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Population Dynamics of the Checkerspot Butterfly Euphydryas editha

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Summary

Populations of the butterfly *Euphydryas editha* differ in their stability and in their response to stresses such as drought. These differences depend in detailed fashion on the nature of the relationships between the butterfly and its food-plants, parasites and climate. Extinctions have occurred several times during this study and are probably frequent in many populations of this species.

A central problem in population biology remains the development of generalizations about the distribution and abundance of plants and animals, and the nature of their genetic and phenetic responses to environmental changes. The solution to this problem requires a data base of long-term studies of natural populations of a variety of organisms. In this context, one of us (PRE) selected for study the butterfly *Euphydryas editha* Boisduval (Nymphalidae: nymphalinae). This inconspicuous species was not known for its population cycles, outbreaks, migrations or economic importance, and hence differs from the bulk of insects on which long term data have been gathered. Changes in numbers of this butterfly have been measured in some populations since 1960 (EHRLICH et al., 1975) and in others for shorter periods of time. Concurrent studies have been carried out on the different ecological relationships between *Euphydryas editha* and other organisms (e.g., WHITE, 1974; EHRLICH et al., 1975). It is now possible to describe the probable effects of interpopulation differences in these relationships on the dynamics of *Euphydryas editha* populations. Data are also being gathered on changes in frequency of genes which affect allozyme loci in order to examine the relationships between these frequencies and population dynamic changes. The recent California drought has brought about extinction of some *Euphydryas editha* populations and drastic reduction of others, while leaving a few apparently unaffected. This has provided information on the susceptibility of populations with different ecological relationships to one major kind of environmental stress. It will also permit us to examine the effects of the population size bottlenecks on subsequent changes in allozyme frequencies in several populations.

In contrast to most speakers at this conference, we are studying an organism for which interspecific competition seems rarely of importance. *E. editha* sometimes occurs sympatrically with one or at most two congeners and sometimes not; there is no evidence for biological interference or character displacement in areas of sympatry, or indeed, for any of the kinds of pattern described by DIAMOND (this volume). Thus, if our study is compared to the other insect-plant work in this symposium, we should have a simpler situation in which to look at the population dynamics of our study organism than does ZWÖLFER, who is dealing with complex forms of competition as well as reciprocal interactions between the plant populations and the various insect species which feed upon them. We can hope to interpret the dynamics of *E. editha* populations in terms of the insect's interactions with

resources and sometimes also with parasitoids and predators. Nonetheless, the important variables controlling *E. editha* dynamics are often many and complex, even in situations where the only major interactions are those between the insect, its host plant and climate.

Before describing these interactions we should give some relevant details of the biology of the insect. Eggs are laid in batches, and hatch after about two weeks. If the first-instar larvae find food, they spin a web over part of the plant and remain within the web when not feeding. If there is no food within about 10 cm of the egg-mass, the newly-hatched larvae starve. Even if food is close by, they may fail to locate it, and unless several of them do so, they all die, since first-instar larvae need to cooperate to feed effectively. If the larvae succeed in finding edible plants to sustain them for about 10 days they reach mid-third instar, at which point they will, if deprived of food, search for a few days, then molt and enter diapause. Even if food is still available, diapause at the end of third instar is obligatory for *E. editha* in most populations. It lasts through summer and early winter at low elevation, through late summer and all winter at moderate elevation (2300 m) and during snowcover at high elevation. Diapause is usually broken as soon as food is again available; and larvae grow rapidly to produce the adults. There is sufficient time for only one generation per year, and even so, many individuals in most populations fail to fit their life cycles into the growing season and die either because the host plant has undergone senescence between the time the eggs were laid and the time of hatching, or because the larvae fail to reach third instar during the period in which they can still find food.

This pre-diapause starvation mortality has been quantified for many *E. editha* populations (WHITE, 1974; SINGER, 1972). It is likely to be responsible for the evolution of a behavior very important to the population dynamics of *E. editha* and very frustrating to those of us who attempt to raise the insect in the laboratory. If we mistreat post-diapause 4th or 5th instar larvae in any way, especially by not providing very young or succulent plants as food, they continue to feed for a short while (storing up fat?) then enter a second diapause just as long as the first. This procedure can be repeated, and a single larva can, with two weeks' feeding each year, outlast the tenure of the graduate student attempting to write a dissertation upon its habits.

52 out of 70 diapausing larvae gathered in the field (at Woodside, California, in 1969) weighed between 3.0 and 4.5 mg; however, two of them weighed 9 mg, one weighed 12.5 mg and the largest weighed 16.5 mg. The presence of these large larvae may indicate that second diapause also occurs in the field. The ability to re-enter diapause may increase the chance of individual survival either when food is removed by competing larvae or in unusually dry years when the poor quality of food available to early post-diapause larvae may indicate that there will not be time for the next generation of larvae to reach the minimum size at which they can enter diapause.

The survival of population LO through a year when no host-plants were available to prediapause larvae (R. R. WHITE and M. P. LEVIN, unpublished) seems certain to be a result of «second diapause».

Having given this basic life-history information, we shall now describe the variability of population dynamics between ecologically different populations of *E. editha*. The populations for which the longest run of data is available are on Stanford University's Jasper Ridge Biological Reserve (JR). EHRLICH's early work on these three populations (JRH, JRC and JRG) dramatized the necessity of identifying demographic units in population dynamic studies (EHRLICH, 1965). Analysis of the data for the whole of Jasper Ridge would give an impression of stability, but study of the movement patterns of individual butterflies showed that there were three populations which fluctuated independently of each other and exchanged less than 0.5% of individuals per generation. One of these populations has undergone two extinctions in the last ten years. More recently, these

populations have tended to fluctuate more nearly in synchrony, but it is clear that they *can* be independent of each other.

The reasons for the observed dynamic changes were investigated by SINGER (1972). He found that pre-diapause mortality due to senescence of host plants amounted to about 99%, and that densities of *E. editha* larvae were thereby reduced almost to the density of the adult population 11 months later. This leaves little room for other mortality factors, and there is evidence for this population that mortality in diapause, or predation and parasitism (affecting post-diapause larvae and pupae) have all been low during this study (SINGER, 1971a; EHRLICH et al., 1975). Since the larvae which starved did so when they had eaten little or no food and since the food was dense (several hundred plants per square meter), the feeding of most larvae did not affect the access to food of other individuals (WHITE, 1974). Unavailability of food to any larva was due to its senescence, and not to its consumption by other insects of the same or competing species. Larval survival through this crucial stage could occur either:

1. Where the phase relationship between adult emergence and host plant senescence was favorable – this would vary between years with climatic factors, but within years was highest for insects which lived as post-diapause larvae on the drier, warmer, south-facing aspect of the slope and laid eggs on the north-facing aspect.
2. Where digging by gophers *(Thomomys bottae)* had thinned out the host-plants (*Plantago erecta* Morris) during the winter and the remaining plants, as a result of reduced competition and/or soil tilling, had grown much larger than their fellows, lasting two or three weeks longer into the dry season.
3. Where wandering larvae were able to locate the flowers of the hemiparasitic annual *Orthocarpus densiflorus* (Scrophulariaceae), which served as a very temporary secondary host-plant, for the few days in which the larvae grew to sizes at which they could diapause.

We can regard these three means of survival as three resources, and hence interpret the lack of synchrony between change in numbers of the three identified demographic units as a result of their differential dependence on these three resources. In population JRH, route (3) was responsible for most of the larval survival in the year of study (SINGER, 1972; EHRLICH et al., 1975).

It is much easier to demonstrate the action of density-dependence than its absence; however, by elimination of possible density-dependent agents it seems clear from the biological relationships of *E. editha* at these sites that the three Jasper Ridge (JR) populations have fluctuated independently of their densities at the population density levels which have prevailed since 1959. We have, however, insufficient data as yet to test whether the actual population size changes in practice depend on previous population density levels. We should note, however, that the sedentary nature of the JR *E. editha* (EHRLICH, 1961) makes our findings different from the superficially similar case quoted by ANDREWARTHA and BIRCH (1954) for the grasshopper *Austroicetes cruciata*. In this species also, individuals died from starvation in some areas without competing for food; however, the insect is migratory and the observations may have been made in an area which would not support a population of sedentary grasshoppers, and which received frequent input from more favorable regions. It seems, however, that most *E. editha* populations in the San Francisco Bay Area receive very few immigrants, yet are similar in their lack of density-dependence to those at JR. How do so many populations persist in this condition? Does this indicate that *E. editha* is here at the limits of its ecological tolerance, and could not exist in a drier climate with a shorter growing season? We know something about the answers to these questions. Firstly, with regard to the persistence of these populations, there are several apparently circumstantial factors which are relevant:

1. The phase relationship between insect flight season and plant senescence varied by only 6 days in length in the 4 years 1968–71, and probably varies little in general, because those climatic factors which speed development of the larvae in February and March generally result in earlier senescence of host-plants to the same degree.
2. The effects of year-to-year variation in this phase relationship are mitigated because although the host plants undergo senescence quite rapidly, this senescence starts very early in the flight season in some patches of the habitat. Since female butterflies do not oviposit in dry areas, they are selecting oviposition sites from a smaller and smaller proportion of the habitat as the flight season progresses. Examination of the fates of both real and hypothetical (SINGER, 1971a) egg masses laid in 1971 showed that the probability of an egg-mass hatching into a dry environment was 27% at the very beginning of the flight season, on March 22, rapidly rose to 71% by March 29, but was only 75% on April 4 and 83% at the very end of the flight season on April 16. The pattern in time of senescence of the host-plants gave rise to a slow rate of decline of hatching mortality with advancing time of oviposition, and a plateau at about the time of maximum oviposition in this year. This phenomenon would strongly attenuate the effects of small year-to-year changes in the phase relationship in the JR populations. Even in very dry years, some plants would still, it seems, be suitable.
3. Old data from the Woodside population, prior to its bisection by housing development, show rates of attack by braconid parasitoids on the order of 90%, much higher than any rates recorded recently anywhere in the Bay Area. It is possible that populations existed which had phase relationships between plant senescence and peak oviposition more favorable to larval survival than that at JR. These would also have provided more favorable environments for *Apanteles* spp. (which starve along with their hosts at JR, since larval starvation occurs after parasite attack), and may have provided reservoirs from which recolonization by *E. editha* of other areas could occur after extinctions which may have been caused by a succession of dry years or by fluctuations in density of the secondary host-plant, *O. densiflorus*.

With regard to the question of the limits of ecological tolerance, one might expect that the *Plantago*-feeding ecotype of *E. editha* could not occur southwards of JR, where the growing season is shorter. In fact, it occurs all the way to Baja, California. Southwards from JR initally little initial change in the ecology of *E. editha* is encountered, perhaps because faster larval growth compensates for the shorter growing season. About 200 miles south of JR, however, *Plantago* occurs on a different soil type which permits longer survival of the plant in the dry season. In these areas (such as population CS – see WHITE and SINGER, 1974) both *E. editha* and its host-plant are typically sparse, perhaps because the ecological situation which is in some ways more favorable to both of them than that at JR, has allowed them to come into density equilibrium with each other. Post-diapause larvae remove a large proportion of the host-plants, leaving them so sparsely distributed that high rates of starvation of the next generation of pre-diapause larvae occur, not because of plant senescence but because of plant scarcity. Similar situations have been better documented for other ecotypes of *E. editha* feeding on other host-plant genera (WHITE, 1974) but the situation at CS provides an instructive contrast to that at JR, where both plant and insect are typically dense, where changes in insect density do not affect either insect population trends or plant density in the succeeding year and where observed changes in *Plantago* density have no contemporary or subsequent effect on the density of the insect. Changes in plant quality, not quantity, are the important factors.

Even further south, in the San Diego area, which has a climate with very variable timing and extent of rainfall, populations are found which fluctuate more widely than any other *E. editha* populations known. In some years outbreaks occur, with intense competition for

both larval and adult resources, while in other years high pre-diapause starvation mortality due to plant senescence as at JR reduces larval density at this early stage to a level at which post-diapause larvae do not compete for food (R. R. WHITE and M. P. LEVIN, unpublished Ms). In 1976, in population LO, pre-diapause survival was good enough to result in complete removal of the *Plantago* from the whole habitat by post-diapause larvae in January–February, 1977. Many postdiapause larvae starved, but many became adults. Many, and probably most, of the females, emigrated, as no host-plant remained and no oviposition sites could be found (D. MURPHY and R. R. WHITE, Ms.). Nonetheless, *E. editha* has reappeared at this site in moderate numbers in 1978. The ability of larvae to undergo a second diapause must be responsible for this, since large-scale immigration in one year is unlikely.

South of San Diego, in Baja, California, rainfall becomes even lower and less predictable. The *E. editha* which live here weigh less than one-third as much as JR individuals, and we know little about them. Size differences between individuals in several populations of *E. editha* are maintained when the butterflies are raised in the laboratory under the same conditions. Thus, it seems likely (though not tested for this specific case) that the Baja, California *E. editha* are genetically smaller than those at JR, and thus are able to fit their life cycle into a shorter unpredictable growing season, with larvae which «germinate» along with their host-plants after rainfall, and re-enter diapause if the rains do not persist.

Returning to the question of the sense in which the JR *E. editha* exist at the limits of their ecological tolerance, the answer is complex. Evidently although 99% of individuals at JR die because their life cycles, as individuals, are too long to fit into the season when food is available, the species *E. editha* can exist in much shorter growing seasons than at JR. Various ecological factors have resulted in the adoption here of a high fecundity strategy with resultant high mortality. Earlier flight season would entail lower starvation of pre-diapause larvae but lower fecundity, since there would be less time for female larvae to grow. Assuming that this strategy is optimised, and that a slightly earlier flight season with lower fecundity and lower mortality would result in fewer offspring reaching diapause, then the nature of the population dynamics tells us that such an insect could not exist at JR. It would become extinct, since there are no density-dependent factors which could counteract the effect of lower average numbers of diapausing larvae resulting from each female. However, there could be a selectional «trough» between two possible strategies – one with very low fecundity, early flight season and high survival, and the second the existing strategy of high fecundity with resulting high mortality. Provided that the flight seasons were sufficiently distinct that no gene flow occurred, we could perhaps test this suggestion by introducing small *E. editha* at JR. There seems no reason why they could not coexist with the larger, later individuals, though nectar supply at a very early flight date may prove so poor as to cause emigration.

We have described some of the interactions between insect, plant and climate as they affect the population dynamics of the *Plantago*-feeding ecotype of *E. editha*. The recent succession of *two* unusually dry years has brought about very severe reductions in the JR populations, and in other Bay Area *E. editha* populations. Some of the reasons why these populations should be more stable to climatic fluctuations than their density-independence leads us to expect have already been described. There are however, three reasons why *two* consecutive dry years should have unusually adverse effects:

1. It has been shown (SINGER, 1972) that, in the JRH population, pre-diapause survival on the small south-facing slope occurred in only one year of a four-year study of larval distribution. Not surprisingly, this was an unusually wet year. In the following year, those post-diapause larvae which appeared on the south-facing slope grew faster than the rest and gave rise to earlier adults. Thus, the wet conditions of year 1 affected the

microdistribution of larvae and hence the phase relationship between plants and insects in year 2 in such a way as to increase the survival of pre-diapause larvae in year 2 and hence the population density in year 3. Conversely, it should hold that a dry year will adversely affect the phase relationship in the following year. If this year, too, is dry, the slightly later flight season brought about indirectly by the previous dry year, will tend to increase larval starvation still further.

2. In years when the phase relationship is unfavorable to *E. editha*, most larvae run out of food sooner and enter diapause smaller than they do in more favorable years. This is a second factor tending to make the flight season the following year a little later, since smaller diapausing larvae take longer to reach adult size.
3. In dry years the host plant produces seeds which are both fewer and smaller (R. R. WHITE, unpublished). Since the length of the growing season limits *P. erecta* as well as *E. editha*, and since small plants usually undergo earlier senescence than large plants, the effect of drought on seed size should also cause a carry-over effect to the following year in a manner unfavorable to the butterfly. Any effect of lower seed number on plant size through reduced competition would counteract this, however.

Overall effects of the drought

E. editha occurs in many different habitat types, using at least five genera of host-plants, though it is usually monophagous in each population (SINGER, 1971b). We have generated expectations about the susceptibility of different ecotypes of *E. editha* to climatic fluctuations. In 1971, SINGER wrote: «In populations (e.g., DP) which utilise perennial food-plants the supply of food is approximately constant from year to year. At DP, both population density of *E. editha* and the spatial pattern of survival of pre-diapause larvae are determined by intraspecific competition for food. Macroclimate apparently has no effect on mortality, and senescence of the food-plant is unimportant to *E. editha*. It is predicted that such populations will prove very stable through time, local extinction being unlikely.» (SINGER, 1971a). This expectation has proven completely false. The drought has reduced the DP population by two orders of magnitude and the JR populations by only one order (EHRLICH et al., in prep.). The failure of this prediction serves as a lesson that those populations which are most intensely regulated under most conditions are not necessarily the least susceptible to environmental fluctuations – in this case the answer would depend on the exact nature of the response of the host to drought (keep stored resources for next year??) and the initial density of the insects, which, if high, would result in an overcompensating crash as many eggs would be laid on small plants, and most larvae would die in the classic «scramble» competition resulting. Indeed, in the year 1970 and 1971 the proportion of pre-diapause larvae starving to death at DP was over 99%, almost the same as that at JR. The difference was that plant senescence was relatively late at DP, and the lack of food was due entirely to its consumption by larvae. 100% defoliation occurred in many parts of the habitat. With hindsight, and in the light of recent models such as those of MAY and OSTER (1976) we can see how such an intensely density-dependent situation may be unstable. If this interpretation is correct, the DP population should stage a rapid and dramatic recovery to its former density or higher.

More interesting still has been the large-scale extinction during the drought of populations of *E. editha* which lived in the Sierra foothills and fed on *Collinsia tinctoria*. Three out of four such populations under study have become extinct in the last two years. The surviving population at Indian Flat (IF) is not the one which had the most favorable «phase relationship» for most insects, but does have two factors in its favor:

1. It covers a larger area than the other three.
2. It has a high diversity of plant senescence times, permitting early adults from drier areas to find suitable oviposition sites in shady areas in at least the first of the two dry years.

The reason for extinction of one of these populations, Agua Fria (AF) is quite clear. In 1977, a search of about half the habitat revealed only 23 individual host-plants, and damage from probably one *E. editha* larva was found. In 1978, several thousand plants are present. Clearly, the hosts have a «seed bank» strategy, and do not germinate in dry years. The equivalent strategy of *E. editha*, repeated diapause, probably will not be effective in these circumstances since our laboratory observations indicate that larvae which break diapause die if they are unable to feed at all. They need to find at least *some* food if they are to store reserves and survive a second summer. At AF in 1977, all but one of them found no food at all. Again, our earlier knowledge of these populations led us to expect that they would be more stable to drought than JR, since female insects can predict quite accurately the future senescence time of an individual plant. This they do by ovipositing on unopened buds. In contrast, females at JR seem unable to distinguish between plants which will remain green for one week and those which will last another three or four weeks.

At least one population of *E. editha* (WK), at 1800 m elevation in the Sierra Nevada mountains, has remained stable following the drought. At this site, larvae break diapause and host plant seeds germinate in synchrony when the snow melts over them. Thus, lower winter rainfall results in earlier snowmelt and earlier flight of *E. editha*, affecting the timing of the growing season more than its length. Winds which affect the depth of snow drifting will also be important. Thus, the lack of adverse effect of the drought is not surprising. At even higher elevations (for which we do not yet have data this year) low accumulation of snow in winter («drought») may even lengthen the growing season, which should start early and continue through the summer, fueled by convectional rains.

In conclusion, populations of the butterfly *Euphydryas editha* differ dramatically in their response to drought, which is stressful to some populations and less so or not all to others. The reasons for these differences lie in the details of the relationships which exist in each population between the butterfly and its host plants and parasites or predators. Any possible generalization would need to account for the effects of these specific relationships and their interaction with climate on population dynamics. We cannot generalize about the population dynamics of the species. *E. editha*, since so much interpopulation variability exists.

The history of one population supports theoretical predictions that extreme density-dependence may result in large-scale fluctuations, but other populations of *E. editha* which we have studied fluctuate apparently independently of their densities in response to changes in quality and quantity of food which are simply the result of the interactions between the host-plant and climatic factors. Thus, there is frequently no reciprocal interaction between the insect and its food supply. Susceptibility to climatic stress may be great whether host-plants are annual or perennial – indeed, changes in quality of perennial plants during drought may be as severe in their effects as changes in quantity of annuals.

Extinctions seem to be frequent in populations of more than one ecotype of *E. editha*. We should note that in most instances such extinctions entail the elimination of all genetic material in the population. These events represent large-scale death rather than large-scale emigration, and even if the latter were the case, migrants are unlikely to contribute genetically to other populations for reasons expounded by EHRLICH et al. (1975) and GILBERT and SINGER (1973).

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