


ON THE WINGS OF CHECKERSPOTS
A Model System for Population Biology

Edited by
Paul R. Ehrlich
Ilkka Hanski

OXFORD
UNIVERSITY PRESS

2004

RO-4-116



3

Structure and Dynamics of *Euphydryas editha* Populations

JESSICA J. HELLMANN, STUART B. WEISS, JOHN F. McLAUGHLIN,
PAUL R. EHRLICH, DENNIS D. MURPHY, AND ALAN E. LAUNER

3.1 Introduction

The research reported in this volume began more than 40 years ago with studies of the Bay checkerspot butterfly, a subspecies of the widely distributed Edith's checkerspot butterfly. Working initially with the populations on Stanford University's Jasper Ridge Biological Preserve, Ehrlich and colleagues asked some fundamental questions: why does the Bay checkerspot butterfly inhabit the area that it does? Why does it not occur elsewhere? Why is it sometimes abundant and sometimes rare? How does population size relate to genetic variability? Are these populations evolving at a rate that can be detected on an ecological time scale? Answers to such questions from checkerspots and other well-selected systems have helped produce a comprehensive picture of how the world works at the population level. As research on the Bay checkerspot proceeded, however, many questions took on new applied and conservation significance. Work at Jasper Ridge and other sites established that Edith's checkerspot butterfly populations were quite unstable and that many habitats were threatened by human development and habitat degradation. Most recently, the Jasper Ridge populations that were the focus of the Ehrlich group's long-term study have become extinct.

We review here the current understanding of population structure and dynamics that has emerged

from four decades of work on Edith's checkerspot butterfly, *Euphydryas editha*. We focus primarily on the Bay checkerspot, which has been studied from 1959 to the present. This butterfly is typically assigned to the subspecies *bayensis*, a name we will continue to use to avoid confusion. The first descriptions of *E. editha* were apparently based on specimens from the San Francisco Bay area; hence technically the proper name is *E. editha editha*. Other studies exploring the dynamics of *E. editha* have been pursued at Rabbit Meadow in the Sierra Nevada mountain range since 1979 (chapter 9) and opportunistically at other sites (e.g., Parmesan 1996). As this chapter and subsequent chapters illustrate, *E. editha* displays a diversity of population dynamic patterns. The dynamics of *E. editha* populations in the San Francisco Bay area provide a foundation for exploring this diversity and its relationship to factors such as habitat size and isolation, disturbance history, position within the species' range, and adaptation to local food resources. A major conclusion emerging from this research is that the interplay between habitat quality and climate is a critical determinant of the dynamics of local populations.

We begin with a description of the Bay checkerspot and the characteristics that make it distinct from other *E. editha*. Second, we turn to the factors that play a role in its population dynamics. Third, we discuss the factors that may lead to ex-

inction of Bay checkerspot populations, particularly those factors responsible for the documented disappearance at Jasper Ridge. Fourth, we discuss our understanding of the dynamics of *E. editha* in the San Francisco Bay region, knowledge that developed as research expanded to include an increasing number of populations at different sites. Finally, we briefly contrast the Bay checkerspot with other *E. editha* ecotypes. In this chapter and others, we use the term "ecotype" to refer to groups of populations with similar ecological characteristics such as larval food plants, timing of life cycle, and climatic zone of their habitat. Ecotype can be used in either a general or specific sense. For example, populations of the Bay checkerspot form one specific ecotype found in one small region of California. The Bay checkerspot joins with other coastal populations, however, to form a more general ecotype living in coastal grasslands and typically feeding on annual hosts. These populations contrast with ecotypes using predominantly perennial hosts and/or found in very different habitat types such as at higher elevations in the Sierra Nevada.

3.2 Habitat and Life History of *Euphydryas editha bayensis*

Euphydryas editha is distributed from British Columbia to Baja California and from the coast of California east to Colorado, Wyoming, and Alberta, Canada (White and Singer 1974) (chapter 2). Across this range, populations are typically scattered, discrete, and isolated (Scott 1986). Figure 3.1 shows the locations of the best studied populations in California and western Nevada. Groups of populations often differ from each other in host plant usage and timing of life cycle events (e.g., summer versus winter diapause). In coastal areas, *E. editha* larvae feed on *Plantago* and occasionally on *Castilleja* and *Collinsia*. Noncoastal populations feed on *Pedicularis*, *Penstemon*, *Collinsia*, *Castilleja*, and, less commonly, on other scrophulariaceous plants (chapters 6 and 7).

The Bay checkerspot butterfly is confined to patches of native grassland in the San Francisco Bay area, California, which occur almost exclusively on serpentine-based soils (figure 3.2). These patches are surrounded by chaparral, oak woodlands, and non-native grassland on nonserpentine substrates. Serpentine soils maintain a native flora because their

unusual chemical composition helps prevent domination by invasive grasses (Tadros 1957). These chemicals include high concentrations of nickel, chromium, and magnesium and relatively low levels of major nutrients, including phosphorous and nitrogen (Walker 1954).

The largest habitat patch occupied by *E. editha bayensis* is Morgan Hill, a >1500 ha site near the southern edge of the subspecies range just south of San Jose (figure 3.2). (In various publications, Morgan Hill has been called Kirby Canyon, East Hills, and Coyote Ridge, and it contains the Kirby Canyon Butterfly Reserve.) A smaller number of more isolated habitat patches, including Jasper Ridge, are found on the San Francisco peninsula and on the east side of San Francisco Bay. In general, the grassland patches inhabited by *E. editha* are larger and more isolated than patches used by *Melitaea cinxia* in the Åland Islands, as described in chapter 4 (see figure 4.3). Before the introduction of Eurasian grasses approximately 200 years ago, the habitat of the Bay checkerspot butterfly may have been much more widespread (Ehrlich and Murphy 1987a, Cushman et al. 1994). The degree to which this more extensive habitat was continuous versus patchy is unknown.

Populations of *E. editha bayensis* feed on the annual forbs, *Plantago erecta*, *Castilleja densiflora*, and *C. exserta* (figure 3.3). (These *Castilleja* species were formerly in the genus *Orthocarpus*.) Key events of the butterfly's annual life cycle coincide with the growing season of these and other native, annual grassland plants. Prediapause larvae hatch in the late spring and feed on presenescent plants until they are sufficiently mature to enter an obligatory diapause during the summer drought (figure 2.2). Of the prediapause hosts, *P. erecta* is typically the most widespread and consistently abundant from year to year, while *Castilleja* species tend to be spatially and temporally more variable (figure 3.4). Larvae that survive to diapause emerge as winter rains begin and continue feeding (largely on *P. erecta*) until they pupate in the early spring. Adults emerge after approximately two weeks, and the adult flight season lasts four to five weeks, depending on weather conditions and population size (Hellmann et al. 2003). Adults feed on nectar from a variety of native flowers, most notably *Muilla maritima*, *Layia platyglossa*, *Lasthenia californica*, *Allium serratum*, and *Lomatium macrocarpum*.

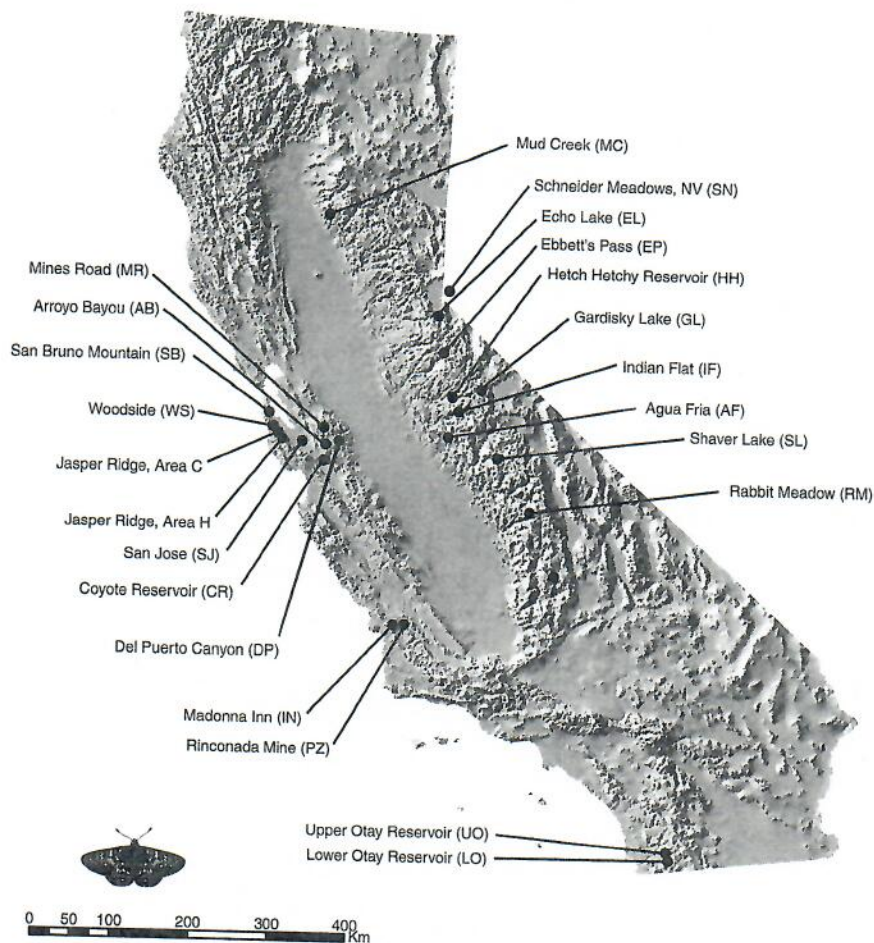


Figure 3.1. Map of the locations of the best studied *Euphydryas* populations in California and in far western Nevada.

3.3 Population Sizes and Spatial Structures

Traditional methods of analyzing mark–recapture data work well for univoltine organisms like the Bay checkerspot that have closed, discrete populations and in which all individuals are of reproductive age (for more complicated systems, see Schwarz and Seber 1999). Research on the dynamics of *E. editha bayensis* began with an intensive mark–recapture experiment in 1960 at the Jasper Ridge Biological Preserve (Ehrlich and Davidson 1960; figure 3.5). Mark–recapture experiments have been repeated at Jasper Ridge most years since, producing one of the most comprehensive data sets on the dynamics of a suite of invertebrate populations (NERC Centre for

Population Biology 1999, Hellmann et al. 2003). Estimates of population size are calculated from mark–recapture data using the ratio of marked to unmarked adult butterflies captured on a particular sampling day (Jolly 1965). Daily estimates are then summed over an entire flight season using Scott's (1973) method to estimate the total number of adults flying in a single season. It appears that handling by researchers in these experiments has minimal impact on the behavior and longevity of the butterflies (e.g., Orive and Baughman 1989).

The intensity of mark–recapture surveys at Jasper Ridge varied over the years. Years with intensive surveys (57% of study years in the habitat patch labeled “area C” and 50% in the habitat labeled “area H”; figure 1.2) had sample sizes of as many

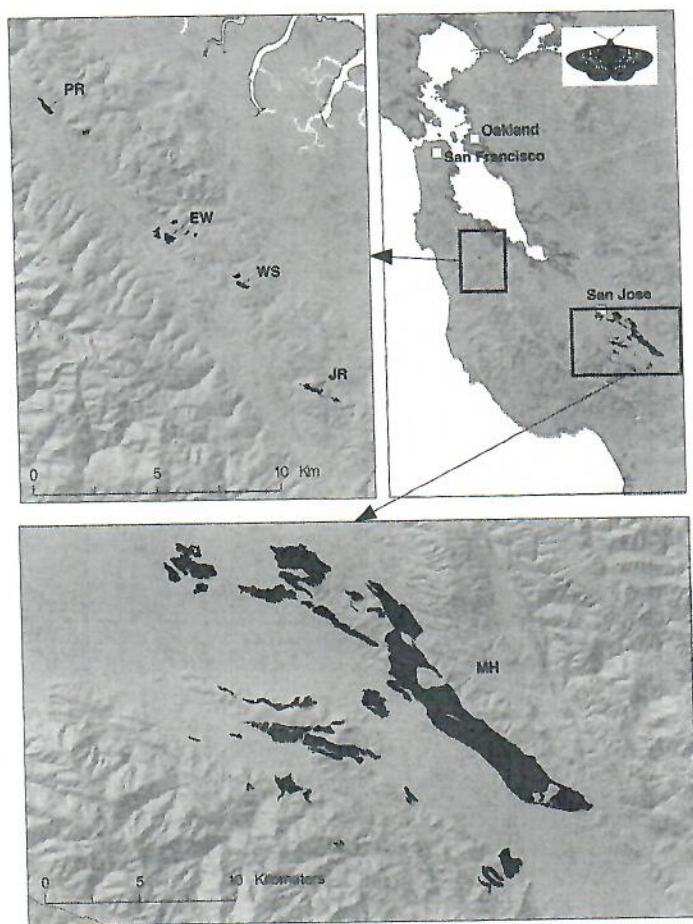


Figure 3.2. Map of the two main groups of serpentine grassland habitats in the San Francisco Bay Area. One cluster of *E. editha* populations is at Morgan Hill (MH), south of San Jose (bottom panel). The other cluster is in the vicinity of the Jasper Ridge Biological Preserve (JR, left panel). Of these latter patches, only the habitat at Edgewood County Park (EW) was extant in 2000. PR is Pulgas Ridge. WS was the site of the Woodside population.

as 500–2000 individuals when populations were large, recapture rates > 20%, and sampling spread over the entire season. Remaining years had lower rates of recaptures or data for only portions of the flight season were collected (eight years). The most striking finding from the first year of mark–recapture study at Jasper Ridge was the discovery that adult butterflies were confined to serpentine grassland. These areas are dominated by native plants (total about 7 ha) and are located within a larger expanse of grassland dominated by non-native plants

(figure 2.6). Early recapture results (figure 3.6) clearly showed that these circumscribed areas contained three separate populations that rarely exchanged individuals; migration rates between two of the populations averaged < 2.6% of 1048 adults recaptured in 1960–63 (Ehrlich et al. 1975; table 3.1, figure 2.6). Because populations were largely independent, they have been deemed “demographic units” (Brown and Ehrlich 1980), synonymous to “local populations” in the *Melitaea cinxia* metapopulation in the Åland islands, Finland (chap-



Zdravko Kolev' 2003

Figure 3.3. The larval host plants of the Bay checkerspot butterfly, *Plantago erecta*, *Castilleja exserta*, and *Castilleja densiflora*. The two *Castilleja* species are typically grouped into one host type in checkerspot studies (e.g., Hellman 2002). Drawings by Zdravko Kolev.

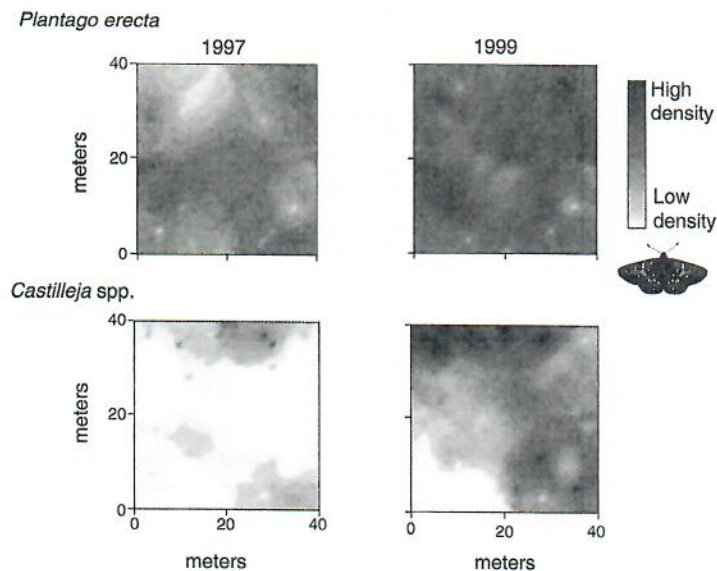


Figure 3.4. Contour diagram of the abundance and distribution of *E. editha bayensis* host plants on representative slopes in two survey years at Morgan Hill (Hellmann 2000). Dark shades represent high density; light shades represent low density or absence. In general, *Plantago erecta* is spread relatively evenly across slopes and throughout the study area, whereas the occurrence of *Castilleja* is spatially and temporally variable.

ter 4).
units a
chapar
easily f
area C
dispers
Recapt
tinued
recapt
The
at Jasp
plation
closely
the esti
until its
lation i
see also
patch h
study p
recolon
kerspot

Table 1
of early
mover
at Jasp

Year
1960
1961
1962
1963



Figure 3.5. Marking *Euphydryas editha* number 30, using a modern felt-tip pen with a flow rate not requiring wing support (see figure 2). Photo by Paul R. Ehrlich.

ter 4). The areas occupied by these demographic units are partially separated from one another by chaparral and oak woodland, but a butterfly could easily fly from one area to another (distance from area C to area H is 700 m). The rarity of inter-area dispersal shows that *E. editha* is fairly sedentary. Recaptures outside of areas of original capture continued to be infrequent in subsequent years of mark-recapture sampling (Ehrlich 1961b, 1965).

The long-term data from the three habitat patches at Jasper Ridge give a retrospective view of the population dynamic similarities and differences among closely neighboring populations. Figure 3.7 shows the estimated size of each population at Jasper Ridge until its extinction (Hellmann et al. 2003). The population in area G (between areas C and H; figure 1.2, see also figure 12.1) was ephemeral. At its peak, this patch had approximately 200 adults, and over the study period the population was extirpated twice and recolonized once (Ehrlich et al. 1975). Just one checkerspot butterfly has been observed in area G since

1973. Populations in areas C and H fluctuated in the range of hundreds to thousands of adults until approximately 1983 when the population in area C began a relatively rapid decline and then disappeared by 1991. The decline of the population in area H was less abrupt; its fluctuations continued around a long-term decline that began in the mid-1970s and accelerated in the late 1980s until its extinction in 1997 (McGarrahan 1997). Recognition of the distinctiveness of these three demographic units was critical to subsequent study of their dynamics.

The populations at Jasper Ridge show variability in several parameters in addition to population size (Hellmann et al. 2003). Considering years with recapture rates >20%, the average sex ratio of adult males to females was 1.08 in area C ($\sigma = 0.13$; $n = 14$) and 2.02 in area H ($\sigma = 1.12$; $n = 17$; Ehrlich et al. 1984; chapter 5). The number of adult females was greater than the number of adult males in six years in area C, whereas female-biased sex ratios were never observed in area H. These results suggest that mortality or dispersal rates by sex differed in the two habitat patches, given that the primary sex ratio is close to 1:1. Data also suggest that the adult sex ratio may have been skewed toward males when total population size was low (Hellmann et al. 2003). The population in area C almost always flew later than the population in area H, and females almost always flew later than males in both populations (Iwasa et al. 1983). Loss rate, a parameter that includes mortality and dispersal, differed qualitatively between the sexes and populations. In general, females showed higher rates of mortality and/or dispersal from each population than did males, but because interpatch dispersal was rare, differential mortality by sex appears to have occurred in some years.

Table 3.1. Data reproduced from Ehrlich (1965) of early mark-recapture data, reflecting the movement of individuals among habitat patches at Jasper Ridge.

Year	Recapture in Area of Previous Capture	Total Recaptures	Percent in Area of Previous Capture
1960	216	224	96.4
1961	411	425	96.7
1962	159	164	97.0
1963	235	235	100.0

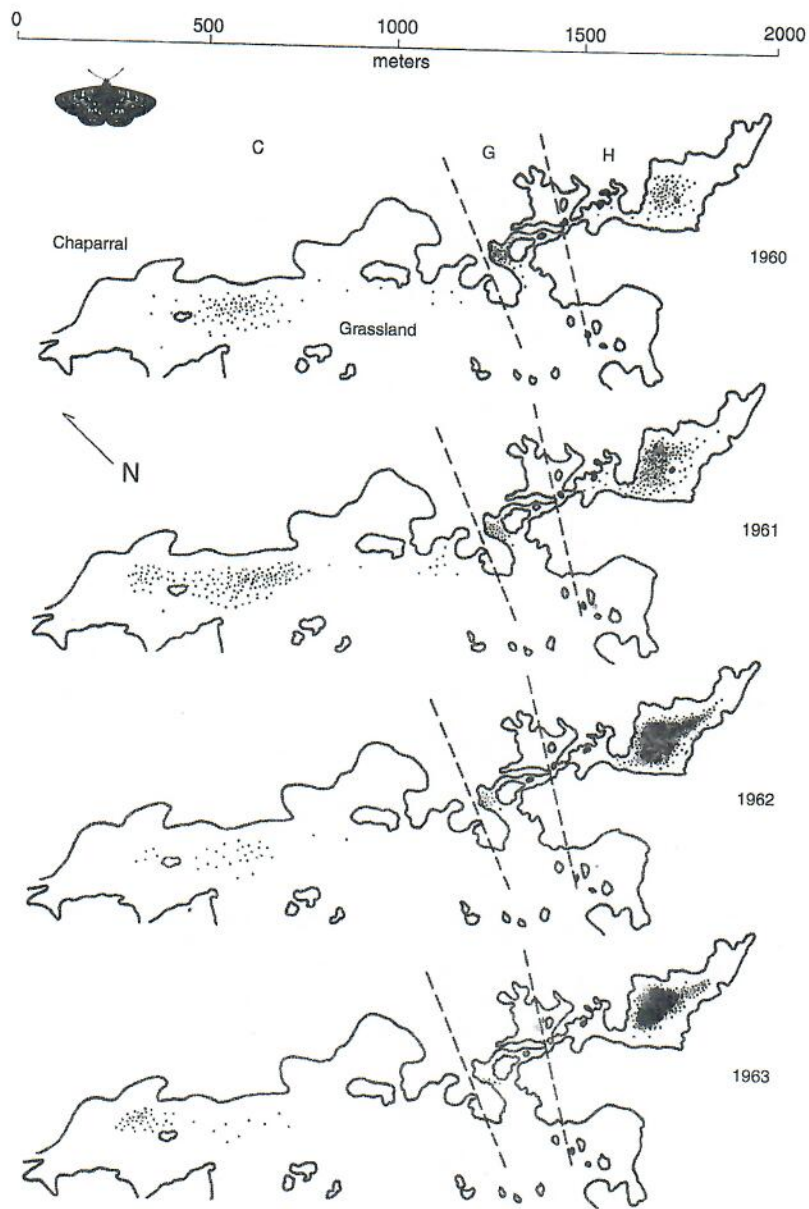


Figure 3.6. Geographic representation of the relatively independent dynamics of populations in areas C, G, and H at Jasper Ridge. Dots represent the position of first capture of an individual. Note the decline of the population in G while the population in H was exploding (more than 10-fold increase) and the population in C fluctuated (after Ehrlich 1965).

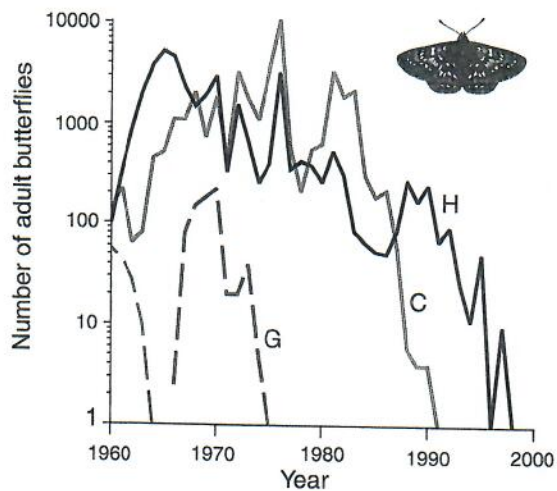


Figure 3.7. Estimated adult population sizes at Jasper Ridge calculated from results of mark-release-recapture surveys (Hellmann et al. 2003).

At Bay checkerspot butterfly sites beyond Jasper Ridge, the primary method of estimating abundance has involved counting postdiapause larvae. Large postdiapause larvae are relatively easy to detect in the short grassland vegetation, and their numbers are estimated using a timed search technique that is extrapolated to an entire habitat patch (Murphy and Weiss 1988b). For postdiapause larval sampling, the habitat is stratified into "thermal strata" based on potential March 21 clear-sky insolation, or the amount of in-coming solar radiation. Insolation is determined by latitude, date, time of day, slope, aspect, topographic shading, and cloud cover; thermal strata within a habitat primarily reflect topography (section 3.4). Multiple samples in each stratum allow errors to be estimated, and recently the method has been extended to cover > 1000 ha of habitats. This method is preferred over mark-recapture of adults in large, well-mixed populations.

Very few populations of Bay checkerspot remain. Those that have been monitored, apart from Jasper Ridge, are at Morgan Hill and Edgewood Park (figure 3.2). Morgan Hill has fluctuated from 12,000 to 500,000 adults, never reaching very low numbers (figure 3.8), while Edgewood Park declined from 100,000 adults in 1981 to near-extinction in 2002.

3.4 Factors Affecting Population Dynamics

With this quick summary of the abundance and demography of the Bay area *E. editha* populations,

we now ask: what causes checkerspot populations to change in size and distribution across space? One notable aspect of checkerspots is that adult females lay a large number of eggs. This reproductive output represents a huge potential for growth, but in most populations and in most years, nearly all immature individuals die before reaching reproductive stage (chapter 7). Determining the causes of this mortality is key to understanding and predicting the dynamics of this butterfly. Research at Jasper Ridge and other sites now suggests that prediapause larval host plant use, weather, and topographic diversity combine to determine the dynamics of Bay checkerspot populations.

The Relationship between Larvae and Plants

Singer (1971b, 1972) was the first to ask how populations of *E. editha bayensis* use food resources and how they are affected by food availability over time. Singer found that larvae from eggs laid at Jasper Ridge in 1969 and 1970 had difficulty reaching diapause. Although the butterflies chose nonsenescent host plants for oviposition, senescence often occurred during the two weeks before eggs hatch. This caused approximately 80% of larvae to starve soon after hatching. In 1970 this figure rose to approximately 99%, when hosts underwent senescence before the larvae had reached a size at which they could respond to lack of food by entering diapause. Field observations of larvae that did survive this critical period indicated that they could do so in three ways. First, they came from eggs laid near

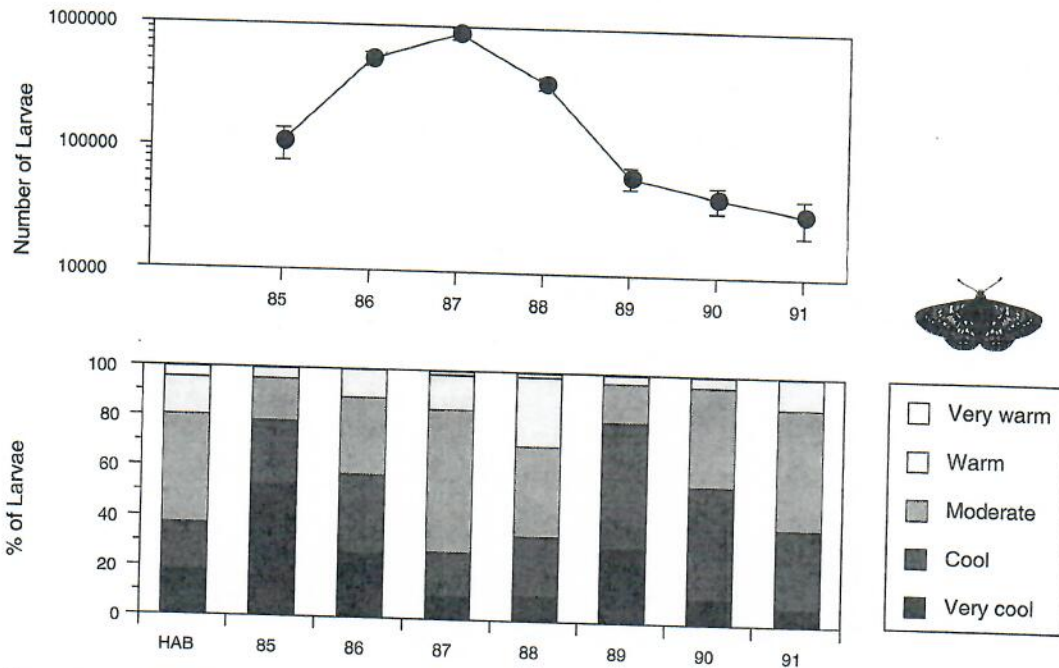


Figure 3.8. Changes in population size of *E. editha* in the Kirby Canyon Preserve at Morgan Hill in 1985–91 (see also Hellmann et al. 2003). Error bars show 95% confidence intervals. The lower panel shows proportional representation of larvae in different thermal strata. “HAB” refers to the proportion of the different slope types in the habitat as a whole.

Plantago erecta on gopher mounds, where *P. erecta* stayed green longer than plants on soil untilled by gophers. Second, they came from eggs laid near *P. erecta* that lasted for sufficient time without gopher activity, usually on a cooler, north-facing slope. And third, they came from eggs laid on or near *Castilleja*, a host that tended to remain edible longer than *P. erecta*. These three situations involved three different resource types for prediapause larvae. Singer concluded that the timing of host senescence relative to the timing of larval growth was the primary determinant of the number of larvae that survived to adulthood and that prediapause larval survivorship was the primary factor responsible for changes in population size.

More recent work by Hellmann (2002c) on the interaction between larvae and plants built upon Singer’s observations between prediapause larval survival and host plant use and explores how variation in host plant phenology, host availability, and host use affects larval growth and survivorship. Using field enclosures (0.75 × 0.75 m), Hellmann observed how larvae forage in the serpentine grassland. She found that prediapause larvae dispersed

widely among host plants and shifted from approximately equal use of the two host species toward exclusive use of *Castilleja* as the growing season progressed (figure 3.9a). This shift and subsequent survivorship to diapause was independent of the host on which larvae originally hatched. These results suggest that larvae select and modify their diet over time, and what they choose to eat correlates with changing quality of plants.

Hellmann also quantified how environmental conditions and the host plant species available to foraging larvae affect their growth and survivorship (Hellmann 2002c). Using the controlled conditions of a greenhouse, she manipulated the surface temperature of containers holding either both *Castilleja* and *P. erecta* or only *P. erecta*, into which she introduced prediapause larvae. These treatments replicated dissimilar microclimates occurring in the field (moderate vs. extreme surface temperatures) and the two types of host plant environments that larvae experience (one vs. two hosts). The experiments confirmed that temperature affects the rate of host plant senescence; high temperature accelerates the loss of water, nitrogen, and phosphorous

A. Fi

Proportion of larvae

B. Gr

Proportion of larvae

Figure studies hatche data at 30°C) *P. erect*

and doe *Castillej*. tration c variable Larvae f show a s in their d to *Castil*. This shift ure beca in contai container ture incre

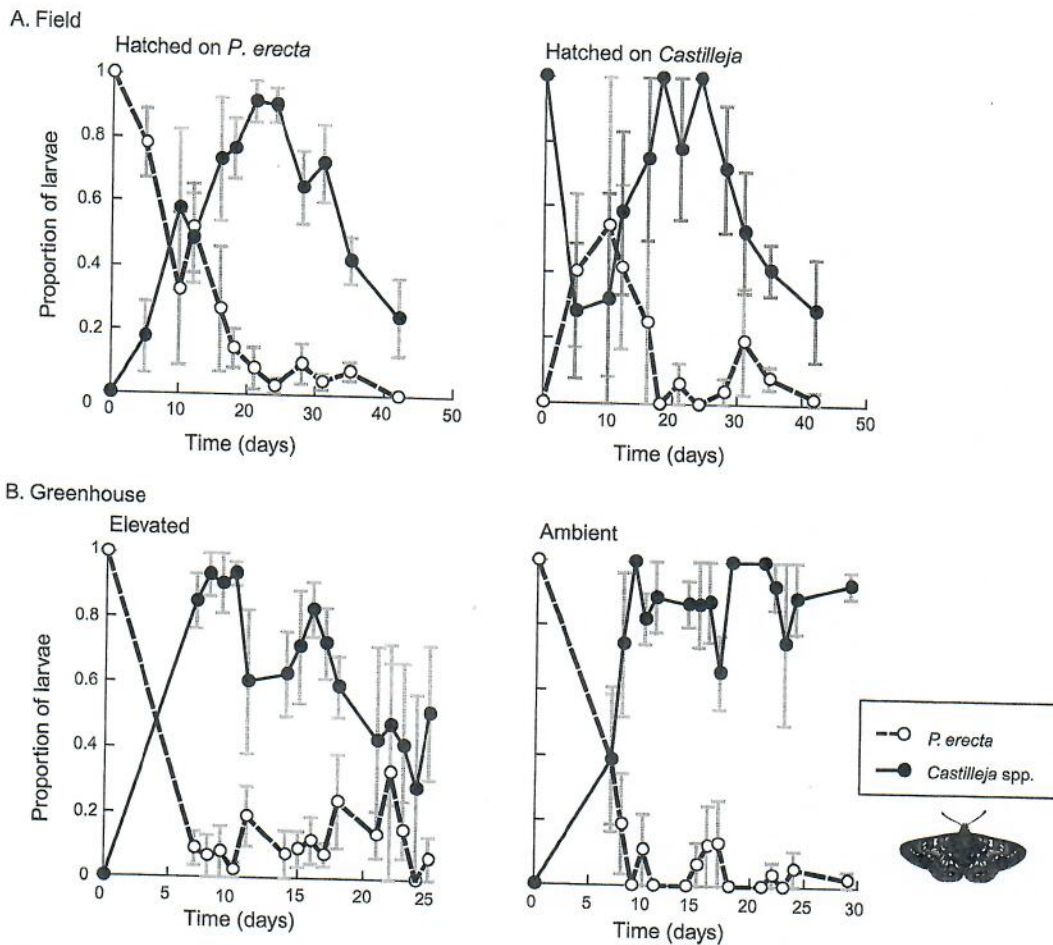


Figure 3.9. Fraction of larvae on different substrates through time in (A) field and (B) greenhouse studies (Hellmann 2002c). In (A), two types of data are shown: containers with larvae that all hatched on *Plantago erecta* and those with larvae that all hatched on *Castilleja*. In (B), two types of data are also shown: containers with larvae under elevated temperature (surface temperature = 30°C) and under ambient temperature (surface temperature = 20°C). In (B), all larvae hatched on *P. erecta*.

and does so more strongly in *P. erecta* than in *Castilleja*. *Castilleja* had a higher average concentration of nitrogen and phosphorous but was more variable in nutrient content than was *P. erecta*. Larvae feeding on plants in the greenhouse did not show a strong preference for *P. erecta* at any point in their development, and those that could dispersed to *Castilleja* as the season progressed (figure 3.9b). This shift happened earlier under elevated temperature because plants senesced quickly. Survivorship in containers with only *P. erecta* was lower than in containers with both hosts, and elevated temperature increased larval survival in containers with both

hosts. This is because higher temperatures accelerate larval growth, enabling larvae to shorten their development. Elevated temperature seems to allow larvae to stay in phase with *Castilleja*, but not with *P. erecta*.

In general, growth rates of ectothermic animals increase rapidly with increasing temperature to an optimum and subsequently decrease until a lethal temperature is reached (Sharpe and DeMichele 1977, Ratte 1984). Reflecting this pattern, Fleishman et al. (2000b) found a relationship between stage of pre-diapause larval development and microclimate (topographic position) in the field; *E. editha bayensis* lar-

vae on warm slopes tended to grow faster than larvae on cool slopes. Environmental conditions, such as temperature, directly affect larval growth and indirectly affect larval feeding via host plant senescence. The balance of these effects on the number of larvae surviving to diapause seems to depend at least in part, on the host species that larvae consume (Hellmann et al. in review).

The apparent inferiority of *P. erecta* as a larval host raises the question: why do adult females oviposit on this species at all? A partial answer may be in the relative consistency of *P. erecta* abundance among years (figure 3.4) and varying nutrient content among individual plants. Laying eggs on *Castilleja* is an option for females in only some years. The dispersal abilities of larvae suggest that adults may choose an optimal neighborhood, rather than an individual plant, in which to lay eggs (Hellmann et al. in review). The most desirable location to lay an egg is an area where both hosts are available. Singer (1971a) suggested that females may restrict their search to areas rich in flowers, enhancing opportunities for larvae to diversify their diet. An interesting aspect of diet evolution in this and other small foragers is the potential influence of spatial scale on natural selection. Plasticity of larval behavior may be selected in environments where individuals can make their own resource decisions, when resources (host plants or slope exposures) are fine grained. In environments where alternative resources are spread far apart or coarse grained, selection may act primarily on the oviposition choice of adults.

Another key factor in the relationship of larvae and host plants is the timing of adult emergence, a factor that largely determines the start of larval feeding. Murphy et al. (1983) and Cushman et al. (1994) estimated how the reproductive success of females changes over time due to the constraints of host plant senescence (see also Murphy et al. 1983). They posited that reproductive success drops sharply as the season progresses, based on an estimation of daily fecundity (number of eggs produced by a female as a function of size and age) and the mortality rate of prediapause larvae from eggs laid at different times in the season (as a function of the time larvae have to feed until the host plant senesces). They concluded that under conditions of relatively high larval mortality, few females (as low as 11%) have enough surviving offspring to replace themselves, and because the earliest emerging females contribute the majority of individuals to the next

generation, effective population size may be substantially smaller than census population size in *E. editha bayensis*. On the other hand, previous studies suggested that by selecting hosts that had not senesced, which is a smaller and smaller subset of plants as time goes on, reproductive success may hold constant for some portion of the flight season. In 1970, for example, Singer and Ehrlich (1979) reported that groups of eggs laid two and three weeks after the beginning of the flight season had a nearly equal chance of surviving at egg hatch (71% and 74% of groups, respectively, died). Including *Castilleja* in the larval diet also extends the foraging period and may boost larval survival relative to feeding only on *P. erecta*, particularly for eggs laid later in the season (Singer 1972, Hellmann 2002a). Cushman et al.'s (1994) analysis considers effects of senescence on larvae, not on oviposition, and considers only the dynamics of *P. erecta*; therefore the pressures for early emergence described in their analysis are likely to be mitigated somewhat by adaptive strategies of host choice during the flight season (chapter 6).

The Significance of Weather

Studies of Bay checkerspot larvae and their host plants indicated that butterfly abundance is strongly mediated by abiotic conditions. Ehrlich (1965) first suggested that the population dynamics of Jasper Ridge *E. editha* might be climate-sensitive, but year-to-year changes in population size were not correlated among the three principal populations at Jasper Ridge (figure 3.6), subject to the same yearly fluctuations in weather. Comparisons of distribution maps of larval survival with maps of their resources showed that populations in areas C and H depended on different resources (Singer 1971a). Spring survival of larvae in area C was correlated with abundance of *P. erecta*, which had its growth period extended by the digging of gophers. Survival in area H was correlated with the abundance of late-senescent *Castilleja* and of *P. erecta*. From 1969 to 1971, this difference appeared to cause suitable habitat patches to differ in area C in each year, while the larval distribution in area H was more stable. Singer (1971b) suggested that a year without suitable habitat patches was more likely to occur in area C than in area H. Therefore, he predicted that area C should be the less stable of the two populations, and its persistence might depend on intermittent recolonization from area H. Over the period 1961–

69,
win
vers
the
the
tor
197
mor
mul
shov
in tl
pop
pop
to w
F
baye
be s
trem
nia
usua
pop
Bay
sis d
Dob
extre
in ar
are l
plan
diffe
latio
abilit
is ne
cipit
and j
sugg

N_{t+1}/N_t
1
1
1
1

69, the population in area H fared better after dry winters, while the population in area C did the reverse, performing better following wet winters. Thus the data began to indicate a dissimilar response in the two populations to a major environmental factor (rainfall) driving population dynamics (Singer 1971b; figure 3.10). Taking advantage of the much more extensive data set that has by now been accumulated, McLaughlin et al. (2002a, 2002b) have shown that weather conditions play a dominant role in the long-term dynamics and extinction of the populations at Jasper Ridge, and indeed that the two populations C and H exhibited dissimilar responses to weather events (for details, see section 3.5).

Further evidence of the sensitivity of *E. editha bayensis* populations to weather conditions can be seen in their gross responses to weather extremes. Ehrlich et al. (1980) found that the California drought of 1975–77 was “correlated with unusual size changes” in a number of *E. editha* populations in distinct habitat types. Each of five Bay checkerspot populations included in their analysis declined over the drought period (figure 3.11). Dobkin et al. (1987) showed that several years of extremely heavy rainfall caused population declines in area H at Jasper Ridge. Both drought and deluge are hypothesized to alter the timing of the insect-plant interaction, much like temperature, but in different ways. Drought deleteriously affects populations by reducing the period of host plant availability, but deluge slows larval growth. Further work is needed to understand how temperature and precipitation combine to affect the timing of larval and plant development; work by Hellmann (2002c) suggests that both temperature and moisture avail-

ability are critical determinants of plant senescence and larval growth rates.

Historical sensitivity to climate and weather suggests that checkerspot populations will be strongly affected by shifts in climate (Murphy and Weiss 1992, Parmesan 1996, Parmesan et al. 1999). Mechanistic models of the relationship between larvae and plants suggest that the dynamics of Bay checkerspot populations in particular will be markedly affected by climate change (Hellmann et al. 2004). Small changes in the temporal overlap of larvae and host plants, as could be caused by a shift in mean regional temperature, may result in significant changes in population growth rates. One model of host plant senescence and larval movement between host plants indicates that if senescence relative to diapause occurs 10% sooner, a currently viable population could be extirpated in fewer than 60 years (Hellmann et al. 2004). Populations of mobile larvae that are able to take advantage of longer-lasting hosts (*Castilleja*) will fare better under such a scenario, suggesting the importance of polyphagy in buffering populations against environmental variation and change. More recent evidence suggests that climate change in the form of increased climatic variability may already be affecting checkerspot butterfly populations (McLaughlin et al. 2002a; section 3.5).

Microclimate and Spatial Variation of Environmental Factors

Weather varies across time and space, of course, and weather and topography interact to create a spatial component in the dynamics of local checkerspot

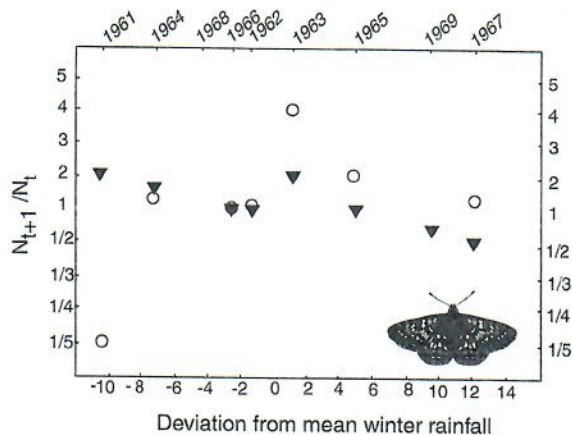


Figure 3.10. Early illustration of the relationship between rainfall (deviation from mean of winter rainfall, November–March of year t in inches) and proportional change in population size between years t and $t + 1$ in area C (open circles) and area H (filled triangles) at Jasper Ridge, as based on Singer (1971a). Correlation between the difference of the N_{t+1}/N_t values for the two habitats and the corresponding rainfall value is significant at $p = .017$ (Spearman rank correlation), suggesting a dissimilar response in the two populations.

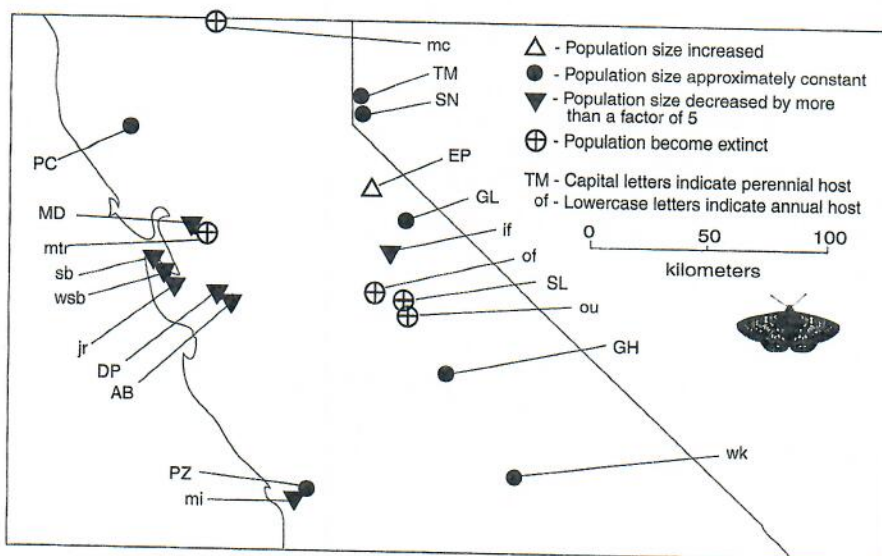


Figure 3.11. Responses of *Euphydryas editha* populations to the California drought of 1975–77 (after Ehrlich et al. 1980).

populations. Using a combination of biophysical modeling, empirical field studies, and population modeling, Weiss et al. (1988) examined the complex relationships among weather, topography, and dynamics of the Bay checkerspot butterfly at Morgan Hill. Topoclimates, or topographically mediated microclimates, strongly affect the distribution and abundance of larvae and butterflies within a habitat (Geiger 1965). We commonly think of weather as a mean condition that applies over an entire region at a given time, but for many small animals and plants, weather is a local phenomenon. Weather experienced by individual organisms is affected by factors such as surrounding vegetation and soil type and, strongly, by topography.

Initial site surveys at Morgan Hill indicated that the size of the population and the habitat that supported it were at least two orders of magnitude larger than at other known sites (figure 3.2). Approximately 1500 ha of serpentine grassland exist along a main ridge, and adjacent smaller patches of habitat are found on numerous side ridges and in canyons across an elevational range of 300 m (figure 3.12, plate V). Slopes facing all compass directions reach 40°. Surveys in 1984 and 1985 indicated that adults, host plants, and nectar sources were widespread across the habitat but that postdiapause larvae were found primarily on cooler north- and east-facing slopes. Abundance and survival appeared to vary by slope also at Jasper Ridge (Singer

1972), but the Morgan Hill site offers much more topographic diversity, habitat area, and denser populations in which to study this phenomenon.

Using insolation models for tilted surfaces (measurements of in-coming solar radiation) and field measurements of temperature, Weiss and colleagues translated the complex terrain of the Morgan Hill into a thermal gradient. Weiss et al. (1988) observed striking spatial variation in surface temperature across the grassland in relation to insolation (figure 3.13), similar to that observed at Jasper Ridge by Dobkin et al. (1987). Surface temperatures in short grassland vegetation with a high proportion of bare soil are strongly influenced by insolation. Noontime surface temperatures on south-facing slopes can exceed air temperature by 20–30°C through the growing season, and those on flat areas exceed air temperatures by 5–12°C. In contrast, surface temperatures on north-facing slopes can be at or below air temperature. Within a slope there can be as much as a 15°C difference between the warmest and coolest spots. For small foraging caterpillars, this variation can be the difference between successful foraging and overheating, finding senescent or nonsenescent host plants, or growing slowly or quickly. We briefly discuss the effects of topography on several life stages and aspects of *E. editha bayensis* life history.

Topography influences postdiapause larval growth. Postdiapause larvae must grow from about 3 mg to 300–500 mg to reach a size at which they



Figure 3.12. Aerial photograph of the Morgan Hill, showing topographic heterogeneity. Photo by Paul R. Ehrlich.

can pupate. After larvae break diapause and begin feeding in the winter, maximum air temperatures are well below the body temperatures required for larval growth. Postdiapause larvae are efficient solar collectors; their black color (plate VIII.2) maximizes absorption of insolation, and their setae (the hairy structures protruding from the body) minimize convective heat loss (Weiss et al. 1988). When basking, last instar larvae reach temperatures 10–12°C above air temperatures near the ground. Because insolation varies across slopes, ground-level temperatures, larval body temperature, and larval growth rates also vary spatially. Field collections of larvae demonstrated that those on warmer slopes were several weeks ahead in development compared to those on cooler slopes. Weiss and colleagues (1987) weighed cohorts of postdiapause larvae, marked them, and released them on various slopes through the growing season. Gains in larval mass were a linear function of slope-specific insolation, with a maximum growth rate of about 50 mg/day for last instars. Postdiapause larvae also could disperse up to 10–20 m/day, which allowed them to transfer from cooler to warmer slopes and speed their development by a week or more.

Topography also modifies the development of pupae. Placement of pupae on various slopes in the

field showed that pupae, like larvae, develop faster on warmer slopes than on cooler slopes and that development rate is proportional to insolation (Weiss et al. 1988, Weiss and Murphy, 1993). Extreme heat experienced in some portions of the habitat also appears to cause pupal mortality. Ninety percent of one sample of pupae placed on a south-facing slope during a March heat wave ($T_{air} > 30^{\circ}\text{C}$) were killed by surface temperatures that were well over 40°C (Weiss, unpub. data). Pupae are likely to be better protected than other life stages, however, in most field situations, because they are normally in sheltered positions and protected by a small amount of silk webbing (plate VIII.5).

Differences in larval and pupal development across slopes lead to differences in adult emergence times across the topoclimatic gradient. Empirical relationships between insolation, air temperature, and the growth and development rates of postdiapause larvae and pupae have been integrated into a climate-based computer model (Weiss et al. 1993) (also implemented in a Geographic Information System [Weiss and Weiss 1998]) that predicts dates of adult emergence across complex topography. The models predict the course of development by summing slope-specific insolation over time, with adult emergence requiring a total of 630 MJ/m² of inso-

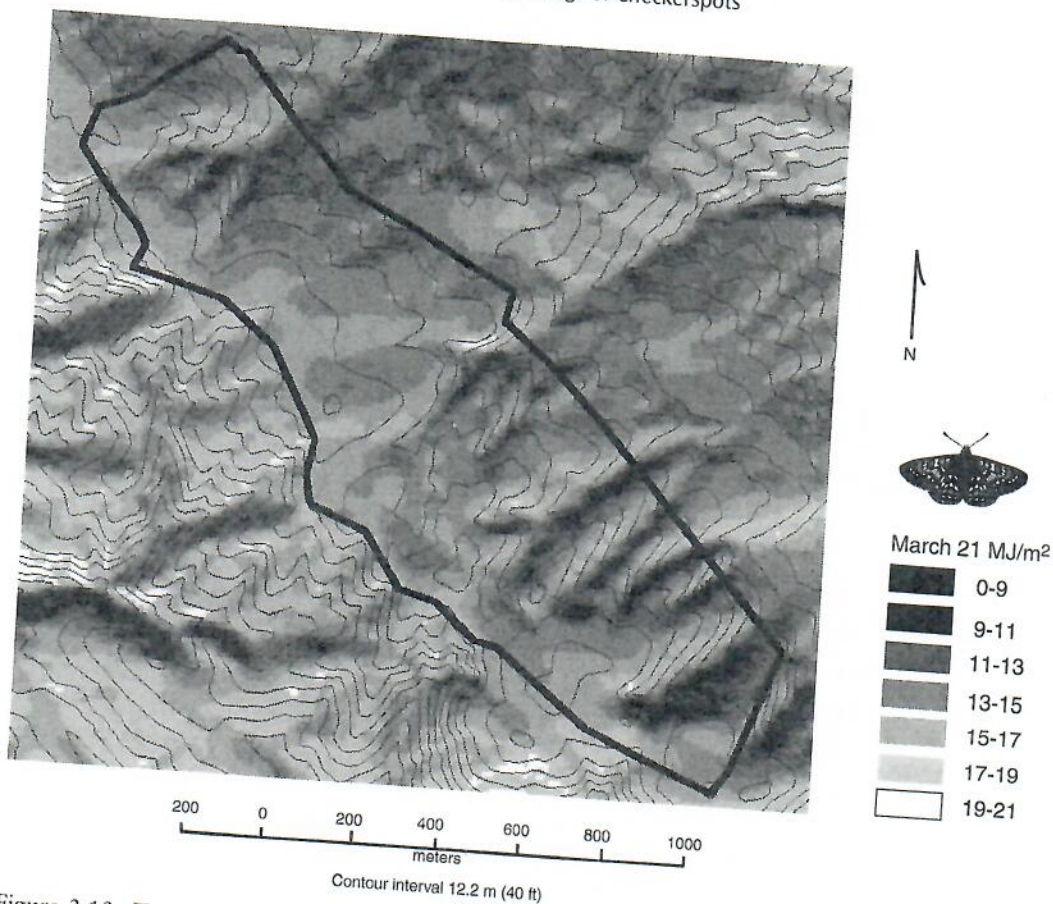


Figure 3.13. Topographic map of the Kirby Canyon Butterfly Preserve (~100 ha) at Morgan Hill showing March 21 insolation. Morgan Hill is the largest and most topographically diverse of the Bay checkerspot habitats.

lation accumulated over sunny days (larvae grow slowly under cloudy and rainy conditions). The model also allows for simulation of adult emergence curves for any given weather sequence, topographic configuration, and distribution of larvae. The results of simulation for the years 1976–89 indicate that the spatial variation in adult emergence (the difference between extreme north- and south-facing slopes) is about 43 days, greater than the amount of year-to-year variation in emergence (28 days) on the same slope. The emergence curve is also affected by the distribution of postdiapause larvae on different slopes. Observed changes in larval distribution were shown to alter mean emergence date in this model by 10–12 days. These results suggest that the size and shape of the emergence curve for adult butterflies is determined by macroclimate, topoclimate, and historical larval distributions and var-

ies among sites due to local topography and differences in larval distributions.

Just as development and emergence vary in space with topography and topoclimate, so does host plant phenology. Recall that larvae experience different host plant conditions in different locations within a given habitat area just as they do in different years (Fleishman et al. 2000b, Hellmann 2002c). To estimate when the host plants undergo the various stages of their life cycle, Weiss et al. (1988) set up transects in the field to assess visually their dates of initial flowering, peak flowering, average flowering, and senescence. *Plantago erecta* phenology at Morgan Hill exhibited a four-week difference in peak flowering between years (1990 and 1991) and a two to four week difference between slope extremes within the same year (south 22°; north 30°; figure 3.14). Data for *Castilleja densiflorus* and *C.*

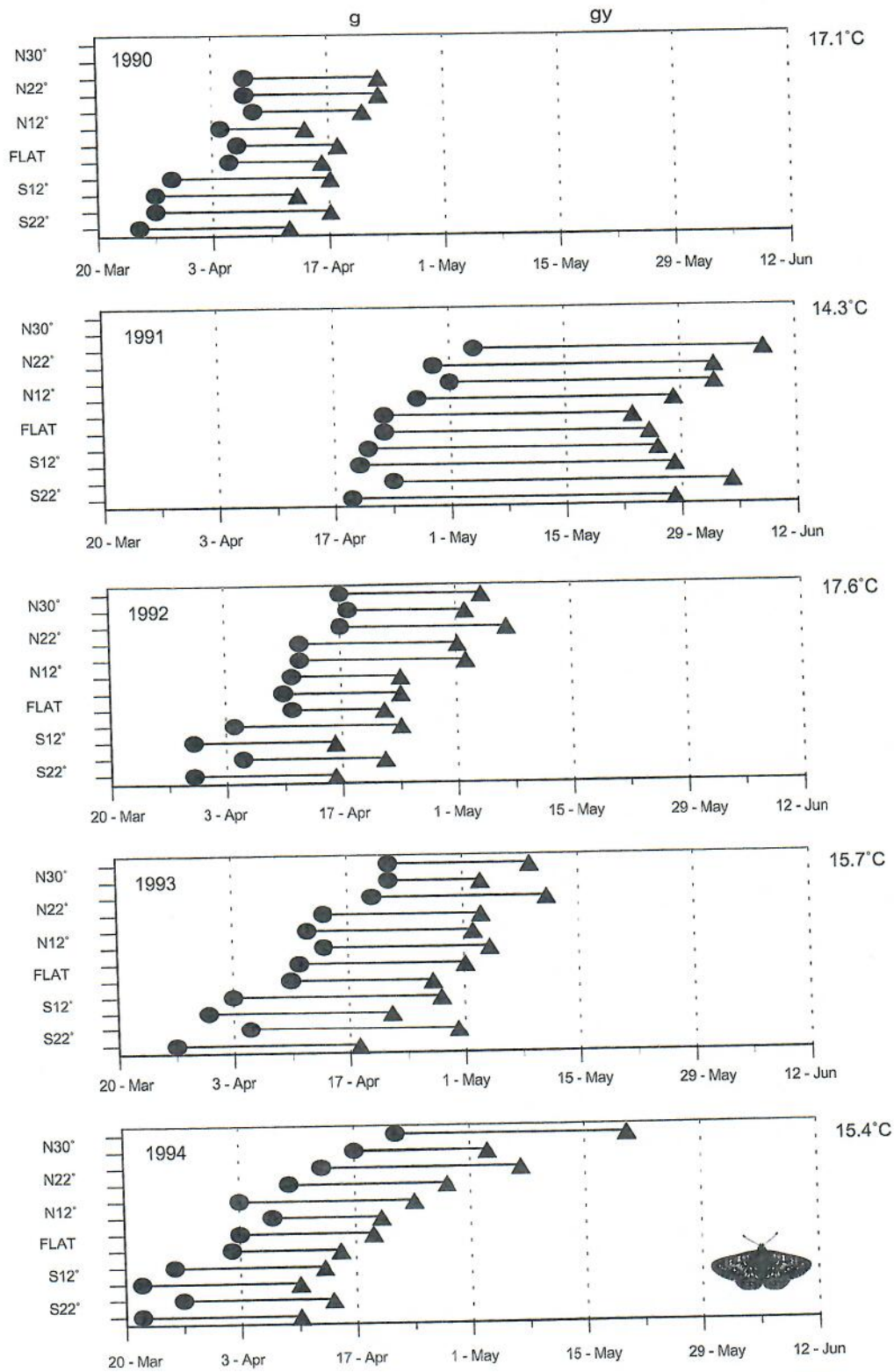


Figure 3.14. Timing of peak flowering (circles) and senescence (triangles) assessed visually across slopes at Morgan Hill from 1990 to 1994 for *Plantago erecta*. Mean temperature in April is given on the right.

exserta were similar, but those species flowered, on average, 10 and 17 days later than *P. erecta*. Warmer temperatures in April shortened the time to senescence, and cooler temperatures prolonged it. Nectar sources also showed the same phenological patterns, so that topographic diversity assures availability of nectar through the flight season. These observations of senescence are similar to other visual assessments made at Jasper Ridge (Dobkin et al. 1987) and are confirmed by nutrient analysis of plants grown in the greenhouse (Hellmann 2002c).

Integration over Space and Time

The distribution of postdiapause larvae across habitats and over time reflects the significance of larval-plant interactions, weather, and topography to Bay checkerspot populations. Singer's early study of spatial patterns of larval survival at Jasper Ridge (Singer 1971b, 1972) and later studies at the larger Morgan Hill site showed that the distribution of postdiapause larvae generally expands and contracts over the topoclimatic gradient. The hypothesis is that the interaction of climate and topography drives this process: favorable weather leads to relatively high survival on a range of slope types, but unfavorable weather precludes survival on all but the coolest of slopes (assuming that host plant resources are equally abundant on slopes of all exposures). At Morgan Hill, for example, postdiapause larvae cover a wide range of slope types when abundance is high, but when population size is small, a greater proportion of larvae are found on moderate to cool slopes (Weiss et al. 1988, 1993). This phenomenon is illustrated for the period 1985-91 in figure 3.8. From 1985 to 1987, the Morgan Hill population grew from 100,000 to nearly 1 million larvae, while at the same time the proportion of larvae on warmer slopes increased markedly. During the large decline from 1988 to 1989, the larval population retreated back to cooler slopes. Postdiapause larvae indicate where prediapause larvae survived to diapause in the previous spring, reflecting patterns of host senescence that vary with slope exposure and gross environmental conditions.

Effect of Other Factors on Population Dynamics

Factors other than prediapause mortality from starvation seem to play a secondary role in the dynam-

ics of *E. editha bayensis* populations. Estimates based on field-collected larvae suggest that parasitism is low in most extant populations in the Bay area (White 1986; chapter 8). Birds and other vertebrate predators are rarely observed feeding on adults or larvae. Spider predation may occur, as does parasitism or predation of pupae (White 1986) and some egg predation. Habitat-wide resource limitation due to larval host plant defoliation has not been observed in populations of this ecotype. Finally, nectar availability may be important in extending adult fecundity and the number of eggs laid (Murphy et al. 1983), but like predation, it does not appear to affect dynamics to the degree that host senescence does. In other populations of *E. editha*, the influence of these factors can be quite different, however. For example, Moore (1989a) found a high level of parasitism, and David Boughton (pers. comm.) reports intense resource competition at Rabbit Meadow in the Sierra Nevada mountains.

3.5 Population Extinctions

Theoretically oriented ecologists have historically been preoccupied with the necessity of some density-dependent factors operating in population dynamics to keep populations from reaching excessive densities. Empiricists have often been more preoccupied with the question of which factors are mostly responsible for the observed population dynamics. Controversies have occurred over how to interpret empirical results in which no evidence for density dependence could be found. These views can be largely reconciled if one assumes that density-dependent factors can act either constantly or so infrequently that they have little observable effect on short-term population behavior. It is in this perspective that we should view the results on *Euphydryas editha bayensis* population dynamics, with the apparent dominance of weather-related density-independent processes.

In this section, we examine the causes of population extinction in *E. editha bayensis*. By analyzing actual extinction events, well documented for the Jasper Ridge populations (figure 3.7), we may uncover which factors affect *E. editha* populations most strongly. Drawing upon the population processes outlined above, we explore five possible explanations for the population losses we have seen at Jasper Ridge (table 3.2).

Table 3.2. Hypotheses about the causes of extinctions in *Euphydryas editha bayensis* populations at Jasper Ridge Biological Preserve.

Hypothesis	Predictions ^a	Evaluation
1. Habitat loss	(a) Extinctions below threshold in habitat number and isolation	(a) Yes
2. Weather	(b) Spatial synchrony within large habitats	(b) No
	(a) Extinctions follow severe or protracted droughts	(a) Yes: JRC; no: JRH
	(b) Extinction in JRC before JRH	(b) Yes
	(c) Weather variables forecast population fluctuations	(c) Yes
	(d) Declining long-term trend in growing season rainfall	(d) No; increasing trend
3. Plant declines	(e) Long-term increased variation in rainfall or temperature	(e) Yes; increased variability in rainfall
	(a) Correlation between plant cover (year $t - 1$) and butterfly population size, N_t	(a) No: <i>Lasthenia</i> ; yes: <i>Plantago</i> and JRH
4. Parasitoids	(b) Similar responses in JRC and JRH to plant declines	(b) No; inverse responses
	(a) Strong or complex endogenous population dynamics	(a) No; endogenous component weak, both populations
5. Human impact	(b) Generalist parasitoid: density-independent mortality	(b) No; asynchronous dynamics, driven by weather
	(a) Detectable effects of destructive sampling	(a) Maybe (Harrison et al. 1991)
	(b) Large population decreases following intensive study	(b) No

^aJRC, Jasper Ridge habitat area C; JRH, Jasper Ridge habitat area H.

Unfavorable Weather

As outlined in section 3.4, populations of the Bay-area ecotype of *Euphydryas editha* decline after years with extreme weather (hot and dry or cold and wet) because these extremes reduce the temporal overlap of larvae and plants (Singer 1972, Cushman et al. 1994, Hellmann 2002c). Based on this observation, extinctions should follow a sequence of several years of unfavorable weather, conditions that push population size steadily lower. Our understanding of topographic effects on *E. editha bayensis* also suggests that when extinctions do occur, they should happen sooner in habitats with relatively little topographic heterogeneity because topographic diversity reduces the impact of extreme weather (Singer and Ehrlich 1979, Dobkin et al. 1987, Ehrlich and Murphy 1987a, Weiss et al. 1988).

Unfavorable weather, such as droughts in 1976–77 and the late 1980s, and extremely wet winters of 1996 and 1998, did precede large declines in abundance at Jasper Ridge. Extinctions of populations in areas C (1991) and H (1998) followed such events (figure 3.7). Furthermore, extinction occurred first in area C, the larger but more topographically homogeneous patch. More refined predictions have recently been made by McLaughlin et al. (2002b), who modeled the population dynam-

ics that would result from various mechanisms acting on the Jasper Ridge populations, including endogenous (density-dependent) factors, exogenous effects of weather, and combined influences of both endogenous and exogenous factors. The structure of the model is explained in box 3.1. In both areas C and H, McLaughlin et al. found that population fluctuations were largely driven by climatic variability: rainfall in year t predicted population size in year $t + 1$. The timing and the form of the weather effects differed between the two areas. In area C, where the topography is more homogenous and thus microclimates are more uniform, the effect of weather was severe. In area H, where topography and microclimates are more variable, the population showed damped oscillations over time and weaker effects of weather on population size. Differences in the dynamics of the two populations are evident in the dissimilar shapes of the response surfaces produced by the models (figure 3.15).

Historical data indicate that extreme weather became more frequent toward the demise of the populations' at Jasper Ridge. Seasonal rainfall data from San Jose, California (National Climatic Data Center [NCDC] 2001), the longest climate data set available in the region, show an upward but not statistically significant trend in the total seasonal rainfall, but, more important, they show an increase

BOX 3.1 Model of Population Dynamics at Jasper Ridge

Population modeling provides a powerful approach for testing hypotheses about population dynamics (Kendall et al. 1999). Population dynamics can be reconstructed from time-series data using response surface methodology (RSM; Box and Draper 1987, Turchin and Taylor 1992, Turchin 1996). RSM predicts population growth rates using generalized polynomial regression of transformed independent variables. The method is highly flexible: it evaluates diverse functional forms, considers several model dimensions (number of variables included), and can detect nonlinearities and time lags in population dynamics (Turchin 1995). Other methods sharing these advantages (Sugihara and May 1990, Ellner et al. 1991) require longer time series than are available for *E. editha bayensis*.

Changes in population size can be caused by endogenous (density-dependent) feedback, exogenous factors (e.g., weather events), or interactions between endogenous and exogenous factors. These three kinds of dynamics can be modeled using time-lagged population data, weather data, and combinations of population and weather data (Lewellen and Vessey 1998). Details about the modeling method and results for *E. editha bayensis* are in McLaughlin et al. (2002b).

Modeling Endogenous Dynamics To model endogenous effects of multiple factors when only population data are available, RSM uses an equation containing multiple time lags. Equation 3.1 represents per capita rate of population change, N_t/N_{t-1} , as a function of population size in d previous years, N_{t-i} , and exogenous noise, ϵ_t :

$$N_t/N_{t-1} = f(N_{t-1}, N_{t-2}, \dots, N_{t-d}, \epsilon_t). \quad (3.1)$$

The response surface (figure 3.15) is constructed by approximating f , using polynomial combinations of transformed predictor variables ($X \equiv N_{t-i}^{\theta_i}$) and r log-transformed rate of population change, $r_t \equiv \log_e(N_t/N_{t-1})$. Equation 3.1 reduces to equation 3.2 for a two-dimensional model ($d = 2$) with quadratic dependence ($q = 2$) on transformed predictor variables $X \equiv N_{t-1}^{\theta_1}$, $Y \equiv N_{t-2}^{\theta_2}$:

$$r_t = a_0 + a_1X + a_2Y + a_{11}X^2 + a_{22}Y^2 + a_{12}XY + \epsilon_t. \quad (3.2)$$

Model dimension (d), polynomial degree (q), and variable transformations (θ_i) are determined in different steps to avoid selecting spuriously complex models. The best model is selected with cross-validation, which identifies the model with greatest prediction accuracy (Efron and Tibshirani 1993, Turchin 1996). Prediction accuracy is measured with the prediction coefficient of determination, R_p^2 (Turchin 1996), for log-transformed population size ($L_t = \log N_t$), which depends on the ratio of the mean square prediction error to population variance,

$$R_p^2 = 1 - \frac{\sum_i (L_i - \hat{L}_i)^2}{\sum_i (L_i - \bar{L})^2}, \quad (3.3)$$

where \hat{L}_i is abundance predicted in year i , and \bar{L} is the mean of the log-transformed abundances L_i . Potential values for R_p^2 range from 1, indicating perfect prediction, to $-\infty$. RSM includes a given variable only if that variable increases prediction accuracy.

Modeling Exogenous Dynamics Models for exogenously driven changes in *E. editha bayensis* populations contained total growing season (October–April) rainfall
(continued)

for each year as a predictor variable. Exogenous models included rainfall data from either the current growing season (W_t), the growing season in the year preceding adult flight (W_{t-1}), or both:

$$N_t/N_{t-1} = f(W_t, W_{t-1}). \quad (3.4)$$

Mixed Endogenous-Exogenous Models A third class of models includes both lagged population size and total growing season rainfall as predictor variables. Equation 3.5 is a two-variable mixed model containing the endogenous variable N_{t-1} and the exogenous variable, W_{t-1} :

$$N_t/N_{t-1} = f(N_{t-1}, W_{t-1}). \quad (3.5)$$

In practice, equation 3.5 is transformed to a form analogous to equation 3.2.

Simulating Population Dynamics Simulating population trajectories reveals dynamical properties extracted by each kind of model. Simulations with endogenous models run freely from a starting population size. Simulations with exogenous or mixed endogenous-exogenous models can be run with the observed sequence of precipitation data (McLaughlin et al. 2002b) or with precipitation data representing various climate scenarios (McLaughlin et al. 2002a). Simulation results in figure 3.17 were obtained using random samples of precipitation data (figure 3.16) from decades with low (figure 3.17a, b) and high (figure 3.17c, d) variability.

in variance over time (figure 3.16). McLaughlin et al. (2002a) found that variance in seasonal precipitation was significantly higher in intervals just before the extinction of the two populations than in the early part of the time series. Simulation of population responses confirmed that increased variability can cause greater population fluctuations and increased extinction risk. Based on a shift in the variance of the precipitation record, McLaughlin et al. (2002b) divided the precipitation data into two periods corresponding to the past (pre-1971) and the present climate (post-1971). Using the model described in box 3.1, they simulated replicate trajectories for each population using the data, adjusted to reflect conditions at Jasper Ridge before and after 1971. They found that under the historical regime, conditions prevailing before 1971, simulated populations in area C persisted an average of 444 years and populations in area H an average of 162 years (figure 3.17). Under the current regime (post-1971), however, the average persistence time of the population shifted significantly downward to an average of 19 years for the population in area C and 52 years for the population in area H. This strongly suggests that it was not just unlucky sequences of weather, but shifts in the underlying

climate that caused the demise of the Jasper Ridge populations.

Loss of Habitat Connectivity

Numerous factors may have set the stage for climate to drive population extinctions in *Euphydryas editha*. In particular, widespread declines in the area and connectivity of native grasslands likely reduced the available habitat for this butterfly, possibly affecting its ability to withstand weather extremes. Any reduction in population size or rates of butterfly immigration from neighboring populations may have decreased the life span of the Jasper Ridge populations and be the ultimate cause for population losses. Unfortunately, the process of invasion by Eurasian grasses into California was essentially complete before *E. editha* came under scientific study (Murphy and Ehrlich 1989). However, several indirect pieces of evidence support the influence of habitat loss on population sustainability and time to extinction.

Because currently suitable habitat is distributed in discrete patches (figure 3.2), we can use metapopulation theory to examine the likelihood of regional persistence of the Bay checkerspot butterfly (see box

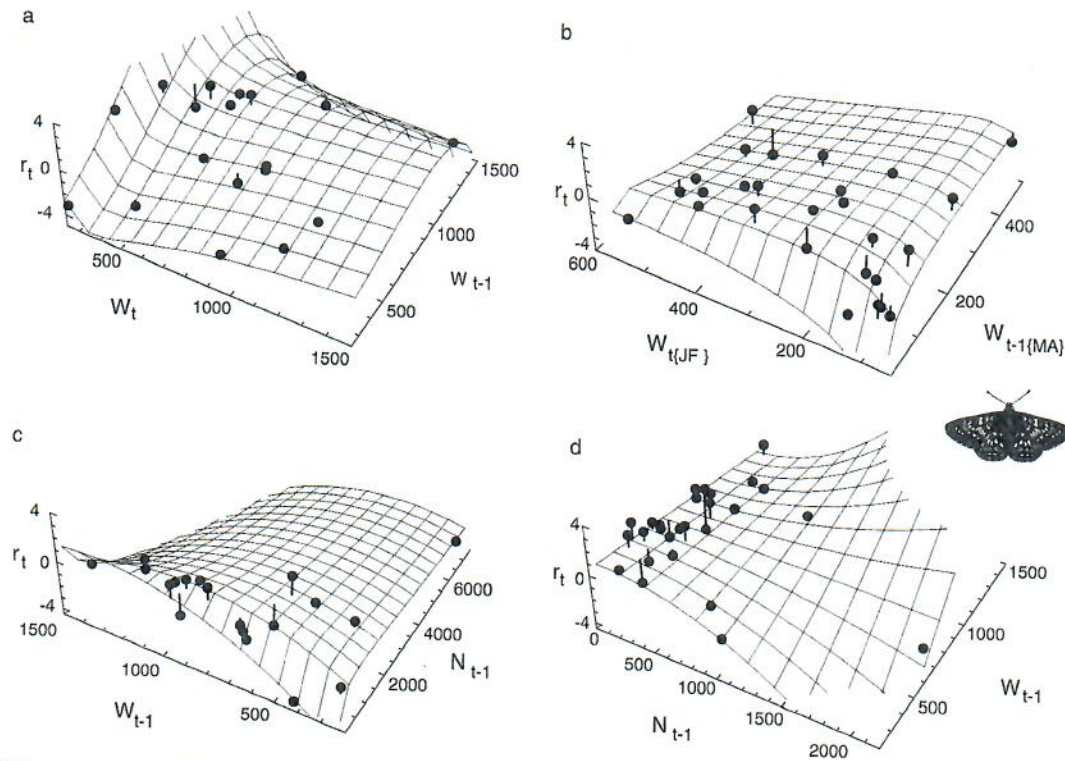


Figure 3.15. Response surfaces for population growth of *Euphydryas editha* at Jasper Ridge. Estimates of growth rate (r_t) are plotted against population size in the previous year (N_{t-1}) and/or rainfall (W) using the exogenous and mixed endogenous–exogenous models of box 3.1 (McLaughlin et al. 2002b). Points are the observed growth rate. The lines from these symbols to the surface illustrate the magnitude of residual variation. The data for the population in area C are shown in (a) using an exogenous model with total growing season rainfall in the current and preceding year as predictor variables and in (c) using a mixed endogenous–exogenous model. The data for the population in area H are shown in (b) using an exogenous model with winter (January–February) rainfall in the current year and spring (March–April) rainfall in the preceding year as predictor variables and in (d) using a mixed endogenous–exogenous model.

12.1). As a rule of thumb, a meta-population consisting of extinction-prone but well-connected local populations should inhabit a network of at least 15–20 patches to be viable (Gurney and Nisbet 1978, Hanski et al. 1995b, Hanski and Ovaskainen 2000). Viability here means that the lifetime of the metapopulation is much longer than the lifetime of an average local population. Empirical data on butterfly metapopulations in Europe support the existence of a threshold value of around 20 patches (Thomas 1994a, Hanski et al. 1995b). This value exceeds the current number of Bay area habitat patches by a factor of at least 2 (Murphy and Weiss 1988a). Furthermore, some of these patches are currently so isolated that it is doubtful whether any migration occurs among them (figure 3.2). A caveat here is that some remaining habi-

tat patches may be sufficiently large (such as Morgan Hill) that their expected time to extinction of their populations is very long. The small and isolated habitats at Jasper Ridge, however, do not likely fall into this category. For the Bay checkerspot butterfly to persist to modern times at Jasper Ridge, the populations in areas C and H must have been linked to large, high-quality “reservoir” habitats that were close by. No such sites have occurred since the 1970s, suggesting that the loss of neighbors or larger habitat areas was the ultimate reason that populations like those at Jasper Ridge could no longer persist. Before the 1970s, the Woodside population, less than 5 km away (figure 3.2), may have filled this reservoir role. This population was reported to have had a very high population density.

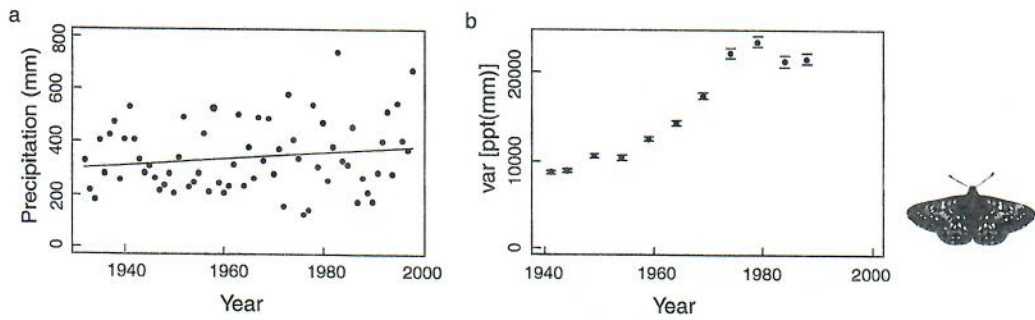


Figure 3.16. Historical precipitation records for San Jose, California, the longest sequence of local weather data on record (McLaughlin et al. 2002a). The total rainfall accumulated during the growing season from 1932 to 2000 is given in (a), where the regression line shows a nonsignificant increase in rainfall over this period ($p = 0.15$). The variance in rainfall, shown in (b), is calculated as bootstrap means and standard deviations in 20-year intervals. Values are plotted at the 11th year of each interval. Variance is significantly higher at the end (just before extinction of *E. editha* at Jasper Ridge) than at the beginning of the time series ($p = .001$).

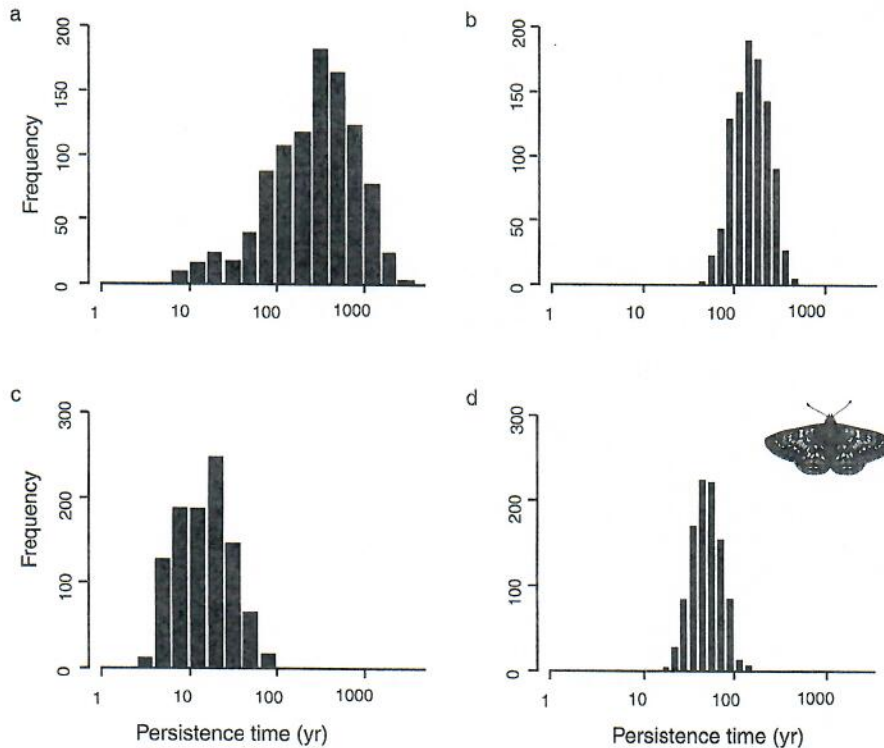


Figure 3.17. Distributions of persistence times in many replicate simulations of the two Jasper Ridge populations under historical and present climate. Simulations were performed using the bootstrapped precipitation data from San Jose (figure 3.16) before and after 1971 and the population models built for Jasper Ridge (McLaughlin et al. 2002a, 2002b; box 3.1). The distribution of times to extinction for simulated populations in area C are given on the left (a and c); the distribution for area H are on the right side (b and d). The mean of the distribution under the historical climate (1932–70), top panels (a and b), is significantly higher than the mean persistence time under the present climate (1971–2000), bottom panels (c and d); $p < .001$).

Loss of serpentine grasslands outside the preserve in more recent decades is not likely to be the proximate cause of declines at Jasper Ridge. The distance between Jasper Ridge and its nearest serpentine habitat exceeds by 100-fold the radius within which adults have been observed to detect habitat and lies at the upper limit of observed adult dispersal (Harrison 1989). Therefore, it is unlikely that the population dynamics at Jasper Ridge were significantly affected by immigration from other populations (or changes in those populations due to any recent habitat losses). Populations at Jasper Ridge may have been rescued by neighboring populations historically, but most recently, the influence of neighbors on the dynamics of the populations at Jasper Ridge was small (see also section 3.6).

Declines in Larval Host Plants or Adult Nectar Sources

Checkerspot butterflies require plants for larval foraging and adult nectaring. Changes in these resources could have caused the extinctions if they became limiting sometime during the lifetime of the Jasper Ridge populations. A decrease in larval host plants one year would reduce adult abundance the following year because adult abundance depends strongly on prediapause larval survival. A decrease in nectar plants also would reduce adult abundance in the following year because nectar abundance limits egg production by adult females, although females emerge with a full or nearly full complement of eggs, and nectar feeding only increases late-

season laying (Murphy et al. 1983, Cushman et al. 1994; but see Boggs 1997b; section 3.4). Recall that the timing of food resources is a prominent feature of the ecology of *E. editha bayensis*, but this factor is not necessarily correlated with total plant abundance.

We can use plant data collected in area C from 1983 to 1993 (Hobbs and Mooney 1995; figure 3.18) to determine whether any changes in plant abundance occurred in the period preceding population extinction. Assuming that changes in plant cover were similar in areas C and H, regression analysis of butterfly abundance against the abundance of *Lasthenia californica*, a major nectar source, and *Plantago erecta*, a larval food plant, indicates that plant declines were not responsible for the population losses (table 3.3). Relationships between butterfly abundance and plant cover were weak, except for a correlation between population size in area H and *P. erecta* cover. In addition, regression slopes for areas C and H were opposite in sign, and there is no reason to expect this difference because most factors affecting plants, such as rainfall and nitrogen deposition, would affect both habitats (differences in gopher abundance could affect plant abundance and would be site-specific, however). Further, even in years of lowest cover, *L. californica* and *P. erecta* grew in excess of potential checkerspot consumption. A final possibility concerning plants is that the removal of cattle from Jasper Ridge in 1960 led to the extinctions. If changes in plants resulted from cattle removal, however, they appear to have been completed by 1983,

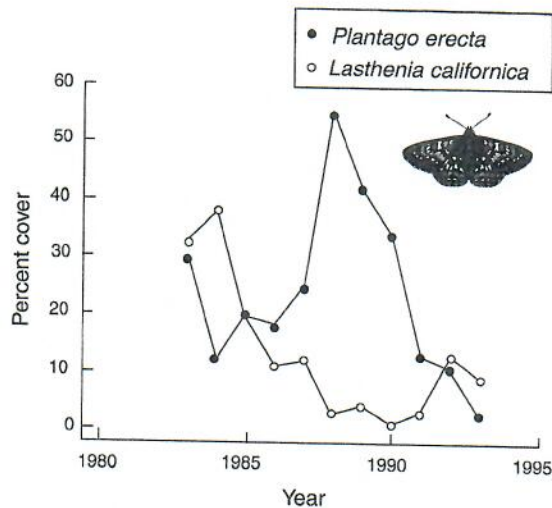


Figure 3.18. Percent cover of *Lasthenia californica*, a nectar plant, and *Plantago erecta*, a host larval plant, at Jasper Ridge as recorded by Hobbs and Mooney (1995).

and th
tion. N
ity tha
resour
years t

Preda:

Long-t
to find
on but
ter 8).
that p
tion lo
the Jas
of thre
density
butter
et al. 2
undar
oscilla
events
dynar
weak
parasi
Altern
(which
shoulc
enous)
ogeno
of the
genera
ics in
not in
sitoid

Table 3.3. Results of simple linear regression of *E. editha bayensis* adult male abundance versus preceding year percent cover of plants used by *E. editha bayensis* adults (*Lasthenia californica*) and larvae (*Plantago erecta*).

Population	Plant Species	<i>n</i>	<i>b</i>	<i>p</i> { <i>b</i> = 0}	<i>r</i> ²
JRC	<i>Lasthenia californica</i>	5	0.15	.271	.38
JRH	<i>Lasthenia californica</i>	11	-0.02	.549	.04
JRC	<i>Plantago erecta</i>	5	-0.08	.762	.04
JRH	<i>Plantago erecta</i>	11	0.06	.015	.50

To normalize distributions, abundance data for males were log-transformed and plant percent cover data were arcsine transformed. Plant cover data were recorded from plots in area C during 1983–93, by Hobbs and Mooney (1995). *b* = slope of regression line. For area C, regressions include data from 1983–88 only because the abundance of *E. editha bayensis* males reached zero in 1988 and never exceeded four individuals thereafter (see figure 3.18).

and this happened well before population extinction. Nevertheless, we cannot rule out the possibility that cattle removal caused a subtle change in the resources of the butterfly population that took many years to lead to extinction.

Predation

Long-term research with *E. editha bayensis* has failed to find a strong influence of predators or parasitoids on butterfly population dynamics (section 3.4; chapter 8). Nevertheless, there are a number of parasitoids that potentially could have contributed to population losses at Jasper Ridge. In the model built for the Jasper Ridge populations (box 3.1), the effect of three specialist parasitoids should appear in the density-dependent (endogenous) component of the butterfly's dynamics (Ehrlich 1965, McLaughlin et al. 2002b). Extinctions would result either from undamped oscillations or from parasitoid-induced oscillations compounded by density-independent events. However, the endogenous component in the dynamics of both Jasper Ridge populations was weak to nonexistent, suggesting that specialist parasitoids had little effect on population declines. Alternatively, the effect of generalist parasitoids (which attack other hosts in addition to *E. editha*) should appear in the density-independent (exogenous) component of the butterfly's dynamics. Exogenous factors strongly influenced changes in size of the populations of both areas C and H, but a generalist also would have caused different dynamics in areas C and H because the populations were not in close synchrony. Furthermore, such a parasitoid also would have been strongly affected by

weather because rainfall explained most of the fluctuations in the Jasper Ridge population models. This combination seems unlikely, however.

Human Disturbance

A final possible explanation for extinction at Jasper Ridge is the destruction of individual butterflies or habitat disturbance caused by people, including researchers. Adults were routinely removed from the populations (Harrison 1991), decreasing reproductive success, and eggs, pupae, or larvae must have been trampled by researchers or visitors. Other impacts could have included trampled plants and compacted soils (Murphy and Ehrlich 1989). If sampling or handling of individuals were responsible for population losses, population decreases should have been particularly severe in years after destructive sampling or intensive study: notably 1964 when all butterflies that were captured were removed from the populations, and 1981 when the population in area H was sampled intensively with mark-recapture methods.

Populations persisted long after the 1964 sampling season—in fact, growing soon thereafter (Hellmann et al. 2003). Using the 1981 data, Harrison et al. (1991) estimated the effects of adult removals from areas C and H. They concluded that population reductions due to destructive sampling were small relative to variability caused by environmental conditions (effects of sampling on population sizes were not statistically detectable). Nevertheless, they estimated that sampling increased extinction risk between 0 and 15%, depending on female egg production before sampling. The effects of intensive

sampling can also be evaluated qualitatively by examining population growth rates between 1981 and 1982. For both populations, the growth rate [$r_t = \log(N_t/N_{t-1})$] in 1982 was less than the mean growth rate over all years but was within half of a standard error of the mean (table 3.4; Hellmann et al. 2003). This means that there were not unusually large decreases in population size immediately after 1981. We also can use the models outlined in box 3.1 to predict the change in population size that would have occurred in area H if it were not sampled intensively in 1981. In this case, the model underestimates the observed decline between 1981 and 1982 (estimated: $r_{1982} = -0.237$; observed: $r_{1982} = -0.340$), but the magnitude of the underestimate is within the model's prediction uncertainty (table 3.4; see McLaughlin et al. 2002b). Although the 1981–82 decline in area H was greater than would be predicted from weather conditions alone, it was not unusually large.

Assuming that the difference between predicted and observed population declines in 1982 was due to direct human impact and that other human impacts in other years had similar effects, the difference between observed and predicted growth rates (table 3.4) provides an estimate of the direct impact of human activities. After subtracting this effect, mean growth rates since 1969 remain negative for both the C and H area populations (adjusted means: $r_{JRC} = -0.047$; $r_{JRH} = -0.152$). Hence, research and other direct human factors may have reduced persistence time marginally at Jasper Ridge, but impacts of other factors were considerably more important.

We conclude that the likely dominant factors in population extinction at Jasper Ridge were climate change, as the proximate cause of extinction, and

habitat loss in the surroundings, as the ultimate trigger for regional decline of the species.

3.6 Regional Dynamics

Although the Jasper Ridge populations have disappeared, other populations of *Euphydryas editha bayensis* still persist. Widespread events, like drought or heavy rain, affect multiple sites, but local events cause widely separated populations to have qualitatively distinct dynamics. Small amounts of dispersal do link habitats and populations together, though not strongly enough to synchronize their dynamics. Dispersal of even a few individuals can also link distant populations genetically, preventing genetic divergence over time at neutral loci (Roughgarden 1979; chapter 10).

A number of researchers have investigated adult movements of *E. editha* with some conflicting results. Brussard et al. (1974) showed that Bay checkerspot adults fly relatively freely within their local habitat and that sexes showed relatively little difference in movement patterns. They also found no apparent pattern that restricted intrapopulation gene flow; thus local populations should be relatively well-mixed. When a butterfly "decides" to leave, albeit infrequently, it typically moves steadily across nonhabitat in a directed fashion. Work by Harrison (1989) showed that butterflies released in nonhabitat areas do not orient toward distant habitat patches.

As for the propensity to move, Brussard et al. (1974) observed higher rates of movement at the beginning and end of the flight season in *E. editha bayensis*. Similarly, Murphy and White (1984) suggested that populations of *E. editha* in southern

Table 3.4. Population declines from 1981 to 1982 in Jasper Ridge *E. editha bayensis* populations and declines predicted by models of population responses to weather conditions (McLaughlin et al. 2002b).

Population	r_{1982}	\bar{r}_t	SE(\bar{r}_t)	$\hat{r}_{>1982}$	Prediction Error	
					$(r_{1982} - \hat{r}_{1982})$	SE $(\bar{r}_t - \hat{r}_t)$
JRC	-0.463	-0.297	0.381	-0.213	-0.250	0.156
JRH	-0.340	-0.255	0.233	-0.237	-0.103	0.158

Differences between observed and predicted declines provide an upper estimate of the impact of intensive mark-recapture sampling conducted in 1981. Growth rates were calculated as $r_t = \log(N_t/N_{t-1})$. r_{1982} is the growth rate observed in 1982; \hat{r}_{1982} is the growth rate predicted in 1982 using population response models. \bar{r}_t is the mean observed growth rate over all years. SE $(\bar{r}_t - \hat{r}_t)$ is the standard error of the mean difference between observed and predicted growth rates. For JRH, the prediction error in 1982 is within one standard error of the mean prediction error (mean = 0).

California show variable dispersal rates and changes in vagility across generations. In these southern populations, changes were largely driven by changes in resource availability: when resources were scarce, vagility increased. Work by Sisk et al. (2004), in contrast, suggested that dispersal rates of *E. editha bayensis* do not increase when resources are limiting at the end of a flight season. They also did not find a seasonal, locational, or interannual difference in dispersal rates. The relative constancy of low interpatch dispersal at Jasper Ridge over time also suggests that dispersal in *E. editha bayensis* is not strongly correlated with population size.

Evidence for Metapopulations

A metapopulation is a set of local populations connected by migration (Harrison et al. 1988, Hanski 1999b). In metapopulation theory, the risk of extinction of a local population often is assumed to be a function of the area of the respective habitat patch (box 12.1). The probability that a currently unoccupied site will receive colonists from existing populations is assumed to decline with distance. Because populations of *E. editha bayensis* appear to go extinct relatively frequently but exist in a shifting mosaic of distinct populations, some groups of habitat patches may support metapopulations.

To test this hypothesis, Harrison et al. (1988) examined the occupancy and characteristics of small habitat patches surrounding the Morgan Hill colony (figure 3.2). Initial surveys suggested that distance from Morgan Hill was a key factor in whether a patch was occupied by checkerspots. In 1986, 8 small patches within 4.4 km of Morgan Hill were occupied, but none of a possible 15 patches outside this radius were occupied. Assuming that the small habitat patches have ephemeral local populations, these results suggest that the maximum colonization distances are around 4–5 km, which is the same as for *Melitaea cinxia* (van Nouhuys and Hanski 2002a; chapter 4). Harrison (1989) found that butterflies released into nonhabitat could fly up to several kilometers and not locate suitable habitat. She also estimated, however, that the probability that a dispersing female successfully reproduces in her new habitat is small. Transplants of postdiapause larvae in 38 patches produced adults in only 6 sites 1 year later. Harrison et al. (1988) found that a logistic regression including distance from Morgan Hill, topographic composition, and abundance of larval and nectar plants significantly explained the pres-

ence or absence of butterflies in 59 potential patches in the neighborhood of Morgan Hill. This implies that both distance from the source population and habitat quality (topography and plant abundance) determine patch occupancy. Because of this distance-dependent occupancy, local populations in the Morgan Hill area appear to constitute a metapopulation. In particular, they conform to the mainland-island model of metapopulations—a metapopulation with one large source of colonists surrounded by smaller, extinction-prone satellites. The other metapopulation study of *E. editha*, at Rabbit Meadow (chapter 9), exhibits a structure more akin to the classic model (box 12.1) than to the mainland-island model (Hanski 1999b), where all local populations have a significant risk of extinction (C. D. Thomas et al. 1996).

It is important to realize that the total abundance and number of sites occupied by *E. editha bayensis* appears to be steadily declining over time. Recent human development and the invasion of historical habitats by grasses has likely increased the isolation between the sites (considering both actual distances and the hospitality of interpatch matrix to movement), which would decrease the number of occupied sites. As we argued above, there currently are too few habitat patches on the San Francisco Peninsula, including Jasper Ridge, to sustain a metapopulation over the long-term. It also seems unlikely that remaining sites on the peninsula are close enough for much interpatch colonization to occur (figure 3.2). Neighboring sites, which were fairly distant by the 1990s and with relatively small population sizes, did not rescue the populations at Jasper Ridge from extinction. For that matter, the long-lasting population in area H did not rescue its nearest-neighbor populations from extinction (the populations in areas C and G).

Genetic Similarities among Local Populations

Dispersal affects the genetic composition of populations as well as their abundances. Baughman et al. (1990a) examined the genetic differentiation among *E. editha* populations (including *bayensis*) to determine the degree to which populations and subspecies shared either a recent common ancestor or current gene flow. Examining allozyme variation at 19 loci, they concluded that either a significant amount of gene flow occurs among populations or there is strong stabilizing selection. These patterns

may reflect historical connectivity, rather than current gene flow, however (Slatkin 1987). Before the invasion of non-native grasses and/or before the last glaciation (8,000–10,000 years ago), checkerspot populations may have had greater dispersal among habitat patches (section 3.5). Alternatively, the amount of dispersal that could be inferred from Harrison et al.'s (1988) results may be sufficient to prevent significant genetic differentiation among *E. editha bayensis* populations over time. It is not possible at present to estimate which of these explanations is more likely.

Other characters such as morphology and host plant use tell a very different story of population differentiation. Groups of *E. editha* populations defined on the basis of allozyme data do not correlate well with groups delineated by morphology (subspecies classifications) or host plant use (Baughman et al. 1990a). This suggests that host choice is not a good indicator of genetic relatedness or gene flow via dispersal among populations; diet seems to be a relatively plastic trait, and ecotypes using new hosts seem to evolve relatively quickly (Singer et al. 1992a, Radtkey and Singer 1995, C. D. Thomas et al. 1996). This lack of correlation also suggests that the subspecies that have been described for *E. editha* are not natural genetic units.

3.7 Other *Euphydryas editha* Ecotypes

To put the work described above in a broader context, we briefly contrast the qualities of Bay area populations with other *E. editha* populations. One of the early results of extending research beyond Jasper Ridge was that *E. editha* did not have an "ecology" per se but rather that populations and groups of populations had distinctive sets of ecological relationships (Gilbert and Singer 1973, Ehrlich et al. 1975). One of the simplest ways to contrast these relationships is to examine population responses to the abiotic environment, notably drought. We already mentioned (section 3.4) that *E. editha bayensis* populations respond negatively to drought, presumably via effects on the timing of host senescence relative to prediapause larval growth. Populations of *E. editha* in the inner coast range (*E. editha luestherae*) show more variable responses to drought than do *E. editha bayensis*. Two of three study populations remained constant after the 1975–77 drought, for example, but one, at Del Puerto Canyon (Figs. 3.1, 3.11), plunged to

a low of three individuals in 1978 before rebounding the next year. Del Puerto Canyon is one *E. editha* population that appears to show strong density dependence in its dynamics. Intensive competition and overexploitation of food resources is responsible for larval starvation at this site, and drought appears to decrease the abundance of the dominant host, *Pedicularis*, thereby exacerbating resource competition.

In southern California, *E. editha quino* populations are similar to *E. editha bayensis* in the ephemeral nature of their hosts and the effect of weather on phenology, but dissimilar in the frequency with which individuals disperse from their natal habitat in response to weather events. The drought of 1975–77 was less severe in southern than in central California, and populations actually experienced great population explosions during this period. At this time, dispersal out of habitat patches also was observed on a number of occasions (Murphy and White 1984). Populations remain sedentary when food resources are plentiful, but dispersal increases after extreme scarcity of larval host plants arising from high population densities (White 1974). Populations of this ecotype are notorious for disappearing from sites and reappearing, presumably because they are easily extirpated from small or otherwise marginal habitats. Between outbreak years, the ecotype presumably persists in only the largest "reservoir" habitats, from which migrants reoccupy many temporarily vacant sites.

In populations of *E. editha* that feed on *Collinsia tinctoria* between 150 and 1800 m elevation on the western slopes of the Sierra Nevada, adults are able to respond adaptively to host phenology and to oviposit on plants that will last long enough to support larvae to diapause (Singer 1971b). As a consequence, mortality of prediapause larvae from host senescence only occurs in severe drought years. However, these insects are also susceptible to climate in the early postdiapause stage. In the drought year of 1977, most *Collinsia* at these sites remained in the seed bank. At one site, Agua Fria, host density was reduced by two orders of magnitude, and only 23 plants could be found (Singer and Ehrlich 1979). Larvae that emerged from diapause would have been unable to find sufficient food to fuel their return to diapause until the following year. Three of the four studied populations of this ecotype became extinct at this time. The sole survivor of this group of populations was the one (Indian Flat) that covered the largest area and had the greatest diver-

sity of host senescence times due to its many different slope aspects.

In populations at moderate elevations (2000 m), annual hosts undergo senescence but perennial hosts do not, while at the highest elevations (above 3000 m), frequent thunderstorms keep vegetation edible all summer even when low elevations are experiencing drought (figure 3.19). One example of a metapopulation relying on both an annual and a perennial host plant occurs at Rabbit Meadow (2300–2400 m; Singer and Thomas 1996, C. D. Thomas et al. 1996, Boughton 1999). Cleared patches where the annual host was used for oviposition occurred interspersed with undisturbed patches where the (traditional) perennial host was used. Insects in the clearings developed fast and were able to oviposit on phenologically suitable annual hosts. Slower developing insects in the undisturbed patches did migrate to clearings but arrived too late to produce surviving offspring (Boughton 1999). When clearings were unoccupied, the phenological differences between the patches generated a set of sources and sinks, with clearings acting as sinks.

When clearings were occupied, these source–sink relationships were reversed (this system is described in greater detail in chapter 9). It is interesting that larval survival in adjacent populations with different hosts was negatively correlated in this system, so that conditions that were favorable in one habitat were unfavorable in the other. This situation is analogous to that in *E. editha bayensis* populations, where different habitats and slopes with dissimilar topography and host plants buffer populations against fluctuations in the abiotic environment.

Outside of California, we know relatively little about the mechanisms controlling *E. editha* population size. In Colorado, the occurrence of low-rainfall years seems to play a role (Holdren and Ehrlich 1982), and drought may have been influential in recent extinctions of coastal populations in British Columbia (subspecies *taylorii*) (Guppy and Fischer 2001). For each of the *E. editha* ecotypes, the response of a population to extreme weather appears to depend on the details of the relationships between the insect and its host plants. We can generalize from *E. editha bayensis* that ac-

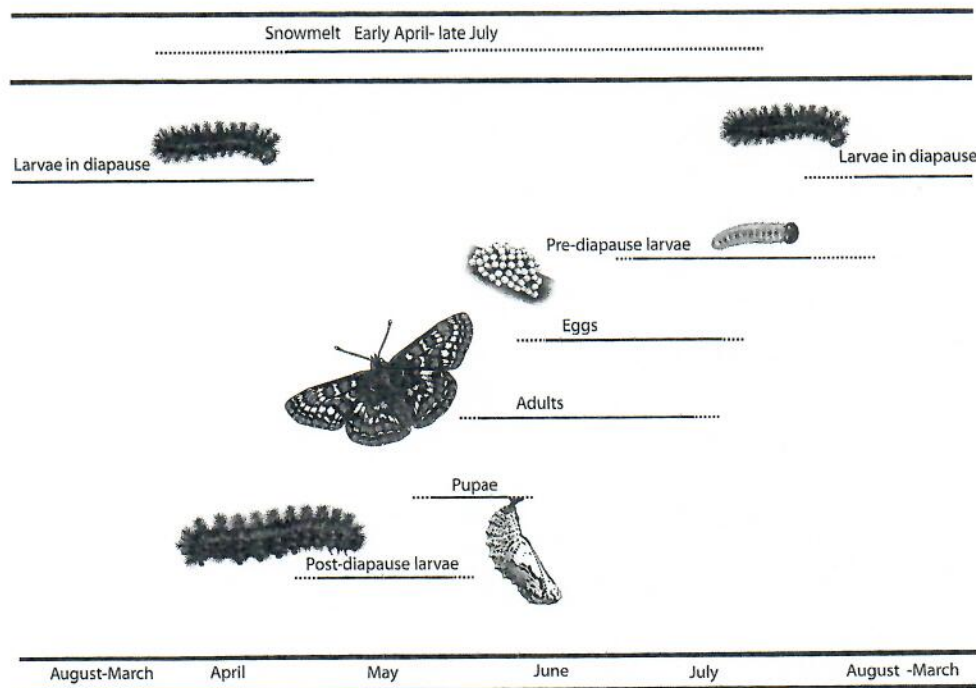


Figure 3.19. Life cycle diagram of noncoastal *E. editha* populations. This life cycle is representative of populations residing at high elevations in the Sierra Nevada. These populations are univoltine, like *E. editha bayensis* (figure 2.2), but diapause during the winter months. Drawings by Zdravko Kolev.

cess (either temporal or sheer abundance) to host resources is an essential, and often the principle, factor limiting population size.

3.8 Conclusion

The type of detailed understanding of local populations outlined in this chapter is essential for managing and conserving checkerspots and other insect species (chapter 13). In the control of pests, for example, an understanding of population abundance, location, and timing, as well as variation in these factors over time, are useful in improving efficiency and effectiveness of pesticide application. To conserve endangered insects, it is important to understand which factors buffer against population declines and which portions of a landscape serve as refugia. All factors taken together, timing of life-history events and the synchrony of butterflies and their resources, appears particularly important in *E. editha bayensis* and possibly other *E. editha* ecotypes and insect taxa. A major theme emerging from studies of this species is the significance of resource diversification in terms of habitat heterogeneity and resource use. This concept has been referred to as a portfolio effect (Boughton and Singer 2004), much

like managing stocks on the stock market: diversification buffers against fluctuating conditions.

The long history of research on *E. editha* has provided a number of particular lessons for population ecology. First is the realization that it is critical to identify demographic units if sensible conclusions are to be drawn about the dynamics of populations. Second is the recognition that demographic units commonly go extinct. Third, conserving large, topographically diverse habitats with multiple plant resources helps populations persist through extreme environmental events (Ehrlich and Murphy 1987a, Weiss and Murphy 1993, Hellmann 2002c, Hellmann et al. 2004). Fourth, the finding that climate change can cause population losses confirms that regional changes in the environment will threaten native biota (Murphy and Weiss 1992, Hill et al. 1999b, Parmesan et al. 1999, C. D. Thomas and Lennon 1999, Hughes 2000, McCarty 2001, McLaughlin et al. 2002a). Phenology and indirect impacts of climate change through host plants may be important ways that taxa are susceptible to climate change (Hellmann 2002c). The ultimate product of research on the Bay checkerspot is the mechanistic understanding of factors controlling population dynamics, as well as a grasp of the complex interactions of these factors across space and time.