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ECOLOGICAL STUDIES ON THE BUTTERFLY *EUPHYDRYAS EDITHA*

A DISSERTATION

SUBMITTED TO THE DEPARTMENT OF BIOLOGY

AND THE COMMITTEE ON GRADUATE STUDIES

OF STANFORD UNIVERSITY

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

By

Michael Christopher Singer

May 1971

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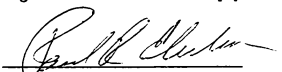

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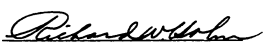

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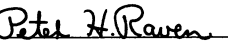

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INTRODUCTION

A long-term study of the Jasper Ridge colony of the butterfly Euphydryas editha Bdv. has combined measurement of population structure and gene flow (Ehrlich 1965) with phenetic (Ehrlich & Mason 1966, Mason, Ehrlich & Emmel 1968), genetic (McReynolds unpubl.) and behavioral (Labine 1966, 1968) studies. It was found that:

(1) The colony comprises three populations, termed C, G and H.

(2) These populations fluctuate in size independently of each other.

(3) The distribution of adult insects is variable from year to year.

(4) The insects do not occupy all the available habitat defined in terms of their known resources.

The detailed ecological investigation of population H described in Chapter One of this dissertation reveals selection pressures acting to restrict gene flow in addition to those given by Labine (1966), provides explanations for observations (2) and (3) above, and redefines larval resources such that observation (4) no longer applies.

The hypotheses generated by such a study can be tested in three ways, since the importance of a particular environmental parameter may be estimated by:

(1) Long-term observation and measurement (e.g. attempts to correlate population size changes with climatic factors).

(2) Experimental manipulations.

(3) Comparisons between populations differing with respect to the parameter concerned.

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In this last respect, the work described in Chapter One has been useful as a guide in the selection of ecological parameters for a broad comparison of populations of E. editha living in many different types of community in western North America. This work, of which Chapter Two forms a part, is being carried out in collaboration with L.E. Gilbert and R.R. White. It stresses interpopulation differences in the relationships between E. editha and other organisms, and aims at the identification of factors which can be used to predict the nature of these differences.

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CHAPTER ONE

ECOLOGY OF THE JASPER RIDGE COLONY OF THE BUTTERFLY EUPHYDRYAS EDITHA

I. Life Cycle.

The flight season of E. editha on Jasper Ridge usually extends from approximately March 18 to April 22, with most females emerging during the last week of March and the first week of April. Labine (1968) has shown that maximum oviposition occurs during the first few days of adult life, i.e., during the first week of April in an average year at Jasper Ridge.

The eggs are laid in masses of 20-350 at or close to the base of one of the food-plants, Plantago erecta Morris. Egg-masses observed in both 1969 and 1970 (n = 62) hatched in 13-14 days in the field. Several hours after all the larvae have hatched, they spin a silk tent around the base of the plant and commence feeding in small groups. Cooperation between larvae in breaking the epidermis of the plant is essential for survival at this stage. The larger the number of larvae, the higher the probability that an individual searching for food will find freshly cut plant tissue, and the higher the feeding efficiency of the group as a whole. Isolated newly-hatched larvae die if offered only mature P. erecta plants, but can survive on P. erecta seedlings or Collinsia heterophylla flowers.

In populations of E. editha in which eggs are laid on unopened Collinsia inflorescences, and the young larvae eat the flowers, egg-mass sizes are characteristically smaller than those in Plantago-

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feeding populations (Table I). This is evidence of the importance of the gregarious habit in allowing very small larvae to survive on tough, mature leaves. Any alternative to this strategy would involve either a flight season timed such that young larvae can eat seedlings, or larger egg size with reduced fecundity.

It is very rare that the plant on which an egg-mass is laid suffices to maintain the resulting larvae to diapause. At some stage, usually during the second instar, the aggregation of larvae disintegrates as individuals undertake a solitary search for food. A similar case has been described by Dethier (1959a) in Melitaea harrisii, an aster-feeding nymphaline butterfly in which heavy mortality occurred during the search for food as larvae dispersed from the plant on which the egg-mass had been placed. Some populations of E. editha - for example population SM (Fig. 11) where P. erecta is sparsely distributed - may correspond exactly to the description given by Dethier, but at Jasper Ridge the situation is rendered more complex by the presence of an alternative food-plant, Orthocarpus densiflorus Benth. (Scrophulariaceae) and by the fact that both of the annual food-plants are undergoing senescence and becoming inedible to the larvae. The interactions of factors influencing survival of prediapause larvae at this stage are discussed in detail in Section 2 of this chapter.

First, second and early third instar larvae respond to senescence of the food-plant by searching until they find edible food or starve. Their random pattern of search corresponds to that described by Dethier for M. harrisii larvae. Those which have reached mid- or late third instar, however, respond to lack of food by searching

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for a diapause site under a small rock or in a tuft of perennial grass, and molting into fourth instar. If food supply does not become limiting, the larvae simply grow larger before entering fourth instar. This molt is unusual in two ways; the head capsule does not increase in size and there is a change of phenotype. The "diapause phenotype" has shorter primary spines and longer secondary spines than the preceding and succeeding instars. This renders the larvae extremely water-repellant and resistant to attack by small Apanteles species. It may also be important in reducing the risk of predation by other invertebrates such as Arachnids. In the Woodside population of E. editha many diapausing larvae have been found sharing crevices with a variety of spiders and other potential predators. Repeated checking of one such site containing 22 larvae showed loss of two larvae in a three-month period; it is probable that these two individuals had merely moved elsewhere in response to being disturbed.

Since third instar larvae may molt and enter diapause at different sizes, there is variability in the weights of diapausing larvae (Table II). The weight at diapause is correlated with the number of subsequent instars, such that most male larvae at Jasper Ridge pass through a total of six instars, whilst females undergo seven. If, however, the quality of prediapause food is good, both sexes may mature in six instars; if poor, both may require seven or more. Thus, the weight of a larva at the third molt, while related to the quality and quantity of available food, is not correlated with the eventual weight of the adult.

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During diapause, larvae are exposed to extremely high temperatures. On a day in early May when the highest ambient air temperature was 76°F, the temperature at a typical diapause site at Woodside reached a maximum of 116°F. Ambient air temperatures of 95-100°F occur each year at some point during the diapause period of E. editha. In contrast, winter brings some risk of flooding before diapause is broken in late December or January. If a diapause site should become unsuitable, larvae are able to undertake a search for a new site at any time during diapause.

After diapause, Jasper Ridge E. editha larvae feed on seedlings of P. erecta. If the quality of the food-plant is poor, larvae may enter a second diapause in fifth or sixth instar, re-assuming the diapause phenotype. This habit is also seen in close relatives of E. editha such as E.chalcedona and Chlosyne leanira (S.O. Mattoon, pers. comm.). It may be a safeguard against years of unusually low rainfall in which the total length of time for which the food-plant is edible is not long enough to allow E. editha to complete its life cycle. Though rare at Jasper Ridge, such years may be quite frequent in the Southern semi-desert parts of the range of E. editha.

While prediapause larvae are adapted to feeding on rather dry, mature leaves in high ambient temperatures, the post-diapause insects feed on young plants under a much colder temperature regime. Profound physiological differences correlated with adaptation to temperature conditions are suggested by the following observations:

(1) Prediapause larvae grow well under laboratory conditions in temperatures of 80°F and over. At 65°F or below they feed

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very little and become disease-prone.

(2) Early post-diapause larvae kept at 80°F re-enter diapause. They feed most rapidly at around 55°-60°F.

These observations were made under low light intensity, since larvae are much blacker in color after diapause, and bask in strong light, thereby increasing the body temperature considerably above ambient levels. In the field, larvae are able to feed on dull days at ambient temperatures of about 45°F and over, and on sunny days at even lower temperatures.

In the low temperatures prevailing at Jasper Ridge in January and February, larvae spend much of their time basking. Those preparing to molt spin a silk platform and assume a semipermanent basking attitude, exposed to the sun. The act of molting itself appears to require high body temperature, and is often delayed for a week or more in dull weather. In many other populations of E. editha, larvae have the reverse problem of heat stress. Those preparing to molt select positions never exposed to full sunlight, and active larvae avoid heat stress by burrowing between rocks or hiding in pine cones (population IF) or by the completely different method of climbing tall grasses or other vegetation (population MC - S.O. Mattoon, pers. comm. - and population DP).

The prepupa spins a silk tent on the ground, usually encompassing several small plants. Within this tent, the larva suspends itself, often just touching the ground. The duration of the pupal state in the field is about 14 days, depending on the prevailing temperature.

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The behavior of adult E. editha in the field has been described by Labine (1966).

II. Microdistribution.

This section discusses the distributions in space of eggs and larvae, and their relationships to the distributions of adults. In an insect such as E. editha, which is sedentary for much of its life cycle, a study of microdistribution becomes in essence a study of microhabitat preferences of the mobile phase and of the spatial distribution of mortality in the sedentary phases.

Eggs

Since egg-masses of E. editha at Jasper Ridge are large, oviposition is infrequent. Furthermore it is not readily observed, as the ovipositing insect assumes a cryptic position, usually embedded in the low vegetation. Oviposition behavior has been studied at Woodside by Labine (1966) and at Jasper Ridge and other populations by Singer (Chapter Two of this dissertation). In some E. editha populations the prediapause food-plants are scarce relative to the insects, and each plant may bear several egg-masses. In these cases, the exact distribution of egg-masses in space may be readily plotted. However, the primary oviposition plant at Jasper Ridge, P. erecta, is abundant and widespread, averaging several hundred plants/m^2 in many areas. In these circumstances, few egg-masses can be found and their overall distribution in space must be surmised from careful observation of criteria used by ovipositing E. editha and subsequent plotting of the distributions of these criteria. Two sets of factors

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are involved, those determining whether or not the insect will alight and those influencing the subsequent probability of oviposition. These factors are discussed below.

Observation of female E. editha at Jasper Ridge indicates that those motivated to oviposit tend to choose green areas in which to alight. Early in the flight season, this results in a random pattern of alighting since all areas contain green plants. However, senescence of most annual plants, including P. erecta, commences during the E. editha flight season. Spatial heterogeneity with respect to this senescence results in a temporary pattern of brown and green in the environment, thereby influencing the pattern of alighting of oviposition-motivated E. editha. The character of this influence differs between populations C and H for the following reasons. Early in the wet season (November-December) activity of gophers (Thomomys bottae) results in drastic thinning out of newly-germinated annual seedlings in some areas. Those plants which are undamaged or which germinate subsequently frequently grow much larger than their counterparts in undisturbed areas. They set more seed and remain green for 1-4 weeks after senescence and drying of other plants. This "gopher effect" is prominent on Jasper Ridge, although in superficially similar E. editha populations elsewhere in the San Francisco Bay Region gopher activity appears to have no effect on the senescence time of P. erecta. During the four years of this study, the pattern of the gopher effect has differed between populations C and H. In H areas of delayed senescence were typically of small size, containing fewer than 20 P. erecta plants.

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Many single, widely-scattered plants were also affected. In contrast, gopher activity in C frequently affected larger areas each containing several hundred individual plants. At least two such areas have been observed in C each year, though the sites affected have differed. These areas were conspicuous from the air, and female E. editha have been observed orienting to them in their search for oviposition sites. In consequence the pattern of alighting, while random early in the flight season, became nonrandom in area C, but remained almost random in H, both because the insects showed much reduced responses to the smaller green areas, and because the areas themselves were widely distributed throughout the population. These observations formed the justification for simulation of alighting behavior of female E. editha in H by the use of random numbers as coordinates on a grid. In 1970, 264 such points were located in H, and each was examined for its suitability as a site for an egg-mass on three occasions during the flight season. The presence of at least four leaves of green P. erecta within 5 cm. of the point chosen was used as a criterion for deposition of a hypothetical egg-mass. The justification for use of such a simple criterion is as follows:

(1) E. editha rarely oviposit where senescent plants only are present - of 41 observed ovipositions (and egg-masses found) at Jasper Ridge, one was not in the presence of green P. erecta.

(2) There is a possibility that insects are able to select those plants which will remain green for longest. This does not happen at Jasper Ridge, since examination of such plants at the very end of the E. editha flight season in both 1969 and 1970,

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two weeks after the peak of oviposition, revealed a total of 8 egg-masses, of which only two were over four days old (eggs can be aged by color).

The same sets of random coordinates were used on March 22, March 29, April 4, and April 16. The distributions of hypothetical egg-masses laid on these dates are shown in Fig. 1. On March 22, 214 of 290 sites examined were judged suitable for oviposition. This number then declined to 194 on March 29, 98 on April 4, and 18 on April 16.

Larvae

Observations of the fates of 62 real egg-masses in 1968 and 1969 indicated that the survival of newly-hatched larvae depends on the presence of food within about 10 cm. of the egg-mass site. It is possible that a plant selected at random before any senescence pattern has appeared has a lower probability of remaining green for a further two weeks than does one selected at a later date from those which still remain green. Thus, it is not intuitively obvious that, within the observed flight season of E. editha, the earliest oviposition results in the lowest hatching mortality. This can, however, be tested by following the fates of the hypothetical egg-masses. For eggs laid on March 22, the conditions on April 4 can be used to estimate survival. The 98 sites which still fulfilled oviposition criteria would evidently be suitable for young larvae. In addition, some survival would be expected at 26 sites in which O. densiflorus plants were growing within 10 cm. of the egg mass; at 8 sites where green P. erecta plants were so placed, and at 2 sites where both plant species were present. Thus a total of 134 out of 214 oviposi-

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tion sites were judged adequate for larval survival at this stage. Similarly, the condition of food-plants and their distance from each site on April 10, 18, and 30, were recorded, and hatching mortalities for the various oviposition dates estimated as follows:

Date Laid	No. Laid	No. Surviving	% Mortality
March 22	181	132	27
March 29	175	51	71
April 4	98	25	75
April 16	18	3	83

Examination of the mark-release-recapture data for 1970 at JRH, with the knowledge that most eggs are laid in the first few days of life of the adult (Labine 1968) shows that in 1970, oviposition commenced about March 20, remained at a low level until March 25, rose rapidly to a peak about March 29, and then declined slowly. Thus, it appears that, at least at Jasper Ridge H in 1970, the probability of survival was highest for egg-masses laid early in the flight season, but did not decline to zero even for the latest ovipositions.

There are no gross differences between the patterns of early and late hypothetical oviposition (Fig. 1) or between the patterns of survival of early and late hypothetical egg-masses (Fig. 2).

It is rare for the plant on which the eggs were laid to support a group of larvae beyond early second instar, even if it does not undergo senescence. Consequently, second and third instar larvae must search for new food. While the food supply, both O. densiflorus and P. erecta, diminishes continually by senescence, the searching capacity of larvae is increasing rapidly during these instars, such

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that the probability of finding food may even rise with time. Since the average rate of disappearance of food-plants is known, this hypothesis can be tested by measuring the searching capacities of first, second and third instar larvae under field conditions. Such experiments are currently in progress.

After senescence of most of the food-plants, but before any larvae have entered diapause, it is possible to census surviving larvae by searching all remaining edible food-plants. Such a census of sq. C3 (see Fig. 3) in May, 1970, revealed 3 larvae in two 25 m^2 plots, or 1 larva per 17 m^2. This compares with the post-diapause estimate of 38 larvae in 900 m^2 (15 larvae observed in standard count) or 1 larva per 22 m^2, and the resulting 1971 adult density over the whole of population H of one adult per 30 m^2 of larval distribution (400 adults in 11,700 m^2).

While the figure given for density of prediapause larvae is certainly not representative of the total area of larval distribution, it does indicate that the bulk of mortality in 1970 could be attributed to the observed starvation of newly-hatched, first and second instar larvae. Survival through this critical prediapause phase depends on the probability of finding one or other of the alternative food-plants. The relative importance of P. erecta and O. densiflorus at this stage can be deduced from comparing the distributions of both plants with the spatial pattern of survival of larvae as revealed by plotting the distribution of post-diapause larvae.

Post-diapause larval distribution is estimated by a standard search technique performed under fair, calm weather conditions. The

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standard search has been calibrated by mark-release-recapture and was shown to reveal 1/3 to 1/2 of the larvae present (Table III). A numbered stake is inserted by each larva revealed in the standard search, and the distribution of stakes later plotted with surveying equipment.

The map of O. densiflorus distribution (Fig. 4) was obtained in 1969 by taking overlapping color photographs from several points in area H, then later re-framing the photographs in the viewfinder of the same camera at the same vantage points, and locating the necessary landmarks with a transit. The pattern of senescence of P. erecta (Fig. 6) was plotted from observations made on March 25 and April 8, 1969.

A comparison of Figs. 4, 5c and 6 shows that, in the drier parts of H near the top of the hill (Squares A1, 2, 3; B1, 2, 3; C2, C3), the distribution of post-diapause larvae in 1970 corresponded almost exactly with the 1969 distribution of O. densiflorus. However, on the North-East facing slope (Square D1) some larvae evidently survived on P. erecta alone. This statement can be made, since larval movements were measured (by marking larvae with paint) and averaged less than two feet per week at January temperatures in 1970. Hence it is not likely that the larvae at the North end of Square D1 (Fig. 5c) had moved the 30 feet from the nearest 1969 O. densiflorus prior to the making of the map in early February, 1970.

The correspondence between Figs. 4 and 5c, thus indicates that O. densiflorus was extremely important for survival of prediapause E. editha larvae in population H in 1969. The case is strengthened by the

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similarity between post-diapause larval distributions in 1969, 1970 and 1971 (Figs. 5b, 5c, and 5d), since the distribution of O. densiflorus in 1968 and 1970 was almost identical to that plotted in 1969. It should be noted, however, that O. densiflorus plants were both smaller and less dense in 1970 than in 1969, although their overall distribution had not changed. 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. On this assumption, the map of post-diapause larval distribution in 1968 (Fig. 5a) shows that considerable numbers of prediapause larvae had survived in the drier parts of H, outside the presumed distribution of O. densiflorus. One might predict that such survival would be greatest in years when heavy rainfall occurs at the time when P. erecta in squares A1-4 and B2-4 would normally commence senescence - i.e. in late March and April. This prediction fits the observed case, in that 1967 rainfall (at Searsville Lake) was 8.91 inches in March and 6.81 inches in April. The means for these months are 3.85 inches and 2.06 inches respectively. In this case, then, unusual climatic conditions in spring of 1967 appear to have influenced the spatial pattern of mortality in H, and hence the spatial distribution of post-diapause larvae in 1968. However, since there was no increase in population size between 1967 and 1968, the increased survival in the drier parts of H appears to have coincided with higher mortality in the damper areas.

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A clue to the reason for this may be afforded by the physiological adaptation of prediapause larvae to warm, dry conditions and dry food (p. 6). Further evidence, albeit slight, lies in the observed fate of three egg-masses placed in H in early February 1970, two months before they would have been laid in the field. The resulting larvae reached early second instar but all died following a day of rain on March 15.

The responsiveness of ovipositing E. editha at Jasper Ridge to only one of the two food-plants required by most larvae results in powerful selection pressure against leaving the population, since P. erecta plants selected at random from outside the population are much less likely to be growing intermingled with O. densiflorus than are those selected close to the area of adult emergence.

III. Population Size Changes at Jasper Ridge.

It has been shown (Ehrlich 1965), that population size changes in areas C, G, and H of Jasper Ridge are not correlated. In two cases observed at Jasper Ridge and Woodside, large reductions in population size were already apparent in the densities of post-diapause larvae (Table IV), indicating that unusually high mortality had occurred either before or during diapause. This mortality estimate excludes predation by insect parasitoids, which is not consummated until late in post-diapause larval or pupal life. Furthermore, such predation in Bay Area E. editha populations in the years 1968-1971 has remained at levels too low to account for observed population size changes (White, Singer & Gilbert unpubl.). Since diapause mortality is also

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usually low (pages 5 and 13), it seems probable that the measured population size changes at Jasper Ridge are correlated with the extent of starvation mortality in prediapause larvae. The extent of this mortality would be expected to vary from year to year, since it depends in a broad sense on the phase relationship between the flight season of E. editha and the senescence of the food-plants. This phase relationship has been observed to vary (Table V), but only within narrow limits, since high rainfall, which delays senescence of the plants, is usually correlated with low temperatures and low sunshine hours, thereby delaying development of post-diapause E. editha larvae.

An accurate estimation of phase relationships in past years from recorded climatological data would be complex, and would require detailed studies since the physiological condition of the plants at any point in time depends on the cummulative effects of conditions which they have experienced. For example, the effect of a six-week drought such as that in late January and February 1971 is dependent on both the initial soil moisture content and the size and condition of the plants. The 1971 drought had no detectable accelerating effect on senescence of P. erecta at Jasper Ridge; however, if rainfall levels in December and early January had not been high, the effect of the same drought may well have been severe.

Even if the phase relationship between senescence of P. erecta and peak oviposition of E. editha females were accurately measured in a given year, this would not suffice as a basis for predicting the population size change of E. editha between this year and the next, since larvae can survive to diapause in three ways:

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(1) by locating nonsenescent P. erecta unaffected by the activities of gophers;

(2) by locating P. erecta maintained green by the "gopher effect";

(3) by locating O. densiflorus blooms.

Of these survival conditions, only (1) is determined by the phase relationship discussed above. Differences between years in survival by method (3) are caused as much by inter-year differences in density of O. densiflorus as by its senescence. A further compounding factor is the interaction between the aspect of the slope and the rate of development of larvae. An example should make this clear. Post-diapause larvae in the driest parts of area H (squares A1-4 and B1-4) grow faster than those in the more North-facing areas, and become adults sooner. The heavy rainfall of spring 1967, besides affecting the 1967 phase relationship between E. editha flight season and food-plant senescence, influenced the 1968 phase relationship also, through its effect on 1968 post-diapause larval distribution.

If it is true that population size changes of E. editha at Jasper Ridge are determined by differences in mortality of prediapause larvae, then the lack of correlation between changes in populations C, G and H can be explained in terms of ecological differences between them. As described in Section II of this chapter, larval survival in H is higher at the top of the hill in wet years, and apparently highest in dry years on the damper North-East facing slope. The overall result seems to be higher survival in years drier than average (Fig. 8).

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Area C is much larger than H and almost entirely level, corresponding in exposure to the dry hilltop of H. It is not surprising, therefore, that the greatest recorded reduction in population size of C followed the lowest recorded winter rainfall, and that survival in C has been consistently higher than in H following wet years but lower than in H following dry years (Fig. 8). Although not plotted accurately in C, the distribution of larvae found in 1969, 1970 and 1971 has differed considerably from year to year (Fig. 9) while larval distribution in H underwent no such fluctuations in these years. By analogy with the study of H (Section I of this chapter), it can be assumed that changes in the distribution of post-diapause larvae in C represent spatial differences in survival from year to year. This is to be expected, since a large proportion of larvae in C survive by method (2) above, i.e. by locating P. erecta maintained green by the activities of gophers. The distribution of gopher activity varies from year to year and may depend on the local distribution of the onions, Brodiaea pulchella and B. terrestris, which constitute a major portion of the diet of these gophers (J. Proctor pers. comm.). O. densiflorus is also important to larvae in C. and this resource too is variable from year to year in its distribution and abundance.

Thus, the changes in adult distribution of E. editha in C measured by Ehrlich (1965) probably reflect changes in the pattern of survival of prediapause larvae, dependent on the activities of gophers and the distribution of O. densiflorus. This model amounts to repeated local extinction of E. editha in most parts of C, followed by recolonisation as adult insects distribute egg-masses over the whole

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area each year. Such a population can persist only if the area occupied is large and hence certain to contain at least one small area of high survival each year. Although C is much larger than H, (see Ehrlich [1965] for map), the factors necessary for survival seem less predictable, and the continued existence of this population may depend on periodic recolonisation by individuals from H.

Area G resembles H in its North-East facing aspect, thereby ensuring survival of larvae in most years without the assistance of either T. bottae or O. densiflorus. However, it resembles C in the unpredictability of appearance of these two resources.

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 G resembles a small section of C in the predictability of these resources. Since E. editha appears to undergo frequent extinction in such small sections of C, it is no surprise that extinction of population G occurred in 1963, followed by recolonisation in 1966. A further important factor may be the high tendency for emigration of adult E. editha from G in certain years. The factors responsible for these movements are being investigated (Gilbert & Singer unpubl.).

IV. Other Populations.

To what extent does the foregoing description of the Jasper Ridge E. editha colony apply to other colonies? Between San Francisco and San Jose, six other colonies have been examined. All are on serpentine soil, and all contain both P. erecta and O. densiflorus. The "gopher

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effect" so prominent in population C of Jasper Ridge is absent in all six colonies. In one colony, EW (see map Fig. 11) senescence of P. erecta occurred so early in the flight season in 1970 that 15 out of 18 egg-masses found were laid on O. densiflorus (see Chapter Two, pages 32 and 33). Southwards from EW, dependence on O. densiflorus appears to diminish clinally through colonies WS, JR and SJ, such that the phase relationship between the flight season of E. editha and senescence of P. erecta is favorable enough in large areas of population SJ to permit high larval survival in the absence of O. densiflorus. This trend continues Southwards from the San Francisco Bay Region through populations CR and MI, both of which are on serpentine soils. Population CR is heavily grazed by cattle and contains no Orthocarpus species, but maintains a very high density of E. editha. Population MI is lightly grazed, and contains some Orthocarpus. Observed distributions of post-diapause larvae suggest that this Orthocarpus may facilitate larval survival in some years, but that most larvae survive on P. erecta alone (observations of L.E. Gilbert, R.R. White & M.C. Singer).

There are no known Plantago-feeding E. editha colonies on serpentine soil south of the San Luis Obispo area. In the vicinity of Santa Maria (populations SM, CS) E. editha populations occur on a soil type known as Oakley Sand, while in the San Diego area (populations DH, OT) soil types have not yet been identified but are neither sand nor serpentine. The present-day ecology of these Southern populations differs markedly from that described for Jasper Ridge. In the Santa Maria area Oakley Sand is extensively cultivated, although its

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low calcium content (a feature shared with serpentine) renders application of fertilisers necessary. Several dense E. editha populations have been reported "in alfalfa fields" or "in ditches between flower and vegetable fields." (W.L. Swisher, pers. comm.) Of those recorded populations investigated, two had disappeared; in one of these P. erecta was no longer present, and in the other it was vanishingly scarce. On this soil type, P. erecta appears to be essentially a plant of disturbed grounds, and, even where present, occurs at much lower densities than on serpentine soils. In population CS fifteen metre square quadrats were thrown in the area of highest E. editha larval density. The number of plants per square metre ranged from zero to 58, with an average of 6.7. P. erecta density at SM was not measured but was much lower than that at CS. This compares with several hundred plants per square metre at Jasper Ridge (A.R. Moldenke, R.R. White unpubl.). In the two populations investigated, CS and SM, periodic disturbance appears to prevent the exclusion of P. erecta by perennial grasses or filaree (Erodium sp.). At SM, major disturbing agents are motorcyclists, while at CS the soil appears to be turned from time to time by the U.S. Air Force. This cultivation is performed only in a band adjacent to the access road, which contains P. erecta and E. editha, and which is divided from adjacent undisturbed areas by a militarily straight line. These latter areas are characterised by scattered shrubs among perennial grasses; P. erecta is absent. The population was visited on April 10th, 1971, approximately one month after the estimated time of peak oviposition and consequently two weeks after hatching of most egg-

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masses. At this time, webs of first and early second instar larvae were found, and an estimated 80% of P. erecta plants were still in edible condition. This observation places mortality of newly-hatched larvae due to senescence of P. erecta at considerably less than 20%, compared to the 70% observed at Jasper Ridge. However, prediapause starvation mortality may still be high, though in this case it can be ascribed to low density of P. erecta rather than to its senescence. It should be noted that a small proportion of E. editha egg-masses at CS are laid on a Collinsia species as yet undetermined; this plant occurs only in a few small areas and undergoes senescence synchronously with P. erecta. It appears equally suitable as a prediapause larval food-plant, and, like P. erecta, occurs only in disturbed areas. Population SM appears similar in general to population CS, but lacks the Collinsia species.

While the general statement that E. editha populations in the Santa Maria area lead a fugitive existence seems tenable, evidence as to the sequence of events following colonisation is lacking. The following sequences seem possible:

(1) The new population increases until reaching a balance with insect parasitoids. Such parasitoids are present at CS and SM.

(2) The new population increases until reaching a balance with its food-plant(s). The seed set of annual food-plants may be progressively reduced by the insects until the density of food reaches the point where massive starvation of pre-diapause larvae ensues. The situations at CS and SM may

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correspond to this model, which can only be postulated where the phase relationship of food-plant senescence and E. editha flight season results in much lower larval mortality through food-plant senescence than that observed in the San Francisco Bay Area.

(3) Human interference is so infrequent as to permit development of climax communities of which P. erecta is not a member.

(4) Human interference is so frequent that it prevents any of the sequences postulated above from going to completion.

Until the recent urbanisation of large sections of San Diego County, E. editha was a widespread insect around San Diego, Chula Vista and La Jolla. The two extant populations investigated, DH and OT, both were characterised by extremely high densities of E. editha in 1971, and also by high starvation mortality of prediapause larvae through senescence of the food-plants, Plantago insularis (at DH) and, probably, P. erecta (at OT). It is possible that larvae at OT transfer to Orthocarpus before diapause, but at DH there are no alternative food-plants (observations of F. Thorne, A.R. Moldenke, M.C. Singer, R.R. White and L.E. Gilbert). Like those in the Santa Maria area, San Diego E. editha populations may be less permanent than those in the San Francisco Bay Region, since both Plantago and Orthocarpus species are prominent during successional stages after fires, which are frequent (A.R. Moldenke, pers. comm.).

These southern populations must be opportunistic in their response to climatic conditions, since San Diego receives almost no

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rainfall in some years. The ability of E. editha larvae to diapause for several years or to re-enter diapause after a brief period of feeding must be essential for long-term survival. Southwards from San Diego, in Baja California, winter rainfall becomes even less predictable. A population of E. editha found near Rosario in 1968 was re-visited in February 1971 (A.R. Moldenke, pers. comm.). It was observed that winter rainfall had been insufficient for germination of the annual Plantago presumably utilised by E. editha, and that no edible food-plants of any kind were available. In contrast, appreciable summer rainfall may be received in exceptional years. On at least two known occasions in the last half-century, this has resulted in a second generation of E. editha in late summer in the San Diego area (F. Thorne, pers. comm.). Thus it seems that southern populations of E. editha resemble desert annual plants in their response to rainfall. Indeed, diapause itself is facultative, and can be omitted from the life cycle if larvae receive tender, non-senescent food. Jasper Ridge E. editha larvae on the other hand, have an obligatory 8 month diapause which cannot be broken in midsummer by experimentally generated "rainfall".

The foregoing comparison of E. editha populations deals only with coastal butterflies living in exposed open grassland areas and feeding on annual food-plants, with oviposition principally on plants of the genus Plantago. High mortality of prediapause larvae owing to lack of food-plant, whether through senescence or outright scarcity of the plants, appears to be a common factor, as is a low

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level of predation by insect parasitoids. Changes in population size from year to year are dependent largely on climatic conditions (except at CS and SM) and local extinction appears to be frequent.

A complete comparative ecology of all known E. editha populations lies beyond the scope of this thesis. However, the following characteristics of other populations stand out in sharp contrast to those described above:

(1) In some populations (e.g. MC) which utilise annual food-plants, female E. editha are able to predict the time at which senescence of the food-plant will occur by ovipositing only on plants which have not yet bloomed, thereby avoiding starvation mortality of first-instar larvae through senescence of the food-plant.

(2) In populations (e.g. DP) which utilise perennial food-plants the supply of food is approximately constant from year to year. At DP, both population density of E. editha and the spatial pattern of survival of prediapause larvae are determined by intraspecific competition for food. Macroclimate apparently has no effect on mortality, and senescence of the food-plant is unimportant to E. editha. It is predicted that such populations will prove very stable through time, local extinction being unlikely.

(3) In other populations which utilise perennial food-plants (e.g. SN) the supply of food does not become limiting, but the level of predation by insect parasitoids is high, and may be the most important factor determining

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the density of E. editha.

(4) In other cases large scale extinction of many E. editha populations over a wide area appears to have occurred since 1961 (in the Mono Basin), in the virtual absence of human interference.

(5) In addition to the grassland areas described, E. editha populations are found in chaparral-covered canyons (details in Gilbert, L.E. & M.C. Singer, Ms. in prep.); in mixed open woodland; on high montane talus slopes; in Great Basin sagebrush and Pinon-juniper communities, and in clearings in Northern coniferous forests.

Comparative studies on E. editha populations in these diverse situations can be used to answer questions such as: "Under what circumstances are populations of E. editha predator-limited?" The answers to this question may have some predictive value in investigations of predator relationships of phytophagous insects in general (White, Singer & Gilbert unpubl.). In a similar vein, the food-plant relationships of several E. editha populations have been investigated and are discussed in the next chapter.

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CHAPTER TWO

FOOD-PLANT PREFERENCE IN EUPHYDRYAS EDITHA

Interpopulation differences in oviposition preference of E. editha have been investigated in two ways; by laboratory testing and by direct observation in the field. Where evidence as to proximate mechanisms responsible for these differences can be obtained, this can be regarded as evidence of the mechanisms involved in microevolutionary changes of oviposition preference in E. editha. Such changes in oligophagous insects are usually assumed to be changes in chemotactic response; the literature on insect food-plant preferences, reviewed by Thorsteinson (1960), stresses such chemotactic responses. This report presents evidence that microevolutionary changes in oviposition preference may occur by means other than changes in chemotaxis. It should be noted that larval food-plant preference is not related to adult oviposition preference in any predictable way. The newly-hatched first instar larvae can exercise no food-plant preference, as they lack sufficient powers of movement to leave the plant on which the eggs were laid. Consequently the distribution of young (prediapause) larvae on the alternative food-plants is determined by the oviposition preference of the adult. Prior to the obligatory diapause, the larvae leave the food-plant. During the post-diapause instars, they have much enhanced powers of movement and their distribution becomes influenced more by their own food-plant preferences than by the oviposition preferences of their parents.

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Laboratory Tests

Wild-collected females are fed, kept for 36-48 hours, and placed in a net cage outdoors for two hours. Then each insect undergoes a succession of two-minute trials with potential food-plants, in randomised order. Deposition of an egg-mass on one of these is considered as a choice of this plant over those tested prior to it. After each trial, the insect is allowed to walk or fly for one minute, then transferred to a plastic dish containing a freshly cut plant. Simultaneous choice experiments are impracticable as the insect will not always lay on the plant which provides the triggering stimulus. This difficulty arises because motivation to oviposit may last for 15 to 30 seconds after receipt of a suitable stimulus. During this time the insect may walk several inches.

The results of these tests are shown in Table VI. Some insects were used twice; hence the number of trials shown in the table is greater than the number of experimental insects. The key to abbreviations used in designating populations precedes under Fig. 11. All food-plants referred to in Table VI are in the family Scrophulariaceae, with the exception of the genus Plantago, which is in the Plantaginaceae.

This method, with the small numbers of insects used, will detect only gross differences in chemotactic response, as there are the following important variables:

(1) The origin and condition of the plant. This cannot be controlled if wild females are used in tests, as the populations of E. editha fly at different times of year.

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(2) The motivational state of the insect. E. editha females may spend a considerable time (several hours) searching for an oviposition site. The threshold stimulus necessary to trigger oviposition is lowered with nonconsummation, as in many types of behavior pattern. There seems to be concomitant lowering of specificity of the response, such that the spectrum of acceptable plants broadens as the insect searches.

In spite of these qualifications Table VI shows striking differences in chemotactic response between some of the populations studied. The insects are divided into three groups. Those in the first group, JR, EW, and DP, oviposit readily on Plantago erecta, Plantago lanceolata, Orthocarpus densiflorus, Pedicularis densiflora, and Collinsia heterophylla. Members of the second group, MC and IF, respond only to plants of the genus Collinsia, (C. heterophylla and C. tinctoria) and those from GL choose mainly Castilleja spp. (C. nana, and C. breweri). Any small intrapopulation variability which may exist has not been detected.

Field Observations

The results given in Table VII were gathered by direct observation of ovipositing females, and by searching for egg masses on all probable food-plant species.

DISCUSSION

There are no observations of oviposition in the field on plant genera refused by the insects in the laboratory. Thus, if one compares Tables VI and VII, the laboratory data suffice to explain

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the observed lack of oviposition in the following cases:

(1) On Plantago or Orthocarpus in population IF.

(2) On Pedicularis in population MC.

(3) On Castilleja in DP, IF and MC.

However, the following observations cannot be predicted from the laboratory data:

(1) The preponderance of Plantago oviposition over Orthocarpus oviposition in JR.

(2) Preponderance of Orthocarpus oviposition over Plantago oviposition at EW.

(3) The lack of Pedicularis oviposition in JR.

(4) Preponderance of Pedicularis oviposition over Collinsia oviposition at DP.

(5) The lack of Penstemon oviposition at GL.

Differences in chemotactic response too small to be detected with the numbers of insects used may contribute to these discrepancies. However, field observations have revealed other contributory factors, as detailed below. Densities of the various food-plants have been estimated in terms of percentage ground cover (Singer, unpubl.). With one exception, discussed below, differences in plant density did not contribute significantly to observed oviposition patterns in the populations studied.

The predominance of oviposition on Plantago erecta at JR appears to result largely from the following factors:

(1) Insects motivated to oviposit tend to choose green areas

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in which to alight. Orthocarpus densiflorus is in bloom during the flight season and the whole plant has a magenta appearance from the air.

(2) Insects which alight toward the top of a suitable plant respond to the stimulus received by dropping to the ground and searching for an oviposition site. The base of a P. erecta provides both further chemical stimuli and, often, a suitable site (Fig. 10). In contrast, the base of an O. densiflorus, during the flight season of E. editha, usually bears no leaves large enough to carry an egg-mass and appears too dry to provide suitable chemotactic stimuli. For this reason, insects which reach a plant by walking are also more likely to oviposit on P. erecta.

This importance of the shape of the plant is largely negated in the laboratory where the plants used in tests are cut, and no longer in their natural growing positions.

These factors result in the observed ratio of oviposition on the two plant species at JR. At EW, the ratio is reversed. This may be caused partly by a difference in density of the plants between the two populations, but is due mainly to differences in their condition. O. densiflorus is approximately 3 to 10 times denser at EW than at JR. It is a hemiparasite (Atsatt, 1970) and its senescence time probably depends on the nature of its parasitic connections with other plants. The senescence time of P. erecta depends on other factors, such as previous winter rainfall and tilling of the soil by gophers. Both species of plant commence senescence during the E. editha flight

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season, but in both 1969 and 1970 senescence of P. erecta occurred 1-2 weeks earlier than that of O. densiflorus in the EW population, whereas at JR senescence of the two plant species proceeded almost simultaneously. When senescent plants were offered to oviposition-motivated insects as described for the other laboratory tests, no ovipositions were observed (8 trials).

Thus, a comparison of the JR and EW E. editha populations suggests that the difference between them in oviposition preference can be largely ascribed to differences in quality of the alternative food-plants at the time of oviposition.

A different mechanism is responsible for the lack of oviposition on Pedicularis at JR. This plant is a hemiparasite of trees and normally grows in the shade of its host. Female E. editha at DP readily fly into the shade when motivated to oviposit, whereas those at JR have never been observed to do so even on hot days. The flight behavior of JR females thus tends to keep them out of contact with Pedicularis, though they frequently fly within 3-4 metres of large stands of this plant. This relationship may well be evolved rather than incidental, since there are powerful selection pressures against Pedicularis oviposition at this locality. These selection pressures are associated with egg-mass predation (Table VIII). Similarly, selection pressures against Collinsia oviposition have been demonstrated at DP, where the observed preponderance of Pedicularis oviposition is probably largely due to the aspect of shade preference in the flight behavior of E. editha as described.

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In the discussion of oviposition at JR, it was noted that the probability of oviposition on Orthocarpus was reduced by the habit of placing the egg-mass close to the ground. This habit has also been subject to evolutionary modification in the populations studied. In the Collinsia spp. feeding populations IF and MC, oviposition is typically upon the lower side of the nodding unopened inflorescence or upon the uppermost pair of unfurled leaves of the plant. Of the four ovipositions on Collinsia heterophylla observed at DP, all were at the base of the plant. Evolutionary modification of this behavior trait could theoretically result in a change of food-plant, since the plant genera differ in availability of suitable oviposition sites close to the ground.

In population GL all of 26 post-diapause larvae collected in 10 hours of searching on 3 separate days were feeding on Penstemon heterodoxus. Laboratory data show oviposition on both P. heterodoxus and Castilleja nana, while field observations indicate that C. nana is the sole oviposition plant. Further examination of the laboratory results indicate a preference for C. nana oviposition significant at the 0.05 level; of 8 ovipositions on this plant, 5 followed rejection of P. heterodoxus, while, of the 3 insects ovipositing on P. heterodoxus, none had been offered C. nana. The observed ratio of C. nana preference to P. heterodoxus preference is thus 5:0. This explains the lack of P. heterodoxus oviposition in the field, on the hypothesis that insects searching for oviposition sites are very likely to find and oviposit on C. nana before reaching the high state of oviposition motivation at which P. heterodoxus becomes acceptable.

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The probability of this state being reached, and hence the proportion of oviposition on P. heterodoxus would depend on the densities of both plants and on their distribution relative to that of the E. editha females. A study of resource distribution and adult behavior in E. editha populations has been carried out (Gilbert, L.E. and M.C. Singer, Ms. in prep.). This study has shown that in some populations (e.g. JR), adult nectar sources, oviposition plants and larval food-plants are all abundant and share almost identical distributions in space. Under such circumstances oviposition motivation would only rarely rise to the point at which secondarily preferred oviposition plants are accepted and oviposition on such plants would be rare.

In contrast, other populations (e.g. MC) show a much wider distribution of E. editha adults than of oviposition plants. This situation arises at least in part from the distribution of nectar sources. Furthermore, oviposition plants are much less abundant than those at JR. In these circumstances, female E. editha have been observed searching for oviposition sites several hundred yards from the nearest available food-plants. This type of population would be predicted to show relatively high oviposition frequencies on secondarily preferred plants if they were present (they are not at MC) and occasional ovipositions on completely inappropriate plants. Several such "mistakes" have been observed in Lepidoptera (Dethier, 1959b).

This line of reasoning leads to a hypothesis about the possible nature of evolutionary change in oviposition preference in a population of an oligophagous insect such as E. editha. It is evident that the instantaneous probability of oviposition on a particular plant

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species in a given insect population depends on many factors, such as the chemical preference, behavior and population structure of the insect, and on the distributions and densities of the various food-plants. A decrease in density of the preferred oviposition plant may instantly increase the probability of oviposition on several secondary food-plants by the mechanisms discussed above. While such secondary oviposition remains at a high level, selection may act to create a hierarchy of secondary preferences, such that the most suitable secondary oviposition plant gradually becomes the primary oviposition source if the decrease in density of the original food-plant continues. In this context it may be significant that population GL:

(1) is the only population to contain P. heterodoxus;

(2) is the only population tested to oviposit on P. heterodoxus in the laboratory;

(3) does not oviposit on P. heterodoxus in the field.

Population GL is close to at least three other Castilleja-ovipositing populations, of which only one, SR, is shown on the map. Prediapause larvae can be raised on P. heterodoxus in the laboratory, and post-diapause larvae normally feed on it in the field. It seems likely that the laboratory oviposition response of GL E. editha to P. heterodoxus indicates evolution of a secondary preference for oviposition on this plant where C. nana is scarce, or intermittently so.

Geographical Distribution of Oviposition Preference

The map (Figure 11) shows some correlation between oviposition preference and overall geography. Thus,insects in coastal populations (DH, OT, SM, CS, MI, SJ, CR, JR) tend to oviposit on Plantago

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species. Inland, on the east slope of the coast range, is a band of Pedicularis feeding populations, exemplified on the map by DP and PC. This band may extend much further North and South than shown. In the foothills of the Sierras, (MC, FR, BB, HH and IF) Collinsia oviposition is the rule whereas the high Sierra populations, GL and SR, and probably high montane populations in Nevada, oviposit on Castilleja spp. Nonetheless, there are sufficient discontinuities (EW, SN) to suggest that local populations of E. editha are capable of responding to specific local situations, no matter where they may occur. Within the Great Basin of Nevada and Eastern California, investigation of four populations of E. editha has revealed oviposition on four different plant genera, as follows:

Population	Oviposition on:
SN	Plantago lanceolata
LC	Pedicularis centranthera
WP	Castilleja lapidicola
WK	Collinsia sp.

Evidently the habit of ovipositing on P. lanceolata, an imported European weed, has been recently acquired. It has appeared independently in many Oregon and Washington E. editha populations. In the McDonald Forest (Benton Co., Oregon) P. lanceolata serves as both the prediapause (D.V. McCorkle, pers. comm.) and post-diapause foodplant for E. editha; however at population SN, post-diapause larvae ignore P. lanceolata and feed on the cotyledons of Collinsia parviflora, which may be the ancestral oviposition plant at this population.

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Food-plant preference of post-diapause larvae is as geographically diverse as oviposition preference of adults. Some examples are given in table IX. Evidently the spotty geographical distribution of E. editha may be partly a result of complex food-plant requirements comparable to those described for the Jasper Ridge colony.

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TABLE I

Egg-cluster Sizes in E. editha

Population	Probability of senescence of food-plant	Oviposition Plant	Source of Data	Mean Cluster Size	Sample Size
DP	low	Pedicularis densiflora	Field	58	27
DH	high	Plantago insularis	Lab.	102	47
WSB	high	Plantago erecta	Lab.	109	19
CR	high	Plantago erecta	Lab.	114	28
SJ	high	Plantago erecta	Lab.	119	8
SS	low	Plantago lanceolata	Lab.	70	39
MC	low	Collinsia tinctoria	Field	35	8

Laboratory data are obtained by averaging over the life spans of individual females. All infertile eggs are excluded, since these are typically laid in small clusters.

TABLE II

Weights of diapausing larvae collected at Woodside; November, 1969

Weight (mg.)	# of larvae:	
1.5	1	
2.0	2	
3.0	10	
3.5	8	
4.0	18	
4.5	16	Mean weight
5.0	6	4.39 mg.
5.5	1	
6.0	3	
8.5	1	
9.0	2	
12.5	1	
16.5	1	

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TABLE III

Calibration of standard larval count technique in different parts of square B3 of Area H, Jasper Ridge; February, 1969.

# larvae marked in first count	# larvae in second count	# marked larvae recovered	Estimated # larvae present	% larvae revealed by count
7	7	3	16	44
8	6	2	24	33
10	8	3	33	37.5
10	10	4	25	40
			Average	38.5%

In these four cases, the standard count technique, performed under fair, calm weather conditions, revealed about 40% of the larvae present. The standard count requires approximately one hour of search time per 500 m^2 searched. The proportion of larvae revealed varies in complex fashion with weather conditions. It is reduced by cool, cloudy weather, in which larvae are less visible; by very hot weather, in which they may hide; and by cold winds, which reduce the visual acuity of the observer. It is nonetheless a convenient means of comparing larval density within and between populations of E. editha living in open grassland areas, since interpopulation differences in density are so great that the number of larvae found per man-hour varies from less than one to over two hundred. No such comparison, however, is possible between populations in which larvae are dispersed over the ground and those in which they are clumped on or around perennial food-plants.

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TABLE IV

Changes in adult and larval densities of *E. editha*

Jasper Ridge, Area H

Year	# postdiapause larvae in standard count	Estimated # of larvae in study area	Estimated # of adults in total area	adult/ larval ratio
1969	344	905	3100	3.42
1970	299	787	2200	2.80
1971	53	139	400	2.88

Woodside "B"

Year	# larvae per man/hour	Estimated # of adults (Lincoln index)
1970	75	2000
1971	13*	400

*Average of 3 samples

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TABLE V

Observed phase relationships between senescence of *P. erecta* and oviposition of *E. editha*, 1968-1971

Year	Est. date of max. oviposition	Est. date at which 50% of *P. erecta* was senescent	Interval between these dates (# of days)
1968	March 26	April 18	23
1969	March 22	April 20	29
1970	March 28	April 22	25
1971	March 27	April 20	24

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TABLE IV

Ovipositions of Euphydryas editha in random sequential tests in the laboratory

The percentage oviposition on each plant species is given; a dash indicates that the plant was not available for testing.

Population	Plantago	Orthocarpus	Pedicularis	Collinsia	Castilleja	Penstemon	# Trials	# Insects
JR	29	21	21	29	0	0	28	20
EW	24	24	20	33	0	0	21	14
DP	26	16	32	26	0	0	38	15
IF	0	0	0	100	0	0	15	8
MC	0	0	0	100	0	0	8	3
GL	19	-	6	6	50	19	16	9

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TABLE VII

Egg-masses of Euphydryas editha observed in

the field (percentages)

A zero indicates that plants of this genus are present in fair quantity and have been searched, but no eggs have been found on them. A dash indicates absence or scarcity of the plant.

Population	Plantago	Orthocarpus	Pedicularis	Collinsia	Castilleja	Penstemon	Total # Observations
JR	98	2	0	-	-	-	41
EW	17	83	-	-	-	-	18
DP	-	-	94	6	0	-	65
IF	0	0	-	100	0	0	25
MC	-	-	0	100	0	0	12
GL	-	-	-	-	100	0	14

TABLE VIII

Disappearance (Predation) of Egg-Masses

Plant Species	Population	% Predation	Sample Size
Pedicularis densiflora	DP	0	18
Pedicularis densiflora	JR	88*	23
Plantago erecta	JR	2	45

*Based on a predation rate of 65.2% in one week; all other figures based on the full two-week duration of the egg-mass.

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TABLE IX

Postdiapause food-plants of *E. editha*

Population	Prediapause food-plant	Postdiapause food-plants in order of importance
JR	*Plantago erecta* *Orthocarpus densiflorus*	*Plantago erecta*
DP	*Pedicularis densiflora*	*Pedicularis densiflora* *Castilleja foliolosa* *Castilleja affinis* *Collinsia bartsioefolia*
SM	*Plantago erecta*	*Plantago erecta*
IF	*Collinsia tinctoria*	*Collinsia tinctoria*
GL	*Castilleja nana*	*Penstemon heterodoxus*
SR	*Castilleja breweri*	*Castilleja breweri* *Pedicularis groenlandica*
SN	*Plantago lanceolata*	*Collinsia parviflora*
SS	*Plantago lanceolata*	*Plantago lanceolata*
MC	*Collinsia tinctoria*	*Lonicera interrupta* *Plectritis ciliosa* *Collinsia sparsiflora*
DH	*Plantago insularis*	*Plantago insularis*
CP	*Collinsia childii*	*Collinsia childii*

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Figure 1:

Distributions of hypothetical egg-masses laid at Jasper Ridge, Area H, 1970.

(a) laid March 22
/ sites devoid of P. erecta
● sites of hypothetical egg-masses

(b) laid March 29
■ sites suitable March 29 but not April 4
● sites suitable March 29 and April 4
/ sites suitable March 29, April 4 and April 16

(c) laid April 4

(d) laid April 16

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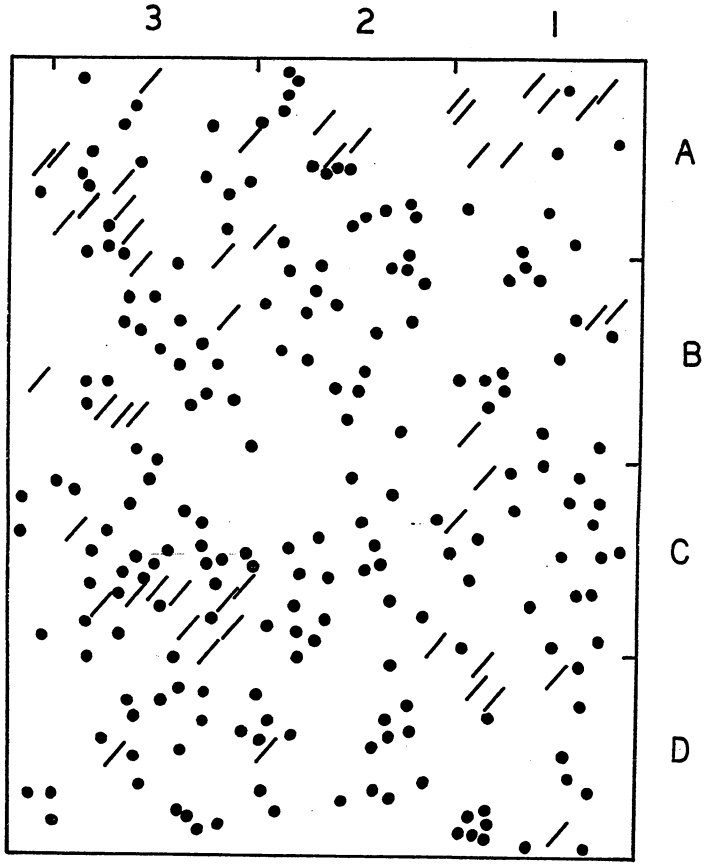

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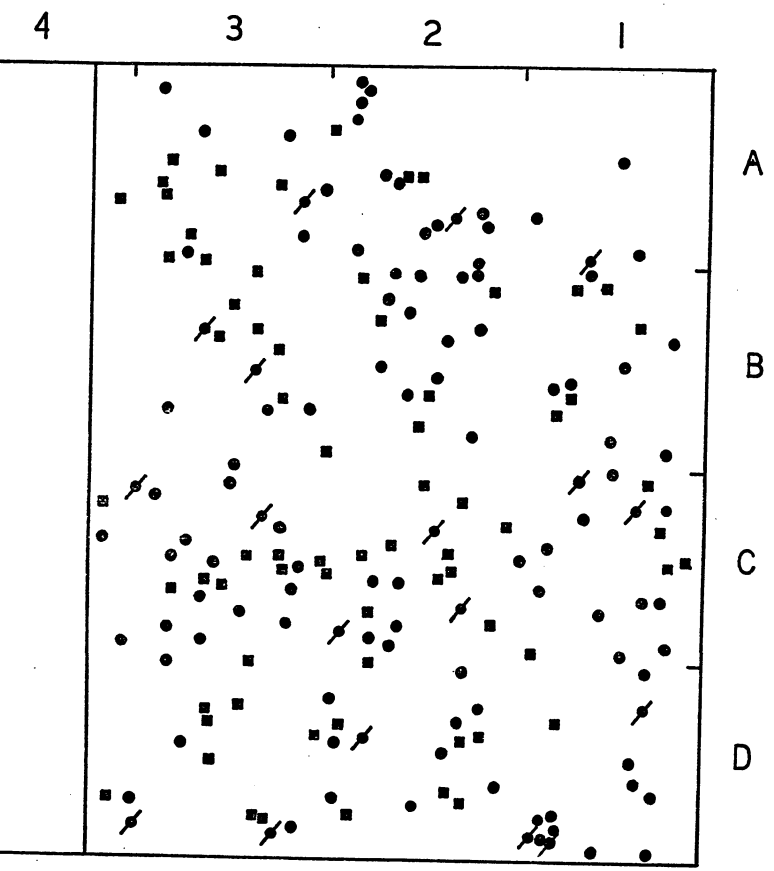

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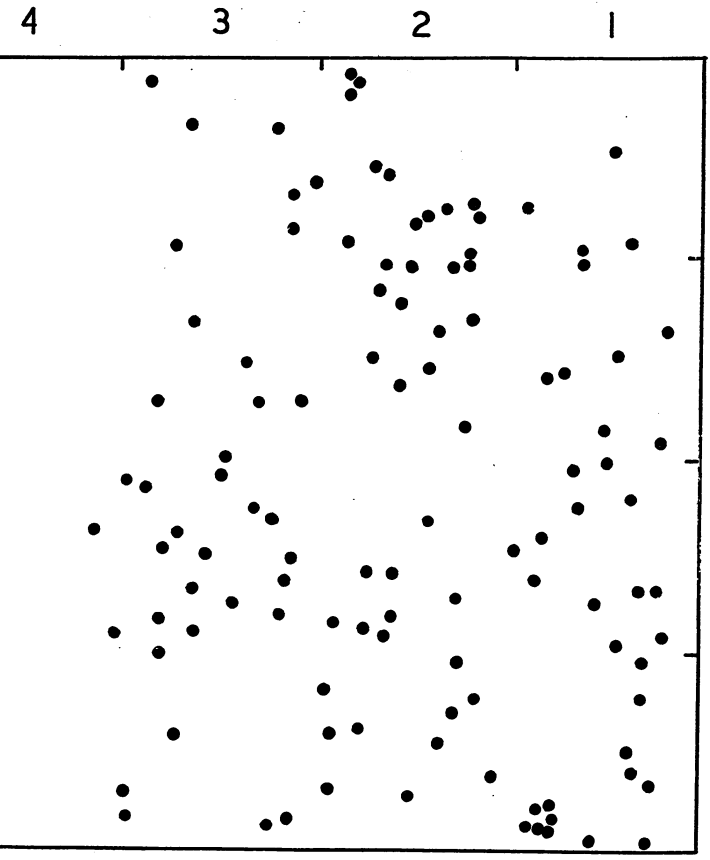

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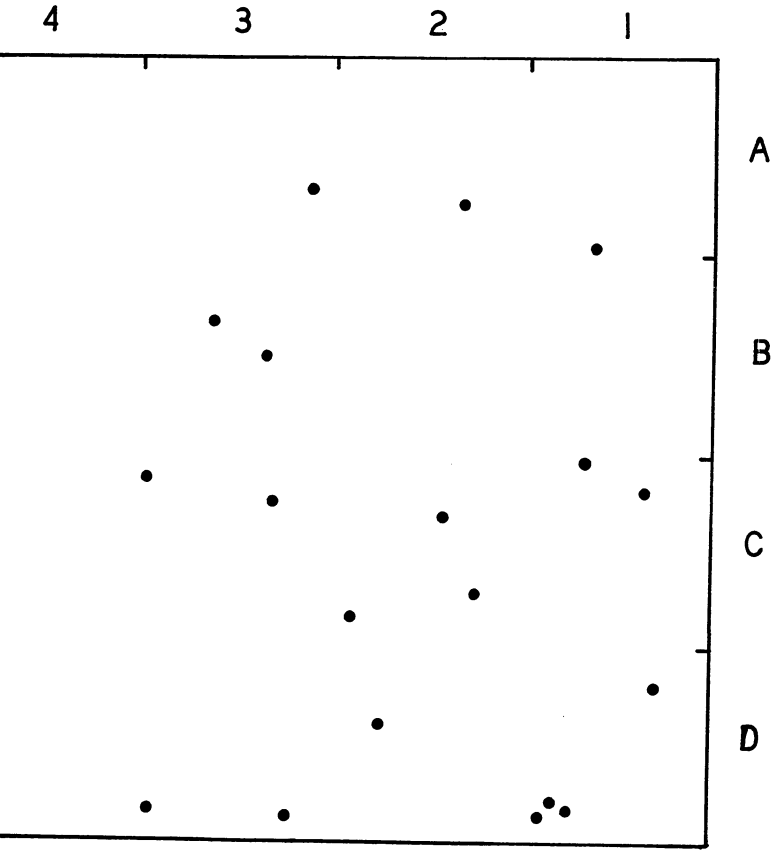

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Figure 2:

Survival of hypothetical egg-masses at Jasper Ridge, Area H, 1970.

(a) laid March 22
(b) laid March 29
(c) laid April 4
(d) laid April 16

Egg-masses killed by gophers

Egg-masses surviving

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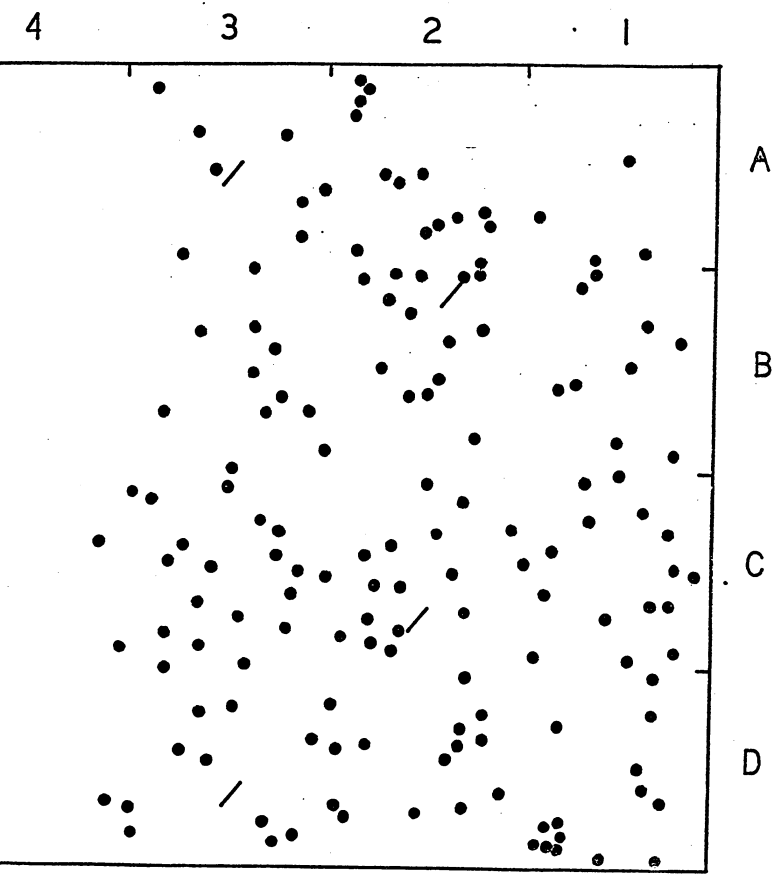

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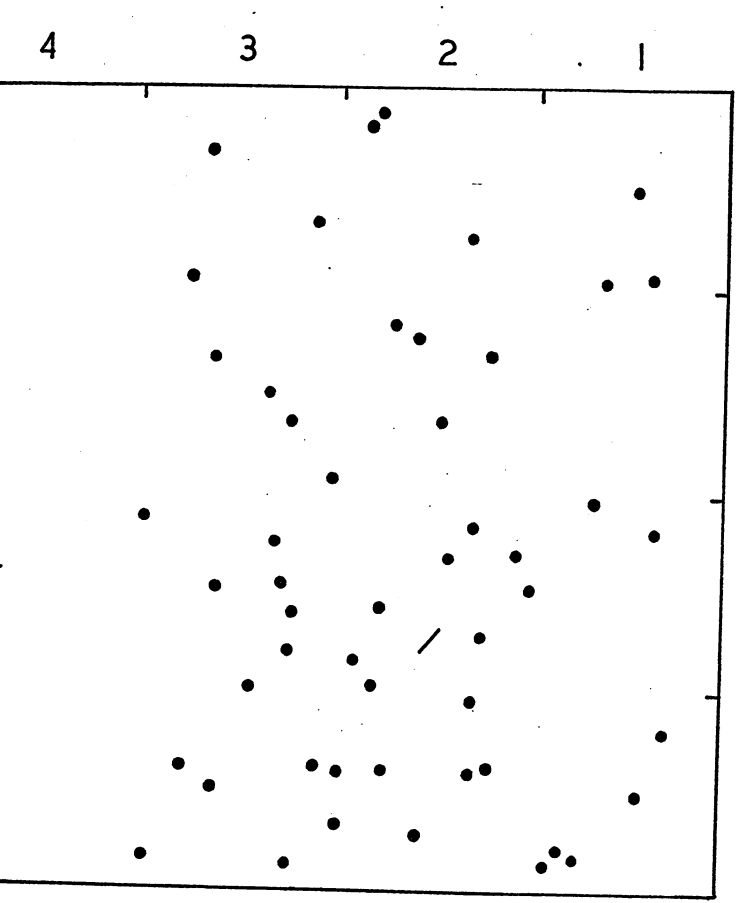

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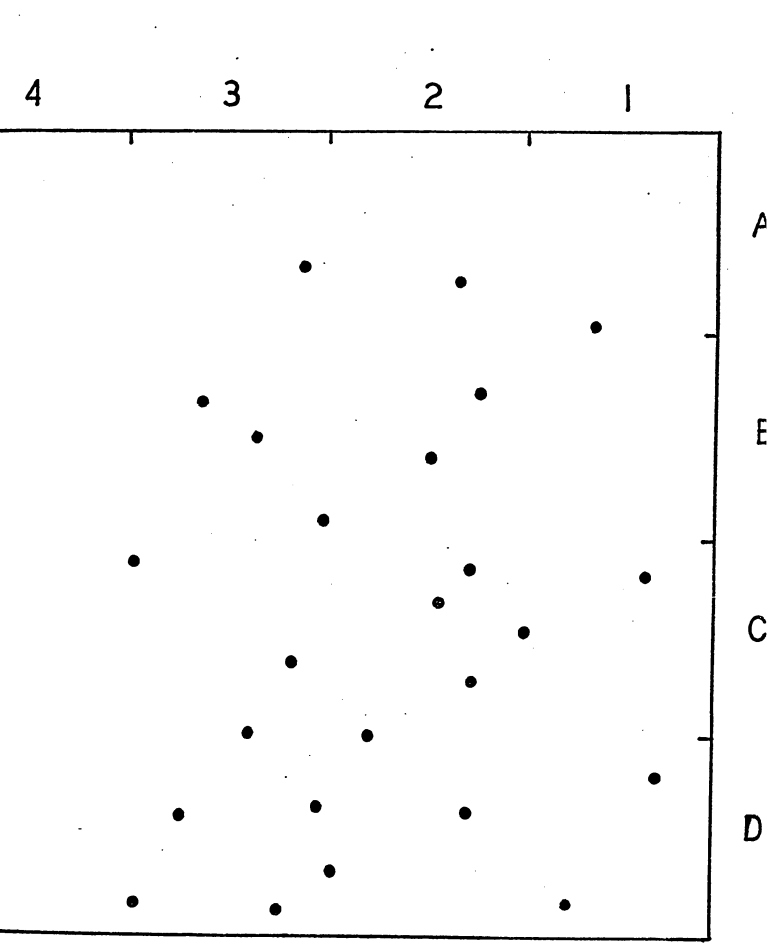

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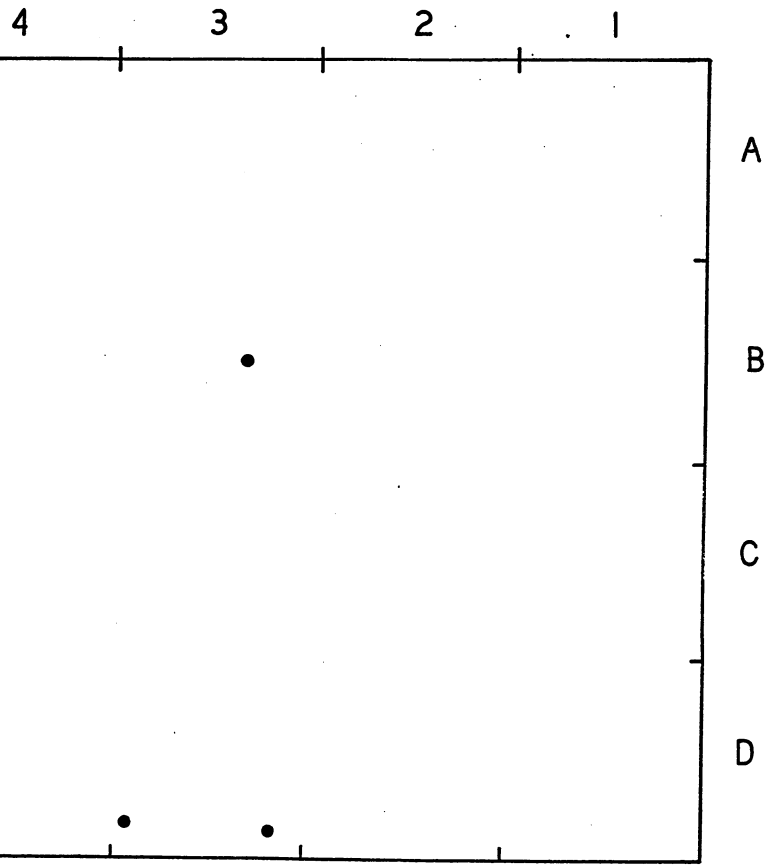

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Figure 3:

Area H, Jasper Ridge, showing:

(a) boundary of chaparral (solid lines)
(b) grid within which microdistribution of larvae has been studied
(c) maximum distribution of larvae observed (based on 1968 census, with the exception of squares F1 and F2, which are based on the 1969 distribution)

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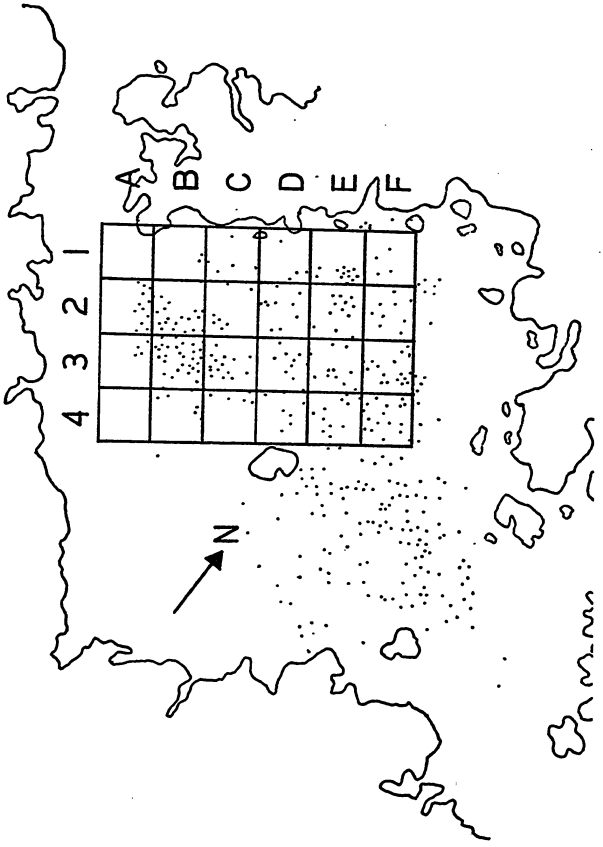

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Figure 4:

Microdistribution of Orthocarpus densiflorus in study area. April, 1969.

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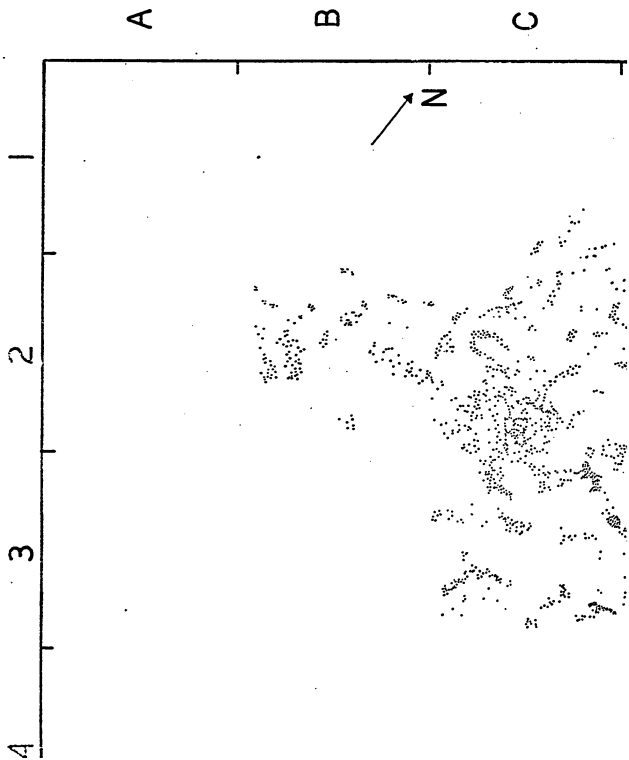

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Figure 5:

Microdistribution of post-diapause larvae of Euphydryas editha in study area.

(a) February, 1968
(b) February, 1969
(c) February, 1970
(d) February, 1971

(b), (c) and (d) are based on the standard count procedure described under Table III, page 41.

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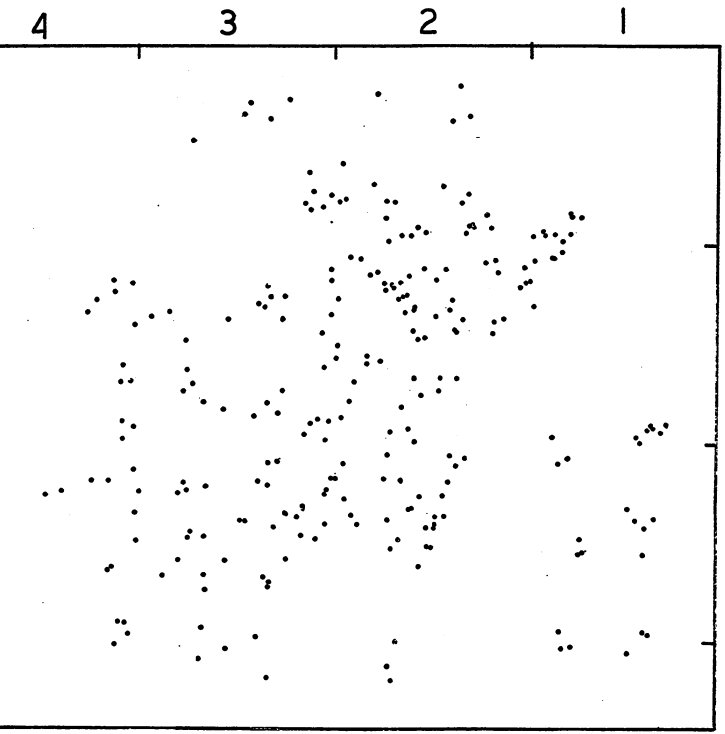

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Figure 6:

Approximate spatial distribution of senescence of Plantago erecta (other than that affected by gophers), in Area H, 1969.

1: areas undergoing earliest senescence (late March)

4: areas undergoing latest senescence (3rd week of April)

The dotted line indicates the boundary of distribution of P. erecta

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Figure 7:

Contour map of Jasper Ridge, Area H. Elevation is given in feet.

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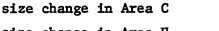
Figure 8:

Population size changes and winter rainfall at Jasper Ridge.



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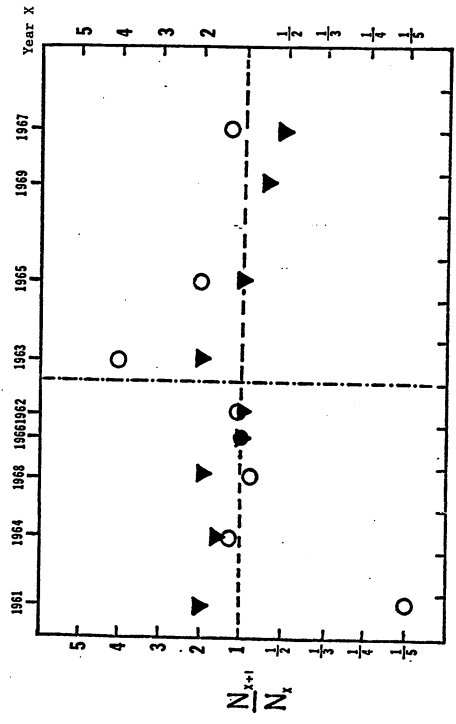

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Figure 9:

Approximate distributions of post-diapause larvae found in Jasper Ridge Area C:

(a) 1969
(b) 1970
(c) 1971

The whole area was searched in each year.

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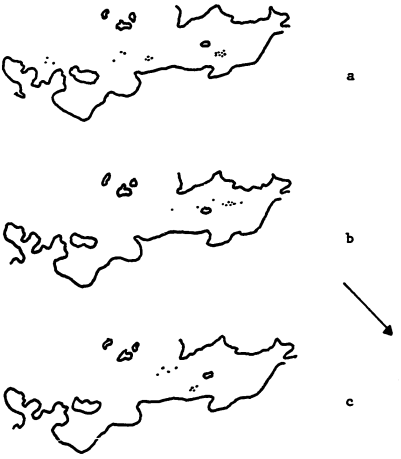

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Figure 10:

Food-plants of *Euphydryas editha*

1. *Plantago erecta*, showing position of typical egg-mass at Jasper Ridge
2. *Orthocarpus densiflorus*
3. *Pedicularis densiflora*, showing positions of typical egg-masses at population DP
4. *Collinsia tinctoria*, showing position of typical egg-mass at population MC
5. *Castilleja nana*, showing position of typical egg-mass at population GL
6. *Penstemon heterodoxus*, a larval food-plant

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Figure 11:

Geographical distribution of oviposition preference in *Euphydryas editha*.

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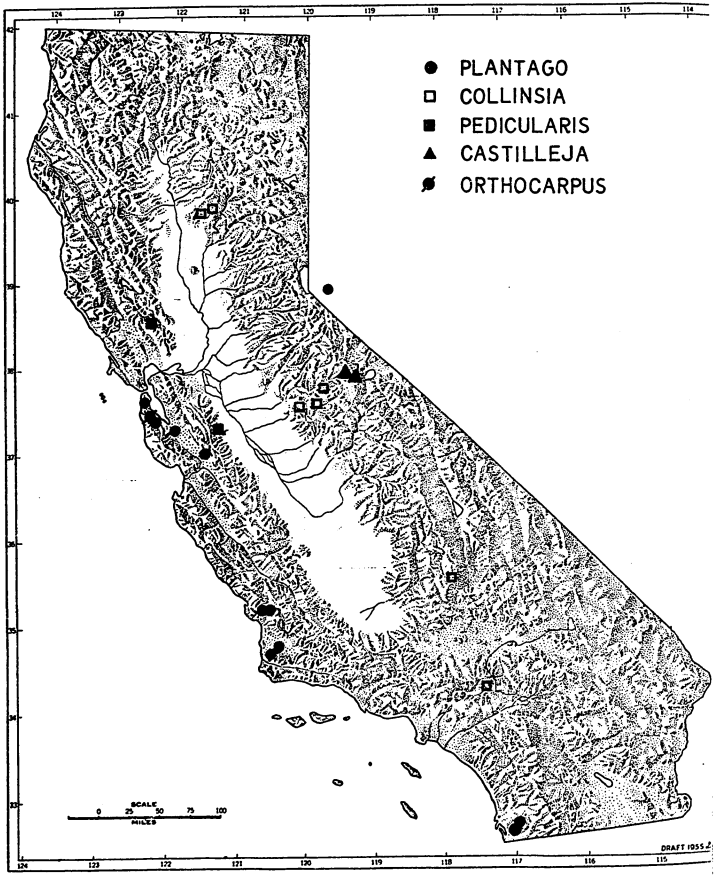

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Figure 12

Key to Populations:

BB Briceburg, Mariposa Co., Calif.

CP Cedar Pines Park, San Bernardino Co.

CR Coyote Res., Santa Clara Co., Calif.

CS Casmalia, Santa Barbara Co., Calif.

DH Dictionary Hill, San Diego Co., Calif.

DP Del Puerto Canyon, Stanislaus Co., Calif.

EW Edgewood Road, San Mateo Co., Calif.

FR Forest Ranch, Butte Co., Calif.

GL Gardisky Lake, Mono Co., Calif.

HH Hetch Hetchy Res., Tuolumne Co., Calif.

IF Indian Flat, Mariposa Co., Calif.

JR Jasper Ridge, San Mateo Co., Calif.

LC Lehman Caves, White Pine Co., Nev.

MC Mud Creek, Butte Co., Calif.

MI Madonna Inn, San Luis Obispo Co., Calif.

OT Otay Reservoir, San Diego Co., Calif.

PC Pope Creek, Napa Co., Calif.

SB San Bruno Mountain, San Mateo Co., Calif.

SJ San Jose, Santa Clara Co., Calif.

SM Santa Maria, Santa Barbara Co., Calif.

SN Snyder Meadow, Ormsby Co., Nev.

SR Saddlebag Reservoir, Mono Co., Calif.

WK Walker Pass, Kern Co., Calif.

WP Wheeler Peak, White Pine Co., Nev.

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