ECOLOGICAL STUDIES OF RHOPALOCERA IN A HIGH SIERRAN COMMUNITY – DONNER PASS, CALIFORNIA. I. BUTTERFLY ASSOCIATIONS AND DISTRIBUTIONAL FACTORS

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The State of California, extending some 1,264 miles along the Pacific Coast of North America, contains 158,693 square miles of dry deserts, moist coastlands, chaparral-covered hills, and great mountain ranges, with unparalleled opportunities for the ecologist and lepidopterist alike. Practically every combination of climatic factors may be found within the state's boundaries. Six life zones, with approximately 4000 species of fern-allies and flowering plants, lie at elevations ranging from 282 feet below sea level to 14,495 feet at the peak of Mount Whitney. Temperatures and rainfall correspond generally with these life zones; average annual rainfall ranges from about 0 inches to 70 inches, and mean temperatures of about 40°F. in boreal regions to high summer temperatures of 130° in the deserts are recorded. Thus California provides many unique locations to study the ecological aspects of a species' adaptation and preference for a particular environment.

One such location – the Donner Pass area in the Sierra Nevada, Placer County, California – was selected for intensive study during the summers of 1956 and 1960. This location encompasses the flora of three life zones and ranges in elevation from 6800 to 8300 feet. This paper reports the general ecological observations made on each of the 76 recorded species, forms and races of Rhopalocera and the four habitats selected for study in the area. Factors involved in butterfly distribution are discussed using examples from this Donner Pass study and the literature.

INTRODUCTION

In this Donner Pass study and past investigations by other authors, two general factors in the ecology of Rhopalocera have been emphasized:

(1) Preference of many species for a particular type of habitat.
(2) Effect of weather (extrinsic environmental conditions) on butterfly flight periods.

A second paper will treat the latter subject. The present paper reports our data on the general ecology of the Donner Pass butterfly fauna.

E. B. FORD (1957), in considering the geographical distributions and ecological preferences of British butterflies, notes that it is often difficult to separate these two distinctions. Many species will normally occur within a particular region and this region, though usually composed of varying habitats, is known as part of the general geographic distribution of each resident or migratory species. However, within that general region, the ecological preferences of each species dictate the distribution of that butterfly.

As yet, few published papers have been devoted entirely to the ecology of butterflies in a particular locality. TILDEN (1959) has done comprehensive studies on the butterfly fauna of Tioga Pass, California. He arranges the 43 species in groups based on their apparent abundance in various sub-alpine and alpine plant associations. Certain habits of alpine butterflies are noted. TILDEN concludes that range is usually determined by the presence of food plants, although food plants of some of these alpine species are presently unknown. In this author's estimation, the occurrence of the adult butterflies is less effected by particular environmental conditions than is that of the plants.

Many authors have noted habitat preferences for single species or groups of Rhopalocera. MUNROE (1951) in reporting collecting conditions in northern Quebec observed a seasonal succession and an altitudinal zonation of the various resident species. The flight season was so short that the time of appearance of species differed in days instead of weeks "as in more temperate climates." Different *Boloria* and *Plebeius* species each had specific habitats, such as "rocky hilltops" and "only on grassy beds of dried-up lakes at from 2200 to 2400 feet." EHRLICH (1954; 1956) treats the *Erebia* in northwestern America from an ecological standpoint. BROWN, EFF and ROTGER discuss the ecological preferences of over 200 species in their book *Colorado Butterflies* (1957). BROWN (1952) also discusses the restricted ecological preferences of *Oeneis oslari* Skinner in the South Park area of Colorado; the type of soil and terrain preferred is apparently directly related to the presence of the food-plant grass.

As in BROWN's paper (1952), many authors have attempted to give possible explanations for the basis of these "ecological preferences" of a species. Probably the most acceptable explanation for limiting factors in the distribution of resident species is the presence of food plants. The "hilltop" controversy of a few years ago brought out possible reasons for congregations of butterflies. SHOUMATOFF (1953) summarizes past authors' hypotheses into two groups: ecological explanations, such as food-plant search, wind, and tropism, and intrinsic factors, such as "liking hilltops," "social ambition," and "gregariousness." ARNHOLD (1952)

notes that *Euchloe olympia* prefers to fly along the leeward side of ridges (near Dresbach, Minnesota); a narrow band of calm is created on the top or side of the banks according to wind direction. Thus wind, as well as food plant, appears to definitely be a factor in the local habitat preference of a species.

Since a species generally is very restricted to one group or species of food plant, it follows that the geographic range of the butterfly will correspond to the range of the required plants. However, climatic factors within the range may prevent the butterfly from existing with its food plant. Since butterflies are poikilothermic ("cold-blooded") and therefore dependent on solar heat for their activity, species cannot live where temperature and solar radiation do not meet their tolerances (Hovanitz, 1958).

EHRLICH (1956) lists climatic factors that could limit *Erebia* distribution in habitats of northwestern America, such as temperature fluctuations, amount of cold, snow cover, rapidity of runoff, and amount of spring flooding of habitat. The influence of any of these factors on butterfly distribution over a large territory would be the subject of a very interesting paper, but that would require an intensive investigation over many years.

The contribution of this paper towards studies of the latter type is to report information on the local habitat preferences of butterflies in a single locality. Perhaps some day we will have enough information to provide a generalized survey of climatic and vegetational factors, and their influence on butterfly distribution, for the entire Sierra Nevada range. However, towards the end of this paper, we have discussed the apparent reasons for habitat preference in the Donner Pass Rhopalocera, and these conclusions may prove to be a step on the way to full understanding of the factors involved in butterfly distribution.

HABITATS OF THE DONNER PASS AREA

The Donner Pass area is located on the crest of the Sierra Nevada range at an elevation of 6800 to 8383 feet, 15 miles northwest of Lake Tahoe, in Placer County, California. Flora and fauna of both the east and west slopes of the Sierra meet along this crest. Adding to the desirability of the study area is the union of three life zones here — Transition, Canadian, and Hudsonian — with Canadian zone vegetation comprising most of the territory. Four habitats within the Donner Pass area were studied: wet meadow, dry meadow, forest, and montane.

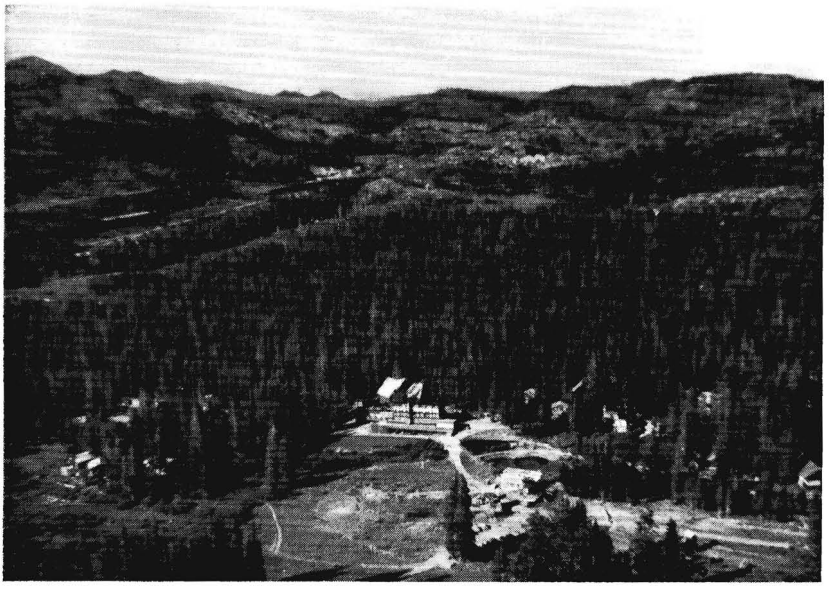
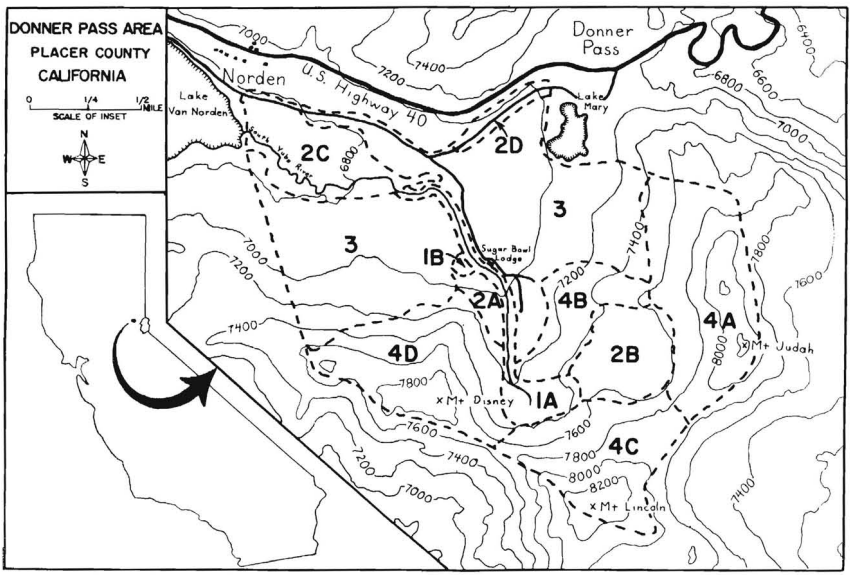


Fig. 1. The Donner Pass area, looking N.N.E. from Mt. Disney (7,953′). In center of photograph is Sugar Bowl Lodge, with the dry and wet portions of the Lodge meadow at lower center and at left. Lake Mary is at upper center; long railroad snowsheds and Highway 40 are at upper left. The actual Pass is slightly to the left of upper center.



Sketch map of the State of California showing the locality studied, and topographical map (inset) of the Donner Pass area showing the habitats (numbered 1A through 4D) described in the text. Primarily from Geological Survey map, Norden Quadrangle, California, 7.5 Minute Series, U. S. Dept. of the Interior (1955).

1. Wet Meadow

A. Sugar Bowl and South Yuba River

The Sugar Bowl is a small bowl-shaped valley (elevation 7260 feet) formed by the confrontation of Mt. Disney, Mt. Lincoln, and the high ridge connecting the two peaks. A heavy snow pack on these slopes, coupled with scattered springs, provides a considerable flow of water into this area. Here also is the source of the South Yuba River, which flows into Lake Van Norden. Thus there is an abundance of plants due to the moisture and rich soil. Willows (*Salix*) are found in scattered thickets in the Sugar Bowl and along most of the length of the river. Grasses (*Poa* species) and sedges (*Carex*) are common throughout the area. Other common plants are Cow Parsnip (*Heracleum lanatum*), Sierra Sweet Cicely (*Osmorrhiza occidentalis*), Scarlet Gilia (*Gilia aggregata*), Common Monkey Flower (*Mimulus guttatus*), and Elephant Heads (*Pedicularis grœnlandica*).

B. Wet Portion of Lodge Meadow

This area (elevation 7000 feet) is located at the base of Mt. Disney, where numerous springs provide a very wet environment. About one-half of it is covered with willows. In the other portions one finds a large number of grasses and flowers. Some of the more common plants are Indian Paint Brush (*Castilleia miniata*), Common Monkey Flower (*Mimulus guttatus*), Columbine (*Aquilegia truncata*), Larkspur (*Delphinium pauciflorum*), Tiger Lily (*Lilium pardalinum*), and Meadow Rue (*Thalictrum fendleri*).

2. Dry Meadow

A. Lodge Meadow and Adjacent Portions

This flat area near the Sugar Bowl Lodge supports many flowering plants despite its dryness in July and August. Fireweed (*Epilobium angustifolium*), Common Yarrow (*Achillea millefolium*), and Pussy Paws (*Calyptridium umbellatum*) are common. Elevation: 6960 to 7000 feet.

B. Emigrant Meadow

Emigrant Meadow (elevation 7500 to 7600 feet) is a dry flat expanse with few plants; two species are Yellow-bud Penstemon (*Penstemon lætus*) and *Saxifraga æstivalis*.

C. Summit Valley

Summit Valley (elevation 6800 feet) is a large flat meadow which is marshy in the spring, but dry throughout July and August. Grasses dominate most of the area but in some places Pussy Paws, Yarrow, and Pepper Grass (*Lepidium perfoliatum*) can be found.

3. Forest

Dense forest covers about one-half of the total study area, particularly between 6800- and 7600-foot elevations. This is almost all Canadian zone forest. Some of the forest trees and plants near Lake Mary and Lake Van Norden are typical Transition zone inhabitants, and the higher montane forest is typical of the lower Hudsonian zone. The majority of the forest trees are Red Fir (*Abies magnifica*), Lodgepole Pine (*Pinus contorta*), Silver Pine (*Pinus monticola*), and Mountain Hemlock (*Tsuga mertensiana*).

On the forest floor a great variety of plants are found. Collecting was usually good in small clearings or near the forest edge; many butterfly species were found beneath an aerial transportation system (used in winter), which cuts a swath through the forest from Highway 40 to Sugar Bowl Lodge. Some of the forest plants are the Spotted Coral Root Orchid (*Corallorrhiza maculata*), Fireweed, Corn Lily (*Veratrum californicum*), Yarrow, Pine Drops (*Pterospora andromedea*), and Alpine Shooting Star (*Dodecatheon alpinum*).

4. Montane

A. Mount Judah

Mount Judah (8,243′) appears barren due to the large granite boulders scattered over its talus slopes. The dry, almost soilless environment discourages most trees. The flora includes Alum Root (*Heuchera micrantha*), Rabbit Brush (*Chrysothamnus nauseosus*), Sage Brush (*Artemisia tridentata*), and Mule-Ears (*Wyethia mollis*).

B. Rocky Slope leading to Mount Judah

Seemingly a jumble of small granite rocks, this area (elevation 7160 to 7400 feet) supports many plants; included in this flora are scattered Lodgepole Pines (*P. contorta*), *Wyethia mollis, Lupinus,* and *Sedum* species.

C. Mount Lincoln

Mount Lincoln (8,383′) is quite similar to Mount Judah. One minor difference is the presence of Mountain Hemlock (*Tsuga mertensiana*).

D. Mount Disney and Crow's Nest

This twin-peaked mountain is part of a long ridge and supports a flora similar to the other peaks, although Mt. Disney (7,953′) has more species. Found here are Red Fir, Lobb's Buckwheat (*Eriogonum lobbii*), Mountain Alder (*Alnus tenuifolia*), *Chrysopsis brewerii,* and Western Pennyroyal (*Monardella odoratissima*).

Local Distribution and Ecological Preferences of Species Recorded

The phrase "flight period" refers herein to the first and last records for the species. Observations were made from June 17 to August 26 (1960, unless otherwise noted); obviously, some species were already flying before the first day of observation. Nomenclature of species follows Ehrlich (1961a). Subspecific names are used for clarity with certain polymorphic western species, such as in *Speyeria.*

A. PAPILIONIDÆ

1. *Papilio zelicaon* Luc. Flight period: June 17-August 6. Uncommon; males found typically on peaks of area (bare rocks) and never observed visiting flowers. Females on lower slopes of Mt. Judah, flying around food plant (*Cymopterus terebinthinus*) and ovipositing single eggs (observed fresh female depositing eggs, around 10 a.m. on June 27); one female seen visiting Western Pennyroyal (*Monardella odoratissima*).

2. *Papilio indra indra* Reak. Flight period: June 17-July 10. Males occasionally seen around 3 peaks of area and lower slopes of Mt. Judah (landed on rocks and opened wings to "sun" themselves). Males frequently seen at muddy places. Females occasionally (June 27, June 30) seen ovipositing single eggs on *Cymopterus terebinthinus.* L. M. Martin has found several hundred *indra* larvæ on this *Cymopterus* at Kaiser Peak (10,000′), Fresno Co., Calif.

3. *Papilio rutulus* Luc. Flight period: June 17 - July 15. Males occasionally seen around willows and in forest; one female observed laying eggs on willow in Summit Valley.

4. *Papilio eurymedon* Luc. Flight period: June 17 - July 24. Males common in wooded areas; females on lower slopes of Mt. Judah.

Reported food plants available: *Ceanothus velutinus* and *prostratus,* and *Prunus emarginata.*

5. *Parnassius clodius baldur* Edw. Flight period: June 27-July 25. Found almost everywhere, but particularly abundant on the lower slopes of Mt. Judah (females laying eggs on or near *Sedum* in this location).

B. PIERIDÆ

1. *Neophasia menapia* F. & F. Flight period: August 8-August 15. Only on lower slopes of Mt. Judah and Lake Van Norden area; males flying around upper tips of *Pinus contorta;* no females seen.

2. *Pieris sisymbrii* Bdv. Flight period: June 20 - June 28. Lower slopes of Mt. Judah, but only seven adults observed during summer (1960). Species of Cruciferæ (recorded food plants) present in area.

3. *Pieris protodice* L. Flight period: June 23 - August 25. Most common in dry meadows; known food plants (Cruciferæ), such as mustard species, were present; double-brooded.

4. *Pieris rapæ* L. Flight period: June 18 - August 14. Dry and wet meadows; reported food plants (Cruciferæ) abundant.

5. *Euchloe creusa hyantis* Edw. Flight period: June 21 - July 13. Only on lower slopes of Mt. Judah; food plants (Cruciferæ) present.

6. *Anthocaris sara* form *julia* Edw. Flight period: June 18 - July 16. Lower slopes of Mt. Judah and open wooded slopes; rarely seen in meadows. Food plants (mustard species) present; several mature larvæ found in mid-June (1956). Males identical to typical white *reakirtii* were occasionally taken in fresh condition. *A. julia* is a yellow- tinted, high-altitude form of *sara,* while the lowland, spring form of *sara* is *reakirtii.*

7. *Colias eurytheme* Bdv. Flight period: June 17 - August 26. Found in all habitats, but most abundant in Summit Valley meadows. Females seen ovipositing on clover (*Trifolium*).

8. *Colias eurytheme* form *amphidusa* Bdv. Flight period: July 1 - August 26. Appeared in early July and by August this strongly-marked form was dominant over typical *eurytheme.*

9. *Colias philodice eriphyle* Edw. Flight period: (July 1). Only 3 found — in dry meadows of Summit Valley.

C. DANAIDÆ

1. *Danaus plexippus* L. Flight period: June 23 - August 25. No milkweed species in area and individuals seen were likely strays from lower elevations.

D. SATYRIDÆ

1. *Cœnonympha tullia californica* Westwood. Flight period: (late June). Seen only in 1956 (wet winter) in late June on Mt. Judah (grassy areas). Flight period in 1960 (dry winter) may have finished by June 17.

2. *Cercyonis sthenele oetus* Bdv. Flight period: July 11 - August 20. Found only on high western slope (above 8000 feet) and around peak of Mt. Judah; landing on sagebrush stems (*Artemisia tridentata*). Food plant likely to be grasses, which were abundant on mountain. Adults (both sexes) visited Western Pennyroyal blooms.

E. NYMPHALIDÆ

1. *Speyeria cybele leto* Behr. Flight period: July 15 - August 3. Five fresh specimens seen on lower slopes (6,980′) of Mt. Disney, visiting Western Pennyroyal flowers. Possible food plants (*Viola* species) for *leto* and the following *Speyeria* species were present in wet meadows.

2. *Speyeria zerene zerene* Bdv. Flight period: August 2 - August 25. Uncommon; both sexes visited Western Pennyroyal on lower slopes (6,980′) of Mt. Disney.

3. *Speyeria coronis snyderi* Skin. Flight period: July 3 - July 15. Females proportionately more common than males; flying around Western Pennyroyal on Mt. Disney (6,980′).

4. *Speyeria atlantis irene* Bdv. Flight period: July 12 - August 26. Both sexes almost as abundant as *S. mormonia arge;* adults visited Western Pennyroyal. Females occasionally seen in wooded areas.

5. *Speyeria mormonia arge* Stkr. Flight period: June 29 - August 26. The most abundant *Speyeria* and found throughout the Pass area; adults avidly visited Western Pennyroyal.

6. *Boloria epithore* Edw. Flight period: June 17 - July 22. Very abundant in forest and around Pine-mat Manzanita (*Arctostaphylos nevadensis*). Food plant is reported as *Viola* (violets).

7. *Chlosyne palla* Bdv. Flight period: (July 7). Only 1 worn male seen. Food plants (*Castilleia* and *Aster* species are reported) abundant in area. As *palla* is recorded from higher elevations than Donner Pass, some unknown climatic factor may prevent its establishment, or possibly the species has not extended its range to this particular area yet.

8. *Chlosyne hoffmanni hoffmanni* Behr. Flight period: June 25-August 6. Found throughout the area; very abundant where its food plant (*Chrysopsis breweri*) grows, especially on open slopes of Mt. Disney and Mt. Judah. Mature larvæ fairly common at end of June; females

laid egg masses, each containing 30 to 110 eggs. These eggs hatched in approximately 3 weeks, and larvæ grew quite slowly, staying together in communal webs. By last week in August, every larva observed had assumed a lethargic state. Larvæ were still in webs, though plants were dying.

9. *Phyciodes campestris montana* Behr. Flight period: June 18-August 25. Practically as abundant as *C. hoffmanni;* found most commonly where *Aster* species (recorded food) were growing in meadows. Females were observed hovering around *Aster integrifolius.*

10. *Phyciodes mylitta* Edw. Flight period: June 20-August 5. Scarce in area, although its reported food plant, thistle (*Cirsium*), was fairly abundant along Lake Mary road (dry location).

11. *Polygonia zephyrus* Edw. Flight period: June 20-August 18. Over-wintering individuals collected in late June and early July; fresh males collected in early August on *Monardella odoratissima.* Food plant (*Ribes viscosissimum* – Sticky Currant) common in Lodge meadow. Mature larvæ found by second week of July.

12. *Nymphalis californica* Bdv. Flight period: June 17-August 20. Over-wintering individuals numerous during late June. Swarms of larvæ found on *Ceanothus* in first two weeks of July on peak of Mt. Disney (lone location). About July 15, individuals began to hatch and on July 21, the species reached its peak of abundance with an estimated 5,000 seen in one hour in a 100′ x 100′ area on Mt. Judah. On this date, the butterflies began flying in a westerly direction at about 10 a.m. On July 22, population counts were about "normal" again.

13. *Nymphalis milberti* Godt. Flight period: June 17-August 6. Apparently a stray species in this area. Adults visited Western Pennyroyal. *Urtica,* the usual food for *milberti* and also *atalanta,* was not growing in the Pass area; it is abundant along streams at nearby, lower elevations.

14. *Nymphalis antiopa* L. Flight period: June 19-August 15. Over-wintering individuals seen during late June and early July. Fresh specimens seen during late July and early August. Food plant: willows.

15. *Vanessa cardui* L. Flight period: June 22-August 16. Seen around rocky peaks of the 3 mountains. Food plant: thistle.

16. *Vanessa atalanta* L. Flight period: June 22-July 21. Only several males seen, flying around peaks with *cardui.* No food plant in area.

17. *Vanessa virginiensis* Dru. Flight period: June 18-August 25. Also found around peaks with *cardui.* Larvæ were found during July on *Gnaphalium palustre* (Cudweed); this food plant grew only in one clump at the base of Mt. Disney.

18. *Vanessa carye* Hbn. Flight period: June 18-August 19. Found frequently throughout the area. Food plant probably *Lupinus* here.

19. *Precis lavinia* Cramer. Flight period: June 18-August 18. Males common in dry meadows; females common in wet meadows, and occasionally seen hovering over *Plantago* (*Mimulus* also in the area).

20. *Limenitis lorquini* Bdv. & Lec. Flight period: June 23-August 10. Frequently seen in willows (food plant) along the South Yuba River.

F. LYCÆNIDÆ

1. *Satyrium californica* Edw. Flight period: July 20-August 10. A distinct inhabitant of the area along the Lake Mary road. Adults flew around and landed on *Eriogonum nudum* blooms. Reported food plant is *Quercus;* Huckleberry Oak (*Quercus vaccinifolia*) was found in this area.

2. *Satyrium sylvinus* Bdv. Flight period: July 18-August 26. Found most commonly around willows (recorded food plant) on the lower slopes of Mt. Judah; adults landed on *Eriogonum nudum* flowers.

3. *Satyrium sæpium* Bdv. Flight period: July 20-August 16. Found only along Lake Mary road; females observed ovipositing on *Ceanothus velutinus.* Adults landed on *Eriogonum nudum* and Elderberry (*Sambucus velutina*).

4. *Satyrium behrii* Edw. Flight period: (August 4). One found in 1960; fairly abundant in 1956 on rocky slopes of Mt. Judah. Adults landed on *Eriogonum* blooms. Probable food plant: *Lupinus* species.

5. *Satyrium fuliginosa* Edw. Flight period: July 10-August 9. Fairly common on lower slopes of Mt. Judah. Females seen ovipositing on lupines (food plant).

6. *Strymon melinus* Hbn. Flight period: July 7-August 15. Found flying around *Eriogonum* blooms; fairly abundant. Reported food plant: *Polygonum alpinum* (Knotweed), present in several areas.

7. *Callophrys johnsoni* Skin. Flight period: (June 28). Probably a resident of the area, but extremely restricted colony. Female observed flying around *Arceuthobium* (a mistletoe and recorded food plant) on Mountain Hemlock at lower end of Sugar Bowl.

8. *Callophrys nelsoni* Bdv. Found rarely in 1956; foodplant (believed to be Incense Cedar – *Libocedrus*) not found in Pass area.

9. *Callophrys augustinus iroides* Bdv. Flight period: June 28 - July. Found rarely in late June and July on rocky slopes; adults fed on *Eriogonum.* Food plant: *Ceanothus* and *Sedum* reported by authors.

10. *Callophrys eryphon* Bdv. Flight period: June 28 - July 10. Only occasionally captured (on semi-forested, talus slope) but all fresh specimens. Food plant: probably *Pinus contorta.*

11. *Callophrys dumetorum perplexa* B. & Benj. Flight period: June 22-July 9. Occasionally found in the high montane areas (above 7,500'). Food plant probably an *Eriogonum* species.

12. *Lycæna arota virginiensis* Edw. Flight period: July 20-August 11. Found only along the Lake Mary road; fairly abundant. Males hatched in mid-July, females appeared in early August. Females were ovipositing on *Ribes montigenum* (Gooseberry) during first two weeks of August (eggs hatch the following spring).

13. *Lycæna editha* Mead. Flight period: July 15-August 19. Fairly common throughout the entire area, especially in dry meadows. A possible food plant (*Potentilla drummondii*) occurs in the Lodge meadow.

14. *Lycæna nivalis* Bdv. Flight period: July 3-August 17. Rather scarce; males more abundant than females. Found in dry meadows. Food plant is unknown.

15. *Lycæna cupreus* Edw. Flight period: June 17-July 15. Found in dry meadows. Adults frequently visited flowers of *Calyptridium umbellatum* (Pussy Paws). In early July, mature larvæ were found feeding on the blossoms of this plant; being pink in color, they blended well with the flowers.

16. *Lycæna heteronea* Bdv. Flight period: August 6-August 16. One small colony found near a tiny stream (elevation 7160') on Mt. Judah. Observed food plant was *Eriogonum nudum*, and the adults frequently visited the flowers of this buckwheat.

17. *Everes comyntas amyntula* Bdv. Flight period: June 17-July 1. One colony found on the top of Mt. Judah (8,234'). Here the species' observed food plant, *Astragalus whitneyii* (Milkvetch or "locoweed") grew on top of the narrow ridge connecting the two peaks of Mt. Judah. A constant wind blew; both sexes landed on the plants and flew up only occasionally.

18. *Plebejus anna* Edw. Flight period: June 26-August 19. Found throughout the area but common only on the moist lower slope of Mt. Disney. Food plant unknown in spite of the species' abundance.

19. *Plebejus sæpiolus* Bdv. Flight period: June 19-August 17. Found only in wet portions of Lodge meadow and Summit Valley (very abundant). Females (all *rufescens* form) oviposited on *Trifolium hybridum* (Alsike Clover) throughout late June and July.

20. *Plebejus icarioides* Bdv. Flight period: June 22-August 3. Found throughout the area; especially common in areas with wide-spread patches of *Lupinus* (food plant)—usually on rocky talus slopes.

21. *Plebejus shasta* Edw. Flight period: June 30-August 18. Found throughout the area, and very common in dry meadows on mountain slopes. Some adults seen landing on *Monardella odoratissima* blooms. Food plant is unknown.

22. *Plebejus acmon* West. & Hew. Flight period: June 18-August 15. Found only in Lodge meadow in late June and along Lake Mary road in early August. Females oviposited on *Eriogonum nudum* (food plant).

23. *Plebejus acmon lupini* Bdv. Flight period: June 25-July 25. Found only in Sugar Bowl and on Mt. Judah. Food plant probably *Eriogonum*. TILDEN (1959) suggests this insect may be a species distinct from *acmon*.

24. *Agriades glandon podarce* F. & F. Flight period: June 27-August 3. A small colony found in wet portion of Lodge meadow; fairly abundant here. Food plant perhaps *Vaccinium nivictum* (Sierra Bilberry), found in same area.

25. *Glaucopsyche lygdamus behrii* Edw. Flight period: June 17-July 16. Found throughout the area in late June, but most common on the moist lower slope of Mt. Disney. Food plant here probably *Lupinus*.

26. *Philotes enoptes* Bdv. Flight period: June 26-July 13. Males found landing on moist ground and flying on lower slopes of Mt. Judah. One female seen ovipositing on *Eriogonum nudum*.

27. *Philotes battoides intermedia* B. & McD. Flight period: June 25-July 13. Found on moist stream banks on lower slope of Mt. Judah. Several females seen around *Eriogonum nudum*.

28. *Celastrina argiolus echo* Edw. Flight period: June 17-July 15. Fairly common in all habitats. Food plant probably among *Ceanothus, Vaccinium, Spiræa,* and *Actinomeris* species (all recorded food plants) found in the pass area.

G. HESPERIIDÆ

1. *Thorybes nevada* Scud. Flight period: June 17-July 13. Abundant in dry and wet meadows. Food plant unknown.

2. *Pyrgus ruralis* Bdv. Flight period: June 17-July 11. Found in every habitat. Food plant probably *Potentilla drummondii* (larvæ known to feed on *P. tenuiloba* elsewhere).

3. *Pyrgus communis* Grt. Flight period: June 17-August 19. Abundant in every habitat. Particularly found around muddy places. Females seen ovipositing on *Sidalcea glaucescens* (Mallow Family) and larvæ found all summer.

4. *Erynnis juvenalis* Fabr. Flight period: June 19-July 25. Males collected on the 3 peaks and occasionally elsewhere; no females seen. Food plant unknown for this area.

5. *Erynnis afranius* Lint. Flight period: June 17-August 5. Males collected on the three peaks; 1 female collected in Lodge meadow. Food plant possibly columbine (food plant of the related *E. lucilius*)—*Aquilegia* grew in the meadows.

6. *Hesperia juba* Scud. Flight period: June 17-July 1. Occasionally seen in both dry and wet meadows.

7. *Hesperia nevada* Scud. Flight period: June 22-July 10. A large thriving colony was found at the very peak of Mt. Judah. Males appeared in late June and females appeared in early July. Females were observed ovipositing on a species of grass.

8. *Hesperia harpalus* Edw. Flight period: (August 8-August 11) A small colony was found on the lower slope (7,240′) of Mount Judah. Two females were seen ovipositing on a grass species, and other females were observed hovering over the grasses in this small area.

9. *Polites sonora* Scud. Flight period: June 23-August 25. Found in every habitat but most common in dry meadows. Food plant: likely grasses, as in other Hesperiinæ.

10. *Polites sabuleti tecumseh* Grin. Flight period: June 19-August 19. Distributed in every habitat but particularly common in the dry meadows (especially in Summit Valley). Most abundant in late June and early July, though the species was collected throughout the summer.

H. Possible Future Additions to the Butterfly Fauna of Donner Pass

Papilio brucei Edw. could be established in the area and overlooked in 1956 and 1960. Its food plant on Kaiser Peak (10,000 to 10,300 feet; Fresno County, California) reported by L. M. MARTIN to be *Cymopterus terebinthinus,* which was present on Mt. Judah (8,243′).

Colias eurytheme form *autumnalis* Cockerell might have been flying right after snowmelt in early June.

Euphydryas chalcedona macglashanii Rivers has its type locality as "Truckee" (10 miles east of the Pass) and COMSTOCK (1927) notes it as occurring in the mountains north of Lake Tahoe in late June and early July.

Euphydryas chalcedona sierra Wright is common in the Lake Tahoe region, 15 miles from Donner Pass, and has been collected at Gold Lake, 30 miles north of the Pass.

Phædrotes piasus Bdv. is recorded from similar elevations in northern California and its food plant (*Lupinus*) is common in Donner Pass.

Ochlodes sylvanoides Bdv. was common in Squaw Valley (August 11, 1960), 10 miles southeast of the Pass. Apparently-similar habitats are available in the Lake Van Norden meadows.

Speyeria callippe juba Bdv. was found at Emigrant Gap, 15 miles west of the Pass area. Other *callippe* forms have been reported from the Lake Tahoe and Gold Lake regions.

Table I. DISTRIBUTION OF RHOPALOCERA SPECIES IN THE DONNER PASS AREA.

Species	Habitat									
A. PAPILIONIDÆ	1	2A	2B	2C	2D	3	4A	4B	4C	4D
Papilio zelicaon	—	—	—	—	—	—	X	X	X	X
Papilio indra	—	—	—	—	—	—	—	X	—	—
Papilio rutulus	X	—	—	X	—	X	—	—	—	—
Papilio eurymedon	X	X	—	X	—	X	—	X	—	X
Parnassius clodius	—	X	—	—	—	—	X	X	X	X
B. PIERIDÆ										
Neophasia menapia	—	—	—	X	—	—	—	X	—	—
Pieris sisymbrii	—	—	—	—	—	—	X	X	X	X
Pieris protodice	X	X	X	X	X	X	—	X	—	—
Pieris rapæ	X	X	—	X	X	X	—	—	—	—
Euchloe creusa	—	—	—	—	—	—	—	X	—	—
Anthocaris sara	X	X	—	—	—	X	—	X	—	X
Colias eurytheme	X	X	X	X	X	X	X	X	X	X
Colias philodice	—	—	—	X	—	—	—	—	—	—
C. DANAIDÆ										
Danaus plexippus	X	X	X	X	X	X	X	X	X	X
D. SATYRIDÆ										
Cœnonympha tullia	—	—	—	—	—	—	—	X	—	—
Cercyonis sthenele	—	—	—	—	—	—	X	—	—	—
E. NYMPHALIDÆ										
Speyeria cybele	—	—	—	—	—	—	—	—	—	X
Speyeria zerene	X	X	—	X	X	X	—	X	—	X
Speyeria coronis	—	X	—	—	—	—	—	—	—	X
Speyeria atlantis	X	X	—	X	X	X	X	X	X	X
Speyeria mormonia	X	X	X	X	X	X	X	X	X	X
Boloria epithore	X	X	X	X	X	X	X	X	X	X
Chlosyne palla	—	—	—	—	—	—	—	X	—	—
Chlosyne hoffmanni	X	X	X	X	X	X	X	X	X	X
Phyciodes campestris	X	X	X	X	X	X	X	X	X	X
Phyciodes mylitta	—	X	—	X	—	—	—	—	—	—

Polygonia zephyrus	X	X	X	X	X	X	X	X	X	X
Nymphalis californica	X	X	X	X	X	X	X	X	X	X
Nymphalis milberti	X	X	—	—	—	X	—	—	—	—
Nymphalis antiopa	X	X	—	X	—	X	—	—	—	X
Vanessa cardui	—	—	—	—	—	—	X	—	X	X
Vanessa atalanta	—	—	—	—	—	—	X	—	X	X
Vanessa virginiensis	—	X	—	—	X	—	X	X	X	X
Vanessa carye	—	X	—	—	X	—	X	X	X	X
Precis lavinia	X	X	X	X	X	—	—	—	—	—
Limenitis lorquini	X	—	—	—	—	—	—	—	—	—
F. LYCÆNIDÆ										
Satyrium californica	X	X	—	—	X	—	—	X	—	—
Satyrium sylvinus	X	X	—	—	X	—	—	X	—	—
Satyrium sæpium	X	X	—	—	X	—	—	X	—	—
Satyrium behrii	—	X	—	—	X	—	—	—	—	—
Satyrium fuliginosa	—	—	—	—	X	—	X	X	X	X
Strymon melinus	X	X	—	—	X	—	—	X	—	—
Callophrys johnsoni	X	—	—	—	—	—	—	—	—	—
Callophrys nelsoni	—	—	—	—	—	—	—	X	—	—
Callophrys augustinus	X	—	—	—	X	—	X	X	—	X
Callophrys eryphon	X	—	—	—	—	X	—	—	—	X
Callophrys dumetorum	X	X	—	—	—	—	X	X	X	X
Lycæna arota	—	—	—	—	X	—	—	—	—	—
Lycæna editha	X	X	X	X	X	—	X	X	X	X
Lycæna nivalis	X	X	X	X	X	—	—	—	—	X
Lycæna cupreus	X	X	X	X	X	—	—	—	—	—
Lycæna heteronea	X	X	—	—	—	—	X	X	—	X
Everes comyntas	—	—	—	—	—	—	X	—	—	—
Plebejus anna	X	X	X	X	X	X	X	X	X	X
Plebejus sæpiolus	X	—	—	X	—	—	—	—	—	—
Plebejus icarioides	—	X	—	—	X	—	X	X	X	X
Plebejus shasta	—	X	—	—	—	—	X	X	X	X
Plebejus acmon	—	X	—	—	X	—	—	—	—	—
Plebejus acmon lupini	X	—	—	—	—	—	—	X	—	—
Agriades glandon	X	—	—	—	—	—	—	—	—	—
Glaucopsyche lygdamus	X	X	—	X	X	X	X	X	X	X
Philotes enoptes	X	—	—	—	X	—	—	X	—	—
Philotes battoides	X	—	—	—	X	—	—	X	—	—
Celastrina argiolus	X	X	—	—	—	X	X	X	X	X
G. HESPERIIDÆ										
Thorybes nevada	X	X	X	X	X	X	X	X	X	X
Pyrgus ruralis	X	X	X	X	X	X	X	X	X	X
Pyrgus communis	X	X	X	X	X	X	X	X	X	X
Erynnis juvenalis	—	X	—	—	—	—	X	X	X	X
Erynnis afranius	—	X	—	X	—	—	X	X	X	X
Hesperia juba	—	X	—	X	—	—	X	X	X	X
Hesperia nevada	—	—	—	—	—	—	X	—	—	—
Hesperia harpalus	—	—	—	—	—	—	—	X	—	—
Polites sonora	X	X	X	X	X	X	X	X	X	X
Polites sabuleti	X	X	X	X	X	X	X	X	X	X

Discussion

From this study several factors important in determining the distribution of a species within a local habitat have emerged. The explanations for the "ecological preferences" of the butterflies in the Donner Pass area (and presumably elsewhere) fall ideally into the following categories.

I. Larval Food Plant

As pointed out in the introduction, the specific larval food plant required by most species limits the distribution of the butterfly to areas where the food plant grows. But within the geographical range of the food plant, two quite different distributions of the plant are possible: (1) a "closed" range, where plant and butterfly are confined to very restricted areas within a habitat; (2) an "open" range, where the plant and butterfly are widespread in a given habitat; or, alternately, an "open" range where the food plant is widespread but the butterfly is confined in distribution.

A. Closed Range

In some butterfly species, such as *Euphydryas editha* in the San Francisco Bay region, the adults seem to "choose" to remain within a very specific area despite the fact that its food plant is available in a somewhat greater area. This apparent "choice" factor, Ehrlich (1961b) terms "intrinsic barriers" to dispersal.

In the Donner Pass area also, some species were found with apparent intrinsic barriers to dispersal. *Everes comyntas amyntula* and *Hesperia nevada* were restricted to the very top of Mt. Judah, and each species was always found within a few feet of its respective food plant, which was also restricted to the ridge (8,240′) here. With a constant, strong wind and the weak flight of *Everes*, any dispersal away from the food plant would seem to be dangerous for the survival of the species there. *Hesperia nevada* seemed just to "choose" to remain in this territory.

Examples from lower elevations also come out of the Lycænidæ and Hesperiidæ. Certain lycænids (*Lycæna heteronea* and *Satyrium californica*, for example) and skippers, such as *Hesperia harpalus*, were found only in the immediate vicinity of food-plant colonies. Such restricted plants are found only in areas with particular soil and moisture requirements. Willows, the larval food plant of *Limenitis lorquini*, are found only in wet areas and *Limenitis* stays among the willows, despite its strong flight. One might hypothesize that a specifically developed physiology (weak flight and a single food plant with specific

soil and moisture requirements) or an intrinsic "choice" factor (plus a single food plant) has caused these butterfly species to be restricted even within a habitat the size of those studied (refer to map).

B. Open Range

In this category we include food plants that enjoy a wide distribution throughout one or more habitats, and that have their corresponding butterfly species occurring with them. Examples are numerous: *Pieris protodice, Anthocaris, Colias, Chlosyne hoffmanni, Precis lavinia, Boloria epithore, Plebejus sæpiolus,* and many others.

C. Open Food Plant Range but Restricted Butterfly Distribution

This is a very common circumstance in temperate North America. The food plant will occur over a wide region, yet the butterfly species will be distributed in only part of the habitats available to it. (This, of course, is assuming the same elevation and general climate prevails throughout these habitats.) The following explanations are offered:

(1) The species is a weak flier and is only increasing its range very slowly. Ehrlich (1954) postulates that species of this nature (e.g. *Erebia*) may have wind as an important dispersal agent.

(2) The species may be a fairly strong flier but it never strays far from its its colony in a particular habitat. Ehrlich (1961b) has offered an *intrinsic barrier* explanation for this phenomena.

(3) The species (a weak or only fair flier) exists in a habitat surrounded by an almost insurmountable barrier, such as mountains, a forested area, or even a wide river. Bauer (1959) notes that the southward spread of *Erebia vidleri* Elwes and *Boloria chariclea* Schneider from Washington into Oregon has been barred by the Columbia River gorge.

(4) To the casual observer, habitats may appear to be suitable because of similar climate and elevation, but microclimates in the area may preclude any settling of the butterfly species. Besides severe cold in the winter, there may be flooding from spring runoff, lack of sufficient solar radiation due to frequent cloudiness or northerly exposure, an abundance of parasites and predators, feeding heavily on butterflies of the area (single strays from elsewhere would be destroyed too frequently for permanent settlement), and extreme temperature fluctuations within the immediate area of the food plants (bare rocks with sun reflection, for instance).

Three examples of this "open but restricted" phenomena in the Donner Pass area are offered from the hairstreak group. *Satyrium sylvinus* was found around willows at the base of Mt. Judah, but in Summit Valley (same elevation—about 6800 feet) the species was absent despite the abundance of willows. Food plants for *Callophrys eryphon* and *C. augustinus iroides* were quite numerous and widely distributed, but these hairstreaks were found only rarely in both 1956 and 1960.

II. Adult Feeding Plant

This distributional factor has not been noted by most authors, but in the Donner Pass area, the adult feeding habits of some butterfly species dictated the apparent distribution of the imagos. The most obvious examples of this intrinsic ecological factor were the members of the *Speyeria* group. The fritillary species were very rarely found in the moist areas where the larval food plant (*Viola* species) grows (and then only females). This is the complete opposite of the first case considered (I-A) where certain species were extremely restricted to the food-plant area. Instead, *Speyeria* occasionally would be seen flying very rapidly through dry meadows or on rocky slopes where no larval food plants were known to occur. We are indebted to L. M. Martin for pointing out that single-egg-laying species, such as *Speyeria*, often must fly a considerable distance between each oviposition. Usually, the adult *Speyeria* congregated around flowering Western Pennyroyal to feed during most of the day.

Thus preferences of the adult butterfly for a certain feeding plant can be very important in determining the distribution of some species within a habitat that may not even contain the larval food plant!

III. Strong Fliers or Inter-Habitat Migrants

Examples in this group are familiar to every North American lepidopterist: *Vanessa cardui, V. atalanta, V. virginiensis, Nymphalis californica, Danaus plexippus,* and *Polygonia zephyrus.* Members of this category often fly many miles and one or more thousand feet in elevation away from the nearest food plants.

Vanessa cardui and *V. atalanta* were found only at elevations over 8,200 feet, while thistles (food plant for *cardui*) grew to around 6,800 feet and no food plants were found for *atalanta.* No larval food plant for *Danaus plexippus* was available for many miles around, but individuals of this renowned migrant were seen rather frequently above 7,000 feet.

For two species (*Nymphalis californica* and *Polygonia zephyrus*), the larval food plant was found only in one locality, while the adults flew in every habitat. The strong flight of these species has granted considerable freedom of movement to the adults, and thus the butterflies often appear far from their larval food plants. Yet this "migrating" tendency does not imperil the survival of the species, for the adults hatch close to their food plants and can mate and lay eggs before flying off, or else can find new food-plant sources in their movements.

IV. MOUNTAIN-TOP ATTRACTION

No paper of this type would be complete without entering the "mountain-top controversy." We have already mentioned (III) the *Vanessa* species flying about the peaks. There were two other strong fliers in the study area that were restricted mainly to the highest peaks: *Papilio zelicaon* and *P. indra*. Elsewhere in California, *P. zelicaon* is found wherever a suitable food plant (Umbelliferæ) grows. On the Donner Pass peaks, the available food plant for both *zelicaon* and *indra* was *Cymopterus* and this plant's range included the tops of the peaks down to 7,100 feet. For these strong fliers, the winds along the high ridges and peaks may prove enticing, if one concedes that the species can indeed "choose" to remain there. On the other hand, the closeness of their food plant would make the adults' appearance around the peaks seem but natural.

CONCLUSIONS

Using the ecological data obtained from our research in the Donner Pass area, we have found *first* that the distribution of butterflies in a Sierran community is apparently governed by the inherent physiology of each species; in other words, by *intrinsic* factors. This physiology may be dependent upon one or more of the following factors: (1) the *larval food plant;* (2) the *adult feeding plant;* (3) the *development of wing muscles for flight,* i.e., how strongly or weakly the butterfly flies; (4) other *unknown intrinsic factors,* such as the preference of some species for mountain-tops and the lack of any dispersal tendency, as in *Satyrium sylvinus.*

Secondly, we have found that the distribution of butterflies depends upon various *extrinsic* factors which work on the *intrinsic* factors of each species. Among extrinsic factors we have noted climate, food-plant distribution, elevation above sea level, natural barriers to dispersal, wind, and presence of parasites and predators.

Thus in the search for explanations of butterfly distribution we must consider all the above factors, for each factor has its examples and many butterflies are not easily categorized. The real basis for the distribution and "ecological preferences" of a species must be sought in the evolution and adaptation of physiological mechanisms for exploiting a particular habitat in nature.

Summary

The local distributions, ecological preferences, and flight periods of 76 species, forms, and races of Rhopalocera in the Donner Pass area, Placer County, California, U. S. A., are reported. Factors involved in determining butterfly distribution are discussed. It is concluded that the distribution of a butterfly species is determined by (1) *intrinsic factors,* including larval food plant, adult feeding plant, strength of flight, and unknown factors, such as intrinsic barriers to dispersal; and (2) *extrinsic factors,* including climate, food-plant distribution, elevation above sea level, natural barriers to dispersal, and presence of parasites and predators. These extrinsic conditions work on intrinsic physiological factors, which have evolved for exploitation of a particular environment, and so determine the geographical range and local distribution of a species.

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SATYRIUM BEHRII (LYCÆNIDÆ) IN OREGON

Prompted by the recent record of *Satyrium behrii* Edwards from Nevada (Philip, *Journ. lepid. soc.* 15: 56; 1961) the Reverend A. I. GOOD, of Wooster, Ohio, wrote to inform me of his capture of the species in Oregon, another of the states whence *behrii* was previously unreported (cf. Clench, *in* Ehrlich & Ehrlich, *How to know the butterflies*: 192; 1961).

Rev. GOOD took a single fresh male on 5 July 1961 at John Day (Grant Co.), the only individual he saw in nearly a month of collecting in the area. He has generously presented the specimen to Carnegie Museum.

E. J. NEWCOMER, of Yakima, Washington, has also reported in correspondence the capture of S. *behrii* in Oregon. He took it at two localities: Camp Sherman (Jefferson Co.), 22 July; and Pringle Falls (Deschutes Co.), 23 July. There is also a record of the species from Ft. Klamath (Klamath Co.) in the Museum of Comparative Zoology at Harvard.

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