

ASSOCIATION OF WITHIN-TERRITORY VEGETATION CHARACTERISTICS AND FITNESS COMPONENTS OF CALIFORNIA GNATCATCHERS

GERALD T. BRADEN,^{1,3} ROBERT L. MCKERNAN,¹ AND SHAWN M. POWELL²

¹ San Bernardino County Museum, 2024 Orange Tree Lane,
Redlands, California 92374, USA; and

² Department of Forestry and Wildlife Management, University of Massachusetts,
Amherst, Massachusetts 01003, USA

ABSTRACT.—Correlations among habitat characteristics and fitness components of California Gnatcatchers (*Poliophtila californica californica*) were examined using within-territory vegetation and life-history data for 41 pairs of gnatcatchers at four sites from 1993 through 1995. Gnatcatchers nested earlier, had more successful nests, produced more fledglings, had a longer nesting period, and had lower fledgling costs when their territories were associated with increased grass and forb cover, increased perennial structure, increased horizontal perennial homogeneity, decreased vertical perennial homogeneity, and decreased perennial diversity. Within-territory vegetation variables, derived from the correlation of vegetation and life-history variables, were able to discriminate among gnatcatcher pairs grouped by site. Survival of adult gnatcatchers was significantly higher in the gnatcatcher group that had average within-territory vegetation characteristics associated with maximization of other life-history variables and was significantly lower in the gnatcatcher group that had average within-territory vegetation characteristics associated with minimization of other life-history variables. Survival of juveniles was not associated with within-territory vegetation. The finite rate of population increase (λ) was >1 for the gnatcatcher group where within-territory vegetation and life-history variables were maximized, approximately equal to 1 for gnatcatcher groups where within-territory vegetation and life-history variables were moderate, and <1 for the gnatcatcher group where within-territory vegetation and life-history variables were minimal. Our study suggests that within-territory vegetation characteristics are associated with adult survival and λ , but site characteristics independent of vegetation also could have contributed to such an association. Received 3 September 1996, accepted 1 April 1997.

SPECIES ABUNDANCE can be a misleading indicator of habitat quality and reproductive success (Van Horne 1983, Pulliam 1988, Martin 1992, Vickery et al. 1992a). Assuming that habitat features associated with fitness components (i.e. increased reproductive output and survival) will be chosen more often over time, preservation of (or management for) such features should increase fitness and promote short-term increases in abundance (Martin 1992). For most bird species, however, specific habitat features associated with increased fitness are poorly understood (but see Vickery et al. 1992b). Most studies have taken a qualitative approach to linking fitness components with habitat or nest location (e.g. Walkinshaw 1953, Graber 1961, Nolan 1963, Thompson and Nolan 1973, Stewart et al. 1977, Knapton 1978, Middleton 1979, Fischer 1980, Zimmerman 1982).

Although these studies provide valuable information on life history, they lack quantitative assessments of the association between habitat and fitness.

This study focuses on identifying the association between habitat features and fitness components for the California Gnatcatcher (*Poliophtila californica californica*), a small, sedentary passerine endemic to the coastal sage scrub community of southern California and northern Baja California (Atwood 1991). The California Gnatcatcher is listed as a threatened species. The current population estimate for the United States is approximately 2,000 pairs (Atwood 1992). The decline of this species has been concomitant with the disappearance and degradation of the coastal sage scrub habitat throughout southern California (Atwood 1993).

The coastal sage scrub community is a Mediterranean habitat characterized by facultatively drought-deciduous, mesophilic shrubs from

³ E-mail: gbraden@co.san-bernardino.ca.us

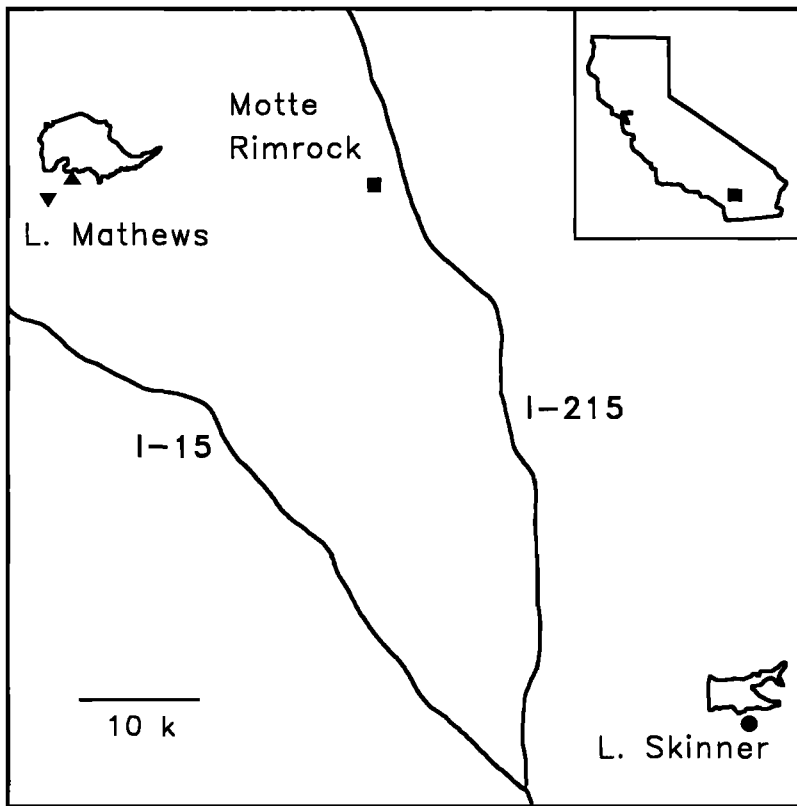


FIG. 1. Location of the California Gnatcatcher study areas. Circle is Lake Skinner, triangle up is Lake Mathews Site 1, triangle down is Lake Mathews Site 2, and square is University of California Motte Ecological Reserve. Scale is approximate.

0.5 to 2.0 m tall (see Westman 1981, Mooney 1988, O'Leary 1990a). This community has been heavily modified by agriculture, invasion of exotic weeds, increased frequency of fire, air pollution, livestock grazing, and urban expansion (Klopatek et al. 1979; Westman 1981, 1985; O'Leary 1990a). Large areas of coastal sage scrub have been converted, or are undergoing conversion, to non-native grasslands (Kirkpatrick and Hutchinson 1980, Malanson 1985), and it is generally accepted that 70 to 90% of this habitat type has been lost over the last 100 years (Westman 1981, O'Leary 1990a).

We identified within-territory vegetation variables that are associated with life-history variables in California Gnatcatchers and then used these vegetation variables to explore whether average within-territory vegetation of gnatcatcher groups also is associated with juvenile survival, adult survival, and the finite rate of population growth (λ).

STUDY AREAS AND METHODS

All study sites were in western Riverside County, California (Fig. 1), and were dominated by the Riversidean coastal sage scrub sub-association (O'Leary 1990a). The Lake Skinner site was located within the Western Riverside County Multi-Species Reserve. Vegetation data at this site were collected in 1995 and life-history data from 1992 through 1995. The site was heavily dominated by perennial shrubs that included California buckwheat (*Eriogonum fasciculatum*) with relatively smaller proportions of California sage (*Artemisia californica*), bush penstemon (*Keckiella antirrhinoides*), and white sage (*Salvia apiana*). A few territories were dominated almost entirely by black sage (*Salvia mellifera*). Two study sites were located within the proposed Lake Mathews Multi-Species Reserve. Vegetation data at these sites were collected in 1993 and 1995 and life-history data from 1993 through 1995. Territories occupied by gnatcatchers in 1993 along the lakeshore were no longer occupied by 1995. Occupied territories in 1995 were approximately 1.6 km from the lakeshore.

Therefore, vegetation and life-history data for 1993 were from a different, although relatively close, study area than data collected in 1995. The study area in 1993 is hereafter referred to as Lake Mathews Site 1, and was dominated by the perennial shrubs *Encelia californica* and California sage. The 1995 study area, hereafter referred to as Lake Mathews Site 2, also was dominated by *E. californica* and California sage but had substantial proportions of California buckwheat, bush penstemon, white sage, and black sage. The fourth study site was located at the Motte Rimrock Ecological Reserve, which is a part of the University of California Reserve System. Vegetation data at this site were collected in 1993 and life-history data in 1993 and 1994. The Motte Site was dominated by black sage, *E. californica*, and California sage. Cover of annual plant species at all sites was dominated by wild oats (*Avena* sp.), brome (*Bromus* sp.), storksbill (*Erodium* sp.), mustard (*Brassica* sp.), and other introduced grasses and forbs. Native grasses and annuals consisted of relatively rare and patchy clumps of bunchgrasses (*Stipa* sp.); onion (*Allium* sp.), fiddleneck (*Amsinckia* sp.), mariposa lily (*Calochortus* sp.), cryptantha (*Cryptantha* sp.), blue dicks (*Dichelostemma capitatum*), goldfields (*Lasthenia* sp.), and baby blue-eyes (*Nemophila menziesii*) were seasonally abundant. All study sites had been affected to some degree by fire, dryland farming, grazing, or various forms of recreation over the previous 100 years.

Vegetation data.—Vegetation within gnatcatcher territories was sampled using radial transects ($n = 10$ per territory) located randomly within each territory. Transect locations were based on random compass orientations and distances from arbitrary starting points within each territory. Vegetation data were collected concurrently for each pair at all sites from May through early July to minimize potential differences in vegetation due to seasonal changes. Each transect consisted of two perpendicular 10-m tapes, centered on the 5-m mark, with one tape oriented north-south. We sampled vegetation at 1-m intervals using a fiberglass rod that was 0.5 cm in diameter, 2 m long, and marked at decimeter intervals. At each interval we recorded height of annual vegetation, height of perennial shrubs, height of dead wood, species of perennial shrub, litter depth, number of perennial shrub rod contacts (hits) per decimeter, and physiognomic cover type. Physiognomic cover types consisted of perennial shrub, non-native grass, native grass, grass-forb mix, dead wood, bare ground, and rock. Physiognomic cover types were not necessarily mutually exclusive. Finally, we recorded the four point-quarter distances to the closest perennial plants from the intersection of the two tapes for each transect.

Twenty-three habitat variables were derived from the vegetation data for each territory using the transect as the sample unit. These variables described

different aspects of the physiognomic cover, perennial and annual characteristics, and spatial perennial structure of the habitat for 41 gnatcatcher territories. Diversity of perennial species was calculated as $1/\sum p_i^2$ (Hill 1973), where p_i is the proportion of perennial species i within a territory.

We described the perennial spatial structure of the habitat within gnatcatcher territories based on variables relating to vertical and horizontal structure. Variables related to vertical structure consisted of the number of rod hits below 0.5 m, the number of rod hits from 0.5 to 1.0 m, the number of rod hits from 1.0 to 1.5 m, the coefficient of variation (CV) in perennial height, and the perennial homogeneity among the three height classes. We used 0.5-m height classes because the mean height of nests was approximately 0.5 m (Braden unpubl. data). We used the diversity formula of Hill (1973) and the proportions of hits in the three height classes as a measure of perennial homogeneity among height classes. Variables related to horizontal structure consisted of the mean point-quarter distances, the CV in point quarter-distances, the total number of rod hits, the CV in hits per rod, the mean number of rod hits among transects, and the homogeneity of hits among transects. We used the diversity formula of Hill (1973) and the proportion of hits among the 10 transects in each territory to calculate the homogeneity in hits among transects.

Life-history data.—Adult birds were uniquely color-banded at the beginning of the study and as needed at the onset of each breeding season; all observations were of banded birds. Nestlings were banded at eight days of age. Territories were visited two to four times a week throughout the breeding season, which extended from late February or early March to early July or early August. Territory boundaries were determined using spot-mapping, and territories were delineated using the MCPAAL (Stuwe 1985) harmonic mean algorithm with a grid width of 25. The 95% contour was used to designate territory size in order to eliminate outliers. Nests were visited at two- to five-day intervals and monitored for the onset of egg laying, clutch size, and number of nestlings and fledglings. An effort was made to locate all nesting attempts, including nests that were abandoned before completion. Although some nesting events undoubtedly were undetected, all attempts that resulted in fledglings were observed. A nest was considered successful if one or more young fledged, regardless of the fate of the fledgling. Young were considered to have fledged if they were detected within five or more days after leaving the nest.

Association of vegetation with life-history variables.—We used canonical correlation analysis to examine the association between life-history and vegetation variables. Variables were entered and removed such that all variables in the reduced life-history variable set were significantly correlated with all variables in

the reduced habitat variable set and vice versa. The final canonical correlation consisted of the fewest variables that explained the greatest amount of variation between habitat and life-history variables, with no dependencies within the two variable sets.

To determine if vegetation variables were associated with adult and juvenile survival and the intrinsic rate of population growth, we compared vegetation within territories among different groups of gnatcatcher pairs. Because gnatcatcher pairs occurred at different sites, we used site as a grouping factor and stepwise discriminant analysis to determine if vegetation within territories varied among the four gnatcatcher groups. Stepwise discriminant analysis was likely to select the most important within-territory vegetation variables but unlikely to use all variables that were associated with other life-history traits. Therefore, we used ANOVA to compare gnatcatcher groups using all the within-territory vegetation variables that were associated with other life-history variables. We then calculated adult survival, juvenile survival, and the finite rate of population growth for the different groups of gnatcatcher pairs and compared them against each group's standing relative to within-territory vegetation variables.

Survival was calculated as the proportion of banded gnatcatchers from the previous breeding season known to be alive at the beginning of the next breeding season. Two years of dispersal studies indicated that 95% of the banded juveniles were found within a 1.5-km radius of their natal territory and that adults rarely dispersed more than one territory width (i.e. 200 m) from the previous year (Braden unpubl. data). Therefore, study areas and suitable habitat within a 1.5-km radius from each study area were searched at the onset of each breeding season for banded individuals. Adults or juveniles presumed to be dead by this method were never detected in subsequent seasons.

Survival among different groups of gnatcatchers was compared using contingency tables of surviving versus non-surviving individuals. Contingency table subdivisions followed Zar (1984). The finite rate of population increase (λ) for each gnatcatcher group was determined by using adult survival, juvenile survival, mean number of fledglings per pair, and Pulliam's (1988) model:

$$\lambda = P_A + P_j\beta, \quad (1)$$

where P_A is the adult survival rate during the non-breeding season, P_j is the survival rate of juveniles during the same period, and β is the number of juveniles produced at the end of the breeding season. Lambda values should be viewed as maximum values because there was no consideration of environmental stochasticity.

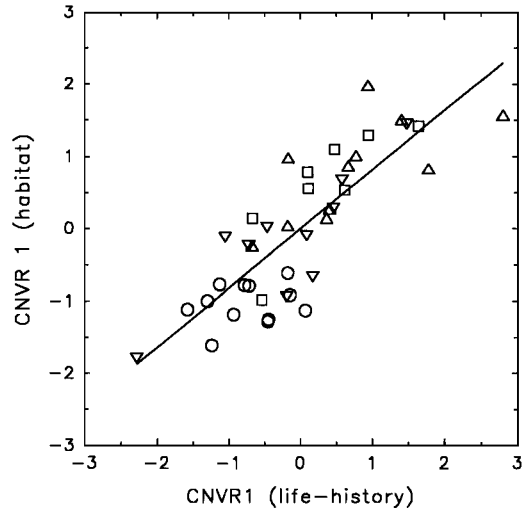


FIG. 2. Canonical correlation of the first canonical variables (CNVR 1) for within-territory vegetation and life-history data sets. Circles are gnatcatcher pairs at Lake Skinner (1995), triangles down are pairs at Lake Mathews Site 2 (1995), triangles up are pairs at Lake Mathews Site 1 (1993), and squares are pairs at Motte Reserve (1993).

RESULTS

Association between vegetation and life-history variables.—Eight within-territory vegetation variables were significantly correlated with five life-history variables ($P = 0.003$, $r^2 = 0.67$). There were no dependencies within variable sets, and the correlation between habitat and life-history variable sets was described by the first canonical variable for each set (Fig. 2). A second canonical variable approached significance. However, including additional life-history or vegetation variables invariably resulted in a lack of significance between at least one variable in the vegetation set with all variables in the life-history set or vice versa.

The correlation coefficients indicated that increased grass-forb cover, number of hits below 0.5 m, total number of hits, and homogeneity of hits among transects, accompanied by decreased perennial diversity, CV in hits, homogeneity in hits among height classes, and CV in point-quarter distance among perennials were associated with increased fledging success, increased nesting success, early date of first nest, a longer nesting season, and lower cost per fledgling (Table 1).

TABLE 1. Canonical correlation of life-history and within-territory vegetation variables for California Gnatcatcher pairs. Values are correlation coefficients (r) of life-history variables with all vegetation variables, and vice versa, and canonical variable correlation coefficients (CNVR) of each variable with the first canonical axis. See text for description of variables; CV is coefficient of variation.

	r	CNVR
Life-history variables		
No. of fledglings	0.627	-0.674
No. of successful nests	0.494	-0.422
Date of first nest	-0.546	0.640
No. days from first to last nest	0.576	-0.754
No. fledglings/no. of nest days	-0.562	0.659
Vegetation variables		
Grass-forb cover	0.473	-0.659
Perennial diversity	-0.579	0.640
No. hits below 0.5 m	0.579	-0.704
Total no. of hits	0.611	-0.664
CV in hits	-0.459	0.562
Homogeneity in hits among transects	0.557	-0.682
Homogeneity in hits among vertical height classes	-0.406	0.513
CV in point-quarter distances of perennials	-0.404	0.504

Association among vegetation, survival, and λ .—Stepwise discriminant analysis did not discriminate among the four gnatcatcher groups using within-territory vegetation due to similarities of vegetation at the Motte and Lake Mathews Site 1. When these two groups of gnatcatchers were combined, there was a significant discrimination ($P < 0.0001$, $r^2 = 0.63$), with an 85.4% correct jackknifed classification among at Lake Skinner, Lake Mathews Site 2, and the combined Motte and Lake Mathews gnatcatcher territories. The discriminant function selected grass-forb cover, number of hits below 0.5 m, and total number of hits as the most useful variables for distinguishing the three gnatcatcher groups, based on within-territory vegetation.

Within-territory vegetation variables that were positively associated with increased fledging success, increased nest success, early date of first nest, a longer nesting season, and lower cost per fledgling (Table 1) were significantly higher for territories at Lake Skinner than for territories at the combined Motte and Lake Mathews Site 1, with values at Lake Mathews Site 2 in between (Table 2). Within-territory vegetation variables that were negatively

associated with increased fledging success, increased nest success, early date of first nest, a longer nesting season, and lower cost per fledgling (Table 1) were significantly lower for territories at Lake Skinner than for territories at the combined Motte and Lake Mathews Site 1, with values for territories at Lake Mathews Site 2 in between (Table 2).

Adult survival was consistent with the gradient for within-territory vegetation structure among the three groups of gnatcatchers (Table 3). Adult survival was significantly higher at Lake Skinner and Lake Mathews Site 2 than at the combined Motte and Lake Mathews Site 1 ($P < 0.01$). Fledging success also was consistent with the gradient in within-territory vegetation among the three gnatcatcher groups (Table 2). There were no significant differences in juvenile survival among the three groups ($P > 0.30$), indicating no association of juvenile survival and within-territory vegetation.

The finite rate of population growth also reflected the same gradient among gnatcatcher groups as did within-territory vegetation (Tables 2 and 3). At Lake Skinner, where within-territory vegetation values indicated maximization of life-history variables, the λ value was concordant with a growing population, or source habitat ($\lambda > 1$). At the combined Motte and Lake Mathews Site 1, where within-territory vegetation values indicated minimization of life-history variables, the λ value was concordant with a declining population, or sink habitat ($\lambda < 1$). At Lake Mathews Site 2, where within-territory vegetation indicated moderate life-history values, the λ value was approximately 1. The results suggest that within-territory vegetation variables that were associated with life-history variables may also be associated with adult survival and the intrinsic rate of population growth, but not with juvenile survival.

Potential confounding effects.—There were no significant differences in fledging success among years within a site. Thus, annual differences in fledging success within sites were not confounding factors in the association of within-territory vegetation and fledging success. These results also suggest that annual within-site vegetation growth, if present, did not influence fledging success. Because perennial structure and spatial homogeneity were associated with fledging success, any significant change in

TABLE 2. Vegetation and life-history variables ($\bar{x} \pm SE$) from 41 California Gnatcatcher territories deemed important from canonical correlation analysis. Different superscripts in the same row represent multiple comparisons among study areas where $P \leq 0.05$.

	Motte/Lake Mathews 1 ^a	Lake Mathews 2	Lake Skinner
Life-history variables			
No. of fledglings	1.4 ± 0.44 ^A	3.1 ± 0.50 ^{A,B}	3.8 ± 0.77 ^B
No. of successful nests	0.4 ± 0.14 ^A	1.2 ± 0.25 ^B	1.1 ± 0.19 ^B
Date of first nest	85.4 ± 3.8 ^A	75.9 ± 4.2 ^{A,B}	71.4 ± 2.4 ^B
No. days from first to last nest	72.7 ± 6.0 ^A	94.8 ± 7.3 ^{A,B}	109.4 ± 5.3 ^B
No. fledglings/no. of nest days	0.97 ± 0.043	0.94 ± 0.037	0.94 ± 0.038
Vegetation variables			
Grass-forb cover	8.1 ± 1.0 ^A	33.8 ± 2.9 ^B	37.3 ± 2.2 ^B
Perennial diversity	1.7 ± 0.05 ^{A,B}	1.9 ± 0.08 ^B	1.6 ± 0.06 ^A
No. hits below 0.5 m	25.5 ± 1.1 ^A	32.8 ± 1.5 ^B	69.7 ± 2.5 ^C
Total no. of hits	53.5 ± 2.1 ^A	70.8 ± 3.4 ^B	113.3 ± 3.8 ^C
CV in hits	147.7 ± 5.6 ^A	125.8 ± 4.9 ^B	92.3 ± 2.2 ^C
Homogeneity in hits among transects	8.1 ± 0.28 ^A	8.5 ± 0.29 ^{A,B}	9.1 ± 0.10 ^B
Homogeneity in hits among vertical height classes	2.1 ± 0.03 ^A	2.2 ± 0.03 ^A	1.9 ± 0.2 ^B
CV in point-quarter distances of perennials	35.9 ± 1.4 ^A	34.9 ± 1.5 ^A	27.2 ± 1.1 ^B

^a Motte and Lake Mathews 1 study areas combined.

perennial vegetation due to growth of vegetation should have been reflected in differences in fledging success within sites. However, within-site fledging success was not significantly different among years.

DISCUSSION

Our results identified vegetation characteristics of gnatcatcher territories that were significantly correlated with life-history characteristics of gnatcatcher pairs. Within-territory vegetation variables accounted for 67% of the variation in life-history variables. Date of the first nest, number of successful nests, number of fledglings, length of the nesting season, and cost per fledgling were associated with grass-forb cover, the number of rod hits below 0.5 m, the total number of rod hits, the homogeneity

of hits among radial transects, perennial diversity, the CV in rod hits, the homogeneity in hits among height classes, and the CV in point-quarter distances among perennials. These same within-territory vegetation variables suggest that on average, the vegetation within gnatcatcher territories was better at some site than at others.

The gradient in within-territory vegetation among gnatcatcher groups was coincident with the gradient in adult survival and λ among gnatcatcher groups. Gnatcatcher pairs at Lake Skinner, where the average within-territory vegetation indicated maximization of other life-history parameters, had a λ value >1 and significantly higher adult survival, which is consistent with increased fitness. Gnatcatcher pairs at Lake Mathews Site 2, where the average within-territory vegetation suggested

TABLE 3. Survival and intrinsic rate of population increase (λ) for different groups of California Gnatcatcher pairs. Values are proportion surviving (sample size in parentheses). Overall values for adult survival with different superscripts are different among groups at $P < 0.01$. Juvenile survival did not differ among groups ($P > 0.30$). Lambda values are not adjusted for environmental stochasticity.

Group	Adults			Juveniles			λ
	1993–94	1994–95	Overall ^a	1993–94	1994–95	Overall ^a	
Lake Skinner	0.50 (26)	0.44 (25)	0.47 ^A	0.22 (23)	0.32 (28)	0.28	1.50
Lake Mathews 2	— ^b	0.60 (10)	0.60 ^A	—	0.14 (7)	0.14	1.03
Motte	0.21 (14)	—	0.17 ^B	0.00 (6)	—	0.15	0.38
Lake Mathews 1	0.19 (21)	0.08 (12)		0.57 (7)	0.00 (14)		

^a Overall and lambda values for Motte represent combined data from Motte and Lake Mathews 1 study areas.

^b —, no data.

moderate values for other life-history parameters, had a λ value equal to 1 and high adult survival, which is consistent with moderate fitness. Gnatcatcher pairs at the combined Motte and Lake Mathews Site 1, where the average within-territory vegetation suggested minimization of other life-history parameters, had a λ value < 1 and significantly lower adult survival, which is consistent with lowered fitness.

Gnatcatcher pairs were grouped by site because (1) survival and λ were calculated based on groups of gnatcatcher pairs; and (2) stepwise discriminant analysis and ANOVA comparisons indicated that grouping gnatcatcher pairs by sites, based on similarities of within-territory vegetation, made sense biologically. But, using site as a grouping factor introduced the possibility that survival and λ were influenced by unmeasured site characteristics that were not related to within-territory vegetation. Thus, our results suggest that within-territory vegetation is associated with adult survival and λ .

Six of the eight habitat variables that were associated with fitness components were measures of habitat structure. Collectively, these variables were a measure of spatial perennial structure, horizontal homogeneity, and vertical homogeneity. The correlation coefficients of these six variables indicated that fitness components decreased with reductions in spatial perennial structure, decreased horizontal homogeneity, and increased vertical homogeneity within Gnatcatcher territories. These observations suggest that habitat disturbances that potentially affect perennial structure and homogeneity within gnatcatcher territories, such as fire, grazing, or urban expansion, also may affect gnatcatcher fitness.

Seven of the eight habitat variables were related to the structure of perennial vegetation within gnatcatcher territories in such a way as to suggest that fitness components increase as the coastal sage habitat within their territories matured. Assuming that the maturation of coastal sage scrub results in an increased occupation of space by perennial shrubs, then maturation should lead to increased numbers of hits below 0.5 m, the total number of hits, and the homogeneity in hits among transects. The same increase in the occupation of space by perennial shrubs with coastal sage scrub maturation should lead to decreased CV in hits, CV

in point-quarter distances among perennial shrubs, and homogeneity among vertical height classes. Homogeneity among vertical height classes should decrease due to the disproportionate amount of perennial structure below 0.5 m. One of the two remaining habitat variables, decreasing perennial diversity, has been associated with maturation of coastal sage scrub (Westman 1981), especially after fires (Westman et al. 1981, O'Leary 1990b). Future studies should be directed at testing this hypothesis.

Our results suggest that preservation of, or management for, within-territory vegetation characteristics that were associated with life-history variables, possibly including adult survival and λ , should increase fitness and promote short-term increases in abundance of California Gnatcatchers. Our results may be useful as part of an assessment of areas of coastal sage scrub already occupied by California Gnatcatcher but should not be relied upon without further studies of habitat-fitness relationships. Application of our results to areas of coastal sage scrub that are not occupied by gnatcatchers is problematic because we did not compare occupied versus unoccupied gnatcatcher territories. The suitability of coastal sage scrub habitats for gnatcatchers is likely to consist of many factors in addition to the within-territory vegetation variables described here. Our results suggest that average within-territory vegetation is not the same among sites; therefore, some areas of occupied habitat are more important than others.

It is noteworthy that territory size was not correlated with vegetation variables. Given the scope and intensity of the within-territory vegetation measurements, it is unlikely that correlations between territory size and vegetation characteristics existed but were undetected by us. More likely, territory size is correlated with life-history variables. Gnatcatcher territories averaged 3.4 ha (Braden unpubl. data), which is relatively large for a small passerine. Gnatcatchers undertake two to eight spatially distant nesting attempts per season. Spatially distant nesting attempts are associated with nest depredation in several species of passerines (Harvey et al. 1979, Greig-Smith 1982), and territory occupancy has been shown to be negatively related to predation risk for some bird species (Blancher and Robertson 1985, Marz-

luff 1988). Also, Marzluff (1988) and Martin (1992) argued that nest predation may affect territory occupancy and size. Additional studies are needed to determine whether territory size in California Gnatcatchers is related to nest predation.

In summary, our results identify within-territory vegetation variables that were associated with life-history variables. These same variables also may be associated with adult survival and the intrinsic rate of population growth. Six of the eight vegetation variables that were associated with life-history variables indicated that increased perennial spatial composition and horizontal homogeneity, accompanied by decreased perennial vertical homogeneity and diversity within gnatcatcher territories, were associated with increases in the number of successful nests, length of the nesting season, start of the nesting season, fledging success, cost per fledgling, and perhaps adult survival and λ . Preservation of and management for these habitat characteristics should promote fitness and short-term population growth for California Gnatcatchers.

ACKNOWLEDGMENTS

Kent Beeman, Gene Cardiff, Marnie Crook, Arthur Davenport, Kim Ferree, Cin Greyraven, Christine Harker, Stacy Love, Chet McGaugh, Tracy Meyers, Steve Myers, and Mary Beth Woulfe helped collect the data. Dr. David Moriarty reviewed a draft of the manuscript. The study was funded by the Metropolitan Water District of California via the Southwestern Riverside County Multi-Species Reserve Management Committee and the U.S. Fish and Wildlife Service, Carlsbad, California. We thank them all.

LITERATURE CITED

- ATWOOD, J. L. 1991. Subspecies limits and geographic patterns of morphological variation in California Gnatcatchers (*Polioptila californica*). *Bulletin of the Southern California Academy of Sciences* 90:118-133.
- ATWOOD, J. L. 1992. A maximum estimate of the California Gnatcatcher's population size in the United States. *Western Birds* 23:1-9.
- ATWOOD, J. L. 1993. California Gnatcatchers and coastal sage scrub: The biological basis for endangered species listing. Pages 149-169 *in* *Interface between ecology and land development in California* (J. E. Keeley, Ed.). Southern California Academy of Sciences, Los Angeles.
- BLANCHER, P. J., AND R. J. ROBERTSON. 1985. Site consistency in kingbird breeding performance: Implications for site fidelity. *Journal of Animal Ecology* 54:1017-1027.
- FISCHER, D. H. 1980. Breeding biology of Curve-billed Thrashers and Long-billed Thrashers in south Texas. *Condor* 82:392-397.
- GRABER, J. W. 1961. Distribution, habitat requirements, and life-history of the Black-capped Vireo (*Vireo atricapilla*). *Ecological Monographs* 31: 313-336.
- GREIG-SMITH, P. W. 1982. Dispersal between nest sites by Stone Chats *Saxicola torquata* in relation to previous breeding success. *Ornis Scandinavica* 13:232-238.
- HARVEY, P. H., P. J. GREENWOOD, AND C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). *Journal of Animal Ecology* 48:305-313.
- HILL, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54: 427-432.
- KIRKPATRICK, J. B., AND C. F. HUTCHINSON. 1980. The environmental relationships of California coastal sage scrub and some of its component communities and species. *Journal of Biogeography* 7:23-28.
- KLOPATEK, J. M., R. J. OLSON, C. J. EMERSON, AND J. L. JONES. 1979. Land use conflicts with natural vegetation in the United States. *Environmental Conservation* 6:191-199.
- KNAPTON, R. W. 1978. Breeding ecology of the Clay-colored Sparrow. *Living Bird* 17:137-57.
- MALANSON, G. P. 1985. Fire management in coastal sage scrub, southern California, USA. *Environmental Conservation* 12:141-146.
- MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455-473 *In* *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- MARZLUFF, J. M. 1988. Do Pinon Jays alter nest placement based on prior experience? *Animal Behaviour* 36:1-10.
- MIDDLETON, A. L. A. 1979. Influence of age and habitat on reproduction by the American Goldfinch. *Ecology* 60:418-432.
- MOONEY, H. A. 1988. Southern coastal scrub. Pages 471-489 *In* *The terrestrial vegetation of California* (M. G. Barbour and J. Major, Eds.). California Native Plants Society Special Publication No. 9.
- NOLAN, V., JR. 1963. Reproductive success of birds in a deciduous scrub habitat. *Ecology* 44:305-313.
- O'LEARY, J. F. 1990a. Coastal sage scrub: General characteristics and consideration for biological conservation. Pages 24-41 *In* *Endangered plant communities of southern California* (A. A.

- Schoenherr, Ed.). Southern California Botanists Special Publication No. 3.
- O'LEARY, J. F. 1990b. Postfire diversity patterns in two subassociations of California coastal sage scrub. *Journal of Vegetation Science* 1:173-180.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- STEWART, R. M., R. P. HENDERSON, AND K. DARLING. 1977. Breeding ecology of the Wilson's Warbler in the High Sierra Nevada, California. *Living Bird* 16:83-102.
- STUWE, M. 1985. MCPAAL v1.2: Micro-computer programs for the analysis of animal locations. Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia.
- THOMPSON, C. F., AND V. NOLAN, JR. 1973. Population biology of the Yellow-breasted Chat (*Icteria virens* L.) in southern Indiana. *Ecological Monographs* 43:145-171.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992a. Is density an indicator of breeding success? *Auk* 109:706-710.
- VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992b. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. *Auk* 109:697-705.
- WALKINSHAW, L. H. 1953. Life-history of the Prothonotary Warbler. *Wilson Bulletin* 65:152-168.
- WESTMAN, W. E. 1981. Diversity relationships and succession in California coastal sage scrub. *Ecology* 62:170-184.
- WESTMAN, W. E. 1985. Air pollution injury to coastal sage scrub in the Santa Monica Mountains, southern California. *Water, Air, and Soil Pollution* 26:19-41.
- WESTMAN, W. E., J. F. O'LEARY, AND G. P. MALANSON. 1981. The effects of fire intensity, aspect, and substrate on post-fire growth of California coastal sage scrub. Pages 151-179 *In* Components of productivity of Mediterranean-climate regions: Basic and applied aspects (N. S. Margaris and H. A. Mooney, Eds.). W. Junk, The Hague.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.
- ZIMMERMAN, J. L. 1982. Nesting success of Dickcissels (*Spiza americana*) in preferred and less preferred habitats. *Auk* 99:292-298.

Associate Editor: R. L. Hutto