

DOES NEST PLACEMENT AFFECT THE FATE OR PRODUCTIVITY OF CALIFORNIA GNATCATCHER NESTS?

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ABSTRACT.—I monitored 384 California Gnatcatcher (*Poliioptila californica*) nests at five study areas in western Riverside County, California, from 1992 through 1995. Overall, 78.9% of the nesting attempts failed (52.9% from nest predation), and 21.1% fledged young. Vegetation measurements were taken at 207 of 384 nest locations and at 207 randomly selected locations within gnatcatcher territories. Nest placement was not random in that gnatcatchers placed their nests in locations with greater cover and height of perennial vegetation, increased horizontal structural homogeneity, and increased vertical structural homogeneity relative to random locations. The volume of gnatcatcher nest shrubs was lower than that of random shrubs, and concealment was higher at nests than at random shrubs. Nevertheless, variables that differed significantly between nests and random locations were not significantly associated with nesting success, nest predation, nest abandonment, or productivity. The use of specific perennial shrub species as nest substrates was not proportional to the availabilities of the shrub species within the study areas, yet I found no relationship between nesting success and the species of nest shrub. Nesting success appeared to be unrelated to the abundance of perennial shrubs at four of five study areas. My results suggest that factors affecting the fate of California Gnatcatcher nests operate at scales larger than the nest site or nest patch. Received 12 August 1998, accepted 29 January 1999.

NEST PREDATION is the primary cause of nest failure for a wide diversity of avian species (Ricklefs 1969, Martin 1988). Because nest predation affects fitness directly, natural selection should favor life-history or nest-placement characteristics that decrease predation. Furthermore, nesting success may be affected by factors operating at different or even multiple spatial scales (Martin 1992, Sedgwick and Knopf 1992). Therefore, understanding how nest placement affects nest fate is an important step toward understanding nest-site selection and potentially the structure of avian assemblages. Accordingly, many studies have found that nest failure, usually due to predation, will affect the nest placement of land birds (Peterson and Best 1985, Martin and Roper 1988, Holway 1991, Morton et al. 1993). However, studies have also found that nest placement does not always appear to influence nest predation or nesting success (Holway 1991, Filliater et al. 1994, Howlett and Stutchbury 1996, Wilson and Cooper 1998).

The California Gnatcatcher (*Poliioptila californica*) is a small shrub-nesting passerine endemic to the coastal sage scrub of southern California and northern Baja, Mexico. The coastal sage

scrub community is a Mediterranean-type habitat typified by facultatively drought-deciduous mesophilic shrubs from 0.5 to 2.0 m tall (Westman 1981, Mooney 1988). The California Gnatcatcher is listed as a federally threatened species because of habitat loss.

I examined the effects of nest placement on success, predation, abandonment, and productivity of California Gnatcatcher nests to test the hypothesis that an open-cup nester that experiences high nest failure, mostly due to predation, has nest-placement characteristics that increase nesting success or productivity and decrease nest predation. Specifically, I used nests and random habitat measurements to define variables that may be important to nest placement at two spatial scales and then used those variables to determine if nest placement affects nesting success and other productivity measures. In addition, I examined whether nesting success is related to the orientation of the nest within the shrub, slope aspect of the nest shrub, height of the nest, or species and abundance of the nest shrub.

STUDY AREA AND METHODS

I monitored 384 California Gnatcatcher nests at five study areas in western Riverside County, Cali-

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fornia, from 1992 through 1995. Thirty-five nests were monitored at the North and South Hills of the Domenigoni Valley in 1992 (hereafter referred to as the Hills study area), 47 nests were monitored at the University of California Motte Rimrock Reserve in 1993 and 1994, 53 nests were monitored at Lake Mathews Site 1 in 1993 and 1994, 60 nests were monitored at Lake Mathews Site 2 in 1994 and 1995, and 189 nests were monitored at Lake Skinner from 1992 through 1995. All study areas were dominated by the Riversidian coastal sage scrub subassociation (Westman 1981, O'Leary 1990), but vegetation cover and composition were heterogeneous among study areas. For a map and detailed descriptions of the study areas see Braden et al. (1997a, b).

Nest fates.—Nests were visited at intervals of three to five days. The frequency of nest checks was consistent among study areas and throughout the duration of the study. Nests were considered successful if one or more young fledged (i.e. left the nest). Because nestlings were banded when they were eight days old as part of a life-history study, the exact or at least approximate fledging dates were known. Each nest could be unambiguously attributed to specific pairs because all adults were uniquely color banded. Nests were considered lost to predation if some or all of the eggs disappeared, eggs were damaged, or eggs or egg shell fragments occurred in the vicinity of the nest, as long as the adult birds no longer attended the nest. Shredded or damaged nest structures were always interpreted as predation. Nests were classified as abandoned when there was no indication of predation and the nest was no longer attended by the adults. Because nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) was shown to have little influence on nesting success of gnatcatchers at these study areas (Braden et al. 1997b), cowbird parasitism was not considered further in this study. The number of depredated nests was probably underestimated because the disappearance of an egg during egg laying, but before the nest was checked, could have resulted in the nest being classified as abandoned.

Vegetation data.—Vegetation data were collected only at the 207 gnatcatcher nests in which at least one egg was laid or at nests that were clearly depredated and at 207 randomly selected locations. Vegetation data were collected for 24 nests at the Hills study area, 25 at Motte, 33 at Lake Mathews Site 1, 38 at Lake Mathews Site 2, and 87 at Lake Skinner. Both nest and random location vegetation data were collected using radial transects. I located random radial transects by flinging a measuring rod over my shoulder after I moved a random distance and direction from a gnatcatcher nest. Distances were calculated as a random number between 10 and 100 m to locate the random transect within the known territory of the gnatcatcher pair associated with each nest. Each nest was used to establish a single random location for

vegetation measurements. Random location transects were centered on the shrub closest to the measuring rod if the rod did not land in a shrub.

Radial transects consisted of two perpendicular 10-m tapes centered over a nest shrub or randomly located shrub, with one tape oriented north and south. Data were recorded at 1-m intervals along each tape using a fiberglass rod that was 0.5 cm in diameter and 2 m long. The total number of points measured along each radial transect was 21. The number of rod contacts (hits) with a perennial shrub per decimeter, height of annual plants, perennial shrub height, and the species of perennial shrub were recorded at each of the 21 points. At the intersection of the two transects, I recorded the point-quarter distance (Mueller-Dombois and Ellenberg 1974) to the closest perennial shrub for each of the four quarters, the slope and slope aspect at the intersection, and the length, width, and height of the shrub at the intersection. Nest height, distance of nest from the edge of the shrub, and width of the nest shrub at nest height were measured for nests but not at random locations (because there were no nests from which to measure). Nest data were collected after the nest was no longer active, usually within three weeks. Vegetation data were collected at all study areas from April through early July and included nests that were initiated in March through July, effectively the length of the breeding season. I used the vegetation data to generate variables that described the habitat of nests and random locations.

I defined the habitat at nests and random locations in terms of the nest patch and the nest site. The nest patch was defined by 12 variables: annual cover, perennial cover, average point-quarter distance, coefficient of variation in point-quarter distances, mean annual height, mean perennial height, number of hits from 0.0 to 0.5 m, number of hits from 0.5 to 1.0 m, number of hits from 1.0 to 1.5 m, total number of rod hits, horizontal diversity, and foliage height diversity. Annual and perennial cover per transect were calculated as the number of points with annual and perennial hits divided by 21, and mean annual and perennial height were calculated as the sum of annual and perennial height at all points divided by 21. I used the point-quarter distance as a measure of horizontal perennial structure and shrub density and the coefficient of variation in point-quarter distance as a measure of the variability in horizontal perennial structure. Horizontal structural diversity was calculated using the total rod hits for each of the 21 points in a transect and the heterogeneity index (*HI*) of Wiens and Rotenberry (1981):

$$HI = (\text{maximum no. of rod hits} \\ - \text{minimum no. of rod hits}) \\ \div \text{mean no. of rod hits.} \quad (1)$$

A value of zero for *HI* indicated that perennial struc-

ture was evenly distributed across horizontal space. Foliage height diversity was calculated using the number of hits in each of three 0.5-m height classes and the diversity formula of Hill (1973):

$$1/\sum p_i^2 \quad (2)$$

where p_i is the proportion of perennial rod hits among foliage height class i within a radial transect. Nearly all perennial plants were less than 1.5 m tall, and the mean nest height was $74.4 \pm \text{SD of } 15.2 \text{ cm}$ ($n = 207$).

I defined the nest site using 12 variables that described the location of the nest shrub or random shrub and to define the location of the nest within the shrub: nest height above ground, distance of the nest from the top of the shrub, proportional distance of the nest from the top of the shrub, distance of the nest from the edge of the shrub, proportional distance of the nest from the edge of the shrub, distance of the nest from the center of the shrub, width of the shrub at nest height, slope at the nest shrub, slope aspect at the nest shrub, species of nest shrub, nest-shrub volume, and nest concealment. The slope at the nest shrub, slope aspect of the nest shrub, species of nest shrub, nest-shrub volume, and nest concealment were measured for nests and random locations. All other variables were measured at nests only. Shrub volumes were calculated using the length, width, and height of each shrub. Slopes were measured as a value from 0 to 90° using a clinometer at nest or non-nest sites. Concealment was measured by placing a card with a 10 × 10 cm grid on top of the nest and counting the number of 1.0-cm² squares that were clearly visible from 0.5 m above the nest. Concealment values for random locations were measured by positioning the 10 × 10 cm grid card in a random shrub using the proportional height and distance from the edge of a true nest, along with a random orientation in the shrub. Concealment measurements initially were taken from the four cardinal compass directions in addition to above the nest, but a preliminary analysis indicated that concealment from the top was a better indicator of a nest shrub versus a random shrub.

Nest placement and fitness measures.—I used two-factor ANOVA to compare variables for nests versus random locations grouped by study area. Variables that differed significantly between nests and random locations were deemed important to nest placement and used in subsequent analyses. I used two-factor ANOVA to determine if nest-placement variables differed significantly among successful, depredated, and abandoned nests grouped by fate and study area. To examine nest productivity, I arbitrarily defined three or more fledglings per nest as high nest productivity and fewer than three as low productivity. I then used two-factor ANOVA to determine if nest-placement variables differed for nests with high

versus low productivity grouped by study area. Three of the five study areas had few successful four-egg nests, so I restricted the analysis of nest placement versus productivity to Lake Mathews Site 2 and Lake Skinner.

Multivariate analysis.—I used stepwise discriminant analysis to determine if nest-placement variables that were significantly different from random locations could discriminate among successful, depredated, or abandoned nests and to determine if nest placement affected nest productivity. I used data from all study areas in stepwise discriminant analyses of nesting success, predation, and abandonment. I restricted the stepwise discriminant analyses of nest productivity to Lake Mathews Site 2 and Lake Skinner.

Nest orientation, slope, nest height, and nesting success.—I used Rayleigh's test (Zar 1984) to evaluate the mean angle of the slope aspect of nests and the mean angle of the orientation of nests in the nest shrub. When Rayleigh's tests were significant, I used the Watson-Williams test to determine if the mean angles for the orientation or slope aspect of successful nests were significantly different than the mean angles for orientation or slope aspect of all other nests at a study area. I restricted analyses of nest orientation and nest-slope aspect to Lake Mathews Site 1, Lake Mathews Site 2, and Lake Skinner because the other study areas did not have enough successful nests for a meaningful analysis. Study areas were analyzed separately because slope aspects were heterogeneous among study areas.

Sockman (1997) found that California Gnatcatcher nests in the upper and lower thirds of nest shrubs were depredated more often than nests in the middle third. I used a goodness-of-fit test with the log-likelihood ratio G -statistic to determine if nest height affected nest predation or nesting success by dividing nest heights into three classes defined by $<1 \text{ SD}$, $\pm 1 \text{ SD}$, and $>1 \text{ SD}$ from the mean nest height. I tested nest heights from individual study areas separately and for all study areas combined.

Nest-shrub use, availability, and success.—I used the goodness-of-fit Bonferroni technique (Byers et al. 1984) with the G -statistic to determine when perennial shrubs were overused, underused, or used in proportion to availability as nest shrubs. Expected frequencies were obtained from random-location transects. Observed frequencies were based on shrubs in which California Gnatcatchers built their nests.

Because multiple nests from a single pair may not be independent samples, I ran all tests using a reduced data set consisting of only one nest for each pair, selected at random.

RESULTS

Statistical results using the reduced data set ($n = 76$) did not vary from the results using all

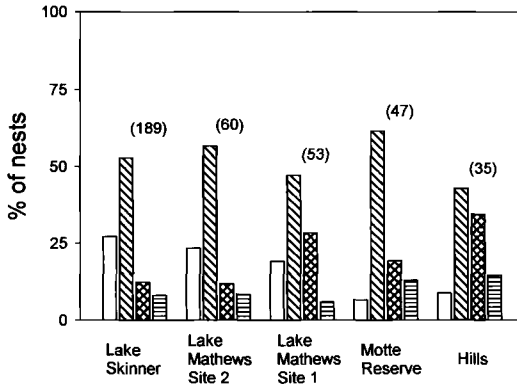


FIG. 1. Fates of California Gnatcatcher nests at five study areas in Riverside County, California. Clear bars = successful nests; diagonal left = depredated nests; crosshatching = abandoned nests; horizontal lines = nests with infertile eggs, dead nestlings, nests destroyed by rain, nests failed due to parasitism, or nests with unknown outcomes. Values are percent of total nests per study area and should be considered as estimates of the true values. Sample sizes are in parentheses.

207 nests. Therefore, I used the larger data set. California Gnatcatchers had low nesting success, mostly due to predation (Fig. 1). Overall, nest predation accounted for 52.9% (203/384)

of nest fates and 67% (203/303) of nest failures. Nesting success varied among study areas, but overall only one of five nests was successful. Low nesting success resulting mostly from nest predation was consistent within study areas.

Nest placement and nesting success, predation, and abandonment.—Nest placement by California Gnatcatchers was not random (Table 1). The distance between shrubs, variation in the distance between shrubs, annual cover, mean annual height, horizontal diversity, and foliage height diversity were significantly lower for nest patches than for random locations. Perennial cover, mean perennial height, the number of hits between 0.5 and 1.0 m, and total rod hits were significantly higher for nest patches than for random locations. Shrub volume was lower and concealment was higher for California Gnatcatcher nest sites than for random locations.

Twelve of 15 nest-placement variables differed significantly between nests and random locations (Table 1), but none of them differed significantly among successful, depredated, or abandoned nests (Table 2). Also, none of seven other nest-site variables differed significantly among successful, depredated, and abandoned nests. Similarly, none of the 15 nest-placement

TABLE 1. Results of two-factor ANOVA comparing California Gnatcatcher nests ($n = 205$) and random locations ($n = 205$). Values are $\bar{x} \pm SD$; P -values are for nests versus random locations and among study areas.

Variable	Nests	Random	P	
			Nest vs. random	Among study areas
Nest-patch variables				
CV of point-quarter distance	0.30 ± 0.14	0.32 ± 0.17	*	**
Average point-quarter distance (m)	1.6 ± 0.63	1.9 ± 0.73	***	*
Perennial cover (%)	81.0 ± 13.1	73.1 ± 18.8	***	***
Mean perennial height (m)	0.77 ± 0.20	0.66 ± 0.23	***	***
Annual cover (%)	69.1 ± 24.5	74.7 ± 22.9	**	***
Mean annual height (cm)	13.9 ± 8.59	18.5 ± 12.80	***	***
Hits from 0 to 0.50 m	43.7 ± 23.9	41.1 ± 24.8	ns	***
Hits from 0.50 to 1.0 m	35.1 ± 17.9	27.9 ± 17.2	***	***
Hits from 1.0 to 1.5 m ^a	5.1 ± 6.6	4.1 ± 5.9	ns	***
Total rod hits	84.2 ± 38.7	73.4 ± 39.1	**	***
Horizontal diversity	2.09 ± 0.29	2.00 ± 0.36	***	***
Foliage height diversity	3.27 ± 1.06	4.02 ± 1.84	***	***
Nest-site variables				
Nest-shrub volume (m ³)	3.58 ± 3.60	3.97 ± 3.65	*	***
Nest concealment (%)	83.1 ± 20.3	53.7 ± 30.3	***	ns
Slope at the nest (°) ^a	15.5 ± 6.12	15.7 ± 6.78	ns	***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, $P > 0.05$.

^aSignificant interaction between comparisons of nest versus random × among study areas.

TABLE 2. Results of ANOVA comparing California Gnatcatcher nest-patch and nest-site variables. Values are $\bar{x} \pm SD$; *P*-values are for comparisons among fates and among study areas. All study area \times fate interactions were nonsignificant ($P > 0.05$).

Variable	Successful (<i>n</i> = 53)	Depredated (<i>n</i> = 102)	Abandoned (<i>n</i> = 45)	<i>P</i>	
				Fate	Among study areas
Nest-patch variables					
CV of point-quarter distance	0.30 \pm 0.12	0.28 \pm 0.13	0.32 \pm 0.17	ns	ns
Average point-quarter distance (m)	1.59 \pm 0.75	1.51 \pm 0.63	1.59 \pm 0.49	ns	ns
Perennial cover (%)	71.9 \pm 22.5	67.3 \pm 25.5	70.1 \pm 24.7	ns	***
Perennial height (m)	0.79 \pm 0.18	0.77 \pm 0.021	0.73 \pm 0.17	ns	***
Annual cover (%)	71.1 \pm 22.5	67.3 \pm 25.5	70.0 \pm 24.7	ns	***
Annual height (cm)	16.9 \pm 7.32	13.4 \pm 9.64	11.4 \pm 6.07	ns	***
Hits from 0.50 to 1.0 m	36.3 \pm 17.9	35.3 \pm 18.7	33.0 \pm 16.3	ns	**
Total rod hits	89.8 \pm 38.6	85.3 \pm 40.6	74.7 \pm 32.5	ns	***
Horizontal diversity	2.06 \pm 0.30	2.10 \pm 0.30	2.11 \pm 0.28	ns	***
Foliage height diversity	3.04 \pm 0.62	3.28 \pm 1.08	3.52 \pm 1.34	ns	**
Nest-site variables					
Nest-shrub volume (m ³)	3.68 \pm 4.09	3.60 \pm 3.62	3.44 \pm 2.96	ns	***
Nest concealment (%)	81.6 \pm 22.5	83.6 \pm 20.1	84.2 \pm 18.2	ns	ns
Nest to shrub center (m)	0.47 \pm 0.28	0.39 \pm 0.23	0.44 \pm 0.25	ns	ns
Nest to shrub edge (m)	0.44 \pm 0.33	0.49 \pm 0.38	0.50 \pm 0.34	ns	**
Distance from shrub edge (prop.)	0.53 \pm 0.19	0.48 \pm 0.22	0.49 \pm 0.22	ns	*
Distance from top of shrub (m)	0.46 \pm 0.19	0.46 \pm 0.23	0.43 \pm 0.19	ns	ns
Distance from top of shrub (prop.)	0.62 \pm 0.11	0.64 \pm 0.12	0.64 \pm 0.13	ns	ns
Nest height above ground (m)	0.70 \pm 0.13	0.77 \pm 0.16	0.75 \pm 0.16	ns	**
Width of shrub at nest height (m)	0.91 \pm 0.51	0.88 \pm 0.43	0.94 \pm 0.33	ns	*

variables were significantly different for nests that produced two or fewer fledglings versus three or more fledglings ($P \geq 0.20$).

Multivariate analysis.—Discriminant function analysis distinguished successful, depredated, and abandoned nests when data from all study areas were combined ($r^2 = 0.05$, $n = 172$, $P < 0.001$). However, the discriminant function explained only 5.0% of the variation among nest fates. When the five study areas were analyzed separately, discriminant functions among nest fates were not significant.

Nests with high productivity could not be discriminated from nests with low productivity for both study areas combined or for the Lake Mathews Site 2 separately. Nest with high versus low productivity at the Lake Skinner study area could be separated by a significant discriminant function ($r^2 = 0.16$, $n = 36$, $P < 0.05$), but the function explained only 16% of the variation in productivity.

Nest orientation, nest-slope aspect, nest height, and nesting success.—Successful gnatcatcher nests were randomly oriented in nest shrubs at Lake Mathews Site 1 ($z = .45$, $r = 0.27$, $n = 6$, $P > 0.50$), Lake Mathews Site 2 ($z = 0.04$, $r =$

0.05 , $n = 12$, $P > 0.50$), and Lake Skinner ($z = 1.18$, $r = 0.20$, $n = 31$, $P > 0.10$), indicating that nesting success was unrelated to nest orientation.

Slope aspects at the nest shrub for successful nests at Lake Mathews Site 2 ($z = 0.08$, $r = 0.08$, $n = 12$, $P > 0.50$) and Lake Skinner ($z = 0.78$, $r = 0.16$, $n = 31$, $P > 0.50$) were random. Slope aspect at the nest shrub for successful nests at Lake Mathews Site 1 was not random (mean angle = 183° , $z = 3.07$, $r = 0.72$, $n = 6$, $P < 0.05$), but neither was the slope aspect of this study area (mean angle = 181° , $z = 0.354$, $r = 0.35$, $n = 37$, $P < 0.02$). Furthermore, the mean angle of the slope aspect at successful nests was not significantly different than the mean angle of the slope aspects of unsuccessful nests ($F = 0.51$, $df = 1$ and 25 , $r = 0.134$, $n = 35$, $P > 0.25$).

Nesting success and nest predation were not related to the height class the nest occupied in the nest shrub at all five study areas or for all study areas combined, indicating that nest height was not a factor in nest depredation or nesting success ($P > 0.20$ for all comparisons).

Nest-shrub use, availability, and nesting success.—Most gnatcatcher nests were placed in

California buckwheat (*Eriogonum fasciculatum*), California sage (*Artemisia californica*), black sage (*Salvia mellifera*), brittlebush (*Encelia farinosa*), white sage (*Salvia apiana*), bush penstemon (*Keckiella antirrhinoides*), or *Opuntia* spp. However, use of various shrub species as a nesting substrate, and the availability of these species, varied among study areas (Fig. 2).

Furthermore, gnatcatchers showed no consistent preference for a particular nest substrate. Brittlebush was preferred as a nest substrate relative to its availability at Lake Mathews Site 1 but was used in proportion to its availability at Motte, Hills, and Lake Mathews Site 2 study areas. California sage was avoided at Lake Mathews Site 2 but was used in proportion to availability at Lake Skinner (Fig. 2).

Nesting success was not associated with a specific shrub at any of the study areas ($P \geq 0.20$ for all comparisons). Nesting success was significantly higher for nests placed in the most abundant shrub species than for nests in the least abundant shrub species at Lake Skinner ($P \leq 0.05$). However, nests in abundant shrubs were neither more nor less successful than nests placed in the scarcest shrubs at the other four study areas ($P \geq 0.25$ for all comparisons), and I found no evidence to suggest that nesting success was related to shrub abundance (although sample sizes were smaller than at Lake Skinner). These results suggest that the species of nest shrub, and to a lesser extent the relative abundance of the nest shrub, were not related to nesting success.

DISCUSSION

Based on previous work at four of the five study areas used in this study, the number of successful nests and the number of fledglings per pair were positively correlated with the density, vertical homogeneity, and horizontal homogeneity of perennial vegetation within California Gnatcatcher territories (Braden et al. 1997a). Consistent with the habitat/fitness relationship, the current study found that gnatcatchers placed their nests in areas with increased perennial cover, density, concealment, and vertical perennial homogeneity compared with random locations. In addition, 78.9% of all gnatcatcher nesting attempts failed, mostly due to predation, which theoretically should result in strong selection to increase nesting success

through nest-site placement. Nevertheless, I detected no relationships between nest placement and nest fate or productivity. At least four possibilities (none of which are mutually exclusive) may account for these unexpected results.

First, the failure to detect a relationship between nest placement and nest fate or productivity may be due to study design. However, nest-placement variables used in this study (i.e. nest orientation, nest height, vegetation density, and patch composition) have been shown to influence nesting success and nest predation in other species (Best and Stauffer 1980, Conner et al. 1986, Li and Martin 1991). The large number of variables used to test for the effects of nest placement on nest fate and productivity favored the possibility of finding a relationship. The fact that both the nest patch and the nest site were examined increases the likelihood of detecting an influence of nest placement on nest fate and productivity. The variables used in this study differed between gnatcatcher nests and random locations, and nest-placement variables also differed among study areas. It seems unlikely that the same variables would fail to detect a major influence of nest placement on nest fate or productivity.

High densities of nest predators have been associated with forest fragments and edges (Wilcove 1985, Robinson 1992). Predation rates in excess of 80% have been reported for forest fragments (Robinson 1992). Thus, landscape effects, through fragmentation processes, may override selection effects on nest placement, accounting for the inability to detect relationships among nest placement, nest fate, and productivity. In support of the "fragmented-landscape" hypothesis, coastal sage scrub communities are known to have been modified by agriculture, fire, exotic weeds, and urban expansion (Klopatek et al. 1979, Westman 1981, O'Leary 1990), and there was a gradient in perennial structure among four of the study areas (Braden et al. 1997a). However, undisturbed coastal sage scrub also varies in patchiness, species composition, and seasonal growth in response to moisture and soil composition (Westman 1981, Mooney 1988, O'Leary 1990). Thus, a gradient in perennial structure among study areas does not necessarily indicate a fragmented landscape.

If increased predation due to fragmentation were overriding nest-selection forces, and

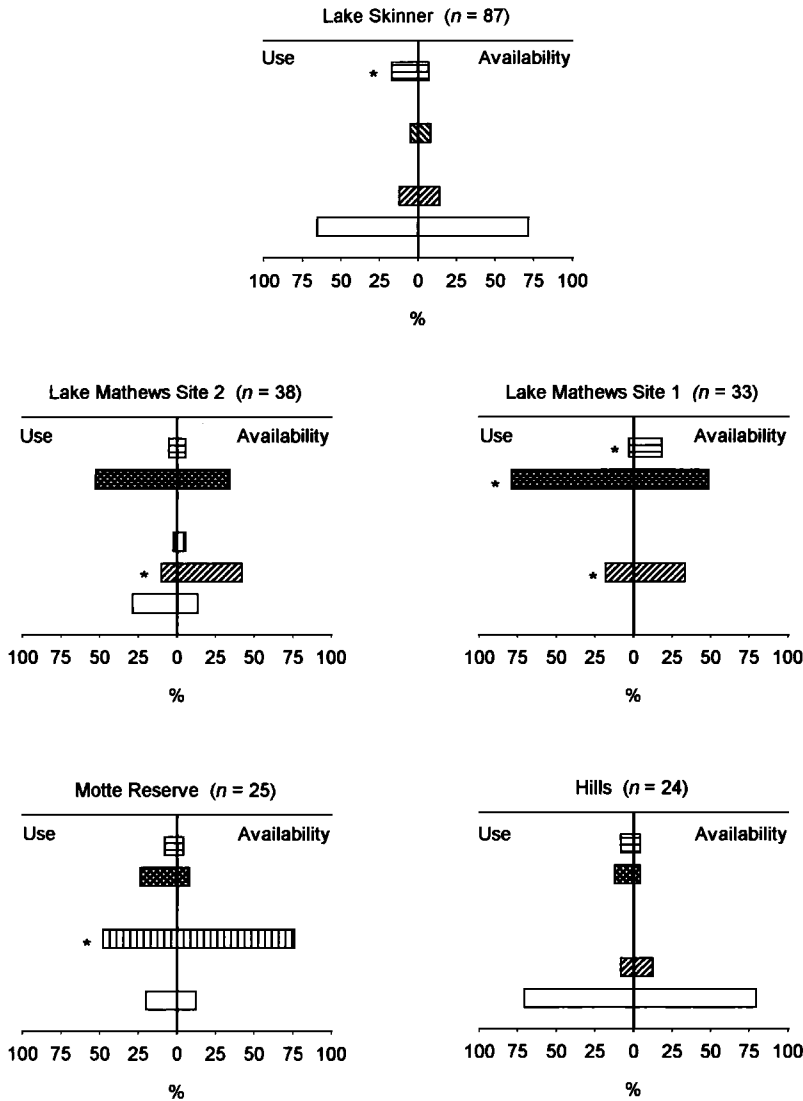


FIG. 2. Comparisons of shrubs used by California Gnatcatcher as nest substrates versus shrub availabilities at five study areas in Riverside County, California. Use versus availability determined by goodness-of-fit using the G-statistic and Bonferroni tests. Asterisks indicate that shrub use was not proportional to shrub availability at $P \leq 0.05$. Sample sizes are numbers of nests. Clear bar = California buckwheat; diagonal right = California sage; vertical bar = black sage; diagonal left = bush penstemon; crosshatching = brittlebush; horizontal lines = rare or uncommon perennial species.

study areas differed in perennial structure, then predation rates among study areas should have differed significantly, which they did not ($\chi^2 = 2.57$, $df = 4$, $P = 0.63$). Predation rates high enough to obscure selective forces for nest placement could result in nonviable populations. However, lambda values for gnatcatcher populations at Lake Skinner, Lake Mathews

Site 2, and Lake Mathews Site 1/Motte were 1.50, 1.03, and 0.38, respectively (Braden et al. 1997a). Although historic lambda values are unknown, a strong relationship between nest placement and nest fate or productivity, if it exists, should be detectable in growing or stable populations because lambda values above 1 suggest that such a selection process would be

effective, even if increased predation within a fragmented landscape were hindering the effectiveness of the selection process. Landscape effects cannot easily account for the failure to detect a relationship between nest placement and nest fate or productivity, nor can landscape effects be entirely discounted.

Filliater et al. (1994) found that nest-site characteristics were not related to nesting success for a population of Northern Cardinals (*Cardinalis cardinalis*). They postulated that environments with a high diversity of predators, each with different search strategies, may exclude the possibility of safe nest placement. Thus, a third possibility for the inability to detect a relationship between nest placement and nest fate or productivity for the California Gnatcatcher is the occurrence of a predator-rich environment. For example, a high diversity or abundance of terrestrial predators might favor nest placement high in a shrub, whereas a concomitantly high diversity of avian predators might favor nests placed low in a shrub. Given this scenario, a predator-rich environment could preclude the possibility of safe nest placement because all nest locations may be subject to similar predation risk. Nest placement could still be nonrandom if gnatcatchers exhibited some general antipredator nest-placement characteristics related to concealment that reduced predation risk from many predators. Nest placement could also be nonrandom for reasons unrelated to nest predation, such as thermoregulation and food availability. My results suggest that nest predators were abundant and varied. Adult gnatcatchers engaged in vigorous agonistic behavior toward gopher snakes (*Pituophis melanoleucus*), common kingsnakes (*Lampropeltis getulus*), coachwhips (*Masticophis flagellum*), Beechey ground squirrels (*Spermophilus beecheyi*), Bewick's Wrens (*Thryomanes bewickii*), Bullock's Orioles (*Icterus bullockii*), Greater Roadrunners (*Geococcyx californianus*), and coyotes (*Canis latrans*).

The occurrence of generalized nest predators is a fourth possibility that could account for the inability to detect a relationship between nest placement and nest fate or productivity. Zimmerman (1984) and Howlett and Stutchbury (1996) hypothesized that nest predators could be non-specialists that elicit cues from potential prey by random close encounters with nests. Random searches by non-specialized

predators could account for the absence of safe nest placement because all placements should be subject to equal predation pressure when predator search patterns are random. In support of the "generalized-predator" hypothesis, Bowman and Harris (1980) found that the spatial heterogeneity of vegetation decreased a predator's foraging efficiency significantly more than nest concealment. Thus, the presence of generalized nest predators could account for the lack of a relationship between nest placement and nest fate or productivity in the present study and for the positive correlation between the density of perennial vegetation and the structure of gnatcatcher territories and nesting success and productivity identified previously (Braden et al. 1997a).

Some passerine species may select habitats based on the availability or abundance of suitable nest sites (Steele 1993) or foraging sites (Sedgwick and Knopf 1992). Also, predators may respond to the cumulative density of species with similar nest sites within the habitat (Martin 1993). Thus, factors affecting nesting success may function at scales larger than the nest site or patch. I did not detect major effects of nest placement on nest fate or productivity at scales of the nest site or patch, but previous work on four of the five gnatcatcher populations used in this study detected a relationship between habitat versus nesting success and the number of fledglings per pair at the scale of the gnatcatcher territory (Braden et al. 1997a), which is approximately 3.4 ha (G. Braden unpubl. data). Therefore, major factors affecting nesting success, and ultimately habitat suitability, for California Gnatcatchers appear to operate at spatial scales larger than the nest site or patch.

Assuming that California Gnatcatchers cannot influence nest fate or productivity through nest placement, how do they compensate for fitness lost through nesting failures? Filliater et al. (1994) postulated that Northern Cardinals nest repeatedly within a breeding season because one of the nesting attempts would be successful due to chance alone. Although my study did not examine life-history traits, it is worth noting that California Gnatcatcher pairs averaged 3.39 ± 1.40 nesting attempts per season (range 1 to 7; G. Braden unpubl. data). Gnatcatchers regularly built new nests within seven days following a nest failure and were

observed to build a nest in two days. Thus, the number of nesting attempts by California Gnatcatchers may be an adaptive response to low nesting success.

In summary, nest placement did not have a major effect on nest fate or productivity for California Gnatcatchers. Small effects may have been present but were not detectable. Possible explanations for the lack of major effects of nest placement on nest fate and productivity include a fragmented landscape, a predator-rich environment, or the occurrence of generalized predators; none of these explanations is mutually exclusive. The fact that nesting success and the number of fledglings previously has been correlated with habitat structure within territories of California Gnatcatchers suggests that factors having major effects on nest fate operate at scales larger than the nest site or nest patch.

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