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Estimating female reproductive success of a threatened butterfly: influence of emergence time and hostplant phenology

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Abstract We estimated lifetime reproductive success of *Euphydryas editha bayensis* (Nymphalidae), a federally listed threatened butterfly, based on age-specific fecundity and both adult and offspring survival. Our results indicate that the relative timing of adult emergence and larval hostplant senescence strongly influenced reproductive success of females. For 1992, we estimated that only 8–21% of the eggs laid by females emerging on the 1st day of the 4-week flight season would produce larvae that reach diapause. This figure dropped to 1–5% for females emerging 7 days into the flight season. Within our entire sample, we estimated that 64–88% of the females produced offspring with less than a 2% probability of reaching diapause. These estimates are particularly striking given that they are based on only one source of larval mortality – prediapause starvation due to hostplant senescence. This dependence of reproductive success on the relative timing of female emergence and hostplant senescence may reduce effective population size and render *E. editha bayensis* especially vulnerable to local extinction events.

Key words Adult emergence time
Conservation biology · *Euphydryas editha bayensis*
Hostplant phenology · Lifetime reproductive success

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Introduction

Individuals in populations differ widely in the number of offspring they produce and the subsequent success of their offspring. Understanding the extent, distribution, and causes of these differences is of central importance to studies of population dynamics, natural selection, and conservation biology (Lomnicki 1978; Arnold and Wade 1984; Clutton-Brock 1988). However, quantifying the lifetime reproductive success of individuals in natural populations has proved to be extremely difficult (Clutton-Brock 1988; Barrowclough and Rockwell 1993). For many vertebrates, individuals have reproductive lifetimes that exceed the duration of most research projects. For many invertebrates, survivorship and fecundity are difficult to quantify due to the small size of individuals and their distribution in the environment. As a result of these and other logistical difficulties, field studies have rarely quantified reproductive success.

Variation in lifetime reproductive success may be especially striking for organisms that are restricted to environments characterized by pronounced variation in the timing and magnitude of seasonal fluctuations (e.g., see Istock 1981; Tallamy and Denno 1981). For such organisms, synchrony between the time of reproduction and resource availability for the resulting offspring is critical to reproductive success. In many cases, developmental phenology and resource availability are influenced strongly by abiotic factors, such as temperature and precipitation, that are difficult for organisms to track precisely. In addition, abiotic factors may have different and sometimes opposing effects on emergence time and juvenile resource availability. For example, with herbivorous insects in mediterranean climates, cooler spring temperatures and increased precipitation may increase hostplant availability and quality, but such conditions may significantly slow larval development and therefore delay adult emergence (see Weiss et al. 1988).

The threatened and federally protected Bay checkerspot butterfly, *Euphydryas editha bayensis* (Nymphalidae), lives in a seasonal mediterranean climate. Previous studies have suggested that its population dynamics are determined largely by starvation levels of prediapause larvae, a process that appears to be mediated by the degree of synchrony between adult emergence and availability of annual hostplants (Singer 1971; Singer and Ehrlich 1979; Dobkin et al. 1987; Weiss et al. 1988). However, these studies have not examined actual variation in reproductive success of individual females as a function of the time of adult emergence. Moving from the population to the individual level is critical for understanding the pressures affecting the evolution of phenology and designing management strategies for endangered species.

Here, we develop and apply a method for estimating the lifetime reproductive success of female butterflies in natural populations. We use this method to ask how reproductive success varies among females with different dates of adult emergence relative to the timing of larval hostplant senescence.

Methods

Study sites and organisms

We conducted field work at Kirby Canyon (Santa Clara County, California, USA) and Stanford University's Jasper Ridge Biological Preserve (San Mateo County, California, USA). These areas support rich native grassland communities on serpentine-based soils, which possess a unique chemical composition that has resisted the invasion of Eurasian annual grasses and forbs. The sites have a mediterranean climate consisting of a cool rainy season from approximately October to April and a warm dry season from May to September.

Euphydryas editha bayensis is a univoltine butterfly currently restricted to the grasslands on serpentine soils in the San Francisco Bay Area. Although there is substantial phenological variation among years, adult butterflies usually have a 3–5 week flight season, between early March and late April (Singer and Ehrlich 1979). Checkerspot butterfly populations are patchily distributed and movement of adults between adjacent populations is highly restricted (Ehrlich 1961, 1965). Extinction of local populations is frequent and plays a significant role in the butterfly's metapopulation dynamics (Ehrlich et al. 1980; Harrison et al. 1988).

Females lay egg masses of 20–200 eggs near the base of *Plantago erecta* (Plantaginaceae) and less frequently *Orthocarpus densiflorus* and *O. purpurascens* (Scrophulariaceae) (Singer 1972). Eggs hatch in approximately 2 weeks (Labine 1968; Singer and Ehrlich 1979). Larvae feed for 12–14 days until they reach the fourth instar, when they enter an obligatory dry-season diapause (Ehrlich 1965; Singer 1972). At the start of the next rainy season (5–6 months later), surviving larvae break diapause and resume feeding on newly germinated *P. erecta*. Postdiapause larvae feed until they reach 300–500 mg and then pupate (Weiss et al. 1988).

Overview: estimating lifetime reproductive success

The lifetime reproductive success of an individual female is equal to her lifetime fecundity multiplied by the proportion of her offspring that attain reproductive age. Because lifetime fecundity depends on both reproductive lifespan and daily fecundity, we estimate these parameters in *E. editha bayensis*. Daily fecundity depends on both female age and body weight, particularly in species that rely heavily on larval reserves for egg production, such as *E. editha bayensis* (Labine 1968; Boggs 1986; C. L. Boggs, unpublished data).

The proportion of offspring that attain reproductive age depends on the hatching success of eggs, pre- and postdiapause larval mortality, and pupal mortality. Here, we use prediapause larval mortality to provide an upper estimate of lifetime reproductive success. We feel this is a reasonable approximation, given that prediapause mortality due to hostplant senescence commonly exceeds 90% in *E. editha bayensis* (Singer 1972; Singer and Ehrlich 1979; Dobkin et al. 1987). To determine prediapause larval mortality, we therefore document patterns of hostplant senescence. In addition, we estimate dates of female emergence because these determine dates of egg deposition, which in turn may have a profound effect on whether larvae have sufficient time to reach diapause.

Lifetime fecundity

Age-specific adult survival

We estimated age-specific survival probabilities using field data on 120 female butterflies from an intensive mark-recapture study on *E. editha bayensis* in 1981 at Jasper Ridge (see Ehrlich et al. 1984; Murphy et al. 1986). We used these data to calculate the conditional probabilities of survival – e.g., the probabilities that a female butterfly surviving to the age of 4 days would live to the age of 5, 6, 7, and so on to 16 days. Conditional probabilities are simply the probability of an individual reaching a future age divided by the probability of its reaching its current age.

Age-specific fecundity

We gathered three kinds of data to estimate age-specific fecundity for *E. editha bayensis*. First, in the field, we determined the relationship between wing wear and age, as this allowed us to link data on field and greenhouse butterflies. Second, we generated regression equations to predict daily fecundity from wing wear and weights of greenhouse females. And third, we weighed field-caught females and assessed their wing-wear condition.

Relationship between wing wear and age. To determine the relationship between age and wing-wear categories, we again used data from the 1981 mark-recapture study at Jasper Ridge. The wing-wear condition of all individuals was rated at capture according to a standardized scale, with categories ranging from 0.5 (newly emerged) to 3.5 (severely battered and/or worn), increasing by 0.5 increments (consistency in wing-wear assignments was achieved by using laminated voucher specimens in the field; see Murphy et al. 1986). Using data on 86 females that were captured more than once and caught first as newly emerged (0.5) individuals, we determined the number of days between captures and the corresponding change in wing-wear condition. By assuming that 0.5 and 1.0 individuals were 1 day old, we estimated the mean age of butterflies in each of the seven wing-wear categories, rounding up or down to the nearest day in all cases. We assumed that the relationship between age and wing wear did not differ among years and populations. We used these data to assign wing-wear categories to greenhouse females of known ages. The midpoint for the age range of each wear category was as close as possible to the mean age estimated from field data for that wear category.

Predicting daily fecundity from body weight and wing wear. We conducted a greenhouse study to determine the influence of adult weight and age on female fecundity. Late-instar larvae collected from Kirby Canyon were fed greenhouse-cultivated *P. erecta* until pupation. Adult females obtained from these larvae were allowed to mate either on the day of eclosion ($n = 12$) or within 2 days of eclosion ($n = 9$). We obtained matings by placing females in cylindrical 0.035-m^3 net cages with at least twice as many young males obtained from pupal stocks and/or the field.

We housed mated females individually in net cages with ambient light and controlled temperature (mean ± SD daily maximum and minimum temperatures were 34.0±3.3 and 12.6±2.0°C, respectively). Each cage allowed both sun and shade for butterfly thermoregulation, and contained three pots of flowering *Layia platyglossa* (Asteraceae) for nectar feeding and one pot of *P. erecta* for oviposition. We placed butterflies on flowers and the hostplant at least twice a day to make sure that opportunities for feeding and oviposition were available. At sunset every day, we weighed each female in a glassine envelope to the nearest 0.1 mg and counted the number of eggs she laid that day.

Weights and wing-wear categories of field-caught females. Every 5–7 days during the 1992 flight season (from late March to late April 1992), we captured butterflies in a 40 x 400 m plot at Kirby Canyon to weigh and assess the wing-wear condition of each female. The plot traversed a major ridge that included four microclimatic zones defined by Weiss et al. (1988): warm (south- and west-facing slopes; tilt >11°), moderate (all aspects; tilt <11°), cool (north- and north-east-facing slopes; tilt >11°), and very cool (north- and north-east-facing slopes; tilt >17°). We sampled the butterfly population four times during the flight season; butterflies were not present 5 days prior to the first sample nor 5 days after the fourth sample.

We captured 40 butterflies per slope type per sample date, except for the last sample date when we were able to capture only 15 per slope type. We rated the wing condition of all captured individuals according to the standardized scale described above (omitting the 0.5 wear class). We weighed all females in glassine envelopes to the nearest milligram and immediately released them at their sites of capture.

Calculating lifetime fecundity of field-caught females

We calculated lifetime fecundity in three steps. First, we estimated the total potential fecundity of field-caught females by substituting their respective weights and wing-wear categories into the greenhouse-based regressions predicting past and future fecundity. Second, we multiplied total potential fecundity by the proportion of eggs laid each day by greenhouse females, thus generating age-specific fecundity for field-caught females. Third, we multiplied future age-specific fecundity by the conditional survival probabilities to account for future adult mortality. We also estimated the emergence date of each female based on age at capture and capture date.

Offspring survival

We used the average proportion of senescent hostplants at the time of diapause to estimate prediapause larval mortality. We focused exclusively on the phenology of *Plantago erecta*, as *Orthocarpus* made up less than 1% of the hostplants on our study site in 1992 (S. B. Weiss, unpublished data). We classified as "presenescent" those hostplants that were green and suitable for larval feeding, and as "senescent" those that were dried out and no longer edible.

To determine the slope-specific availability of hostplants to prediapause larvae throughout the season, we established three parallel line transects (400 m long and 20 m apart) within the Kirby Canyon plot described earlier. For each 100-m section of the three line transects, we visually estimated the proportion of *P. erecta* that were presenescent in ten 1-m^2 quadrats. The first quadrat was placed along the transect at a randomly chosen distance from the terminus, while all remaining quadrats were 10 m apart. We monitored *P. erecta* every 6–9 days (from late March to mid-May 1992) for a total of six times during the season, beginning when 100% of the *P. erecta* were presenescent and concluding when all plants had senesced.

To estimate the availability of *P. erecta* to larvae, we calculated the day-specific proportion of hostplants over all slopes that were presenescent 24 and 28 days into the future. We linearly interpolated between sample dates to generate these day-specific profiles from our weekly data. We selected 24 and 28 days because they represented low and high estimates of the development time from egg to larval diapause (12–14 days for eggs to hatch; 12–14 days for larvae to reach diapause).

Lifetime reproductive success

Using the data generated above, we estimated the daily reproductive success of each female as her age-specific fecundity, adjusted for her own probability of survival, multiplied by the estimated probability of larval survival to diapause. We calculated larval survival probabilities as the proportion of hostplants that were presenescent 24 and 28 days following a given day's egg production. We then summed all daily reproductive success values to obtain an estimate of lifetime reproductive success.

Results

Lifetime fecundity

We based calculations of lifetime fecundity of field-caught females on estimates of adult survival probability and age-specific fecundity. Adult survival probabilities varied with age, and are shown in Fig 1.

We determined the relationship between age-specific fecundity and adult female weight and age using greenhouse females. Greenhouse females lived a maximum of 19 days, with just over 50% surviving to 11 days (see Fig. 2). In contrast, the maximum lifespan observed in the field was 14 days, with just over 50% surviving to 4 days (Fig. 1). Fecundity varied substantially with age, with the shape of the curve matching that previously observed in another population of *E. editha bayensis* (Labine 1968). Egg-laying occurred from day 1 to 16, with 62% of each female's eggs being deposited between days 2 and 5 (Fig. 2).

Ages of greenhouse females were initially recorded as "days since adult eclosion". To convert these data from days to wing-wear category ratings, we used the relation-

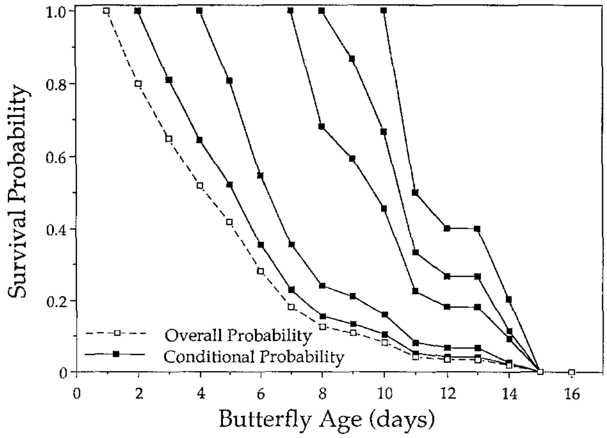

Fig. 1 Estimated adult survival probabilities for *Euphydryas editha bayensis* plotted as a function of butterfly age. The *single dashed line* corresponds to the estimated overall survival probabilities. The *five solid lines* correspond to the estimated conditional survival probabilities for butterflies that had already survived to the age of 2, 4, 7, 8, and 10 days, respectively

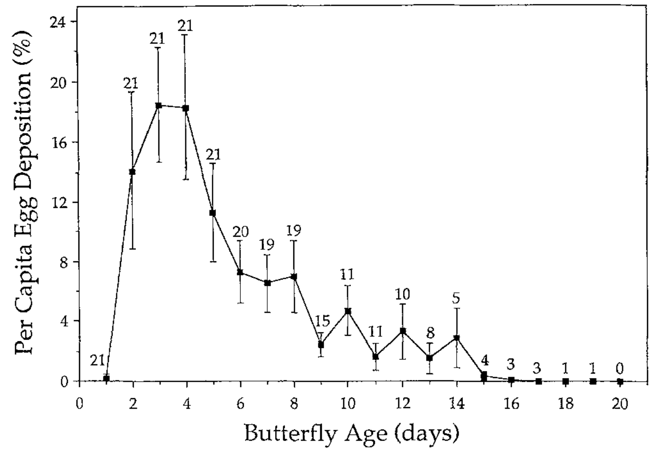

Fig. 2 Mean age-specific fecundity of 21 *E. editha bayensis* reared in the greenhouse. *Vertical bars* correspond to ±1 SE. *Numbers* above the error bars indicate the number of butterflies that produced eggs on that day

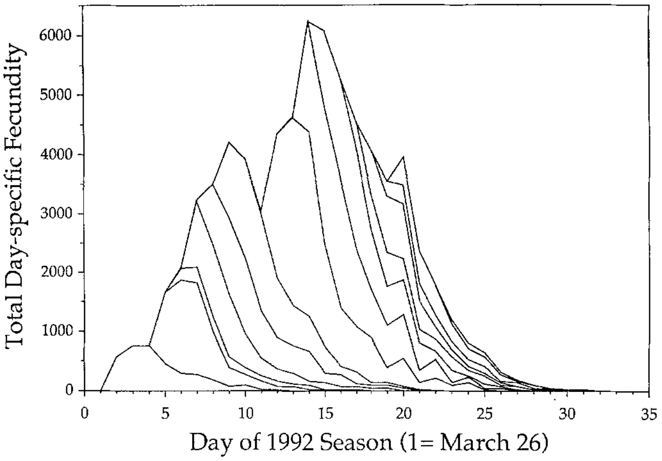

Fig. 4 The summation of day-specific fecundity curves for field-caught *Euphydryas editha bayensis*, where each of the 14 *curves* corresponds to a cohort of females that emerged on the same day (ranging from day 1 to 22). Total day-specific fecundity of all 211 butterflies is given by the *outer line*

Table 1 Relationship between wing-wear categories and estimated age (in days) of field-caught female *Euphydryas editha bayensis* in 1981. Included are the assignment of wing-wear categories to greenhouse-reared females of known age. Field data are for 86 females caught more than once and first caught in the newly emerged condition (i.e., category 0.5). Sample sizes indicate the number of captures (e.g., 137, 114) and not the number of butterflies (86)

FIELD			GREENHOUSE
Wing-wear Category	n	Estimated mean age (SE)	Age range
1.0	137	1.65 (0.15)	1–2
1.5	114	4.19 (0.15)	3–5
2.0	14	7.14 (0.44)	6–7
2.5	22	7.82 (0.35)	8
3.0	4	10.25 (0.82)	9–11
3.5	1	15.00	12–19

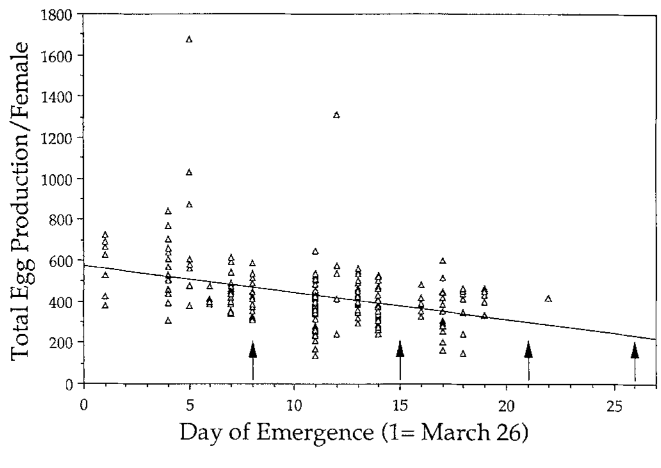

Fig. 3 Estimated total fecundity of 211 field-caught *E. editha bayensis* plotted as a function of their respective emergence dates. The *solid line* corresponds to a linear regression model (see text). *Arrows* indicate the dates when butterflies were sampled

ship between estimated age and wing-wear categories for 86 field-caught *E. editha bayensis* in 1981 (Table 1). Table 1 also shows the assignments of wing-wear categories to greenhouse-reared females of known age, which allowed us to link data from field and greenhouse butterflies.

Butterfly weight and wing wear had a substantial influence on greenhouse female fecundity. Stepwise multiple regressions based on weight and assigned wing wear predicted a significant amount of variation in past and future female fecundity [square root of past fecundity = $-25.01+0.04(\text{weight})+26.49(\text{wear})-4.24(\text{wear})^2$, $r^2 = 0.57$, $F_{3,226} = 98.4$, $P<0.001$; square root of future fecundity = $-5.76+0.13(\text{weight})-0.26(\text{wear})^2$, $r^2 = 0.72$, $F_{2,227} = 292.6$, $P<0.001$).

Using these regressions, we calculated total fecundity, adjusted for future adult mortality, for our sample of field-caught females. Estimated lifetime fecundity varied considerably among individuals, ranging from 135 to 1680 and decreasing significantly with later emergence dates (Fig. 3; $y = 574.1-13.1x$, $r^2 = 0.13$, $F_{1,209} = 31.2$, $P = 0.0001$). The outer line in Fig. 4 shows the total day-specific fecundity of all 211 females throughout the 1992 field season. Figure 4 also shows the day-specific fecundity curves that make up this overall relationship, with each of the 14 curves corresponding to a cohort of females that emerged on the same day.

Offspring survival

The proportion of presenescent host plants decreased dramatically throughout the season (Fig. 5a). However, timing of senescence did not differ significantly among the four slope types (repeated-measure ANOVA, slope-time interaction, $F_{5,596} = 1.3$, $P = 0.251$). Figure 5b illustrates the day-specific proportion of presenescent host-plants available at diapause, assuming 24- and 28-day development periods. We used average values across

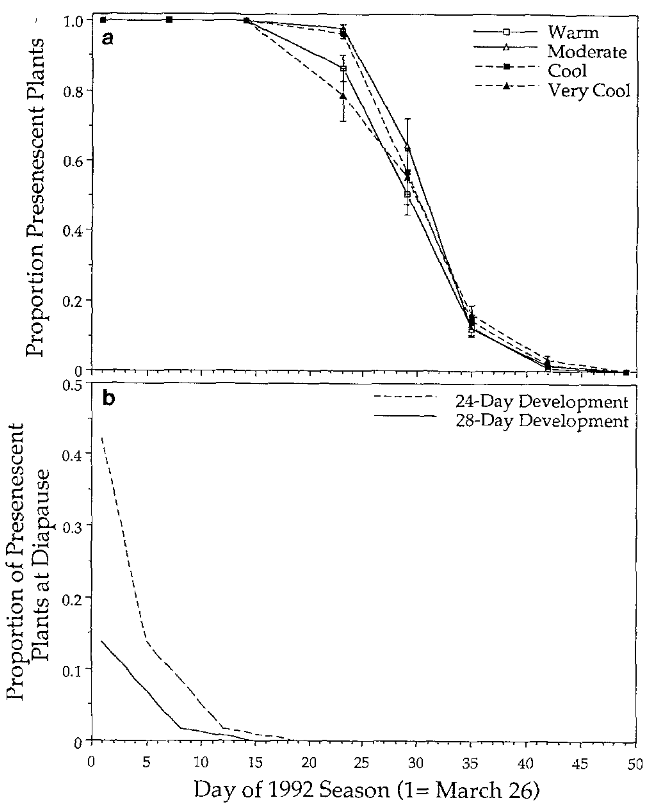

Fig. 5 **a** Proportion of presenescent *Plantago erecta* plants throughout the field season and **b** the proportion of presenescent *P. erecta* at larval diapause, 24 and 28 days in the future. The *four lines* in **a** correspond to different habitat-types in the study area

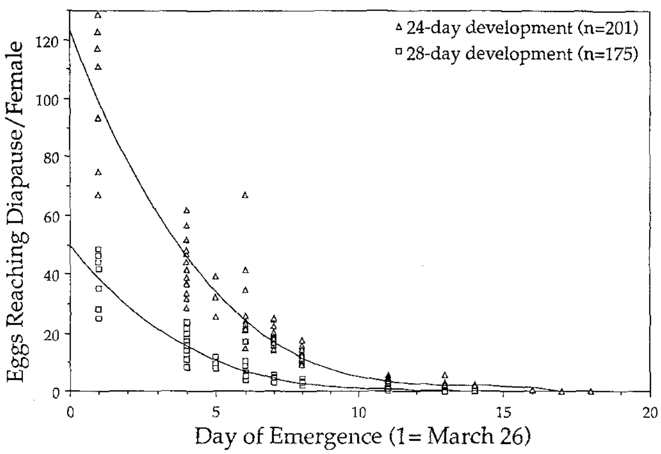

Fig. 6 Number of *E. editha bayensis* eggs that were estimated to reach larval diapause plotted as a function of each female's day of emergence. Separate estimates are shown for 24-day (n = 201) and 28-day (n = 175) development periods. The *solid lines* correspond to third-order polynomial regression models (see text)

Table 2 The estimated influence of emergence date on the reproductive success of female *E. editha bayensis*. Development from egg to diapausing larva is assumed to take either 24 or 28 days

Female emergence day	n	Estimated % eggs reaching diapause	
		24-day development	28-day development
1	7	20.6	7.8
4	15	10.4	4.0
5	3	7.2	2.2
6	12	5.4–7.5[a]	1.4–1.9[a]
7	16	4.6	1.0
8	23	3.5	0.9
11	46	1.0–1.2[a]	0.2–0.3[a]
13	28	0.6–0.8[a]	0–0.1[a]
14	25	0.5	0
16	8	0.2	0
17	14	0.1	0
18	4	0	0
19	9	0	0
22	1	0	0

[a] Some females were captured on different censuses, but were estimated to have the same emergence date. These females had different estimates of reproductive success because their conditional survival probabilities differed

slopes in Fig. 5b, given that the four slopes did not differ significantly in host plant phenology (Fig. 5a).

Assuming a 24-day development period (from egg to diapausing larva), eggs laid after day 19 of the flight season had no chance of reaching larval diapause, whereas those laid on day 7 had a 10% chance (Fig. 5b). Assuming a 28-day development period, eggs laid after day 15 had no chance of reaching diapause, and those laid on day 3 had a 10% chance.

Lifetime reproductive success

Day of emergence was strongly related to lifetime reproductive success (Fig. 6). A large percentage of females were estimated to have attained at least some level of reproductive success under either developmental scenario (95.3% for the 24-day larval development regime and 82.9% for the 28-day regime; Table 2). However, in both scenarios, the number of offspring reaching larval diapause per female decreased dramatically with day of emergence (Fig. 6; 24-day development: $r^2 = 0.91$, $y = 123.7–26.3x+1.9x^2–0.05x^3$, $F_{3,197} = 688.9$, $P = 0.0001$; 28-day development: $r^2 = 0.93$, $y = 49.8–12.2x+1.0x^2–0.3x^3$, $F_{3,171} = 753.1$, $P = 0.0001$).

Although we estimated that many females successfully reproduced to some degree, the percentage of offspring reaching larval diapause was extremely low for most individuals. We estimated that between 8% (28-day development) and 21% (24-day development) of the eggs laid by females emerging on the 1st day of the flight season would produce larvae that successfully reach diapause. For females emerging on the 7th day, larval success dropped to 1–5% (Table 2).

Discussion

Results from our analysis quantitatively illustrate the dire consequences faced by *Euphydryas editha bayensis* that failed to emerge early in the 1992 flight season. We estimated that 64–88% of the females in our sample had less than 2% of their eggs reach larval diapause. These results are particularly striking given that we considered only adult mortality and prediapause larval starvation due to hostplant senescence. Clearly, larvae (and pupae) face many other sources of mortality, including the effects of natural enemies and problems associated with larval development. Thus, our methods were conservative and provided an upper bound on the lifetime reproductive success of female butterflies.

In *E. editha bayensis*, mortality rates are approximately 50% during the diapause stage, 20% during the postdiapause stage, and 50% during the the pupal stage (White 1986; Weiss et al. 1988; R. R. White, unpublished data). Thus, a female *E. editha bayensis* must on average produce ten offspring that reach larval diapause if two of them are to become adults (that is, if she is to achieve replacement fertility). An estimated 33% of the female butterflies in our sample achieved replacement fertility under a 24-day development period, whereas this number dropped to 11% under a 28-day development period. On the sample level, we estimated that our field-caught females would need to have 2110 eggs reach larval diapause in order to maintain a stable population size (211 females × 10 eggs). Under the 24-day development scenario, the sample attained exactly 100% of this replacement value, whereas the sample attained only 38% replacement under the 28-day scenario. If our sample of 211 females is representative of the population as a whole, these estimates suggest that the population at best would have persisted at the same level in 1993, and at worst would have declined by as much as 62%.

Our method for estimating lifetime reproductive success assumes that failure to recapture butterflies approximates *Euphydryas* mortality. As pointed out by Ehrlich (1961), Ehrlich et al. (1984), and others, the disappearances of butterflies from a given site can be due to either death or emigration, two events that cannot be readily distinguished from one another using standard mark-recapture techniques and analyses. Hence, pooling the two may have caused us to overestimate age-specific adult mortality. However, while we were concerned primarily with individual reproductive success, which is halted by death but not necessarily by emigration, we were also interested in the interaction between the timing of oviposition and hostplant senescence. Thus, while emigration may not always terminate a female's reproduction, it does terminate her contribution to the local population.

To estimate lifetime reproductive success, we assumed that fecundity schedules for greenhouse females matched those of field individuals. However, maximum temperatures were probably greater in the greenhouse than the field. Early age-specific fecundity is known to increase with temperature in other butterfly species (e.g., Boggs 1986), suggesting that, if anything, the age-specific fecundity curve may have been shifted forward in the greenhouse relative to the field. If so, we would have overestimated the reproductive success of females in the field, because larvae resulting from eggs laid earlier in the season have a greater chance of locating edible hostplants and therefore surviving to diapause. Our estimates of reproductive success are thus conservative with respect to not only causes of larval mortality, but also timing of egg deposition.

We have assumed that the probability of larvae surviving to diapause was equal to the average proportion of presenescent hostplants available at the time of diapause. This assumes that larvae were randomly distributed with respect to senescent and presenescent hostplants at all times. Given the lack of information on the actual distribution of prediapause larvae among hostplants, our assumption represents the null hypothesis.

Although we failed to detect significant differences in hostplant phenologies across slope types in 1992, such differences often occur in this system. For example, among-slope differences were observed on our study plot in 1990 and 1993, and at other Kirby Canyon sites in 1992 (S. B. Weiss, J. H. Cushman, and A. J. Hobday, unpublished data). In those years and sites where differences were apparent, *Plantago erecta* senesced first on the warmest slopes and last on the coolest slopes (Weiss et al. 1988). Thus, larvae will typically have the greatest chance of reaching diapause when they are located on the coolest slopes (Singer 1972; Weiss et al. 1988). However, individuals develop faster on warmer slopes as postdiapause larvae and pupae, and hence are the first to emerge in the spring (Weiss et al. 1988).

Our results clearly demonstrate that, in 1992, only the offspring of females that emerged early in the flight season had a reasonable chance of surviving to larval diapause. Thus, factors that lead to early adult emergence will result in greatly increased reproductive success. However, the timing of the adult flight period is constrained both by the need for cool temperatures to prolong hostplant senescence during the prediapause larval stage as well as warmer temperatures to increase development rates during the postdiapause larval stage.

Given that only a few early emerging females appear to contribute most of the offspring to the next generation and that females generally mate only once (Labine 1968), the effective population size (N_e) of this threatened butterfly is likely to be significantly lower than the observed population size (N). Even in those years and/or at those sites where N is large, N_e may still be relatively small due to the persistent effects of emergence time on reproductive success. This suggests that genetic factors may affect population viability, even when N is large. This hypothesis contrasts with suggestions by Ehrlich (1983) and Murphy et al. (1990) that genetic factors could be safely ignored when considering the extinction of butterfly populations, as most populations do not remain at the small sizes required for serious genetic problems to occur (small populations either go extinct or recover to larger sizes). These conjectures were based on the assumption that N_e is the same order of magnitude as N (also see Mueller et al. 1985). However, if $\mathrm{N_e}$ is commonly one or two orders of magnitude lower than N, as suggested by this study, then genetic stochasticity may well affect population persistence.

The phenological scramble for survival and the assured mortality of most *E. editha bayensis* larvae leads to an obvious question – why is the life history of this subspecies so apparently incompatible with its climate and the associated patterns of resource availability? The answer to this question may lie in the relatively recent history of human settlement of coastal California, and the concomitant invasion of grasslands by alien plant species that have outcompeted native species under all but a few rare edaphic conditions. Presumably, many of the native plant species, and the insects that depend on them, that are now restricted to porous, rapidly drying serpentine soils, were once more widely distributed on soils that dried later in the spring. Thus, the race between developing prediapause larvae and plant senescence, the major current source of mortality, may be a rather new artefact of anthropogenic habitat disruption. Serpentine-based soils may historically have provided only marginal habitat for this and other species that were comparatively better adapted to other physical circumstances (see further discussion by Murphy et al. 1983; Murphy and Ehrlich 1989).

The method that we have used to estimate the lifetime reproductive success of *E. editha bayensis* should be applicable to many other insect taxa, especially other univoltine Lepidoptera. It should work best for those species for which there is a close correlation between the initial body weight of adult females and their lifetime fecundity. The strength of this correlation, and therefore the usefulness of our method, should be greatest for those species that do not rely heavily on adult feeding for oogenesis (Boggs 1986). Because the procedure is fairly non-intrusive, it will be particularly appropriate for threatened and endangered taxa.

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