Conservation Lessons from Long-Term Studies of Checkerspot Butterflies

PAUL R. EHRLICH*
Center for Conservation Biology
Department of Biological Sciences
Stanford University
Stanford, California 94305

DENNIS D. MURPHY
Center for Conservation Biology
Department of Biological Sciences
Stanford University
Stanford, California 94305

Abstract: *Long-term studies of checkerspot butterflies (*Euphydryas *spp.) are used to draw conservation lessons with implications for the design and management of reserves for invertebrates. We discuss;*

1. *The importance of determining the structure of and patterns of mating within demographic units.*
2. *The lack of congruence between migration and gene flow.*
3. *The crucial role of habitat diversity in the protection of species which otherwise require only small areas of habitat.*
4. *The importance of identifying and preserving "reservoir" populations within metapopulations.*
5. *The necessity of identifying subtle habitat requirements.*
6. *The key role of environmental stochasticity in the extinction of small populations.*
7. *The difficulty of protecting metapopulations and of introducing populations into "empty" habitat patches.*

We conclude, among other things, that the size of reserves required to preserve herbivorous insects is often underestimated; that a "minimum viable metapopulation" approach to their conservation may be needed; that long-term studies of the biology of populations of sample invertebrate groups would greatly aid conservation biologists; and that more effort is needed to inform the public and decision makers about the need to conserve populations *as well as species.*

**Correspondence and requests for reprints should be addressed to this author.*

Paper submitted 1/5/87; revised manuscript accepted 4/7/87.

Resumen: *Se discuten las implicaciones que los estudios sobre las mariposas del género* Euphydryas *tienen para el diseño y manejo de reservas para invertebrados. Se desarrollan los siguientes temas:*

1. *La importancia que tiene el determinar la estructura y los patrones de apareamiento dentro de las unidades demográficas.*
2. *La falta de congruencia entre la migración y el intercambio de genes.*
3. *La importancia de la diversidad de hábitat en la protección de aquellas especies que requieren áreas pequeñas.*
4. *La importancia de identificar y proteger "reservas" de poblaciones dentro de metapoblaciones.*
5. *La necesidad de identificar aquellas características sutiles del hábitat que requiere la especie.*
6. *La importancia que tienen los eventos estocásticos del medio ambiente en la extinción de las poblaciones pequeñas.*
7. *La dificultad para proteger metapoblaciones y para introducir poblaciones en fragmentos de hábitat "vacíos" ("empty" habitat patches).*

Concluímos, entre otras cosas, que es común el subestimar el tamaño de las reservas necesario para la sobrevivencia de las poblaciones de insectos herbivoros; que se necesita enfocar la conservación de estos insectos desde un punto de vista de "metapoblación mínima viable"; que estudios a largo plazo de la biología de poblaciones de grupos de invertebrados selectos serán de mucho valor para los biólogos; y que es necesario informar al público y a las personas que toman decisiones en el campo de la conservación sobre la necesidad de conservar poblaciones *y especies.*

Introduction

Field research in population biology tends to be short in duration and narrow in geographic scope. This situation presents a major impediment to the application of basic research to problems confronting conservation biologists, since conservation biology is by definition concerned with the maintenance of populations and species over the long term. "Snapshots" of the histories of single populations over brief periods repeatedly have proven to give at best a partial, and at worst an erroneous, impression of the factors controlling the distribution and abundance of plants and animals.

One of the few long-term studies of a suite of invertebrate species over a substantial portion of their ranges has been carried out on checkerspot butterflies (genus *Euphydryas*). The ecology and population genetics of checkerspot butterflies in the western United States have been under intensive study for the past 27 years (e.g., Ehrlich 1961, 1965; Singer 1971; Ehrlich et al. 1975; Singer & Ehrlich 1979; Brown & Ehrlich 1980; Singer 1982; Murphy et al. 1983, 1984, 1986; Murphy 1984; Brussard et al. 1985). Here we summarize some of that work, highlighting findings of particular importance to conservation biology, including the design and management of nature reserves. Our findings should give particular insight into the conservation biology of herbivorous insects.

Population Biology

Physical Environment and Population Structure

1. *An important lesson for conservation biology from the earliest studies of* Euphydryas *is that the movement of individuals between habitat patches or reserves does not necessarily mean that gene flow is occurring. It also does not mean that, in case of extinction, recolonization of one patch by individuals from the other will occur readily.*

The most extensively studied colony of *Euphydryas* is that of *E. editha* on Stanford University's Jasper Ridge Biological Preserve. There the butterflies occupy an island of serpentine-based grassland approximately 9 hectares in extent, surrounded by chaparral and sandstone-based grassland. Despite essentially continuous habitat, uninterrupted by barriers to the butterfly's flight (Ehrlich 1961), the colony was found to consist of three separate demographic units—populations sufficiently isolated to have independent dynamics, though not necessarily enough to be independent genetic units. In each season, fewer than 5 percent of the individuals marked in one demographic unit were recaptured in another, so migration between extant units did not dramatically influence their dynamics. Nonetheless, this consistent finding suggests that *E. editha* exists as "metapopulations"; that is, populations subdivided into groups that occupy clusters of habitat patches and interact extensively.

Furthermore, because of the combination of late-season timing of migration and the reproductive strategy of the butterflies, individual movements are clearly much more frequent than the movement of genes. Males "plug" females after they inseminate them, effectively preventing another insemination for a week or more (Labine 1964). Most females are mated and plugged within hours of eclosion, so that after the first week of the female flight period an immigrant male has a comparatively small chance of being able to inseminate females. Later, when females become receptive to second inseminations, the probability of offspring survival becomes very small because of time constraints on larval development *(discussed below)*. These same constraints make it unlikely that any but the earliest migrant females will make a genetic contribution to the recipient population, or serve as effective founders.

2. *Understanding the scale and structure of populations is crucial to designing and managing reserves.*

The dynamic histories of the three demographic units on Jasper Ridge, in areas C, G, and H (Ehrlich 1965), have been documented since 1960 (Fig. 1). Note that Jasper Ridge area G went extinct in 1964, was re-established in 1966, and then went extinct again in 1974. If the mark–recapture studies had addressed the entire grassland as a single area, and the butterflies had been considered as a single demographic unit (solid line in Fig. 1), the extinction events would have been overlooked, and the safety of the Jasper Ridge population from stochastic extinctions of its component demographic units would have been overestimated.

3. *Understanding the patterns of mating within demographic units is also required if conservation efforts are to succeed, because those patterns may change with density.*

We have found population structure in some locations other than Jasper Ridge to be much looser (demographic units much less well defined), and this structure is reflected in the genetics of the populations. Spatial autocorrelation of allele frequencies in Great Basin populations, for example, suggests that discrete demographic units may occupy habitat areas of dozens of square kilometers and individuals may move much greater distances (Wright et al. 1987). Yet, even in more or less continuous habitat, special physical features may be crucial to population structure. In Colorado, where diffuse demographic units of *Euphydryas editha* occupy many square kilometers of montane sagebrush communities, hilltops appear to constitute important rendezvous points at which males aggregate when population densities are low and to which females travel to seek mates (Ehrlich & Wheye 1986).

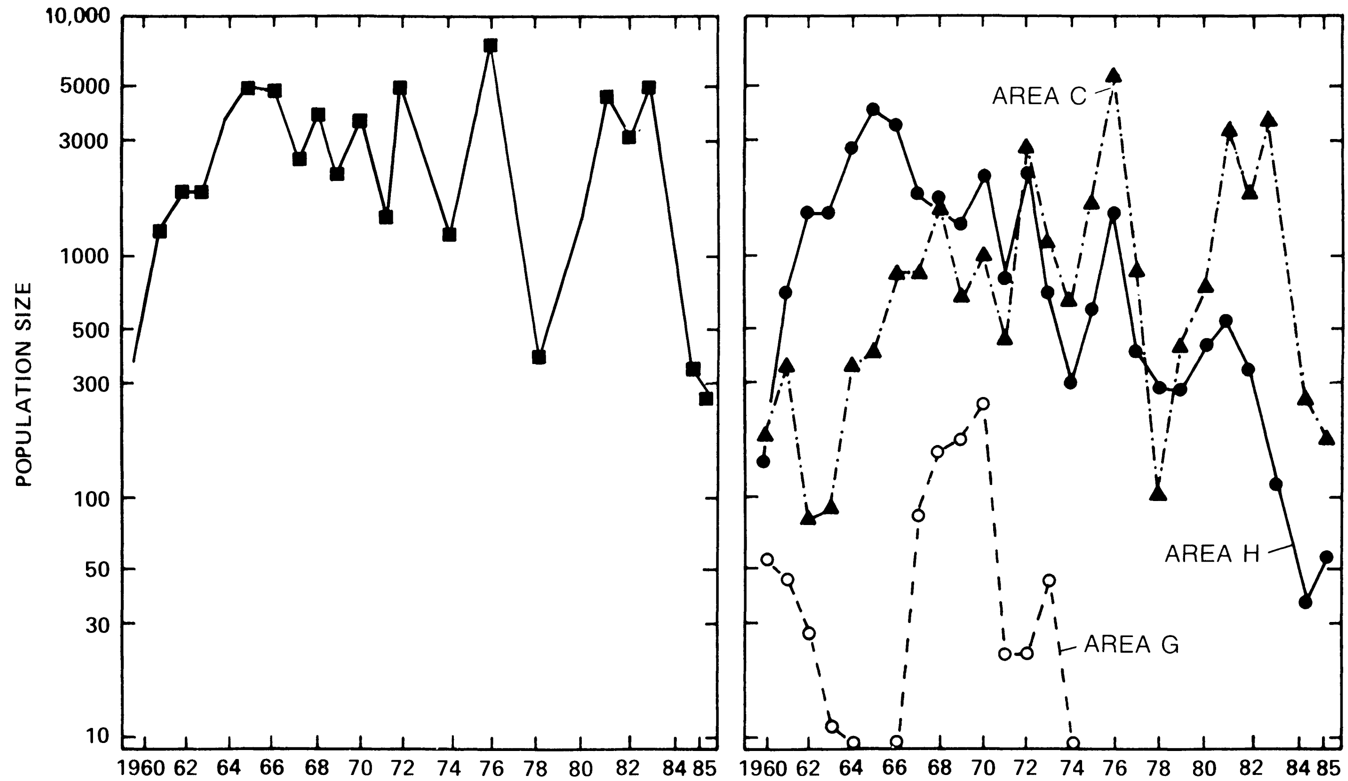

Figure 1. Jasper Ridge population size changes had the separate demographic units not been identified (left). Population size changes of the demographic units in Jasper Ridge areas C, G, and H (right). Note extinction and recolonization events in area G.

At low population densities, such mating aggregations may play a crucial role in keeping a population viable. At high densities, however, males that move to hilltops may have relatively small chances of mating (Ehrlich & Wheye 1986). Thus, while such an environmental feature may seem unimportant if the study of a demographic unit was done in a year of abundance, its inclusion may prove critical if a reserve is sliced out of continuous habitat.

4. *Topographic heterogeneity or other aspects of habitat diversity may be key determinants of the habitat suitability of an area for the maintenance of populations of many insect herbivores that otherwise require only small areas of habitat.*

Topography is a crucial consideration in the conservation biology of threatened populations of *Euphydryas editha bayensis* in the San Francisco Bay area of California, the ecotype represented at Jasper Ridge. For more than a century, the ecotype has been confined to patches of serpentine-based grassland. Earlier it may have been much more widespread, but lack of knowledge of the California grassland flora before the introduction of now virtually ubiquitous Eurasian weeds makes reconstruction of prior distributions impossible. For the last century, areas of suitable habitat have been declining in the face of development, and populations in those serpentine habitats that remain are often subject to extinction as a result of climatic events such as the California drought of the mid-1970s (Ehrlich et al. 1980) and the "El Nino" weather of 1982–1983 (Dobkin et al. 1987).

The sizes of populations of the Bay Area ecotype are controlled in a density-independent fashion. Eggs are laid in the spring, and upon hatching, larvae are immediately in a race to reach the size at which they can enter an obligatory diapause in which they pass the summer dry season of California's Mediterranean climate. The larvae lose this race if they cannot grow large enough before their annual food plants senesce. There is a complex phase relationship in the timing of the insect's developmental cycle and that of the plant (Singer 1972, Singer & Ehrlich 1979). This relationship is mediated by the macroclimate interacting with the microclimate, and the latter varies significantly with slope and exposure (Dobkin et al. 1987).

The remaining patches of serpentine habitat most suitable for the long-term maintenance of populations are the largest and most topographically diverse. A large area of habitat alone is clearly not sufficient to guarantee the persistence of checkerspots. Extinctions have been observed in large habitats that lack topographic heterogeneity. The Coyote Reservoir population, the most densely populated of known Bay Area colonies in 1971, was extinct by 1976. The Coyote Reservoir site consists almost entirely of an east-facing slope. Topographic heterogeneity allows some areas within a serpentine patch to have a favorable microclimate for larval development in any weather regime; north-facing slopes will be favored in most years, while south-facing slopes contribute to population increases in wet years. High survival rates on south-facing slopes in wet years appear to push population numbers high enough in topographically diverse locations to allow demographic units to survive substantial declines during inevitable drought years.

5. *If conservation options are limited, top priority should be given to identifying and preserving reservoir populations, if any.*

The overall pattern in the San Francisco Bay area appears to be one in which just one population south of the bay (Morgan Hill, Santa Clara County) is large enough (Fig. 2) and stable enough to act as a "reservoir population" of *E. editha bayensis* (Fig. 3). A reservoir population may be defined as a demographic unit which can be expected to persist through essentially all natural environmental perturbations. A reservoir population is one that can act as a relatively permanent source of colonists to habitats that cannot permanently maintain what might be called "satellite" populations. We suggest that since all demographic units will eventually become extinct, that the terms "reservoir population" and "satellite population" only be used where it is estimated that the former will persist at least 10 times as long as the latter.

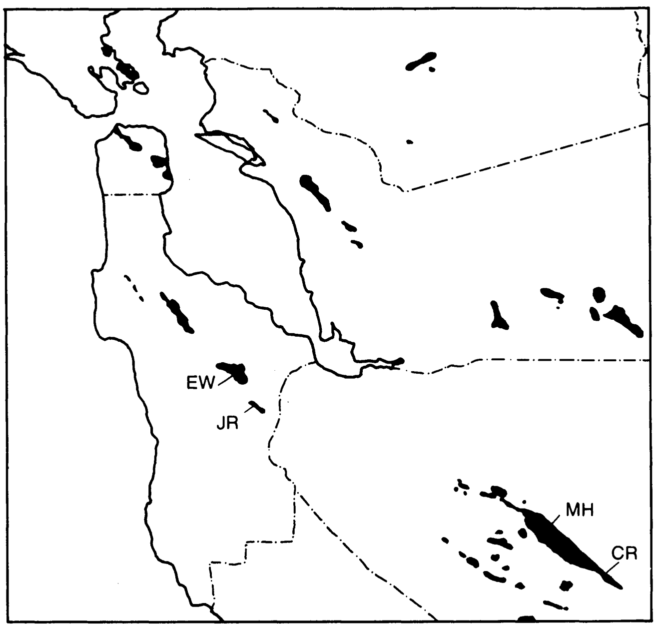

Figure 2. Distribution of San Francisco Bay Area serpentine soils, including grassland habitats of Euphydryas editha. *EW = Edgewood Park (part of the San Mateo-Woodside grassland system), JR = Jasper Ridge, CR = Coyote Reservoir, and MH = Morgan Hill.*

The extensive San Mateo-Woodside system of serpentine-based grasslands has been severely fragmented, and only at Edgewood Park is the remnant habitat greater than 10 ha in extent. The ability of the population there to function as a reservoir is doubtful, as it has undergone dramatic population fluctuations itself ($>10^5$ individuals in 1981 to $<10^2$ in 1985). All other sites, including Jasper Ridge Reserve, are too small for truly long-term maintenance of the butterfly's populations through extended drought. It seems likely that if the California drought had continued for another year, all three demographic units in the reserve might have become extinct. Indeed, weather conditions seem not to have been optimal since 1981, and neither the Jasper Ridge area C nor area H population has been able to rebuild to the high density levels of the early 1970s.

Resources and Population Dynamics

6. *Natural history investigations should be undertaken before a reserve is designed in an attempt to identify subtle habitat requirements that could potentially play key roles in the long-term survival of populations to be protected.*

Independent fluctuations in size of the demographic units on Jasper Ridge result, at least in part, from rather subtle differences in the means by which larvae survive to diapause each spring. In both populations, survival is greatest for eggs laid on north-facing slopes or other comparatively mesic areas by early emerging females from south-facing slopes. In the area H demographic unit, many survivors are larvae that wander from drying *Plantago* and locate the flowers of later-senescing *Orthocarpus densiflorus* on which the larvae feed to diapause. At nearby Edgewood Park, females often oviposit directly on *Orthocarpus* (Singer 1971). In contrast, many survivors to diapause in Jasper Ridge area C come from eggs laid on *Plantago* on soil tilled by gophers *(Thomomys),* where plants are large and exhibit delayed senescence—although *Orthocarpus* plays a role as a secondary food source in this area also.

While the primary resource determinants of habitat suitability clearly are oviposition and larval host plants, other resources may play crucial roles in population persistence and habitat suitability. The availability of nectar, for instance, is very important in maintaining egg production by females in the latter stages of reproduction. A paucity of middle- and late-season nectar has been implicated in the extinction of the Jasper Ridge area G population (Murphy et al. 1983). The presence of standing water has been shown to affect population structure

Figure 3. Newly emerged Euphydryas editha bayensis *female in the area H serpentine grassland of the Jasper Ridge Biological Preserve.*

in *Euphydryas* (Ehrlich & White 1980) and in *Chlosyne*, a genus closely related to *Euphydryas* (Schrier et al. 1976). Males travel relatively long distances to sip from moist earth around puddles, presumably to obtain sodium (Arms et al. 1974, Adler & Pearson 1982). The presence of both nectar and standing water, additionally, have been shown to be determinants of overall butterfly species numbers in Great Basin riparian communities (Murphy & Wilcox 1986).

7. *Under severe environmental conditions, the degree of oligophagy may be a crucial determinant of extinction proneness.*

We used mark–recapture studies and detailed statistical analysis in an attempt to identify adult population dynamic parameters that might be unique to particularly extinction-prone species. But, population studies of highly endangered *Euphydryas editha* and ubiquitous, unthreatened *Euphydryas chalcedona* on Jasper Ridge revealed few differences (Murphy et al. 1986). Indeed, both species appear to move freely within suitable habitat and exchange individuals at low rates with other colonies at distances of several kilometers or more.

Ease of recolonization well may be determined, however, primarily by patterns of resource use, rather than interspecific differences in vagility. The Bay Area ecotypes of *Euphydryas chalcedona* feed on perennial host plants and appear to accept a wide variety of hosts. *E. editha*, by contrast, feeds on annuals and exhibits narrower host tolerance. Furthermore, within the California range of *E. editha*, populations feeding on perennials (e.g., on *Pedicularis densiflora* in the inner coast ranges and on *Castilleja nana* in the alpine Sierra Nevada) have suffered fewer documented "natural" extinctions than those feeding on annuals (e.g., on *Plantago* and *Orthocarpus* in outer coast ranges and on *Collinsia tinctoria* in the Sierra foothills). These observations suggest that wide host tolerance and the incorporation of less ephemeral hosts into the larval diet may confer resistance to extinction.

Dispersal, Patch Dynamics, and Gene Flow

8. *Recolonization of empty patches may not occur in most years; many populations may be re-established in rare years of explosive dispersal.*

The need to monitor populations for many generations is underscored by our observation of populations of *Euphydryas editha* in southern California. Individuals in those populations exhibit rather sedentary behavior similar to Jasper Ridge butterflies. Dispersal in southern California populations increases, however, in particularly dry years when oviposition plants and adult nectar sources are sparse. Yet, in 1977, a year of substantial rainfall in southern California, the populations exploded in size, and adults dispersed en masse from population centers (Murphy & White 1984). These circumstances (not repeated since) allowed insight into the abiotic and biotic forces that can determine patterns of dispersal in the species.

Dry winters seem to result in increased vagility because larval host plants and adult nectar sources are sparse from the lack of precipitation and because postdiapause larvae defoliate a higher proportion of available host plants before adult females emerge to oviposit. When wet years precede dry years, defoliation is intensified in the dry years because larval populations are larger. Furthermore, consecutive years of adequate rainfall apparently result in butterfly population build-ups such that entire standing crops of host plants may be defoliated; massive postdiapause mortality of larvae then occurs and virtually all emerging adults disperse. Population size, dispersal, and the likelihood of local extinction, therefore, are determined by density-independent factors in most years, but by density-dependent factors in a very few years. These rare years, however, appear to be one of the keys to the natural recolonization of habitats unable to support populations over the long term. Thus not only may gene flow and recolonization potential be difficult to estimate from data on movement of individuals, but the amount of dispersal itself may vary dramatically from year to year.

Minimum Viable Population Size

9. *Environmental stochasticity, especially variation in host quantity, quality, and phenology, is the major cause of extinction, particularly in small populations.*

A general constancy has been found in allozyme frequencies and in average heterozygosity in California *Euphydryas* populations, despite wide fluctuations in population sizes and after local "bottlenecks" where N_e may have fallen well below 50. This suggests that deleterious genetic effects, such as inbreeding depression or loss of variation, may be relatively unimportant in the persistence of *Euphydryas* populations.

Although rates of dispersal from Jasper Ridge demographic units appear to be inversely correlated with population size (Gilbert & Singer 1973), recent observations in area H indicate that *E. editha* populations can persist for numerous generations at surprisingly small sizes. It appears that levels of dispersal in *Euphydryas* are complexly related both to population density itself, and to the abundance (or scarcity) of resources. The population in Jasper Ridge area H has been estimated to consist of less than 100 individuals for four consecutive years (in two of those years, N_e was certainly less than 10!). Thus, while the role of demographic stochasticity has not been determined and could be significant in certain circumstances, our present evidence indicates that small population size in and of itself will not ordinarily lead to population extinction. Small populations, of course, are particularly susceptible to extinction due to environmental events such as drought.

Even large populations are at risk, however, when drought reaches dramatic proportions (on the order of half "normal" rainfall), or if several less extreme drought years occur in succession. Such conditions are effectively "natural" catastrophes. Likewise, the major cause of anthropogenic extinction of *Euphydryas editha* populations has not been a gradual deterioration of local environments leading eventually to population extinctions, but rather a catastrophic loss of habitats. For example, in the San Francisco Bay area the paving over of patches of serpentine grassland has led to the endangerment of *E. editha bayensis.*

Management and Politics

10. *Habitat patches and metapopulations are difficult to protect.*

In the Outer Coast Ranges of central California, native grassland persists as remnant patches on serpentine and other highly weathered soils. Unique chemical characteristics, including high levels of magnesium, nickel, and chromium, and low levels of calcium, nitrogen, and phosphorus, appear to account for the resistance of serpentine soils to invasion by non-native grasses and forbs, and the resultant exclusion of many native plant species. The high degree of ecotypic differentiation and endemism in serpentine-based grassland communities make them an obvious target for conservation efforts, but they exist as dispersed small units, ranging from less than a hectare to a few thousand hectares in extent, with most less than 10 ha. If a continuous national park or other reserve of reasonable configuration was established that contained all the serpentine patches in the San Francisco Bay area, it would necessarily include the homes and businesses of millions of people.

Most of the native grassland remnants are privately owned, hence conservation efforts must follow one of two paths: acquisition of property, obviously an expensive proposition; or invocation of the Endangered Species Act. Unfortunately, the 1982 reauthorization of the Act largely removed protection from "take" for endangered and threatened plants. *Euphydryas editha bayensis* is, at present, the only animal restricted to the native grassland community that has been proposed for federal endangered species protection.

Two major problems exist in using this butterfly as a tool to protect serpentine-based grassland habitat. First, because some number of demographic units within the metapopulation are always extinct and their sites awaiting recolonization, the butterfly may not be present in many of the remnants with the highest plant diversity (Murphy & Ehrlich 1987). Since the Endangered Species Act focuses on protecting "species," temporarily vacant habitat patches have no legal protection. Second, invertebrates can be protected only if an entire described subspecies is threatened or endangered. An opponent to the listing of *Euphydryas editha bayensis* has challenged the validity of the traditional taxonomic treatment of the subspecies. As biologists well know, the subspecies is an arbitrary taxonomic category. This challenge, which promises to become a protracted battle, ultimately may compromise future attempts to protect infraspecific genetic diversity of invertebrates.

Finally, because small reserves in largely urban areas have neighbors, maintaining good relations with those neighbors may be critical to the integrity of the reserve. Jasper Ridge has an extremely active docent program, and docents lead carefully guided tours of the facility on which, among other things, the importance of *Euphydryas* work is explained. Tours were routed away from area H after it was discovered that, even with the most careful supervision, it was impossible to prevent trails from widening in response to increased foot traffic. The area around the preserve is suburban, and some homes share common boundaries with it. Educational programs, fencing, and patrolling at Jasper Ridge have generally been able to keep intrusion to a minimum in the past decade, but constant vigilance has been required, and in one case Stanford University has had to resort to extensive and expensive litigation to maintain the integrity of the preserve.

Simply finding the funds to establish small reserves to protect the elements of a metapopulation is only the first, and in many cases the easiest, step. Finding the additional funds and engaging the time of interested people to manage them are clearly major challenges. Furthermore, it has yet to be determined whether, even if the sites that can support the demographic units of a metapopulation (such as that of *E. e. bayensis*) can be preserved, the metapopulation itself can be protected. It may be, for example, that complete urbanization of intervening areas would so interfere with dispersal and recolonization that the entire system would collapse to extinction.

Thus, political problems often involve more than finding ways to protect reserves. Conservation biologists working with butterflies and other vagile organisms must always be concerned with land use patterns adjacent to reserves. They must work to make those areas more hospitable to organisms that disperse out of the protected area. Conservation biologists also must actively campaign for abatement threats such as acid precipitation and rapid anthropogenic climate change. No amount of careful management of reserves will prevent extinctions from such adverse conditions.

11. *The ease of maintaining a metapopulation or re-establishing extinct metapopulations by introducing insects into "empty" habitat is difficult to predict.*

It may be a long time before the success of a transplant experiment can be evaluated, even when a univoltine insect is involved. Re-establishment of demographic units known to have gone extinct and their establishment in "empty" habitats that seem suitable both appear to be possible management options for the conservation of *Euphydryas.* Two transplantation experiments have been carried out in connection with our studies of the allozyme genetics of *E. editha.* The failure of one transplant of 500 larvae to Agua Fria in the foothills of the California Sierra Nevada was due, at least in part, to human disturbance of a portion of the habitat. Another, to Arroyo Bayou in the Inner Coast Range of central California, again with 500 larval colonists, appears to have resulted in establishment of a demographic unit, although there are signs that natural immigration also played a part.

Our most interesting result with transplant experiments thus far have been achieved with another checkerspot species, *Euphydryas gillettii.* One of two attempts to transplant a colony for northwestern Wyoming to central Colorado was successful (Holdren & Ehrlich 1981). A population founded in 1977 with 83 egg masses (about 10^4 eggs) has persisted through the 1986 field season. Most important to conservation is that in nine generations the population has fluctuated in size, but has never exceeded 200 individuals, and has not spread from the immediate vicinity of the release, despite extensive adjacent and apparently suitable habitat (Ehrlich & Holdren, unpublished data). The population thus has never expanded to occupy a variety of sites and slopes and, therefore, may yet go extinct. Indeed, this underscores the difficulty of assessing habitat quality or suitability in general.

Unfortunately, population density constitutes the best bioassay of habitat quality. Furthermore, even if habitat is adequate to sustain a population for many ordinary years, the key to long-term habitat suitability is whether a habitat can support a population during extreme years (for *E. editha,* years of drought or deluge).

We are now embarking on a series of experiments to re-establish *E. editha bayensis* populations in isolated patches of habitat that we know previously supported demographic units, and in others that appear suitable but whose previous record of occupancy (or lack of it) is unknown. This work, which may involve as many as 70 patches, should greatly expand our understanding of the problems that managers will face in maintaining these and related organisms with similar "metapopulation dynamics." It is, however, already clear from work with

Euphydryas and with many other organisms (e.g., Ehrlich 1986, 1987) that simply introducing a group of colonists into entirely suitable habitat is no guarantee of establishment.

12. *Introduced mammalian herbivores may have complex impacts on endangered herbivorous insects.*

In the Bay Area, grassland habitat supporting high densities of *Euphydryas editha* host plants are early and intermediate successional stages leading to a stable climax community dominated by perennial bunchgrasses (Murphy & Ehrlich 1987). Native ruminant grazers (including the now extirpated tule elk and pronghorn antelope) undoubtedly played a role in creating successional habitat. In the absence of these species, domesticated livestock now affect the landscape physically and biologically and can alter profoundly the plant species composition, hence suitability of habitat for *Euphydryas editha*.

The physical presence of cattle directly affects the butterfly in its nonvagile stages. Mortality from being stepped on or buried under cow pats obviously can be significant, and is proportional to the density of cattle in a given area (White 1986). A more subtle effect of cattle is the physical alteration of the landscape from the action of hooves, including the terracing of steep slopes. Larvae are often found exclusively on cattle terraces on north-facing slopes in winter when the sun is low in the sky, sunlight is at a premium, and the terraces receive more isolation than the slopes.

The effect of cattle on the species composition of grasslands is more complicated. The physical action of hooves provides continual ground disturbance, which may or may not favor the butterfly's host plants. Selective grazing of introduced annual grasses reduces their ability to invade and outcompete the native flora, although native forbs and bunchgrasses are also consumed by cattle. Cattle droppings add concentrated nutrients that favor the establishment of introduced grasses in localized areas. The areas around salt licks and watering troughs can be almost completely dominated by introduced grasses. On both grazed and ungrazed sites, the butterfly host plants are interspersed with patches of introduced grasses. In ungrazed sites, invasion of introduced grasses appears to be facilitated by large gopher mounds. The dynamic balance of these processes is poorly understood.

13. *Endangered populations of insects may be "studied to death."*

In the course of the intensive study in 1981 in Jasper Ridge area H *(above),* it became apparent that roughly150–200 investigator hours spent collecting in an area of approximately 2.5 ha had a significant impact on the vegetation of the area. Although investigators took care always to wear tennis shoes (rather than cleated boots), some crushing of areas of herbage was obvious at the end of the experiment, although no long-term damage to the vegetation appears to have been done. We were concerned, however, that some pupae, egg masses, and larvae of the butterflies (which are close to the soil surface) may have been destroyed by trampling, which, in turn, could have serious consequences for the population. Sadly, research areas, especially those close to major centers, tend to be small and thus vulnerable to serious disturbance from research activities themselves and to interference between research projects. At the Jasper Ridge Preserve and the Rocky Mountain Biological Laboratory, the field stations we know best, both problems are causing growing concern among researchers and managers. Since it is questionable whether intensive mark–recapture experiments in such limited habitat areas can add to one's knowledge of the population (Murphy et al. 1986), it seems to us that managers should advocate instead the use of noncapture methods to estimate population sizes over the long-term.

Conclusions

What are the most important lessons for conservation biology to come out of the *Euphydryas* work? We think the first is that the size requirements of reserves designed to protect herbivorous insects may often be underestimated. Populations of such insects seem often to be subject primarily to density-independent population regulation, and thus their waiting time to extinction may be relatively short. A reserve that simply encompasses the location of a single demographic unit, even if it provides adequate marginal buffering and security from intrusion, may soon lose the organisms it was designed to protect. If such insects are to be conserved, in many if not most cases, a series of demographic units, selected for the diversity of their habitats, should be set aside. Where necessary, either corridors among the sites should be established or active management planned so that stochastic extinctions of demographic units can be followed by assured recolonizations.

In short, the "minimum viable population" sort of approach that many conservation biologists favor for vertebrate species, while risky enough for them, may not work at all for many invertebrates. Instead, concern there should be shifted toward "minimum viable metapopulations." This means that, in some cases, vertebrates or plants will prove inadequate as "umbrella species" for invertebrates. While the grizzly bear, because of its gigantic home range requirements, may protect many invertebrates, including checkerspot butterflies, in the Yellowstone ecosystem, preserving one patch of serpentine soil-based grassland for the last known population of the San Mateo Thornmint *(Acanthomintha obovata duttoni)* will do little to aid in the long-term maintenance of *Euphydryas editha bayensis.*

It is also clear that the level of effort that has gone into uncovering the details of *Euphydryas* biology cannot be expended on more than a minute fraction of potentially endangered invertebrate species—most of which, even in the temperate zones, have yet to be recognized as endangered. This leads to two conclusions. First, strategies for invertebrate conservation must be established on the basis of long-term studies of a few species or taxonomic groups chosen as representative. Second, in the absence of better information, conservative assumptions should be made about the long-term requirements of invertebrates. We probably should make a best guess about the habitat area required to preserve a species, and then at least double that area to reach a recommended minimum reserve size.

We cannot emphasize too strongly the importance of making studies of sample groups over the *long term*. We have, for example, drastically altered our original conclusions repeatedly after observing populations under different climatic regimes. Doing a long-term study also often allows time for observing the behavior of different ecotypes of the same species, which in the *Euphydryas* system led to drastic revisions of many early ideas about the biology of these organisms. Fortunately, the National Science Foundation is already aware of the need to conduct long-term studies (e.g., Callahan 1984), and conservation biologists in the United States should do all they can to encourage increased funding by Congress of the Foundation's program to support such research.

Finally, there is a great need for conservation biologists to emphasize the conservation of *populations* along with the conservation of species. We have seen here how the attrition of populations of *Euphydryas editha bayensis* has endangered the entire ecotype. A similar attrition, we believe, is gradually endangering many, if not most, other organisms. Focusing on the loss of species is focusing on the closing scene of what is ordinarily a long process. It leads to underestimates of the scale and severity of the current extinction crisis. When public statements are made on that crisis, the critical importance of the loss of populations should always be mentioned.

Literature Cited

Adler, P.E.; Pearson, D.L. Why do male butterflies visit mud puddles? *Can. J. Zool. 60*:322–325;1982.

Arms, K.; Feeney, P.; Lederhouse, R. Sodium: Stimulus for puddling behavior by tiger swallowtail butterflies *(Papilio glaucus). Science 185*:373–374;1974.

Brown, I.L.; Ehrlich, P.R. Population biology of the checkerspot butterfly *Euphydryas chalcedona*. Structure of the Jasper Ridge colony. *Oecologia 47*:239–251;1980.

Brussard, P.F; Ehrlich, P.R.; Murphy, D.D.; Wilcox, B.A.; Wright, J. Genetic distances and the taxonomy of checkerspot butterflies (Nymphalidae: Nymphalinae). *J. Kans. Ent. Soc. 58*:403–412;1985.

Callahan, J.T. Long term ecological research. *BioScience 34*:363–367;1984.

Dobkin, D.S.; Olivieri, I.; Ehrlich, P.R. Rainfall and the interaction of microclimate with larval resources in the population dynamics of checkerspot butterflies *(Euphydryas editha)* inhabiting serpentine grasslands. *Oecologia 71*:161–166;1987.

Ehrlich, P.R. The attributed of invaders and invasion processes: vertebrates. In: H.A. Mooney, J.A. Drake, eds. *Biological Invasions: A Global Perspective.*

Ehrlich, P.R. Which animal will invade? In: H.A. Mooney, J.A. Drake, eds. *Ecology of Biological Invasions of North America and Hawaii. Ecological Studies, Vol. 58.* New York: Springer-Verlag;1986:79–95.

Ehrlich, P.R. The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. *Evolution 19*:327–336;1965.

Ehrlich, P.R.; Murphy, D.D. The population biology of checkerspot butterflies *(Euphydryas)* – a review. *Biol. Zentral. 100*:613–629;1981.

Ehrlich, P.R.; Murphy, D.D.; Singer, M.C.; Sherwood, C.B.; White, R.R.; Brown, I.L. Extinction, reduction, stability and increase: The responses of checkerspot butterfly populations to the California drought. *Oecologia 46*:101–105;1980.

Ehrlich, P.R.; White, R.R. Colorado checkerspot butterflies: Isolation, neutrality, and the biospecies. *Amer. Nat. 115*:328–341;1980.

Ehrlich, P.R.; White, R.R.; Singer, M.C.; McKechnie, S.W.; Gilbert, L.E. Checkerspot butterflies: A historical perspective. *Science 188*:221–228;1975.

Ehrlich, P.R.; Launer, A.E.; Murphy, D.D. Can sex ratio be determined? The case of a population of checkerspot butterflies. *Amer. Nat. 124*:527–539;1984.

Ehrlich, P.R.; Wheye, D. Non-adaptive "hilltopping" behavior in male checkerspot butterflies *(Euphydryas editha). Amer. Nat. 127*:447–483;1986.

Gilbert, L.E.; Singer, M.C. Patterns of dispersal and gene flow in a butterfly species. *Amer. Nat. 107*:58–72;1973.

Holdren, C.E.; Ehrlich, P.R. Long-range dispersal in checkerspot butterflies: Transplant experiments with *Euphydryas gillettii. Oecologia 50*:125–129;1981.

Holdren, C.E.; Ehrlich, P.R. Ecological determinants of food plant choice in the checkerspot butterfly *Euphydryas editha* in Colorado. *Oecologia 52*:417–423;1982.

Labine, P.A. Population biology of the butterfly, *Euphydryas editha*. I. Barriers to multiple inseminations. *Evolution 18*:335–336;1964.

McKechnie, S.W.; Ehrlich, P.R.; White, R.R. Population genetics of *Euphydryas* butterflies. I. Genetic variation and the neutrality hypothesis. *Genetics 81*:571–594;1975.

Mueller, L.E.; Wilcox, B.A.; Ehrlich, P.R.; Murphy, D.D. A direct assessment of the role of genetic drift in determining allele frequency variation in populations of *Euphydryas editha*. *Genetics 110*:495–511;1985.

Murphy, D.D. Nectar sources as constraints on the distribution of egg masses by the checkerspot butterfly, *Euphydryas chalcedona* (Lepidoptera: Nymphalidae). *Environ. Entomol. 12*:463–466;1983.

Murphy, D.D. Butterflies and their nectar plants: The role of the checkerspot butterfly *Euphydryas editha* as a pollen vector. *Oikos 43*:113–117;1984.

Murphy, D.D.; Launer, A.E.; Ehrlich, P.R. The role of nectar feeding in egg production and population dynamics of the checkerspot butterfly, *Euphydryas editha*. *Oecologia 56*:257–263;1983.

Murphy, D.D.; Menninger, M.S.; Ehrlich, P.R. Nectar source distribution as a determinant of oviposition host species in *Euphydryas chalcedona*. *Oecologia 62*:269–271;1984.

Murphy, D.D.; Menninger, M.S.; Ehrlich, P.R.; Wilcox, B.A. Local population dynamics of adult butterflies and the conservation status of two closely related species, San Francisco Bay, USA. *Biol. Conserv. 37*:201–233;1986.

Murphy, D.D.; White, R.R. Rainfall, resources, and dispersal in southern populations of *Euphydryas editha* (Lepidoptera: Nymphalidae). *Pan-Pac. Ent. 60*:350–354;1984.

Murphy, D.D.; Wilcox, B.A. Butterfly diversity in natural forest fragments: A test of the validity of vertebrate-based management. In: J. Verner et al., eds. *Wildlife 2000: Modeling Wildlife Habitat Relationships*. Madison, WS: Univ. Wisconsin Press;1986:287–292.

Murphy, D.D.; Ehrlich, P.R. The conservation biology of California's remnant native grasslands. In: Mooney, H.A., L.F. Hueneke, eds. *California Grasslands: Structure and Productivity;* (in press)1987.

Schrier, R.D.; Cullenward, M.J.; Ehrlich, P.R.; White, R.R. The structure and genetics of a montane population of the checkerspot butterfly, *Chlosyne palla*. *Oecologia 25*:279–289;1976.

Singer, M.C. Evolution of foodplant preferences in the butterfly *Euphydryas editha*. *Evolution 35*:383–389;1971.

Singer, M.C. Complex components of habitat suitability within a butterfly colony. *Science 173*:75–77;1972.

Singer, M.C. Quantification of host specificity by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. *Oecologia 52*:224–229;1982.

Singer, M.C.; Ehrlich, P.R. Population dynamics of the checkerspot butterfly *Euphydryas editha*. *Fortrschr. Zool. 25*:53–60;1979.

Wheye, D.; Ehrlich, P.R. The use of fluorescent pigments to study insect behavior: Investigating mating patterns in a butterfly population. *Ecol. Entomol. 10*:231–234;1985.

White, R.R. Pupal mortality in the bay checkerspot butterfly. *J. Res. Lepid. 25*:52–62;1986.

White, R.R.; Singer, M.C. Geographical distribution of host plant choice in *Euphydryas editha* (Nymphalidae). *J. Lepid. Soc. 28*:103–107;1974.

Wilcox, B.A.; Murphy, D.D. Conservation strategy: The effects of fragmentation on extinction. *Amer. Nat. 125*:879–887;1985.

Wright, J.; Brussard, P.F.; Murphy D.D.; Ehrlich, P.R.; Wilcox, B.A. Genetic population structure in *Euphydryas editha:* The search for an appropriate spatial scale. *Evolution* (submitted for publication)