GEOGRAPHIC VARIATION IN CACTUS WREN SONGS

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ABSTRACT: We compared Cactus Wren (*Campylorhynchus brunneicapillus*) songs recorded in three regions of coastal southern California (Ventura and Los Angeles counties, Orange County, and San Diego County), Baja California, and the Sonoran and Chihuahuan deserts. On the basis of four measures of the fine structure of individual notes, songs of wrens from Baja California south of 31° N latitude were most distinct; songs of birds from the three regions of coastal southern California were similar and most like songs given by birds in Baja California. Cactus Wrens in coastal southern California are geographically isolated, morphologically different, and differ in song behavior from those in Baja California. Compared with Sonoran and Chihuahuan desert populations, Cactus Wrens in coastal southern California are geographically isolated, differ in song behavior, and occur in a unique and unusual ecological setting. These characteristics suggest that the U.S. Fish and Wildlife Service should reconsider its 1994 decision denying coastal Cactus Wrens protection under the Endangered Species Act because the population was deemed to not meet the definition of a "distinct population segment."

The Cactus Wren (*Campylorhynchus brunneicapillus*) is one of the most familiar and conspicuous members of the avifauna of North America's arid regions. Distributed commonly and widely throughout the lowlands of Baja California and the Mojave, Sonoran, and Chihuahuan deserts, the species also occurs in coastal southern California and extreme northwestern Baja California (American Ornithologists' Union 1998).

Rea and Weaver (1990) reviewed the nomenclatural history and distributional limits of various subspecies of the Cactus Wren in detail; these authors observed that the peninsular forms (*C. b. bryanti* and *affinis*) are so distinct morphologically from the continental populations (*C. b. brunneicapillus*, *anthonyi*, *couesi*, *seri*, and *guttatus*) that the two groups "look like different species." More recently, on the basis of differences in mitochondrial DNA (mtDNA), Zink et al. (2001) similarly concluded that the peninsular and continental forms represent "evolutionarily significant unit[s] (Moritz 1994), if not phylogenetic species (Cracraft 1989)."

Particular attention has recently focused on the taxonomy of Cactus Wren populations found in coastal southern California, from Ventura County south through San Diego County and into extreme northwestern Baja California. These populations are geographically separated from both the peninsular birds of Baja California and from populations in the Sonoran and Mojave deserts of California. Rea (1986) suggested that the coastal population of Cactus Wrens inhabiting southern California and extreme northwestern Baja California be recognized as a newly described subspecies, *C. b. sandiegensis*. Later, Rea and Weaver (1990) revised the proposed distribution (and spelling) of *sandiegensis* to extend from Valle de las Palmas (32° 24′ N latitude) in

extreme northwestern Baja California only as far north as southern Orange County (San Juan Creek), California; they assigned wrens on the coastal slope of Ventura, Los Angeles, Riverside, San Bernardino, and northern Orange counties to the wide-ranging Sonoran Desert subspecies *anthonyi* (= *couesi*, *sensu* American Ornithologists' Union 1957). However, Rea and Weaver (1990) commented that "some individuals [from the Los Angeles area] show some genetic influence of *C. b. sandiegensis*."

Although Rea and Weaver's (1990) evaluation of *sandiegensis* was based on plumage characters, they also stated that "we can recognize a distinct song dialect in southern coastal wrens [*sandiegensis*]. The vocalizations have a slightly lower frequency and lower pitch than more northern [coastal *anthonyi*] and eastern [desert *anthonyi*] birds, and have a raspy quality not heard in adjacent populations . . . central and northern Orange County wrens sing the Los Angeles Basin dialect." Sibley (2000) confused the issue by ascribing Rea and Weaver's (1990) description of the plumage and vocal characteristics of *sandiegensis* to all Cactus Wrens in coastal southern California, including coastal populations of *anthonyi*. Proudfoot et al. (2000) placed *sandiegensis* (and, inexplicably, *seri*) within the peninsular group, presumably on the basis of distribution.

The distribution and nomenclature of Cactus Wren subspecies is especially important with regard to the coastal birds of southern California and extreme northwestern Baja California. These wrens are entirely restricted to the coastal sage scrub plant community (Rea and Weaver 1990), widely considered to be one of the most threatened habitat types in the United States as a result of intense pressure for urban development (Hanes 1976, Kirkpatrick and Hutchinson 1977, Mooney 1977, Westman 1987, O'Leary 1990). Because of these threats, in 1990 the U. S. Fish and Wildlife Service (USFWS) was petitioned by the San Diego Biodiversity Project and Palomar Audubon Society to list the San Diego Cactus Wren (*C. b. sandiegensis*) as an endangered species under the U.S. Endangered Species Act (ESA). The ESA uses the term "species" to include "any distinct population segment of any species of vertebrate." That is, from a legal standpoint, the word "species" may or may not have any taxonomic connotation. The USFWS rarely uses population-level listings; when they are applied, such rulings require proof not only that a population is imperiled but also that it is both discrete and significant (U.S. Department of the Interior and U.S. Department of Commerce 1996).

In response to several unpublished letters disputing the subspecific validity of *sandiegensis*, the USWFS suggested that "Cactus Wrens residing in coastal southern California may . . . constitute a distinct vertebrate population segment that could qualify for listing under the [ESA]" (USFWS 1994) and expanded the subject of the original petition from *sandiegensis* to include all Cactus Wrens found in the coastal sage scrub of southern California and extreme northwestern Baja California. Thus, circumventing the question of subspecies limits, the USFWS opted instead to assess whether *sandiegensis* and coastal populations of *anthonyi*, combined, should be afforded protection under the ESA.

The USFWS found that "all of the published literature on the status of coastal sage scrub vegetation types in California supports the conclusion

that this plant community is one of the most depleted habitat types in the United States," and that "numbers of Cactus Wrens residing in coastal sage scrub of coastal southern California have declined as a result . . . of the same factors that have . . . impacted" the California Gnatcatcher (*Polioptila c. californica*), formally designated as threatened (USFWS 1994: 45660). Nonetheless, the USFWS's final conclusion was that coastal Cactus Wrens "do not constitute a distinct vertebrate population segment" and therefore were not "a listable entity" (USFWS 1994: 45660).

The rationale supporting this decision hinged on three points (USFWS 1994: 45660). First, by broadening the petition to include all of California's coastal Cactus Wrens, including *sandiegensis* and coastal populations of *anthonyi*, the USFWS not surprisingly concluded that "no apparent morphological or other morphometric differences . . . distinguish coastal birds from other Cactus Wrens;" Rea and Weaver (1990:99–100) had earlier observed that "northern coastal Cactus Wrens [*anthonyi*, coastal populations] . . . are not taxonomically separable from adjacent desert *anthonyi*." Second, the USFWS stated that coastal Cactus Wrens lack distinctive behavioral characteristics distinguishing them from desert populations. Third, the USFWS claimed that the coastal sage scrub inhabited by Cactus Wrens in coastal southern California and extreme northwestern Baja California transitions gradually into plant communities of the Baja California peninsula that are also occupied by the species, thereby proving that the wrens of coastal southern California are "not isolated in habitat."

This paper examines the conclusion that "coastal Cactus Wrens" (*sensu* USFWS 1994) do not represent a "listable entity" under the ESA. In particular, we discuss the USFWS's contention that coastal populations do not differ behaviorally from desert birds by comparing songs recorded throughout much of the species' range. We also consider the USFWS's statement that coastal Cactus Wrens are not ecologically isolated from conspecifics in the Baja California peninsula, especially in light of vocal, morphologic, and genetic differences between continental and peninsular populations.

METHODS

We recorded songs of 157 Cactus Wrens from 1982 to 1992 in the coastal sage scrub of southern California (Ventura and Los Angeles counties, n = 24 individuals; southern Orange County, n = 17; San Diego County, n = 17), Baja California south of 31° N latitude (n = 19), the Sonoran desert of southeastern California, southern Arizona, and northern Sonora, Mexico (n = 49), and the Chihuahuan desert of southern Texas (n = 31) (Figure 1). We used a Marantz PMD221 cassette recorder and a Sennheiser ME88 directional microphone. Recordings used in this study have been deposited in the Macaulay Library, Cornell Laboratory of Ornithology.

We measured four characteristics of each song by means of Canary bioacoustics software version 1.2 (Charif et al. 1995). We chose variables that could be measured consistently from all recordings and because they seemed likely to reflect the verbal descriptions ("slower . . . lower pitch . . . raspy quality") used by Rea and Weaver's (1990) discussion of the song of *sandiegensis*. RATE was defined as the number of notes per unit time, with

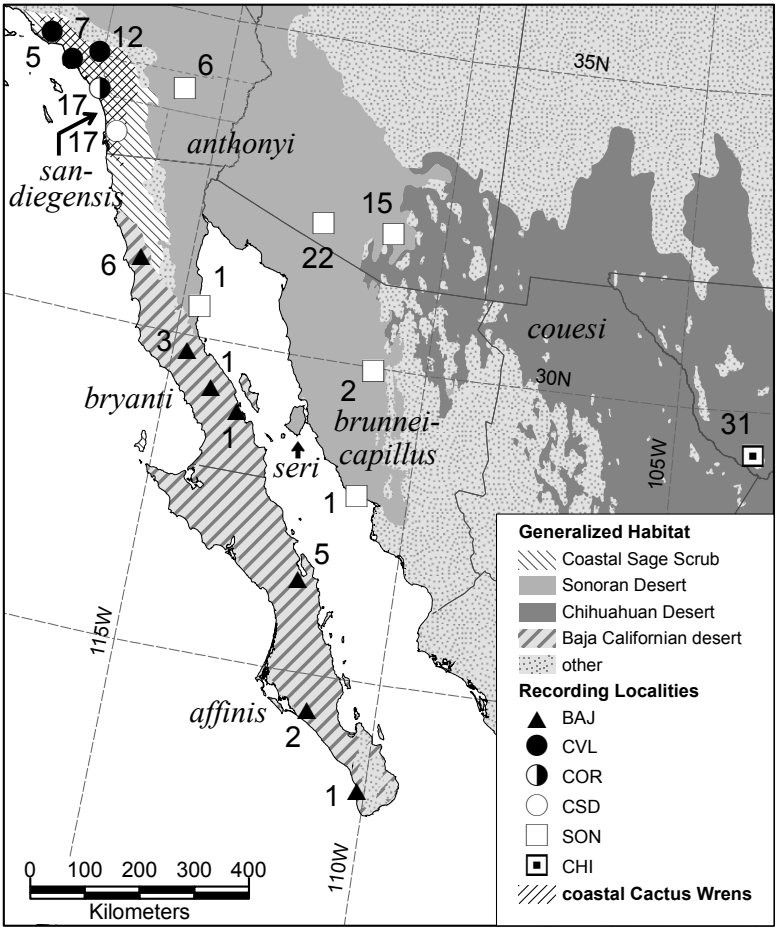

Figure 1. Localities where we sampled Cactus Wren songs relative to generalized habitat and subspecies distributions. Numbers indicate multiple individuals recorded at a single location (for clarity, nearby localities are represented by a single point). Boundaries of broad ecological regions follow Olson et al. (2001); "Baja Californian desert" consists of ecoregions described as "Baja California desert," "Gulf of California xeric scrub," and "San Lucan xeric scrub." Area defined by Olson et al. (2001) as "California coastal scrub and chaparral" referred to here as "coastal sage scrub" (current extent of community much reduced from that shown here). CVL, coastal, Ventura and Los Angeles counties; COR, coastal, Orange County; CSD, coastal, San Diego County; SON, Sonoran Desert; CHI, Chihuahuan Desert; BAJ, Baja Californian desert.

Δ time calculated between times (in seconds) of peak intensity of selected notes; at least three successive notes were included in this measurement, and values were then averaged (Figure 2). Measurements of RATE were obtained with the spectrogram display set at time resolution = 2.902 milliseconds. Frequency and intensity measures were obtained from that note of the song at that note's peak intensity; the spectrogram's frequency resolution for these measurements was set at 5.38 Hz. Peak frequencies (kHz) and average intensities (W/m^2) were measured from each resulting 11.6-millisecond time "slice" and then used to calculate the mean frequency (FREQ) as well as coefficients of variation describing each note's variability in frequency (CV_FREQ) and intensity (CV_INTEN). To avoid possible inclusion of various background noises, frequency measurements were made after sounds <0.75 kHz and >2.5 kHz were filtered from the signal.

Songs that we subjectively judged to be typical of a particular individual were selected randomly for analysis. Cactus Wrens have a large vocal repertoire, including many variations of their adult song (Proudfoot et al. 2000). However, most of our recordings covered relatively short intervals, during which only a single song type was usually evident. Also, any variability that might be introduced into the analysis by inclusion of nonhomologous song types would have no geographic basis and would thus serve only to lower the likelihood of detecting differences among regions. Nonetheless, to address the possibility that some recordings might represent nonhomologous song

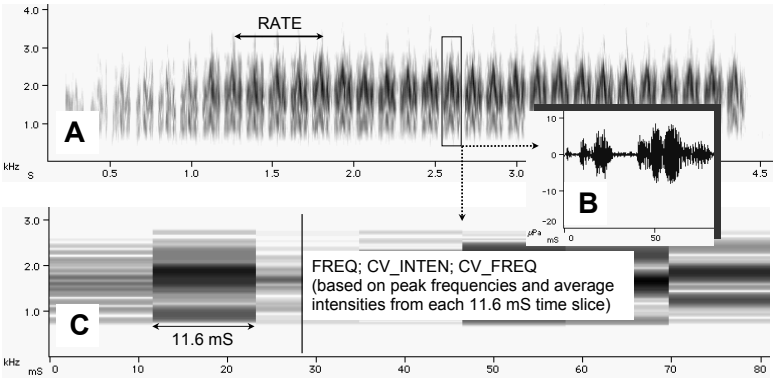

Figure 2. Measurements used in analysis of variation in Cactus Wren songs. A, spectrogram display, frequency resolution 43.07 Hz, time resolution 2.902 milliseconds, used as basis of the variable RATE (notes per unit time). B, waveform display, showing instantaneous pressure (ΔPa) as a function of time, for a single selected note. Such variations were measured from displays like that shown for a single note in C (spectrogram display, frequency resolution 5.38 Hz, time resolution 11.6 milliseconds), with the selected note being chosen as that where the peak intensity of sound occurred within the song. Peak frequencies (kHz) and average intensities (W/m^2) were measured from each 11.6-millisecond time "slice" of this note and then used to calculate the mean frequency (FREQ) and coefficients of variation (standard deviation/mean) for intensity (CV_INTEN) and frequency (CV_FREQ).

types, we excluded from analysis six songs (Baja California, 2 individuals; Sonoran Desert, 1; Ventura and Los Angeles counties, 1; San Diego County, 2) that were identified as multivariate outliers by jackknife Euclidean distances >2.5 standard deviations (Tabachnik and Fidell 1989, McCune and Grace 2002, Sall et al. 2004).

Quantitative analyses were performed using JMP-IN 5.1 statistical software (Sall et al. 2004). Variables were $\log_{10}$-transformed to improve normality of distributions.

RESULTS

Although Cactus Wren songs were superficially similar throughout the sampled range (Figure 3), we detected significant differences among the six regions in the fine structure of individual syllables (Figure 4). Mean frequency (FREQ) was higher in birds from the Baja California desert than in populations from all the other regions. The other measured variables (RATE, CV_INTEN, and CV_FREQ) all varied significantly by region, although the multiple comparison tests elucidated no consistent, obvious geographic patterns.

Multivariate means of the six regions differed significantly (MANOVA; Wilks' $\lambda = 0.53$, approx. $F_{20,472} = 5.00$, $P < 0.0001$; Figure 5). Song characteristics of the continental populations appeared to transition gradually from the Chihuahuan Desert to the Sonoran Desert and thence from north to south in coastal southern California. Songs of the peninsular populations showed the greatest contrast with songs of birds from the Sonoran and Chihuahuan deserts; songs of birds from coastal southern California were intermediate in their characteristics between those given by the Sonoran Desert and Baja California peninsula populations. Recordings from Baja California were significantly different from those of the geographically adjacent regions of the Sonoran Desert and the coastal sage scrub of San Diego County (MANOVA, least squares means contrasts; $P < 0.0001$ and $P = 0.001$, respectively). Songs of birds in the Sonoran Desert differed from those of the combined coastal populations ($P < 0.001$) and, marginally, from the geographically adjacent birds of coastal Ventura and Los Angeles counties ($P = 0.048$). Recordings of wrens from the coastal sage scrub of Ventura and Los Angeles counties differed marginally from those from coastal San Diego County ($P = 0.048$). Songs of birds from southern Orange County did not differ statistically from those recorded in coastal San Diego County ($P = 0.258$) or from birds recorded in Ventura and Los Angeles counties ($P = 0.567$), consistent with K. L. Weaver's observation (in litt., 2006) that northern and southern coastal dialects can be recognized in this area.

Hierarchical cluster analyses based on the mean values for each of the six regions yielded two different "solutions," depending on the algorithms used for construction of the clusters. Group-average (UPGMA), centroid, Ward's minimum-variance, and complete (farthest-neighbor) linkage methods all produced dendrograms in which the most fundamental division was between the Sonoran and Chihuahuan Desert samples versus the other four sampling regions (Figure 6). In each of these approaches, the three coastal Cactus Wren samples (Los Angeles and Ventura counties; Orange

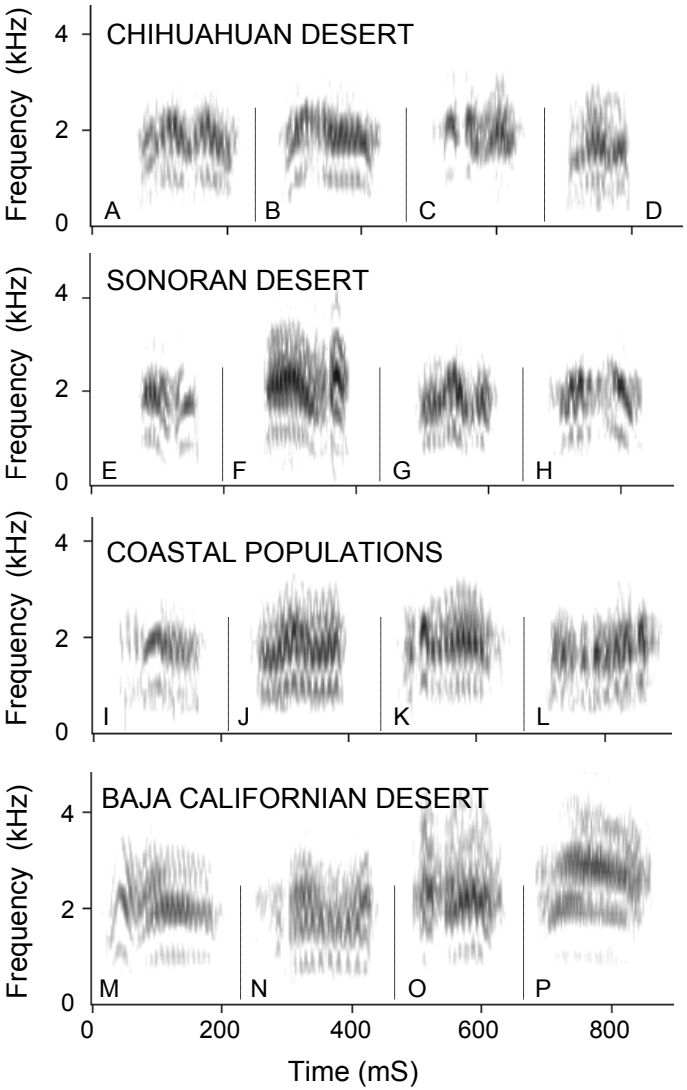

Figure 3. Variation in single notes from Cactus Wren songs recorded in four major arid regions of southwestern North America. A–D: Texas, Brewster Co., Big Bend National Park; E: California, Riverside Co., Joshua Tree National Park, Cottonwood Springs; F: Arizona, Pima Co., 3 km SE of Quijotoa; G–H: Arizona, Pima Co., Organ Pipe Cactus National Monument; I: California, Orange Co., Caspers Regional Park; J: California, San Diego Co., Lake Hodges; K: California, Los Angeles Co., Point Vicente; L: California, Ventura Co., Camarillo; M, O, P: Baja California Sur, 30 km S of Mulege; N: Baja California Sur, 15 mi SE of Santa Rita. Frequency resolution 43.07 Hz, time resolution 2.902 milliseconds.

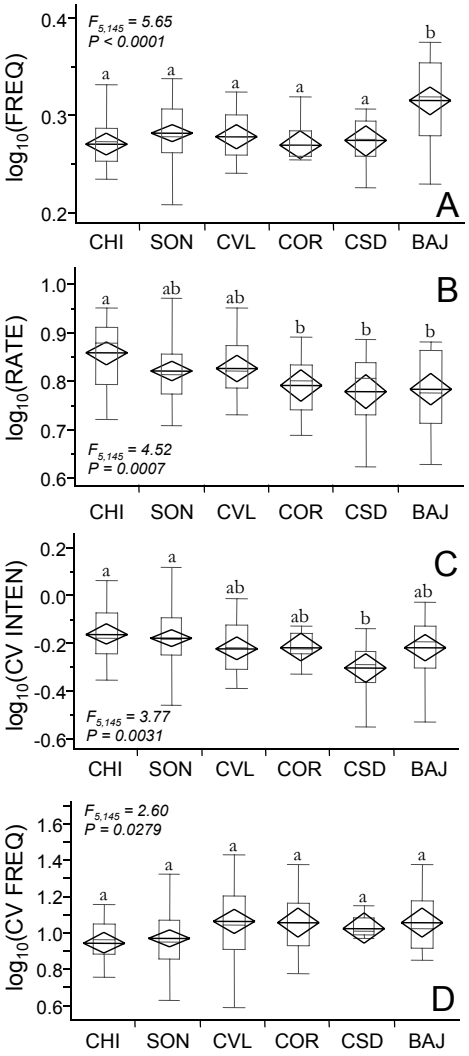

Figure 4. Univariate comparisons of four measures of Cactus Wren songs by six sampling regions. A, FREQ; B, RATE; C, CV_INTEN; D, CV_FREQ. Diamonds, indicating means and 95% confidence intervals, imposed on quantile box plots. Shared letters (a, b) identify means that are not significantly different ($P > 0.05$) according to the Tukey–Kramer honest significant difference test. CVL, coastal, Ventura and Los Angeles counties; COR. coastal, Orange County; CSD. coastal, San Diego County; SON. Sonoran Desert; CHI. Chihuahuan Desert; BAJ. Baja Californian desert.

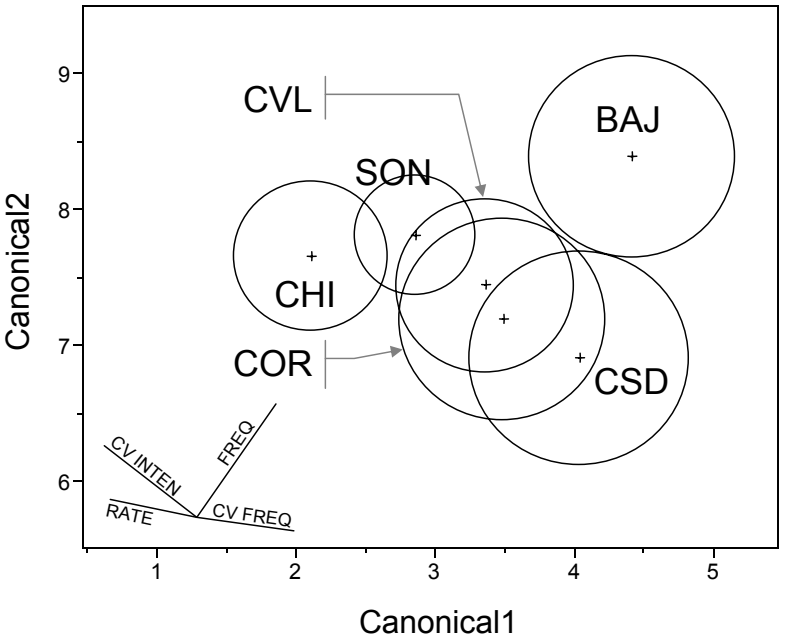

Figure 5. Multivariate means of Cactus Wren songs based on four measured variables by six sampling regions. Circles represent 95% confidence estimates. CVL, coastal, Ventura and Los Angeles counties; COR, coastal, Orange County; CSD, coastal, San Diego County; SON, Sonoran Desert; CHI, Chihuahuan Desert; BAJ, Baja Californian desert. Weightings of the four variables on each canonical axis indicated by biplot rays.

County; San Diego County) were grouped together. McCune and Mefford (1999) recommended Ward's method "as a general-purpose linkage method that minimizes distortions in the underlying space." Single-linkage (nearest-neighbor) cluster analysis, found by Milligan (1980) to perform poorly in simulations, similarly grouped together the three coastal California samples but associated these with the Sonoran and Chihuahuan Desert samples instead of with those from Baja California (Figure 6).

Discriminant-function analysis based on vocal characteristics yielded a relatively poor level of discrimination among these three primary groups (Baja California, coastal southern California, and Sonoran and Chihuahuan deserts) (Table 1). Using a cutoff in which the classification "decision" was based simply on the largest of the three calculated probabilities, rates of correct classification were 74% (Baja California), 61% (Sonoran and Chihuahuan deserts), and 60% (coastal southern California). However, only 32% of predicted probabilities used in the classification were >70%, and 20% were <50% probability. Incorrect classifications were fairly evenly distributed between alternate groups; for example, 10 songs of wrens from

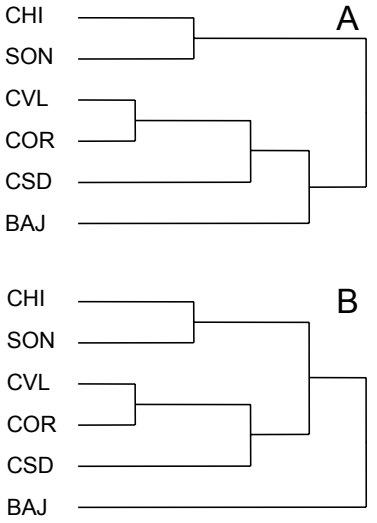

Figure 6. Dendrograms (Euclidean distance measures) based on mean values of FREQ, RATE, CV_INTEN, and CV_FREQ for six sampling regions. Dendrogram A obtained from group-average (UPGMA), centroid, Ward's minimum-variance, and complete (farthest-neighbor) linkage methods; dendrogram B shows results from single-linkage (nearest-neighbor) cluster analysis. CVL, coastal, Ventura and Los Angeles counties; COR. coastal, Orange County; CSD. coastal, San Diego County; SON. Sonoran Desert; CHI. Chihuahuan Desert; BAJ. Baja Californian desert.

coastal southern California were considered to belong to the Baja California group, and 13 were assigned to the desert category. These results merely emphasize the fact that although there are average multivariate differences among Cactus Wren songs from various geographic regions, the differences are subtle; many individuals cannot be correctly assigned to a geographic region on the basis of song characteristics measured here.

DISCUSSION

Vocal Variation

Cactus Wrens differ slightly in the fine structure of their songs over their extensive geographic range. We identified three major groupings from among our six sampling regions: (1) Sonoran and Chihuahuan deserts, (2) coastal southern California, and (3) the Baja California peninsula. However, these differences are subtle; songs given by individual birds are not easily classified correctly into one of the three groups. Although songs recorded in San Diego County (*sandiegensis*) differ statistically from recordings of coastal examples of *anthonyi* obtained in Ventura and Los Angeles counties, songs from both of these coastal regions were more like each other than those given by desert populations of *anthonyi*. Songs of birds from the

Table 1 Results of Discriminant Function Analysis of Cactus Wren Songs by Three Major Geographic Areas Identified by Cluster Analysis[a]

		Classification by Discriminant Function		
Actual Origin	*n*	Baja California	Coastal	Desert
Baja California[b]	19	14	3	2
Coastal[c]	58	10	35	13
Desert[d]	80	11	20	49

[a]Calculations based on correlation matrix of mean frequency, rate, and variations of frequency and intensity. Analysis used equal prior probabilities; classification "decisions" reflect the highest probability among the three groups.

[b]Desert regions south of 31° N.

[c]Ventura, Los Angeles, Orange and San Diego counties.

[d]Sonoran and Chihuahuan deserts.

Baja California desert were the most distinctive, being higher in frequency than those of other populations but generally similar in the other measured variables to populations in coastal southern California.

The biological basis and significance of these vocal differences is unknown; we have not conducted playback experiments to evaluate whether the birds themselves even perceive these differences. We did not assess whether these variations reflect learned dialects, genetic differences, or some combination of the two. Some other species of wrens feature pronounced song dialects that, in general, represent learned behaviors (Kroodsma 1977), and such may be the case here. Eggert's (1996) finding of localized genetic differentiation among Cactus Wrens from seven sampling areas in coastal southern California at least suggests that the small, fragmented populations in this region are adequately isolated to permit development of unique song dialects.

Conservation Implications

Should coastal Cactus Wrens be protected under the federal Endangered Species Act? The USFWS (1994) previously concluded that coastal populations have been affected by habitat losses at least as severe as those affecting the nominate subspecies of the California Gnatcatcher, which it listed as threatened in 1993 (USFWS 1993, Atwood 1993). Because in southern California the Cactus Wren has a much smaller population and is more ecologically restricted than the California Gnatcatcher (Rea and Weaver 1990), its conservation status is far more precarious. There is little doubt that the coastal populations of the Cactus Wren in southern California and extreme northwestern Baja California are severely threatened. Do these coastal birds, including but not limited to *sandiegensis*, represent a "distinct population segment" that can be considered a "listable entity" under the ESA (USFWS 1994)?

The federal government has published a policy by which it evaluates

whether a "distinct population segment" meets the ESA's definition of a "species" (U.S. Department of the Interior and U.S. Department of Commerce 1996). In particular, distinct population segments must be shown to be (1) "discrete" and (2) "significant" relative to other populations of the species.

According to the U.S. Department of the Interior and U.S. Department of Commerce (1996: 4725), populations are considered discrete when they are "markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation." The policy also allows for "some limited interchange" among discrete population segments (U.S. Department of the Interior and U.S. Department of Commerce, 1996: 4724).

Cactus Wrens in coastal southern California are clearly isolated ecologically and geographically from desert populations to the east. The profound differences between coastal sage scrub and vegetation of the Sonoran Desert have long been acknowledged by numerous authors (Shreve and Wiggins 1964, Bender 1982, Holland 1986, Barbour and Major 1988, Davis et al. 1994, Davis et al. 1995, Sawyer and Keeler-Wolf 1995, Keeler-Wolf and Barbour 1997). There are few localities where coastal sage scrub actually comes into close proximity with vegetation characteristic of the Sonoran Desert. In a distributional pattern reminiscent of that of the California and Black-tailed (*Polioptila melanura*) Gnatcatchers (Atwood 1988), San Gorgonio Pass, Riverside County, appears to be the most likely area of contact between Cactus Wrens of coastal and desert populations (Rea and Weaver 1990).

However, ongoing habitat loss caused by suburban development in southern California has largely, if not completely, isolated coastal Cactus Wrens from populations in the Sonoran Desert. As early as 1923, W. L. Dawson commented that "all proper desert areas west of San Gorgonio Pass are being threatened sharply by the human invasion. Those joyous bits of desert 'washes' . . . have become . . . cluttered up with bungalows and chicken coops . . . The Cactus Wren has receded from many parts of the San Diego–Ventura section already, and is in danger of being altogether cut off" (Dawson 1923: 667). The "bungalows and chicken coops" of southern California in the early 1920s have now been replaced by sprawling cities inhabited by over 14 million people (Southern California Association of Governments 2000; www.scag.ca.gov/census).

The USFWS's status review (USFWS 1991) concluded that "although historically connected with interior, desert populations of the Cactus Wren through the San Gorgonio Pass in Riverside County, the range of the coastal Cactus Wren now appears to be geographically disjunct as a result of the continuing urbanization of this corridor. The range limit of the coastal Cactus Wren at the west end of the San Gorgonio Pass coincides with that of the coastal sage scrub plant community. The hiatus of suitable habitat formed by the Transverse and Peninsular ranges also serves to maintain and define the disjunct distribution of coastal and interior populations of the Cactus Wren." K. L. Garrett (in litt., 1992) stated that "all of the coastal slope [Cactus Wren] populations are now functionally isolated from the desert ones," and R. L. McKernan (in litt., 1992) concurred that the "once contiguous population . . . of Cactus Wrens through the San Gorgonio Pass no longer exist[s]."

Atwood (unpubl. data) found that the average dispersal distance of juvenile coastal Cactus Wrens on the Palos Verdes Peninsula is significantly lower (1.6 ± 2.28 km, n = 71; mean ± standard deviation) than movements of dispersing California Gnatcatchers (3.2 ± 2.07 km, n = 76) in the same landscape, suggesting that coastal Cactus Wrens may be more vulnerable than gnatcatchers to the isolating effects of habitat loss and fragmentation.

Cactus Wrens in coastal southern California are also isolated ecologically and geographically from populations of the Baja California peninsula. The USFWS's (1994) assertion that the coastal sage scrub community of southern California transitions gradually into the central Baja Californian desert is not commonly held (Thorne 1976, Westman 1983, Holland 1986, Hickman 1993, Zippin and Vanderwier 1994, and Keeler-Wolf and Barbour 1997). Furthermore, the conclusion by Zink et al. (2001) that wrens in Baja California south of approximately 31° N latitude represent a genetic clade different from other populations suggests that the main comparison of relevance to the question of ecological isolation is between coastal wrens and populations in the Sonoran Desert, not between coastal wrens and Baja California populations.

Cactus Wrens have a patchy, discontinuous distribution along the narrow coastal plain of northwestern Baja California. Grinnell (1921) specifically corrected earlier authors who supposed a continuous distribution of *bryanti* from the vicinity of San Telmo (31° N) north into coastal southern California. Bancroft (1923, 1946) was unable to locate the species between Valle de las Palmas and San Telmo. Wilbur (1987) described Cactus Wrens as "very local" between Tijuana and San Telmo, specifically noting their occurrence only at Punta Banda, Ensenada (31° 43′ N) (Short and Crossin 1967); Unitt et al. (1995) ascribed wrens at this locality to *bryanti*. Although recent field work in northwestern Baja California shows that Cactus Wrens do occur, in small numbers, between San Telmo and Ensenada (R. A. Erickson in litt., 2005), there are no known records between Punta Banda and Valle de las Palmas. As in the vicinity of the San Gorgonio Pass, much of the area from Tijuana south to San Telmo has been heavily affected by grazing, farming, and urban development (F. Roberts in litt., 1994). Whatever tenuous contact zone might have existed historically between Cactus Wrens in coastal southern California and those in peninsular Baja California has likely been reduced or severed.

Are there behavioral characteristics that distinguish coastal Cactus Wrens from conspecifics in the Sonoran and Chihuahuan deserts and from the genetically distinct birds of Baja California? On the basis of the observation that both groups "almost always nest in cactus," the USFWS (1994: 45660) argued that there is no evidence of behavioral differences between desert and coastal wrens. In this study, we found that songs given by birds in coastal southern California differ significantly from those of neighboring populations in the Sonoran Desert and peninsular Baja California. Although these vocal differences have unknown biological significance, and may reflect only local, learned dialects, their existence is nonetheless consistent with the observed isolation of the coastal birds from other Cactus Wren populations.

The final aspect of evaluating whether a population warrants recognition as a distinct population segment involves considering its "importance to

the taxon to which it belongs" (U.S. Department of the Interior and U.S. Department of Commerce 1996: 4725); populations must be determined to be significant after having been found to be discrete. The U.S. Department of the Interior and U.S. Department of Commerce (1996: 4725) listed four types of evidence, any one of which is sufficient to demonstrate the biological or ecological "significance" of a discrete population. These include instances where (a) the population segment represents the sole surviving natural occurrence of a taxon that may be common as an introduced population outside its historic range, (b) loss of the population segment would result in a significant gap in the range of a taxon, (c) the population segment differs markedly from other populations of the species in its genetic characteristics, or (d) the population segment persists "in an ecological setting unusual or unique for the taxon." Of these four types of evidence, (b), (c), and (d) are of particular relevance to assessing the "significance" of coastal Cactus Wrens.

Throughout their extensive North American range, Cactus Wrens occupy arid, desert habitats—except in coastal southern California and extreme northwestern Baja California, where they occur in a dramatically different community, coastal sage scrub, that is dominated by completely different plant species, subject to completely different climatic conditions and ecosystem processes, and occupied by a completely different suite of potential predators and competitors. The rationale recently put forward by the USFWS (2003: 20231) in support of its proposed recognition of U.S. populations of the California Gnatcatcher as a distinct population segment is equally valid with regard to coastal Cactus Wrens: "the ecological setting inhabited by the species north of the border is . . . unique within its range. The species' ability to exist under these conditions suggests unique behavioral and/or physiological adaptations."

On the basis of examination of variation in the mitochondrial gene NADH dehydrogenase subunit 2 (ND2), Zink et al. (2001) concluded that there are two major lineages of Cactus Wrens, one consisting of subspecies in Baja California south of approximately 31° N latitude (*bryanti* and *affinis*), the other including all other populations (*couesi*, *anthonyi*, *brunneicapillus*, and *guttatus*). The subspecies *sandiegensis* and *seri* were not studied in this analysis.

The only Cactus Wrens from the coastal slope of southern California sampled by Zink et al. (2001) were six individuals from the Palos Verdes Peninsula, Los Angeles County. However, because mtDNA is transmitted via the mother only, and because the samples used by Zink et al. study consisted of feathers taken from three juveniles in each of two nests (Atwood unpubl. data), presumably only two females were actually represented. In these individuals the mitochondrial gene studied was similar to that in birds from the Sonoran and Chihuahuan deserts and differed from that in birds of the Baja California peninsula.

Farther south, along the coast of northwestern Baja California, Zink et al. (2001) collected four specimens at Camalu, approximately 31° N latitude. Of these, one belonged to the "eastern haplotype" (i.e., the widespread *couesi–anthonyi* group of the Sonoran and Chihuahuan deserts), one to the "southern haplotype" (i.e., the *bryanti–affinis* group of Baja California). The remaining two specimens "proved difficult to sequence but were definitively

typed as southern" (Zink et al. 2001:6).

The co-occurrence of both genetic clades at this locality is intriguing but impossible to interpret without comparable data from Cactus Wren populations in coastal southern California and northwestern Baja California. Does the presence of the *couesi–anthonyi* ("eastern," *sensu* Zink et al. 2001) haplotype at Camalu reflect a connection, along the coast of Baja California and into coastal southern California, with wren populations to the north? Or, instead, a connection to the east with wren populations in the Sonoran Desert near San Felipe? Similarly, it is also impossible to conclude, from available genetic data, whether *sandiegensis* belongs to the *bryanti–affinis* clade, to the *couesi–anthonyi* clade, or, as suggested by P. Unitt (in litt., 2007), whether *sandiegensis* might have arisen "through secondary intergradation between *anthonyi* and *bryanti*, then formed a more stabilized population when gene flow from the north and south was restricted."

Zink (2004: 562) argued that if the goal of conservation is to "protect historically unique segments of biological species" there are only two groups of Cactus Wrens that might conceivably "merit conservation attention": (1) populations in central and southern Baja California (the *bryanti–affinis* lineage) and (2) all other populations of the species (the *couesi– anthonyi* group). Under this logic and the assumption—with very limited data—that all coastal Cactus Wrens are correctly included within the *couesi–anthonyi* group, then Cactus Wrens found on the coastal slope of southern California would not be given special conservation consideration. Zink's premise, however, is inconsistent with the Endangered Species Act and its legal or policy interpretations. Genetic differentiation is merely one of several criteria by which populations can be considered "discrete and significant." Restricting conservation efforts only to those populations that have been isolated long enough to permit divergence of mtDNA could interfere with exactly the types of processes that might, in the future, yield new genetic types.

We believe that all Cactus Wrens in coastal southern California and extreme northwestern Baja California, including but not limited to *sandiegensis*, meet the federal government's definition of a "distinct population segment" that is both discrete and significant, and that protection of these birds under the U.S. Endangered Species Act is warranted. Compared with wrens in Baja California south of 31° N latitude, coastal Cactus Wrens differ morphologically, are isolated geographically, and have different songs. Compared with Sonoran and Chihuahuan desert populations, coastal Cactus Wrens are isolated geographically, have different songs, and occur in a unique and unusual ecological setting. The USFWS's (1994) conclusion that the coastal Cactus Wren, although threatened with extinction, does not constitute a "listable entity," should be revisited.

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