Biological Conservation **46** (1988) 183–200

Ecological Studies and the Conservation of the Bay Checkerspot Butterfly, *Euphydryas editha bayensis*

Dennis D. Murphy & Stuart B. Weiss

Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, California 94305, USA

(Received 13 November 1987; revised version received 4 February 1988; accepted 10 March 1988)

ABSTRACT

The historical decline of the bay checkerspot butterfly Euphydryas editha bayensis *is discussed and pertinent ecological information presented. The distribution of the butterfly has become highly restricted as its habitat has been destroyed by development and its numbers reduced by severe drought. Habitat loss and fragmentation disrupts the ability of habitat patches to support populations as key topographic features are eliminated. The continued survival of the butterfly is dependent on a reservoir population which provides colonists for smaller habitat patches in the vicinity. The political struggle to gain federal protection for the butterfly is reviewed.*

INTRODUCTION

Butterflies are showy, conspicuous, taxonomically well-known, and frequently collected by amateurs, making them an almost ideal group for field studies in population biology. Information has been accumulated on their distributions, natural histories and population dynamics, thus opening a window through which we may view both the status of butterfly populations themselves, and the health of the ecological communities of which they are a part. Many published biological studies provide substantial information pertaining to the conservation of endangered butterfly taxa (Arnold, 1983; J. A. Thomas, 1983, 1984; Gall, 1984; Warren *et al.*, 1984; C. D. Thomas, 1985; Warren, 1987*a,b,c*). We think, however, that

Biol. Conserv. 0006-3207/88/$03·50

the bay checkerspot butterfly *Euphydryas editha bayensis*, which is discussed here, merits additional attention due to the particularly detailed understanding of its ecology.

A quarter century of intensive biological studies of this butterfly has documented fluctuating local populations in response to climatic extremes and several waves of anthropogenic assaults on this butterfly, which is now at the brink of extinction. Two centuries ago, the bay checkerspot may have been one of the most abundant and widespread butterflies in the central Coast Range of California. After decades of habitat destruction and fragmentation, its fate rests on the persistence of a single population. Despite substantial data documenting the need for protection measures, action was delayed due to political pressures. This paper reviews the historical decline of the butterfly and applies the large body of information derived from long-term studies to assess its current conservation status and prospects for continued survival.

HABITAT AND LIFE CYCLE

E. e. bayensis is restricted to habitat patches of native California grassland containing a mixture of its larval host plants (*Plantago erecta*, the primary oviposition plant, and *Orthocarpus densiflorus* or *O. purpurascens*, secondary hosts used when *Plantago* becomes senescent [Singer, 1972]) and adult nectar sources (*Lasthenia chrysostoma*, *Layia platyglossa*, *Allium breweri*, and *Lomatium* spp.). With one exception, the only areas containing this mixture of grassland forbs are outcrops of serpentine soil (Ehrlich & Murphy, 1987*a*). Serpentine rock weathers to a shallow, nutrient-poor soil, low in nitrogen and calcium, and very high in magnesium, nickel, and chromium. Serpentine-derived soil is easily saturated with rain, but dries rapidly, and as a result is an exceedingly harsh environment for plants. For these reasons, the grasses and forbs introduced from Europe which now dominate most Californian grasslands have been unable to establish fully on serpentine soils, although they can constitute a significant part of the serpentine-based grassland community (Murphy & Ehrlich, in press).

The Mediterranean climate of central California is characterized by a cool rainy season, from October through April, and a warm summer drought, from May through September. The quantity and temporal distribution of rainfall varies greatly from year to year. Butterfly host plants germinate any time from early October to late December, and senesce from early April to mid May.

E. e. bayensis is univoltine; adults fly from late February to early May, females laying masses of up to 200 eggs at the bases of *Plantago* and

Orthocarpus. Newly-hatched larvae form webs and feed gregariously until the oviposition plant is defoliated or senesces. Larvae that have not by then reached obligatory size for diapause must disperse to find additional hosts to continue growing. Only larvae which reach the fourth instar before the dry season are able to enter diapause. They break diapause the following rainy season after *Plantago* germinates, and then feed from approximately November to late February or early March, followed by pupation.

CURRENT AND HISTORICAL DISTRIBUTION

The bay checkerspot butterfly is presently restricted to grasslands on outcrops of serpentine soil. The recent exception was the San Bruno Mountain population, which appears to have become extinct (the last adult butterflies were observed in 1984). This population inhabited grasslands

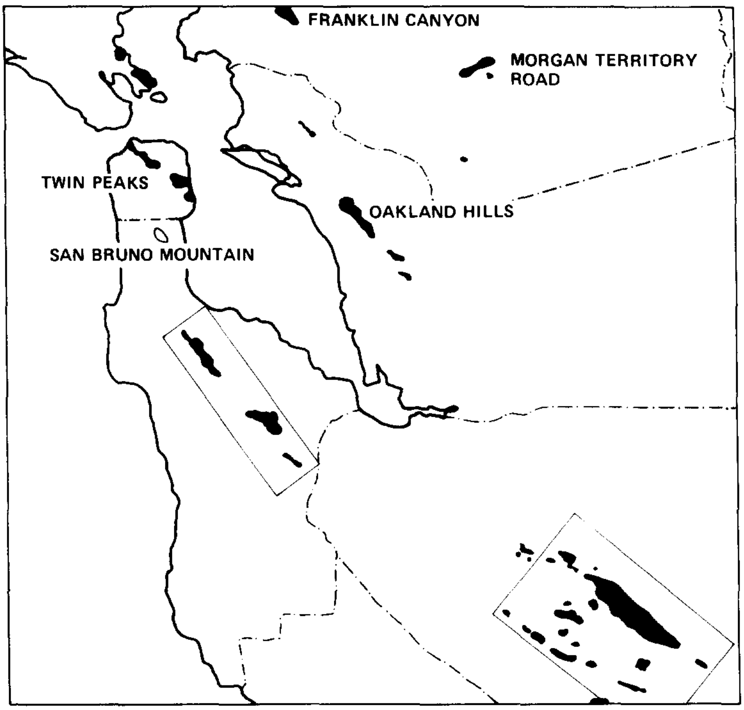

Fig. 1. The range of the bay checkerspot butterfly. Populations were once known from the serpentine soil-based grassland patches with location labels (in black); all are now extinct. The San Bruno Mountain population, its habitat marked with an open circle, did not reside on serpentine; it is also now extinct. Extant populations are now restricted to the San Mateo region (see box left-center and Fig. 2) and the Santa Clara region (see box lower right and Fig. 3).

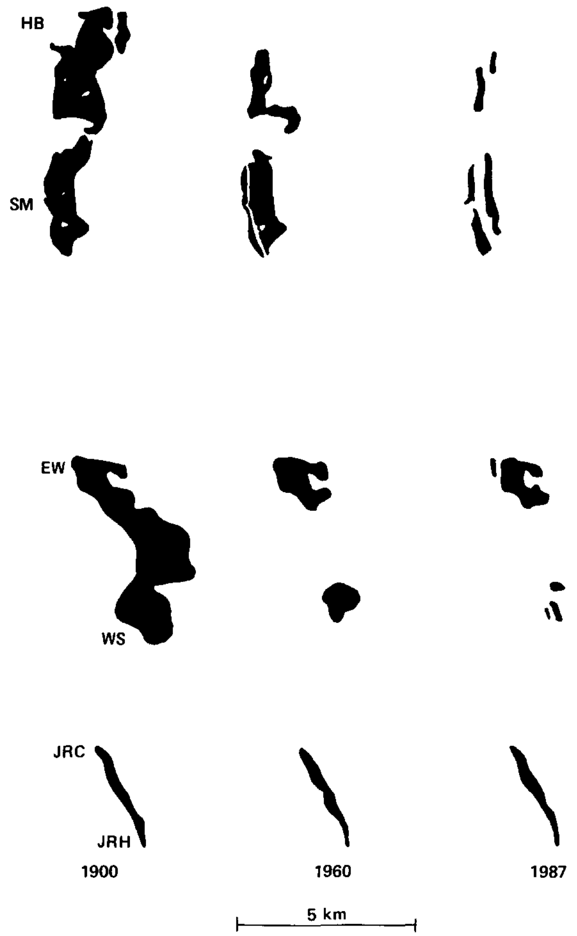

Fig. 2. Historical decline of serpentine grassland habitat in San Mateo County. Populations once existed in all six labeled areas (Hillsborough, San Mateo, Edgewood, Woodside, Jasper Ridge area C, and Jasper Ridge area H). Extant populations are now found at Edgewood and Jasper Ridge, and a few adults have been observed at San Mateo.

across steep slopes on shallow soils where *Plantago*, *Orthocarpus* and nectar sources were abundant in a matrix of native perennial bunchgrasses. Following several wildfires, much of this habitat has been invaded by introduced grasses and forbs, particularly of the genus *Erodium*, leading to severe fragmentation and isolation of the small remaining patches.

The remnant distribution of its habitat suggests that *E. e. bayensis* was once distributed widely in many grassland areas around San Francisco Bay. The first habitat fragmentation occurred when grassland communities other than those on serpentine soil were replaced by the mix of alien annual grasses and forbs seen today, leaving those on serpentine as nearly the only suitable habitats for the butterfly. Yet, even then, the butterfly still exhibited a relatively wide distribution (Fig. 1), its range extending in the early 1950s across five San Francisco Bay Area counties and comprising more than a dozen distinct populations. The butterfly has since been extirpated from San Francisco, Alameda, and Contra Costa Counties. In San Mateo County, only two serpentine soil-based grasslands have remained largely undisturbed, at Jasper Ridge (JR) and Edgewood Park (EW) (Fig. 2). The type locality of *E. e. bayensis* at Hillsborough (HB) was destroyed in the 1950s, a large nearby habitat at San Mateo (SM) was reduced to a remnant by freeway construction in the 1960s, and most of the habitat at Woodside (WS) was converted to a housing development in 1980 (see also Table 1).

Habitats supporting populations in Santa Clara County have suffered less disturbance, but populations there were severely reduced by the drought of 1975–77 (Fig. 3). Known colonies at Silver Creek Hills, Coyote Reservoir, and on the western fringe of the Santa Clara Valley went extinct in 1977 (Murphy & Ehrlich, 1980). In the past three years, however, butterflies have

TABLE 1
Causes of Previous Extinctions and Current Threats to Bay Checkerspot Butterfly Populations[a]

Population	*County*	*Causes of extinction*	*Current threats*
Twin Peaks	San Francisco	Urbanization	
San Bruno Mountain	San Mateo	Invasion by non-native plants, fire	
Hillsborough	San Mateo	Freeway construction suburbanization	
San Mateo	San Mateo	Freeway construction	
Edgewood	San Mateo		Golf course development
Woodside	San Mateo	Freeway construction suburbanization	
Jasper Ridge	San Mateo		Climatic fluctuations
Oakland Hills	Alameda	Urbanization	
Franklin Canyon	Contra Costa	Unknown	
Morgan Territory	Contra Costa	Drought, overgrazing	
Silver Creek Hills	Santa Clara	Drought, overgrazing	Suburbanization
Morgan Hill	Santa Clara		Resource development, extreme drought
Coyote Reservoir	Santa Clara	Drought, overgrazing	
Hale Avenue	Santa Clara	Drought	

[a] The Silver Creek Hills and Hale Avenue populations were documented as extinct, and the habitat patches have been subsequently recolonized.

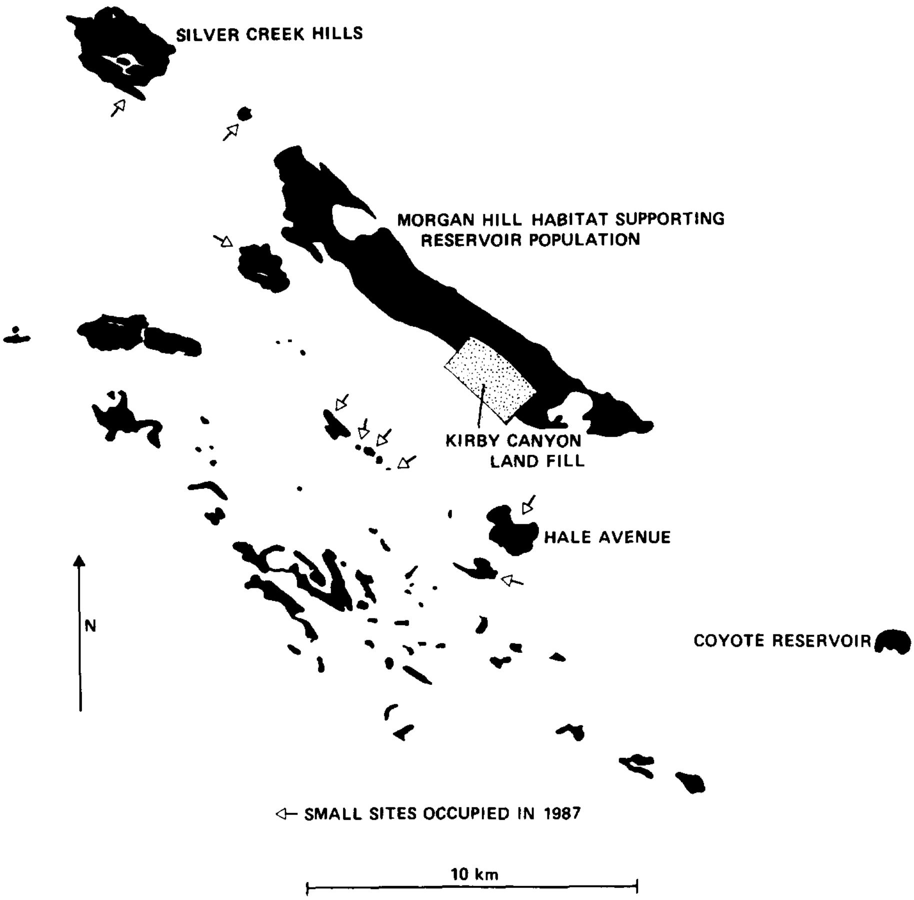

Fig. 3. Habitat patches in the Santa Clara Valley (in black). The large patch supports the Morgan Hill reservoir population (the Kirby Canyon landfill is shown as the stippled area). Smaller patches supporting satellite populations are identified with arrows. Patches occupied previous to the mid-1970s drought are identified (see text).

moved northward from Morgan Hill over virtually continuous habitat, and in 1987 were found at the Silver Creek Hills for the first time in a decade. Serpentine outcrops on the western fringe of the Santa Clara Valley were apparently also recently recolonized. Coyote Reservoir, more isolated from the source of colonists at Morgan Hill, has not been recolonized naturally, nor have apparently suitable habitats further west of the Santa Clara Valley.

POPULATION FLUCTUATIONS AND HABITAT QUALITY

Given the remnant distribution of habitat patches, an issue central to the conservation of the bay checkerspot butterfly is that of habitat quality. Here we discuss the characteristics of habitat patches which affect their ability to support a butterfly population over the long-term.

E. e. bayensis populations fluctuate widely in size from year to year (Ehrlich *et al.*, 1975), apparently primarily because of variation in prediapause mortality rates. These usually range from 90% to 99%, as most larvae fail to reach diapause before their host plants senesce (Singer, 1972).

The level of prediapause survival is determined by the phase relationship between adult flight and host plant senescence, which is largely determined by a complex combination of weather patterns and topography (Singer, 1972; Ehrlich *et al.*, 1975). Drought years result in a 'poor' phase relationship when host plants senesce early, although this can be partially compensated for by faster larval and pupal development. A two-year drought in central California from 1975 to 1977 caused dramatic population decreases (Singer & Ehrlich, 1979; Ehrlich *et al.*, 1980). During the first drought year, the primary contribution to prediapause survival was from early-flying females that had developed on warm slopes and laid eggs on cool slopes where host plants senesced later. During the second drought year, when virtually no females developed early on warm slopes, the poor phase relationship was exacerbated and several populations went extinct. Extremely wet winters, such as the 'El Nino' season of 1982–83, can also result in poor phase relationships because larval and pupal development are slowed far more than host plant availability is extended (Dobkin *et al.*, 1987).

The effects of extreme weather can be either buffered or exacerbated by topography. Local topography creates an array of microclimates, because insolation levels depend on the slope and aspect of a given portion of habitat. Low wintertime insolation creates low ground-level temperatures and long periods of shade, particularly on the steepest northern exposures. Larval growth rates depend directly on insolation levels (Weiss *et al.*, 1987). Insolation differences affect the timing of diapause termination and determine subsequent larval growth rates. The difference in eclosion date between the earliest and latest developing postdiapause larvae can exceed two months (Weiss *et al.*, in press).

Dispersal by postdiapause larvae from cool to warmer slopes can speed development by several weeks (Weiss *et al.*, 1987). The earlier larvae move, the greater the decrease in their development times, although early postdiapause larvae are greatly constrained by their small size and the irregularities of grassland surfaces (Weiss & Murphy, 1988). Large postdiapause larvae may move over 10 m per day. Larvae, additionally, often disperse dozens of meters in search of pupation sites. The exposures of slopes on which pupation takes place affect the length of the pupal stage, with warm slopes advancing adult eclosion and cool slopes retarding it (White, 1986; Weiss *et al.*, in press). Host plants on the warmest slopes senesce up to one month before those on the coolest slopes.

As the foregoing discussion implies, the pattern of rainfall during postdiapause feeding and pupal development determines the eclosion date for adults, while rain falling in March and April determines the date of host plant senescence. If larvae and pupae develop quickly and host plant senescence is delayed by spring rainfall, the subsequent generation of prediapause larvae can survive on slopes warmer than where females developed—that is, the population experiences 'thermal advance'. Conversely, if senescence is early because of drought, or larvae and pupae develop slowly because of extended rains, offspring can only survive on slopes cooler than where females developed. This situation may be described as 'thermal retreat'.

Since topography influences development rates and larval survival, the topography of a habitat patch determines its ability to support a butterfly population in the long-term, i.e., its habitat quality. The overall distribution of slope exposures, which determines the range of microclimates across a site, is the primary determinant of habitat quality. Cool slopes support the 'core' of a bay checkerspot population by serving as an essential refuge in years of thermal retreat. The resiliency of a population through consecutive years of thermal retreat depends on the initial distribution of a larval population (preceding a drought or deluge year) across the thermal gradient from warm to cool slopes. A high proportion of larvae on warmer slopes buffers the population against thermal retreat; but, if a population has retreated to the coolest slope available in a habitat patch, and then undergoes another thermal retreat, population extinction might be expected.

A second topographic characteristic that determines habitat quality is the spatial arrangement of slopes within a habitat patch. Key areas are those where cool slopes directly abut warm slopes over a scale of 1–30 m. Such proximity allows postdiapause larvae to disperse readily from cool to warm microclimates, and thus to advance development rates. Narrow ridgelines and 'V'-shaped gullies create the most abrupt interfaces, often on a scale of < 10 m. The rounded shapes of most Californian coastal foothills create more gradual transitions over longer distances, especially near hilltops, in hollows, and in saddle areas. Hillsides terraced by cattle provide sufficient flat habitat for larval basking, such that larvae can grow faster on otherwise cool slopes. Hence, even microtopography on a scale of 10 cm can be important (Weiss *et al.*, in press).

A third topographic component of habitat quality is regional in scale; the amount of rainfall received by a site depends on its location in relation to local rain shadows. Average yearly rainfall in the Bay Area varies greatly over short distances, from 1500 mm on the western slopes of the Santa Cruz Mountains, to 330 mm on the floor of the Santa Clara Valley, a scant 20 km away (Gilliam, 1962). Rainfall totals for each storm are important in determining soil moisture, especially in autumn when seeds germinate, and in spring when soil moisture cues plant senescence (Gulmon *et al.*, 1983). Larval and pupal development, and adult flight, are suppressed on cool overcast days, regardless of the amount of rain that falls on a specific site. Smaller habitat patches in regions of higher rainfall may provide higher quality habitat than patches of similar size and topography in drier rain shadow areas. This is supported by the drought-induced extinctions of populations in Santa Clara County on all but the largest habitat patch, while smaller populations in wetter San Mateo County persisted (with severe reductions in butterfly numbers).

The stringent requirements of topographic diversity and rainfall mean that large habitat size by itself does not guarantee population persistence. Population extinctions have been documented in large habitat areas that lack topographic diversity. Coyote Reservoir, for instance, is a large habitat area that consists mostly of east-facing slopes. The habitat supported the densest larval population known in 1971, but that population was extinct by 1977. Likewise, within the 2000 ha habitat supporting the largest population at Morgan Hill, a 500 ha reserve with largely western exposure could be selected that would fail to provide for the long-term survival of the butterfly. Conversely, 100 ha on the crest and eastern flank of the same ridge, in the most topographically diverse section of habitat, would probably provide an adequate refuge for effectively permanent protection of the bay checkerspot.

The complexity of these determinants of habitat quality explains why the fragmentation and loss of even small areas can compromise the ability of a habitat patch to support a bay checkerspot population. For example, the 'San Mateo' serpentine patch (SM, Fig. 2) still contains many hectares of serpentine grassland supporting larval host plants and adult nectar sources, yet it cannot support a butterfly population. The remaining habitat consists nearly exclusively of warm south- and west-facing slopes, with only a minute area of cooler slopes. In general, the loss of the coolest portions of a habitat patch may not cause a decline in the size of a local butterfly population for many years, but such areas provide the only refuge when consecutive years of thermal retreat occur, and the absence of such areas may result in population extinction.

Finally, livestock grazing has profound impacts on the habitat quality of serpentine-based grasslands for the bay checkerspot. Grazing regimes can have different effects on different slope exposures. In general, grazing helps maintain the forb-dominated, intermediate grassland successional stages favored by the butterfly and can reduce localized shading from taller grassland plant species. In the Morgan Hill area, removal of grazing results in grasslands dominated by non-native annual grasses within a few years. Yet, overgrazing in drought years, during which grassland biomass is low, has been implicated in several extinctions. Hence, an as yet undetermined level of livestock grazing is probably necessary to provide high quality habitat for the butterfly, at least in the southern populations. In contrast, a similar increase in non-native grasses at Jasper Ridge and Edgewood has not been observed since cattle were removed. The reasons for this difference between the southern and northern habitats remain undetermined, and clearly need more investigation.

METAPOPULATION DYNAMICS

Wilcox & Murphy (1985), following Levins (1970), described the present distribution of the bay checkerspot as a metapopulation, or 'population of populations', in which extinction, dispersal, and recolonization allow regional persistence of the species. Both theory and common sense suggest that the small demographic units that constitute many of the surviving populations of the bay checkerspot are particularly vulnerable to extinction (Leigh, 1981; Goodman, 1987). The extinctions on undisturbed habitat documented since 1960 support this view. Yet, despite the stringent habitat requirements of the butterfly discussed above, successful recolonization of empty habitat patches has been documented (Ehrlich *et al.*, 1975, Harrison *et al.*, in press). The long-term survival of the butterfly, therefore, appears to depend not only on the persistence of extant populations, but also on the number of empty suitable habitat patches, and on the spatial arrangement of both.

While a number of distinct, functioning metapopulations may have existed as recently as 20 years ago, only one remains largely intact (Fig. 3). This, the complex Morgan Hill metapopulation, is comprised of a single 'reservoir population', which can be expected to persist through essentially all natural environmental perturbations, and a large number of surrounding habitat patches able to support 'satellite populations' that exist for short periods (Ehrlich & Murphy, 1987*a*). Of more than 60 such patches surveyed in the past two years, only eight were found to support butterflies, all with fewer than several hundred individuals. Harrison *et al.* (in press) point out that the pattern of patch occupancy resembles that of a 'Boorman–Levitt metapopulation', in which a source population provides migrants to transient recipient populations.

The eight habitat patches supporting the butterfly are in fact significantly closer to the reservoir population than 15 other equally or more suitable habitat patches containing the necessary plant resources with no resident populations. Furthermore, the occupied patches are not significantly larger in area than other suitable but unoccupied patches; hence a 'distance effect', and not an 'area effect', appears to best explain the observed pattern of occupancy (Harrison *et al.*, in press).

Historical observations indicate that this distribution represents recent colonization from the Morgan Hill reservoir population. As noted above, previously robust populations in extensive habitat patches at Silver Creek Hills and Coyote Reservoir went extinct during the 1975–77 drought, and with them apparently all other Morgan Hill satellite populations. The most likely circumstance for the recent colonization of empty habitat patches is that an early emerging (warm slope) female from the source population oviposited on a cool slope in the empty patch.

The observed northward spread of butterflies from Morgan Hill toward Silver Creek Hills from 1985 to 1987 took place during a period of thermal advance, and topographic features of the source and recipient patches played roles in the successful colonizations. A larger Morgan Hill reservoir population generated more migrants, a higher proportion of potential migrant females eclosed relatively early in the flight season, and favorable weather apparently allowed migrants to oviposit well before host plant senescence. Certainly, colonization would be more difficult in a period of thermal retreat (during a low rainfall year).

Migration of adults from occupied to unoccupied patches, then, may be the limiting factor in the metapopulation dynamics of this butterfly. Adults transferring between Jasper Ridge area H and area C, only 500 m apart, across unsuitable habitat, have averaged less than 2% of total recaptures during the past 25 years (Ehrlich, 1961, 1965; Ehrlich *et al.*, 1975). Furthermore, adults dispersing between habitat patches do not necessarily contribute to the next generation. Females tend to disperse late in the flight season, often later than the latest date at which offspring can reach diapause. Male migrants entering a new population generally find most females already mated and unavailable (Labine, 1964). This led Ehrlich *et al.* (1975) to suggest that gene flow is very restricted in this species.

Nonetheless, adequate levels of exchange to tie populations genetically at loci not under selection (Slatkin, 1987) certainly must occur among directly adjacent populations, such as those on Jasper Ridge. This may explain the apparent lack of deleterious genetic effects following population bottlenecks observed at Jasper Ridge (Mueller *et al.*, 1985). Indeed, inbreeding in small populations of this species appears to be a minor factor contributing to local extinction compared to the effects of environmental fluctuations. The high degree of genetic similarity among geographically separated populations of *E. e. bayensis* (McKechnie *et al.*, 1975) may perhaps be explained by the extinction–recolonization dynamic described above. Slatkin (1985) discusses how the re-establishment of populations after local extinction can encourage genetic homogeneity across wide geographic distances.

With rates of migration between nearly contiguous demographic units relatively low, movement by the bay checkerspot butterfly to geographically distant habitats (greater than 10 km) is undoubtedly limited. Moreover, the tendency for adults to disperse at increased rates from areas supporting low densities of conspecifics (Gilbert & Singer, 1973) indicates that the absence of adults may contribute to deter potential migrants from establishing in unoccupied habitat patches. Natural re-establishment of populations in disrupted habitat island systems where patches are highly isolated is therefore probably infrequent.

CONSERVATION PRESCRIPTIONS

While the habitat requirements of *E. e. bayensis* are complex, the conservation prescriptions to ensure long-term survival are relatively simple. The lone remaining reservoir population at Morgan Hill in Santa Clara County must be preserved. The large size and topographic diversity of this habitat support the most fecund and resilient of known populations. Observations of natural recolonization of surrounding smaller habitat patches are encouraging, but those observations emphasize the importance of Morgan Hill as a reservoir population. Although the present pattern of habitat patch occupancy does not indicate that satellite populations are a key source of colonists (Harrison *et al.*, in press), recolonizations of small patches relatively far from the reservoir site may prove to be facilitated by the proximity, size, and quality of intervening habitat patches. If so, the loss of a single small patch might affect the likelihood of recolonization and gene flow among other small habitat patches. The vulnerability of smaller patches to drought is well documented; hence, the protection of as many small patches as possible, whether they support populations or not, ought to be the second conservation directive. If future extinctions occur on small patches, artificial reintroductions remain a viable option, and may be necessary in the more isolated patches.

The prospects for the bay checkerspot butterfly in San Mateo County on the San Francisco Peninsula are less bright. Jasper Ridge does not appear capable of supporting populations of the butterfly indefinitely (Ehrlich *et al.*, 1980). One of three small demographic units that were present there in the early 1960s has gone extinct; and in the vacant area *Orthocarpus* and nectar sources have been 'replaced' via grassland succession by native bunch-grasses. Another demographic unit, in area H, underwent a four-year bottleneck in which the effective population size (N_e) was probably never greater than 15 (Mueller *et al.*, 1985). The area C demographic unit, which numbered nearly 5000 individuals in 1981, was reduced to fewer than

300 individuals in 1986. The Edgewood Park demographic units have shown dramatic reductions from a cumulative high of more than 100 000 butterflies in 1981, to fewer than 1000 in 1985. The overall population appears to have increased since 1985, but plans for Edgewood Park currently include a golf course development which would destroy some habitat and could mean the demise of this population. The San Bruno Mountain population is now extinct; no adults have been observed for three seasons despite intensive searches during the flight periods.

The few remaining habitat patches in San Mateo County must be fully protected; no further disturbance can be tolerated. The San Bruno Mountain site should be re-established, perhaps from Morgan Hill stock, thus allowing biologists to gauge the likelihood of success for future artificial transplants. Should drought or deluge soon strike again and cause the extinctions of the Jasper Ridge and/or Edgewood sets of populations, reintroduction using Morgan Hill stock would be appropriate.

POLITICS

Dramatic decreases in the sizes of the Jasper Ridge demographic units, the conversion of the habitat of the Woodside population, and action toward golf course development at Edgewood, prompted a petition to the US Fish and Wildlife Service to place the bay checkerspot butterfly on the federal endangered species list in 1980. Endangered species listings came to a virtual standstill, however, under the then new Reagan administration in 1981. Only in 1982, when Stanford biologists threatened to file a lawsuit, did listing activity proceed. The listing proposal, with critical habitat outlines, appeared in the Federal Register in 1985.

The Morgan Hill reservoir population, on previously inaccessible private property, was discovered in 1983. Waste Management, Inc. promptly initiated a habitat conservation plan which would allow them to develop a sanitary solid waste landfill on the site (Fig. 3). The plan, among other considerations: (1) sets aside the highest quality butterfly habitat adjacent to the landfill site; (2) establishes funding for further studies of the ecology and genetics of the butterfly; (3) regulates grazing to provide the greatest possible density of larval host plants and nectar resources; and (4) provides funding for the identification of empty habitat patches and re-establishment of butterfly populations therein (Murphy, 1988). Co-operating with the Fish and Wildlife Service and listing proponents, Waste Management, Inc. avoided a protracted battle over the butterfly and has benefited from a surge of positive public relations.

Conversely, United Technologies, Inc., a defense contractor and owner of neighboring portions of habitat supporting the bay checkerspot reservoir population at Morgan Hill, took a negative stance following the 1983 discovery. They challenged the listing proposal and hired an entomologist to promote the arguments that (1) the butterfly was much more widely distributed than previously documented and (2) the overall distribution of the subspecies was inaccurately portrayed by the petitioners. Yet, their intensive helicopter searches located only two additional records of adults on nearby habitat patches in Santa Clara County. The latter argument, however, proved non-trivial. While the United States Endangered Species Act can confer protection to the entirety of described subspecies of invertebrates, it cannot protect either 'undescribed' populations or specific populations within the extent of described subspecies. Implicit in the United Technologies' contention that ecologically similar populations 200 km to the south should also be recognized as *E. e. bayensis*, was that the addition of populations to the taxon would negate the need to protect it. Despite the documented losses of populations in the San Francisco Bay Area and language in Section 3 of the Act defining endangered species as those which are 'in danger of extinction throughout all *or a significant portion* of its range' (emphasis ours), the US Fish and Wildlife Service chose to convene a panel of experts to rule on the taxonomic validity of the subspecies. The panel acknowledged the inherently arbitrary nature of all subspecies designations, but deemed that the narrow geographic range of *E. e. bayensis* presented by the petitioners was consistent with the *Code of Zoological Nomenclature*, previous systematic treatments, and popular works. In essence, the panel suggested that traditional acceptance is the best criterion for measuring the validity of a subspecies, and implied that taxonomic disagreements generated by clearly self-serving interests do not constitute legitimate challenges to that validity. *E. e. bayensis* was listed as 'a threatened species' 7 years after the first petition was filed in 1980 (United States Federal Register, Sept. 18 1987).

Not to be lost in conservation efforts specifically directed at the bay checkerspot is that the butterfly now survives in minute remnants of a once extensive ecosystem. The native California grassland ecosystem on serpentine soil is itself gravely endangered. Language in the 1982 re-authorization of the Endangered Species Act severely weakened regulations concerning threatened and endangered plants, restricting protection to plants solely on federal land, and there only from personal acquisition and not habitat destruction. As the only animal currently conferred protection and completely restricted to native California grasslands, the bay checkerspot must act as an umbrella of sorts to protect this remnant ecosystem. The butterfly may prove to be inadequate to that task for several reasons: (1) because remnant native grasslands requiring protection extend well beyond the present distribution of the butterfly; (2) because several of the habitat patches with the richest diversity of plants and lepidoptera, within or adjacent to the distribution of the butterfly, do not appear to have previously supported the bay checkerspot; (3) because temporarily empty habitat patches, which could support the butterfly, normally would not receive protection, even though those habitat areas may be crucial to overall metapopulation dynamics and the long-term persistence of the taxon.

CONCLUSIONS

Euphydryas editha bayensis shares with many, if not most, herbivorous insects traits which make conservation plans for them comparatively straightforward. Since populations are largely regulated by abiotic factors, heterogeneity in the physical structure of the habitat (for this butterfly, topography in particular) is a key determinant of habitat quality. Habitat heterogeneity, in fact, may be more important to many such species than habitat size, since the resource biomass required to sustain invertebrate populations may be met in relatively small habitat areas. Nonetheless, like most herbivorous insects, *E. e. bayensis* has highly specific resource requirements—for instance, the presence of appropriate combinations of larval hosts and nectar resources, which may only be available in particularly exacting circumstances (in this case, a narrowly-defined successional stage with appropriate levels of vertebrate grazing). Those exacting circumstances, of course, may more often be met in habitats of large overall size. Indeed, the most difficult conservation prescription to meet may be protection of the entirety of the last metapopulation complex in Santa Clara County. Losses of single habitat patches may ultimately prove to confound the extinction–recolonization dynamic of the entire metapopulation, and may make some local population extinction events permanent.

Thousands of generations may have fine-tuned the bay checkerspot to an environment rather different from that in which we presently find it. The use by *Euphydryas editha* of the secondary larval host plant, *Orthocarpus*, for example, may be an artifact of the recent restriction of the butterfly to serpentine-based grasslands where host plant senescence proceeds several weeks earlier than in surrounding grasslands. Similarly, the sedentary flight behavior exhibited by this butterfly seems better adapted to a more continuous distribution of suitable habitat, which probably existed in central California prior to the invasion of Eurasian weeds.

Ehrlich & Murphy (1987*b*) list a number of characteristics of ecological systems in habitat patches that can affect resource relationships and structures of surviving populations. These include high edge to interior ratios, lack of microhabitat heterogeneity, and increased rates of selective extinctions which impact community interactions. Indeed, like *E. e. bayensis*, most threatened or endangered species under study reside in remnant habitats; as such, we must be exceedingly careful when drawing conclusions to be incorporated into conservation plans and management schemes. Moreover, as the need for a responsible livestock grazing program in the preservation agenda of *E. e. bayensis* illustrates, the conservation of endangered species will often necessitate substantial hands-on management. This management is all the more difficult when we attempt to preserve species in remnant environments, in which many of the selective forces are anthropogenic in origin.

ACKNOWLEDGEMENTS

We wish to express our appreciation to all those before us whose research on the bay checkerspot provided the foundation for our own, particularly Michael C. Singer and Paul R. Ehrlich. Much of this work was supported by a continuing NSF grant to Professor Ehrlich (DEB82-06961). Waste Management, Inc. also provided support for this work, allowing us complete access to the Morgan Hill study site and participating in the Kirby Canyon Conservation Agreement. We would like to dedicate this paper to all who have contributed towards the protection of the bay checkerspot butterfly and its habitat, including scientists, environmental groups, the US Fish and Wildlife Service, and Waste Management, Inc.

REFERENCES

Arnold, R. A. (1983). Ecological studies of six endangered butterflies (Lepidoptera: Lycaenidae): Island biogeography, patch dynamics, and the design of nature reserves. *Univ. Calif. Publs in Entomology*, **99**.

Dobkin, D. S., Olivieri, I. & Ehrlich, P. R. (1987). Rainfall and the interaction of microclimate with larval resources in the population dynamics of checkerspot butterflies (*Euphydryas editha*) inhabiting serpentine grassland. *Oecologia*, **71**, 161–76.

Ehrlich, P. R. (1961). Intrinsic barriers to dispersal in the checkerspot butterfly. *Science, N.Y.*, **134**, 108–9.

Ehrlich, P. R. (1965). The population biology of the butterfly *Euphydryas editha*, II. The structure of the Jasper Ridge colony. *Evolution*, **19**, 327–36.

Ehrlich, P. R. & Murphy, D. D. (1987*a*). Conservation lessons from long-term studies of checkerspot butterflies. *Conserv. Biol.*, **1**, 122–31.

Ehrlich, P. R. & Murphy, D. D. (1987*b*). Monitoring populations on remnants of native vegetation. In *Nature Conservation: The Role of Remnants of Native*

Vegetation, ed. D. Saunders *et al.* Surrey Beatty, Chipping Norton, NSW, pp. 201–10.

Ehrlich, P. R., Murphy, D. D., Singer, M. C., Sherwood, C. B., White, R. R. & Brown, I. L. (1980). Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia*, **46**, 101–5.

Ehrlich, P. R., White, R. R., Singer, M. C., McKechnie, S. W. & Gilbert, L. E. (1975). Checkerspot butterflies: a historical perspective. *Science, N.Y.*, **188**, 221–8.

Gall, L. (1984). Population structure and recommendations for conservation of the narrowly endemic alpine butterfly, *Boloria acroenema* (Lepidoptera: Nymphalidae). *Biol. Conserv.*, **28**, 111–38.

Gilbert, L. E. & Singer, M. C. (1973). Dispersal and gene flow in a butterfly species. *Am. Nat.*, **107**, 58–73.

Gilliam, H. (1962). *Weather of the San Francisco Bay Region*. University of California Press, Berkeley, CA.

Goodman, D. (1987). The minimum viable population problem, I. The demography of chance extinction. In *Viable Populations for Conservation*, ed. M. Soule. Cambridge University Press, Cambridge, pp. 11–34.

Gulmon, S. L., Chiarello, N. R., Mooney, H. A. Chu, C. C. (1983). Phenology and resource use in three co-occurring grassland annuals. *Oecologia*, **58**, 33–42.

Harrison, S., Murphy, D. D. & Ehrlich, P. R. (in press). Metapopulation ecology of the checkerspot butterfly *Euphydryas editha bayensis*. *Amer. Nat.*

Labine, P. (1964). Population biology of the butterfly *Euphydryas editha*, I. Barriers to multiple insemination. *Evolution*, **18**, 335–6.

Leigh, E. G. (1981). The average lifetime of a population in a varying environment. *J. Theor. Biol.*, **90**, 213–39.

Levins, R. (1970). Extinction. In *Lectures on Mathematics in the Life Sciences*, ed. M. Gerstenhaber, American Mathematical Society, Providence, R.I. pp. 77–107.

McKechnie, S. W., Ehrlich, P. R. & White, R. R. (1975). Population genetics of *Euphydryas* butterflies, I. Genetic variation and the neutrality hypothesis. *Genetics*, **81**, 571–94.

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

Murphy, D. D. (1988). The Kirby Canyon conservation agreement; A model for the resolution of land use conflicts involving threatened invertebrates. *Environ. Conserv.*, **15**, 45–8.

Murphy, D. D. & Ehrlich, P. R. (1980). Two California checkerspot subspecies: one new, the other on the verge of extinction. *J. Lepid. Soc.*, **34**, 316–20.

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

Singer, M. C. (1972). Complex components of habitat suitability within a butterfly colony. *Science, N.Y.*, **176**, 75–77.

Singer, M. C. & Ehrlich, P. R. (1979). Population dynamics of the checkerspot butterfly *Euphydryas editha*. *Fortschr. Zool.*, **25**, 53–60.

Slatkin, M. (1985). Gene flow in natural populations. *Ann. Rev. Ecol. Syst.*, **16**, 393–430.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science, N.Y.*, **236**, 787–92.

Thomas, C. D. (1985). The status and conservation of the butterfly *Plebejus argus* L. (Lepidoptera: Lycaenidae) in northwest Britain. *Biol. Conserv.*, **33**, 29–51.

Thomas, J. A. (1983). The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. *J. Appl. Ecol.*, **20**, 59–83.

Thomas, J. A. (1984). The behaviour and habitat requirements of *Maculinea nausithous* (the dusky large blue butterfly) and *M. telius* (the scarce large blue) in France. *Biol. Conserv.*, **28**, 325–47.

Warren, M. S., Thomas, C. D. & Thomas, J. A. (1984). The status of the heath fritillary butterfly *Mellicta athalia* Rott. in Britain. *Biol. Conserv.*, **29**, 287–305.

Warren, M. S. (1987*a*). Ecology and conservation of the heath fritillary butterfly *Mellicta athalia*, I. Host selection and phenology. *J. Appl. Ecol.*, **24**, 467–82.

Warren, M. S. (1987*b*). Ecology and conservation of the heath fritillary butterfly *Mellicta athalia*, II. Adult population structure and mobility. *J. Appl. Ecol.*, **24**, 483–97.

Warren, M. S. (1987*c*). Ecology and conservation of the heath fritillary butterfly *Mellicta athalia*, III. Population dynamics and the effect of habitat management. *J. Appl. Ecol.*, **24**, 498–512.

Weiss, S. B. & Murphy, D. D. (1988). Fractal geometry and caterpillar dispersal; or how many inches do inchworms inch? *Func. Ecol.*, **2**, 116–18.

Weiss, S. B., Murphy, D. D. & White, R. R. (in press). Sun, slope, and butterflies: Topographic determinants of habitat quality for *Euphydryas editha*. *Ecology*.

Weiss, S. B., White, R. R., Murphy, D. D. & Ehrlich, P. R. (1987). Growth and dispersal of larvae of the checkerspot butterfly *Euphydryas editha*. *Oikos*, **50**, 161–6.

White, R. R. (1986). Pupal mortality in the bay checkerspot butterfly. *J. Res. Lep.*, **25**, 52–62.

Wilcox, B. A. & Murphy, D. D. (1985). Conservation strategy: The effects of fragmentation on extinction. *Amer. Nat.*, **125**, 879–87.