

Pupal Mortality in the Bay Checkerspot Butterfly (Lepidoptera: Nymphalidae)

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Abstract. Mortality for pupae of *Euphydryas editha bayensis* (Lepidoptera: Nymphalidae) placed in the field ranged from 53 to 89%. Predation and cold weather during the period of pupation were the major mortality factors. Mortality during this stage is high enough to affect total numbers of adults and other life stages and variable enough to affect the population dynamics of these butterflies. Studies of these and other holometabolous insect species should include estimates of pupal mortality.

Introduction

Few complete life tables have been published for natural populations of butterflies (see Dempster, 1983). This is partly because at least one life stage of these holometabolous insects is difficult or impossible to observe in the field. For example, *Euphydryas editha bayensis* Sternitzky (1937) (the Bay Checkerspot butterfly) is among the most thoroughly studied insects, but only its adult stage is easily observable. Eggs and prediapause larvae have only recently been found in numbers, and diapausing larvae remain essentially a "black box" to us. Many post-diapause larval samples have been collected and some data on parasitoid rates have been published (Ehrlich, 1965; White, 1973 and Stamp, 1984). Pupae are almost never seen.

Prior to this study the only information on pupal mortality in *Euphydryas editha* was Singer's observation that several out of 20 pupae placed out at Jasper Ridge were eaten and the wooden tongue depressors used to mark them had been chewed on by rodents (Singer, 1971).

Life table data for butterfly populations that have been published show pupal mortalities ranging from 0 to 100%, but averaging around 60% (Table 1). Most of the pupal mortality identified was due to predation. With this background I did an experiment designed to quantify pupal mortality in the Bay Checkerspot butterfly.

Materials and Methods

Large post-diapause larvae were collected in late February and early March from field sites at Edgewood Park (EW) in 1982 and 1983 and Morgan Hill (MH) in 1984. Both sites are serpentine grasslands (Krucke-

Table 1. Available data on lepidopteran pupal mortality.

Species	Pupal Mortality	Major Factor	n	Source
<i>Pieris rapae</i>	.31	parasitoids	large	Harcourt 1966
	.38	virus	42	Dempster 1967
	.08	virus	27	Dempster 1967
	.05	virus	65	Dempster 1967
<i>Papilio machaon</i>	.59	predation	150	Wiklund 1975
	.90	predation	158	Wiklund 1975
<i>Papilio xuthus</i>	.83	parasitoids	12	Watanabe 1976
	.12	predation	25	Watanabe 1976
<i>Artopoetes pryori</i>	.45	predation	42	Watanabe & Omata 1978
<i>Papilio glaucus</i>	1.00	predation	112	West & Hazel 1982
	.80	predation	109	
	.88	predation	128	
	.55	predation	127	
<i>Battus philenor</i>	.91	predation	140	West & Hazel 1982
	.94	predation	139	
	.77	predation	80	
	.96	predation	80	
<i>Battus philenor</i>	.14	predation	64	Sims & Shapiro 1983
	.67	predation	109	
<i>Agraulis vanillae</i>	.08	predation	364	I.L. Brown pers. comm.

berg, 1984; Sommers, 1984; Crittenden and Grundmann, 1984) where adverse soil conditions favor the native plants on which the butterflies depend. Edgewood Park is in San Mateo County at 37° 27' 50" latitude, 122° 17' 10" longitude, and 660' (200m) elevation. Morgan Hill is in Santa Clara County at 37° 11' 28" latitude, 121° 40' longitude, and 1000' (300m) elevation. For comparison, Jasper Ridge is in San Mateo County at 37° 25' latitude, 122° 19' longitude, and 550' (170m) elevation. Rainy weather in 1982 and 1983 and a large population in 1984 (at MH) allowed longer collection periods than normal. Larvae were kept in groups of about four in plastic petri dishes (37mm in height, 150mm diameter) and fed daily until they pupated, on average about a week. They were fed primarily the Eurasian weed *Plantago lanceolata* L., which they seem to prefer in the laboratory but which is rarely used in the field (Tilden, 1958). Supplementary feeding with the normal foodplants (*Plantago erecta* Morris and *Orthocarpus* spp.) was done when possible.

As soon as pupae hardened enough to permit handling they were placed in the field. Transects were laid out in areas from which larvae had been collected (areas of relatively high larval densities). Pupae were placed directly on the soil or foliage every 25cm (my span plus 2cm) along the

transects (Fig. 1). Edgewood Park is open to the public and I wanted my transects to be inconspicuous to people as well as to potential predators, so I marked each pupa with a tiny (7 x 4mm) paper flag mounted on an insect pin. These I could easily relocate. A typed number on the flag identified each pupa. An acrylic spray (Krylon Crystal Clear 1301) applied to the page before cutting the flags out made the numbers proof against rain.

Pupae were checked every three to seven days, depending on weather conditions, and their fates were recorded as follows:

(1) Parasitized — two kinds of parasitoids emerged from pupae. One was a tachinid fly (*Siphosturmia melitaeae* Coquillett, determined by Paul Arnaud, Calif. Academy of Sciences) the larva of which bored out the side of the pupa and then itself pupated, sometimes near enough to be found. The exit hole was larger than that made by the piercing predators. The other parasitoid was a large ichneumonid which caused the pupae to change to an orangish hue. In emerging from an infected pupa, this wasp cut a circular cap off the top of the pupa. This cut (Fig. 2) was entirely different from the typical lines of fracture resulting from butterfly eclosion (Fig. 3). Butterflies that successfully eclosed left behind a case fractured along typical lines and very much thinner than that left by even the most thorough predator.

(2) Stepped on — pupae crushed. The evidence often included signs of trampling, showing the outline of a footprint, usually of cattle.

(3) Died intact — pupae remaining, apparently unmolested, throughout the study. They eventually either shrank and were found to be empty, or they turned black and contained a foul black liquid (probably due to a virus).

(4) Vanished — pupae not relocated, although their marking flags were. None of the traces mentioned below were found.

(5) Predated — pupae clearly damaged by one predator or another. One predator left behind $\frac{1}{4}$ to $\frac{1}{2}$ of the pupal case, the inside of which was well cleaned out. Another made rough gashes (Fig. 4) and ate most of the contents, leaving the inside of the case coated with gore. Another predator or suite of predators pierced the pupal case and sucked out some or all of the contents. The damage in the two latter cases was consistent with "tasting but not eating". Related species are known to be unpalatable as adults and to a lesser extent as pupae (Bowers, 1980, 1981).

Degree Days (F.) were calculated according to Rahn (1971): $[(\text{daily max} \leq 86) + (\text{daily min} \geq 50)]/2 - 50$.

Results

Total pupal mortality ranged from 53 to 89% (Fig. 5). The major mortality factors, in order of increasing importance, were the following:

Parasitism was a minor factor, taking 1-10% of the pupae. The tachinid (*Siphosturmia melitaeae*) is endemic to virtually all *E. editha bayensis* populations, but its average infection rate is only 7.8% (45 samples from



Fig. 1. Pupa of *Euphydryas editha* as placed in the field.



Fig. 2. Remains of *E. editha* pupa placed in the field at Edgewood Park in 1983. Note the precise circular break made by a parasitoid as it emerged.



Fig. 3. Remains of *E. editha* pupa from which an adult butterfly successfully emerged. Note the thinness of the cast shell and fracture lines typical of normal emergence.

1963-1984, 407 tachinids/5212 larvae) and was only 1-2% in these three samples. Presumably the tachinid infects prediapause larvae, but death of the host does not occur until the pupal stage. Infected pupae can often be identified by their low weights. Healthy female pupae average about 380mg and males about 280mg. Tachinid parasitized pupae weigh under 200mg.

A large ichneumonid was found to oviposit in pupae in the field, a phenomenon previously undetected. The first observation was actually of a female (probably parthenogenetic) wasp palping a pupa in the field. This predatory species is probably generally unimportant, having taken 10/239 pupae in 1982, 3/160 in 1983, and 0/260 at MH in 1984 (nor did it turn up in a larger sample at MH in 1985). Since it is necessary to collect or observe pupae in order to detect it, it is not surprising that this predator is known to date only from EW.

Crushing generally was found to be a minor factor, but the large number of cattle grazing at MH raised it to 10% in the 1984 study. There are no cattle at EW and horses are supposed to be restricted to trails. Cattle were evicted from Jasper Ridge in 1960 (P. R. Ehrlich pers. comm.).

The proportion of pupae that died intact varied from 9 to 34% and apparently changed with weather patterns. The higher mortality that occurred in 1982 was undoubtedly a result of the very unusual cold and rainy weather. The number of Degree Days measured at Jasper Ridge from January 1 to March 31 in 1982 was 263, 1983 it was 353, and in 1984 it was 570. I expect that this pattern of high mortality occurs whenever late win-

ter weather is cold.

Pupae that vanished without a trace before any others in their age class had eclosed were "taken" by something, presumably a predator. Pupae disappearing while others in their age class were eclosing might have successfully eclosed and their cast cases might have blown away or been otherwise removed. This possibility could not be distinguished from removal by a predator. Here I estimated the proportion of the missing pupae to have eclosed by taking the proportion of same age class of pupae which did leave evidence of having eclosed. The remaining proportion I considered to have been eaten. The effect of this estimate is probably to underestimate predation (the accuracy of this estimate is important only in the 1983 sample). Weather-delayed pupae lasted much longer than normal in 1983; 42% of them disappeared. In this unusually late year (Fig. 6) an opportunistic predator (perhaps a bird or rodent) took larger propor-



Fig. 4. Pupa of *E. editha* placed in the field at Edgewood Park, 1983, showing evidence of predation. The damage is consistent with "tasting but not eating" as might occur when a naive predator attacks an unpalatable subject.

tions of pupae later in the season. In the other two years this form of mortality was very low (Fig. 5). This temperature dependent pattern parallels that observed by Pollard (1979) for *Ladoga camilla* (Nymphalidae).

Predators that left physical remains took 23 to 32% of the pupae, making such predation the least variable factor over the three year study.

One habitat difference at MH allowed a refinement of the experimental technique used. As at any serpentine grassland site there were small areas of a fraction to several square meters in which the foliage was extremely sparse, especially due to lack of the common bunch grasses. These bare areas at MH alternated with areas of denser foliage so that my transects regularly passed in and out of them. I recorded whether pupae were placed in areas of denser foliage, bare areas, or in-between sorts of areas. Analysis of the data for MH in 1984 showed that pupal mortality varied significantly with microhabitat ($G = 21.41$, $df = 8$, $P < .01$; Table 2). Being crushed was more likely in barer spots ($G = 8.07$, $df = 2$, $P < .025$). Dying intact was less frequent in barer spots ($G = 7.79$, $df = 2$, $P < .025$). Neither the "eaten" group nor the "vanished" group varied significantly with microhabitat, but one might add these together as presumed predation. In that case, predation was less frequent in spots with more foliage ($G = 5.992$, $df = 2$, $P = .05$). Successful eclosion was not significantly better, but was nearly so, in spots with more foliage ($G = 4.73$, $df = 2$, $P < .10$).

Table 2. Fates of pupae placed in field at MH in 1984, according to ground cover of spot where pupae were put.

	Bare	Mixed	Dense Foliage	n
Eclosed successfully	.430	.412	.565	122
Died in place	.035	.078	.141	21
Stepped on	.158	.078	.043	26
Eaten	.237	.314	.174	59
Vanished	.140	.118	.076	29
Totals	114	51	92	257

Discussion

The weather of any given study is unusual and this study merely represents an extreme of that situation (Kerr, 1985). Both 1982 and 1983 were very cool, wet, and therefore late years. They differed significantly in that there were some normally sunny days early in 1982 so that development to pupation was probably normal. Then the cold set in and pupae became subject to attack by fungi and viruses. In 1983 there was an extensive period of cold, but when that ended temperatures were warm enough to allow normal pupation. On the other hand, 1984, was an extremely dry year. The rains ended very early and normal temperatures followed. Flight began and ended early (Fig. 6).

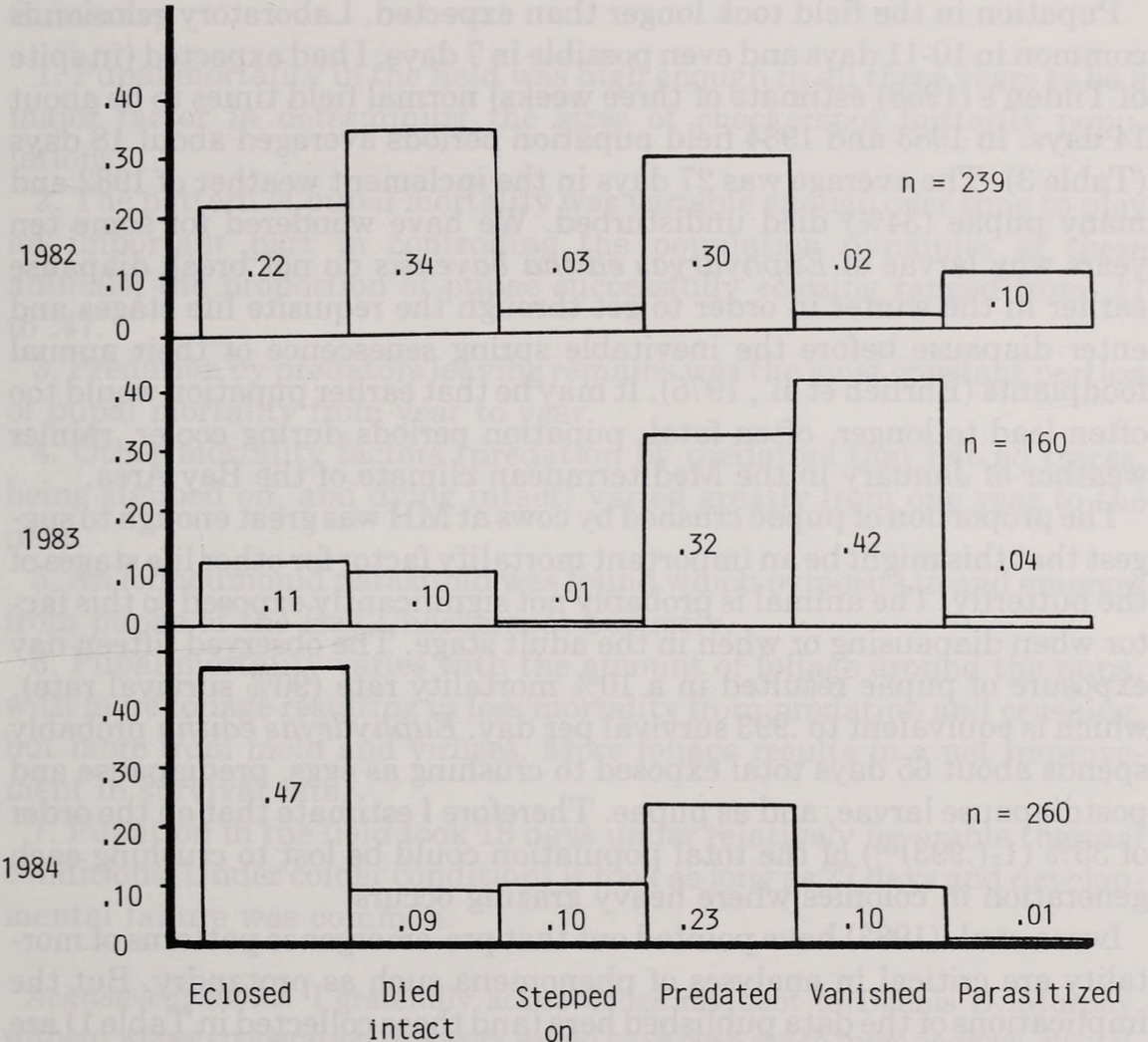


Fig. 5. Successful emergence and mortality rates by cause in three samples of *Euphydryas editha* pupae which were place in the field.

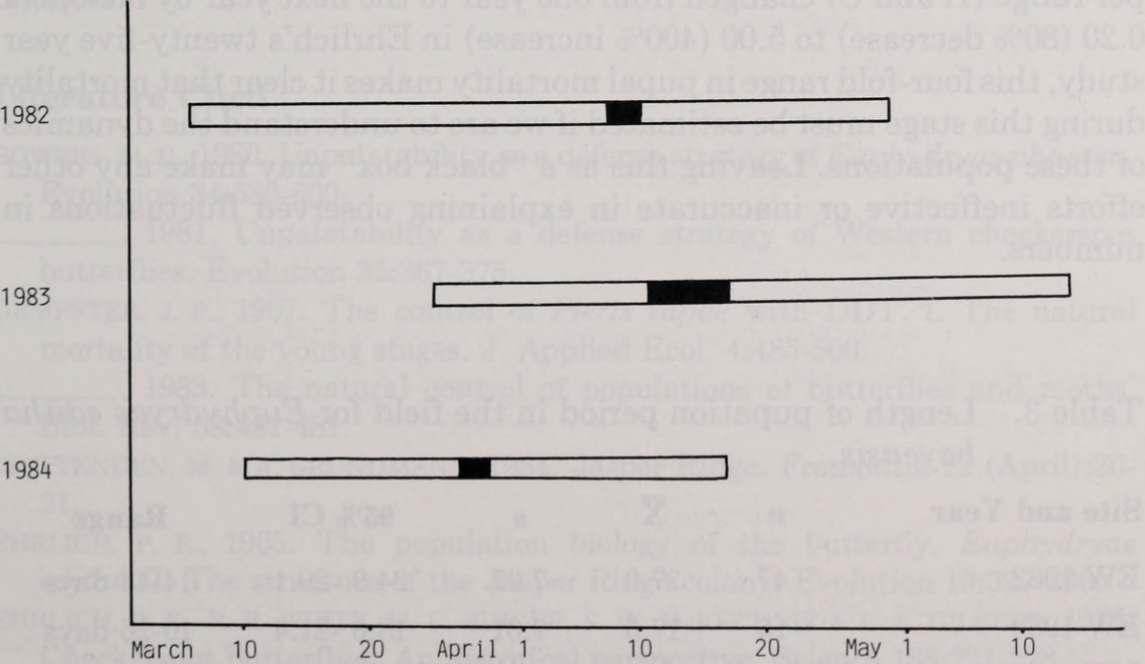


Fig. 6. Flight seasons of *E. editha* at Edgewood Park, from first to last adult seen. Shaded areas represent peak flight.

Pupation in the field took longer than expected. Laboratory eclosion is common in 10-11 days and even possible in 7 days, I had expected (in spite of Tilden's (1958) estimate of three weeks) normal field times to be about 14 days. In 1983 and 1984 field pupation periods averaged about 18 days (Table 3). The average was 27 days in the inclement weather of 1982 and many pupae (34%) died undisturbed. We have wondered for some ten years why larvae of *Euphydryas editha bayensis* do not break diapause earlier in the winter in order to get through the requisite life stages and enter diapause before the inevitable spring senescence of their annual foodplants (Ehrlich et al., 1975). It may be that earlier pupation would too often lead to longer, often fatal, pupation periods during cooler, rainier weather of January in the Mediterranean climate of the Bay Area.

The proportion of pupae crushed by cows at MH was great enough to suggest that this might be an important mortality factor for other life stages of the butterfly. The animal is probably not significantly exposed to this factor when diapausing or when in the adult stage. The observed fifteen day exposure of pupae resulted in a 10% mortality rate (90% survival rate), which is equivalent to .993 survival per day. *Euphydryas editha* probably spends about 65 days total exposed to crushing as eggs, prediapause and postdiapause larvae, and as pupae. Therefore I estimate that on the order of 35% ($1-(.993)^{65}$) of the total population could be lost to crushing each generation in colonies where heavy grazing occurs.

Iwasa et al. (1983) have pointed out that pre-emergence patterns of mortality are critical in analyses of phenomena such as protandry. But the implications of the data published here (and those collected in Table 1) are of more general importance. Successful eclosion varied from 11 to 47% of the pupae placed in the field. Given that estimated adult numbers at Jasper Ridge (H and C) changed from one year to the next year by factors of 0.20 (80% decrease) to 5.00 (400% increase) in Ehrlich's twenty-five year study, this four-fold range in pupal mortality makes it clear that mortality during this stage must be estimated if we are to understand the dynamics of these populations. Leaving this as a "black box" may make any other efforts ineffective or inaccurate in explaining observed fluctuations in numbers.

Table 3. Length of pupation period in the field for *Euphydryas editha bayensis*.

Site and Year	n	\bar{X}	s	95% CI	Range
EW 1982	47	27.0	7.02	24.9 -29.1	14-43 days
EW 1983	15	17.5	7.01	13.6 -21.4	10-26 days
MH 1984 males	52	19.9	4.38	18.7 -21.1	12-27 days
females	69	16.6	4.04	15.7 -17.6	12.23 days

Summary

1. Pupal mortality in the field was high enough in all three years to be a major factor in determining the sizes of checkerspot butterfly populations.

2. The pattern of pupal mortality was variable enough over time to play an important part in controlling the population dynamics of these animals; the proportion of pupae successfully eclosing ranged from .11 to .47.

3. Predation by predators leaving remains was the most constant portion of pupal mortality from year to year.

4. Other mortality factors (predation by predators that left no traces, being stepped on, and dying intact) varied greatly from one year to the next.

5. An ichneumonid parasitoid was found which oviposits in and emerges from pupae of the Bay Checkerspot butterfly.

6. Pupal mortality varies with the amount of foliage around the pupa, with more foliage resulting in less mortality from predation and crushing, but more from mold and viruses. More foliage results in a net improvement in survival rate.

7. Pupation in the field took 18 days under relatively favorable thermal conditions. Under colder conditions it took as long as 27 days and developmental failure was common.

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