CALIFORNIA GNATCATCHER TERRITORIAL BEHAVIOR

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To conserve and manage endangered and threatened species effectively requires an understanding of their overall distribution as well as a more detailed understanding of individuals' use of space. Nonmigratory birds' use of an area in the breeding season may differ from their use of it in the nonbreeding season. Amid ever-increasing pressure to develop, determining if habitat is occupied is crucial to planning preserves. Knowledge of typical territorial behavior can be important in designing survey methods for determining population densities and in ensuring the conservation of habitat necessary for breeding and overwintering.

We studied the ecology of 57 pairs of the California Gnatcatcher (*Polioptila californica*) in southwestern San Diego County from 1989 to 1992 (see Grishaver et al. 1998, Preston et al. 1998). Currently, there is little published information on the species' territory size and territorial behavior. This paper describes the gnatcatchers' unusually large territory and various aspects of males' and females' territorial behavior.

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), 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 in Jamacha Valley, the 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. We did not collect data sufficient for analysis at Amber Ridge between July 1989 and September 1990 when over half of the site was graded for development. Approximately 65 ha were retained in open space. Both sites are dominated by coastal sage scrub (Mooney 1977, Westman 1981).

Field Methods

In November 1988, we mist-netted and banded adult California Gnatcatchers with U. S. Fish and Wildlife Service aluminum bands and unique combinations of color bands. Throughout the remainder of the study, we banded additional juvenile and adult gnatcatchers opportunistically. Nestlings were banded at an age of 9 or 10 days.

We recorded the number of pairs, the identity of individuals within a pair, and any changes in pair composition. Individual mortality and immigration of new birds into the study areas were also noted. We visited each territory an average of 12 to 16 times during the nonbreeding (1 September–28 February) and breeding (1 March–31 August) seasons. We used tape-recorded vocalizations to elicit responses from a resident pair only if extended searching failed to reveal one or both members of the pair. If a tape was used, we waited 5–10 minutes prior to beginning data collection to allow the gnatcatchers to resume their normal activities. We determined the breeding status of each pair during each observation period.

We collected territory/home-range data by following each resident individual or pair and mapping its location every 30 seconds on an aerial photograph (photo scales 1:3300 and 1:4800). A repeating timer indicated the beginning of each 30-second interval. We recorded when none, one, or both gnatcatchers were in view, and then calculated the proportion of time each individual was in view or out of sight during the observation period.

We defined a territorial dispute as any aggressive intraspecific behavior directed at an intruding nonresident individual. Territorial disputes typically entailed mewing, scolding, bill clicking, and aggressive display postures directed toward the intruding gnatcatcher(s) by one or both members of the resident pair. Disputes often resulted in pursuit and sometimes in an attack on the intruding bird(s) by the resident bird(s). For each observed territorial dispute, we recorded the identity of all participants, their age and sex, and the beginning and ending locations of the dispute.

Data Analysis

The size and configuration of each pair's territory/home range were calculated by combining all mapped locations for each pair for each breeding and nonbreeding season. A minimum convex polygon, indicating the extent of the territory/home range, was hand-drawn around the outermost locations in a conservative connect-the-dots manner without any buffer area. Territory/home-range size was determined by hand-planimetering the perimeter of the polygon and using a computer to calculate its area.

We defined the home range as the entire area used by a pair and the territory as the area actively defended by the pair through aggressive, agonistic interactions. Paired t tests were used to determine if there were significant differences between the sizes of breeding territories and home ranges. The area observed to be used by the birds during any particular period of time is a subset of the home range. Thus, use areas determined during a restricted period may underestimate the true home range. To assess the point at which each pair had been sampled sufficiently to represent its true home range, we plotted area used versus cumulative field effort (number of hours and number of days of observation). Initial search effort, periods when both gnatcatchers disappeared from view and could not be quickly relocated, and brief nest checks were not included in calculation of field effort. The rate of increase in territory size was calculated for each observation day and averaged for each pair over the entire breeding season. Average rates of increase for individual pairs (ha/observation day) were

averaged for all pairs to yield an overall average rate of increase in territory size per observation day. The average rates of increase between successive nest attempts, during the fledging phase, and during the post-breeding phase were compared with the overall mean rate of increase to determine if territory-delineation rates were higher during these intervals. At the Rancho San Diego site we also kept records of the amount of time a subset of established pairs wandered outside of their territories of the previous breeding season during the 1989–1990 and 1990–1991 nonbreeding seasons.

We categorized territorial disputes by the age and sex of all participants and compiled disputes according to the age of the intruder for each month of the year. Locations where territorial disputes originated and terminated were added to the maps showing territory boundaries (see above). We also measured the distance from the ending location of the dispute to the nearest territory boundary.

We plotted average territory sizes obtained from other studies of the California Gnatcatcher against distance from the coast. By means of SAS software (SAS 1996), we used a Pearson's correlation to determine if there was a significant relationship between territory size and distance from the coast.

RESULTS

Field Effort

We delineated breeding territories and/or nonbreeding home ranges for 57 pairs of the California Gnatcatcher. For 16 of these pairs, one or both individuals were observed in two consecutive breeding and/or nonbreeding seasons. Our total field effort averaged 16.0 [standard error (SE) ± 1.6] visits to a territory to collect territory/home-range data during the breeding season, 12.8 (± 0.9) visits during the nonbreeding season. Observation periods were of variable duration (range 15–275 minutes). Excluding the nonbreeding seasons at the Amber Ridge site, we observed each pair an average of 70.2 minutes per territory visit. Individual breeding-season and nonbreeding-season observation periods averaged 57 to 86 minutes per territory visit. During the nonbreeding seasons at Amber Ridge, field effort was substantially lower with an average of 44 minutes of observation per visit.

Territory and Home-Range Size

Data for both sites and all years combined, the mean size of a gnatcatcher's breeding territory was 8.1 ha (SE ± 0.5, n = 45 pairs). There was no significant difference in territory size between the two study areas (7.8 ± 0.7 ha, n = 30 pairs at Rancho San Diego versus 8.7 ± 0.8 ha, n = 15 pairs at Amber Ridge), although there was variability from year to year (Figure 1). Nonbreeding home ranges at both sites averaged 12.4 ha (SE ± 1.1, n = 51 pairs). At Rancho San Diego nonbreeding home ranges (mean = 14.0 ha, SE ± 1.2, n = 41 pairs) were over twice as large as at Amber Ridge (mean = 5.8 ha, SE ± 0.4, n = 10 pairs). This may be attributed partially to a lower level of effort at Amber Ridge during the nonbreeding season for both

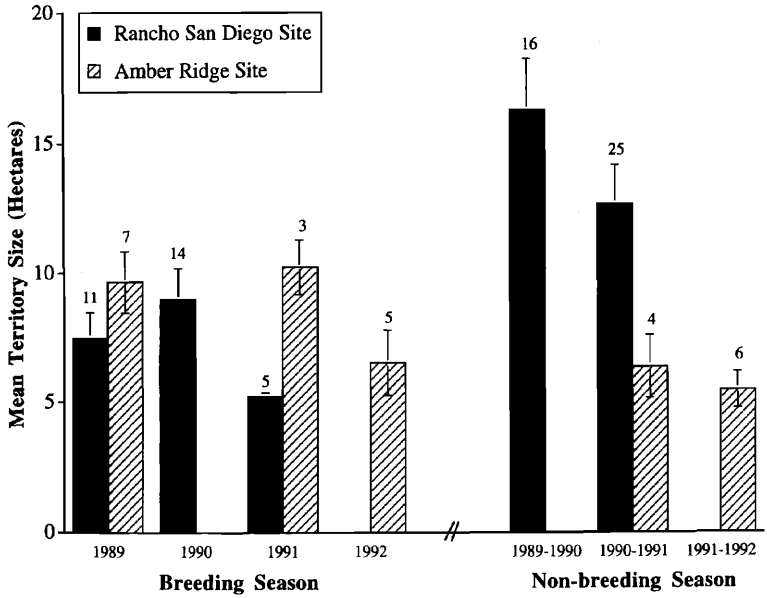

Figure 1. Mean sizes (± standard error) of California Gnatcatcher breeding territories and nonbreeding home ranges at Amber Ridge and Rancho San Diego study sites in southern San Diego County. Sample sizes for each site and year are listed above the error bar for that year.

number of visits and observation-period duration (see below). At Rancho San Diego, the mean difference in home-range size between the breeding and nonbreeding seasons for pairs for which both areas were estimated was 7.2 ± 1.5 ha, an average proportional increase of 78% (SE ± 16.2%, n = 18). This mean difference was significant (paired t test, n = 18 pairs, P = 0.005).

We obtained average territory sizes from other studies of the California Gnatcatcher and found a significant correlation ($P < 0.001$) between territory size and distance from the coast (Figure 2).

Population Dynamics

We observed fluctuations in the number of pairs at both sites over the course of the two studies. Numbers at both sites were higher during the nonbreeding periods owing to postbreeding immigration of juveniles and to relatively high weather-related mortality during January and February just before the breeding season. At one site in the Rancho San Diego study area we observed a 50% reduction in the number of pairs over one year, despite substantial immigration and settlement of juveniles on the site. The primary cause of mortality was severe cold, wet weather from December to February. There were also year-to-year differences in population densities that appeared associated with weather conditions such as cold rains and extended

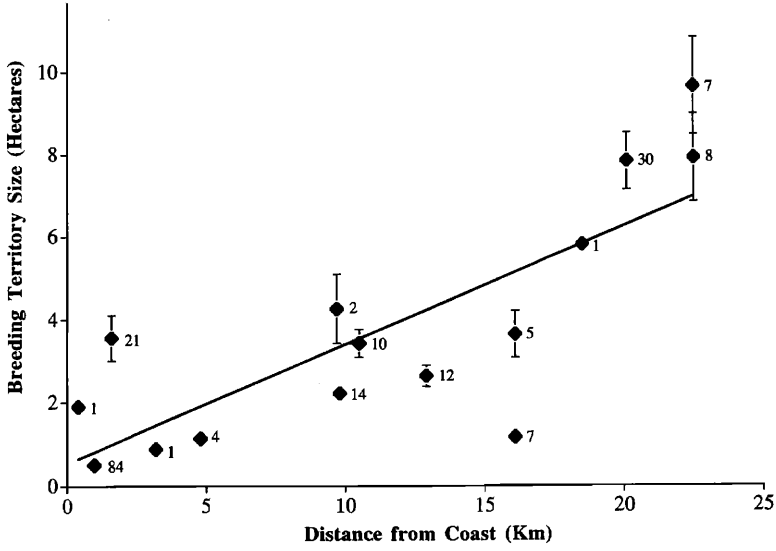

Figure 2. California Gnatcatcher territory size versus distance from the coast in southern California; $r^2 = 0.628$; $P < 0.001$. Average territory sizes obtained from the following sources: this study, R. A. Erickson (pers. comm.) for coastal Orange County, S. Taylor (pers. comm.) for Marine Corps Air Station Miramar, Mock et al. (unpubl. data) for Miramar and southwest Poway, Sweetwater Environmental Biologists (1986), RECON (1987), Impact Sciences, Inc. (1990), Bontrager (1991), McMillen et al. (1991), MBA (1993), Mooney Associates (1994), Atwood et al. (1998a).

drought. Our study extended over the last two years (1989–1990) of a five-year drought and one year (1992) of above-average rainfall.

Over half of the Amber Ridge site was graded for development in the fall of 1989, resulting in a decrease in the gnatcatcher population in adjacent undeveloped habitat. The population gradually increased, however, in this remaining habitat during the two years following grading.

Territory Size and Level of Field Effort

Our estimate of the size of a California Gnatcatcher territory increased as the level of field effort increased (Figure 3). The average rate of increase for 18 territories was 0.3 ha (SE ± 0.04) per day of observation. This rate of increase was not linear for all territories, as some followed a stair-step pattern. Since gnatcatchers often focus their activity around their nests (Atwood et al. 1998a), during the breeding season they often use different parts of their territory selectively. We found that the rate of increase between the termination of a nesting attempt and the beginning of another attempt was 25% higher than the rate of increase during a nest attempt.

Field observations suggested that prior to leaving the natal territory and becoming independent, fledglings were led around the perimeter of the

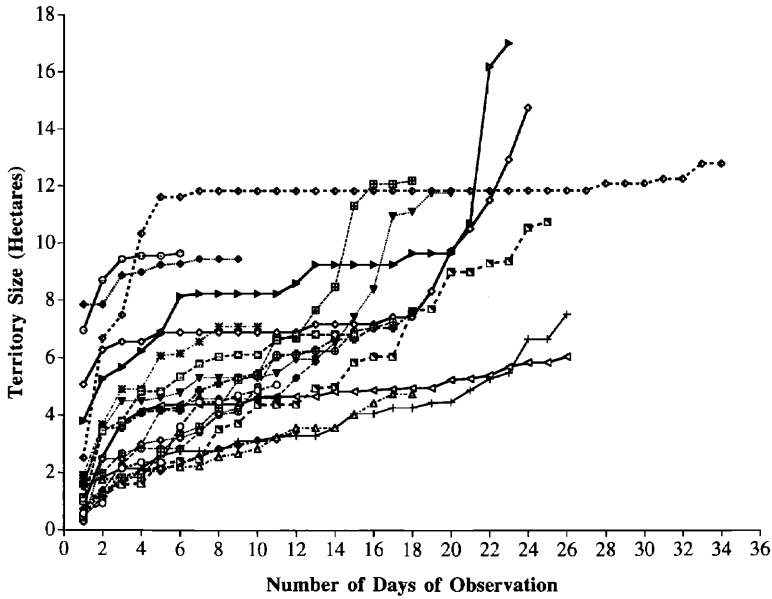

Figure 3. Estimates of California Gnatcatcher breeding-territory size (n = 19) as a function of observation effort.

territory by the adults. Therefore, we expected that the rate of increase in the delineated territory would be higher late in the fledgling stage. We found that the rate of increase in delineated territory was 25% higher (0.4 ha/observation period, n = 24 periods) when pairs had older fledglings (fledged for 14 or more days). The rate of increase was also higher (0.6 ha/observation day) for pairs that had completed nesting prior to the end of the breeding season. Typically we saw this expansion of territory in a subset of the pairs beginning in late June or July. This increased territory growth most likely reflects the beginning of the expansion of the home range in the nonbreeding season.

The observed size of 12 of 18 (66.7%) territories increased on the last visit of the breeding season (average increase on the last observation day was 0.3 ha). The average territory size delineated after eight visits was 5.4 (SE ± 0.6) ha. When data from all visits (mean = 18.2 visits, range 9–34 visits/territory) were included, the territory averaged 8.6 ha (SE ± 0.9), 59% larger than the same territories delineated with eight visits (paired t test, mean difference = 3.2 ha, $P < 0.006$, n = 18). The eight-visit dataset represented only a portion of the complete breeding season for most of the pairs, and the average territory may have been larger if the eight visits had been more evenly spaced throughout the entire breeding season.

During the nonbreeding season, 11 pairs of California Gnatcatchers spent substantial portions of their time wandering outside of their established

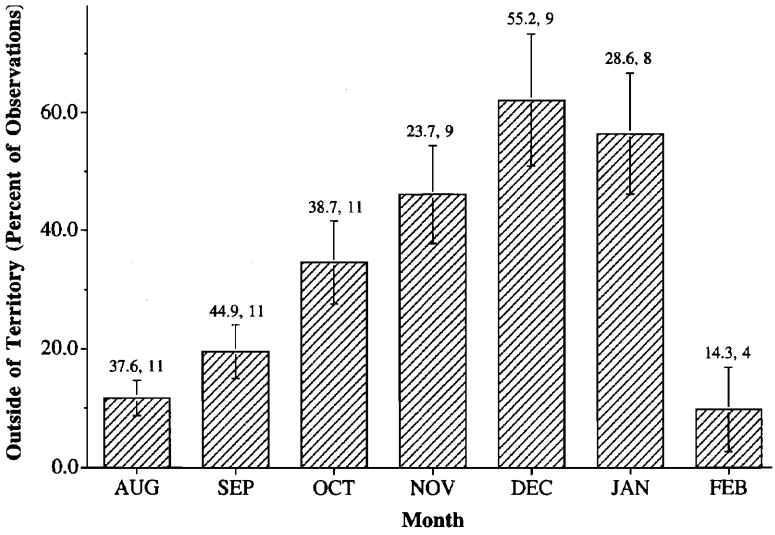

Figure 4. Mean (± standard error) percentage of time California Gnatcatchers wandered outside of defended territories in the nonbreeding season at Rancho San Diego. Number of hours of observation and number of pairs specified for each month.

territory into neighboring territories or into undefended habitat (Figure 4). This expansion of their home range peaked in December with an average of 62.1% (SE ± 11.2%) of their time spent outside of their defended territory.

Throughout the breeding and nonbreeding seasons territory boundaries as determined by patterns of spatial use and the locations of territorial displays were relatively fixed. Existing boundaries could be somewhat altered during the postbreeding season, however, through immigration and territory establishment by juveniles. Occasionally pairs of first-year birds were able to insert a territory between large existing territories. Weather-related mortality in late winter was also associated with adjustments to territory boundaries. Typically, territories adjacent to a vacated territory expanded to include all or part of the vacated territory.

Territorial Behavior

Despite wandering outside of their territory during the nonbreeding season, gnatcatchers defended territory boundaries throughout the year (Figure 5). Territorial disputes involving an adult intruder accounted for 53.5% of 129 observed disputes, those involving juvenile intruders 42.6%, intruders of unknown age or sex 3.9%. Territorial disputes with adult intruders were distributed equally between the nonbreeding and breeding seasons, with some monthly variation. Because of the high level of extraterritorial wandering and trespassing into occupied habitat during the nonbreeding season, it might be expected that the frequency of territorial disputes then would be higher. During the nonbreeding season, however,

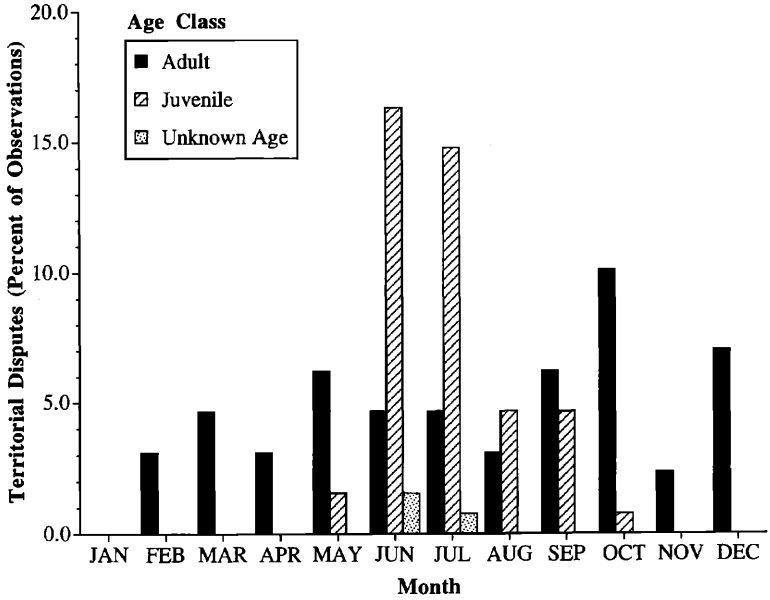

Figure 5. Temporal distribution of territorial disputes of adult and juvenile California Gnatcatchers; 129 territorial disputes were recorded for 29 pairs.

territory holders spent a large proportion of time wandering outside of their own defended territories, so intrusion of neighboring pairs into their territory often went undetected. Quiet and secretive behavior by gnatcatchers intruding into neighboring territories, coupled with their evasive behavior when encountering territory holders, may also account for a lower-than-expected number of territorial disputes during the nonbreeding season. Disputes involving juvenile intruders peaked in the late spring and early summer as juveniles dispersed through occupied habitat and began establishing their own territories. By November, disputes with juveniles ceased as juveniles established their own territories by October. The lack of juvenile intruders after late fall may also be attributed to the difficulty in differentiating between first-year and older birds after this time of the year.

Adult male gnatcatchers were involved in the majority of territorial interactions, acting alone or with the female as a defender of their territory, in 87.6% of the disputes. The female was involved as a defender (alone or with her mate) in 50.4 % of disputes. The male was the sole defender in 49.6% of disputes, while the female was the sole defender in 12.4%. Males defended their territories primarily against other males, juveniles (unknown sex), and pairs. Rarely did the male chase out a lone female. Females most often chased other females or juveniles (unknown sex) out of their territory and rarely chased out lone males. Adult males were intruders in 42.6% of the disputes, adult females were intruders in 20.9%. The remainder of disputes involved juveniles of undetermined sex or unidentified birds.

Territorial chases typically were terminated by a resident pair near their territory boundary (as determined independently by territorial delineation). In 74% of 115 territorial disputes, aggressive chases terminated within 30 m of the resident pair's current breeding-season territory boundary or, in the nonbreeding season, the previous breeding season's boundary. This percentage includes disputes that terminated both inside and outside of the territory. Of the remaining territorial disputes, 17.4% ended between 30 and 60 m from the territory boundary, and 8.7% ended greater than 60 m from it.

Two established pairs meeting at a boundary between adjacent territories often sat on high perches (e.g., *Malosma laurina* or *Baccharis sarothroides*) and scolded, clicked their bills, and engaged in defensive postures such as tail fanning and pumping, without actual contact or a prolonged chase. After a few minutes these disputes usually dissipated and the participants returned to their own territories. If an intruder crossed over a territory boundary it was most likely scolded and then aggressively attacked and/or chased out of the territory by the resident gnatcatcher(s). The resident male typically did most of the active chasing and aggressive behaviors with the female following at a distance or remaining behind and not actively participating. The female was not as actively involved as the male in aggressive interactions beyond initial scolding. If an intruder was a lone adult female, however, the resident female took the lead in chasing the intruding female out of the territory.

We observed a number of instances where a gnatcatcher had lost its mate or was temporarily separated from its mate. In these cases, the lone resident would usually scold any intruders, including prospective mates. In the absence of pursuit by a resident of the same sex, however, intruders of the opposite sex refused to leave. The intruder typically stayed close, giving frequent contact notes. Usually the lone resident would eventually begin foraging with the prospective mate. If the lone resident was unpaired, it often accepted the intruder as its mate within a few days. If the resident was only temporarily separated from its mate, however, the return of its mate would result in the chasing of the intruder out of the territory. Males that were unpaired or had lost their mates spent extensive time vocalizing and searching. If after a day or so they failed to find their mate, they tried to attract another female to their territory by persistently vocalizing and patrolling their territory. Unpaired males would also leave their territory to look for mates in adjacent habitat. One established male lost his mate late in the breeding season and remained unpaired through the following February, when he relocated nearly 4 km from his established territory and bred at the new territory with a new mate.

California Gnatcatchers use areas of marginal habitat, such as riparian edges or weedy areas, for foraging during the winter (this study, Campbell et al. 1998). These areas are not inhabited during the breeding season but are used by gnatcatchers wandering outside of defended territory boundaries in the nonbreeding season. Because these are not defended areas, gnatcatchers sometimes gather there in small groups and forage together without territorial behavior. Members of these groups even remain in contact with one another while foraging by exchanging contact notes. We observed as many as five individuals (a juvenile, female, and three males) foraging together in undefended habitat during the nonbreeding season.

DISCUSSION

Territory Size and Density

California Gnatcatcher populations can vary considerably from year to year (this study, Atwood 1998b, Erickson and Miner 1998). Population levels may be altered over the short term by factors such as weather (e.g., drought, floods; this study, Erickson and Miner 1998), adjacent grading or clearing of habitat (this study), or fire (Atwood et al. 1998c). Other characteristics of a site may influence population levels over the long term, such as climate (Mock 1998), elevation (Atwood and Bolsinger 1992), composition of the vegetation communities (Weaver 1998), and distance from the coast (this study). California Gnatcatcher occupancy of an area can vary over time. During our study, some areas of suitable habitat were unoccupied during years of low population density and became occupied as the population increased.

California Gnatcatcher territories range from an average of less than 1 ha to the relatively large territories of 8+ ha we observed in our study. The territory sizes we recorded were unusually large relative to the body mass of the species in comparison to those of other passerines (Figure 6). In our study individual breeding-season territories ranged from 2.83 to 18.5 ha, considerably larger than recorded in most other studies. There may be several reasons for such large territories in our study areas. In coastal southern California there appears to be a trend of increasing territory size with increasing distance from the coast (Figure 2). Habitats may vary in the resources they offer gnatcatchers, so that habitat quality may be higher along the coast than farther inland. The composition of the vegetation at more mesic coastal sites and more arid inland sites differ (Weaver 1998). Habitat quality defined in terms of food resources or vegetation physiognomy and composition has been shown to affect territory size in some passerines (Schoener 1968, Davies 1978, Wiens et al. 1985, Smith and Shugart 1987, Haggerty 1998). Territories near the coast may also be constrained by development and a lack of suitable habitat. The number of pairs inhabiting a site may influence territory size. The five-year drought ending in 1991 may have resulted in larger territories at our sites. When habitat is abundant and population densities are relatively low, gnatcatchers appear to be able to defend much larger areas without interfering with their normal reproductive activities (Grishaver et al. 1998). Population densities have also been shown to be related to territory size in some birds (Krebs 1971, Morse 1976, Wiens et al. 1985, Smith and Shugart 1987).

Bontrager (1991) noticed an 82% increase in home-range size during the nonbreeding season, similar to our increase of 78%. This extra-territorial wandering appears to have two functions. California Gnatcatchers wandering into neighboring territories are able to assess the status of the neighboring territory holders. Gnatcatchers are short-lived birds and may benefit by being able to determine the pairing status of potential mates in case their current mate should die. We observed gnatcatchers expand their own territory into neighboring territories with the death of one or both members of the neighboring pair. Thus by assessing the status of other territories around their own, gnatcatchers have the opportunity to acquire resources

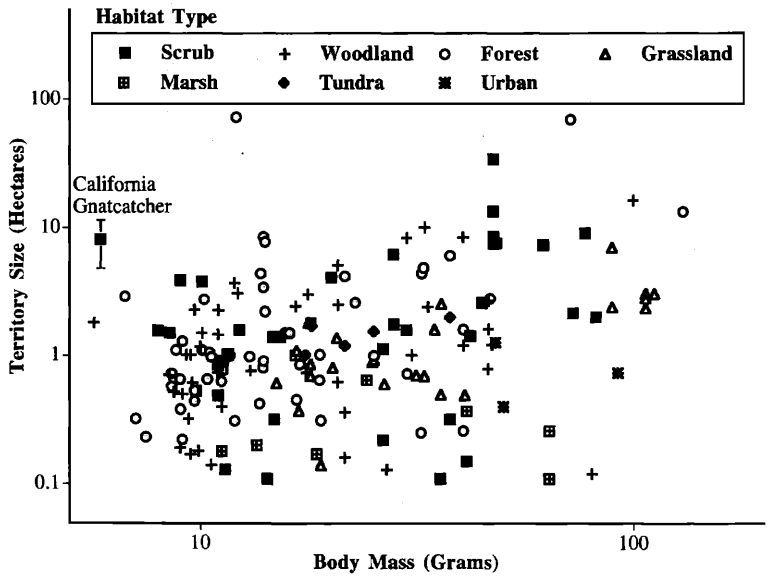

Figure 6. Relationship between body mass and territory size for various species of passerines, distinguished by habitat. The mean and range of breeding-territory sizes for the California Gnatcatchers in our study (n = 45 territories) are shown. Territory sizes for other species obtained from Schoener (1968), Wiens (1969), Krebs (1971), Ralph and Pearson (1971), Zimmerman (1971), Catchpole (1972), Anderson and Anderson (1973), Morse (1976), Cody (1978), Nolan (1978), Rice (1978), Root (1969), Seastedt and MacLean (1979), Zach and Falls (1979), Saether (1983), Wiens et al. (1985), Prescott and Middleton (1988), Matthysen (1990), and Poole and Gill (1992–1997).

and information (e.g., more habitat, potential mates). A second function of extra-territorial wandering is the use of nondefended habitat for supplemental foraging during winter when food resources are likely limited (this study, Campbell et al. 1998). This foraging, often in edge or riparian habitats, may be important in the overwinter survival of gnatcatchers in drier and colder inland sage scrub.

Fluctuations in population levels, territory size, amount of habitat occupied, and habitat requirements between the breeding and nonbreeding seasons have important implications for the conservation and management of the California Gnatcatcher. In many cases planning decisions for proposed development projects are based on the number of gnatcatchers detected during multiple visits to the site during the breeding season. Information on use of nonbreeding habitat has only begun to be considered. Attempts are often made to define habitat use through the delineation of territories. There is substantial debate, however, over methods for delineating occupied habitat through territory mapping, often with the aid of computer modeling (Anderson 1982, Atwood et al. 1998a, Hansteen et al. 1997). Using the same data

set, different computer programs yield different estimates of territory size (Worton 1989, Call et al. 1992, Hansteen et al. 1997). The amount and temporal distribution of data-collection effort also affect estimates of territory size (Figure 4; Anderson 1982, Atwood et al. 1998a).

There is also disagreement over the interval between data points necessary to achieve statistical independence of each point (Anderson 1982, Hansteen et al. 1998). The 30-second interval used in this study does not afford such independence. In another study of gnatcatcher territories in coastal San Diego, we recorded the birds' locations at 1- and 5-minute intervals and found that territories defined from locations recorded at only the 5-minute intervals were substantially smaller (Spencer and Mock unpublished data). This result is similar to that from other home-range studies (Anderson 1982, Call et al. 1992, Hansteen et al. 1997). The need is for territory-delineation techniques that fully document the home range used by a pair while maximizing the statistical independence of data points. It is important, however, that biologically relevant observations not be ignored for the sake of meeting strict statistical criteria.

Atwood et al. (1998a) recommended that standard methods for determining gnatcatcher territory size and configuration be developed. Such standardization is important for comparing results of various studies so we may gain a better understanding of how territories vary in time and space. Determining territory size and configuration should take into account that gnatcatchers' use of space varies through time. They tend to maintain fairly constant territory boundaries throughout the year, however, even with this variation. Territory boundaries appear to change primarily in response to local changes in population densities resulting from juveniles' immigration and adults' mortality. Because of fluctuations in habitat occupancy, population densities, and territory sizes over time, we should move away from depending almost exclusively on territory delineations and population estimates in making land-use decisions. Development of habitat-suitability models that adequately evaluate habitat quality and long-term viability could minimize decision making based on information that varies significantly from year to year (e.g., population density and territory size).

Territorial Behavior

In our study paired male and female gnatcatchers jointly defended territories year round. We observed each sex defending its territory primarily against adults of the same sex. This behavior may be important in maintaining the integrity of the pair by minimizing the intruder's competition for a mate (Gowaty et al. 1989, Slagsvold 1993, Meek and Robertson 1994). It may be a means for a territory holder's recognizing its mate or for an intruder's determining that a territory holder is unpaired. This pattern of territorial behavior may also be important in a resident's preventing its mate from engaging in extra-pair copulations. Alternatively, by tolerating intruders of the opposite sex, territory-holders can solicit extra-pair copulations. Extra-pair matings are considered to be an important part of the mating strategies of many apparently monogamous passerine species (Birkhead and Møller 1992). Although, we did not observe any extra-pair copulations, we did observe a male entering another male's territory, quietly visiting the

active nest. He approached the nest very closely, avoiding detection by the resident male. This observation, combined with territorial defense aimed at the same sex, could indicate that California Gnatcatchers engage in extra-pair matings. Similar behavior is seen in species known to participate in extra-pair copulations (Gowaty et al. 1989, Slagsvold 1993, Meek and Robertson 1994). Breeding-season aggression between resident females and intruding females has also been attributed to preventing conspecific brood-parasitism (Hobson and Sealy 1990).

The male is the most active in territorial defense, but the female also plays an active if less intensive role (e.g., scolding but not chasing). The female's participation contrasts with the situation in many other passerine species, in which the male is the sole defender of the territory (Davies 1978, Welty 1982, Hunt et al. 1995). The female California Gnatcatcher's significant role in territorial defense may be attributed partially to year-round defense of a territory unusually large relative to body size. Female participation may be required to maintain a large territory successfully and thereby ensure acquisition of resources necessary for survival and successful reproduction.

SUMMARY

We studied the territorial behavior of 57 pairs of the California Gnatcatchers at two sites in southwestern San Diego County from 1989 to 1992. At our sites pairs defended unusually large year-round territories. Breeding-season territories averaged 8.1 ha (SE ± 0.5, n = 45). During the nonbreeding season, gnatcatchers wandered into adjacent territories and unoccupied habitat, using a home range that was typically 78% (SE ± 16.2) larger than their breeding territory. The number and duration of these forays peaked in December, when the birds spent an average of 62% of their time away from their defended area. Despite the increase in forays outside of established territories during the nonbreeding season, pairs continued to defend and sometimes to expand their previous breeding-season territories. Disputes involving adult intruders were equally distributed between breeding and nonbreeding seasons. Juvenile intruders accounted for 42.6% of all territorial disputes. Female gnatcatchers, in contrast to many other passerine species, actively participate in territorial defense and were involved in 50% of all territorial disputes. Over 70% of disputes terminated within 30 m of the boundaries of the breeding-season territory, regardless of season. Knowledge of California Gnatcatcher territory size and territorial behavior is important in designing preserves and in developing practical survey methods for assessing population densities of this threatened species.

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