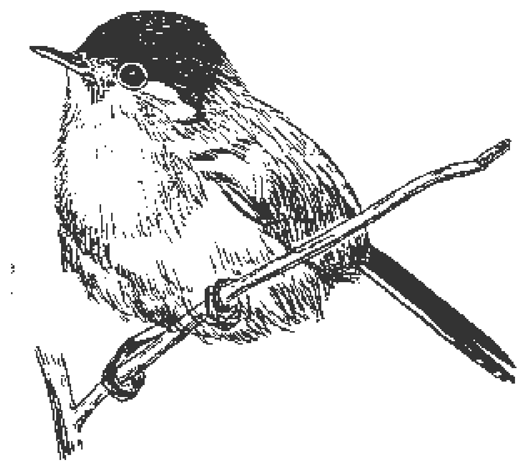
Effects of Fire on California Gnatcatcher Populations
On Camp Pendleton Marine Corps Base

Final Report



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Report Submitted to Marine Corps Base Camp Pendleton
pursuant to requirements of Contract No. N68711-98-LT-80045.

March 1, 2002

Recommended citation:

Atwood, J.L., A. Pairis, M.R. Fugagli and C.A. Reynolds. 2002. Effects of fire on California gnatcatcher populations on Camp Pendleton Marine Corps Base. Unpubl. technical report, prepared for U.S. Marine Corps, Oceanside, California (Contract No. N68711-98-LT-80045); Antioch New England Institute, Keene, New Hampshire. March 1, 2002.

EXECUTIVE SUMMARY

The influence of fire on California gnatcatcher population dynamics was studied on Camp Pendleton Marine Corps Base, San Diego Co., California from 1999 – 2001. Work was conducted in 50 113 ha focal study plots placed randomly in coastal sage scrub vegetation on the Base. Plots were characterized as old (mean number of years since last fire >= 20), middle-aged (mean number of years since last fire < 20 and >= 10), or young (mean number of years since last fire < 10) according to their fire history, as mapped in 1996 by the Base GIS layer YSLF96. Pair and nest locations were similarly classified according to the GIS fire history.

Annual censuses found 220 pairs in 1999, but only 51 and 50 pairs, respectively, during 2000 and 2001. The population crash that occurred between 1999 and 2000 was, for the most part, not caused by human disturbance or habitat loss. Most pairs were located in areas mapped as not having burned for 20 years or more.

When the population crash occurred, declines were more profound in areas dominated by younger habitat. In 1999, 13% of the total pairs were located in areas that had burned < 10 years previously; in 2000 and 2001, 0% and 6%, respectively, of all pairs were located in areas of younger habitat. In other words, although gnatcatchers may occur in areas of younger habitat during periods of high population levels, at low population levels they tend to persist mostly in areas that have not burned for 20 years or more. Maintenance of such “old-growth” areas may be essential to the long-term viability of a population.

A total of 342 California gnatcatcher nests were found and monitored during the study. Nests located in areas mapped as having burned within 10 years had significantly higher rates of daily nest survivorship than nests located in older habitats. Thus, although fewer pairs of gnatcatchers occured in areas of younger habitat, those that did often had higher rates of reproductive success than pairs located in older areas. Differences in predator communities among variously-aged habitat may explain this observation, but more detailed study is needed.

Preliminary analysis of vegetation characteristics failed to uncover significant differences in habitat structure or species composition among territories classified as being located in old, middle-aged, or young areas.

INTRODUCTION

Under contract to the U.S. Marine Corps, Antioch New England Institute studied California gnatcatcher (*Polioptila californica*) ecology and behavior on Camp Pendleton Marine Corps Base, San Diego Co., California from 1999–2001. The general purpose of this work was to collect information of value to Base biologists responsible for management of sensitive natural resources, including Federally Threatened and Endangered Species such as the California gnatcatcher. In particular, the study collected data needed to assess how gnatcatcher habitat quality and distribution is influenced by fire. Although a natural element in southern California's coastal ecosystem, wildfires occur at greater-than-typical frequencies on Camp Pendleton as a result of military training activities central to the Base's mission. This report summarizes results from the 1999, 2000, and 2001 field seasons.

Few systematic studies of California gnatcatchers and fire have previously been conducted, although a number of reports have made various comments regarding the topic. Anthropogenic wildfires are a frequent occurrence in coastal southern California, and thus represent an important factor affecting the dynamics of California gnatcatcher populations. Gnatcatcher re-occupancy of burned areas varies, probably mostly in relation to the time required for coastal sage scrub recovery – which, in turn, may be influenced by fire intensity, the seasonal timing of the burn, soil type and topography, post-fire rainfall patterns, and pre-fire habitat condition. Given the relatively poor dispersal capabilities of California gnatcatchers, and their general tendency to avoid moving through habitats other than coastal sage scrub (Atwood and Bontrager 2001), the presence and proximity of suitable source populations may also influence the speed with which the species returns to an area that has recovered from fire.

Bontrager et al. (1995a) reported successful nesting by gnatcatchers in small coastal sage scrub refugia in the first spring following a late October burn (Bontrager et al. 1995a), but 4–5 years of vegetation recovery is apparently the more typical minimum

(Mayer and Wirtz 1995; Beyers and Wirtz 1997; Wirtz et al. 1997). Some sites may remain unoccupied by California gnatcatchers even 10 years after a fire, especially in more arid, inland areas (Anderson 1991; Mock and Bolger 1992). Furthermore, high fire frequency may cause permanent conversion of coastal sage scrub to grassland (Westman and O'Leary 1986; Zedler et al. 1983); Malanson (1984) found that repeated fires at 10 year intervals may reduce or eliminate *Artemisia californica*, a dominant plant species common in most areas occupied by California gnatcatchers. Tracts of coastal sage scrub may be degraded by invasion of exotic annuals such as *Bromus diandrus* and *B. madritensis*, which competitively exclude dominant scrub species following fire or grazing (Minnich and Dezzani 1998).

Immediately north of Camp Pendleton, the October 1993 Laguna Canyon fire burned 93% of a 2750 ha tract of coastal sage scrub that had been occupied during the preceding breeding season by 127 pairs of California gnatcatchers (LSA Associates 1995; Bontrager et al. 1995a). Within the burned area, gnatcatchers initially persisted in unburned or lightly-burned patches of scrub where stands of fire-resistant *Opuntia* acted as buffers; surveys during spring 1994 found 9% of the estimated pre-fire population of gnatcatchers (Bontrager et al. 1995a). Pair counts remained essentially stable (5-12 pairs) from 1994-1996, with significant reoccupancy of the area beginning when the percent cover of climax shrubs reached 50–60% (Harmsworth Associates 1999a). In 1997 the population increased from 12 to 27 pairs, and in 1998 73 pairs were found (LSA Associates 1994; Griffith Wildlife Biology 1996; Harmsworth Associates 1996, 1997, 1999a). In 1998 the amount of coastal sage scrub present on the site was approximately 41% of the pre-fire condition; the 73 pairs found in 1998 represented 57% of the pre-fire population present at this site (based on Harmsworth Associates 1999a).

Fire history may influence not only gnatcatcher presence on a site, but potentially may also modify the species' behavior in ways that have important demographic consequences. Increased territorial interactions were noted by Bontrager et al. (1995a) in unburned refugia thought to have received as many as 500 individuals displaced by fire. LSA Associates (1997, 1998) suggested that territorial crowding, measured by the number of borders shared with neighboring pairs, may reduce reproductive output. Gnatcatcher pairs in the recovering burn area in Orange Co. had higher rates of reproductive success than at nearby sites (1996 – 5.22 fledglings/pair ± 1.18 SE; 1997 – 5.55 ± 0.77 SE) during the first two years after fire (Harmsworth Associates 1996, 1997); by 1998, when densities were comparable to pre-fire conditions, reproductive success within the burn was lower (4.3 fledglings/pair ± 1.07 SE; Harmsworth Associates 1999a), and not significantly different from that in nearby study areas (based on Harmsworth Associates 1999b). Greater rates of reproductive success immediately following fire may reflect reduced levels of interspecific competition and/or lowered populations of predator species (Harmsworth Associates 1997; D. R. Bontrager, pers. comm.).

Atwood and Bontrager (2001) concluded that "the subject of fire is fundamental to many management issues. Frequency, intensity, timing, and extent of fire all are important topics with relevance to long-term maintenance of viable coastal age scrub habitat and stable gnatcatcher populations. We are only at the earliest stages of understanding how California gnatcatcher populations respond to these recurring, large-scale "catastrophes" that are central to the functioning of this ecosystem." This study attempts to address this topic in terms of 4 primary questions:

1) Where are California gnatcatcher pairs located on Camp Pendleton relative to fire history (number of years post-burn);
2) Does consistency of habitat occupancy by gnatcatchers vary among tracts of habitat with differing fire histories;
3) Does reproductive success of gnatcatcher pairs differ among tracts of habitat with differing fire histories; and
4) Do vegetation characteristics vary among tracts of coastal sage scrub with differing fire histories.

METHODS

The study integrated gnatcatcher distribution and reproductive success data collected during 1999 – 2001, vegetation measurements collected in 2001 – 2002, and general habitat data derived from GIS layers provided by the Marine Corps GIS Branch (1997). These various types of information sources are described below.

Distribution and annual variation – Although Base-wide survey work conducted in 1998 yielded a fairly accurate picture of California gnatcatcher distribution on Camp Pendleton (Atwood et al. 1999), several aspects of this study made it difficult to understand population dynamics of the species on the Base. Specifically, the 1998 work did not include any study of reproductive success, and the absence of a color-banded birds often made it difficult to certainly determine whether a given area was occupied by one or several closely-spaced pairs. Also, because the 1998 survey protocol followed NCCP guidelines, it was likely that some pairs would be missed, even though detection of putative core populations (the objective of the NCCP process) would be accomplished (Atwood et al. 1999).

In this study, distribution surveys were conducted annually within 50 focal study plots, each defined by a 1.2 km diameter circle (113 ha), placed throughout the Base (Fig. 1). Fire history and vegetation characteristics of each plot, derived from Base-provided GIS layers (see below), are provided in Tables 1 and 2. Photos of each plot are provided in Appendix A, as well as in digital format (*.jpg files) on the enclosed CD.

All major areas of natural habitat within each plot were surveyed for breeding California gnatcatchers during February – June of each year of the study (1999 – 2001). In 1999, placements of pair locations were estimated by field workers through inspection

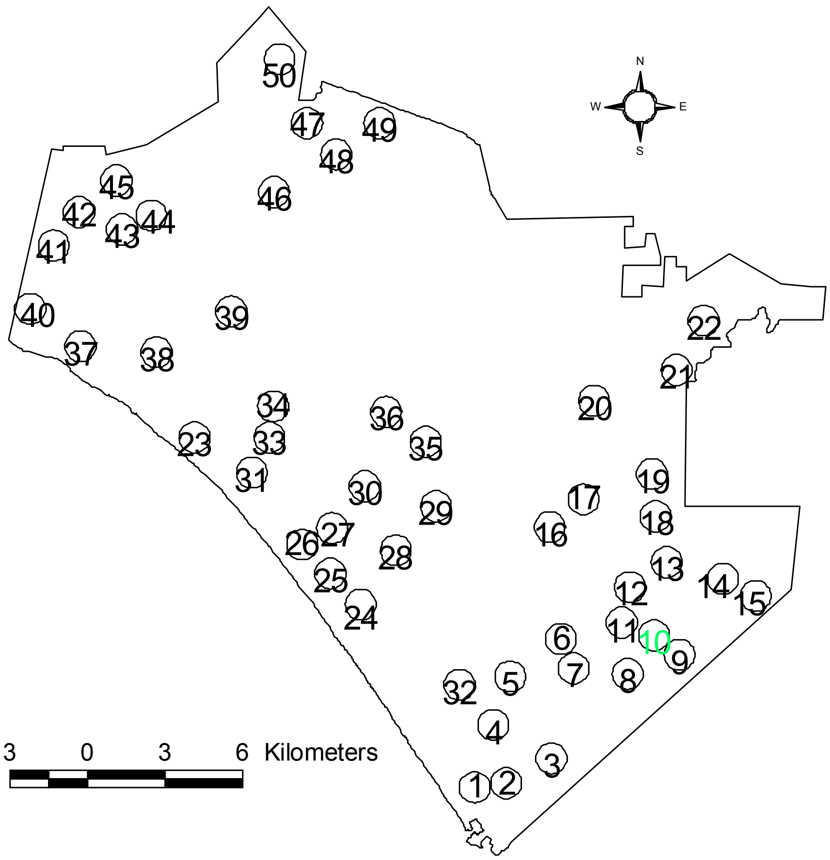

Fig. 1. Location of 50 113 ha focal study plots on Camp Pendleton Marine Corps Base.

Table 1. Fire history characteristics of 50 study plots on Camp Pendleton, based on GIS layer YSLF96. Weighting of means based on total area (ha) of differently-aged polygons within each plot. Plots categorized as "OLD" (mean number of years since last fire >= 20), "MIDDLE-AGED" (mean number of years since last fire < 20 and >= 10), and "YOUNG" (mean number of years since last fire < 10).

Plot	Mean YSLF	Category
1	24.0	OLD
2	23.8	OLD
3	21.9	OLD
4	20.3	OLD
5	9.6	YOUNG
6	17.4	MIDDLE-AGED
7	17.4	MIDDLE-AGED
8	21.5	OLD
9	23.6	OLD
10	16.8	MIDDLE-AGED
11	13.4	MIDDLE-AGED
12	21.4	OLD
13	13.6	MIDDLE-AGED
14	23.5	OLD
15	14.4	MIDDLE-AGED
16	11.0	MIDDLE-AGED
17	21.6	OLD
18	23.8	OLD
19	22.8	OLD
20	20.8	OLD
21	7.3	YOUNG
22	9.2	YOUNG
23	6.0	YOUNG
24	23.9	OLD
25	18.1	MIDDLE-AGED
26	17.7	MIDDLE-AGED
27	15.0	MIDDLE-AGED
28	15.5	MIDDLE-AGED
29	15.9	MIDDLE-AGED
30	8.9	YOUNG
31	6.3	YOUNG
32	1.5	YOUNG
33	6.1	YOUNG
34	13.5	MIDDLE-AGED
35	17.6	MIDDLE-AGED
36	7.4	YOUNG
37	23.0	OLD
38	9.7	YOUNG
39	3.1	YOUNG
40	24.0	OLD

Table 1. Fire history characteristics of 50 study plots on Camp Pendleton, based on GIS layer YSLF96 (cont'd).

Plot	Mean YSLF	Category
41	23.8	OLD
42	11.9	MIDDLE-AGED
43	18.3	MIDDLE-AGED
44	17.9	MIDDLE-AGED
45	17.2	MIDDLE-AGED
46	7.2	YOUNG
47	10.1	MIDDLE-AGED
48	8.3	YOUNG
49	22.1	OLD
50	24.0	OLD

Table 2. Vegetation characteristics of 50 study plots on Camp Pendleton. Categories derived from GIS layer VEG95.

	Area (ha) of vegetation categories [a]						
PLOT	CSS	GRS	CHP	RIP	AGR	OAK	MAR
01	22.1	6.6	0.0	2.0	34.9	0.0	46.9
02	72.8	8.6	0.0	3.4	15.8	0.0	12.0
03	87.4	24.0	0.0	0.0	1.1	0.0	0.0
04	49.1	63.5	0.0	0.0	0.0	0.0	0.0
05	94.2	14.2	0.0	4.2	0.0	0.0	0.0
06	25.4	77.6	0.0	0.0	9.5	0.0	0.0
07	27.3	84.6	0.0	0.0	0.0	0.0	0.6
08	23.9	82.6	0.0	0.8	5.3	0.0	0.0
09	40.8	70.8	0.0	1.0	0.0	0.0	0.0
10	39.0	59.4	0.0	2.4	11.8	0.0	0.0
11	16.2	75.3	0.0	12.0	9.0	0.0	0.0
12	63.5	22.9	3.1	0.0	23.0	0.0	0.0
13	31.7	35.7	11.8	0.0	33.4	0.0	0.0
14	82.8	18.3	0.0	10.1	1.3	0.0	0.0
15	102.2	0.0	0.0	10.3	0.0	0.0	0.0
16	0.0	108.9	0.0	3.6	0.0	0.0	0.0
17	4.0	101.7	0.0	6.4	0.4	0.0	0.0

Table 2. Vegetation characteristics of 50 study plots on Camp Pendleton (cont'd).

	Area (ha) of vegetation categories [a]						
PLOT	CSS	GRS	CHP	RIP	AGR	OAK	MAR
18	0.4	17.4	0.0	4.8	90.0	0.0	0.0
19	21.2	6.0	0.0	16.8	64.9	0.0	3.6
20	79.2	0.0	0.0	0.0	0.0	33.4	0.0
21	100.7	0.0	0.0	11.5	0.3	0.0	0.0
22	112.3	0.2	0.0	0.0	0.0	0.0	0.0
23	98.6	0.0	0.0	0.3	13.6	0.0	0.0
24	10.7	63.3	0.0	38.6	0.0	0.0	0.0
25	17.1	94.0	0.0	0.0	1.5	0.0	0.0
26	20.9	91.6	0.0	0.0	0.0	0.0	0.0
27	81.7	29.1	0.0	1.7	0.0	0.0	0.0
28	97.6	12.4	0.0	2.6	0.0	0.0	0.0
29	46.1	37.4	0.0	20.2	8.9	0.0	0.0
30	73.6	39.0	0.0	0.0	0.0	0.0	0.0
31	109.1	0.0	0.0	3.4	0.0	0.0	0.0
32	25.6	84.8	0.0	0.0	2.2	0.0	0.0
33	95.2	14.6	0.0	2.8	0.0	0.0	0.0
34	80.8	30.0	0.0	0.0	0.0	1.7	0.0
35	5.9	94.4	0.0	10.9	0.0	1.4	0.0
36	5.6	97.1	0.0	9.1	0.3	0.4	0.0
37	48.0	0.0	0.0	27.2	37.3	0.0	0.0
38	93.8	18.7	0.0	0.0	0.0	0.0	0.0
39	44.1	38.1	0.0	25.8	3.6	0.9	0.0
40	23.6	0.0	0.0	11.6	76.1	0.0	0.0
41	72.2	1.1	0.0	0.0	39.2	0.0	0.0
42	34.0	42.6	0.0	9.7	26.1	0.0	0.0
43	17.2	83.9	0.0	1.2	10.2	0.0	0.0
44	16.3	78.8	0.0	17.5	0.0	0.0	0.0
45	45.6	66.9	0.0	0.0	0.0	0.0	0.0
46	72.2	33.5	0.0	0.0	0.0	6.9	0.0
47	84.5	0.0	21.4	6.6	0.0	0.0	0.0
48	92.6	0.5	18.1	1.4	0.0	0.0	0.0
49	0.0	0.0	102.9	9.6	0.0	0.0	0.0
50	72.2	0.0	28.1	0.0	0.0	12.2	0.0

[a] CSS = coastal sage scrub; GRS = grassland; CHP = chaparral; RIP = riparian; AGR = developed, disturbed, agriculture; OAK = oak woodland; MAR = marsh.

of topographic maps and aerial photographs. In 2000 and 2001, pair locations were derived from actual nest sites positioned with a Garmin 12XL GPS unit; if multiple nests of a particular pair were found within a single year, the centroid of a minimum convex polygon (calculated using Spatial Movements extension, ArcView 3.2) defining these nest points was used as representative of that pair's location. Pair locations for all 3 years are contained in the ArcView 3.2 shapefile PAIRS99_01; each pair was assigned a unique identifying number (Pair_ID), consisting of the year, plot number, and a 2-digit number (e.g. 00-37-03). Nest locations from 2000 and 2001 are contained in the ArcView shapefile NESTS99_01; nests were similarly assigned unique identifying numbers, consisting of the Pair_ID followed by a single digit decimal value indicating the nesting attempt by that pair (e.g., the Nest_ID for the second nesting attempt in 2000 by pair 3 in Plot 37 was identified as 00-37-03.2).

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 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 biologists would revisit the site in order to obtain simultaneous observations of all birds in question, or banders would attempt to mark at least some individuals to enhance ability to discriminate among closely-spaced pairs. Annual population estimates within each plot were based on observations of uniquely banded birds, the locations of simultaneously active nests, or simultaneous observations of unbanded birds. Survey intensity exceeded the minimum effort required by U.S. Fish and Wildlife Service (USFWS) protocols (USFWS 1997).

Reproductive Success – Nest monitoring associated with this study was limited to pairs found within (or immediately adjacent to) the focal study plots, and followed procedures that have been used by the Principal Investigator elsewhere in southern California. Territories were regularly visited from early March through July, and nests were located through direct observation of nest building, nest exchanges, or feeding of nestlings.

To minimize potential impacts associated with monitoring activities, visits by biologists to nests were limited to 1 – 2 dates from the beginning of nest building to fledging. The initial visit was made when feeding of nestlings was first observed, with the objective of estimating the age of juveniles that were present based on developmental criteria described in Atwood and Bontrager (2001). Date for a follow-up banding visit and/or a date when nestlings could be expected to fledge were then determined. Banding visits were made in 1999 and 2000 when nestlings were approximately 8 – 9 days of age; handling of nestling gnatcatchers before this age is impractical due to the birds' small size, and banding of older nestlings may cause premature fledging (Atwood and Bontrager 2001). Systematic banding of nestlings was not attempted in 2001 because of the project's anticipated termination the following year. Nests were not visited when western scrub-jays (*Aphelocoma californica*), loggerhead shrikes (*Lanius ludovicianus*), or brown-headed cowbirds (*Molothrus ater*) were seen nearby. On dates when nests were not directly inspected, observations of adult gnatcatcher behavior were made from vantage points located at least 50 m from the nest site. This approach allowed us to determine if the nest was still active and attended, or if failure had occurred. If no evidence of activity was seen near the nest location (including feeding of recently-fledged young), field observers would approach and inspect the nest and confirm that failure had occurred.

Mist nets were used to capture adult and fledgling gnatcatchers for banding during 1999 and 2000; birds were attracted to the vicinity of the nets by playback of recorded vocalizations. Three plastic colored leg bands were used in conjunction with the numbered USFWS band to provide a unique color combination. Lists of birds banded during the study are provided in Appendix B.

Analysis of reproductive success data was not based on overall plot characteristics, thus allowing use of data collected from nests not located within actual plot boundaries. Nests were classified as being located in habitat that was "OLD" (number of years since last fire >= 20), "MIDDLE-AGED" (number of years since last fire < 20 and >= 10), and "YOUNG" (number of years since last fire < 10).

We used 2 methods to calculate rates of nest survivorship. First, we applied the traditional technique described by Mayfield (1961, 1975). Secondly, we used the program MAYFIELD, available interactively at http://www.mbr.nbs.gov/software/ mayfield.html. Although the two techniques aim at producing similar results, they use different mathematical algorithms; especially, the traditional approach does not address statistical issues raised by irregularly-spaced nest monitoring visits (Bart and Robson 1982). The program CONTRAST, also available interactively at the National Biological Service's Patuxent website http://www.mbr.nbs.gov/software/, was used to test for significant differences among nests located in OLD, MIDDLE-AGED, and YOUNG habitat.

Habitat Data – Several sources of spatial data formed the basis of many of the analyses conducted in this study. In particular, these sources included (1) the GIS vegetation layer VEG95, and (2) the fire history layer YSLF96 (Marine Corps Base GIS Branch 1997), and (3) the gnatcatcher distribution layer CAGN98, showing the results of the Base-wide population survey conducted by Atwood et al. (1999).

The GIS layer VEG95, showing the results of habitat mapping conducted in 1995, indicates at least 23,433 ha of natural vegetation classified as various types of coastal sage scrub on Camp Pendleton. In this study we expanded the Coastal Sage Scrub vegetation categories provided in VEG95 to include Coastal Bluff Scrub (Holland classification code 31000), Coastal Scrub (Holland classification code 32000), Coastal Sage-Chaparral Scrub (Holland classification code 37G00), and Flat-topped Buckwheat (Holland classification code 37K00). Other vegetation categories we used in this analysis included: (1) Chaparral; (2) Grassland; (3) Disturbed, including agricultural and developed land; and (4) Other.

Previous field work on gnatcatcher distribution on Camp Pendleton suggested that some mapping inaccuracies exist within the vegetation data layer VEG95; approximately

35% of 620 California gnatcatcher pair locations found by Atwood et al. (1999) were located in areas classified as grassland, chaparral, or disturbed (ruderal) vegetation as opposed to the species' more typical coastal sage scrub community. While in some cases gnatcatcher territories may actually have been located in these less preferred plant communities, most of the apparent discrepancies are more likely the result of inaccurate mapping of vegetation boundaries and/or territory locations.

As an important part of this study we compared the vegetation data contained in VEG95 with 1994 USGS aerial photographs downloaded at 1 m resolution from http://terraserver.homeadvisor.msn.com/default.asp. Overlays showing the relationship between VEG95 and these aerial photographs are provided for each of the 50 focal study plots in Appendix C. Although VEG95 provides a gross overview of the distribution of habitats on Camp Pendleton, it is evident that it contains many inaccuracies at a fine scale. This lack of accurate spatial resolution in the available vegetation map limited the type of analyses we were able to conduct.

Similar problems may also be associated with the fire history data layer, YSLF96. Even assuming that all fires have been identified in this cumulative data layer, the possibility exists that small, unburned inclusions within a fire's primary perimeter may not have been mapped; the GIS layer, therefore, may imply that some areas burned which, in fact, had not. Such small unburned patches, where fire may have jumped over a narrow ravine or bypassed a particular slope, represent important habitat islands that may differ markedly from the condition of the immediately surrounding landscape. Three percent of 620 gnatcatcher territories found by Atwood et al. (1999) were located in areas shown by YSLF96 as having been recently burned (<= 5 years since last fire), possibly reflecting failure to map the presence of small, unburned patches of habitat within a fire's overall boundaries.

In addition to habitat data derived from Base GIS layers, we also collected vegetation transect data during June 2001 and January 2002. To promote comparability of results, vegetation work followed protocols used by Braden et al. (1997). Vegetation associated with 40 gnatcatcher territories identified during 1999 and 2000 was sampled;

we stratified our selection to ensure inclusion of territories of varied fire histories. GPS coordinates, topographic maps, and aerial photos were used in the field to select transect starting positions. Once a site was located, five radial lines, of random lengths ranging from 1-100 m, were laid out at 60 degree intervals. Beginning at the end of each of these radial lines, measurements were taken along 5 m long transects oriented along each cardinal direction. We used a 2 m long PVC pipe, marked in 10 cm intervals, as a visual reference.

The following information was recorded along each of these 5 m transects at 1 m intervals: height (m) of all annual vegetation, perennial shrubs, and dead wood that fell within 10 cm of the marker pole, species of perennial shrub, litter depth, and number of perennial shrub contacts (hits) per 10 cm interval. Vertical structure was described by summarizing the total number of hits at intervals < 0.5 m (HITS_LT0.5), 0.5–1.0 m (HITS_0.5-1.0), 1.0-1.5 m (HITS_1.0-1.5), and 1.5-2.0 m (HITS_1.5-2.0). The total number of rod hits in each territory and the mean number of hits per transect were used as indices of horizontal structure.

In order to avoid undue disturbance of pairs with nests or fledglings, we elected to postpone collecting vegetation measurements until after the breeding season had been completed on several of our most densely-occupied plots. Although this decision introduced a seasonal component to the data collection that would have been desirable to avoid, we believe that because the January 2002 sampling occurred before significant rainfall had caused new vegetation growth that spring 2001 and winter 2002 data may be considered comparable. We readily acknowledge that this is not a perfect arrangement, but felt that we should err on the side of caution and avoid disturbing pairs that were actively engaged in nesting activities.

Additional analyses of vegetation and survivorship data collected during this study are anticipated as part of Ms. Pairis' doctoral research, and will be provided to Camp Pendleton as soon as available.

RESULTS

Distribution and annual variation

Total numbers of gnatcatchers within the 50 focal study plots varied 220 pairs in 1999 to 51 and 50 pairs, respectively, in 2000 and 2001 (Table 3). On only one plot was a population change apparently attributable to human-caused habitat alteration. The coastal sage scrub vegetation in Plot 09, which supported 20 pairs of gnatcatchers in 1999, was decimated by horse grazing before and during the 2000 breeding season, and by 2001 zero pairs were present. Other changes in pair numbers among the study plots were most likely due to various natural factors, such as mortality resulting from particular, poorly-understood interactions of winter rainfall and temperature (Atwood and Bontrager 2001). Because of the human-related impacts to gnatcatcher habitat on Plot 09 during the course of this study, we excluded this Plot in our analyses of annual variability in population size relative to fire history, described below.

Table 3. Counts of California gnatcatchers within 50 focal study plots, 1999 – 2001. Unlisted plots did not support gnatcatchers during any of the three years of the study.

PLOT	1999	2000	2001
2	30	10	9
3	3	0	0
4	20	5	5
6	2	0	0
7	4	2	0
8	3	1	0
9	20	6	0
10	5	0	0
11	2	0	0
12	1	1	0
13	11	0	2

Table 3. Counts of California gnatcatchers within 50 focal study plots, 1999 – 2001 (cont'd).

PLOT	1999	2000	2001
14	9	0	0
18	2	1	0
19	11	3	3
24	4	1	1
25	13	2	5
26	7	3	5
37	13	5	3
40	18	7	6
41	23	4	9
42	7	0	1
43	5	0	1
45	7	0	0
TOTALS	220	51	50

Although gnatcatcher pairs were occasionally found in specific polygons mapped as having burned < 10 years previously (see below), no plots that were classified, on average, as YOUNG were found to support pairs of gnatcatchers. In 1999, 13% of pair locations fell in polygons mapped as having burned < 10 years previously, and 75% were in areas that had not burned for 20 years or more. In 2000 and 2001, 0% and 6%, respectively, of pairs were located in areas of YOUNG habitat, and 95% (2000) and 89% (2001) were in areas mapped as OLD habitat (Table 4).

Table 4. Location of California pairs relative to habitat of varying ages since last fire. Counts include pairs that were adjacent to, but technically outside of, focal study plot boundaries.

YEAR	YOUNG	MID	OLD	total
1999	30	27	170	227
2000	0	3	63	66
2001	4	3	59	66

The percent change in number of pairs present during high (1999) vs. low (2000) population levels was greater on MIDDLE-AGED (x = 0.90, SD = 0.187, n = 11) than OLD (x = 0.64, SD = 0.250, n = 11) plots (Wilcoxon rank sum test, P = 0.01). That is, when gnatcatcher populations "crashed" between 1999 and 2000, the declines were more profound in areas dominated by younger habitat (Table 5). Pair counts in OLD plots were more stable over the 3-year study than in plots classified as MIDDLE-AGED; coefficients of variability (CV) were significantly smaller in OLD plots (Wilcoxon rank sum test, P = 0.02).

Table 5. Annual variation in counts of California gnatcatcher pairs within focal study plots occupied during 1999 – 2001. Unlisted plots did not support gnatcatchers during any of the three years of the study.

		YEAR					
PLOT	YSLF [a]	1999	2000	2001	x	SD	CV
02	OLD	30	10	9	16	11.846	72.5
03	OLD	3	0	0	1	1.733	173.2
04	OLD	20	5	5	10	8.663	86.6
06	MIDDLE-AGED	2	0	0	1	1.155	173.2
07	MIDDLE-AGED	4	2	0	2	2.000	100.0
08	OLD	3	1	0	1	1.528	114.6
09	OLD	20	6	0	9	1.263	118.4
10	MIDDLE-AGED	5	0	0	2	2.887	173.2
11	MIDDLE-AGED	2	0	0	1	1.155	173.2
12	OLD	1	1	0	1	0.577	86.6
13	MIDDLE-AGED	11	0	2	4	5.859	135.2
14	MIDDLE-AGED	9	0	0	3	5.196	173.2
18	OLD	2	1	0	1	1.000	100.0
19	OLD	11	3	3	6	4.619	81.5
24	OLD	4	1	1	2	1.733	86.6
25	MIDDLE-AGED	13	2	5	7	5.686	85.3
26	MIDDLE-AGED	7	3	5	5	2.000	40.0
37	OLD	13	5	3	7	5.292	75.6
40	OLD	18	7	6	10	6.658	64.4
41	OLD	23	4	9	12	9.849	82.1
42	MIDDLE-AGED	7	0	1	3	3.786	142.0
43	MIDDLE-AGED	5	0	1	2	2.646	132.3
45	MIDDLE-AGED	7	0	0	2	4.415	173.2

Although not directly related to the question of fire impacts on gnatcatcher populations, we also used our focal survey data to make a Base-wide population estimate of the species. Typically such estimates have been derived from a labor-intensive (and costly) survey of all potential gnatcatcher habitat on Camp Pendleton; the most recent of these Base-wide surveys was completed in 1998 by Atwood et al. (1999). Here, we used plot-based counts to estimate the Base-wide gnatcatcher population; because we wished to compare this estimate with the results of Atwood et al.'s (1999) Base-wide survey, we used 1999 plot data. By substituting as the independent variable the total area of 16,213 ha of coastal sage scrub mapped as being present on the Base (excluding live fire and security areas not surveyed by Atwood et al. in 1998), the resulting regression equation:

$$COUNT = 37.479 + (0.033 * \text{CSS area in ha})$$

predicted a total of 573 pairs of gnatcatchers on Camp Pendleton – a value surprisingly close to the much more difficult-to-obtain population estimate of 620 pairs obtained through Atwood et al.'s (1999) Base-wide survey.

Reproductive Success

A total of 342 California gnatcatcher nests were found and monitored during the 3-year study. We used these data to calculate rates of daily nest survival as indicators of reproductive success in habitat with differing fire histories.

First, especially in light of the substantial change in population size between 1999 and 2000, we tested for the possibility of significant annual variation in reproductive success that would have prevented our pooling of data across years. Four plots were selected for analysis as being represented by adequate samples of nests during each of the 3 years (Table 6).

Table 6. Plots and sample sizes (number of nests) used for Mayfield analyses of among-year variation in reproductive success.

Plot	1999	2000	2001
02	30	17	17
37	17	12	6
40	9	11	9
41	16	9	11

In only one of the plots (Plot 37) did we find a significant among-year difference in estimates of daily nest survivorship rates (Table 7); this case not only involved an estimate derived from the smallest sample (6 nests in 2001) used in these calculations, but nest survivorship may also have been adversely impacted by the activities of other researchers working on the plot. In general, we found no evidence for among-year variation in reproductive success, and consequently decided to pool all of our available data for use in evaluating fire impacts on reproductive success.

Table 7. Among-year comparisons of estimated daily nest survivorship rates on 4 focal study plots. Estimates based on traditional Mayfield approach and Patuxent Wildlife Research Center program MAYFIELD. Probability values testing the hypothesis of among-year homogeneity of estimates based on program CONTRAST.

DAILY NEST SURVIVORSHIP								
	Traditional				Patuxent			
PLOT	1999	2000	2001	P	1999	2000	2001	P
02	0.879	0.811	0.837	0.69	0.970	0.956	0.977	0.42
37	0.705	0.875	0.769	0.12	0.940	0.971	0.945	0.29
40	0.909	0.964	0.700	0.03	0.982	0.991	0.938	0.12
41	0.833	0.882	0.793	0.61	0.966	0.965	0.962	0.98

We found significant differences in rates of daily nest survivorship among nests located in OLD (n = 301), MIDDLE-AGED (n = 25), and YOUNG (n = 16) habitat (ANOVA, $P < 0.01$). Regardless of the estimation technique, daily nest survivorship was higher for nests situated in YOUNG habitat than in areas classified as MIDDLE-AGED or OLD (Fig. 2; Table 8).

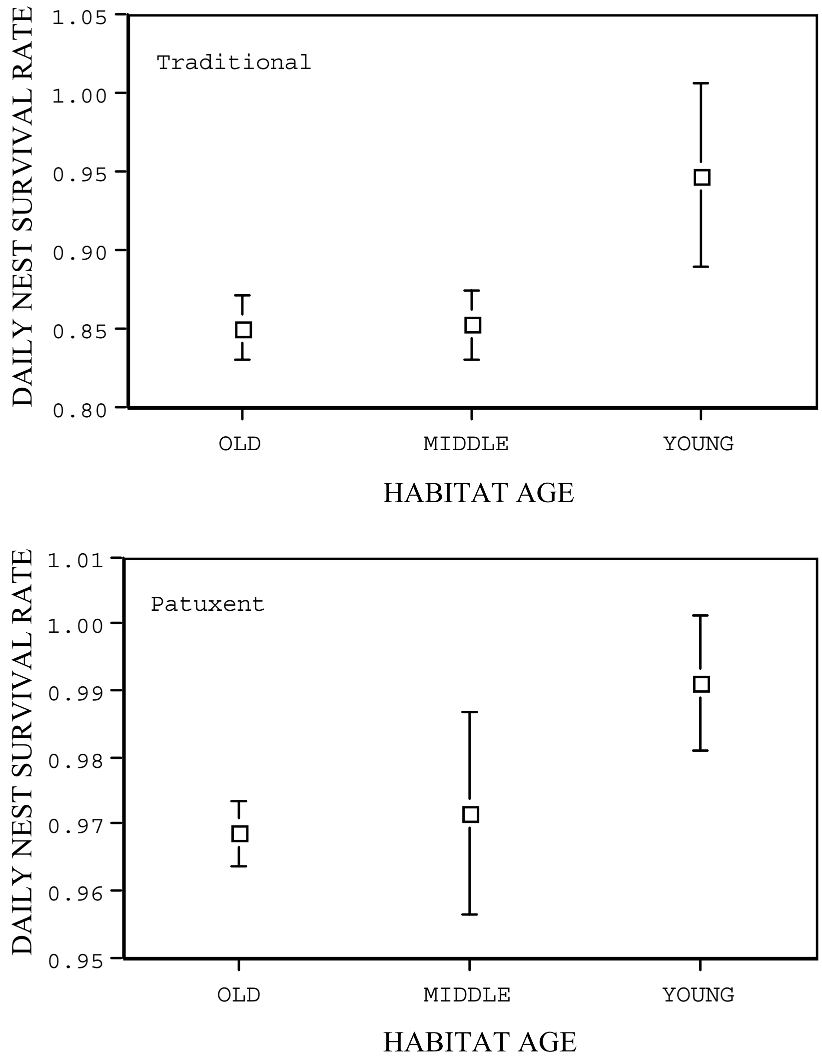

Fig. 2. Comparison of reproductive success (measured by daily nest survival rates) among habitats of varying fire histories. Results obtained by two methods of calculating daily nest survival rates are shown. Error bars represent 95% confidence range.

Table 8. Comparison of daily nest survival estimates obtained by two different analytic approaches. Probability values testing the hypothesis of homogeneity of estimates among habitat of differing fire histories based on program CONTRAST.

	Nest Survivorship			
ANALYSIS	OLD	MID	YOUNG	P
Traditional	0.851	0.853	0.947	0.008
Patuxent	0.969	0.972	0.991	0.000

Habitat Data

There was no significant difference in the mean height of perennial plants found within California gnatcatcher territories, although values representative of YOUNG habitats were slightly smaller than those found in MIDDLE-AGED and OLD territories (Table 9; ANOVA, P = 0.29).

Table 9. Comparison of mean height of perennial plants among California gnatcatcher territories with differing fire histories.

AGE	n	MEAN	SE	Lower 95%	Upper 95%
OLD	12	1.00	0.06	0.87	1.13
MID	3	1.12	0.13	0.86	1.39
YOUNG	10	0.90	0.07	0.76	1.05

Similarly, no significant differences were found in measures of general vegetation structure; neither indices of vertical structure (HITS_LT0.5, HITS_0.5-1.0, HITS_1.0-1.5, or HITS_1.5-2.0), or horizontal structure (TOTAL_HITS) differed significantly among territories classified as belonging to different fire histories (ANOVA, P > 0.05).

DISCUSSION

In general, California gnatcatchers occupy areas of habitat that have not burned for at least 20 years. Many variables influence this generality, especially physical and climatic factors that affect rates of vegetation recovery following a burn. Nonetheless, both this study and work in southern Orange Co. have found that the majority of gnatcatcher pairs in a region are located in areas that have not burned for at least 10 years. On Camp Pendleton, the percent of total pairs that were located in "old-growth" habitat (>= 20 years since last fire) varied during this study from 75 – 95%.

This is not to suggest that younger areas of habitat are never occupied by California gnatcatchers. In fact, considerable numbers of pairs may be distributed within a fairly recently burned landscape where the vegetation has substantially recovered. However, this study found that such areas of younger habitat are less likely to be occupied during population "crashes", which occur fairly often in California gnatcatchers. That is, under high population levels, gnatcatchers may appear to be widespread on the landscape, with almost all areas of suitable habitat being occupied. But, under low population levels, the only areas of habitat that are consistently occupied are those that have not burned for 20 years or more. Such "old-growth" habitats may provide essential refugia during population crashes.

Surprisingly, although areas of older habitat were more consistently occupied than areas which had been burned more recently, gnatcatchers that nested in younger habitat had higher rates of reproductive success (as measured by estimates of daily nest survivorship) than pairs in older habitat. Thus, although fewer pairs may occur in areas of younger habitat, those that do often have higher rates of reproductive success than pairs with territories in older areas. Differences in predator communities among variously-aged habitat may explain this observation, but more detailed study is needed.

More study is needed to clarify what actual variables among habitats of different fire histories are relevant to California gnatcatcher population dynamics. Our preliminary analysis found no obvious contrasts in vegetation structure or composition between territories located in old, middle-aged, or young habitat, but further work on prey abundance, habitat homogeneity, and structure of predator communities all remains to be completed.

ACKNOWLEDGMENTS

Various people assisted us at different stages of this project, and we wish to express our gratitude to all. Don Schroeder provided able assistance in finding and monitoring gnatcatcher nests. Andrea Petersen graciously provided a home-away-from-home for numerous assistants; her hospitality went above and beyond the call of duty. Jill Turner put in endless hours of GIS work. Jaimie Contois, Amy Smith, Jessica Ganas, and Melissa Diven all waded through fields of *Artemisia* collecting vegetaion data. Jim Gruber and Sherman Morrison smoothed difficult administrative headches.   Tim Burr, John Lovio, Bill Berry, and Rob Lovich all were patient and understanding, despite our tardy reports and infrequent communication. We thank all of you.

This project was funded by the Assistant Chief of Staff, Environmental Security, Natural Resources Division, Marine Corps Base Camp Pendleton, United States Marine Corps.

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APPENDIX A

Photographs of focal study plots on Camp Pendleton
Marine Corps Base.
For location of Plots see Figure 1. Mean years since last
fire (YSLF) for each plot represent average age of polygons
contained within plot, weighted by polygon area.

Plot 01: N33.13752 W117.23531 Mean YSLF=24.0. June 2001.

Plot 01: N33.13752 W117.23531 Mean YSLF=24.0. June 2001.