SIX YEARS OF SYNCHRONOUS CALIFORNIA GNATCATCHER POPULATION FLUCTUATIONS AT TWO LOCATIONS IN COASTAL ORANGE COUNTY, CALIFORNIA

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Bird populations and distributions are known to be influenced by environmental factors (e.g., Graber and Graber 1979, Cawthorne and Marchant 1980, Root 1988a,b,c, Arcese et al. 1992, Mehlman 1997). Nevertheless, "whether and how most animal populations are regulated remains one of the principal unanswered questions in ecology" (Rodenhouse et al. 1997). Another major gap in our understanding concerns the scale over which species' populations fluctuate (Holmes et al. 1986).

Atwood and Bolsinger (1992) analyzed the upper elevational limits of the California Gnatcatcher (*Polioptila californica*), but otherwise little has been published on environmental factors affecting this species. In particular, Atwood (1993) noted that data concerning annual survivorship had not yet been published. We compared the results of California Gnatcatcher surveys conducted at two locations in coastal southern California over the same 6-year period in the 1990s. A cursory examination of the data suggested that annual fluctuations in the number of breeding pairs were similar, presumably in response to similar environmental influences. A more thorough analysis and consideration of these issues is presented here.

STUDY AREAS

The coastal terrace at Crystal Cove State Park, between Newport Beach and Laguna Beach, Orange County, California, is described in more detail elsewhere (Miner et al. 1998). The study site lies between Pacific Coast Highway and the bluffs overlooking the Pacific Ocean in the vicinity of Pelican and Reef points. Total size of the study area is approximately 93 hectares; the elevation is approximately 20–40 meters. Habitat on the site is a mixture of coastal sage scrub and annual grassland. Dominant scrub species include California sagebrush (*Artemisia californica*; plant taxonomy and nomenclature follow Hickman 1993), California buckwheat (*Eriogonum fasciculatum*), California encelia (*Encelia californica*), black sage (*Salvia mellifera*), goldenbush (*Isocoma menziesii*), deerweed (*Lotus scoparius*), and coyote brush (*Baccharis pilularis*).

"Site 2" is also on the coast of Orange County, approximately 11 km away. It covers approximately 100 hectares and, like the Crystal Cove site, the terrain is mostly gentle. The elevation range is 0–35 meters. The habitat is a mixture of coastal sage scrub and annual grassland, with California

encelia strongly dominant over most of the site. Unlike Crystal Cove, Site 2 is located adjacent to a considerable expanse of wetland and ruderal habitat that may serve as a buffer and allow for a higher gnatcatcher population than would be possible at a site otherwise susceptible to seasonal desiccation (Campbell et al. 1998). Because of a combination of natural and unnatural features, the gnatcatcher populations at both sites are rather discrete, but movement in and out of both populations is known to occur.

METHODS

Gnatcatcher surveys at Crystal Cove began in 1991. Final estimates of nesting pairs each year were based on an analysis of all data collected during the breeding season (February through July), although not all areas necessarily received equal coverage. Color-banding of some birds greatly assisted in this process. In general, all areas were carefully surveyed at least twice with the occasional use of taped gnatcatcher vocalizations.

Sporadic gnatcatcher surveys were conducted at Site 2 in 1990 and 1991, but comprehensive coverage during the breeding season did not begin until the following year. Three complete surveys were conducted from March to May 1992 and in July/August 1997, with two surveys done in March/early April in each of the intervening years. As at Crystal Cove, taped gnatcatcher vocalizations were occasionally used during these surveys.

Because of the limitations of our coverage, our observations of single males (or females) were considered to represent pairs unless further visits gave us sufficient confidence that single birds were indeed unpaired. We acknowledge that these data may not represent completely accurate censuses of these areas, but we consider them to be careful estimates.

In order to assess the influence of weather on these gnatcatcher populations, we obtained temperature and rainfall data from Newport Beach Harbor and summed rainfall totals from November through February to obtain a cumulative seasonal amount for each season from 1990–1991 to 1996–1997. Similarly, we averaged monthly average temperature maxima and minima to obtain single seasonal averages for the same period. Long-term seasonal averages were derived from long-term monthly averages in the same fashion.

RESULTS

Our annual estimates of the number of nesting pairs at each site fluctuated rather synchronously from 1991 to 1997 (Figure 1; $r = 0.759$, $P = 0.02$). Weather during the study period was generally milder than average, with lower maximum temperatures and, especially, higher minimum temperatures (Figure 2). Seasonal temperatures varied rather little, and no correlation with population size was found. Rainfall did vary (following a prolonged drought, the study period was generally wetter than average) and was inversely correlated with population size ($r = -0.706$, $P = 0.025$ at Crystal Cove; $r = -0.429$, $P = 0.15$ at Site 2).

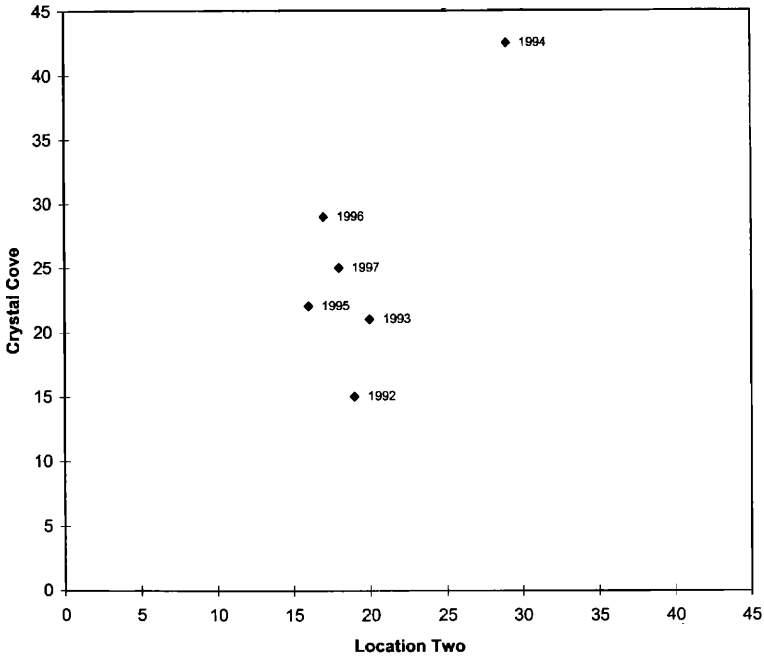

Figure 1. Numbers of California Gnatcatchers over 6 years at two locations in coastal Orange County, California.

DISCUSSION

The considerable variation in population size at these sites may seem unusual given the statement by Welty and Baptista (1988:405) that "the great majority of bird populations seem relatively constant in number except for seasonal fluctuations." Evidence is mounting, however, that annual population swings of this magnitude are common among passerines (e.g., Wiens 1989, DeSante 1990, Arcese et al. 1992). There is a large body of work concerning the variability of bird communities (e.g., Noon et al. 1985, Holmes et al. 1986, Böhning-Gaese et al. 1994), but it is usually difficult to tease out details on individual species from community discussions. Koenig (1998), using Breeding Bird Survey and Christmas Bird Count data, found little large-scale synchrony among California landbird populations, especially in resident species.

The general population trends documented here are similar to those shown during the same period on the Palos Verdes Peninsula, coastal Los Angeles County, and in the San Joaquin Hills of coastal Orange County

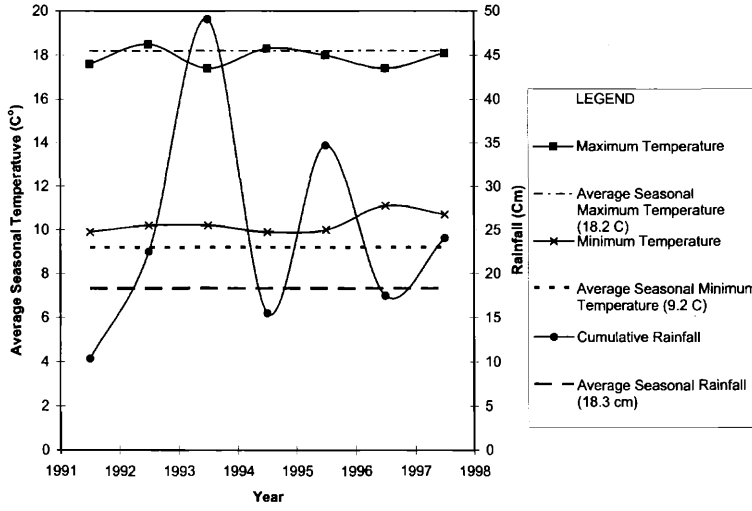

Figure 2. Temperature and precipitation during the study period.

(Atwood et al. 1998a,b). Weather data presented here, coupled with demographic data gathered by Atwood et al. (1998b), are useful in attempting to explain these population trends.

Rainfall appears to be a mixed blessing for California Gnatcatchers and can be viewed in two ways. The inverse correlation shown in Figure 3 suggests that overwinter survivorship may be reduced in years of above-average rainfall (several days of continuous rain may decrease food availability; Holmes et al. 1986), limiting population levels in the nesting season to follow. This is precisely the pattern shown by Atwood et al. (1998b): survivorship was greatest prior to the population peaks in 1994 and 1996. Another view of Figure 3 suggests that above-average rainfall in this arid landscape allows for increased productivity and an increase in the nesting population the following year (cf. DeSante and Geupel 1987). Again, at least partial support has been provided by Atwood et al. (1988b), as reproductive success was greatest in 1993, one year prior to the population spike shown in Figure 3. Displacement of some birds by the October 1993 Laguna Canyon Fire, separated from the Crystal Cove study site by the width of Pacific Coast Highway, probably accentuated the 1994 peak at Crystal Cove, as suggested by Bontrager et al. (1995) and Atwood et al. (1998a).

Both of these phenomena have been proposed as major regulating factors in other passerines, and it is likely that the two interact with one another over time to influence gnatcatcher population levels. Sherry and Holmes (1993) noted that, in general, species mostly resident in the temperate zone tend to be limited mainly by winter mortality (e.g., Root 1988c, Arcese et al. 1992, Mehlman 1997), especially smaller species (Graber and Graber 1979, Cawthorne and Marchant 1980) such as the California Gnatcatcher. How-

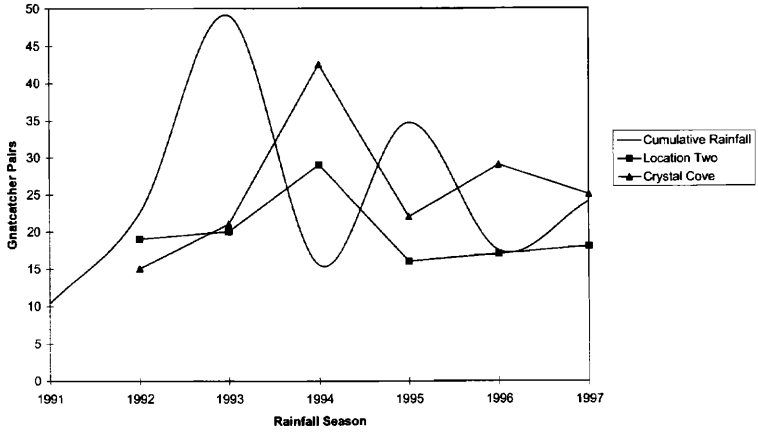

Figure 3. Previous season rainfall vs. numbers of California Gnatcatcher pairs at two locations in coastal Orange County, 1991–1997.

ever, O'Connor (1991) stated that weather is usually considered merely as a transient influence on bird populations. A number of other authors (Nolan 1978, DeSante and Geupel 1987, Johnson and Geupel 1996, Chase et al. 1997) have emphasized productivity in determining population size, especially among migratory species.

Only additional data and analysis will clarify how these and other factors regulate California Gnatcatcher populations. No one factor is likely to account wholly for a given population level (Newton 1991). Our analysis does not consider the impact of minimum temperature or short-term severe weather, which may be more important than seasonal averages (Arcese et al. 1992, Atwood 1993, Mock 1998). Nor do we yet understand the potential effect of metapopulation dynamics on analyses such as ours. O'Connor (1991) suggested that when primary habitats are saturated, secondary habitats are often colonized, and when those are in turn colonized fully, further habitats come into use. Hence primary habitats will usually be saturated and vary little from year to year, but secondary habitats may vary substantially.

In conclusion, our data suggest that the synchrony observed is produced by common population responses to commonly experienced weather patterns, perhaps related to higher mortality in wetter years.

SUMMARY

Similar methods were used to estimate the breeding populations of the California Gnatcatcher at two large sites (ca. 100 ha) in coastal Orange County, California, from 1992 to 1997. Population fluctuations were highly correlated ($r = 0.759$, $P \leq 0.02$), and seasonal rainfall and population levels were inversely related. Demographic data obtained elsewhere suggest that increased rainfall may increase winter mortality, at the same time that it

increases productivity in the following nesting season. The potential for synchronous population fluctuations on a regional scale has obvious management implications. Permanent or long-term monitoring at selected sites may improve the reliability of interpretations of short-term data and assist in planning for potential population bottlenecks.

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