IS THE CALIFORNIA GNATCATCHER A GOOD UMBRELLA SPECIES?

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Conservation of biodiversity is best attained by establishing habitat reserves that are designed for multiple species and sustain entire ecosystems (Noss 1983, Hunter et al. 1988, Scott et al. 1988, Brussard 1991). Most existing habitat reserves have been established primarily on the the basis of the ecological requirements of only one or a few species. This is a consequence of two basic limitations of the multiple-species approach to the design of habitat reserves: the single-species focus of the Endangered Species Act (ESA), and the lack of detailed autecological studies upon which multiple-species conservation decisions can be confidently based. Recent attempts to address conservation at the species and ecosystem levels simultaneously through habitat-based conservation planning and Section 10(a) of the ESA may be a feasible solution to the single-species focus of the ESA (Noss et al. 1997). However, we will always be faced with a lack of sufficient autecological data.

The concept of umbrella species has evolved in recent years in an attempt to overcome the single-species limitations of the existing legal framework and current level of ecological understanding. Fundamental to this concept is the assumption that preservation of the critical habitat of one species will also protect viable populations of other species that share that habitat (Murphy 1988, Simberloff 1988, Murphy et al. 1990, Noss 1990, Bean et al. 1991, Rohlf 1991, Noss et al. 1996). Testing of the effectiveness of each proposed reserve umbrella should be undertaken before a valid assesment of the protection provided other species under the umbrella can be made. After a thourough survey of the literature, however, Noss et al. (1996) could not find a single definitive study that evaluated the level of protection afforded other species of vertebrates within a proposed umbrella-species reserve.

Launer and Murphy (1994) investigated the effectiveness of a single-species-reserve umbrella to protect plants, and Berger (1997) evaluated the effectiveness of the Black Rhinoceros (*Diceros bicornis*) as an umbrella species in protecting six species of large herbivores. If species that are targets for reserve design are also to be used as umbrellas for conservation of greater biodiversity, then it is essential that we examine the broadest effects of reserve umbrellas to preserve species at all levels as well as important components of ecosystem structure and function. Noss et al. (1996) attempted a broad evaluation of the effectiveness of a reserve designed for large carnivores in Idaho to protect the wider diversity of vertebrates. As far as we are aware, however, our research is the first attempt to evaluate the effectiveness of an umbrella species in protecting a wide variety of plants and animals in numerous taxa and at many trophic levels.

Determination of the precise level of protection afforded every other species contained within an umbrella requires detailed autecological studies and population-viability analyses of each species. Such a process would be excessively time-consuming and thus impractical in light of the rapid rate of species extinction (Diamond 1984, Gilpin 1987). Therefore, a methodological compromise is needed through which a reasonable estimate of the level of protection for each species in the reserve can be made. The purpose of this research is to apply one possible set of methods that require a relatively modest amount of time and data to determine the degree to which a single-species-reserve umbrella protects other species of concern. We hope that these or similar methods may be applied to current and future reserve-design efforts to improve estimates of other proposed umbrella species' effectiveness.

We selected the California Gnatcatcher (*Polioptila californica*) as the target for a single-species-reserve design and investigated how the umbrella of a California Gnatcatcher habitat reserve will protect populations of each of the other species evaluated in this study on the basis of the other species' ecological differences. Our general expectations of the effectivenesss of the reserve umbrella are that species occurring in some habitats will be better protected than species occurring in other habitats, that species requiring smaller areas will be better protected than those requiring larger areas, that species at lower trophic levels will be better protected than those at higher levels, and that species that do not have specialized habitat requirements will be better protected than those with more exacting requirements.

METHODS

Our primary goal is to investigate the usefulness of our methods in evaluating the umbrella effects of a single-species reserve. The reserve we have designed and subsequently analyzed is hypothetical and not intended to be implemented on the basis of this design exercise. Our design was based on the best scientific data available at the time; however, several assumptions were made to simplify the number of issues that need to be considered in designing the reserve: (1) planned future land uses were not considered, and therefore all existing habitat was assumed to be available for inclusion in the reserve; (2) the cost of land acquisition was not a factor in the reserve's delineation, and it was assumed that all land within the reserve could be acquired; (3) habitat within the reserve would be permanently protected from future development; and (4) all habitat within the study area that was not included in the final reserve design would not be protected and was not considered usable habitat for reserve species. We ignored the question of genetic stochasticity.

The gnatcatcher was chosen as the target species because it requires a relatively large area for a bird of its size. Therefore, it has greater potential to be an effective umbrella species. Furthermore, numerous studies associated with this and other conservation projects around the study area have resulted in good estimates of parameters for population modeling and the gnatcatcher's habitat requirements for reserve design. The study area (52,414 ha) was within a portion of the gnatcatcher's distribution in the Otay

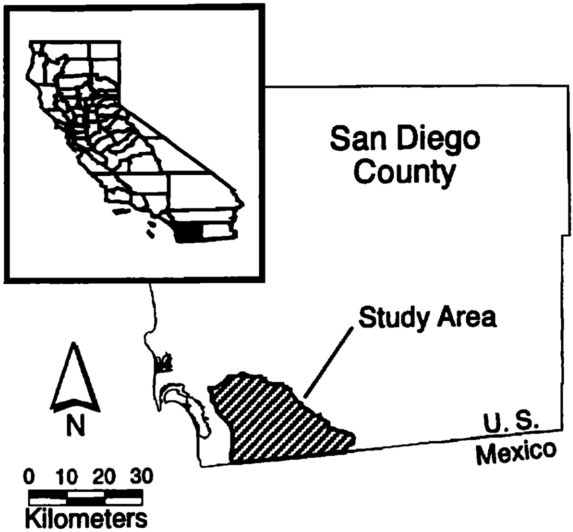

Figure 1. Location of hypothetical reserve designed to test the umbrella effect of the California Gnatctcher.

region of southwestern San Diego County (Figure 1) and was selected because it contains several of the largest subpopulations in the United States as well as one of the largest contiguous patches of coastal sage scrub (CSS).

The two main tools used in designing a habitat reserve for the gnatcatcher are a geographic-information-system (GIS) database (Ogden 1993) and a metapopulation-simulation model (Akçakaya and Ferson 1992). Detailed descriptions of the reserve-design process and umbrella-evaluation method are contained in Fleury (1994). The important GIS coverages used for this analysis were vegetation communities, soils, slope, elevation, and locations of the gnatcatcher and sensitive plant species. The population parameters used for modeling the gnatcatcher in this study are based on best available data [see Mock (1993) and Ogden (1992)].

Coastal sage scrub is the primary habitat of the gnatcatcher in San Diego County and elsewhere in southern California (Anderson 1991, Atwood 1980, 1988, 1991, Braden et al. 1997). The CSS in the study area has been estimated to be able to support approximately one pair of gnatcatchers per 10 ha (Ogden 1992). On the bases of the distribution of CSS and gnatcatcher sightings over a 9-year period (1986 to 1994) the gnatcatchers in the study area appear to be distributed in 10 subpopulations (Mock 1993) and were modeled as such. Known dispersal distances for juveniles (Mock 1993) are greater than the distance between the two most distant subpopulations; therefore, the model allowed migration between all subpopulations.

The gnatcatcher reserve was designed to meet the following objectives: (1) to contain habitat sufficient to support a population of gnatcatchers for at least 200 years with 99% certainty, (2) to maintain contiguity with major areas of gnatcatcher habitat outside of the study area, (3) to follow accepted principles of reserve design such as maintaining large contiguous areas, minimizing the perimeter-to-core-area ratio, and using naturally occurring boundaries, and (4) to exclude smaller isolated patches of habitat unless their inclusion is necessary for long-term population viability. The first objective of the reserve design (to support a viable population for at least 200 years with 99% certainty) is valid only within the hypothetical constructs of this exercise. If the assumptions we made to simplify the reserve-design process (see above) were relaxed, then this first objective would probably not be met. This is not a concern within the context of this study, which seeks to evaluate the umbrella effects of a hypothetical single-species reserve, but would be a problem if the results of our reserve design were implemented in the real world.

The reserve was designed simultaneously at the landscape level and at the population level. At the landscape level, the larger patches of high-quality gnatcatcher habitat were identified as reserve cores, and smaller fragmented patches that did not contribute to connectivity between large patches were excluded. Four key subpopulations were located in a line running from north to south through the center of the study area.

At the population level, the metapopulation-simulation model was run with these four subpopulations to determine the minimum viable population size necessary to meet the reserve's goal of 99% certainty of population viability for 200 years under this metapopulation structure. Then linkage corridors were added to the core subpopulation centers to accommodate migration between the subpopulations and to maintain contiguity with the gnatcatcher populations to the north and south of the study area. A buffer of 50 m (based on Paton 1994) was added around the perimeter of the reserve to couteract edge effects (Wilcove 1985, Lovejoy et al. 1986, Temple 1987, Saunders et al. 1991, Alberts et al. 1993).

One hundred twenty species in the study area are listed as endangered, threatened, or declining on federal, state, or local lists (e.g., USFWS, California Department of Fish and Game, California Native Plant Society, Audubon Blue List, or county and city lists of species of concern). Some of these species are not sensitive over their whole range but are included because of their limited or declining occurrence in San Diego County or elsewhere. Forty of the 120 species were selected with a stratified ramdom-sampling scheme to be analyzed for their level of protection under the umbrella. The stratification ensured that all major life-history groups were represented in the study (e.g., herbaceous plants, birds of prey, large mammalian carnivores, etc.). The area within the reserve was evaluated for the presence, quantity, quality, and spatial distribution of the habitat of each of the 40 species to determine how well the other species were protected within the reserve.

Several conditions must be met for a species to be well protected within the reserve. The habitat must be relatively cohesive, and there must be enough habitat to support a minimum population typically of at least several hundred individuals (although the number could be much higher depending on the life history of the species). If all habitat occurs in only one area, it is more vulnerable to catastrophes such as brush fire; optimally, therefore, the habitat should occur in several areas. Habitat patches must be connected so that individuals can disperse from one patch to the next. We developed four criteria on the basis of these conditions to determine the level of protection the reserve umbrella provided for each species: (1) large unfragmented blocks of the species' habitat must occur within the reserve, (2) species' numbers within the reserve must be at least several hundred, (3) the large blocks of habitat must occur in at least three distinct areas, and (4) the habitat must be well connected relative to the species' dispersal ability.

We categorized each species' level of protection as "good," "marginal," or "poor." If all four criteria were met, we considered the species well protected within the reserve; if only two or three criteria were met (depending on the species and circumstance), we considered the species marginally protected; and if zero, one, or in some cases two criteria were met, we considered the species poorly protected.

RESULTS

Approximately 11% of the 52,414-ha study area was contained within the gnatcatcher reserve (Figure 2). Seventy-three percent of the habitat in the reserve was CSS (4166 ha), of which 3370 ha was high-quality gnatcatcher habitat and, from an average density of one pair per 10 ha of high-quality habitat, was estimated to support a gnatcatcher population of 337 pairs. In addition to CSS, there was also chaparral, grassland, and open water covering from 5 to 10% of the reserve. Approximately 90% of our reserve area is also included within the reserve boundary of the final San Diego County Multiple Species Conservation Program (MSCP). Therefore, we believe that our reserve delineation is realistic, even though we did not consider other nonecological "real-world" constraints, such as the cost of land acquisition.

Fourteen of the 40 species analyzed (35%) were well protected by the reserve umbrella. Ten species (25%) were marginally protected, and 16

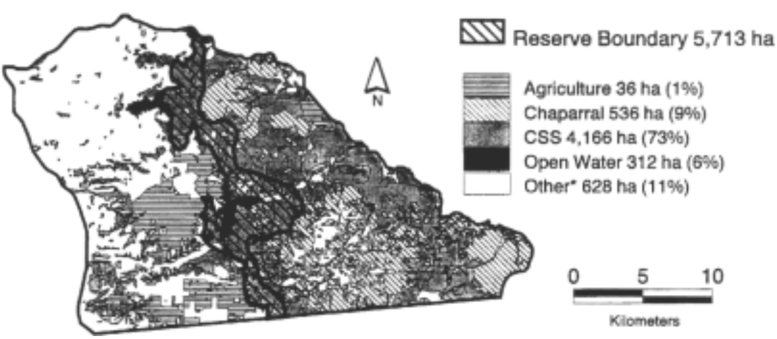

Figure 2. Distribution of hypothetical gnacatcher reserve and habitat types in Otay region of San Diego County. Other habitat and land-use types within the reserve include grassland (6%), riparian wetland (3%), stands of Tecate cypress (*Cupressus forbesii*) (1%), disturbed habitat (1%), and developed (<1%).

species (40%) were poorly protected (Table 1). Not surprisingly, the gnatcatcher is a good umbrella species for some species but not for others. It is more interesting, however, to examine the results for trends in level of protection for species grouped by the ecological factors (i.e., primary habitat, area requirements, trophic level, and need for rare and localized habitat types such as rock outcrops, or caves) relevant to determining each species' level of protection. The 40 species selected from the original list of 120 sensitive species are listed in Table 2 along with their level of protection under the gnatcatcher-reserve umbrella and their primary habitat, area requirement, trophic level, and requirement for rare and localized habitat.

Table 1 Effect of Habitat, Area Requirement, Trophic Level, and Need for Rare and Localized Habitat Types on Level of Protection Afforded by a Reserved Designed for the California Gnatcatcher

	Level of protection[a]		
Category	Good	Marginal	Poor
All species (40)	14 (35%)	10 (25%)	16 (40%)
Coastal sage scrub species (22)			
Primary habitat (CSS)	13 (59%)	3 (14%)	6 (27%)
Area requirement			
<2 ha (plants)	2 (50%)	1 (25%)	1 (25%)
<2 ha (animals)	9 (82%)	1 (9%)	1 (9%)
2–10 ha	2 (67%)	1 (33%)	0 (0%)
>10 ha	0 (0%)	0 (0%)	4 (100%)
Trophic level			
Producer	2 (50%)	1 (25%)	1 (25%)
1° consumer	6 (75%)	1 (12.5%)	1 (12.5%)
2° consumer	5 (50%)	1 (10%)	4 (40%)
Need for rare and localized habitat types			
Yes	0 (0%)	0 (0%)	3 (100%)
No	13 (68%)	3 (16%)	3 (16%)
Non-CSS species (18)			
Primary habitat (not CSS)	1 (6%)	7 (39%)	10 (55%)
Area requirement			
<2 ha (plants)	0 (0%)	3 (75%)	1 (25%)
<2 ha (animals)	1 (14%)	3 (43%)	3 (43%)
2–10 ha	0 (0%)	1 (100%)	0 (0%)
>10 ha	0 (0%)	0 (0%)	6 (100%)
Trophic level			
Producer	0 (0%)	3 (75%)	1 (25%)
1° consumer	1 (25%)	1 (25%)	2 (50%)
2° consumer	0 (0%)	3 (43%)	4 (57%)
3° consumer	0 (0%)	0 (0%)	3 (100%)
Need for rare and localized habitat types			
Yes	1 (14%)	2 (29%)	4 (57%)
No	0 (0%)	5 (45%)	6 (55%)

[a]Figures are numbers of species.

First, we examined level of protection by primary habitat. Of the 14 species classified as well protected, only one did not occur in CSS. Therefore, insufficiency of proper habitat appears to be the major factor in determining level of protection for non-CSS species. Nine of the 22 species occurring primarily in CSS, however, were categorized as marginally or poorly protected, suggesting that other factors were also important (Table 1). Because there is only one non-CSS species that was well protected, we focused the remainder of our analysis on the CSS species.

Next, we grouped animal species into three categories of area requirement (<2 ha, 2–10 ha, and >10 ha per individual) and looked at level of protection. Plants were analyzed separately because they use space so differently from animals. There are trends in all three animal categories and a weak trend for plants, suggesting that species that require 10 ha or less tended to be well protected and all species requiring greater than 10 ha were poorly protected (Table 1).

Next we examined level of protection by trophic level. Analyzing the results in terms of trophic level seems somewhat redundant because trophic level affects level of protection through area requirements (i.e., species at higher trophic levels generally require larger areas). Furthermore, trophic level may be confounded because many species forage at more than one trophic level. Although there were no tertiary consumers in CSS, there was a tendency for primary consumers and plants to be well protected (Table 1). There was no distinguishable trend for secondary consumers.

Finally, we grouped species by need for rare and localized habitat types. Examples of potentially rare and localized habitat types are larval host plants, vernal pools, cliffs, and caves. There were only two CSS species requiring rare and localized habitat types and both were poorly protected. At the same time, the majority of CSS species that did not require rare and localized habitat types were well protected (Table 1).

DISCUSSION

Our results indicate that a single-species reserve designed for the gnatcatcher is a good umbrella for some species but not for others, and that much of the patterning of species protection can be explained by species' differences in ecological characteristics. Results of the single-species reserve-design effort are of obvious importance to the overall study's results because they set the limits within which each of the other species may be evaluated. Although the basic question is whether the gnatcatcher-reserve umbrella protects populations of other species, the more interesting question is, why or why not?

Population size and distribution are two critical factors that determine viability of a population (Shaffer 1981, Shaffer 1985, Gilpin 1987, Soulé 1987). Many factors, including the four factors evaluated in this study (presence, abundance, distribution, and connectivity of habitat), can limit the size or distribution of a population.

Co-occurrence of species in the same habitat is the fundamental basis for the umbrella-species concept (Murphy 1988, Simberloff 1988, Murphy et al. 1990, Noss 1990, Bean et al. 1991, Rohlf 1991). However, as

Table 2 Level of Protection under the Gnatcatcher-Reserve Umbrella for 40 Selected Species

Species	Level of protection	Number of criteria for protection met	Habitat[a]	Area requirement	Trophic level[b]	Need for rare or localized habitat types
Plants						
Otay Mesa mint, *Pogogyne nudiuscula*	Marginal	2	VP	<2 ha	1°P	Yes
San Diego ambrosia, *Ambrosia pumila*	Poor	1	CSS, dist. CSS, dist. Chp	<2 ha	1°P	No
Orcutt's brodiaea, *Brodiaea orcuttii*	Marginal	2	G, VP, seeps, wet meadows, streams	<2 ha	1°P	Yes
San Diego goldenstar, *Muilla clevelandii*	Good	4	G, CSS, Chp (open)	<2 ha	1°P	No
Coast barrel cactus, *Ferocactus viridescens*	Good	4	CSS	<2 ha	1°P	No
Palmer's ericameria, *Ericameria palmeri* ssp. *palmeri*	Marginal	2	RS (edges), CSS	<2 ha	1°P	No
Otay manzanita, *Arctostaphylos otayensis*	Poor	1	Chp	<2 ha	1°P	No
Tecate cypress, *Cupressus forbesii*	Marginal	3	CF, Chp, drainages	<2 ha	1°P	No
Invertebrates						
Hermes copper butterfly, *Lycaena hermes*	Good	4	CSS, Chp (open) (on *Rhamnus crocea*)	<2 ha	1°C	Yes
Quino checkerspot butterfly, *Euphydryas editha quino*	Marginal	4[c]	CSS, VP, NG	<2 ha	1°C	No
Thorne's hairstreak butterfly, *Mitoura thornei*	Poor	1	CF (Tecate cypress)	<2 ha	1°C	Yes
Harbison's dun skipper, *Euphyes vestris harbisoni*	Good	4	RW, RS, OW (on *Carex spissa*)	<2 ha	1°C	Yes
Riverside fairy shrimp, *Streptocephalus woottoni*	Poor	0	VP	<2 ha	1°C	Yes
Amphibians and reptiles						
California red-legged frog, *Rana aurora draytonii*	Marginal	4[c]	RA	<2 ha	2°C	No
Coronado skink, *Eumeces skiltonianus interparietalis*	Good	4	G, CSS, Chp (open)	<2 ha	2°C	No
Granite spiny lizard, *Sceloporus orcutti*	Poor	0	CHP, OW, with rocks formations	<2 ha	2°C	Yes
San Diego horned lizard, *Phrynosoma coronatum blainvillii*	Good	4	CSS, Chp (open)	<2 ha	2°C	No
Orange-throated whiptail, *Cnemidophorus hyperythrus beldingi*	Good	4	CSS, Chp, G	<2 ha	2°C	No
Birds						
San Diego Cactus Wren, *Campylorhynchus brunneicapillus sandiegensis*	Poor	1	CSS (in *Opuntia* spp.)	<2 ha	2°C	Yes

Blue-gray Gnatcatcher, *Polioptila caerulea obscura*	Marginal	4[d]	OW, RW, CSS, Chp	2–10 ha	2°C	No
Tricolored Blackbird, *Agelaius tricolor*	Marginal	3	FWM	<2 ha	2°C	Yes
Canada Goose, *Branta canadensis moffitti*	Marginal	4[d]	AGF, G, FWM	<2 ha	1°C	No
California Horned Lark, *Eremophila alpestris actia*	Marginal	3	G (open), AGF	2–10 ha	2°C	No
Ferruginous Hawk, *Buteo regalis*	Poor[d]	1	G, AGF	>10 ha	2°C	No
Sharp-shinned Hawk, *Accipiter striatus velox*	Poor	1[d]	All habitats	>10 ha	3°C	No
Merlin, *Falco columbarius* sspp.	Poor	1[d]	G, AGF	>10 ha	3°C	No
Long-eared Owl, *Asio otus wilsonianus*	Poor	1	RW, OW, CF (near open scrub and G)	>10 ha	2°C	No
Red-shouldered Hawk, *Buteo lineatus elegans*	Poor	1	RW, OW, CF, urban	>10 ha	3°C	No
Mammals						
San Diego desert woodrat, *Neotoma lepida intermedia*	Good	4	CSS, Chp	<2 ha	1°C	No
Southern grasshopper mouse, *Onychomys torridus ramona*	Good	4	CSS, Chp (open)	<2 ha	2°C	No
Dulzura pocket mouse, *Chaetodipus californicus femoralis*	Good	4	CSS, Chp, OW, CF	<2 ha	C	No
Northwestern San Diego pocket mouse, *Chaetodipus fallax fallax*	Good	4	CSS, Chp (open)	<2 ha	1°C	No
San Diego black-tailed jackrabbit, *Lepus californicus bennettii*	Good	4	CSS, Chp (open)	<2 ha	1°C	No
California mastiff bat, *Eumops perotis californicus*	Poor	1	CC, MMStr., OW, CF	>10 ha	2°C	Yes
Townsend's big-eared bat, *Corynorhinus townsendii townsendii*	Poor	1	CC, MMStr. (near water), most native habitats	>10 ha	2°C	Yes
Mexican long-tongued bat, *Choeronycteris mexicana*	Poor	1	CC, MMStr., most native habitats	>10 ha	1°C	Yes
Ringtail, *Bassariscus astutus octavus*	Good	4	CSS, Chp, RW, RS	2–10 ha	2°C	No
Bobcat, *Lynx rufus californicus*	Poor	1	All native habitats	>10 ha	2°C	No
Mule deer, *Odocoileus hemionus fuliginatus*	Good	4	CSS, Chp, RW, OW	2–10 ha	1°C	No
Mountain lion, *Puma concolor californica*	Poor	1	CSS, Chp, RW, OW, CF	>10 ha	2°C	No

[a]AGF, agricultural fields; CC, caves, crevices, mines; CF, coniferous forest; Chp, chaparral; CSS, coastal sage scrub; Dist., disturbed habitat; FWM, freshwater marsh; G, grassland; MMStr., man-made structures; NG, native grassland; OW, oak woodland; RA, aquatic riparian; RF, riparian forest; RS, riparian scrub; RW, riparian woodland; VP, vernal pool.

[b]1°P, producer; 1°C, primary consumer; 2°C, secondary consumer; 3°C, tertiary consumer.

[c]Habitat is intact but species is currently extirpated from reserve; therefore, criterion would be met only if species successfully recolonized or were successfully reintroduced.

[d]Species occurs within the reserve during winter only; therefore, the criterion is met during winter only.

demonstrated here, sharing of habitat is not the only determinant of the umbrella's effectiveness. Indeed, only 59% of the species in this study that occur in CSS were considered well protected. For the other CSS species, other factors had an overriding effect. On the other hand, all but one non-CSS species were marginally or poorly protected, indicating that reserve umbrellas should be extended only to species that have habitat requirements very similar to those of the targeted umbrella species.

Often, when area requirements are discussed in the context of the umbrella-species concept they are discussed with respect to the requirement of the umbrella species itself (Shaffer 1981, Noss 1990), while the area requirements of other species are largely ignored. Ideally, the best umbrella species are those with vast area requirements, such as the mountain lion (*Puma concolor*) and grizzly bear (*Ursus arctos*), because the umbrella of these species' reserves should protect almost all of the other species of that region (Noss et al. 1996). Implementing such a large habitat reserve would be immensely challenging because of economic as well as jurisdictional constraints and complexities (Bean et al. 1991). The area requirement of breeding gnatcatchers in our study area is approximately 10 ha per pair. Our analysis revealed that species requiring more than 10 ha per individual were not well preserved, indicating that species with area requirements much larger than that of the umbrella species are not likely to be well protected.

Trophic level may initially appear functionally similar to species' area requirement, ranking wide-ranging carnivores high as umbrella species (Noss et al. 1996). However, trophic level may not be equally as useful as area requirement for most species. As previously mentioned, population size is one of two critical factors determining population viability. Population density (individuals/area) is the reciprocal of area requirement (area/individual). Population density, if extrapolated over the area of habitat, can be used to estimate population size, which is important in determining level of protection within a reserve.

There are at least three reasons why trophic level is not clearly related to population density or size. First, there is no direct relationship between trophic level and density. Species at the same trophic level may occur at very different densities (e.g., a bird as a secondary consumer feeding on insects versus a large carnivore as a secondary consumer feeding on herbivorous rodents and ungulates). Second, social behavior (coloniality) or mobility may allow species at higher trophic levels to occur at densities higher than expected (although increased local densities are likely to even out when averaged over larger areas). And third, a species may frequently forage at more than one trophic level by consuming a variety of foods. Therefore, it is possible that the weak relationship between trophic level and level of protection identified in this analysis is due predominantly to the correlation with the effect of area requirement.

The need for rare and localized habitat types was the bane of many species that otherwise would have been considered well protected in this study. Only 10% of the species requiring rare and localized habitat types were well protected within the reserve. Such habitat specialists are likely to be poorly protected by a single-species-reserve umbrella unless the umbrella species has similar specialized habitat requirements.

It is not possible to predict from these results which species are protected under the umbrella of a different single-species reserve. If different target species were chosen, the result would have undoubtedly been different. Likewise, had we chosen a different configuration for the gnatcatcher reserve our results probably would have differed. There are certain underlying ecological characteristics, however, that are likely to be common to most species that are protected and lacking in most species that are not, regardless of the particular single-species reserve. Specifically, we expect that species that share the same primary habitat as the umbrella species, that have area requirements equal to or less than the umbrella species, and that do not require rare and localized habitat types to be best protected under the reserve umbrella.

Why does this single-species-reserve umbrella protect the species it does? The simple answer is that the reserve encompasses enough habitat to support large enough populations of the well-protected species. It also encompassed habitats that were distributed widely enough to counter the detrimental effects of environmental stochasticity while being connected enough to allow dispersal throughout the habitat.

Although the umbrella-species concept has been briefly discussed many times in the conservation-biology literature (e.g., Murphy 1988, Simberloff 1988, Murphy et al. 1990, Noss 1990), these discussions typically have overlooked the many confounding factors that may restrict the ability of a reserve umbrella to protect a given species. One discussion that does address many of these problems is that of Mühlenberg et al. (1991), who acknowledged the problem of rare and localized habitat types also identified in this research. They recommended a hierarchical approach in which representative species with various area requirements and habitat characteristics are selected as target species. The initial reserve design is completed with the species with the largest area requirement functioning as the umbrella species. Then the design is modified using other target species with successively smaller area requirements and different habitat characteristics as additional umbrella species. Along with this hierarchical approach Mühlenberg et al. (1991) discussed a variety of additional important considerations and methods, from detailed population studies to population-viability simulations to policy strategies. Several of their recommended methods are analogous to those developed here and are being applied in multispecies conservation plans in the Southwest (e.g., San Diego County MSCP, California Natural Communities Conservation Planning (NCCP), and the Lower Colorado River MSCP).

Lambeck (1997) proposed an application of the umbrella-species concept to reserve design by identifying suites of focal species, each of which contributes different spatial and compositional attributes to the reserve. Lambeck's focal species are defined by limiting factors within the ecosystem. Species that are most limited by (i.e., have large) area requirements are used to define the minimum suitable area for that habitat type. The area-limited focal species are analagous to "traditional" umbrella species. Other focal species are added to the suite on the basis of other limiting factors and act as functional umbrellas for other components of the reserve. For example, dispersal-limited species are used to define the acceptable degree of connectivity; resource-limited species (e.g., those requiring rare and localized habitat types) define essential habitat components; process-limited species (e.g., those depending on fire or flood) define the minimum level at which processes are managed. Lambeck's (1997) broader application of the umbrella-species concept includes structure and function in addition to the composition aspect of reserve design typically addressed by the umbrella-species concept.

Several multispecies habitat-conservation plans are currently under development and implementation in California and other states [e.g., Southern California Coastal Sage Scrub NCCP; Coachella Valley (California) MSHCP; Lower Colorado River MHCP (California, Arizona, and Nevada); Placer County (California) NCCP; Balcones Canyonlands (Texas) HCP; and Brevard County (Florida) HCP]. Although earlier habitat-conservation plans typically identified one or a few target species to function as umbrella species, recent regional HCP programs have significantly increased the number of species incorporated into the reserve-design process that may function as umbrella species (e.g., the San Diego County MSCP identified 97 nominal target species). The political context of habitat-conservation planning along with constraints of time and money, however, generally do not allow for rigorous scientific study to determine whether these species are the most effective basis to aid conservation-planning decisions (i.e., they may not be the best umbrella species)—a serious concern for some conservationists (Atwood and Noss 1994, Noss et al. 1996, Noss et al. 1997). As these reserve-design efforts continue, a species-by-species evaluation of the effectiveness of the reserve umbrella in protecting viable populations is a critical next step.

Fortunately, since this project's inception, the reactive single-species approach to reserve design has, to a significant extent, been replaced (at least conceptually) with a proactive ecosystem-level approach to conservation (Atwood and Noss 1994, Mantell 1994, Noss and Cooperrider 1994, Knight and Bates 1995). But multispecies and ecosystem-level projects are still limited by the amount of available autecological data and therefore must focus on a subset group of target species. These target species must function as umbrellas for the remaining species in the ecosystem. Therefore, the umbrella-species concept is still, and will likely always be, a necessary pragmatic approach for reserve design and management.

SUMMARY

In this case study of the umbrella-species concept, we analyzed the effectiveness of a reserve designed for a single species to protect a wide variety of other plants and animals that were not the target of the reserve design. We selected the California Gnatcatcher as the umbrella species and the Otay region of San Diego County as our study area. We then designed a hypothetical reserve based on the habitat requirements of the gnatcatcher alone. We assessed the level of protection this reserve provided 40 other sensitive plant and animal species occurring in the study area. The gnatcatcher functioned as a suitable umbrella species for less than half of the species we evaluated. Generally, the species best protected under the gnatcatcher-reserve umbrella were species that had area requirements equal

to or less than the gnatcatcher's and habitat requirements similar to the gnatcatcher's, as well as species at lower trophic levels and species that were not habitat specialists. The methods developed in this study require a relatively modest amount of time and data to estimate the degree to which a single-species-reserve umbrella protects other species of concern and may be useful if applied in other single- and multiple-species conservation plans.

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