Evaluating the California Gnatcatcher as an Umbrella Species for Conservation of Southern California Coastal Sage Scrub

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Abstract: *Designing reserves that preserve the habitat of many coexisting and threatened species often involves use of conservation surrogates, such as umbrella species. Typically, animals with legal protection are used as umbrella species, and these selections are overwhelmingly vertebrates. The tacit assumption that vertebrates automatically serve as conservation umbrellas for invertebrates rarely has been justified. The California Gnatcatcher (* Polioptila californica, *Muscicapidae), is a federally listed and endangered species in the United States and has been used as an umbrella species for the conservation of coastal sage scrub in southern California. Conservation planning efforts for this community follow a general paradigm of using vertebrate-based reserve designs as de facto protection for invertebrate cohabitants. To test the effectiveness of this strategy, I surveyed 50 patches of coastal sage scrub in San Diego County for three species of Lepidoptera: Mormon metalmark (*Apodemia mormo, *Riodinidae), Bernardino blue, (*Euphilotes bernardino, *Lycaenidae), and Electra buckmoth (* Hemileuca electra, *Saturniidae). The presence of the gnatcatcher was a poor indicator of the presence of these insects. Only the largest or most recently separated habitat patches supported all three species of Lepidoptera, but the gnatcatcher was present on nearly every site, regardless of size. Results indicate that vertebrates do not automatically function as umbrella species for invertebrate cohabitants. Reserve designs based on vertebrate umbrella species, which assume invertebrates will be protected, may result in the loss of a large portion of invertebrate diversity.*

Evaluando a la Perlita de California como una Especie Sombrilla para la Conservación del Matorral de Salvia Costero del Sur de California

Resumen: *El diseño de reservas que preservan el hábitat de muchas especies coexistentes y amenazadas a menudo implica el uso de abstracciones, tal como las especies sombrilla. Típicamente, animales protegidos legalmente son utilizados como especies sombrilla, y estas selecciones son, en sugran mayoría, vertebrados. Raramente se ha justificado el superesto tácito de que los vertebrados automáticamente funcionan como sombrillas de conservación para invertebrados. La Perlita de California (* Polioptila californica, *Muscicapidae), es una especie enlistada federalmente y en peligro en los Estados Unidos y se ha utilizado como una especie sombrilla para la conservación del matorral de salvia costero en el sur de California. Los esfuerzos de planificación de la conservación de esta comunidad siguen un paradigma general de utilizar reservas diseñadas con base en vertebrados como protección de hecho para cohabitantes invertebrados. Para probar la efectividad de esa estrategia, busqué tres especies de Lepidoptera:* Apodemia mormo *(Riodinidae),* Euphilotes bernardino *(Lycaenidae) y* Hemileuca electra *(Saturniidae) en 50 parches de matorral de salvia costero en el Condado de San Diego. La presencia de la perlita fue un indicador pobre de la presencia de estos insectos. Las tres especies de mariposas solo estuvieron presentes en los parches más grandes o los separados más recientemente, pero la perlita estuvo presente en casi todos los sitios, independientemente del tamaño. Los resultados indican que los vertebrados no funcionan automáticamente como especies sombrilla para cohabitantes invertebrados. El diseño de reservas fundamentado en especies de vertebrados sombrilla, que asumen que los invertebrados serán protegidos, puede resultar en la pérdida de una porción grande de la diversidad de invertebrados.*

Paper submitted April 24, 2000; revised manuscript accepted October 18, 2000.

Introduction

Endangered species frequently are threatened by habitat destruction, a problem that is most severe when development occurs in regions of high endemism (Dobson et al. 1997). Because threatened species often exist in habitats that are mostly destroyed, reserves support ad hoc assemblages of a portion of the remaining habitat. Conservation efficiency—choosing portions of habitat that support the highest number of threatened species—is usually the priority (Andelman & Fagan 2000). Designing reserves that preserve the habitat of many coexisting and threatened species often invokes the use of conservation surrogates. These surrogate species are thought to represent the conservation needs of threatened sympatric species dependent on the same habitat (Simberloff 1998). The surrogate approach focuses the management and design of reserves on one or a few, often charismatic, threatened species (Caro & O'Doherty 1999). One such surrogate strategy is the umbrella species concept. An effective umbrella species must represent the conservation needs of cohabitants. Wilcox (1984) suggests that to provide a "protective umbrella," a "target species" should have a "minimum area requirement [that] is at least as comprehensive as the rest of the community." The putative "umbrella" is a species with a relatively large range requirement compared to sympatric species such that it theoretically confers protection to other species that share the same habitat or ecoregion and are also threatened (Andelman & Fagan 2000). Although surrogate approaches such as the umbrella strategy have become widespread and popular shortcuts for the conservation of threatened habitats, they are controversial and rarely validated (Andelman & Fagan 2000).

Shortcut conservation strategies such as the use of umbrella species are seen as alternatives to ecosystem approaches, which require monitoring of multiple biotic and abiotic factors (Hanley 1993; Launer & Murphy 1994; Tracy & Brussard 1994). Unfortunately, the effectiveness of both umbrella and ecosystem approaches is debatable (Franklin 1994; Hobbs 1994; Walker 1995; Lambeck 1997; Caro & O'Doherty 1999), and attempts to define a balance between species and ecosystem-based management have resulted in acrimony (Beattie & Oliver 1999; Goldstein 1999; Risser 1999; Walker 1999).

Conservation based on umbrella species is popular, likely because managing a single species is more straightforward and easier to evaluate than managing a complex of amorphous, abstract ecosystems. Furthermore many laws, such as the U.S. Endangered Species Act, mandate species-level management. Often the animals considered for use as umbrellas are legislatively protected species—mostly vertebrates (Andelman & Fagan 2000). The U.S. endangered species list, for example, contains 331 vertebrates but only 45 insects and arachnids (U.S. Fish and Wildlife Service 2000). Although the majority of legally protected animals are vertebrates, the majority (between 80% and 97%) of animals in terrestrial ecosystems are invertebrates (Erwin 1997).

Even if there was strong evidence supporting the use of vertebrates as umbrellas for other vertebrates, umbrella strategies based on vertebrates must also protect invertebrates, which are an essential part of ecosystems (Allen-Wardell et al. 1998). There is evidence that invertebrates maintain a finer spatial relationship to their habitat and require different reserve designs that may not be incorporated into management plans based on a vertebrate umbrella species (Murphy & Wilcox 1986). Although Martikainen et al. (1998) found that a woodpecker was an adequate umbrella species for a threatened woodland beetle assemblage, other studies question the effectiveness of a vertebrate as a conservation umbrella for invertebrates (Kerr 1997; Oliver et al. 1998; Simberloff 1998). Yet invertebrates are regularly and specifically ignored or given the lowest priority in otherwise thorough conservation management and monitoring programs at all levels, even when guidelines suggest their inclusion (California Department of Fish and Game 1993; Overton 1994). Therefore, most endangered-species reserves are vertebrate-based, and the legally protected vertebrates serve as automatic but unsubstantiated umbrella species for invertebrates dependent on the same habitat.

I sought to evaluate the effectiveness of a vertebrate as an umbrella species for invertebrates restricted to the same habitat. I focused on coastal southern California because it is a global hotspot of endemism, with nearly 100 species proposed for or currently under legislative protection (Atwood 1993; McCaull 1994; Medail and Quezel 1999). Although the ecoregion has been the subject of evaluations of different surrogate-species approaches (Chase et al. 1998, 2000; Andelman & Fagan 2000), the effectiveness of a vertebrate species as a surrogate for invertbrate species has not been evaluated.

The vertebrate umbrella species for southern California coastal sage scrub (CSS) is the California Gnatcatcher (*Polioptila californica*, Muscicapidae) (CAGN), a songbird listed as threatened under the U.S. Endangered Species Act (Atwood 1993; McCaull 1994). The California Gnatcatcher has been used as an umbrella species for this community because it is almost completely restricted to nesting in California coastal sage scrub vegetation types and it is legislatively protected (Atwood 1993; California Department of Fish and Game 1993). There are some indications that the California Gnatcatcher does not function as an umbrella for other vertebrates (Chase et al. 2000), but the fate of the California coastal sage scrub invertebrate community has not been evaluated.

California coastal sage scrub is arguably the most endangered habitat in the United States, with more than 85% of its original area lost to agriculture and urban development by 1980 (Westman 1981). California coastal sage scrub is a drought-deciduous plant community composed of a variety of low-growing (<1 m), aromatic shrubs, including *Salvia apiana* (Lamiaceae), *Salvia mellifera*, *Artemisia californica* (Asteraceae), *Eriogonom fasciculatum* (Polygonaceae), and *Encelia californica* (Asteraceae) (Holland & Keil 1995; Minnich & Dezzani 1998). California coastal sage scrub habitat is found only below 300 m elevation in parts of Los Angeles, Orange, Riverside, and San Diego counties, California. California coastal sage scrub was never extensive, originally encompassing only 1.2 million ha and has borne the brunt of urbanization associated with the metropolitan corridor from Los Angeles to San Diego.

Land values in coastal southern California are among the highest in the nation, and much of the remaining California coastal sage scrub is in private hands. Preservation of remaining California coastal sage scrub, along with riparian, beach, and native grassland communities, has been a hotly contested issue, pitting environmentalists, the U.S. Fish and Wildlife Service (USFWS), and the California Department of Fish and Game (CDFG) against developers and local governments anxious to reap the economic benefits of continued development. In an effort to avoid litigation, a variety of compromise proposals have surfaced, including the Multiple Species Conservation Program and the Multiple Habitat Conservation Plan in San Diego County (CDFG 1993).

Under both these proposals, vegetation communities have legally protected vertebrates designated as putative umbrella, or "target," species for planning reserve designs in remaining habitat. In exchange for being allowed to commercially develop a piece of property and "take" a protected species, a private landowner is required to contribute land or a negotiated sum to the purchase and conservation of property elsewhere that is designated as a mitigation land bank. These mitigation banks are to be expanded until all available California coastal sage scrub has been developed or preserved in perpetuity (CDFG 1993). The USFWS is charged with negotiating with municipal governments, landowners, and private interest groups to establish the reserve designs and determine mitigation-bank contributions. The former U.S. Secretary of the Interior, Bruce Babbitt, touted this compromise between government and private landowners as a model for future urban conservation planning (Pierce 1996). Although ostensibly habitat-based, the Multiple Habitat Conservation Plan and the Multiple Species Conservation Program for California coastal sage scrub were designed to preserve habitat with the highest concentration of California Gnatcatchers (Ogden Environmental and Energy Services), effectively making the plan species-based and the bird the umbrella species for California coastal sage scrub. Reserve planning efforts for California coastal sage scrub represent a near-perfect model for testing the effectiveness of vertebrate umbrella species for invertebrate conservation.

I compared USFWS distribution data for the California Gnatcatcher to those for three California coastal sage scrub insects to evaluate the bird as an umbrella species. The evaluation consisted of two questions: (1) Is the probability of finding the vertebrate umbrella, in this case the California Gnatcatcher, on the habitat patch equal to the probability of finding each of the insects on the habitat patch? A good umbrella species will occur at a level of frequency equal to that of the species to be protected under it. An umbrella that is ubiquitous or rare is not helpful for identifying patches that support the most invertebrates (Fleishman et al. 2000). (2) Is the vertebrate umbrella more or less sensitive than the insects to habitat fragment size? If the putative umbrella persists on smaller patches than do the insects, then it does not indicate minimum patch size for the insects for which it is supposed to be a surrogate.

Methods

I surveyed 50 California coastal sage scrub patches for three Lepidoptera that occurred historically throughout the regions of the Multiple Habitat Conservation Plan and Multiple Species Conservation Program in central and northern San Diego County, California. I selected two butterflies, *Euphilotes bernardino* (Lycaenidae) and *Apodemia mormo* (Riodinidae), and a moth, *Hemileuca electra* (Saturniidae). I determined their pattern of co-occurrence with the California Gnatcatcher and the minimum patch size for each species.

Insect Species Selection

To evaluate the value of the California Gnatcatcher as an umbrella species for invertebrates, it was necessary to survey for insects whose life histories are well known. Choosing insects that in coastal southern California are obligate California coastal sage scrub inhabitants is essential, because their presence alone demonstrates patch conditions in California coastal sage scrub. Insect surveys that include generalists and other facultative California coastal sage scrub insects likely will be misleading because their populations are sustained in adjacent non-California coastal sage scrub areas. Their transient presence in a California patch has nothing to do with the condition of local California coastal sage scrub.

In addition to insects dependent on California coastal sage scrub, I chose relatively mobile insects that would provide a conservative measure of the effects of habitat fragmentation on invertebrates and thereby avoid inaccurate rejection of the California Gnatcatcher as a general invertebrate umbrella. I surveyed three species of California coastal sage scrub Lepidoptera because they are highly vagile compared with most invertebrates, and flight provides resistance against the negative effects of habitat fragmentation (Murphy & Wilcox 1986). Therefore, the Lepidoptera represent a conservative estimate of extinction risk for the rest of the invertebrate community, and if the three Lepidoptera are not successful in maintaining populations across a reserve based on the California Gnatcatcher, then less-mobile invertebrate species are unlikely to fare better. I defined California coastal sage scrub Lepidoptera as those having larvae that, in coastal southern California, are solely dependent on plants that help define the California coastal sage scrub vegetation community (Scott 1986; Tuskes et al. 1996; Minnich & Dezzani 1998).

Hemileuca electra is a saturniid moth that flies in October and has a generation time of 1 year or more (Powell 1987; Tuskes et al. 1996). *Euphilotes bernardino* is a small blue or brown lycaenid butterfly whose congeners are often specialized for microhabitats, including two other species that are listed as threatened or endangered in California (Arnold 1980; Scott 1986). There is one generation per year, and adults are active in late spring (late May, early June). The third species, *Apodemia mormo*, flies from February until late November in the study area and has multiple broods (Scott 1986). There appear to be peak flights of *A. mormo* in late spring and October that coincide with the flights of *E. bernardino* and *H. electra*, respectively. In coastal southern California, the larvae of all three species feed only on *Eriogonom fasciculatum* (Opler & Powell 1961; Mattoni 1989; Tuskes & McElfresh 1995), a characteristic plant of the coastal sage scrub vegetation community (Minnich & Dezzani 1998).

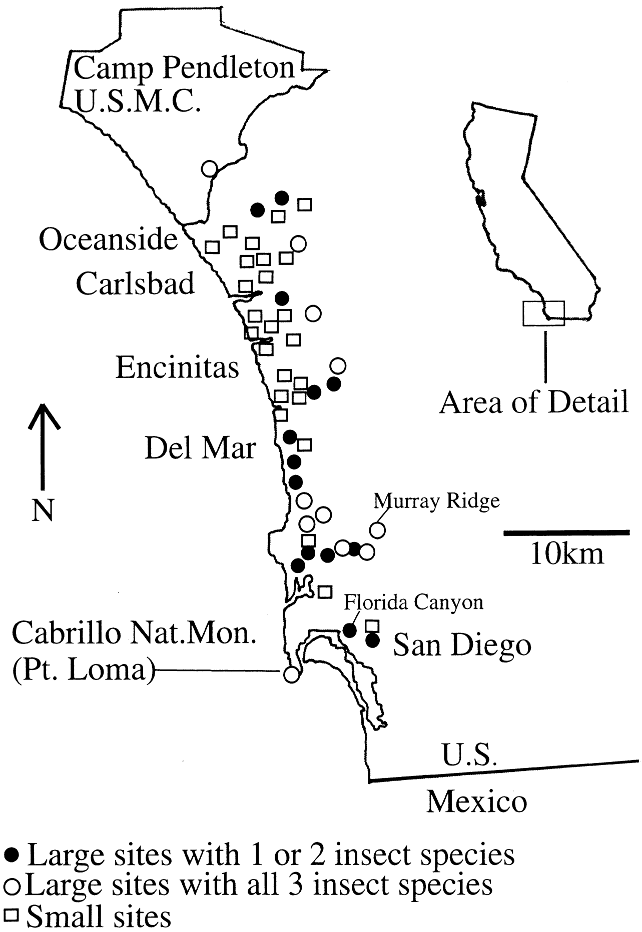

Figure 1. Location of 50 habitat patches in western San Diego County surveyed for three species of Lepidoptera. Small sites are <9 ha; large sites are >9 ha. H. electra *always occurred with both* A. mormo *and* E. bernardino.

Site Selection

California coastal sage scrub vegetation sites were selected based on geographic information system maps used by the USFWS (Ogden et al. 1993, 1999). These maps identify patches being considered for development or inclusion into mitigation reserves (Fig. 1). Area of patches was calculated from digitized versions of the maps based on aerial photographs taken in 1995, but the maps do not reflect fine-scale gradients in habitat quality, and patches of equal size do not necessarily contain equal amounts of California coastal sage scrub vegetation. I surveyed 50 patches ranging in size from 1.3 to 334.4 ha. To standardize emergence phenology of the adult stage during survey periods, all patches chosen were within 10 km of the Pacific Ocean in central and northern San Diego County. I included nearly all such California coastal sage scrub patches from U.S. Marine Corps Base Camp Pendelton to the city of San Diego. Sites within the study area that were not included were either inaccessible because of unwilling landowners or so severely degraded that I was unable to locate California coastal sage scrub. There were only two sites of the 50 in the study area that the USFWS did not consider inhabited by the California Gnatcatcher. Because the purpose of my study was to evaluate the California Gnatcatcher as an umbrella species, it was not necessary to locate an equal number of sites without the bird. The effectiveness of an umbrella species is contingent simply upon it having the same frequency of occurrence (here, in response to habitat fragmentation) as the species it is supposed to protect.

Survey Methodology

During October 1997 and late May to early June 1998, I surveyed an initial group of 25 sites. During October 1998 and late May to early June 1999, I surveyed an additional, independent group of 25 sites across the same region. Survey methodology was identical for both groups. I visited each patch of 9 ha or smaller, for a minimum of 30 minutes per visit, on three separate dates during one fall and one spring field season (9 ha was the maximum area I could survey thoroughly in a 30-minute visit). For every additional 5 ha, I spent an additional 30 minutes surveying a site during each visit or until the target species was found, whichever came first. All host plants at each site were located during an initial visit.

The two butterflies in the survey oviposit, court, mate, perch, and gather nectar almost exclusively on or near the host plant, *Eriogonum fasciculatum*. Studies of endangered congeners indicate that most individuals are found within a few meters of the host plant (Arnold 1980; Scott 1986). Therefore, I focused survey time on visiting all individual host plants at every site on every visit until I found the butterflies or exhausted the allotted time. Searches for the butterflies were conducted only during weather conditions under which the butterflies had previously been observed to be active in the study area (>17° C).

Adult *H. electra* do not feed, and adults are difficult to catch or see on the wing, especially at low population densities. Adult males are strongly attracted to pheromone produced by females, however, and the males are easily lured and caught. Pheromone for *H. electra* was synthesized by McElfresh and Millar (1999). Tests on the coastal subspecies of *H. electra* confirmed its attractiveness to males (Rubinoff 1998). Pherocom (Trece, Salinas, California) sticky traps baited with synthetic pheromone-infused rubber septa were set in every patch. To ensure that pheromone had been broadcast over the full course of the survey, I replaced septa after 2 weeks and confirmed that old septa were still attractive to males after use by attracting males in large patches where they occur.

To avoid inaccurately rejecting the California Gnatcatcher as an umbrella species for the Lepidoptera, I defined habitat occupancy as generously as possible. Once a lepidopteran was found on site, I considered that site occupied and habitable. Further survey visits for that insect were not conducted. Sighting of a single individual during one visit was sufficient for a site to be considered occupied. As a result of this generous assessment of the California Gnatcatcher as an umbrella species, I may have overestimated the number of patches actually occupied by the insects.

Analysis

Because I surveyed nearly all California coastal sage scrub patches within the study area, it was possible to calculate (rather than estimate) actual frequencies of occurrence for each of the Lepidoptera and the California Gnatcatcher in the study area. Sites were arbitrarily divided at the midpoint between the 25 smallest and 25 largest to facilitate examination of the effect of patch size on the frequency of occurrence and co-occurrence of the species and to display the distribution of patch size across the study area (Fig. 1). To determine the effectiveness of the California Gnatcatcher as an umbrella species, I used a test of the difference between two frequencies (with alpha 0.01), which analyzes the significance of the difference in frequency of occurrence for each of the species over small, large, and all sites (Daniel 1995). I also used the test of difference between frequencies to assess the significance of the difference between co-occurrence of the species at the small and large sites. Areas of the sites were log-transformed for analyses.

I calculated and graphed the relationship between the number of species found in the sites and the log (area) of the sites using DeltaGraph 4.5 (SPSS 2000) and JMP 3.0.2 (SAS Institute 1994). I used the Shapiro-Wilkes test (for normality of distribution) on the residuals of linear functions to find the best fit for the data. I calculated correlations of occurrence between the species and with log (area) using JMP 3.0.2 (SAS 1994). I also calculated a logistic regression for the occurrence of the species as a function of patch size (JMP 3.0.2 [SAS 1994]).

Results

Species Distribution

The California Gnatcatcher occurs in 48 of the 50 patches (Ogden et al. 1999). All three Lepidoptera occurred significantly less frequently ($p < 0.01$; Table 1): *A. mormo*, the most widespread of the Lepidoptera in the survey, occurred in 38 patches, *E. bernardino* in 33, and *H. electra* in only 11 of the largest patches. In the 25 small patches of <10.7 ha, the difference in occurrence was even more pronounced, and *H. electra* was not found (Table 1). The smallest site in which *A. mormo* occurred was 1.3 ha, and *E. bernardino* did not occur on sites of <2.0 ha. *H. electra* was present only on sites of ≥12.5 ha and always with both of the other insects. Frequency of occurrence increased with size of site for all three Lepidoptera. Frequency of occurrence of the bird was not affected by patch size.

Correlation among Patch Size and Occurrence of Umbrella and Insect Species

The probability of a California coastal sage scrub patch containing all four species—three Lepidoptera and the California Gnatcatcher—increased with increasing patch size (Fig. 2). There was a direct relationship be-

Table 1. Frequency of occurrence of California Gnatcatcher and three Lepidoptera.

	Small sites (n = 25)*	*Large sites* (n = 25)*	*All sites (n = 50)*
California Gnatcatcher	0.96	0.96	0.96
Apodemia mormo	0.60	0.96	0.78
Euphilotes bernardino	0.36	0.96	0.66
Hemileuca electra	0	0.44	0.22

**Small sites < 9 hectares < large sites.*

tween the size of a patch and the number of species that occurred on it ($r^2 = 0.50$; Fig. 2). All but one site larger than 14.8 ha supported the California Gnatcatcher, *A. mormo*, and *E. bernardino*. *H. electra* did not occur consistently in patches of <49.6 ha, however, and there were only five sites larger than that in the study area. Logistic regressions for species presence as a function of area revealed that the size of a patch was a strong indicator of the presence of all three Lepidoptera (Table 2). Distribution of the California Gnatcatcher was not explained by patch size (Table 2). The frequency of co-occurrence between the three Lepidoptera and the California Gnatcatcher was significantly higher in the large sites than it was in the small ones, for all species combinations ($p < 0.01$; Table 3). *A. mormo* was the most likely to co-occur with the California Gnatcatcher, followed by *E. bernardino*. *A. mormo* and *E. bernardino* were equally likely to co-occur with *H. electra* at large sites. The insects were significantly (chi-square, $p < 0.005$) more likely to co-occur on patches than would be expected by random association. An analysis of correlations of occurrence revealed a strong association for the co-occurrence of the three insects and with increasing patch size, but because the California Gnatcher occurs on nearly every site, there was poor or no correlation of occurrence of any insect, or patch size, with the presence of the California Gnatcatcher (Table 4). In other words, patch size, not the presence of the California Gnatcatcher, was the predictor for the presence of the insects.

Survey Effectiveness

Survey effectiveness for the Lepidoptera was high. In over 80% of the sites where I found any of the insects, they were detected on the first visit in which they were being sought, and further visits in search of the insect were unnecessary (Fig. 3). In nearly every site where any of the insects were found, they were found by the end of the second visit; there was no statistical advantage in surveying uninhabited sites a third time, but this third visit was always made if the insects were not found on the first two visits. The amount of *E. fasciculatum* on sites varied from less than five individual plants to hillsides dominated by it. Larger patches did not always have more host plants than smaller ones.

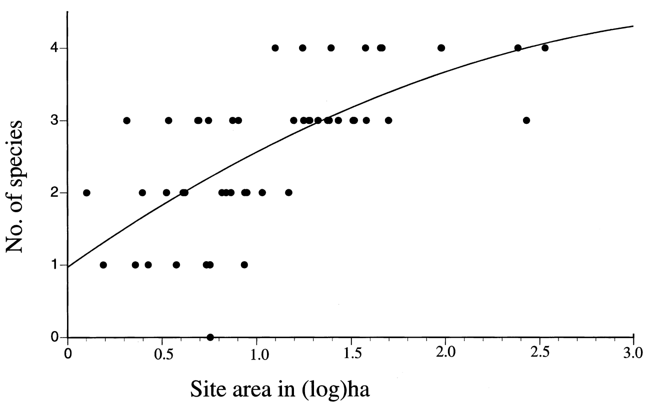

Figure 2. Relationship between occurrence of species and California coastal scrub sage patch size. A quadratic function, $f(x) = -0.24x^2 + 1.8x + 0.97$, was the best fit ($r^2 = 0.50$) based on normalcy of distribution (Shapiro-Wilkes) of residuals around zero.

Table 2. Logistic regression for presence or absence of California gnatcatcher and three Lepidoptera as a function of patch area (in hectares) of California coastal sage scrub.

	r^2 *(measure of fit with area)*	*Likelihood ratio chi-square*	p
California gnatcatcher	0.0845	1.419	0.233
Apodemia mormo	0.1612	8.88	0.002
Euphilotes bernardino	0.3837	24.59	0.0001
Hemileuca electra	0.5074	26.73	0.0000

Discussion

I defined occupancy generously for the Lepidoptera, counting any patch where I had seen a single individual at any time as occupied. This probably resulted in an overestimate of the number of patches on which the insects were actually resident. Even with this overestimation, the California Gnatcatcher is recorded in signifi-

Table 3. Frequency of co-occurrence of California Gnatcatcher and three lepidoptera at 50 sites of California coastal sage scrub.*

	California Gnatcatcher	A. mormo	E. bernardino
Small sites			
California Gnatcatcher	–	–	–
A. mormo	0.60	–	–
E. bernardino	0.36	0.28	–
H. electra	0	0	0
Large sites			
California Gnatcatcher	–	–	–
A. mormo	0.92	–	–
E. bernardino	0.96	0.92	–
H. electra	0.40	0.44	0.44
All sites			
California Gnatcatcher	–	–	–
A. mormo	0.76	–	–
E. bernardino	0.66	0.60	–
H. electra	0.20	0.22	0.22

**All species showed a significant difference in frequency of co-occurence at small versus large sites ($p < 0.01$).*

Table 4. Correlations between presence of California Gnatcatcher, insects, and size of patch (ln ha).

	California Gnatcatcher	A. mormo	E. bernardino	H. electra	*ln ha*
California Gnatcatcher	1.000	0.1243	0.0689	−0.1380	−0.1778
A. mormo		1.000	0.4864	0.2984	0.3817
E. bernardino			1.000	0.3812	0.5907
H. electra				1.000	0.6694
ln ha					1.000

cantly more patches than any of the three Lepidoptera surveyed, an undesirable quality for an umbrella species (Lambeck 1997; Simberloff 1998). The California Gnatcatcher does not appear to be as sensitive to patch size and composition as the three Lepidoptera. If all remaining patches containing the gnatcatcher were to be preserved, the bird would be a superior choice as an umbrella species, because it occurs on nearly every patch in the study region. Few patches will be preserved, however, and California coastal sage scrub is so severely fragmented that the structure of reserves is becoming an ad hoc assemblage of remnant habitat islands in a sea of urban development. Furthermore, these three Lepidoptera are more mobile than many invertebrates, for some of which even dirt roads may provide significant barriers to dispersal (Mader 1984). If these three Lepidoptera are not able to recolonize or exchange genetic material between isolated patches of California coastal sage scrub, then populations of less vagile California coastal sage scrub invertebrates are even more likely to be threatened. The conservation needs of the invertebrate community must be considered in reserve design, or many sensitive species will be lost. Therefore, an umbrella species whose presence indicates a high probability of an intact ecosystem should be used in a conservation plan of this scale; for California coastal sage scrub, the California Gnatcatcher is not such a species.

Because the California Gnatcatcher is used as an umbrella but persists on patches unoccupied by other California coastal sage scrub species, the presence of the bird is not only uninformative of conservation value but potentially misleading. Use of such a "false" umbrella could result in the sacrifice of patches that are of higher

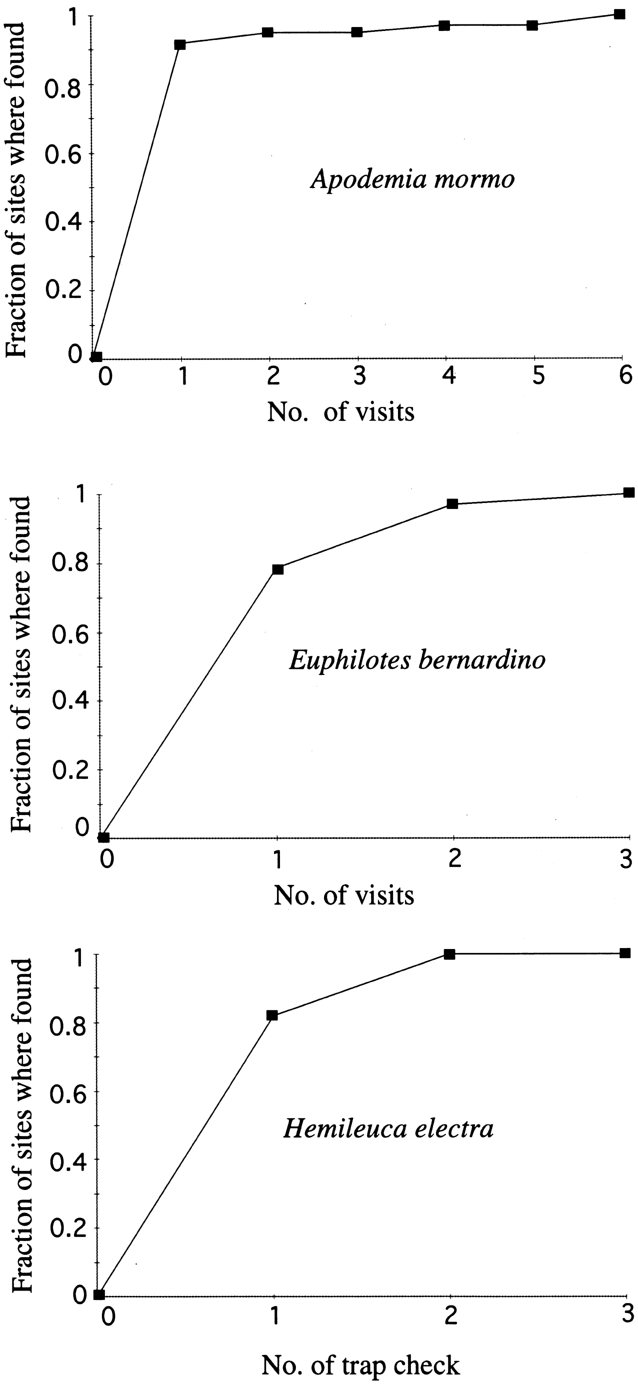

Figure 3. Survey efficiency for each lepidopteran species, showing the fraction of visits required to find each species at sites where it occurred. For Apodemia mormo*, up to six visits (during spring and fall because* A. mormo *flies during both) were made to each site. For* Euphilotes bernardino*, which flies only in May–June, sites were visited up to three times. For* Hemileuca electra*, which flies in October, sites were visited up to three times. Presence of* H. electra *was determined by pheromone-baited traps that remained in the habitat patches continually during the flight period.*

conservation value due to the faulty assumption that patches actually inhabited by only the California Gnatcatcher will serve the same conservation role. Higher-value patches are defined as those that contain a greater number of California coastal sage scrub species. When evaluating and preserving high-quality habitat, selecting the most sensitive species (sensu Lambeck 1997) is essential to a successful conservation program. Species that are most likely to suffer population decline due to a threat, such as habitat fragmentation or invasive weeds, should be used to dictate the threshold at which that threat can occur in a reserve system (Lambeck 1997). Ideally, under these circumstances, an umbrella species would occur with equal or less frequency than the biota it is expected to represent. Otherwise, reserves might preserve only the most resilient, and probably ubiquitous, species.

In coastal San Diego County, the larvae of the three insect species in the survey feed only on California coastal sage scrub plants; therefore, the presence of the insects indicates the presence of California coastal sage scrub vegetation. Moreover, the occurrence of these insects is related to the size of patches (Tables 2 & 4; Fig. 2). This association does not fully explain the data ($r^2 = 0.50$), so there must be other factors beyond size alone that determine suitable habitat and insect presence, such as time since isolation and habitat quality.

Time since isolation is likely to be crucial in determining whether or not a population of insects persists in a patch (MacArthur & Wilson 1967). Florida Canyon, a fairly large patch (15.7 ha), was a historical site for *H. electra* (Wright 1907), but I did not find it there. In contrast, Murray Ridge, a smaller site (12.5 ha) with fewer host plants, still maintains populations of the moth. Florida Canyon is in urban San Diego and has been completely surrounded by development for more than 60 years. Murray Ridge was separated from large tracts of contiguous habitat to the east only in the past decade. Many smaller sites that contain *H. electra* may also lose the species as their population size decreases and their time since isolation increases, and such a pattern of delayed extinction is likely to mislead reserve planners who assume that the current distribution of animals is sustainable.

The quality of California coastal sage scrub is also a factor in comparing habitat patches. The insects show a strong pattern (chi-square, $p < 0.005$) of co-occurrence, implying that some patches are of higher quality. Maps used by the USFWS that identify California coastal sage scrub quantify the size of patches but do not distinguish a largely intact California coastal sage scrub ecosystem from a patch with a few dozen native shrubs in the midst of alien weeds. From the perspective of some California coastal sage scrub species, the amount of actual resources available in two equally sized patches identified as California coastal sage scrub can vary tremendously; bigger is not necessarily better. This makes prioritization of patches for conservation far more complicated and perhaps beyond the scope of current planning efforts.

Conclusion

The large-scale, landscape-level, multiple-species conservation plans for coastal southern California are considered models for future conservation planning across the United States (Hebert 1996). The implementation of these plans has required compromises by both private landowners and the federal government. But the strategy of using a single vertebrate species as an umbrella species for the whole fauna of the California coastal sage scrub is flawed. Further land development is scheduled, and many of the patches in the study have already been converted to other uses. Given that a larger reserve system than currently exists was unlikely to preserve even three relatively mobile insects, the future is bleak for California coastal sage scrub invertebrate biodiversity as a whole.

Although these results confirm the same message of failure communicated by other studies of umbrella species (Simberloff 1998; Caro & O'Doherty 1999; Andelman & Fagan 2000), they represent one of the first tests of an in-situ, vertebrate-based reserve to preserve obligate invertebrate cohabitants. Vertebrates cannot be assumed to be effective umbrella species for invertebrates. Assuming that any single species will function as a conservation surrogate may be an error worse than making decisions without the use of umbrellas at all. A reserve-planning strategy based on vertebrate umbrella species clearly can lead to faulty valuation of patch biodiversity and can fail to save parts of the invertebrate community.

This study should not serve as an endorsement for the use of invertebrate umbrella species over vertebrates. Lepidopteran umbrella species do not guarantee the maintenance of general (Launer & Murphy 1994), or even invertebrate, biodiversity: 17 years of management for an endangered butterfly at the Antioch sand dunes National Wildlife Refuge in California did not prevent the extinction of more than half the dune-restricted insects in the same habitat (Powell 1983; Maffei 1997). Single-species umbrellas are unlikely to meet the conservation requirements of all of their cohabitants. Conservation shortcuts must include comprehensive strategies that address the varied needs of threatened species in remnant habitats. Lambeck (1997) suggests a strategy of multiple umbrella species which theoretically combines the management simplicity of umbrella species with the effectiveness of ecosystem-level planning. New (1997) argues that a suite of lepidopteran species would be an effective conservation umbrella for endangered communities. *H. electra*, *E. bernardino*, and *A. mormo* could be used in conjunction with other California coastal sage scrub invertebrates to test this idea. Multiple-species planning represents a more comprehensive way for umbrella-based conservation to overcome the array of known and unknown factors that limit or threaten populations in reserves. With modifications, multiple-species conservation programs may become effective, but using them as a national (or international) standard for conservation planning will not ensure the survival of endemic invertebrate communities, which are an undervalued but essential component of biodiversity.

Acknowledgments

This research would not have been possible without cooperation from the following people and agencies: M. Wells of Torrey Pines State Reserve; D. Lydy of The U.S. Navy, Point Loma; T. Walker of Tri-Canyon Parks (San Diego), Environmental Protection Services, U.S. Marine Corps Camp Pendleton; and particularly S. Weber, Chief of Natural Resources at Cabrillo National Monument, and J. Brown, then of Dudek and Associates. E. Hein and J. Vanderweir of the U.S. Fish and Wildlife Service provided invaluable technical advice and assistance. S. McElfresh and J. Millar of the University of California, Riverside, generously shared synthesized pheromone. The support and hospitality of the Brown and Long families was essential. D. Faulkner of the San Diego Museum of Natural History kindly researched historic collecting records. I thank J. Powell; S. Welter at the University of California, Berkeley; J. Brown of the United States National Museum; and especially F. Sperling, U.C. Berkeley and University of Alberta, for advice and feedback during all stages of this effort. Labmates M. Caterino, A. Cognato, J. Herbeck, and J. Kruse, as well as E. Fleishman of Stanford University, were helpful reviewers. I received financial support from the Achievement Rewards for College Scholars foundation, the Margaret C. Walker fund, a Harvey I. Magy fellowship, Sigma Xi, and an Agriculture Experiment Station grant to F. Sperling.

Literature Cited

Allen-Wardell, G., et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conservation Biology **12:**8–17.

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates, or expensive mistakes? Proceedings of the National Academy of Sciences of the United States of America **97:**5954–5959.

Arnold, R. A. 1980. Ecological studies of six endangered butterflies (Lepidoptera, Lycaenidae): island biogeography, patch dynamics, and the design of habitat preserves. Publications in entomology 99. University of California Press, Berkeley.

Atwood, J. L. 1993. California Gnatcatchers and coastal sage scrub: The biological basis for endangered species listing. Pages 149–166 in J. E. Keeley, editor. Interface between ecology and land development in California. Southern California Academy of Sciences, Los Angeles.

Beattie, A. J., and I. Oliver. 1999. Biodiversity buzzwords: another reply to Goldstein. Conservation Biology **13:**1514.

California Department of Fish and Game. 1993. Southern California coastal sage scrub natural communities conservation plan. Scientific review panel conservation guidelines and documentation. California Department of Fish and Game, Sacramento, California.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology **13:**805–814.

Chase, M. K., J. T. Rotenberry, and M. D. Misenhelter. 1998. Is the California Gnatcatcher an indicator of bird-species richness in coastal sage scrub? Western Birds **29:**468–474.

Chase, M. K., W. B. Kristan III, A. J. Lynam, M. V. Price, and J. T. Rotenberry. 2000. Single species as indicators of species richness and composition in California coastal sage scrub birds and small mammals. Conservation Biology **14:**474–487.

Daniel, W. W. 1995. Biostatistics. Wiley, New York.

Dobson, A. P., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science **275:**550–553.

Erwin, T. L. 1997. Biodiversity at its utmost: tropical forest beetles. Pages 27–40 in M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, editors. Biodiversity. II. Understanding and protecting our biological resources. Joseph Henry Press, Washington, D.C.

Fleishman, E., D. D. Murphy, and P. F. Brussard. 2000. A new method for selection of umbrella species for conservation planning. Ecological Applications **10:**569–579.

Franklin, J. F. 1994. Preserving biodiversity: species in landscapes. Response to Tracy and Brussard, 1994. Ecological Applications **4:** 208–209.

Goldstein, P. Z. 1999. Clarifying the role of species in ecosystem management: a reply. Conservation Biology **13:**1515–1517.

Hanley, T. A. 1993. Balancing economic development, biological conservation, and human culture: the Sitka black-tailed deer *Odocoileus hemionus sitkensis* as an ecological indicator. Biological Conservation **66:**61–67.

Hebert, H. J. 1996. Orange County coast a testing ground for the Endangered Species Act. San Diego Daily Transcript, 17 July:1c, 3c.

Hobbs, R. J. 1994. Landscape ecology and conservation: moving from description to application. Pacific Conservation Biology **1:**170–176.

Holland, V., and D. Keil. 1995. California vegetation. Kendall/Hunt, Dubuque, Iowa.

Kerr, J. T. 1997. Species richness, endemism, and the choice of areas for conservation. Conservation Biology **11:**1094–1100.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology **11:**849–856.

Launer, A. E., and D. D. Murphy. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. Biological Conservation **69:**145–153.

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

Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation **29:**81–96.

Maffei, W. A. 1997. Survey of Antioch Dunes National Wildlife Refuge for 17 listed insect taxa. Report. U.S. Fish and Wildlife Service, Newark.

Martikainen, P., L. Kaila, and Y. Haila. 1998. Threatened beetles in White-Backed Woodpecker habitats. Conservation Biology **12:**293–301.

Mattoni, R. H. T. 1989. The Euphilotes battoides complex: recognition of a species and description of a new subspecies. (Lycaenidae). Journal of Research on the Lepidoptera **27:**173–185.

McCaull, J. 1994. The Natural Community Conservation Planning Program and the coastal sage scrub ecosystem of southern California. Pages 281–292 in R. E. Grumbine, editor. Environmental policy and biodiversity. Island Press, Washington, D.C.

McElfresh, J. S., and J. G. Millar. 1999. Geographic variation in sex pheromone blend of *Hemileuca electra* from southern California. Journal of Chemical Ecology **25:**2505–2525.

Medail, F., and P. Quezel. 1999. Biodiversity hotspots in the Mediterranean basin: setting global conservation priorities. Conservation Biology **13:**1510–1513.

Minnich, R. A., and R. J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris plain, California. Western Birds **29:**366–391.

Murphy, D. D., and B. A. Wilcox. 1986. Butterfly diversity in natural habitat fragments: a test of the validity of vertebrate-based management. Pages 287–292 in J. Varner, M. L. Morrison and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison.

New, T. R. 1997. Are Lepidoptera an effective 'umbrella group' for biodiversity conservation? Journal of Insect Conservation **1:**5–12.

Ogden, Dudek, and Associates. 1993. Vegetation communities with sensitive species and vernal pools. Prepared for the Multiple Habitat Conservation Program. San Diego Association of Governments, San Diego.

Ogden, Dudek, and Associates. 1999. Vegetation communities with sensitive species and vernal pools. Prepared for the Multiple Habitat Conservation Program. San Diego Association of Governments, San Diego.

Ogden Environmental and Energy Services. 1996. Multiple species conservation program. Volumes 1 and 2. San Diego, California.

Oliver, I., A. J. Beattie, and A. York. 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in eastern Australia. Conservation Biology **12:**822–835.

Opler, P., and J. A. Powell. 1961. Taxonomic and distributional studies on the western components of the *Apodemia mormo* complex (Riodinidae). Journal of the Lepidopterists' Society **15:**145–171.

Overton, H. B. 1994. Inventory and monitoring plan (for terrestrial plants, algal turf, mammals, birds, reptiles, marine invertebrates, and marine vertebrates). Internal planning document. Cabrillo National Monument, National Park Service, San Diego.

Pierce, E. 1996. Some activists doubt environment plan. San Diego Union Tribune, 6 August:B–1.

Powell, J. A. 1983. Changes in the insect fauna of a deteriorating riverine sand dune community during 50 years of human exploitation. Report. U.S. Fish and Wildlife Service, Sacramento.

Powell, J. A. 1987. Records of prolonged diapause in Lepidoptera. Journal of Research on the Lepidoptera **25:**83–109.

Risser, P. G. 1999. Examining relationships between ecosystem function and biodiversity: reply to Goldstein. Conservation Biology **13:**438–439.

Rubinoff, D. 1998. Field observations on mating behavior and predation of *Hemileuca electra* (Saturniidae). The Journal of the Lepidopterists' Society **52:**212–214.

SAS Institute. 1994. JMP 3.02 statistical discovery software. Cary, North Carolina.

SPSS. 2000. DeltaGraph 4.5. Chicago.

Scott, J. A. 1986. The butterflies of North America. Stanford University Press, Stanford, California.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management pass in the landscape era? Biological Conservation **83:**247–257.

Tracy, C. R., and P. F. Brussard. 1994. Preserving biodiversity: species in landscapes. Ecological Applications **4:**205–207.

Tuskes, P. M., and S. McElfresh. 1995. The biology and distribution of *Hemileuca electra* (Saturniidae) populations in the United States and Mexico, with descriptions of two new subspecies. Journal of the Lepidopterists' Society **49:**49–71.

Tuskes, P. M., J. P. Tuttle, and M. M. Collins. 1996. The wild silkmoths of North America. Cornell University Press, Ithaca, New York.

U. S. Fish and Wildlife Service. 2000. United States endangered species list. Washington, D.C.

Walker, B. H. 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology **9:**747–752.

Walker, B. H. 1999. The ecosystem approach to conservation: reply to Goldstein. Conservation Biology **13:**436–437.

Westman, W. E. 1981. Diversity relations and succession in Californian coastal sage scrub. Ecology **62:**439–455.

Wilcox, B. A. 1984. In situ conservation of genetic resources: determinants of minimum area requirements. Pages 639–647 in J. A. McNeely and K.R. Miller, editors. National parks: conservation and development. Smithsonian Institution Press, Washington, D.C.

Wright, W. S. 1907. Field notes, 10 October 1907. Deposited in San Diego Museum of Natural History, San Diego.