CHAPTER 9

Genetics and the Extinction of Butterfly Populations

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Introduction

Butterflies are both excellent indicators of the health of ecological systems (Pyle, 1976; Ehrlich and Ehrlich, 1981) and major tools used by biologists to investigate the properties of natural populations. Consequently, they are of central importance to all those interested in preserving and managing Earth's biotic resources. It is therefore appropriate to examine the state of knowledge of the genetics of extinction in this key group.

The relationship between the dynamics and the genetics of natural populations remains largely *terra incognita*. The dynamics of relatively few carefully defined demographic units (populations that change in size independently) have been followed for any length of time, and until recently it has been extremely difficult to study the genetics of most such populations because of the problem of determining gene frequencies at samples of loci.

A thorough understanding of the interactions between the size and the hereditary characteristics of populations nevertheless is crucially important to humanity. It would permit more effective manipulations of economically important organisms—for example, of insects that prey on pests

of crops. And, more important, it would provide insight into the best tactics for ending the current epidemic of extinctions (Ehrlich and Ehrlich, 1981).

There is reason to hope, however, that knowledge of these dynamic genetic interactions, at least in certain groups of butterflies, will soon be much more extensive. The dynamics of some populations of Nearctic checkerspots (*Euphydryas* in the family Nymphalidae, the brush-footed butterflies, subfamily Nymphalinae) are now understood; changes in some demographic units have been traced for more than two decades (e.g., Ehrlich et al., 1975; Ehrlich and Murphy, 1981); and numerous population extinctions have been observed. Allozyme frequencies have been traced in a number of populations for 5 to 8 years, and these data are now being analyzed (Ehrlich et al., 1983).

Overall, then, the stage may be set for a substantial improvement in the understanding of how population size and gene frequencies interact, at least in butterflies. A breakthrough cannot come too soon, because of the increasingly precarious position of Earth's biota (Ehrlich and Ehrlich, 1981).

In this chapter, I attempt to summarize what is known about the extinction of butterfly populations, and to speculate about the genetics of extinction in these organisms. The speculations, I must emphasize, are just that—little enough is known about the genetics of *any* natural populations, and virtually nothing is known about the genetics of extinction.

Natural Extinctions

1. *Euphydryas*

Among the best documented extinctions of butterfly populations from natural causes are the two extinctions of the area G demographic unit of *Euphydryas editha bayensis* (San Francisco Bay region checkerspot) on Stanford University's Jasper Ridge Biological Reserve, California. From the time of the first census in 1960, this unit, which at its largest occupied an area of about 0.6 hectare, declined continuously from about 60 individuals until it became extinct in 1964–1965. It was naturally reestablished in 1966, reached a population size of several hundred in 1970, and then declined again to extinction in 1974–1975. During the same period, demographic units adjacent to G on either side (Jasper Ridge C and H) fluctuated in size but persisted (Ehrlich, 1965; Ehrlich et al., 1975).

All populations of *E. e. bayensis* (indeed, most *Euphydryas* populations in western North America) are extremely time-constrained in their development. The food plants of *E. e. bayensis* are vernal annuals that senesce

rapidly in April–May. Butterflies lay their eggs on the plants, and before the plants dry up the larvae must complete the third instar and enter the resting state (diapause) in which the dry summer is passed. The larvae emerge from diapause after the fall–winter rains set in and the seeds of their food plants have germinated.

On the order of 99% of mortality in these populations occurs when pre-diapause larvae fail to reach the obligatory diapause instar before their food plants senesce (Singer, 1972). Year-to-year variation in that mortality, controlled largely by the complex phase relationship of the butterflies with the local climate (Singer and Ehrlich, 1979), is the cause of observed population trends. Adult populations tend to decline in springs following dry springs (because in dry springs the larval food plants senesce more rapidly, are sparser, and are of poorer quality because there has been little rainfall) and to increase following wet springs. In all years it is plant senescence that limits food availability—on Jasper Ridge, competition among larvae has not been a factor in more than two decades, and there is no sign of density-dependent population "regulation."

Within this general picture of the dynamics of *E. e. bayensis*, how does one explain the extinctions of the demographic unit in area G? It might be tempting to invoke a genetic explanation, since G is the smallest demographic unit. Could, perhaps, loss of heterozygosity as the population size shrank in the early 1960s (and as a result of a founder effect when it was reestablished) have made it more vulnerable to adverse conditions? There is little sign in our data that such an explanation is correct (Ehrlich et al., 1983). Populations of *E. editha* (Edith's checkerspot) show remarkable stability of both gene frequencies and heterozygosity through wide-ranging fluctuations of population size—including bottlenecking, as discussed below.

Instead, the explanation of the area G extinctions appears to lie in the relationship of *E. e. bayensis* with its adult nectar resources. Females lay masses of eggs every two days or so. In most years the time constraints are such that only larvae from the first one or two egg masses have any chance of reaching diapause. Females emerge with large numbers of mature eggs and large fat reserves, and the size of their first two egg masses is unaffected by the presence or absence of nectar resources. In wet years, however, larvae from third, fourth, and fifth egg masses may survive. *Those* egg masses will be larger if adequate nectar resources are available than they will be if sources are inadequate (Murphy et al., 1982).

It appears, then, that nectar resources play a key role in enhancing reproduction in favorable years. This permits demographic units to build to relatively large sizes, which provide buffering against extinction in these populations, as they have density-independent population regulation. In this context the probable cause of the area G extinctions becomes clear. Although larval resources in the area are adequate, nectar resources (unlike

those in areas C and H) are both scarce and badly timed for the butterflies (Murphy et al., 1982). Therefore the G demographic unit has not been able to reach population sizes that would adequately buffer it against droughts, and it has twice gone extinct.

The dynamics of a number of California populations of *Euphydryas editha* and of its sympatric close relative, *E. chalcedona* (chalcedon checkerspot), have been monitored for a decade or more. The *E. editha* populations belong to an array of ecotypes, suites of populations adapted to diverse ecological conditions (Gilbert and Singer, 1973; White and Singer, 1974; Ehrlich and Murphy, 1981). Within ecotypes the populations tend to be more similar to one another in their ecological characteristics than to populations of other ecotypes, even when the latter are geographically closer.

This long-term monitoring has allowed our research group to take advantage of a "natural experiment" — the California drought of 1975–1977 — to study the response of *Euphydryas* demographic units to stress. Several populations of *E. editha* went extinct, and others were reduced in size by fivefold or more.

These responses differed among *E. editha* ecotypes. Within and between species, the responses appeared to be largely a function of the fine-tuning of the relationship of the populations to their larval food plants (Ehrlich, et al., 1980) and of habitat changes induced by human activities (such as grazing) that altered the vulnerability of the populations to extinction.

Information on allozyme frequencies is available for several populations that went through drought-induced bottlenecks in population size. Preliminary results show a surprising lack of influence of dynamic changes on allele frequencies and genetic variability. Polymorphic loci tend to maintain the same predominant alleles in roughly the same frequencies through dramatic changes in population size (Ehrlich et al., 1983). Furthermore, when there have been some indications of loss of genetic variability, it appears to have been rapidly restored.

There are three possible explanations, which are not mutually exclusive, for these observations:

1. The variation is "neutral," but population size at the bottleneck has been underestimated (some populations with effective population size, N_e, less than 20), so drift would not be expected to have had substantial effects on allele frequencies.
2. The variation is under selective control, and the polymorphisms are maintained by marginal overdominance (e.g., Gillespie, 1977), heterogeneity of the environment (Hedrick et al., 1976; Watt, 1977), or some other mechanism, and population size has been underestimated or the bottleneck has not existed long enough, as in explanation 1.

3. Genetic variability is lost, but there is sufficient gene flow from populations of the same ecotype (Ehrlich and Murphy, 1981) to restore the pre-bottleneck variability.

Preliminary data on the genetics of Great Basin populations of *E. editha* (Wilcox, Murphy, Ehrlich, and Brussard, in preparation) indicate that they have lower levels of heterozygosity than those in California (McKechnie et al., 1975) or Colorado (Ehrlich and White, 1980). These populations appear to be strongly isolated from one another and may not be subject to the large fluctuations in populations size that are found in some California ecotypes. This could indicate a mechanism-controlling level of variability that has little to do with the dynamic history of the populations.

One tentative conclusion may be drawn about the role of genetics in the extinction of *Euphydryas* populations. There is no sign of the sort of situation thought to be common in the extinction of populations of vertebrates or of *Drosophila* strains in laboratories—that is, small population size resulting in inbreeding depression, which in itself contributes to extinction (for overview see Frankel and Soulé, 1981). This conclusion is not grounded in evidence that *Euphydryas* are especially resistant to inbreeding depression. Rather it follows from the observation that *Euphydryas* populations *do not persist at the small sizes required for strong inbreeding to continue over several generations.* In short, when *Euphydryas* populations are reduced to 30 to 50 individuals, they appear either to go extinct promptly or to rebound to sizes an order of magnitude or more larger. Since the dynamics of most *Euphydryas* populations are largely density-independent, stochastic (random) extinction is the likely fate of any demographic unit that gets small enough to suffer a substantial decay of genetic variability. This is indicated not only by our frequent observations of population extinctions in nature, but by the difficulty of reestablishing extinct populations (Murphy, Ehrlich, and Wilcox, unpublished observations) and of transplanting species to previously unoccupied suitable habitats.

In the latter case (Holdren and Ehrlich, 1981, and unpublished observations), eggs and larvae of *Euphydryas gillettii* (Gillett's checkerspot) were transplanted south across the Wyoming Basin gap in the Rocky Mountains to sites in Colorado that had suitable larval and adult resources. Each transplant was made with the rough equivalent of the reproductive output of populations of 30 to 50 individuals. One transplant population fluctuated for three generations at an estimated size below 30 individuals, perhaps dropping below 10, and then increased in 1981 to more than 100 individuals. The other produced only one known adult in the first generation and then went extinct.

It may be, therefore, that for insect populations similar in their dynamics to *Euphydryas* conservation biologists need not concern themselves with the genetic effects of temporarily small population size. This is

probably just as well, since the process of evaluating allozyme frequencies in a population of, say, 60 adults requires exterminating the population! What is of greater interest is sorting out the ecological factors that make populations of different ecotypes differentially susceptible to extinction (Murphy and Wilcox, in preparation).

2. *Glaucopsyche*

It also seems unlikely that genetic factors were directly involved in the extinction of a montane population of the silvery blue, *Glaucopsyche lygdamus* (family Lycaenidae, the gossamer-winged butterflies). A late season snowstorm destroyed the lupine inflorescences that are the basic resource for *Glaucopsyche* larvae, and a large population disappeared as the result of that single climatic event (Ehrlich et al., 1972).

That extinction illuminated a possible reason for the very early flowering of the perennial lupine plants (*Lupinus;* they normally set seed long before the end of the growing season). The risks of early flowering may be more than compensated by its impact on *Glaucopsyche*, which must oviposit on the buds. By sacrificing one season's reproduction, the plants gained a decade of virtual freedom from the attacks of their major seed predator (Ehrlich, 1982).

Nothing is known about the genetics of *Glaucopsyche* populations, but observations in connection with their food plant relationships (e.g., Breedlove and Ehrlich, 1972) make it seem unlikely that small populations would benefit greatly from the increased resources available to the average individual. In only the most unusual cases does it seem likely that density effects play crucial roles in the dynamics of populations of *Glaucopsyche* or of many other temperate zone lycaenines. My guess would be that, owing to their small size (wingspreads usually under 3 cm) and the frequent abundance of their food plants, they would more readily maintain substantial numbers than many *Euphydryas* demographic units. Inbreeding problems would be rather rare and extinctions a result of catastrophes rather than of declines in population size in response to "normal" variation in weather patterns.

Anthropogenic Extinctions

A number of species and many populations of butterflies have gone extinct as a result of human activities. One of the earliest recorded losses was that

of a subspecies of the sthenele brown, *Cercyonis sthenele sthenele* (Nymphalidae, subfamily Satyrinae, the satyrs and wood nymphs). It disappeared under the spreading city of San Francisco in 1880 (Ehrlich and Ehrlich, 1981). *Glaucopsyche xerces* (Xerces blue) followed it in 1943, and five species of butterflies are now threatened or endangered in the San Francisco Bay area. Several populations of *Euphydryas editha bayensis* are known to have been paved over in that region, the most recent being one at Woodside that was largely destroyed in April 1980 while under study by our group. The sites of many other well-known butterfly populations are now under concrete in the Los Angeles basin and around other cities. In such cases, once again, one would not expect loss of genetic variability to play an important role. Inbred or outbred, organisms cannot persist without suitable habitat.

1. *Euphydryas editha*

The entire *E. editha bayensis* ecotype may be unusually susceptible to anthropogenic extinction, in spite of the existence of two demographic units on Stanford University's biological preserve. For at least several hundred years, its populations appear to have existed in isolated patches of grassland growing on serpentine soil. These patches are differentially affected by droughts and, presumably, other environmental stresses, and thus in any season the demographic units occupying them are differentially susceptible to extinction. Those units have probably gone extinct frequently and then have been reestablished in time by migrants from other colonies of these relatively sedentary insects. The ecotype thus has persisted as a shifting mosaic of fluctuating populations, not as static, permanent occupants of given sites.

As humanity has removed patch after patch from the mosaic of suitable habitat, the probability of successful recolonization has declined. The number of remaining patches is now so small that the entire ecotype is threatened with extinction. If the two remaining demographic units on Jasper Ridge go extinct, as they nearly did during the recent drought, recolonization from the other remaining major reservoir (Edgewood, 10 km away) would probably not occur before that colony went extinct as well (Murphy and Ehrlich, 1980).

The precariousness of the situation of *E. e. bayensis* was underscored in 1981–1982 when the Edgewood population, by two orders of magnitude the largest surviving demographic unit, was subjected to repeated Malathion sprayings as part of the program to attempt to control the Mediterranean fruit fly (*Ceratitis capitata*). The *Euphydryas* larvae were in diapause when the spraying occurred, but our data suggest that they nonetheless suffered considerable mortality, probably from "direct hits" on

poorly sheltered individuals. The population declined from over 100,000 to considerably fewer than 10,000 adults. It is not at all clear that broadcast spraying is the appropriate response to medfly infestations (which will certainly recur), but the level of competence of the state and federal agencies with the responsibility for pest control provides little hope that a more sophisticated approach will be taken next time. The impact of the program on other butterfly populations in the treated areas is not known, but local pest outbreaks (Ehrlich group, unpublished observations) indicated substantial effects on nontarget organisms—as one would expect, the predators of pests were more severely affected than the herbivorous pests themselves.

The "mosaic" pattern of population regulation (Ehrlich and Birch, 1967; Ricklefs, 1973) exhibited by *E. editha bayensis* has also been described for populations of the checkered white, *Pieris protodice* (family Pieridae, the whites and sulphurs), in the Central Valley of California (Shapiro, 1978). The degree to which this sort of pattern applies to other butterflies, and the rates of population turnover that prevail, remain to be documented. But, as indicated above, I believe the pattern is a common one in populations of insects.

For the mosaic pattern to operate, individuals from one demographic unit must be genetically suited for life in the patch once occupied by another. Our group has used as a working hypothesis that within the *E. e. bayensis* ecotype this is the case—even though substantial differences in the detailed ecology between populations as close in distance (10 km) as those on Jasper Ridge and at Edgewood have been discovered. This assumption is soon to be tested with transplant experiments, but there is evidence from other butterflies that small genetic differences can prevent successful recolonization of empty habitat patches.

2. *Lycaena dispar*

The large copper, *Lycaena dispar* (Lycaenidae, Lycaeninae), became extinct in England in the middle of the last century when most of its marsh habitats were destroyed and collectors wiped out the few remaining colonies. In 1927, a colony was reestablished at Woodwalton Fen, using stock from Holland. With the help of constant management it survived until 1968, when a heavy flood wiped it out. In 1970, the butterfly was reintroduced again, but the scientist who has the most intimate knowledge of its biology believes that it cannot survive without constant husbandry (Duffey, 1977).

A major problem is the genetic differentiation of the Dutch stock from the now-extinct English stock. Subtle differences in the habitat requirements of the two strains make it unlikely that the reintroductions can persist unaided. To put it another way, if *L. dispar* in England once had a

mosaic population dynamic pattern like that of *E. editha*, Dutch populations probably were not part of the mosaic. Instead they belonged to a different ecotype.

3. *Maculinea arion*

The problem of fine genetic adjustment to habitat requirements is beautifully exemplified by the story of the extinction of the large blue, *Maculinea arion* (Lycaenidae), in England (Thomas, 1980a, 1980b). Two of the basic habitat requirements of the species were its larval food plant, wild thyme (*Thymus praecox*), and one species of ant (*Myrmica sabuleti*) with which, like many lycaenids, it had a symbiotic relationship. The ants tended the larvae in return for droplets of sugary solution from larval honey glands. Last instar larvae were removed from the plants by the ants and taken into the ant nests where they lived as social parasites, being fed by the ants and eating ant brood.

The end for *M. arion* in England came when economic conditions changed and the grazing of sheep was discontinued in the areas where the blue still survived. Sheep kept areas in a condition similar to the downland localities where *M. arion* had originally thrived. The cessation of grazing permitted the thyme to grow luxuriantly, but made conditions unsatisfactory for *Myrmica sabuleti*. Under such circumstances that ant is rapidly replaced by *Myrmica scabrinodis*, an unsuitable host, whenever grazing is even slightly relaxed. Thus removal of sheep deprived *M. arion* of a necessary resource, and it went extinct.

4. *Papilio machaon*

Relatively little is known about the population biology of larger butterflies, in part perhaps because they tend to be more difficult to subject to mark–release–recapture experiments. An interesting exception is the English populations of the swallowtail *Papilio machaon* (family Papilionidae). The habitat of this species in Cambridgeshire was greatly reduced when once-extensive marshy peatland (fens) were drained. There is evidence that in the process a low-mobility phenotype evolved before the last remnant population went extinct at Wicken Fen in the early 1950s (Dempster et al., 1976).

Attempts to reestablish the species at Wicken failed repeatedly. Interestingly, investigations during the last attempt in the 1970s (Dempster and Hall, 1980) revealed no signs of inbreeding depression as the population got smaller. For instance, egg viabilities that were carefully monitored in the field showed no reduction as extinction approached.

Discussion

As stated at the beginning, butterflies are key indicator organisms for the health of ecosystems, systems that provide *Homo sapiens* with indispensible services without which civilization cannot persist (Ehrlich and Ehrlich, 1981). And butterflies are the only sizable group of invertebrates that are routinely studied and collected alive by large numbers of amateur naturalists. Only in large mammals, birds, a few groups of reptiles and fishes, and (in some regions) vascular plants are the decline and disappearance of populations and species equally likely to be noted.

In addition, far more is known about the host plant relationships of butterflies than about the diets of any comparable group of herbivores. Therefore not only are butterflies representative of the smaller animals in terrestrial ecosystems, they provide some index to the status of plant communities as well. It is probably fair to say that proximate causes of the vast majority of butterfly extinctions are changes in the populations of their larval food plants or adult resources.

Despite the great interest in butterflies, the monitoring of their populations is grossly inadequate in most overdeveloped countries (England represents an exception) and virtually nonexistent in less-developed nations—especially in those with rapidly disappearing stands of tropical moist forest. What is known, however, is not reassuring. There appears to be an accelerating global trend toward the loss of butterfly populations and species as a result of the expanding activities of *Homo sapiens* (e.g., Arnold, 1980, 1981, 1982; Bielewicz, 1967; Brown, 1970; Chew, 1981; Ehrlich et al., 1980; Emets, 1977; Kloppers, 1976; Lamas Mueller, 1974; Morton, 1982; Pyle, 1976; Pyle et al., 1981; Zukowski, 1959). This trend is caused primarily by habitat destruction, and, of course, it parallels that of a general despoliation of Earth's biota.

The steps necessary to arrest this general trend must be aimed at the conservation of entire ecosystems; they have been discussed in detail elsewhere (e.g., Myers, 1979; Ehrlich, 1980; Ehrlich and Ehrlich, 1981; Frankel and Soulé, 1981). Some of these steps could and should be initiated with no further knowledge of the biology of extinction in butterflies or other organisms. But further research should go on simultaneously, as it can provide insight into both the interpretation of observed extinctions and the tactics of conservation of butterflies and other organisms with similar population biologies.

We obviously need to learn much more about the relationship between genetics and dynamics in butterfly populations. Can inbreeding depression be ignored as a factor leading to extinction in many (or most) butterfly populations, as suggested above? Or is my hypothesis based on too restricted a sample of kinds of populations? Only further research will tell,

especially on the dynamics and genetics of relatively vagile species (e.g., Brown and Ehrlich, 1980; Brussard and Ehrlich, 1970a, 1970b, 1970c).

We do not even know how frequently phenotypic changes accompany dynamic events. Ford and Ford (1930) in a classic paper associated phenotypic changes—especially changes in "variability"—with fluctuations in population size in *Euphydryas aurinia* (marsh fritillary). But modern attempts to do the same sort of thing have been few, and the results have been less than definitive (e.g., Ehrlich and Mason, 1966; Mason et al., 1968).

In fact, with the exception of the work by Dempster and his colleagues on *Papilio machaon*, I know of no studies successfully relating phenetic or genetic changes in butterfly populations to *any* human disturbance of the environment. There has been no equivalent of "industrial melanism," the darkening of moth species in areas subject to heavy pollution (Kettlewell, 1973), discovered in butterflies. One might, for example, expect model-mimic resemblances to become less precise where humanity has reduced populations of visual predators. And various forms of pollution, from pesticide drift to acid rains, might be placing selective pressures on populations. In spite of the existence of large butterfly collections made over long periods of time, people have not attempted to look carefully even at phenetic trends over decades. One reason for this undoubtedly is the nonrandom nature of the samples in most collections.

Thus, although more is known about the biology of extinction in the butterflies than in most groups of animals, the surface has just been scratched. Long-term monitoring of many more populations in diverse groups of butterflies should be started, so that information can be gathered on such things as rates of natural and anthropogenic extinctions and the dynamic and genetic events preceding them. If such research is not begun soon and pursued with skill and vigor, however, it seems likely that the phenomenon under study will itself terminate the opportunities for investigation.

Summary

Butterflies, because they are well-known biologically and the object of the attention of numerous amateur naturalists, serve as a crucial indicator of the health of ecosystems, and thus of humanity's life-support systems.

Natural extinctions of butterfly populations appear to be common occurrences, especially in response to stresses on their larval food plants. These extinctions, however, are normally followed by recolonization of habitat patches, and a mosaic pattern of population "regulation" prevails.

Anthropogenic extinctions of butterflies are becoming increasingly common as a result of widespread habitat destruction.

Little is known about the genetics of extinction in butterflies. What data there are indicate that inbreeding effects, as populations decline, are not important factors in the disappearance of populations. In contrast, fine genetic adjustments to habitat conditions often appear to make reestablishment of populations with stock from other ecotypes quite difficult.

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