CALIFORNIA GNATCATCHER VOCALIZATION BEHAVIOR

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Some passerine songs and calls have fairly specific functions (Kroodsma 1981, Catchpole 1982, Merila and Sorjonen 1994). Other songs or calls may have more than one function with the meaning varying with the context in which the song or call is given and received (Lein 1981, Catchpole 1982, Howes-Jones 1985, Nelson and Croner 1991, Slagsvold et al. 1994). Characteristics of the repertoire and singing behavior, such as switching from one song to another, shifting song frequencies, song flights, song rate, tempo, volume, complexity, and length, can convey information on the motivation of the singer (Hill and Lein 1987, Radesater et al. 1987, Highsmith 1989, Staicer 1989, Schnase et al. 1991, Aweida 1995, Byers 1995, Ritchison 1995). Birds' vocalizations can function to attract mates, establish and defend territories, maintain pair bonds, attract females for extra-pair copulations, stimulate a female's reproductive condition, coordinate nest exchanges, and convey information about the presence or absence of potential predators (Kroodsma 1981, Catchpole 1982, Ritchison 1991, 1995, Neudorf and Tarof 1998).

We investigated the vocalization behavior of the California Gnatcatcher (*Polioptila californica*) to determine the function of the various calls made by males and females. In this species the male does not sing a complex song as in many other passerines. We also investigated the annual cycle in vocalization rates and in the percentage of pairs detectable during surveys. Vocalizations play an important role in the detection of gnatcatchers by observers and thus are important in identifying occupied habitat.

Atwood (1988) used sound spectrograms to characterize gnatcatcher vocalizations in his comparison of the California and Black-tailed (*P. melanura*). To date, however, there has been no detailed description of California Gnatcatcher vocalization behavior. We studied over 50 pairs of California Gnatcatchers in southwestern San Diego County from 1989 to 1992 (Grishaver et al. 1998, Preston et al. 1998). This paper examines the vocalization behavior of 21 of these pairs.

MATERIALS AND METHODS

Study Area

We studied California Gnatcatchers at two sites in the unincorporated Rancho San Diego area of southwestern San Diego County (32° 40′ N, 117° W). The two sites are located approximately 19–23 km inland from the coast and 21 km north of the U.S.–Mexican border. Elevations range from

90 to 370 m above mean sea level. At the 1200-ha Rancho San Diego site along the Sweetwater River our study extended from November 1988 to August 1991. At the 111-ha Amber Ridge site, 2.5 km to the northeast, it extended from November 1988 to July 1992. Both sites are dominated by coastal sage scrub (Mooney 1977, Westman 1981).

Field Methods

Our methods, including banding each individual with a unique combination of colors, are detailed in Preston et al. (1998). We visited each territory an average of 12 times during the nonbreeding season (1 September–28 February) and 16 times during the breeding season (1 March–31 August). Between 1 September 1989 and 31 July 1991, two observers noted all vocalizations of a subset of pairs in the two study areas, simultaneously with our observations for studies of territoriality, time budgets, and breeding biology. We recorded the frequency of different vocalizations given by males and females. Notes were also made indicating when birds were out of hearing range or when the identity of the vocalizing bird could not be determined. Intervals when the pair appeared separated (out of vocal contact with one another) were also noted. We categorized vocalizations on the basis of descriptions by Atwood (1988). Vocalizations included the mew (Atwood Type I), scold (modified Atwood Type I), churr (Atwood Type II), alarm (Atwood Type V), and warbling (Atwood Type VI). We also recorded contact notes (not described by Atwood), which are quiet, short buzzes given by both male and female when close together.

To calculate the monthly detectability of resident gnatcatchers at the Amber Ridge site between October 1990 and July 1992, we recorded the time spent in each occupied territory searching for resident pairs.

Data Analysis

We summarized, by observation period, the frequency of each type of vocalization for an established pair of gnatcatchers. We did not include data from unpaired birds or birds believed to be in the process of establishing their territories. The frequency of a pair's vocalizations was divided by the number of minutes one or both of the pair were within the range of the observer's hearing and was expressed as an hourly rate. Monthly means and standard errors were calculated for each type of vocalization and for each stage of the nesting cycle. The pre-nest-building stage was the 2-week period preceding the first signs of nest building for each pair at the beginning of the breeding season. Nest building was the period when birds were observed constructing a nest. Egg laying was the period between the end of nest building and the beginning of incubation. Incubation started when birds were first observed sitting on eggs. The brooding stage began with hatching of the first egg and ended when parents no longer brooded their young, typically when the nestlings were 9 days old. The older-nestling stage extended from then until the chicks fledged, usually at an age of 14 days. The fledgling period began when the first nestling had left the nest and continued, in the absence of another nesting attempt, until the fledglings left their natal territory. If the adults began construction of another nest while still attending fledglings, the stage was classified as nest building since most observations were near the nest, typically some distance away from the fledglings. The eighth stage of the nesting cycle was the nonbreeding period.

Using the methods described above. we calculated separate hourly vocalization rates for males and females. We calculated the mean and standard error of vocalization rates for each type of call for both males and females by month and by stage of the nesting cycle. To look at the effect of time of day on vocalization rate, we categorized vocalizations as early morning (0600–0959) or late morning/mid-day (1000–1359). Observations after 1400 were insufficient to be included in the statistical analysis. We compared differences between males and females by analysis-of-variance tests after $\log_{10}$-transforming vocalization rates by month and by stage of the nesting cycle. We also compared vocalization rates for the two daily time periods.

Monthly percent detectability was calculated by totaling our number of visits to all territories in the study area in which we detected one or both of the pair. This total was divided by the total number of visits to all established territories for that month. A visit was defined as "no detection" if we spent >30 minutes within an established territory and did not locate that pair. Visits to territories with known nests were excluded from this analysis since gnatcatchers were almost always detected if the active nest location was known, artificially inflating the measure of detectability.

RESULTS

Vocalization Behavior

Between 1989 and 1991, we recorded 327 hours of vocalizations during 241 observation periods of 21 gnatcatcher pairs at the two study sites. The number of hours of data collection per pair averaged 15.6 (standard error ± 3.9, range 1.1–70.5). This measure of field effort excludes any periods when both members of a pair were outside of the observer's hearing range. Data-collection levels were similar for males (310.2 hours) and females (297.2 hours).

We tallied 50,347 vocalizations during the study. Mews constituted 52.2% of all vocalizations, contact notes 31.6%, churrs 11.9%, scolds 3.3%, and other vocalizations 1.1%. The mean monthly rate of vocalizations peaked in February with 237.6 vocalizations/hour and was lowest in June with 67.4 vocalizations/hour (Figure 1). The monthly patterns for different types of vocalizations were similar except for churrs, which were most frequent from January through June.

Mean vocalization rates varied with stage of nesting, with highest rates before nest building and lowest rates while eggs and young were in the nest (Figure 2). Churrs were highest during the early stages of breeding, whereas mews peaked at later stages of the nesting cycle. Contact notes were lowest when the nest was active and the male and female were often separated by relatively great distances (e.g., one bird was foraging while the other was tending the nest).

Male and female gnatcatchers shared all calls except the churr, given only by males. Males called significantly more frequently than females from February through June ($P < 0.005$) (Figure 3). Merging vocalization rates for

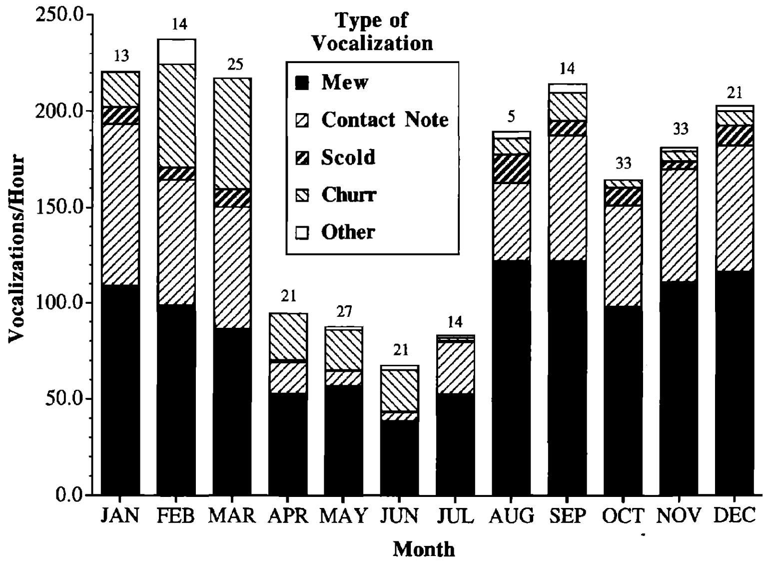

Figure 1. Mean monthly rates of California Gnatcatcher vocalization types. Twenty-one pairs were observed for 327 hours at the Amber Ridge and Rancho San Diego study sites. The number of observations is listed above each month.

the entire year also yielded a significant difference between males and females ($P < 0.001$). In 9 of the 20 pairs with observations sufficient for this comparison, the males' and females' vocalization rates differed significantly. For all but one of these pairs, the male's rate was greater than the female's.

Except during the fledgling stage males' and females' vocalization rates differed significantly during all stages of the nesting cycle (Figure 4). The difference at the fledgling stage appears not significant only because observations at this stage were too few (n = 8 observation periods each for males and females). Conversely, the sample size for the nonbreeding period was the largest (n = 141 observation periods each for males and females), and even though the difference in vocalization rates appears small it was significant.

There was no significant difference in vocalization rates between the early morning (0600-0900) and middle of the day (1000-1300).

Detectability

On the basis of repeated surveys of nine territories between 1 October 1990 and 31 July 1992 at Amber Ridge, the gnatcatchers' detectability was lowest from October to February (Figure 5). There were two replicates for all months except August and September. There may be some bias in detectability over the course of the study due to the two observers' increasing familiarity with the population. Some pairs were easier to detect than others. Monthly detectability of any one pair varied from 20 to 100%.

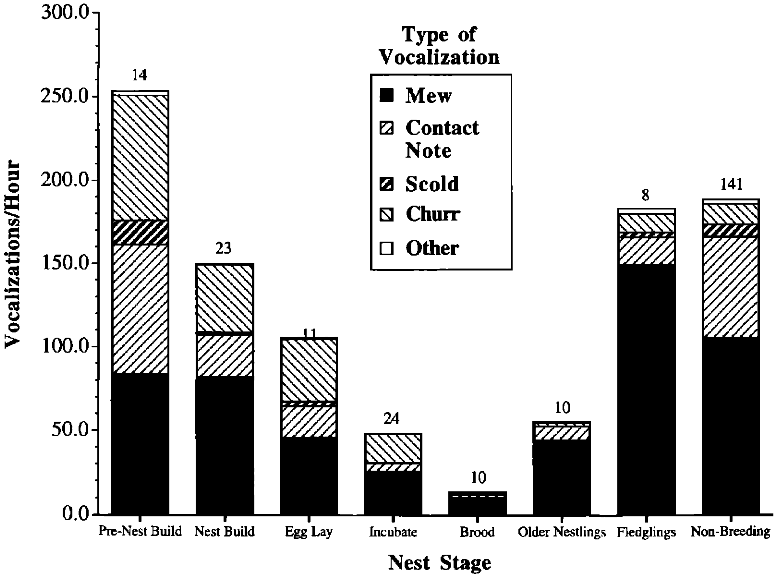

Figure 2. Mean rates of California Gnatcatcher vocalization types during each stage of the nesting cycle. Twenty-one pairs were observed for 327 hours at the Amber Ridge and Rancho San Diego study sites. The number of observation periods is listed above each stage of the nesting cycle.

DISCUSSION

Vocalization Behavior

California Gnatcatchers emit several unique calls (Atwood 1988) but lack a longer, more complex vocalization characteristic of the songs of males of many passerine species. The division between calls and songs, however, is rather arbitrary and artificial (Catchpole 1982). We consider gnatcatcher calls to encompass functions similar to those of typical passerine songs.

From our observations and the descriptions of vocalizations by Atwood (1988), it appears that some gnatcatcher calls have very specific functions. We heard alarm calls consistently when a potential predator or human approached the gnatcatcher or its nest too closely. Churrs, restricted to males, are important in mate attraction, facilitation of nesting, and pair-bond maintenance. The contexts in which this call was heard and the seasonal pattern of churr rates (Figures 1 and 2) are consistent with other studies that have found certain vocalizations to have similar functions in other passerines (Howes-Jones 1985, Kroodsma 1981, Staicer 1989, Merila and Sorjonen 1994, Ritchison 1995). The rate of churring is highest during the pre-nesting and early nesting periods, relatively low in the nonbreeding and later breeding stages. The male initiates and plays a dominant role in nest building (Grishaver et al. 1998). Churrs are an important component of nest-building behavior and may entice the female to the nest site. Churrs during the pre-

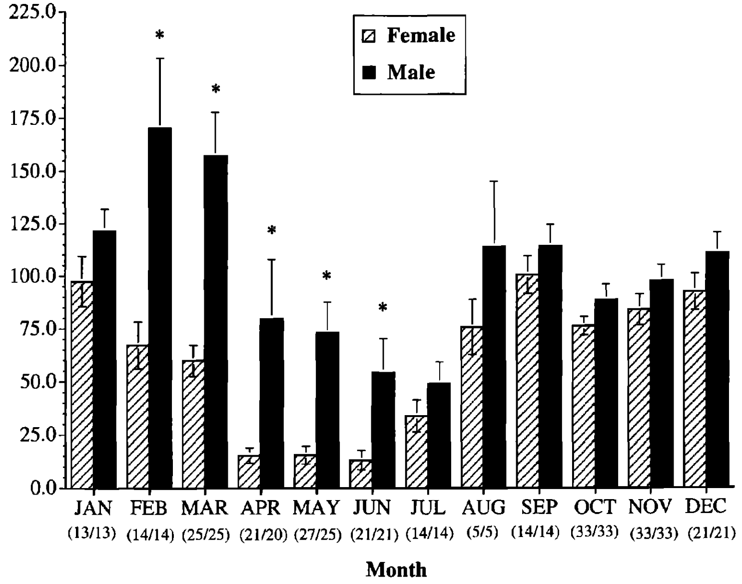

Figure 3. Mean (± standard error) monthly rates of total vocalizations for male and female California Gnatcatchers. Twenty-one pairs were observed at the Amber Ridge and Rancho San Diego study sites. Females were observed for a total of 297.2 hours, males for 310.2 hours. The number of observation periods for each sex is listed in parentheses below each month (male/female). *, difference between the sexes is significant ($P < 0.005$, analysis of variance).

breeding stage may stimulate the female into reproductive condition. Churrs were also associated with periods when the male and female became separated, especially during the earlier phases of the nesting cycle (from prenesting to incubation). This call was also frequently heard during pair formation, although we quantified vocalizations only for established pairs. In one case a newly unpaired male left his territory at the start of the breeding season and entered the territory of a female who had also lost her mate. The male churred extremely often over several days and appeared to be trying to lead the female back to his territory. The fact that the male was not defending his own territory while churring extensively and was unpaired and attempting to attract a mate suggests that churrs function primarily in mate attraction and not in territorial defense. The California Gnatcatcher may indulge in extra-pair copulations (Preston et al. 1998). If so, churrs may also function to attract females for such copulations, although we did not document this.

The mew call appears to be used in a variety of situations. Atwood (1988) described it as important in territorial advertisement and in interactions between the sexes. The contexts in which we observed gnatcatchers mewing support Atwood's interpretation of multiple functions for this call. California Gnatcatchers mew often throughout the year (Figures 1 and 2), consistent

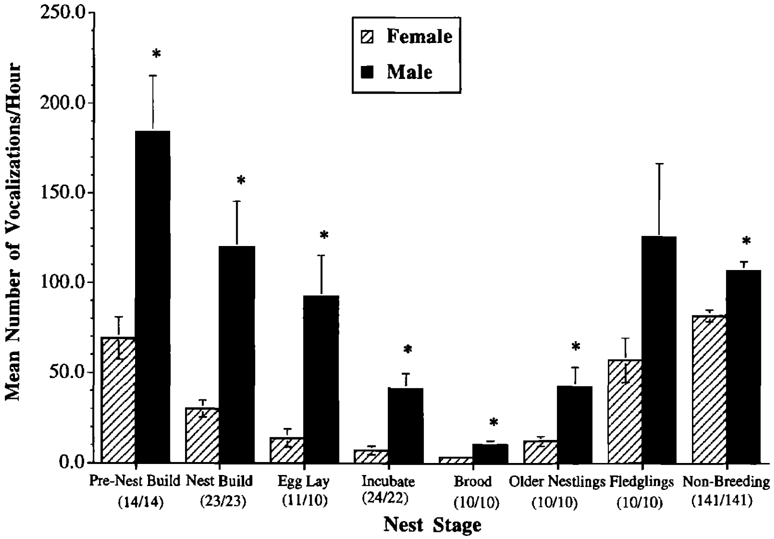

Figure 4. Mean (± standard error) rates of total vocalizations for male and female California Gnatcatchers during each stage of the breeding cycle. Twenty-one pairs were observed at the Amber Ridge and Rancho San Diego study sites. Females were observed for a total of 297.2 hours, males for 310.2 hours. The number of observation periods for each sex is listed in parentheses below each month (male/female). *, difference between the sexes is significant ($P < 0.005$, analysis of variance).

with the call's functioning to maintain pair bonds and territories year round. Atwood also attributed a scolding function to the mew. In our study we recorded this scolding call separately because we could distinguish it easily and because of the specific scolding context in which it was used. This scolding type of mew was used by territory holders in interactions with intruding gnatcatchers and in mobbing potential nest predators. It was also used when members of a pair came together after short-term separations. Because of the variability in the mew call, it is likely that variations in its rate, duration, frequency, pitch, and volume relay specific information.

To determine the functions of various gnatcatcher calls definitively will require further spectrographic analysis of the various subtleties of the calls, more quantification of the context of each call, and of the behavioral responses of receivers of these calls.

Detectability

The study at Amber Ridge indicates pairs were most detectable from March to September (Figure 5). Best and Petersen (1982, 1985) found that the detectability of two other arid shrubland passerines, the Sage (*Amphispiza belli*) and Brewer's (*Spizella breweri*) Sparrows, varied with the stage of the nesting cycle. The Sage Sparrow's detectability was relatively low (25-80%) with some fluctuation according to breeding stage,

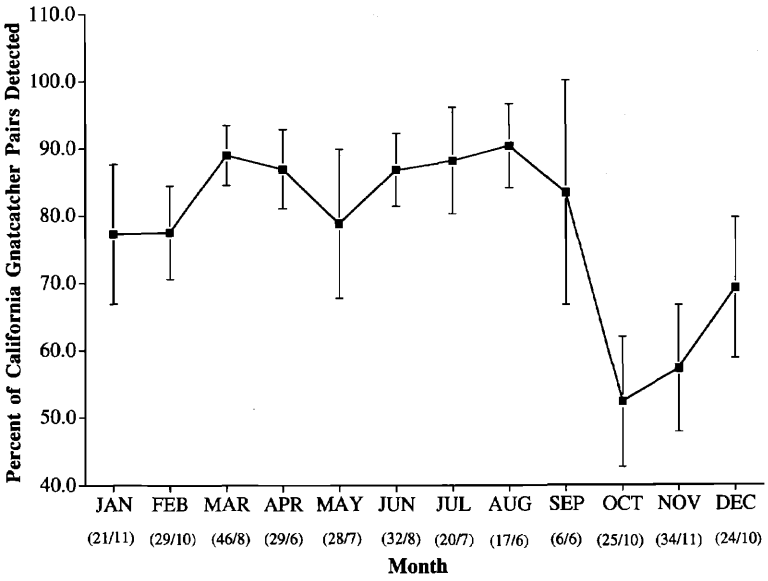

Figure 5. Mean (± standard error) rates of monthly percent detectability of California Gnatcatchers in occupied territories at the Amber Ridge study site. Sample sizes are listed in parentheses below each month as number of visits to all territories/number of territories.

whereas Brewer's Sparrow varied pronouncedly in detectability, being highly detectable (100%) during the early breeding season and dramatically less detectable (30–60%) after pairing.

Our study suggests that the California Gnatcatcher's detectability (P_d) varies between 70% and 90% from December through September. Detectability is lowest in October and November (52–57%). Therefore, the probability (P_m) of missing a gnatcatcher present at a site diminishes greatly with each successive visit. A maximum value of P_m set at 5% requires five visits for a P_d of 50%. P_d values greater than 70% require only three visits for the 5% P_m threshold to be met. Therefore three to five visits are adequate in most months of the year in areas with relatively large gnatcatcher populations. In areas where P_d may be lower, however, such as near the limits of the gnatcatcher's range, additional visits might be necessary.

The pattern of detectability of the gnatcatchers at Amber Ridge differed somewhat from the pattern of variation in vocalization rates (Figures 1 and 5). Gnatcatchers emit easily detectable calls (e.g., mews and churrs) at the highest rate between August and March. Since vocalizations are the primary means of detecting gnatcatchers, we expect that gnatcatchers are more detectable during these months. The slightly lowered detectability at Amber Ridge from October to February (52% to 78%) may be partially explained by the birds' high rate of extra-territorial wandering between November and January (Preston et al. 1998). As we became familiar with each territory, we may have biased our efforts in areas where we expected to find gnatcatchers. Gnatcatchers outside of their defended territory call less frequently than when they are in their territory. Simpson (1985) documented the same pattern in the Carolina Wren (*Thryothorus ludovicianus*). Resident birds wandering into territories of neighboring pairs or into supplemental foraging areas not defended by any birds may not be detected by an observer using a taped recording to elicit territorial behavior.

It is important to note that we directed substantial effort toward following each pair during the breeding season and to finding all nests. As a result, we spent more time looking for hard-to-detect pairs during the breeding season than during the nonbreeding season. This increase may have contributed to higher detectability during the breeding season than would have been expected from vocalization patterns. The majority of nests were found at the nest-building stage (Grishaver et al. 1998), when gnatcatchers are relatively conspicuous and vocal (Figure 2). Subsequent observations at known nests were not used to determine detectability (see Methods). This precluded the inclusion of many observations from the incubation, brooding, and nestling stages of the nesting cycle when gnatcatchers are substantially less vocal, hence detectability in the breeding season may have been overestimated. Our experience in locating and following California Gnatcatchers suggests that gnatcatchers are more difficult to detect during the egg-laying, incubation, and early nestling stages. At these times adults are significantly quieter (Figure 2) and more secretive, especially near the nest. Detection rates by observers unfamiliar with a gnatcatcher pair during the breeding season would probably be lower than suggested by this analysis.

While California Gnatcatchers do not sing complex songs, they do have a variety of calls that appear to have specific functions. The pattern of these calls and the behavior of the birds during the annual cycle can influence their detectability during surveys, with important consequences for survey methods and determination of population densities.

SUMMARY

We collected vocalization data on 21 pairs of California Gnatcatchers throughout the annual cycle to describe their seasonal pattern of vocalizing and to determine the functions of multiple call types. By understanding their vocalization behavior, we can improve our survey methods for assessing densities of this threatened species. Vocalization rates were highest from August through March (the non-breeding, pre-nesting, nest-building, and fledgling phases of the nesting cycle) and lowest from April to June (primarily during the egg-laying, incubation, and nestling phases). Males were significantly more vocal than females from February to June. The percentage of pairs detected during regular surveys varied by month, being lowest during October and November.

ACKNOWLEDGMENTS

We thank the staff of the biology group at Ogden Environmental and Energy Services Company for their assistance on this project, particularly Jerre Stallcup, Steve Lacy, David King, and Eric Bailey. We thank John Rotenberry for his comments on the manuscript. Philip Unitt was helpful with the final editing. Funds for these studies were provided by the Home Capital Development Corporation, the Weingarten, Siegel, Fletcher Group, Inc., and Ogden Environmental and Energy Services.

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Accepted 7 July 1998