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The Trouble with Butterflies

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The existence in this and other journals documents that of the vast diversity of insects available, the butterflies is a group of animals very frequently studied. Butterflies are disproportionately the subject of notes, articles, and books. Virtually all butterfly books aimed at general audiences, if they say anything to justify themselves, state the case in very modest terms. Authors too numerous to cite mention the captivating sight of colorful butterflies on the wing.

Many professional biologists doing scientific research with butterflies can refer back to childhood interest in catching and collecting these animals. Research scientists among us, however, often make the claim that butterflies are better suited for scientific research purposes than are most other organisms. Such claims are commonly found in grant proposals. The separate points made in favor of butterflies are generally valid.

(1) The taxonomy of butterflies is reasonably well-worked out.

(2) Their geographic distributions are well known.

(3) Their life cycles are usually understood.

(4) Their ecological relationships are at least partly known.

(5) They are conspicuous in diurnal flight and relatively easy to handle.

(6) Compared to vertebrates, they are small and have short life cycles.

(7) Since many people, both professional and amateur, do research on butterflies, there often exists the critical intellectual mass necessary for scientific progress.

While these characteristics are helpful to the scientist, balance is lost by the failure to mention, let alone discuss frankly, those traits commonly found in butterflies which are a hindrance.

Perhaps the most disadvantageous trait is that one or more of the life stages of these holometabolous insects is almost always unobservable. It is also true that species with diapause stages are very difficult to work with in the laboratory and that specific ecological relationships, such as those involving larval food plants, are often unknown. Genetic systems are usually polygenic, electrophoretic, or unknown. Here I discuss the problems that butterflies commonly present to scientists.

In the worst cases, we are not even thinking about the difficult problems, but are simply proceeding with experiments on questions that seem tractable. Final answers to questions of causes of distributions and dynamics of populations must remain unavailable as long as one or more life stage is ignored as too difficult to work with. In the best cases, we are regularly designing and performing experiments that fail to overcome the problems inherent in our experimental organisms. We are rarely and sporadically publishing the negative results, so we are not evoking all of the peer comment possible.

Unobservable Life Stage

Perhaps the only truly complete life history description (with a good physical description for each life stage) in the literature is Wright's (1983) for *Lycaena epixanthe*. The situation for population biology studies involving all life stages is similar. Very few complete life tables have been published for natural populations of butterflies (see Dempster 1983). I (White 1986) have found only seven butterfly life tables in the literature (Harcourt 1966, Dempster 1967, Watanabe 1976, and Watanabe & Omata 1978) in which each stage is represented by a sample size of more than ten individuals. This is so because one or more of the life stages is difficult or impossible to observe in the field. The reader is doubtless aware of some of the problems presented by his own research organism and may not care to hear about them from me. This is especially so since my own research organism has plenty of its own disadvantages. I will therefore discuss my own system.

The Bay Checkerspot butterfly, *Euphydryas editha bayensis* Sternitzky (1937), is one of the most thoroughly studied of insects (Ehrlich 1984), but only its adult stage is easily observed by the biologist (Fig. 1). Adult butterflies might seem easily observable, but even this life-stage puts the observer to great effort. Only in the 1981 study (Ehrlich et al. 1984) where three very experienced people worked virtually each day of the flight season is it thought that virtually all the male *Euphydryas editha* in one generation of one population (Jasper Ridge H) were captured (n = 316). Even in this case the authors estimated that only 162/221 (73%) of the females were handled during the season. In the course of the twenty-five year study at Jasper Ridge (Stanford University's biological preserve) the estimated proportion of males handled has averaged 60% and has sometimes fallen as low as 30%. The proportion of females handled has always been smaller. These values are very good for field studies in general, but they nonetheless make it clear that even the most "apparent" life-stage of the Bay Checkerspot butterfly is partially unobservable. Each of the other life stages is more difficult to observe in nature.

The distribution of egg masses probably averages about one per ten square meters in denser populations, rising to one per two square meters in the best years (assuming five masses per female, maximum of 2000 females in JRH 1960–1984, area of 2 ha. = 20,000 sq m). Since the size of an egg mass is about 10 sq mm, the average proportion of the substrate

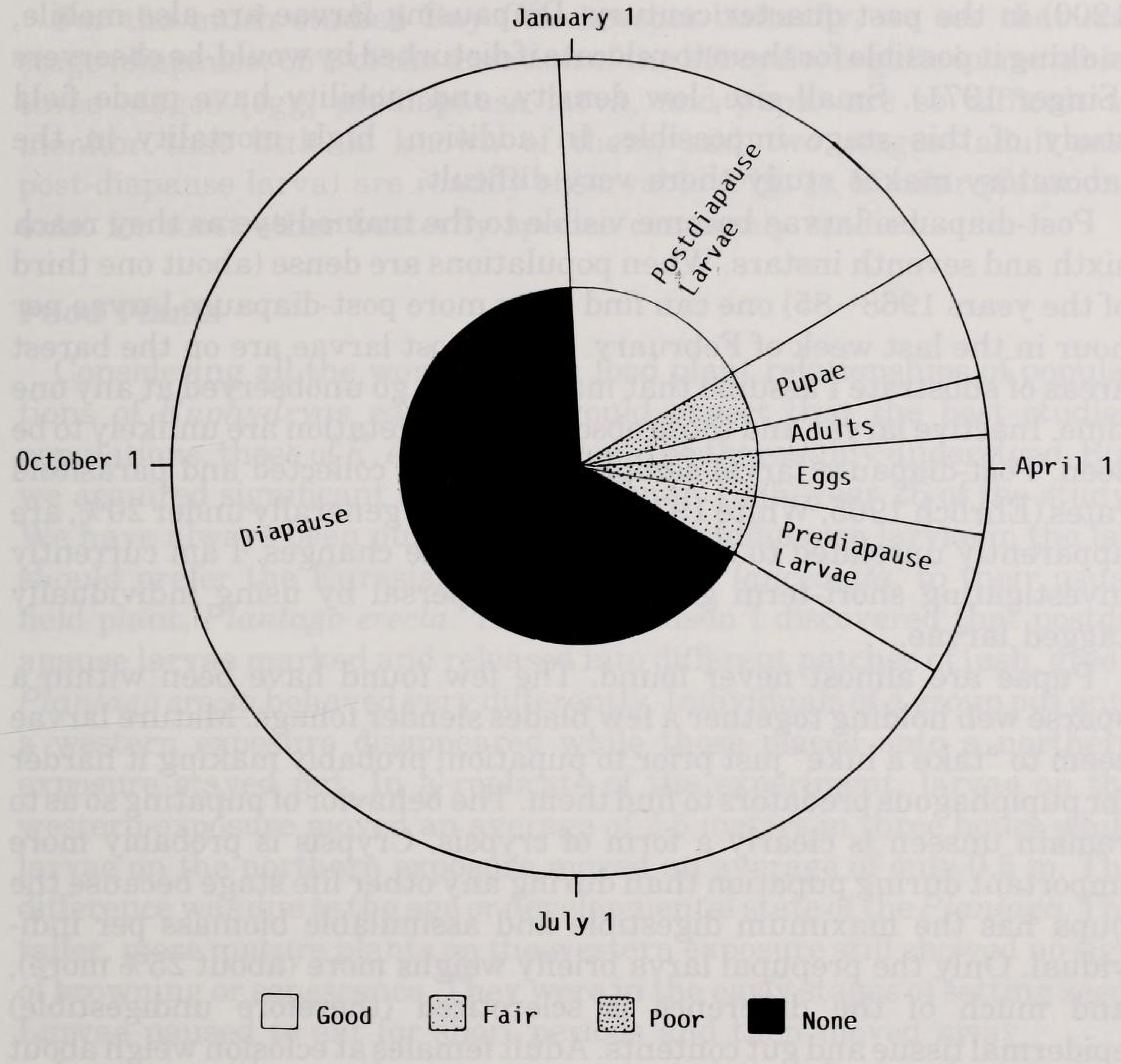

Fig. 1. The annual life cycle of *Euphydryas editha bayensis*, divided proportionately by length of life stages. The outer circle names the life stage. The inner circle indicates our current level of information.

covered by eggs is about 0.000001 (10 sq mm/10(1000 mm × 1000 mm) = one millionth). Egg masses therefore have been and continue to be very difficult to monitor. Only one of the extant Bay Checkerspot populations is currently dense enough to allow numbers of egg masses to be found.

Prediapause larvae disperse in search of food as their annual food plants senesce, making accurate assessment of their fates extremely difficult. An exception occurs when larval growth is slower than "normal" relative to plant senescence schedules. When host plants senesce before the adult flight season ends, it is a certainty that more than 98% of the prediapause larvae will starve due to lack of edible plants (Singer & Ehrlich 1979).

Diapausing fourth instar larvae (4–20 mg, about 3–6 mm long) are hidden in the soil, sometimes under rocks, probably in peak densities of no more than one or two per square meter. This density would allow for 40,000 diapausing larvae at JRH (2 × 20,000 sq m), a habitat where the maximum adult population has not exceeded 4000 (averaging about

1200) in the past quarter century. Diapausing larvae are also mobile, making it possible for them to relocate if disturbed by would-be observers (Singer 1971). Small size, low density, and mobility have made field study of this stage impossible. In addition, high mortality in the laboratory makes study there very difficult.

Post-diapause larvae become visible to the trained eye as they reach sixth and seventh instars. When populations are dense (about one third of the years 1968–85) one can find 40 or more post-diapause larvae per hour in the last week of February. Since most larvae are on the barest areas of substrate I assume that many larvae go unobserved at any one time. Inactive larvae and those obscured by vegetation are unlikely to be seen. Post-diapause larval samples have been collected and parasitoid rates (Ehrlich 1965, White 1973, Stamp 1984), generally under 20%, are apparently unrelated to adult population size changes. I am currently investigating short-term growth and dispersal by using individually tagged larvae.

Pupae are almost never found. The few found have been within a sparse web holding together a few blades slender foliage. Mature larvae seem to "take a hike" just prior to pupation, probably making it harder for pupiphagous predators to find them. The behavior of pupating so as to remain unseen is clearly a form of crypsis. Crypsis is probably more important during pupation than during any other life stage because the pupa has the maximum digestible and assimilable biomass per individual. Only the prepupal larva briefly weighs more (about 25% more), and much of the difference is sclerotized (therefore undigestible) epidermal tissue and gut contents. Adult females at eclosion weigh about 75% of their freshly formed pupal weight. Adult males weigh only about 50% of their pupal weight and both sexes progressively lose unsclerotized tissue weight as their adult lives go on, making older butterflies less and less energetically rewarding to predators. The pupa is shorter and of greater diameter than the preceding mature larva and than the succeeding adult, so sclerotized surface area is minimized relative to potentially digestible volume. During the pupal stage larval tissues are being degraded into the universal biochemical building blocks (easily usable by any potential consumer) in order to build new, adult tissues. In addition, the sclerotized tissue is relatively segregated from the contents and therefore easy for a predator to separate from digestible contents. And, obviously, the pupa itself has virtually no behavioral means of defense other than by twitching.

Thus, the pupal stage is the most rewarding and the most defenseless life stage and we might expect pupiphagy to be important in the population biology of butterflies. Indeed, in 13 of 21 samples of pupal mortality of eight species of butterfly (White 1986, Smith 1986), mortality exceeded 50%. In 11/13 of those cases predation was the major factor. The only work on field mortality of *Euphydryas editha* pupae is my own (White 1986, and unpub.), and that depends on pupae placed artificially in the field. Ideal data would come from pupae formed naturally, *in situ*.

For the much studied Bay Checkerspot butterfly, we see that one stage (diapause, 65% of the duration of the life cycle) is quite intractable, three stages (egg, prediapause larva, and pupa) are so difficult to monitor that little is known of them, and two stages (adult and post-diapause larva) are readily observable (Fig. 1). Similar situations exist for most other butterfly species commonly studied.

Food Plants

Considering all the work done on food plant relationships of populations of *Euphydryas editha* one would expect that the best studied populations, those of *E. e. bayensis* would be thoroughly understood. But we acquired significant new information in 1985, year 26 of the study. We have always been puzzled as to why postdiapause larvae in the lab should prefer the Eurasian weed, *Plantago lanceolata*, to their usual field plant, *Plantago erecta*. This past season I discovered that postdiapause larvae marked and released into different patches of lush, green *Plantago erecta* behaved very differently. Individuals of a group put onto a western exposure disappeared while those placed onto a northern exposure stayed put. In a replicate of the experiment, larvae on the western exposure moved an average of 2.5 meters in three hours while larvae on the northern exposure moved an average of only 0.5 m. The difference was due to the age or developmental state of the *Plantago*. The taller, more mature plants on the western exposure still showed no sign of browning or senescence. They were in the early stages of setting seed. Larvae paused to eat for short periods and then moved away.

Larvae on the northern exposure tasted the shorter, less mature plants there and kept right on eating. For many years biologists have been pulling up handfulls of the larger plants to feed their laboratory larvae. We have avoided the much harder-to-harvest, smaller plants, and we have thereby been providing almost inedible fare. Small wonder that the Eurasian weed was preferred.

Conclusion

In terms of ecological relationships such as larval food plant, much progress has been made (compare Howe 1975 to Opler & Krizek 1984 and to Scott 1986), yet much remains to be done.

With respect to observational difficulty, butterflies are no worse than many other organisms studied. For instance, most of the interesting social interactions of many rodents occur underground, out of sight of the biologist. Similarly, root systems of plants have been difficult for plant ecologists to study (Cody 1986). Still, it is the responsibility of those working on butterflies to devote proportionately more time to the investigation and discussion of the more difficult life stages. Because the failure to discuss problem areas in print ultimatley retards progress, it would be beneficial for authors to include such discussions. More attention being thus focussed on problem areas ought to result in more experimental effort being spent there. Alternatively, much research could be switched to more tractable species (such as *Agraulis vanillae*).

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