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THE TAXONOMY, DISTRIBUTION, AND STATUS OF COASTAL CALIFORNIA CACTUS WRENS

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The southern coastal sage scrub is a distinctive plant community of southern California (Munz and Keck 1959, Mooney 1977). Beginning very narrowly in the Santa Barbara region, it is best developed in Ventura, Los Angeles, Orange, and San Diego counties, and ends in northwestern Baja California, where a different plant assemblage, the maritime desert scrub, begins (Thorne 1976). One very prominent feature of coastal sage scrub is thickets of cactus, including the Coastal Cholla, *Opuntia prolifera*, and two species of prickly-pears, *Opuntia littoralis* and *O. oricola*. The coastal sage scrub is the primary habitat of two birds, the California Gnatcatcher, *Polioptila californica californica*, and the San Diego Cactus Wren, *Campylorhynchus brunneicapillus sandiegensis*, that are declining rapidly because of loss of habitat to urbanization. (For explanation of variations in the spelling of the Cactus Wren's scientific name, see Appendix 1).

This paper has four goals. First, we present the characters distinguishing *C. b. sandiegensis* as a valid subspecies distinct from adjacent races of Baja California and the interior continental deserts. The characters are given in sufficient detail that anyone with a specimen in hand should be able to identify it. Second, we evaluate the taxonomic status of the Cactus Wrens occupying Ventura, Los Angeles, and Orange counties. In the original description (Rea 1986:119), these were referred to as less typical *sandiegensis*, and the birds from the San Fernando Valley, Los Angeles Co., were called *anthonyi* (Phillips 1986:120). Third, we analyze the habitat requirements of *C. b. sandiegensis*. And finally, we present census data from the last ten years demonstrating the rapid decline of the San Diego Cactus Wren due to habitat loss.

TAXONOMIC BACKGROUND

Taxonomists have long recognized that the Cactus Wren population isolated along the California coast is distinctive, but opinions differed as to

the significance of the difference (Table 1). Debate often focused on whether the wrens belonged to a continental or a peninsular subspecies. The peninsular forms in Baja California (*C. b. bryanti* and *C. b. affinis*, including "*C. b. purus*") have the entire tail black barred with white, except for the central brown pair of rectrices, have little or no buff wash on the flanks and abdomen, and have large spots rather uniformly distributed over the underparts. The black throat spots are mostly double on each feather. In contrast, the various continental forms have quite a different appearance. Their tails are essentially black except for the brown central pair. The black feathers have a subterminal white bar with additional white bars being restricted to the outer one or two pairs of rectrices. The birds have a strong cinnamon-buff wash on the abdomen and a cluster of large black spots on the throat. There is usually a single large spot along the shaft of each throat feather. The remaining underparts are more finely spotted.

The differences between the two groups of subspecies are readily apparent in the field as well as in the hand. Actually the two groups look like different species.

Furthermore, the two subspecies nearest the southern California coastal population differ strongly in dorsal coloration. *Campylorhynchus b. bryanti* of northern Baja (31°–29°N) is rather uniform dark umber brown above, whereas *C. b. anthonyi* of the deserts of southern California, adjacent northeast Baja California, southern Arizona, and northwestern Sonora has a brownish gray back that contrasts with the darker, strongly rufous crown and nape (see Figure 1 for distributions).

When A. W. Anthony (1894) erected the subspecies *C. b. bryanti* for the Cactus Wrens of northern Baja California (type locality San Telmo), he referred San Diego County birds to his new race. He wrote, "east of the Cuyamaca Mts., I am unable to find any indication of either *bryanti* or

Table 1 Historical Treatment of Coastal Cactus Wrens

Author	Date	Disposition
A. W. Anthony	1894	Race different from that in Baja or desert (unnamed)
E. A. Mearns	1902	*bryanti*
H. S. Swarth	1904	*couesi*
R. Ridgway	1904	*bryanti* (not typical) in San Diego region; *couesi* in Los Angeles region
F. Stephens	1904	*bryanti* "blending into *couesi* (or *anthonyi*)"
J. Grinnell	1915	"Meeting ground of *couesi* and *bryanti*" in same locality, possibly without intergradation
J. Grinnell	1921	*couesi* with slight tendency toward *bryanti*
G. Bancroft	1923	Distinct disjunct subspecies (unnamed)
J. Grinnell	1928	*couesi*
Grinnell and Miller	1944	*couesi*
G. Bancroft	1946	Western "group"
A. M. Rea	1986	Described subspecies *sandiegensis*
M. R. Browning	1990	Recognized *sandiegensis*

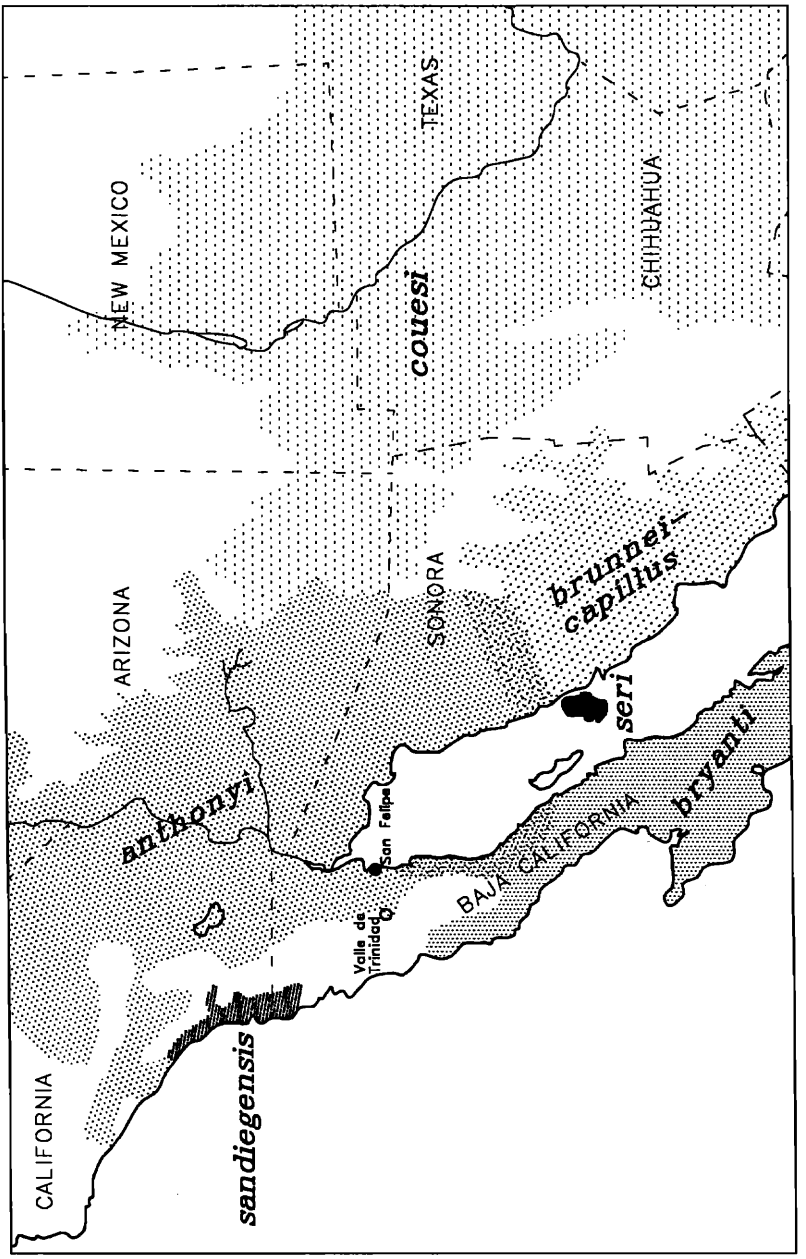

Figure 1. Distributions of subspecies of the Cactus Wren in the southwestern United States and northwestern Mexico. Overlapping of patterns suggests probable areas of intergradation.

affinis," noting that birds from the interior or desert portion of the county are unlike those of Baja California but the same as those from the rest of the Sonoran Desert of southern California, Arizona, and New Mexico. He also noted that the rufous wash of the underparts "is not so pronounced in western San Diego County skins as those from San Bernardino County (Cal.), Arizona, and New Mexico." In an addendum Anthony noted, "Owing to the lack of material, I am unable to make a satisfactory disposition of the Cactus Wren from north of the boundary. The series at hand points toward a race inhabiting the southwestern part of California, differing from the bird of Arizona, New Mexico, and Texas." Also in 1894, Anthony collected four specimens (now in the Carnegie Museum, Pittsburgh) from Valle de las Palmas and Carrizo Valley, a bit southeast of Tijuana in Baja California. These also show the San Diego combination of characters.

The Cactus Wren as a species had been described originally by Lafresnaye in 1835 from "Californie." Edgar A. Mearns (1902) attempted to determine where, in what was broadly conceived in the 1830s as constituting California, the original specimen might have been taken because, as Mearns explained, "the Cactus Wren of the portion of California west of the Coast Range Mountains is different from that of east." At his request, Robert Ridgway at the Smithsonian Institution examined the type specimen preserved at the Boston Society of Natural History. He concluded that it best matched material from Guaymas, Sonora, thus fixing this as the type locality. Mearns then described the subspecies *C. b. anthonyi* with type locality near Tacna, Yuma County, Arizona, and gave its range as "interior deserts of the southwestern United States, south into the Mexican states of Chihuahua, Sonora, and northeastern Lower California (east of the Coast Range)." He retained the population west of the Peninsular Ranges in *bryanti*.

Swarth (1904) took exception to Mearns' treatment, considering *C. b. anthonyi* and *C. b. bryanti* (at least as represented in southern California) both synonyms of *C. b. couesi* (type locality Laredo, lower Rio Grande, Texas). Swarth conceded that *bryanti* might be a valid race from the Baja California area Anthony ascribed to it. Swarth's inability to see more than one subspecies is hardly surprising because his specimens were all from the range of *anthonyi* as we define it here.

The same year Ridgway (1904) completed the third volume of his monumental Birds of North and Middle America. He treated *C. b. anthonyi* as a synonym of *C. b. couesi* of the lower Rio Grande, ranging west to Orange, Los Angeles, and *interior* San Diego counties, and included the "coast district of San Diego County" in the range of *C. b. bryanti* of northern Baja California.

Before the volume was issued, Ridgway received Swarth's publication and noted in an addendum (Ridgway 1904:753–754) that he agreed with Swarth in synonymizing *anthonyi* but not with Swarth's treatment of *bryanti*: "Mr. Swarth's California material apparently did not contain a specimen from the coast district (or any other portion?) of San Diego County, to which *H. b. bryanti* (not typical, however) is restricted in its California range." The third edition of the A.O.U. Check-list (1910) essentially followed Ridgway's (1904) treatment.

Frank Stephens (1904) likewise responded to Swarth's paper. Stephens gave an excellent analysis of the northwest continental and the two peninsular races. On the basis of a "hasty study" of A. W. Anthony's specimens, Stephens assigned two skins from San Diego to *bryanti*, noted the difference in crown color between the birds of coastal San Diego and the interior, but concluded there were "more *couesi* [or *anthonyi*, if distinct] south of the border than *bryanti* north of it." He did not specify whether he had desert or only coastal specimens in the series he was examining.

Initially, Joseph Grinnell (1915) believed that two forms of Cactus Wren occupied southwestern California. He listed *couesi* as "a common resident locally in the San Diegan district from San Diego northwest as far as Santa Paula, Ventura County." On the basis of the A. W. Anthony series as well as recently collected specimens in the Museum of Vertebrate Zoology, he listed *bryanti* as "sparingly and locally resident in the vicinity of San Diego. The metropolis of this form is to the southward, San Diego apparently being the meeting ground of *H. b. couesi* and *H. b. bryanti*, for the two are known to have nested in the same locality. These two forms thus have no wide area of intergradation, if actual blending occurs at all."

Grinnell (1921) later reexamined A. W. Anthony's specimens. He concluded that "specimens from San Diego County, California, which have been labeled '*bryanti*' prove to exhibit only a slight tendency in that direction, being much nearer *H. b. couesi*. Those individuals showing nearly or quite complete white barring of the tail do not show the other diagnostic features of *bryanti*, namely very heavy spotting below and dark upper surface."

Griffing Bancroft (1923) next pointed out that birds from the San Diego district are different from both *bryanti* and *couesi*, and he thought that they constituted a distinct subspecies. Furthermore, he noted the coastal birds were perfectly isolated except for perhaps through the narrow San Gorgonio Pass in Riverside and San Bernardino counties (see also Grinnell and Swarth 1913). He found only one place where the birds extended south of the international boundary, about 32 km east of Tijuana. Laurence M. Huey, curator of birds at the San Diego Natural History Museum, took specimens there, finding them "identical with the birds of southwestern California."

Bancroft (1923) surveyed the remaining area between the border and San Telmo (31°N) many times without finding the wren or its nests. The habitat was not suitable. Good cholla stands, Bancroft reported, "are confined to a narrow strip very near the ocean" where mesas drop off abruptly to the coast; inland there are but "small isolated patches" of habitat without wrens. Bancroft concluded from both field work and specimens that *C. b. bryanti* did not come closer than "150 miles" of California.

Grinnell (1928:211–212) mapped a "station of record" 32 km east of Tijuana as *C. b. couesi*. On the basis of specimens, he also concluded that this race occurs from northeastern Baja California south along the gulf coast to a little below 31°N. Grinnell's map shows a wide hiatus in the Cactus Wren's distribution between the San Diego–Tijuana region and the San Telmo region at 31°N, a north–south distance of 160 km.

The fourth and fifth editions of the A.O.U. Check-list (1931, 1957) likewise considered the Cactus Wrens of all of southern California to be *C. b. couesi* with *bryanti* restricted to Baja, coming north only to 31°N.

Bancroft (1946) believed birds of coastal southern California to have the darkest eggs of any of the peninsular or continental forms he studied, further exemplifying, he said, the distinctiveness of this isolated population. On the basis of larger sample sizes now available, this apparent difference in egg color does not stand up (Lloyd Kiff pers. comm.).

After examining specimens in major U.S. museums, Rea prefers to recognize *couesi* and *anthonyi* as distinct. *C. b. anthonyi* has a more rufescent crown and a paler, grayer ground color of the back, whereas *couesi* has a darker brown crown and a darker, warmer brown back. *C. b. couesi* occupies Texas, southern New Mexico, and adjacent Mexico, with some individuals scattered across the higher elevations of the species' range in central Arizona (Rea 1983). Phillips (1986) reluctantly recognized *anthonyi* and synonymized *couesi* with a query in *C. b. guttatus* (Gould) of central Mexico. Kenneth C. Parkes (pers. comm.) notes that "*guttatus* is distinctly shorter-tailed, has the interscapular area less grayish, and has larger and rounder spots on the flanks" than Texas specimens and suggests that *couesi* and nominate *brunneicapillus* may be indistinguishable.

While preparing a revision of the Cactus Wrens of southern Arizona (Rea 1983:206), Rea noted and set aside various specimens in the San Diego Natural History Museum collection labeled as "*couesi*" but having anomalous characters. Generally their spotting below was too heavy and they had too much white in the tail for either *couesi* or *anthonyi*, but their backs were not as dark as *bryanti*. When their localities were checked, all proved to be of coastal origin. Later this population was described as the subspecies *C. b. sandiegensis* Rea, 1986 (type locality San Diego Wild Animal Park, 3.7 km west of San Pasqual, adjacent to San Pasqual Battlefield State Park, San Diego Co., California).

CHARACTER ANALYSIS

Methods

We examined specimens from the following collections: San Diego Natural History Museum (SD), Pomona College (PC), Los Angeles County Museum (LA), University of California, Los Angeles (UCLA), University of California, Santa Barbara (UCSB), Museum of Vertebrate Zoology, Berkeley (MVZ), University of Arizona, Tucson (ARIZ), University of New Mexico, Albuquerque (UNM), National Museum of Natural History, Washington, D.C. (US), Carnegie Museum, Pittsburgh (CM), and American Museum of Natural History, New York (AMNH).

We believe that we have located virtually all extant adult specimens from coastal populations (46 from the San Diego vicinity and 67 from the northern coastal region). No specimens known to us exist from northern San Diego County or most of Orange County (see Figure 2).

Cactus Wrens are exposed to bright sunlight much of the day. As a result, their plumage undergoes significant seasonal color change due to fading

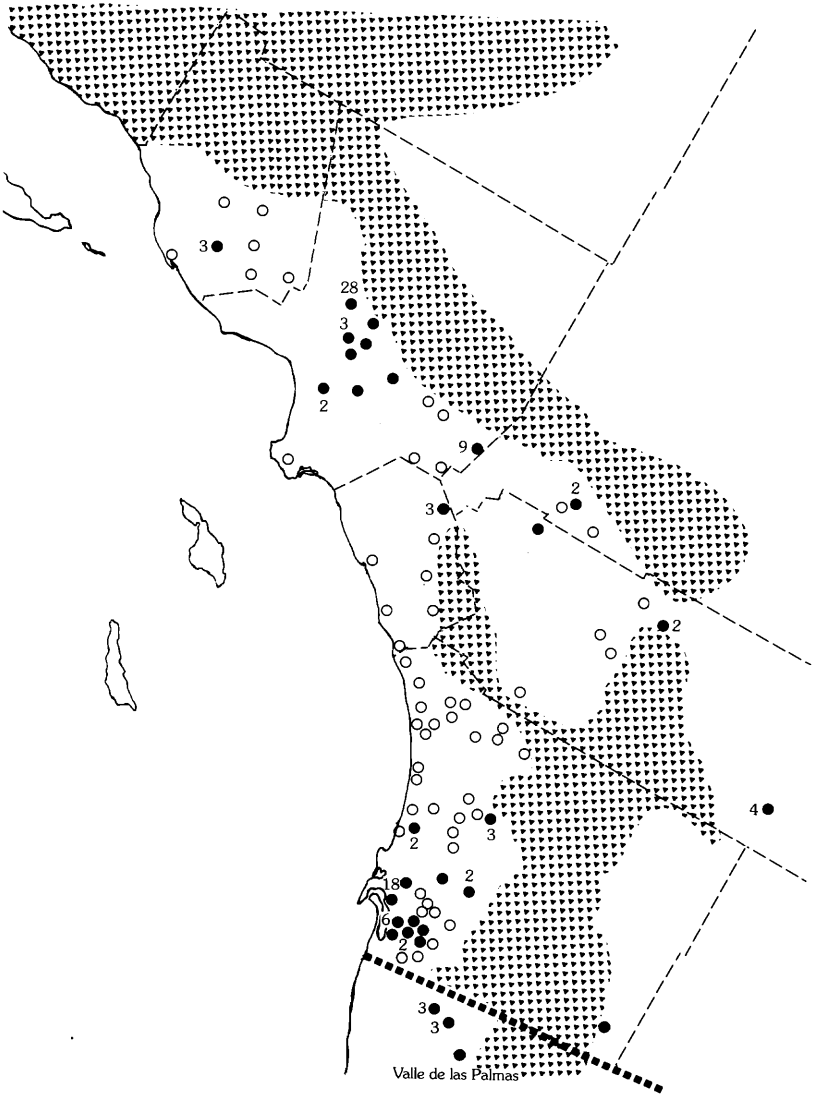

Figure 2. Distribution of the Cactus Wren in coastal southern California and northwestern Baja California. Dots, localities from which adult specimens were examined; numbers, number of adult specimens examined from that locality (if more than one); circles, additional localities from which the Cactus Wren has been reported or collected (some localities in close proximity have been lumped; see Figure 13 for more detail).

and wear. November-taken specimens, for example, are not comparable to January specimens, nor are these comparable with March skins. Insofar as possible, we made color comparisons only among specimens taken within six weeks of each others' collection date. Post-mortem color changes (foxing) also occur in this species. Dorsal browns become more rufescent within the first decade the specimen is in the museum.

Comparisons were made with 94 specimens from the peninsula (races *C. b. bryanti* and *C. b. affinis*) and approximately 300 specimens from the continent (*C. b. anthonyi*, *C. b. couesi*, *C. b. brunneicapillus*, and *C. b. guttatus*).

Scoring of Characters

Seven characters (Table 2, Figures 3 and 4) distinguish the continental desert populations of Cactus Wrens, the races *C. b. anthonyi* and *C. b. couesi*, from the Baja California peninsular races *C. b. bryanti* and *C. b. affinis*.

1. Chin/gular area. The chin and interramal area are immaculate in over three-quarters of the specimens from the continental deserts. An occasional specimen from the western or Colorado desert lacks this white patch, having spots going as far forward as in peninsular wrens. Peninsular specimens are spotted on the chin all the way through to the interramal area.

Table 2 Characters Distinguishing Subspecies of the Cactus Wren[a]

Character	*C. b. anthonyi*	*C. b. bryanti*
1. Chin/gular area	Broadly white in >75% (1)	Speckled (2)
2. Chest spot shape	Always single, large central reniform spot (1)	Mostly double, irregular marks (2)
3. Abdominal spotting	Fine, linear to narrowly rhomboid, contrasting with throat/chest (1)	Heavy, oval to diamond-shaped, not strongly contrasted to chest (2)
4. Chest patch	Spots aggregated to form black patch (1)	No strong aggregation into patch (2)
5. Flank/abdomen color	Conspicuous buffy wash across flanks and lower abdomen (1)	Largely white, weak ochre wash ± restricted to flanks or absent (2)
6. Back color	Warm ground color of nape contrasting with grayer interscapulars and lower back (1)	Warm ground color of nape continuing through interscapulars and lower back without demarcation (2)
7. Tail barring	Largely black (states 1–3, see Table 3)	Largely white-barred (states 7–9)

[a]Score values in parentheses

2. Chest spot shape. Chest spots of continental desert birds are single, occupying the middle of the feather, and centered on the shaft (Figure 5a). An occasional individual has some split spots along the lateral margins of the chest. The spots' shape is variable but is most often kidney- or even

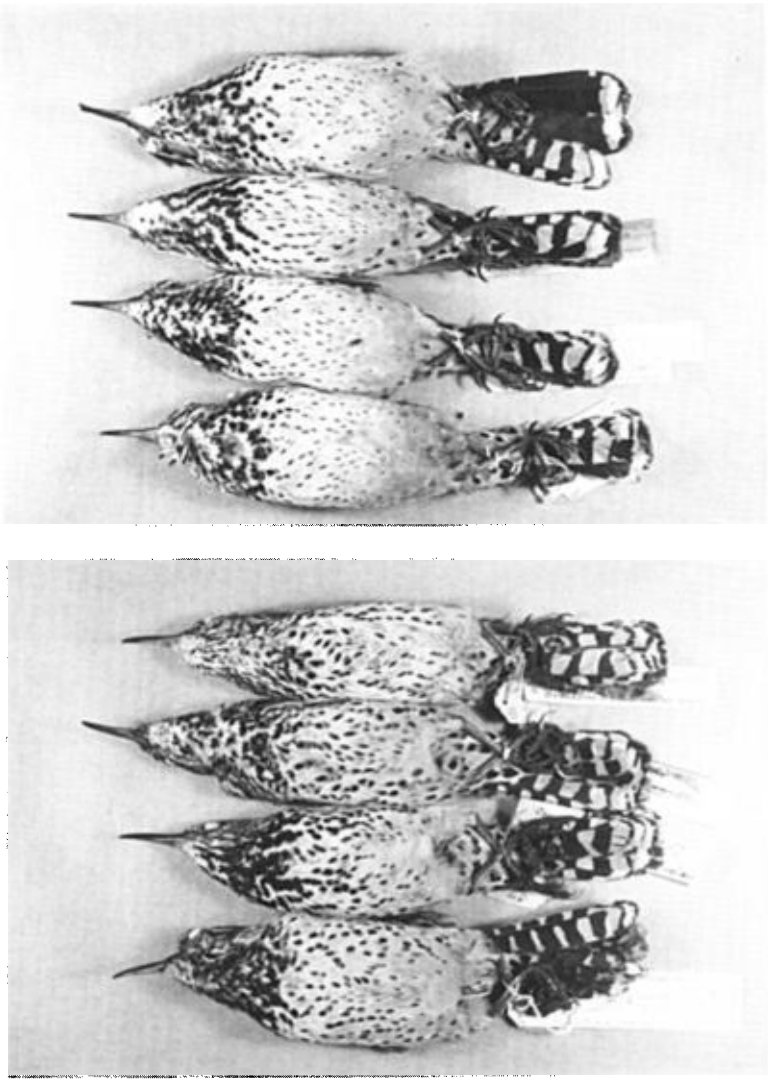

Figure 3. Underparts of two subspecies of the Cactus Wren. Upper, *C. b. anthonyi*; lower, *C. b. sandiegensis*.

chevron-shaped, with the proximal margin concave. In both peninsular subspecies the central part of the chest feather is white, and irregularly shaped spots occupy the two distal lateral corners of the feather (Figure 5b).

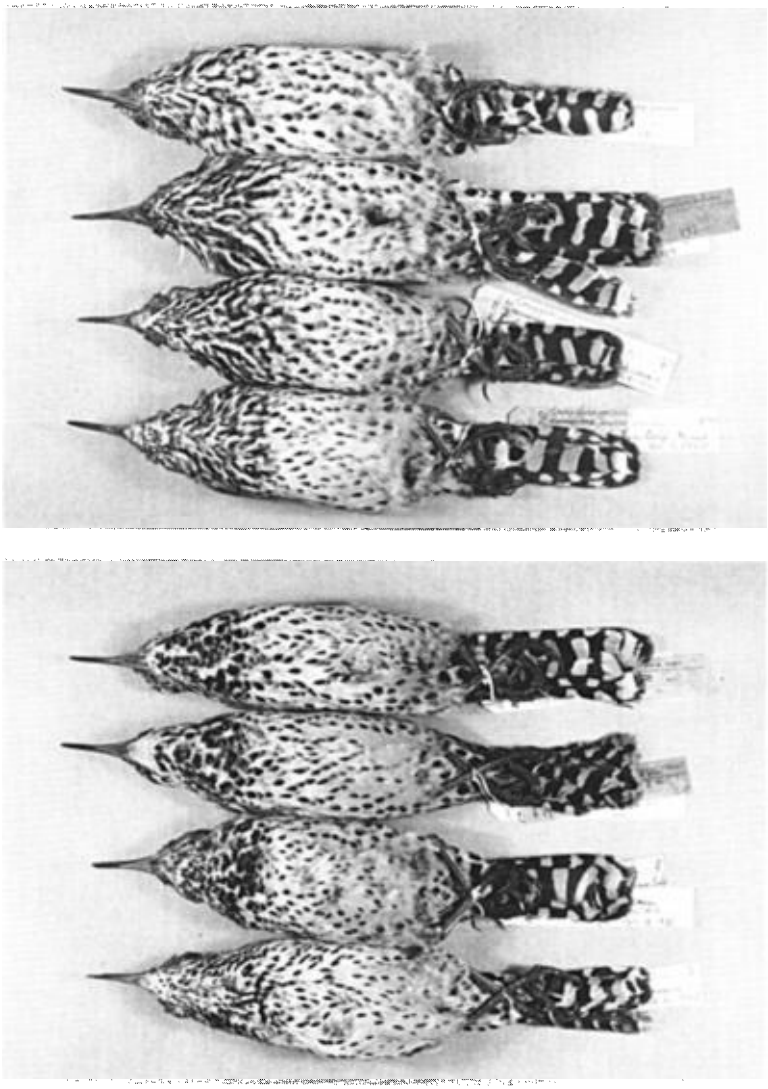

Figure 4. Underparts of two subspecies of the Cactus Wren. Upper, *C. b. bryanti*; lower, *C. b. sandiegensis*.

3. Abdominal spotting. In continental Cactus Wrens the flanks and belly are largely pale because the spots of this region are fine, either linear or rhomboid, strongly contrasting with the large single spots on the chest. In peninsular forms the abdominal spots are large and oval, giving the appearance of a bird with an almost uniformly marked undersurface. Spots on the crissum of *bryanti* are two or more times larger than those of *anthonyi*.

4. Chest patch. Because of the larger size of the chest spots of continental birds as well as the contrasting fineness of the spotting on the rest of the underparts, there is a conspicuous aggregation of the spots into a black chest patch. This is only weakly correlated with sex. In some cases a male may be more densely spotted than a female, but most anatomically sexed specimens cannot be segregated on this criterion. Peninsular Cactus Wrens are more uniformly marked below, with nonaggregated (double) chest spots and large oval abdominal spots. In other words, a chest patch is lacking.

5. Flank/abdomen color. Until their plumage is worn and faded, continental Cactus Wrens have a strong buffy wash across the flanks and abdomen, contrasting with the white ground color of the remaining underparts. In peninsular birds this wash is usually entirely absent. Some individuals have a weak wash, but the color is more yellowish, nearest Pale Ochraceous Buff of Ridgway (1912). Both the quality and the quantity of the color differ. An occasional peninsular specimen has a distinct wash below, but this invades the entire underparts to the chest. This color may be adventitious, the result of a bird dust-bathing in red (iron-oxide) clay soils.

6. Back color. In *anthonyi*, the ground color of the back is brownish gray, distinctly contrasting with the rufous of the crown and nape. The crowns of peninsular birds are even more strongly rufescent, with the warmer, darker brown tones extending down through the ground color of the entire dorsum. (The shape of the white dorsal streaks, bordered by fuscous or blackish streaks, appears not to vary geographically, at least in the northwestern Mexico and the southwestern U.S.)

7. Tail markings. Continental forms of adult Cactus Wrens have essentially black tails except for the brown central pair of rectrices and the white subterminal bar across the remainder (Table 3). White bars and spots are restricted primarily to the outer (sixth) rectrix. Rectrix 5 may have a trace of white or a distinct spot or bar on the inner web (states 1–3 in Figure 6). Peninsular forms have distinct white bars and spots on the inner webs of rectrices 3–6, their tails thus being completely barred.

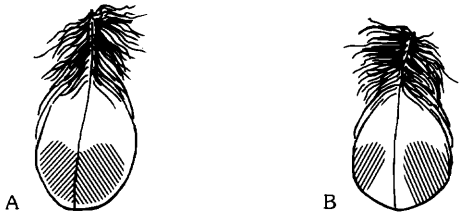

Figure 5. Chest-spot shapes in two groups of subspecies of the Cactus Wren. A, continental subspecies; B, peninsular subspecies.

The pattern in juvenal rectrices differs from that in adults in that the distal white marking is not a simple subterminal bar running across the tail. Usually there is a terminal spot at the rachis running back onto the inner vane as an irregularly shaped bar, which may or may not be actually connected to the spot (Figure 7). This produces tails more extensively marked with white in juveniles than in adults from the same populations. Juvenal rectrices are also more rounded and less truncated at their tips. Occasional first-winter birds fail to molt their rectrices. In the analysis of these individuals, we have considered the distal spot and bar or splotch to be one rather than two separate markings. Specimens in juvenal plumage proved so variable in most other characters that we did not attempt to score them, except where noted specifically in the text.

Each adult specimen examined was scored for the seven character states (Table 2). Characters 1 through 6 were scored 1.0 for the state normally found in the western continental desert form (*C. b. anthonyi*) and 2.0 for the state normally found in the northern peninsular form (*C. b. bryanti*). Conditions intermediate between these were scored 1.5. Tails were scored 1–3 for states normally found in *anthonyi*, 4–6 for intermediate states, and 7–9 for states found in *bryanti*. Tails with conditions intermediate between the states given in Table 3 and Figure 6 were encountered. Some characters readily admit intermediate states (tail pattern, as noted, and abdominal color); others, such as chest spotting, are either/or.

Not every available specimen could be scored for all seven distinguishing characters. Some fall individuals were still molting their rectrices when collected. Others had missing or broken tail feathers. (Loose rectrices should be attached to the specimen or its label, as they are critical in the evaluation of coastal birds.) A frequent problem we encountered with Los Angeles area specimens was evaluating colors. Because of considerable

Table 3 Tail Patterns of Cactus Wrens[a]

State	Rectrix 5	Rectrix 4	Rectrix 3
States normally found on wrens from continental deserts[b]			
1	No white	No white	No white
2	Trace white	No white	No white
3	White spot (distinct)	No white	No white
States normally found on wrens from coastal sage scrub, San Diego region			
4	Several distinct spots	Trace or none	Trace or none
5	Spots and bar(s)	Spots and bar(s)	Trace
6	Distinct white bars	Spots and bars	Spots
States normally found on wrens from peninsular Baja California			
7	Distinct white bars	Distinct white bars	Spots
8	Distinct white bars	Distinct white bars	Spots and bars
9	----------Entire tail barred (except central pair)----------		

[a]Inner webs, exclusive of white subterminal bar
[b]States 1–3 may have reduced white even on rectrix 6

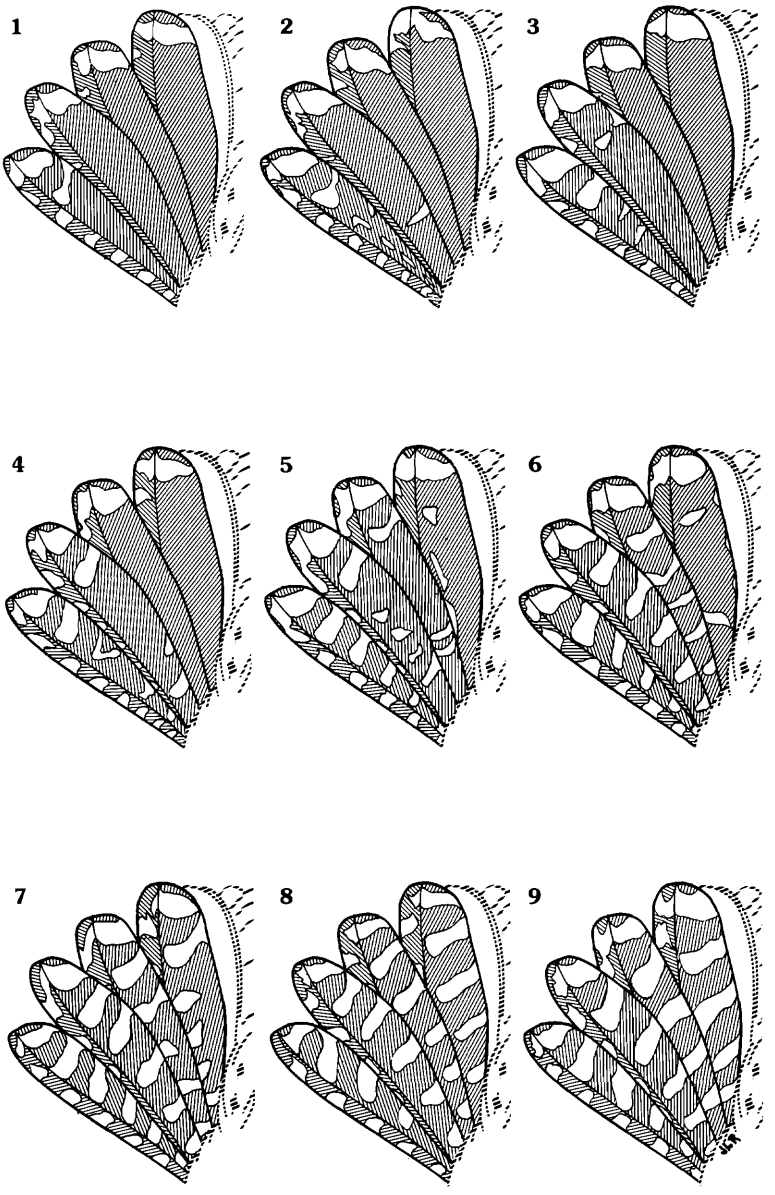

Figure 6. Variations in tail patterns of adult Cactus Wrens. Outer (6th) rectrix at left in each set. Character states correspond to descriptions in Table 3. States 1–3, continental deserts; 4–6, southern coastal sage scrub, San Diego area; 7–9, peninsular Baja California.

soot staining, character 5 (the extent and color of the abdominal wash) was particularly difficult to access. Even early fall specimens of this region scarcely a month after molt were already severely blackened.

The following formula was used to calculate an index for each character for each population:

$$\frac{\text{Character value} \times \text{number of individuals with that character}}{\text{Total number of scored specimens}} = \text{Index}$$

For example, from the northern coastal or Los Angeles population, 65 of the 67 specimens could be scored for chin spotting (character 1). Of these, 52 had distinctly white chins (value 1), 12 had some spotting encroaching into the chin (value 1.5), and one had the interramal area fully spotted (value 2).

$$\begin{aligned} 1 \times 52 &= 52 \\ 1.5 \times 12 &= 18 \\ 2 \times 1 &= 22 \\ \hline & 72 \end{aligned}$$

$$\frac{72}{65} = 1.11$$

The index shows the average value for the entire sample scored but does not show the range of variability within the population.

Pooled Characters of Two Populations

Of the 46 adult specimens of the Cactus Wren known from coastal San Diego County and northwestern Baja California, 315 individual characters could be scored out of a possible 322 (46 × 7; there were seven missing

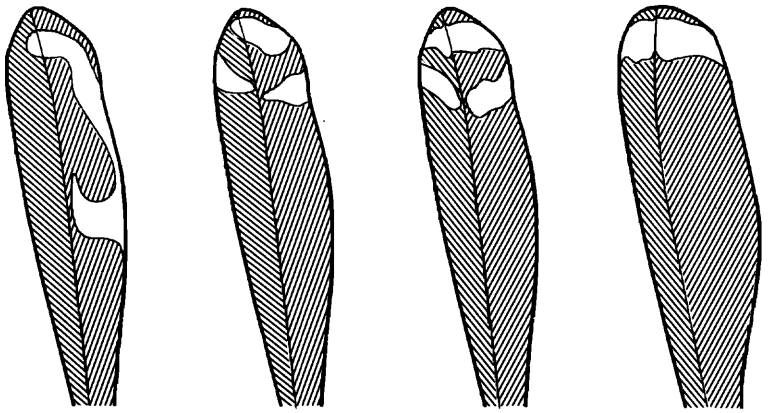

Figure 7. Variations in tail patterns of juvenile Cactus Wrens, showing the "single" subterminal bar. Right feather is of an adult for comparison.

character scores). The pooled results (Table 4) are plotted in Figure 8. Total scores for five characters (1, 3, 4, 5, and 7) are at or near the mean between pure *anthonyi* (1.0) and pure *bryanti* (2.0). In two characters (2, type of chest spot; 6, back color), San Diego birds scored nearer *anthonyi*.

Of the 67 available adult specimens of the Cactus Wren from the Los Angeles region (Ventura, Los Angeles, and extreme northern Orange counties), 429 individual characters could be scored (there were 40 missing character scores). The pooled results (Table 4) are plotted in Figure 9. In only two characters (5, reduction of buff on abdomen; 7, increase in white tail markings) was there an approach toward peninsular birds.

Three specimens (MVZ) from Santa Ana Canyon in northern Orange County are indistinguishable from transmontane *anthonyi* in characters 1 through 6. Their tails score 4.5, 3, and 6, indicating a very slight tendency toward the peninsular subspecies.

The San Diego-Area Population

In making subspecific identifications, however, taxonomists need to be able to identify *individual specimens*; averages or pooled characters are not sufficient. The standard frequently used for evaluating a subspecies is the so-called seventy-five percent rule (Amadon 1949). In its more rigorous interpretation, "before a population is given subspecific status, at least 75

Table 4 Pooled Characters of Coastal Cactus Wrens

Character	Sample Size	Index[a]
San Diego-vicinity population		
1. Chin/gular area	45	1.34
2. Chest spot shape	44	1.26
3. Abdominal spotting	46	1.49
4. Chest patch	46	1.50
5. Flank/abdomen color	46	1.46
6. Back color	43	1.22
7. Tail barring	45	5.18
Northern coastal population		
1. Chin/gular area	65	1.11
2. Chest spot shape	64	1.00
3. Abdominal spotting	67	1.06
4. Chest patch	65	1.03
5. Flank/abdomen color	55	1.22
6. Back color	59	1.03
7. Tail barring	54	3.44

[a]For characters 1–6, a value of 1.0 indicates the condition typical of *C. b. anthonyi*; a value of 2.0 indicates the condition typical of *C. b. bryanti*. For character 7, a value of 1.0 indicates the least barring, a condition found only in *C. b. anthonyi*; a value of 9.0 indicates the most barring, a condition found only in *C. b. bryanti* and *C. b. affinis*.

percent of the individuals [constituting] it must be separable from 99+ percent of the individuals of all other populations of the same species which may overlap with it as regards the geographically variable characters. An equivalent statement is that 97 percent of one of two compared populations must be separable from 97 percent of the other."

As noted above, at least seven characters or variables distinguish southwestern Cactus Wrens. For the two coastal segments, the Los Angeles and San Diego regions, we determined how many characters distinguished an *individual* specimen from adjacent subspecies—in other words, how many of the available specimens were distinguishable from *anthonyi* on the basis of no character, only one character, only two characters, etc., to all seven variables (Figures 10a and 11a). The same comparison was made with *bryanti* (Figures 10b and 11b). Of 46 known specimens from coastal San Diego County and adjacent Baja California, that is, of *sandiegensis* as we here define it, all are distinguishable from *anthonyi* by at least one character, while 86.9% (40 individuals) are distinguishable from it by three or more

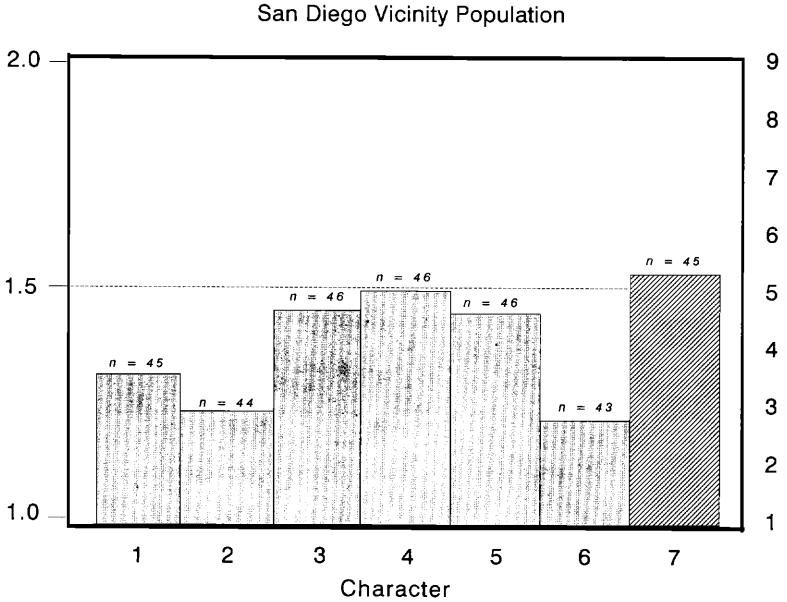

Figure 8. Pooled characters of the San Diego-area population of the Cactus Wren (*C. b. sandiegensis*) (see Tables 2 and 4). Characters 1–6 go with the left vertical axis. Character 7, tail barring (cross-hatched), goes with the right vertical axis. Low scores (near 1) indicate continental values (*anthonyi* and *couesi*), while high scores (near 2 or, for tails, near 9) indicate peninsular values (*bryanti* and *affinis*). Height of bar represents the mean score for all specimens of the population scored for that particular character; *n*, number of individuals scored.

The San Diego population is strongly intermediate for characters 3, 4, 5, and 7 (see text), less strongly intermediate for characters 1, 2, and 6.

characters. By the same comparison to *bryanti*, the northern peninsular form, 97.8% of *sandiegensis* (45 individuals) are separable on the basis of three or more characters. Even more rigorously, 89.1% (41 individuals) are distinguishable from peninsular birds by four or more characters. No specimen from the range of *sandiegensis* was indistinguishable from *bryanti*, nor was any distinguishable on the basis of only a single variable. As noted by the white bars in Figure 11b, two specimens, one each falling into the two- and three-character-only categories, were defective and could not be scored for all possible characters.

The population named *sandiegensis* thus meets the criterion of a valid subspecies. Based on a mosaic of characters, it is completely distinguishable from disjunct populations to the east (*anthonyi*) and the south (*bryanti*). If we could present a seven-dimensional figure, we could demonstrate this 100% separation graphically. Two variables are the most that can be shown easily in a scatter diagram. The two that allow the most discrimination,

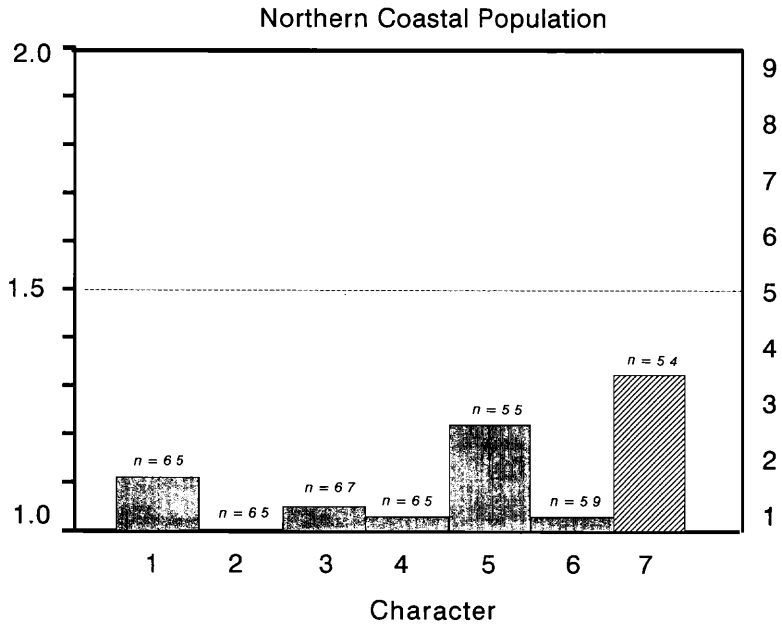

Figure 9. Pooled characters of the Los Angeles-area population of the Cactus Wren (see Tables 2 and 4). Characters 1–6 go with the left vertical axis. Character 7, tail barring (cross-hatched), goes with the right vertical axis. Low scores (near 1) indicate continental values (*anthonyi* and *couesi*), while high scores (near 2 or, for tails, near 9) indicate peninsular values (*bryanti* and *affinis*). Height of bar represents the mean score for all specimens of the population scored for that particular character; *n*, number of individuals scored.

The northern coastal population is very near the desert (continental) *anthonyi* but shows some peninsular genetic influence in characters 1, 5, and 7.

abdominal spotting and tail barring, together distinguish 89% of *sandiegensis* from 86% of *anthonyi* from the lower Colorado River valley (Figure 12). While it is not possible to predict in individual specimens which characters will distinguish *sandiegensis*, there is a greater probability that these will be chest patch (3), abdominal spotting (4), abdominal color (5), or tail pattern (7). Because of the aggregate nature of the characters, all possible characters should be considered in identifying an individual to subspecies (see Amadon 1949:254–255). A single character, even among the four most likely (3, 4, 5, 7), may not be distinguishing.

At least in historic times, the San Diego Cactus Wren has been isolated from conspecific populations to the south by a hiatus of about 160 km owing to a lack of suitable habitat. This population extends no farther south than does the coastal sage scrub habitat. There may be a few pairs scattered throughout the hiatus, but it is doubtful that any sizable colonies exist here. To the east, the coastal subspecies is broadly separated from desert *anthonyi* by unsuitable habitat (the chaparral, oak woodland, and coniferous forests of the Peninsular Ranges). The desert subspecies reaches

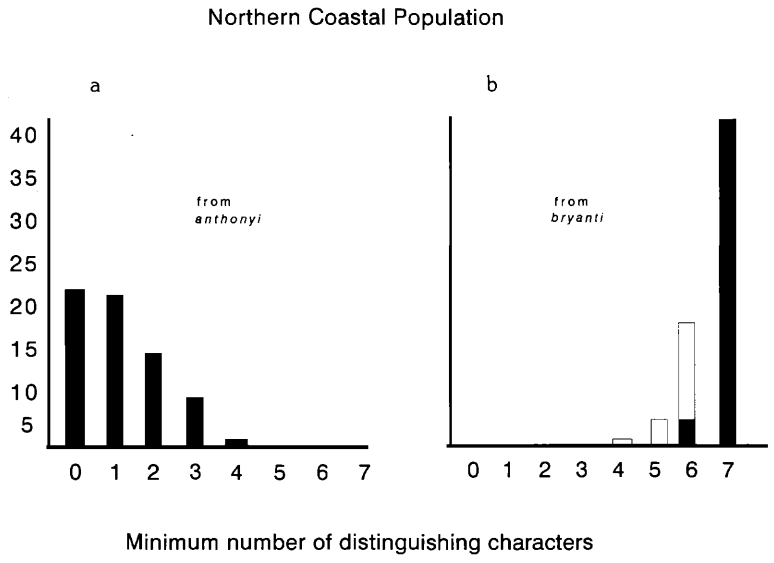

Figure 10. Number of characters (horizontal axis) distinguishing the San Diego-area population of the Cactus Wren (*C. b. sandiegensis*) from desert *anthonyi* (left) and peninsular *bryanti* (right). (Number of individuals on vertical axis.) Black bars, specimens scored for all possible character states; white bars, defective specimens lacking scores for one or more character states.

All but six specimens from the San Diego area were distinguishable from desert *anthonyi* on the basis of three or more characters, while all but two were distinguishable from peninsular *bryanti* on the basis of three or more characters (four specimens could not be scored for all characters).

eastern San Diego County, ascending east-facing slopes to an elevation of at least 1190 m (SD 42688).

The Los Angeles-Area Population

Results for coastal Cactus Wrens north of San Diego County are graphed in Figure 11. Only 10.9% (seven individuals) are distinguishable from continental forms by three or more characters. (The highest-scoring specimen, SD 45699, is one of the only three available from Ventura County, the northernmost locality.) Of 67 specimens, 22 (32.8%) are completely indistinguishable from *anthonyi*. Peninsular characters are only weakly reflected in northern coastal birds. All 67 specimens are distinguishable from *bryanti* on the basis of four or more characters. Even here, the lower limits may be artifacts, since the three specimens falling into the four- or five-character-only categories and 15 of the 19 falling in the six-only category were defective (that is, could not be scored for all seven characters). Of 67 scored specimens, at least 45 (67.2%) were distinguishable from the peninsular populations by all seven characters. Thus, while the northern

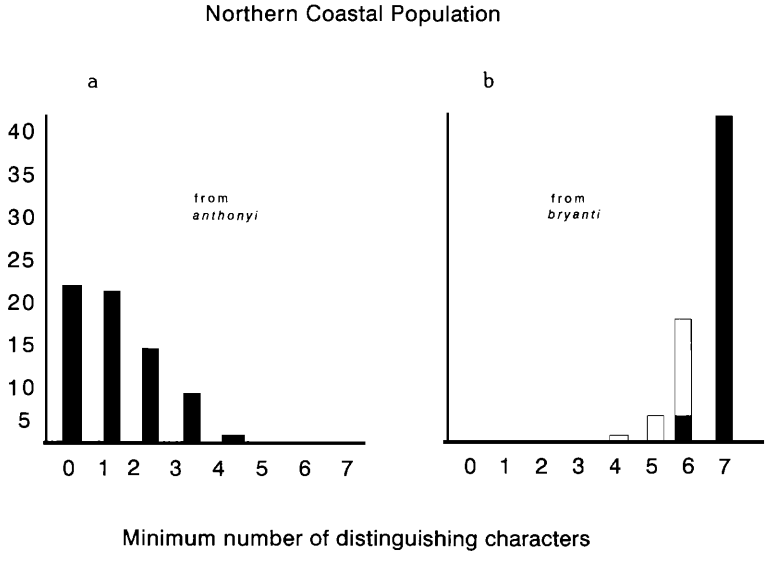

Figure 11. Number of characters (horizontal axis) distinguishing the Los Angeles-area population of the Cactus Wren from desert *anthonyi* (left) and peninsular *bryanti* (right). (Number of individuals on vertical axis.) Black bars, specimens scored for all possible character states; white bars, defective specimens lacking scores for one or more character states.

Only five Los Angeles-area specimens were distinguishable from *anthonyi* on the basis of three or more characters, while 43 specimens were distinguishable from *bryanti* on the basis of six or seven characters (18 specimens could not be scored for all characters).

coastal Cactus Wrens are readily distinguishable from *bryanti*, they are not taxonomically separable from adjacent desert *anthonyi*. The Los Angeles-area population tends only slightly toward *sandiegensis*, mostly in tail pattern, more weakly in reduced abdominal buff and invasion of chin spotting into gular region.

As an isolated character, how reliable is tail pattern? Our initial criterion, based on a somewhat superficial examination of several hundred specimens, was that continental birds had largely black rectrices except for the subterminal white bar and outer (6th) rectrix, while peninsular birds had completely barred or spotted rectrices (this is exclusive of the brown central pair in all populations). Baja California specimens indeed cluster in categories 8 and 9, with few scoring as low as 7. To evaluate the range of variation in continental birds, we scored 35 specimens from the Tucson region, eastern Pima Co., Arizona, well outside the influence of *bryanti*. Here, 77% of the tails ranked, as expected categories 1 to 3.5, with a mean of 2.9. However, seven specimens scored 4, and one scored 4.5. Thus the somewhat higher tail values for the northern coastal wren population in themselves are not necessarily indications of *sandiegensis* influence. Coupled with reduced buffy abdominal wash, the higher tail scores probably do reflect some genetic influence from the south. Unfortunately, the extensive soiling of Los Angeles Basin birds makes this color character difficult to

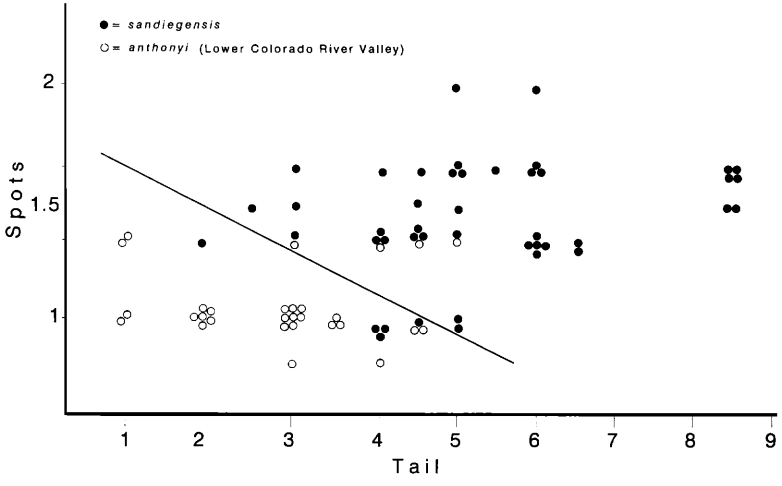

Figure 12. Scatter diagram of abdominal spotting (character 3) plotted against tail pattern (character 7) in two races of the Cactus Wren. All but five specimens of *C. b. sandiegensis* (89.1%) are separated from all but four specimens of *C. b. anthonyi* by the line effecting maximum separation. Northern specimens from Los Angeles and Ventura counties east to the Coachella Valley have been excluded; these show slight genetic influence of *sandiegensis*. For scoring of characters, see Tables 2 and 3 and Figure 6.

evaluate. Nine northern specimens (15.6% of those scorable) had tail values of 5 to 6, which we interpret as an indication of *sandiegensis* genes.

Although their distribution is patchy, coastal Cactus Wrens, as noted earlier, extend as far north as southern Ventura County. Los Angeles Basin birds were narrowly connected with desert birds through San Gorgonio Pass, an avenue of possible gene flow of desert characters west into the Los Angeles area, resulting in the present genetic condition of that population. Several Coachella Valley specimens (SD) suggest possible gene flow in the opposite direction.

Specimens from Northeastern Baja California

Desert *anthonyi* and peninsular *bryanti* (or *affinis*?) must come into contact along the gulf coast east of the Sierra San Pedro Mártir, between San Felipe and latitude 29°N (see Figure 1). Apparently Cactus Wrens have never been collected there because the region lacks adequate roads. This area merits further study, as the two gnatcatcher species, *Polioptila melanura* and *P. californica*, overlap there without interbreeding (Atwood 1988). There is indirect evidence that this is not the case with Cactus Wrens. The few specimens available from San Felipe on the northern peninsular gulf coast (SD, all spring) suggest that this population is influenced by a peninsular form. Nine of the 11 San Felipe specimens are in juvenal plumage. Their tails score 3, 3.5, 4 (2), 4.5 (2), 5, and 8 (2). One (SD 32660) is far along in postjuvenal molt. Its large single chest spots, small abdominal spots, and paler upperparts are those of *anthonyi*, but its dilute abdominal wash is yellowish buff as in *bryanti* rather than buffy ochre as in *anthonyi*. One adult (SD 32658) has single chest spots and a tail score of 3.5 but rather heavy abdominal spotting and dark upperparts, suggesting *bryanti* (or *affinis*) influence. The other adult (SD 10463) looks like *anthonyi* but has a distinct white spot on all the black rectrices.

Two spring adult males (SD) from Aguajito Spring, Valle de la Trinidad, Baja California, are indistinguishable from *sandiegensis*. One has large single chest spots and a heavy chest patch, while the other has twin spots and chevrons on the throat and chest. Both have relatively heavy flank spotting, reduced abdominal buff, and dorsal coloration warmer than that of *couesi* or *anthonyi* in comparable seasonal wear. Their tail scores are 4 and 5. The other six characters average 1.5 and 1.46, respectively.

Four juveniles from Valle de la Trinidad (SD, 14 July) lack abdominal spots and are only lightly spotted on the throat. Their upperpart colors are warm, as in *bryanti*. Two have mostly black tails (2, 2) and two have heavily barred tails (8, 9). This colony, apparently isolated from *sandiegensis*, seems anomalous. At this locality Atwood (1988:18) discovered limited contact between the California Gnatcatcher and the Black-tailed Gnatcatcher. Atwood stated that "the former species occurs primarily in widespread sage scrub vegetation dominated by *Artemisia*, *Salvia*, and *Rhus*, whereas the latter is generally restricted to typical (but limited in extent) Sonoran desert wash vegetation dominated by *Prosopis*."

Like *sandiegensis*, the Cactus Wrens of Tiburón Island (*C. b. seri*) combine characters of the two major evolutionary groups. They resemble

continental birds from the adjacent mainland (characters 1[?], 2, 4[?], 7) but have larger spotting on the abdomen (character 3). In reduction of abdominal buff wash (character 5), they are intermediate toward peninsular birds. Their bills are shorter than either peninsular, continental, or coastal forms (Rea 1986). They occupy a range approximately half the size of that of *C. b. sandiegensis*, as here restricted.

Field Identification

Our experience with this bird indicates that nearly all adults of *sandiegensis* individuals can be identified as such in the field except when they are in worn plumage (late spring and summer). San Diego Cactus Wrens have a smudgy appearance, as the large spots of the flanks and abdomen present an extension of the dark chest patch. Most individuals also show a light buffy wash on the flanks. In contrast, north coastal and desert birds can be readily recognized by the clear demarcation between the black chest patch and light belly, which is very finely speckled. The richer cinnamon buff of most of these individuals extends across both flanks and abdomen.

We also can recognize a distinct song dialect in southern coastal wrens. Their vocalizations have a slightly slower frequency and lower pitch than more northern and eastern birds, and have a raspy quality not heard in adjacent populations. This behavioral aspect deserves further study.

Subspecies Limits

Too few specimens exist to determine whether there is north–south clinal variation within *sandiegensis*. There are large gaps in specimen representation, with nothing from northern San Diego County (including all of Camp Pendleton) or southern Orange County. We included these areas in the range of *sandiegensis* on the basis of field observations and vocalizations (San Diego-type dialect). Central and northern Orange County wrens sing the Los Angeles Basin dialect. Within the northern coastal segment (even with the larger sample size, 67 adult specimens), we were unable to segregate a coastal versus a more interior subset or a northwest to southeast cline in characters. Considerable individual variation occurs at each locality. The largest sample from a single locality (28 specimens from the San Fernando Valley) shows a scattering of intermediate traits in all characters except 2 (chest spot shape). Scores of one sample, of nine adults and two juveniles from Claremont, were discordant. While body scores were consistently low except apparently for character 5 (abdominal color), 10 tails scored high (from 4 to 5.5) and one scored low (2).

Only three specimens (SD) are known to us from the isolated Ventura County population. Owing to molt or seasonal wear, these could not be scored for all characters. One (SD 45699) shows southern influence in characters 3, 4, 5, and 7. Habitat just east of Camarillo is still rather extensive and population numbers are relatively high for the north.

Northern coastal Cactus Wrens, with their very different genetic composition, must have had an evolutionary history different from that of *sandiegensis*. Either they were derived directly from *anthonyi* ancestors

from the desert, then received genetic influence from the south along the coast, or a pre-existing *sandiegensis*-like population has continued to experience genetic swamping by desert birds. Before urbanization of the Los Angeles Basin, colonies were open to at least narrow genetic contact through the San Gorgonio Pass. During hotter, dryer periods of the Holocene (if there were any), the contact here presumably would have been greater. But there was at least some contact with the south, as evidenced by occasional individual characters such as large ventral spots, white-barred tails, or reduced abdominal buff.

POPULATION STATUS

Methods

To determine the distribution and numbers of the San Diego Cactus Wren, we reviewed localities on specimen labels (both study skins and egg sets), checked areas of previously known occurrence, solicited information from local field ornithologists, and surveyed areas where appropriate habitat was likely to occur.

The generalized vegetation map of San Diego County (Oberbauer 1977) helped us determine where large blocks of coastal sage scrub occurred within that county. Our early surveys also indicated that the distribution of cacti, in which the wren nests almost exclusively, is correlated strongly with soil type. The maps of the *Soil Survey of the San Diego Area* (Bowman 1973) suggested additional, smaller areas potentially supporting cactus associations. Locations with cacti were then surveyed on foot. We began field surveys in 1980, with the greatest effort in 1984 and 1985. During 1988, 1989, and 1990, we revisited most areas that had wrens in 1984 and 1985. Through August 1990, approximately 285 hours had been devoted to field surveys.

Censusing was by direct count, aided by playing tapes of Cactus Wren songs, to which the wrens are very responsive. During field surveys, we also collected data on nests. We obtained information on territory size, shape, and location by conducting breeding bird censuses (Weaver 1982, Weaver in press) and winter bird censuses (unpublished) in accordance with procedures suggested by Hall (1964), Kolb (1965), and Van Velzen (1972).

Distribution

Our review of specimens confirms the San Diego Cactus Wren's occurrence from the San Dieguito River in west-central San Diego County to the Tijuana and Valle de las Palmas regions in northwestern Baja California (Figure 13). Our field observations also indicate that *sandiegensis* ranges north through northwestern San Diego County to San Juan Creek in southern Orange County.

The Peninsular Ranges of San Diego County and northern Baja California separate *sandiegensis* from the nearest populations of the desert race, *anthonyi*, by a minimum of 50 km. The Agua Tibia Mountains on the northern border of San Diego County separate *sandiegensis* by only 14 km from Riverside County birds that are very similar in appearance to the

northern coastal population. The Plano Trabuco separates it from northern coastal birds by less than 5 km in southern Orange County. The Cactus Wrens of the Coto de Caza area, near Trabuco Canyon, Orange County, should be studied because they are situated between *anthonyi*-like and *sandiegensis*-like populations.

Coastal Cactus Wrens recently occurred as far inland as Pauma Valley in San Diego County, 48 km from the coast (a population now exterminated), but most live within 32 km of the sea. Most wrens live at elevations of less than 150 m. We have found them as high as 400 m in San Diego County, while Schneebeck (1978) recorded the birds in Orange County at the upper limits of the coastal sage scrub at 450 m above sea level.

The wren's distribution is highly fragmented, and most populations consist of only a few pairs. In San Diego County, the wrens are concentrated along the Otay River and its tributaries, near Lake Jennings, in the interior valleys of the San Dieguito River, and near the Santa Margarita River. In Orange County, most wrens are found along the mid-section of San Juan Creek and its northeastern tributaries. A detailed account of distribution and numbers is given in the Appendix 2.

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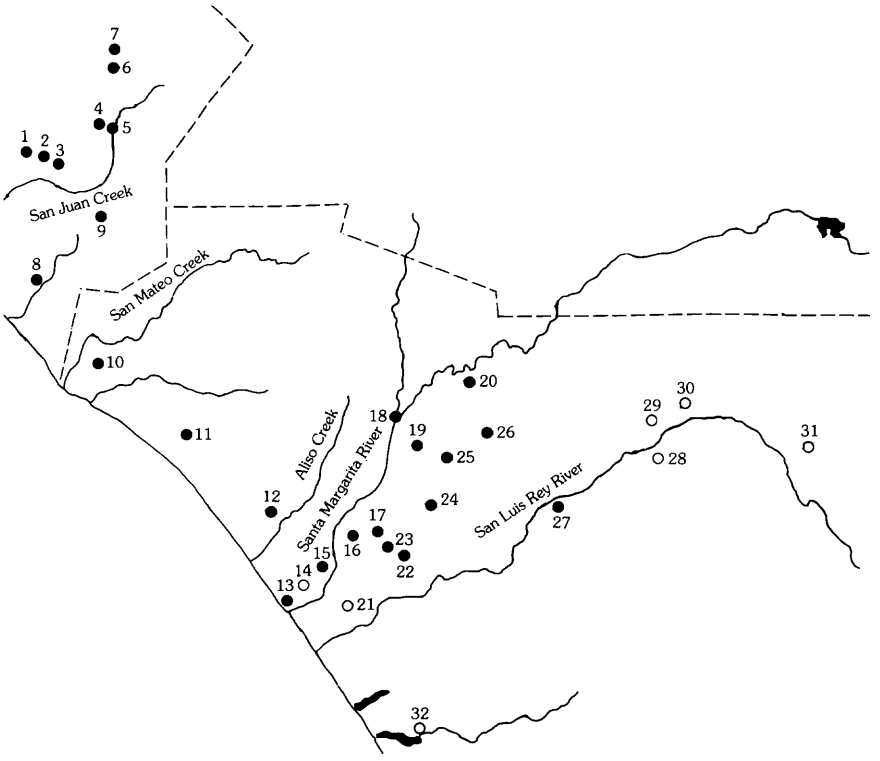

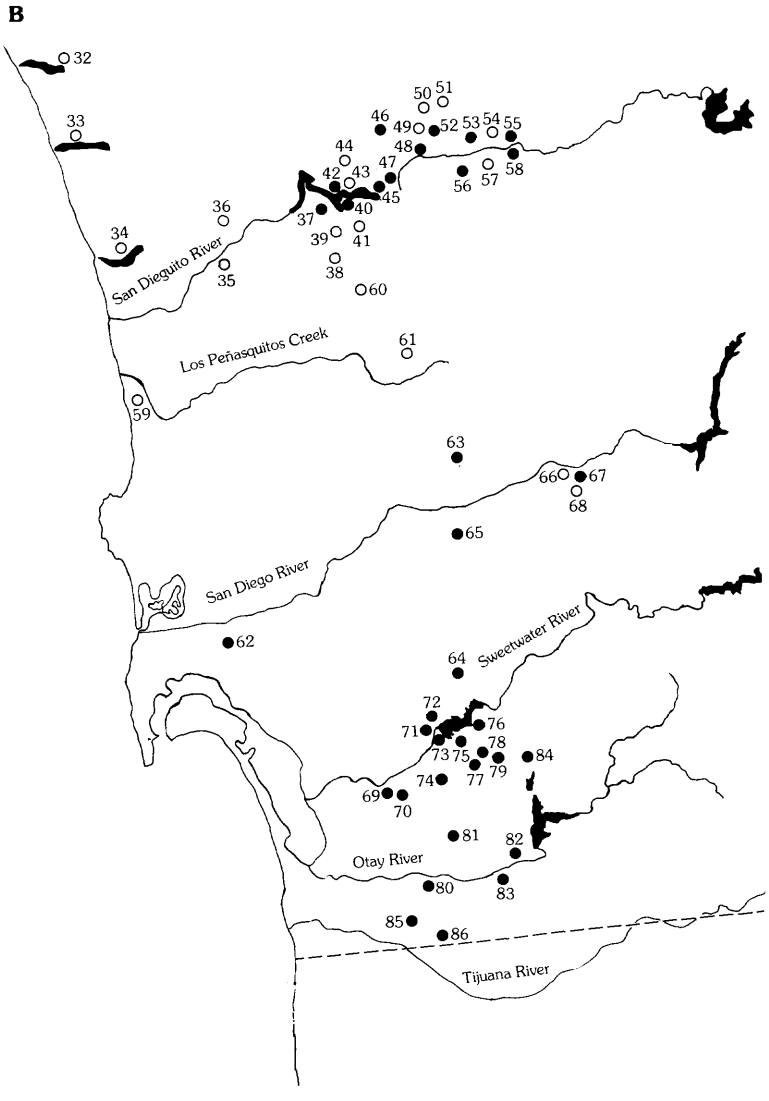

Figure 13. Localities where the San Diego Cactus Wren (*C. b. sandiegensis*) has occurred since 1980. A, southern Orange County and northern San Diego County; B, central and southern San Diego County. Solid circles, colonies still extant; open circles, colonies lost during the 1980s. The single locality in Baja California where the San Diego Cactus Wren has been reported since 1980, Valle de las Palmas, is shown in Figure 2.

Areas that were not checked but would appear to provide suitable habitat include northwestern Camp Pendleton below the Border Patrol checkpoint in San Diego County (Larry Salata pers. comm.) and Gabino Canyon and the north end of Cañada Gobernadora in southern Orange County. Additional surveys are also recommended for the Starr Ranch Audubon Sanctuary in Orange County.

Current Numbers

Our counts and those of other active field workers conducted over the past decade show that the San Diego Cactus Wren has a very small and rapidly declining population. As of fall 1990, approximately 200 pairs still inhabit San Diego County and 150 pairs still inhabit Orange County. In Baja California, fewer than 10 pairs are present at Valle de las Palmas south of Tecate, the only currently known area of occurrence south of the border. The habitat here has been seriously degraded by burning, grazing, and conversion to vineyards during the past two decades (Marcos Camacho pers. comm.)

Former numbers of *sandiegensis* are speculative, but the scattered populations still present in the early to mid-1980s suggest that they were once numerous near all of the lagoons and coastal canyons in San Diego and southern Orange counties.

The decrease in this bird's numbers has been apparent to field workers for decades. Dawson (1923:667) first called attention to the seriousness of the decline of the coastal population: "All proper desert areas west of San Gorgonio Pass are being threatened by human invasion. The Cactus Wren has receded from many parts of the San Diego–Ventura section already, and is in danger of being altogether cut off."

Willett (1933) noted the species' decline at its northern limits: "Reported by Evermann (1886) as rather common resident of Ventura County in early 80s, but apparently much less plentiful in that section at the present time, as land has been largely cleared for agricultural purposes." Whereas J. S. Appleton had found the bird a "formerly common resident of Simi Valley, southern Ventura County," by 1933 it had not been seen there "for several years past."

In 1944, Grinnell and Miller described the range of the coastal populations of southern California as "much restricted as compared with conditions in 1880s and 1890s, owing to great reduction of requisite habitat." Sams and Stott (1959) observed that the wren was "found sparingly in the coastal lowlands (near San Diego)," and, referring to the San Diego County coast, Unitt (1984) stated that "in 1981, the species is found in very few localities."

By August 1990, we could find no wrens at 26 of the 78 sites (33%) in San Diego County where they had been recorded in the preceding decade. Even more alarming, the wrens have disappeared from 14 of the 27 sites that we or other field observers had censused in 1984–85 and again in 1988–90, and have decreased in numbers at another seven locations. We noted increases at only three sites. The number of pairs at these 27 sites dropped from 145 to only 102, a 30% decrease. We noted habitat

destruction at most of these sites. Grazing, clearing for agriculture, and fires contributed to the decrease, but construction of houses accounted for the majority of the population reductions or local extirpations. We do not know the extent of population losses in Orange County, but these must be substantial due to the accelerating growth in the south end of the county.

Continuing declines in population are a certainty. Well over 50% of all wrens occur on privately owned lands. Virtually all of these areas are in imminent danger of development in the 1990s. Those wrens found on public lands, including the largest remaining colonies, also face a dubious future. Many lie in the path of proposed highways (as across Rancho Mission Viejo along the proposed Foothill Transportation corridor in Orange County and in the Sweetwater and Otay River valleys in San Diego County or along existing highways where increasing pressure for "improvements" will greatly reduce habitat for the wren (as in Caspers Wilderness Park).

Another cause for concern includes the accidental fires resulting from training exercises on Camp Pendleton and policies that encourage "controlled" burns, such as those that have taken place at the San Diego Wild Animal Park. Benson (1969) considered fire to be the chief limiting factor in the distribution of cacti in southern California, so it is disconcerting to see preventable habitat destruction of a rapidly vanishing natural resource.

Isolated populations of birds of the coastal sage scrub have high rates of extinction according to a recent study in San Diego County (Soulé et al. 1988). Our studies of the Cactus Wren certainly corroborate this. Soulé's team found the wren in only one of the 37 canyons they surveyed. Their studies emphasized that sage scrub birds disappear from isolated "islands" of habitat owing to their low initial numbers and their inability to cross urbanized areas to repopulate these remnants.

All 26 sites in San Diego County where we documented the bird's disappearance had populations of fewer than five pairs. Eighteen of these still retain sage scrub remnants that should support, on a strictly spatial basis, at least a pair of wrens. From their recent history of disappearance, it should be of concern that in this county, which supports the largest remaining numbers of wrens, only 10 of the 52 remaining sites support five or more pairs.

ECOLOGY

Habitat Requirements

San Diego Cactus Wrens adhere strictly to coastal sage scrub throughout the year. Areas supporting this plant community are dry, receiving even less rainfall than the chaparral above, at higher elevations. Coastal sage scrub may extend inland as far as 50 km, but more often is within 30 km of the coast. Species diversity is high. Some characteristic shrubs include Flat-top Buckwheat, *Eriogonum fasciculatum*; California Sagebrush, *Artemisia californica*; White Sage, *Salvia apiana*, and Black Sage, *S. mellifera*. Often there are scattered shrubs approaching tree size—Laurel Sumac, *Malosma laurina*, and Lemonadeberry, *Rhus integrifolia*. Some compo-

nents of this community are from the Sonoran Desert or have their closest relatives there: Coast Barrel Cactus, *Ferocactus viridescens*; Fish-hook Cactus, *Mammillaria dioica*; California Wolfberry, *Lycium californicum*; Bladderpod, *Cleome isomeris* (= *Isomeris arborea*); San Diego Sunflower, *Viguiera laciniata*; Chalk-lettuce, *Dudleya pulverulenta*; California Encelia, *Encelia californica*; Our Lord's Candle, *Yucca whipplei*; Spanish Dagger or Mojave Yucca, *Yucca schidigera*; Jojoba, *Simmondsia chinensis*

Figure 14. Nest of the San Diego Cactus Wren in *Opuntia littoralis* on Bernardo Mountain, near Escondido, San Diego County, November 1988.

Photo by Kenneth L. Weaver

(see Raven and Axelrod 1978). Our breeding and winter censuses indicate that the wrens prefer areas dominated by California Sagebrush and Flat-top Buckwheat and tend to avoid locations dominated by sages.

The wren's chief requisite, though, is tall *Opuntia* cacti. The wrens supplement their insect diet in fall and winter by feeding on the fruit of two species of *Opuntia*. Most important, the cacti provide the only firm support for the wren's bulky, pouch-shaped nests, which are used not only for raising young but also for nighttime roosting throughout the year (Figure 14).

The bird's almost exclusive selection of tall cacti for nest placement is corroborated by our nest records. We have located 584 nests in coastal San Diego and Orange counties. All but two were found in *Opuntia*. The exceptions were located in particularly robust individuals of the Yellow Bush Penstemon (*Keckiella antirrhinoides*). The median height of cacti in which the wrens placed their nests was 138 cm (n = 98, range 74–226 cm), while the median height of the nests was 94 cm above ground (range 40–165 cm). The wrens are absent from areas where only low, sprawling cacti grow.

Nest counts are not a reliable indicator of wren populations. We have found up to a dozen nests within the territory of a single pair of wrens.

The wrens nest in three native species of *Opuntia*: the Coastal Cholla (*Opuntia prolifera*) and two species of prickly-pear (*O. littoralis* and *O. oricola*). Coastal Cholla is the typical choice in southern San Diego County

Figure 15. Sage scrub dominated by Coastal Cholla (*Opuntia prolifera*) near Sweetwater Dam, San Diego County, May 1990. Coast Barrel Cacti (*Ferocactus viridescens*) are also common at this locality.

Photo by William T. Everett

where large prickly-pears are scarce (Figure 15). Definite nesting preferences by the wren are not obvious where both cholla and prickly-pears grow abundantly. For example, of 32 nests found at Agua Hedionda Lagoon, 16 were located in cholla, 16 in prickly-pears; Santa Margarita River nests included 18 (42%) in cholla, 39 (58%) in prickly-pears.

The two species of prickly-pear offer the only nesting sites in the interior valleys of the San Dieguito and San Luis Rey rivers in San Diego County. Nest selection varies greatly. Twenty-eight of 34 nests (82%) on Bernardo Mountain near Escondido (Figure 16) were built in the more abundant *Opuntia littoralis*, but all 11 nests of a remnant population near Pala were found in *O. oricola* (Figure 17).

Tall *Opuntia* cacti capable of supporting the wren's nests are found primarily on south-facing slopes or at the bases of hillsides within 400 m of river valleys. They are also on hillsides along tributary canyons, mainly those with south- and west-facing slopes. Along San Juan Creek in Orange County (Figures 18 and 19) and the Otay River in San Diego County, tall *Opuntia* cacti grow right on the edges of the washes, a situation that once probably existed along many other rivers. Dense patches inhabited by wrens are also found where coastal sage scrub forms a ground cover in the very open woodland of Coast Live Oaks (*Quercus agrifolia*) and California Sycamores (*Platanus racemosa*) along San Juan Creek and some of its tributaries, such as Bell and Crow canyons (Nagata 1982; Gundy and

Figure 16. Sage scrub dominated by the prickly-pear *Opuntia littoralis* on the south slope of Bernardo Mountain, near Escondido, San Diego County, November 1988.

Photo by Kenneth L. Weaver

Flanagan 1978). The association of the wrens with tall *Opuntia* growing along canyons is so striking that the simplest way to locate the birds is by watershed.

Using spot-mapping techniques (Hall 1964), we determined the approximate size of territories for 13 pairs of wrens in south Escondido in San Diego County. Territories ranged in size from 0.8 ha to 2 ha, with an

Figure 17. Sage scrub dominated by the prickly-pear *Opuntia oricola* at San Pasqual Battlefield Historical Park, San Diego County, May 1990. The type locality of *C. b. sandiegensis*, the San Diego Wild Animal Park at San Pasqual, is less than 1 km away.

Photo by Kenneth L. Weaver

average of 1.3 ha. In Arizona, Anderson and Anderson (1973) found territories to range from 1.2 to 2.8 ha and average 1.9 ha.

San Diego Cactus Wrens we studied centered their territories on narrow draws, where cacti tend to be more abundant and taller than on adjacent slopes. Most territories tend to be roughly elliptical, corresponding to the downslope flow of the draws. Thus, there is a vertical as well as a spatial requirement for hillside-inhabiting wrens, a factor that has not been taken into consideration in mitigation efforts. The wash-dwelling wrens of San

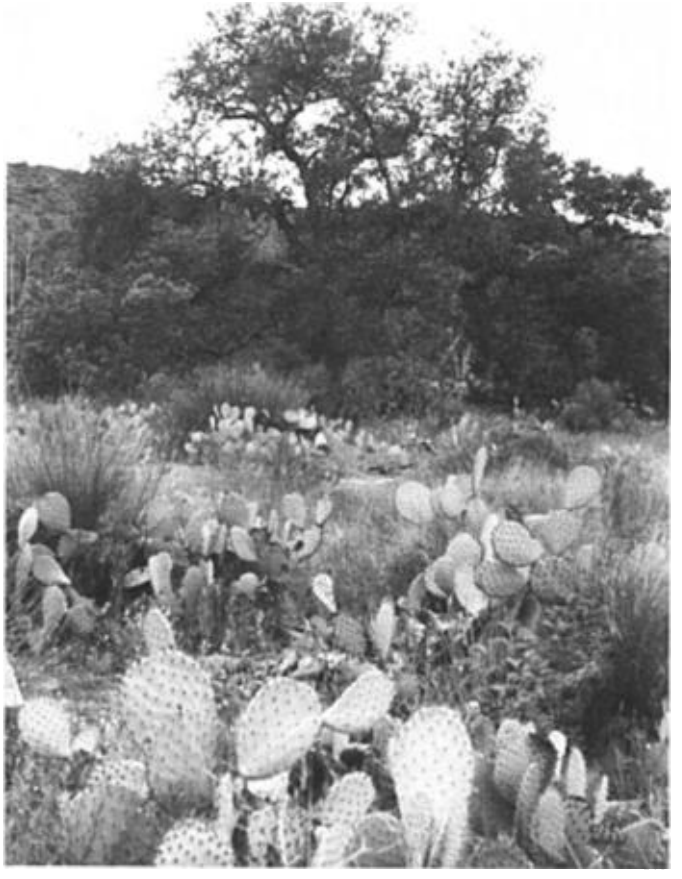

Figure 18. Wash inhabited by San Diego Cactus Wrens in San Juan Creek, Casper's Wilderness Park, Orange County, April 1990.

Photo by Kenneth L. Weaver

Juan Creek lack a vertical component to their territories. However, the narrow distribution of cacti along the creek also causes the birds' territories to be elliptical or rectangular.

Associated Fauna

The avifauna associated with the San Diego Cactus Wren forms a small but distinctive assemblage. Birds recorded in significant numbers (greater than three pairs) on our census plots are the California Quail (*Callipepla*

Figure 19. Wash inhabited by San Diego Cactus Wrens in San Juan Creek, Casper's Wilderness Park, Orange County, April 1990.

Photo by Kenneth L. Weaver

californica), Costa's Hummingbird (*Calypte costae*), Bushtit (*Aegithalos minimus*), California Towhee (*Pipilo crissalis*), California Gnatcatcher (*Polioptila californica*), Rufous-crowned Sparrow (*Aimophila ruficeps*), and Sage Sparrow (*Amphispiza belli*). Where sumacs and other tall shrubs occurred, Bewick's Wren (*Troglogytes bewickii*), California Thrasher (*Toxostoma redivivum*), Wrentit (*Chamaea fasciata*), and Rufous-sided Towhee (*Pipilo erythrophthalmus*) also occurred in significant numbers.

A wide variety of mammals frequents the coastal sage scrub. Several rodents, such as the San Diego Pocket Mouse (*Perognathus fallax*), Agile Kangaroo Rat (*Dipodomys agilis*), and Desert Woodrat (*Neotoma lepida*), show a distinct preference for this habitat (Bleich 1973).

Although no reptiles are limited entirely to coastal sage scrub, two lizards restricted to southern California and listed by the California Department of Fish and Game as threatened, the Coast Horned Lizard (*Phrynosoma coronatum*) and the Orange-throated Whiptail (*Cnemidophorus hyperythrus*), are particularly common in this habitat (Eric Lichtwardt pers. comm.). The Red Diamond Rattlesnake (*Crotalus ruber*), in its U.S. distribution found only in southwestern California, is also especially abundant in the coastal sage scrub (Richard Zembal pers. comm.).

Certain insects are found primarily or exclusively in the coastal sage scrub, usually because of association with certain plants. Two examples are the moths *Megathymus comstocki* and *Tegeticula yuccasella* (on *Yucca schidigera*).

PALEOBIOGEOGRAPHY

The modern southern coastal sage scrub community that supports the San Diego Cactus Wren is itself anomalous in the otherwise mesic chaparral of the California Floristic Province. Most of the plant genera characterizing southern coastal sage scrub community, enumerated under Habitat Requirements, have their evolutionary centers of diversity in deserts, which themselves were more restricted in area generally and in more southern latitudes during the Pleistocene Epoch. Axelrod (1966) attributed these relictual desert components along the coast to the Xerothermic period (also called the Hypsithermal or Altithermal period) that followed the Wisconsin glaciation. According to Raven and Axelrod (1978:33), "The continued trend toward spreading drought, as in the Xerothermic periods of the Quaternary, allowed many taxa that are primarily associated with deserts to invade the dryer parts of the California Floristic Province." Many of these desert plant genera have evolved endemic species along the coast.

Axelrod (1978) believed that the southern coastal sage as a community is relatively young, occupying its present area only since the last glaciation, 12,000 years ago. He hypothesized that when grasslands in semiarid open areas among forests and woodlands began to lose summer precipitation, coastal sage vegetation replaced them. Tectonic events during the Quaternary Period elevated lowlands into mesas, which were then dissected by erosion, producing the slopes and thin, well-drained soils favored by coastal sage scrub. Sonoran Desert vegetation was moving northward on the

continent about the same time. Modern plant communities in the Southwest were probably in place by 4000 years ago (Van Devender et al. 1987).

Presumably, the California Gnatcatcher, which has evolved to the species level, and the San Diego Cactus Wren, which has not, invaded coastal areas between 12,000 and 4000 years ago. (Both represent genera having centers of diversity in subtropical or tropical regions.) Whether the subspecies *C. b. sandiegensis* represents a genetic mixing of traits derived from a dual invasion of *anthonyi* from the east and *bryanti* from the south is unknown. Alternatively, the San Diego Cactus Wren may have been derived from the intergrading of continental and peninsular birds in northeast Baja California (area of overlapping patterns in Figure 1) and later invaded its current range. Specimens (SD) from Valle de la Trinidad have traits characteristic of the subspecies *sandiegensis*, and specimens from San Felipe tend in that direction. In the modern vegetation, the coastal wrens, so far as known, are separated from Valle de la Trinidad by 140 km. The coastal California Gnatcatcher, however, with a broader niche in the sage scrub (it is not dependent on cactus), reaches and narrowly overlaps the desert Black-tailed Gnatcatcher in Valle de la Trinidad (Atwood 1988).

The taxonomic differences between the Cactus Wrens of the Los Angeles and San Diego areas are interesting in the light of apparent differences in the vegetative community. Axelrod (1950, 1966) has suggested that two segments of southern coastal sage scrub be recognized, a Venturan component and a San Diegan component.

CONSERVATION RECOMMENDATIONS

The San Diego Cactus Wren is particularly vulnerable because of the bird's restriction to a single type of habitat and strict dependence on a single genus of cacti for placement of its breeding and roosting nests. Rampant urbanization has caused an extremely fragmented distribution and a rapidly shrinking population. Most populations now consist of fewer than five pairs, and the bird appears to be unable to colonize suitable habitat that is surrounded by development. We believe this bird will not survive unless the following steps are taken:

1. Listing of *C. b. sandiegensis* as an endangered subspecies by the federal government;
2. Protection of large blocks of its habitat, the coastal sage scrub;
3. Maintenance of the habitat, including local suppression of fires.

SUMMARY

The Cactus Wrens of southern Orange County, coastal San Diego County, and extreme northwestern Baja California form a distinct subspecies, *Campylorhynchus brunneicapillus sandiegensis*. They are easily distinguishable in the hand and in the field from neighboring populations to the north, south, and east. Based on a mosaic of seven characters, *C. b. sandiegensis* differs from *C. b. anthonyi* of the transmontane desert by larger ventral spotting, reduced abdominal buff, and greater white tail

barring, and from *C. b. bryanti* of Baja California by its less brown dorsum, less barred tail, generally single-spotted chest feathers, and tendency toward a chest patch. This sedentary bird is highly dependent on coastal sage scrub containing tall *Opuntia* cacti. Fewer than 400 pairs remain. Rapid habitat destruction places this bird in serious danger of extinction. Cactus Wrens from the Los Angeles area of southern California are not taxonomically distinguishable from *C. b. anthonyi* of the adjacent desert, although some individuals show some genetic influence of *C. b. sandiegensis*.

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Unfortunately, we had difficulty in acquiring a number of Cactus Wren records. This is a result of serious flaws in the way California's environmental impact review process is administered. Proprietary rights to scientific data gathered during biological surveys are assigned to landowners, not to the public. Dissemination of this information thus may be restricted; biologists who work for consulting firms may be restricted from sharing their data with the scientific community. We know of several instances where consultants have actually been fired when they reported rare birds and other wildlife. The environmental assessment process is in dire need of reform.

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APPENDIX 1. HISTORY OF THE NAME *CAMPYLORHYNCHUS*

Readers will note variations in the gender of the scientific name of the Cactus Wren. The species was described by Lafresnaye in 1835 as *Picolaptes brunneicapillus*. The generic name *Picolaptes* Lesson, 1830, with the type species *P. spixii*, is now a synonym of *Xiphorhynchus* Swainson, 1827, in the family Dendrocolaptidae (woodcreepers). The generic name *Campylorhynchus* was first proposed by Spix in 1824 for what is now *C. turdinus*, and the generic name was used by Gray in 1847 in combination with the specific name as *brunneicapillus*. The A.O.U. (1886, 1889) followed Gray. However, Palmer (1893), following the convention of nomenclature of that time, concluded that *Campylorhynchus* should be treated as a junior synonym of *Campylirhynchus* Megerle, 1821, a generic name of a beetle. The A.O.U. (1910, 1931) used the next available generic name, *Heleodytes* Cabanis, 1851, for the Cactus Wren. The fifth edition of the Check-list (A.O.U. 1957, first printing) returned to the use of *Campylorhynchus* Spix because the name is not preoccupied under current rules of nomenclature, but scientific names of the Cactus Wren were treated as neuter in gender. (In the second printing, an incorrect mixture of both masculine and neuter was used.) The neuter was followed in the original description of the San Diego Cactus Wren (Rea 1986), in conformity with other taxa in the genus written by Phillips (1986). In this paper, the masculine is used, as in the original species combination by Gray, the thirty-second supplement to the A.O.U. Check-list (1973), the sixth edition of the A.O.U. Check-list (1983), and according to the latest edition of the International Code of Zoological Nomenclature, which specifies that genera with the masculine ending *-us* be treated as masculine regardless of their derivation and gender in language of origin.

APPENDIX 2. RECORDS OF THE SAN DIEGO CACTUS WREN SINCE 1980

Location	Most Recent Survey[a] Count	Most Recent Survey[a] Territorial Males	Previous Survey Count[b]	Previous Survey Territorial Males	Notes[c]
San Juan Creek[d]					
1. Rancho Mission Viejo	—	64	NPR	—	D
2. Rancho Mission Viejo	—	32	NPR	—	D
3. Rancho Mission Viejo	—	15	NPR	—	D
4. Caspers Park[e]	—	3	KS	—	
5. Caspers Park	19	13	KS	—	
6. Starr Ranch[e]	—	1	NPR	—	
7. Starr Ranch[e]	—	2	KS	—	
Segunda Deshecha Cañada					
8. San Clemente	1	1	NPR	—	
San Mateo/San Onofre Creeks					
9. Rancho Mission Viejo	—	13	NPR	—	D
10. Camp Pendleton	—	5	KS	—	
Unnamed creek					
11. Camp Pendleton	—	1	NPR	—	
Aliso Creek					
12. Camp Pendleton	—	2	NPR	—	
Santa Margarita River					
13. Camp Pendleton	—	1	NPR	—	
14. Camp Pendleton	0	0	1	1	
15. Camp Pendleton	—	5	11	10	
16. Camp Pendleton	—	3	KS	—	
17. Camp Pendleton	—	1	NPR	—	
18. Camp Pendleton	1	1	NPR	—	
19. Naval Weapons Station	17	—	NPR	—	
20. Naval Weapons Station	2	—	NPR	—	
San Luis Rey River					
21. Camp Pendleton	ON	—	KS	—	
22. Camp Pendleton	—	1	NPR	—	
23. Camp Pendleton	—	3	11	9	F
24. Camp Pendleton	—	2	NPR	—	
25. Camp Pendleton/ Naval Weapons Station	11	—	NPR	—	
26. Naval Weapons Station	1	—	NPR	—	
27. Bonsall	5	2	3	2	
28. Lilac	0	0	N	—	

Continued

Location	Most Recent Survey[a] Count	Most Recent Survey[a] Territorial Males	Previous Survey Count[b]	Previous Survey Territorial Males	Notes[c]
29. Pala	0	0	2	1	
30. Pala	0	0	N	—	
31. Pauma Valley	0	0	3	3	F
Agua Hedionda Creek					
32. Agua Hedionda Lagoon	0	0	5	4	R
San Marcos Creek					
33. Batiquitos Lagoon	0	0	1	1	R
Escondido Creek					
34. San Elijo Lagoon	0	0	—	2	A
San Dieguito River					
35. Rancho Santa Fe	0	0	N	—	
36. Rancho Sante Fe	ON	—	NPR	—	
37. Rancho Bernardo	—	1	NPR	—	
38. Rancho Bernardo	0	0	3	1	R
39. Rancho Bernardo	0	0	KS	—	R
40. Rancho Bernardo	5	1	5	1	D
41. Rancho Bernardo	0	0	3	2	R
42. Escondido	21	12	23	18	F, R
43. Escondido	0	0	1	1	R
44. Escondido	0	0	1	1	R
45. Escondido	20	13	—	19	R
46. Escondido	1	1	8	4	F
47. Escondido	2	1	3	2	R, G
48. Escondido	4	3	3	2	R
49. San Pasqual Valley	0	0	2	2	R, A
50. San Pasqual Valley	0	0	6	3	R, A
51. San Pasqual Valley	0	0	1	1	R
52. San Pasqual Valley	2	2	—	5	G
53. San Pasqual Valley	54	38	54	48	F
54. San Pasqual Valley	0	0	1	1	A
55. San Pasqual Valley	2	1	2	2	
56. San Pasqual Valley	6	4	—	6	
57. San Pasqual Valley	0	0	1	1	A
58. San Pasqual Valley	2	1	2	1	
Los Peñasquitos Creek					
59. Torrey Pines State Res.	0	0	1	1	
60. Poway	0	0	5	2	R
61. Poway	0	0	N	—	R

Continued

Location	Most Recent Survey[a] Count	Most Recent Survey[a] Territorial Males	Previous Survey Count[b]	Previous Survey Territorial Males	Notes[c]
San Diego River					
62. San Diego	1	1	1	1	
63. Santee	3	2	10	—	D
64. Spring Valley	—	1	NPR	—	R
65. El Cajon	1	1	1	1	
66. Lakeside	0	0	1	1	
67. Lakeside	33	18	10	8	D
68. Lakeside	0	0	1	1	
Sweetwater River					
69. Chula Vista	5	—	NPR	—	D
70. Chula Vista	2	1	NPR	—	
71. Sunnyside	1	—	NPR	—	D
72. San Diego	N	—	NPR	—	D
73. Sweetwater Reservoir	13	8	KS	—	D
74. Sunnyside	3	2	KS	—	D
75. Mother Miguel Mt.	—	3	—	2	D
76. Mother Miguel Mt.	2	2	10	5	D
77. S of Mother Miguel Mt.	—	1	NPR	—	D
78. S of Mother Miguel Mt.	2	1	NPR	—	D
79. S of Mother Miguel Mt.	1	1	6	3	D
Otay River					
80. Dennery Canyon	6	3	NPR	—	D
81. Rancho Otay	6	—	6	—	D
82. Rancho Otay	27	—	37	—	D
83. Rancho Otay	16	—	2	—	D
84. Proctor Valley	1	—	1	1	D
Tijuana River					
85. Otay Mesa	2	1	NPR	—	D
86. Spring Canyon	2	1	NPR	—	D
87. Valle de las Palmas	5	1	KS	—	A

[a]N, nests found; ON, remnants of old nests found.
[b]KS, known site, no record available; NPR, no previous record.
[c]A, habitat destruction due to agricultural clearing; D, proposed development; F, habitat destruction due to fire; G, habitat destruction due to grazing; R, habitat destruction due to residential construction.
[d]Results of Orange County Breeding Bird Atlas indicate a minimum of 50 pairs in this portion of the San Juan Creek drainage basin but data are not listed according to specific locations.
[e]Data resulting from breeding bird censuses, not strictly surveys.

Details of San Diego Cactus Wren Locations and Surveys

Orange County, California

San Juan Creek

1. Rancho Mission Viejo, W side of Cañada Chiquita, from San Juan Creek N approx. 5 mi. Oct 1989–Jan 1990 (DB).
2. Rancho Mission Viejo, W side of Cañada Gobernadora from San Juan Creek N 3 mi., W across ridge to E side Cañada Chiquita, then N 2 mi. Oct 1989–Jan 1990 (DB).
3. Rancho Mission Viejo, W side of Cañada Gobernadora from San Juan Creek N approx. 2.25 mi. Oct 1989–Jan 1990 (DB).
4. Caspers Regional Park, Bell Canyon. 23 Apr–24 May 1981 (PF & KA).
5. Caspers Regional Park, San Juan Creek, from park road crossing to 1.5 mi. E. 12 Feb and 19 Apr 1990 (KW).
6. Starr Ranch Audubon Sanctuary, Crow Canyon, 5.5 mi. SE of Trabuco Oaks Post Office. 16 Apr–24 May 1981 (JN).
7. Starr Ranch Audubon Sanctuary, S side of Pruesker Peak, 5.1 mi. N of entrance to Caspers Regional Park. 15 Apr–20 May 1982 (RB).

Segunda Deshecha Cañada

8. San Clemente, NW corner intersection of Marblehead Dr. and Avenida Pico. 19 Apr 1990 (KW).

San Mateo Creek

9. Rancho Mission Viejo, Cristianitos Canyon area from Hwy. 74 S approx. 3 mi. Oct 1989–Jan 1990 (DB).

San Diego County, California

San Mateo/San Onofre Creeks

10. Camp Pendleton, NW and S slopes of ridge on N side of Basilone Rd., approx. 1.5 mi. E of Interstate 5. 1983 (HW); spring 1989 (LS).

Unnamed creek

11. Camp Pendleton, SW slope of Horno Hill, approx. 0.5 mi. NW of intersection of old Highway 1 and Horno Canyon. Spring 1989 (LS).

Aliso Creek

12. Camp Pendleton, SW slope below hills 765 and 693, S side of Las Pulgas Rd., E side of Stuart Mesa Rd. Spring 1989 (LS).

Santa Margarita River

13. Camp Pendleton, N side of mouth of Santa Margarita R., W of Interstate 5. Spring 1989 (LS).
14. Camp Pendleton, N side of Santa Margarita R., W of Stuart Mesa Rd. 18 Jul 1984 (KW); spring 1989 (LS).
15. Camp Pendleton, N side of Santa Margarita R., between Stuart Mesa Rd. and Basilone Rd. 18 Jul and 4 Aug 1984 (KW); spring 1989 (LS).
16. Camp Pendleton, N side of Pueblitos Canyon, E of Vandegrift Blvd. Spring 1989 (LS).
17. Camp Pendleton, W slope of hill 492, NE side of head of Pueblitos Canyon, SE of base radio tower. Spring 1989 (LS).
18. Camp Pendleton, 300 yards S of confluence of Santa Margarita R. and De Luz Creek. 1982 (RZ).

19. Naval Weapons Station (Fallbrook Annex), W slopes of hills 650, 592, and 472, W and SW edge of base. Spring 1989 (DS).
20. Naval Weapons Station (Fallbrook Annex), ridge line between water tanks, NE end of base. Spring 1989 (DS).

San Luis Rey River

21. Camp Pendleton, Wire Mt., N of Santa Margarita School. 18 July 1984 (KW).
22. Camp Pendleton, E side of Windmill Canyon, SE slope of hill 425, E of golf course club house. Spring 1989 (LS).
23. Camp Pendleton, W side of Windmill Canyon, W of golf course, N to base radio tower. 4 Aug 1984 (KW); spring 1989 (LS).
24. Camp Pendleton, Pilgrim Creek N of Vandegrift Blvd. and S of firing range. Spring 1989 (LS).
25. Camp Pendleton/Naval Weapons Station (Fallbrook Annex), Pilgrim Creek on Camp Pendleton immediately S of border with Naval Weapons Station N 0.5 mi. to slopes E and W of Fallbrook Rd. Spring 1989 (LS); spring 1990 (DS).
26. Naval Weapons Station (Fallbrook Annex), E border of base, approx. 0.5 mi. S of Fallbrook Community Air Park. Spring 1990 (DS).
27. Bonsall, N side West Lilac Rd. 1.3 mi. E of intersection with Camino del Rey. 18 Aug 1989 (KW); 25 Aug 1990 (KW).
28. Lilac, E side of Couser Canyon Rd., 1 mi. S of intersection with Hwy. 76. 27 Dec 1989 (KW); 21 Jun 1990 (KW).
29. Pala, N side of Hwy. 76, 4 mi. E of intersection with Interstate 15. 16 Mar 1985 (KW); 25 Aug 1990 (KW).
30. Pala, N side of Hwy. 76, hill W of intersection with Pala Rd. 16 Mar 1985 (KW); 13 Nov 1988 (KW).
31. Pauma Valley, uppermost Adams Dr. 16 Apr 1985 (KW); 3 Feb 1990 (KW).

Agua Hedionda Creek

32. Carlsbad, Agua Hedionda Lagoon, N side of Lake Dr., W of intersection with Kelly Dr. 3 Mar 1984 (KW); 3 Dec 1988 (KW).

San Marcos Creek

33. Carlsbad, Batiquitos Lagoon, W side Batiquitos Dr. 20 May 1984 (KW); 3 Dec 1988 (KW).

Escondido Creek

34. Encinitas, San Elijo Lagoon, NE of intersection of Interstate 15 and Manchester Ave. 6 Sep 1981 (DK & CE); 1 Apr 1984 (KW).

San Dieguito River

35. Rancho Santa Fe, SE side of confluence of Lusardi Creek and San Dieguito R. Aug 1983 (HW); 9 Mar 1985 (KW).
36. Rancho Santa Fe, NW of intersection of Del Dios Hwy. and Camino del Norte. 9 Mar 1985 (KW).
37. Rancho Bernardo, hills W of SE arm of Lake Hodges, W of Interstate 15. "Early 1980s" (EM).
38. Rancho Bernardo, W of intersection of Camino del Norte and West Bernardo Dr. 25 Aug 1984 (KW); 23 Dec 1989 (KW).
39. Rancho Bernardo, Westwood area, N of Rancho Bernardo Rd. and W of Interstate 15. "Early 1980s" (EM).
40. Rancho Bernardo, ridge E of SE arm of Lake Hodges, W of Interstate 15. 1 Sep 1984 (KW); 16 Jun 1988 (PU), 18 May, 6 and 30 Jun 1990 (RB & PU).
41. Rancho Bernardo, NE of Interstate 15 and Bernardo Center Dr., W of Escala Dr. 1981 (KW).

42. Escondido, S slope of Bernardo Mt., hill 506 S of Lake Hodges boat landing. 8 Apr and 1 Sep 1984 (KW); 20 and 27 Nov 1988 (KW).
43. Escondido, N side of Lake Hodges, W of Interstate 15. 30 May 1981 (KW); 16 Jun 1985 (KW).
44. Escondido, N side of Clarence Lane W of Centre City Pkwy. 27 Jul 1981 (KW); 20 Apr 1990 (KW).
45. Escondido, S side of hill 765, NE of Lake Hodges. 28 Apr 1983 (KW); 25 Feb 1989 (KW).
46. Escondido, N of El Dorado Dr. between Bear Valley Pkwy. and Summit Dr. 28 Feb–20 Jun 1981 (KW); 20 Apr 1990 (KW).
47. Escondido, intersection of San Pasqual Rd. and Sunset. 18 Mar 1984 (KW); 13 Feb 1989 (KW).
48. Escondido, SE of intersection of San Pasqual Rd. and Old Pasqual Rd. 18 Mar 1984 (KW); 13 Feb 1989 (KW).
49. San Pasqual Valley, NE side of intersection of Cloverdale Rd. and Hwy. 78. 10 Mar 1984 (KW); 20 Apr 1990 (KW).
50. San Pasqual Valley, NE and SE of intersection of Cloverdale Rd. and Rockwood R. 23 Mar 1984 (KW); 13 Feb 1989 (KW).
51. San Pasqual Valley, E side of Rockwood Rd. 1 mi. N of intersection with Cloverdale Rd. 1989 (JG); 20 Apr 1990 (KW).
52. San Pasqual Valley, S side of hill 1017, N of Hwy. 78, E of Cloverdale Rd. 10 Mar 1984 (KW); 31 Dec 1988 (KW).
53. San Pasqual Valley, San Pasqual State Historical Park and San Diego Wild Animal Park, from 0.5 mi. E of entrance to Wild Animal Park to Guejito Creek. 2, 9, and 26 Jun and 3 Jul 1984 (KW); 17 and 31 Mar, 4 and 20 Apr 1990 (KW).
54. San Pasqual Valley, NW of Hwy. 78 bridge over Guejito Creek. 5 Jun 1983 (KW); 20 Apr 1990 (KW).
55. San Pasqual Valley, N side of Santa Ysabel Creek, due N of Crane's Peak. 9 Jun 1984 (KW); 20 Apr 1990 (KW).
56. San Pasqual Valley, SE of intersection of Bandy Canyon Rd. and Santa Ysabel Creek Rd. 23 Mar 1984 (KW); 13 Feb 1989 (KW).
57. San Pasqual Valley, S side of Bandy Canyon Rd., approx. 1.5 mi. E of intersection with Santa Ysabel Creek Rd. 23 Mar 1984 (KW); 20 Apr 1990 (KW).
58. San Pasqual Valley, W slope of Crane's Peak. 23 Mar 1984 (KW); 20 Apr 1990 (KW).

Los Peñasquitos Creek

59. San Diego, Los Peñasquitos Lagoon, Torrey Pines State Reserve, W of railroad tracks. 14 Mar 1984 (RW); 2 Mar 1985 (KW).
60. Poway, W of La Manda Rd. and N of Camino del Norte. 25 Aug 1984 (KW); 23 Dec 1989 (KW).
61. Poway, S of Gate Dr. 1981 (HW); 15 Aug 1984 (KW).

San Diego River

62. San Diego, Mission Hills, canyon between Fort Stockton Dr. and Washington Pl. 20 Mar 1986 (CE); 20 May 1990 (SH).
63. Santee, Fanita Ranch, E side of Sycamore Canyon NE of Santee Lakes. 29–27 Jul 1983 (CE); 13 May and 2 Jun 1989, 27 Jul 1990 (PU).
64. Spring Valley, N slope of Dictionary Hill, W of Lamar, S of Crest Dr. 18 Nov–2 Dec 1989 (GG).
65. El Cajon, Fletcher Hills, ridge between Travelodge Dr. and Murray Dr. Jul 1989 (EM); Mar 1990 (HW).
66. Lakeside, N of intersection of Lake Jennings Park Rd. and El Monte Rd. 13 Apr 1985 (KW); 9 Mar 1990 (KW).

67. Lakeside, Lake Jennings County Park and vicinity S of El Monte Rd. and E of Lake Jennings Park Rd. 13 Apr and 3 May 1985 (KW); 9 Mar 1990 (KW).
68. Lakeside, S of Lake Jennings Park Rd., N of Helix Water District building. 13 Apr 1985 (KW); 9 Mar 1990 (KW).

Sweetwater River

69. Chula Vista, E of Interstate 805 between Bonita Rd. and H St. 15 Aug 1989 (fide AMR).
70. Chula Vista, NW of intersection of East H St. and Ridgeback Rd. 27 Dec 1988 (KW).
71. Sunnyside, NW of intersection of Sweetwater Rd. and Quarry Rd. 4 May 1990 (PB, EB).
72. San Diego, Paradise Hills, Hwy. 54 at Briarwood Dr. Aug 1989 (JB).
73. Sweetwater Reservoir, SE of dam. 5 and 24 May 1990 (SS, SV, KW).
74. Sunnyside, Long Canyon W of Corral Canyon Rd. 27 Dec 1988 (KW).
75. Mother Miguel Mt., SW base, E end of San Miguel Rd., N of Wild Man's Canyon. 1989 (EL); 6 Apr 1990 (PU).
76. Mother Miguel Mt., W slopes. 23 Mar 1989 (EL); 6 and 18 Apr 1990 (PU).
77. S of Mother Miguel Mt., N side of Proctor Valley Rd. approx. 1 mi. W of intersection with Rancho Janal Dr. 18 Apr 1990 (JL).
78. S of Mother Miguel Mt., approx. 0.5 mi. N of Proctor Valley Rd. at S end of Wild Man's Canyon. 1989 (EL).
79. S of Mother Miguel Mt., 0.5 mi. N of Proctor Valley Rd., approx. 0.25 mi. W of intersection with Rancho Janal Dr. 1989 (EL); 6 Apr 1990 (PU).

Otay River

80. Dennery Canyon, N of Otay Mesa Rd., E of Interstate 805, and W of Otay Valley Rd. 15 Mar 1988 (HW).
81. Rancho Otay, Poggi Canyon. 1986–1988 (fide NG).
82. Rancho Otay, Otay R. SW of Lower Otay Reservoir, including Salt and Wolf canyons. 1986–1987 (fide NG).
83. Rancho Otay, Johnson Canyon (S of Otay River). 1986–1987 (fide NG); 7 Jun, 16–17 Jul 1990 (PB, SS, SV).
84. Proctor Valley, NW side of Proctor Valley Rd. N of Upper Otay Reservoir. 1987 (fide NG); 10 Mar 1989 (PU).

Tijuana River

85. Otay Mesa, W of Brown Field, S of Otay Mesa Rd. 22 Sep 1983 (RW).
86. Spring Canyon, SW of intersection of Otay Mesa Rd. and Cactus Rd. "Before 1986" (HW).

Baja California

87. Valle de las Palmas, E of Hwy. 3 on S-facing slopes, 0.5–1.0 mi. N of town of Valle de las Palmas. 27 Jul 1986 (AMR).

Sources: Richard Barber, Raymond Bransfield (Am. Birds 37:95, 1983), John Beezley, Tim Burr (U.S. Navy), Claude Edwards, Patricia Flanagan and Kent Armstrong (Am. Birds 36:88, 1982), Pam Beare (Caltrans), Ellen Berryman (Caltrans), David R. Bontrager, Nancy Gilbert (U.S. Fish and Wildlife Service), Glenn Greenwald, John Griffith, Steve Huemner, David King, Eric Lichtwardt, John Lovio, Julia Nagata (Am. Birds 36:87, 1982), Esther McNeil, Amadeo M. Rea, Larry Salata (U.S. Fish and Wildlife Service), Sue Scatolini (Caltrans), Doreen Stadtlander (U.S. Fish and Wildlife Service), Philip Unitt, Sandy Vissman (Caltrans), Kenneth Weaver, Richard Webster, Harold Wier, Richard Zembal (U.S. Fish and Wildlife Service).