ECOLOGICAL STUDIES OF RHOPALOCERA IN A HIGH SIERRAN COMMUNITY – DONNER PASS, CALIFORNIA. II. METEOROLOGIC INFLUENCE ON FLIGHT ACTIVITY

by THOMAS C. EMMEL and JOHN F. EMMEL

The present paper reports a study of Rhopalocera flight patterns and meteorological fluctuations at Donner Pass (Placer County) – a typical Canadian Zone area in the Sierra Nevada mountain range of California. The authors have spent a total of over six months in two different years investigating the Donner Pass region. The senior author (T. C. E.) surveyed the area in 1956, delineating vegetation zones and general Rhopalocera distribution and activity in the various habitats. A subsequent intensive investigation was planned in the spring of 1960 and that summer one of us (J. F. E.) obtained the meteorologic and flight activity data described in this report.

INTRODUCTION

Probably since the first collector in medieval Europe stopped outside with a net in his hands, it has been observed that times of emergence and flight of butterflies and most other insects tend to be adjusted to the surrounding environmental conditions. In our previous paper (1962), we noted that climatic factors govern the general distribution of butterflies; anyone interested in this phase of zoogeography should read WILTSHIRE (1957), who discusses the influence of desert, plain, and mountain climates on the distribution of Iraq's Lepidoptera. But within the area of distribution, weather directly affects the seasonal occurrence and fluctuation in numbers of the insects.

Some of the most striking examples of this important effect are found among the butterfly species of the southwestern deserts. BAUER (1955) remarks that *Papilio rudkini* Comstock has a very irregular flight period in the desert mountains, with captures recorded from January through November. BAUER states that rainfall seems to be "the deciding factor as to when it may be found."

HOVANITZ (1948) has studied the differences in field activity of the two female color phases of *Colias eurytheme* Boisduval during the day. He found different frequencies of each color phase (within the population of a specific locality) at different times of the morning and afternoon. Total activity was found to be dependent upon various temperature and solar radiation combinations; further discussion on certain aspects of his important studies of flight activity will be considered later.

Ehrlich (1954) states that *Erebia rossii* Curtis flies on "the warmest, stillest, brightest days." An interesting aspect of local climatic influence on butterfly species is this author's comment that, because of the weak flight of this *Erebia*, "prevailing winds cannot be discounted as a possible major guiding agency in the dispersal and subspeciation of *rossii*."

Other investigations have found climatic influence on mosquito populations. Platt *et al.* (1958) found "a 100% positive correlation . . . between relative humidity and the abundance of *Aedes vexans*," while Goodwin and Love (1957) found that extremely high air temperatures would greatly decrease numbers of mosquitoes. Many other examples of environmental studies with various invertebrates can be found in the literature.

In our previous paper, we considered the influence of vegetation and altitude (as well as various intrinsic factors) on the occurrence of butterfly species in a particular area. In this present paper, we wish to consider what governs the apparent rarity and abundance of a species within an area where it occurs. Lack (1954) found that food abundance is a limiting factor on bird populations, but this is obviously not the case with most butterflies, as the food plant is generally much more abundant than the butterfly (see Emmel & Emmel, 1962). A study of population size for each species in Donner Pass was not intended. Instead, we present herein data on the relative daily abundance of each of six butterfly species (from five families), along with records of daily weather conditions, and an attempt is made to show how these extrinsic (meteorologic) conditions affect the *flight activity* on each day within the flight period.

Description of Study Area

Donner Pass has had a long history of climatic influence on the lives of men and beasts. The heavy snows of the region attained unfortunate fame in 1846, when the Donner Party was trapped below the Pass. Even today, miles of strong wooden snow sheds stand over the railroad tracks for protection against the fierce storms.

Snowmelt occurs in early June, while snow flurries can be expected in early September. Sandwiched between nine months of winter – spring, summer, and fall in the Donner Pass area must rapidly pass in seccession. Thus it is that butterflies and plants come out together as soon as bare ground appears, and the flight or growth seasons are measured in weeks instead of months.

The Lodge meadow area was the particular region studied for collecting data on daily flight numbers of the six most abundant Rhopalocera.

The Lodge meadow area studied in Donner Pass, Placer County, California. Moist in June, the meadow becomes progressively drier during the summer and plants such as Yarrow (in the foreground) become dominant on the gentle slope between the South Yuba River and the base of Mt. Disney.

This study area, approximately 500 by 800 feet, is bounded on the north by the South Yuba River, on the west by willow thickets and forest, on the south by the slope of Mt. Disney, and on the east by a dirt road and forest. It lies at an elevation of approximately 6960 feet above sea level. In June, the meadow here was wet and grasses, with many wildflowers, grew in verdant abundance. As the summer progressed, the meadow dried slowly and such plants as Yarrow (*Achillea millefolium*) and Fireweed (*Epilobium angustifolium*) replaced the earlier wet meadow inhabitants. The reader is referred to our earlier paper for further habitat description.

Methods

Within the Lodge meadow area, daily counts on numbers of butterflies in flight were made. The method employed was counting by direct observation in a two hour period: 10-12 A.M., Pacific Standard Time.

Table 1. MAXIMUM NUMBERS OF INDIVIDUALS OBSERVED IN ANY TWO-HOUR PERIOD FOR SIX SPECIES.

Species	Number observed	Date
Parnassius clodius baldur	40	June 27
Colias eurytheme	55	June 23
Chlosyne hoffmanni	120	July 7
Nymphalis californica	650	July 21
Plebejus icarioides	39	June 28
Pyrgus communis	52	July 20

These counts were made through continuous crossings of the study area by the observer. In using numbers seen per two-hour period as an index of abundance, we are following EHRLICH's suggestion (1959).

Determination of the size of natural populations is very difficult, as pointed out by BROWN (1951). One can only obtain crude estimates and the results should be interpreted "as estimates of the *lower* possibility of size." In our case, a complete count of the population (possible in "marking" experiments; see Ehrlich, 1961) was not necessary; we desired to compare the *relative* numbers of flying adults from day to day.

In order to avoid false comparisons of one species' abundance with that of another species (which may not prefer the meadow habitat as much as others), all comparisons were calculated as follows. The number of individuals on each day was divided by the maximum number counted on any one day (see Table I) during the summer to obtain the percent of flying butterflies for each date. That is if Y = number of individuals observed, then Y/Y max $\times$ 100 = percentage or index of activity. Obviously, the above method of counting and of calculation has statistical limitations but the authors believe the results are accurate enough for the purpose: to compare relative abundance of flying butterflies with meteorological conditions on a day-to-day basis.

Meteorological data were obtained from standard instruments maintained by the staff of the Audubon Camp in the Lodge meadow. Relative humidity and barometric pressure were taken at 5:30 P.M., P. S. T. Degree of cloudiness figures represent approximations of the areas of visible sky and of clouds during the daylight hours.

RESULTS AND DISCUSSION

The six butterfly species selected for the flight activity graph (Fig. 3) represent five major Rhopalocera groups found in the Donner Pass area. These were: *Parnassius clodius baldur* Edw. (Papilionidæ), *Colias*

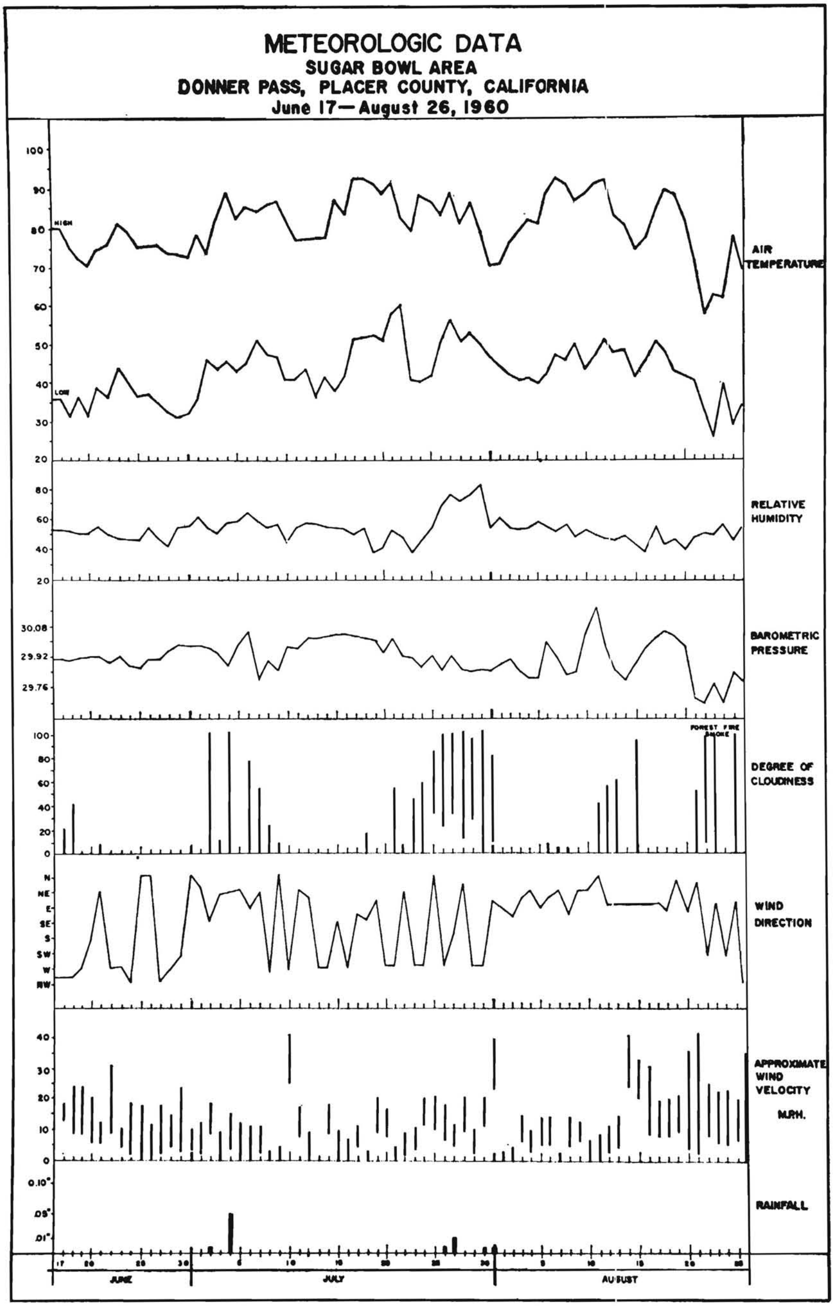
METEOROLOGIC DATA
SUGAR BOWL AREA
DONNER PASS, PLACER COUNTY, CALIFORNIA
June 17—August 26, 1960
HIGH
LOW
AIR TEMPERATURE
RELATIVE HUMIDITY
BAROMETRIC PRESSURE
30.08
29.92
29.76
FOREST FIRE SMOKE
DEGREE OF CLOUDINESS
N
NE
E
SE
S
SW
W
NW
WIND DIRECTION
APPROXIMATE WIND VELOCITY M.P.H.
0.10"
.05"
.01"
RAINFALL
JUNE
JULY
AUGUST

Figure 2

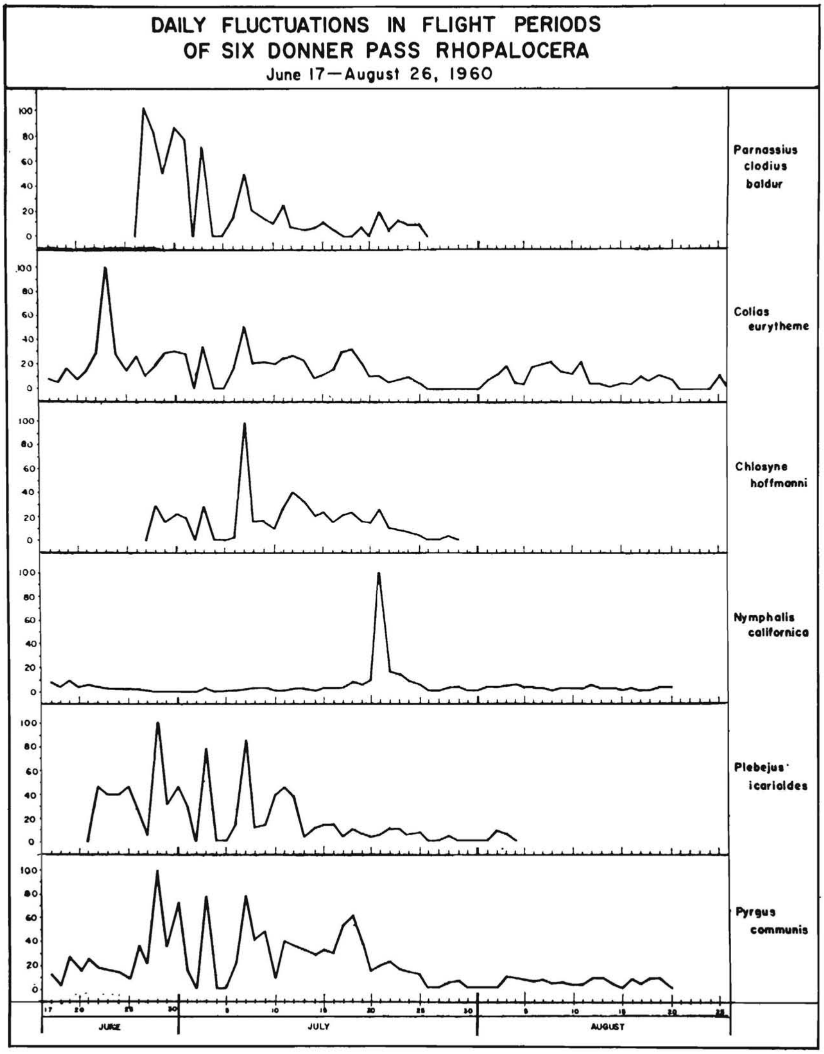

Figure 3

eurytheme Bdv. (Pieridæ), *Chlosyne hoffmanni hoffmanni* Behr and *Nymphalis californica* Bdv. (Nymphalidæ), *Plebejus icarioides* Bdv. (Lycænidæ), and *Pyrgus communis* Grt. (Hesperiidæ).

The flight periods of three species (*C. eurytheme, N. californica, P. communis*) began before June 17, the date of first observations, and extended into late August (two generations of adults occurring within this time). The flight periods of the other three butterflies began in late

June after observations were underway, and terminated in late July. Thus it is interesting to compare the effects of meteorological conditions on each of the long-term and short-term fliers, which we shall do (individually) during the following discussion of our data.

A. General Trends of Activity

For four species (and perhaps *C. eurytheme,* too), there seemed to occur a large emergence and much flight activity at one time, near or at the beginning of each species' flight season. The "hump" of high activity slopes down to rather low levels after about 10 to 15 days. The peak flight dates for these particular species were:

P. clodius: June 27-July 7
C. hoffmanni: July 7-12
P. icarioides: June 23-July 11
P. communis: June 26-July 9

Following these peak periods in each species was a long "trailing-off" period, in which few individuals were found, and those collected were usually worn and old.

Colias eurytheme, from our data, appears to have two "humps" of higher flight activity, one extending from late June to early July and a second beginning in the first week of August. This second occurrence, with a week or so of low abundance of typical *eurytheme,* represents for the most part the emergence of the form "amphidusa", which replaced typical *eurytheme* to a very considerable extent during August.

Nymphalis californica occurred at low population levels throughout the summer, but on July 21, a mass emergence took place with the new adults migrating out of the area that afternoon in a westerly direction. Notes on this butterfly's ecology are mentioned in our previous paper. The possible cause of this mass emergence will be treated shortly.

To our knowledge, none of the six species exhibited sexual dichronism in respect to the time of emergence; that is, both sexes of these species emerged concurrently (synchronous) or with not more than several days' difference. It would be interesting to graph flight-period data on a *Speyeria* species or *Lycæna arota* Bdv., for instance; one would likely find two peaks or perhaps a long plateau if the males remained at a state of high activity until the females emerged *en masse.*

B. Stimulus for Emergence of Short-term Fliers

By considering the meteorological and flight activity data in Figures 2 and 3, it is possible to see certain weather situations that could account for butterfly emergence.

Parnassius clodius and *Chlosyne hoffmanni* apparently began to emerge around the 26th of June. For the previous seven days weather conditions had been generally mild, with the daily high temperatures between 70 and 80 degrees, no cloudiness or rain, steady humidity and barometric pressure levels, and fairly low-velocity afternoon winds. Up to June 22, however, the night temperature was often near freezing; on June 23, the low was 43° F. This rather high "low" temperature (for June) could have provided the necessary stimulus for almost immediate emergence, especially in the case of *Plebejus icarioides,* which emerged in numbers from June 22 on.

The stimulus for the mass emergence of *Nymphalis californica* was evidently a five-day period of very high temperatures. The mature larvæ were very abundant in the first week of July, and the pupal stage lasted approximately two weeks. It is interesting to note that immediately after this date, the barometric pressure fell, with high degrees of cloudiness, high relative humidity and some rain. It is perhaps not impossible that the butterflies could "sense" this drop in pressure, or, more likely, the several days of unusually high temperatures. FRANK SALA (1961) and others have remarked on the apparent ability of the members of the *Saturnia albofasciata* group to "choose" to emerge on precisely a certain day after the beginning of the warm "Santanna" winds in southern California (see Stevenson, 1960) during late fall.

C. CORRELATIONS OF METEOROLOGICAL DATA WITH DAILY FLIGHT ACTIVITY

I. TEMPERATURE

Our hypothesis before collecting the data reported herein was that a positive correlation would be found between increase in temperature and increase in butterfly activity. For several reasons, this hypothesis was not substantiated. First, the daily high temperature never fell below 70° F. until August 21. This meant the high temperature ranged from 70 to about 95 degrees, and all Sierran species known to the authors would be active in such a range. Thus it was found in a scatter-dot correlation diagram (plotting per cent of butterfly activity versus the number of degrees Fahrenheit) that the butterflies were both highly active and inactive under the same temperature conditions, with no noted increase in butterfly numbers with increase in temperature. On July 5, for instance, at a high temperature of 90°, no butterflies flew in the morning. This was due to a heavy rain on the preceding day (which thoroughly wetted the vegetation); this is the sort of interrelationship of the data that must be taken into account. However, in areas of very high temperatures (well above 90° around noon), HOVANITZ (1948) found that with *Colias* "a period of minimum diurnal activity occurred about the middle of the day," so there may even be a negative response in activity with such temperatures.

Secondly, as the high-low temperatures were recorded as such for the entire 24-hour day, the "high" temperature does not necessarily reflect the situation between 10 and 12 o'clock in the morning. Thus a cool temperature in the morning may have limited flight during that time. But in the three *Colias* populations studied by HOVANITZ (1948), "the activity of the females was greatest at some point during the morning," and this point was found by him to be "earlier in the day in the more southern populations."

II. RELATIVE HUMIDITY AND BAROMETRIC PRESSURE

Relative humidity generally ranged between 40 and 60 per cent; by definition, this factor is dependent upon temperature. The only sharp change (remembering that this condition was only measured at 5:30 P.M.), outside of times of rain, was an increase to the 80 per cent level from July 27 to 29. Unfortunately, there was no considerable butterfly activity at the end of July (both preceding and following these dates), so no conclusions on the effect of relative humidity on butterfly activity can be drawn from our study.

Cloudiness and rain were accompanied by a drop in barometric pressure, but it is believed that the former factors' physical effects of decreasing solar radiation and of wetting the vegetation were probably the significant causes of drops in flight activity, rather than the drop in pressure (but refer to our previous remarks on *Nymphalis californica* emergence).

For both these meteorological factors, studies in tropical habitats with hourly changes in humidity and barometric pressure would likely provide more interesting and conclusive evidence for effects on flight activity.

III. DEGREE OF CLOUDINESS

The effect of degree of daily cloudiness on flight activity is believed here to be shown of considerable significance. By considering the period of highest activity (June 27 to July 9) in four species, and graphing degree of cloudiness versus percentage of activity during this time, we find an apparent direct negative correlation; that is, with increasing cloudiness butterfly activity decreases. On clear days during this period, flight activity varied from 0 to 100%, with other factors being responsible for this spread of activity. The seven days of varying cloudiness during this time of high butterfly emergence made correlation work possible; the other three general periods of cloudiness (late July and in August) occurred towards the end of times of emergence and abundance of the species considered.

Amount of solar radiation or light intensity is dependent upon degree of cloudiness in a significant way. Direct sunlight is lessened or completely obscured by clouds, and these six butterflies do not fly when the extreme situation occurs. Thus here exists a direct correlation between flight activity and solar radiation. There is also a close correlation between solar radiation and daily temperature. HOVANITZ (1948) found in *Colias* that "activity is greatest along a peak line ranging from high temperature and low solar radiation to low temperature and high solar radiation."

A unique opportunity to study the effects of smoke on flight activity was provided by a large forest fire near the Pass, beginning August 20. Virtually all flight activity of all species halted when thick clouds of smoke severely obscured the sun and even filled the valleys of the area.

IV. WIND DIRECTION AND VELOCITY

No general correlations with flight activity were attempted, as it was obvious that from comparing the graphs wind direction and velocity usually are independent factors not acting on butterflies to any measurable extent (July 10 being the exception with regard to wind velocity). This is likely because of the rather sheltered valley in which the Lodge meadow is located, where the winds are of a mild nature. The wind speed and direction would seemingly prove to be relevant factors in more exposed situations, such as where the habitat is located on the leeward or windward side of a peak or a steep hillside, or perhaps in an extensive, flat, arctic-alpine area where winds could sweep butterflies away if they did not become inactive during windy hours.

V. RAINFALL

Rainfall was light in the Pass during the summer of 1960, as it was for the entire state. Rain (over 0.05 inches) on July 4 eliminated any flight activity on that and the following day; likewise, nearly trace amounts of rain (with a high degree of cloudiness) on July 2, 26, 27, 30 and 31 halted all flight of butterflies. Thus a correlation between precipitation in the form of rain and butterfly activity exists; if rain occurs, there will be "no" flight activity during that time. We are, of course, limiting this conclusion to just this particular temperate zone locality. The summer rains in the Sierras are cold and accompanied by a noticeable drop in air temperature. Precipitation is also accompanied by increasing cloudiness, a drop in barometric pressure, and an increase in relative humidity; it is felt that from this study the first two factors are the influential ones on butterfly flight activity. We already noted in the introduction that some workers have found insect abundance to be correlated with relative humidity.

D. The Interrelationships of Factors, and Statistics

The interrelationships among the meteorological factors considered in this paper are obvious. Rainfall will always be associated with degree of cloudiness, which in turn is linked with amount of solar radiation or light intensity (not measured in this study, other than very approximately by daily cloudiness). In high mountain areas, a decrease in solar radiation may be more important than temperature in influencing flight activity, as evidenced by the negative correlation of degree of cloudiness and butterfly numbers found in this study. Other relationships have been stated earlier.

The task of determining the particular factor (out of two or more conditions) responsible for affecting activity is indeed a formidable one. With butterfly activity as the dependent variable, one could determine multiple correlations for various combinations of independent meteorological variables, as Hovanitz (1948) did for certain of his data (and as we have done). But as noted above, in the Pass area the meteorological conditions are not independent of each other. One statistical method of dealing with this type of situation is the use of an equation for linear regression.

Andrewartha (1953: pp.568-583) illustrates the use of the regression equation in considering fluctuations in the numbers of a population of *Thrips imaginis* (order Thysanoptera), where weather is an important influence on numbers. The reader is referred to his book for the form and discussion of this equation, but we may mention several points here. In using the equation, the deviation from the usual number of insects is compared with the departure from the usual weather, and the extent of each condition's effect on insect numbers for any particular day is derived. This equation may be accurately used only with a large quantity of data, which our study did not provide.

E. Additional General Remarks

As noted in our discussion of temperature effects, Hovanitz found the highest period of activity of *Colias* females in the morning, with a considerable decrease in activity during the hottest portion of the day.

In the Donner Pass study area, we found the greatest activity in most species occurred between approximately 9:45 A.M. and 12:30 P.M., although because of the low population numbers we did not make an attempt to graph hourly activity during any one day HOVANITZ was able to count 1245 butterflies in 55 minutes in his Imperial Valley study).

Our suggestion for future long-term studies in areas unfamiliar to the investigator (in terms of peak flight activity) would be to record, for several days, flight activity by the hour – from as early as 6 A.M. to as late as 7 P.M. (e. g. in the tropics and during the arctic summer). Then if one is interested in fluctuations over the entire flight period of the species, he could choose from the data the normal "peak" for the species during the day, and thus obtain larger daily samples for correlation work.

It would be highly interesting to obtain additional information on the peak activity of a single species (such as *Colias*) in northern and southern localities – to discover whether it is indeed true that highest activity occurs earlier in the morning in southern localities. This phenomenon would very likely be linked with a particular level of solar radiation, for in many bird species, the morning or evening period of calling is intimately determined by a minimum and maximum level of light intensity. Such suggested studies would require exact measurements of foot-candles of light.

Additionally, comparative studies of times of high activity during the day in various species and genera would shed further light on this aspect of butterfly physiology. The senior author has observed *Cercyonis* flying at 7 A.M. in Washington state, *Caligo* and various satyrid butterflies flying only at twilight in Yucatan (Mexico), and certain Mexican *Thecla* flying only at mid-day for an hour or so. Accurate measurements of light intensity at such hours (both at the beginning and end of activity) over a number of days would undoubtedly prove of high interest. LLOYD MARTIN has pointed out that some species must fly before mating; this presents one reason for activity in the early morning hours.

SUMMARY AND CONCLUSIONS

1. The beginning of each of the flight periods of four species considered is dominated by a large "hump" of high activity, representing mass emergence of the adults over a period of up to about 10 days. Following this peak period is a long "trailing-off" period, in which individuals become progressively fewer and more worn.

2. Two different generations of one species, such as in *Colias eurytheme*, will show two distinct periods of abundance, determined

by their respective times of emergence. C. L. REMINGTON (personal communication) has pointed out that "amphidusa" is best considered a seasonal form "induced mainly by photoperiod;" if photoperiod measurements had been taken throughout the summer, the decreasing photoperiods in July and August may have nicely tied in with this observation of two points of abundance.

3. A five-day period of generally mild weather, coupled with high diurnal temperatures and a rise in the low nocturnal temperatures, apparently stimulated the mass emergence period of *Parnassius clodius, Chlosyne hoffmanni, Plebejus icarioides,* and *Nymphalis californica.*

4. Temperature was not found to be correlated with flight activity. This was perhaps principally because of the constantly-high diurnal temperatures throughout the greater part of the summer.

5. Relative humidity and barometric recorded under the stated conditions (5:30 P.M.), did not show any particular deviations during the early-summer peak of butterfly activity. Thus no conclusions on possible effects can be drawn. It is suggested that studies in tropical areas might elucidate the influence of these factors.

6. Degree of cloudiness, with its accompanying influence on solar radiation or light intensity, was shown to be directly correlated in a negative way with flight activity; i.e., along a line of increasing cloudiness, butterfly activity decreases. On clear, warm days, all degrees of activity occurred.

7. Butterfly activity in the Lodge meadow area was usually independent of wind direction and wind velocity.

8. Rainfall, accompanying cloudiness and barometric pressure and relative humidity changes, definitely is correlated with flight activity in a negative sense; that is, with any amount of rain, butterfly activity ceases.

9. The interrelationships of meteorological factors makes interpretation of the effect of any single factor quite difficult. Multiple-correlation graphs and the linear regression equation are two statistical methods for dealing with this type of situation.

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(TCE) Reed College, Portland 2, Oreg., U. S. A.

(JFE) Stanford University, Palo Alto, Calif., U. S. A.