Distribution of the Bay Checkerspot Butterfly, Euphydryas editha bayensis: Evidence for a Metapopulation Model

Susan Harrison; Dennis D. Murphy; Paul R. Ehrlich

DISTRIBUTION OF THE BAY CHECKERSPOT BUTTERFLY, *EUPHYDRYAS EDITHA BAYENSIS*: EVIDENCE FOR A METAPOPULATION MODEL

SUSAN HARRISON, DENNIS D. MURPHY, AND PAUL R. EHRLICH

Department of Biological Sciences, Stanford University, Stanford, California 94305

Small populations may be highly vulnerable to extinction by demographic accident or environmental adversity (Richter-Dyn and Goel 1972; Leigh 1981). Empirical observation supports the idea that local populations are often transient (Andrewartha and Birch 1954, 1985; Spight 1974; Ehrlich et al. 1980; Washburn and Corneli 1981). A tendency for local populations to become extinct, combined with a relatively low ability to disperse to and colonize new habitats, can lead a species to exhibit the "shifting mosaic" type of population dynamics first described by Levins (1970). Such species persist as "metapopulations," or populations of populations, as long as new populations are founded at a rate that balances the extinction of established ones (Levins 1970).

For ecological purposes, a metapopulation may be defined as a set of populations (i.e., independent demographic units; Ehrlich 1965) that are interdependent over ecological time. That is, although member populations may change in size independently, their probabilities of existing at a given time are not independent of one another, because they are linked by processes of extinction and mutual recolonization, processes that occur, say, on the order of every 10 to 100 generations.

Population ecologists since Andrewartha and Birch (1954) have recognized that models of single, isolated populations are inadequate for describing the dynamics of species in which populations are short-lived. Yet the metapopulation remains a poorly developed concept in empirical biology. With some exceptions (Gill 1978; Fritz 1979; Pokki 1981; Schoener and Spiller 1987), few studies have assessed the relative roles of within- and between-population processes in the population dynamics of a species or attempted to determine the rates and patterns of population extinction and colonization in a natural metapopulation. This may be, in part, because many metapopulations function on intractably large scales of time and space. Another practical problem is that of identifying a discrete metapopulation and delimiting it from other metapopulations of the same species.

The bay checkerspot butterfly (*Euphydryas editha bayensis*) exhibits the two features that predispose a species to "shifting mosaic" metapopulation dynamics.

First, its local populations are prone to relatively frequent extinction (Ehrlich et al. 1980). Extinctions are caused, at least in part, by aberrant weather patterns, which disrupt the delicate synchrony between the butterfly's annual life cycle and that of its host plant (Singer and Ehrlich 1979). Second, the sedentary behavior of the butterfly (Ehrlich 1961), combined with the patchy distribution of its habitat (see the section "Study System," below), limits its potential rates of colonization of empty habitats. It has been suggested that small populations of the bay checkerspot may "persist" by means of occasional recolonization, rather than through the regulation of population size (Singer and Ehrlich 1979).

In this paper, we analyze a system of habitat patches and small populations of the bay checkerspot butterfly that appear to constitute a discrete metapopulation, and we attempt to infer its extent, temporal dynamics, and equilibrium configuration. To do this, it is first necessary to define and measure habitat suitability in order to determine the number of occupied and unoccupied habitat patches. We then test the hypothesis that distance-dependent dispersal from a large source population influences the spatial pattern of habitat occupancy. Finally, historical information and simulation modeling are used to estimate hypothetical distance-dependent rates of colonization and area-dependent rates of extinction for each habitat patch in this system. These rates are not amenable to direct measurement, since the relevant time scale appears to be one of decades.

STUDY SYSTEM

Life History and Habitat

The bay checkerspot butterfly is univoltine, with adults appearing in March and April. Eggs are laid in masses of 25–150, and each female produces about 4–15 masses (C. Boggs, unpubl. data). Eggs hatch in 2–3 wk, and the larvae feed for 10–14 days before entering summer diapause in the fourth instar, during May. Diapause ends in the late autumn; post-diapause larvae feed during the rainy season, December–February, and then pupate.

The principal host plant of the bay checkerspot butterfly is an annual plantain, *Plantago erecta*. Species of owl's clover, *Orthocarpus*, are alternative hosts; they receive fewer egg masses than *P. erecta*, but some pre-diapause larvae move to *Orthocarpus* from *P. erecta* (Singer and Ehrlich 1979). The habitat of the bay checkerspot consists of grassland based on serpentine soil, which supports its larvae's host plants as well as its nectar sources *Lasthenia chrysostoma*, *Lomatium macrocarpum*, *Layia platyglossa*, and *Linanthus androsaceus* (Murphy 1984).

Serpentine outcrops, which are associated with faulting, are abundant in southern Santa Clara County, California (Bailey and Everhart 1964; Lindsey 1974). Some of these outcrops support native grassland and thus provide potential checkerspot habitat; others either support chaparral or grasslands dominated by introduced species or have been developed. The study area of roughly 15 by 30 km is located in the vicinity of Morgan Hill, California. It is bounded on the southwest by the Santa Cruz Mountains, in which the serpentine tends to support chaparral;
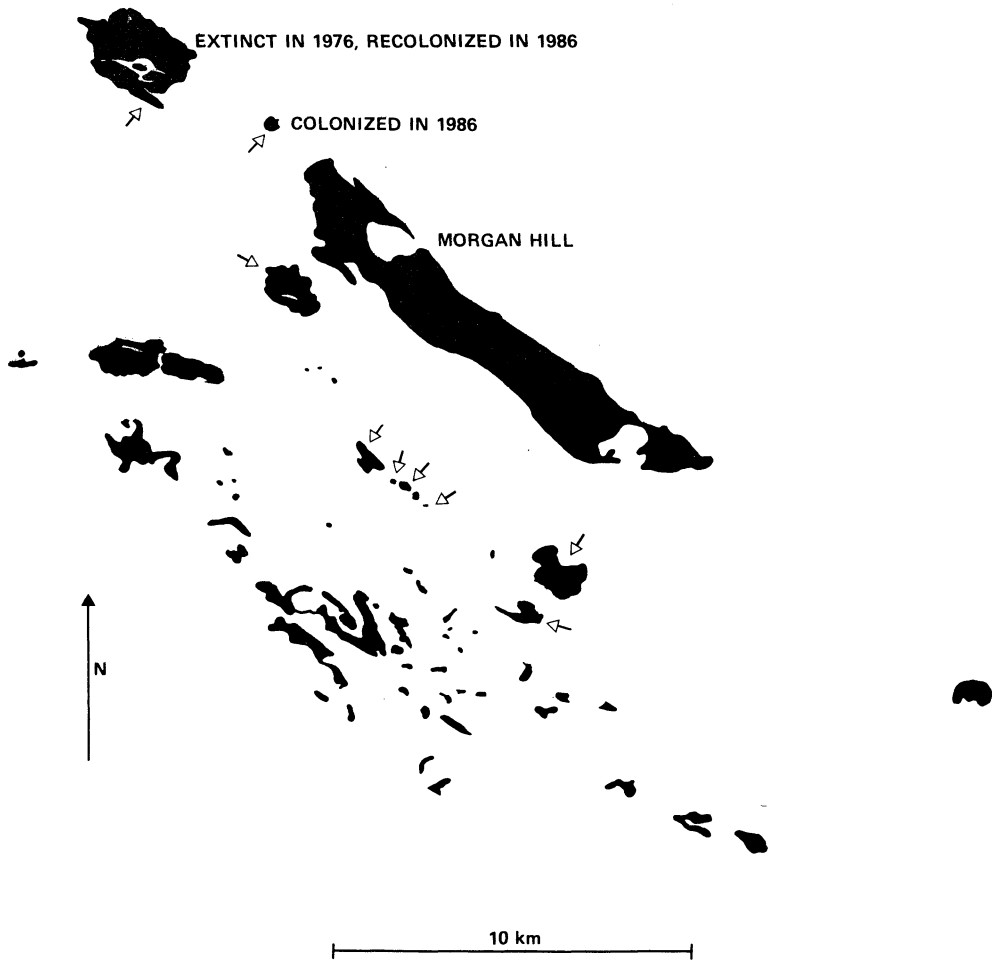
FIG. 1.—Distribution of serpentine grasslands in southern Santa Clara County, California, and butterfly populations in 1987. Population MH is located on the large patch labeled "Morgan Hill." Arrows indicate the locations of the seven small populations measured by the mark-recapture technique in 1987. Two additional patches at the upper left, colonized in 1986, also support populations.

on the northeast by the Inner Coast Range, which contains little serpentine; and on the northwest by the San Jose metropolitan area. There is no clear boundary on the southeast, although serpentine outcrops become sparse about 10–15 km southeast of Morgan Hill. Figure 1 shows the approximate distribution of serpentine grasslands and the locations of the bay checkerspot populations observed in 1987.

The area contains one very large patch (ca. 2000 ha) of serpentine grassland (see fig. 1), undoubtedly the largest existing habitat of the bay checkerspot. This patch supports a checkerspot population estimated to number in the hundreds of thousands of adults in each year from 1984 to 1986 (Murphy and Weiss, MS). The

population and its habitat patch are both referred to here as MH. Approximately 60 other patches of serpentine grassland are found in the region described above, ranging in size from 0.1 to 250 ha (see "Methods"). These small patches surround MH on its northwestern to southwestern side at distances of 1.4 to 20.8 km, measured from the Coyote Fault, which forms the western border of MH.

Distribution of Butterfly Populations

In a preliminary survey in 1986, adult checkerspot butterflies were found on eight of the small patches, 1.4–4.4 km from MH. No adult checkerspots were found in 1986 on approximately 15 patches of apparently suitable habitat, 4.9–20.8 km from MH. Distance-dependent colonization of the small patches by migrants from MH could explain the spatial pattern seen in 1986. However, a spatial gradient in habitat quality is an alternative that must be considered.

Habitat Quality

Most colonization-extinction models (e.g., MacArthur and Wilson 1967) propose that the sizes of island populations, and hence their expected extinction rates, are functions of island area. For populations of the bay checkerspot butterfly, the area of serpentine grassland patches probably is important, at least to the extent that some minimum size must exist below which a patch cannot support a population. However, other characteristics of patches are likely to influence habitat quality for the butterfly, including topography and resource abundance.

Steep southern and southwestern slopes, which receive high winter and spring insolation, are markedly different environments for the bay checkerspot butterfly from northern and northeastern slopes (Singer and Ehrlich 1979; Dobkin et al. 1987; Weiss et al., in press). Pre-diapause larvae must complete development to the fourth instar (the diapausing stage) in springtime before the host plant on which they feed senesces. Their survival at this stage is the primary determinant of size changes in the bay checkerspot populations at Jasper Ridge Biological Preserve, San Mateo County, California (Singer and Ehrlich 1979). In most years, eggs from southern and southwestern slopes contribute little to future population size because *Plantago erecta* senesces early on these slopes, and the larvae on them die. But in unusually wet years, when plant senescence on warm slopes is delayed, larvae on warm slopes contribute disproportionately to the population 2 yr hence, because greater insolation causes these larvae to develop faster, to emerge and oviposit sooner, and thus to give their own progeny a head start in the next year's race against senescence (Weiss et al., in press). Because topography and yearly weather interact in this complex fashion to affect population growth and because the study patches vary in their slope composition, patch area probably needs to be divided into several topographical categories in order to be a good indicator of habitat quality for the checkerspot butterfly.

In addition to varying in area and topography, the patches of serpentine grassland differ in the densities of the bay checkerspot's plant resources they support. Land use is a major factor: grasslands that are lightly to moderately grazed tend to contain a higher proportion of native species, including the host and nectar plants of the butterfly, than do ungrazed or heavily grazed grasslands (L. Huenneke,

unpubl. data; pers. obs.). The abundance of host and nectar plants exerts a significant impact on the population dynamics of the bay checkerspot butterfly. When present in sufficient densities, *Orthocarpus* (which usually senesce later in the season than does *P. erecta*) appear to abet the survival of bay checkerspot populations through dry years, when *P. erecta* tends to senesce early (Singer and Ehrlich 1979), and thus may be a factor in preventing extinction. Abundant nectar may allow females to produce extra egg masses toward the end of the flight season, which in turn may cause a population in a nectar-rich habitat to build up a "buffer" during favorable years that decreases its risk of extinction in bad years (Murphy et al. 1983).

History of Extinction

Some information exists on the causes, location, and timing of local extinctions of the bay checkerspot butterfly in the Morgan Hill area. The severe drought of 1975–1977 caused the disappearance of numerous *Euphydryas editha* populations around California (Ehrlich et al. 1980). In the Morgan Hill area, three bay checkerspot populations (which did not include MH) were known before the drought. All three were found to be extinct in 1978 (Murphy and Ehrlich 1980). One of the three populations inhabited the largest habitat patch (excluding MH) in this area. The most likely scenario, in light of this information, is that all the populations that existed on the small patches in the Morgan Hill region at that time became extinct in 1975–1977. It is inconceivable that the MH population could have disappeared in the drought, because of its present large size, though it may have been severely reduced in numbers. The small populations seen in the 1986 preliminary survey thus may have been the product of 9 yr of recolonization, following complete extinction in the drought.

The 1975–1977 drought was the most extreme in California's recorded history; however, it has been called a "50-yr drought" because of the frequency of severe droughts in the past. Major droughts occurred in California in the years 1923–1924, 1863–1864, 1857, and 1827–1829 (California Department of Water Resources 1977; Kahrl 1979).

METHODS

Number of Populations and Potential Habitats

Potential habitat for the bay checkerspot butterfly was systematically sought during January and February 1987 on the serpentine outcrops shown on geologic overlays of seven 1:24,000 topographical quadrangles: Santa Teresa Hills, San Jose East, Mount Madonna, Morgan Hill, Gilroy, Chittenden, and Loma Prieta, California (U.S. Geological Survey). Fifty-nine outcrops on which the larval host *Plantago erecta* was found were designated patches of potential habitat. Patches were each searched for populations of the bay checkerspot three to five times, depending on their sizes, during the 1987 adult flight season (March–April). The patches on which bay checkerspot populations were found in 1987 are henceforth referred to as "occupied" patches.

The eight sites on which adult bay checkerspots had been found in the 1986

TABLE 1

CORRELATION MATRIX OF DISTANCE AND HABITAT-QUALITY VARIABLES

	M	P	L	O	WA	MCA
M	1.0					
P	0.18	1.0				
L	0.39	0.32	1.0			
O	0.17	0.02	0.33	1.0		
WA	−0.21	−0.03	−0.07	−0.07	1.0	
MCA	−0.21	−0.14	0.07	0.13	0.67*	1.0

NOTE.—M, distance from MH; P, *Plantago* density; L, *Lasthenia* density; O, *Orthocarpus* density; WA, warm area; MCA, moderate area + cool area.
  * $P < 0.05$.

preliminary survey were searched for larvae during the 1987 post-diapause larval season (February), to ascertain whether breeding was occurring on these sites.

Measurement of Habitat Quality

From the geologic overlays, the distance in kilometers from the nearest edge of MH, the area in hectares (using a digitizer), and the percentages of warm, moderate, and cool slopes were measured for each patch. (Maps were field-corrected, when necessary, for differences between the serpentine shown on the map and the extent of serpentine grassland.) Topography was measured using the grid system described elsewhere (Murphy and Weiss, MS). Warm, moderate, and cool slopes were defined in terms of aspect and tilt angle. Warm slopes face south, southwest, or southeast at an angle of more than 7°; cool slopes, north at more than 7° or northeast at more than 12°; moderate, all other slopes. These slope categories correspond to clear-sky solar-radiation values of >6.0, <5.0, and 5.0–6.0 kwh m^{-2} d^{-1}, respectively, on March 21 at the 37.5°N latitude of Morgan Hill (Weiss et al., in press).

Density indexes for *Plantago erecta*, *Orthocarpus*, and *Lasthenia chrysostoma* were obtained using transects. Three to 10 transects (depending on the size of the patch) were walked from one edge of the habitat patch (defined by the first *P. erecta* found inside the boundary of the serpentine shown on the geologic overlay) to the other. Every 10 paces, the presence or absence (within a ½-m radius) of each of the three plants was noted. The percentage of these sample points at which a plant was present was used as an index of the density of that plant on the patch. No significant correlations were found between patch area and the plant-density indexes (see table 1; "Results"), indicating that this method was unbiased with respect to patch area.

Logistic regression (Cox 1970) was used to test the influence of distance from MH, warm area, moderate area plus cool area, and densities of the three plant species on the presence or absence of butterflies on 59 grassland patches. Logistic regression tests the effects of one or several independent variables (which may be discrete or continuous) on a binary dependent variable: in this case, presence versus absence of butterfly populations. The model has the form

$$p = e^r/(1 + e^r),$$

where p is the probability of a "success" (e.g., presence of butterflies), and r is a regression equation (constant $+ aX_1 + bX_2 + cX_3 + \ldots + fX_6$). The BMDP stepwise logistic-regression procedure PLR (BMD 1985) was used to estimate the regression parameters. Significance limits for removing and entering variables at each step were set at $P < 0.10$, such that the procedure included in the final model only the independent variables whose effects were significant at this level.

Estimation of Population Sizes

Sizes of the seven populations extant in both 1986 and 1987 were estimated using a mark-recapture technique. Each site was visited three times at 3–4-day intervals. Each butterfly handled was marked to indicate the day and site on which it was captured. The site-specific mark allowed the detection of movements between the seven sites by marked butterflies. Population sizes and their variances were estimated using the Fisher-Ford technique on data for combined sexes (Begon 1979). Combining sexes reduced the total variance for each population and did not consistently bias the estimates in either direction compared with estimates derived from analyzing data separately for males and females. Population estimates and their standard deviations are shown in table 2.

Sizes of the seven populations were regressed on total patch area. Because the variance of the population-size estimates increases linearly with the mean, a logarithmic transformation was employed (Sokal and Rohlf 1981).

RESULTS

Pattern of Patch Occupancy

Seven breeding populations existed in both 1986 and 1987. Two additional sites appear to have been recently colonized, since populations were found on them in 1987 but not in 1986 (mark-recapture estimates were not attempted on these sites since numbers appeared extremely low). One site on which a single adult was found in 1986, but no larvae or adults were found in 1987, was not categorized as supporting a population. The habitats supporting the nine 1987 populations were 1.4–4.4 km from MH.

Distance and Quality Effects

In the logistic-regression analysis, all six variables were significant ($P < 0.10$) in explaining the presence or absence of butterflies on the 59 patches of potential habitat. The best-fitting regression expression for presence or absence versus the distance and quality of patches is

$$r = -9.79 \text{ (distance)} + 1.01 \text{ (moderate area} + \text{cool area)}$$
$$- 1.22 \text{ (warm area)} + 0.85 \text{ (Plantago)} \tag{1}$$
$$+ 0.32 \text{ (Lasthenia)} + 0.18 \text{ (Orthocarpus)} - 35.68 .$$

The one-sample Kolmogorov-Smirnov test for the goodness of fit of data to an

TABLE 2

Suitable Habitat Patches

Patch Number	Distance from MH (km)	Area (ha)	Quality (eq. 2)	Exp N (eq. 3)	Obs $N \pm$ SD
1	4.6	121.2	66.34	325	0
2	6.0	92.7	37.55	282	0
3	7.9	58.4	60.39	221	0
4	4.4	249.9	268.12	476	*
5	2.0	21.5	5.80	130	*
6	1.4	106.0	132.54	299	344 ± 131.1
7	3.6	19.0	18.32	122	69 ± 32.2
8	4.1	0.9	5.32	24	10 ± 5.47
9	4.0	3.2	7.73	47	158 ± 54.8
10	4.0	2.5	7.05	42	56 ± 25.1
11	4.0	55.0	38.01	217	176 ± 70.8
12	2.7	83.0	76.07	270	287 ± 101.6
13	4.9	2.4	10.22	31	0
14	6.4	2.6	5.39	28	0
15	6.9	3.7	4.98	51	0
16	7.8	2.8	5.25	44	0
17	7.7	0.5	6.56	18	0
18	7.7	0.4	7.09	19	0
19	7.4	1.3	13.64	29	0
20	8.3	5.8	5.99	65	0
21	8.4	1.5	6.31	32	0
22	8.8	0.9	8.93	24	0
23	9.3	6.4	7.44	68	0
24	7.0	0.3	7.27	14	0
25	20.8	19.2	23.03	122	0
26	20.5	1.2	12.92	28	0
27	10.4	20.9	17.39	128	0

Note.—Quality is as defined in the logistic-regression analysis of butterfly presence and absence (eq. 2). Exp N, expected population sizes from the area regression (eq. 3). Obs N, observed sizes of the seven populations extant in 1987.
 * The two populations founded in 1986.

intrinsic hypothesis indicates that this model cannot be rejected at the 0.20 level (Kolmogorov-Smirnov $D = 0.045$, $n = 59$; Sokal and Rohlf 1981).

This result indicates that the likelihood of a patch's being inhabited by butterflies depends on both its distance from MH and its "quality," in terms of the five habitat variables. In order to define quality, it is necessary to separate its effects from the strong effect of distance from MH. This can be done by repeating the logistic-regression analysis on a subset of the data: those patches (nine occupied and six unoccupied) that are within 4.4 km of MH, which is the distance of the farthest patch occupied in 1987. Within this radius, distance has no relation to occupancy (Wilcoxon rank test, $U = 33$, df $= 6, 9$; Sokal and Rohlf 1981). The result of this second logistic-regression analysis is the expression

$$\text{quality} = 1.45 \text{ (moderate area + cool area)} - 0.54 \text{ (warm area)}$$

$$+ 0.60 \text{ (}Plantago\text{)} + 0.09 \text{ (}Lasthenia\text{)} \tag{2}$$

$$+ 0.10 \text{ (}Orthocarpus\text{)} - 47.61 \text{ .}$$

This model likewise cannot be rejected at the 0.20 level (Kolmogorov-Smirnov $D = 0.004$, $n = 16$; Sokal and Rohlf 1981).

The only significant correlation between variables is that of the area of warm slopes to the area of the moderate slopes plus the cool slopes on a patch (table 1). The absence of significant correlations between distance and the habitat variables indicates that the distribution of butterfly populations is probably not the result of a spatial gradient in habitat quality.

The negative coefficient seen in the regression for the warm-area term is not readily explainable on biological grounds. It is evidently a byproduct of the significant correlation (table 1) between the warm area and the moderate area plus cool area; removal of the latter term from the second regression changes the warm-area coefficient from -0.54 to -0.05. The term is left in because, with respect to habitat quality, this analysis is intended only to provide the descriptive fit that best categorizes patches; it is not aimed at testing the biological significance of specific habitat variables.

The second logistic-regression formula (eq. 2) constitutes a quantitative definition of habitat quality, separated from the effects of distance. It can be employed to determine which of the distant, unoccupied patches are probably suitable for butterfly populations and which are not. "Quality" as in equation (2) was calculated for all patches, including the 43 that are more than 4.4 km from MH. The lowest-quality patch that was occupied (patch 8 in table 2) supported a population estimated at 12 ± 5.47 SD in 1987. If this patch is used as a minimum standard for a habitable patch, a total of 27 patches can be considered of adequate quality, that is, as good as or better than patch 8. Table 2 shows these 27 patches (9 occupied and 18 unoccupied) and their distances from MH, areas, and habitat-quality scores. The other 32 patches, lower in quality than one that supported only 12 butterflies in 1987, are presumed to be of inadequate quality to support checkerspot populations.

These results suggest that the distribution of butterfly populations is controlled in an absolute, "threshold" manner by the distance from MH and by the five habitat variables studied (fig. 2). Only those patches that are both "good enough" (as good as the poorest occupied patch) and "near enough" (as near to MH as the most distant occupied patch) are inhabited. Of the remainder, 6 are near enough but too low in quality, 18 are good enough but too distant, and 26 are both too far from MH and too low in quality to support populations.

Population Sizes

Population-size estimates and their standard deviations are shown in table 2. The logarithm of patch area is a significant predictor of the logarithm of population size:

$$\ln N = 3.24 + 0.53 \ln(\text{total area}) \tag{3}$$

($r = 0.84$, df $= 5$, $P < 0.05$).

In separate simple regressions, the only other habitat variable that was significant in predicting population sizes was $\ln(\text{warm area})$ ($r = 0.81$, df $= 5$, $P < 0.05$).
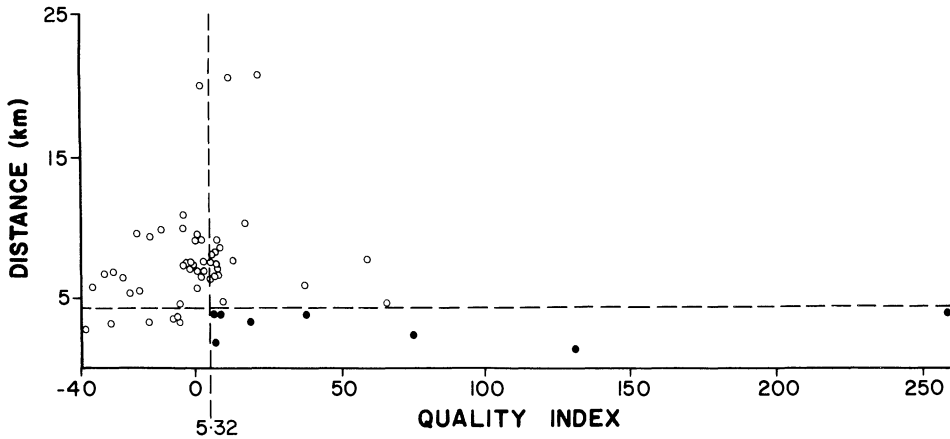
FIG. 2.—Habitat-quality scores versus distance from MH, for the 59 patches of potential habitat for the bay checkerspot in the study area.

The relationship of observed population sizes to patch areas (eq. 3) can be used to predict the sizes of the populations that would have been present in 1987 on the suitable but distant sites, had these been colonized. These estimates are shown in table 2.

Transfers

Of the 114 marked butterflies that were recaptured, 14 (12.4%) were recaptured on sites other than those on which they were marked. These transfers are shown in table 3.

DISCUSSION

These results indicate that in the study area suitable habitat patches for the bay checkerspot butterfly remain unoccupied because they are too distant from a source of colonists. This constitutes evidence for the existence of a metapopulation with a "mainland and islands," or "Boorman-Levitt," structure (Boorman and Levitt 1973; Wilson 1975).

Do MH plus the 27 small, suitable habitat patches constitute a single, discrete metapopulation? Whether the entire collection of patches can be considered a metapopulation depends on whether all the patches are interconnected by at least occasional dispersal. The question is then whether colonists from MH (or from other patches) ever reach the most distant patches.

The pattern of patch occupancy can be used to calculate the annual rates of colonization of suitable patches as functions of their distances from MH, if two assumptions are made. (1) Complete extinction of the small populations occurred in 1975–1977, and few extinctions have occurred since then; thus, the 1987 pattern results from 10 yr of colonization. (2) All or nearly all colonization of the small patches has come from MH. A curve describing rates of immigration with distance

TABLE 3

Transfers of Marked Butterflies between
the Seven Populations in 1987

Date	Sex	From Patch	To Patch	Distance Moved (km)
4-9	M	10	9	0.1
4-12	M	10	9	0.1
4-12	M	10	9	0.1
4-12	F	9	8	0.2
4-14	M	9	7	0.8
4-15	M	10	9	0.1
4-15	M	10	9	0.1
4-15	M	10	9	0.1
4-15	M	9	8	0.2
4-15	F	7	10	0.9
4-15	M	9	10	0.1
4-16	F	12	11	0.8
4-16	M	10	9	0.1
4-16	M	11	12	0.8

and time can then be fitted to the 1987 data on patch occupancy and used to estimate annual rates of immigration for each patch.

The negative-exponential function has extensive empirical (Wolfenbarger 1949; Diamond et al. 1976; Gilpin and Diamond 1976, 1981) and theoretical (Kitching 1971) support as a description of immigration with distance for organisms dispersing between discrete habitats. According to this model, the probability per unit of time of colonization of a given patch is

$$I = e^{-D/D'},   (4)$$

where D is the distance from the source to the target patch, and D' is a species-specific dispersal constant representing the average distance moved by successful colonists. In the absence of data on long-distance movements by checkerspot butterflies, D' must be fitted from the available data. (The conclusions are not markedly altered if, in place of eq. 4, we use an immigration function based on the "random walk": $I = \exp(-D^2/D')/D$ [Gilpin and Diamond 1976]; Harrison, unpubl. data.)

The cumulative probability of colonization after 10 yr of immigration with no extinction can be represented by

$$P(T) = P(T - 1) + I[1 - P(T - 1)],   (5)$$

where $P(T)$ is the probability that a patch is colonized by year T, and I, immigration rate, is the negative exponential of distance as in equation (4). Equation (5) was fitted to the data on patch occupancy (table 2) using a computer simulation. The best-fit value of D' was 1.7 km (fig. 3; fit = 1 - (mean squared error)$^{1/2}$ = 0.762).

Values of D' from 1.5 to 2.0 yield the relationships of yearly immigration rates to distance from MH shown in figure 4. Using the best-fitting value of $D' = 1.7$
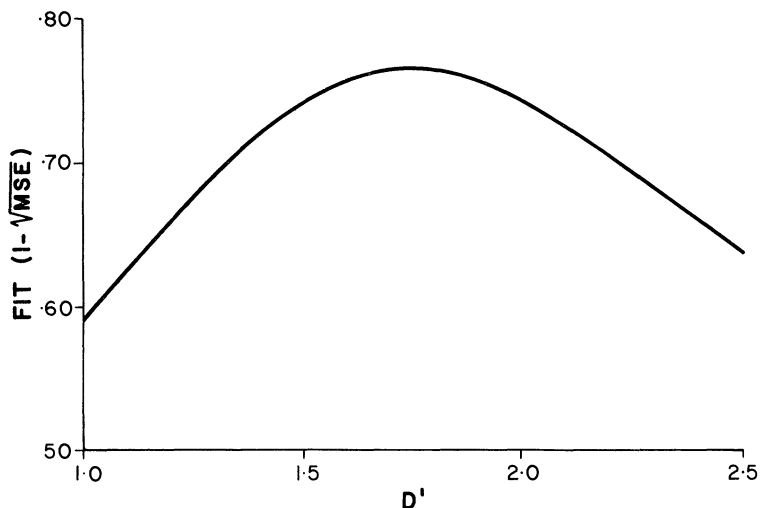
FIG. 3.—Fit of the dispersal constant D' in the negative-exponential immigration function $(I = e^{-D/D'})$ to the 1987 pattern of patch occupancy, assuming 10 yr of cumulative colonization.

km, the cumulative probability of colonization with time for patches at various distances from MH is as shown in figure 5.

The lowest possible rate of extinction that can be assumed, given what is known, is once in roughly 50 yr, but this rate is attained only if all populations survive from their founding until the next major drought. This is probably an underestimate of extinction, but as an outside limit for population persistence, it implies that any patch with a low cumulative probability of being colonized after 50 yr has a correspondingly low probability of ever supporting a population. Using the above function for colonization with distance, we can calculate for each patch the time until its chance of becoming colonized equals or is greater than 50% (table 4). The maximum predicted occupancy after 50 yr equals the sum of all patches' 50-yr colonization probabilities, or 16.72 patches.

By this estimation, which is conservative with respect to its assumptions about extinction, the radius of the Morgan Hill metapopulation is about 7 or 8 km. Patches at a greater distance from MH than this are unlikely ever to support populations, since catastrophic extinction events will occur more frequently than these patches are likely to be colonized. The metapopulation in 1987 was then six or seven populations short of its expected maximum, to be reached in an estimated 30 more years.

This conclusion is subject to two modifications, one positive and one negative in relation to the metapopulation's spatial extent. The negative one has already been mentioned: extinctions of small populations probably occur more frequently than once every 50 yr. The positive one is that the foregoing calculations have assumed that all colonization must come from MH. How would "stepping stone" coloniza-
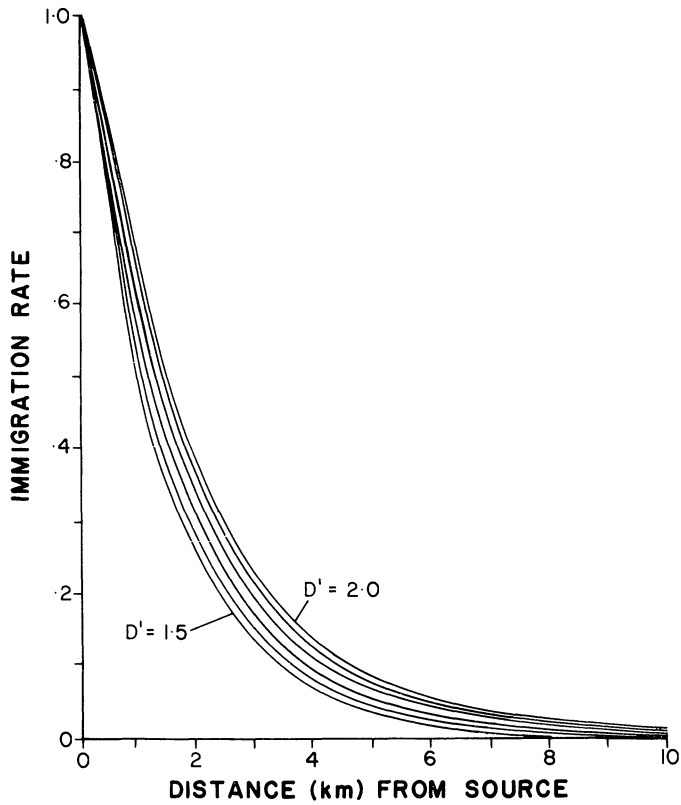
Fig. 4.—Predicted yearly immigration rates as a negative-exponential function of distance ($I = e^{-D/D'}$), for values of the dispersal constant D' from 1.5 to 2.0 km.
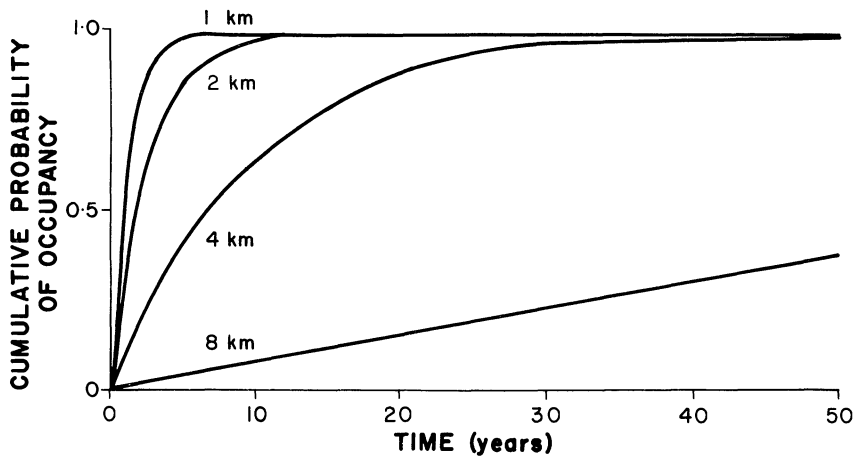

Fig. 5.—Predicted cumulative probabilities of colonization after 50 yr for patches 1, 2, 4, and 8 km from MH ($D' = 1.7$ km).

TABLE 4

EXPECTED NUMBER OF YEARS TO 50% PROBABILITY
OF COLONIZATION FOR THE FOURTEEN NEAREST
HABITAT PATCHES

Patch Number	Distance (km)	Time (yr)
6	1.4	2
5	2.0	2
12	2.7	4
7	3.6	6
9	4.0	7
10	4.1	8
4	4.4	9
1	4.6	11
13	4.9	13
2	6.0	24
14	6.4	30
15	6.9	40
19	7.4	>50
16	7.8	>50

NOTE.—Using equations (4) and (5); $D' = 1.7$ km. The catastrophic-extinction model predicts that the radius of the metapopulation is about 7 km.

tion between the small patches affect the chances of colonization of distant patches?

Stepping-Stone Effects on Colonization Rates

Significant stepping-stone colonization seems unlikely, a priori, because of the difference, of three to four orders of magnitude, between the sizes of MH and the small populations. If per capita rates of dispersal and successful colonization are so low that MH, with at least 400,000 adults in 1987 (Murphy and Weiss, MS), has provided colonists to only nine patches in 10 yr, then several small populations of 10–500 adult butterflies are unlikely to add greatly to the net rates of colonization in the system.

However, per capita rates of emigration by the bay checkerspot from the populations at Jasper Ridge appeared to be higher at low population sizes (Gilbert and Singer 1973). A significant inverse relationship between population size and per capita dispersal could augment the importance of stepping-stone colonization in the MH system.

Stepping-stone colonization can be modeled using the following extension of the immigration function given earlier:

$$I_i = e^{-D/D'} + b \sum_{j=1}^{26} e^{-D_{ij}/D'} p_j, \qquad (6)$$

where I_i is the yearly rate of immigration to patch i, j's are all patches other than i, D_{ij}'s are the distances from patch i to each patch j, and p_j's are the probabilities at each time unit that each patch j is occupied. The first term represents the immigra-

TABLE 5

Effects of Varying Degrees of Stepping-Stone Colonization

b	Best-Fit Value of D' (km)	Best Fit to 10-Yr Data $1 - (MSE)^{1/2}$	Patches >50% Likely to Be Colonized within 50 Yr
0	1.7	0.762	1, 2, 4–15, 24
0.0001	1.7	0.762	1, 2, 4–15, 24
0.001	1.7	0.761	1, 2, 4–15, 19, 24
0.01	1.7	0.747	1, 2, 4–21, 24
0.1	1.3	0.608	1–22, 24–27

Note.—The constant b weights the small patches versus population MH in the absolute numbers of colonists produced. D', fitted dispersal constant in the negative-exponential function; MSE, mean squared error of model.

tion from MH, and the second term gives the immigration from all occupied small patches. The constant b weights the difference between MH and the stepping-stone populations in their production of colonists. If per capita dispersal rates are the same in large and small populations, then b is simply N_j/N_{MH}, or roughly 0.0001–0.001.

To test the possible results of stepping-stone colonization, a 50-generation simulation of the 27 patches was created, in which the cumulative colonization probability for each patch in each generation was calculated using equation (5) and the stepping-stone formula for immigration rates (eq. 6). At $t = 0$, the cumulative probability of colonization of each patch is zero. At $t = 1$, the cumulative probability equals the immigration rate from MH, that is, the negative exponential of the distance of the patch from MH. In each successive generation, each patch's immigration rate equals its immigration rate from MH plus the sum of its immigration rates from all other patches. Interpatch immigration rates equal the negative exponential of the interpatch distance (measured from the geologic overlay maps) divided by the constant D', times the cumulative probability that the other patch has been colonized, times the constant b. Probability accumulates over time as in equation (5).

Values of $b = 0$ (no stepping-stone behavior), $b = 0.0001$, $b = 0.001$ (per capita dispersal in small populations 1–10 times that in the large one), $b = 0.01$ (per capita dispersal in small populations 10–100 times as high), and $b = 0.1$ (per capita dispersal in small populations 100–1000 times as high) were used. The value of the dispersal constant D' that gives each value of b the best possible fit to the data under the 10-yr model (as in fig. 3) was used. The results of this simulation are presented in table 5.

Table 5 shows that values of b must be very high to have an appreciable effect on the colonization of patches, even after 50 yr. When $b = 0.01$, 6 more patches are occupied than when $b = 0$; $b = 0.1$ yields 12 more occupied patches than when $b = 0$. But these values of b imply extremely high dispersal tendencies in butterflies from small populations, relative to those in the large population. Under the more probable assumption of $b = 0.001$, only one more patch is likely to be colonized within 50 yr; the most distant patch more than 50% likely to be occupied

is 7.4 km instead of 7.0 km from MH. Note that values of b that greatly increase patch occupancy (i.e., 0.01, 0.1) also appear to worsen the fit of the immigration function to the data, hinting that stepping-stone colonization has not been impor- tant in producing the existing pattern.

This result accords qualitatively with the theoretical results of Gilpin (1980), who found that stepping-stone islands are unlikely to increase immigration rates to distant islands, except under certain circumstances: (1) a narrow range of parame- ter values, with respect to the species' dispersal ability and the spacing of stepping stones; (2) a chain of stepping stones; (3) very large (i.e., comparable to the mainland in size) stepping stones. None of these conditions appears to pertain to the MH metapopulation. However, some transfers of butterflies between adjacent populations were detected during the mark-recapture study, suggesting that the question of stepping-stone colonization deserves further empirical investigation.

Continuous Extinction

The other issue that strongly affects the spatial extent and dynamics of the metapopulation is the rate and temporal pattern of extinction. If extinctions of populations are caused only by major, devastating droughts, such as that of 1975– 1977, then they are probably (1) infrequent; (2) completely correlated between all the patches, which are all subject to the same macroclimatic regime; and (3) virtually independent of population size over the range in question (10–500 adults). According to 27 yr of study of other populations of *Euphydryas editha* (Ehrlich et al. 1975, 1980; Singer and Ehrlich 1979; Ehrlich and Murphy 1981), conditions 1 and 2 are unlikely to be true. Extinctions probably occur more often than extreme drought years and are caused in part by factors specific to particular populations (local environmental changes, interaction of weather patterns with local topography and vegetation). As for condition 3, no known data bear directly on the relationship of extinction probabilities to population size in *Euphydryas*.

The best evidence concerning the effects of environmental variability on the sizes, hence chances of extinction, for bay checkerspot populations is in the population-size data from Jasper Ridge. Populations JRC and JRH were measured by the mark-recapture method from 1968 to 1986 (unpubl. data, analyzed by the Jolly-Seber method). Yearly changes in the sizes of both populations over this time period are significantly, though weakly, correlated with rainfall patterns, indicating that the two populations fluctuate in response to the same environmen- tal factors. But they do so according to such different numerical relationships that the size changes of JRC and JRH are not significantly correlated with each other over time ($r = 0.001$, df $= 18$; Ehrlich, A. J. Milgram, and Murphy, MS).

In both JRC and JRH, the proportional change in population size, $\Delta N = N_{T+1}/N_T$, is not significantly correlated with N_T, the population size in year T (JRC, $r = -0.29$; JRH, $r = -0.34$; df $= 16$, $P > 0.10$). In fact, no significant relationship was found, in either population, between N_T and N_{T+1} (JRC, $r = 0.06$; JRH, $r = 0.25$; df $= 16$, $P > 0.10$). The Durbin-Watson test (Neter et al. 1985) also did not indicate significant temporal autocorrelation (JRC, $D = 1.90$; JRH, $D = 1.50$; $n = 19$, $P > 0.05$). This uncorrelated behavior allows ΔN to be treated as a random variable, with a distribution that can be estimated from the JRC and JRH data.
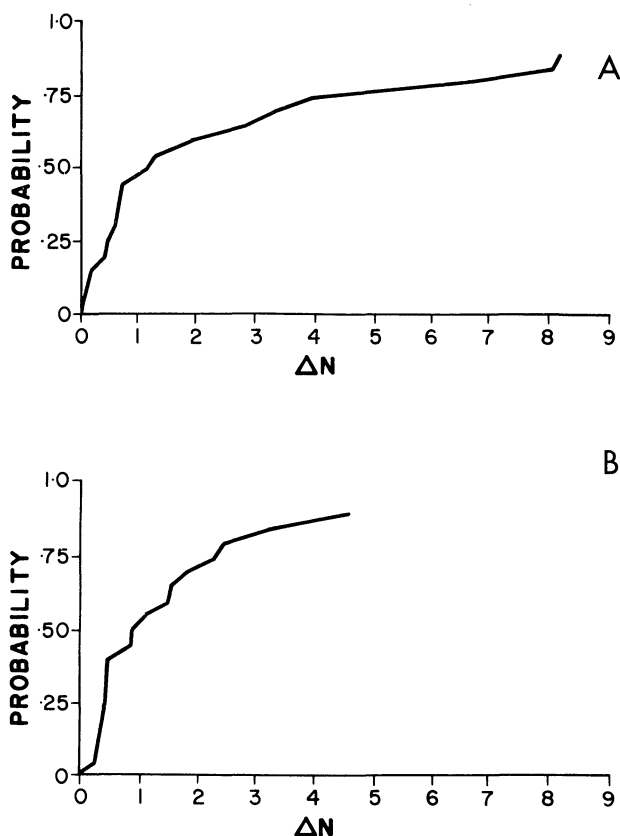
Fig. 6.—Cumulative probability distributions of values of yearly population-size change, ΔN, from 19 yr of data on the sizes of the bay checkerspot populations at Jasper Ridge: A, population JRC; B, population JRH.

Figure 6 shows the cumulative probability distributions of ΔN for JRC and JRH, respectively, from the 19-yr data. As this figure suggests, JRC experienced somewhat greater variation in size over the period 1968–1986 than did JRH: the range of ΔN values is greater.

The mean times to extinction of checkerspot populations of different initial sizes were calculated via simulation. A population of a given initial size is iterated through a series of yearly size changes, drawn at random from the distributions of ΔN shown in figure 6; the population becomes extinct when it crosses a threshold of minimum population size. The simulation calculates the mean number of years (T_e) until extinction from 1000 replicate runs. The simulation was run for initial population sizes of 10–500 in steps of 10 and for minimum-size thresholds (N_c) of 2, 4, 6, 8, and 10 (since the smallest actual population in the MH system in 1987 was estimated at 12). Separate runs were performed using the JRC and JRH distributions of ΔN.

Results of the time-to-extinction simulation are presented in figure 7. In each
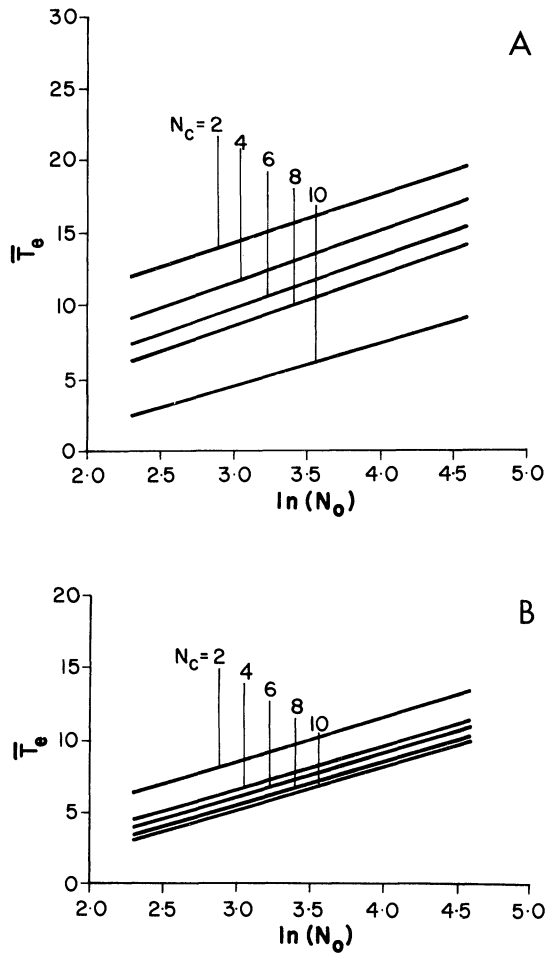
FIG. 7.—Predicted times to extinction of bay checkerspot populations as functions of their initial sizes, for different values of the minimum-size threshold, N_c, using the distribution of ΔN values: A, population JRC; B, population JRH.

case, the mean time to extinction depends linearly on the logarithm of initial population size ($r = 0.94$–0.99, df $= 48$, $P < 0.001$), a relationship predicted by many models of environmental stochasticity (e.g., Leigh 1981; review in Quinn and Hastings 1987). The slope of this regression differs slightly depending on whether JRC or JRH data are used. The minimum-size threshold, N_c, has a nonlinear negative effect on the mean time to extinction.

According to these results, the smallest population in the MH metapopulation ($N = 12$; table 2) has an expected mean time to extinction of 1–13 yr, depending on the chosen value of N_c and on whether the JRC or the JRH data are used to obtain ΔN. The largest potential population ($N = 476$, based on the area relationship) has an expected mean time to extinction of 12–26 yr. The upper values of

these ranges (those calculated using $N_c = 2$ and JRC data) are still well below the 50 yr that was previously assumed to be the maximum lifetime for a population. There are shortcomings in applying data from Jasper Ridge to the populations at Morgan Hill, since the two areas are not climatically identical and the Jasper Ridge populations have 30-yr histories of sampling and experimentation. But if the simulation result is at all valid, it indicates that recolonization is the key to "persistence" for bay checkerspot populations numbering in the tens to hundreds.

The reciprocal of the expected mean time to extinction of a population is its expected yearly probability of extinction. This rate can be compared with its expected yearly colonization rate, the negative exponential of its distance from MH. Table 6 lists, for each of the 27 suitable patches, the minimum and maximum expected yearly extinction rate (using, respectively, JRC data and $N_c = 2$; JRH data and $N_c = 10$) and the expected yearly probabilities of colonization (using the best-fit values of the constant D' under the assumption of continuous extinction: 1.8 km for the minimum extinction rates and 2.2 km for the maximum extinction rates). The actual 1987 population size is used for occupied patches, and the expected population sizes (from the area relationship, eq. 3) are used for the others. For minimum and maximum expected extinction rates, the predicted probability of each island's being colonized at equilibrium is also given. This probability equals $I/(e + I)$, the colonization rate divided by the sum of colonization and extinction rates (Gilpin and Diamond 1976, 1981). The number of patches expected to be occupied at equilibrium equals the sum over all patches of $I/(e + I)$: 10.57 and 8.21 for the minimum and maximum estimates of extinction rates, respectively.

The continuous-extinction model thus predicts that populations in the MH metapopulation will "wink in and out" around an equilibrium occupancy of 8–11 patches. The patches that are most likely to support populations are the 10 or 11 with predicted equilibrium probabilities greater than 50% (table 6); these include all 9 of the currently occupied patches.

Which is closer to the truth, the catastrophic 50-yr extinction model, which predicts 7 more colonizations over the next three decades, or the continuous-extinction model, which predicts constant turnover of populations and an equilibrium number of 8 to 11 populations? The absolute nature of the distance and habitat-quality thresholds (fig. 2) lends support to the 50-yr catastrophic scenario; continuous turnover would be expected to produce a somewhat more random pattern of occupancy than figure 2 evidences. But both catastrophic and continuous modes of extinction have undoubtedly played a role in this metapopulation.

Continuous rates of colonization have been assumed here, but it is possible that colonization, like extinction, is partly episodic in nature. No data from the MH metapopulation suggest what the yearly pattern of dispersal might be. At Jasper Ridge, yearly rates of transfer of female butterflies between populations JRC and JRH were neither constant nor extremely episodic during 1974–1985; transfers averaged 2.7% ± 4.1% of female recaptures (J. Baughman, unpubl. data). But colonization is more than just dispersal, and the probability that an immigrant landing on an empty patch will successfully found a population certainly varies from year to year.

TABLE 6

PREDICTED PROBABILITIES OF COLONIZATION AND EXTINCTION, AND EQUILIBRIUM PROBABILITIES
OF OCCUPANCY, FOR SUITABLE PATCHES UNDER THE CONTINUOUS-EXTINCTION MODEL

PATCH NUMBER	DISTANCE FROM MH (km)	AREA (ha)	MINIMUM EXTINCTION RATE ($D' = 1.8$ km)			MAXIMUM EXTINCTION RATE ($D' = 2.2$ km)		
			Extinction	Colonization	Equilibrium	Extinction	Colonization	Equilibrium
1	4.6	121.2	.04	.08	.66	.09	.12	.58
2	6.0	92.7	.04	.04	.47	.09	.07	.42
3	7.9	58.4	.04	.01	.24	.10	.03	.22
4	4.4	250.0	.04	.09	.68	.08	.14	.63
5	2.0	21.5	.05	.33	.87	.12	.40	.77
6	1.4	106.0	.04	.46	.92	.09	.53	.85
7	3.6	19.0	.05	.14	.73	.15	.19	.56
8	4.1	0.9	.08	.10	.56	.80	.16	.16
9	4.0	3.2	.05	.11	.68	.11	.16	.60
10	4.0	2.5	.06	.11	.64	.17	.16	.49
11	4.0	55.0	.05	.11	.68	.11	.16	.60
12	2.7	83.0	.04	.22	.85	.09	.29	.77
13	4.9	1.4	.06	.07	.52	.24	.11	.31
14	6.4	2.6	.06	.03	.32	.26	.05	.17
15	6.9	3.7	.06	.02	.27	.18	.04	.19
16	7.8	2.8	.06	.01	.18	.19	.03	.13
17	7.7	0.5	.07	.01	.17	.40	.03	.07
18	7.7	0.4	.07	.01	.17	.40	.03	.07
19	7.4	1.3	.06	.02	.21	.25	.03	.12
20	8.3	5.8	.05	.01	.17	.16	.02	.13
21	8.4	1.5	.06	.01	.14	.24	.02	.08
22	8.8	0.9	.07	.01	.10	.30	.02	.06
23	9.3	6.4	.05	.01	.10	.15	.01	.09
24	7.0	0.3	.08	.02	.20	.58	.04	.07
25	20.8	19.2	.05	.00	.00	.12	.00	.00
26	20.5	1.2	.06	.00	.00	.26	.00	.00
27	10.4	20.9	.08	.00	.00	.12	.01	.07
TOTAL EQUILIBRIUM OCCUPANCY					10.57			8.21

NOTE.—Minimum and maximum extinction rates correspond to different assumptions made in the time-to-extinction simulation (see text). The colonization constant D' is fit to the 10-yr data (as in fig. 3) for the minimum and maximum extinction rates, separately. Extinction and colonization refer to the yearly probabilities of extinction and colonization, given either minimum or maximum extinction-rate estimates. Equilibrium is the equilibrium probability of occupancy, equal to colonization divided by the sum of extinction and colonization.

Species with very high dispersal ability still form a single functional population, even in a fragmented habitat. Species of lower dispersal ability tend to form metapopulations, with more or less distinct local populations. A species' rates of dispersal and efficacy at colonizing, relative to the expected lifetimes of its local populations, determine the degree of saturation of its available habitats within a given metapopulation. Spruce grouse were found to occupy 25 (78%) of 32 patches of bog forest in the Adirondack Mountains, New York, in 1976 (Fritz 1979). The field vole (*Microtus agrestis*) occupied, over the period 1972–1977, from 41% to 75% of 69 habitable islands in the Tvarminne Archipelago of Finland, among which it disperses by swimming (Pokki 1981).

In this study, the bay checkerspot butterfly was found to inhabit 9 of 27 available habitats in the Morgan Hill region, and thus would appear to lie toward the low end of this colonization continuum. However, like the metapopulations studied by Pokki (1981) and Schoener and Spiller (1987), and unlike that modeled by Levins (1970), this one has an essentially permanent population as a source of colonists. Hence, the metapopulation as a whole is not subject to collapse, should recolonization of the small populations fail to keep pace with their extinction.

SUMMARY

This study demonstrates the existence of a metapopulation and infers its approximate spatial extent. Habitat variables and distance from a source of colonists are shown to predict the distribution of local populations. Population sizes are shown to correlate with the area of habitat patches. The spatial pattern of populations, combined with historical information, allows the hypothetical estimation of distance-dependent rates of colonization. A colonization model suggests that "stepping stone" colonization is unimportant. Empirical information on population-size changes is used to estimate yearly extinction probabilities for the small populations with respect to their initial sizes. The metapopulation configurations predicted by a "catastrophic" versus a "continuous" model of extinction are contrasted.

ACKNOWLEDGMENTS

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
———. 1985. The ecological web. University of Chicago Press, Chicago.
Bailey, E. H., and D. L. Everhart. 1964. Geology and quicksilver deposits, New Almaden district, California. Prof. Pap. 360. U.S. Geological Survey, Menlo Park, Calif.
Begon, M. 1979. Investigating animal abundance: capture-recapture for biologists. University Park Press, Baltimore, Md.
BMD. 1985. BMDP statistical software manual. University of California Press, Berkeley.
Boorman, S. A., and P. R. Levitt. 1973. Group selection on the boundary of a stable population. Theor. Popul. Biol. 4:85–128.
California Department of Water Resources. 1977. The California drought, 1977: an update. DWR Bull. (2-15-77).

Cox, D. R. 1970. The analysis of binary data. Methuen, London.

Diamond, J. M., M. E. Gilpin, and E. Mayr. 1976. Species-distance relation for birds of the Solomon archipelago: the paradox of the great speciators. Proc. Natl. Acad. Sci. USA 73:2160–2164.

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

Ehrlich, P. R. 1961. Intrinsic barriers to dispersal in the checkerspot butterfly. Science (Wash., D.C.) 134:108–109.

——. 1965. The population biology of the butterfly *Euphydryas editha*. II. The structure of the Jasper Ridge colony. Evolution 19:327–336.

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

Ehrlich, P. R., R. R. White, M. C. Singer, S. W. McKechnie, and L. E. Gilbert. 1975. Checkerspot butterflies: a historical perspective. Science (Wash., D.C.) 188:221–228.

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

Fritz, R. S. 1979. Consequences of insular population structure: distribution and extinction of spruce grouse populations. Oecologia (Berl.) 42:57–65.

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

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecol. Monogr. 48:145–166.

Gilpin, M. E. 1980. The role of stepping stone islands. Theor. Popul. Biol. 17:247–253.

Gilpin, M. E., and J. M. Diamond. 1976. Calculation of immigration and extinction curves from the species-area-distance relation. Proc. Natl. Acad. Sci. USA 73:4130–4134.

——. 1981. Immigration and extinction probabilities for individual species: relation to incidence functions and species colonization curves. Proc. Natl. Acad. Sci. USA 78:392–396.

Kahrl, W. L. 1979. California water atlas. State of California, Sacramento.

Kitching, R. 1971. A simple simulation model of dispersal of animals among units of discrete habitat. Oecologia (Berl.) 7:95–116.

Leigh, E. G. 1981. The average lifetime of a population in a varying environment. J. Theor. Biol. 90:213–239.

Levins, R. 1970. Extinction. Pages 77–107 *in* M. Gerstenhaber, ed. Lectures on mathematics in the life sciences. Vol. 2. American Mathematical Society, Providence, R.I.

Lindsey, W. C. 1974. Soil survey of the eastern Santa Clara area, California. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

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

Murphy, D. D., and P. R. Ehrlich. 1980. Two California bay checkerspot subspecies: one new, one on the verge of extinction. J. Lepid. Soc. 34:316–320.

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

Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models. Irwin Press, Homewood, Ill.

Pokki, J. 1981. Distribution, demography and dispersal of the field vole, *Microtus agrestis* L., in the Tvarminne Archipelago, Finland. Acta Zool. Fenn. 164:1–48.

Quinn, J. F., and A. Hastings. 1987. Extinction in subdivided habitats. Conserv. Biol. 1:198–209.

Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonizing species. Theor. Popul. Biol. 3:406–433.

Schoener, T. W., and D. A. Spiller. 1987. High population persistence in a system with high turnover. Nature (Lond.) 330:474–477.

Singer, M. C. 1972. Complex components of habitat suitability within a butterfly colony. Science (Wash., D.C.) 173:75–77.
Singer, M. C., and P. R. Ehrlich. 1979. Population dynamics of the checkerspot butterfly *Euphydryas editha*. Fortschr. Zool. 25:53–60.
Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2d ed. Freeman, San Francisco.
Spight, T. M. 1974. Sizes of populations of a marine snail. Ecology 55:712–729.
Washburn, J. O., and H. V. Cornell. 1981. Parasitoids, patches and phenology: their possible role in the local extinction of a cynipid gall wasp population. Ecology 62:1597–1607.
Weiss, S. J., R. R. White, and D. D. Murphy. In press. Sun, slope, and butterflies: topographic determinants of habitat quality in *Euphydryas editha*. Ecology.
Wilson, E. O. 1975. Sociobiology. Harvard University Press, Cambridge, Mass.
Wolfenbarger, D. O. 1949. Dispersion of small organisms. Am. Midl. Nat. 35:1–152.