological associations of the butterflies of Staten Island (Richmond County, New York). Journal of Research on the Lepidoptera 12:65–128.

Shields, O. 1966. The butterfly fauna of a yellow pine forest community in the Sierra Nevada, California. Journal of Research on the Lepidoptera 5:127–28.

———. 1978. Erynnis brizo lacustra and Hesperia columbia in the Sierra Nevada. Journal of the Lepidopterists' Society 32:61–62.

Stanford, R. E., and P. A. Opler. 1993. Atlas of western United States butterflies. Denver and Fort Collins, CO: Authors.

Storer, T. I., and R. L. Usinger. 1963. Sierra Nevada natural history. Berkeley and Los Angeles: University of California Press.

Thomas, C. D., D. Ng, M. C. Singer, J. L. Mallet, C. Parmesan, and H. L. Billington. 1987. Incorporation of a European weed into the diet of a North American herbivore. Evolution 41:892–901.

Tilden, J. W. 1959. The butterfly associations of Tioga Pass. Wasmann Journal of Biology 17:249–71.

Tong, M. L., and A. M. Shapiro. 1989. Genetic differentiation among California populations of the Anise Swallowtail, Papilio zelicaon Lucas (Papilionidae). Journal of the Lepidopterists' Society 43:217–28.

Van Dyke, E. C. 1892. Notes on some of the butterflies of the Yosemite Valley and adjacent region. Zoe 3:237–41.

Back to CD-ROM Table of Contents