

Do hypotheses from short-term studies hold in the long-term? An empirical test

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Abstract. 1. A sequence of population estimates for two now-extinct populations of *Euphydryas editha bayensis* is presented. After removing biased sampling days, estimates of demographic parameters from the long-term data were used to test five hypotheses built from studies of shorter duration. Such tests of short-term conclusions are rare.

2. The long-term demographic parameters include sex ratio, mortality, dispersal, mean flight date, and duration of flight season. The two populations differed with respect to sex ratio and mean flight date, and sexes differed with respect to mortality and dispersal.

3. Three of the five hypotheses were supported directly or indirectly by patterns in the parameters. These hypotheses predict that dynamics are asynchronous over the long term, that larval mortality, not adult abundance and mortality, is the primary determinant of changes in population size, and that topography mediates larval mortality.

4. Two hypotheses were not supported or supported only in part. Flight phenology differed between the study populations as predicted, but flight order was opposite that expected from the topographic composition of each habitat. Variability in sex ratio and the occurrence of female-biased ratios in the habitat of one of the populations also suggest that previous observations of sex ratio are not generalisable.

5. Populations were extremely volatile over the study period. Removal of biased sampling days did not change basic trends or fluctuations in the data. This volatility suggests that *E. editha* populations residing in similar habitats may risk immediate extinction.

Key words. Bias reduction, demography, *Euphydryas editha bayensis*, extinction, hypothesis testing, long-term data, population variability.

Introduction

Long-term studies of populations, communities, and ecosystems are vital to understanding ecological processes, and thus can provide critical information to managers and conservation planners (Ehrlich *et al.*, 1975; Callahan, 1984). Such studies maximise the return on a research investment

and should yield generalities applicable to other systems (Ehrlich, 1992, 1997). One model system under continuous study since 1960 is the threatened Bay checkerspot butterfly *Euphydryas editha bayensis*. This butterfly has been studied with annual mark–recapture surveys at the Jasper Ridge Biological Preserve, California, U.S.A. (37°24'N, 122°13'30"W) to gain information on the ecology and evolution of the populations residing there and, more recently, to monitor its decline to extinction.

This paper presents an entire corrected set of abundance estimates for this site now that its populations have become extinct. In order to produce these estimates, objective

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criteria for removing sampling inconsistencies and biases in the survey data are proposed, applied to the raw data, and used to examine their impact on calculated population sizes. Such data cleaning is often performed informally on census data, particularly in systems where recapture numbers are low due to weather, technical problems, or population size, but little attention has been paid to the impact of selective data removal on population estimation.

After data cleaning, demographic parameters were estimated and compared across populations, sexes, and years to examine the factors that affected these populations. These parameter estimates were used to test a set of hypotheses about the ecology of this insect that had been derived previously from shorter-term studies: (1) Populations in close proximity (such as at Jasper Ridge) fluctuate independently (Ehrlich *et al.*, 1975). (2) Variation in larval mortality among years is the primary cause of population fluctuations (Singer, 1972; Ehrlich *et al.*, 1980; Dobkin *et al.*, 1987; Hellmann, 2002). (3) Topography and habitat heterogeneity affect butterfly phenology (Weiss *et al.*, 1987, 1988; Murphy & Weiss, 1988; Weiss & Weiss, 1998). (4) Heterogeneity in topography mediates larval survival on slopes of differing exposure (Dobkin *et al.*, 1987; Weiss *et al.*, 1988; Fleishman *et al.*, 2000). (5) Sex ratios are moderately and consistently male biased in field populations (Ehrlich *et al.*, 1984). By evaluating these hypotheses, it was possible to determine whether results from shorter-term field studies can be scaled up to produce population predictions over several decades. This kind of comparison is possible in relatively few study systems, and the completion of surveys at Jasper Ridge provides one such opportunity. Finally, the variability of the Jasper Ridge populations, as revealed by the complete long-term data, is used to address extinction risk in other populations of this subspecies.

Euphydryas editha at Jasper Ridge

Euphydryas editha bayensis is a univoltine insect that inhabits isolated areas of native grassland in the San Francisco Bay area of central California (Hellmann *et al.*, in press). These habitats experience a Mediterranean-type climate with summer drought. Eggs are laid by adults during the spring growing season, and larvae diapause through the summer as third or fourth instars. Post-diapause larvae emerge with the onset of rain in the late autumn and pupate in March or April.

Initial studies at Jasper Ridge showed that its resident colony was grouped into three distinct populations or demographic units. Each population occupied a habitat patch of serpentine soil-based grassland labelled areas C, G, and H (Ehrlich, 1961; Fig. 1), and these populations exhibited limited inter-patch dispersal (Ehrlich, 1965; Ehrlich *et al.*, 1975). Areas C and H were censused annually with mark-recapture techniques from 1960 (Ehrlich & Davidson, 1960) until the population in area C went extinct in 1991 and the population in area H disappeared in 1998. The population in area G went extinct twice over the study period, was recolonised once, and has been uninhabited

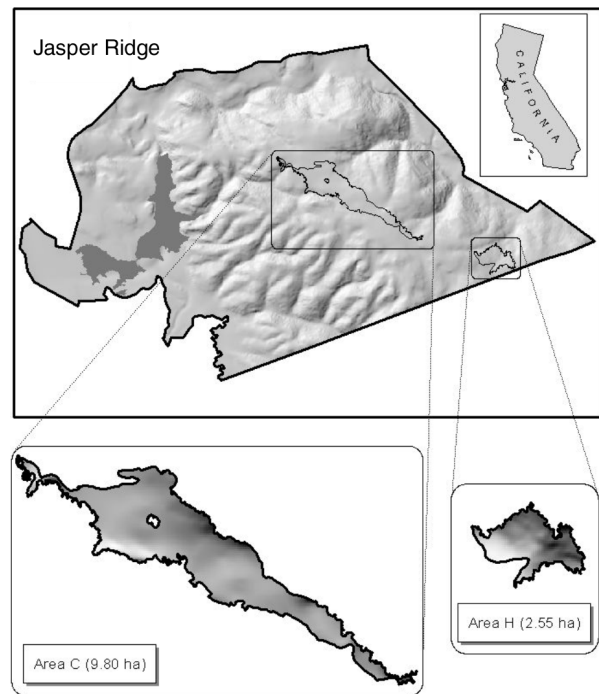


Fig. 1. Map of the Jasper Ridge Biological Preserve and the two patches of serpentine grassland labelled areas C and H. Topographic relief is shown in the first inset, and the solar insolation of each patch is shown with a grey scale (light colours = warm; dark colours = cool).

since 1973. Abundance estimates for area G were reported by Ehrlich *et al.* (1975) but are too brief to include in the analyses presented here. Hence, this synthesis focuses on long-term data from the two habitat areas C and H.

Methods

Mark-recapture studies at Jasper Ridge typically began when the first adults appeared in the early spring each year and were terminated when the number of adults declined to near zero. Each captured insect was marked with a unique number and scored for wing condition (a surrogate for age), sex, area of capture (C or H), and location within each area. Mark-recapture studies were not carried out in 1965–1967; instead, casual observations were made (Ehrlich *et al.*, 1975; Harrison *et al.*, 1991). The populations were sampled poorly in 1968, and sampling records for the period 1969–1971 are incomplete. While monitoring continues, no *E. editha bayensis* have been seen at Jasper Ridge since 1997.

Data preparation and abundance estimation

The raw mark-recapture data were analysed using a program (Jolly3.6) that calculated daily abundance for sampling days using the Jolly-Seber method (Jolly, 1965; Seber, 1965), estimated daily abundance for non-sampling days with linear interpolation, and calculated adult seasonal

abundance using Scott's method I (Scott, 1973). To satisfy the assumption of equal catchability among individuals, males and females were analysed separately. Because days with no capture were not recorded consistently throughout the study period, all days with capture (n) equal to zero between the first and last capture days were removed. These resulting seasonal outputs comprise a set of *original* population estimates. A set of *cleaned* estimates was then created by removing obvious sampling errors from the data with two stages of data cleaning (Appendix 1).

Jolly–Seber is a widely used method of estimating the abundance of insects. Alternative models based on a likelihood approach have been developed recently to estimate daily abundance and other population parameters from mark–recapture data (e.g. Schwarz & Arnason, 1996; Schwarz & Seber, 1999; Schwarz, 2001). These methods allow the consideration of constraints on factors such as the number and timing of births and the occurrence of distinct cohorts. In this case, these features do not apply, and the likelihood model reduces to the classic Jolly–Seber model provided that daily survival rates are less than one and daily birth rates are not less than zero (C. Schwarz, pers. comm.). Such violations were rare in the data set (fewer than two per year). Software implementing the likelihood model (POPAN) truncates large estimates of daily survival rates to one and negative daily birth rates to zero. While truncation avoids errors of overestimation of survival and daily population size, it ignores errors that cause underestimates of abundance and survival. To avoid negative bias due to removing only overestimates, birth and survival estimates were not truncated when calculating total seasonal abundance.

The years 1969–1971 required additional procedures for abundance estimation because the sampling record in these years terminated before many butterflies had emerged. Data from 1981 (an extremely well sampled year) were used to build a non-linear regression model of adult age and fraction of the completed flight season (Appendix 2). This model was then used to estimate what fraction of the flight season had passed by the end of sampling, and the original estimates were modified by this amount. The model generated reasonable predictions for other well-sampled years (data not shown), suggesting that the pattern of emergence observed in 1981 is generalisable to other years.

Reliability ranks

The accuracy of population estimates varies with sampling effort and completeness. To describe this variation, a rank between one (high) and five (low) was assigned to each sex and area data file according to the reliability of each abundance estimate (Tables 1 and 2). These ranks sort the data into groups that have similar sampling intensity.

Population dynamics

Population sizes and annual growth rates were normalised using log transformations: $L_t = \ln(N_t)$ and $r_t = \ln(N_{t+1}/N_t)$. To

summarise fluctuations and trends in the two populations, the mean and variance of L_t and r_t were calculated using cleaned estimates from years with reliability one, two, or three, thus restricting analysis to only those years that were well sampled. Because male population estimates are assumed to be more reliable than female estimates (Ehrlich *et al.*, 1984), r_t was calculated from male data to characterise the total population. Female data were used for comparison with female parameters.

Demographic parameters

The basic demography of the populations was described with measures of sex ratio, mortality, dispersal, timing of flight season, and flight duration; these characteristics were contrasted across sexes and habitat patches (areas). Definitions and calculations of demographic variables are given in Table 3. Because sex ratio is sensitive to error in population estimation, analyses of sex ratio were restricted to data in the top two reliability ranks; other metrics were calculated with ranks one, two, and three (Table 3). Bias in sex ratio was evaluated using a χ^2 test that assumes a binomial distribution (called X^*) (Goldstein, 1964). Pearson correlation analysis or non-parametric comparison tests (Mann–Whitney two-sample, Wilcoxon paired-sample) were used to examine all other parameters (Zar, 1999).

Results

Abundance estimation

The total number of captures, number of individuals marked, reliability ranks, and original and cleaned abundance estimates by sex for the entire study period are given in Table 2. Seasonal abundance could not be estimated in the following cases: a cleaned estimate for females in area C in 1962 could not be generated because no marked insects were recaptured; estimates for both sexes and populations in 1964 could not be calculated because all captured insects were removed; estimation was not possible for both sexes and populations in 1968 and for females in 1970 because the sampling record ceased too early.

Table 1. Reliability classes.

Rank	Description
1	Complete sampling, both frequent and covering duration of season Large sample sizes Recapture rate > 35%
2	Sampled well but not as frequently as rank 1
3	Recapture rate \approx < 20% Sharp peaks in estimated daily population size
4	Insufficient sampling duration No recaptures
5	No mark–recapture data recorded Qualitative abundance estimates

Table 2. Estimated abundance for original (N_O) and cleaned (N_C) mark–recapture data, total number of handles (n), number of unique marks placed in the population (M), and reliability ranks (R). Where possible, 1969–1971 were estimated by the extrapolation algorithm outlined in the methods and Appendix 2. Estimates for 1964, 1965, 1966, 1967, 1968, females of area H in 1970, and females of area C in 1962 were not calculated in this study for reasons stated in the results; estimates were taken instead from Harrison *et al.* (1991) and are denoted with an asterisk.

Year	Population in area C										Population in area H									
	Females					Males					Females					Males				
	n	M	R	N_O	N_C	n	M	R	N_O	N_C	n	M	R	N_O	N_C	n	M	R	N_O	N_C
1960	54	33	2	43	63	102	55	2	66	76	36	21	2	31	37	117	44	2	62	62
1961	66	40	2	82	82	241	109	2	137	138	70	48	2	105	128	348	135	2	211	211
1962	10	10	4	30	40*	26	14	2	24	24	110	91	2	376	394	467	229	2	504	504
1963	21	19	2	37	37	35	20	2	52	44	159	136	3	1258	1427	555	287	2	653	649
1964	30	0	4	84	175*	93	0	4	227	280*	366	0	4	670	1400*	987	0	4	1914	2400*
1965	n/a	n/a	5	n/a	200*	n/a	n/a	5	n/a	320*	n/a	n/a	5	n/a	2000*	n/a	n/a	5	n/a	3200*
1966	n/a	n/a	5	n/a	425*	n/a	n/a	5	n/a	680*	n/a	n/a	5	n/a	1750*	n/a	n/a	5	n/a	2800*
1967	n/a	n/a	5	n/a	425*	n/a	n/a	5	n/a	680*	n/a	n/a	5	n/a	900*	n/a	n/a	5	n/a	1440*
1968	31	31	4	40	800*	382	277	4	351	1280*	212	169	4	192	576*	622	327	4	574	922*
1969	74	38	4	328	457	250	139	4	251	279	237	133	4	449	955	771	425	4	840	965
1970	107	106	4	241	713*	203	165	4	676	1150	63	60	4	n/a	820*	427	338	4	747	2155
1971	90	44	4	139	188	145	88	4	191	250	74	33	4	22	40	271	163	4	216	291
1972	362	253	3	1371	1371	587	415	2	1961	1961	169	101	3	755	733	538	378	2	819	819
1973	412	265	2	923	933	936	452	2	837	837	131	88	2	230	250	546	224	2	359	381
1974	178	93	2	272	272	247	155	3	496	843	62	32	3	72	72	153	81	2	151	183
1975	272	201	2	1776	1756	570	374	2	1809	1809	66	41	3	127	94	227	150	2	315	315
1976	766	634	2	4643	3789	1471	1120	2	6980	6980	204	171	3	2316	2316	702	441	2	1004	1004
1977	252	141	2	310	279	824	327	1	317	327	133	74	2	141	171	361	141	1	186	186
1978	46	18	3	88	165	93	51	3	57	44	54	11	2	68	79	224	86	2	346	346
1979	104	50	2	290	307	230	109	1	253	253	57	16	3	211	211	208	79	2	178	178
1980	240	125	1	385	385	381	171	1	259	259	78	49	2	125	125	173	54	1	137	137
1981	1035	623	1	1492	1492	2183	1026	1	1944	1944	434	165	1	221	228	1860	305	1	322	322
1982	673	381	1	678	678	702	334	3	1223	1223	83	42	2	84	84	285	69	2	183	224
1983	557	382	2	1027	1203	1080	552	2	651	985	8	7	3	11	11	97	51	2	70	74
1984	132	90	2	145	145	211	108	2	162	162	7	6	3	12	12	29	16	2	49	54
1985	124	64	1	107	107	156	62	1	79	79	7	6	3	16	16	43	24	2	37	38
1986	80	63	2	128	128	146	78	2	88	88	10	7	2	18	17	29	15	2	30	34
1987	12	7	3	17	13	59	34	2	41	47	28	23	2	37	37	72	39	2	50	50
1988	2	2	–	6	6	0	0	–	0	0	58	50	2	103	100	243	105	1	178	178
1989	3	3	–	3	3	1	1	–	1	1	44	35	2	46	85	220	73	1	83	84
1990	0	0	–	0	0	2	2	–	4	4	31	27	2	41	41	142	79	3	207	207
1991	0	0	–	0	0	0	0	–	0	0	11	10	3	30	30	110	37	2	38	38
1992											27	23	2	23	24	182	59	1	66	70
1993											17	8	2	8	10	83	17	1	16	16
1994											8	4	2	4	3	30	10	1	8	8
1995											14	10	2	11	9	79	30	2	41	43
1996											0	0	–	0	0	0	0	–	0	0
1997											1	1	–	4	4	7	5	–	6	6
1998											0	0	–	0	0	0	0	–	0	0

The effect of removing sampling errors on total estimated population size was small (Tables 2 and 4). Cleaned and original estimates of total abundance differed by > 100 individuals in only 4 years. In three of these cases, the cleaned estimate was larger than the original estimate. The qualitative dynamics of the cleaned and original data sets were also very similar. The original and cleaned estimates showed the same pattern of growth and decline with only one exception. Cleaning had very little impact on the files with the highest reliability (rank one) but modified a greater proportion of files ranked two and three. (For details, see Appendix 1.)

Population dynamics

Over the study period, both populations exhibited volatile dynamics, including several large peaks into the thousands of individuals and several deep troughs to sizes below 100 (Table 2; Fig. 2). Area C supported relatively large numbers of adults (nearly 3500) in 1981, and the population was largely extinct by 1988. In contrast, area H had relatively few individuals (<≈ 300) for 15 years before the population disappeared. For most of the years when abundance was estimated with mark–recapture data, the size of the population in area C

Table 3. Description of demographic variables.

Variable	Ranks included [†]	Definition
Sex ratio	1, 2	Male estimate/female estimate
Mortality and dispersal	1–3	Scott's method I average ϕ (Scott, 1973)
Mean flight date	1–3	$\sum_i n_i \text{Date}_i / \sum_i n_i$ [‡]
Flight duration	1–3	Last date minus first date any insect captured

[†]See Table 2.[‡]Where n is the number of adults caught on sampling day i and $Date$ is the calendar date of sampling day i .

exceeded that of area H. This pattern changed just prior to the extinction of the population in area C.

In both sites, the mean population growth rate, F_t , was negative and variation around this mean was large (Table 5). Mean growth rate did not differ significantly between populations ($n_C=15$, $n_H=26$, $U=180$, $P=NS$), but the population in area C had a larger variance in its annual growth rate than did area H over the period when both populations were extant (1960–1986: $\sigma_C^2=1.82$, $\sigma_H^2=0.66$; Bartlett's test, $P<0.05$, $n=18$). Changes in population size as measured by r_t of males were correlated poorly between the two populations ($r=0.39$, $P=NS$, $n=18$), but total population sizes were correlated ($r=0.76$, $P<0.001$, $n=19$). In 61% of years ($n=18$), the two populations increased or decreased in the same direction, but this was not statistically different from random (binomial test, $P=NS$). Changes in population size ($N_t - N_{t-1}$) were larger when the populations changed in the same direction than when they changed in different directions ($n_{\text{sync}}=11$, $n_{\text{async}}=7$; C: $U=16$, $P<0.05$; H: $U=17$, $P<0.05$).

Demographic characters

Sex ratio. The number of males exceeded the number of females in 12 of 19 years in area C and in 24 of 28 years in area H (Table 2). Nine of 14 years with high reliability had sex ratios that were significantly different ($\alpha=0.05$) from 1:1 in area C, and 6 of those years were female biased (Table 5). Eleven of 17 years were significantly different from 1:1 in area H, and all were biased toward males. Sex ratio in the two populations also differed significantly (unpaired test, $n_C=14$, $n_H=17$, $U=37$, $P=0.001$; paired

Table 4. Number of data files modified in the cleaning procedure (Appendix 1), excluding the files: 1964 (no recaptures), 1965–1967 (missing files), and 1968–1971 (sampling incomplete). Note that the data in the original and cleaned columns of Table 2 are different for the period 1969–1971 due to the extrapolation procedure (Appendix 2).

	Pre-Jolly	Post-Jolly	Total
Female, area C	3	6	9
Male, area C	3	5	8
Female, area H	4	17	18
Male, area H	5	9	12

test, $n=8$, $T=3$, $P<0.05$; Table 5). Sex ratio and population size were correlated in area C but not in area H (C: $n=14$, $r=0.567$, $P<0.05$; H: $n=17$, $r=-0.23$, $P=NS$). As such, there also was a significant decline in sex ratio through time in area C (C: $n=14$, $r=-0.53$, $P=0.051$; H: $n=17$, $r=0.32$, $P=NS$). There was not a statistically significant correlation between sex ratio and growth rate, r_t , in either population (C: $n=14$, $r=-0.42$; H: $n=16$, $r=-0.45$; both $P=NS$).

Mortality and dispersal. The parameter, ϕ , is a measure of mortality and dispersal of individuals in a study population and is estimated over a season from daily estimates according to Scott (1973) (Jolly, 1965). Low ϕ values represent high loss to mortality or dispersal. In the case of Jasper Ridge, ϕ primarily reflects mortality because dispersal between sites was low (Ehrlich, 1961; Ehrlich *et al.*, 1975). Within a population, sexes had significantly different ϕ values (C: $n=19$, $T=1$, $P<0.001$; H: $n=27$, $T=17$, $P<0.001$), but within a sex, populations were not significantly different (females: $n=19$, $T=60$; males: $n=20$, $T=74$; both $P=NS$). In general, females had a lower ϕ than males (Table 5). For males, ϕ was correlated negatively with r_t in area H but not in area C (C: $n=18$, $r=0.23$, $P=NS$; H: $n=25$, $r=-0.44$, $P<0.05$). There was no relationship between ϕ and r_t for

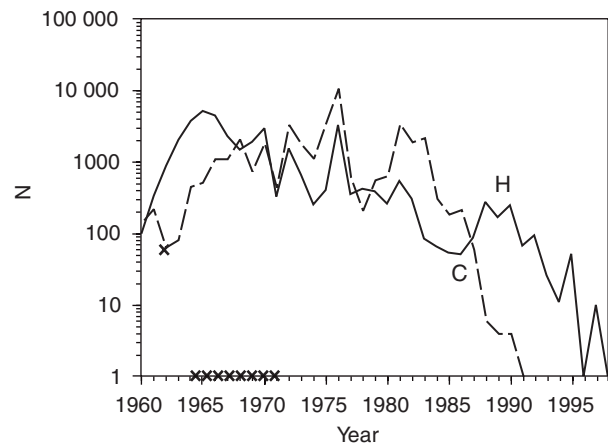


Fig. 2. Size of the Jasper Ridge *Euphydryas editha bayensis* populations through time in log scale. **x** on the x-axis designates the years in which both sexes and both areas had a reliability ranking of four or five (see Tables 1 and 2). **x** on the area C curve refers to a single female estimate with a reliability rank of four.

Table 5. Summary statistics.

	C	H	Combined
Average sex ratio (male estimate/female estimate)	1.08	2.02	1.59
Variance of sex ratio	0.13	1.12	0.88
Average ϕ for females	0.69	0.64	0.66
Variance of ϕ for females	0.03	0.02	0.02
Average ϕ for males	0.83	0.79	0.83
Variance of ϕ for males	0.02	0.02	0.01
Average mean flight date for females (days [†])	40.53	39.50	39.90
Variance of mean flight date for females	61.15	33.30	43.73
Average mean flight date for males (days [†])	36.85	34.89	35.70
Variance of mean flight date for males	47.08	25.73	34.76
Average flight season length (days)	31.42	29.18	30.08
Variance of flight season length	59.44	68.39	64.64
Mean r_t for females [‡]	-0.27	-0.03	-
Variance of r_t for females	1.65	1.50	-
Mean r_t for males [‡]	-0.24	-0.02	-
Variance of r_t for males	1.82	0.92	-
Mean L_t for females [§]	5.68	4.25	-
Variance of L_t for females	2.19	2.50	-
Mean L_t for males [§]	5.68	4.85	-
Variance of L_t for males	2.59	1.42	-

[†]From 1 March.

[‡] $t = 1960$ – 1986 for area C and $t = 1960$ – 1994 for area H.

[§] $t = 1960$ – 1987 for area C and $t = 1960$ – 1995 for area H.

females (C: $n = 16$, $r = -0.05$; H: $n = 25$, $r = -0.19$; both $P = \text{NS}$) and no relationship between ϕ and estimated abundance or a significant trend in ϕ over time (Table 6).

Mean flight dates and flight duration. The mean flight date of area C was later than that of area H (females: $n = 19$, $T = 23$, $P = 0.01$; males: $n = 20$, $T = 30.5$, $P = 0.01$; Table 5, Fig. 3), and, with a single exception, female mean flight date was the same or later than the date for males. There was a strong correlation between populations for mean flight date in both females ($n = 19$, $r = 0.74$, $P < 0.001$) and males ($n = 20$, $r = 0.81$, $P < 0.001$). The amount of time separating male and female mean flight appears larger in area H than in area C but this difference was not statistically significant ($n = 19$, $T = 28$, $P = \text{NS}$; Table 5).

Flight season length was correlated positively between the two populations when a single outlier (1963) was removed ($n = 18$, $r = 0.79$, $P < 0.01$; Table 5, Fig. 4a). (This outlier represents the longest season length recorded in either habitat.) Total seasonal abundance and flight season length were also correlated significantly (C: $n = 19$, $r = 0.75$, $P < 0.01$; H: $n = 28$, $r = 0.61$, $P < 0.01$; Fig. 4b,c).

It is important to note that while time between first and last captures is a common measure of flight season length (e.g. Roy & Sparks, 2000), it is subject to sampling error because adult abundance tends to be very low for several days near the beginning and end of the flight season. These periods of low abundance last longer when total butterfly abundance is small. Nevertheless, the risk of underestimating season length is small because butterflies are unlikely to be overlooked when present: surveyors walk the entire habitat, adults are conspicuous, and plants have low stature.

Discussion

The demography of the checkerspot butterfly populations at the Jasper Ridge Biological Preserve can be used to test hypotheses generated from short-term study. Although there are long-term data sets for numerous species (see NERC Centre for Population Biology, Imperial College, 1999; Inchausti & Halley, 2001), relatively few have the demographic information needed to test key ecological questions.

Table 6. Correlation matrix for metric of mortality and dispersal.

ϕ	Estimated N	Year
Females, area C	$n = 29$, $r = 0.16$, $P = 0.51$	$n = 19$, $r = 0.13$, $P = 0.59$
Females, area H	$n = 27$, $r = 0.13$, $P = 0.52$	$n = 27$, $r = -0.08$, $P = 0.68$
Males, area C	$n = 20$, $r = -0.15$, $P = 0.51$	$n = 20$, $r = 0.48$, $P = 0.03$
Males, area H	$n = 27$, $r = 0.32$, $P = 0.10$	$n = 27$, $r = -0.16$, $P = 0.42$

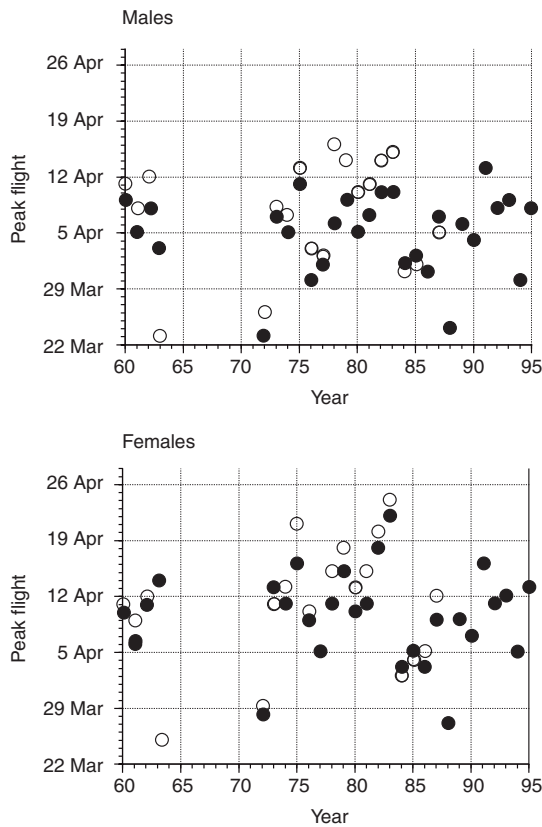


Fig. 3. Date of mean flight. ○ = area C; ● = area H.

Euphydryas editha is unique in that it has been studied using mark-recapture techniques for an exceptionally long period.

Evaluation of short-term hypotheses

Five hypotheses derived from shorter-term data sets were examined using the demographic metrics described in Tables 3 and 5.

(1) Early studies at Jasper Ridge reported that portions of the colony residing there fluctuated independently of one another (Ehrlich *et al.*, 1975). This conclusion was based on low rates of inter-population movement ($\approx 3\%$) and the appearance of dissimilar population fluctuations. Low rates of movement among populations continued over the long term, as indicated by the fact that no individuals were found in area C after 1990 although the population in area H persisted for nearly a decade longer. Poor correlations between growth rates and the fact that common directional changes in population size occurred in only half of the years also suggest continued asynchrony between the populations (however the statistical significance of these metrics could be influenced by measurement error). On the other hand, some synchrony in abundance did occur because large changes in abundances in the two populations typically occurred in the same direction. Analyses presented elsewhere suggest that climatic factors accurately predict

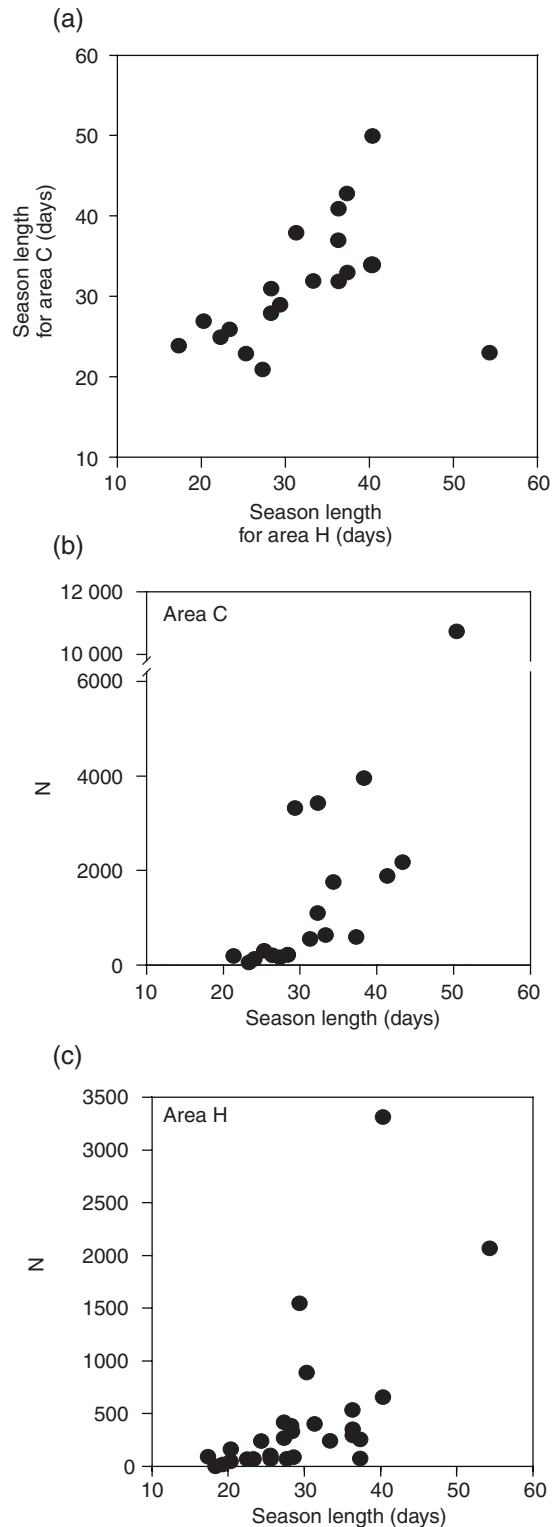


Fig. 4. (a) Correlation between flight season length (number of days between first and last sampling days) of the two populations, and the relationship between season length and abundance for (b) area C and (c) area H. Without the outlier (1963), the relationship in (a) is statistically significant at $\alpha = 0.05$.

changes in population size (McLaughlin *et al.*, 2002a). Thus, low rates of movement probably did preclude dynamical coupling of these populations but qualitative similarities in their dynamics did occur and were probably due to a shared regional climate.

(2) Previous research suggests that the survivorship of eggs and pre-diapausal larvae is the key determinant of population abundance in this taxon (Singer, 1972; Cushman *et al.*, 1994; Fleishman *et al.*, 2000; Hellmann, in press). Larval mortality varies among years depending on the timing of host senescence, as determined by weather and the host species on which larvae feed (Singer, 1972; Hellmann, in press). Based on this hypothesis, adult mortality and abundance should have had relatively little impact on subsequent population size (Ehrlich *et al.*, 1975). Indeed, adult mortality did not appear to influence population growth strongly, as evidenced by the lack of correlation between ϕ and r_t of females. The small amount of variation in adult loss rates (ϕ) relative to the size of population fluctuations also suggests that adult mortality is not a strong determinant of population size. Additionally, loss rates did not differ significantly between the populations as measured by a paired test, indicating that population asynchrony was probably not due to differences in adult dispersal or survival. These pieces of evidence indirectly support the hypothesis that larval survivorship is important to the dynamics of the Bay checkerspot by eliminating adult mortality as a strong factor in determining population fluctuations. The failure of adult abundance to predict changes in population size, however, does not rule out other effects such as year-to-year or habitat differences in adult fecundity that may be caused by differences in nectar availability (see Murphy *et al.*, 1983). Fecundity, however, is a less likely explanation for changes in population size because extended fecundity from nectar feeding results in enhanced reproduction later in the growing season (Labine, 1968; Murphy *et al.*, 1983; Boggs, 1997a,b). Larvae hatching from eggs laid late in the season are thought to have low survivorship and thus contribute little to the next generation (Cushman *et al.*, 1994).

(3) Previous studies suggest that habitat heterogeneity, microclimate, and topography affect the timing and distribution of butterfly development, emergence, and flight (Weiss *et al.*, 1987, 1988; Murphy & Weiss, 1988; Weiss & Weiss, 1998). Based on this hypothesis, the two habitat patches should have supported populations with distinctly different flight times because of their differing topographies. The long-term data support this hypothesis, because mean flight of the population in area C was later than that in area H. The order of this timing was not as predicted, however. If timing of emergence were driven primarily by climatic factors (e.g. thermal insolation), larvae in area C should have developed more quickly than in area H because the slopes in area C are warmer on average (Weiss *et al.*, 1993; Fig. 5). One possible explanation is that larvae in area C tended to concentrate on the coolest exposures. The only data available to evaluate this possibility are from 1983, when post-diapause larvae in area C were found only on cool exposures (S. B. Weiss, unpublished). If larvae primarily occupied those exposures,

the flight season would occur later than the topography of the entire area suggests. Thus, while differential emergence phenologies in different habitats are supported, further research is needed to investigate the factors that influence slope occupancy and the role of this occupancy in determining patterns of emergence.

(4) Previous work has suggested that topography also mediates the effect of weather on larval mortality (Ehrlich *et al.*, 1980; Dobkin *et al.*, 1987; Weiss *et al.*, 1988; Fleishman *et al.*, 2000). This hypothesis predicts that in extremely dry years, a relatively small number of larvae on only the coolest slopes survives to diapause because host plants on warm slopes senesce too early to sustain larvae. In benign years, a greater number of larvae survive on a larger range of slopes because host plants last for long enough to sustain larvae throughout the habitat. This phenomenon is observed in the correlation between flight season length and total population size (Fig. 4). When the population size was low, adults emerged in a tight pulse, suggesting that they came only from cool slopes. When the population size was greater, the emergence curve was wider, suggesting that adults came from a greater diversity of slope exposures.

(5) A 1-year study of sex ratio in *E. editha bayensis* suggested that field ratios are male biased and in the range of 1.75–1.95 (Ehrlich *et al.*, 1984). It was hypothesised that females suffer higher rates of mortality than males due to male harassment and the risks associated with oviposition, such as vulnerability to predators (Bowers *et al.*, 1985). This hypothesis predicts that the long-term data should show consistently male-biased sex ratios of the approximate magnitude measured during the short-term study. As predicted, the majority of years showed ratios that were significantly different from 1:1, suggesting that the ratio of unity commonly observed in Lepidoptera at birth is modified by field conditions (Owen, 1971). The consistency of male-biased ratios was not supported, however. In one of the two habitats, the ratio was occasionally biased towards females; those years were no less well sampled than years that were found to be male biased. This occasional occurrence of female-biased sex ratios warrants additional study to determine the cause of variation in sex-specific mortality and dispersal in this species (Frey & Leong, 1993; Jiggins *et al.*, 1998; Smith *et al.*, 1998; Underwood & Shapiro, 1999). A possible explanation is the differential exposure of the sexes to particular weather events due to differences in the timing of their emergence and flight (Schtickzelle *et al.*, 2002). If these events also cause changes in population size, they may help to explain why sex ratios declined with population size in one of the two habitats. Alternatively, there may be sex-specific tendencies to disperse when population size is small in some habitats (Odendaal *et al.*, 1989; Baguette *et al.*, 1998).

The hypotheses that have proved to be robust to comparison with the long-term data are those based either on a relatively deep understanding of underlying mechanisms or on data from a diversity of sites. Hypothesis 1 is based on multiple years of study (14 years), and hypotheses 2 and 4 resulted from the work of multiple researchers at multiple

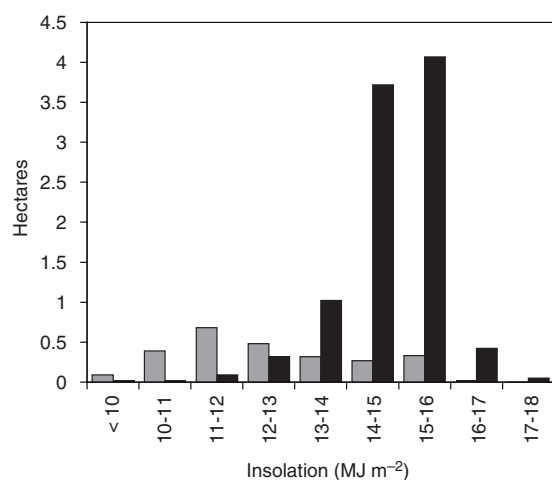


Fig. 5. Distribution of 21 March clear sky solar insolation for areas C and H built from a 5-m digital elevation model and the program SOLARFLUX (Rich *et al.*, 1995). The dark bars represent area C; the light bars represent area H.

locations. The hypotheses that are falsified are those based on a single year of data in the case of sex ratio (hypothesis 5) or multiple-year studies at sites other than Jasper Ridge in the case of topography and timing of emergence (hypothesis 3). These observations suggest that additional time and effort investigating population processes at multiple sites returns a benefit in terms of capturing a population's long-term dynamics (Franklin, 1989).

Population trends and extinction at Jasper Ridge

While the demography of these populations is useful for examining mechanisms of population change, the dominant characteristics of the long-term data are their negative growth rate and large population fluctuations. In retrospect, extinction appears particularly probable given the large variance in population size relative to mean abundance in both habitat areas (Hanson & Tuckwell, 1978; Leigh, 1981; Goodman, 1987; Pollard & Yates, 1992; Foley, 1994; Belovsky *et al.*, 1999; Vucetich *et al.*, 2000). Extinction was likely to occur first in area C because the mean rate of decline and the coefficients of variation in population size [$CV(L_t)$] were larger in area C than in area H. Removing low-sample days to reduce errors in

Table 7. Population demographics for the Kirby Canyon Butterfly Reserve based on counts of post-diapause larvae surveyed annually between 1985 and 2000. The number of adults is estimated as one half the number of estimated larvae (Murphy & Weiss, 1988).

	L_t	r_t
Mean	11.54	0.028
Maximum	13.68	1.58
Minimum	10.19	-1.73
Variance	0.96	0.81

population estimation did not affect the assessment of population fluctuations or long-term population trends.

Comparison with other populations

Contrasting the mean and variance of abundance at Jasper Ridge with other sites suggests whether additional extinctions of this subspecies may occur. Habitats of similar size located 7 km north of Jasper Ridge at Edgewood Park support populations that show variance in abundance that approaches mean population size (i.e. high coefficient of variation) (S. B. Weiss, unpublished). If their dynamics are similar to those at Jasper Ridge, these populations appear destined for extinction as well. In contrast, the largest habitat patch in the region, at the Kirby Canyon Butterfly Reserve (a 100-ha site \approx 50 km south of Jasper Ridge), exhibits similar fluctuations to those at Jasper Ridge but has a larger population size on average. Since 1985, this population has exhibited a slightly positive population growth rate and had a coefficient of variation in population size [$CV(L_t)$] that was an order of magnitude smaller than either area C or H (Table 7). Thus, the expected persistence time for this population should be substantially longer than was the case at Jasper Ridge, but it too is likely to go extinct as indicated by its degree of variability. Recent studies suggest that long-term habitat and climatic changes may be causing regional declines of this species, possibly explaining why Jasper Ridge went extinct and other populations seem to be on a trajectory of extinction (Weiss, 1999; McLaughlin *et al.*, 2002b; Hellmann *et al.*, in press).

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Appendix 1

A variety of sampling scenarios can produce biased observations of butterfly abundance (Sutherland, 1996). These biases can often be removed by systematic data cleaning. The cleaning procedure used here involved two stages, before (pre-Jolly) and after (post-Jolly) daily abundance estimation.

Pre-Jolly cleaning

Data from individual sampling days were deleted if the number of captures on that day was exceptionally small relative to previous and subsequent sampling days. For an individual sampling day, the number of handles or the total number of adult insects captured, n , was compared with the n for the previous and subsequent sampling days. In the example of sampling days a , b , and c , the n value of b was compared with the n value of a and c . b was removed if a and b or b and c were greater than 10 and

$$[a > 3b] \text{ AND } [c > 3b].$$

Two sampling days in sequence were both removed if in a , b , c , and d , b and c were adjacent calendar days with n larger than 10 and the larger of b and c met the above criterion when compared with a and d . Note that in one case (male, area C, 1983), two non-sequential but flanking sampling days were removed because they were both significantly smaller than the number of captures of nearby days. The population estimates of removed days were filled by linear interpolation.

Post-Jolly cleaning

In cases when the number of recaptures (m_i) or the number of recaptures to be captured again later (R_i) was equal to zero, a daily abundance estimate could not be calculated [see Jolly (1965) for definitions of variables]. Therefore, seasonal abundance estimates were recalculated without the estimates

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for mid-season days with either m_i or R_i equal to zero. Mid-season was defined as those days for which there are previous or subsequent sampling days with non-zero m_i and/or R_i values. Again, removed days were filled by interpolation.

Effect of cleaning

Cleaning both increased and decreased estimates, resulting in a net average increase of 3.6 adults in area C (6% of the original estimate) and 12.4 adults in area H (4% of the original estimate) ($\sigma_C = 15\%$, $\sigma_H = 8\%$) (Tables 2 and 3). The occasions on which the difference between the cleaned and original estimates exceeded 100 were distributed relatively evenly among files of rank two and three in the females of area C, males of area C, and females of area H. The largest proportional changes (>25% of the original estimate) were also distributed relatively equally, although they appear most often in the estimates for area C. There were no large changes (>25%) within the last 7 years of either population's existence. The only exception to the rule that the two data sets show the same pattern of population change occurred between 1982 and 1983 in area C. When the sexes were examined separately, a few more of these occasions arose, primarily in files with rank four.

Appendix 2

Using the male data from area H in 1981, a non-linear regression model ($R^2 = 0.965$) was built to describe the relationship between mean wing condition and proportion of the Jolly–Seber abundance estimate (Y). The equation for the regression model is:

$$Y = aX^3[1 - \exp(-bX)]/(c + dX)^3$$

where $a = 1100$, $b = 3.85$, $c = 1.29$, $d = 9.27$, and $X = \text{meancondition} - x_0$, where $x_0 = 1.28$. This model was used to modify original estimates of years with incomplete sampling records.