DISPERSAL CAPABILITY OF THE CALIFORNIA GNATCATCHER: A LANDSCAPE ANALYSIS OF DISTRIBUTION DATA

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Dispersal is the means by which genetic and demographic exchange between subpopulations maintains the viability of the regional metapopulation (Fahrig and Merriam 1985, Lacy 1987, Merriam 1991). Our paper describes potential limitations of existing data on dispersal of juvenile California Gnatcatchers (*Polioptila californica*) and provides a landscape analysis of distribution data from areas of fragmented habitat. This analysis suggests that the dispersal capability of the California Gnatcatcher may be underappreciated.

METHODS

We studied California Gnatcatchers on approximately 842 ha of coastal sage scrub near the Sweetwater River in the unincorporated community of Rancho San Diego in southwestern San Diego County (32° 40' N, 117°W). Rancho San Diego is approximately 21 km from the Pacific coast and 21 km north of the United States–Mexico border. There were two primary study areas within 2 km of each other. Gnatcatchers were color-banded at the larger study area (1200 ha) from 1989 to 1991 and at the second smaller (111 ha), more easterly, study area (111 ha) from 1989 to 1992. We banded a total of 100 juvenile California Gnatcatchers between 1988 and 1992; 28 individuals were resighted in subsequent years after having dispersed away from their banding locations. We compare this dispersal data to comparable data for the Palos Verdes Peninsula (Atwood et al. 1998).

We evaluate the landscape characteristics of five dispersals of juvenile gnatcatchers to isolated sage scrub fragments at Palos Verdes (Los Angeles County), Encinitas, Point Loma, and the South Park, and Chollas Creek neighborhoods in the city of San Diego. For each dispersal we measured the distance both as a straight line and along a parsimonious landscape route favoring natural vegetation and topography. Vegetation and sighting information were derived from databases for regional habitat-conservation-planning programs maintained by the San Diego Association of Governments and the city of Rancho Palos Verdes. Aerial photographs (1:24,000 scale) were used to interpret the types of highly human-modified habitats.

RESULTS

Dispersal of banded juvenile California Gnatcatchers has been studied at Rancho San Diego (Mock and Bolger 1992), the Palos Verdes Peninsula (Atwood et al. 1998), and Siphon Reservoir, Orange County (Galvin 1998). The first two studies have documented median straight-line dispersal distances

of less than 3 km (Figure 1), whereas the third reports an average dispersal distance of less than 500 m (excluding a single observation at 7.55 km). The dispersal curves for Palos Verdes and Rancho San Diego are similar, but these results likely underestimate the gnatcatcher's typical dispersal distance because of the limitations of a relatively small search area (Barrowclough 1978, Cunningham 1986, Payne 1990). The Palos Verdes Peninsula population is presumably a closed population with restricted options for dispersing birds; this population appears to be able to reach all habitat patches on the peninsula. Potential habitat for dispersing gnatcatchers at Palos Verdes is limited to a relatively small area (less than 900 ha of habitat), and the longest possible straight-line distance between the most distant sage scrub patches on the peninsula is less than 10 km.

Twenty-eight of the 100 juveniles banded during the Rancho San Diego study were detected within the two study areas or were reported by biologists at other nearby sites. The remaining banded juveniles either died or dispersed outside of the study area and remained undetected. Many of the resightings in the Rancho San Diego study occurred during the drought years of 1989 and 1990, when gnatcatcher population densities were relatively low and habitat was readily available near a juvenile's natal territory. Fifteen of 28 banded gnatcatchers resighted at Rancho San Diego dispersed more than one territory away from their banding location (Figure 2). Nine of these 15 gnatcatchers most likely passed through landscapes that were extensively human-modified (residential, disturbed habitats, golf course, busy roads such

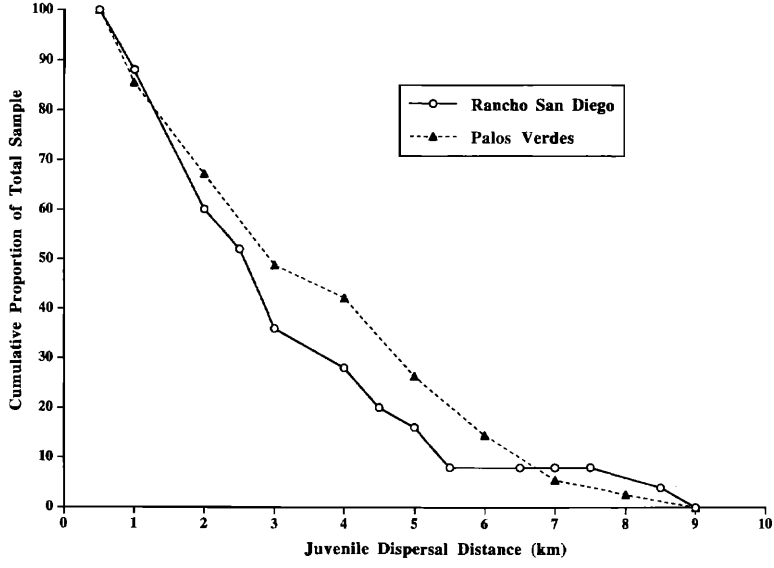

Figure 1. Dispersal-distance curves of California Gnatcatchers at Rancho San Diego (n = 28 individuals; Mock and Bolger 1992) and Palos Verdes (n = 76 individuals; Atwood et al. 1998).

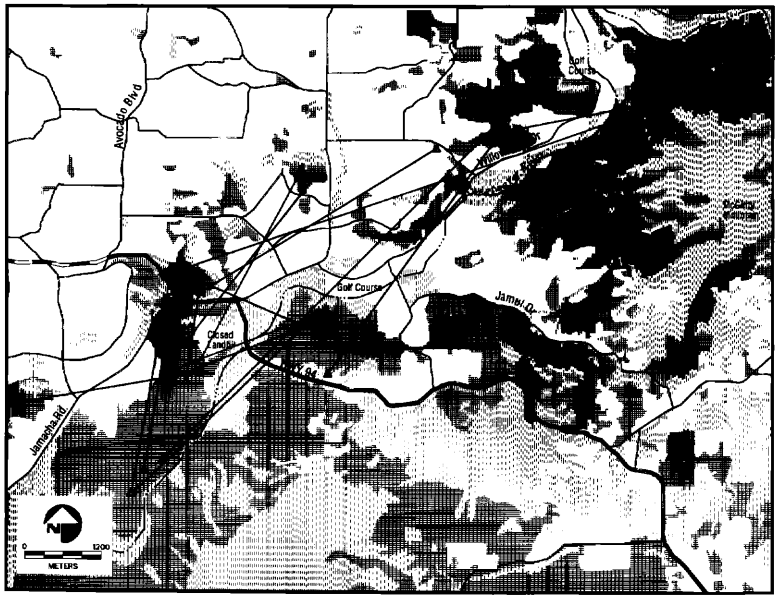

Figure 2. Straight-line dispersal routes for 15 California Gnatcatchers dispersing more than one territory away from their banding location at Rancho San Diego. Vegetation data from regional database. Cross-hatching, coastal sage scrub; vertical dashes, other natural vegetation; no pattern, developed areas; open triangles, California Gnatcatcher sightings.

as highways 54 and 94). Several survey reports have documented dispersal of juvenile California Gnatcatchers across highly man-modified landscapes (Atwood et al. 1998, Everett et al. 1993, Galvin 1998, J. Lovio pers. comm., D. Hunsaker pers. comm.). Recent detailed studies of fragmentation of sage scrub suggest that the gnatcatcher may be able to maintain itself within an archipelago of small patches of habitat (Lovio 1996).

Gnatcatcher occurrences in isolated habitat patches that have been fragmented for over 20 years also suggest dispersal across highly human-modified landscapes. Table 1 compares the straight-line dispersal distance and natural-landscape dispersal distance for the five examples. Figures 3 through 6 show general vegetation coverage of each dispersal location. The vegetation types shown are coastal sage scrub, other natural vegetation (e.g., chaparral, riparian habitats, and grasslands), and developed/agricultural land (highly human-modified landscapes). The types of highly human-modified landscapes crossed by dispersing gnatcatchers are also summarized in the table in order of relative abundance.

Palos Verdes

A banded juvenile California Gnatcatcher on the Palos Verdes Peninsula dispersed to the U.S. Navy Fuel Depot (Figure 3; Atwood et al. 1995). To reach the native vegetation at the fuel depot, the gnatcatcher had to traverse

Table 1 Presumed California Gnatcatcher Dispersal Distances across Highly Human-modified Landscapes[a]

Location	Dispersal distance (km)	Distance across modified landscape (km)	Proportion modified landscape (%)	Type of modified landscape
Straight-line route				
Palos Verdes	3.18	2.27	71	Moderate-density residential, well vegetated
Encinitas	1.10	0.79	72	High-density residential, little vegetation
Point Loma	5.83	5.28	91	Moderate- to high-density residential and commercial, poorly to well vegetated
South Park, San Diego	1.81	1.10	61	High-density residential, little vegetation
Chollas Creek, San Diego	1.73	1.26	73	High-density residential, well vegetated
Mean	2.73	2.14	74	
Natural-landscape route				
Palos Verdes	4.15	1.48	36	Parklike open space, well vegetated
Encinitas	1.26	0.34	27	High-density residential, well vegetated
Point Loma	6.54	2.99	46	Concrete channel; moderate- to high-density residential, well vegetated
South Park, San Diego	2.99	0.39	13	High-density residential, little vegetation
Chollas Creek, San Diego	2.17	0.79	36	High-density residential, well vegetated
Mean	3.42	1.20	32	

[a]Based on landscape analysis (see Figures 3, 4, 5, and 6).

highly human-modified landscapes for at least 1.3 km (Table 1). This route crosses several well-vegetated residential lots, continues along a strip of coastal sage scrub and other natural vegetation, crosses a wooded estate, skirts Palos Verdes Reservoir, and crosses Green Hills Memorial Park to reach the Navy fuel depot. At least two additional individuals have been subsequently documented dispersing between isolated sage scrub patches through human-modified habitats (Atwood et al. 1998).

Encinitas

Bailey noted a dispersing gnatcatcher on 14 June 1993 in a small fragment (less than 4 ha) of chaparral and riparian habitat (Figure 4). We assume it to have been a first-year bird since no gnatcatchers inhabited the site during the previous breeding season (1992). The gnatcatcher was not resighted during two subsequent visits in June. The nearest source population is around San Elijo Lagoon. To reach the fragmented site from San Elijo

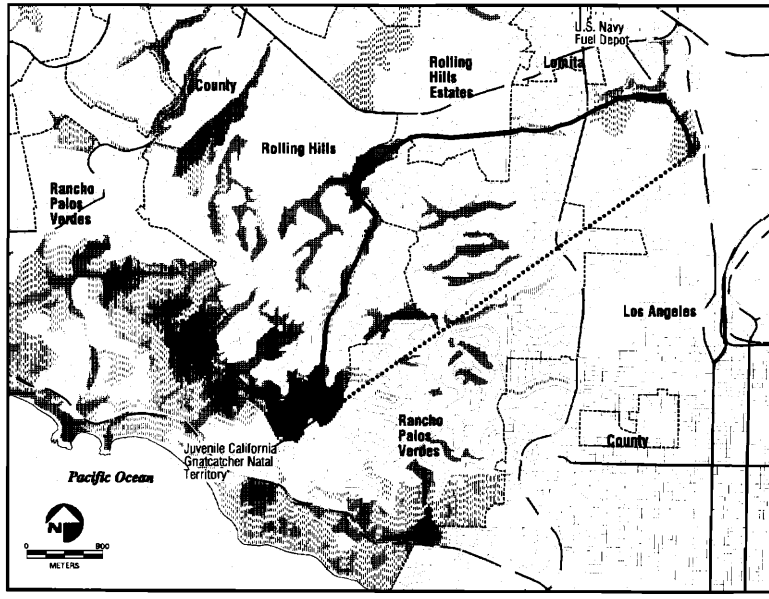

Figure 3. Straight-line (dotted line) and presumed natural-landscape routes (solid line) of juvenile California Gnatcatcher dispersing through highly human-modified landscape at Palos Verdes (Atwood et al. 1995). Vegetation from regional database. Cross-hatching, coastal sage scrub; vertical dashes, other natural vegetation; no pattern, developed areas.

Lagoon, a gnatcatcher would have to traverse a high-density residential neighborhood for at least 0.55 km (Table 1). Many of the homes in this neighborhood are well vegetated with mature ornamental trees and shrubs.

Point Loma

A California Gnatcatcher detected during focused surveys of Point Loma in 1993 was considered to be a dispersing individual (Figure 5; Everett et al. 1993). There were two previous reports of California Gnatcatchers on Point Loma in 1990 and 1992. Two gnatcatchers were detected in August of 1990, but did not remain in the area. Breeding gnatcatchers apparently have not occupied Point Loma for at least three decades and perhaps for much longer (Everett et al. 1993). Everett et al. (1993) concluded that Point Loma currently does not support a breeding gnatcatcher population and is apparently isolated by distance from likely source populations. However, W. E. Haas (pers. comm.) noted a pair of gnatcatchers in the fall of 1995 near the 1993 sighting location.

The source population nearest Point Loma is in Tecolote Canyon near the University of San Diego (Figure 5). To reach the native vegetation on Point Loma from Tecolote Canyon, a gnatcatcher would have to traverse highly human-modified landscapes for at least 4.8 km (Table 1). This route would follow the Tecolote Creek concrete drainage ditch, open space around Mission Bay, the San Diego River channel, Famosa Slough, and the

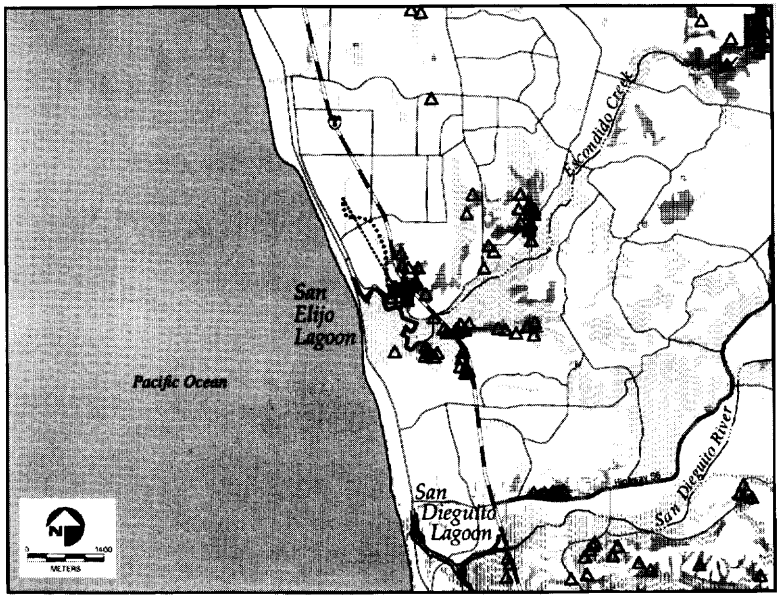

Figure 4. Straight-line (dashed line) and presumed natural-landscape routes (dotted line) of California Gnatcatcher detected in an isolated patch of coastal sage scrub in Encinitas (E. Bailey pers. obs.). Vegetation and gnatcatcher-locality data from regional database. Cross-hatching, coastal sage scrub; vertical dashes, other natural vegetation; no pattern, developed areas; open triangles, California Gnatcatcher sightings.

ridgeline of Point Loma, covered with moderate- to high-density residential neighborhoods having dense mature trees and shrubs. Two freeways and numerous major roads also would have been crossed.

South Park and Chollas Creek, San Diego

In November 1993 Bailey observed a pair of California Gnatcatchers along Home Avenue, east of Interstate 805 (Figure 6). In addition, two gnatcatchers were detected nearby in the fall of the same year adjacent to Interstate 15 near Highway 94 (RECON 1993). These patches of habitat have been fragmented for over 40 years, strongly suggesting gnatcatcher dispersal across highly human-modified landscapes (this assumes local extirpation followed by recolonization rather than the maintenance of a relict population). Nearby source populations are Chollas Community Park and Balboa Park, locations that are also habitat fragments. To reach the native vegetation at Home Avenue from Chollas Community Park, a gnatcatcher would have to traverse highly man-modified landscapes for at least 1.3 km (Table 1). This route crosses a well-vegetated high-density residential area, continues through coastal sage scrub along Chollas Creek, and crosses over a residential and commercial area to the Home Avenue site. To reach native vegetation near Interstate 15 from Balboa Park, a gnatcatcher would have to traverse highly

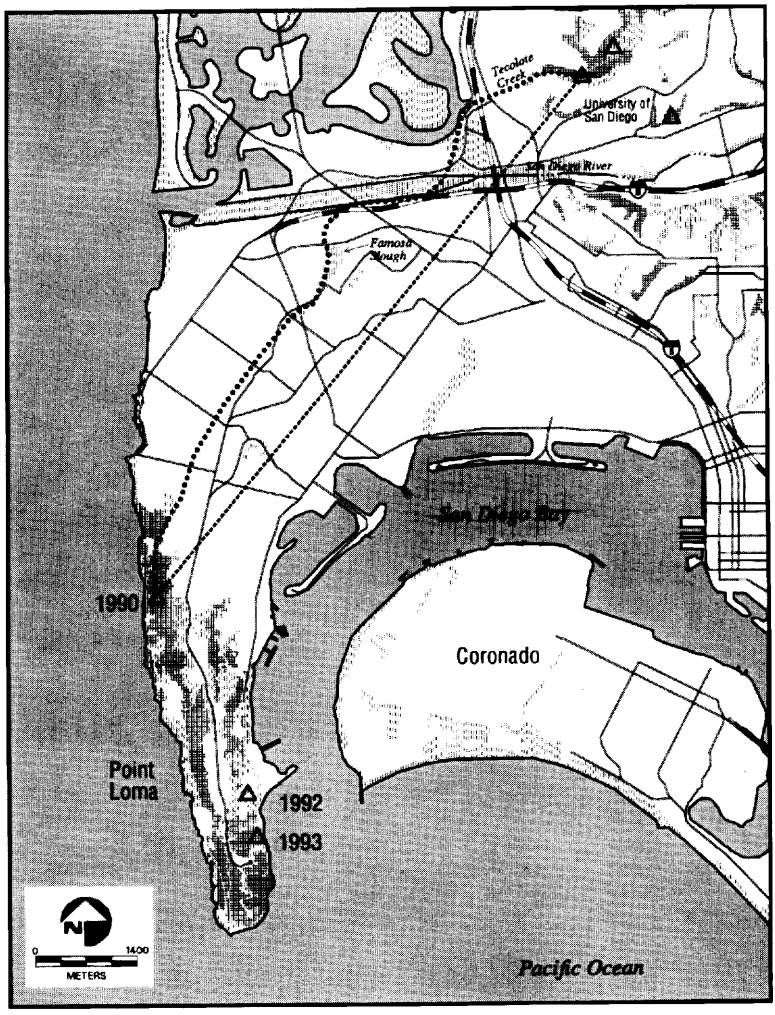

Figure 5. Straight-line (dashed line) and presumed natural-landscape route (dotted line) of California Gnatcatchers detected on Point Loma (Everett et al. 1993). Vegetation from regional database. Cross-hatching, coastal sage scrub patches; vertical dashes, other natural vegetation; no pattern, developed areas; open triangles, California Gnatcatcher sightings, with year of sighting.

human-modified landscapes for at least 0.63 km (Table 1). This route crosses both fragments of native vegetation in canyons and high-density residential areas with little vegetation. Subsequent effort by P. Unitt for the San Diego Bird Atlas has documented a pair nesting at the Interstate 15 site and three

Figure 6. Straight-line (dashed line) and presumed natural-landscape route (dotted line) of California Gnatcatchers detected in central San Diego (E. Bailey pers. obs.) and Chollas Creek (RECON 1993). Vegetation and gnatcatcher-locality data from regional database. Cross hatching, coastal sage scrub; vertical dashes, other natural vegetation; no pattern, developed areas; open triangles, California Gnatcatcher sightings.

gnatcatcher territories within Chollas Canyon between Chollas Park and the Home Avenue site. These subsequent sightings suggest there is a large cluster of habitat islands within an otherwise urban landscape that appears to allow for demographic exchange of gnatcatchers between habitat fragments (P. Unitt pers. comm, Lovio 1996).

DISCUSSION

We conclude that existing banding studies likely underestimate the typical and maximum California Gnatcatcher dispersal distance and that California Gnatcatchers appear to be capable of dispersing relatively long distances across highly human-modified landscapes (0.5 to 5.0 km, assuming a natural-landscape route; Table 1). Gathering an unbiased sample of dispersal distances is likely to be impractical for relatively large landscapes, such as San Diego County (Barrowclough 1978, Cunningham 1986, Payne 1990). An exponential model fitted to the Rancho San Diego dispersal data predicts a maximal dispersal distance of less than 22 km for 95% of juveniles surviving to October. A circle with a 22-km radius encompasses over 1500 km^2 (150,000 ha). A thorough search of sage scrub within such a large area over a short time period in fall (before substantial winter mortality) would be a very costly endeavor. Some conservation biologists have recommended

against extrapolating dispersal data beyond empirically derived maximum values (Brussard et al. 1993:16); however, this conservative interpretation of spatially limited and biased dispersal data will usually result in an underestimation of a species' dispersal capability (Cunningham 1986) and ultimately lead to an overestimation of the metapopulation's vulnerability to extinction.

Although not preferred in a preserve design, "stepping-stone" dispersal corridors may be the only remaining dispersal routes between some core gnatcatcher populations of significant conservation value. Such minimal corridors appear to exist in San Diego County (e.g., Lakeside and Oceanside) and are likely to be critical linkages between substantial populations of the California Gnatcatcher. There are also relatively large islands of gnatcatcher-occupied coastal sage scrub completely surrounded by man-modified landscapes (e.g., Twin Peaks and Van Dam Peak in Poway, Rattlesnake Mountain in Santee, Dictionary Hill west of Sweetwater Reservoir). These habitat fragments cumulatively support several hundred pairs, and their conservation value may be underestimated. Dispersal studies of banded gnatcatcher populations associated with presumed stepping-stone corridors and relatively large isolated patches of coastal sage scrub are recommended.

SUMMARY

In the California Gnatcatcher, dispersal of juveniles is the means by which genetic and demographic exchange between subpopulations maintains the viability of the regional metapopulation. Studies of banded individuals in southern San Diego County and at Palos Verdes in Los Angeles County have documented median dispersal distances of less than 3 km. These measures likely underestimate the gnatcatcher's typical dispersal capacity because of the difficulty of detecting dispersed individuals in open populations and the opportunity for successful dispersal to maximum distances being truncated in small isolated patches of habitat. Spatially isolated occurrences of gnatcatchers suggest juveniles' dispersal capability is greater than empirically documented with banded individuals. Juvenile California Gnatcatchers are apparently able to traverse highly man-modified landscapes for at least short distances. Underestimation of a species' dispersal capability can lead to an overestimation of the metapopulation's vulnerability to extinction. The conservation value of "stepping-stone" corridors and of relatively large patches of gnatcatcher-occupied coastal sage scrub surrounded by man-modified landscapes may be underestimated.

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