

## The Butterfly Fauna of Two Adjacent Plant Communities in the Sierra Nevada Foothills of Mariposa County, California

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**Abstract.**—A butterfly fauna encompassing two plant communities in the Sierra Nevada foothills was surveyed and was found to contain 59 resident and 35 non-resident species. 63% of the residents but just 3% of the non-residents are univoltine, and only 44% of the resident species are shared by both plant communities. Dispersal between them by residents normally found in only one of the plant communities rarely occurs. Information on climate, relative abundance, flight season, dispersal, behavior, and bionomics are presented. Based upon paleobotanic inferences, butterfly species endemic to the Foothill Woodland are pre-Pleistocene, whereas the Yellow Pine Forest endemic subspecies are post-Pleistocene (Holocene).

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Efforts to identify butterfly indicator species for the various life zones of California have achieved only limited success (cf. Grinnell and Grinnell 1907; Garth and Tilden 1963; MacNeill 1964; Shapiro et al. 1979), although identification of indicator taxa that are endemic to, and thus diagnostic of, a particular plant community that is floristically defined appears more promising. For example, Stone and Smith (1990) found that various *Hemileuca* Walker (Saturniidae) taxa often utilize larval foodplants that are dominant or abundant only within a particular plant community in southwestern North America. In recent years, a spate of butterfly faunal surveys has appeared for various areas within California, but these frequently encompass more than one plant community and de-emphasize a community approach to species distributions. Determination of butterfly indicator species for particular plant communities requires that these communities be more selectively surveyed.

Botanists have already laid the groundwork for California's many different plant communities, each of which is characterized by certain key indicator species (cf. Munz and Keck 1949, 1965; Barbour and Major 1990). To date, however, only the butterfly fauna of the Foothill Woodland plant community in central California has been adequately surveyed in a similar manner (Shields 1986).

Butterflies are primarily dependent upon angiosperms for their larval foodplants and adult nectar sources, and a given plant community is largely controlled by climate, being confined as an adaptive and cohesive unit to a particular climatic zone. Crowe (1965) has demonstrated that certain climatic zone adaptations also exist for *Coenonympha* Hübner (Satyridae) and *Callipsyche* Scudder (Lycaenidae) in Oregon. A high fidelity between butterfly indicator species and the plant community they inhabit is expected due to hostplant restriction there and/or a narrow range of temperature and moisture requirements (see Tilden 1959) to which the indicator species are physiologically adapted. Non-indicator butterfly species, in

contrast, are not so restricted by habitat and climate and regularly occur in more than one plant community, be they non-residents or residents, due to their superior vagility compared with plants and thus do not constitute a butterfly community corresponding to its plant community. Though climatic fluctuations can alter the species composition and distribution of plant communities to some degree (see Shapiro et al. 1979), the persistence of many identifiable plant communities in California argues against any wholesale restructuring during the past 8000 years (see Van Devender and Spaulding 1979; Van Devender et al. 1987). Identifying endemic butterfly species that are indicators of a particular plant community is important to do since this butterfly/plant association likely evolved over similar intervals of geologic time, thus indicating their relative age (cf. Janzen 1968; Shields 1986; Farrell et al. 1992). This idea is quite different from maintaining that entire communities persist and migrate as units through Neogene time.

An ecological survey of the butterfly fauna within two adjacent Sierran foothill plant communities is presented here (see Fig. 1). Special attention is given to distinguishing resident from non-resident species, along with selective aspects of abundance, flight period, brood number, behavior, bionomics and dispersal. Several butterfly indicator taxa (ecotypes) are identified as endemic to the Yellow Pine Forest plant community from the completed analysis and will be discussed.

### Methods

A survey of the butterfly fauna was conducted for 28 years between 1961 and 1995 in the Yellow Pine Forest (YPF) plant community and for 17 years between 1970 and 1989 in the Foothill Woodland (FW) plant community (see Fig. 1 and Plant Communities below). At Jerseydale, Mariposa Co., California, casual sampling at irregular intervals was done on 458 days (January–December) in 1961–63, 1965–66, 1970–74, 1976–77, and 1980–95. The summits of Footman Ridge (and sometimes Portuguese Ridge) were visited on 54 days (April–December) in 1971–74, 1976–77, 1980–87, and 1989, and Skelton Canyon on 67 days (January–September, December) in 1970–74, 1976–77, and 1980–89. Resident species were defined as those indigenous to the study area, i.e. breeding and overwintering there, with the first (or only) brood freshly emerging in the habitat the following season. Non-resident species represent migrators or other dispersers that most often did not overwinter, casual or weedy species from nearby or more distant locations, and those hilltopping taxa that were not found at lower elevations within the study area. The flight period of a species was determined from all the dates it was collected or observed during the entire survey, and relative abundance was subjectively assessed from the numbers encountered on those dates. The number of broods for the resident species was checked against Shields (1986) and Scott (1986), and the ecological terminology follows Lincoln et al. (1982). The nomenclature largely follows Miller and Brown (1981), but with a few cited changes by other authors and my personal opinion in the case of some generic assignments.

### Habitat

#### *Habitat Description*

Most of the Jerseydale valley and forest soils are granitic, gabbro, and quartz diorite in composition, with large granitic boulders and slabs frequently exposed. Footman Ridge is largely comprised of slate metamorphic rocks and soils. Skelton

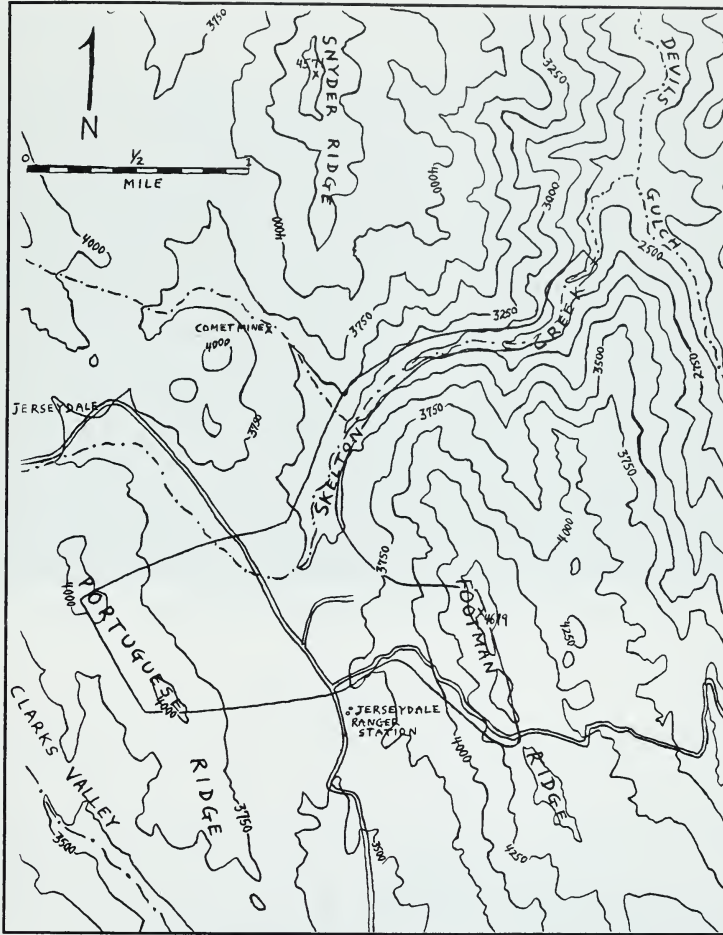


Fig. 1. Topographic map of the study area at Jerseydale, Mariposa County, California. The survey is outlined as the Y-shaped area from Portuguese Ridge to Footman Ridge and Skelton Canyon. Elevation contours are in feet.

Canyon is steep-walled and rockier and consists mainly of various metamorphics including metagabbro, amphibolite, metavolcanics, slate, and greenstone units. The marine metamorphics (Paleozoic) and igneous granites (Mesozoic) form a contact zone mixture near the very top of the canyon. The entire study area is unglaciated.

The forested and riparian habitats at Jerseydale are mostly in their natural state (see Fig. 2), although some timber harvesting occurred in the past. Other disturbances include old logging roads, cattle grazing and several stock pond dams in the Iris-Buttercup meadows, and some disturbed, weedy places especially around habitation. Footman Ridge (see Fig. 3) is relatively undisturbed except for an access road and an old lightning burn with secondary growth. Skelton Canyon is essentially pristine habitat (see Fig. 4) except for a steep jeep road, horse trail, and several abandoned mines.





Fig. 2. Meadow, riparian, and Yellow Pine Forest habitat at Jerseydale.



Fig. 3. The north end of Footman Ridge, viewed from Skelton Canyon.



Fig. 4. Foothill Woodland habitat in Skelton Canyon (foreground).

### *Plant Communities*

The Jerseydale area and the west slope of Footman Ridge are occupied by a species-rich Yellow Pine Forest plant community. The forest indicator trees present (see Munz and Keck 1965) are Ponderosa Pine (*Pinus ponderosa*) (predominant), Sugar Pine (*P. lambertiana*), White Fir (*Abies concolor*), Incense Cedar (*Calocedrus decurrens*), and California Black Oak (*Quercus kelloggii*), and indicator shrubs include Sierra Gooseberry (*Ribes roezlii*), Bear Clover (*Chamaebatia foliolosa*), Mariposa Manzanita (*Arctostaphylos mariposa*), and Deer Brush (*Ceanothus integerrimus*). The warm, southeast-facing slopes of Skelton Canyon, in contrast, are occupied by an ascending Foothill Woodland plant community. Indicator trees present here are Digger Pine (*Pinus sabiniana*), Canyon Oak (*Quercus chrysolepis*), and Buckeye (*Aesculus californica*), and indicator shrubs include Buck Brush (*Ceanothus cuneatus*), Yerba Santa (*Eriodictyon californicum*) and Redbud (*Cercis occidentalis*), with some chaparral community elements present such as Chamise (*Adenostoma fasciculatum*) and Mountain Mahogany (*Cercocarpus betuloides*). Along the northwest-facing slope, upper portion, and mouth of Skelton Canyon, the FW and YPF plant communities intermix in an ecotone, while along the northern slopes and summit of Footman Ridge, the two communities remain distinct but interdigitate as a patch-work of “islands”.

### *Climate*

Summers at Jerseydale are generally warm, with the greatest evaporation occurring in May to October; diurnal and seasonal temperature fluctuations are relatively wide, and winds are usually light to moderate (Gilbert and Peterson 1966). The driest months are May to September, and the wettest months are November to March. Jerseydale's seasonal precipitation falls primarily as rain, which always



Table 1. The 1971 to 1995 precipitation totals (July 1–June 30) for Jerseydale Ranger Station, 1113 m, Mariposa County, California. The 25-year average is 1.07 m (42.15 in).

Year	Meters	Year	Meters
1970–71	.79	1983–84	1.07
1971–72	.57	1984–85	.74
1972–73	1.08	1985–86	1.52
1973–74	1.02	1986–87	.61
1974–75	1.19	1987–88	.67
1975–76	.48	1988–89	.72
1976–77	.42	1989–90	.80
1977–78	1.97	1990–91	.76
1978–79	1.15	1991–92	.87
1979–80	1.35	1992–93	1.65
1980–81	.70	1993–94	.70
1981–82	1.82	1994–95	1.97
1982–83	2.13		

exceeded the snowfall's total water content during the years 1980–95. The 15 year average winter snowfall depth from 1980–81 to 1994–95 was 0.64 m, ranging from a low of 0.12 m in 1983–84 to 1.74 m in 1990–91. The earliest snows usually arrive in mid November, with the latest snows in late March (late April in 1994). Decembers vary from comparatively mild and dry to harsh, with strong winds, frosts, hard freezes, and heavy snowfall. Yearly precipitation totals are shown in Table 1. The climate for Skelton Canyon was not monitored, but it is expected to have less annual precipitation, a longer growing season, more frost-free days, fewer snows, and higher average temperatures than Jerseydale (see Munz and Keck 1949).

Some studies indicate that drought can have a severe effect on butterfly numbers, even leading to local extinction in some highly variable populations, while warm, dry summers, or wet conditions early in the previous year, tend to increase their numbers (cf. Ehrlich and Murphy 1981; Pollard 1988; Pollard and Yates 1993). During the severe drought years at Jerseydale (1972, 1976–77, 1987), butterfly species indeed were generally in very low numbers, with few species becoming common except for *P. napi*, *C. tullia*, *N. californica*, and *L. arota* (see Table 2). Unusually high precipitation occurred from October to April during the 1981–82 and 1982–83 seasons, with late snows in 1981–82 and heavy rains with little snow in 1982–83. 1983 was a high abundance year for *N. menapia*, *P. napi*, *E. hyantis*, *H. grunus*, *M. nelsoni*, and *G. piasus*, and also produced several nymphalid melanics. Following unusually cold weather in late December of 1990 and 1992 (10 day runs of temperatures below 0°C at night), and night-time temperatures approaching –18°C on February 5–7, 1989 and December 28, 1990, butterfly species diversity plummeted from 1989 to 1993, with only partial recovery in 1994 and 1995 and regaining normalcy in 1996.

## Results

### *Resident vs. Non-Resident Species*

The survey area produced 59 resident and 35 non-resident species (see Tables 2 and 3) for a total of 94 species (37% non-resident). Of the 59 resident species,

37 (63%) are univoltines (=one generation per year), the remaining third being bivoltines or multivoltines that overwinter as pupae or, infrequently, as adults. The largest segment of residents are lycaenids (37%), while 54% of the non-residents are nymphalids and hesperiids, only 17% being lycaenids. Of the non-residents, *Z. eurydice*, *P. pulchella*, *A. milberti*, *P. faunus*, *P. satyrus*, *E. brizo*, *E. tristis*, and *H. columbia* represent occasional dispersers from relatively nearby locations where they are permanent residents. The remaining 25 non-residents are primarily non-diapausing multivoltines that are known to migrate, occasionally migrate, or frequently disperse well beyond their normal ranges. Of these, only *C. eurytheme*, *D. plexippus*, the four *Vanessa*, *J. coenia*, and *I. acmon* regularly breed and recolonize within the survey area, though *P. protodice* and *H. ericetorum* do so occasionally. *B. philenor*, *Z. cesonia*, *P. sennae*, *D. gilippus*, *E. claudia*, *L. bachmanii*, and *P. leo* (see Table 3) commonly co-occur in SE Arizona (Bailowitz and Brock 1991) and likely represent long-distance migration dispersal. Excluding these stronger migrants and short-distance dispersers, the remaining 14 non-resident species are oligophagous or polyphagous and disperse upslope from the San Joaquin Valley as regular or occasional species and invaders.

The results that follow will be primarily concerned with the resident species.

#### Abundance

Occasional population outbreaks were noted for *N. menapia*, *N. californica*, *V. cardui*, *M. nelsoni*, *S. californica*, *S. auretteorum*, *I. icarioides*, and *H. ericetorum*. High abundance years for other species included *C. sthenele* (1981), *C. tullia* (1965, 1966), *D. plexippus* (1987–88, 1991), *S. callippe* (1974), *S. hydaspe* (1974, 1976), *N. antiopa* (1970), *L. arota* (1972), *H. grunus* (1983), *I. eryphon* (1974) and *H. harpalus* (1985, 1989). Species generally displaying little fluctuation in abundance from year to year were *P. multicaudata*, *L. lorquini*, *A. bredowii*, *A. halesus*, *P. ruralis*, and *P. melane*. Species exhibiting a marked decline over the years include *P. clodius*, *P. eurymedon*, *C. tullia*, *S. zerene*, *P. gracilis*, and *I. icarioides*. The commonest resident species are *S. callippe*, *S. hydaspe*, *E. chalcadon*, *E. editha*, *A. bredowii*, *L. arota*, *H. grunus*, *M. nelsoni*, *E. propertius*, *O. sylvanoides*, and *O. agricola*. Rarely-encountered species are *P. zelicaon*, *T. leanira*, *A. halesus*, *C. perplexa*, *L. spinetorum*, *E. tristis*, *E. brizo*, *P. ruralis*, *H. columbia*, and *P. melane*.

#### Flight Season

At Jerseydale, hibernants are the earliest to appear, often followed by *P. napi* and *C. argiolus* as the first butterflies to emerge in late February to mid April, depending on the year. In Skelton Canyon, first emergents precede Jerseydale's by about one to eight weeks, usually as *C. argiolus* and *P. sonorensis*, beginning in mid February to mid March. The peak in resident species diversity at Jerseydale is reached in late May to late June and at Skelton Canyon in mid May to mid June, when the greatest variety of annuals and perennials are in bloom. The last resident, nonhibernant butterflies of the season at Jerseydale are present until mid October to mid November, depending on the year, although hibernant *N. californica* fly as late as late October to late December. A few worn individuals of *C. sthenele* and *S. saepium* fly as late as mid August, one fair *S. hydaspe* and worn *H. grunus* into mid October, worn female *S. zerene* into late October, and worn

Table 2. Annotated checklist of resident (indigenous) butterflies from the survey area. J = Jerseydale (Yellow Pine Forest), F = Footman Ridge (YPF & Foothill Woodland), S = Skelton Canyon (Foothill Woodland & ecotone), A = all three localities (allochoric), u = univoltine. References relevant to some taxonomic decisions are cited.

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### Papilionidae

- Parnassius clodius sol* Bryk & Eisner—J,u  
*Papilio eurymedon* Lucas—A  
*Papilio multicaudata* Kirby—A  
*Papilio rutulus rutulus* Lucas—J,S  
*Papilio zelicaon* Lucas—S,F

### Pieridae

- Neophasia menapia menapia* (C. & R. Felder)—J,F,u  
*Pontia sisymbrii sisymbrii* Boisduval—S,F,u  
*Pieris napi castoria* (Reakirt)—J,S (see Shapiro 1975; Ferris 1989)  
*Euchloe ausonides* near *ausonides* (Lucas)—J,u  
*Euchloe hyantis hyantis* (W.H. Edwards)—S,F,u  
*Anthocharis lanceolata lanceolata* Lucas—S,u  
*Anthocharis sara sara* Lucas—J,S

### Satyridae

- Coenonympha tullia californica* (Westwood)—A (see Porter & Geiger, 1988)  
*Cercyonis sthenele silvestris* (W.H. Edwards)—A,u

### Nymphalidae

- Speyeria callippe inornata* (W.H. Edwards)—J.,Fu  
*Speyeria hydaspe* near *viridicornis* (J.A. Comstock)—J,Fu  
*Speyeria zereene zereene* (Boisduval)—J,Fu  
*Thessalia leanira leanira* (C. & R. Felder)—S,u (see Smith and Brock 1988)  
*Charidryas palla palla* (Boisduval)—A,u  
*Phyciodes mylitta mylitta* (W.H. Edwards)—A  
*Euphydryas chalcedona chalcedona* (Doubleday)—S,u  
*Euphydryas editha rubicunda* (Hy. Edwards)—S,u  
*Polygonia gracilis zephyrus* (W.H. Edwards)—J (see Scott 1984)  
*Nymphalis antiopa antiopa* (Linnaeus)—J,S  
*Nymphalis californica* (Boisduval)—A  
*Limenitis lorquini lorquini* (Boisduval)—J,S  
*Adelpha bredowii californica* (Butler)—A

### Lycaenidae

- Lycaena arota arota* (Boisduval)—J,F (see Ballmer and Pratt 1988)  
*Lycaena gorgon* (Boisduval)—S,u  
*Habrodais grunus grunus* (Boisduval)—A,u  
*Atlides halesus estesi* Clench—J,F  
*Satyrium auretteum auretteum* (Boisduval)—S,F,u  
*Satyrium californica* (W.H. Edwards)—A,u  
*Satyrium saepium saepium* (Boisduval)—S,F,u  
*Satyrium sylvinus* near *sylvinus* (Boisduval)—J,S,u  
*Satyrium tetra* (W.H. Edwards)—S,u  
*Callophrys perplexa* near *perplexa* (Barnes & Benjamin)—S,u (see Ballmer and Pratt 1988)  
*Loranthomitoura johnsoni* (Skinner)—J,u  
*Loranthomitoura spinetorum spinetorum* (Hewitson)—J (see Ballmer and Pratt 1992)  
*Mitoura nelsoni nelsoni* (Boisduval)—J,Fu  
*Incisalia augustinus iroides* (Boisduval)—A (see Ferris 1989)  
*Incisalia eryphon eryphon* (Boisduval)—J,u  
*Incisalia mossii* near *windi* Clench—S,u  
*Everes amyntula amyntula* (Boisduval)—A,u  
*Celastrina argiolus echo* (W.H. Edwards)—A (see Eliot and Kawazoe 1983)  
*Philotes sonorensis sonorensis* (Felder & Felder)—S,u  
*Glaucopsyche lygdamus* near *incognitus* Tilden—J,S,u  
*Glaucopsyche piasus* near *piasus* (Boisduval)—J,u  
*Icaricia icarioides icarioides* (Boisduval)—A,u
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Table 2. Continued.

## Hesperiidae

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<i>Thorybes pylades</i> (Scudder)—J,F,u
<i>Erynnis persius</i> ssp. (Scudder)—J,S
<i>Erynnis propertius</i> (Scudder & Burgess)—A
<i>Pyrgus ruralis ruralis</i> (Boisduval)—J,u
<i>Hesperia harpalus</i> near <i>yosemite</i> Leussler—A,u (see MacNeill 1964)
<i>Hesperia juba</i> (Scudder)—J,F
<i>Ochlodes agricola nemorum</i> (Boisduval)—S,u (see Emmel and Emmel 1973)
<i>Ochlodes sylvanoides sylvanoides</i> (Boisduval)—A,u
<i>Poanes melane melane</i> (W.H. Edwards)—J,S (see Burns 1992)
<i>Amblyscirtes vialis</i> (W.H. Edwards)—J,u

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*A. bredowii* into early November (once in mid December). Several unusual autumn occurrences were a fresh female *M. nelsoni* in early October and a *C. argiolus* in mid October. By late October, most species encountered are the common weedy types. By late summer in Skelton Canyon, extremely dry conditions prevail and only three to seven resident species are present.

*Dispersal and Behavior*

Skelton Canyon (FW) resident species that occasionally or rarely disperse up into Jerseydale (casuals) are *P. sisymbrii*, *A. lanceolata*, *E. chalcedona*, *E. editha*, *L. gorgon*, *S. saepium*, *S. auretteum*, *S. tetra*, *C. perplexa*, *I. mossii*, and *O. agricola*. Jerseydale (YPF) resident species that rarely disperse down into Skelton Canyon are *P. clodius*, *S. callippe*, *L. arota*, *M. nelsoni*, *I. eryphon*, and *A. vialis*. Dispersal exchange of these casuals across the ecotone that separates the two plant communities appeared not to lead to their permanent establishment by colonization in the foreign community and, except for *A. lanceolata* and *E. editha*, is usually quite rare or at least not a very regular occurrence, with the ecotone exhibiting no edge effect here. 73% of the resident butterfly species are in common between Jerseydale and Skelton Canyon if casual exchange is included, but decreases dramatically to 44% if casuals are excluded. Species that overwinter as adults at Jerseydale include *P. gracilis*, *N. californica*, *N. antiopa*, and *V. atalanta* (see Scott 1979). Species exhibiting male hilltopping behavior on the highest summit of Footman Ridge (s = singletons) are *P. zelicaon*, *P. eurymedon*, *P. protodice* (s), *P. sisymbrii*, *S. callippe*, all four *Vanessa*, *S. saepium*, *T. pylades* (s), *E. propertius*, *E. tristis* (s), *E. brizo*, *H. harpalus*, and *H. columbia*. Although *L. johnsoni* frequents ridge summits in hilltopping behavior in Napa and Yolo counties (cf. Kelson and Minno 1983; Shields 1986), none was observed doing so on Footman Ridge. Migratory species (excluding strays) are *D. plexippus*, *N. californica*, and *V. cardui* (see Shields 1987; Giuliani and Shields 1995 for Jerseydale observations). In addition, occasional *H. ericetorum* were seen to rapidly migrate NW in the spring of 1985 and 1986. Strongly colonial species are *C. tullia*, *H. grunus*, *L. gorgon*, *S. sylvinus*, *E. amyntula*, *P. sonorensis*, *G. piasus*, and *I. icarioides*.

I saw most taxa visit flowers, but those that rarely or never did (at least in this area) were *Polygonia*, *Nymphalis*, *A. bredowii*, *L. arota*, *H. grunus*, *L. johnsoni*, and *P. sonorensis*. Flowers present that were especially attractive to butterflies include *Erysimum* L. (Brassicaceae); *Eriogonum* Michx. (Polygonaceae); *Arctos-*

Table 3. Annotated checklist of non-resident (immigrant) butterflies from the survey area. J = Jerseydale, F = Footman Ridge, S = Skelton Canyon, A = all three localities.

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Papilionidae

*Battus philenor philenor* (Linnaeus)—J, one stray (12.VII.1983)

Pieridae

*Pontia protodice* Boisduval & Le Conte—J,F; occasional species

*Pieris rapae* (Linnaeus)—J,S; occasional species

*Colias eurytheme* Boisduval—A; frequent invasions, rarely overwinters

*Zerene cesonia* (Stoll)—S, one stray (15.IX.1983)

*Zerene eurydice* (Boisduval)—J, one vagrant

*Phoebis sennae* (Linnaeus)—J, one stray (2.V.1992)

Danaidae

*Danaus gilippus strigosus* (Bates)—J, three strays (16,21,23.X.1988)

*Danaus plexippus* (Linnaeus)—A; seasonal migrant, does not overwinter

Nymphalidae

*Euptoieta claudia* (Cramer)—J, one stray (23.X.1988) (see Shapiro et al. 1990)

*Phyciodes pulchella pulchella* (Boisduval)—J, one vagrant (see Scott 1994)

*Polygonia faunus rusticus* (W.H. Edwards)—J, one vagrant

*Polygonia satyrus satyrus* (W.H. Edwards)—J, several vagrants in 1983

*Aglais milberti milberti* (Godart)—J, one vagrant (see Miller and Miller 1990)

*Vanessa annabella* (Field)—A; occasional species, several migrating

*Vanessa atalanta rubria* (Fruhstorfer)—A; overwinters but absent in summer; several migrating in late April and early May

*Vanessa cardui* (Linnaeus)—A; seasonal migrant, does not overwinter

*Vanessa virginiensis* (Drury)—A, occasional species

*Junonia coenia* (Hübner)—A; common, opportunistic species, rarely overwinters (see Tilden 1973)

Libytheidae

*Libytheana bachmanii larvata* (Strecker)—J, one stray (13.X.1990)

Lycaenidae

*Lycaena helloides* (Boisduval)—J, occasional species

*Strymon melinus pudica* (Hy. Edwards)—A, occasional species

*Brephidium exilis* (Boisduval)—J, occasional species

*Leptotes marina* (Reakirt)—J,S; occasional species

*Everes comyntas* (Godart)—J,S; several vagrants in 1973

*Icaricia acmon acmon* (Westwood & Hewitson)—A; common, opportunistic species, rarely overwinters

Hesperiidae

*Polygonus leo arizonensis* (Skinner)—J, one stray (11.VIII.1984)

*Erynnis brizo* near *lacustra* (W.G. Wright)—F, occasional species (see Shields 1978)

*Erynnis tristis tristis* (Boisduval)—F,J; occasional species

*Pyrgus communis* (Grote)—A, occasional species

*Heliopetes ericetorum* (Boisduval)—A; seasonal migrant, sometimes fairly common, does not overwinter

*Hylephila phyleus phyleus* (Drury)—J, occasional species

*Hesperia columbia* (Scudder)—F, occasional species (see Shields 1978)

*Atalopedes campestris campestris* (Boisduval)—J, occasional species

*Lerodea eufala* (W.H. Edwards)—J, occasional species

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*taphylos* Adans. (Ericaceae); *Apocynum* L. (Apocynaceae); *Asclepias* L. (Asclepiadaceae); *Phlox* L. (Polemoniaceae); *Eriodictyon* Benth. and *Nemophila* Nutt. ex Barton (Hydrophyllaceae); *Monardella* Benth. (Lamiaceae); *Chamaebatia* Benth. and *Prunus* L. (Rosaceae); *Cercis* L. and *Lupinus* L. (Fabaceae); *Ceanothus* L. (Rhamnaceae); *Aesculus* L. (Hippocastanaceae); *Lomatium* Raf. (Apiaceae); *Achillea* L., *Cirsium* Mill., *Haplopappus* Cass., and *Wyethia* Nutt. (As-

teraceae); and *Brodiaea* Sm. (Amaryllidaceae). Species especially fond of visiting mud are *N. californica*, *A. bredowii*, *L. arota*, *A. halesus*, *L. spinetorum*, and *L. johnsoni* (both sexes, to replenish water-loss); and *E. amyntula*, *C. argiolus*, and *I. icarioides* (males only, to restore sodium-loss) (see Adler and Pearson 1982). The shade-loving species are *C. sthenele* and *H. grunus*. The meadow species are *E. ausonides* and *C. tullia*. Riparian species are *P. rutulus*, *P. multicaudata*, *N. antiopa*, *L. lorquini*, *S. sylvinus*, *A. vialis*, and *P. melane*. Species that fly over exposed rocky, south-facing canyon slopes are *P. sisymbrii*, *E. hyantis*, and *P. sonorensis*.

A few possible foodplants were recorded (see also Bionomics section). A worn female *N. californica* was seen attempting to oviposit on *Ceanothus cuneatus* (Hook.) Nutt. A larva found on the outer leaves of *Holodiscus boursieri* (Carr.) Rehd. (Rosaceae) in a sunlit gully in deep forest produced an *L. lorquini* adult. The two violets in the forest where *S. zerene* and *S. hydaspe* fly are *Viola lobata* Benth. and *V. purpurea* Kell. (Violaceae). *H. grunus* adults are closely associated with *Quercus chrysolepis* Liebm.

### Bionomics

A more detailed accounting of the bionomics of 22 resident species is presented below for the survey area.

1. *Parnassius clodius sol*.—Flew from late May to late June. In 1956–58, it was fairly common in forest openings along Skelton Creek where *Dicentra formosa* (Andr.) Walp. (Fumariaceae) occurs. It then declined to one to two individuals per season in the 1960's and early 1970's and was last sighted there in 1983. Its extirpation was probably due to low population levels from the 1958–59 and 1960–61 droughts that were subsequently subjected to double the average precipitation in 1982–83. Adults like to nectar on the flowers of *Wyethia angustifolia* (DC.) Nutt.

2. *Papilio zelicaon*.—Flies in early April to late May (residents), and apparently as vagrants in late July to late August, and is always rather scarce. One female oviposited on *Lomatium utriculatum* (Nutt.) C. & R. (Apiaceae) in Skelton Canyon (Emmel and Shields 1978). Native California umbels produce univoltine *P. zelicaon*, while multivoltine populations use non-native hosts in lowland areas (Sims 1983).

3. *Papilio multicaudata*.—Flies from late April to mid September and is multivoltine. The males patrol along Skelton Creek and forest gullies, and adults nectar on *Cirsium*. Females are occasionally orange. Usually not more than one or two are found on any given day.

4. *Neophasia menapia*.—The flight usually begins in late June and lasts two to four weeks. Males emerge first and reach peak numbers within five to 10 days when the first females emerge. Males actively fly around *Pinus ponderosa*, usually high up, patrolling for perched females, from 7:00 AM to 6:00 PM. Both sexes occasionally descend to the forest floor to nectar on the flowers of Bear Clover (*Chamaebatia*), Blackberry (*Rubus* L., Rosaceae), etc., or to fly in the shade. Occasional wings and dead individuals on the ground and beak-marked wings suggest a fair amount of bird predation. They became very common in 1981 and 1983.

5. *Pieris napi*.—Form *microstriata* J.A. Comstock is sometimes fairly common



and flies from early March to mid May in Skelton Canyon and from late March to early June at Jerseydale, while typical *castoria* is very rare (c. 0.01%) and occurs in late May to late June at Jerseydale. It frequents streamsides where its *Cardamine breweri* Wats. (Brassicaceae) foodplant grows, is fond of nectaring on the flowers of *Arctostaphylos mariposa*, and flies from 9:00 AM to 4:00 PM.

6. *Euchloe ausonides*.—Flies from early April to late May, peaking in early May. It is a resident, flying rapidly over the open, flowery meadows, but is also sometimes associated with *Brassica geniculata* (Desf.) J. Ball. (Brassicaceae) in weedy habitat late into its flight period. The first individuals to appear are fresh, however, and probably utilize a native crucifer. One specimen (5.V.1974) had a nearly solid green underside.

7. *Anthocharis lanceolata*.—On the wing from early April to early June, and is not very common. Males often fly up and down ravines on the southeast-facing slopes of Skelton Canyon, and one was observed to avidly nectar on the purple flowers of its foodplant, *Arabis sparsiflora* Nutt. in T. & G. (Brassicaceae).

8. *Speyeria callippe inornata*.—Males fly from late May to late July, females from mid June to mid August. Adults are occasionally common and inhabit open areas in the forest and forest margins and sometimes hilltop. It frequently nectars on *Monardella*, *Wyethia*, and sometimes *Cirsium*, and the violet where it flies is *Viola quercetorum* Baker & Clausen.

9. *Speyeria hydaspe viridicornis*.—Males fly from early June to early August, females from mid June to mid August. Adults fly along forest paths, margins, and clearings and frequently nectar at *Monardella*, *Wyethia*, and *Apocynum*. Males sometimes fly close to the ground and around small trees, apparently searching for females. One copulating pair was located at 11:05 AM at mint beds (female carried male). It is fairly common.

10. *Lycaena arota*.—Has an extended summer flight from mid June to early September. Both sexes are drawn to mud that is in full sunlight along the creeks and stock pond dams in the hot summer afternoons and are sometimes abundant.

11. *Loranthomitoura spinetorum*.—Is bivoltine at Jerseydale, flying from late April to mid June and mid July to mid August, mostly at mud in the afternoon along creeks and earthen dams.

12. *Loranthomitoura johnsoni*.—The flight lasts from mid July to mid August. Most captures are from sunlit muddy places along Skelton Creek bordered by Incense Cedar-White Fir forest slopes, from 8:30 AM to 3:00 PM, rarely nectaring on watercress. Males and females are about equal in numbers. 1956 and 1963 were its peak years, which were normal precipitation years preceded by three to four subnormal precipitation years. The foodplant at Jerseydale remains unknown. Older females confined with *Arceuthobium campylopodum* Engelm. in Gray (Loranthaceae) and *Phoradendron juniperinum* var. *libocedri* Engelm. in Wats. (Loranthaceae) (which grows on Incense Cedar) reluctantly laid a few ova on each but refused *Arceuthobium abietinum* f. sp. *concoloris* Hawksworth & Wiens and *A. tsugense* (Rosendahl) Jones (cf. Hawksworth and Wiens 1972). One worn female hovered around very small Incense Cedars (2:30 PM, 25.VII.1976) in a clearing where only these small trees are growing commonly. Only the light-colored summer form is present at Jerseydale (see Shields 1965).

13. *Mitoura nelsoni*.—Flies from late April to late June (to mid July in 1963), peaking in late May. Adults nectar on a wide variety of flowers, particularly

*Achillea*, *Ceanothus integerrimus*, *Chamaebatia*, *Potentilla* L. (Roseaceae), *Prunus*, and *Wyethia*, visit mud, and are often common (almost swarming on *Chamaebatia* in late June of 1961). One copulating pair was observed at 10:50 AM on 25.V.1974 in an area with lots of young *Calocedrus* Kurz. (male carried female).

14. *Incisalia mossii windi*.—Flies only in April and nectars on *Lomatium utriculatum* and *Pseudobahia heermannii* (Durand) Rydb. (Asteraceae). The main colony is located about half-way down Skelton Canyon at 825–885 m, with occasional vagrants found further up the canyon. Females differ from typical *windi* in having a greenish-brown upperside and a golden underside with a pronounced white line. The foodplant here may be *Sedum spathulifolium* ssp. *anomalum* (Britton) Clausen & Uhl (Crassulaceae) which grows on steep, shady, north-facing rocky places immediately adjacent to the main colony of *windi*.

15. *Philotes sonorensis*.—Flies at an isolated colony in Skelton Canyon from mid February to late April, peaking in late March to mid April. It emerges when its foodplant, *Dudleya cymosa* (Lem.) Britt. & Rose (Crassulaceae), is about half-grown and stops flying about one to two weeks before *Dudleya* Britt. & Rose anthesis.

16. *Glaucopsyche piasus*.—Flies from early May to mid June. Adults visit lupines (*Lupinus*), other flowers, and mud in direct association with the far more numerous *I. icarioides*. It is perhaps most closely associated with *Lupinus albi-caulis* Dougl. ex Hook. that grows in isolated patches in forest clearings. 1981 and 1983 were its peak years, although it is never very common.

17. *Thorybes pylades*.—Flies from early May to late June and is seldom common. Adults are found around *Lathyrus nevadensis* Wats. and *L. paucifolium* Fern. ssp. *brownii* (Eastw.) Piper (Fabaceae) in the forest understory, visit mud, and occasionally hilltop.

18. *Pyrgus ruralis*.—A total of eight specimens were collected, always in mid to late May, in 1974, 1981, 1983, 1985, and 1994. Flight is low to the ground near patches of *Potentilla glandulosa* Lindl. (Rosaceae) in forest clearings and small gullies, and it sometimes visits mud.

19. *Hesperia juba*.—Is bivoltine, flying from early May to mid June and late August to mid October. Males are sometimes territorial at a particular low spot in the meadow next to a small gully, and adults visit the blooms of *Haplopappus arborescens* (Gray) Hall on Footman Ridge. It is usually fairly scarce but became common in mid September of 1985.

20. *Hesperia harpalus yosemite*.—Flies from early September to mid October, peaking in mid September. Though only rarely found in Skelton Canyon and Jerseydale, it is sometimes fairly common on *Haplopappus* blooms on Footman Ridge where the males are territorial while nectaring and perching along the ridgetop.

21. *Poanes melane*.—Flies in early May to mid June and again in mid September, with few encountered over the years. Males are closely associated with sedgy places along Skelton Creek for 2 km. Its habits at Jerseydale favorably compare with those of *P. melane vitellina* (Herrich-Schäffer) in southeastern Arizona, i.e. a scarce, riparian, canyon-bottom dweller (see Bailowitz and Brock 1991). Some of the earliest California records (1871) are from the Yosemite area, further indicating that its populations are resident in this region (Heppner 1971).

However, the adults also visit flowers in waste areas in the fall, perhaps from immigration.

22. *Amblyscirtes vialis*.—Flies from mid April to late June and is occasionally common. It inhabits shaded creeks, forest clearings, dry gullies, and bends in the dirt roads. One copulating pair was observed at 5:25 PM.

### Discussion

The only resident taxa ecotypes that are confined to the YPF plant community at Jerseydale are *P. clodius sol* and *G. piusus* (western foothill segregate). *Colias occidentalis chrysomelas* Hy. Edwards frequents the YPF in northern California (Garth and Tilden 1963; Shapiro et al. 1979; Ferris, 1993; personal observations) and also inhabits the Douglas-Fir Forest (*Pseudotsuga menziesii*) (Howe 1975), both of which are in the Transition Zone, and *Speyeria cybele leto* (Behr) may be another Transition Zone indicator (Garth and Tilden 1963; Shapiro et al. 1979; personal observations). The geographic ranges of all four are certainly narrower than their hostplant ranges, suggesting that climatic-physiologic adaptation may be restricting them to the Transition Zone environment.

Probable indicator taxa of the FW (and chaparral) that are present in the survey area include *Z. eurydice*, *T. leanira leanira*, *E. chalcedona chalcedona*, *E. editha rubicunda*, *L. gorgon*, *S. auretorum*, *S. tetra*, *S. saepium*, *C. perplexa*, *P. sonorensis*, *E. tristis*, *E. brizo lacustra*, *H. columbia*, and *O. agricola* (cf. Shields 1986). In addition, *A. lanceolata* and *C. sthenele silvestris* are found especially in the Upper Sonoran Zone but are occasionally met with in the Transition Zone (the “selective” indicator category of Oosting 1956).

Paleobotanically, the dominant species of the YPF plant community first appeared in the Sierra Nevada in Kern and Alpine counties during the Middle and Late Miocene, prior to the major uplift of the range during the Pliocene and Early Pleistocene (Axelrod 1957, 1980). The present-day YPF plant community developed at the borders of the mixed conifer forests during the Holocene when such genera as *Dicentra*, *Lathyrus* L., *Potentilla*, *Ribes* L., and *Viola* L. radiated into the drier, bordering vegetation with the opening up of this new subzone (cf. Axelrod 1976; Raven and Axelrod 1978; Van Devender et al. 1987). The history of the FW plant community is outlined in Shields (1986) and extends back to Late Miocene times in central California. The large number of butterfly indicator species inhabiting the FW plant community compared with the remarkably few ecotypes confined to the YPF plant community in California suggests that the former are pre-Pleistocene relics while the latter evolved quite recently during the Late Quaternary.

Of the 44 resident species found in the YPF plant community at Jerseydale, two are indicators and 18 occur from the Upper Sonoran to at least the Canadian life zone (sometimes higher) and show no fidelity to any particular plant community (e.g. *P. rutulus*, *L. lorquini*, *L. johnsoni*, *T. pylades*, etc.), with *A. halesus* descending into the Lower Sonoran. Of the remainder, one group of 14 species also flies in the Upper Sonoran Zone: *P. eurymedon*, *P. multicaudata*, *P. napi*, *E. ausonides*, *A. sara*, *A. lanceolata*, *C. tullia*, *L. arota*, *I. augustinus*, *S. californica*, *S. sylvinus*, *G. lygdamus*, *O. sylvanoides*, and *P. melane*. *S. callippe inornata* generally occurs above the FW plant community and likes drier sites such as forest openings and forest margins within the YPF plant community. However, it



also frequents the YPF/FW ecotone and the contact zone between these plant communities, making its ecological preference difficult to classify. The other group (nine species) occurs from the Transition Zone to at least the Canadian Zone: *N. menapia*, *S. zerene*, *S. hydaspe*, *P. gracilis*, *M. nelsoni*, *I. eryphon*, *P. ruralis*, *H. harpalus*, and *A. vialis* (cf. Garth and Tilden 1963; Shields 1966, 1986). Thus it appears that all of the resident butterfly species of the YPF plant community were fed directly in from the Upper Sonoran and Canadian Zones which border it.

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#### Literature Cited

- Adler, P. H., and D. L. Pearson. 1982. Why do male butterflies visit mud puddles? *Can. J. Zool.*, 60: 322–325.
- Axelrod, D. I. 1957. Late Tertiary floras and the Sierra Nevada uplift. *Bull. Geol. Soc. Am.*, 68:19–46.
- . 1976. History of the coniferous forests, California and Nevada. *Univ. Calif. Pubs. Bot.*, 70: 1–62.
- . 1980. Contributions to the Neogene paleobotany of Central California. *Univ. Calif. Pubs. Geol. Sci.*, 121:1–212.
- Bailowitz, R. A., and J. P. Brock. 1991. Butterflies of southeastern Arizona. Sonoran Arthropod Studies, Inc., Tucson, 342 pp.
- Ballmer, G. R., and G. F. Pratt. 1988. A survey of the last instar larvae of the Lycaenidae of California. *J. Res. Lepid.*, 27: 1–81.
- , and ———. 1992. *Loranthomitoura*, a new genus of Eumaeini. *Trop. Lepid.*, 3:37–46.
- Barbour, M. G., and J. Major. 1990. Terrestrial vegetation of California. *Calif. Native Plant Soc. Spec. Pub.*, 9:1–1020.
- Burns, J. M. 1992. Genitalic recasting of *Poanes* and *Paratrytone*. *J. Lepid. Soc.*, 46:1–23.
- Crowe, C. R. 1965. The climatological tool in Lepidoptera research. *J. Res. Lepid.*, 4:23–36.
- Ehrlich, P. R., and D. D. Murphy. 1981. The population biology of checkerspot butterflies (*Euphydryas*). *Biol. Zbl.*, 100:613–629.
- Eliot, J. N., and A. Kawazoe. 1983. The butterflies of the *Lycaenopsis* group. British Museum (Natural History), Hampshire, 309 pp.
- Emmel, J. F., and O. Shields. 1978. Larval foodplant records for *Papilio zelicaon* in the western United States. *J. Res. Lepid.*, 17:56–67.
- Emmel, T. C., and J. F. Emmel. 1973. The butterflies of southern California. *Nat. Hist. Mus. Los Angeles Co., Sci. Ser.*, 26:1–148.
- Farrell, B. D., C. Mitter, and D. J. Futuyma. 1992. Diversification at the insect-plant interface. *BioScience*, 42(1):34–42.
- Ferris, C. D. 1989. Supplement to: A catalogue/checklist of the butterflies of America north of Mexico. *Lepid. Soc. Mem.*, 3:1–103.
- . 1993. Reassessment of the *Colias alexandra* group, the legume-feeding species, and preliminary cladistic analysis of the North American *Colias*. *Bull. Allyn Mus.*, 138:1–91.
- Garth, J. S., and J. W. Tilden. 1963. Yosemite butterflies. *J. Res. Lepid.*, 2:1–96.

- Gilbert, D. E., and G. D. Peterson, Jr. 1966. Climate and plantclimate map of Mariposa County. University of California Agricultural Extension Service, 80 pp.
- Giuliani, D., and O. Shields. 1995. Large-scale migrations of the Painted Lady Butterfly, *Vanessa cardui*, in Inyo County, California, during 1991. *Bull. Southern Calif. Acad. Sci.*, 94:149–168.
- Grinnell, J., and F. Grinnell, Jr. 1907. The butterflies of the San Bernardino Mountains, California. *J. New York Entomol. Soc.*, 15:37–49.
- Hawksworth, F. G., and D. Wiens. 1972. Biology and classification of Dwarf Mistletoes (*Arceuthobium*). U.S. Dept. Agr.-Forest Service, Agriculture Handbook, 401:1–234.
- Heppner, J. B. 1971. The distribution of *Paratrytone melane* and its spread into San Diego County. *J. Res. Lepid.*, 10:287–300.
- Howe, W. H. 1975. The butterflies of North America. Doubleday & Co.; Garden City, New York, 633 pp. 97 pls.
- Janzen, D. H. 1968. Host plants as islands in evolutionary and contemporary time. *Amer. Nat.*, 102: 592–595.
- Kelson, R. V., and M. C. Minno. 1983. Observations of hilltopping *Mitoura spinetorum* and *M. johnsoni* in California. *J. Lepid. Soc.*, 37:310–311.
- Lincoln, R. L., G. A. Boxshall, and P. F. Clark. 1982. A dictionary of ecology, evolution and systematics. Cambridge Univ. Press, Cambridge, 298 pp.
- MacNeill, C. D. 1964. The skippers of the genus *Hesperia* in western North America with special reference to California. *Univ. Calif. Pubs. Entomol.*, 35:1–230.
- Miller, L. D., and F. M. Brown. 1981. A catalogue/checklist of the butterflies of America north of Mexico. *Lepid. Soc. Mem.*, 2:1–280.
- , and J. Y. Miller. 1990. Nearctic *Aglais* and *Nymphalis*: Laurasia revisited? *The Entomologist*, 109:106–115.
- Munz, P. A., and D. D. Keck. 1949. California plant communities. *El Aliso*, 2:87–105.
- , and ———. 1965. A California flora. University of California Press, Berkeley & Los Angeles, 1681 pp.
- Oosting, H. J. 1956. The study of plant communities. 2nd ed. W.H. Freeman & Co., San Francisco, 440 pp.
- Pollard, E. 1988. Temperature, rainfall and butterfly numbers. *J. Appl. Ecol.*, 25:819–828.
- , and T. J. Yates. 1993. Monitoring butterflies for ecology and conservation. Chapman & Hall, London, 274 pp.
- Porter, A. H., and H. Geiger. 1988. Genetic and phenotypic population structure of the *Coenonympha tullia* complex in California: no evidence for species boundaries. *Can. J. Zool.* 66:2751–2765.
- Raven, P. H., and D. I. Axelrod. 1978. Origin and relationships of the California flora. *Univ. Calif. Pubs. Bot.*, 72:1–134.
- Scott, J. A. 1979. Hibernial diapause of North American Papilionoidea and Hesperioidea. *J. Res. Lepid.*, 18:171–200.
- . 1984. A review of *Polygonia progne (oreas)* and *P. gracilis (zephyrus)*, including a new subspecies from the southern Rocky Mountains. *J. Res. Lepid.*, 23:197–210.
- . 1986. The butterflies of North America. Stanford Univ. Press, Stanford, 583 pp., 64 pls.
- . 1994. Biology and systematics of *Phyciodes (Phyciodes)*. *Papilio*, new ser., 7:1–120.
- Shapiro, A. M. 1975. Photoperiodic responses of phenologically aberrant populations of pierid butterflies. *Great Basin Nat.*, 35:310–316.
- , C. A. Palm, and K. L. Wcislo. 1979. The ecology and biogeography of the butterflies of the Trinity Alps and Mount Eddy, northern California. *J. Res. Lepid.*, 18:69–151.
- , S. O. Mattoon, G. T. Austin, and O. Shields. 1990. Northward dispersal of *Euptoieta claudia* in California and Nevada in 1988. *J. Lepid. Soc.*, 44:201–202.
- Shields, O. 1965. *Callophrys (Mitoura) spinetorum* and *C. (M.) johnsoni*: their known range, habits, variation, and history. *J. Res. Lepid.*, 4:233–250.
- . 1966. The butterfly fauna of a Yellow Pine Forest community in the Sierra Nevada, California. *J. Res. Lepid.*, 5:127–128.
- . 1978. *Erynnis brizo lacustra* and *Hesperia columbia* in the Sierra Nevada. *J. Lepid. Soc.*, 32:61–62.
- . 1986. Butterflies of the Foothill Woodland (and chaparral) plant community in central California: their ecology, affinities, and ancestry. *Utahensis*, 6(3):18–40.

- . 1987. Two related migrations of the California Tortoise Shell butterfly in Mariposa County, California, in 1986. *J. Lepid. Soc.*, 41:209–211.
- Sims, S. R. 1983. Prolonged diapause and pupal survival of *Papilio zelicaon* Lucas. *J. Lepid. Soc.*, 37:29–37.
- Smith, M. J., and J. P. Brock. 1988. A review of the *Thessalia leanira* complex in the southwestern United States, with a description of two new subspecies of *Thessalia fulvia*. *Bull. Allyn Mus.*, 118:1–21.
- Stone, S. E., and M. J. Smith. 1990. Buckmoths in relation to Southwestern vegetation and foodplants. *Desert Plants*, 10:13–30.
- Tilden, J. W. 1959. The butterfly associations of Tioga Pass. *Wasmann J. Biol.*, 17:249–271.
- . 1973. *Junonia* and *Precis*, a correction. *J. Res. Lepid.*, 12:216.
- Van Devender, T. R., and W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. *Science*, 204:701–710.
- , R. S. Thompson, and J. L. Betancourt. 1987. Vegetation history of the deserts of southwestern North America; the nature and timing of the Late Wisconsin-Holocene transition. Pp. 323–352 in *The geology of North America*, vol. K-3. The Geological Society of America; Boulder, Colorado.

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