lina are chalky white (not slightly greenish as *C. angulifera*) affording protective coloration on the equally chalky white undersides of sweet-bay leaves. The larvae tended to be gregarious, especially in the early instars, but this pattern largely disappears in later instars. Few larvae survived under unsleaved conditions with both avian and hymenopterous predators being responsible for losses to larvae reared in the open. Approximately 60 percent of cocoons collected in the field had fallen prey to parasitic wasps.

Since the breeding behavior of *C. carolina* is so strongly diurnal, reproductive isolation from *C. angulifera*, which is totally nocturnal, would seem to be complete under natural conditions (*7*). It also does not appear to overlap the late afternoon breeding pattern of *C. promethea* to any great extent. Where these species overlap in their ranges, the difference in circadian activity no doubt serves as an effective isolating mechanism in otherwise reproductively compatible forms.

It is unclear whether *C. carolina* might be more closely related to *C. promethea* than *C. angulifera* as previously supposed, especially when one considers that the first two species are diurnal and exhibit an identical type of cocoon structure, dissimilar to that of *C. angulifera*. In general, insects with "complete" metamorphosis, such as moths, can be regarded as two organisms in one from the point of view of evolution. Natural selection for certain characteristics may occur in larval stages independently of differences or similarities in imagoes.

Also of great theoretical interest to moth speciation would be experiments crossing the three species of *Callosamia*. Interspecies matings in the genus are readily accomplished by hand-pairing methods (*8*) or by manipulation of the photoperiod. If the time of mating activity is genetically fixed, then when during the 24-hour cycle would hybrids of *C. carolina* and *C. angulifera* mate, or hybrids of *C. carolina* and *C. promethea*? Considerable genetic information of evolutionary significance might be obtained by a study of the behavioral patterns of these hybrid crosses of species in the genus *Callosamia*.

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3. F. M. Jones, *Entomol. News* **20**, 49 (1909).
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5. High densities of *C. carolina* were encountered only in the bigger bay swamps, such as the vast Parker's Island bayhead located 10 miles southeast of Lake Placid, Highlands County, Florida. The species occurred sparingly in many small bayheads and could not be found at all in some.
6. M. M. Collins and R. D. Weast, *Wild Silk Moths of the United States* (Collins, Cedar Rapids, Iowa, 1961).
7. Collins and Weast (*6*) found that *C. angulifera* breeds between 7:30 p.m. and midnight, and that *C. promethea* breeds in late afternoon, generally from about 4 p.m. until dusk.
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24 September 1971; revised 12 January 1972 ■

Complex Components of Habitat Suitability within a Butterfly Colony

Abstract. *The microdistribution of adult* Euphydryas editha *changes from year to year, and the colony is subdivided into three populations that fluctuate independently in size. These observations are attributed largely to fluctuations in time and space of three complex larval resources associated with the availability of food. This complexity also entails selection pressure favoring the observed low dispersal tendency of adults.*

A long-term study of the colony of the nymphaline butterfly *Euphydryas editha* Bvd. at Jasper Ridge (San Mateo County, California) combined measurement of poulation structure and gene flow (*1*) with phenetic (*2*), genetic, and behavioral (*3*) studies. It was found that (i) The colony comprises three populations, termed C, G, and H; (ii) these populations fluctuate in size independently of each other; (iii) the distribution of adult insects is variable from year to year; and (iv) the insects do not occupy all the available habitat, as defined in terms of their known resources.

Detailed ecological investigation described here reveals selection pressures that act to restrict gene flow, provides explanations for observations ii and iii above, and redefines larval resources so that observation (iv) no longer applies.

At Jasper Ridge, *E. editha* is a univoltine insect with a flight season usually extending from about 18 March to 22 April. The eggs are laid in masses of 20 to 350 at or close to the base of a food plant, *Plantago erecta* Morris (Plantaginacae). They hatch after 13 to 15 days. The young larvae feed for about 3 weeks and then enter a summer diapause which is broken in late December or January.

In 1968, the fates of 30 masses of eggs laid throughout the flight season were followed. In 23 of these, the *P. erecta* plants underwent senescence between the time of oviposition and hatching of the eggs, and the first instar larvae starved. No larvae from these egg masses were observed to reach the middle of third instar, the earliest stage at which larvae are capable of entering diapause if deprived of food. It was predicted that the microhabitat patches in which senescence of *P. erecta* occurred latest would be the areas of highest postdiapause larval density in January 1969. This prediction was not fulfilled (*4*).

In April and May 1969, a detailed study of population H showed that mortality of newly hatched larvae was about 80 percent. The remaining larvae could survive in three sets of circumstances.

1) The eggs are laid very early in the flight season, on *Plantago erecta* that will remain green for a further 5 weeks.

2) Eggs are laid on, or larvae are able to locate, *P. erecta* plants that have grown much larger than their fellows and that remain green for longer into the dry season, as a result of local soil tilling by gophers (*Thomomys bottae*) during the preceding winter.

3) Larvae are able to locate flowers of the hemiparasitic annual plant *Orthocarpus densiflorus* Benth. (Scrophulariaceae), on which they feed.

In each population, the degree of type 1 survival depends on the relative timing of the flight season of *E. editha* and the senescence of most of the *P. erecta* plants. This phase relation is most favorable on slopes facing north, and its variation from year to year depends in complex fashion on climatic factors (*4*).

Type 2 survival depends on the extent, timing, and spatial pattern of gopher activity, which is variable from year to year. Of those *P. erecta* plants that remain green for the longest as a result of gopher activity, more than 50 percent are eaten by the gophers themselves during the period when *E. editha* larvae are feeding on them. This evidently lessens the contribution of the "gopher effect" to the survival of prediapause *E. editha* larvae.

Survival of type 3 also varies from year to year depending upon the density and senescence time of *O. densiflorus*. If the senescence time of this plant is dependent on climatic factors, then these are not the same factors that determine the senescence time of *P. erecta*.

In 1969 an attempt was made to quantify the relative importance of these three resources to *E. editha* larvae in population H of Jasper Ridge. The distributions of *O. densiflorus* and of the "gopher effect," and the pattern of senescence of *P. erecta* unaffected by gophers, were plotted and compared with the spatial pattern of survival of larvae derived from an estimated (*5*) distribution of egg masses (Fig. 1a) and the measured distribution of postdiapause larvae in early 1970 (Fig. 1b).

A comparison of the contour map (Fig. 2) with Fig. 1, a, b, and d, shows that, in the drier parts of area H near the top of the hill (squares A, 1–3; B, 1–3; C, 2 and 3), the pattern of survival of prediapause larvae coincided almost exactly with the distribution of *O. densiflorus* (Fig. 1d). However, on the slope facing northeast (square D1) a few larvae evidently survived on *P. erecta* alone.

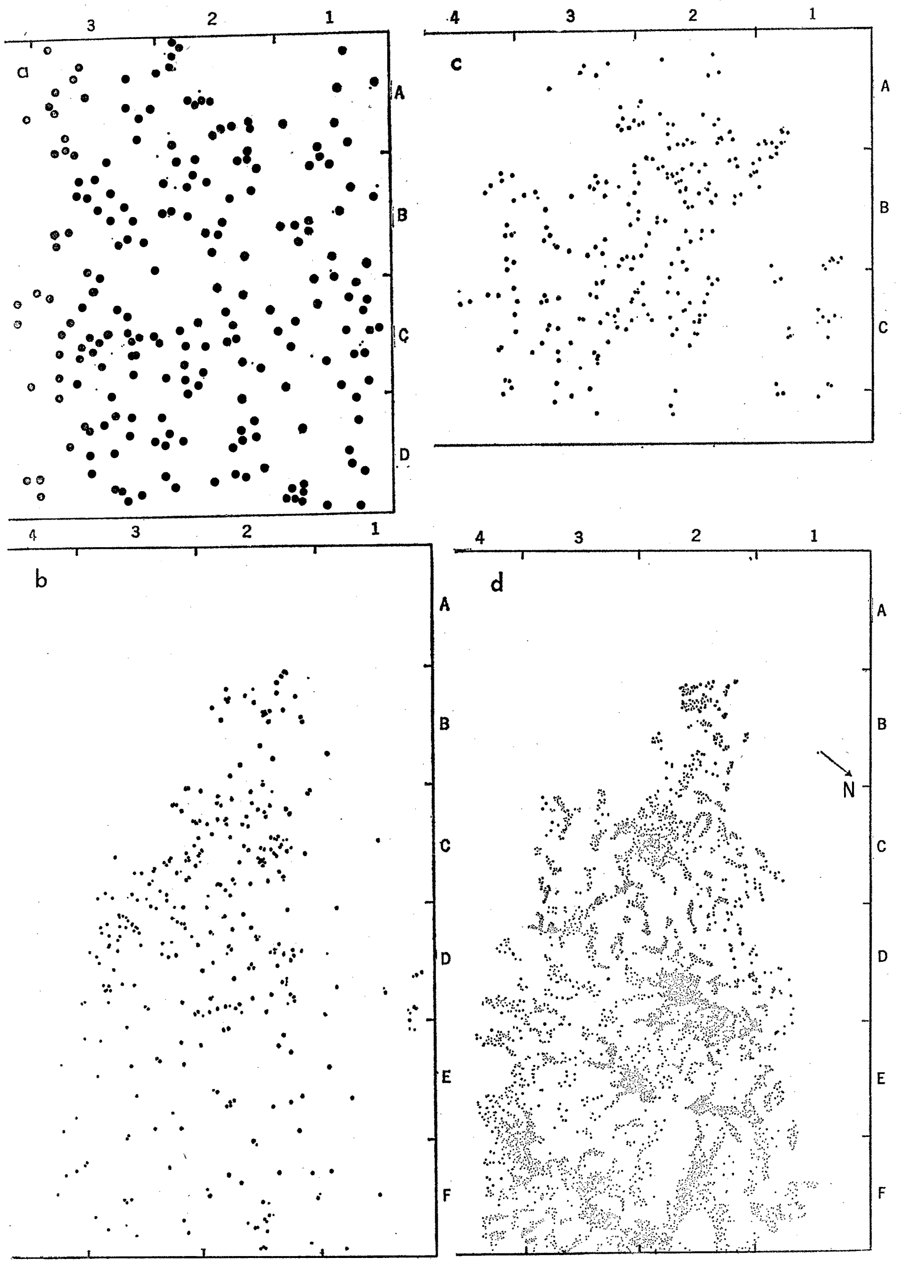

Fig. 1. Microdistributions of (a) *E. editha* egg masses (*5*), (b) postdiapause larvae in February 1970, (c) postdiapause larvae in February 1968, and (d) *Orthocarpus densiflorus* in April 1969 within the study area grid for population H at Jasper Ridge.

The spatial patterns of gopher activity and senescence of *P. erecta* were not correlated with the pattern of survival of larvae (*4*).

It appears that the secondary food plant, *O. densiflorus*, was extremely important for the survival of prediapause *E. editha* larvae in 1969. This hypothesis is further supported by the similarity between the distributions of postdiapause larvae in 1969, 1970, and 1971, since the distributions of *O. densiflorus* in 1968 and 1970 were almost identical to that in 1969. In 1967 the importance of *O. densiflorus* to *E. editha* larvae was not known, and its distribution was not observed. It seems probable, however, that this distribution was broadly similar to those seen in subsequent years. However, the map of distribution of postdiapause larvae in 1968 (Fig. 1c) shows that many had survived in the drier parts of area H, outside the region of presumed distribution of *O. densiflorus*. One might predict that such survival would be greatest in years when heavy rainfall occurred at the time when *P. erecta* in squares A, 1–4 and B, 2–4 would normally have commenced senescence, that is, in late March and April. This prediction fits the observed case, in that 1967 rainfall was 22.6 cm in March and 17.3 cm in April. The means for rainfall in these months are 9.8 and 5.3 cm respectively. In this case, then, unusual climatic conditions in the spring of 1967 appear to have influenced the spatial distribution of postdiapause larvae in 1968. Since postdiapause larvae in the driest parts of area H (squares A, 1–4; B, 1–4) grow faster than those in more north-facing areas, these larvae become adults sooner. Thus the heavy rainfall in the spring of 1967, besides affecting the phase relation between the *E. editha* flight season and food plant senescence in 1967, also influenced the phase relation in 1968 through its effect on the distribution of postdiapause larvae.

The foregoing discussion epitomizes the difficulty of formulating any model that might predict changes in population size for Jasper Ridge *E. editha* or correlate these changes with environmental variables. However, some qualitative deductions can be made, and are relevant to the questions raised by Ehrlich (*1*). It remains true that changes in population size in areas C, G, and H are not correlated (*6*). It was initially suggested that these populations may undergo predator-prey cycles out of phase with each other, since three species of insect parasitoids are present (*1*). However, the observed rate of such predation has been too low to make this explanation valid for the years 1968 to 1971. Furthermore, although mortality caused by parasites is not evident until the pupal or late prepupal stage, changes in adult density have been correlated with changes in the preceding densities of postdiapause larvae (*4*), a result that indicates that the mortality factors responsible for changes in population size have been acting before or during diapause. Since comparison of pre- and postdiapause densities indicates that diapause mortality has been low, it seems that changes in population size from year to year at Jasper Ridge have been determined by differences in mortality of prediapause larvae. If this is true, then the lack of correlation between such changes in populations C, G, and H can be explained in terms of ecological differences between them, some of which will now be summarized.

The importance of *O. densiflorus* for larval survival in area H has already been described. On the other hand, the "gopher effect" is more prominent in area C than in area H, and the distributions of both gophers and *O. densiflorus* are variable. This has resulted in considerable differences between postdiapause larval distributions in 1969, 1970, and 1971. By analogy with the study of area H, it may be assumed that these changes represent spatial differences in larval survival from year to year. This phenomenon may explain Ehrlich's observation (*1*) that the distribution of *E. editha* adults varies within population C.

Area G resembles area H in that it faces northeast, thereby ensuring survival of larvae in most years without the assistance of either gophers or *O. densiflorus*. The "gopher effect" was prominent in 1968 and 1970 but absent in 1969 and 1971. *O. densiflorus* has varied greatly in abundance; five plants were counted in 1970, and 203 in 1971. Thus area G resembles a small section of area C in the predictability of these resources. Since *E. editha* appears to undergo frequent extinction in such small sections of area C, it is no surprise that extinction of population G occurred in 1963, followed by recolonization in 1966 (*1*). A further important factor may be the high tendency for emigration of adult *E. editha* from area G in certain years.

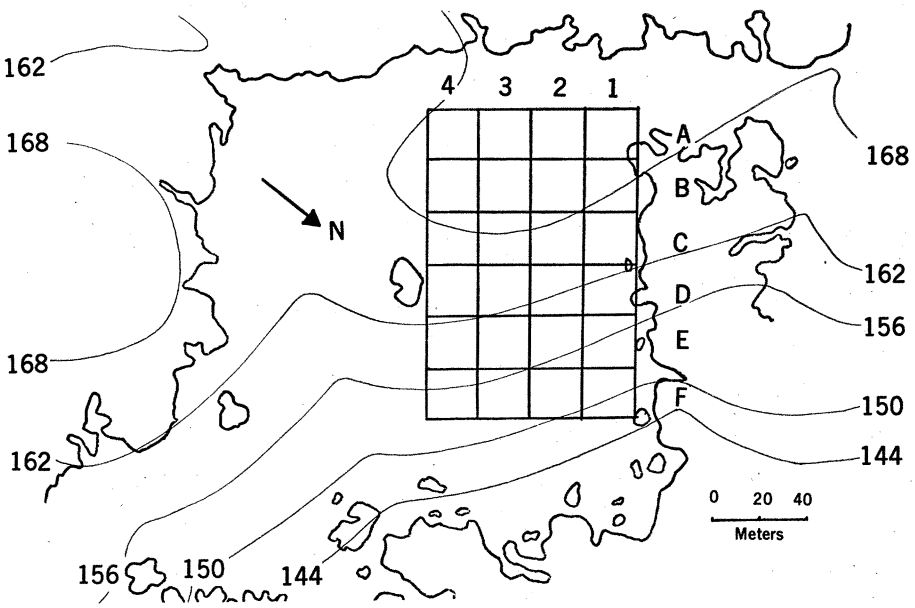

Fig. 2. Contour map of the area of Jasper Ridge inhabited by population H, showing altitude in meters, boundary of grassland and chaparral (solid line), and position of study area grid in the grassland.

The conclusions of this work are as follows:

1) Independent fluctuations in size of the three *E. editha* populations at Jasper Ridge are attributed largely to their differential dependence on three fluctuating larval resources.

2) Changes in microdistribution from year to year probably reflect changes in the spatial pattern of survival of prediapause larvae.

3) The adult insects do indeed occupy all the area available to them, that is, the area where larval and adult resources overlap.

4) The observed low dispersal rate of adult insects, which results in the subdivision of the Jasper Ridge colony into three populations, is brought about by a complex set of factors. One important selection pressure stems from the complexity of larval resource requirements and the consequent inability of ovipositing adults to respond to them appropriately. Specifically, oviposition sites are chosen with respect to one species of food plant only, while most larvae require a site where two species of food plants are intermingled. Since the correlation between the distributions of these two plant species is higher on Jasper Ridge than in the San Francisco Bay region as a whole, female *E. editha* that disperse stand a reduced chance of locating a suitable habitat for larvae (*7*).

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5. In many *E. editha* populations egg masses are conspicuous, and their distributions can be readily plotted. At Jasper Ridge, however, this is not practicable. The estimated distribution was obtained from observation of the flight behavior of oviposition matinated females and of criteria used in selection of an oviposition site. The pattern of alighting was simulated by the use of random numbers as coordinates on the grid, and each point selected was examined for its suitability as an oviposition site. In addition, egg masses and small larvae have been found in squares A, 1–4, where postdiapause larvae do not occur in most years.
6. P. F. Brussard, P. R. Ehrlich, M. C. Singer, unpublished manuscript.
7. In some *E. editha* populations, larval resources are less complex and less cryptic to the adults than those described here. Insects in such populations differ greatly in their dispersal characteristics from the Jasper Ridge individuals.

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