CALIFORNIA GNATCATCHERS, CACTUS WRENS, AND CONSERVATION OF COASTAL SAGE SCRUB ON THE PALOS VERDES PENINSULA

PROGRESS REPORT NO. 4 (1996)

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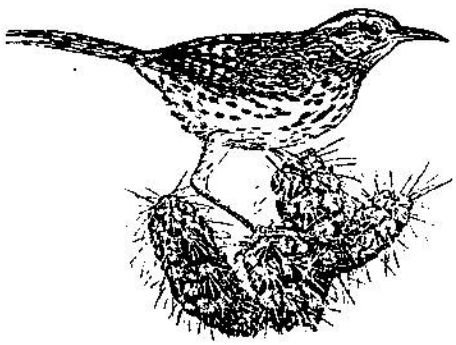

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INTRODUCTION

A critical aspect of the the State of California's Natural Community Conservation Planning (NCCP) program is the central role that science is intended to play in the formulation of land-use planning decisions and policies. By applying principles of modern conservation biology to data on the distribution, ecology, and population dynamics of selected plant and animal species, the objective of NCCP is to design regional reserves that will ensure the long-term viability of rare and declining habitat types. Such a "proactive" conservation approach, if successful, may potentially halt the decline of sensitive species dependent on the habitat type being considered, and thereby reduce the need to protect biodiversity through the cumbersome regulatory framework afforded by endangered species laws. Conversely, NCCP will also identify areas that are scientifically determined to be less important from a biological standpoint, and where economic development may consequently proceed without fear of triggering further additions to federal or state endangered species lists.

The pilot project of the NCCP program has focused on a plant community known as coastal sage scrub, which is patchily distributed in southern California in the coastal lowlands west of the Transverse and Peninsular ranges. Historically, coastal sage scrub was a dominant feature of the southern California landscape, where it occurred in a natural matrix that also included grassland, chaparral, and oak woodland communities. Today, as a result of urban and agricultural impacts, 70-90% of the historic acreage of coastal sage scrub is estimated to have been lost, and those tracts of scrub that remain in the region generally occur as "islands" surrounded by ever-increasing "seas" of urban development. Habitat loss and fragmentation has caused nearly 100 species and subspecies of plants and animals belonging to the coastal sage scrub community to decline to the point that federal and state wildlife agencies have formally designated them as endangered or threatened, or identified them as potential candidates for such listing (Atwood 1993).

The NCCP coastal sage scrub Scientific Review Panel selected three "target species" to use as the focus of conservation planning efforts for this habitat type: California Gnatcatcher (*Polioptila californica*), Cactus Wren (*Campylorhynchus brunneicapillus*), and orange-throated whiptail (*Cnemidophorus hyperythrus*). Although different or additional species are, in practice, being used as surrogates for coastal sage scrub conservation planning in some areas of southern California, virtually all NCCP efforts that have been initiated to date have included maintaining biologically viable populations of California gnatcatchers and cactus wrens as a principal objective. Consequently, sound ecological and behavioral information about these species will play a critical role in the preparation of NCCP plans.

To provide some of the biological information needed to develop scientifically credible conservation plans, Manomet Observatory for Conservation Sciences began, in 1992, an intensive, long-term study of California Gnatcatcher and Cactus Wren ecology and population dynamics, especially focusing on populations of these species that occur on the Palos Verdes Peninsula, Los Angeles Co., California. The primary objectives of Manomet's study have been largely defined by the research needs identified in the NCCP coastal sage scrub conservation guidelines prepared by the California Department of Fish and Game. These objectives include: (1) develop GIS data layers delineating the extent of coastal sage scrub vegetation and the distribution of California gnatcatchers and cactus

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wrens; (2) determine the extent and causes of annual variation in gnatcatcher and wren reproductive success, survivorship, and territory size; and (3) collect data on factors affecting the dispersal behavior of gnatcatchers and wrens.

This report, prepared pursuant to the requirements of U.S. Navy Contract No. N68711-95-C-7615, summarizes data collected during the 1996 breeding season including, where appropriate, comparison of results with those obtained during 1993 (Atwood et al. 1994), 1994 (Atwood et al. 1995a), and 1995 (Atwood et al. 1995b). Because of the continuing process of data entry and editing, the results presented here supersede those presented in previous progress reports. At the present time, Manomet's Palos Verdes study is anticipated to continue at least through 1997.

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METHODS

Population surveys. -- All major areas of natural habitat on the Palos Verdes Peninsula were surveyed for breeding California Gnatcatchers and Cactus Wrens during February - June of each year of the study (1993 -1996). The Peninsula's isolation from other natural areas in the Los Angeles basin renders it a "closed system" with regard to the movements of these non-migratory species. Furthermore, because of the limited amount of extant natural habitat present on the Peninsula, it is feasible each year to find and identify most or all surviving individuals.

Surveys were generally conducted before 11:00 h and after 16:00 h, under weather conditions deemed acceptable in terms of wind and temperature. Tape recordings of gnatcatcher and wren vocalizations were used to elicit responses. In areas where closely adjacent territories of unbanded birds posed potential confusion over the number of pairs actually present, teams of 2 - 4 biologists would revisit the site in order to obtain simultaneous observations of all birds in question. Funding limitations prevented us from precisely following the gnatcatcher survey protocols recommended by the NCCP scientific review panel or the U.S. Fish and Wildlife Service (USFWS), and some areas were only visited on one or two dates. Nonetheless, because of the limited amount of suitable habitat and the fact that our population estimates were based on observations of uniquely banded birds, the locations of simultaneously active nests, or simultaneous observations of unbanded birds, we feel confident in the accuracy of our results. There was no substantial change in our survey effort or technique among the four years reported here.

This research was conducted under U.S. Fish and Wildlife Service Endangered Species recovery permit PRT-800922, U.S. Fish and Wildlife Service Master Bird-Banding Permit 09996, State of California Scientific Collecting Permit 1025, and a California Department of Fish and Game Memorandum of Understanding dated 25 August 1992 (as amended).

Breeding biology and reproductive success. -- Study of California Gnatcatcher breeding biology included documentation of total reproductive output of 9 pairs during 1993, 20 pairs during 1994, 21 pairs during 1995, and 18 pairs during 1996; data from 4, 4, 10, and 8 pairs of Cactus Wrens were similarly obtained in each of these years, respectively. Occupied territories were visited from 1 - 3 days per week, beginning in early March and continuing through late June or mid-July. Nests were located through direct observation of nest building, nest exchanges, or feeding of nestlings. In all cases, we believe that we discovered all of the successful nesting attempts of each of these focal pairs. The number of juveniles fledged per successful nest was based on counts obtained 1 - 5 days after fledging.

To minimize impacts that might potentially result from monitoring activities, visits by biologists to California Gnatcatcher nests were generally limited to 3 dates from the beginning of nest building to fledging, especially during 1994 and 1995. Visits were planned to occur once near the beginning of incubation, once during the first week of the nestling stage (in order to estimate age of juveniles and thereby schedule a follow-up banding visit), and once to band nestlings at approximately 8 days of age. We made no effort to expand the presently available data on clutch size, as our primary goal was to determine the total number of fledglings produced annually by each pair. Nests were not visited when Scrub Jays (*Aphelocoma coerulescens*), Loggerhead Shrikes (*Lanius ludovicianus*), or Brown-

headed Cowbirds (*Molothrus ater*) were seen nearby. Cactus Wren nests were irregularly inspected due their generally inaccessible locations.

We used Japanese mist nets to capture adult and fledgling gnatcatchers and wrens for banding; birds were usually attracted to the vicinity of the nets by playback of recorded vocalizations. Most nestling gnatcatchers were banded at approximately 8 - 9 days of age; handling before this age was impractical due to the birds' small size. Nestling cactus wrens were generally banded at approximately 10 days of age. Banding efforts as reported to the USFWS Bird-Banding Laboratory are provided in Appendix A.

Dispersal behavior and survivorship. -- Maximum direct-line distances were used as the basis for evaluating the dispersal behavior of juvenile California Gnatcatchers and Cactus Wrens. To reduce the likelihood of including observations of birds that had not yet begun to disperse from their natal territories, we excluded all resightings obtained < 150 days after the initial banding date. For gnatcatchers, only observations of juveniles that were banded as nestlings are included here. Movements of hatch-year and nestling Cactus Wrens were included in the dispersal analyses for that species.

Survivorship estimates for both species (adults and juveniles) were calculated between the nesting seasons of 1993 - 1994, from 1994 - 1995, and from 1995 - 1996.

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RESULTS

Population size and distribution. -- Twenty-six to 56 breeding pairs of California Gnatcatchers were found on the Palos Verdes Peninsula during the 1993 - 1996 nesting seasons, with 36 pairs estimated to be present in 1996. The Peninsula's gnatcatcher population was at its highest level (56 pairs) in 1994. A 54% decrease between 1994 and 1995 was followed by a 38% increase from 1995 to 1996. The majority of pairs (1993 - 86%; 1994 - 86%; 1995 - 77%; 1996 - 72%) were located in polygons classified as Sagebrush Scrub or Cactus Scrub (Table 1). During 1993 - 1996 most gnatcatchers on the Peninsula (35 of 36 pairs) occurred within the jurisdictional boundaries of the City of Rancho Palos Verdes (Fig. 1; Table 1).

Fifty, 61, 63, and 57 breeding pairs of Cactus Wrens were found on the Palos Verdes Peninsula during 1993, 1994, 1995 and 1996, respectively. Because of difficulties associated with censusing this species, we believe these results indicate an essentially stable population during these years. The majority of pairs (1993 - 84%; 1994 - 77%; 1995 - 81%; 1996 - 91%) were located in polygons classified as Sagebrush Scrub or Cactus Scrub (Table 1); as breeding pairs of this species are invariably associated with patches of *Opuntia*, location of pairs in polygons delineated as habitats such as Grassland merely reflects inherent inaccuracies in mapping of vegetation and pair locations, as well as in definitions of vegetation subassociations (Atwood et al. 1994). During 1993 - 1996 most Cactus Wrens on the Peninsula (54 of 57 pairs) occurred within the jurisdictional boundaries of the City of Rancho Palos Verdes (Fig. 2; Table 1).

TABLE 1. DISTRIBUTION OF CALIFORNIA GNATCATCHERS AND CACTUS WRENS ON THE PALOS VERDES PENINSULA BY HABITAT TYPE AND CIVIL JURISDICTION.

	HABITAT TYPE [a]						JURISDICTION [b]				
	SS	CS	SL	LS	GS	GR	RPV	PVE	RH	RHE	SP
California Gnatcatcher											
1993 (51 total)	35	9	2	2	2	1	42	3	1	0	5
1994 (56 total)	39	9	1	1	5	1	46	3	1	1	5
1995 (26 total)	16	4	2	1	2	1	23	2	1	0	0
1996 (36 total)	25	1	0	0	6	4	35	1	0	0	0
Cactus Wren											
1993 (50 total)	18	24	2	2	4	0	46	4	0	0	0
1994 (61 total)	18	29	3	1	8	2	53	6	2	0	0
1995 (63 total)	22	29	1	0	9	2	58	5	0	0	0
1996 (57 total)	29	23	1	0	2	2	54	2	1	0	0

[a] SS = Sagebrush Scrub; CS = Cactus Scrub; SL = Sage - Lemonadeberry Scrub; LS = Lemonadeberry Scrub; GS = Grassland - Scrub Ecotone; GR = Grassland.

[b] RPV = Rancho Palos Verdes; PVE = Palos Verdes Estates; RH = Rolling Hills; RHE = Rolling Hills Estates; SP = San Pedro.

FIGURE 1. APPROXIMATE DISTRIBUTION OF CALIFORNIA GNATCATCHER PAIRS, 1996.

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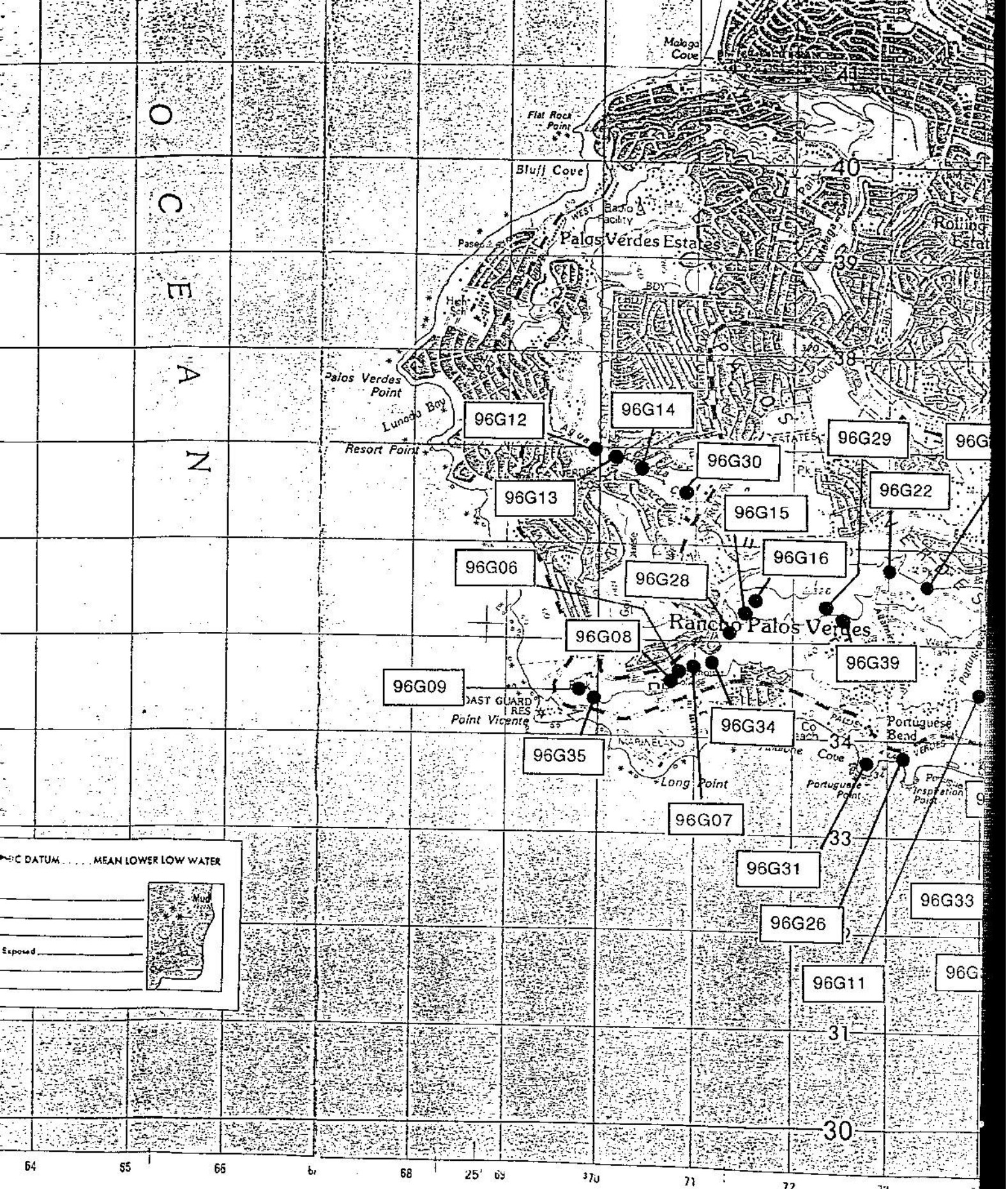

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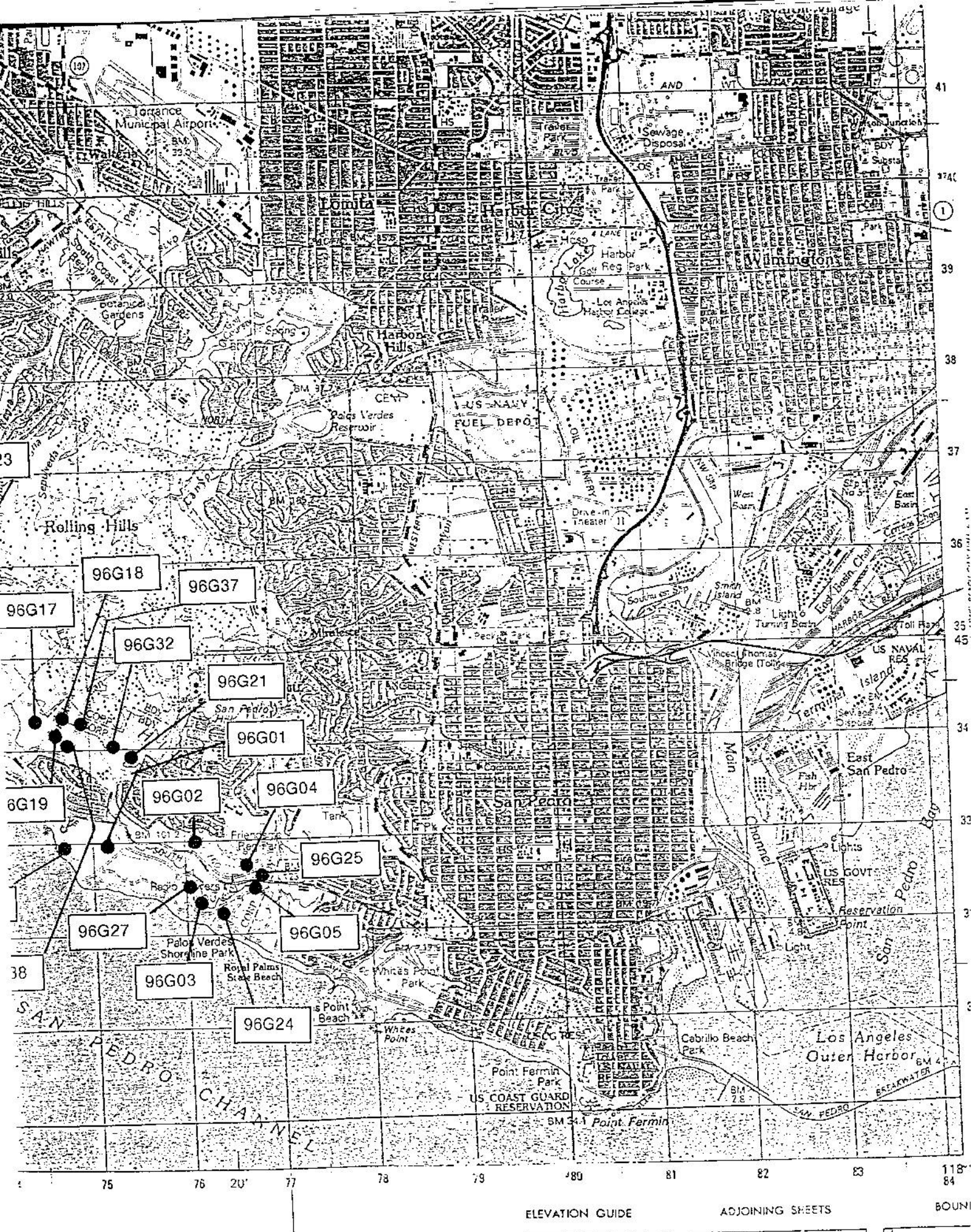
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Torrance Municipal Airport
Lomita
Harbor City
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Rolling Hills
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Palos Verdes Reservoir
U.S. NAVY FUEL DEPOT
Harbor Lake Golf Course
Harbor Reg Park
Los Angeles Harbor College
Sewage Disposal
Drive-in Theater
West Basin
East Basin
Smith Island
Light 6
Turning Basin
Vincent Thomas Bridge (Toll)
US NAVAL RES
Terminal Island
San Pedro
East San Pedro
Fish Hbr
Main Channel
San Pedro Bay
Lights
US GOVT RES
Reservation Point
Light
Friendship Park
Palos Verdes Shoreline Park
Royal Palms State Beach
White Point Park
Point Fermin Park
US COAST GUARD RESERVATION
Point Fermin
Cabrillo Beach Park
Los Angeles Outer Harbor
BREAKWATER
SAN PEDRO CHANNEL
Botanical Gardens
South Coast Regional Park
Seaport
Pacific Coast Hwy
Western Ave
Normandie Ave
Vermont Ave
Figueroa St
Anaheim St
Harbor Blvd
Alameda St
Avalon Blvd
Main St
Broad Ave
Gaffey St
Pacific Ave
Beacon St
Front St
Miraleste
Peck Park
Mary Star of the Sea
Trailer Park
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Oil Refinery
Sewage Disposal
Sewage Treatment
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FIGURE 2. APPROXIMATE DISTRIBUTION OF CACTUS WREN PAIRS, 1996.

NOTE THAT DUE TO MAP SCALE AND THE CLOSE PROXIMITY OF SOME TERRITORIES, SOME SOLID CIRCLES REPRESENT MULTIPLE PAIRS.

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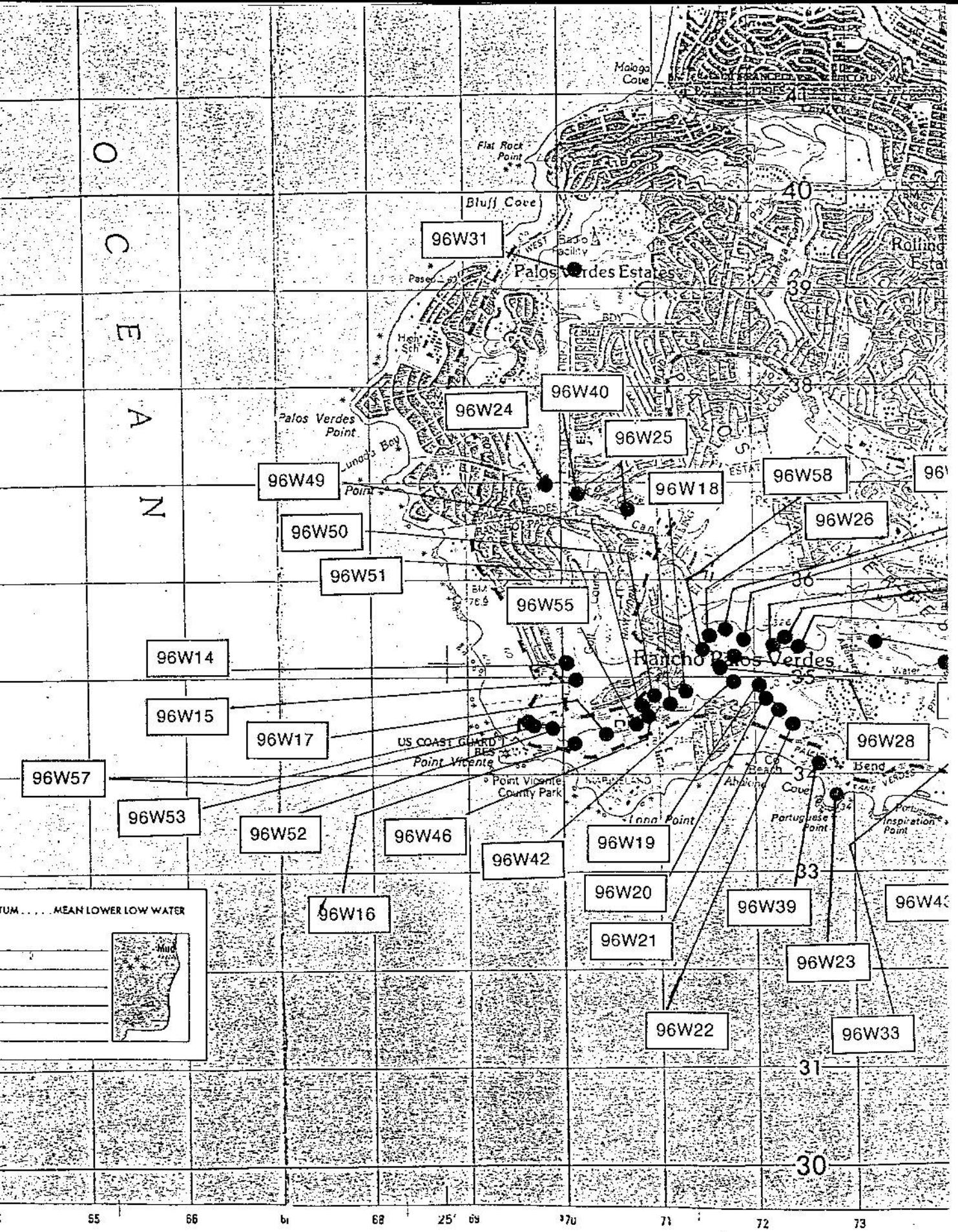
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Flat Rock Point
Bluff Cove
Palos Verdes Estates
Palos Verdes Point
Point Vicente
Point Vicente County Park
Rancho Palos Verdes
Portuguese Bend
Portuguese Point
Inspiration Point
Abalone Cove
Long Point
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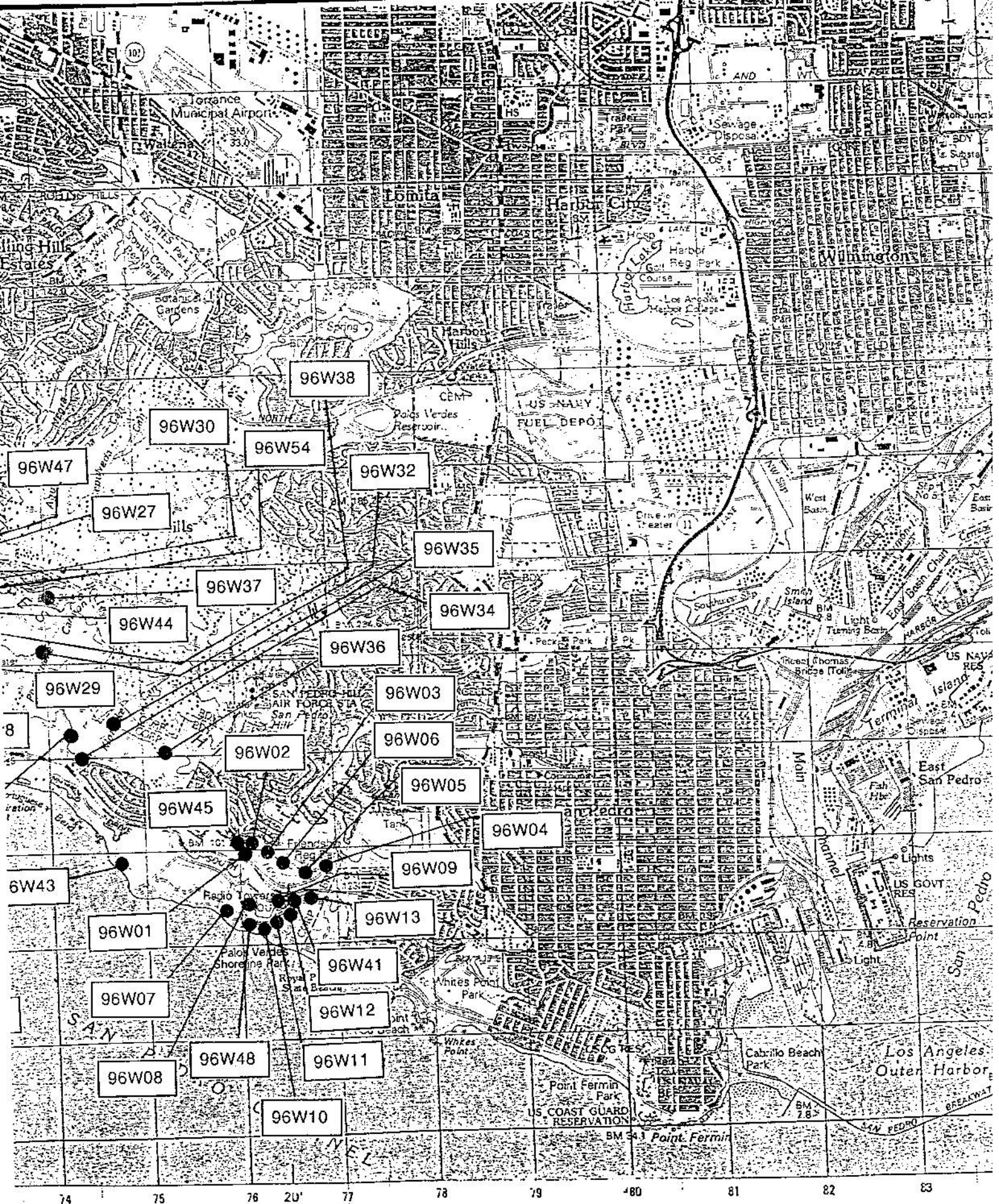

Torrance Municipal Airport
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Harbor City
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Los Angeles Harbor College
Sewage Disposal
Trailer Park
Botanical Gardens
Sandpits
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US NAVY FUEL DEPOT
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Cabrillo Beach Park
Los Angeles Outer Harbor
Point Fermin Park
US COAST GUARD RESERVATION
Point Fermin
SAN PEDRO HILL AIR FORCE STA
San Pedro Hill
Friendship Reg Park
Radio Towers
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2352 II
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During each year of the study period, a substantial portion of the Peninsula's gnatcatcher population was concentrated in three patches, located in the vicinities of Agua Amarga Canyon, Edward's Canyon (McCarrell's Canyon), and Klondike Canyon (Fig. 3, patch numbers 22, 27, and 33, respectively). These three areas, which encompassed only approximately 25% of the total area of coastal sage scrub (all subassociations) present on the Peninsula, supported from 53% - 69% of the total breeding population of gnatcatchers found from 1993 - 1996.

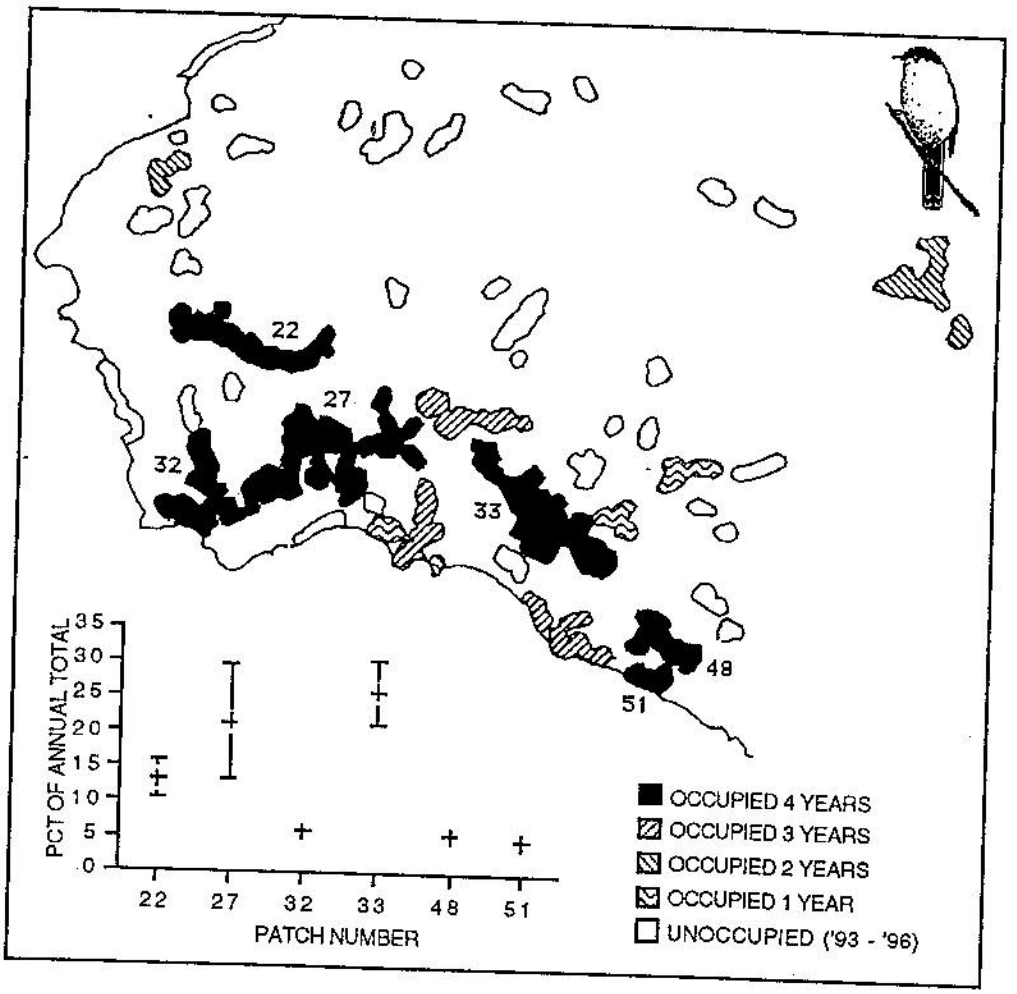

FIGURE 3. CALIFORNIA GNATCATCHER OCCUPANCY OF MAJOR TRACTS OF COASTAL SAGE SCRUB, 1993 - 1996. EACH PATCH DEFINED BY 75 M BUFFER SURROUNDING POLYGONS DESIGNATED AS SAGEBRUSH SCRUB OR CACTUS SCRUB. GRAPH (INSET) SHOWS MEAN ANNUAL PERCENT OF TOTAL BREEDING PAIRS (± 2S.E.) FOUND IN PATCHES (NUMBERED ON MAP) OCCUPIED CONSISTENTLY FROM 1993 - 1996.

Reproductive success. -- Table 2 summarizes data on gnatcatcher and wren reproductive success on the Peninsula since 1993. The have been no significant annual differences in reproductive success of either species from 1993 – 1996 (Kruskal-Wallis test; California gnatcatcher, H corrected for ties = 4.4, P = 0.22; cactus wren, H corrected for ties = 0.3, P = 0.97).

TABLE 2. REPRODUCTIVE SUCCESS (NUMBER OF FLEDGLINGS PRODUCED PER PAIR PER YEAR) OF CALIFORNIA GNATCATCHERS AND CACTUS WRENS ON THE PALOS VERDES PENINSULA, 1993 - 1996.

YEAR	X (# fledglings)	s.d.	n (pairs)	Range (# fledglings/pair)
California Gnatcatcher				
1993	3.89	1.69	9	0 - 6
1994	2.70	2.34	20	0 - 8
1995	2.62	3.09	21	0 - 7
1996	2.72	2.37	18	0 - 8
Cactus Wren				
1993	3.50	2.18	4	0 – 9
1994	3.00	2.58	4	0 – 6
1995	3.40	1.05	10	0 – 9
1996	3.63	0.71	8	2 – 8

Survivorship. -- Table 3 summarizes California Gnatcatcher survivorship data from adult and juvenile gnatcatcher and wren cohorts known to be alive in 1993, 1994, and 1995. Results indicate that adult gnatcatcher survivorship from 1993 - 1994 and from 1995 - 1996 was similar (0.52 and 0.48, respectively), whereas juvenile gnatcatcher survivorship showed greater year-to-year variations. Survivorship of both adult and juvenile gnatcatchers appeared to be reduced from 1993 - 1994 (0.19 and 0.16, respectively).

TABLE 3. SURVIVORSHIP OF CALIFORNIA GNATCATCHERS AND CACTUS WRENS ON THE PALOS VERDES PENINSULA, 1993 - 1996.

YEAR	# BANDED	NUMBER SURVIVED TO YEAR+1	SURVIVAL RATE
California Gnatcatcher			
ADULTS			
1993	25	13	0.5200
1994	74	14	0.1892
1995	40	19	0.4750
JUVENILES			
1993	74	19	0.2568
1994	77	12	0.1558
1995	51	22	0.4314
Cactus Wren			
ADULTS			
1992	33	19	0.5758
1993	46	25	0.5435
1994	52	29	0.5577
1996	46	28	0.6087
JUVENILES			
1992	61	21	0.3443
1993	33	12	0.3636
1994	64	13	0.2031
1995	96	15	0.1563

Dispersal behavior. -- Gnatcatcher dispersal data were restricted to only those observations obtained ≥ 150 days after banding. The mean dispersal distance of gnatcatchers banded as nestlings of unknown sex and later found to be males was 2.85 km (s.d. = 2.12, n = 23); for females, the mean distance was 3.33 km (s.d.= 1.91, n = 28). There was no significant difference in dispersal distances between the sexes (Mann-Whitney U-test, Z corrected for ties = -0.985, P = 0.32), or among observations based on the 1993, 1994, and 1995 nestling cohorts (Kruskal-Wallis test, H corrected for ties = 4.73, P = 0.094) (Table 4). Figure 4 presents dispersal data based on movements of the 1993 – 1995 gnatcatcher nestling cohorts.

TABLE 4. MEAN DISPERSAL DISTANCES OF 1993, 1994, AND 1995 CALIFORNIA GNATCATCHER NESTLING COHORTS.

YEAR	MEAN (km)	S.D.	RANGE	n
1993	2.37	1.84	0.5 – 6.6	21
1994	3.73	2.59	0.3 – 8.3	12
1995	3.53	1.95	0.7 – 6.6	21

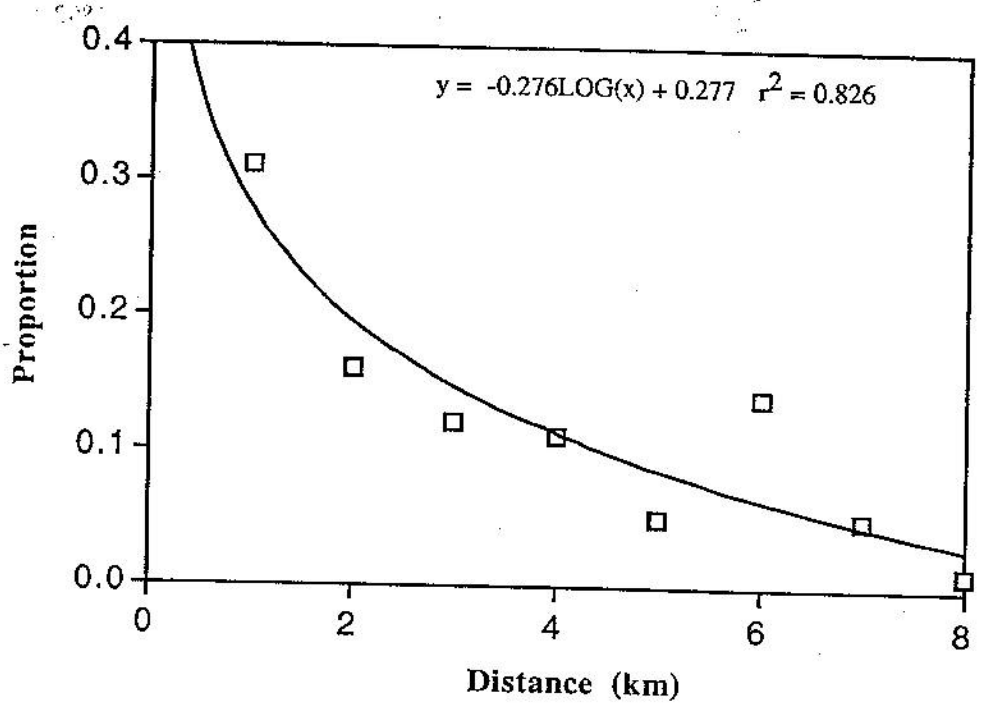

FIGURE 4. DISPERSAL CURVE (LOGARITHMIC MODEL) BASED ON RESIGHTINGS OF CALIFORNIA GNATCATCHERS HATCHED IN 1993 – 1995.

Figure 5 presents dispersal data based on movements of the 1993, 1994, and 1995 cactus wren juvenile cohorts. The mean dispersal distance of wrens banded as juveniles (both sexes combined due to small samples) was 1.86 km (s.d. = 2.17, n = 22). Small numbers of recoveries from the 1993 and 1994 cohorts precluded any analysis of among-year differences.

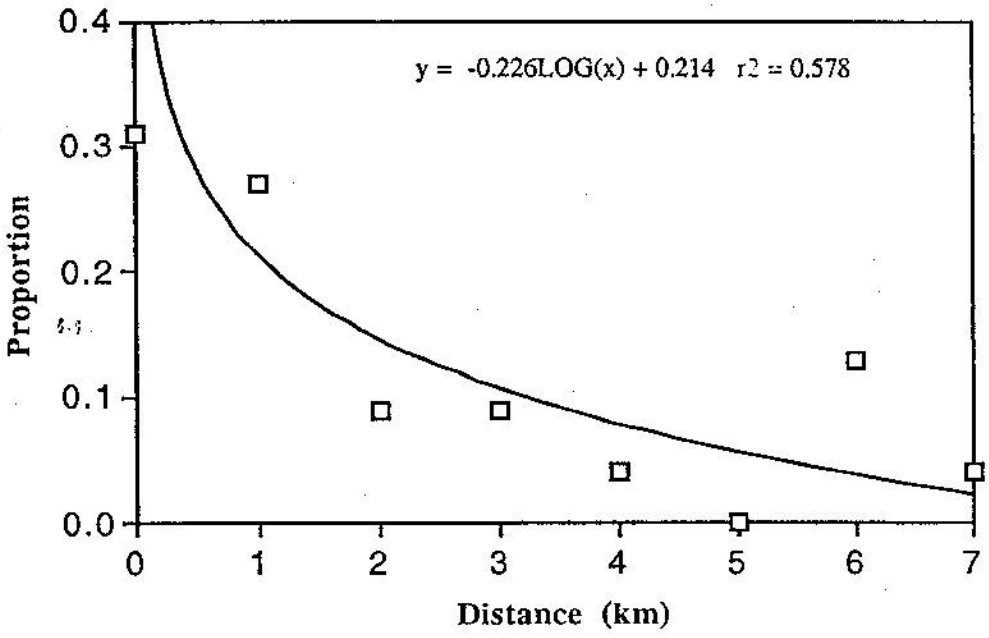

FIGURE 5. DISPERSAL CURVE (LOGARITHMIC MODEL) BASED ON RESIGHTINGS OF CACTUS WRENS HATCHED IN 1993 - 1995.

Miscellaneous. -- A single female gnatcatcher (SG-KR) was present on the U.S. Navy Fuel Depot (DFSP) located in San Pedro until at least 21 March 1996. On 4 April 1996 a nest was located near Rancho Palos Verdes City Hall that, on 8 May 1996, was determined to be attended by SG-KR and a banded male (SR-YM). SG-KR remained at this new location through the end of the 1996 breeding season, and successfully 3 fledglings out of 4 nesting attempts. The distance between DFSP and Rancho Palos Verdes City Hall is approximately 10.5 km (assuming straight-line movement). Movement of SG-KR during the 1996 breeding season was not unexpected given the absence of potential mates at the Fuel Depot.

On 9 July 1996, a different (unbanded) gnatcatcher, probably a juvenile, appeared at the Fuel Depot and was still present in early August. The sex of this bird has not yet been determined. This is the second known instance of this relatively isolated island of habitat being colonized by gnatcatchers presumed to have originated elsewhere on the Peninsula.

Habitat restoration efforts near the northern end of the Ocean Trails project have succeeded in establishing an area of *Encelia*-dominated coastal sage scrub on a tract of land that previously supported only disturbed grassland habitat. On several occasions during 1996, gnatcatcher pair 96G33, whose nest site was located in a small patch of

Artemisia situated adjacent to the restoration area, was observed foraging in the newly-established scrub. Details of the restoration activity, including initial palette of plant species used, timing of activities, and plant density and species composition at the end of the project, will hopefully be presented elsewhere. Knowledge of coastal sage scrub restoration remains limited, and improvements of available techniques will only be possible through careful documentation of failed and, as appears to be the case at Ocean Trails, successful efforts to create habitat that is suitable for species such as gnatcatchers. Especially in areas such as the Palos Verdes Peninsula, where extant tracts of coastal sage scrub are so few and so small that protection of viable gnatcatcher populations is an extremely difficult challenge, creation of a successful habitat reserve system will almost surely involve not only protection of most areas of existing habitat, but also restoration of coastal sage scrub in areas presently covered by disturbed grassland.

Finally, we describe here two unusual observations of gnatcatcher behavior that we made in 1996. Pair 96G15 (KS-YM male, MS-GR female) were siblings raised during successive nesting attempts in 1995 by pair 95G01. Pair 96G15 began two nests together in 1996, neither of which was completed. The female disappeared early in the season; subsequently, the male was frequently seen calling loudly and twice was observed quite far (up to 6 km on 12 April) from his original territory. On 15 April we observed KS-YM diligently building a nest, with no sign of a female anywhere in the vicinity. Material was still being added to this nest on 23 April and 26 April, and the nest appeared complete when we inspected it on 2 May. Later, on 13 May and 21 May, KS-YM was seen approximately 3 km from the original site. He was then resighted near the nest on 17 June, and remained (unpaired) in this vicinity throughout the remainder of the season. The nest was never used.

On 30 July 1996 we found a nest that contained nestlings that were mostly covered with a thin layer (< 1 mm) of dried mud. The mud was heaviest on the upperparts of the 2 nestlings that were positioned highest in the nest, and the nestling at the bottom was mostly clean. We do not know how mud got onto the nestlings.

Adult gnatcatchers have been reported to shade their nests during hot weather (Woods 1928). The territory of the pair (96G30) whose nest had mud-coated nestlings included a shallow, and in many places muddy stream. We speculate that the parents may have returned to brood the nestlings after bathing, thereby depositing a thin layer of mud on the nestlings. Although intentional belly-wetting as a method of cooling nests has been observed in many species of Charadriiformes (Begg and Maclean 1976, Maclean 1975 and references therein, Roberts 1977), we are unaware of any descriptions of such behavior in passerines.

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RECOMMENDATIONS FOR FURTHER STUDY

Manomet's Palos Verdes project is expected to continue at least through 1997. Future acquisition of data on California Gnatcatcher and Cactus Wren distribution, reproductive success, survivorship, and dispersal will follow the basic procedures used during 1993 - 1996. Data collected in this study have already been used in population viability analyses of Orange County gnatcatcher populations (Akçakaya and Atwood, in press; Appendix B), and should be applied to similar projects in the future.

Additionally, the possibility of reintroducing gnatcatchers to the DFSP should be evaluated by the U.S. Navy, USFWS, and California Department of Fish and Game. Relocating gnatcatchers has never been attempted (and, in fact, would obviously require careful consideration and special permitting). In most areas of southern California, such an approach is probably irrelevant, as habitat conservation plans can be built around extant tracts of natural land that support established gnatcatcher populations. However, on the Palos Verdes Peninsula, and possibly in other portions of the highly urbanized Los Angeles basin, maintenance of viable gnatcatcher populations may require more intensive management efforts, possibly including reintroduction programs. Federal ownership of the DFSP, the obvious willingness of the U.S. Navy to manage this land for rare species and engage in active habitat restoration programs, and the documented movements of gnatcatchers between the DFSP and other portions of the Peninsula, all suggest that such an idea should at least be discussed.

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Banding Schedules Submitted to USFWS Bird-Banding Laboratory, October 1996.

(None of the birds banded in 1996 would be expected to still be alive in 2009.)

A Habitat-based Metapopulation Model of the California Gnatcatcher

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Abstract. We present an analysis of the metapopulation dynamics of the federally threatened coastal California Gnatcatcher (*Polioptila c. californica*) for an approximately 850 km^2 region of Orange County, California. We developed and validated a habitat suitability model for this species using data on topography, vegetation, and locations of gnatcatcher pair observations. Using this habitat model, we calculated the spatial structure of the metapopulation, including size and location of habitat patches and the distances among them. We used data based on field studies to estimate parameters such as survival, fecundity, dispersal, and catastrophes, and combined these parameters with the spatial structure to build a stage-structured, stochastic, spatially-explicit metapopulation model. The model predicted a fast decline and high risk of population extinction with most combinations of parameters. Results were most sensitive to density-dependent effects, the probability of weather-related catastrophes, adult survival, and adult fecundity. Based on data used in the model, the greatest difference in results was given when the simulation's time horizon was only a few decades, suggesting that modeling based on longer or shorter time horizons may underestimate the effects of alternative management actions.

Introduction

The California Gnatcatcher's northernmost subspecies (*Polioptila c. californica*) has declined due to extensive agricultural and urban development of coastal sage scrub, the species' primary habitat type in southern California and northwestern Baja California (Atwood 1993). Listed in 1993 as threatened under the U.S. Endangered Species Act (ESA), protection of the gnatcatcher and its habitat has become a major focus in the inaugural application of the State of California's Natural Community Conservation Planning (NCCP) program (Atwood & Noss 1994). This voluntary, regional land-use planning process, aimed at delineating core tracts of essential natural habitat while allowing economic development in areas of lower biological significance, has been described as a potential model for resolving conflicts between conservation and economic concerns (Reid & Murphy 1995). Because participation in the NCCP program was formally recognized as an alternative to the requirements for incidental "take" permits as authorized under Section 10(a) of the ESA, most NCCP efforts in southern California have revolved around planning decisions intended to conserve gnatcatchers and their habitat.

We analyze the viability of a California Gnatcatcher metapopulation in central and coastal Orange County. Our aims are (1) to develop a habitat suitability model for California Gnatcatcher, (2) to demonstrate how this model can be linked to a metapopulation model for viability analysis, and (3) to analyze the sensitivity of the viability of this species to uncertainties in model parameters.

The NCCP plans that were recently prepared for central and coastal Orange County did not incorporate these results, in part because our analysis was not completed until after the planning process was well underway. Nonetheless, it is our hope that these results will contribute to future NCCP planning efforts elsewhere in southern California, as well as provide a basis for long-term habitat management within the NCCP coastal sage scrub reserve system in central and coastal Orange County.

The Model

We developed a spatially-explicit, stage-structured, stochastic model of the California Gnatcatcher metapopulation in central and coastal Orange County, based on habitat suitability maps we developed, and on demographic data from Atwood et al. (1995,1996a). We used the population viability analysis program RAMAS/GIS, which is designed to link landscape data from a geographic information system with a metapopulation model (Akçakaya 1995; for another application of the program, see Akçakaya et al. 1995; for reviews see Kingston 1995 and Boyce 1996).

We used data on the current distribution of the species' habitat to find the spatial structure of the metapopulation, i.e., to identify the location, size and shape of habitat patches in which (sub)populations of the metapopulation exist. In addition to spatial structure, we incorporated parameters related to demography, such as carrying capacities, initial abundances and vital rates of each population, the amount of year-to-year variability in vital rates, as well as the rate of dispersal between patches, and the degree of similarity of environmental fluctuations that different populations experience.

We accounted for uncertainties arising from measurement errors and lack of data by making three estimates of each parameter; i.e., by estimating lower and upper bounds, in addition to a "medium" estimate. We used these ranges to estimate upper and lower bounds on the estimated viability of the species. In most cases, the estimation of a range is quite arbitrary; we used ranges such as ±20 to 100% for parameters based on crude estimates and ranges such as ±5 to 10% for parameters based on more reliable data.

Habitat and census data

The habitat variables and census data that formed the basis of our analysis were provided by the GIAS lab of Southern California Edison in the form of digital raster (grid) maps with a resolution of 100 m. These maps described topography, vegetation, and gnatcatcher distribution in approximately 853 km^2 of central and coastal Orange County.

Topographical data layers included elevation, slope, and aspect, with each grid cell being represented by the value at the cell's central point. The values for elevation map (named **ELV**) are elevation in meters above sea level, the values for the slope map (**SLP**) are in percentages (i.e., 0 for flat areas; 100 for a 45° incline), and the values for aspect (**ASP**) are in units of degrees from north (e.g., 180 for south, 90 for east and west, 0 for north), ranging from 0 to 180.

Vegetation maps, originally prepared by Jones and Stokes (1993) from color aerial photographs, were converted from ARC/Info coverages to grid (raster) format. Because field experience suggested that the Jones and Stokes (1993) classification of various coastal sage scrub subassociations might include a relatively high degree of subjective interpretation, and because a preliminary analysis failed to detect any consistent patterns regarding presence or absence of gnatcatchers in different subassociations, we combined the original 20 subassociations of coastal sage scrub into a single, generalized map. The total amount of coastal sage scrub was calculated for each map cell, with values ranging from 0 m^2 (no coastal sage scrub) to 10,000 m^2 (full cover). Because of uncertainties regarding accuracy of the raw vegetation data, each cell in the coastal sage scrub (**CSS**) data layer was assigned the value of a 9-cell (3×3) moving average of these area estimates.

We also used the Jones and Stokes (1993) vegetation data to create maps of wetland vegetation (including riparian habitat), woody vegetation (combining chaparral, woodland, and forest categories), and grasslands. Based on these maps, we created three data layers describing distance of each cell to (1) the nearest cell with at least 10% cover of trees or other woody vegetation (**DTR**), (2) the nearest cell of grassland (**DGR**), and (3) the nearest cell of wetland or riparian vegetation (**DWT**). We believe that variables describing distance to woody vegetation or grassland provide a more objective characterization of coastal sage scrub subassociations than do the classifications used by Jones and Stokes (1993). For example, coastal sage scrub dominated by *Artemisia californica* generally occurs in closer proximity to grassland areas, while subassociations dominated by *Salvia mellifera* often occurs near chaparral or oak woodland (and distant from grassland). We truncated distance values > 2 km for these data layers.

In surveys of California gnatcatchers (conducted in Orange County in 1991-92, and 1994), 325 pairs and 80 single individuals were found in 1991-92, and 238 pairs and 80 single individuals were located in 1994. Cells where one or more pairs were recorded were assigned a value of 1 (present) (n = 547). In a separate data layer, which we used for validation purposes, we also assigned a value of 1 (present) to all cells (n = 129) where single birds were observed.

Finally, because distributional surveys did not certainly document gnatcatcher absence within the study area, we randomly added 273 (50% of the number of cells where pairs were observed) points intended to represent locations unsuitable for gnatcatchers. We selected these "absent" localities randomly, but with the following constraints: (1) "Absent" localities were not placed within 300 m of cells where pairs or single individuals were observed. Because the species' territory size may be larger than one 1 ha (Atwood et al. 1996b), it is likely that cells surrounding an observation point would support suitable habitat even though no observations were obtained in these cells. Similarly, we consider it likely that many observations of single birds occurred in suitable breeding habitat, and that areas near these points should not be used to characterize unsuitable habitat. (2) "Absent" localities were not placed within 300 m of other randomly-placed points, because too much clustering would lead to redundancy and not add information to the analysis. (3) "Absent" localities were not placed in cells dominated by agricultural fields, water, rural development, or residential development. All of these habitat types are clearly not suitable gnatcatcher habitat, and their inclusion would not add information to the analysis.

Habitat suitability map and patch structure

We used logistic regression (SAS Institute 1990) to calculate a habitat suitability function, which was then used to calculate for each cell an index of habitat suitability. Logistic

regression is indicated in cases where the response (dependent) variable is binary (e.g., 0 or 1). We used a stepwise approach with a significance level of P=0.05 for adding and removing variables. After all variables were tested, we started adding interaction terms (and removing those that became non-significant). In this phase, we retained all previously-added single variables, even if they became not significant with the addition of an interaction term.

The link between the habitat map and the metapopulation model was characterized by two parameters. *Threshold HS* is the minimum habitat suitability (HS) value below which the habitat is not suitable for reproduction and/or survival. *Neighborhood distance* is used to identify nearby cells that belong to the same patch, and may represent, for example, the foraging distance of the species. These parameters are used by a patch-recognition algorithm that delineates patches on the habitat map. Given these two parameters, the program finds clusters or groups of nearby cells (i.e., within the neighborhood distance of each other) that have HS values higher than or equal to the threshold HS, and label them as patches.

We used 0.5 (i.e., 50%) as the threshold HS; only those cells that had a habitat value of 0.5 or above were considered when habitat patches were analyzed (see below). We used a neighborhood distance of 3 cells, which corresponds to assuming that any two suitable locations within about 300 m of each other are in the same habitat patch. We analyzed the sensitivity of extinction risk to these two parameters by using a range of 0.45 to 0.55 for the Threshold HS parameter, and a range of 250 m to 350 m for the Neighborhood distance parameter (see Table 1).

Carrying capacities and initial abundances

The program allows the calculation of carrying capacities (K) based on the total habitat value of each patch (i.e., the sum of habitat values of all cells that are included in a patch). We estimated carrying capacities based on territory sizes, which were estimated to be 4.69 ha on average in Orange County (Bontrager, 1991). We used 1/4.69=0.213 as a scaling constant in calculating K of each patch, by multiplying it with the total habitat value in each patch. We used total habitat value instead of the total area as the argument, because the latter includes areas with low habitat value. The sum of habitat values in a patch is also related to the area of the patch, but weighted by the amount of habitat in each cell, so that territories in areas with low habitat value are assumed to be larger. We used ±20% of this parameter as the upper and lower limits. We excluded patches with $K \leq 5$, because only larger populations would have at least one pair of adults at stable stage distribution (see next section).

We specified the initial number of individuals in each patch as a fixed proportion of the carrying capacity of that patch. We estimated this proportion based on the ratio of the total number of observed pair locations (for both 1992 and 1994, but excluding the 1994 locations within 150 m of 1992 locations) (503) to the number of pairs (629) predicted by the above calculation of the total carrying capacity. Thus, each patch had a population of 503/629, or 80% of its carrying capacity at the beginning of the simulation. For the lower limit, we used 52% (based on only the 1992 pairs), and for the upper limit we used 100% (assuming some of the singles represent pairs). For all simulations, we assumed that the populations have a stable distribution of individuals to stages at the start of the simulation.

Stage structure

We modeled the dynamics within each patch with a stage-structured, stochastic matrix model with two stages (juveniles and adults). In parameterizing this stage-structured model, we assumed that (1) all reproduction in the population takes place in a relatively short breeding season (a "birth-pulse" population, see Caswell 1989), (2) the population is censused immediately after each breeding season (a post-reproductive census, see Caswell 1989), (3) all adults breed (so that the proportion of last year's adults who are breeders this year is simply the survival rate of adults), (4) the maternity rate (number of fledglings per breeder) is the same whether none, one or both of the breeders are nesting for the first time (i.e., were juveniles last year), and (5) the stage matrix is the same in all populations. With these assumptions, the stage matrix is

$$\begin{bmatrix} P_{JB} \cdot M & S_a \cdot M \\ S_j & S_a \end{bmatrix},$$

where S_a is survival rate of adults; S_j is survival rate of juveniles; P_{JB} is proportion of last year's juveniles that are breeders this year; and M is maternity or fertility (number of fledglings per breeder).

The two elements in the first row of the matrix are fecundities. Adult fecundity (F_a) is equal to $S_a \cdot M$, juvenile fecundity (F_j) is equal to $P_{JB} \cdot M$. We estimated P_{JB}, S_a and S_j based on data from the California Gnatcatcher population on the Palos Verdes peninsula (Atwood et al. 1996a), and M based on data from Orange County (Woehler 1996, Bontrager 1996). There were no comparable data on survival from Orange County. The data set represented 3 transitions: 1993 to 1994, 1994 to 1995 and 1995 to 1996.

The data for 1994-1995 suggests a sharp decline, which is what was observed on the Palos Verdes Peninsula (Atwood et al., 1996a), as well as in coastal Orange County (Erickson & Pluff, 1996; Chambers Group and LSA Associates, unpubl. data). This may be a result of the exceptionally wet/cold winter of 1994-95. One hypothesis is that gnatcatchers, due to

their small body size and high metabolic rates, have higher mortality under such weather conditions (e.g., Mock 1996). If this is correct, the survival rates for 1994-95 would be an exception rather than the rule. For this reason, we used the average of 1993-94 and 1995-96 transitions to estimate the average stage matrix, and the 1994-95 data as a basis for modeling catastrophes (see Table 2 and *Catastrophes*, below).

To calculate upper and lower bound on vital rates, we assumed a measurement error of ±1 individual in the recovery (re-sighting) of banded individuals. The rationale for these limits is based on the assumption of birth-pulse population. The parameters are estimated assuming that the census is made exactly at the same time each year. If the census is actually made, say, one day earlier than this exact time, then the re-sighting might be an overestimate (if a bird actually dies before the "correct" time). At a practical level, ± a number for re-sighting is more reasonable than, say, ±10% of the vital rate itself, as the latter does not account for differences in sample size for different vital rates. The number 1 (instead of, say, 2) is used as a minimum, but even this gave quite large uncertainties at the risk level (see *Results*, below). The resulting ranges are listed in Table 1.

Environmental and demographic stochasticity

We modeled environmental stochasticity by sampling the set of vital rates used to project the dynamics of each population from random (lognormal) distributions with means taken from the mean stage matrix, and standard deviations taken from a "standard deviations matrix". The sampling was done at each time step (in this case each year), thus the required standard deviation is one among years. We estimated these standard deviations based on the variability of survival rates and fecundities from the two transitions (1993-94 and 1995-96; see Table 2). We used the 1994-95 transition to model catastrophes (see below), so we did not include this transition in estimating the standard deviations.

We incorporated demographic stochasticity by sampling number of survivors from a binomial distribution and number of offspring from a Poisson distribution (Akçakaya 1991). In addition, we incorporated demographic stochasticity in dispersal (see below).

Catastrophes

One type of catastrophe that may affect species living in coastal sage scrub is fire. Coastal sage scrub is frequently subject to fire, especially in areas where the habitat occurs in close proximity to human population centers (Westman 1982; Keeley 1982). Two fires have occurred within the study area since 1948 (Fig. 5 in NCCP Habitat Conservation Plan prepared by R.J. Meade Consulting, Inc. 1995). In 1982 a fire was located in the area

identified here as the second largest patch, and in 1993 one occurred in the area identified as the largest patch. The 1993 fire destroyed habitat occupied by approximately 127 gnatcatcher pairs (Atwood et al. 1996a), corresponding to about 48% of the initial abundance in the modeled population occupying the largest patch. Based on this, we assumed two fires, one affecting the second largest patch in year 34, and the other affecting the largest patch in year 45, in the 50-year simulations of our model (see below). We assumed that each fire will decrease K by 48% and K will increase to its original level in 10 years in each case. Although these assumptions ignore long-term affects of fires, such as potential conversion of coastal sage scrub to grassland (Anderson 1991), we do believe they capture most of its short and medium-term effects on gnatcatcher populations. We analyzed the sensitivity of results to fire by running simulations with only one fire (in the largest patch), and with 2 additional fires affecting the largest and second largest patches in years 25 and 14, respectively.

Another type of catastrophe with direct impact on gnatcatcher populations may be extreme weather conditions, such as those which may have characterized the winter of 1994-95. In this model, we used the demographic parameters estimated from 1994-95 to model such catastrophes. We assumed that the effect of such a catastrophe is a sharp decline in vital rates beyond the normal year-to-year fluctuations (see *Environmental and demographic stochasticity*, above). After a catastrophe year, the vital rates are again sampled from the average stage matrix (estimated based on the average of 1993-94 and 1995-96 transitions) with the standard deviations given above.

The frequency of such extreme population caused by weather conditions is difficult, if not impossible to estimate, because it is not clear which aspect of the weather makes the crucial difference. A statistical estimation is possible only after several years of vital rate estimates. In the absence of such information, we focused on the minimum temperatures in October through December. In the two weather stations closest to the study area (Tustin and Newport), frequency of average of the three monthly minimum temperatures less than equal to that in 1994 was about 14% in the last 98 years. Thus we chose the annual catastrophe probability of 0.14. We used the range 0.07–0.28 to evaluate the sensitivity of results to this assumption.

Density dependence and Allee effects

For most simulations, we assumed a ceiling-type density dependence model for each population, and used the carrying capacities calculated based on habitat data as population ceilings. This model allows the populations to fluctuate independent of the population size (N), according to the stage matrix and the standard deviations matrix, until the population reaches the ceiling. The population then remains at this level until a population

fluctuation takes it below the ceiling. We also modeled density dependence with a contest model (which uses the Beverton-Holt equation) with the assumption that each population grows with a rate of 15% when N is low, and is stable with 0% growth when $N=K$.

Allee effects, which may cause a reduction in vital rates when population size becomes very small, are not well-studied for this species. In the current model, we incorporated Allee effects by specifying a local extinction threshold for each population. Once any population falls to or below its local threshold, the model assumes the population to be extinct by setting the abundance to zero. The patch then remains unoccupied, unless it is colonized by dispersers from another patch. We set the local thresholds at 0%, 2% and 4% of the carrying capacity of the patch. By considering a population to be extinct once it reaches or falls below its threshold, the model need not accurately predict the dynamics of the populations at these low abundance levels.

In addition, we specified a metapopulation extinction threshold of 30, 60 or 120 individuals (about 1%, 2% and 4% of the total initial metapopulation size), and calculated the viability results in terms of falling below this threshold (see below).

Metapopulation dynamics: Correlation-distance function

Parameters related to dynamics at the metapopulation level include the interdependence of environmental fluctuations among populations, and patterns of dispersal. The relatively small study area (with the maximum distance between any two patches about 40 km), and the apparent dependence of gnatcatcher biology to weather conditions suggests that weather patterns such those seen in southern California (affecting substantial areas) impose a correlation structure on the metapopulation dynamics. In a study of the southern California metapopulation of the spotted owl, LaHaye et al. (1994) found strong, distance-dependent spatial autocorrelation among rainfall, and used this relationship between rainfall correlation and distance as a basis for setting correlation among population dynamics. In the current model, we used three different correlation-distance functions to set the correlation of vital rates among populations (see Fig. 1). The function is $C = \exp(-d/b)$, where C is the coefficient of correlation between the vital rates of two populations, d is the distance (km) between the centers of these two populations, and b is a parameter that describes how fast the correlation declines with increased distance between populations. We used b values of 100 (high correlation), 30 (medium correlation) and 10 (low correlation).

Metapopulation dynamics: Dispersal

In this model, dispersal refers to the movement of birds among habitat patches, and dispersal rate (proportion dispersing from target population to source population) may depend on the distance between source and target populations, the abundance in the population, and whether the bird is a juvenile or an adult.

We estimated the distance dependence of dispersal based on data for 1993 and 1994 from Atwood et al. (1996a), who report the number of juveniles that dispersed different distances. We divided the number of dispersing juvenile birds in each distance class by the total sample size (32) to obtain proportion dispersing, and used this as the dependent variable. We used the mid-point of each distance class (in km) as the independent variable (d) in the exponential model $M = a \cdot \exp(-d/b)$. In this model, M is the dispersal rate, d is the distance (km), and a and b are model parameters. The parameter b is the average dispersal distance. The model was fitted with a=0.4 and b=2.5 km (see Fig. 2). In addition, the above equation was modified to reflect a maximum dispersal distance of 15 km. Because of the relative isolation and small size of the Palos Verdes peninsula where these data were collected, we used the fitted function to model minimum dispersal, and set the average dispersal distance to 3.0 and 3.5 km for medium and high dispersal. The distance metric we used in this study is one between the center of the source population to the edge of the target population. The asymmetry of this measure of distance allows for more realistic modeling of dispersal between a large and a small patch.

We assumed that adults have negligible dispersal among populations (they can disperse within the same patch), and used dispersal parameters discussed above only for the juvenile stage. We incorporated demographic stochasticity in dispersal among populations by sampling the number of dispersers from a binomial distribution with sample size equal to the number of juveniles in the source population, and probability equal to the dispersal rate based on distance.

We modeled density dependence in dispersal for each population such that the dispersal rate was directly proportional to population size. We modeled two levels of density dependence in dispersal, in addition to density-independent dispersal (Fig. 3). Under strong density-dependent dispersal, when the population size (N) is lower than the carrying capacity (K), the proportion dispersing is lower, in proportion to the ratio of N/K. When dispersal is density-independent ("none" on the graph), the dispersal rate is M regardless of abundance.

Analysis and viability measures used

The analysis of the dynamics of the California Gnatcatcher metapopulation with the model described above consisted of a series of simulations. Each simulation consisted of 10,000 replications, and each replication projected the abundance of the each population for 50 time steps (years). At each time step, the number of juveniles and adults at each population were projected using a set of vital rates, drawn from a random (lognormal) distribution (also see "Demographic stochasticity" above).

The mean values of these vital rates (survival and fecundity) were taken from the stage matrix, and the standard deviation of vital rates are those given by the standard deviation matrix. The sampled stage matrices of different populations were correlated according to one of three sets of correlations (see above), whereas the elements of the stage matrix within a population were perfectly correlated. The number of individuals in each stage of each population, as well as the number of dispersers were always integer numbers. These calculations followed the algorithm described by Akçakaya (1995).

To analyze the sensitivity of model results to each parameter, we ran three simulations for each parameter, using the lower, medium and upper estimates of that parameter, and the medium estimates of all the other parameters (Table 1). We used three measures to express the predicted viability of the metapopulation: (1) median time to fall below the metapopulation extinction threshold, (2) risk of falling below the metapopulation threshold anytime within 20 years, and (3) risk of falling below the threshold anytime within 50 years.

Results

Habitat suitability map

The results of the logistic regression analysis are summarized in Table 3. The goodness of fit statistics given at the end of the table show that the regression is highly significant, and the probability column shows that regression coefficients are also statistically significant. Slope, aspect and distance from wetlands were non-significant.

The frequency distribution of habitat suitability values in the landscape is given in Fig. 4. Only 24% has habitat values of 0.5 or above, and the average habitat suitability is about 0.30. The locations where gnatcatcher pairs were observed have habitat values ranging from 0.14 to 1.00, with an average of 0.86. The frequency distribution of the habitat suitability values of locations with gnatcatcher observations is given in Fig. 5a. About 95% of the observations are in locations with habitat values of 0.5 or above.

Validation of the habitat function

Despite the highly significant fit of the data, and the obvious difference between the distribution of habitat suitability (HS) values at all locations and at locations with gnatcatcher observations, this analysis does not provide an independent validation of the habitat function, because these are the observations we used in the statistical analysis. One method of validation is to separate the current observations in two, and use only one set for estimation and the other set for testing. We separated the observation locations and random points into two sets, diving the map roughly in half with all coastal observations in the southern half, and all inland observations in the northern half. We re-estimated the habitat function with the northern half of the data set, which gave a slightly different equation from the one estimated with the whole data set. We used this equation to predict the habitat suitability values of observed pair locations in the southern half of the data set. Because these observations were not used in the estimation of the function, they can be used to validate the model.

The results of this validation (Fig. 5b) show the frequency distribution of the habitat suitability values of locations with gnatcatcher pairs in the south, based on the habitat suitability function estimated with the northern half of the data set. Except for the small sample size (since only half the data are used), the results are similar to those in the previous figure: a large proportion (90%) of the observations are in cells with predicted habitat values of 0.5 or more. The habitat function estimated from the northern half successfully predicted the observations in the southern half.

We made two additional types of validation. We used the function estimated with the location of pairs to predict the HS values of locations of single birds. About 89% of the single locations were predicted to have a HS value of 0.5 or more. We used a function estimated with the location of pairs in 1992 to predict the HS values of locations of pairs in 1994. About 82% of the pair locations in 1994 were predicted to have a HS value of 0.5 or more. The habitat function estimated with observations of pairs successfully predicted the observations of singles, and the habitat function based on 1992 pairs successfully predicted the observations of 1994 pairs.

Patch structure

Given the habitat map, and the (medium) parameter estimates described above, the program found 13 habitat patches (clusters of suitable cells within the neighborhood distance of each other). The 2 largest patches made up about 84% of the total area of all patches (Table 4). A map of the patch structure is given in Fig. 6. The shades of gray on the map represent the habitat suitability (the darker the color, the higher the suitability), the

black outline is the border of the study area, and the thin white outlines are the outer borders of patches. Not all cells within the patch boundaries are suitable at the threshold level of 0.5, as discussed above. In other words, the patches have "holes" in them, as represented by the lighter gray regions within patches. Such areas are not counted in the area of patches, and the habitat values in these areas are not used in the calculation of carrying capacities (K) or initial abundances (N_0) reported in the table. The total carrying capacity was 3357 birds, or (at stable distribution) 629 adult pairs. The total initial abundance was 2952 birds, or 553 adult pairs.

Viability

With most parameter combinations, the model predicted a fast decline and a high risk of extinction of the gnatcatcher populations. With medium estimates of all variables, the risk of falling below the metapopulation threshold of 60 individuals was about 19% in 20 years and about 76% in 50 years. The median time to fall below the threshold was about 34 years. The sensitivities of these three results to each parameter are listed in Table 5, which gives the difference between the risk result predicted by the upper and lower limits of each parameter, as well as the difference as a percentage of the risk result with medium parameter estimates. The first column indicates whether higher parameter value resulted in higher (+) or lower (–) viability. For example, higher adult fecundity resulted in higher viability, and the difference in median time to fall below the threshold between high and low estimates of adult fecundity was 14.7 years. This corresponded to 43.57% of the median time (33.8 years) with the medium estimate of all parameters, including adult fecundity. The difference in risk (of falling below the metapopulation threshold of 60 individuals within 20 years) between the low and high adult fecundity was about 0.145, or 77% of the risk (0.189) with the medium estimate. The final column indicates the year at which the difference in risk of decline (with the high and low values of the parameter) was the largest.

These sensitivity results are taken from cumulative time to decline curves (see Fig. 7 as an example). In this figure, the curves show the probability of falling below the metapopulation threshold, as a function of time. The vertical dashed lines show the median time to decline. The arrows show the four sensitivity results listed in Table 9: the difference between median time to decline (A), the difference in risk of decline in 20 years (B) and 50 years (C), and the maximum difference in risk of decline (D), which in this case occurred around year 40.

The results were most sensitive to the probability of weather-related catastrophes, and also very sensitive to adult fecundity, juvenile fecundity, and parameters related to density dependence (the type of density dependence, and Allee effects that describe density effects at low abundances). All of these five parameters caused more than 10 years difference in median time to extinction, and/or a difference of more than 0.2 in risk of extinction (falling below the metapopulation threshold) in 50 years.

The results showed moderate sensitivity to seven other parameters: juvenile survival, adult survival, metapopulation extinction threshold, threshold habitat suitability, carrying capacities, standard deviation of fluctuations in vital rates, and density dependence in dispersal. The results were not sensitive to neighborhood distance, initial abundances, dispersal distance, correlation among population fluctuations, and the number of fires.

Discussion

The results of three types of validation of the habitat suitability function suggest that this function is a good estimator of the quality of habitat in occupied locations. However, the major weakness of this function is the lack of data on absences (locations where gnatcatchers are absent), which forced us to use random locations. This might have caused an overestimation of habitat quality in certain locations. If such data become available, the function may be narrowed down, excluding some of the areas now included as habitat in the patches. Another limitation of the habitat map is its geographic coverage. The coastal sage scrub in the study area may be connected to similar habitat in southern Orange county and elsewhere. One of potential improvements to the model involves expanding it to include the populations of California Gnatcatcher in other areas.

One of the specific aims of this analysis was to demonstrate how uncertainty and variability can be incorporated in models for determining the threat a species faces. We incorporated natural variation (resulting from temporal fluctuations in environmental factors) in the form of randomly distributed vital rates (survivals and fecundities), and as natural catastrophes. We also modeled demographic stochasticity in reproduction, survival and dispersal. We used these types of natural variation (environmental and demographic) to express the model results in probabilistic terms (e.g., risk of decline).

Most parameters are not precisely known because of measurement errors and lack of data. In such cases, we made three estimates of the parameter; estimating lower and upper bounds, in addition to a "medium" estimate. We thus incorporated uncertainty that results from lack of knowledge in the form of parameter ranges. We used these ranges to estimate

upper and lower bounds on the estimated viability of the species. In other words, we used natural variability to estimate risks, and uncertainties to estimate the uncertainty of these risk estimates.

The sensitivity of results to catastrophe probability is not surprising: because we did not have enough data to correlate vital rates with weather-related variables, we used a wide range for this parameter. The deterministic, long-term growth rate (eigenvalue, λ) predicted by the stage matrix (with medium values of vital rates) was above 1.0, and declines and extinctions occurred mostly due to catastrophic declines in the vital rates, as well as year-to-year environmental fluctuations and Allee effects. The declines predicted by the model also explains the insensitivity of metapopulation viability to fires. We modeled fires as causing a decrease in carrying capacity (K), but the populations were most of time well below K, and thus were not affected by a decline in K caused by fires.

A surprising result was the negative (but weak) effect of dispersal distance on viability, which can be explained by a type of source-sink dynamics. Although all populations in our model had the same vital rates (hence the same λ), the smaller populations were more prone to extinction as a result of demographic stochasticity. Increased dispersal distance meant a larger number of dispersers going from the more stable larger populations to these smaller and more extinction-prone populations. To demonstrate that the smaller populations indeed act as sink populations, we ran two other simulations, with 9 largest and 5 largest populations, by simply deleting the smaller populations. The results of these simulations showed that when the smaller populations were excluded, the risk of decline to any level was lower (Fig. 8). We made this comparison only to demonstrate that small populations can act as sink populations, even if their vital rates are the same as the larger populations. However, this result should not be interpreted in terms of reserve design. The reason is that we also assumed that there was no dispersal to the patches we deleted from the model, i.e., dispersal was only to the patches that remained in the model. There is, of course, no guarantee that gnatcatchers would not attempt to disperse to these areas whether or not they are part of a reserve system.

Increased dispersal had a similar effect of increasing extinction risk in another model: Akçakaya and Baur (1996) concluded that when some populations were modeled as being subject to more severe catastrophes than others, it created a type of source-sink dynamics, which caused this effect. When catastrophes were evenly distributed increased dispersal caused a decrease in extinction risks.

Two of the model parameters, threshold habitat suitability, and metapopulation extinction threshold, have necessarily arbitrary values. The rationale for selecting any value for these thresholds is similar to the one used in deciding a probability level for statistical significance. Just as the level of statistical significance depends on priorities (e.g., whether

one wants to minimize Type I or Type II error), so do these parameters. Threshold habitat suitability reflects a compromise between making sure that no suitable habitat is left out, and making sure that unsuitable habitat is not included in patches. Similarly, the extinction threshold depends on whether it is more important not to overestimate or not to underestimate extinction risks. It is therefore positive that the results were only moderately sensitive to these parameters.

The results point to a need to better estimate two groups of ecological parameters. One group is the vital rates (especially fecundity), and the frequency and amount of change in vital rates caused by catastrophes. The other group includes density dependence parameters, including Allee effects. Detailed data on vital rates may also help estimate these parameters, for example by comparing fecundities in regions with different density of gnatcatchers. Such a data set may also help link the vital rates to local habitat suitability, eliminating one of the stronger assumptions of our model (that vital rates are the same for all populations).

The sensitivity of results suggests that the results should not be interpreted in absolute terms. Specifically, it would be inappropriate to use the results of this model to conclude that gnatcatcher populations in Central/Coastal Orange County are either threatened by extinction or secure from such a threat. There is simply too much uncertainty about most of the parameters to predict with confidence what the population size will be in 50 years, or what the risk of extinction might be. Despite this uncertainty, we believe the model can have practical use in two areas.

The sensitivity analysis described is one potential use of modeling in the conservation and management of the coastal sage scrub community; it gives information about which parameters need to estimated more carefully. Once a model is developed, it can be improved with such analyses carried out at least once a year to incorporate new data collected during that year.

The second use of such a model is to rank management options in terms their predicted effect on the viability of target species. Results of population viability models such as this one are less reliable if interpreted as absolute predictions than if interpreted as relative to other sets of assumptions or scenarios. Even if results of a model are sensitive to various model parameters, it is possible that relative rankings of management options will not be as sensitive. In other words, the specific predictions of the model may change as a function of parameters and assumptions, but all assumptions may still predict that a particular management option ranks better than its alternatives in terms of the viability of the species. This would make such a relative ranking a much more reliable prediction than a prediction of exactly what the population size would be 50 years from now.

In principle, all possible management actions can be represented as changes in habitat suitability or demographic parameters (including their variances, and the initial values of variables such as abundances in each stage and each population). The consequences of these parameters sets can be estimated by the model in terms of the viability of the species, and then used to rank alternative management actions, to prioritize conservation measures, and to evaluate the importance of different parameters.

The uncertainty of model results depends on the time horizon of the simulation. The cumulative time to quasi-extinction results showed that the greatest difference between the results given by different parameter combinations occurred around 30 to 40 years. This suggests that the results are most sensitive to changes in parameters when the time horizon is only a few decades. This might be an appropriate time horizon, if the model is used in the future to compare alternative management options. Longer or shorter time horizons may underestimate the effects of management actions, as the model results may not be as sensitive to changes in parameters (as a function of the simulated effect of the management action). As more demographic and ecological data accumulate, it will become possible to make assessments with longer time horizons.

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Table 1. Low, medium and high estimates of parameters used in the model of the California Gnatcatcher metapopulation.

Parameter	*Parameter estimate*		
	Low	Medium	High
Habitat-demography link:			
Threshold HS	0.45	0.50	0.55
Neighborhood distance (m)	250	300	350
Carrying capacity (K) multiplier[a]	0.170	0.213	0.256
Initial abundance (as % of K)	52	80	100
Mean dispersal distance (km)	2.5	3.0	3.5
Stage matrix:			
Juvenile survival rate (S_j)	0.3275	0.3441	0.3606
Juvenile fecundity (F_j)	0.4901	0.5376	0.5874
Adult survival rate (S_a)	0.4650	0.4975	0.5300
Adult fecundity (F_a)	0.7975	0.8899	0.9876
Density dependence:			
Density dependence type		ceiling	contest
Allee effects (local threshold as % of K)	0	2	4
Density-dependent dispersal	none	weak	strong
Stochasticity:			
Standard deviations[b]	0.8 S	S	1.2 S
Correlation of fluctuations (b)	10	30	100
Catastrophe (weather) probability	0.07	0.14	0.28
Number of fires	1	2	4
Metapopulation extinction threshold	30	60	120

[a] This parameter is multiplied with the total habitat suitability value of the patch to calculate carrying capacity and initial abundance in the patch.
[b] S represents the standard deviations given in Table 2.

Table 2. Stage matrix parameters: juvenile survival rate (S_j), proportion juveniles that become breeders (P_{JB}), juvenile fecundity ($F_j=P_{JB}\cdot M$), adult survival rate (S_a) and adult fecundity ($F_a=S_a\cdot M$).

Year	M	S_j	P_{JB}	F_j	S_a	F_a
1993	1.7[a]	0.2568[c]	0.1757[c]	0.2986	0.5200[c]	0.8840
1994	2.3[a]	0.1558[c]	0.0909[c]	0.2102	0.1892[c]	0.4375
1995	1.9[b]	0.4314[c]	0.4118[c]	0.7766	0.4750[c]	0.8958
Average for (93,95)		0.3441	0.2937	0.5376	0.4975	0.8899
St. dev. for (93,95)		0.0873	0.1180	0.2390	0.0225	0.0059

[a] from Woehler (1996)
[b] average of M from Woehler (1996) and Bontrager (1996)
[c] from Atwood et al. (1995, 1996a)

Table 3. Results of logistic regression for habitat function of California Gnatcatcher. The habitat variables are coastal sage scrub (CSS), elevation (ELV), distance from grassland (DGR) and distance from trees (DTR). Slope, aspect and distance from wetlands were non-significant.

Variable	Regr.coefficient	SE	Wald χ^2	Prob.
CSS	$6.7494\cdot10^{-4}$	$1.6781\cdot10^{-4}$	16.1762	0.0001
ELV	$-8.9122\cdot10^{-3}$	$2.4068\cdot10^{-3}$	13.7118	0.0002
DGR	$-2.6755\cdot10^{-3}$	$0.5961\cdot10^{-3}$	20.1444	0.0001
DTR	$-1.8863\cdot10^{-3}$	$0.3759\cdot10^{-3}$	25.1813	0.0001
CSS•ELV	$-18.3337\cdot10^{-7}$	$5.8438\cdot10^{-7}$	9.8427	0.0017
CSS•DTR	$4.2860\cdot10^{-7}$	$1.2153\cdot10^{-7}$	12.4385	0.0004
ELV•DTR	$8.5879\cdot10^{-6}$	$2.6093\cdot10^{-6}$	10.8326	0.0010
constant	1.8223	0.5797	9.8806	0.0017

Goodness of fit (chi-square for covariates):
Log likelihood statistic = 523.783 with 7 df (P=0.0001)
Score statistic = 374.544 with 7 df (P=0.0001)

Table 4. Carrying capacities, initial abundances and areas of the patches identified by the model with medium values of parameters.

Rank	K	Init. abund.	Area (km^2)	Area as % of patches
1	1721	1514	101.0	49.82
2	1130	994	68.8	33.92
3	133	117	8.2	4.03
4	124	109	8.8	4.33
5	72	63	4.3	2.10
6	39	34	3.1	1.51
7	36	32	2.5	1.21
8	32	28	2.1	1.05
9	32	28	2.0	0.99
10	13	11	0.7	0.35
11	11	10	0.6	0.28
12	7	6	0.4	0.19
13	7	6	0.4	0.21
Total	3357	2952	202.7	100.00

Table 5. Sensitivity of model results to parameters: difference in median time to decline and probability of decline between models with high and low values of each parameter.

		Median time to decline (yr)		Prob. of decline in 20 years		Prob. of decline in 50 years		Max. diff. (year)[d]
Parameter	eff.[a]	abs.[b]	perc.[c]	abs.[b]	perc.[c]	abs.[b]	perc.[c]	
Threshold HS	–	8.7	25.7%	0.0837	44.2%	0.1617	21.4%	41
Neighborhood distance	+	3.1	9.2%	0.0382	20.2%	0.0604	8.0%	35
Carrying capacity	+	6.7	19.8%	0.0857	45.2%	0.1119	14.8%	35
Initial abundance	+	3.0	8.9%	0.0656	34.6%	0.0307	4.1%	26
Dispersal distance	–	5.2	15.4%	0.0502	26.5%	0.1119	14.8%	41
Juvenile survival	+	7.5	22.2%	0.0771	40.7%	0.1452	19.2%	42
Juvenile fecundity	+	11.8	34.9%	0.1056	55.7%	0.2332	30.8%	38
Adult survival	+	8.4	24.9%	0.0875	46.2%	0.1662	21.9%	38
Adult fecundity	+	14.7	43.5%	0.1452	76.6%	0.2888	38.1%	40
Density dependence	+	14.7	43.5%	0.0812	42.8%	0.2393	31.6%	47
Allee effects (local threshold)	–	10.3	30.5%	0.1605	84.7%	0.1627	21.5%	34
Density dependent dispersal	+	7.2	21.3%	0.0719	37.9%	0.1278	16.9%	36
Standard deviations	–	7.8	23.1%	0.0914	48.2%	0.1205	15.9%	33
Correlation	–	2.8	8.3%	0.0402	21.2%	0.0334	4.4%	33
Catastrophe (weather) prob.	–	61.3	181.4%	0.6546	345.4%	0.7342	96.9%	32
Number of fires	–	0.5	1.5%	0.0119	6.3%	0.0160	2.1%	43
Metapopulation threshold	–	7.2	21.3%	0.1204	63.5%	0.1021	13.5%	31

[a] Effect on metapopulation viability.
[b] Absolute difference between the results of the two models with high and low values of the parameter.
[c] Difference as a percentage of the result with the medium value of the parameter.
[d] Year at which the difference in risk of decline (with the high and low values of the parameter) was the largest.

Figure legends

Figure 1. Correlation-distance functions [$y=\exp(-x/b)$] used in the model. The function gives the correlation between the vital rates of two populations separated by the indicated distance.

Figure 2. Proportion of dispersing juveniles as a function of distance (in km). Data are from Atwood et al. (1996a) for 1993 and 1994. The curve is the function $y=0.4\cdot\exp(-x/2.5)$.

Figure 3. Total rate of dispersal as a function of population size, used to model density-dependent dispersal for each population. M is the total rate of dispersal from the population to all other populations, given by the dispersal distance function. K is the carrying capacity. The parameters M and K are different for each population.

Figure 4. Frequency distribution of habitat suitability (HS) values for California Gnatcatchers in the study area. The HS values were calculated for each of 85,333 1-ha cells in the study area, with a habitat function that was estimated by regression of presence-absence data on habitat variables.

Figure 5. Frequency distribution of the habitat suitability (HS) values of locations where California Gnatcatcher pairs were observed in (a) all of the study area, and (b) in the southern part of the study area. The HS values in (b) are predicted using data only from the northern half of the data set, and thus are used as one of three validations of the habitat function.

Figure 6. Patch structure of the model, superimposed on the habitat suitability map of California Gnatcatcher in Orange County. The shades of gray represent the habitat suitability (the darker the color, the higher the suitability), the black outline is the border of the study area, and the thin white outlines are the outer borders of patches.

Figure 7. Sensitivity of risk of decline to adult fecundity (F_a). The curves show the probability of falling below the metapopulation threshold as a function of time. The vertical dashed lines show the median time to decline. The arrows show four sensitivity results: the difference between median time to decline (A), the difference in risk of decline in 20 years (B) and 50 years (C), and the maximum difference in risk of decline (D), which in this case occurred around year 40.

Figure 8. Risk of decline (by 80 to 100% from the initial metapopulation abundance) predicted by models with 13, 9 and 5 populations. The vertical line marks the metapopulation extinction threshold of 60 individuals.

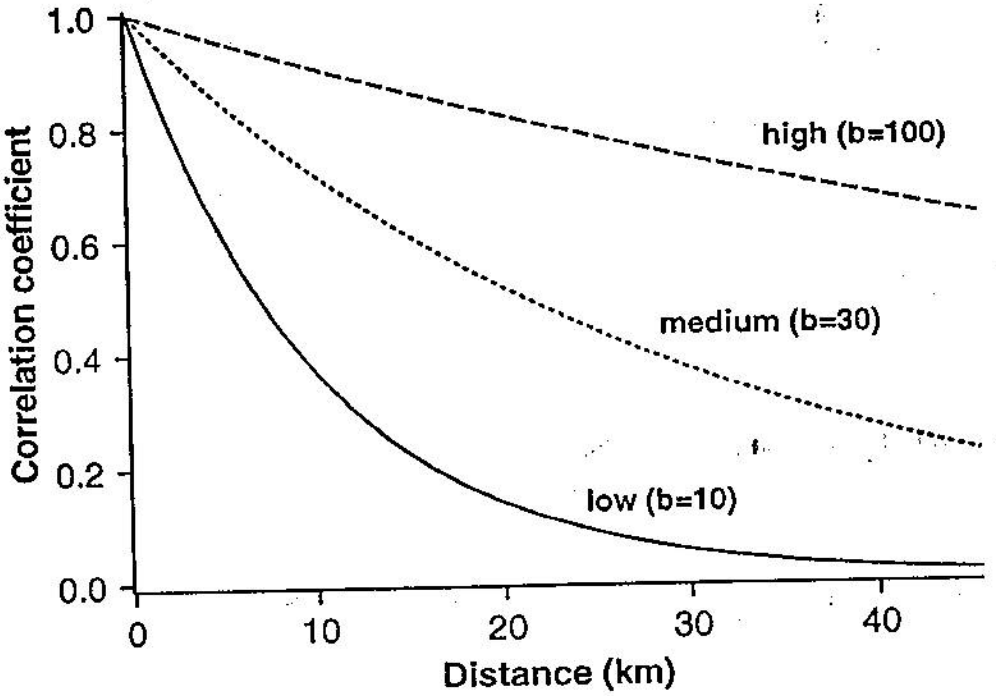

1.0
0.8
0.6
0.4
0.2
0.0
Correlation coefficient
high (b=100)
medium (b=30)
low (b=10)
0
10
20
30
40
Distance (km)

FIG 1

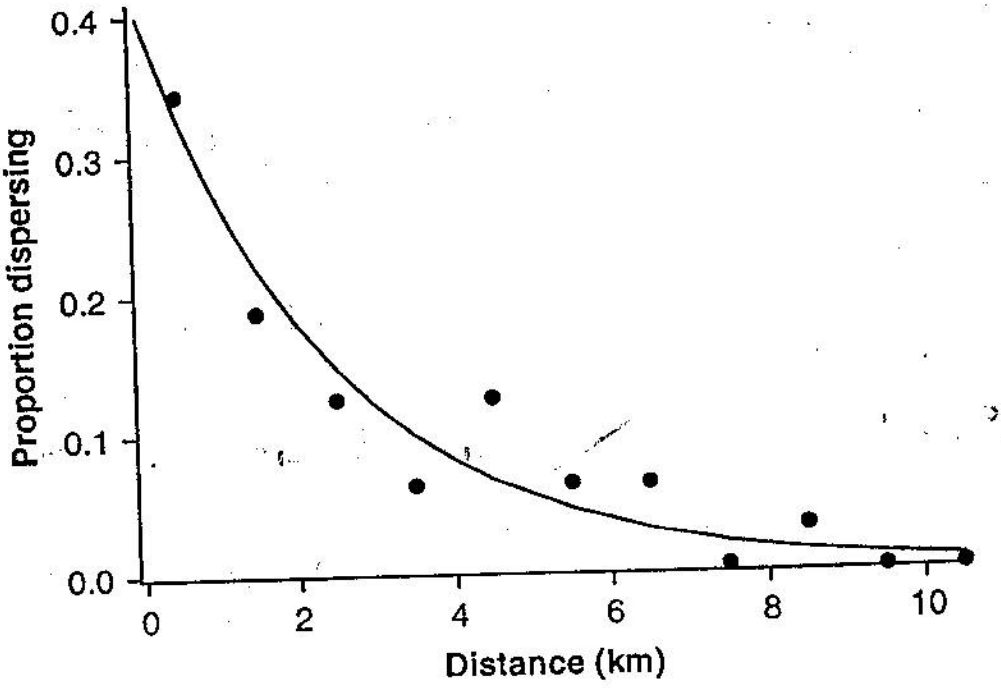


FIG 2

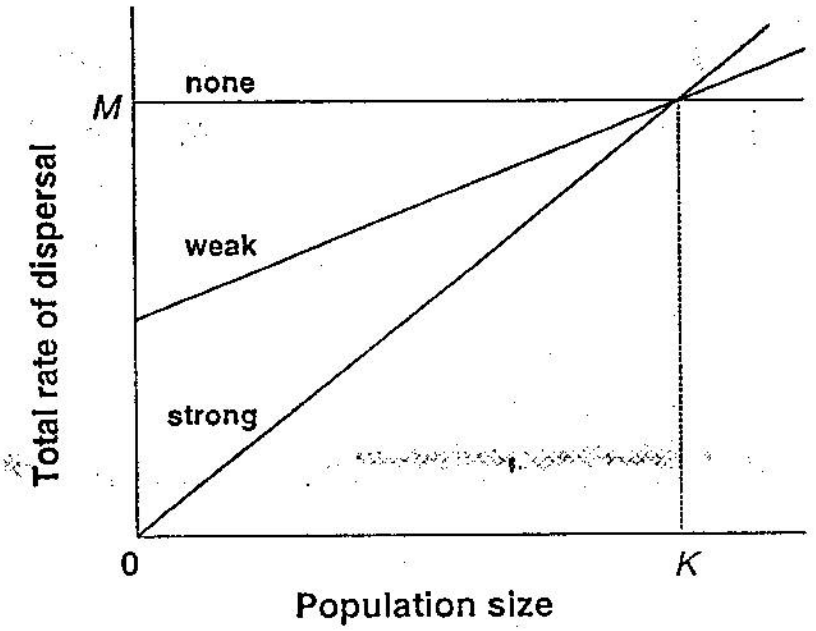

none
M
weak
strong
Total rate of dispersal
0
K
Population size

FIG 3

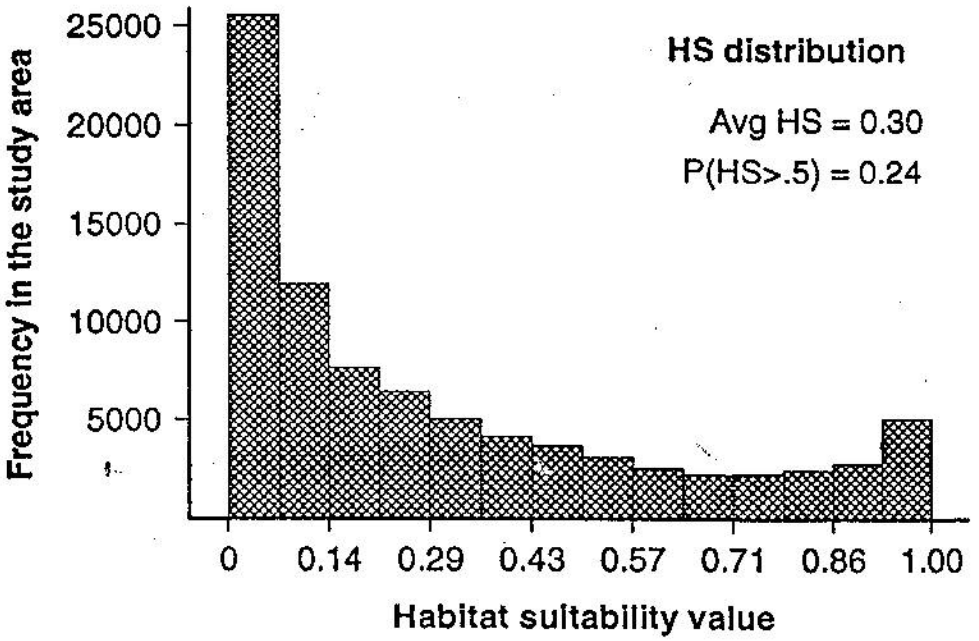
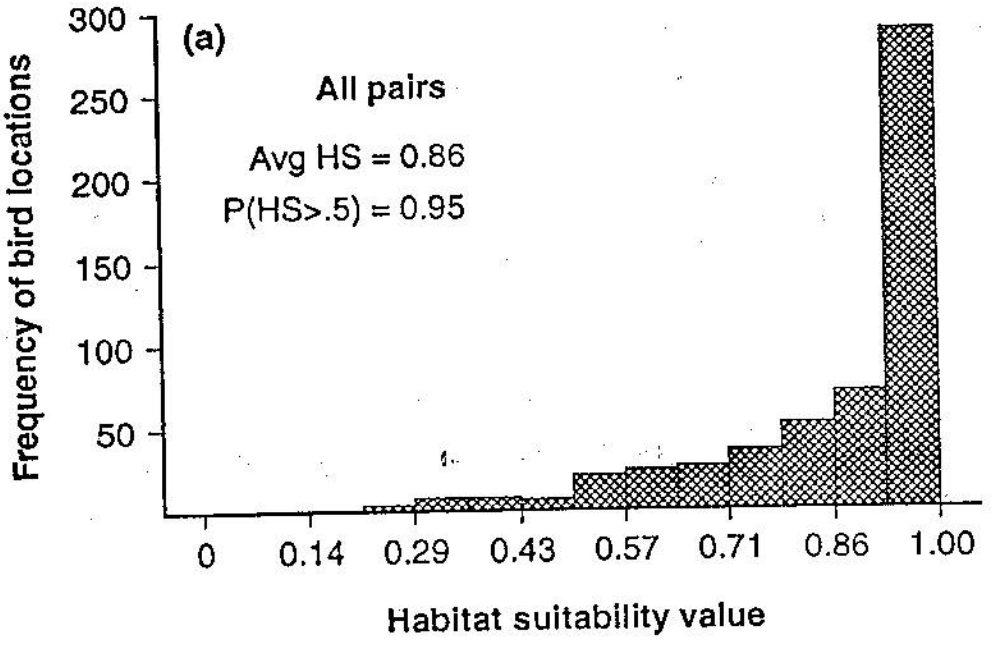

HS distribution
Avg HS = 0.30
P(HS>.5) = 0.24
Frequency in the study area
25000
20000
15000
10000
5000
0
0.14
0.29
0.43
0.57
0.71
0.86
1.00
Habitat suitability value

FIG 4


(a)
All pairs
Avg HS = 0.86
P(HS>.5) = 0.95
Frequency of bird locations
300
250
200
150
100
50
0
0.14
0.29
0.43
0.57
0.71
0.86
1.00
Habitat suitability value

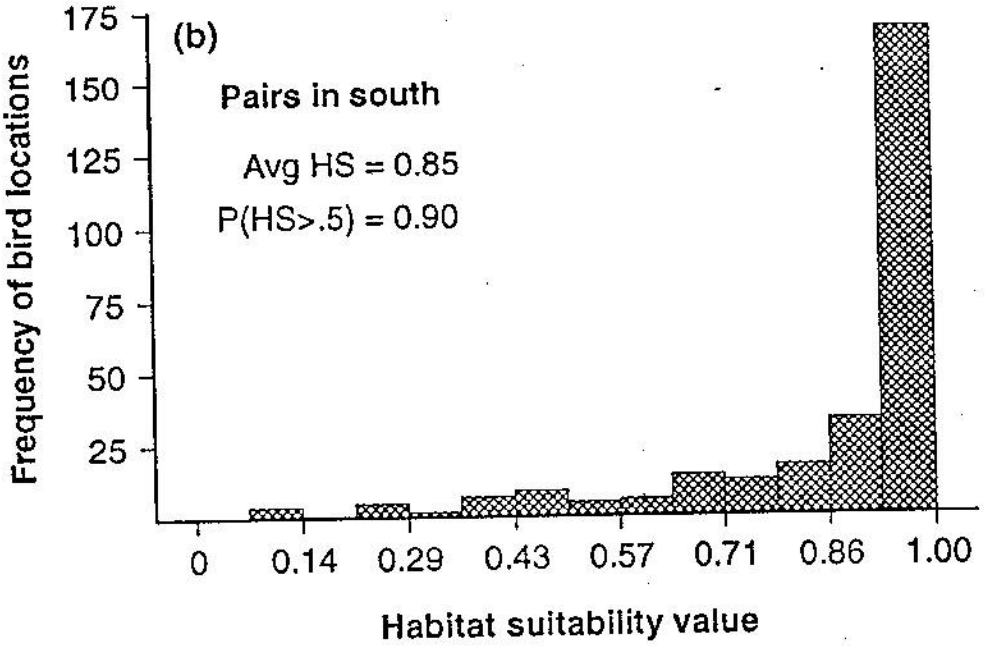

(b)
Pairs in south
Avg HS = 0.85
P(HS>.5) = 0.90
Frequency of bird locations
175
150
125
100
75
50
25
0
0.14
0.29
0.43
0.57
0.71
0.86
1.00
Habitat suitability value

FIG 5

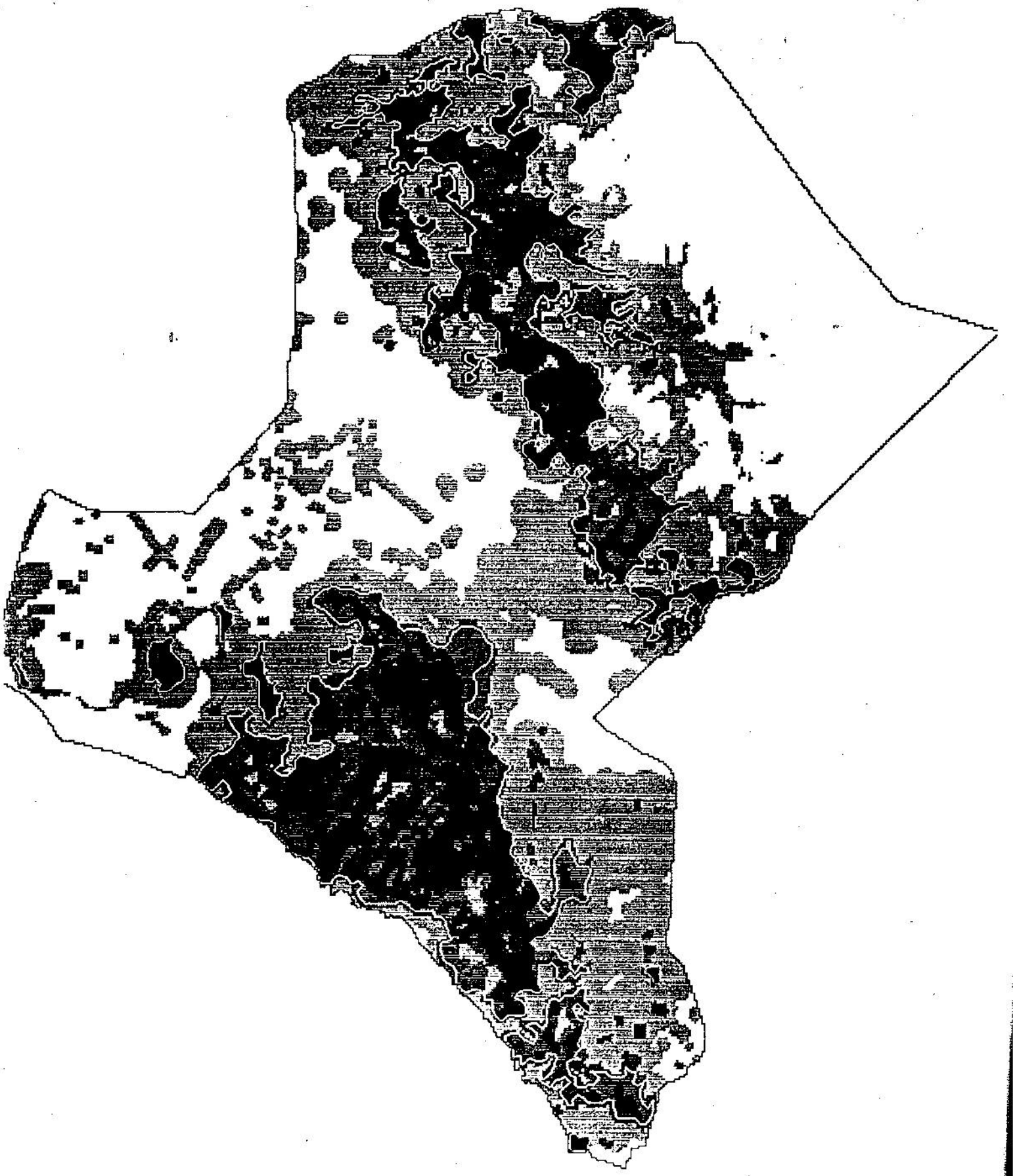


FIG 6

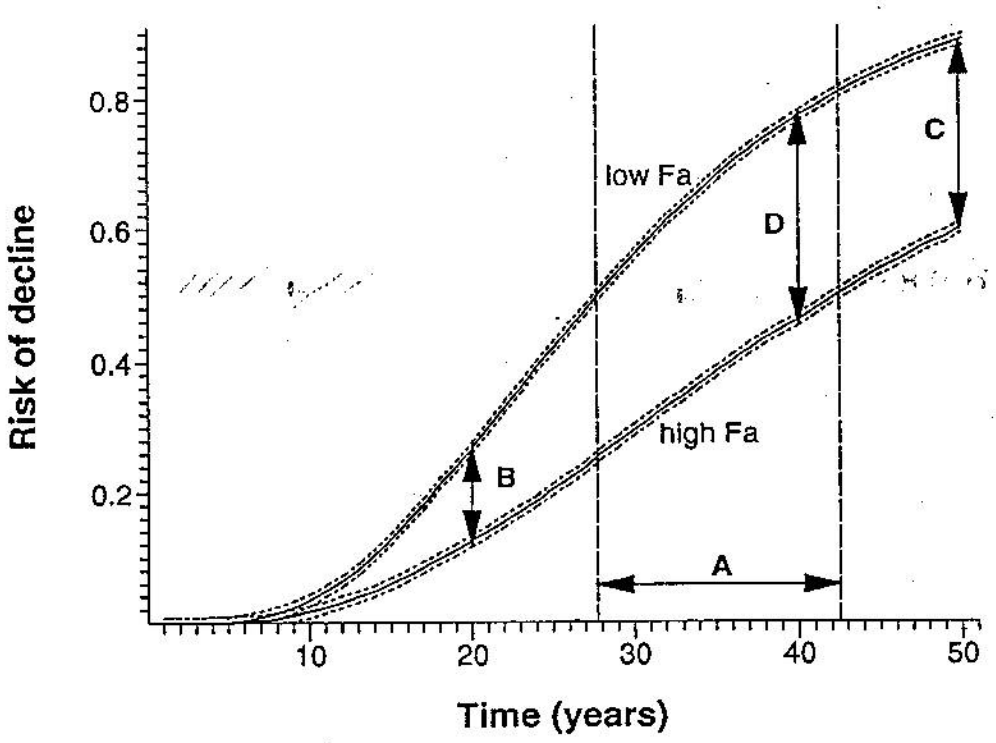

Risk of decline
0.8
0.6
0.4
0.2
low Fa
high Fa
A
B
C
D
10
20
30
40
50
Time (years)

FIG 7

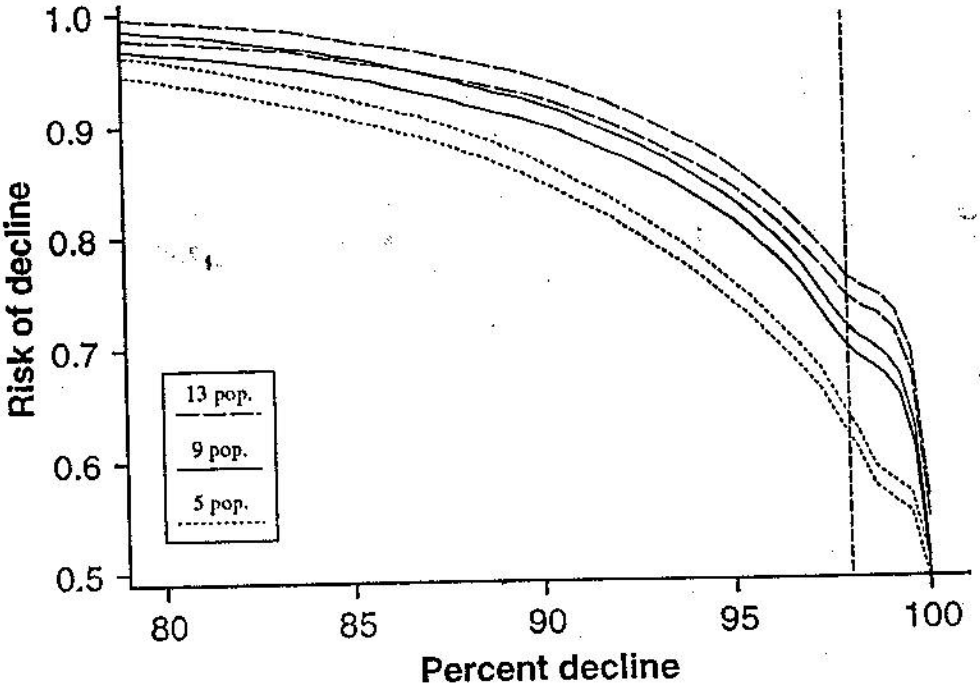

1.0
0.9
0.8
0.7
0.6
0.5
Risk of decline
13 pop.
9 pop.
5 pop.
80
85
90
95
100
Percent decline

FIG 8