ENERGETIC CONSTRAINTS TO THE DISTRIBUTION AND ABUNDANCE OF THE CALIFORNIA GNATCATCHER

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The relation of physiology to distribution in terrestrial vertebrates is neither direct, simple, nor obvious—George Bartholomew, 1958

Year-to-year variations in temperature, precipitation, and food supply affect the survival and reproduction of organisms. Annual fluctuations in birth rate and survival are often expressions of this environmental variability. It is generally believed that the viability of most populations decreases with increasing environmental variation (Burgman et al. 1993). A long series of years in which survival and/or birth rate are low may threaten the existence of a population. In the absence of human-caused threats, environmental variation is probably the greatest threat to population viability (Dennis et al. 1991, Järvinen and Väsänen 1984, Stacey and Taper 1992, Virkkala 1991).

The traditional view is that survival of small birds is most influenced by a combination of precipitation and cold weather, being low when the two coincide (Gessaman and Worthen 1982, Lustick and Adams 1977). Winter is typically the time of year with the highest mortality (Ricklefs 1969, Gessaman and Worthen 1982). Empirical work has demonstrated a linkage between variation in weather, food resources, and songbird demography (e.g., Holmes et al. 1991, Martin 1987, Sullivan 1989). Some studies suggest a causal link between physiology and species distribution (e.g., Yarbrough 1971, Ketterson and King 1977, Weathers 1979, Weathers and van Riper 1982, Hayworth and Weathers 1984, Root 1988, Hinsley et al. 1993). Earlier researchers, however, considered behavioral and ecological factors to be more important than physiological factors in limiting a species' distribution (e.g., Bartholomew 1958, Sturkie 1965).

The assumption that variation in climate can be a major factor influencing population viability is supported by analyses of the geographic limits of songbird distributions (Root 1988). Correlative evidence indicates that the winter distribution and abundance patterns of many bird species may be limited by their winter energy requirements. Root (1988) found that several species of songbirds appeared to be limited to areas where the January mean minimum temperature (JMMT) resulted in thermal compensation (i.e., thermoregulation plus basal requirements) less than 2.49 (standard error 0.07) times a species' basal metabolic requirement. The distribution-limiting isotherm is termed T_{dis}.

The purpose of this paper is to evaluate the relevance of the Root model to the distribution and abundance of the California Gnatcatcher (*Polioptila californica*). Thousands of acres of otherwise apparently suitable coastal sage scrub (CSS) in the eastern portion of its range in California appear to support few gnatcatchers (Atwood and Bolsinger 1992, Mock 1993, D.

Padley, P. Unitt, B. Wagner, J. Newman pers. comm.), suggesting possible systematic differences in environmental conditions between coastal and inland areas that influence where gnatcatchers are able to persist. Substantial California Gnatcatcher mortality associated with cold, wet weather conditions has been documented (Mock and Bolger 1992).

METHODS

To evaluate the energetic-constraints hypothesis, I obtained historical climate data for weather stations throughout southern California (sources: National Climatic Data Center, North Carolina; Univ. Calif. Agricultural Extension Service 1970). I categorized weather-station locations shown in Figure 1 as to whether they were associated with the gnatcatcher's historical distribution [Atwood 1993, San Diego County regional geographic-information system (GIS) database, J. Newman, D. Padley pers. comm.). Annual total precipitation and JMMT were evaluated relative to elevation and distance from the coast.

I calculated a predicted range of T_{dis} from allometric equations in Root (1988), then compared my prediction with a detailed energetics model developed by Webster and Weathers (1990) for the Verdin (*Auriparus flaviceps*; mass 6 g) wintering in Riverside County. I adapted the model for the gnatcatcher by using temperature data from weather stations along the eastern boundary of the gnatcatcher's known distribution in San Diego County.

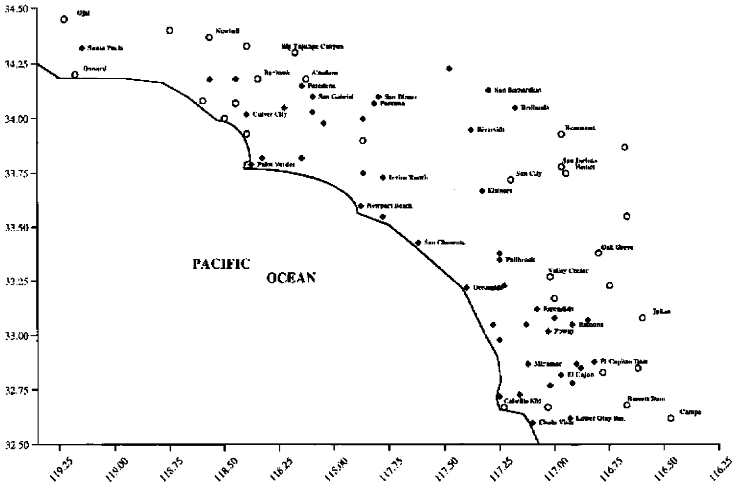

Figure 1. Distribution of weather stations within the southern California range of the California Gnatcatcher. Filled diamonds, locations with gnatcatcher populations; open circles, gnatcatchers absent.

RESULTS AND DISCUSSION

The current known distribution (Figure 1) and abundance of the California Gnatcatcher in California is concentrated along the coast in maritime-influenced areas of Orange and San Diego counties (Atwood 1993, county GIS databases). Much of the potentially suitable habitat in the peripheral portions of the documented range of the gnatcatcher has not been extensively surveyed; however, surveys of these areas typically have yielded relatively few new gnatcatcher sightings. For example, 1992 surveys of 2400 acres of CSS in Marron Valley, southeast of Otay Mountain, detected only three individuals and CSS around Gregory Mountain, east of Interstate 15 near Pala, also appears to be unoccupied (Ogden Environmental unpublished data).

Likewise, surveys in Riverside County suggest that CSS near Beaumont, Hemet, San Jacinto, and Sun City lacks substantial populations of the California Gnatcatcher (D. Padley, J. Newman pers. comm.). The interior valleys of Los Angeles County historically supported gnatcatchers, but populations are lacking in the Santa Monica Mountains and foothills of San Gabriel Mountains (Atwood 1993). Ventura County historically supported birds near Santa Paula, and there is a recent sighting of a single individual near Moorpark (Atwood 1993, C. A. Jones and R. S. Ramirez unpubl.).

Winter weather patterns within the range of the gnatcatcher are influenced by distance from the coast (maritime influence) and elevation, correlated factors (Figure 2). January mean minimum temperature is influenced significantly by both distance from the coast and elevation. Step-wise multiple regression of JMMT on distance and elevation showed that these factors account for a significant portion of the regression variance (r^2 = 0.554, n = 52, F = 32.7, $P < 0.0001$): JMMT = 7.239 − 0.0043(elevation) − 0.0363(distance).

Mean annual total precipitation (MATP) is primarily correlated with elevation (r^2 = 0.279, n = 78, F = 29.4, $P < 0.0001$): MATP = 0.0211(elevation) + 32.849. Distance from the coast is not a significant factor; however, inland areas tend to experience more days of precipitation (r^2 = 0.661, n = 19, F = 36.04, $P < 0.0001$): days precipitation > 0.25 cm = 0.048(distance) + 4.222. This increased frequency of rain exposes gnatcatchers farther inland to more frequent thermal stress usually associated with the combination of cold temperatures and wet weather (Lustick and Adams 1977).

The apparent eastern limit of the California Gnatcatcher appears to coincide with a T_{dis} of 2.5°C (Figure 2), a value within the 95% confidence interval for the predicted T_{dis} derived from allometric equations developed by Root (1988). Ratios of resting metabolic rate to basal metabolic rate (RMR:BMR) calculated from the energetics model for the wintering Verdin suggest that California Gnatcatchers may be more sensitive to cold weather than most of the 14 species analyzed by Root (1988) (mean RMR:BMR 2.49, standard error 0.07, lower 95% confidence interval approximately 2.35). RMR:BMR for San Diego County areas lacking gnatcatchers mostly exceed 2.2 (Table 1). RMR:BMR for marginally occupied areas are between 2.10 and 2.15. Areas with substantial gnatcatcher occupation have ratios less than 2.10.

Overall, the eastern range limits of the California Gnatcatcher are generally consistent with the energetic-constraint hypothesis. Most CSS

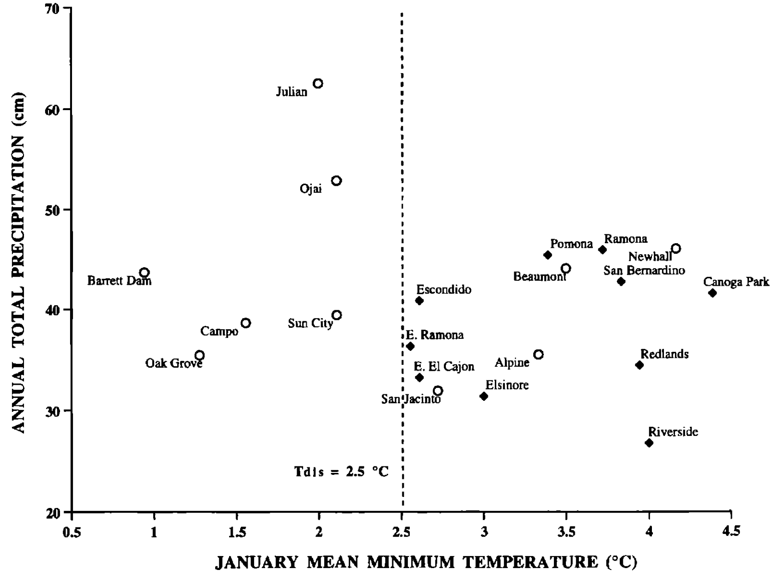

Figure 2. January mean minimum temperature and precipitation at weather stations where the January mean minimum temperature is less than 4.5°C. The energetics model predicts the California Gnatcatcher's occurrence only where T_{dis} > 2.5°C. Filled diamonds, locations with gnatcatcher populations; open circles, gnatcatchers absent.

above 450 m elevation does not appear to support substantial populations (Atwood and Bolsinger 1992; county GIS databases). Winter weather above this elevation is generally colder and wetter than below it. Annual over-winter survival of gnatcatchers at higher elevations is probably insufficient to sustain populations. One exception to this elevational limit is north of El Capitan Reservoir at the headwaters of the San Diego River (Figure 1), site of the most inland known population in San Diego County. The JMMT for this location is 5.1°C, well above the T_{dis} value of 2.5°C. Perhaps the San Diego River and El Capitan Reservoir have a moderating effect on JMMT in this area, allowing gnatcatchers to sustain themselves over the winter.

Root (1988) reported a T_{dis} of −1.1 °C for the closely related Black-tailed Gnatcatcher (*Polioptila melanura*). The Black-tailed Gnatcatcher's distribution in western Arizona becomes restricted as elevation increases, especially above 600 m, despite apparently suitable habitat above this elevation (Hunter 1988, Rosenberg et al. 1991). The difference in elevational limits between the Black-tailed and California Gnatcatchers is reflected in their different values of T_{dis}. Black-tailed Gnatcatchers have also been documented as roosting communally in thermal refugia (e.g., Verdin nests) during winter, a behavioral adaptation enhancing over-winter survival (Walsberg 1990). California Gnatcatchers associated with the Cactus Wren (*Campylorhynchus brunneicapillus*) may also seek shelter in that species' covered nests when available.

Table 1 Calculated Ratios of Resting Metabolic Rate to Basal Metabolic Rate for the California Gnatcatcher along the Eastern Edge of Its Range in San Diego County

Weather station location	Gnatcatcher population[a]	January mean maximum temperature (°C)	January mean minimum temperature (°C)	Calculated RMR:BMR ratio[b]
Alpine	No	17.3	3.3	2.15
Barrett Dam	No	17.4	0.9	2.22
Campo	No	15.8	1.6	2.27
Julian	No	12.7	2.0	2.38
Oak Grove	No	14.7	1.3	2.32
East El Cajon	Marginal	19.4	2.6	2.10
East Ramona	Marginal	18.4	2.6	2.14
Escondido	Marginal	18.5	2.6	2.13
Ramona	Marginal	17.2	3.7	2.15
El Cajon	Yes	18.7	5.5	2.04
El Capitan Dam	Yes	19.7	5.1	2.01

[a] Marginal indicates areas with few gnatcatcher sightings.

[b] Ratio of resting metabolic rate (RMR) to basal metabolic rate (BMR) calculated from energetics model for the Verdin in winter (Webster and Weathers 1990). Model assumed daytime and nighttime wind speeds of 8.0 and 0.8 km/hr, respectively.

There are a few weather stations with JMMT values greater than 2.5°C that currently do not have any nearby documented gnatcatcher populations (Alpine, San Jacinto, Beaumont, Newhall; Figure 2). This analysis suggests that gnatcatcher occupation of coastal sage scrub around these locations is not constrained by winter weather. Surveys of suitable habitat in these areas may reveal previously undocumented populations of the California Gnatcatcher.

The California Gnatcatcher appears to be lacking in the coastally situated Santa Monica Mountains and much of coastal Ventura County (Atwood 1993). Historically, gnatcatchers were known from near Santa Paula, and there is a recent sighting of a single individual near Moorpark (Atwood 1993, C. A. Jones and R. S. Ramirez unpubl.). From this analysis, the absence of gnatcatchers from the Santa Monica Mountains appears anomalous; the energetic-constraint hypothesis is not a likely explanation for the lack of gnatcatchers in the Santa Monica Mountains. This area supports substantial tracts of dense coastal sage scrub dominated by black and purple sage (*Salvia mellifera* and *S. leucophylla*; Westman 1981). Both of these species produce possibly insecticidal chemicals that may reduce insect densities, especially during droughts (Muller and Muller 1964, Muller and del Moral 1966, Tyson et al. 1974). Black-sage-dominated sage scrub has been reported as being less preferred by California Gnatcatchers (Bontrager 1991, Bontrager et al. 1995, Sweetwater Environmental Biologists 1994, Mock unpubl. data). The dominance of this less preferred subassociation may be one factor contributing to the gnatcatcher's absence from this coastal area.

This research provides a preliminary test of the long-standing hypothesis within ecology that abiotic environmental factors, such as extreme weather, play a role in shaping a species' distribution and abundance (Root 1988). It provides a scientific basis for giving priority in habitat acquisition and habitat-management programs toward areas likely to support resilient gnatcatcher populations (Root and Schneider 1993). Coastal areas support the majority of documented gnatcatcher-occupied habitat and these areas have JMMT well above the T_{dis} value of 2.5°C.

Additional field surveys are recommended for areas where JMMT is less than 4.4°C to test the energetic-constraint hypothesis further. Laboratory studies documenting the physiological response of the California Gnatcatcher to temperature and wind are also needed if a detailed energetics model for this species is to be developed. Alternative hypotheses to explain the absence of gnatcatchers from the Santa Monica Mountains and coastal Ventura County need to be developed and evaluated.

SUMMARY

The California Gnatcatcher's current distribution appears to be limited to only a portion of the available coastal sage scrub. I evaluate the hypothesis that abiotic environmental factors (i.e., thermal environment and precipitation) are the primary forces constraining the species' distribution and abundance. Root (1988) proposed that distributions of small sedentary songbirds are limited to where the January mean minimum temperature results in a resting metabolism less than 2.49 times the species' basal metabolic requirement, defining a limiting isotherm T_{dis}. The limiting T_{dis} for the California Gnatcatcher, based on a detailed energetic model for the Verdin, appears to be 2.5°C, within the 95% confidence interval of the Root model. The lack of gnatcatchers in the Santa Monica Mountains and coastal Ventura County is not consistent with the energetic-limitation hypothesis. These coastal areas are dominated by sage scrub subassociations believed to be less preferred by gnatcatchers.

ACKNOWLEDGMENTS

M. Webster graciously provided the Verdin energetics model program. Graphics and GIS support was provided by the San Diego office of Ogden Environmental and Energy Services. Funding for this study was provided by Ogden Environmental and Energy Services. Review of the manuscript was provided by C. Hunter, J. Rotenberry, P. Unitt, and an anonymous reviewer. I am grateful to all of the above individuals and organizations for their contributions to this study.

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Accepted 7 July 1998