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INTER-PEAK DISPERSAL IN ALPINE CHECKERSPOT BUTTERFLIES (NYMPHALIDAE)

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ABSTRACT. Inter-peak transfer was demonstrated for the first time in butterflies. Dispersal rates were lower for females than for males. Dispersal—as measured by velocity per day, distance moved between recaptures, and net range of individuals—was greater from more sparsely populated, less favorable areas.

In spite of field work during the past ten years (e.g., Scott, 1975; Brussard & Ehrlich, 1970; Gilbert & Singer, 1973; Watt et al., 1977; Watanabe, 1978) there remain many important questions about the vagility of butterflies in natural populations. Much of the work done involved very localized areas, small colonies of animals, or both. The remainder of the data involve larger areas, but suffer from various defects, especially inadequate coverage of the study area (e.g., Schrier et al., 1976).

In the former case local demographic units have been identified and dispersal within them has been characterized. A demographic or ecological population is a local concentration of individuals that may be counted in a demographic sense, and which is the essential unit of ecological impact in terms of resource utilization or carrying capacity. These units have independent dynamic behaviors. They may or may not be independent genetic units (demes). This assertion can rarely be made regarding migration between such colonies. This is unfortunate because the reproductively successful transfer of only a few individuals can, under some circumstances, meld two colonies into one Mendelian population (McKechnie et al., 1975; Ehrlich & White, 1980; Lewontin, 1974).

It is partly for logistical reasons that few studies of larger areas have been done. It is far more difficult to observe dispersal between than within demographic units. In studies of larger areas a few workers have shown that demographic units exchange significant numbers of individuals (Watanabe, 1978; Watt et al., 1977; Brussard & Ehrlich, 1970; Ehrlich & Gilbert, 1973). Thus the Mendelian populations defined by gene flow may contain several distinct demographic units.

Individuals of most species are far from uniformly distributed in space. This may be due to obviously discontinuous resource distributions or to less obvious factors. Whenever organisms occur in apparently discrete units, questions about inter-colony vagility arise. In the case of such a distribution the question of whether there are nu-

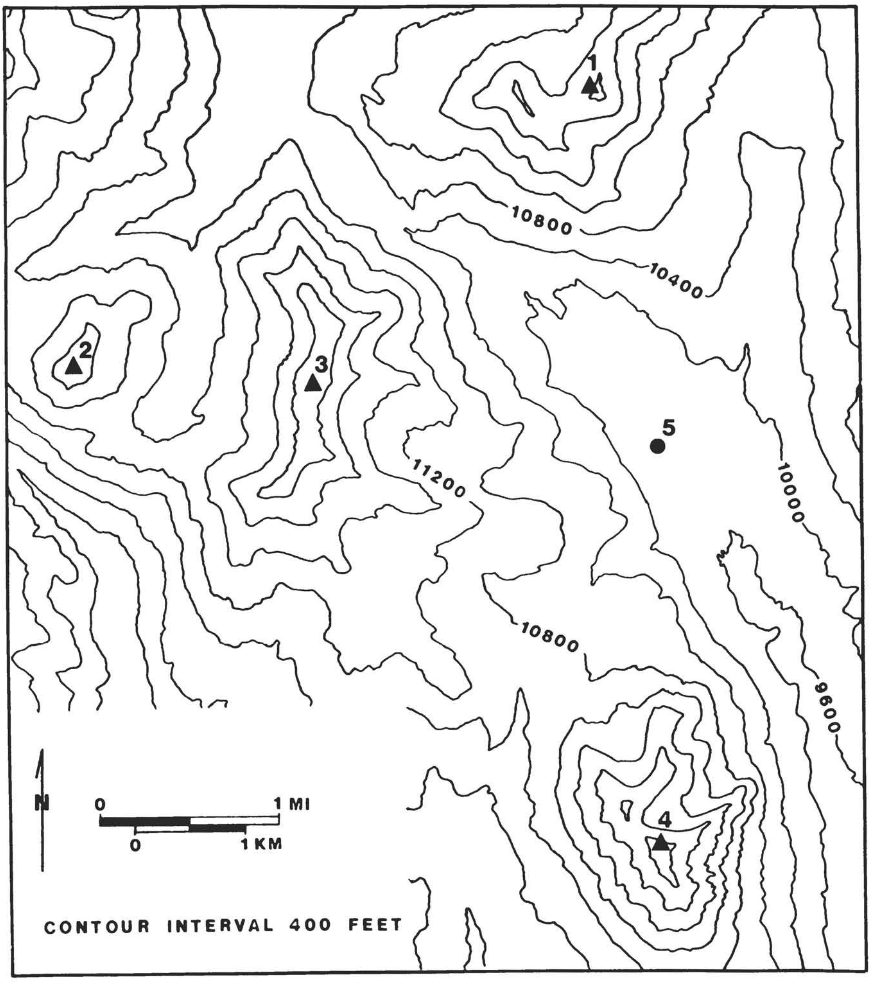

FIG. 1. Contour map of study area. **1**, Bellview; **2**, Cinnamon; **3**, Mt. Baldy; **4**, Gothic; **5**, release-point on road at 9700 ft, equidistant from the peaks of 1, 3, and 4.

merous, separately evolving populations or a single evolving species can be answered only with vagility (realized dispersal) data which allow assessment of the magnitude of gene flow (Ehrlich & Raven, 1969).

MATERIALS AND METHODS

To determine the structure of high altitude checkerspot butterfly populations four colonies of *Euphydras anicia* (Doubleday) were selected for study. *E. anicia* is found throughout Colorado at both high and low elevations. Populations occurring in alpine zones are sometimes given the subspecific name *eurytion* (Mead), and seem to form a distinct group within the species (Brown et al., 1957; Howe, 1975). Alpine populations of the species occur from New Mexico northward to Wyoming and Montana.

The four colonies selected occupied the alpine zones of the following peaks (Fig. 1) in Gunnison Co., Colorado: Cinnamon Mt., 12,300 ft (3747 m); Mt. Baldy, 12,800 ft (3900 m); Bellview Mt., 12,500 ft (3808 m); and Gothic Mt., 12,600 ft (3840 m). Each of these peaks had a modest colony of *E. anicia*. Larval foodplants, *Besseya alpina* Rydberg (White, 1979), did not occur below 11,500 ft (3500 m), so each peak was separated from each other peak by habitat unfavorable to *E. anicia*. *Besseya alpina* is strictly an alpine plant (Harrington, 1954).

From 5 to 31 July 1978, a mark-release-recapture program was conducted. Each butterfly was given its own number in a magic marker code (Ehrlich & Davidson, 1960), with different colors used for marking on the separate peaks. Each peak was climbed in turn and as many butterflies as possible marked on each. The condition, sex, and capture site of each butterfly was recorded with its number. These data (Appendix) allowed the mapping of intra-peak movements, while the colors used in the marks signified the peak on which the butterfly had first been marked.

The time of ascent from base camp to *Euphydryas* habitat was about 2 h; descents took about 1 h. Four days were missed due to inclement weather and early descents from the peaks were forced four times by thunderstorms. Poor weather reduced flight on three additional days.

Population sizes were estimated from mark-release-recapture data by the Lincoln Index method using males only and then multiplying by two (Ehrlich et al., 1975). This provided estimates for all days except the first day that butterflies were marked on a given peak. It was assumed that the population changed at a constant (geometric) rate between marking days. Estimates of the numbers of individuals that flew at a given site over the course of the flight season were made by summing the numbers estimated for each calendar day and dividing by the estimated average residence time. The first and last days of the flight season were estimated from the number of butterflies handled on the first and last marking days. The average residence time was calculated as the reciprocal of one minus the probability of presence from one day to the next.

The probability of daily presence was assumed to be constant over the season and was estimated from recapture data as follows: on the third and each subsequent marking day it is possible to compare the rates of recapture of different classes of marks, that is, those marked on different days. The geometric mean of the resulting ratios was calculated, weighting each sample (comparison of one class to another) by approximately the harmonic mean of the numbers of butterflies recovered from each class.

RESULTS AND DISCUSSION

The sizes of these *Euphydryas* populations, while at least an order of magnitude smaller than that at Cumberland Pass (Cullenward et al., 1979), were larger than expected, based on the modest sizes of these alpine zones. The estimates given below are rough, based on mark-release-recapture data. In spite of relatively small areas of available habitat, population sizes were greater than a few hundred individuals per peak. During the season there were probably 3000–5000 butterflies on Gothic Mountain, 1600–3200 on Bellview, 500–1000 on Baldy, and 400–600 on Cinnamon. The total present on all four peaks on any one day might have been 2000–4000.

The flight seasons differed from one peak to another and were atypically long for *Euphydryas* (White, unpubl.; M. C. Singer, pers. comm.). The season on Bellview preceded the season on Gothic by a week to ten days. The lengths of the flight seasons were estimated as six weeks or more, based on numbers flying at the start and finish of the study. This concurs with previous estimates for *E. anicia* (Cullenward et al., 1979).

Residence times, estimated by the method described, were greater than residence time estimated by the method of Ehrlich (1961), as expected. Butterflies seemed to live about as long as most *Euphydryas* under field conditions (Gothic males—10.4 days, Bellview males—8.9 days). Ten butterflies were recaptured more than two weeks after marking.

Recaptures of 189 marked individuals (229 recapture events) indicated the following. First, there were differences between the sexes. Second, patterns of movement varied between topographic areas within single peaks. Third, the patterns varied among peaks. Fourth, some inter-peak dispersal occurred.

Dividing Bellview and Gothic into areas of high and low butterfly density, one observes the same kind of difference that Cullenward et al. (1979) found for *E. anicia* at Cumberland Pass (CL) in 1976. More densely populated areas possess larger proportions of females, more nectar, and more foodplants. They tended to be north-facing slopes (BV, CL) protected from weather (of other directional origins than north) by higher ridges and shoulders. Less densely populated areas tended to be ridges and peaks, sometimes above the more densely populated areas. Butterflies marked in the more favorable areas were

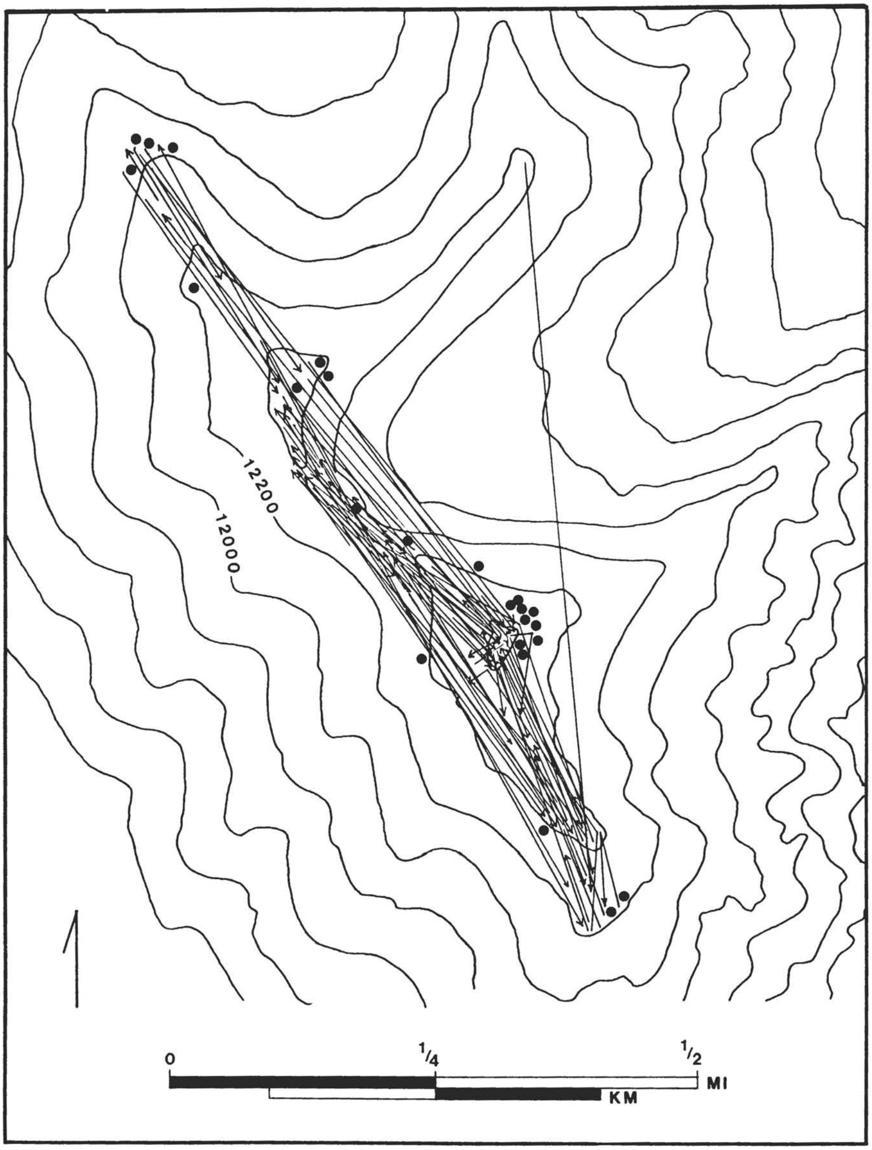

FIG. 2. Contour map of Gothic Mountain showing movements of *E. anicia* males. Each dot represents two recaptures in area of original capture.

more likely to be recaptured than those marked in the less favorable areas (Bellview males, 34/121 vs. 26/185, df = 1, G = 9.02, P < .005; Sokal & Rohlf, 1969).

Female *E. anicia* were recaptured in numbers only on Bellview in

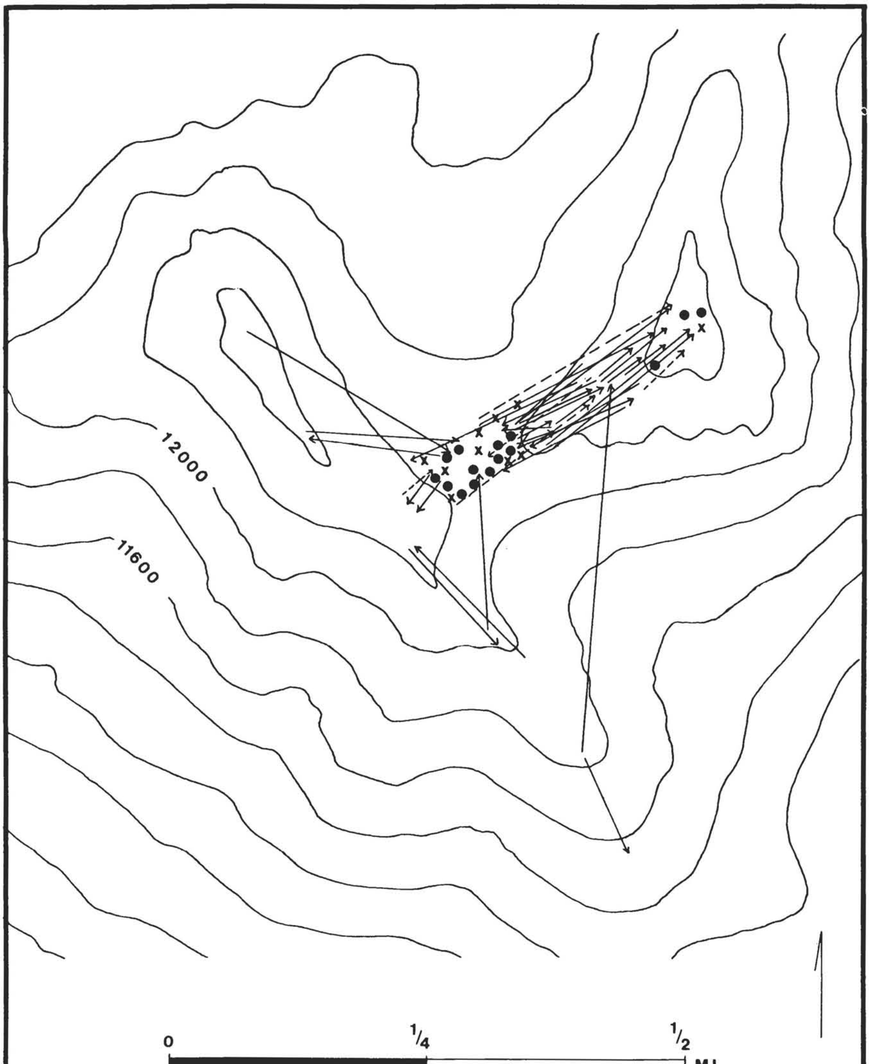

FIG. 3. Contour map of Bellview showing movements of *E. anicia*. Dots represent males and x's represent females recaptured at or near point of previous capture. Solid arrows represent male movements, dashed arrows represent female movements.

this study (Fig. 3). Average movement between recaptures was 18 ± 59 m ($\bar{x} \pm s$; n = 25), similar to that observed at Cumberland (18 ± 44 m, n = 32). Males on Bellview averaged 65 m between recaptures (n = 63, s = 109 m), comparable to the 75 m observed at Cumberland (n = 173, s = 129 m). This sexual difference has been found for all alpine *Euphydryas* populations studied (White, 1973).

Dispersal differences among peaks paralleled those found within peaks. Dispersal within Gothic appears to be more extensive than at Bellview. Gothic males moved 146 ± 222 m between recaptures (n = 109, s = 222 m), more than twice as far as those on Bellview (Fig. 2). Velocity per day (v_i of Scott, 1975) averaged 23 m for Gothic males and 8 m for Bellview males. In addition, the kurtoses (departures from a normal curve) of the data from the two sites differed (GM, n = 107, $g_2 = 5.61$, s.e. = 0.47; BV, n = 62, $g_2 = 7.11$, s.e. = .60; t = 1.94, df = 167, $.05 < P < .06$; Sokal & Rohlf, 1969; J. Matta, pers. comm.). The pattern of movement on Gothic was not as leptokurtotic as that on Bellview. Gothic Mountain, while divisible into more favorable and less favorable areas, had no area with the very high density of butterflies observed in the favorable areas of Bellview and Cumberland. Favorability of *Euphydryas anicia* habitat is defined as having both nectar and larval foodplants in densities such that a flight of a few meters would pass by examples of each. Mt. Baldy was less favorable than Gothic, and less densely populated.

Transfers from one peak to another were observed only from Baldy to Cinnamon (see below). Long distance dispersal, then, seems to arise from less densely populated, less favorable areas. It is unclear whether the different kinds of areas selectively favor different, genetically determined (intrinsic) dispersal behavior or whether the butterflies native to any area would respond similarly. If the latter case is correct, a corollary question is whether the butterflies respond to male density, female density, nectar availability, or to a combination of factors.

Whatever the cause of the observed movements within the peaks, it seems likely that the result is spatially extensive demes possessing large numbers of individuals. Dispersal increases the effective area of a deme and thus keeps the numbers of individuals within demes high, even as densities decrease. Such behavior would decrease the effects of genetic drift among areas within peaks, and increase the rate of colonization of new or empty habitats within peaks. Observed dispersal makes it clear that separate population units do not exist within peaks of the size studied. Each peak contains an essentially panmictic unit.

One displacement experiment was attempted. Fifty-seven males and 28 females were moved from Bellview down to a point on the road approximately equidistant from Bellview, Baldy, and Gothic. One female was recovered in her area of origin on Bellview 3 days after release. One male was recovered 300 m downslope from origin on Bellview 13 days after release and one male was recovered on Gothic Mountain 2 days after release. The low recovery rate may be due to the tired condition of the displaced animals and to inadequate subsequent coverage of these peaks. The recovered animals moved 3 km from an elevation of 2955 m to at least 3534 m. Such movements indicate the potential for dispersal that these butterflies possess.

Two *bona fide* transfers between peaks were observed. One male moved 2 km from the west end of Baldy to Cinnamon Mt.; another male moved 2.2 km from the east end of Baldy to Cinnamon Mt. Three percent of the butterflies marked on this sparsely populated area of Baldy are thus known to have transferred out. These transfers are notable in five respects. The elevation between the peaks dropped 300–450 m. The flora changed from alpine to alpine-meadow; there were no oviposition plants in the intervening areas. The transfers were against the prevailing winds. The peak of origin seemed relatively unfavorable as an *Euphydryas* habitat. This may indicate purposeful movement from one peak (demographic unit) to another at a rate between 0.1% and 10%, assuming the real rate is within an order of magnitude of that observed (2/229 recapture events). Assuming post-transfer reproductive success, such a rate would almost eliminate genetic drift as a force differentiating the demographic units. One would not expect significant differences in the frequencies of selectively neutral alleles among populations experiencing such transfer rates. So far no significant genetic differences have been found among these populations (C. E. Holdren, P. R. Ehrlich, unpubl.), so that in some respects all four peak colonies appear to be part of the same large deme.

CONCLUSIONS

The following conclusions are drawn from these data:

1. Transfer among separate peaks probably occurs at rates between .001 and 0.10, great enough to limit divergence of neutral allele frequencies by genetic drift, assuming that transfers are reproductively successful.
2. Demes of this species are large in area and fairly large in numbers of individuals; they may include several separate peaks.
3. Dispersal rates increase as the apparent favorability of the point of origin decreases.
4. Flight seasons are long and vary in timing from one peak to another.
5. Female *E. anicia* are more sedentary than males.

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APPENDIX
Mark-release-recapture data

	GM (males)	BV (males)	BV (females)	GM (males)[3]	CM (males)[4]
Number marked[1]	412	288	115	76	69
Number sampled	78	114	40	1	0
Number retaken[2]	85	51	25	20	8
Recapture events[2]	109	63	25	24	6
Average distance moved between recapture events (d)[5]	146 m	65 m	18 m	—	—
s	222 m	109 m	59 m	—	—
Net range of individuals (R)	169 m	67 m	18 m	—	—
s	232 m	111 m	59 m	—	—
Average time between recapture events (t_i)	5.7 days	6.7 days	6.2 days	—	—
Average time from first to last capture (T)	7.0 days	7.3 days	6.2 days	—	—
Average velocity per day (v)	22.6 m/day	8.0	3.0	—	—

[1] Omits last day at each site.
[2] Omits displaced butterflies (3 recaptured individuals, 3 events).
[3] Twelve females marked, 1 sampled, no recaptures.
[4] Nine females marked, none recaptured.
[5] d_i, R, t_i, T, and v refer to statistics of Scott (1975).