dence of approximately 1 percent in English (*13*) and Canadian (*14*) whites. The 8 percent incidence of phenotype $B_{0-1}C$ is the highest value yet reported for any of the faster-moving transferrin B types, although its incidence is somewhat lower than the average value of 10 percent for type CD_1 in Negro populations and the high of 15.6 percent CD_1 reported for a large population in the New Guinea highlands (*15*).

No factors are known which could maintain the transferrin polymorphism (*16*), although some of the variants may be important for resistance to infectious disease. In this connection it may be possible to relate the wide prevalence of tuberculosis and streptococcal infections in Navajo populations (*17*) to the work of Martin and Jandl on the inhibition by transferrin of viral multiplication and cytopathogenic effects (*18*). If the frequencies of the unusual genes are stable, the similar incidence of $B_{0-1}C$ in Navajos and of CD_1 in Negroes suggests that selective factors of approximately equivalent intensity may be operating in the two populations. The development of a method for the separation and isolation of rare transferrins from the serum of heterozygotes (*19*) has permitted experiments to be undertaken to investigate the nature of the chemical differences among the various transferrin types (*20*).

Note added in proof. Since the submission of this report, we have identified in a Chinese population a transferrin variant of slightly greater electrophoretic mobility than the Negro D_1. The conditions required to demonstrate this difference suggest that the Chinese variant will prove slower-moving than the D_1 of Harris *et al.* (*5*).

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Intrinsic Barriers to Dispersal in Checkerspot Butterfly

Abstract. Capture-recapture studies revealed that the checkerspot butterfly *Euphydryas editha* is extraordinarily sedentary. Since no physical barriers prevent interchange between various portions of the study colony, it is concluded that intrinsic factors play the major role in limiting movement. The few available data on dispersal are discussed.

It is generally accepted (*1*) that most flying organisms display a high degree of vagility, the ability to cross barriers. Nevertheless, as Mayr (*2*) has pointed out, birds are usually quite sedentary and make little use of their dispersal potential. Similarly, the few butterflies which have been studied with any degree of rigor—*Maniola jurtina* L. (*3*), *Polyommatus icarus* Rott. (*4*), *Papilio glaucus* L. (*5*), *Anthocaris sara* Boisduval (*6*), and *Pieris protodice* Boisduval and Leconte (*7*)—have shown a remarkable lack of wanderlust. The present report on *Euphydryas editha* Boisduval (Nymphalidae: Nymphalinae) further underscores the importance of differentiating *potential* and *actual* vagility and emphasizes the dangers of casual assumptions about dispersal patterns, "gene flow," and the like.

In the San Francisco Bay region, *Euphydryas editha* is confined to areas of serpentine outcropping, where its food plant, *Plantago erecta* Morris, is especially abundant. In the spring of 1960 a capture-recapture study was made of the adult population of this butterfly on Stanford University's Jasper Ridge Biological Experimental Area, as part of a long-term investigation of microevolution in this species. There *E. editha* is found only in a hilltop island of grassland, surrounded by dense chaparral and scattered oak woodlands. During the 25-day flight period (31 March to 24 April) 185 individuals were given distinguishing marks and released (*8*). Of these individuals 97 were recaptured at least once, accounting for a total of 224 recaptures. The population size (total number of individuals involved in the flight) was estimated to be between 250 and 400. Sampling was done once a day, so that all recaptures of any given individual were on different days.

Prior to the flight period the region occupied by the colony was arbitrarily divided into eight areas (A to H), and during the flight period a careful record was made of the areas in which the individuals were captured and recaptured. Centers of abundance were found in three areas (C, G, H). Only 12 captures and recaptures were made in areas peripheral to C (A, B, D, E, F), and for analysis areas A to F were lumped as area C. The distribution of individuals taken is shown on the map (Fig. 1). Each dot represents the *first* capture of an individual; placement of the dots within each of the eight areas is approximate. This pattern of distribution, although representing only part of the data, agrees with the impressions of the total distributional picture formed in the field by the investigator and his assistant.

Of the 97 individuals which were marked and subsequently recaptured at least once, only eight were found to have changed areas during the study, and each of these changed areas only once. Therefore 216 of the 224 (96.4 percent) recaptures were in the area of previous capture.

For reasons which will be dealt with in a future paper, the frequency of recaptures varied from area to area. Scoring only those individuals which were recaptured at least once, and ignoring the eight which changed areas, the mean number of recaptures $\pm$ standard error (N) per individual were: area C, 1.79 ± 0.210 (34); area G, 2.96 ± 0.523 (24); and area H, 2.52 ± 0.350 (31). The five individuals with the highest number of recaptures in each area had the following scores: area C, 6, 5, 4, 3, 3; area G, 10, 8, 7, 6, 5; and area H, 9, 7, 5, 5, 4. However, if one looks not at the number of times an individual was recaptured but at the number of days it spent "in residence," a different picture emerges. Assuming that no individuals changed areas and then changed back without being detected (a reasonably safe assumption, as this was never observed), one can record the number of days elapsed between initial release and final recapture as the observed number of days in residence. Considering only the individuals recaptured at least once, and again ignoring the eight which changed areas, the average male in area C was known to have been in residence 5.81 days, in area G, 6.33 days, and in area H, 5.61 days. The equivalent figures for females were C, 4.43 days, G, 3.38 days, and H, 3.38 days. An analysis of variance showed a significant effect of sex ($F = 5.78$, $P < .025$) and no sign whatever of an area effect ($F = .19$) or of a sex-area interaction ($F = .12$).

Close scrutiny of the records of the eight individuals that switched areas revealed little of importance. Four were males and four females. Four individuals moved northwest along the main axis of the colony, four moved southeast. Five had wing lengths above the mean for their sex, and three below (no significant difference). Six showed a deterioration in condition between their last capture in their original area and their first recapture in the new area. Two were scored as "fresh" both before and after moving. It would be interesting to know what proportion of dispersing individuals have completed most or all of their reproductive activities before leaving their original area.

It is evident that on Jasper Ridge in 1960 most individuals of *Euphydryas editha*, as long as they remained within the colony, restricted their activities to a very limited area. This lack of movement is shown by the repeated recapture of many individuals in the same location (nearly all of the 71 area G recaptures were made within a space 100 ft in diameter), and by the extreme infrequency of recaptures in areas other than that of original release. No insurmountable physical barriers separate the various sections of the colony. The butterflies were observed on several occasions to fly over the chaparral when chased. As can be seen from the map, in no place does a continuous growth of chaparral or woodland totally separate sections of the colony. In addition, the locations of the main concentrations of individuals remained static, although in areas C and H open space in which the food plant was common was available immediately adjacent to the concentrations. Cursory study of the vegetation and exposure of the areas has not produced a satisfactory explanation of this phenomenon, and further investigations are being made. While it is not known what factors control the spatial distribution of the individuals, it seems that the butterflies "choose" to remain within a circumscribed area—in other words the barriers to dispersal are *intrinsic*.

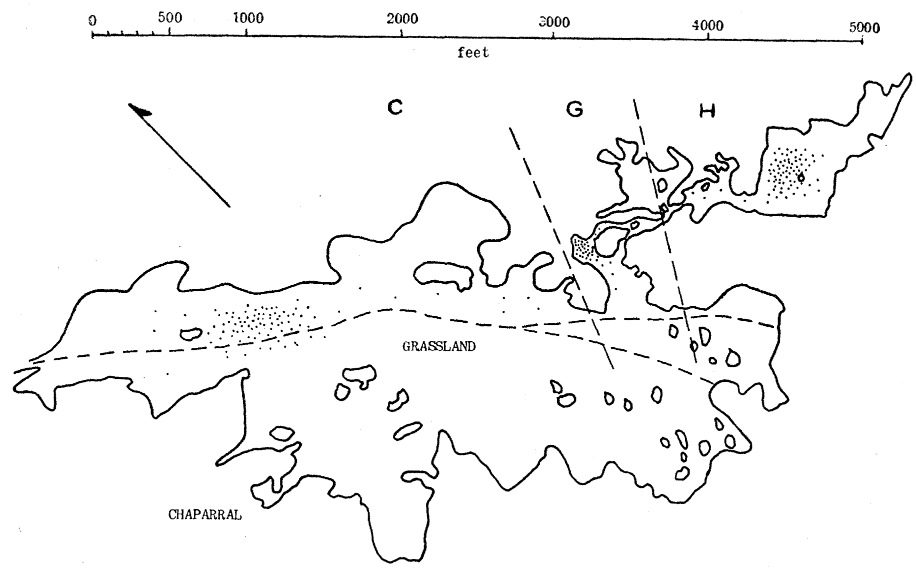

Fig. 1. Distribution of *Euphydryas editha* in Jasper Ridge area, 1960. Each dot represents a single capture. Recaptures are not shown.

Perhaps the most intriguing question raised by the investigation is that of the fate of the 88 individuals which were marked and released but never recaptured. It seems unlikely that the handling procedure affected them (a great many individuals went through the routine repeatedly without any detectable damage). An examination was made of the distribution of recapture frequencies of the first 96 specimens released; these were selected because there was an opportunity to recapture them on a minimum of eight subsequent field days. This showed a disproportionately large 0 class, due to excesses in areas C and H (only 2 of 20 individuals of this group released in G were not recaptured). This difference between the subareas might suggest that individuals are likely to be blown out of the larger, more exposed areas, and thus be lost. However, the general lack of interarea exchange and observations of the butterfly's behavior militate against the idea that the wind would have such a major effect. It is also difficult to hypothesize a mortality factor which could produce this distribution of recaptures. Perhaps there is a heterogeneity of dispersal behavior among individuals within the areas, and differences in the proportions of sedentary and dispersal-prone individuals among areas. Such heterogeneity has been suggested by dispersal data gathered for various groups of Diptera (*9*), and this type of polymorphism could have a distinct selective advantage in a species such as *E. editha* which occurs in rather limited, scattered colonies (*10*).

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