Checkerspot Butterflies: A Historical Perspective

Long-term studies of *Euphydryas* butterflies have revealed much about the biology of natural populations.

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Two major problems blocking our understanding of the genetics and dynamics of natural populations have been the large degree of bias in the sample of populations investigated and the failure to cope with the intimate relationship between genetics and dynamics. In general, microevolutionary studies have been done on populations that have attracted attention because unusual circumstances have permitted natural selection to be easily observed (*1*). On the other hand, studies of the dynamics of natural populations have often focused on organisms of economic significance (*2*) and have only rarely included a significant genetic component. The division between genetic and ecological approaches has been highlighted recently by the proliferation of investigations of allozyme variation in natural populations. Gel electrophoresis has been applied shotgun style to samples which, all too often, may have contained material from more than one population, were of organisms that are basically unknown ecologically, and for which the genetic basis of the observed variation has rarely been elucidated.

It was apparent by the middle 1950's that long-term studies were needed that would consider all aspects of the biology of populations sampled more or less randomly from nature. Such studies seemed to hold the key to questions which then, as now, seemed central to the fields of population genetics and population ecology: What kinds of selection pressures predominate in nature? What is the relationship between these pressures and observable variation? How does the dynamics of a population interact with its genetics? Is population size "controlled" or "regulated"? What are the units of evolution?

In 1959 our group embarked upon such long-term studies with an investigation of a colony of checkerspot butterflies, *Euphydryas editha* Boisduval (Nymphalidae: Nymphalinae), living in a grassland area containing serpentine intrusions at an altitude of about 200 meters on Jasper Ridge, Stanford University campus. In the intervening 15 years we have expanded our investigations to 47 additional populations of *E. editha* in California and Oregon, 25 populations of the closely related sympatric species, *E. chalcedona* Doubleday and Hewitson, and, most recently, three Colorado populations of *E. anicia* Doubleday and Hewitson. We have also studied the biology of many other butterfly populations, but our purpose in this article is to summarize our findings on *Euphydryas* and to see what contributions have been made toward answering the questions outlined above.

It is typical of science today that results are presented as if research programs always proceeded in a certain logical order. Hypotheses are generated and tested seriatim, and theories and laws are formulated. Our progress has not been so orderly. It seemed to us, therefore, that it might be useful to those embarking on similar long-term ventures to structure our discussion historically. Its framework is thus basically the perspective of the senior author but, as will be obvious, many of the major discoveries were made independently by colleagues in the population biology group at Stanford.

Initial Information and Biases

The existence of the *E. editha* colony on Jasper Ridge was made known to Ehrlich by the late O. E. Sette who had sampled the colony (which he described as a "population") several times starting in 1934. Plans were made to begin studying the insect during the spring flight season in 1960. Initial information (*3*) indicated that there was a single panmictic population on the Ridge, that the adults flew in late March and April, that the larval foodplant was the annual plantain *Plantago erecta* Morris, and that there was a larval diapause during the dry season (May to November). Ehrlich's initial biases were that the dynamics of the population would prove to operate in a largely density independent fashion, that selection would account for most or all observed changes in phenotype except when the population was greatly reduced in size, and that findings in the Jasper Ridge population would permit understanding of most, if not all, populations of *Euphydryas editha*—at the very least all central California populations.

Population Structure of the Jasper Ridge Colony

Experiments in 1960, in which individual butterflies of the Jasper Ridge colony were marked, released, and recaptured, quickly did away with one preconception. Although the colony occupied a continuous island of grassland in a sea of chaparral, it was found to consist of three largely isolated populations separated by "intrinsic" barriers to dispersal (*4*). That is, individuals "chose" not to move, although there were no physical impediments to movement. In four generations (1960 to 1963), 1021 of 1048 (97.4 percent) of all recapture events were in the area (arbitrarily designated C, G, and H) of previous capture. The three populations, which became known as C, G, and H, have remained distinct through 15 years of study (although population G has undergone extinction and reestablishment twice).

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Although early results indicated only infrequent movement of individuals among populations on Jasper Ridge, this information was not sufficient to allow inferences to be drawn about levels of gene flow among the populations. Working on this problem, Labine (*5*) discovered that in the process of depositing its spermatophore, the male butterfly adds a "plug" which, once it has dried, effectively prevents another insemination. In addition, she obtained evidence indicating that the presence of a spermatophore in the bursa copulatrix makes a female less receptive to the advances of males. The plug deteriorates with time, permitting an eventual second insemination in some individuals. Labine (*6*) was able to obtain evidence of sperm precedence (fertilization of eggs by sperm from the last male only) in *E. editha*, indicating the "plugging" was a mechanism evolved to protect the male's genetic investment.

Most female *E. editha* are mated immediately on emergence, with no particular ritual. Thus, except at the very beginning of the flight season, a male migrating into a new population would normally find few, if any "unplugged" females receptive to fertilization. Furthermore, for reasons explained in the section on population dynamics below, a female entering a population (or a female fertilized by a migrant male) in the middle or late part of the flight season is much less likely to lay eggs that will make a genetic contribution to the population than is a resident female. Furthermore there is some evidence that the probability of migration increases with age (*7*) and decreases with abundance (*8*). Therefore, gene flow among even large, closely adjacent populations, separated only by "intrinsic" barriers to movement, would appear to be minimal. These observations led to the prediction (*7, 8*) that there would be considerable genetic differentiation among the Jasper Ridge populations, especially in view of slight differences in flight times and nectar sources and greater differences in both slope of the terrain and the dynamics of the populations.

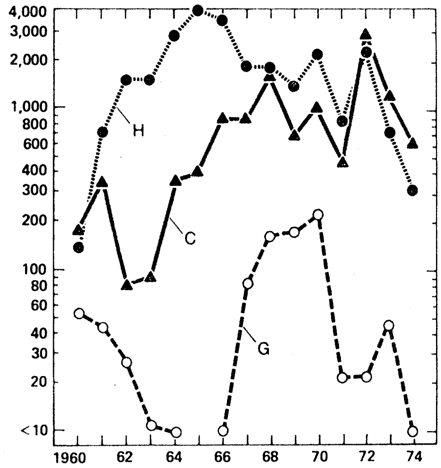

Fig. 1. Sizes of the three *Euphydryas editha* populations (*H*, *C*, and *G*) on Jasper Ridge, 1960 to 1974.

Besides the restriction of movement among populations C, G, and H on Jasper Ridge, it was early observed that the microdistribution of the adult butterflies differed from year to year. Each year, not all of the area that contained *P. erecta* and appeared to be suitable for the larvae was occupied (*7*). On Jasper Ridge, *P. erecta* grows both on serpentine soil and on soil derived from sandstone; adult butterflies, however, are restricted to locations on the Ridge where *P. erecta* grows on serpentine soil. This puzzling behavior is now, as we shall see, fairly well understood. Transfer experiments also indicated that adults transported into an area already occupied by *E. editha* showed no more tendency to leave than did those captured and released in the same area. If, however, individuals were moved to unsuitable areas they readily crossed "barriers" and were able to locate suitable areas with a frequency that made random search unlikely (*9*).

Population Dynamics of the Jasper Ridge Colony

The immediate discovery that one Jasper Ridge "population" was actually three populations permitted us to estimate size changes in C, G, and H independently. Estimates for the first 15 years of the study are illustrated in Fig. 1. Several different capture-recapture techniques were used in making the estimates (*10*).

Figure 1 indicates that the three populations have varied in size relatively independently. For instance, in the early 1960's population H exploded to several thousand while population C remained below 500 and G underwent extinction (only one male was seen in 1964). It was suspected from the beginning that adult mortality played very little role in determining population size. Predators and adverse weather seemed to have little impact on the adult population, and a single female was found capable of laying as many as 1200 eggs (*11*), the bulk of them at the start of the flight season.

As a partial test of the hypothesis that patterns of adult mortality were not major determinants of abundance, heavy predation pressure was artificially applied to the colony in 1964 and 1965 (*12*). This did not result in any significant decrease in the sizes of the populations in 1965 and 1966. One problem with these experiments, however, was our inability to remove more than an estimated 5 to 25 percent of the females in the population. Nevertheless, we believe that even this represents a substantial increase in premature adult mortality.

These experiments, capture-recapture data, and observations have satisfied us that adult mortality was not a major factor in the dynamics of the Jasper Ridge colony. We thus turned in the mid-1960's to a consideration of the larval biology. Since macroclimatic conditions are more or less the same for all three populations it seemed unlikely that they could account for the observed incongruity of the dynamics of the three populations. Availability of the foodplant *P. erecta* did not appear to be a limiting factor, since it was abundant in all areas, while the larvae (especially young larvae) were very difficult to find.

Our attention was thus focused on two factors: parasitism and microclimate. We found three different parasitoids infecting the Jasper Ridge colony, but these caused only low to moderate mortality rates (3 to 24 percent), and this mortality varied in a pattern which made it highly unlikely that it was a major factor in determining the size of the *E. editha* populations.

If parasitism were not the key to the dynamics of the Jasper Ridge populations, could it be microclimate? One of the persistent puzzles of the biology of these populations was the incongruity of the distributions of the butterflies and of *P. erecta*. Because no biochemical differences were detected between *P. erecta* growing on serpentine soil and *P. erecta* growing on sandstone-derived soil, it had been hypothesized (*13*) that *E. editha* was restricted to serpentine soil on Jasper Ridge because it provided a more favorable environment for larval diapause.

The work of Singer (*14*) on the larval biology of the butterfly showed this hypothesis to be completely erroneous. Careful study showed that young larvae suffered heavy mortality from starvation because of the senescence of the annual plantain. Indeed, mortality among prediapause larvae could be 90 percent or more. Larval survival occurred only in one or more of the following circumstances: (i) when the eggs were laid very early in the season on *P. erecta* which would remain green for five more weeks; (ii) when eggs were laid on *P. erecta* growing on soil tilled by pocket gophers, *Thomomys bottae*, because such plants had deeper root systems and remained green after most plants had senesced; or (iii) when the larvae were able to locate plants of the hemiparisitic annual, *Orthocarpus densiflorus* Benth. (Scrophulariaceae), on which they could feed and reach a satisfactory size for successful diapause.

The availability of *Orthocarpus* appears to be the critical factor in larval survival in the Jasper Ridge populations: good years for *Orthocarpus* are followed by years of large adult *E. editha* populations, bad years by small *E. editha* populations (Fig. 2). This explains the coincidence of the distributions of *E. editha* and serpentine soil, for on Jasper Ridge *O. densiflorus* is confined to serpentine soil.

The discovery of a critical secondary foodplant for *E. editha* highlights the pitfalls into which preconceptions can lead an investigator. Ehrlich "knew" from the literature, from watching oviposition behavior, from observations of the feeding behavior of postdiapause larvae, and from successful laboratory rearings, that the foodplant of *E. editha* was *P. erecta*, and this "knowledge" was conveyed to others working on the project. The idea of systematically searching for secondary foodplants simply did not occur to anyone in the group and it took Singer's detailed observations to uncover the key to the dynamics of the Jasper Ridge colony—that is, the prediapause larval survival of any given year is determined by the effects of microclimate on both the rate of senescence of *P. erecta* and the distribution and abundance of the alternative foodplant, *O. densiflorus*.

A second factor, availability of nectar sources, may also play an important role in the dynamics of Jasper Ridge *E. editha* populations under some circumstances. At least in population G in some years, a shortage of the principal adult resource, flowers of *Lomatium* spp., may result in dispersal of adults and depression of the population size in the next generation.

We have described the distribution of mortality for Jasper Ridge populations of *E. editha*, but the question of why the organism is programmed (we hypothesize genetically) to behave so as to produce the observed rather than some alternative distribution remains unexplained. Judged by the physiological capabilities of other *E. editha* populations, those on Jasper Ridge might have evolved one of a wide variety of evolutionary strategies. Singer's observation of high density–independent mortality resulting from foodplant senescence thus raises a series of questions. Why has *E. editha* not circumvented this mortality by evolving an ability to diapause successfully at a smaller size, thus shortening the prediapause growth period? If this is not possible, why do the females not lay larger eggs and give the newly hatched larvae a head start toward achieving the size at which diapause can occur? Or why do the females not fly earlier in the season? Our answers to these questions are, of course, partly speculative. It would seem that *E. editha* could have "chosen" any one of the following strategies:

1) A short postdiapause larval feeding period would result in smaller adults, capable of laying a small number of small eggs, the larvae of which would then have a longer time for prediapause feeding before senescence of food plants and thus lower prediapause mortality.

2) A long postdiapause larval feeding period would result in larger adults capable of (i) laying a few large eggs, the larvae of which would require a shorter prediapause growth period and would therefore suffer lower prediapause mortality, or (ii) laying many small eggs, the larvae of which would require a longer prediapause growth period and would therefore suffer higher prediapause mortality.

At Jasper Ridge, evolutionary choice of strategy (ii) has been made, there being a high mortality rate among many prediapause larvae. That this results in the highest probability of an individual successfully passing its genes on to the next generation must be presumed. Evidently, the production of fewer offspring that are capable of growing larger before food becomes unavailable has not been able to overbalance the advantage of the production of many offspring. If one considers the extremely high prediapause mortality, the shortening of postdiapause larval feeding time must exact a large price in potential egg productivity. Presumably, the rapid increase in air temperature and intensity of insolation during February means that much more growth is achieved during a day late in the

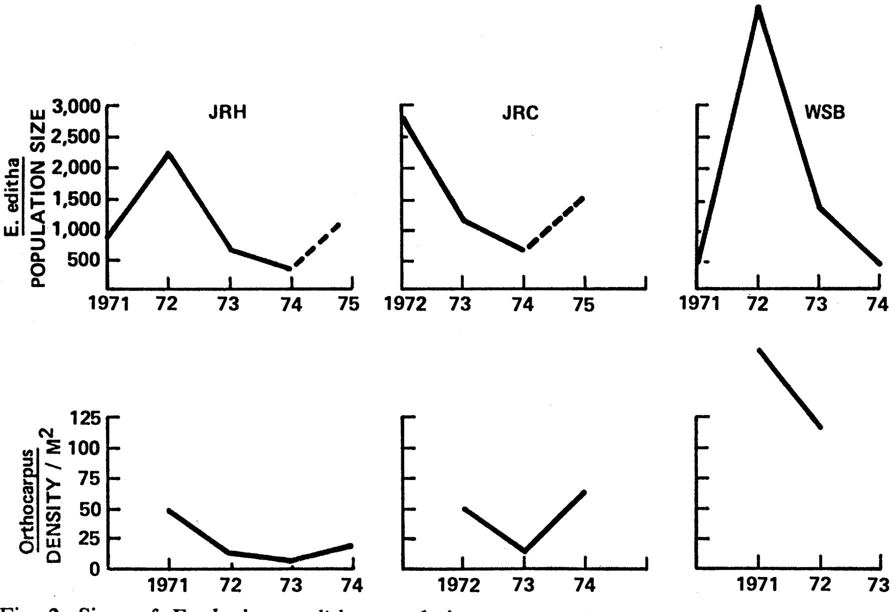

Fig. 2. Sizes of *Euphydryas editha* populations compared to density of the secondary larval foodplant, *Orthocarpus*, in the previous year. Solid lines connect sample points. Dashed lines indicate predictions (*JHR*, Jasper Ridge, population H; *JRC*, Jasper Ridge, population C; *WSB*, another *E. editha* population in San Mateo County, 6.4 km from Jasper Ridge).

month than during one early in the month—and it is late days that would be lost by early pupation.

Additional risks would probably accompany earlier emergence of females, including death from inclement weather and from mice or other predators attacking immobile adults on cold days. They might weigh in the calculus that leads *E. editha* at Jasper Ridge to expose many prediapause larvae to a situation where they have a low probability rather than exposing few larvae to a situation where they have a good chance of achieving adequate size for diapause.

Comparative Structure and Dynamics of Euphydryas Populations

As increased effort was put into investigations of the Jasper Ridge colony of *E. editha* we realized that even a complete understanding of its biology would not permit the induction of many generalities about the dynamics of butterfly populations, let alone insect or animal populations. Therefore, work was begun in the early 1960's on other butterfly populations only distantly related to *Euphydryas* and showing, at least superficially, very different population structure and dynamics (*15*). At the same time we began to expand our interest in *Euphydryas* to see if other populations included under the rubric *E. editha* were similar to the Jasper Ridge populations, and to investigate differences between populations of *E. editha* and of its often sympatric congener *E. chalcedona.*

It was quickly discovered that other *E. editha* populations were unlike those on Jasper Ridge both in structure (*8*) and in the factors controlling their dynamics. For instance, a population living in chaparral at Del Puerto Canyon, Stanislaus County, California (some 84 kilometers ESE of Jasper Ridge), presents an entirely different picture.

The primary plant used for oviposition is *Pedicularis densiflora* Benth. (Scrophulariaceae), with two other plants of the same family, *Castilleja affinis* H. and A. and *Castilleja foliolosa* H. and A., occasionally serving as secondary hosts. *Pedicularis densiflora* is present at Jasper Ridge, but we have never seen it used for oviposition or as a larval foodplant (*16*). Larvae in the Del Puerto population frequently defoliate patches of foodplant and die of starvation. Unlike at Jasper Ridge where density-dependent mortality has not been observed (theoretically nectar sources could be limiting at densities higher than we have seen), density-dependent mortality is very important at Del Puerto.

At Jasper Ridge there are normally abundant adult nectar resources encompassed within the area occupied by the larval foodplants. At Del Puerto this is not the case, and the adults in that population are relatively vagile, moving considerable distances between stands of nectar sources and sites where larval foodplants grow. Some 40 percent of recorded movements in this population are 250 m or more, while almost 70 percent of movements at Jasper Ridge are less than 50 m, and less than 5 percent are as much as 250 m. Further investigations have shown wide variation in biological characteristics among populations of *E. editha.* These characteristics are summarized in Table 1.

Investigations of *Euphydryas chalcedona*, which occurs sympatrically with *E. editha* throughout most of its range, indicate that these organisms generally have distinctly different strategies from those of *E. editha* in the same locality. For instance, only at Arroyo Bayou (where *E. editha* is relatively rare) do both species depend on the same primary foodplant; we have yet to discover the two species utilizing the same primary foodplant at a locality where both are abundant. At Jasper Ridge, Brown and Ehrlich (*17*) have shown that *E. chalcedona*, in addition to utilizing different foodplants (mainly *Diplacus aurantiacus* Jepson and *Scrophularia californica* Cham.; Scrophulariaceae) and flying later, has an entirely different population structure and behavior from *E. editha.* Its distribution is patchy throughout the chaparral where its foodplants grow and there is considerable movement among patches. The *E. chalcedona* colony on Jasper Ridge is not a series of isolated populations as is the *E. editha* colony, but approaches what may effectively be a single panmictic population. Dynamic changes in the *E. chalcedona* colony are synchronous across the ridge, pre-

Table 1. Ecological, behavioral, and phenotypical diversity among *Euphydryas editha*

Characteristic	Jasper Ridge	Del Puerto	Arroyo Bayou	Agua Fria
Location	San Mateo County	Stanislaus County	Santa Clara County	Mariposa County
Elevation (meters)	170	450	720	610
Habitat stability	Climactic	Climactic	Climactic	Riparian
Flight period	March–April	May–June	May–June	April–May
Primary oviposition plant	*Plantago erecta*	*Pedicularis densiflora*	*Pedicularis densiflora*	*Collinsia tinctoria*
Secondary food plants	*Orthocarpus*, necessary	Several, not very important	Not known	*Lonicera* is used by a few larvae
Availability of flowers for nectar	Very dense locally	Common along trails and gullies	Common, but not dense locally	Common, dense locally
Flight habits	Sedentary, 1 to 5 percent transfer 600 m between captures	Will move up to 1200 m for nectar when necessary	Not known	Short movements up and down stream
Population size	A few hundred to a few thousand	Over 1000	A few hundred at most	200 to 600
Population control factors	Early spring rainfall and density of edible foodplant in April and May	Intraspecific competition for food	Interspecific competition with *E. chalcedona* for food	Parasitoid mortality is 40 percent
Adult male forewing (mm)	22.5 ± 0.2	20.9 ± 0.2	21.6 ± 0.4	24.4 ± 0.1
Average egg weight (mg)	0.227 ± 0.005	0.229 ± 0.004	0.226 ± 0.006	0.251 ± .004
Average No. of eggs per mass (in field)	113.0* ($N = 55$ in laboratory)	52.3 ± 4.1	85.1 ± 12.6†	39.1 ± 4.8

* Standard error not available. † Laboratory data.

sumably reflecting a combination of macroclimatic effects on foodplants and the greater degree of vagility of the organisms.

Strategies of Euphydryas chalcedona versus Those of Euphydryas editha

The flight of *E. chalcedona* usually begins and continues later than that of *E. editha* at the same site, but can precede it, as it does at Del Puerto. The eggs of *E. chalcedona* are usually laid on perennials (*Castilleja, Diplacus, Penstemon, Scrophularia, Symphoricarpos, Pedicularis*) as opposed to the annuals (*Plantago, Collinsia*) often used by *E. editha*. Some populations make consistent use of composites as oviposition sites in addition to the primary scrophulariacious plant. The egg masses of *E. chalcedona* are always large (more than 100 eggs per mass), the eggs being heavier and more variable within a population than those of *E. editha*. Capture-recapture studies at Jasper Ridge and Del Puerto and observations at a number of other populations indicate that *E. chalcedona* populations are always as vagile as the most vagile *E. editha* population (that is, that of Del Puerto). Abundant throughout the chaparral areas of California, *E. chalcedona* rarely lives in grassland and occurs as scattered individuals and rare populations (such as Snyder Meadow in Douglas County, Nevada, and Echo Lake in El Dorado County, California) above 1600 m. While sharing many nectar sources with *E. editha, E. chalcedona* is most commonly found visiting *Eriodictyon* or *Aesculus*, which *E. editha* rarely uses. Some populations seem to be limited by larval starvation which results from lack of food in drier years (the Jasper Ridge, Del Puerto, and Lower Otay populations), but limiting factors of most populations remain undetermined. Parasitism has been ruled out, mortality due to parasitoids averaging about 6 percent in *E. chalcedona* ($N = 2134$) and almost 14 percent in *E. editha* ($N = 6202$).

In two high altitude locations studied (2700 m and 3200 m), *E. editha* larval foodplants (*Castilleja nana* Eastw. and *Penstemon heterodoxus* A. Gray) tend to be on flat or gently sloping areas, and those are also the densest part of the adult colony. Butterflies are also seen occasionally along ridge tops, where the foodplants are sparse. Individuals fly close to the ground and for only short distances (*18*). At the highest location where we have studied *E. chalcedona* (2300 m), the larval foodplant (*Penstemon newberryi* A. Gray) occurs on the flanks of a ridge. Adults are commonly found flying over the ridge top, and on nectar sources below and on the ridge top, generally following the rule that *E. chalcedona* is more vagile than *E. editha*.

Our investigations of a third *Euphydryas* species, *E. anicia*, are too preliminary to draw any firm conclusions. Above Cumberland Pass, Gunnison County, Colorado, at an altitude of almost 4000 m, both sexes were commonly taking nectar on ridges above the swales where the plant used for oviposition, *Besseya alpina* Rydberg, grows (*19*). Both sexes were also common in the areas where larval foodplants and nectar grew together, but were rare where the larval foodplants grew alone. This "hilltopping" behavior has been frequently observed in *E. anicia* in Colorado. Thus *E. anicia* at present appears to be more like *E. chalcedona* in population structure than *E. editha*, at least at high altitude.

Phenetics and Genetics

Unfortunately, *E. editha* does not thrive in the laboratory. Although it is possible to culture the species for several generations, larval mortality tends to be high, with many individuals never successfully breaking diapause. This fact, and a failure to find any obvious characteristics that were inherited in Mendelian fashion made genetic analysis difficult early in our investigations. We therefore turned to what we described as the "phenetics" (*20*) of the Jasper Ridge populations. Detailed measurements of various components of the color pattern and of wing length were made and examined for intercorrelations, asymmetry, differences between populations, and generation to generation changes in the populations through time (*20, 21*). We had expected that we would find phenetic differences between the Jasper Ridge C and H populations because of their different exposures, the

populations. All counties are in California except Benton, which is in Oregon.

Mud Creek	Ebbett's Pass	Sulfur Springs	Lower Otay
Butte County	Alpine County	Benton County	San Diego County
610	2730	150	180
Riparian	Climactic	Successional	Climactic
May–June	June–July	April–May	February–March
Collinsia tinctoria	*Castilleja nana*	*Plantago lanceolata*	*Plantago insularis; P. hookeriana*
Several, often necessary	Postdiapause larvae use *Penstemon heterodoxus*	None known	None in most years
Dense locally	Dense locally	Not dense	Very sparse to common, depending on rainfall that year
Some movement	Very sedentary	Not known	Long movements in drier years, shorter movements in better years
Over 1000 most years	A few hundred	A few hundred at most	1000 to many thousands
May and June rainfall suspected; density of edible foodplants; some intraspecific competition	Combination of predation, parasitism, and intraspecific competition for food	Not known	Winter rainfall, especially late winter; density of edible plants; significant competition
22.7 ± 0.2	18.2 ± 0.8	20.7 ± 0.1	19.7 ± 0.1 to 21.1 ± 0.2 mm, depending on food supply
0.209 ± .006	0.231 ± .006	0.277 ± .005	0.181 ± .005 mg
17.9 ± 1.6	14.9 ± 1.5	70* ($N = 39$, in laboratory)	39.2 (minimum figure)

great differences in the dynamics of the two populations, and the low level of gene flow between them. Contrary to our expectations, however, little evidence was found of phenetic or genetic differentiation among the populations in characters where high heritability within populations was indicated. Largely concordant changes in populations C and H in a number of pattern characters affecting lightness of wing color were observed. It is tempting to speculate that these pattern changes were caused by strong, fluctuating natural selection, but the possibility that they might be caused by a complex penetrance system cannot be excluded.

This approach to the genetic questions was time consuming and produced results that were difficult to interpret. We were therefore delighted when the now classic work of Lewontin and Hubby (*22*) brought to our attention the possibility that gel electrophoresis would allow us to sample a number of loci in our populations and follow directly any changes in gene frequencies.

Considerable difficulty was experienced in finding electrophoresis systems that would give satisfactory results with our material, but eventually we were able to evaluate allozyme variation at eight polymorphic loci. In 1973 we surveyed 21 populations of *E. editha* and 10 populations of *E. chalcedona* (*23*). Our results showed that the amount of genetic variability in these butterflies is quite similar to that recently demonstrated in other animal populations of diverse groups (*24*).

One of our findings confirmed the results we obtained, but did not expect, in the phenetic analyses: we could detect little genetic differentiation between the Jasper Ridge C and H populations. Nei's (*25*) index of genetic diversity was .009 for the difference between them. Only one locus, Bdh (β-hydroxybutyric acid dehydrogenase), showed significantly different gene frequencies. This difference persisted in 1974 (*23*).

The overall pattern of variation in gene frequencies was in many ways inconsistent with the hypothesis that allozyme variation is selectively neutral. Gene frequencies at some loci in various isolated *E. editha* populations were more similar than would be expected if drift alone were operating. At other loci there were great divergences, in some cases correlated with obvious environmental factors. In addition, the amounts of heterozygosity and the number of alleles at a locus were correlated more strongly than would be expected under the neutralist hypothesis (*26*).

It has been assumed from the beginning of this work that knowledge of patterns of gene flow among the populations studied is critical to an interpretation of patterns of genetic variation. Fortunately, because of extensive capture-recapture work (*4, 7, 9, 18, 23*) we can estimate levels of gene flow among *Euphydryas* populations with considerable assurance. Between most pairs of *E. editha* populations $4\ Nm$ (*27*) is estimated to be less than 0.1, but there is one pair, populations C and H of Jasper Ridge, between which it is much greater. Between this pair $4\ Nm$ averages about 120 (m being 3 percent, N averaging about 1000). We initially thought that this level of gene flow would be low enough to insure that genetic differentiation between populations C and H would occur. Theoretical work (*28*) suggests, however, that such a level of gene flow will prevent differentiation if only drift is occurring (although there could be differentiation with relatively weak selection). In spite of a level of gene flow sufficient to counteract the effects of drift, differentiation between the C and H populations occurred at one locus. On the other hand, many populations show great genetic similarity even though spatial, temporal, and ecological factors have been found to prevent significant gene flow among them. Thus our data support the generalization (*29*) that differentiation will occur in the presence of gene flow or will not occur in its absence depending on the selective regime.

Variation in the *E. editha* adult phenotype supports this view. Some populations are ecologically different, geographically close, and similar in appearance or very different in appearance. Equally geographically distant but ecologically similar populations may have similar phenotypes. It is interesting that pupal and larval phenotypes vary independently of each other, and of the adult phenotype (*30*).

What Have We Learned?

A number of points of broad interest have emerged from this work:

1) Any discussion of modes of population "regulation" must be based on census data from populations whose limits have been clearly established. Data on, say, the abundance of rice-boring moths gathered by hanging light traps over valleys are worse than useless. The captures may be an index of the size of one population or the average size of 100 populations, and thus may give a totally fallacious impression of the dynamics of the populations. Failure to discriminate the three Jasper Ridge populations of *E. editha* would have meant that independent fluctuations in population size and two population extinctions would not have been detected. The entire picture of the dynamics of the colony would have been biased toward stability.

2) Care must be taken not to equate immigration of genetically distinct individuals with gene flow. A careful evaluation is necessary to determine the probability of reproductive success of immigrants relative to that of natives. Mechanisms that limit multiple matings, or late movement and developmental periods tightly tied to seasonal events, will militate against effective gene flow.

3) The ecology of populations within a taxonomic species may show greater differences than that of two populations in different taxonomic species. For instance, the structure and dynamics as well as the foodplants of the *E. chalcedona* population on Jasper Ridge are more similar to the *E. editha* population at Del Puerto Canyon than either is to the *E. editha* populations on Jasper Ridge. In spite of this, there is no question that both the phenetic and phyletic relationships are properly reflected in the species assignments. As has been pointed out elsewhere (*29*), partly on the basis of the work on *Euphydryas*, "species" are not normally evolutionary units. It is clear that in many cases they are not ecological units either (*31*).

4) Populations of the same species may show patterns of changes in size that are either largely density-dependent or largely density-independent. Indeed, in the same population, density-dependent mortality may predominate in one generation and density-independent in the next.

5) Populations may be completely isolated from one another and yet show very little phenetic or genetic differentiation, while maintaining abundant within-population variation (*32*).

What Must We Learn?

Some of the major questions which interested us at the start of this research remain unanswered. We do not, for instance, know how the genetics and dynamics of the populations interact. What will happen to allozyme variability as population size changes? We are now, however, in a position to seek an answer to that question; indeed, our second annual set of samples is now being assayed as part of a program which will follow gene frequencies at eight loci and size changes in a small number of *E. editha* and *E. chalcedona* populations. We will therefore at least be able to examine the behavior of a small sample of the genotype as population size changes. We are also measuring wing characters again, to see if phenetic variability is correlated with genetic variability.

More difficult questions are posed by our results and those of workers on other organisms. What selective forces are responsible for observed trends in gene frequency? Is the sample of loci we are studying in any sense a random sample? How can we determine what pressures are acting on the remainder of the genotype? These questions are related to questions of the "integration" of genotypes and "choice" of evolutionary strategies—questions among the most difficult facing population biologists today.

Related Projects

In evaluating the usefulness of detailed, long-term studies such as our investigations of *Euphydryas*, it is important to consider other work that was stimulated by the main line of investigation. In this case, such "spin-offs" have been numerous. Labine's discovery of the "plugging" mechanism in *E. editha* has led our group into broad investigations of reproductive strategies in butterflies, and we are only now beginning to obtain significant results. Studies of foodplant preferences in this butterfly have also provided the bases for speculations on the nature of evolutionary change in foodplant preferences in oligophagous insects (*16*).

A question about the use of both Plantaginaceae and Scrophulariaceae as foodplants led to a project with P. H. Raven in which the entire pattern of foodplant utilization by butterflies was examined. It quickly became apparent that the butterflies and their larval foodplants were involved in reciprocal evolutionary interactions for which the term "coevolution" was coined (*33*). Abundant circumstantial evidence indicated that plant secondary compounds played a key role in this coevolutionary interaction as defense mechanisms for the plants. A decade ago this notion was controversial, as was the idea that herbivore populations place heavy selection pressures on plant populations and could limit their distributions (*31, 34*). This controversy stimulated our group to put part of its efforts into detailed investigations of butterfly-plant interactions (*16, 35–37*) which, along with the work of Janzen (*38*), Feeny (*39*), Whittaker and Feeny (*40*), and others, has tended to confirm the role of secondary compounds and the high impact of herbivores on plants.

The whole emerging field of plant-herbivore coevolution has, of course, enormous potential for uncovering better ways of protecting crops from pests than broadcast use of pesticides. Indeed, recent work (*36*) indicates that the successful biochemical strategies of wild plants are exactly the opposite of the unsuccessful agricultural strategies of *Homo sapiens*. And this is not the only area in which results of research tracing back to the long-term *Euphydryas* project may be of significance to current human problems. Studies of the population structure of the tropical butterfly *Heliconius ethilla* (*37*) have reinforced the idea that rather large areas of forest must be preserved if a decay of species diversity of invertebrates is to be avoided. Like various tropical bees, the *Heliconius* "trapline" (make regular circuits visiting scattered plants) in order to obtain pollen that provides necessary amino acids (*41*), and approximately 1 square kilometer of forest is required to support a population.

Conclusion

We have found that long-term studies that are basically autecological in approach have led both to rather broad conclusions about the characteristics of animal populations and to a necessary involvement in quite complicated questions about community ecology. The generality of our conclusions can only be tested by providing more sample points in the universe of animal diversity—that is, by similar long-term, in-depth studies of the population biology of carefully selected organisms.

With time running short as extinction threatens many natural populations, and with money running short as scientists discover that the public does not intend to provide them with unlimited support, population biologists can ill afford the shotgun approach to gathering field data which has dominated so far. We question the usefulness of gathering, grinding, and electrophoresing samples of random organisms from populations of unknown dimensions and poorly understood ecology. And, conversely, we hope ecologists will focus more of their attention on fewer organisms, especially on those (such as *Drosophila*) for which there is already a backlog of genetic data.

Similar focusing of attention should improve the harvest of ideas in community ecology. There has been a cheering explosion of theory in this area in the past 15 years or so, but often the detailed information required to test the theory is not available. For instance, many aspects of niche theory need testing in groups other than birds and lizards. Some obvious vertebrate groups that are beginning to acquire the characteristics of good "sample points" are reef fishes and cichlids (*42*) as well as various groups of mammals. In the invertebrates, butterflies (of course) and perhaps orthopterans and land snails come to mind. We may well find that entirely different bodies of theory will be required to explain community structure in such organisms.

We find it sad that even today much field work is done in almost total isolation from theory (and we do not mean only mathematical theory) and as a result adds little to man's understanding of nature. We hope, however, that this era is ending.

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Putting a Face Together

Chimpanzees and children reconstruct and transform disassembled figures.

David Premack

Chimpanzees do not, so far as is known, construct copies of existing or imaginary figures by any device—drawing, assembling pieces of existing material, or otherwise. In this apparent failure to reproduce or transform parts of the visual world, the ape differs from man no less profoundly than it does in the case of language. Man is never found without reproduction or transformation of his visual world, any more than he is found without language. He decorates his body; draws on walls, in the sand, and elsewhere; throws pots; carves and sculpts statuary; marks tools and other surfaces with calendric inscriptions or other possible forms of protowriting (*1*).

Attempting to account for the ape's lack of visual production revives all of the questions raised by its lack of language. Is the deficiency motor, cognitive, motivational, or some combination of the three? To address these questions I devised a form of visual production which reduced motor demands to a minimum. Then an inability to draw or otherwise fashion visual products would not obscure a possible mental capacity for such tasks. A similar approach in language, eliminating the burden of speech sounds through the use of hand signs or plastic words, revealed an unsuspected linguistic capacity (*2*). Moreover, if evidence of the cognitive factor should be found later on, it could be profitable to return to the motor factor and study rather than simply discard it. But to start with I put the emphasis elsewhere, even as I have bypassed the phonological problem for the time being rather than study it.

An example of the simple visual device used is shown in Fig. 1. An enlarged photograph of a chimpanzee's head (Peony's), with the face blanked out, was mounted on stiff material. The eyes, nose, and mouth were cut out from another identical photograph. Since the pieces did not interlock as in a jigsaw puzzle, placement of an individual piece could not be guided by its conformity to the other pieces. Each piece was mounted on stiff material and was large enough to be easily handled by the chimpanzee. Two sets of facial elements were used, one that preserved normal size relations (Fig. 1, top) and another in which all elements were of the same size (Fig. 1, bottom) (*3*).

The subject's task, deliberately made as simple as possible, was to use all four pieces at least once. The blanked-out face was placed before the subject with the four facial pieces in a scattered arrangement alongside the puzzle, some pieces right side up, others with their blank or white side showing. Once the animal completed the task, it was praised by being told, for example, "That's good, Peony," or the equivalent in an affectionate tone, and given a piece of fruit. At the end of each trial the trainer traced the subject's construction on a translucent grid, removed the pieces from the board, and,

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