VARIATION IN LIFE-HISTORY TRAITS AND NEST-SITE SELECTION AFFECTS RISK OF NEST PREDATION IN THE CALIFORNIA GNATCATCHER

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ABSTRACT.—I monitored nests and reproduction of California Gnatcatchers (*Polioptila californica californica*) at Miramar Naval Air Station, California, in 1994 and 1995 to determine correlates of nest placement, life-history traits, and nest predation. One in four nests survived to fledging, with the majority of losses caused by predation. Predation rate over the entire nesting cycle did not change seasonally and was lower in nests with full clutch sizes than in those with submodal clutch sizes. When the nest sample was divided into thirds according to nest height and then according to rate of disturbance by investigators, the upper and lower thirds suffered greater rates of predation than the middle third, and nests disturbed most often by investigators suffered greater predation rates than those disturbed less frequently. Finally, the probability of incubation lasting the full period (at least 14 days) dropped seasonally from about 0.9 for incubation initiated in mid-March to less than 0.2 for nest initiated in early July, despite there being no apparent relationship between incubation length and mean daily high or low temperatures over the laying and incubation stages. These results indicate that reproductive success is related to variation in nest-site selection and life-history traits, as well as to variation in environmental variables and investigator activity. *Received 2 May 1996, accepted 6 December 1996.*

NEST PREDATION is the primary cause of reproductive failure in land birds (Ricklefs 1969). Many investigators have shown that life-history traits and nest-site selection affect the risk of nest predation (Nice 1957; Nolan 1978; Longcore and Jones 1969; Roseberry and Klimstra 1970; Best 1978; Best and Stauffer 1980; Martin 1988, 1993; Martin and Roper 1988; Hanski and Laurila 1993; Morton et al. 1993; Seitz and Zegers 1993; Hartley and Shepard 1994), indicating that optimal values for these traits exist in some species.

The California Gnatcatcher (*Polioptila californica californica*) is an open-nesting, nonmigratory passerine that lives in coastal sage scrub in southern California. Breeding adults are sexually dichromatic, and males and females participate in all aspects of parental care. Nests of California Gnatcatchers in San Diego County increase seasonally in height and relative height (nest height relative to height of nest plant), and nest height increases with height of the nest plant (Sockman unpubl. data). Nest concealment, however, apparently does not in-

crease seasonally despite the fact that foliage density increases seasonally. I attribute these findings to seasonal differences in nest placement (increasing nest height) that offset changes in overall vegetation density and serve to maintain an optimum level of concealment based on microclimate requirements and the need to minimize nest predation. Support for this hypothesis relies on data showing changes in risk of nest predation with respect to nest placement. Here, I provide these data in addition to data on basic life-history traits and how these traits affect reproductive success.

Concern for the California Gnatcatcher, which is listed as a threatened species, has resulted in studies aimed at understanding its requirements. Yet, published accounts of their life history are scant. I examined fecundity, reproductive success, and duration of the incubation and nestling stages for seasonal variation and for correlations among these traits. Using these results and data on nest placement, I tested whether rate of nest predation: (1) differs seasonally and according to nest-plant species (hereafter substrate), nest-site characteristics, and disturbance by investigators (see Major 1990); (2) increases with increasing clutch size and brood size (because nestlings and parental

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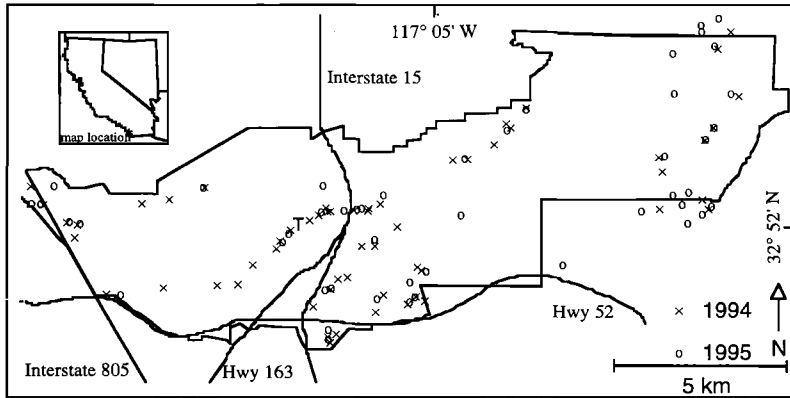
FIG. 1. Spatial distribution of breeding pairs of California Gnatcatchers, Miramar Naval Air Station, 1994 and 1995. "T" marks approximate location at which temperature was measured.

activity provide cues to potential predators); and (3) is highest during the nestling phase due to the increased activity at nests associated with nestlings.

STUDY AREA AND METHODS

Study area.—The study was conducted at Miramar Naval Air Station in San Diego County, California (see Fig. 1). The site consists of 9,561 ha of elevated marine terraces and low foothills, with several extensive canyons and ridges. Elevation ranges from 80 to 330 m. Dominant habitat types are chaparral and coastal sage scrub that together cover approximately 60% of the site (O'Leary et al. 1994). Potentially important nest predators (see Atwood 1993) include Greater Roadrunners (*Geococcyx californianus*), Western Scrub-Jays (*Aphelocoma californica*), Common Ravens (*Corvus corax*), raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), and coyotes (*Canis latrans*). Other potential predators, such as several species of snakes, also occur but are less abundant than the species listed above.

Data collection.—Nests were found by searching suitable habitat and by observing paired birds. Data were collected from mid-March to mid-August of 1994 and 1995, which spanned the period from egg laying through fledging for the entire study population. Each nest was assigned to one of two habitat types, wash or upland, and the nest substrate species was recorded.

Nests were checked with binoculars from a distance of 10 m, usually once every two to four days from the time they were found. Nests could be observed safely from this distance without flushing the attending adult. Which nests were visited at high frequency was determined mostly prior to the breeding season, when locations of wintering pairs were iden-

tified during surveys. Several of these pairs were selected for territory and dispersal studies that carried into the breeding season. Therefore, these nests received more visits than those of pairs that were not used for these studies. Selection of nests for territory and dispersal studies was based on geographic location so that the entire study site was represented as evenly as possible. Communication among investigators in the field contributed to a small amount of variation in nest visitation rates. However, the distribution of visitor frequency probably was approximately random with respect to nest-site characteristics and life-history traits. Therefore, analyses of nest predation and investigator disturbance were unlikely to be biased by other variables (see below). Each approach to a nest by an investigator was recorded as a single visit (disturbance), regardless of whether the adult was flushed or the nest was checked from a distance.

Once laying was complete, I recorded nest height; substrate height; percent concealment (percent of the nest laterally obscured by vegetation) estimated from the north, south, east, and west sides 1 m from the nest and at nest level; and percent concealment from 1 m directly above the nest. It usually took less than 3 min to obtain these measurements. Each of these measurements was taken a second time once the nest had either failed or fledged young, and if at least one week had elapsed since the measurements were first taken. Because the primary interest was the state of the nest just prior to its termination (usually caused by predation), in most cases only the latter measurements were used in the analyses. However, the condition of some depredated nests precluded the collection of second measurements. For these nests, I used the first measurements in the analyses.

If no bird was seen near the nest, the nest was inspected to verify its status. California Gnatcatchers typically lay one egg per day for four days (at which

point the clutch is complete); the modal incubation period is 14 days. Therefore, the age of nests found during laying could be determined directly. If a nest was found during incubation, the adult was flushed each time the nest was checked until hatching occurred. Nests found after hatching were aged by estimating the age of the nestlings. Nestlings typically remained in the nest 14 days after hatching, resulting in a 31-day nesting cycle from the time the first egg was laid.

A nest was assumed to have been depredated when it was found empty after having previously contained at least one egg or nestling, except when fledging had occurred. Fledging was obvious because nests remained intact, and fledglings (accompanied by highly attentive and aggressive parents) usually were detected nearby. Cases in which only part of a clutch or brood disappeared were not counted as depredations unless they eventually resulted in a total loss. Abandoned nests were analyzed separately from depredated nests. Nest visits enabled me to determine clutch size, number of hatchlings and fledglings, hatching success (hatchlings per egg), fledging success (fledglings per egg laid and per egg hatched), and duration of the incubation and nestling periods.

Personnel of Miramar Naval Air Station recorded daily high and low temperatures from a central location (Fig. 1). I calculated for each nest the mean daily high and low temperatures for the entire nesting cycle and for the laying plus incubation periods.

Analyses.—To maximize the statistical independence among sampling units, analyses were based on one value for each variable measured per breeding pair per year. When multiple nests were available for a pair, one nest was randomly selected for analysis. Based on banding data, most pair bonds dissolved between years, and territory locations differed notably from 1994 to 1995. Therefore, I believe that giving equal weight to nesting events in similar parts of the study site but during different years satisfied the assumptions of statistical independence. Nonetheless, data were analyzed for between-year differences in dependent variables.

I used forward-stepping logistic regressions to examine variation in the dependent variables clutch size (<4 vs. ≥4 eggs), number of hatchlings (<4 vs. ≥4), number of fledglings (<4 vs. ≥4), hatching success (<1 vs. 1 hatchling per egg laid), fledging success (<1 vs. 1 fledgling per egg laid or per egg hatched), and duration of incubation and nestling periods (each <14 vs. ≥14 days). Independent variables included year, date of clutch initiation, mean daily high and low temperatures, clutch size (incubation period and nestling period analyses only), duration of the incubation period (all analyses except clutch size and incubation period), duration of the nestling period (fledging success analyses only), and number of hatchlings (nestling period analysis only).

Relative nest height was calculated as the nest height relative to the substrate height, and nest ceiling as the difference between substrate height and nest height. Nest-failure rates, their standard errors, and the probability of a nest surviving the entire cycle were calculated according to Mayfield (1961, 1975) as amended by Hensler and Nichols (1981) and Johnson (1979). To determine whether failure rates differed among subsets of nests, I used Johnson's (1990) method, which requires the calculation of a test statistic that is compared with a χ^2 distribution with df = 1.

The distribution of nests according to nest placement and investigator disturbance was not uniform. To establish adequate sample sizes among the groups of nests being compared in any single analysis, I divided the nest sample into thirds according to each of these independent variables. For example, variation in predation rate with respect to nest height was examined by comparing predation rates among the lowest, middle, and highest thirds of nests.

RESULTS

EGGS, NESTLINGS, AND DURATION OF INCUBATION AND NESTLING STAGES

A total of 171 nests, representing 107 independent pair-year combinations, was found during the two breeding seasons. There were no significant differences (Goodness of fit tests, df = 1) between 1994 and 1995 in clutch size (P = 0.29), number of hatchlings (P = 0.50), number of fledglings (P = 0.92), number of laying days (P = 0.59), number of nestling days (P = 0.46), total nest-cycle days (P = 0.89), and number of incubation days (P = 0.05). Therefore, I pooled these data (see Figs. 2 and 3). I also pooled the 1994 and 1995 data on hatchlings per egg ($\bar{x}$ = 0.91 ± SD of 0.13, n = 55), fledglings per egg ($\bar{x}$ = 0.96 ± 0.18, n = 36), and fledglings per hatchling ($\bar{x}$ = 0.91 ± 0.13, n = 33) after determining that they did not differ between years (t-tests, P = 0.7). Because these variables were calculated from different sets of nests (depending on how long nests survived), the number of fledglings per egg was higher than the number of hatchlings per egg.

Differences in clutch size, numbers of hatchlings and nestlings, hatching and fledging success, and duration of the nestling stage were not explained by any of the independent variables (improvement χ^2 from logistic regression, P ≥ 0.08 for all tests), but duration of the incubation stage was related to timing of nesting (no other independent variable explained a sig-
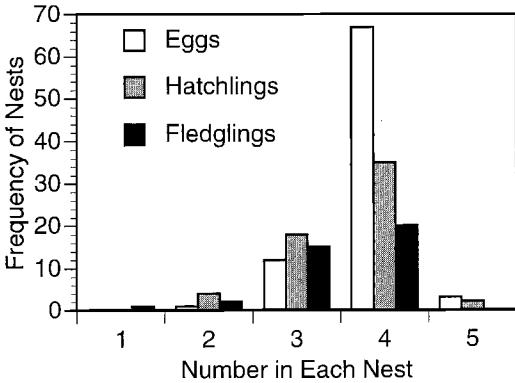
FIG. 2. Frequency distribution of clutch size, number of hatchlings, and number of fledglings in California Gnatcatcher nests, 1994 and 1995 combined.
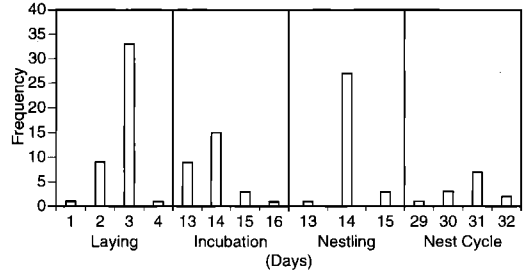

FIG. 3. Frequency distribution of number of laying, incubation, nestling, and total nest-cycle days in California Gnatcatchers, 1994 and 1995 combined.

nificant amount of variation in duration of incubation [$P \geq 0.1$ for all tests]). The probability of gnatcatchers incubating eggs for at least 14 days declined from nearly 0.9 early in the nesting season to less than 0.2 for nests initiated late in the season (Fig. 4).

NEST FAILURE

The rate of nest failure was high, with approximately one in four nests surviving from laying through fledging (Table 1). Most nest failures were caused by predation (presumably by birds and mammals), and failure rates did not differ significantly between years. Two nests that were infested with Argentine ants (*Iridomyrmex humilis*) were considered to have been depredated. Two other nests were parasitized by a Brown-headed Cowbird (*Molothrus ater*). The cowbird egg was removed from each nest, and the nests eventually were depredated. Finally, several nests were abandoned for unknown reasons. These nests were not considered depredated, but obviously they had been deserted as evidenced by the presence of cold eggs or dead nestlings.

Stage of nesting cycle.—In 1994 ($\chi^2 = 1.93, P = 0.165$) and in both years of the study combined ($\chi^2 = 1.33, P = 0.249$), predation rates did not differ significantly across the nesting cycle. In 1995, however, nest-predation rate was significantly higher ($\chi^2 = 11.36, P = 0.001$) during laying (daily predation rate = $0.097 \pm$ SE of 0.035, $n = 31$ nests) than during either incubation ($0.021 \pm 0.008, n = 36$) or brood rearing (0.028

$\pm 0.009, n = 31$). Only in 1995 were differences in overall failure rates (predation and abandonment) across the nesting cycle statistically significant ($\chi^2 = 6.99, P = 0.008$), and this was due to the change in predation rate.

Investigator disturbance.—Some gnatcatcher pairs deserted following the discovery of a nest during construction; these nests were excluded from analyses. Desertion was rare after egg laying began, however. To determine whether nest visits affected predation rates, I divided nest samples into thirds according to the rate of visitation by investigators. Mean rates of visitation for the upper, middle, and lower thirds
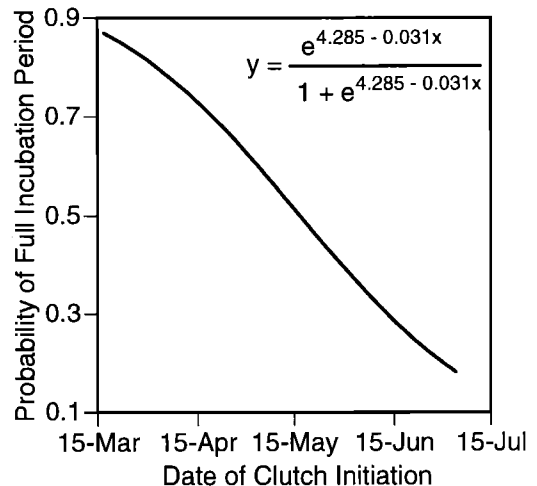

FIG. 4. Seasonal decrease in the probability of a full (≥ 14 days) incubation period in California Gnatcatcher nests. The improvement in fit of the logistic regression model with only a constant by the addition of the independent variable (date of clutch initiation) was statistically significant ($\chi^2 = 3.95$, df = 1, $P = 0.047$).

TABLE 1. Daily nest-failure rates ($\pm$ SE) and probability of a nest surviving the entire nesting cycle for California Gnatcatchers. Test statistics and P-values are for comparisons of failure rates between years (after Johnson 1990).

Cause of failure	1994 and 1995 ($n = 107$ nests)		1994 ($n = 58$ nests)		1995 ($n = 49$ nests)		χ^2	P
	Failure rate	Prob. survival	Failure rate	Prob. survival	Failure rate	Prob. survival		
Predation	0.036 ± 0.005	0.319	0.040 ± 0.007	0.279	0.032 ± 0.007	0.370	0.12	0.73
Abandon-ment	0.007 ± 0.002	0.801	0.006 ± 0.003	0.827	0.008 ± 0.003	0.774	0.03	0.85
Total[a]	0.043 ± 0.005	0.253	0.046 ± 0.007	0.229	0.040 ± 0.007	0.284	0.06	0.81

[a] Predation plus abandonment.

were 0.85, 0.54, and 0.42 visits per day, respectively. Nests in the upper third incurred a significantly ($\chi^2 = 10.71$, $P = 0.001$) greater rate of predation (0.066 ± 0.013, $n = 36$) than did nests in the middle (0.027 ± 0.007, $n = 36$) and lower third (0.030 ± 0.007, $n = 35$); the latter two groups did not appear to differ in daily predation rates.

Clutch and brood size.—One in 13 nests with small clutch sizes survived through fledging, yielding a considerably high rate of nest failure for this subgroup. Mayfield estimates revealed a substantial drop in predation rate when nests had ≥ 4 eggs compared with those having smaller clutch sizes (Table 2). Whether for all nests combined or for nests with ≥ 4 eggs, I observed no significant relationship between predation rate and brood size.

Timing of nesting and nest-site selection.—I examined predation with respect to timing of nesting as measured by the date of clutch initiation. Nest-predation rate during the nestling period declined seasonally, but there was no seasonal difference in predation rate during laying ($\chi^2 = 2.34$, $P = 0.126$), incubation ($\chi^2 = 2.32$, $P = 0.128$), or for the entire nesting cycle (Fig. 5).

Nest predation was lowest over the entire nesting cycle for nests at intermediate absolute heights and for nests at intermediate heights relative to substrate height (Fig. 6). Nest-predation rate also varied according to nest ceiling, with nests in the middle and high end of the ceiling range incurring greater predation than nests with low ceilings. Because absolute nest height was related to relative nest height and nest ceiling, results of these analyses were not independent.

Nest concealment.—Daily predation rate was not significantly related to average percent concealment ($\chi^2 = 2.84$, $P = 0.092$) or percent concealment from above ($\chi^2 = 1.76$, $P = 0.185$), although it tended to increase as average percent concealment decreased. Mean average percent concealment values for the least, moderately, and most concealed nests were 54.4, 68.6, and 83.1%, respectively. Daily predation rate ($\bar{x} \pm$ SE) was 0.049 ± 0.010 ($n = 37$ nests) for the least concealed nests, 0.037 ± 0.009 ($n = 33$) for moderately concealed nests, and 0.028 ± 0.007 ($n = 37$) for the most concealed nests. Changes in predation rate according to properties of substrates, including height ($\chi^2 = 0.77$,

TABLE 2. Daily nest-predation rates ($\pm$ SE, number of nests in parentheses) of California Gnatcatchers with respect to number of eggs or hatchlings. Test statistics and P-values are for comparisons between nests with <4 vs. ≥ 4 eggs or hatchlings (after Johnson 1990).

	No. of eggs or hatchlings		χ^2	P
	<4	≥ 4		
Eggs	0.057 ± 0.018 (13)	0.026 ± 0.005 (70)	5.10	0.024
Hatchlings (all nests)	0.018 ± 0.006 (22)	0.014 ± 0.004 (37)	0.38	0.536
Hatchlings (≥ 4 eggs)[a]	0.014 ± 0.006 (16)	0.011 ± 0.004 (31)	0.26	0.612

[a] Considering only nests in which ≥ 4 eggs were laid.
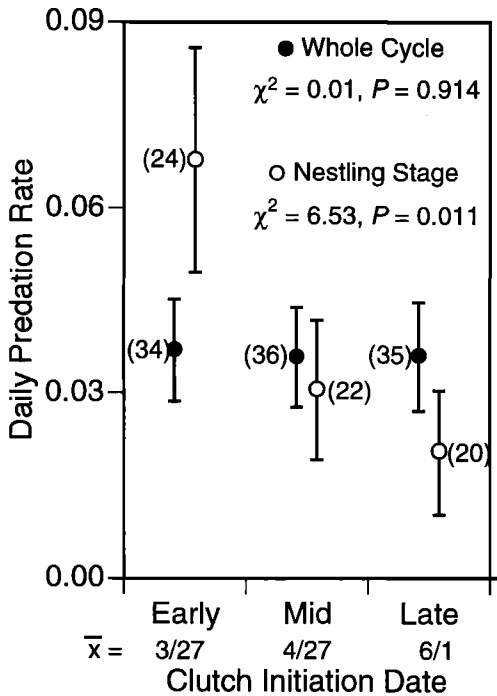
FIG. 5. Daily nest-predation rate with respect to reproductive schedule during the nestling stage and over the whole nesting cycle for California Gnatcatchers. Whiskers are ± 1 SE, with number of nests in parentheses.

$P = 0.381$) and species ($\chi^2 = 0.72$, $P = 0.395$), were not apparent.

DISCUSSION

Nest-predation risk was evaluated in terms of daily predation rate because the method for calculating standard errors of survivorship estimates for the entire nesting cycle has not been established. What might seem to be small daily predation rates need to be considered in terms of the entire nesting cycle. For example, daily predation rates of 0.03 and 0.06 correspond to survivorship estimates of 39% and a 15% for a 31-day nesting cycle (Mayfield 1961, 1975).

The gnatcatcher nests that were visited most frequently by investigators suffered the highest predation rates. This indicates that: (1) the extent of nest monitoring should be considered carefully before conducting a study, and (2) that the number of nests surviving to completion probably underestimates the true survivorship for this species. It is unlikely, however,

that results in other analyses are biased with respect to the independent variables, which themselves were not related to the rate of visitation (see Methods).

Determining the influence of clutch size and number of hatchlings on nest predation was difficult due to the scarcity of nests with small numbers of eggs and nestlings. Although estimates based on small samples may be inaccurate, the importance of a large sample size in Mayfield estimates decreases as the true predation rate increases (Hensler and Nichols 1981). The fairly substantial effect of clutch size on nest predation, and the fact that only 1 in 13 nests survived to completion, suggest that the Mayfield estimates were accurate. An additional concern is that small clutches may have resulted from partial predation during laying. I never observed partial predation during incubation or brood-rearing, however, making this possibility small.

The evolution of clutch size in passerines has been hypothesized to reflect risk of nest predation, with smaller clutches evolving when predation risk is high and vice versa (see Slagsvold 1982, Lima 1987, Martin 1992). Intraspecific variation in clutch size within the same study area leads to the prediction that nests with large clutches should suffer higher predation rates than nests with smaller clutches because fewer nestlings would require fewer nest visits by parents, thus yielding fewer cues for predators. In some open-nesting sparrows (Best 1978, Morton et al. 1993) and in Eurasian Blackbirds (*Turdus merula*; Cresswell 1997), nest-failure rates do not vary with clutch and brood size. My results suggested otherwise. I offer two possible explanations.

The first is that parents producing small clutches may be less capable of defending nests from predators. Like many other species (Montgomerie and Weatherhead 1988, Morton et al. 1993), California Gnatcatchers engage in vigorous vocal and flight behavior in response to a threat near their nest. In some cases, these behaviors may thwart predation. Still, this explanation seems invalid for gnatcatchers, because clutch size can either increase or decrease seasonally among nests of an individual female.

Second, the reduced investment in a small clutch may provide less impetus for defense. To investigate this further, I compared failure
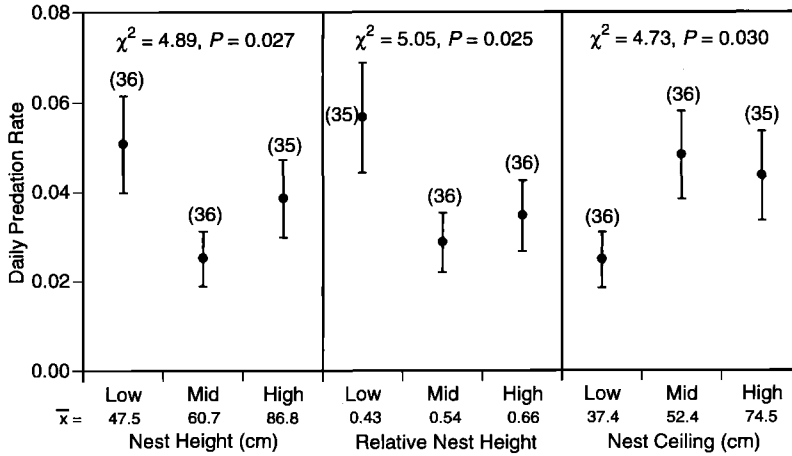
FIG. 6. Daily nest-predation rate with respect to nest height, relative nest height, and nest ceiling for California Gnatcatchers. Whiskers are ± 1 SE, with number of nests in parentheses.

rates between nests with small broods and those with full broods and found no difference when all nests were used and when just nests with complete clutches were used. The actual contents of a nest (i.e. the exact numbers of eggs or nestlings) therefore are unlikely to affect failure rate, even when clutch size is controlled for in analyses comparing brood sizes. This could be determined more conclusively by manipulating egg numbers and observing the effect on nest failure rate.

In some species, nests built low in the vegetation face greater risk of mammalian predation than those built higher in the vegetation (Nolan 1978, but see Filliater et al. 1994), whereas those built too high sometimes experience greater risk of avian predation (Morton et al. 1993). If the change in mammalian predation risk differs from the change in avian predation risk, then some intermediate height would exist where predation risk from both sources combined is lowest. My results were consistent with this prediction, but whether they were a function of differing rates of change in predation risk from aerial versus ground-dwelling predators remains to be determined. Neither variation in habitat type nor nest concealment were likely factors in this result, because these parameters do not appear to change with nest height (Sockman unpubl. data) nor to affect predation rate, irrespective of nest height. Moreover, changes in substrate height and species provided little explanation for variation in predation rate.

Best (1978) observed a similar pattern in Field Sparrows (*Spizella pusilla*); i.e. high and low nests were more susceptible to predation than nests of intermediate height (although differences were not significant). He attributed this to differences in the foraging strategies of predators (i.e. aerial vs. ground-dwelling). Later, Best and Stauffer (1980) reported a drop in mammalian predation as nest height increased, but again, the differences were not statistically significant.

In environments where the risk of nest predation is high, nest placement can have an important influence on reproductive success (Nolan 1978, Best and Stauffer 1980, Wilcove 1985, Martin 1988, Hanski and Laurila 1993, Martin 1993, Morton et al. 1993, Nour et al. 1993, Cresswell 1997; but see Best 1978, Filliater et al. 1994, Howlett and Stutchbury 1996). However, the extent to which predation risk actually drives nest placement, or whether advantages gained by specific nest placements are epiphenomena, remains unknown for many species. For example, because of thermoregulatory needs of embryos and newly hatched nestlings in altricial species, nest microclimate (as affected by nest placement) has an important influence on parents that must balance energetic constraints between time spent on versus off the nest (Zerba and Morton 1983, Walsberg 1985).

Although determining whether predation risk causes variation in nest placement and life-history traits was beyond the scope of my

study, the influence of predation on nest height and clutch size provides a basis for future investigations. Moreover, my results are immediately applicable to the management of California Gnatcatchers. Failure to preserve habitat of specific age (i.e. height) structure may induce unnaturally high rates of reproductive failure, because gnatcatchers would be unable to nest at optimal heights. Additionally, the influence of investigators on nest predation should be an important consideration for future studies involving this heavily monitored species.

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Associate Editor: I. J. Ball