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SUN, SLOPE, AND BUTTERFLIES: TOPOGRAPHIC DETERMINANTS OF HABITAT QUALITY FOR *EUPHYDRYAS EDITHA*[1]

Stuart B. Weiss, Dennis D. Murphy,[2] and Raymond R. White[3]
Department of Biological Sciences, Stanford University, Stanford, California 94305 USA

Abstract. Thermal environments in a large, topographically diverse serpentine soil-based grassland were quantified and ranked using a computer model of clear sky insolation and shading on different slopes to determine the effects of microclimate on the rates of development of each of the life stages of the butterfly *Euphydryas editha bayensis*. Larvae developed to pupation earlier on warm slopes than on progressively cooler slopes. Availability of sunlight can be limiting for larvae, which bask in direct sun to raise body temperature. Larvae can disperse >10 m/d, allowing them to transfer between microclimates. Pupae on warmer slopes also developed faster than those on cooler slopes.

Microclimate also affects the phenology of host plants of larvae and nectar sources of adults. Larval and pupal development and host-plant phenology determine the phase relationship between adult butterfly flight and host-plant senescence, which in turn determines mortality rates of prediapause larvae. Adult females that eclosed early in the season could have their offspring survive on almost all slopes; survivorship of offspring from adults that eclosed in the middle of the flight season was restricted to cooler slopes in the habitat. Some butterflies eclosed too late for their offspring to survive on any slope.

Topographic diversity on several scales is a prime indicator of habitat quality for this butterfly. Areas of high local topographic diversity on a scale of tens of metres appear particularly important for long-term population persistence under variable climatic conditions.

Key words: butterfly; Euphydryas editha; *habitat quality; microclimate; phenology; thermal ecology; thermoregulation; topography.*

INTRODUCTION

Thermal conditions influence activity patterns and growth of insects in all life stages. In Lepidoptera, for example, thermoregulatory behavior or positioning has been reported for eggs (Williams 1981), larvae (e.g., Sherman and Watt 1973, Casey 1976, Rawlins and Lederhouse 1981, Kevan et al. 1982, Knapp and Casey 1986), and pupae (Kevan et al. 1982). Adult thermoregulatory behavior has long been studied in a wide variety of butterflies (e.g., Clench 1966, Watt 1968, Kingsolver 1985). In highly seasonal and variable environments butterflies and other insects can be under great time pressure to complete their life cycles, which places a premium on timely development (Andrewartha and Birch 1954).

The life cycles of *Euphydryas* butterflies, for example, are so constrained (Singer 1972, Ehrlich and Murphy 1981). The most intensively studied populations of *Euphydryas* are those of *E. editha* inhabiting serpentine soil-based grasslands in the Coast Ranges of central California (Ehrlich et al. 1975, Ehrlich and Murphy 1981). Dynamics of these populations appear to be largely determined by levels of starvation of prediapause larvae, a process mediated by a complex phase relationship between adult flight and senescence of annual host plants, which limits the length of the growing season (Singer 1972, Singer and Ehrlich 1979). Thermal microenvironments created by different slope exposures play an important role in determining both development rates of the immature stages of the butterfly and timing of plant senescence when seasonal rains stop in early spring (Singer 1972, Singer and Ehrlich 1979, Dobkin et al. 1987). The highest survivorship of prediapause larvae comes from early-flying females, which lay egg masses on cool north-facing slopes where host plants remain edible later in the season. The females that fly earliest, however, are those that developed as postdiapause larvae on warmer south-facing slopes, where prediapause starvation rates are highest. The importance of this paradox in the persistence of *Euphydryas editha* populations under extremes of drought and deluge has been qualitatively addressed for the well-studied Jasper Ridge colony on the Stanford University campus (Singer and Ehrlich 1979, Ehrlich et al. 1980, Dobkin et al. 1987).

This study initiates a quantitative assessment of the roles that microclimates on different slope exposures play in determining the phase relationship between the adult flight period of *Euphydryas editha bayensis* and

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[1] Manuscript received 4 May 1987; revised 29 January 1988; accepted 8 February 1988.

[2] Address reprint requests to D. D. Murphy.

[3] Present address: Biology S-56, City College of San Francisco, San Francisco, California 94112-1898 USA.

the senescence of its host plants. Theoretical modeling of solar exposure characteristics is combined with experimental and observational studies of the phenologies of the life stages and host plants of the butterfly in a habitat that supports a large, dense population. The ultimate goal of this and future studies is to untangle the complex relationships among topography, microclimate, and the population dynamics of *Euphydryas editha bayensis.* The first step taken here is to identify the topographic features of the serpentine soil-based grassland habitat patches that determine long-term habitat quality for this butterfly.

MATERIALS AND METHODS

Study site

The Morgan Hill study site (37°11′ N, 121°40′ W, elevation 150–400 m) consists of ≈2000 ha of serpentine soil-based grassland habitat, including a 5-km ridge running northwest to southeast with numerous lateral offshoots separated by canyons, some of which contain intermittent streams. The habitat is topographically complex with a wide variety of slope exposures ranging up to 40° in tilt in all compass directions (Fig. 1A, B). The site has been grazed by cattle for many decades.

The mediterranean climate in the San Francisco Bay area has a cool rainy season from October through April and a warm drought from May through September. The distribution and quantity of local rainfall varies considerably from year to year, and with elevation and rain shadows of nearby mountain ranges (Gilliam 1962). Average winter daily maximum temperatures range from 14° to 18°C, and minima rarely fall far below freezing. Average annual rainfall (measured from 1 July to 30 June) is 330 mm at San Jose, the closest regularly recorded climate station to the study site.

Study organism

Euphydryas editha bayensis is a univoltine butterfly restricted to outcrops of serpentine soil, where unique chemical constituents prevent complete invasion of native grasslands by Eurasian annual grasses and forbs (McNaughton 1968, Murphy and Ehrlich 1988). Few transfers of adult butterflies occur even between adjacent habitat patches (Ehrlich 1965, Ehrlich et al. 1975). Extinctions of local populations in small habitat patches are frequent and appear to play a significant role in the population biology of this butterfly (Ehrlich et al. 1980).

Adult butterflies of this subspecies fly from late February into early May. Females lay egg masses of 20–200 eggs ($\bar{X} = 63.4$, SD = 22.1, $n = 48$; D. Ng, *personal communication*) near the base of *Plantago erecta,* and less frequently on *Orthocarpus densiflorus* and *O. purpurascens.* Eggs hatch after ≈2 wk, and newly hatched larvae spin webs as they gregariously consume the host plant. Larvae feed until they reach the fourth instar, when they enter an obligatory diapause for the dry season. Prediapause larvae race to complete necessary growth before their annual host plants senesce following the end of the rainy season. Larvae often transfer from *Plantago* to *Orthocarpus,* because *Orthocarpus* remains edible later in the season (Singer 1972). Starvation rates can approach 95-99% at this stage. This factor is thought to determine adult population size the subsequent year (Singer 1972, Ehrlich et al. 1975).

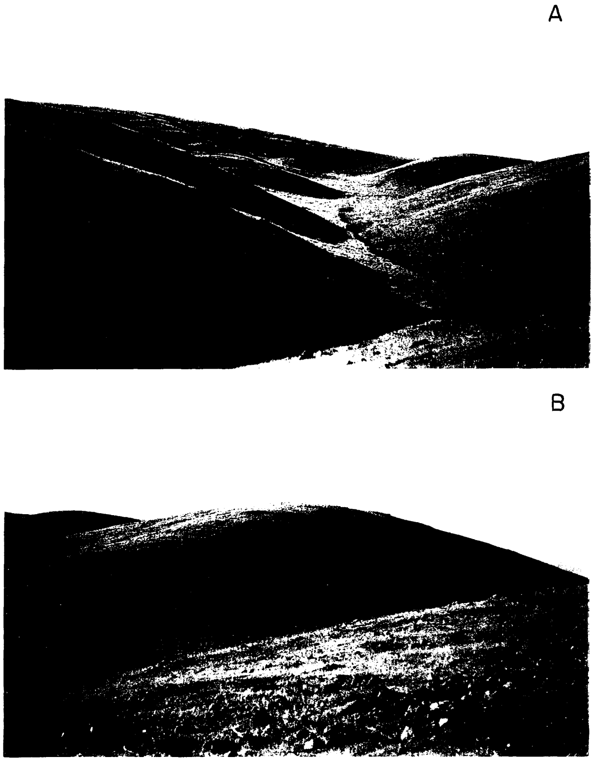

FIG. 1 (A) Portion of study area, showing representative topography and winter shading. (B) Portion of study area showing terracing from cattle grazing.

Surviving larvae break diapause and resume feeding on newly germinating *Plantago* at the start of the next rainy season. Postdiapause *Euphydryas* larvae are well-adapted solar energy collectors and spend much of their time basking (Singer 1971, Porter 1982). Their largely black ground color maximizes absorption of radiation and numerous setae may act as insulation against convective heat loss (Casey and Hegel 1981, Kevan et al. 1982). Postdiapause larvae feed until they reach 300–500 mg and then pupate.

Pupae are cryptic in this species as in many Lepidoptera; larvae draw together a few slender blades of vegetation and suspend themselves a few millimetres above the ground (White 1986). In this position, pupae are often exposed to direct sunlight and receive heat from the ground in a low convection microhabitat.

Theoretical solar calculations

Variations in thermal environments across grassland surfaces (Fig. 1) are the direct result of relative inputs of solar radiation on different slope exposures, and are virtually exclusively determined by the contours of the landscape itself. The boundary layer on slopes receiving higher insolation is warmer than that on slopes receiving lower insolation, even on the scale of plowed furrows and ant mounds (Geiger 1965). Such temperature differences have been experimentally verified on warm SE 13° and cool N 17° slopes in the serpentine soil-based grassland at Jasper Ridge (Dobkin et al. 1987). Insolation differences at these scales are determined by the geometry of the earth's orbit, daily rotation, tilt of axis, and tilt and azimuth of the surface (Lunde 1980).

Hourly solar incidence angles and theoretical clear sky insolation values for the 21st d of each month on different slope exposures were calculated with a program run on an Apple II computer, using standard equations (Lunde 1980).

Two interrelated solar exposure characteristics were extracted from the program: shading levels and total insolation received by the ground. Shading levels are based on a maximum solar incidence angle of 80°. Sunlight arriving parallel to a slope has an incidence angle of 90°; sunlight striking a slope at maximal intensity has an incidence angle of 0°. Field observations indicate that larvae usually cannot find adequate sun for basking in the grassland habitat at high incidence angles because of local shading by low vegetation. 80° is a first approximation of the lower bound of suitable growing conditions. Direct beam insolation levels at this incidence angle are $<1\%$ of normal incidence radiation.

Direct beam insolation striking the ground is calculated as the direct beam radiation from the sun, corrected for atmospheric scattering and absorption according to solar altitude, multiplied by the cosine of the incidence angle. Insolation values include both direct and sky diffuse radiation, but not reflected radiation.

Absolute insolation values are greatly affected by cloud cover and smog. Calculated clear sky insolation, therefore, is used in this study only to rank slopes. Slopes with a western component are ranked higher than equivalent slopes with an eastern component, even where theoretical insolation values are the same (Geiger 1965), because air temperature maxima occur in the early afternoon when western exposures receive their maximal insolation. Morning radiation fog, in addition, can reduce insolation on eastern exposures.

Topographic measurements

Slope, tilt, and azimuth were measured with a clinometer and compass. Microtopography was measured at a scale of 10 cm along a 59-m transect using a measuring tape and clinometer.

Larval and pupal studies

Densities of late-instar postdiapause larvae were recorded in the field in 1 m^2 every 5 × 5 m in a rough grid. *Plantago* was noted as present or absent. Counts were normalized using the square root transformation $[(Y + 0.5)^{1/2}]$, and compared using paired *t* tests (Sokal and Rohlf 1981). Samples of 15–100 postdiapause larvae were collected in areas away from these larval density samples, were then refrigerated for transport, and weighed upon return to the laboratory to measure mean mass in the field at different times. Sampled areas were chosen for relative uniformity of slope exposure and central location within the large habitat.

Additional postdiapause larvae were collected from the field, weighed in the laboratory, and marked individually using enamel paint (Weiss et al. 1987, White and Singer 1987). The next day, these larvae were released in the field at selected sites and were recovered several days later. Larvae were ordered by mass and every other larva placed in separate groups. Mass gains and dispersal distances and directions were recorded. Groups of 100 and 200 large final-instar larvae were marked and released to assess pre-pupation dispersal and choice of pupation sites.

Pupae were obtained by lab rearing and were placed into the field in situations simulating field pupation (see also White 1986).

Body temperature measurements

Larval and pupal body temperatures (T_b) were measured using a Keithley Model 872 thermocouple/digital thermometer pressed firmly against the middle of the body, and the maximum temperature achieved was recorded. While this procedure measures only surface temperatures, the small masses of larvae and pupae preclude large differences in T_b within the animals (May 1979). Ambient temperatures (T_a) were measured in the shade directly adjacent to larvae or pupae.

Plant phenology

Sixteen 10 × 10 m plots were selected to represent a variety of slope exposures. Larval host plants, *Plantago erecta, Orthocarpus densiflorus,* and *O. purpurascens,* were monitored weekly to determine the start of flowering, start of senescence, and completion of senescence. Adult nectar sources in bloom were counted; *Lomatium* spp. were counted in the entire large plot, *Lasthenia chrysostoma* were counted in nine 0.25 × 0.25 m quadrats randomly placed each week within the larger plot.

Phase relationship

The phase relationships between female eclosion and host-plant senescence on various slopes were calculated with the following assumptions: (1) starting at the final sample on each slope, larvae gain mass at the rates observed in the larval mark-recapture experiments for the appropriate slope exposures (40–50 mg/d), and no mass gain occurs on rainy days; (2) larvae reach their maximum mass (average 400 mg for females) and then take 2 d to pupate; (3) the length of the pupal stage is

TABLE 1. Densities of postdiapause larvae, 1985 and 1986. Insolation ranks are based on 21 March values. CD = coefficient of dispersion ($S^2/\bar{X}$).

Insolation rank	Slope exposure	Date	No. 1-m² quadrats	No. larvae found	Density† All	Density† *P. erecta*	CD
			1985				
(1)	Flat	11 Feb	100	5	0.05	0.082	0.93
(2)	N 11°	11 Feb	100	14	0.14	0.18	1.25
(2)	N 11°	11 Feb	100	17	0.17	0.19	0.94
(3)	N 20°	28 Feb	100	34	0.34	0.40	1.56
			1986				
(2)	Flat	10 Jan	114	51	0.45	0.51	1.39
(6)	N 11°	1 Feb	112	99	0.84	1.00	1.76
(1)	SE 11°	1 Feb	50	21	0.42	0.42	1.27
(4)	E 20°	3 Feb	49	54	1.12	1.22	1.94*
(5)	NW 15°	3 Feb	48	49	1.02	1.02	1.27
(3)	W 15°	7 Feb	61	28	0.46	0.50	1.68
(7)	N 20°	24 Feb	98	82	0.84	0.91	1.06

† The first density figure is for all quadrats, the second is for quadrats containing *Plantago erecta.*

* Indicates non-Poisson distribution, $P < .05$.

that observed in the pupal placements closest in slope and time of season (exact matches were not always possible for the early larvae from each slope); and (4) prediapause larval development takes 4.5 wk from freshly laid eggs to the fourth instar (determined by field observations of egg masses and larval webs, based on 1985 field data for time from fresh eggs to larval diapause in the fourth instar, which did not vary significantly with slope exposure [D. Ng, *personal communication*]). The phenology of the individuals that emerged earliest from each slope was calculated in a similar manner, using the heaviest larvae from the next-to-last sample on each slope.

RESULTS

Postdiapause larvae

The distribution of postdiapause larvae is an indication of where oviposition rates and survivorship to diapause were highest the previous spring (Singer 1972). Larvae were more dense on the N 20° slope than on flat areas in 1985 (Table 1, $t = 3.01$, $P < .01$). The N 20° slope exhibited higher larval density than the combined N 11° samples ($t = 2.78$, $P < .01$). The difference in larval densities between the combined N 11° samples and the flat sample was not significant ($t = 1.47$, $.1 < P < .2$). In 1986, larval densities on the flat and N 11° slopes differed significantly ($t = 3.21$, $P < .01$) as did the flat and N 20° slopes ($t = 3.30$, $P < .01$), but larval densities on the N 20° and N 11° slopes did not significantly differ.

The insolation curves for selected slope exposures are the basis for ranking slopes on a temperature gradient from warm to cool (Fig. 2). Insolation differences between slopes are greatest in December and January when the solar altitude is lowest. (References below to warmer and cooler slopes are based on calculated insolation.)

The temporal phasing of postdiapause larval growth is determined by slope exposure. Larvae on warmer slopes reached higher masses sooner than those on cooler slopes (Fig. 3, S is warmer than F > N > N′). Male larvae reach their maximum mass between 250 and 300 mg and then pupate, while female larvae pupate between 350 and 500 mg. The temporal differences in mass gains, therefore, lead to differences in pupation dates between larval cohorts on different slopes. Average dates of pupation on south-facing and steep north-facing slopes are almost one full month apart.

Variation in body mass among individuals within each larval sample created a temporal spread of pu-

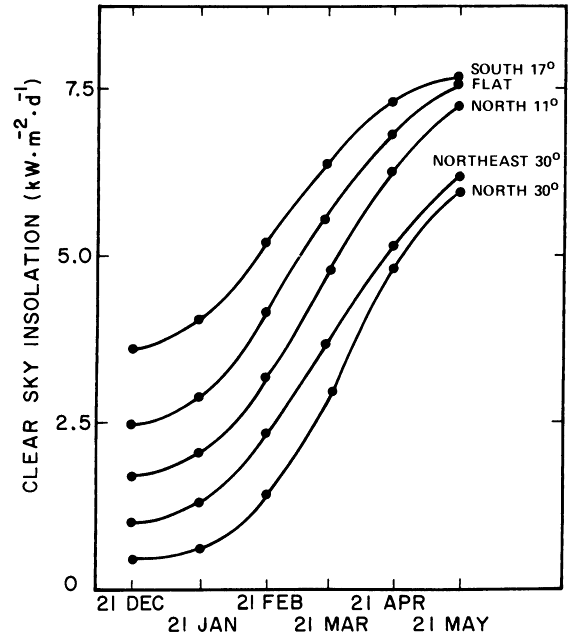

FIG. 2. Theoretical clear sky insolation at 37.5° N latitude striking selected surfaces with the indicated aspect and tilt.

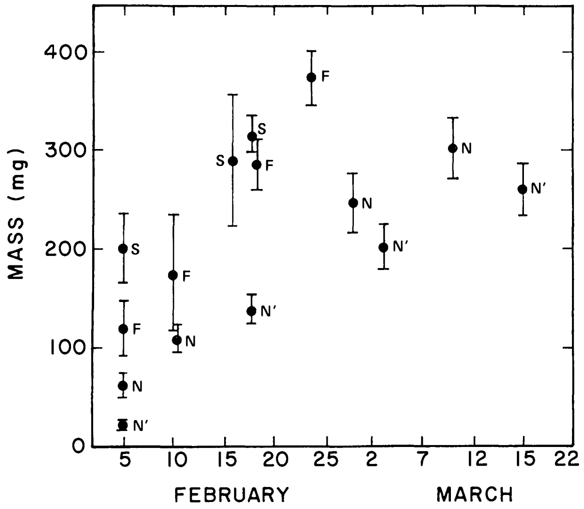

FIG. 3. Mean postdiapause larval mass in the field on different slope exposures. Error bars are 95% confidence intervals (*t* test). S = south-facing 6–11°, F = flat, N = north-facing 11–17°, N′ = north-facing 22–30°.

pation times within larval cohorts on distinct slope exposures. The standard deviations of mean mass in the final samples from each slope ranged from 87 to 109 mg, or ≈2–3 d of mass gain (see below, and Weiss et al. 1987).

Mark-recapture experiments showed that individual last-instar larvae gained mass faster on warmer slopes than on cooler slopes during the same time periods (Table 2). Average daily mass gains ranged from 34 mg/d on a NE 30° slope in late February to 56 mg/d on a N 11° slope in mid-March. Failure to recover all larvae did produce small differences in initial mass between groups, but the small differences in initial mass did not significantly affect mass gains (ANCOVA $F = 0.557$ for 11 February experiment; $F = 0.072$ for 23 February experiment). More extensive experimentation in 1986 revealed a tight linear relationship between calculated insolation and larval mass gains in the sixth and seventh instars (Weiss et al. 1987).

Larvae basking in direct sun reach body temperatures (T_b) well above ground-level ambient temperature (T_a). Fig. 4 is a composite of measurements under full sun conditions on different dates and at different times of day. Direct beam radiation levels, wind, larval size, and orientation are not controlled (therefore, no regression line has been drawn). T_b can exceed T_a by as much as 19°C. Average temperature excesses are in the range of 10°–12°. Under heavy overcast and artificial shading, temperature excesses are <2°.

Simultaneous measurements of larval T_b on a north-facing and a south-facing slope showed highly significant temperature differences (Fig. 5, $P < .001$, Mann-Whitney *U* test). The difference in mean T_b between the two groups was only 3.2°, while the difference in T_a was 6°. This observation suggests, but does not prove, that larvae on the south-facing slope may be in an optimal temperature range between 30° and 35°, while those on the north-facing slope may have to orient to maximize T_b. Measurements of T_a further confirm the contention that slopes receiving higher insolation are warmer than those receiving lower insolation.

Shaded slopes inhibit larval growth, since larvae in shade cannot bask and raise T_b above T_a. Many slopes are shaded for long periods in December and January (Fig. 6, see also Fig. 1), when daily maximum ambient air temperatures are 12°–15°. Larvae at these temperatures in the laboratory are inactive and do not gain mass (S. B. Weiss, *personal observation*).

Microtopography on a scale of 10 cm provides an array of thermal environments that can affect larval growth. The most striking examples of microtopographic effects are on slopes that are terraced by grazing cattle (Fig. 1B). Approximately 10% of the habitat on a terraced N 30° slope has a tilt angle of <10° (Fig. 7), providing adequate solar exposure for larvae to bask when the remainder of the slope is in shade (Figs. 1 and 6). Such microtopography would play a less important role on many slopes.

Postdiapause larvae are capable of moving considerable distances, as much as 10 m/d (Table 3). The reason for the long dispersal distances on the SW 13° slope in March appears to be that postdiapause larvae would not feed on *Plantago* once the plants were in flower and moved substantial distances in search of higher quality food. Larvae moving 10–100 m from nearly all possible diapause sites can experience wide ranges of thermal environments, thus can significantly increase or decrease their daily mass gains.

The actual proportion of larvae moving between slopes is undetermined; some evidence that larvae do indeed transfer between microclimates is presented in

TABLE 2. Growth of marked last-instar larvae during the indicated period. In addition to ANCOVA, differences were also tested by Mann-Whitney *U* test.

Slope exposure	Dates	Time interval (d)	*N*	Gain in mass (mg) ($\bar{X} \pm$ SD)	Rate of gain (mg/d)	ANCOVA	*U* test
N-NW 15°	11–16 Feb	5.5	7	194 ± 21	35	$F = 2.72$ NS	$P = .05$
S 12°	11–16 Feb	5.5	7	246 ± 61	45		
NE 30°	23–26 Feb	2.9	13	98 ± 22	34	$F = 4.69, P < .05$	$P < .005$
S 17°	23–26 Feb	3.3	13	128 ± 23	39		
N 11°	13–16 Mar	3.2	14	179 ± 26	56		

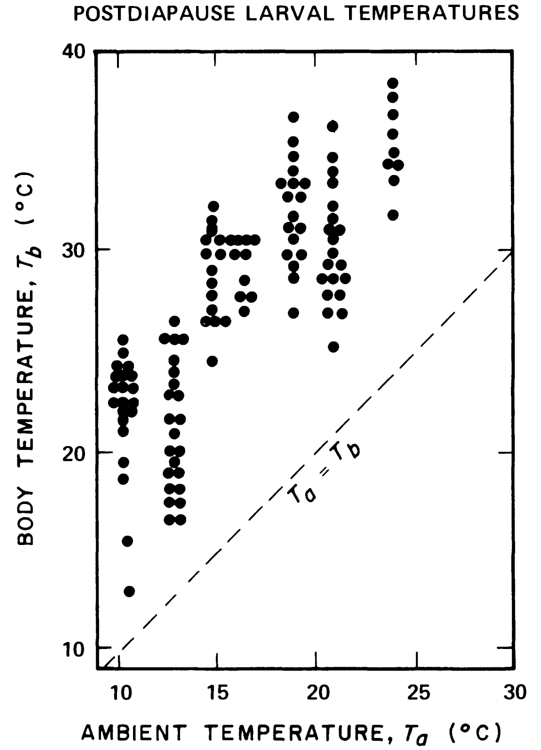

FIG. 4. Postdiapause larval body temperatures. T_a is ambient temperature measured at ground level adjacent to larvae, T_b is body temperature. This figure is a composite of all temperature measurements taken on various slopes at different times of the growing season.

the E 20° larval sample from 1986 in Table 1. It was the only sample with a significantly clumped distribution; 80% of the larvae were found at the top of the slope 10–15 m from a N 17° slope on the other side of the ridge. All other larval density samples were taken in areas at least 30 m away from other slopes.

Regardless of their original location, postdiapause larvae disperse widely just prior to pupation. Releases of groups of 100 and 200 marked larvae that were almost large enough to pupate resulted in no larvae or pupae found within 10 m of the release point.

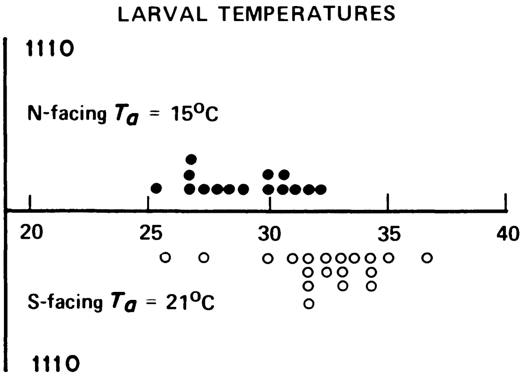

FIG. 5. Postdiapause larval body temperatures measured simultaneously on a south- and a north-facing slope.

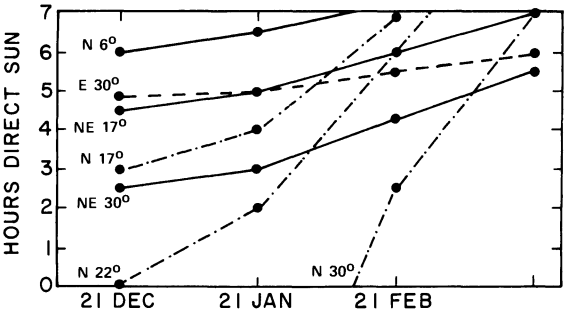

FIG. 6. Number of hours of direct sun striking selected slopes at 37.5° N latitude, based on a maximum solar incidence angle of 80° (see Materials and Methods).

Pupal development

Pupal development times varied with slope and time of year (Table 4). Pupae on warm slopes developed faster than pupae on cooler slopes. Pairwise comparisons between cohorts placed in the field on the same dates (which factors out differences in macroclimate conditions) show significant differences in pupal duration between slopes (samples 1 and 2: $t = 3.82$, $P < .01$; 4 and 5: $t = 2.17$, $P < .05$; 6 and 7: $t = 4.31$, $P < .01$; 8 and 9: $t = 3.50$, $P < .01$). Potential sources of variation in development times within pupal cohorts include microtopography, vegetation cover density, and genetic and phenetic variability among individuals.

Pupal T_b varied by both slope exposure and time of day (Fig. 8). Pupae on a SE 13° slope were warmer than those on a N 11° slope at 0930 ($P < .001$, all comparisons Mann-Whitney U test) and at 1230 ($P < .001$). Pupae were warmer at 1230 than at 0930 on both slopes ($P < .001$).

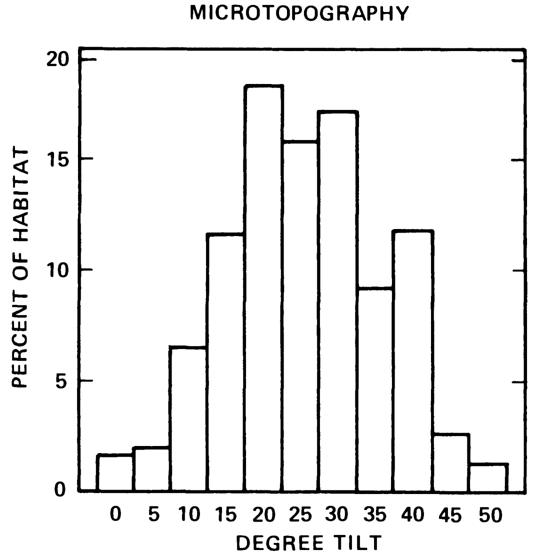

FIG. 7. Microtopography of a terraced north-facing 30° slope. Y axis is percent of habitat with indicted tilt angle. Tilt angle measurements were taken for every 10-cm interval along a 5900–cm transect run directly uphill.

TABLE 3. Larval dispersal. N = number recovered/number released.

			Larval dispersal (m/d)		
Slope exposure	Dates	N	$\bar{X}$	SD	Range
N-NW 15°	11–16 Feb	9/20	0.36	0.16	0.11–0.68
S 12°	11–16 Feb	15/20	1.09	0.76	0.11–2.72
NE 30°	23–26 Feb	12/34	1.43	1.51	0.09–4.14
S 17°	23–26 Feb	15/35	1.14	1.06	0.30–4.72
N 11°	13–16 Mar	17/21	0.48	0.27	0.06–0.93
N 11°	17–17 Mar	13/13	0.94	0.62	0.20–2.00
SW 13°	17–17 Mar	14/14	4.98	4.00	1.00–15.20

Phase relationship

The phenology of *Plantago* followed predictable patterns based on the relative insolation levels of the monitored plots (Figs. 9 and 10). *Plantago* senescence took place sooner on slopes with higher insolation ($\tau = 0.81$, Kendall Rank Correlation Test, $P < .01$). The phenology of *Orthocarpus* followed patterns similar to those of *Plantago.* In most cases, *Orthocarpus* underwent senescence 1 wk later than *Plantago* on the same slopes, with a few scattered plants remaining edible up to 2 wk later on some slopes. The last edible *Orthocarpus* was observed on a N 30° slope on 10 May.

The calculated phase relationship for 1985 between adult female butterfly eclosion and host-plant senescence is shown in Fig. 11. Average female eclosion from south-facing slopes and flat areas was early enough for egg masses from those females to reach diapause size on *Plantago* alone. Average female eclosion from moderate north-facing and steep north-facing slopes was too late by several days to allow larvae to reach diapause on *Plantago* alone; the use of *Orthocarpus* as a secondary host plant was necessary in those areas.

The variance in mass within larval samples translated into some females eclosing significantly earlier than average, up to 2 wk in extreme cases (Fig. 11, see top line for each plot). The earliest adult female was observed in the field on 24 February. Offspring of these early females from each slope could survive to diapause on slopes with higher insolation than their slopes of origin. The earliest female eclosion dates indicate that some females from cool north-facing slopes were in phase with flat areas. In contrast, the females emerging latest from steep north-facing slopes were too late to successfully oviposit anywhere. On 14 April, 24/277 (8.7%) female butterflies that were handled had wing-wear ratings of 1.0 or 1.5, indicating an age of 4 d or less (see Iwasa et al. 1983 and Ehrlich et al. 1984). A substantial portion of the population, therefore, was excluded from successful reproduction because of the solar exposure of the slope on which they had developed.

The results of favorable phase relationships during the 1985 flight season are seen clearly in comparisons of larval densities between 1985 and 1986 (Table 1). All equivalent slopes had higher densities in 1986 (flat: $t = 3.97$, $P < .001$; N 11°: $t = 8.2$, $P < .001$; 20°: $t = 3.79$, $P < .01$). Densities in flat areas increased by a factor of 8, while those on north-facing slopes increased by a factor of 4–5. The high density on the SE 11° slope in 1986 contrasts with densities too low to sample by quadrats in 1985 on similar slopes.

The availability of nectar was determined by slope exposure (Figs. 12 and 13). *Lomatium* was the only nectar source available to the earliest adults in late February and early March. *Lasthenia* was observed to be the most frequently used nectar source when available. Only nectar available before 10 April could contribute to realized fecundity. Thus, the south-facing slopes and flat areas contributed the greatest amount of nectar for adults. *Lasthenia* on cool slopes made minimal contributions to adult reproductive output.

TABLE 4. Pupal phenology and mortality. Survival = number of butterflies eclosed/number of pupae placed in field. 95% confidence interval is based on t test. See Results: Pupal Development for comparisons of paired samples on the same start date.

			Survival		Pupal duration (d)		
Sample number	Placement date	Slope exposure	Ratio	Proportion	$\bar{X}$	SD	95% CI
1	16 Feb	W 25°	5/9	(0.56)	19.0	5.2	12.5–25.5
2	16 Feb	NW 25°	5/8	(0.63)	32.3	5.8	25.1–39.4
3	19 Feb–2 Mar	S 16°	41/80	(0.51)	20.7	2.4	18.9–21.5
4	2 Mar	Flat	11/26	(0.42)	25.8	3.9	23.4–28.2
5	2 Mar	N 6°	14/29	(0.50)	29.2	4.0	26.5–31.9
6	8 Mar	Flat	36/49	(0.74)	19.3	2.3	18.5–20.1
7	8 Mar	N 6°	44/68	(0.65)	22.6	4.1	21.4–23.8
8	12 Mar	SE 11°	15/26	(0.58)	15.8	2.6	14.4–17.2
9	12 Mar	N 11°	10/25	(0.40)	19.7	2.8	17.7–21.7
10	22 Mar	NE 30°	15/33	(0.46)	18.5	2.5	17.1–19.9

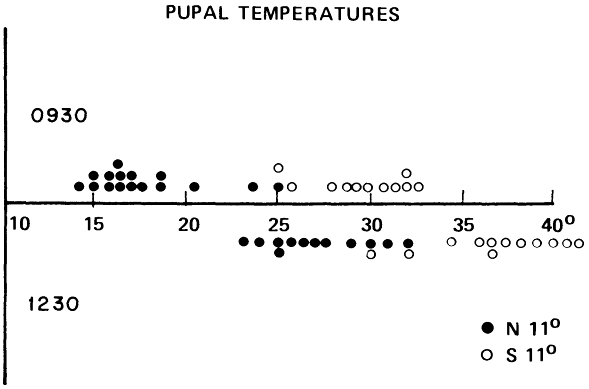

FIG. 8. Body temperatures of pupae placed on opposing N 11° and S 11° slopes at 0930 and 1230.

DISCUSSION: HABITAT QUALITY

The chances of successful reproduction for *Euphydryas editha* females in their serpentine soil-based grassland environments are dependent on the timing of adult eclosion. The phenology of larval and pupal development is affected by slope exposure, variation among individuals on a given slope exposure, and larval dispersal between slopes. These factors all act within the context of the unique pattern of rainy, cloudy, and clear days that each growing season affords. The early emergence of some females allows successful oviposition on many slopes; later females are successful on a limited number of cooler slopes. Locations that provide differential survival and reproductive success effectively differ in habitat quality. Habitat quality, as so defined, provides a framework for exploring the role of topography in persistence of *Euphydryas editha bayensis* populations.

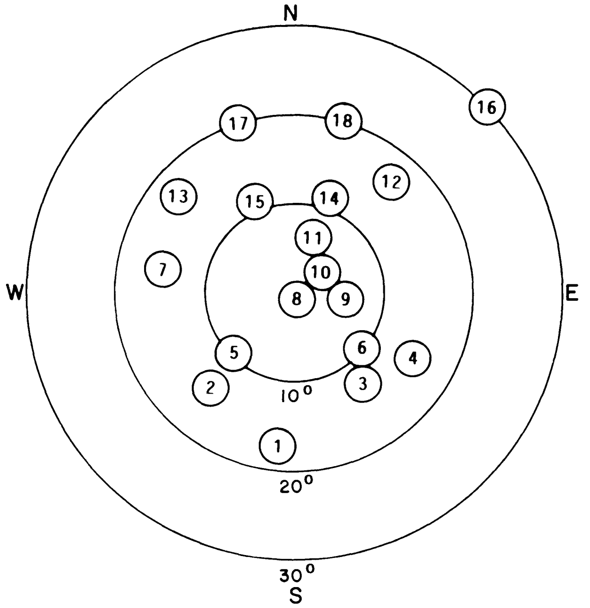

FIG. 9. Tilt and azimuth of plant phenology plots. Plots are numbered in order of insolation received; 1 = highest, 18 = lowest.

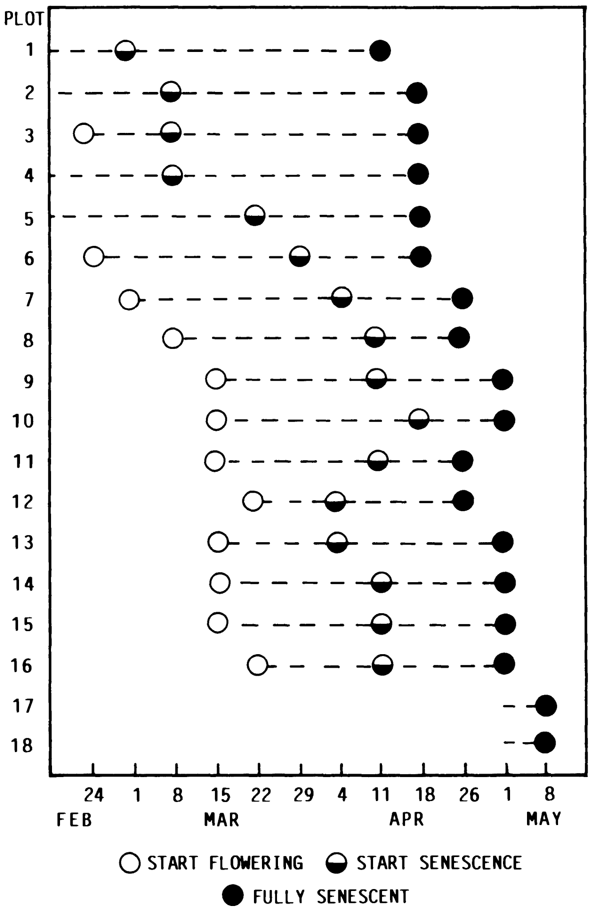

FIG. 10. *Plantago* phenology. Plot numbers refer to Fig. 9. Symbols and dashed lines track the phenology from flowering through complete host-plant senescence for each plot.

Habitat quality has both short-term and long-term components. Short-term local habitat quality varies among the different life stages of *Euphydryas editha,* and changes from month to month, and from year to year. Larvae from egg masses laid on cooler slopes nearly always will have a better chance to reach diapause than those laid concurrently on warmer slopes, because of the later onset of plant senescence on cooler slopes. Females lay more egg masses in cooler areas later in the flight season as *Plantago* on warmer slopes undergoes senescence. Cool slopes, then, are high quality habitat for prediapause larvae, and become better relative to warmer slopes as the flight season progresses.

The relatively fewer larvae that survive to diapause on warmer slopes develop sooner as postdiapause larvae than those on cooler slopes. Adult females from these larvae can successfully oviposit on a wider variety of slopes, and should exhibit greater reproductive success in most years. Warmer slopes, therefore, are high-

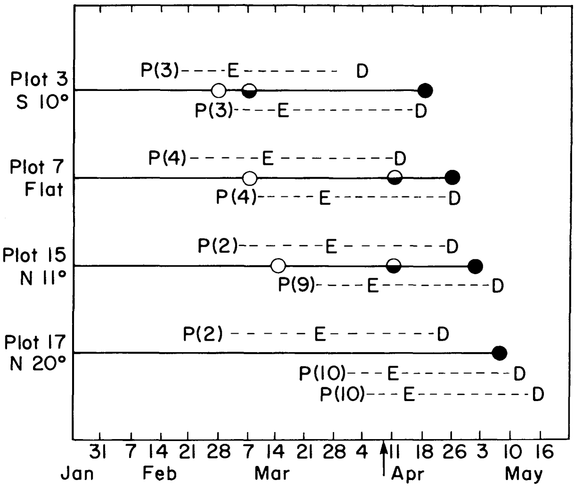

FIG. 11. Phase relationship. P = pupation date, E = eclosion date, D = diapause date. Symbols for *Plantago* phenology (in solid lines) are the same as Fig. 10. The sequences just below the *Plantago* lines are calculated from larval masses for average females from that slope exposure (see Fig. 3). Sequences above the *Plantago* lines are for the earliest females, calculated from the mass of the largest larva from a particular slope (for Plot 3 the largest larva was a 475-mg individual from 5 February; Plot 7, 422 mg, 10 February; Plot 15, 260 mg, 18 February; Plot 17, 422 mg, 18 February). The bottom line for Plot 17 is for the latest females (70 mg, 17 March). The numbers following the pupation dates, e.g., P(3), indicate the pupal cohort from Table 4 used for measurement of pupal duration. The arrow at 10 April indicates the last day egg masses could be laid with some chance of survival on the coolest slopes.

quality habitat for postdiapause larvae, except later in the season when *Plantago* flowers and is unsuitable for food. Warmer slopes similarly are high-quality habitat for pupae, where they develop faster. But, it is important to note that in 1985, eggs laid by all but average and late females from steep north-facing slopes had at least some chance of survival to diapause, even if only on the coolest slopes in the habitat.

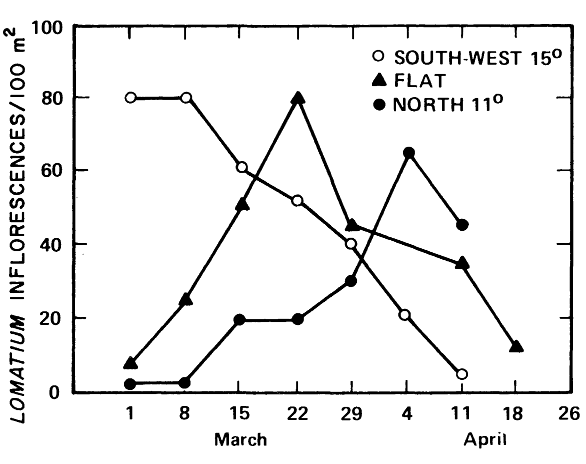

FIG. 12. *Lomatium* phenology for three selected 10 × 10 m plots. Counts are of inflorescences available as adult nectar sources in the whole plot on each date.

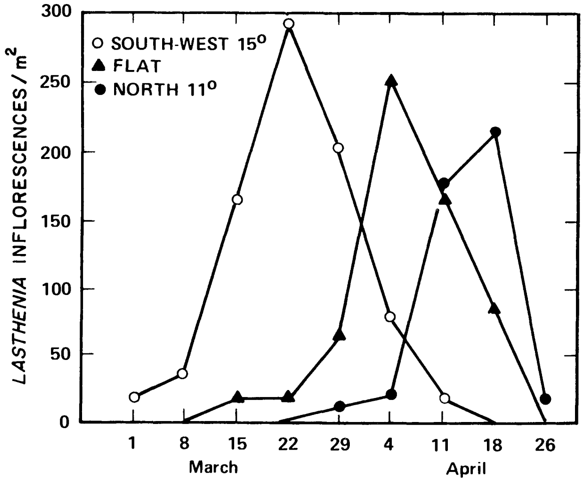

FIG. 13. *Lasthenia* phenology in three selected 10 × 10 m plots. Counts are means of number of inflorescences available as adult nectar sources in 9 0.25 × 0.25 m plots randomly placed each week, corrected to inflorescences per square metre.

This spatial shift in local habitat quality within a butterfly generation confirms the proposed mechanism by which a 2-yr drought, such as that of 1975–1977, can lead to especially severe reductions in population size (Singer and Ehrlich 1979, Ehrlich et al. 1980). Host-plant senescence proceeds very rapidly under drought conditions, and prediapause larvae survive only on cooler slopes, primarily from egg masses laid by females that developed on warmer slopes. During the second drought year, no females eclose early from warmer slopes. Females eclosing later from cool slopes have virtually no chance of successful reproduction anywhere.

In years with extraordinarily wet winters and springs, such as 1982–1983, postdiapause larvae on warmer slopes are much more likely to develop in time to reproduce successfully than those on cooler slopes. Under these weather conditions, feeding and basking periods are merely short breaks between successive storms. Prolonged rains in 1982–1983 led to severe population reductions in Jasper Ridge area H and several other populations. Cool, wet weather delayed postdiapause larval and pupal development much more than the timing of plant senescence, hence prediapause larval starvation was very high (Dobkin et al. 1987).

Dispersing larvae can partially ameliorate drought or deluge effects by moving to warmer slopes to speed their growth. Larvae ready to pupate also can disperse to warmer slopes and eclose as adults earlier. Certain topographic features facilitate interslope transfers; for instance, dispersal across shallow "V"-shaped gullies can provide large temperature changes over just a few metres. Dispersal across ridgelines allows the same effect over slightly greater distances. Thus, habitat quality is not just a feature of an immediate habitat area, but also of adjacent areas on a scale of tens of metres.

Local topographic diversity also can influence the survival of prediapause larvae, albeit over shorter distances given the more limited dispersal capabilities of these smaller larvae (Weiss and Murphy 1988). Prediapause larvae on a warm slope immediately adjacent to a cool slope might find edible plants on the cooler slope. Conversely, larvae searching for diapause sites might enter warmer areas, develop faster as postdiapause larvae, and eclose as adults earlier the next year.

Long-term habitat quality may be defined as the ability of a given habitat patch to support a viable population over decades and centuries. In favorable years, populations on high-quality habitat will increase, which buffers them against inevitable unfavorable weather patterns in subsequent years. Unfavorable weather patterns should not have as drastic an effect on population size in high-quality habitat patches as in low-quality patches.

Several topographic elements contribute to long-term habitat quality. First is the overall range of slope exposures. Even small areas of cool steep north-facing slopes will confer to a population resistance to extinction during short or mild periods of drought. A lack of relatively warmer areas will tend to retard postdiapause development, resulting in later flight periods and confounding the phase relationships between the butterflies and their host plants. A wide variety of microclimates assures that at least some survival, timely development, and reproduction can occur under most macroclimatic conditions. Even slopes with the very highest insolation, where the chances of prediapause survivorship are vanishingly small, can contribute in some years by providing early season nectar, which increases female fecundity and lifespan and affects adult movements (Murphy 1983, Murphy et al. 1983).

A second factor contributing to long-term habitat quality is the spatial interfacing between slope exposures. Areas with high local diversity of slope exposures, especially where cooler slopes extensively abut warmer slopes, confer to populations greater resilience in the face of extreme macroclimate variability when postdiapause larvae disperse.

Third, the amount of rainfall actually received by a site is important in determining soil moisture when rains stop in the spring, hence in determining the timing of plant senescence. The primary determinant of *Plantago* senescence is soil moisture at 0.15 m depth in the soil (Gulmon et al. 1983). Rainfall in the San Francisco Bay area varies widely over short distances with local rain shadows and elevation changes (Gilliam 1962). Cloudy weather has the same inhibiting effect on larval growth and pupal development whether 5 or 50 mm of rain actually falls. Habitats in higher rainfall regions should be more resistant to droughts, when extra rainfall can make a significant contribution to extending the spring annual plant growing season.

These principles have importance to the conservation of this butterfly, which is now listed by the United States Fish and Wildlife Service as a "threatened species" (United States Federal Register, 18 September 1987). Even small reductions in overall range of microclimates or disturbance of areas of high local topographic diveristy within a habitat patch can reduce long-term habitat quality. Such losses might not be apparent until consecutive years of severe drought or deluge, but then could have an impact disproportional to the size of the disrupted area. The importance of microclimate diversity on population dynamics probably applies to numerous small ectothermic animals. The design of preserves for such animals clearly must consider habitat heterogeneity as well as overall habitat size. Smaller, more topographically diverse preserves may well constitute higher quality long-term habitat for organisms such as *Euphydryas editha* than would larger, more homogeneous preserves.

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