CALIFORNIA GNATCATCHER USE OF HABITATS OTHER THAN COASTAL SAGE SCRUB: CONSERVATION AND MANAGEMENT IMPLICATIONS

KURT F. CAMPBELL, Campbell BioConsulting, 40950 Via Media, Temecula, California 92591-1722

RICHARD A. ERICKSON, LSA Associates, Inc., One Park Plaza, Suite 500, Irvine, California 92614

WILLIAM E. HAAS, Varanus Biological Services, Inc., 7950 Silverton Ave., Suite 116, San Diego, California 92126

MICHAEL A. PATTEN, Department of Biology, University of California, Riverside, California 92521

That California Gnatcatchers (*Polioptila californica*) within the United States are dependent on coastal sage scrub habitats is well established (Atwood 1993, USFWS 1991, 1993). Our effort in this paper is to look not at whether these habitats are necessary on a large scale, but rather to raise the question of whether they are always sufficient, at both local and larger scales.

Existing literature on these birds makes little mention of their occurrence outside of coastal sage scrub habitats. Some sources specifically state that the species is restricted to coastal sage scrub (Woods 1949, USFWS 1991). The earliest clear, published indication to the contrary was provided by Unitt (1984): "Elizabeth Copper (pers. comm.) suggests that the gnatcatchers leave the sage scrub for more humid habitats nearby in late summer when most sage scrub plants are dry and brown."

Throughout the species' U.S. range since 1990, we have found numerous instances of California Gnatcatchers making potentially significant use of habitats other than coastal sage scrub (hereafter, non-CSS). Many of these instances were noted without systematic study, but we also document systematic use of non-CSS by closely monitored birds over several years. We neither propose nor anticipate that the species is broadening its general habitat requirements, nor that in California the birds regularly nest independently of coastal sage scrub. We do believe that such use of non-CSS is frequent, at least in some situations, and potentially important to the long-term viability of U.S. populations.

METHODS AND RESULTS

We examined the literature on the California Gnatcatcher for discussions of non-CSS use and reviewed our own extensive combined field experience. Campbell, Erickson, and Patten have performed focused surveys or habitat assessments for the California Gnatcatcher at well over 200 sites since 1988, throughout most of the U.S. range of the species, and at all times of year. Haas has studied the species intensively at several sites in one portion of the range, over several years.

We found little published indication that the species is found outside of its typical habitat. An example is Woods' (1949) statement, "few landbirds confine themselves so rigidly to their characteristic habitat." Apart from

Unitt's (1984) reference mentioned above, we found no explicit discussions of whether the species' habitat preferences may vary seasonally or among various roles (e.g., during dispersal; for juveniles versus adults; during breeding versus nonbreeding). Some authors have noted use of non-CSS, but the potential importance of such use has never been addressed.

We present details of 51 occurrences of California Gnatcatchers using non-CSS for significant periods, many involving multiple birds (Table 1). These observations were not the result of systematic study at coastal sage scrub edge and thus may underestimate the occurrence of such behavior. Observations are ordered by county and grouped by month. Observations of only brief non-CSS habitat use or use of minor CSS habitat variations are not included. Plant nomenclature and taxonomy follow Hickman (1993).

We also present information from longer-term studies of California Gnatcatcher populations in San Diego County, data that complement Table 1. We have recorded substantial use of non-CSS habitat while monitoring gnatcatcher behavior at several locations including Mission Trails Regional Park, Lake Hodges, Sweetwater Reservoir and Dam, Fallbrook Naval Weapons Station, and Marine Corps (formerly Naval) Air Station Miramar. Three of these locations have been monitored for three years or more with color-banded birds. These data are based on standardized spot-mapping (Ralph et al. 1993) and include year-round data from most locations. Anecdotal observations of non-CSS use were made as well during those studies, but we present only graphic summaries of spot-mapping data over several months, as these data are not tested statistically.

At least one pair of California Gnatcatchers seasonally shifted in habitat from predominantly CSS habitat to non-CSS (in this case, cottonwood–willow riparian and willow scrub; Figure 1). In the case of some monitored pairs, the change appeared to be in part due to seasonal expansion of use areas.

Another pair showed an alternative (but not mutually exclusive) form of habitat shifting, from its breeding-season use area (high-quality coastal sage scrub) in the early morning to an alternative habitat (cottonwood–willow riparian; Figure 2) in the afternoon. It used non-CSS primarily along the habitat edge adjacent to the breeding territory.

During the cold, wet winter and spring of 1993 Haas observed three pairs engaging in a third type of shift (Figure 3). The study site covered 20 ha in San Diego County with sage scrub on slopes and in washes, chaparral on ridge tops and mesas. In March and April gnatcatchers used the chaparral, dominated by chamise (*Adenostoma fasciculatum*) and black sage (*Salvia mellifera*), not only for foraging but also for nest placement, building seven nests in chamise. Later in the year, when the sage scrub was no longer laden with dew in the early morning, two of the pairs placed their third or fourth nests there. At this time, all three pairs foraged extensively outside the chamise in sage scrub and chaparral broom (*Baccharis sarothroides*). Use of chamise chaparral by the California Gnatcatcher, even almost exclusive use year round by some individuals or pairs, has been recorded in several studies (T. Conkle pers. comm.).

Data from 1520 observations at two study sites (predominantly coastal sage scrub during the breeding season) show a definite increase from spring to summer in use of several types of non-CSS (including riparian and

Table 1 Observations of the California Gnatcatcher Using Habitats Other than Coastal Sage Scrub

Location and use of non-CSS	Dominant plants or vegetation type	CSS proximity	Number, age, sex	Year	Observer
Rancho Palos Verdes, Los Angeles Co.					
Jan–Mar	Bx	<200 m	4–5	1992	RAE
Jun	Bx	adjacent	1 pair, 2 juveniles	1992	KFC
Sep–Dec	Bx	<200 m	4–5	1991	RAE
Jan–Mar; regular	Bx, Al, Orn	<100 m	3–4	1991	RAE
Newport Beach, Orange Co.					
Mar–Apr; most of territory	Bs, Sx	<100 m	1–2 pairs	1991	RAE
Mar–Apr; most of territory	Bs, Sx	<100 m	2 pairs	1992	RAE
Mar–Apr; most of territory	Bs, Sx	<100 m	2 pairs	1993	RAE
Mar–Apr; most of territory	Bs, Sx	<100 m	2 pairs	1994	RAE
Mar–Apr; most of territory	Bs, Sx	<100 m	1 pair	1996	RAE
Oct; seen once	Rud	<150 m	2	1997	RAE
Oct–Nov	Rud	<600 m	5	1990	RAE
Oct–Nov	Rud	<600 m	5	1991	RAE
Irvine, Orange Co.					
nesting season; most of territory	Bs	± 75 m	1–2 pairs	1991	RAE
nesting season; most of territory	Bs	± 75 m	1–2 pairs	1992	RAE
nesting season; most of territory	Bs	± 75 m	1–2 pairs	1993	RAE
nesting season; most of territory	Bs	± 75 m	1 pair	1994	RAE
nesting season; most of territory	Bs	± 75 m	1 pair	1996	RAE
nesting season; most of territory	Bs	± 75 m	male on territory	1997	RAE
nesting season; regular	Bx, Hi, AGr	adjacent	several pairs and their young	1992	RAE
nesting season; repeated	Bx, Hi, AGr	<100 m	several pairs and their young	1993	RAE
nesting season; repeated	Bx, Hi, AGr	<100 m	several pairs and their young	1994	RAE
nesting season; repeated	Bx, Hi, AGr	<100 m	several pairs and their young	1995	RAE
nesting season; repeated	Bx, Hi, AGr	<100 m	several pairs and their young	1996	RAE

(*continued*

Table 1 *(Continued)*

Location and use of non-CSS	Dominant plants or vegetation type	CSS proximity	Number, age, sex	Year	Observer
nesting season; repeated	Bx, Hi, AGr	<100 m	several pairs and their young	1997	RAE
nesting season; most of territory	Rud	<250 m	1 pair	1996	RAE
nesting season; most of territory	Rud	<250 m	2 pair; 1 successful	1997	RAE
Sep	Bx, Hi, AGr	<250 m	3 juv.	1996	RAE
Sep–Oct	Bx, Hi, AGr	<250 m	5–6, mostly juv.	1993	RAE
Sand Canyon Res., Orange Co.					
May–Jun	Sx	<100 m	1 pair and young	1995	RAE
Los Coyotes Hills, Orange Co.					
May–Aug; postfledging	Bs, Rud	adjacent	5 pairs and young	1991	KFC
San Clemente, Orange Co.					
Jan–Mar; regular	Bx, Al, Orn	<100 m	3–4	1991	RAE
Jul; seen once	Bx, Rud	<300 m	1 juvenile	1991	RAE
Sep–Dec; regular	Bx, Al, Orn	<200 m	3–4	1990	RAE
Crystal Cove State Park, Orange Co.					
Aug–Sep	Bx, Rud	<200 m	5–6, mostly juv.	1993	RAE
Costa Mesa, Orange Co.					
Oct–Nov	Rud	<400 m	5	1990	RAE
Oct–Nov	Rud	<400 m	5	1991	RAE
Laguna Niguel, Orange Co.					
Dec; seen once	St	100+ m	2	1991	RAE
Lake Elsinore, Riverside Co.					
May–June; nesting; not seen outside in 3 visits	Af	adjacent	1 pair	1995	KFC
S of L. Mathews, Riverside Co.					
May–Jun; all of territory	Af	30 m	1 pair	1996	KFC
Jul–Aug	Sx, Sm	adjacent	3+	1995	KFC
Harrison Res., Riverside Co.					
May–Jul; postnesting	low Rip	adjacent	1 pair, no young	1995	KFC

Alberhill Cr., Riverside Co.					
Jun; postfledging	low Rip	50+ m	1 ad., 2 juv.	1992	MAP
Domenigoni Hills, Riverside Co.					
Jun–Jul; postfledging	Hi	adjacent	2 pairs and young	1995	KFC
Railroad Canyon, Riverside Co.					
Jun–Jul; postfledging	Sx, Pf	adjacent	1 pair, 3 young	1994	KFC
Aug–Sep; postfledging	Sx, Pf	adjacent	1 pair, 3 young	1995	KFC
W of L. Mathews, Riverside Co.					
Jul	Bs	150+ m	1 male	1994	KFC
Good Hope, Riverside Co.					
Sep	Bs	20 m	1 female, 1 juv.	1995	KFC
Cajalco Creek, Riverside Co.					
Oct	low Rip	adjacent	2	1993	MAP
San Dieguito Cr., San Diego Co.					
June	Hi, Im	± 50 m	1 pair, 3 young	1998	KFC
July	Tam	± 520 m	1 male	1998	KFC
Sweetwater Res., San Diego Co.					
Nov	St	>100 m	1 male	1994	KFC
Nov	St	adjacent	2; male and female	1994	KFC

[a]Af, *Adenostoma fasciculatum*; Agr, annual grassland; Al, *Atriplex lentiformis*; Bs, *Baccharis salicifolia*; Bx, *Brassica* sp.; Hi, *Hirschfeldia incana*; Im, *Isocoma menziesii*; Orn, ornamentals; Pf, *Populus fremontii*; Rip, riparian; Ru, ruderal (weedy); Sm, *Sambucus mexicana*; St, *Salsola tragus*; Sx, *Salix* sp., Tam, *Tamarix* sp.

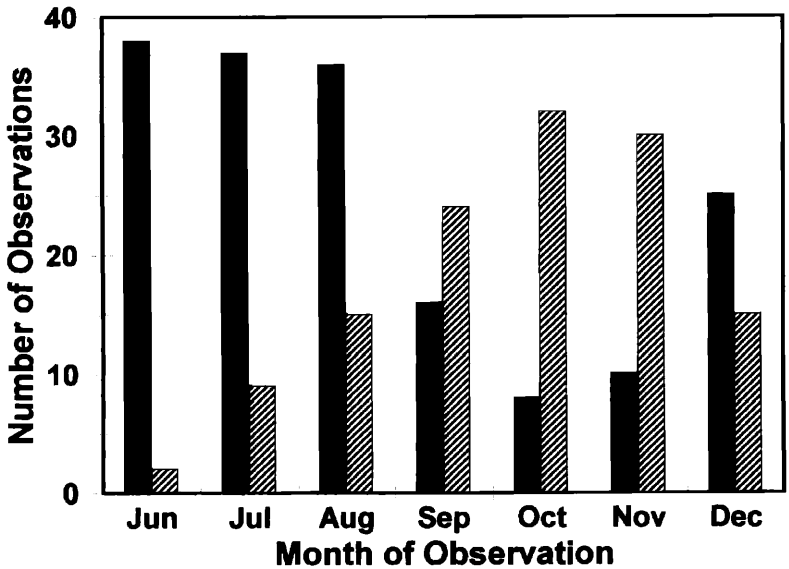

Figure 1. California Gnatcatcher vegetation use, Lake Hodges, Escondido. Data collected June–December 1994; based on two 2-hour spot-mapping visits per month (n = 40 observations/month). Solid bars, observations in coastal sage scrub; cross-hatched bars, observations in riparian habitat.

chaparral) and several plant species, especially Mexican elderberry (*Sambucus mexicanus*), willows (*Salix* spp.), coyote brush (*Baccharis pilularis*), and mulefat (*B. salicifolia*) (Figure 4). Not all pairs from which the data are drawn have access to non-CSS in or adjacent to their use areas.

DISCUSSION

California Gnatcatchers have been observed using non-CSS throughout the year. Given that there is some bias because much of our field work was during the breeding season, the highest rates of non-CSS use appear to be from May to November. Systematic variation in habitat use by time of day is possible (Figure 2).

The majority of our observations likely reflect short-distance movements, with gnatcatchers moving from territories located in coastal sage scrub to adjacent non-CSS. A few observations were of gnatcatchers whose nesting territories include or are located within non-CSS. We have no indication that the pattern is more prevalent coastally or inland, farther north or farther south, at higher or lower elevations, in smaller or larger patches of coastal sage scrub, among sink or source populations, or at the core or periphery of the species' U.S. range. Adults of both sexes, as well as juveniles, have been observed foraging in non-CSS for extended periods, although it appeared the birds most often engaged in such activity subsequent to nesting. Most non-

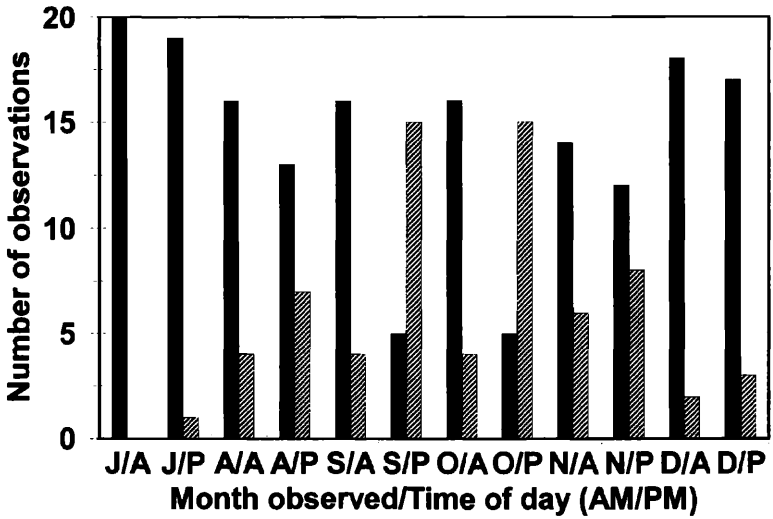

Figure 2. Morning-to-afternoon habitat shift of a pair of California Gnatcatchers in Mission Trails Regional Park, San Diego, July (J) to December (D) 1993. Data based on two 2-hour spot-mapping visits per month (n = 40 observations/month). Morning data (A) collected between 7 and 10 AM; afternoon data (P) collected between 2 and 5 PM. AM and PM data collected on same day. Solid bars, observations in coastal sage scrub; cross-hatched bars, observations in riparian habitat.

CSS use involves areas more mesic than coastal sage scrub, although some of the ruderal areas are only moderately so. An exception is the site on which Figure 3 is based, where gnatcatchers used chaparral adjacent to sage scrub. The sage scrub at this site may have been too cold and wet early in the spring, as the birds used it later. Mature woodland and forest appear to be visited only rarely. Perhaps a more consistent difference from coastal sage scrub is that the non-CSS used frequently has a somewhat greater average height and foliage density and is composed of plant species that are not summer-deciduous. Although many of our observations were of birds at the base of slopes covered with coastal sage scrub, we saw no indication that birds moved in response to degree of slope, aspect, hydrology, or from exposed to protected sites.

The edges of coastal sage scrub, scrub marginal or poor in certain resources, scrub heavily invaded by nonnative plant species, or where California Gnatcatchers in high density are adjacent to productive non-CSS may be the areas where use of alternative habitat is most common. Natural fragmentation of coastal sage scrub is relatively high (Mooney 1988) and increasing with human alteration of the landscape. Geographically, coastal sage scrub itself varies considerably in floristics and phenology (e.g., Kirkpatrick and Hutchinson 1977, White and Padley 1997), and the factors behind California Gnatcatcher use of non-CSS are likely affected by such variation. Annual variation in weather may play an important role, causing significant yearly variations in, for instance, insect abundance in coastal sage

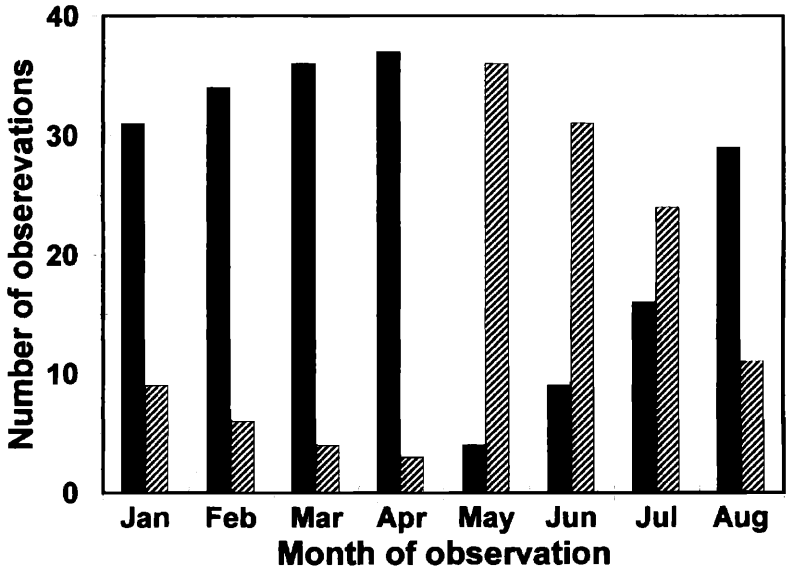

Figure 3. California Gnatcatcher use of chamise chaparral during breeding season, Marine Corps (formerly Naval) Air Station Miramar, San Diego. Shift in habitat in May corresponds to shift to nest placement in coastal sage scrub. Solid bars, observations in chamise chaparral; cross-hatched bars, observations in coastal sage and *Baccharis* scrub.

scrub in late spring and summer (e.g., Roach 1989), pushing birds out of coastal sage scrub or luring them into other habitats.

The California Gnatcatcher may parallel the riparian Least Bell's Vireo (*Vireo bellii pusillus*), whose "use of non-riparian habitats, primarily areas of coastal sage scrub and chaparral vegetation, varied over the nesting cycle, and was related to territory location and habitat composition" (Kus and Miner 1989). These researchers revealed that at one site 23 pairs of Bell's Vireos, 43% of those studied in one year, included nonriparian areas within their home range.

Four causes, which are not mutually exclusive, for the gnatcatcher's use of non-CSS appear possible. In each case, fledglings are especially likely to be susceptible; the apparent peak period of non-CSS use in the species is from around the time birds are fledged to at least several months thereafter.

First, improved food resources may play a role. Coastal sage scrub is highly seasonal in plant growth and insect abundance (O'Leary 1989, Roach 1989, R. Redak unpubl. data). Although California Gnatcatchers appear to be well adapted to this habitat, it may be that at times of food stress, as a result of an unusual paucity of resources in the environment (e.g., drought and/or habitat degradation), more usual stress periods in the bird's cycles (e.g., molt, juveniles' foraging inefficiency combined with energy demands of fledglings), or a combination of these factors, individuals may receive significant benefit by

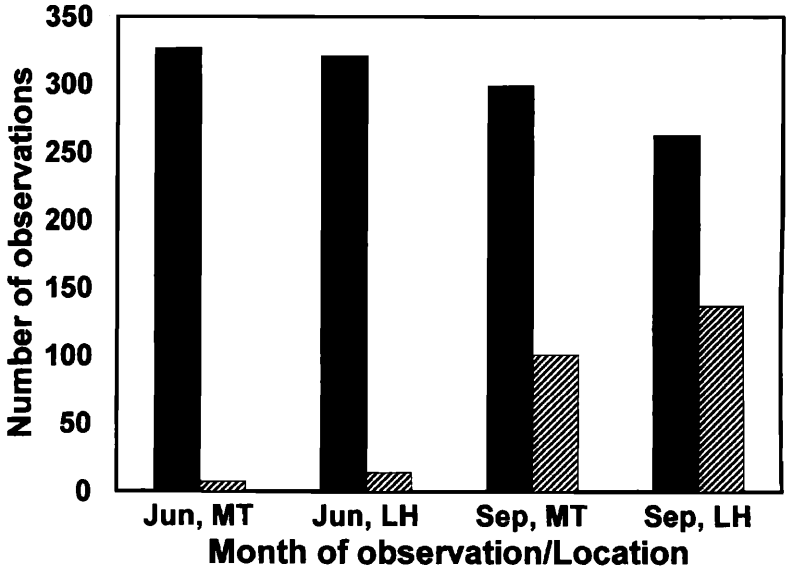

Figure 4. Shift in California Gnatcatcher habitat use from June to September at Mission Trails Regional Park and Lake Hodges, San Diego. Data based on 2-hour spot-mapping visits (10 pairs of gnatcatchers/site; 20 observations/pair/visit, n = 1520). Solid bars, observations in coastal sage scrub; cross-hatched bars, observations in riparian habitat.

foraging in non-CSS. Coastal sage scrub is summer-deciduous (Mooney 1988), unlike riparian habitats in the region, which remain green, dense, and mesic through summer (Holstein 1984). Comparing the close correlation of insect biomass and spring peaks of primary productivity in California upland vegetation, Holstein noted that comparable data for California riparian communities appear unavailable, but that the extremely high summer productivity of such communities undoubtedly induces similarly high summer peaks of insect biomass. These in turn attract insectivorous birds.

Second, gnatcatchers with non-CSS experience as juveniles may have higher survival rates during dispersal and other movements than those without such experience. Coastal sage scrub has always been relatively fragmented as well as subject to fires, and is becoming increasingly so (Mooney 1988, O'Leary 1989, Atwood 1993). Thus there is a potentially substantial and increasing selection pressure for success (i.e., finding resources and avoiding predation) during movement through non-CSS. Gnatcatchers that have been familiarized with such habitats, through foraging forays as juveniles led by parents, may have enhanced likelihood of survival later, and thus the behavioral trait of providing non-CSS habitat experience to young would increase as well.

Third, improved microclimate is another possible factor in non-CSS use. Temperature extremes can be an important factor regulating behavior and

small- and large-scale distribution in birds (e.g., Mugaas and King 1981, Barrows 1981). In a seasonally hot environment such as coastal sage scrub, it is reasonable to expect that fledglings may be susceptible to temperature peaks at the very time when shade and water are scarcest. Temporary movement of birds into more shaded habitats may allow them to avoid heat stress, as well as to seek water (whether directly or through food resources).

Fourth, a lowered predation rate for fledglings is yet another factor that may select for non-CSS use. With most songbirds, postfledgling juveniles suffer relatively high predation. It is possible that predation rates on fledglings may be lower in non-CSS, such as willow riparian, where cover is more dense. If so, such habitats act as nurseries. An analog of this hypothesis may be found in the work of Evens and Page (1986), who studied predation on the Black Rail (*Laterallus jamaicensis*) during high tides in the San Francisco Bay area and concluded that vegetation peripheral to marshes may partly offset predation risk by providing rails with alternative cover at high tides. Rails in upland habitat adjacent to marshes during high tide were taken less often by avian predators than were those where cover peripheral to the marsh was lacking.

An additional factor that may add to the importance of non-CSS adjacent to coastal sage scrub is buffering. In addition to providing potentially direct benefits to gnatcatchers as discussed here, non-CSS may lower mortality within coastal sage scrub by lowering the incidence of predation from exotic species such as domestic cats and habitat loss from the many small fires set at the urban–wildland interface. Kelly and Rotenberry (1993) discussed the importance of buffering in reserve design and suggested methods for designing effective buffers. They did not explicitly address the effects or resource value of different kinds of habitats as buffers except in the context of "boundary permeability" for disturbance, and thus such functions are a potential additional value of buffers.

In addition to the potential advantages, however, inclusion or retention of non-CSS within or adjacent to areas being managed for the California Gnatcatcher may pose two distinct disadvantages: (1) frequency of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) and predation by a variety of predators may be higher with some adjacent habitats (e.g., low riparian) than with others (e.g., grassland), and (2) concerns regarding brush clearance for fire suppression along the urban–wildland interface may be aggravated when "nonhabitat" areas are being protected at the perceived cost of endangering human structures and lives. A tradeoff situation may exist. A nest located close to retained non-CSS may face a high risk of brood parasitism or predation but may make it easier for gnatcatchers to benefit from the non-CSS as well. As brood parasitism of the California Gnatcatcher appears to be rather patchy (Braden et al. 1997), proximity to non-CSS may result in very different conditions for birds in different places.

RECOMMENDATIONS

Determining the importance of non-CSS to the California Gnatcatcher's survival will be a formidable task. Needed are studies addressing: (1) the

frequency and pattern with which non-CSS is used by pairs occupying territories adjacent to a variety of habitat types, (2) productivity of such pairs, and (3) survivorship of their offspring. Some of these issues could be addressed through minor adjustments to the methods and assumptions of ongoing and planned research projects.

Area–habitat relationships are the subject of much recent and ongoing research. It is important, however, to separate the broader issues of edge effects from the more focused issue addressed here. If non-CSS is available to a gnatcatcher, what are the costs and benefits of using it rather than adjacent coastal sage scrub? For example, does it allow birds to avoid other, potentially more costly behavior, such as maintaining a substantially larger territory composed of pure coastal sage scrub?

In the short term, management practices should include consideration of the potential importance of non-CSS located adjacent to coastal sage scrub inhabited by California Gnatcatchers. As Kus and Miner (1989) noted in examining use of nonriparian habitat by the Least Bell's Vireo, "these observations suggest that planning boundaries intended to protect resources essential for breeding vireos should include upland areas bordering riparian habitats."

Areas with moderate to high vegetative density that are not summer-deciduous but are adjacent to coastal sage scrub should be retained, especially habitats such as mulefat scrub, chaparral, and disturbed riparian. Gnatcatchers' use of these habitats may be at least locally critical. We do not know how valuable such habitats are, but they are clearly more valuable than sites that are barren or regularly disturbed and are very likely less valuable than an equivalent area of high-quality sage scrub. The question that will arise repeatedly in management is where along that spectrum each patch of non-CSS in question lies. Probably some non-CSS is more valuable than some coastal sage scrub, if the quality of the latter is too poor, or other factors (e.g., patch size and shape; disturbance factors) are important.

Reserve design should reflect the need for landscape-level planning rather than treat habitats as isolates. For example, the value of a potential mitigation site is partly reflected in the presence of usable non-CSS, in addition to more traditional measures such as the quality and acreage of coastal sage scrub. The potential buffer from human impacts, as well as the alternative habitat resources, may spell the difference between a vital, long-term natural reserve and the dubious expediency of a simple acreage ratio. Finally, those performing impact analyses under the California Environmental Quality Act, National Environmental Policy Act, or other regulations should recognize that avoidance of impacts to coastal sage scrub alone is not a guarantee that impacts to gnatcatchers have been avoided. Removal of habitat up to, but not including, coastal sage scrub may well allow for persistence of gnatcatchers at a given site only if ideal conditions prevail indefinitely, an obviously unrealistic assumption.

It is critical for our understanding of what constitutes California Gnatcatcher habitat that definitions be drawn from actual use by the birds, not from scale-dependent abstractions such as "coastal sage scrub." Failure to protect adjacent non-CSS adequately at the scales of both regional planning and particular sites may critically affect the species' long-term viability. It

may be possible to save "the habitat" by artificially restricting our understanding of it and yet lose the species intended for protection.

SUMMARY

The California Gnatcatcher, while clearly dependent on coastal sage scrub within its U.S. range, regularly uses other habitats and shows seasonal and perhaps daily patterns in such use. Our data do not reveal patterns with regard to many possible environmental variables, such as geographic or topographic trends. There does appear to be some pattern of non-CSS use emphasizing shrubby or weedy habitats that are mesic and not summer-deciduous. Use of such habitats appears to be most frequent immediately upon fledging of young and continues through fall and winter, with smaller numbers of birds using such areas during the breeding season. Improved food resources, higher survival rates during juveniles' dispersal, fire avoidance, cooler microclimate during heat stress, and lower predation rates for juveniles may all be factors contributing to the gnatcatcher's use of alternative habitats. Non-CSS may also provide a buffer to human impacts on and natural variation in coastal sage scrub. Conversely, it may facilitate increased brood parasitism by cowbirds as well as predation at some sites.

The gnatcatcher's use of non-CSS habitats has implications for reserve design and management, restoration efforts, and environmental-impact analyses. The political ramifications of preserving non-CSS for gnatcatchers should be factored into planning and management decisions because of issues such as the perceived need of the human community for safety from wildfire. The importance of non-CSS to the California Gnatcatcher and other coastal sage scrub species should be examined through intermediate-term (8–15 yr) local studies of population dynamics and habitat use under a range of environmental conditions, addressing both productivity and survivorship.

ACKNOWLEDGMENTS

Anecdotal data (Table 1) are from the field work of Campbell, Erickson, and Patten; data from spot mapping are from the field work of Haas and Varanus Biological Services. We thank Elizabeth Copper for her early recognition of the use of alternative habitats by California Gnatcatchers. Brian E. Daniels was the first to point out to Campbell such a pattern of habitat use. Jonathan L. Atwood, Jutta C. Burger, Tricia A. Campbell, and John T. Rotenberry provided invaluable discussions, criticisms, and suggestions. We thank our clients for access to fascinating areas and permission to use the data, particularly the U.S. Marine Corps for use of data derived under contract at Marine Corps Air Station Miramar.

LITERATURE CITED

Atwood, J. L. 1993. California Gnatcatchers and coastal sage scrub: The biological basis for endangered species listing, in Interface between Ecology and Land Development in California (J. E. Keeley, ed.), pp. 149–169. S. Calif. Acad. Sci., Los Angeles.

Barrows, C. W. 1981. Roost selection by Spotted Owls: An adaptation to heat stress. Condor 83:302–309.

Braden, G. T., McKernan, R. L., and Powell, S. M. 1997. Effects of nest parasitism

by the Brown-headed Cowbird on nesting success of the California Gnatcatcher. Condor 99:858–865.

Evens, J., and Page, G. W. 1986. Predation on Black Rails during high tides in salt marshes. Condor 88:107–109.

Hickman, J. C., ed. 1993. The Jepson Manual: Higher Plants of California. Univ. of Calif. Press, Berkeley.

Holstein, G. 1984. California riparian forests: Deciduous islands in an evergreen sea, in California Riparian Systems: Ecology, Conservation, and Productive Management (R. E. Warner and K. M. Hendrix, eds.), pp. 2–22. Univ. of Calif. Press, Berkeley.

Kelly, P. A., and Rotenberry, J. T. 1993. Buffer zones for ecological reserves in southern California: Replacing guesswork with science, in Interface between Ecology and Land Development in California (J. E. Keeley, ed.), pp. 85–92. S. Calif. Acad. Sci., Los Angeles.

Kirkpatrick, J. B., and Hutchinson, C. F. 1977. The community composition of Californian coastal sage scrub. Vegetatio 35:21–33.

Kus, B. E., and Miner, K. L. 1989. Use of non-riparian habitats by Least Bell's Vireos, in Proceedings of the California Riparian Systems Conference: Protection, management, and restoration for the 1990's (D. L. Abell, tech. coord.), pp. 299–303. U.S. Forest Service, Pac. Southwest Forest & Range Exp. Sta. Gen. Tech. Rep. PSW-110.

Mooney, H. A. 1988. Southern coastal scrub, in Terrestrial Vegetation of California, 2nd ed. (M. G. Barbour and J. Major, eds.), pp. 471–489. Spec. Publ. 9, Calif. Native Plant Soc., Sacramento.

Mugaas, J. N., and King, J. R. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie: A study of thermal and behavioral energetics. Studies Avian Biol. 5:1–78.

O'Leary, J. F. 1989. Californian coastal sage scrub: General characteristics and considerations for biological conservation, in Endangered plant communities of southern California (A. A. Schoenherr, ed.), pp. 24–41. S. Calif. Botanists Spec. Publ. 3.

Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E., and DeSante, D. F. 1993. Handbook of field methods for monitoring landbirds. U.S. Forest Service, Pac. Southwest Res. Sta., Gen. Tech. Rep. PSW-GTR-144.

Roach, J. D. 1989. The influence of vegetation structure and arthropod abundance on the reproductive success of California Black-tailed Gnatcatchers. M.S. thesis, San Diego State Univ.

Unitt, P. 1984. The birds of San Diego County. San Diego Soc. Nat. Hist. Memoir 13.

U.S. Fish & Wildlife Service. 1991. Proposed rule to list the Coastal California Gnatcatcher as endangered. Fed. Reg. 56:47053–47060.

U.S. Fish & Wildlife Service. 1993. Determination of threatened status for the coastal California Gnatcatcher. Fed. Reg. 58:16742–16757.

White, S. D., and Padley, W. D. 1997. Coastal sage scrub series of western Riverside County, California. Madroño 44:95–105.

Woods, R. S. 1949. *Polioptila melanura californica* Brewster: Black-tailed Gnatcatcher, in Life histories of North American thrushes, kinglets, and their allies (A. C. Bent, ed.), pp. 374–382. U.S. Natl. Mus. Bull. 196.

Accepted 23 July 1998