

An Environment-metapopulation Approach to Population Viability Analysis for a Threatened Invertebrate

DENNIS D. MURPHY

Center for Conservation Biology
Department of Biological Sciences
Stanford University
Stanford, CA 94305-5020, U.S.A.

KATHY E. FREAS

Center for Conservation Biology
Department of Biological Sciences
Stanford University
Stanford, CA 94305-5020, U.S.A.

STUART B. WEISS

Center for Conservation Biology
Department of Biological Sciences
Stanford University
Stanford, CA 94305-5020, U.S.A.

Abstract: *Most previous population viability analyses of endangered species have focused on large vertebrates: long-lived species with low rates of population increase, long generation times, and comparatively low habitat specificity. Habitat fragmentation not only reduces the distribution of such species, but reduces population densities to levels at which genetic and demographic constraints threaten population persistence. Many other endangered species, in contrast, are characterized by small body size, high rates of population increase, short generation times, and high habitat specificity. Habitat fragmentation reduces distributions of such species, but within remnant habitats population densities may continue to be high. Population viability analyses for these species — which include many small vertebrates, invertebrates, and plants — must focus on the environmental factors and metapopulation characteristics that determine population persistence.*

Population viability analysis for the threatened Bay checkerspot butterfly (Euphydryas editha bayensis) exemplifies the environment-metapopulation approach. Variation in thermal conditions and rainfall through time (macroclimate) and across local topography (topoclimate) drives the population dynamics of this insect. Because of the great sen-

Resumen: *Los análisis previamente realizados sobre la viabilidad de las poblaciones de especies en peligro de extinción, se han concentrado en vertebrados grandes: especies longevas, con tasas bajas de incremento poblacional, períodos generacionales largos y, comparativamente, baja especificidad de requerimientos de hábitat. La fragmentación del hábitat no solamente reduce la distribución de dichas especies, sino también, reduce las densidades poblacionales a niveles en los cuales las limitaciones genéticas y demográficas amenazan la persistencia de las poblaciones. En contraste, muchas otras especies en peligro de extinción se caracterizan por ser pequeñas de tamaño, tener tasas altas de incremento poblacional, períodos generacionales cortos y una alta especificidad de hábitat. La fragmentación del hábitat reduce la distribución de dichas especies, pero su densidad poblacional puede continuar siendo alta dentro del hábitat remanente. Los análisis de viabilidad poblacional para estas especies, que incluyen a muchos vertebrados pequeños, invertebrados y plantas, deben enfocarse en factores ambientales y características metapoblacionales que determinan la persistencia de sus poblaciones.*

El análisis de viabilidad poblacional de la mariposa Bay checkerspot (Euphydryas editha bayensis) ejemplifica el en-

sitivity of larvae and host plants to thermal differences between slope exposures and to annual variation in rainfall, extinction of local butterfly populations is common. Both habitat patch quality (size, topographic diversity, and resource abundance) and distance from a reservoir population affect the likelihood of patch occupancy. An understanding of metapopulation dynamics, therefore, is necessary to explain the regional distribution of the butterfly at any given time.

Although parameterization of key life stages of the Bay checkerspot butterfly is not yet complete, insights from previous studies can be used to help make decisions in reserve design and management of the species.

The systematic treatment of the probabilistic phenomena that determine population persistence has made population viability analysis (PVA) one of just a few quantitative techniques available to conservation biologists (see Soulé 1987). To date, most PVA practitioners have focused on the analysis of populations of what have been called "charismatic megavertebrates," including the grizzly bear (Shaffer 1981), Spotted Owl (Marcot & Holthausen 1987), and Red-Cockaded Woodpecker (U.S. Fish and Wildlife Service 1985). This focus of conservation attention on large vertebrates has been appropriate. Large vertebrates not only garner the greatest public interest and sentiment, they include some of the most endangered species. Furthermore, many large vertebrates serve as "umbrellas" for other species; protection of such umbrella species and their habitats may confer protection on myriad less obvious species.

As our conservation efforts mature, however, attention will increasingly be directed at species that, like endangered large vertebrates, exist in remnant distributions, but share few of the life history characteristics that put large vertebrates at risk of extinction. In areas such as urban and suburban corridors, where large vertebrates are but distant memories, small mammals, small cold-blooded vertebrates, invertebrates, and many plants are now the subjects of conservation efforts. The purpose of this paper is to discuss the key elements of population viability analysis for species that are characterized by life history traits that are distinct from those of large vertebrates.

Shaffer (1981, 1985; and see Soulé 1987) identified four categories of phenomena that affect the persistence

of all populations. First are genetic factors that negatively affect the ability of individuals to survive and reproduce, and the ability of populations to adapt to changing environments. Second are demographic factors that affect population size and persistence, including such factors as sex ratio, reproductive output, and age at first reproduction. Third, all populations are affected by environmental factors, including changes in climate and other habitat characteristics. These and other largely stochastic processes affect the availability of key resources for a particular population, as do natural catastrophes, such as fire, flood, and intense or sustained drought. Fourth are interactions between local populations. These interactions, referred to as metapopulation dynamics, affect levels of gene flow between extant populations, patterns of habitat patch occupancy, and recolonization rates following local extinction events. Naturally, these different types of phenomena can act in concert to produce amplified effects. For instance, a large isolated population subjected to a three-year drought may be reduced to a size at which inbreeding is likely. The results may include reduced reproductive success and, if numbers are low enough, extinction.

foque ambiental y metapoblacional. Las variaciones de las condiciones térmicas y pluviales, a través del tiempo (macroclima), al igual que a través de la topografía local (topoclima), determina la dinámica de poblaciones de este insecto. La extinción de poblaciones locales es común, debido a la gran sensibilidad de las larvas y las planta anfitrionas a las diferencias térmicas entre pendientes de diferente exposición y a las variaciones anuales de la pluviosidad.

La calidad de los segmentos de habitat (tamaño, diversidad topográfica, y abundancia de recursos) y su distancia de "reservorios de población" afecta la posibilidad de ocupación de un segmento de habitat individual. El entendimiento de la dinámica de una metapoblación es, entonces, necesario para explicar la distribución regional de la mariposa en cualquier momento dado en el tiempo.

Aunque la parametrización de las etapas claves en la vida de la mariposa Bay checkerspot no ha sido aún completada, conocimientos generados por estudios previos pueden ser utilizados para asistir en la toma de decisiones para el diseño de reservas y el manejo de especies.

of all populations. First are genetic factors that negatively affect the ability of individuals to survive and reproduce, and the ability of populations to adapt to changing environments. Second are demographic factors that affect population size and persistence, including such factors as sex ratio, reproductive output, and age at first reproduction. Third, all populations are affected by environmental factors, including changes in climate and other habitat characteristics. These and other largely stochastic processes affect the availability of key resources for a particular population, as do natural catastrophes, such as fire, flood, and intense or sustained drought. Fourth are interactions between local populations. These interactions, referred to as metapopulation dynamics, affect levels of gene flow between extant populations, patterns of habitat patch occupancy, and recolonization rates following local extinction events. Naturally, these different types of phenomena can act in concert to produce amplified effects. For instance, a large isolated population subjected to a three-year drought may be reduced to a size at which inbreeding is likely. The results may include reduced reproductive success and, if numbers are low enough, extinction.

Gilpin and Soulé (1986) have described the consequences of the phenomena that affect population persistence as "extinction vortices." Feedback loops between genetic, demographic, and environmental phenomena determine the vulnerability of populations to extinction through one or more vortices. The vulnerability of a population or species to each vortex may be predicted based on its life history characteristics.

Although broad categories of phenomena affecting population persistence can be described, and these descriptions can be quantified to project extinction probabilities, Shaffer and Gilpin and Soulé have stressed that there are no universally applicable rules for PVA. Critical evaluation of the fundamental biology of a target species is essential to determining the phenomena that may affect the persistence of its populations. From a practical standpoint, however, conservation biologists need rules both to guide and to streamline efforts to preserve endangered species. With this in mind, and to simplify and direct initial efforts in population viability analysis, we posit that target organisms align into two broad (and, unfortunately, not always distinct) groups. Most populations of endangered large vertebrates upon which we focus our concern are subject to deleterious effects from habitat loss *and* from significant declines in population sizes and densities. For relatively large-bodied, long-lived organisms with low reproductive rates, long generation times, and relatively low habitat specificity, habitat fragmentation reduces population size and density to a point at which demographic and genetic constraints can threaten population persistence. The other group of species is characterized by short generation time, small body size, high rates of population increase, and high habitat specificity. Populations of such species may also be reduced to remnant distributions as a result of habitat fragmentation, but they often continue to exist in comparatively high densities within remaining suitable habitat. Such species represent an opportunity to expand the PVA "paradigm" to incorporate new or alternative insights into analyses. PVA for those species must focus on the environmental factors and metapopulation characteristics that determine local population persistence.

Butterflies are logical choices for investigating the elements of population viability analyses that focus on environmental and metapopulation phenomena. Butterflies comprise an important taxonomic group in conservation, particularly in the United States and Great Britain. Ten North American taxa now are listed as endangered or threatened by the U.S. Fish and Wildlife Service; three dozen more are candidates for such protection. Most of these taxa occur in urban coastal areas and may serve as umbrella species conferring protection on small remnant native habitats. Butterfly conservation is widely practiced in Great Britain, where intensive management maintains suitable butterfly habitats (J. A. Thomas 1984a).

The primary role of environmental factors in determining butterfly population dynamics is apparent from reviews of butterfly population ecology (Gilbert & Singer 1975; Dempster 1983; Ehrlich 1984; J. A. Thomas 1984a). Most documented population extinctions have resulted from habitat deterioration combined with ex-

treme weather events. Decreases in the quality and/or abundance of larval host plants and adult nectar sources are caused by changes in plant community composition, particularly changes associated with succession, disturbance, and grazing regimes. But, because many butterfly species are especially sensitive to thermal conditions, habitat changes that disrupt microclimatic regimes can cause habitat deterioration without elimination of plant resources. Examples of key environmental factors that affect population dynamics of butterflies include shading levels along woodland rides, solar exposure and wind shelter, sward height in grasslands, water levels in wetlands, successional stages in woodlands and host plant diversity, complex interactions with mutualistic ants, local habitat disturbance, and forest microclimate at overwintering sites (see Table 1).

Extreme weather often is the proximate cause of declines or extinctions of butterfly populations. Drought in northwestern Europe has caused widespread declines in numerous butterfly species (Thomas 1984a), as has drought in California (Ehrlich et al. 1980). A late season snowstorm extinguished a subalpine butterfly population in Colorado (Ehrlich et al. 1972). And, the 1982–83 El Niño event brought unusually wet weather and widespread declines in butterfly populations in California (e.g., Dobkin et al. 1987).

In contrast to environmental variation, demographic stochasticity appears to play a major role in butterfly persistence only when a population has been depressed to minuscule size (<20 individuals) due to habitat deterioration or other environmental events. Such small populations either promptly rebound in numbers or are driven to extinction by the next environmental perturbation. Within-habitat dispersal by butterflies expedites the mixing of individuals, which can ameliorate negative demographic effects, for example those associated with biased sex ratios. Demographic stochasticity, however, has been implicated in one extinction, that of *Maculinia arion* (the large blue), but only after environmental factors reduced the population to just five individuals (J. A. Thomas 1984a).

Nor has inbreeding and other deleterious genetic effects associated with small population sizes been implicated in butterfly extinctions. Dispersal between habitats and populations facilitates gene flow between extant populations and allows comparatively ready recolonization of temporarily unoccupied habitats. Studies of British butterflies support the assertion that if populations persist at sizes sufficiently small to manifest the effects of inbreeding, extinction is likely to occur for other reasons. Indeed, populations of checkerspot butterflies (*Euphydryas* spp.) have been observed to undergo severe bottlenecks with ($N_e < 20$), then bound in numbers with no loss of detectable electrophoretic variation (Mueller et al. 1985; Ehrlich & Murphy 1987a).

Table 1. Factors found to regulate temperate zone butterfly distribution and population size.

<i>Species</i>	<i>Location</i>	<i>Environmental factors</i>	<i>Reference</i>
<i>M. arion</i>	Britain	grazing sward height decline in ant hosts soil type	Thomas (1980)
<i>P. argus</i>	Britain	solar exposure	Thomas (1985)
<i>L. dispar</i>	Britain	water level in wetland	Duffey (1968)
<i>P. machaon</i>	Britain	water level in wetland	Dempster et al. (1976)
<i>L. bellargus</i>	Britain	sward height solar exposure wind exposure soil type	Thomas (1983)
<i>L. sinapis</i>	Britain	shade levels in woodland	Warren (1985)
<i>M. athalia</i>	Britain	woodland succession alternative hosts	Warren (1987a,b,c); Warren et al. (1984)
<i>L. camilla</i>	Britain	woodland succession	Pollard (1979)
<i>M. nausithous</i>	France	water levels in bogs vegetation height density of host ants	Thomas (1984b)
<i>M. telius</i>	France	water levels in bogs vegetation height density of host ants	Thomas (1984b)
<i>E. editha bayensis</i>	U.S.	soil type solar exposure alternative host plants	Murphy and Weiss (1988a)
<i>P. icarioides missionensis</i>	U.S.	local disturbance wind exposure alternative host plants	Weiss and Murphy (1989) Reid and Murphy (1986)
<i>I. mossii bayensis</i>	U.S.	solar exposure rock outcrops	Weiss and Murphy (1989)
<i>S. callippe callippe</i>	U.S.	fog frequency presence of hilltops	Weiss and Murphy (1989)
<i>D. Plexippus</i>	U.S.	forest microclimate	Calvert and Brower (1987)

Long-term subdivision of insect populations into small groups, however, can certainly significantly reduce genetic variation (Laing et al. 1976), but the implications of such circumstances for population persistence are unclear.

Importantly, butterflies almost invariably exist as regional metapopulations. Small habitats tend to support small populations, often with as few as 100 individuals, that frequently are extirpated by events that are part of normal environmental variation. The continued existence of such "satellite" populations requires the presence of one or more large reservoir populations which provide colonists to smaller, outlying habitat patches (J. A. Thomas 1984a; Ehrlich & Murphy 1987a).

Each species, subspecies, ecotype, or even local population has unique ecological characteristics that prevent ready generalizations about population dynamics. Not surprisingly, PVA for butterflies is therefore dependent upon detailed autecological studies that identify key environmental variables. As we illustrate below, quantification of environmental variables in the context of a metapopulation model appears to be an appropriate PVA structure for butterflies and other organisms sharing similar life history characteristics. The theoretical and empirical underpinnings of this approach are devel-

oped in detail by Andrewartha and Birch (1954, 1986) in their discussions of population dynamics, and by den Boer (1968, 1981) in his theory of "spreading of risk."

Environmental Factors and Population Persistence in the Bay Checkerspot Butterfly

Practical application of an "environment-metapopulation" approach to PVA is illustrated by long-term studies of the Bay checkerspot butterfly, *Euphydryas editha bayensis*, currently listed as a threatened species by the U.S. Fish and Wildlife Service (see also Ehrlich et al. 1975, Ehrlich & Murphy 1987a, 1987b, and 1981; Murphy & Weiss 1988a). The butterfly exists as two metapopulations, one highly fragmented in San Mateo County, the other more or less intact in Santa Clara County, California. It is restricted to habitat patches of native grassland that support a mixture of its larval host plants (*Plantago* and *Orthocarpus*) and adult nectar sources (including *Lomatium*, *Lasthenia*, *Layia*, and others) (Murphy et al. 1983; Murphy & Weiss 1988a). With one exception, the areas that support the appropriate mixture of grassland plant species are outcrops of serpentine soil, where introduced grasses and forbs

from Europe have been largely unable to invade native plant communities (Murphy & Ehrlich 1988). The first environmental factor that determines the distribution and abundance of this butterfly, then, is geological — the distribution of outcrops of serpentine rock.

The Mediterranean climate of central California is characterized by a cool rainy season (October–April) and a warm summer drought (May–September). The annual host plants on which Bay checkerspot butterfly larvae feed and adults lay eggs germinate following the first heavy extended rains in November or December. The butterfly is univoltine; adults fly in the latter part of the rainy season, from late February to early May. During this period, females lay masses of up to 200 eggs at the bases of their host plants. Newly hatched larvae form webs and feed gregariously on the oviposition plant until it is defoliated or until the larvae are large enough to enter diapause. Diapause extends through the summer drought and is broken by the onset of late autumn rains when larvae resume feeding.

The quantity and temporal distribution of rainfall varies greatly from year to year. Population size in the Bay checkerspot butterfly is largely regulated by the mortality rate of prediapause larvae each spring (Singer 1972; Singer & Ehrlich 1979). This mortality is controlled by the amount and timing of rainfall and the timing of adult butterfly emergence. Timing of emergence is determined by incident solar radiation on habitat slopes where larvae develop (Weiss et al. 1988). These environmental variables determine two proximate factors that regulate population size. The first is the phase relationship between the development of prediapause larvae and *Plantago* senescence. Spring rainfall delays senescence of *Plantago* until late in the prediapause larval feeding period. The later in the larval growth period that host plants senesce, the more larvae survive. The density of *Orthocarpus* is the second factor that affects population size. High densities of this secondary larval host plant increase the probability that larvae will continue to feed when *Plantago* senesces.

Recent studies have identified how topography within habitat patches determines the phase relationship between larval development and host plant senescence (Weiss et al. 1988; Weiss & Murphy 1989). Thermal microenvironments created by topographic variation (referred to as topoclimate) strongly influence both the development rates of immature stages (eggs, larvae, and pupae) and the timing of host plant senescence at the end of the rainy season. Postdiapause larvae gain mass faster on warmer slopes than on cooler slopes, in direct relation to insolation (Weiss et al. 1987). Faster larval development allows earlier adult emergence, which in turn allows earlier reproduction — crucial in the rapidly drying environment. The larvae that hatch from eggs laid on cool slopes by females that emerged early from warm slopes are those most likely

to reach diapause before host plants senesce, because host plants on cool slopes senesce later than those on warm slopes. This paradox, in which opposing slopes provide greater habitat quality at different stages in the butterfly life cycle, has implications for both reserve design and PVA. Topographic heterogeneity within habitat patches may be the most important physical feature in determining the persistence of Bay checkerspot butterfly populations once they are established.

The distribution and density of postdiapause larvae along topoclimate gradients change from year to year as the phase relationship between larval development and host plant senescence varies (Singer 1972; Murphy & Weiss 1986b). Consecutive years of drought, such as occurred from 1975–77, can cause severe butterfly population declines and even extinctions when host plants senesce particularly early (Ehrlich et al. 1980). Very wet years, such as during the El Niño of 1982–83, also can result in declines in population size when larval and pupal development are delayed by overcast weather longer than the host plant growing season is extended by added moisture (Dobkin et al. 1987). By and large, in a favorable year (a year with mean or slightly greater rainfall), more larvae survive on warmer slopes than survived there in the previous generation. In a less favorable year (particularly during drought), a higher proportion of larvae survive on cooler slopes than survived there in the previous generation. For example, larvae were found primarily on cool slope exposures at the Morgan Hill population in 1984, but by 1987 (after three years of favorable weather) the population had grown ten-fold and the majority of larvae were found on warmer slope exposures (Murphy & Weiss 1988b). The spatial distribution of larvae in a given year, and the amount and timing of rainfall during that growing season, determine the pattern of adult emergence, hence determine the mortality rates and spatial distribution of the subsequent generation. Weather, therefore, has important year-to-year carry-over effects on population size.

Parameterization of Environmental Factors

This qualitative understanding of the interactive effects of macroclimate and topoclimate is useful for conservation decision-making. Habitats can be ranked according to topographic criteria including overall diversity of topoclimate, spatial relationships between various topoclimate, and location relative to rain shadows of local mountain ranges (Weiss et al. 1988). Furthermore, macroclimate-topoclimate interactions have been formalized into a simulation model that predicts emergence dates for Bay checkerspot butterflies, given data on temperature, clear day insolation, larval growth rates, weight at molting, and duration of pupal stages (Weiss

et al., in preparation). The model takes an iterative cohort approach. A population is considered a collection of cohorts, each composed of individuals of a single developmental stage and exposed to identical environmental conditions (Currey & Feldman 1987). Rates of larval and pupal development are determined for cohorts exposed to insolation levels corresponding to a variety of slope exposures. The effects on larval growth of fog and low ambient morning temperatures, which occur during the growing season, are simulated by reducing cumulative exposure to insolation.

The model predicts the phenology of larval growth over a wide range of slopes, and allows comparison of flight season phenologies between years with different weather patterns, or between habitats with different topographic features. Initial results, based on 13 years of weather data from 1975 through 1987, indicate that the timing and duration of rainfall during the growing season are the best predictors of developmental phenology and adult emergence for a given habitat patch. But the complexity of larval developmental responses on different slope exposures rules out simple generalizations and emphasizes the importance of immediate population history in determining larval distribution across a topoclimate gradient. Nevertheless, this model allows identification of the effects of weather factors on changes in population size.

The results of two model runs illustrate the effects of weather on dates of adult emergence on different slopes. In 1976–77, the driest year on record for central California, postdiapause larval development began one month earlier than in 1982–83, the second wettest year ever recorded. The mean predicted date of adult emergence in the dry year, however, was only nine days earlier than the mean predicted date of emergence in the wet year (Fig. 1 and Fig. 2) (March 29, 1977, versus April 7, 1983). In the drought year, the spread in predicted emergence dates for cohorts on the warmest slope (S 11°) and the coolest slope (N 25°) was 37 days. The extended rains of 1982–83 delayed larval development to produce a 52-day spread in predicted emergence dates between slope extremes. Emergence dates can translate into butterfly population responses when the senescence times of host plants are known. Senescence dates theoretically may be predicted from late season rainfall, temperature, and insolation.

Importantly, the predictions of the model underscore the role of habitat heterogeneity in habitat quality. (Habitat heterogeneity can refer to any habitat features that vary in space, time, or both. For this species, habitat heterogeneity means topographic diversity.) The unique topography of an individual habitat patch determines how the butterfly population it supports will respond to specific weather events. For example, at Stanford's Jasper Ridge Preserve, butterfly populations on two separate habitat patches with different topographic

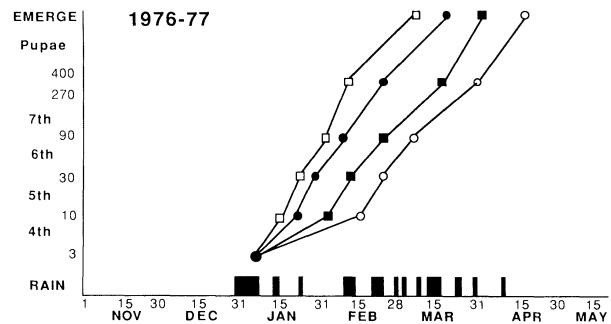


Figure 1. Postdiapause development (simulated) for 1976–77, a severe drought year. The y axis denotes larval development stages as mass in mg at molts (inner numbers) and larval instar (outer numbers/ words). For example, the sixth instar starts at 30 mg and molts into the seventh at 90 mg. The four lines track development on four different slopes. The earliest is south-facing, 11° tilt, followed by horizontal, N 17°, and N 25°. Rainfall days are denoted by black bars just above the X axis.

conditions, just 500 m apart, exhibited asynchronous changes in population size in 6 of 25 years from 1960–1985 (Ehrlich & Murphy 1987a). These differences effectively spread the risk of regional extirpation by reducing the probability of simultaneous local population extinction events.

Appropriate parameterization of weather influences on Bay checkerspot populations requires a model that quantitatively predicts the effects of host plant senescence timing on butterfly population size. Two alternate routes to predict population persistence can then be

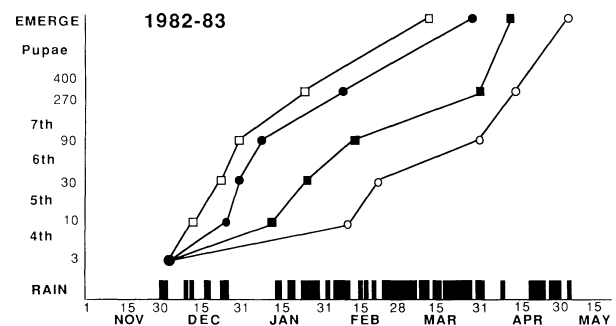


Figure 2. Postdiapause development (simulated) in 1982–83, a very wet year. Notation is the same as Figure 1. Note the differences between 1976–77 and 1982–83. Larvae started development later and emerged earlier in the drought year, while the deluges in 1982–83 extended the larval growth period and spread it out. Such differences in developmental phenology between slopes and between years can be interpreted to predict change in population numbers the next year.

followed. The first is based on extended time series of randomly generated weather sequences and estimates of the probability distribution of persistence times for various combinations of physical habitat configurations (area and topographic diversity), initial population sizes, and initial larval distributions along the topographic gradient. The predictive ability of this approach is constrained by the assumption that future weather patterns will be similar to those in the past, on which generated weather sequences are based. Incipient global warming and associated regional climate changes would present obvious violations of that assumption (see Murphy & Weiss 1989).

An alternative approach defines specific weather sequences that have a high probability of producing extinction events. Existing weather data, paleoecological records (such as tree rings), and predictions from global climate models can be examined for the frequencies of such events. The use of insolation as the phenological "accounting unit" allows quantification of the shifts in larval distributions between slopes. The probability distribution of the magnitude of such shifts can be estimated from model runs using historical weather records. This approach collapses the complex population response into a single output — the direction and magnitude of the shift of larval densities along the to-

poclimate gradient, which we have referred to as thermal advance or retreat (see Murphy & Weiss 1988b). If weather forces the larval population away from a substantial portion of the available topoclimate in a habitat (for example, from warm and moderate slopes to cool ones), extinction often will follow.

Metapopulation Dynamics and Population Persistence

The sensitivity of Bay checkerspot butterfly populations to year-to-year differences in rainfall and to differences in insolation between slope exposures suggests that local populations of the butterfly may be particularly susceptible to extinction. Observations of the extinction, recolonization, and subsequent extinction of a small population on Stanford's Jasper Ridge Biological Preserve bear witness to that supposition (Ehrlich et al. 1975), as does the apparent extinction of all populations save one in neighboring Santa Clara County during the 1975–77 drought in California (Murphy & Ehrlich 1980; Murphy & Weiss 1988a). That this species survives today implies that it persists as a metapopulation, or a collection of interdependent populations affected by recurrent extinctions and linked by recolonizations.



Figure 3. Black areas are serpentine soil-based grassland patches that constitute habitat for *Euphydryas editha bayensis*. As described in the text, the butterfly currently occurs in only a small number of these habitat patches. The metapopulation model predicts that habitat patches closer than 7 km to the largest patch, which supports the Morgan Hill reservoir population, are most likely to be occupied at any given time, thus should be prime targets for protection.

Recent studies of the dynamics of the Morgan Hill metapopulation (Harrison et al. 1988) provide a framework for considering metapopulation structure in PVA. In an effort to determine the extent, dynamics, and "equilibrium" configuration of the metapopulation unit, Harrison et al. first documented the distribution of the butterfly. In the study case, the disproportionately large size of one habitat island in the system and the huge population it supports suggested that it acted as a reservoir of colonists for surrounding smaller patches (Fig. 3). Adult butterflies were found on eight small patches within 5 km of the largest habitat area, while none were found in apparently suitable habitat patches at distances greater than 5 km.

The quality of all habitat patches was assessed to determine whether habitat quality of patches decreases with increasing distance from the largest habitat patch, a circumstance that could explain the pattern of patch occupancy. Patch size, topographic diversity, and resource abundance were measured as components of habitat quality for each patch. Results indicated that both habitat quality and distance from the reservoir population contribute to patterns of patch occupancy. That is, to be occupied, a habitat patch must be both near enough to the reservoir population and good enough in habitat quality characteristics. Historical information and simulation modeling then were used to estimate distance-dependent rates of extinction for each habitat patch in the system. (Since the time scale of the extinction-recolonization process is on the order of decades, rates could not be directly measured.)

Although the Harrison et al. study was not designed to address issues in population viability analysis, the extinction-recolonization predictions of the simulation model have value in conservation decision-making. The model assumes that all satellite populations in the region went extinct during the sustained drought of 1975–77 and later were reestablished, with few subsequent extinctions (see Murphy & Weiss 1988); and that the colonists of the small patches came from the reservoir population. A curve describing rates of immigration with distance based on 1987 data on patch occupancy was used to estimate annual rates of immigration for each patch. It was concluded that the radius of the Morgan Hill metapopulation is probably no greater than about 7 km, and patches more distant from the Morgan Hill main population are unlikely to support populations, since catastrophic environmental events (e.g., severe drought sequences) occur more frequently than those patches are likely to be colonized. The number of patches occupied within the distribution of the metapopulation in 1987 was six populations short of the maximum predicted by the model, a maximum expected to occur an estimated 30 years after a drought. (It is sobering to note that the return of a "50-year drought" took but 11 years, from 1977 to 1988, and the

loss of several populations, extant within the metapopulation matrix in 1988, is expected.)

In addition to dispersal from reservoir to satellite habitat patches, individuals sometimes disperse between adjacent outlying satellite patches. The model predicted that this "stepping-stone" colonization can increase immigration rates to distant islands, but only when: (1) a narrow range of parameter values exists with respect to the dispersal ability of the species, and (2) the islands are arranged linearly or are very large (i.e., comparable in size to the mainland). These conditions are met only in the outlying habitat patches located northwest of the reservoir population at Morgan Hill (Fig. 3). Indeed, apparent stepping-stone colonization has been observed in this area (Murphy & Weiss 1988a).

Metapopulation Parameters

As noted above, we are not yet at the point where risks and extinction probabilities can be parameterized; that is, we cannot say "the populations on Jasper Ridge Preserve have 95% probability of surviving X number of years." However, a Monte Carlo simulation based on the responses of the Jasper Ridge Preserve population (Harrison et al. 1988) could have application in a PVA for the Bay checkerspot butterfly. The results of that analysis indicated that (1) persistence times for populations increase with the natural logarithm of initial population size, and (2) small populations persist only for short periods. The importance of initial population size suggests that a large population such as that at Morgan Hill will prove quite resistant to extinction. Application of this Monte Carlo approach requires reasonably long-term records of population sizes, which now are only available for Jasper Ridge on the Stanford University campus. Generalization of Jasper Ridge data to other populations is steeped in uncertainty because each population has unique responses to weather based on its topography and recent history. Small differences in population responses were found to significantly affect persistence time (Harrison et al. 1988).

Recent estimates of the impacts of sampling on population size trajectories of the Jasper Ridge populations offer another approach that could have application to PVA (Harrison et al. 1990). That treatment assumed varying levels of density dependence and estimated population sizes in the absence of sampling. For the purposes of PVA, population size could be estimated based on varying levels of weather-induced mortality.

Discussion

Understanding the environmental parameters that determine population persistence and the factors associated with metapopulation structure that determine hab-

itat patch occupancy are the most important steps in population viability analysis for small-bodied, short-lived species with high reproductive rates and high habitat specificity. Our solar thermal model, which incorporates environmental parameters (insolation, rainfall, temperature) and field measurements of larval growth, provides the basis for a PVA for the Bay checkerspot butterfly. That habitat quality plays a role in patch occupancy, but appears to be less important to metapopulation dynamics than patch distance from the reservoir population, simplifies conservation efforts aimed at this threatened butterfly, at least under conditions prevalent in Santa Clara County, California. Even without a complete PVA, it is clear that the key conservation goal is to secure the habitat area that supports the reservoir population at Kirby Canyon (Murphy 1988). Furthermore, it appears reasonable to conclude that small, "low quality," serpentine soil-based grassland patches more than 7 km from the large reservoir patch are not likely to support the Bay checkerspot butterfly. Populations residing in large, high quality habitat patches within 7 km of the largest patch may be subject to extinction, but because they are likely to be rapidly recolonized, they should be targeted for preservation. Finally, because of the importance of distance to patch occupancy, the preservation of small, relatively low quality patches close to the largest patch could be as important, or more important, to the integrity of metapopulation dynamics in this system than preservation of larger, higher quality patches further away.

This observation does not consider other conservation goals, such as the preservation of other species, particularly the large number of narrowly endemic plant species associated with serpentine soil-based grasslands. Recognition by reserve designers of the crucial role of topographic diversity as a determinant of habitat quality for the Bay checkerspot butterfly, however, may bridge the gap between single-species conservation and whole ecosystem conservation. Many plants within the serpentine grassland are restricted to just one or several topoclimate. For such species, the Bay checkerspot butterfly may act as an effective "umbrella" species.

While PVA for the Bay checkerspot butterfly relies on nearly three decades of research (clearly an advantage that is rarely encountered in conservation), several hurdles remain before an accurate predictive model can emerge. First, even after successful parameterization of the key factors affecting population persistence, we face the challenge of determining the variances associated with the parameter estimates. This task is particularly daunting for a species that experiences year-to-year population size changes of an order of magnitude or greater. Appropriate quantification of life history features and reproductive characteristics is especially difficult. The distributions of individuals sharing similar fates are often "clumped" within habitats, because this

species lays its eggs in clusters and resource availability is slope-specific during certain periods. Second, factors other than topography bear on resource availability in ways that are incompletely understood. For example, the larval host plants and adult nectar sources of the Bay checkerspot butterfly are all early successional stage species. A moderate amount of grazing by cattle, which prevents habitat succession to a grass-dominated plant community, appears to be important to maintaining habitat quality for the butterfly. However, the effects of grazing intensity and timing are essentially unknown. Third, although metapopulation dynamics has been identified as playing an important role in the regional distribution and persistence of this butterfly, an understanding of the colonization process itself and the characteristics of effective dispersal corridors between habitat patches remains to be established (but see Harrison 1989).

Nevertheless, this "first cut" attempt at the structure of a PVA for the Bay checkerspot butterfly provides a guide for conservation efforts that target species with similar life history traits — short generation time, high potential rate of population increase, and high habitat specificity. Although we would like to produce a PVA with the finest resolution possible, PVA itself really is not an academic exercise. Population viability analysis that is of practical value to reserve designers and land managers must be simple enough to be usable and appropriately cost-efficient in this era of limited conservation funding. In this context, there is, of course, no substitute for common sense. As we have stressed, focusing on genetic or demographic factors in efforts to preserve local populations that have high densities is in most cases a misallocation of effort. An effective population viability analysis for this broad group of organisms should target the habitat features and resources that support populations across the widest range of likely environmental conditions. Understanding the key environmental elements that determine habitat quality can help differentiate between temporarily empty habitat patches and unsuitable ones, thereby allowing limited land-acquisition funds to be allocated optimally. In addition, a habitat-focused PVA can suggest where habitat restoration can make a significant contribution to species survival (Weiss & Murphy 1989).

Interestingly, the roots of PVA for species like the Bay checkerspot butterfly lie in the pest insect management literature. The analogue of PVA is the life table-based key factor analysis used to identify mortality factors correlated with population dynamics of insect pests. Eradication and conservation efforts both seek to identify the intrinsic and extrinsic factors that regulate populations. Microclimate calculations, degree-day summations, the use of Leslie matrices, and the iterative cohort approach to population modeling are all employed in integrated pest management (see Currey & Feldman 1987) and

have practical application in insect conservation. With that in mind, we should take great satisfaction, indeed, in borrowing from the literature on boll weevil control to help save the Bay checkerspot butterfly and the innumerable other highly endangered small and unsung species that challenge conservation biologists today.

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