BREEDING AND DISPERSAL BIOLOGY OF THE CALIFORNIA GNATCATCHER IN CENTRAL ORANGE COUNTY

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The California Gnatcatcher (*Polioptila californica*) is a persistent nester, attempting up to seven nests after repeated failures (Bontrager 1991). I collected data on the dispersal and breeding biology of the gnatcatcher, particularly relating to nesting success and nest location, in Orange County, California. Dispersal patterns can broadly be classified as breeding dispersal, "the movement of individuals, which have reproduced, between successive breeding sites" and natal dispersal, "the movement an animal takes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate" (Howard 1960, Greenwood 1980). Natal dispersal is the primary means by which genetic diversity and interpopulation movements are maintained in nonmigratory, territorial birds, especially those occupying a highly fragmented landscape. Natal dispersal is therefore an important aspect of the biology of the California Gnatcatcher, yet few studies have investigated it (G. Braden unpubl. data, Atwood 1993, Bailey and Mock 1998).

STUDY AREAS AND METHODS

My main study site, Siphon Reservoir, is located in central Orange County, in the foothills of the Anaheim Hills (Figure 1). The site comprises 53 ha of coastal sage scrub surrounding the reservoir, dominated by California sagebrush (*Artemisia californica*) and California buckwheat (*Eriogonum fasciculatum*), with white sage (*Salvia apiana*), black sage (*Salvia mellifera*), brittlebush (*Encelia californica*), and prickly pear cactus (*Opuntia littoralis*) also common (from visual estimates; no quantitative vegetation sampling conducted). The sage scrub is divided into two continuous sections, one to the east and one to the west of the reservoir; the sections are connected via a thin strip of riparian vegetation dominated by willows (*Salix* spp.) and mulefat (*Baccharis salicifolia*). Small areas dominated by grasses and mustard (*Brassica* spp.) are interspersed among the coastal sage scrub. The study site is surrounded by orange groves, nurseries, and other agricultural land. The nearest patch of sage scrub lies approximately 1 km to the northeast.

In addition to the main study site at Siphon Reservoir, I surveyed four other areas for gnatcatchers: Rattlesnake Reservoir, Bee Canyon, Peter's Canyon, and Gypsum Canyon, as part of the dispersal aspect of this study (Figure 1). The size and vegetation composition of each of these areas are similar to that at Siphon Reservoir, all being dominated by California sagebrush and California buckwheat (from visual estimates). At Gypsum Canyon, however, the ground cover is somewhat reduced by cattle grazing.

I established the number and location of breeding pairs of gnatcatchers at the main study site in March, following standard survey protocol. Breeding

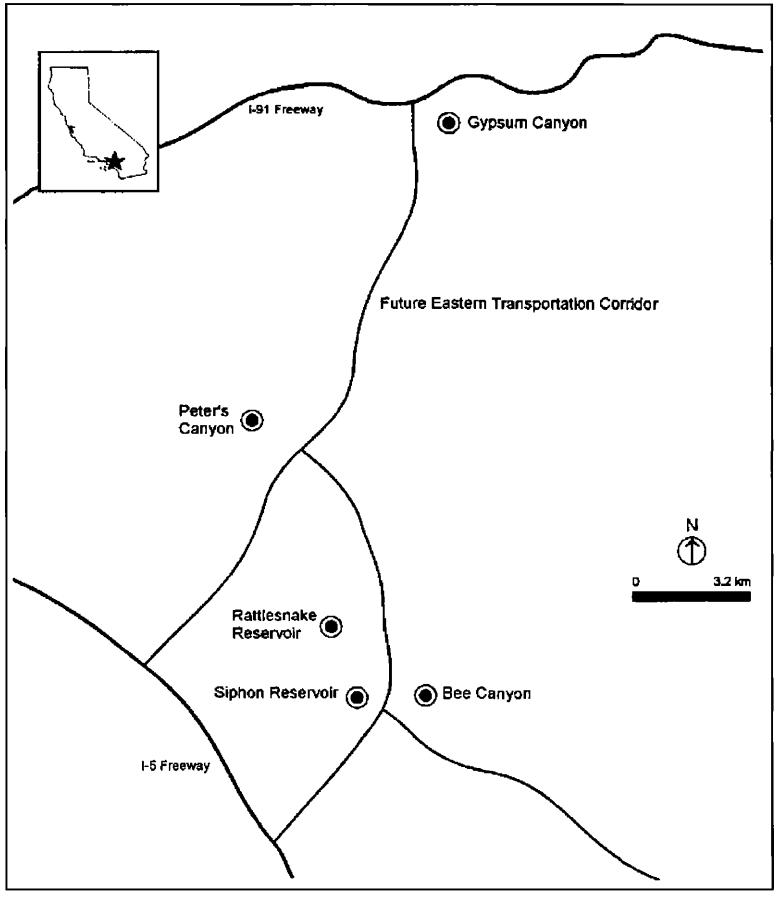

Figure 1. Locations of California Gnatcatcher study sites, Orange County, California.

territories were visited once or twice a week from late March to the end of the breeding season (late July). Nests were visited once per week and monitored for the onset of egg laying, clutch size, nest parasitism, number of nestlings, and number of fledglings. I attempted to locate all nests, including those abandoned prior to egg laying. Although some unsuccessful nesting attempts went undetected, I believe all nesting attempts that resulted in fledglings were located. Nestlings were banded at 8 or 14 days of age. Juveniles were captured with mist nets and banded toward the end of the breeding season, as were several adults. Nest-site characteristics were recorded after gnatcatchers were finished with the nest, after either nest failure or successful fledging of chicks.

I selected sites for the dispersal surveys along a transect running from the main study site (the banding site) toward Highway 91 (Figure 1) in such a way as to represent all distances along the dispersal curve adequately. Each of the selected study sites covered the same area and was vegetated (from visual assessment) like the main study site. The selection of the study sites was complicated by the location of suitable gnatcatcher habitat and by the requirement for not selecting sites separated from the banding site by large areas of developed land. The main study site covered distances from 0 to 1.5 km from the banding site; Bee Canyon is 2.2 km from the banding site (from the center of both sites), Rattlesnake Reservoir at 2.9 km, Peter's Canyon at 7.3 km, and Gypsum Canyon at 16.4 km.

I surveyed for dispersal at each of the five study sites in November and December. Each site was surveyed nine times to ensure that all banded birds were located. Biologists were rotated from site to site to reduce observer bias. Every effort was made to ensure that each site was surveyed for the same length of time. Dispersal distances were calculated as straight-line distances from the site where the bird was banded to the site where it was relocated; mean distances were used in cases of multiple resightings. Dispersal angles were calculated for each observation relative to true north, banding location, and site of relocation; the first angle was used in cases of multiple resightings. The results were tested for a significant direction of mean dispersal.

RESULTS

I located 24 pairs of California Gnatcatchers at the main study site. No unpaired individuals were detected. These pairs were spaced uniformly through the available habitat with no large areas of unoccupied coastal sage scrub. Although I did not map territories during the study, enough data on the birds' locations were collected to define the centers of activity for each of the 24 pairs. All of the gnatcatchers, except for one pair, appeared to remain in the same area throughout the breeding season, although there were some shifts in centers of activity associated with new nest locations. One pair appeared to move to a small area of unoccupied coastal sage scrub adjacent to a second pair after its first nest failed. Because no gnatcatchers were banded at the start of the study, however, these observations cannot be confirmed.

Breeding behavior (in the form of pair bonding and nest-site searching) was first observed in early March, and most pairs had built their first nests by early April. The first chicks hatched on 10 April, and the first chicks fledged on 24 April. Many of the early successful breeders had fledglings by early May. The gnatcatchers continued their breeding cycle throughout May and June, but most pairs had stopped new nesting attempts by early July. The last new nests built were located in the first week of July, and the last chicks fledged on 21 July.

Seventeen of the 24 pairs (71%) nested successfully. Clutch size ranged from three to five with a mean of 3.94 [standard deviation (SD) 0.34]; in total 134 eggs were laid. Eighty-five chicks hatched, of which 74 fledged successfully. The population as a whole had a mean of 3.1 fledglings per pair.

Of the 46 nests located during the breeding season, 21 (45.6%) successfully produced fledglings. Of the 25 unsuccessful nests, 13 (28%) were abandoned or destroyed before eggs were laid, 9 (20%) were depredated with eggs, and 3 (7%) were depredated with chicks. Of the nine nests lost at the egg stage, five were depredated by snakes and four were completely destroyed. Four of the nests lost during the nest-building stage were also completely destroyed, while the others were abandoned. During the breeding season, gnatcatchers were observed aggressively mobbing Greater Roadrunners (*Geococcyx californianus*), Western Scrub Jays (*Aphelocoma californica*), and Cactus Wrens (*Campylorhynchus brunneicapillus*), suggesting that they recognized these species as potential nest predators or destroyers. Other potential nest predators observed in the study site include the American Crow (*Corvus brachyrhynchos*), Common Raven (*C. corax*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), gopher snake (*Pituophis melanoleucus*), and common kingsnake (*Lampropeltis getulus*).

No evidence of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) on the California Gnatcatcher was observed at the main study site, where an intensive cowbird-trapping program was conducted throughout the study.

There were marked differences in the nesting success of individual pairs of gnatcatchers. Four pairs of gnatcatchers (17% of total) raised two broods, 13 pairs (54%) raised one brood, and six pairs (19%) did not raise any broods. Two pairs each raised eight fledglings from their two nesting attempts, while three pairs did not raise any fledglings from three or four nesting attempts. It was unknown whether the differences in breeding success were related to breeding experience, nest or territory location, habitat quality, differences in reproductive fitness between the pairs, or accidents.

The nesting substrates used by gnatcatchers at the main study site were California sagebrush, 23 nests (56.1%); California buckwheat, 11 nests (26.8%); brittlebush, 4 nests (9.8%); white sage, 1 nest (2.4%); black sage, 1 nest (2.4%) and prickly pear cactus, 1 nest (2.4%). The numbers of these nests that were successful were California sagebrush, 8 nests (42.1%); California buckwheat, 7 nests (36.8%); brittlebush, 2 nests (10.5%); white sage, 1 nest (5.3%); black sage, 1 nest (5.3%) and prickly pear cactus, no nests. Although nesting success for nests built in California buckwheat was greater than for those built in California sagebrush or brittlebush, it was not significantly so (χ^2 test, $P > 0.05$).

Nest height ranged from 0.3 to 1.4 m above the ground (mean 0.61 m, SD 0.25 m) and from 0.08 to 1.10 m below the top of the canopy (mean 0.25 m, SD 0.19 m). There were no significant differences in nest height above the ground or in height below the canopy between successful and unsuccessful nests (Student's t test, $P > 0.05$).

Nest location ranged from 0.3 to 97.6 m to the edge of the shrub canopy (mean 3.1 m, SD 4.8 m) and from 0.3 to 121.9 m to the edge of the coastal sage scrub habitat (mean 21.0 m, SD 39.5 m). There were no significant differences between successful and unsuccessful nests in nest location relative to the distance to the edge of the shrub canopy or the edge of the coastal sage scrub (Student's t test, $P > 0.05$).

Fifteen banded gnatcatchers were located during the dispersal surveys, three of which had been banded as adults, 12 as nestlings or juveniles. For adults, this gave a resighting rate of 75% (3 of 4 banded adults relocated), for juveniles, 32% (12 of 38). Gnatcatchers mist-netted and banded as juveniles were much more likely to be resighted than those banded as nestlings. Seven of the 10 (70%) gnatcatchers banded as juveniles were relocated, while only 5 of the 31 (16%) banded as nestlings were relocated.

Of the 12 banded juvenile gnatcatchers that were relocated, all but one were recorded at the main study site (the banding site). The other banded gnatcatcher was located at Peter's Canyon. The mean dispersal distance of juvenile gnatcatchers was 1.05 km (SD 2.06 km, range 0.01–7.55 km), but this figure was skewed by the one individual that dispersed 7.55 km. This individual excluded, the mean dispersal distance was only 0.46 km (SD 0.25, range 0.01–0.80 km). Most of the juvenile gnatcatchers dispersed between 0.3 and 0.8 km from their nests (Figure 2). The mean dispersal distance of gnatcatchers mist-netted and banded as juveniles (mean 0.19, SD 0.19, range 0.01–0.41) was much lower than of those banded as nestlings (mean 0.58, SD 0.25, range 0.24–0.80, not including the outlier), indicating that many of the juvenile gnatcatchers caught in the mist nets may have already undergone some dispersal. Even if this is so, clearly most of the juveniles did not disperse far from their natal area. Dispersal direction was

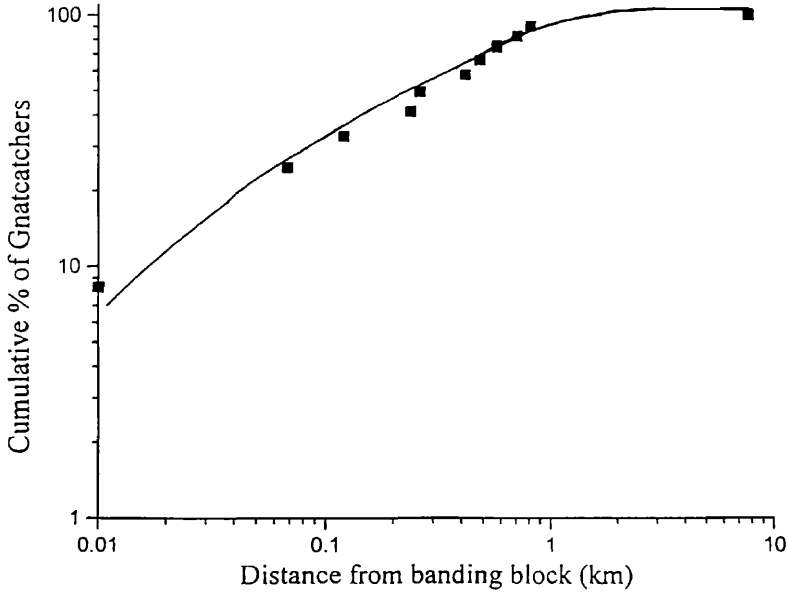

Figure 2. Cumulative percentage of dispersed young California Gnatcatchers relative to distance from banding area.

not significant (χ^2 test, $P > 0.05$), indicating that juveniles dispersed in a random direction after leaving their natal territory.

The banded gnatcatchers exhibited a range of behaviors relating to dispersal and home-range establishment. Of the 12 relocated juveniles, six had paired and established home ranges. Interestingly, four of the five males relocated were paired, only two of the seven females. Throughout the dispersal surveys gnatcatchers were observed most frequently in coastal sage scrub; however, they were also observed regularly in riparian and grassland areas, especially those adjacent to coastal sage scrub. Although no quantitative data were collected, gnatcatchers appeared to use these habitat types more frequently during the nonbreeding season than during the breeding season (see also Campbell et al. 1998).

Survey rates (defined as the mean acres surveyed per minute per biologist) were used to assess if each site was surveyed with equal effort. Despite conscious efforts to maintain equal effort there were significant differences in survey rates between sites (Duncan's multiple-rank range test, $F = 11.1$, $P < 0.01$). Mean survey rates for Gypsum Canyon (0.308 acres/min/biologist) were significantly higher than for other sites, rates for Siphon Reservoir (0.200) were significantly lower. Mean survey rates at Bee Canyon (0.241), Rattlesnake Reservoir (0.254), and Peter's Canyon (0.240) were not significantly different from each other. Many factors affect survey rates, including weather, topography, habitat type, and the number of gnatcatchers located, especially the number of banded gnatcatchers. During this study, surveys were generally quickest at Gypsum Canyon, as the habitat there was very open, with much less ground cover than at the other sites and because there were fewer gnatcatchers there. Surveys took longer at Siphon Reservoir mainly because of the large number of banded gnatcatchers. Observers generally took less than 5 minutes to determine if a located gnatcatcher was unbanded; however, it frequently took up to half an hour to record the band combination of the banded birds. These differences in mean survey rates probably did not affect the results since all areas were surveyed nine times and there was little probability of detecting new birds after six or seven surveys (Figure 3).

Throughout the dispersal surveys many of the banded gnatcatchers were relocated on more than one occasion. On the basis of data from Siphon Reservoir (the only site where more than one banded gnatcatcher was located), the mean probability of detecting one of the banded gnatcatchers was 0.38. This probability was calculated by dividing the mean number of banded birds recorded during each survey by the total number of banded birds present at the site (it is assumed that all banded birds at the site were located). With this probability of detection, probability theory implies that it takes seven surveys to locate 95% of the banded birds.

Another way of determining the minimum number of surveys required to detect all banded gnatcatchers is to plot the cumulative number of new sightings against the number of surveys performed. This plot indicates that just four surveys were required to detect 93% of the banded birds, and all banded birds were recorded after five surveys (Figure 3).

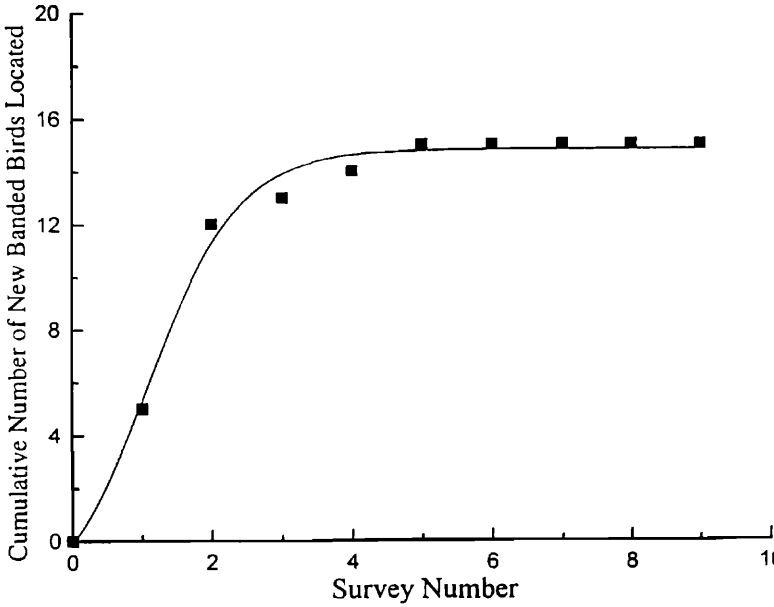

Figure 3. Cumulative number of new banded California Gnatcatchers located during each survey.

DISCUSSION

The main study site at Siphon Reservoir contained a relatively high number of gnatcatcher pairs (24) for 53 ha of suitable habitat. Although home ranges or territories were not mapped in this study, the mean home range for the gnatcatchers can be estimated by dividing the total available habitat by the number of pairs present, giving a mean home range of 2.2 ha. The calculation is valid under the assumptions that gnatcatchers do maintain home ranges, that these home ranges do not overlap, that all available habitat was used, and that the pairs were not using areas beyond the study site. Many other studies have indicated that gnatcatchers do maintain and defend territories (Bontrager 1991, Atwood 1993). My observations at Siphon Reservoir indicate that the breeding gnatcatcher pairs used all of the available habitat and never left the site. Estimates of the California Gnatcatcher's home range vary widely, from as little as 1 or 2 ha (Tattersall 1988, Atwood 1993) to as much as 9.3 ha (Preston et al. 1998). Preston et al. (1998) found a correlation between territory size and distance inland, with the larger territories inland. My estimates are consistent with other estimates for coastal sites.

Nesting success at Siphon Reservoir was relatively high. Seventeen of the 24 pairs (74%) successfully raised fledglings, compared to only 42% in

Rancho Mission Viejo (Bontrager 1991), 58% at Lake Mathews (J. and J. Griffith unpubl. data), and 65% at Rancho San Diego (P. Mock unpubl. data). The 74 chicks fledged represent a mean of 3.1 fledglings per pair, again comparing favorably with results from other studies, 1.4–3.8 fledglings/pair at Riverside (Braden et al. 1997), 2.99 fledglings/pair at Palos Verdes (J. Atwood unpubl. data), 4.65 fledglings/pair at UCI Reserve (E. Woehler unpubl. data), and 0.78 fledglings/nest in San Diego (Sockman 1997).

California sagebrush and California buckwheat were the most commonly used nesting substrates, accounting for over 80% of all known nest sites at Siphon Reservoir. Other studies also found these to be the most commonly used substrates (Atwood 1993, Bontrager 1991, Roach 1989). It is not known whether the preferences for California sagebrush and California buckwheat as a nesting substrate reflect a preference for these plants or the fact they are the two most abundant species in the coastal sage scrub. Most studies, including this one, have found that gnatcatchers nest more frequently in California sagebrush than in California buckwheat. I found nesting success to be higher in California buckwheat than in California sagebrush, but the difference was not significant ($P > 0.05$).

At Siphon Reservoir, the mean nest height was 0.61 m above the ground, slightly lower than recorded in most other studies: 1.04 m in southern California (Atwood 1993); 0.66 m at Rancho San Diego (Roach 1989); 0.87 m near Perris (Tattersall 1988); 0.86 m at Palos Verdes (J. Atwood unpubl. data). The mean distance of the nest below the canopy (0.25 m) was also slightly less: 1 m near Rancho San Diego (Roach 1989); 0.45 m at UCI Reserve (J. Simonsen unpubl. data); 0.42 m at Palos Verdes (J. Atwood unpubl. data).

The mean dispersal distance of juvenile gnatcatchers banded at Siphon Reservoir was 1.05 km, significantly lower than the means of 2.04 km at Riverside (G. Braden unpubl. data) and 2.4 km at Palos Verdes (J. Atwood unpubl. data). The mean dispersal distance at Siphon Reservoir might be an underestimate since some of the relocated banded birds were not banded as nestlings but as fledglings and may have already undergone some dispersal when they were banded in mid July. Other biases in the data set, including small sample size and the fact that not all suitable habitat within the potential dispersal range could be surveyed, make direct comparisons problematic. However, the general dispersal pattern (most of the juveniles staying close to their natal areas and a few dispersing a long distance) is similar to that observed elsewhere (J. Atwood, G. Braden unpubl. data, Bailey and Mock 1998).

These data indicate that gnatcatchers can and do disperse long distances dispersal across unfavorable habitat but that the frequency of these events is low. More typically, gnatcatchers disperse short distances through contiguous coastal sage scrub. As coastal sage scrub becomes more fragmented and gnatcatcher populations more isolated, short-distance dispersal will become more difficult and the long-distance dispersal may not be sufficient to maintain genetic diversity and interpopulation movement.

Of the 12 banded juvenile gnatcatchers that were relocated, all but one were recorded at the main study site (the banding site). That so many young

birds were recorded at the main study site might indicate that the population there was not at saturation level or that its rate of turnover was high. Since the surveys were conducted during the winter, however, I do not know if these birds were able to establish territories and breed successfully in the study area.

My data indicate that six surveys are sufficient to detect over 95% of gnatcatchers at any site. This is an important consideration for both presence/absence surveys and where complete censuses are required.

Because of the impracticality of surveying all potential habitat for banded gnatcatchers, most dispersal studies probably underestimate dispersal distance. Isolated occurences (Bailey and Mock 1998) and sightings of banded birds (G. Braden pers. comm.) confirm long-distance dispersal. The question, then, is not if gnatcatchers can disperse long distances but the frequency of long-distance dispersal.

SUMMARY

I conducted an intensive study of the breeding and dispersal biology of the California Gnatcatcher at five locations in central Orange County in 1995. Twenty-four pairs of gnatcatchers attempted nesting at the main study site, Siphon Reservoir. Seventeen (71%) nested successfully. A total of 134 eggs was recorded, from which 85 chicks hatched and 74 chicks fledged. Twenty-one of the 46 nests located (45%) were successful. Twenty-eight percent of the nests were abandoned before eggs were laid, 20% were depredated while eggs were in the nest, and 7% were depredated while chicks were in the nest. There was no incidence of brood parasitism by the Brown-headed Cowbird. Mean number of fledglings per pair was 3.1. There were marked differences in nesting success between individual pairs; several pairs raised two broods. The majority of gnatcatchers built their nests in *Artemisia californica* (56.1%) or *Eriogonum fasciculatum* (26.8%). Mean nest height above the ground was 0.61 m, and mean distance of the nest below the canopy 0.25 m. Mean distance from nests to the nearest edge of the shrub canopy was 3.1 m, mean distance to the edge of the coastal sage scrub habitat 21.0 m. There were no significant differences for any of these measurements between successful and unsuccessful nests. Fifteen of the 45 individually color-banded gnatcatchers were relocated during the dispersal surveys, three banded as adults, 12 banded as young. Mean dispersal distance of juveniles was 1.05 km (SD 2.06 km), although this was heavily skewed by one individual that moved 7.55 km. This bird excluded, the mean dispersal distance was just 0.46 km (SD 0.25). Juveniles dispersed in random directions after leaving their natal territories.

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LITERATURE CITED

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

Bailey, E. A., and Mock, P. J. 1998. Dispersal capability of the California Gnatcatcher: A landscape analysis of distribution data. W. Birds 29:351–360.

Bontrager, D. R. 1991. Habitat requirements, home range and breeding biology of the California Gnatcatcher (*Polioptila californica*) in south Orange County, California. Prepared for Santa Margarita Company, Rancho Santa Margarita, CA (available from Wilson Ornithol. Soc., Mus. Zool., Univ. Mich., Ann Arbor, MI 48109-1079).

Braden, G. T., McKernan, R. L., and Powell, S. M. 1997. Association of within-territory vegetation characteristics and fitness components of California Gnatcatchers. Auk 114:601–609.

Campbell, K. F., Erickson, R. A., Haas, W. E., and Patten, M. A. 1998. California Gnatcatcher use of habitats other than coastal sage scrub: Conservation and management implications. W. Birds 29:421–433.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Am. Midland Nat. 63:152–161.

Preston, K. L., Mock, P. J., Grishaver, M. A., Bailey, E. A., and King, D. F. 1998. California Gnatcatcher territorial behavior. W. Birds 29:242–257.

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

Sockman, K. W. 1977. Variation in life-history traits and nest-site selection affects risk of nest predation in the California Gnatcatcher. Auk 114:324–332.

Tattersall, E. 1988. The California Black-tailed Gnatcatcher. M. S. thesis, Univ. Calif., Riverside.

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