BREEDING BEHAVIOR OF THE CALIFORNIA GNATCATCHER IN SOUTHWESTERN SAN DIEGO COUNTY, CALIFORNIA

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We intensively studied various aspects of habitat use, breeding biology, home-range requirements and dispersal patterns of a population of the California Gnatcatcher (*Polioptila californica*) in southwestern San Diego County from 1989 to 1992. When this field effort was initiated, few quantitative demographic studies of the species were available to aid in making informed decisions regarding the conservation and management of this species (Atwood 1993). In this paper, we detail our observations of the gnatcatcher's breeding behavior and nesting success. Other analyses are reported in several companion papers (Preston et al. 1998a, b, Bailey and Mock 1998, Mock 1998).

METHODS

We studied California Gnatcatchers on approximately 842 ha of coastal sage scrub near the Sweetwater River in the unincorporated community of Rancho San Diego in southwestern San Diego County (32° 40′ N, 117° W). Rancho San Diego is approximately 21 km from the Pacific coast and 21 km north of the United States–Mexico border. Elevation varies from 92 to 366 m above mean sea level. The slope gradient varies widely, from flat river floodplain to slopes greater than 50%. There were two primary study areas within 3 km of each other. We collected data on breeding biology at the larger study area (1200 ha) from 1989 to 1991, from the second smaller, more easterly study area (111 ha) from 1989 to 1992. Over half of the smaller study area was graded for development in the fall of 1989, eliminating the gnatcatchers from most of the shallow slopes that previously supported them.

We banded 318 California Gnatcatchers from 1988 to 1992. Of these, 218 were adults, juveniles, or fledglings caught in mist nets and 100 were nestlings from 33 nests. Birds were banded with unique combinations of a single USFWS metal band and one or two plastic color bands. The seams of the color bands were sealed with acetone to prevent them from opening. The smallest color bands commercially available (AC Hughes size XF) are slightly too large for gnatcatchers. After some initial problems with band slippage, especially in very young birds, we reduced the band size slightly according to the procedure described by Thomas (1983). No further problems were noted.

Most nests (75%) were found while they were being built. Territories of color-banded gnatcatchers were visited two to three times each week during the breeding season. Nest checks were conducted so as to minimize nest predation associated with the observer (Martin and Geupel 1993). Nest checks were infrequent and timed to determine nesting stage (e.g., eggs laid or eggs hatching) and when nestlings were of an age suitable for banding. We determined the fate of each nest found. Mayfield estimates of daily nest survival were calculated for the different phases of the nesting cycle for each year and for the entire study period (Mayfield 1961, 1975).

After each nest attempt was completed, we recorded the species of plant in which the nest was located, measured the dimensions of each nest (depth and width of the inner cup, length and width of the entire nest, distance from the nest to the nearest opening in the host plant, distance from the ground to the nest rim), and height, width, breadth of the host plant. We measured the distances from the host plant to the nearest neighboring shrubs on the east, west, north, and south. Nest locations were plotted on a topographic map, then digitized into a geographic-information system (GIS) from which percent slope was determined for each nest location.

We observed behavior at the nest with binoculars from a distance of at least 10 m. We defined rounds of nest building as periods of work broken by intervals of less than 10 minutes. The number of trips made to the nest by each member of the pair was recorded. We defined a shift of incubation or brooding as the complete interval that an individual spent on the nest. We always determined the duration of incubation shifts for pairs of consecutive shifts between which the sexes exchanged roles. Observations of nesting behavior were usually made for periods lasting 1 hour or more. The number of trips to feed nestlings was recorded for each parent. Postfledging young were considered fledglings until they left their natal territory, juveniles thereafter. Parental care of fledglings was documented for all intensively monitored pairs. We recorded the date when juveniles immigrating into the study area established territories and banded these birds shortly after their initial detection.

We sampled vegetation structure and composition within gnatcatcher territories by means of 130 belt transects of 60 m^2. Each transect sampled an area 30 m long and 2 m wide. At least three transects were positioned within a territory, but larger territories often had additional transects. Transects were placed within each territory to sample representative vegetation within the territory. Each transect paralleled the vertical aspect of the slope. Information recorded included species, height, width, and length of each shrub rooted within the belt. Area of each shrub was calculated as if it were an ellipse $[(0.5 \text{ length}) \times (0.5 \text{ width}) \times \pi]$. Relative cover of each species was calculated as (total area for a species/total area of all species) × 100%. Daily temperature and precipitation records from 1988 through 1992 from one of the study sites and approximately 8 km away in La Mesa were obtained from the San Diego County Department of Flood Control.

All descriptive statistics are expressed as the mean ± standard error (SE) and sample size (n). Statistical tests for preferences in nest-site selection relative to percent slope and host-plant species followed Bonferroni's inequality test described by Neu et al. (1974). Comparisons between unsuccessful and successful nests are made with a t test or Z test for proportions with continuity correction (Zar 1984). We did chi-squared analyses for the Mayfield nest-survival estimates to test for differences between years and nesting stages, as well as initial survival of dependent juvenile gnatcatchers. The level of significance for all statistical tests was set at $\alpha = 0.05$.

RESULTS

Nest Placement and Nest Sites

We documented 134 nesting attempts over four breeding seasons (1989–1992). Of these nest attempts, 101 (75.4%) were detected during nest building or egg laying, 18 (13.4%) during incubation, 7 (5.2%) with nestlings, and 8 (6.0%) post-fledging. California Gnatcatcher nests are built from grasses and various bark fibers. The cup is lined with fine grasses, fur, feathers, and downy flower parts such as those of *Baccharis sarothroides*. Nest measurements were not obtained from all nests studied because often predators destroyed nests or gnatcatchers took material from old nests to build subsequent nests. Dimensions of intact nests (in cm; mean ± SE): outer length 6.8 ± 0.22 (n = 57); cup depth 3.6 ± 0.07 (n = 67); outer diameter 6.2 ± 0.07 (n = 74); inner-cup diameter 3.8 ± 0.07 (n = 62).

Within a breeding season, patterns of nest dispersion within a pair's territory varied. Some pairs clumped nesting attempts within a small area of their territory, often associated with a drainage, whereas other pairs distributed nests widely throughout their entire territory. Nest placement within the host shrub ranged from 30 to 292 cm above the ground (mean 82.1 ± 2.9 cm, n = 101). Nests were placed within the shrub an average of 16.4 ± 1.4 cm (n = 75) from the nearest outside edge of the shrub. The mean height of shrubs supporting gnatcatcher nests was 135 ± 3.6 cm (n = 103), and the diameter of host shrubs averaged 197 ± 11.7 cm (n = 73). Mean distances between the nest shrub and neighboring shrubs ranged from 153 to 176 cm, indicating that the surroundings of the nest shrub could be characterized as relatively open sage scrub. Plant species were selected for nest support as a function of their relative availability (Table 1). There was no significant preference or avoidance of any plant species for nesting relative to its dominance within the study areas (Neu test of proportions, $P > 0.05$). The smaller study area supported less cover of *Artemisia* and *Malosma* and more *Viguiera* and *Baccharis* than the larger study area (Table 1).

Nesting Behavior and Phenology

Both male and female gnatcatchers participated in all stages of the nesting cycle, although each sex allocates its effort differently (Figure 1). Males selected the nest site and did most of the nest building and nestling feeding, while females spent more time incubating eggs and brooding nestlings. The time spent during each stage of the cycle was documented for 23 pairs monitored through the entire breeding season (Figure 2). The birds nested persistently and were involved in some aspect of the breeding cycle for most of the breeding season.

Table 1 Plant Species Supporting California Gnatcatcher Nests and Relative Plant Dominance at Rancho San Diego

	Area 1		Area 2	
Plant species	Relative dominance (mean ± SE)	% Nests (*n* = 84)	Relative dominance (Mean ± SE)	% Nests (*n* = 47)
Artemisia californica, California sagebrush	37.6 ± 2.3	35.7	12.8 ± 7.2	14.9
Eriogonum fasciculatum, Flat-top buckwheat	28.4 ± 2.4	30.9	38.9 ± 8.4	36.2
Malosma laurina, Laurel sumac	15.7 ± 1.9	10.7	4.5 ± 4.5	4.2
Rhamnus crocea, Redberry	2.6 ± 0.5	4.8	0	0
Baccharis sarothroides, Broom baccharis	0.6 ± 0.3	1.2	6.7 ± 3.7	2.1
Gutierrezia californica, California matchweed	0.6 ± 0.1	0	0	0
Viguiera laciniata, San Diego sunflower	*a*	1.2	28.2 ± 5.2	27.7
Salvia apiana, White sage	*a*	7.1	*a*	8.5
Brickellia californica, California brickellbush	*a*	0	*a*	6.4
Adolphia californica, California spinebush	*a*	2.4	*a*	0
Simmondsia chinensis, Jojoba	*a*	2.4	*a*	0
Hazardia squarrosa, Sawtooth goldenbush	*a*	1.2	*a*	0
Adenostoma fasciculatum, Chamise	*a*	1.2	*a*	0
Xylococcus bicolor, Mission manzanita	*a*	1.2	*a*	0

[a]Relative dominance less than 0.6 for area 1 and less than 4.5 for area 2.

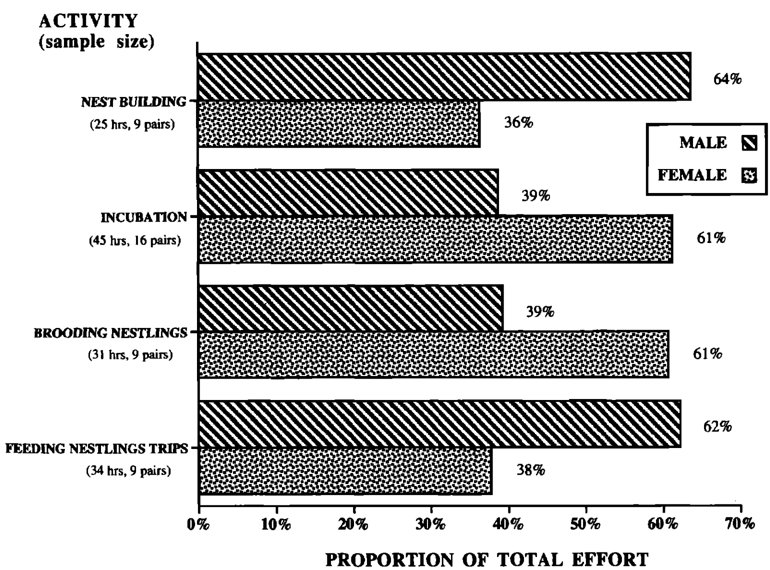

Figure 1. Allocation of effort by sex at each stage of the breeding cycle of the California Gnatcatcher.

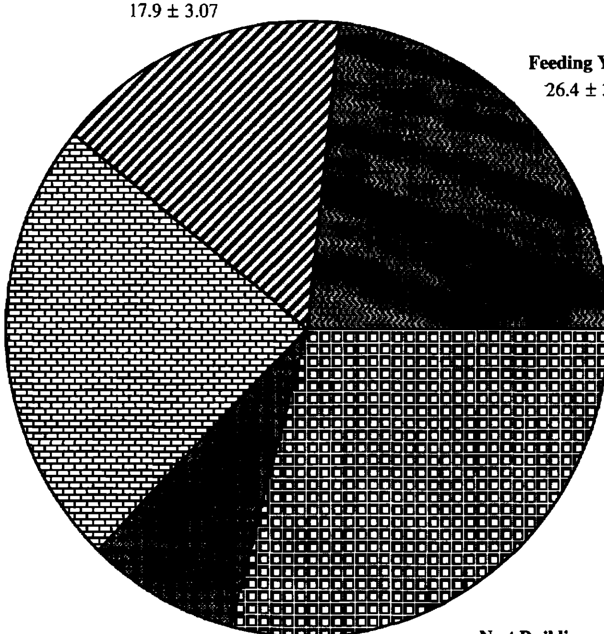

Figure 2. Time budget of the California Gnatcatcher during its nesting season. Figures are days, plus or minus standard deviation. N = 23 pairs; mean season duration 113 ± 6.5 days.

Nest Building

California Gnatcatchers began to molt into breeding plumage in February (Figure 3). The timing of the appearance of the males' black caps varied from year to year and appeared to depend on the amount and timing of winter precipitation. Over the four years studied, the molt began six to seven weeks after the first significant rain (>12 mm) in December. Nest building began two to four weeks after apparent completion of the molt. Nesting attempts were usually initiated between early March and mid-June with the largest number of nests started in April and May. The length of the breeding season from earliest nest building to the latest fledging (excluding the postfledging period) ranged from 102 (1990) to 173 days (1991; mean 121.3 ± 17.3 days, n = 4 years).

Male gnatcatchers appeared to select the nest site and have the dominant role in nest construction. Frequently, while a pair was foraging together, the male abruptly stopped foraging and flew to a shrub that was later used as a new nest site. The male vocalized persistently until the female joined him. The male began bringing nesting material to the site and formed the nest disc in a fork of the shrub. During the female's first few visits to the nest site

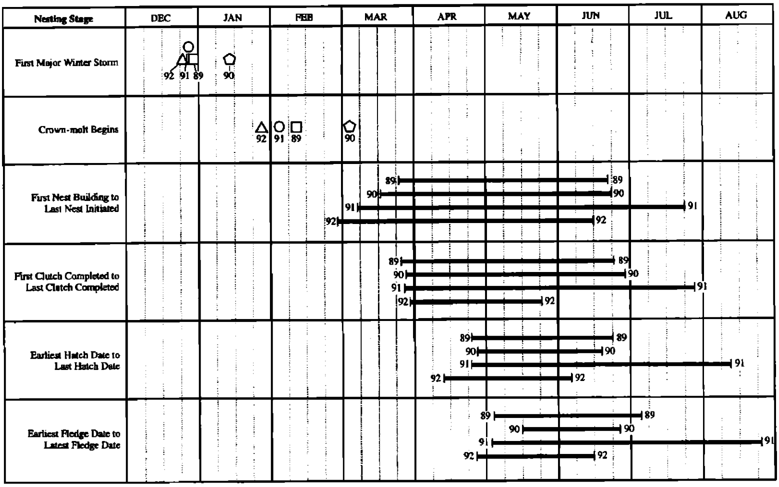

Figure 3. Nesting phenology of the California Gnatcatchers at Rancho San Diego, 1989–1992.

she did not bring in any nesting material but eventually began providing material and shaping the cup. The male allocated more time to nest building than did the female at all stages of nest construction except for lining the nest (Figure 4). The average number of nest visits per hour during nest building was 22.7 ± 2.3 for males and 12.7 ± 1.4 for females (paired t test: P = 0.001, n = 9 pairs).

Gnatcatchers often raised more than one brood. Early and late in the breeding season initiation of nest building often did not lead to egg laying. The average number of nesting attempts per pair per breeding season ranged from 3.3 to 7.3 (n = 4 seasons); one pair attempted to nest 10 times within a single breeding season in 1992 (Table 2). The number of nesting attempts in 1992 was higher than in the other three years (7.3 vs. 4.0–4.7 attempts per pair). A nest can be constructed in as few as 4 days, but the length of time between nest initiation and egg laying decreased as the season progressed. Although the nest appeared complete after 5 or 6 days, the female, and occasionally the male, visited the nest regularly to supplement the lining. For nests initiated in March, the interval between nest initiation and laying of the first egg averaged 10.9 days (± 0.69, n = 12). Nests initiated in April required an average of 7.0 ± 0.25 days (n = 11), those in May or June, 5.2 ± 0.19 days (n = 14). In an unusual case in 1990, a pair spent 30 days building their first nest of the season before finally laying. Several March rain storms washed away neighbors' nests, but this pair's nest survived undamaged.

Egg Laying

The first clutches were initiated in late March (earliest date: 22 March 1989; Figure 3). Egg laying appeared to be delayed in wetter years when a

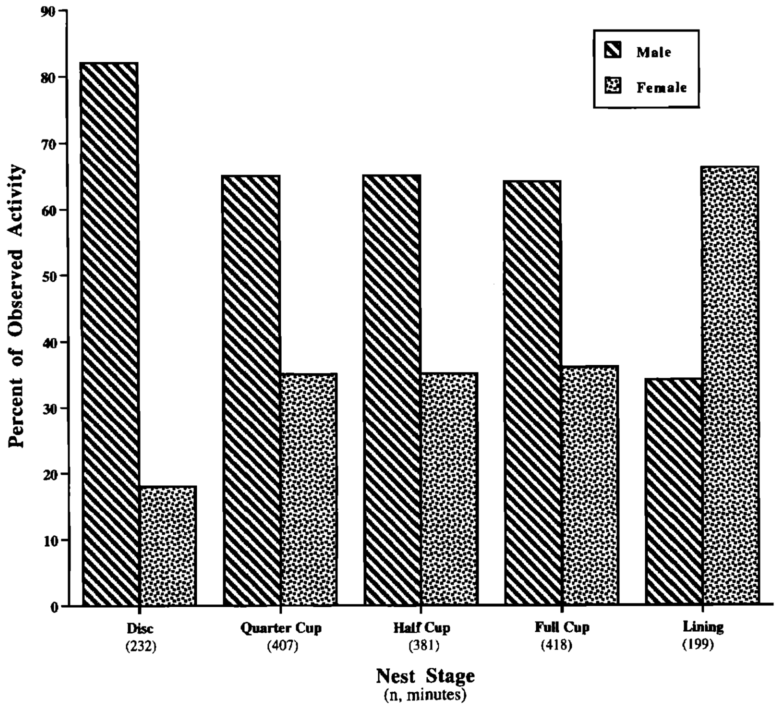

Figure 4. Relative participation of male and female California Gnatcatchers at each stage of nest building, based on 27.3 hours of total observation time of 9 pairs. Figures are numbers of minutes.

number of early nests were destroyed by rain storms. Initiation of the last clutch of the season varied more from year to year, with egg laying ceasing from late May in 1992 to late July in 1991.

California Gnatcatchers typically lay clutches of three or four eggs (mean clutch size 3.61 ± 0.06, n = 69). Clutch size varied significantly by year and may have been influenced by precipitation. In 1989, the fourth year of a drought, only 38% of the clutches contained four eggs (n = 24). In the following three years more rain fell and an average of 74% of the nests contained four eggs (n = 45 clutches). No complete clutches had less than three eggs. One five-egg clutch was the result of partial predation of a four-egg clutch, followed by laying of three-egg replacement clutch in the same nest. This was the only observed instance of partial predation followed by additional laying. The average number of eggs laid per female in one breeding season was 8.8 ± 0.55 (n = 23), the maximum 15.

Incubation

Gnatcatchers begin incubation with the penultimate egg, and eggs hatch after 14 days (mean incubation period 14.3 ± 0.13 days, n = 25). Both

Table 2 California Gnatcatcher Breeding Success at Rancho San Diego, 1989–1992[a]

	1989	1990	1991	1992	All years combined
Percentage of pairs successful	70.8	59.1	100.0	60.0	70.0
	(24)	(22)	(9)	(5)	(60)
Number of nests built per pair per complete season[b]	3.25 ± 0.62	3.5 ± 0.60	4.3 ± 0.60	7.3 ± 1.8	4.2 ± 0.84
	(8)	(6)	(7)	(4)	(25)
Number of eggs per complete clutch	3.38 ± 0.10	3.72 ± 0.11	3.67 ± 0.13	3.83 ± 0.11	3.61 ± 0.06
	(24)	(18)	(15)	(12)	(69)
Hatching rate (%)	61.1	72.7	75.0	31.0	62.0
No. eggs hatched/no. laid	52/85	48/66	39/52	13/42	152/245
Number of fledglings per successful pair	2.9 ± 0.14	2.8 ± 0.41	4.4 ± 1.16	2.7 ± 0.88	3.5 ± 0.20
	(17)	(13)	(8)	(3)	(41)
Fledging rate (%)	76.9	64.6	97.4	53.8	76.3
No. fledged/no. hatched	40/52	31/48	38/39	7/13	116/152
Percentage of successful pairs attempting a second brood	50.0	57.1	55.6	33.3	51.9
	(8)	(7)	(9)	(3)	(27)
Percentage of successful pairs raising multiple broods[b]	25.0	28.6	22.2	33.3	25.9
	(8)	(7)	(9)	(3)	(27)
Estimated number of fledglings per pair[c]	2.1	1.6	4.4	1.6	2.4

[a]Figures are means plus or minus standard error, with sample size (n) in parentheses.

[b]Includes only pairs that survived through July and all of whose unsuccessful nests were believed to have been located.

[c]Assumes no successful nests went undetected, so estimate is conservative (potential underestimate).

members of the pair incubated, the female longer (Figure 1). The average duration of an incubation shift was 35.9 ± 2.4 minutes for females and 22.8 ± 1.4 minutes for males (paired t test, $P < 0.001$, $n = 46$ paired comparisons). Females appeared to control the duration of the incubation shift. Males would approach the nest several times before females relinquished their position, whereas males invariably vacated the nest as soon as the female approached. We did not attempt to observe incubation behavior at night; however, Woods (1928) and C. Reynolds (pers. comm.) reported that females are on the nest then.

Nestlings

Nestlings remained in the nest 10 to 15 days (mean 13.3 ± 0.29 days, $n = 23$ nests). Table 3 details development of nestlings. For the first 4 days following hatching, the pair brooded the nest nearly continuously. Brooding decreased as the nestlings became better insulated and required more

Table 3 Development of Nestling California Gnatcatchers

Age	Characteristics
Day 1	Nestlings are tiny (egg sized). Body is pink and "skinny." The head is dark, eyes are closed.
Day 2	Nestlings are slightly plumper and darker. They hold their heads up and open their mouths when the nest moves. There are small bumps along the edges of the wings where primaries and secondaries will come in.
Day 3	Body is becoming darker. Pin-feather nubs are visible on the back. No nubs are visible on top of the head. Pin feathers are emerging on edges of the wings. Eyes are still closed.
Day 4	Pin feathers are visible in rows on head and body.
Day 5	Pin feathers have elongated; pink skin is visible between rows. Eyes are still closed.
Day 6	Eyes are open. Pin feathers are beginning to cover large areas of the back.
Day 7	Rows of pin feathers are visible on the top of the head. Feathers on the body are in sheaths and bare skin shows between the rows.
Day 8	All feathers are still in sheaths. The tail is about 6 mm long. Birds may be banded at this age with cut-down bands. Nestlings chirp when handled.
Day 9	The tips of the primaries and the body feathers are unsheathed. The head looks feathered. Banding is optimum today. Birds return easily to nest.
Day 10	All feathers are losing sheaths; 50–75% are out of sheaths. The body is beginning to look downy. Not much bare skin shows, except ventrally. Broods of four are not easily returned to the nest; the last bird replaced often will not stay in nest and may induce others to fledge.
Day 11	All feathers are out of sheaths. Nestlings have short tails and a yellow gape. They hop out of the nest if disturbed and do not stay in nest if replaced.
Day 12	Nestlings hop out of the nest if approached. They do not stay in nest if replaced. Survival as fledglings at this age is very good. The main problem with banding at this age is that it is very difficult to handle the birds. They pop out and escape before a hand can be placed over the nest.
Day 13	If approached, the nestlings hop out of the nest and fly a short distance.
Day 14	If the nest is approached, the nestlings fly out, with initial unrehearsed flights of over 10 feet.

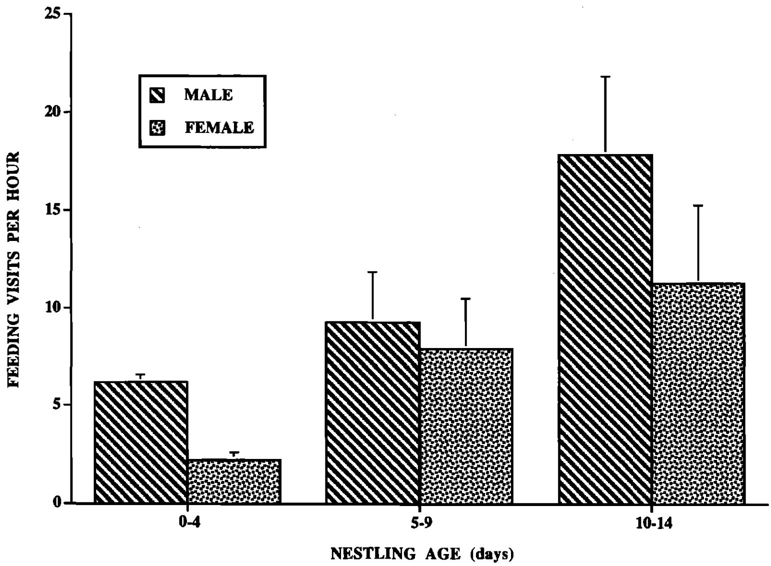

Figure 5. Nestling-feeding rates of male and female California Gnatcatchers, based on 34 hours of total observation time of 9 pairs.

frequent feeding. Nestlings were brooded 89% of the time for the first two days, 66% of the time by day 7, and not brooded at all by day 11 (n = 31 hours of observation of 9 pairs). Females brooded more than males (60.7% versus 39.3% of the total brooding time; Figure 1), a division of labor similar to that observed during the incubation period.

Both males and females fed the nestlings, but males brought food more frequently. In 34 hours of observation of 9 pairs, we found that the male made 62.2% of the trips to the nest, the female 37.8% (Figure 1). Nestling-feeding rates increased with nestling age (Figure 5). When the female was brooding, males often brought food to the nest, gave it to the female, and she fed the nestlings. Females were never observed bringing food to brooding males. We did not document the type of food the parents brought but did observe that the size of prey increased as the young grew. Initially the parents brought food so small that it was barely visible in their beaks. Older young were fed larger insects and caterpillars; these were consumed whole.

Fledglings

Parents cared for fledglings for 21 to 35 days (mean 24.5 ± 1.0, n = 21 broods) after fledging before excluding them from their territory. During the first week the brood stayed close together, often lined up next to each other on a single branch near the nest. They flew short distances toward the parents if called. During the second week, fledglings begged for food more loudly and occasionally flew toward an approaching parent. They still remained close to their siblings, usually perched in the same bush. They did not appear to feed themselves, but searching behavior was emerging. By the second week, fledglings began to mew when separated from the family group, but the majority of their vocalizations were begging notes. By the third week out of the nest, fledglings began to feed themselves, although they continued to beg for food from their parents. The family ranged widely in the parents' territory. By the end of the third week, the family groups spent much of their time at the boundaries of their territory, and by the end of the fourth week, parents chased their fledglings out of the territory, scolding at them and clicking their bills. The length of the fledgling period was dependent on whether the pair initiated another nesting attempt. Early in the breeding season, the parents typically began a subsequent nest within three weeks after the first brood fledged. They continued to feed the fledglings during the early stages of the new nest, but the fledglings were generally expelled from the territory by the fourth week. At the end of the season, however, fledglings remained in the parents' territory for up to five weeks.

We determined the interval between nest attempts in 40 instances. For 29 pairs whose nest was destroyed before young were fledged, a new nest was begun within one day following the destruction. For pairs nesting successfully, the timing of a second nesting attempt depended on the number of young fledged. For two pairs successfully fledging four young, a new nest was begun an average of 20.5 ± 0.05 days after the first nest. The next nest was begun 16 days later for both pairs that fledged three young. The six pairs fledging two young began new nests an average of 12.8 ± 1.14 days later.

In one case, we monitored a pair that fledged only one young from a partially depredated nest. This pair began a new nest only six days later. They fed the fledgling while nest-building, even allowing it to sit in the same bush as the new nest. During egg laying and incubation it was kept some distance away and the male alone fed it. It was not excluded from the parent's territory until the new clutch hatched. Parents with a larger number of fledglings often flew great distances between the new nest and the first fledglings. In all cases, the first young were excluded from the territory by the time the subsequent clutch hatched.

Of 77 fledglings from 25 closely monitored nests, the greatest mortality (13%) occurred in the first week after fledging. About 79% of these fledglings survived for three weeks and became independent. During the first three weeks of the fledgling period larger broods were more susceptible to mortality than smaller broods ($\chi^2 = 6.04$, df = 2, $P = 0.049$). For broods with one or two fledglings, survival to three weeks of age was 94.1% ($n = 17$ fledglings from 11 broods). Broods with three fledglings had a survivorship of 88.9% ($n = 27$ fledglings from 9 broods). The remaining broods had four fledglings, and half of these experienced some mortality, for a survival rate of 71.2% ($n = 52$ fledglings from 13 broods).

Nesting Success

Average annual breeding success ranged from 1.6 to 4.4 fledglings per pair over four seasons (Table 2). About 70% of the 60 pairs monitored raised at least one fledgling each season (range 60–100%). Over half of the successful pairs attempted to raise more than one brood, and a quarter of these fledged two broods; one pair raised three broods. About 33.6% of 134 nesting attempts with known outcomes produced fledglings (Figure 6). Approximately 43% of these nests failed because of predation, while 12% were abandoned, most prior to completion of the nest and before egg laying. Predation varied from 31% in 1991 to 50% in 1989. Seven clutches suffered partial predation, and four of these the pair continued to incubate. During the nestling stage three nests suffered partial predation, but all of these eventually fledged at least one young.

From the condition of the nest and its contents following predation, we attempted to categorize the likely predator (Best and Stauffer 1980). Nests left intact were most likely the victims of snakes or small rodents, whereas nests completely torn apart were more likely attacked by larger mammalian predators. Snakes swallow eggs whole and are therefore less likely to leave broken shells in or near the nest as may rodents or predatory birds. Nests with linings slightly pulled up and nests with punctured eggs may have been disturbed by avian predators. We also observed instances of mice taking over gnatcatcher nests and filling them with their own nesting material.

On the basis of these criteria, we believe snakes were the most common predator (32.8%; Figure 7). We observed snakes to be abundant and diverse in the study area [e.g., California whipsnake (*Masticophis lateralis*), gopher snake (*Pituophis melanoleucus*), and common kingsnake (*Lampropeltis getulus*)], as is typical in coastal sage scrub (T. Case pers comm.). The second important group of likely predators was mid-sized mammals (29.3%), including the California ground squirrel (*Spermophilus beecheyi*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), coyote (*Canis latrans*),

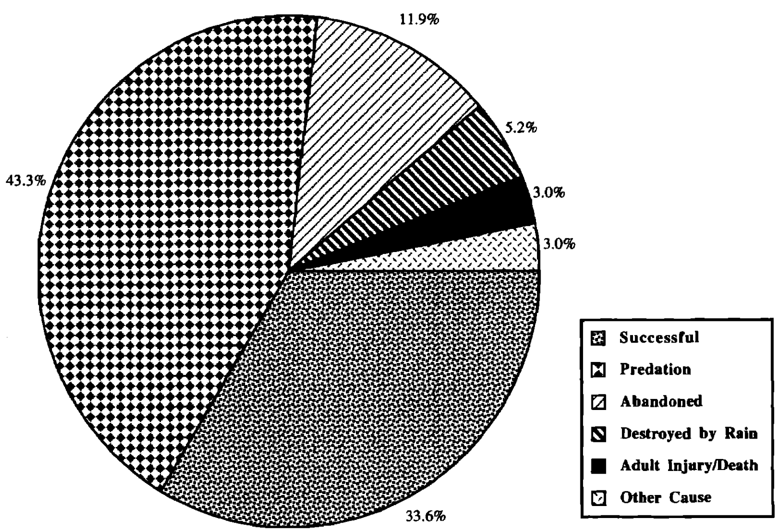

Figure 6. Fates of California Gnatcatcher nests at Rancho San Diego, 1989–1992; n = 134 nests.

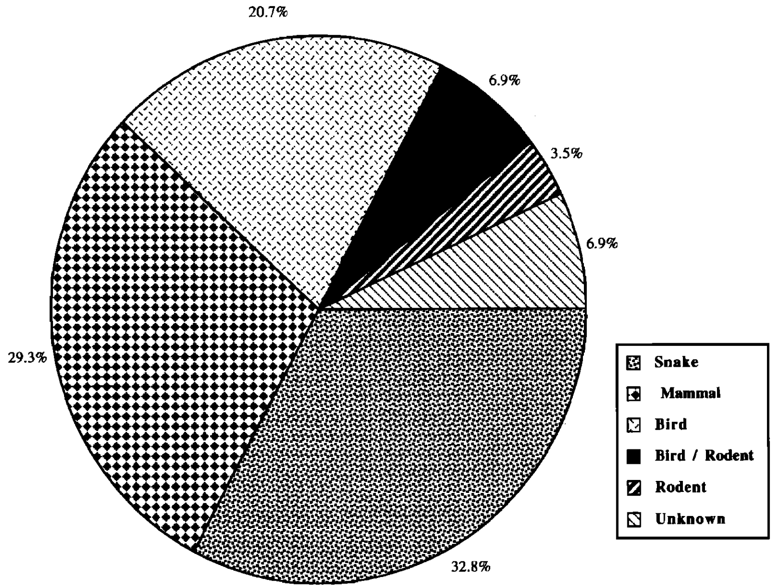

Figure 7. Probable predators of California Gnatcatcher nests at Rancho San Diego, 1989–1992; n = 89 nests.

gray fox (*Urocyon cinereoargenteus*), and bobcat (*Lynx rufus*). There were numerous potential avian predators [e.g., Western Scrub Jay (*Aphelocoma californica*) and Greater Roadrunner (*Geococcyx californianus*)], which appeared to account for at least 20% of the nest predation.

Brown-headed Cowbirds (*Molothrus ater*) parasitized three nests of two adjacent pairs in 1991. In one parasitized nest, the gnatcatcher eggs failed to hatch and the pair reared the cowbird to fledgling size before we removed it. The second parasitized nest failed because of predation, and the third was successful after we removed the cowbird egg during early incubation. During the four years of the study, cowbirds were trapped along the nearby Sweetwater River, which may have minimized cowbird parasitism of gnatcatcher nests. All three incidents of cowbird parasitism occurred in 1991, when gnatcatchers laid later in the summer than in other years.

We calculated Mayfield estimates for daily survival during each stage of the nest cycle for each year and for the entire study (Table 4). We calculated nest survival with and without the nest-building phase included (Table 5). There was significant annual variation in nest success (χ^2 = 29.1, df = 3, $P <$ 0.001). Nest survival was highest in 1989 and 1991, particularly low in 1992 if nest building is included in the estimate. Nest survival also varied significantly with stage of the nesting cycle (χ^2 = 30.9, df = 3, $P < 0.001$). Nest failure was highest during nest building. Although the daily survival rate during egg laying was relatively low, this phase lasted only two days, making the overall survivorship during egg laying relatively high in comparison to the

Table 4 Estimated Daily Survival Rates of California Gnatcatcher Nests at Rancho San Diego, 1989–1992[a]

Year	Daily survival rate			
	Nest building	Egg laying	Incubation	Nestling
1989	0.907 ± 0.028	0.909 ± 0.061	0.970 ± 0.012	0.981 ± 0.011
1990	0.943 ± 0.021	0.963 ± 0.036	0.942 ± 0.017	0.963 ± 0.018
1991	0.917 ± 0.024	0.842 ± 0.083	0.973 ± 0.013	1.000 ± 0.083
1992	0.841 ± 0.034	1.000 ± 0.258	0.938 ± 0.023	0.963 ± 0.026
All years	0.903 ± 0.014	0.928 ± 0.028	0.957 ± 0.008	0.981 ± 0.006

[a]Mean plus or minus standard error.

incubation (14 days) and nestling (13 days) phases. Daily survival during incubation was substantially lower than during the nestling stage.

One third of the nests produced at least one fledgling (Figure 6). Of the 89 nests that failed, 52% were lost during the nest-building stage, primarily because of rain damage and abandonment. Failure after egg laying we attributed largely to predation, occasionally to infertility, death or injury of adults, trampling, or cowbird parasitism. Over 31% of failed nests were lost during the incubation stage, 10% during the nestling stage, and 7% during egg laying. Nest abandonment prior to egg laying was frequent (11% of all nesting attempts) and tended to occur early and late in the season. About 50% of the abandoned nests were observed in 1992, the year with 120% of normal rainfall. In addition to abandoned nests, we also found five nests with visible rain damage early in the 1992 breeding season. Abandonment in 1992 was also attributable to a truncated laying season, ending in late May. Nest building continued into the third week of June 1992, but no eggs were laid.

Nests initiated in May were significantly more likely to be successful than those begun in February or March, and nests started in February were significantly less likely to be successful than those initiated in April ($P < 0.05$, Z test for proportions, $n = 133$ nests; Figure 8). Over 80% of all successful

Table 5 Probability of a California Gnatcatcher Nest Surviving Each Stage of the Nesting Cycle at Rancho San Diego, 1989–1992

Year	Probability of nest surviving					
	Nest building	Egg laying	Incubation	Nestling	Nest building to fledging	Egg laying to fledging
1989	0.555	0.826	0.657	0.784	0.235	0.433
1990	0.701	0.927	0.434	0.612	0.171	0.231
1991	0.593	0.709	0.680	1.000	0.233	0.516
1992	0.369	1.000	0.408	0.612	0.034	0.230
All years	0.542	0.861	0.541	0.777	0.155	0.348

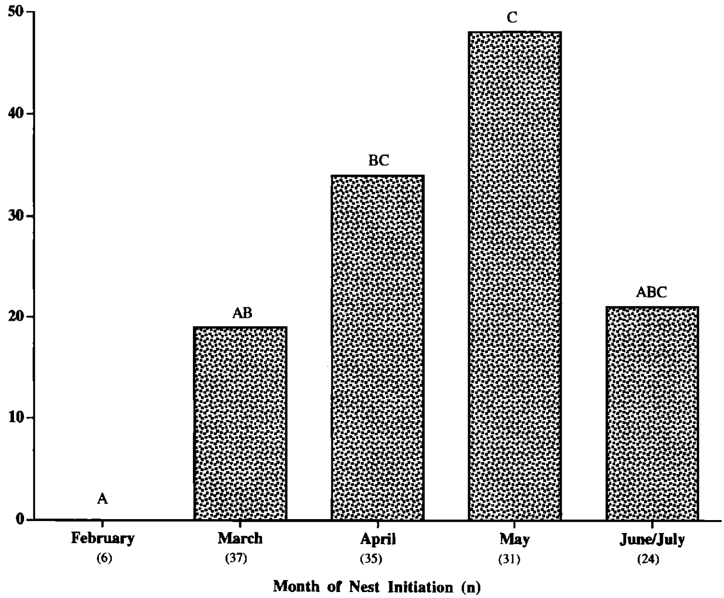

Figure 8. Comparison of the timing of nest initiation and nest success in the California Gnatcatcher; $n = 133$ nests. Comparisons lacking common letter are statistically different (Z test, $P < 0.05$).

nesting attempts were completed in May and June. Cause of nest failure varied by month. All losses of nests due to rain ($n = 8$) occurred in March. Predation was highest during May (34.6% of all depredated nests), followed by April (29.1%), June (21.8%), March (10.9%), and July (3.6%). Over 36% of abandoned nests were deserted in June, 28.6% of nests in March, and 28.6% in April.

Although California Gnatcatchers apparently did not prefer nesting in any particular shrub species (Neu test of proportions, $P > 0.05$; Table 1), the species of nest-host plant appeared to influence nest success (Figure 9). Nests in California sagebrush (*Artemisia californica*) were significantly more likely to be successful than those in flat-topped buckwheat (*Eriogonum fasciculatum*) or San Diego sunflower (*Viguiera laciniata*) ($P < 0.05$, two-tailed Z test for proportions with continuity correction). Nests placed in relatively scarce shrubs (e.g., *Baccharis sarothroides*, *Rhamnus crocea*, and *Brickellia californica*) were significantly more likely to be successful than nests in San Diego sunflower.

The height or diameter of the nest shrub did not significantly influence nest success. The placement of the nest within the shrub, however, did, in that nests placed at an intermediate height from the ground were more likely to be successful. The success of nests less than 70 cm above the ground (20.7%, $n = 29$) was significantly lower ($P < 0.02$, Z test for proportions) than that of nests 70 to 90 cm high (45.0%, $n = 40$). The success of nests

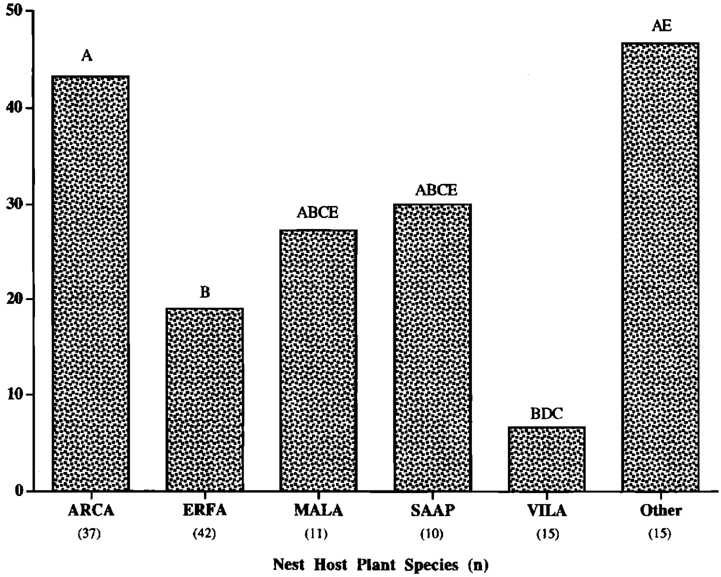

Figure 9. California Gnatcatcher nesting success by host-plant species; n = 130 nests. Comparisons lacking common letter are statistically different (Z test, $P < 0.05$). ARCA, *Artemisia californica*; ERFA, *Eriogonum fasciculatum*; MALA, *Malosma laurina*; SAAP, *Salvia apiana*; VILA, *Viguiera laciniata*.

placed higher than 90 cm from the ground did not vary significantly from that of lower nests (28.1%, n = 32).

Although California Gnatcatchers showed no significant preference for nesting on steeper or shallower slopes, slope had a significant influence on nesting success. Nests were more likely to be successful on shallow slopes (<19.9% slope) than on steeper slopes ($P < 0.05$, Z test for proportions).

DISCUSSION

Nesting Behavior

The California Gnatcatcher is a very persistent nest builder, with up to 10 nesting attempts within a breeding season. Nearly 70% of the pairs monitored successfully produced fledglings each season. About a quarter of the breeding pairs raised two or more broods, although annual variation in the environment, such as drought in 1989 and 1990, is a likely key factor limiting multiple brooding. Unlike many temperate-zone passerines, the California Gnatcatcher has a relatively long nesting season. In 1991 the first nest building was observed on 6 March, the latest nest fledging young on 25 August. Fledglings remained in their natal territory and were dependent on their parents well into September. Woods (1928) and Patten and Campbell (1994) have also reported late-nesting gnatcatchers.

High rates of nest failure account for the high number of nesting attempts by the California Gnatcatcher. It appears to be more persistent in renesting than ecologically similar species in shrubby habitats (Ellison 1998). The Blue-gray Gnatcatcher (*Polioptila caerulea*) may make up to seven nesting attempts and raise up to two broods per season (Root 1969). The ecologically similar Wrentit (*Chamaea fasciata*) makes fewer nesting attempts (up to four), but a similar proportion (20%) of pairs successfully raise two broods (Geupel and DeSante 1990). The differences in renesting effort between the gnatcatchers and Wrentit could be due to the Wrentit's slightly longer nestling period and relatively long dependent-fledgling period (up to 70 days; Erickson 1938, Geupel and DeSante 1990). In addition, the Wrentit studies were conducted in northern California, where the species' reproductive effort could differ from that farther south.

Male California Gnatcatchers participate more in all phases of the nesting cycle (Figure 1) than do many other male passerines, especially in nest building and feeding of young (Silver et al. 1985, Møller 1986). The Blue-gray Gnatcatcher and Wrentit resemble the California Gnatcatcher in the male's providing substantial assistance to the female in nest building, incubation, brooding, and feeding of young (Root 1969, Geupel and DeSante 1990, Ellison 1996). The male Blue-gray, like the male California, often chooses potential nest sites, initiates nest construction, and engages in substantial nest building, especially in renesting attempts, whereas female gnatcatchers of both species are typically responsible for adding the lining and final shaping of the nest cup (Root 1969, Ellison 1996).

Nest Success

Like ours, other studies have shown substantial variation from year to year and from site to site in the California Gnatcatcher's reproductive output. Annual reproductive success in our study ranged from 1.6 to 4.4 fledglings per pair. On the Palos Verdes Peninsula, Los Angeles County, the corresponding range was 2.3–3.9 fledglings per pair (Atwood et al. 1998), in Orange County, 3.4–5.7 (Woehler et al. 1995). From one-year studies, Andros and Schroeder (1995) and Galvin (1998) each reported 2.4 fledglings per pair. Atwood et al. (1998) reported average breeding productivity ranging from 2.3 to 2.6 in Orange County. P. Galvin (pers. comm.) reported annual production exceeding 5.3 fledglings per pair for two consecutive years on his Orange County plot. In Riverside County, the average number of fledglings per pair was 1.9 over 3 years (Braden et al. 1997b).

Notably, the two studies located well away from the coast—Rancho San Diego (this study) and Riverside County (Braden et al. 1997b)—measured the lowest annual productivity (less than two fledglings per pair in some years). Mock (1998) postulated a coastal vs. interior dichotomy in habitat quality and population density due to the difference in climate. Coastal areas are influenced by the more favorable maritime conditions, which presumably allow for higher population densities and productivity. This study and Bontrager (1991) are the only available data gathered during extended drought, highlighting the sensitivity of the California Gnatcatcher's breeding success and survival to weather variations (Mock 1998).

Causes of Nest Failure

Predation was the most common cause of nest failure in our study (Figure 6), responsible for the loss of 43.3% of all nests (range 31–50% each year), a level in the middle of the range reported for other shrub-nesting passerines (Rotenberry and Wiens 1989, Martin 1993, Miller and Knight 1993). For 17 shrub-nesting species (Table 6), the average predation rate was slightly higher, 47%. In three recent studies of the California Gnatcatcher, even higher rates were observed: in Orange County, 50% (Bontrager et al. 1995), in Riverside County, 54.2% (Braden et al. 1997a), in San Diego County, 68% (Sockman 1997). In Riverside County Ellison (1998) also

Table 6 California Gnatcatcher Reproduction Compared with That of Other Shrub-Nesting Songbirds[a]

	Incubation period (days)	Nestling period (days)	Percent success	Percent predation	No. broods per season
Blue-gray Gnatcatcher (*Polioptila caerulea*)	15.0	12.5	24.4	–	2.0
Wrentit (*Chamaea fasciata*)	15.5	15.5	50.4	–	1.5
Northern Mockingbird (*Mimus polyglottos*)	12.2	12.0	49.7	47.1	2.5
Sage Thrasher (*Oreoscoptes montanus*)	15.0	12.3	45.0	–	2.0
Brown Thrasher (*Toxostoma rufum*)	13.1	11.3	43.5	29.0	2.0
Curve-billed Thrasher (*T. curvirostre*)	14.0	14.0	43.8	40.2	2.5
Yellow-breasted Chat (*Icteria virens*)	11.0	8.0	19.7	66.9	2.0
Indigo Bunting (*Passerina cyanea*)	12.5	9.5	36.4	54.0	3.0
Painted Bunting (*P. ciris*)	11.5	13.0	58.8	35.3	3.0
Green-tailed Towhee (*Pipilo chlorurus*)	12.0	12.0	22.0	78.0	2.0
Rufous-sided Towhee (*P. erythrophthalmus*)	12.5	11.0	48.1	51.9	2.0
Abert's Towhee (*P. aberti*)	–	12.5	27.5	63.8	–
Brewer's Sparrow (*Spizella breweri*)	13.0	8.5	79.5	20.5	–
Sage Sparrow (*Amphispiza belli*)	14.2	10.0	56.4	43.2	2.0
White-crowned Sparrow (*Zonotrichia leucophrys*)	12.6	10.0	37.4	51.1	2.5
American Goldfinch (*Carduelis tristis*)	12.3	13.5	45.0	46.6	2.0
Median from all studies	12.6	12.0	44.4	47.1	2.0
California Gnatcatcher	14.3	13.3	32.3	47.3	1.2

[a]Data from Martin (1993).

documented substantially higher nest-predation rates (range 56.5–62.1%) among four species of sparrows nesting in sage scrub, with significant annual differences in some species. In our study area we found evidence of a wide range and abundance of potential nest predators, especially snakes, raccoons, and corvids, often associated with high nest-predation rates (Rotenberry and Wiens 1989, Miller and Knight 1993).

California Gnatcatchers had their lowest daily nest-survival rates during the nest-building and egg-laying stages (Table 4). Based on Mayfield estimates, the chance that a nest in our study area would be successful was 34.8% if the nest-building stage was not included in the estimate (Table 5). Because of abandonment and losses due to rain, however, if nest survival prior to nest completion was factored in, nests had only a 15.5% chance of surviving to fledging (yearly range 3.5–23.5%). Since many investigators do not include the nest-building stage in their nest-survival estimates, our study may be best compared to others with the 34.8%.

Expected survival during incubation was also very low (Table 5). Sockman (1997) found significantly higher nest predation during egg laying during one of the two years of his study. In contrast, Ellison (1998) found nest failure among sage-scrub sparrows to be highest during the nestling stage. During our study, about 23% of gnatcatcher nests failed from causes other than predation (Figure 6), a high proportion in comparison to studies of 17 other shrub-nesting passerine species (mean 7.2%; Martin 1993). Our results, however, resemble those from other studies of the California Gnatcatcher. Braden et al. (1997a) reported 22.6% of nests abandoned and 5.4% lost to weather or infertility. Sockman (1997) estimated a probability of 19.9% that a nest would fail because of abandonment. This higher rate of nest abandonment prior to egg laying in the California Gnatcatcher may be partially the result of weather (this study, Braden et al. 1997).

With an extended breeding season, a female's nutrient reserves may be insufficient for egg laying at the beginning and end of the season when most nest abandonment was observed and when food is likely to be scarce. Since male gnatcatchers are the primary nest builders, the female may not always be physiologically prepared to lay eggs when the first nest is near completion. An extreme example was one pair that initiated nest building on 6 March and began egg laying 5 April, a 30-day interval between nest initiation and the first egg. The last nesting attempts of the season are also frequently abandoned prior to nest completion, most likely because of a decline in food availability late in the season that may preclude continued egg laying (Lack 1968, Drent and Daan 1980, King and Murphy 1985, Martin 1987, Daan et al. 1988, Carey 1996). The intensity of nest monitoring in our study might also have resulted in a higher detectability of nest abandonment. We found most nests (75%) during the nest building, when the birds' behavior is quite conspicuous.

Nest parasitism by the Brown-headed Cowbird does not appear to be a significant factor in the success of California Gnatcatcher nests at two sites studied in San Diego County (this study, Sockman 1997). In Riverside County, however, Braden et al. (1997a) documented a higher incidence of nest parasitism (31.5%), although it was overshadowed by the even more substantial effects of nest predation. Severe brood parasitism appears to be restricted to only a few locations (D. Bontrager, M. Fugagli pers comm.). Gnatcatcher populations have benefited from cowbird-control programs (Braden et al. 1997a).

We identified several factors associated with the nesting success of California Gnatcatchers, including timing of nest initiation, nest host plant, nest height, and steepness of the slope on which the nest was placed. Early and late nests were less successful than nests initiated in April and May (Figure 8). In over 80% of successful nests the young fledged during May and June, the middle of the fledging period. Although predation of nests was highest from April to June, the large numbers of active nests during this period and the high rates of nest failure due to a variety of causes during the early and late months meant that success was still greater for these mid-season nests. At the beginning of the breeding season predation, nest destruction by storms, and abandonment prior to egg laying caused most nest failures. Late in the breeding season, however, the two major causes of nest failure were nest abandonment prior to egg laying and predation. Other studies have also shown that timing of nest initiation affects nest success in some species, primarily because of changes in the abundance of nest predators (Schaub et al. 1992, Filliater et al. 1994).

Although gnatcatchers did not prefer particular shrubs for nesting, we found that the choice of nest shrub did affect nest success (Figure 9), contrary to the findings of Sockman (1997) at Marine Corps Air Station Miramar in central San Diego County. The difference may be due to the two sites' plant-species composition differing substantially. Nesting gnatcatchers at Miramar make extensive use of broom baccharis (*Baccharis sarothroides*) (J. O'Leary, pers. comm.), a shrub species not found commonly at Rancho San Diego (<1% relative dominance). We were not able to distinguish between the contribution of shrub species and other habitat variables, such as steepness of slope, to the likelihood of nest success. In our study, *Viguiera laciniata*, the shrub associated with lowest nest success, grows primarily on the drier, steeper south-facing slopes in areas of sparse vegetation. Gnatcatchers nesting in *Viguiera* had reduced success, but this could be due to the smaller, sparser structure of this shrub or to some factor associated with slope.

Although the size of the nest shrub did not affect nesting success significantly, it is possible that nests built in *Artemisia californica* are less visible because of this shrub's leaf density being higher than that of *Eriogonum fasciculatum* or *Viguiera laciniata*. We did not measure shrub structure, but among all our nests, those placed toward the middle of the shrub were more successful than nests closer to the ground or to the edges. This is consistent with the findings of Sockman (1997), who reported that nests located in the middle third of the bush were more successful, and implies that concealment of the nest is a factor in reducing nest failure. Several other studies have shown that nest concealment is important in reducing nest failure in passerines (e.g., Martin and Roper 1988, Holway 1991, Norment 1993, Ellison 1998), although for some species it may not be important (e.g., Howlett and Stutchberry 1996, Filliater et al. 1994).

Nests can be concealed at the level of a single shrub but also at a larger scale involving the surrounding patch of habitat (Martin and Roper 1988, Knopf and Sedgwick 1992). We examined nest success primarily at the nest site; however, habitat characteristics at this larger scale may also be important. Mean distances between the nest shrub and adjacent shrubs ranged from 1.5 to 1.8 m, suggesting relatively open habitat. Braden et al. (1997b) found that gnatcatchers' nests tend to be more successful and productive when the birds' territories support more grass and forb cover and fewer perennials yet also that the structure of the perennial vegetation is also correlated with nesting success, higher in mature coastal sage scrub.

SUMMARY

We studied the nesting biology of the California Gnatcatcher in southwestern San Diego County from 1989 to 1992. We banded a total of 318 individuals and monitored 134 nests. Gnatcatchers molt into breeding plumage in February and begin nest building two to four weeks after molt. Males select the nest site and are the primary nest builders. Females assist in nest construction and do most of the nest lining. A nest can be constructed in as little as 4 days, but nests built early in the season were worked on for an average of 11 days before eggs were laid. Gnatcatchers are persistent nesters, which is highly adaptable in a habitat that supports many potential nest predators. New nests are begun one day after nest predation and between 6 and 20 days after a brood is fledged, depending on the number of surviving fledglings. Up to 10 nests have been build by a pair in a season. About 75% of all eggs are laid in April and May. The majority of clutches contained 3 eggs in the driest year and 4 eggs in years with more rainfall. The female is the primary incubator and brooder, but the male makes almost twice as many feeding trips to the nestlings. Nestlings fledged at 13 days of age and remained with their parents 3 to 5 weeks. Selection of nest host plant had significant consequences on subsequent nest survival. Landscape-level conditions of the nest site, such as slope gradient, may also affect nest success.

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