would be interesting to have detailed data on specificity (or lack of it) in these other areas.

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FIELD TECHNIQUES FOR INVESTIGATIONS OF POPULATION STRUCTURE IN A "UBIQUITOUS" BUTTERFLY

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Because information about population structure is necessary for a proper understanding of the ecology, evolution, and geographic variation of any species of Lepidoptera, it is surprising that there have been so few effective population studies of these organisms. The investigations of Dowdeswell, Fisher, and Ford (1940, 1949), Turner (1963), Keller, Mattoni, and Seiger (1966) and Ehrlich (1965), among others, are notable exceptions. These studies have all documented essentially similar population structures, and have led to the belief that the subdivision of butterfly species into small isolated or semi-isolated populations with limited interchange of individuals is a general rule.

Studies conducted in 1962, and 1967–1969 on the satyrine *Erebia epipsodea* Butler, however, have revealed a population structure quite different from those previously reported (Brussard & Ehrlich 1970a, 1970b). We have now determined that the population studied in the vicinity of Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado may cover hundreds of square kilometers. There is a great deal of individual movement, and, although these butterflies are capable of recognizing and leaving ecologically unsuitable areas, these areas are not barriers that subdivide the population into smaller units.

Since the population structure shown by *E. epipsodea* may be more typical of Lepidoptera in general than the species previously studied, the purpose of this report is to describe in detail the field techniques used in determining this structure. Details of data analysis are reported elsewhere (Brussard and Ehrlich, 1970a).

When the study began, it was expected that each subalpine meadow or sagebrush flat supported a separate and distinct population, rarely exchanging individuals with adjacent areas, and that the strips of aspen and alpine fir that divided the meadows into discrete units would also serve as the boundaries of the butterfly populations. A capture-mark-recapture program initiated in 1962 used several meadows in the vicinity of RMBL as individual sampling areas. Analysis of the results of this program revealed that out of 735 butterflies collected, marked, and released in 5 localities, less than twenty percent were ever recaptured—far less than one would expect from examining the results of similar studies. Nevertheless, approximately eighty percent of the butterflies recaptured were taken in the area of previous capture. There was no way to determine whether these paradoxical results were caused by high mortality, large population size, or undetected migration.

Additional complications were caused by the short flight season of *E. epipsodea* in this area (approximately three weeks, the exact dates varying somewhat with elevation) and the unpredictable weather characteristic of early summer in the high, mountainous regions of Colorado. In late June and early July the mornings are often cool and cloudy, followed by a brief period of relatively clear sky from mid morning to early afternoon. Clouds and thundershowers usually follow from mid afternoon to early evening. Since it had been shown that *E. epipsodea* does not fly at all in temperatures below 14° C and in any numbers below 18–19° C, nor does it fly when a strong wind is blowing or when the sun is obscured by clouds (Brussard & Ehrlich, 1970c), the time available for collecting in any one day was limited. Any capture-recapture analysis is based on the assumption that marked animals have had time to mix freely with the remainder of the population before recapture. Thus, in order to study the population structure of this insect, it was decided that large numbers of *E. epipsodea* must be marked, released, and recaptured in a systematic manner within the limited period of time available. Furthermore, the sampling program must be designed to (1) give accurate population size estimates and (2) provide quantifiable information on inter-area movement. The development of a systematic sampling program in 1967 gave results which suggested the true nature of the

population structure of this insect. Modifications of this program in 1968 verified and refined the results of the previous year.

Because of the restrictions imposed by the alpine environment, and the large number of butterflies flying in the study areas, it was necessary to develop techniques for rapid handling of the insects in the field. A rapid marking technique was needed, since methods previously described (see, for example, Dowdeswell, Fisher, and Ford 1940 and Ehrlich and Davidson 1960), are far too slow or involve too many people in the marking process. It was found that the "Sharpie" marking pen, manufactured by Sanford's, was the most satisfactory marking device. Because of the fine point, good ink flow and rapid drying, one person using this pen could mark the butterflies quickly and efficiently. Furthermore, the "Sharpie" is available in several colors, each of which can be distinguished from the other after application. Although the color black tended to dry on the tip of the instrument if it were not instantly capped after applying a mark, this difficulty was not experienced with any of the other colors.

Weather permitting, collecting began around 0900 and continued for approximately one hour. The butterflies were netted and placed in individual glassine envelopes which were stored in styrofoam ice chests kept at convenient spots within the study areas. After all butterflies observed in an area had been captured, they were removed from the envelopes with forceps and examined. The recapture event was recorded for marked individuals; freshly caught ones were assigned a number and marked. In addition to date and area of capture, sex and condition were recorded at the time of initial capture and at every subsequent recapture. Damaged individuals or those exhibiting abnormal flight behavior upon release were not returned to the population. There is no evidence that there were any differences in behavior or probability of recapture between marked and unmarked individuals.

The numbering technique used was a modification of the method described by Ehrlich and Davidson (1960). The modifications included adding additional spots near the base of each wing which were assigned values of 100, 200, 400 and 700, increasing the number of individuals that could be marked, per color, to 1000 (Fig. 1). Because of this, and since the "Sharpie" is available in several colors, it was possible to give individual numbers to all butterflies marked in 1968. (In 1967 most insects were individually numbered; however, some were marked with a code pattern indicating area and date of capture.) The advantages of individually numbering all butterflies handled during a flight season are

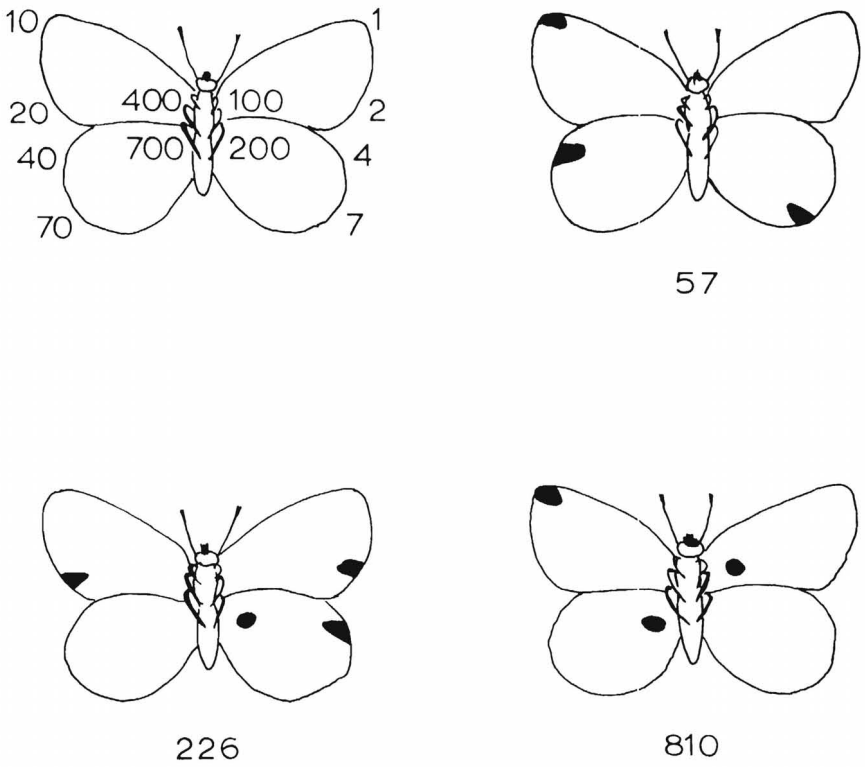

Fig. 1. Modification of Ehrlich and Davidson's (1960) marking system; 1000 butterflies per color can be marked in this fashion.

obvious; considerably more information is accumulated on individual movement, and many more partial histories of recaptured insects can be compiled.

The manner of release of animals as vagile as butterflies assumes great importance in population studies. In order to evaluate the possibility that an abnormally high level of activity occurred subsequent to release, causing excessive dispersal out of the study areas, on two occasions the butterflies were held and released in late afternoon under cloudy conditions. Collecting was delayed the following morning giving the butterflies an opportunity to mix freely with the remainder of the population prior to recapture. The percentage of recapture for that day was then compared to both the day preceding and the day following when normal release procedures were followed. Since there was no significant difference ($p >> .05$), it was assumed that the marking pro-

TABLE 1. Summary of Capture-Recapture Results, 1967

Locality	Days used	Sex	Marked & released	Number of individuals recaptured	% of individuals recaptured	Total number of recaptures*
Visquene Meadow	7	M	204	14	6.4	14
		F	13	0	0	0
Cemetery	11	M	354	123	34.7	180
		F	32	4	12.5	4
Bench Meadow Area	4	M	147	6	4.1	6
		F	3	0	0	0
Naked Hills Peninsula	4	M	111	19	17.1	19
		F	6	0	0	0
Wilson Ranch	4	M	66	2	3.0	2
		F	3	0	0	0
Gothic (combined data for two adjacent plots)	7	M	211	121	57.3	142
		F	72	22	31.9	23

* includes multiple recaptures

cedure did not cause excessive dispersal. An attempt was also made to release the butterflies at points scattered throughout the study area to facilitate free mixing with the rest of the population.

When the capture-recapture program was resumed in 1967, six localities were chosen on the basis of accessibility and apparent abundance of butterflies. In these localities 1222 butterflies were marked and released and an additional 1259 butterflies were captured and examined in peripheral areas. Examination of these data (Table 1) showed that (1) large plots surrounded by even larger expanses of ecologically suitable habitat gave exceedingly small recapture percentages, no matter how long they were sampled (Visquene Meadow, Bench Meadow, Wilson Ranch). (2) Large plots isolated or semi-isolated from other suitable areas gave higher recapture percentages, and the percentages improved with the length of the sampling period. (Cemetery, Naked Hills Peninsula). (3) Two small, adjacent plots, semi-isolated from other areas of suitable habitat and intensively sampled for relatively long periods of time (Gothic) gave satisfyingly high recapture percentages; furthermore, the positioning and size of these plots made it possible to calculate move-

ment of individual butterflies between them. However, when these data were further analyzed in order to get daily population size estimates, it was found that the estimates were highly erratic and not in keeping with field observations. In contrast to the erratic fluctuations in population size estimations from data from the small plots, those estimates made for the larger area (Cemetery), were considerably smoother and tallied more with field observations. The analytical method employed for these estimations was the stochastic model developed by Jolly (1965). The possibility that the difficulties in estimation, especially in the smaller plots, might be reduced by employing a different method of analysis was considered, although the advantages of stochastic models in general and Jolly's method in particular have been pointed out by Southwood (1966). Since the possibility existed that the Jolly method might not be entirely suitable for *E. epipsodea*, these results were compared with results derived from the deterministic models of Dowdeswell, Fisher, and Ford (1940) and Bailey (1951, 1952). In each case the estimates from these deterministic models were consistently 40% to 60% lower than the Jolly estimations. Indeed, on several days, the daily population size estimates based on Bailey's method were lower than that day's catch.

It was concluded, therefore, that the Jolly method was the most suitable analytical tool and that the size of the study plot assumed considerable significance in the estimation of population parameters. The 1968 sampling program, therefore, was designed to gather additional data amenable to analysis by this method.

It had been established during the 1967 season that one worker could usually capture all the *E. epipsodea* flying in an area of approximately 1 hectare (2.5 acres) in one hour. During peak flight season this was approximately 75 insects (Brussard and Ehrlich, 1970a). It was also found that one collector could not adequately cover areas too much larger than 1 ha during the time available for collecting and capture enough butterflies to ensure that recapture percentages were high enough for analysis. In order to utilize an area large enough to give reasonable population size estimates, we employed, in 1968, three field workers for the Cemetery area, trimming the area somewhat (from 7.6 ha to 5.5 ha) to ensure thorough coverage. Since direct evidence of movement of butterflies from site to site along with evidence of re-immigration would provide the main support for the type of population structure that has been advanced for *E. epipsodea* (Brussard and Ehrlich, 1970a), it was also necessary to establish smaller study plots that could be simultaneously covered by each field worker so that these types of data could be

accumulated. To this end, the Gothic area was expanded to include 3 contiguous plots of approximately 1 ha which were sampled simultaneously for 11 days. It was then possible to document thoroughly movement between areas and to estimate its magnitude. The 1968 results confirmed that dispersal and re-immigration did explain the difficulties encountered in obtaining the population size estimates in the small plots (Brussard and Ehrlich, 1970a).

The techniques developed here appear to be very useful in studies designed to establish density and population structures of diurnal Lepidoptera, especially those which appear to be more or less continuously distributed in their habitat, without ecological "barriers." The results of extensive studies such as these are a prerequisite for (and may largely determine the methods to be used in) intensive studies designed to delineate those factors that cause or regulate fluctuations in population size. Many more data pertinent to these phenomena are needed before the important controversy concerning density dependent or density independent population size regulation can be resolved.

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LEPIDOPTERA IN THE UNPUBLISHED FIELD NOTES OF HOWARD GEORGE LACEY, NATURALIST (1856–1929)[1]

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Howard George Lacey was born 15 April 1856 at Wareham, Dorset, England. His elementary education was received at Charterhouse, Hampshire; he studied at Frankfurt, Germany and later received a B.A. degree from Cains College, Cambridge. Although educated for the ministry, he soon gave up this career for that of naturalist. At the age of 26 he came to the United States, arriving in New York 17 June 1882, and proceeded to Kerrville, Texas where he arrived 30 June. Here he bought a ranch in the hill country about seven miles southwest of Kerrville on Turtle Creek (Figure 1) where he spent the next thirty-seven years raising livestock and studying the natural history of the area.

Lacey was a member of the Bournemouth Scientific Society, San Antonio Scientific Society, National Geographic Society, American Audubon Union, and American Ornithologists' Union. He collaborated with the Smithsonian Institution, U. S. Department of Agriculture, and other institutions for the advancement of natural science.

So far as can be determined, he published no scientific papers. Instead, he chose to collect biological specimens which were sent to various contemporary taxonomists and natural history museums. Many of his field collections and observations were recorded in a ledger which is the basis for this account. His ledger is now in the Witte Memorial Museum Library, San Antonio, Texas placed there by his sister Miss Beatrice Lacey.

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