A PHYLOGEOGRAPHIC APPROACH TO MANAGEMENT OF COASTAL CALIFORNIA CACTUS WRENS (*CAMPYLORHYNCHUS BRUNNEICAPILLUS*)

A Thesis

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DEDICATION

This work is dedicated to Oliver Ryder and to the research staff at the Center for Reproduction of Endangered Species of the Zoological Society of San Diego. Without their help and friendship, it would not have been possible.

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ABSTRACT

Species that require management intervention are usually in rapid decline. Conservation biologists often have no time for field studies to determine important factors such as dispersal patterns or natural boundaries of populations and subspecies. Genetic studies can provide a snapshot of these factors to assist in formulating a management plan that is tailored closely to the needs of the species.

Coastal southern California populations of cactus wrens are declining due to the effects of habitat loss and fragmentation; it is estimated that fewer than 400 pairs remain. Previous work has suggested that these populations represent the subspecies *Campylorhynchus brunneicapillus sandiegensis*, which is diagnosable using 7 characters of plumage pattern and color. This study uses phylogenetic methods to re-examine the data used to describe this subspecies. In addition, using primarily non-invasively collected samples, 280 base pairs of the cytochrome b gene were sequenced for birds from 7 coastal sites, 2 desert sites, and 2 sites in Baja California Norte.

Analysis of the morphological data shows that these seven characters do not completely partition the samples geographically, as would be expected if they were sufficient to diagnose a genetically distinct taxon. Analysis of the cytochrome b sequences shows that these populations are genetically distinct, but that there is little support for linking them into a genetically distinct subspecies. They are distinguishable from populations in Baja California and in the California desert.

Genetically distinct populations that are adapted to different habitats may contain the genetic variability needed to allow a species to adapt to changing environments, or provide the raw material for future speciation. As such, their conservation value may be disproportionately large in relation to their size.

This study further shows that it is possible to use non-invasive sampling techniques for population level studies. When planning such a study, the investigator should plan to collect several samples from each specimen, determine a method of demonstrating that the specimen is from the study species, and plan to collect from 1/3 to 1/2 more specimens than is projected to be needed for the study.

INTRODUCTION

One of the most difficult problems faced by conservation biologists has been the determination of the units of conservation management (Vogler and DeSalle 1994). The Endangered Species Act of 1973 (ESA) protects species, subspecies and populations threatened with extinction, but defining these terms for management is often problematic (O'Brien and Mayr 1991). Traditional taxonomic designations, which are frequently based on phenotypic or distributional data, have been and continue to be used as the bases for management and protection under the ESA (O'Brien and Mayr 1991). Genetic studies, however, have called traditional taxonomy into question in a number of cases including the red wolf (*Canis rufus*), which some contend is a gray wolf-coyote hybrid (Wayne and Jenks 1991), and the Florida panther (*Felis concolor coryi)*, whose populations may include animals that evolved in each of the American hemispheres and have recently been combined in Florida (O'Brien et al. 1990).

The New Zealand tuatara, *Sphenodon*, illustrates how the failure to assess the genetic differentiation between populations can adversely impact management success (Daugherty et al. 1990). Prior to formal analysis of allozymes and morphological variation in individuals from 24 of the 30 islands where populations were thought to survive, the tuatara was presumed to be monotypic and protection was afforded on that basis. By the time genetic differences were documented and a second species recognized, 25% of the historical populations had been extirpated (Daugherty et al. 1990). The

second species survives on only one island, and one subspecies is possibly extinct. Even though the tuatara was afforded full protection in 1895, the presumption of monotypy contributed to the lack of management intervention on behalf of these populations.

The management strategy chosen for the now extinct dusky seaside sparrow (*Ammodramus maritimus nigrescens*) was based on morphological taxonomy. In 1980, only six males of this Florida Atlantic coast subspecies could be found and five of these were brought into captivity. These birds were placed in a captive breeding program with females of Scott's seaside sparrow (*A. m. peninsulae*), a Florida Gulf coast subspecies, in a final effort to conserve the genes of the dusky subspecies (Avise and Nelson 1989). A genetic investigation of the evolutionary relationships within the species complex found that although the two subspecies were extremely similar morphologically, there was a considerable genetic distance between them (Avise and Nelson 1989). A better management plan would have bred the dusky males with females from another Atlantic coast subspecies, with whom they showed a closer phylogenetic affinity (Avise and Nelson 1989).

Species that require management intervention are usually in rapid decline. Conservation biologists may not have time for field studies of sufficient length to determine important factors such as levels and distribution of genetic diversity, dispersal patterns or natural boundaries of populations and subspecies. What is needed is a "snapshot" of these factors to formulate a management plan tailored closely enough to the ecology of the species to have a reasonable probability of success (Hamrick et al. 1991). Increasingly, genetic studies are used to help provide this snapshot. For managers that

propose to combine animals from different geographic locations in a single preserve or to maintain genetic variability by moving animals or gametes between populations (Komdeur 1994; Fleischer et al. 1995), genetic studies help to predict which groups will be genetically compatible and which are so different that translocations may lead to outbreeding depression (Templeton et al. 1986). Genetic studies of peripheral populations may find that they are genetically distinct and therefore important to the long-term conservation of species as well as being potential sites of future speciation events (Lesica and Allendorf 1995).

There has long been disagreement over the taxonomic affiliation of cactus wren (*Campylorhynchus brunneicapillus*) populations isolated along the southern California coast (Bancroft 1923; Rea and Weaver 1990). Rea (1986) named the San Diego cactus wren, *Campylorhynchus brunneicapillus sandiegensis*, as a subspecies with a distribution from San Juan Creek in southern Orange County east to the Peninsular Ranges of San Diego County and south to the Tijuana and Valle de las Palmas regions of northwestern Baja California (Figure 1). Table 1 details the characters of plumage spotting and color used to distinguish *C. b. sandiegensis* from the parapatric subspecies *C. b. anthonyi* and the subspecies found in northern Baja California, *C. b. bryanti.* Although Rea and Weaver's study is an exhaustive review and morphological analysis of 121 specimens held by 11 museums, their designation of the subspecies was not accepted by the American Ornithologists' Union's Committee on Classification and Nomenclature. The Committee concluded that *C. b. sandiegensis* is an intermediate form between *C. b. couesi,* whose range they describe as the southwestern United

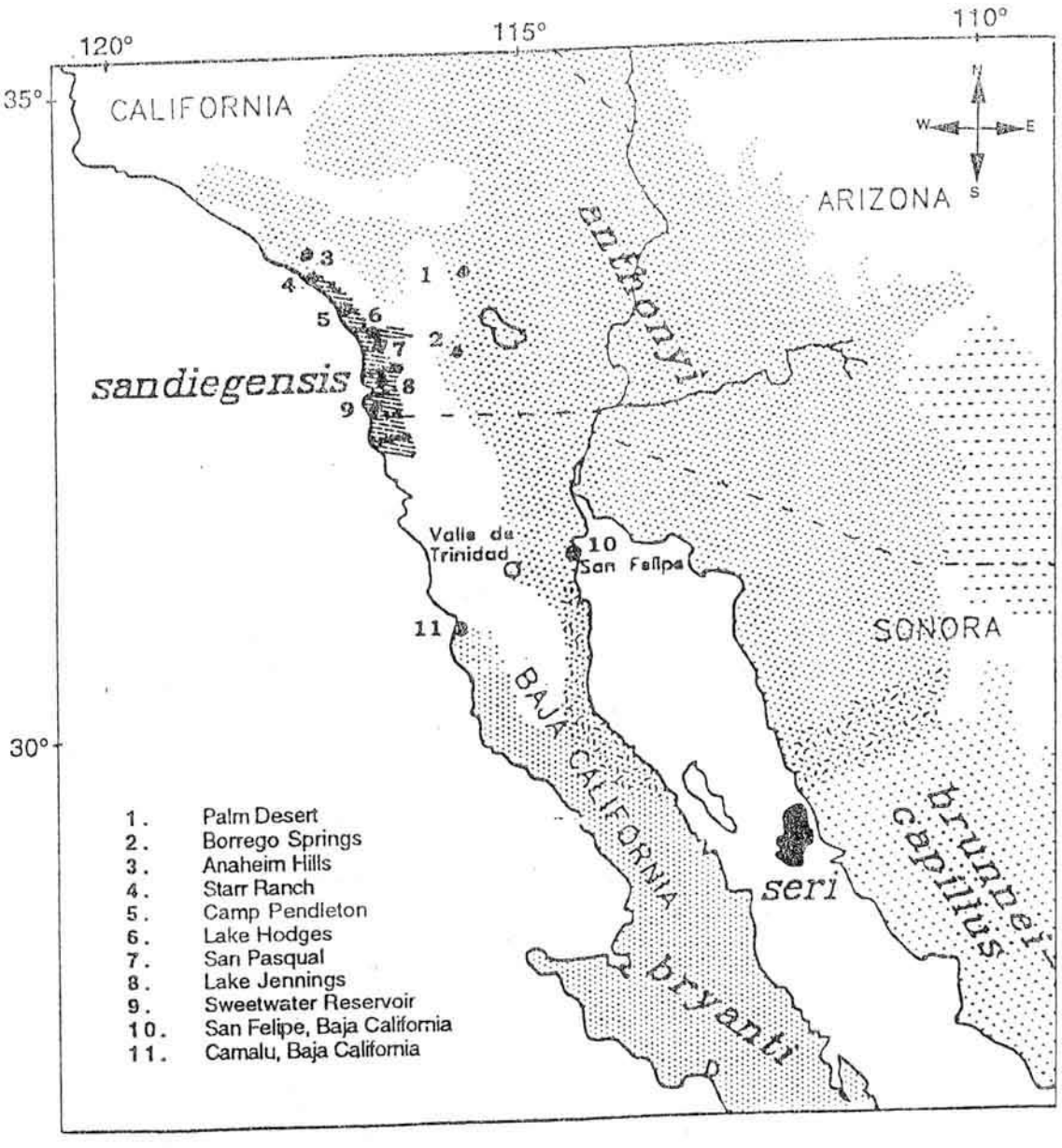


Figure 1. Rea and Weaver's proposed distribution map of C. b. sandiegensis, C. b. anthonyi, *and* C. b. bryanti *(Rea and Weaver 1990). Collection sites 1-11 are shown.*

Table 1. Morphological characters used to distinguish *C. b. anthonyi*, *C. b. bryanti*, and *C. b. sandiegensis* (from Rea and Weaver 1990). Score values are shown in parentheses.

Character Number	Description	*C. b. anthonyi*	*C. b. bryanti*	*C. b. sandiegensis*
1	Chin/gular area	Broadly white in >75% (1)	Speckled (2)	Mostly white, not heavily speckled (1)
2	Chest spot shape	Always single, large spot centered on shaft (1)	Mostly double, irregular marks, shaft is white (2)	Single, large spot centered on shaft (1)
3	Abdominal spotting	Fine, linear to rhomboid - contrasts to throat/chest (1)	Heavy, oval to diamond shaped no strong contrast to chest (2)	Spots larger than *C. b. anthonyi*, no strong contrast to chest (1.5)
4	Chest patch	Spots aggregated to form black patch (1)	No strong aggregation into patch (2)	Tendency of spots to aggregate to form chest patch not as strong (1.5)
5	Flank/ abdominal color	Conspicuous buffy wash across flanks and lower abdomen (1)	Largely white, weak ochre wash, restricted to flanks or absent (2)	Intermediate - buffy color of flanks and abdomen less conspicuous (1.5)
6	Back	Warm color of nape contrasting with grayer interscapulars and lower back (1)	Warm ground color of nape continuing thru inter-scapulars and lower back without demarcation (2)	Dorsum less brown than in *C. b. bryanti* (1.5)
7	Tail barring	Largely black (1-3)	Largely white-barred (7-9)	Barred, but less so than in *C. b. bryanti* (4-6)

States and northern mainland Mexico, and *C. b. bryanti*, whose range they describe as San Diego County, California to northern Baja California, Mexico (Department of the Interior 1994).

Based on the Committee's finding, the U. S. Fish and Wildlife Service ruled that the "coastal population of cactus wren" should be transferred from category 2 (candidate for listing as threatened under the Endangered Species Act) to category 3B. Taxa in category 3B are those that do not meet the Act's definition of distinct species (Department of the Interior 1994).

There is no question that the coastal populations of cactus wrens are declining due to the combined effects of habitat loss and fragmentation (Rea and Weaver 1990; Department of the Interior 1994). Rea and Weaver (1990) estimate that fewer than 400 pairs of San Diego cactus wrens remain, with only 10 locations having more than 5 pairs of birds (Table 2, Appendix). Regardless of their status with the Fish and Wildlife Service, this species is an excellent candidate for a study of management units in a species that has suffered population decline and range fragmentation.

C. brunneicapillus is a monogamous, non-migratory species. A mated pair normally defends one territory throughout their lives (Anderson and Anderson 1973). Nests are pouch-shaped with an entrance at one end (Figure 2). Males and females each maintain a roosting nest, and both contribute to building the breeding nest (Anderson and Anderson 1973). San Diego cactus wrens are found in coastal sage scrub communities and nest almost exclusively in tall *Opuntia* cacti (Rea and Weaver 1990). Their normal diet of insects is supplemented with the fruit of the *Opuntia* in the fall and winter (Rea and Weaver 1990). During their 38-year study of cactus wrens,

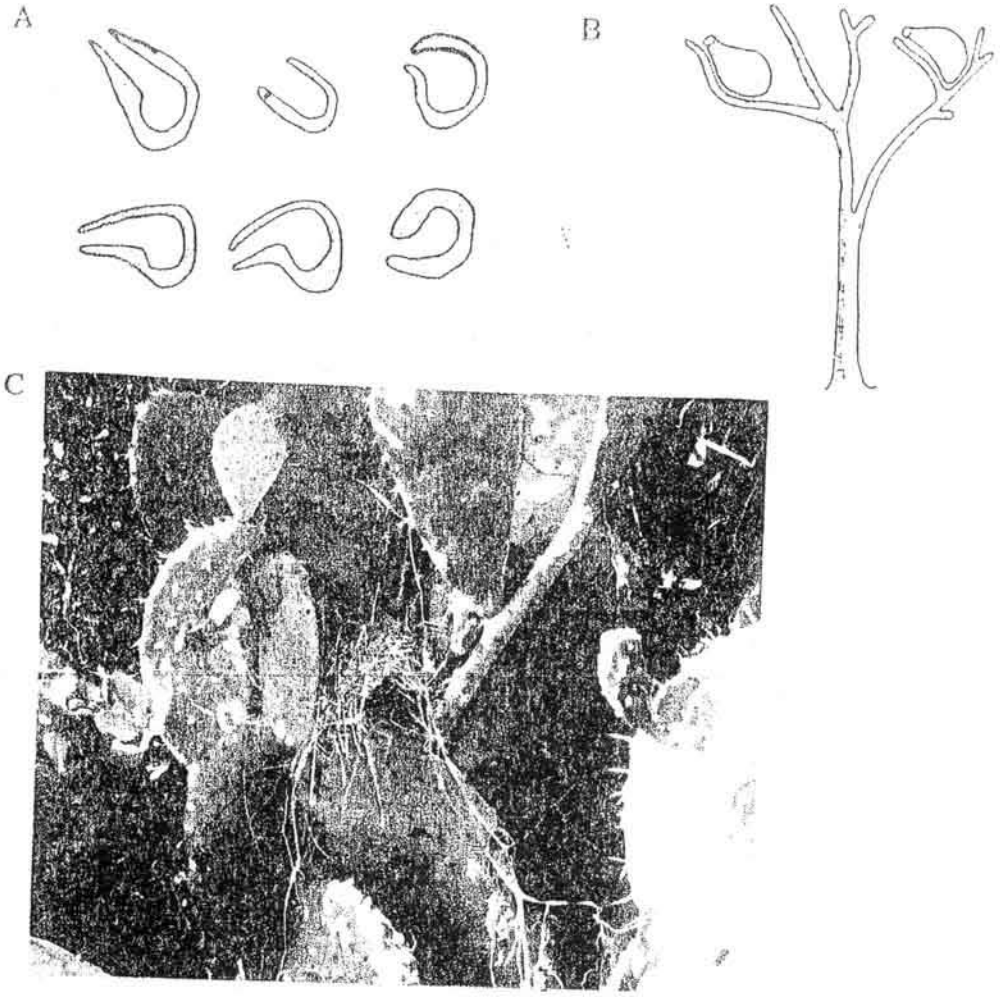


*Figure 2. Variations in the shape of cactus wren nests (**A**), and common locations of nests in cholla cacti (**B**) - the nest entrance usually faces outward (Anderson and Anderson 1973). Photograph of a roosting nest (**C**).*

Anderson and Anderson (1973) observed that young males generally settle near the territory of their parents, taking over their territory in the event of their death, or disperse only as far as needed to avoid aggression from their father. Young females, however, emigrate to the territories of unmated males, making them the longer distance dispersers.

Using genetic data to determine the population structure and taxonomic status of bird species has been complicated by the fact that studies using protein electrophoresis have shown very little genetic variability in birds (Kessler and Avise 1985; Haig and Oring 1988; Gavin et al. 1991). Recent evolutionary age for many avian species (Ball and Avise 1992), high levels of gene flow during migration and rapid colonization of many areas from Pleistocene refugia have all been proposed as reasons for the lack of genetic differences among populations in many species (Ball et al. 1988). Although it has been proposed that birds have a lower rate of molecular evolution than other vertebrates (Kessler and Avise 1985), Shields and Wilson (1987a) used a comparison of mitochondrial DNA (mtDNA) sequence divergence and fossil evidence in five species of geese to show that the mean rate of mtDNA evolution in those species was approximately 2% per million years, the same rate that has been estimated for mammals (Avise et al. 1987).

Because of the previously observed lack of genetic variability, a study of the population genetics of a bird species should use a hypervariable portion of the genome. Mitochondrial DNA, which is maternally inherited and therefore not subject to recombination (Avise et al. 1987), has been shown to evolve at least five to ten times faster than nuclear DNA in primates and rodents (Brown et al. 1982; Miyata et al. 1982). Previous studies of bird

species using mtDNA restriction fragment length polymorphisms (RFLP's) have had some success in determining population structure (Ball et al. 1988; Ball and Avise 1992; Hare and Shields 1992; Gill et al. 1993; Shields and Wilson 1987b).

This study was designed to address three questions:

1) Can the San Diego cactus wren (*C. b. sandiegensis*) be distinguished genetically from the parapatric subspecies *C. b. anthonyi (couesi)* and the allopatric subspecies *C. b. bryanti*, using mtDNA sequencing?

2) Are the genetic distinctions concordant with the observed morphological distinctions (Rea and Weaver 1990)?

3) When the clades derived from the analysis of the mtDNA sequence data are plotted on a map, can we use the patterns that emerge to identify habitat areas containing genetically unique populations and to infer dispersal corridors between populations?

A secondary goal of this study was to show that a genetic study of a species or subspecies may be done using primarily non-invasive sampling techniques. In birds, genetic studies are traditionally done using tissue from animals caught in mist nets, or from blood collected from captured and released birds. Recently, it has been shown that plucked feathers contain sufficient DNA to permit population studies using the polymerase chain reaction (Mundy et al. 1996). Although population studies have been done from shed primate hair (Garner and Ryder 1992; Morin and Woodruff 1992), and bear excrement (Kohn et al. 1995), few have attempted a population study of a bird species using primarily non-invasively collected samples.

MATERIALS AND METHODS

Morphological Data

In describing the differences among the three subspecies, Rea and Weaver (1990) examined 121 specimens held by 11 museums and scored 7 morphological characters for each specimen (Table 1). Their values for each scored character (Table 3, Appendix) were entered into the computer program Phylogenetic Analysis Using Parsimony 3.1.1 (PAUP, Swofford 1993) for phylogenetic analysis. For character 7, scores were rounded to the nearest whole number when entered (i. e. 6.5 was rounded to 7). Characters that Rea and Weaver were unable to score were entered as missing. For comparison with recognized subspecies, five specimens of *C. b. affinis* from Baja California Sur and four specimens of *C. b. couesi* (two from Texas and two from Arizona) were scored and added to the data set. Outgroups were chosen using the relationships among the Certhiidae according to Sibley and Ahlquist (1990) and the relationships among species in the genus *Campylorhynchus* according to Selander (1964). Single specimens of the rufous-naped wren (*C. rufinucha*) and the California gnatcatcher (*Polioptila californica californica*) were scored and added to the data set as outgroups. These additional specimens were held by the San Diego Natural History Museum (SDNHM). For consistency, these specimens were scored after observation of the twenty *C. b. sandiegensis* specimens at the SDNHM that were included in the Rea and Weaver (1990) study. These data were analyzed using a heuristic search in PAUP with all characters weighted

equally and randomization of the order of addition of taxa. To provide a measure of support or stability for the clades that were resolved, bootstrap analysis was performed in PAUP. This involved sampling the original data set with replacement to construct 100 replicates of the same size as the original data set (Swofford 1993). These replicates were used in a heuristic search and a majority-rule consensus was produced for the bootstrap trees. The percentage of bootstrap trees in which a group appeared (bootstrap value) was interpreted as the confidence level for that group.

Sample Collection, DNA Extraction and Sequencing

A permit for collection of feathers at California sites was issued jointly by the California Department of Fish and Game and the United States Fish and Wildlife Service, along with a Memorandum of Understanding allowing work with a "California Bird Species of Special Concern". The sample collection sites for *C. b. sandiegensis* (Figure 1, sites 4-9) were chosen using information from Rea and Weaver (1990) to cover locations reported to have greater than ten birds (Table 2, Appendix). Sites 1 and 2 represent the desert form of *C. b. anthonyi* (*couesi*). Site 3 is within the area represented in Rea and Weaver (1990) as an area of parapatry for *C. b. sandiegensis* and *C. b. anthonyi* (*couesi*). Site 10 represents a possible area of parapatry between *C. b. bryanti* and *C. b. anthonyi* (*couesi*), and site 11 represents *C. b. bryanti*.

At sites 1-4 and 6-9, shed feathers were collected from five nests using a gloved hand or a pair or tongs. Site 5, Camp Pendleton, was the location of a multi-year cactus wren study by John and Jane Griffiths, and four samples (CP1-CP4) were collected by them during banding. The fifth sample from this

site (CP5) was a shed feather collected from a nest. Samples from northern Baja California (MX1-5) were tissue samples provided by Robert Zink of the Bell Museum at the University of Minnesota.

Samples from two recognized subspecies were included for comparison. Tissue and feathers of a cactus wren from Falcon, Texas (*C. b. couesi*) and feathers of a cactus wren from Tucson, Arizona (*C. b. couesi*) were the gift of the University of Arizona. Tissue of the cactus wren from Baja California Sur (*C. b. affinis)* was provided under a loan agreement with the Museum of Natural Science at Louisiana State University. Also provided under this loan agreement were tissue samples for two of the three outgroups used: the rufous-naped wren (*C. rufinucha*), and the band-backed wren (*C. zonatus*). Feathers for the third outgroup, the California gnatcatcher (*Polioptila californica californica*), were provided by the San Diego Natural History Museum. Collection locations for the additional subspecies specimens and all outgroups are shown in Figure 3.

Total genomic DNA was extracted from tissue samples. Tissue was ground in liquid nitrogen and incubated overnight at 50°C in DNA suspension buffer (0.2 M NaCl, 0.05 M Na_2EDTA, pH 8.0), sodium dodecyl sulfate (SDS) at 0.5% total volume and proteinase K at 200 µg/ml of the total volume. The sample was extracted once with an equal volume of phenol, then extracted once with an equal volume of 24:1 chloroform/isoamyl alcohol. DNA was precipitated using 1/10 volume 3 M NaOAc and 2.5 volumes of cold absolute ethanol.

Figure 3. Collection sites of samples used for comparison of the subspecies Campylorhynchus brunneicapillus couesi *and* C. b. affinis, *and for outgroups* C. rufinucha, C. zonatus, *and* Polioptila californica californica.

Total genomic DNA was extracted from feather tips using the InstaGene Purification Matrix (BioRad). Feathers were washed in autoclaved deionized water and the tip cut off with a sterile razor blade. The tip was cut once lengthwise to expose any cells inside and both portions were placed in a 1.5 ml microfuge tube with 0.25 ml InstaGene. Samples were vortexed ten seconds, then incubated overnight at 56°C. They were vortexed again for ten seconds, incubated at 100°C for 15 minutes, then centrifuged at 10,000 rpm for three minutes. Originally the supernatant was placed in another tube and the InstaGene matrix was discarded, but this practice was discontinued. In another study I found that I was unable to amplify a 307 base pair fragment of cytochrome b of California Condor (*Gymnogyps californianus)* using only the supernatant but was able to amplify after adding the supernatant back to the matrix (Eggert et al. submitted). Samples were stored at -20°C when not in use.

The polymerase chain reaction (PCR) was used with primers L14841 and H15149 (Kocher et al. 1989) to amplify a 307 base pair region of the mitochondrial cytochrome b gene. Reactions were carried out in a 70 µl volume containing 40 µl of the InstaGene preparation or 3 µl of the organic preparation, 20 mM Tris-HCl (pH 8.75), 10 mM KCl, 10 mM $(NH_4)_2SO_4$, 2 mM $MgSO_4$, 1% Triton X-100, 1 mg/ml bovine serum albumin (BSA), 28 µM each primer, 7.5 µM each dNTP, and 3.5 units cloned *Pfu* DNA polymerase (Stratagene). When necessary, 15 µl of the PCR products obtained from feather extracts were separated in a 2% low melting agarose (SeaPlaque, FMC) gel and the faint band was excised and melted in 400 µl water. Two µl were used to reamplify the fragment to obtain ample template DNA for

sequencing. PCR products were gel purified in a 2% low melting agarose (SeaPlaque, FMC) gel, from which the bands were excised and extracted once with phenol and once with 24:1 chloroform/isoamyl alcohol. After ethanol precipitation, PCR products were sequenced directly using the Sequenase Version 2.0 sequencing kit (USB) and a modified version of the protocol of Krowczynska and Henderson (1992). All samples were sequenced at least twice using both PCR primers.

Sequence information was aligned by eye and entered into a NEXUS file format to build "gene trees" (Avise 1989). The relationship between outgroup taxa and three recognized subspecies of cactus wren (*C. b. affinis* of Baja California Sur, *C. b. bryanti* of Baja California Norte, and *C. b. couesi* of Texas and Arizona) was assessed using a branch and bound search in PAUP. All characters were weighted equally, and support for each clade was estimated using 100 bootstrap replicates in a branch and bound search.

To assess the relationships among all taxa, the file was used in MacClade 3.0 (Maddison and Maddison 1992) to construct a constraint tree. The outgroup species *Polioptila californica californica* (CAGN) was constrained at the base and all other specimens, including *C. zonatus* (CZ) and *C. rufinucha* (CR), were shown as a polytomy. This tree was then used as a constraint tree in PAUP, where a heuristic search was performed with all characters weighted equally. A majority-rule consensus tree was computed for 100 equally parsimonious trees. To assess the support for the clades that were resolved, 100 bootstrap replicates were analyzed in PAUP, and the bootstrap value was interpreted as the confidence level for a node.

RESULTS

Analysis of Morphological Data

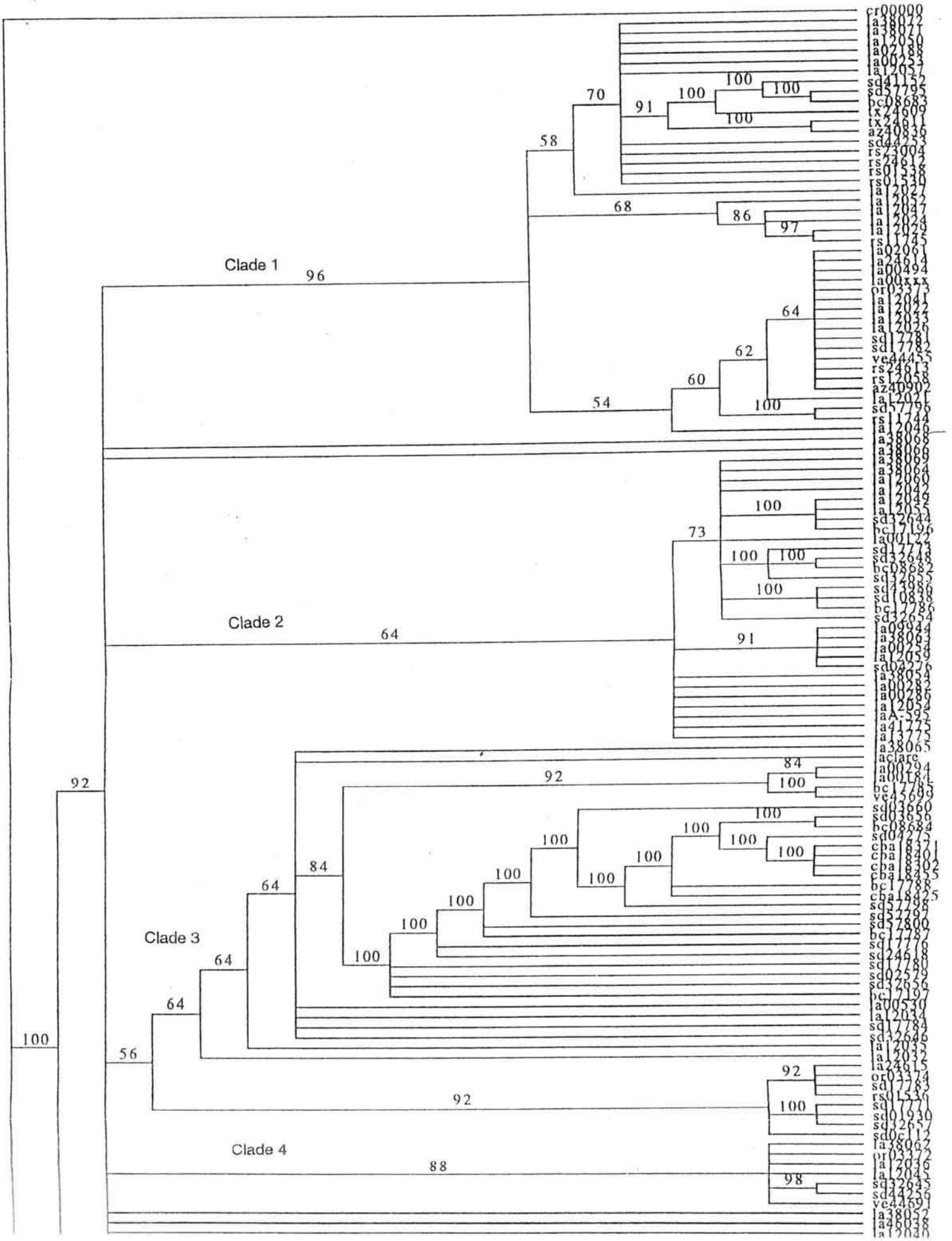
For this study, the data of Rea and Weaver (1990) were supplemented with specimens from two other recognized subspecies and two appropriate outgroups. Two specimens each from Texas and Arizona represent *Campylorhynchus brunneicapillus couesi*, five specimens from Baja California Sur represent *C. b. affinis*, and one specimen each represents the outgroups *C. rufinucha* and *Polioptila californica californica*.. A total of 130 cactus wren specimens and two outgroup specimens were included.

Phylogenetic analysis of the data set divided cactus wrens into four major clades with twelve specimens unresolved. The majority rule consensus tree (Figure 4) contained 177 steps and had a consistency index value of 0.226.

The first clade includes 42 birds with a geographic distribution as follows:

Los Angeles Co.	21	Orange Co.	1
Riverside Co.	8	San Diego Co.	6
Ventura Co.	1	Baja Ca. Norte	1
Texas	2		
Arizona	2		

This group includes all representatives of the recognized subspecies *C. b. couesi*, as well as all but one of the birds from the California desert.


Clade 1
Clade 2
Clade 3
Clade 4

sd12047
fs04295
la12039
cagn001

Figure 4. Majority-rule consensus tree of 100 equally parsimonious trees produced using the seven morphological characters designated by Rea and Weaver (1990) to distinguish Campylorhynchus brunneicapillus sandiegensis. *Clades 1-4 are shown, values are percentages of 100 bootstrap replications that supported each node.*

Thirty-four (81%) of the 42 birds in this clade came from locations north or east of San Diego and Orange counties. Eight (19%) of the 42 came from Orange County, San Diego County, or Baja California Norte.

The second clade includes 29 birds with the following geographic distribution:

Los Angeles Co.	18	San Diego Co.	8
		Baja Ca. Norte	3

This grouping includes only birds from coastal California. More than half (62%) of the birds are from Los Angeles County, while 38% of the birds are from San Diego County and Baja California Norte.

The third clade includes 40 specimens whose geographic distribution is:

Los Angeles Co.	9	Orange Co.	1
Riverside Co.	1	San Diego Co.	18
Ventura Co.	1	Baja Ca. Norte	5
		Baja Ca. Sur	5

This clade includes all specimens of the subspecies *C. b. affinis* of Baja California Sur, as well as the majority of coastal San Diego and Orange County specimens (19/36, 53%). Only one specimen is from the California desert. Also included are five of the nine (56%) specimens from Baja California Norte.

The fourth and smallest clade includes seven specimens from the following counties:

Los Angeles Co.	3	Orange Co.	1
Ventura Co.	1	San Diego Co.	2

Although all of these are coastal California specimens, there is no discernible pattern to their geographic distribution.

The geographic patterns suggested by clades 1-3 are shown in Figure 5. This figure does not include the birds grouped in clade 4 or the twelve birds that were grouped within the cactus wren clade, but were otherwise unresolved. The twelve unresolved birds include nine birds from Los Angeles County, one bird from Riverside County, and two from San Diego County.

The values of characters 1-7 for birds in clades 1-4 are shown in Figure 6.

DNA Extraction and Sequencing

Several shed feathers were collected from each nest to ensure that five samples would be included from each site. Two factors affected the ability to include a sample in this study. First, not every shed feather yielded amplifiable DNA. When a feather extraction failed to produce PCR amplification products, another feather from the nest was extracted and tested in a PCR. This was repeated until a sample produced amplification products. Since cactus wrens line their nests with feathers from old nests or from other species, the origin of feathers found in a nest is not known. To avoid mixing the DNAs of more than one bird, multiple feathers were never extracted at the same time. Successful extractions were accomplished for five nests from every location except Sweetwater Reservoir, where only four samples could be extracted.

The second factor that affected the ability to include a sample was the similarity of the sequence determined to that of samples *C. b. affinis* (CBA) and *C. rufinucha* (CR). Although every effort was made to collect and extract

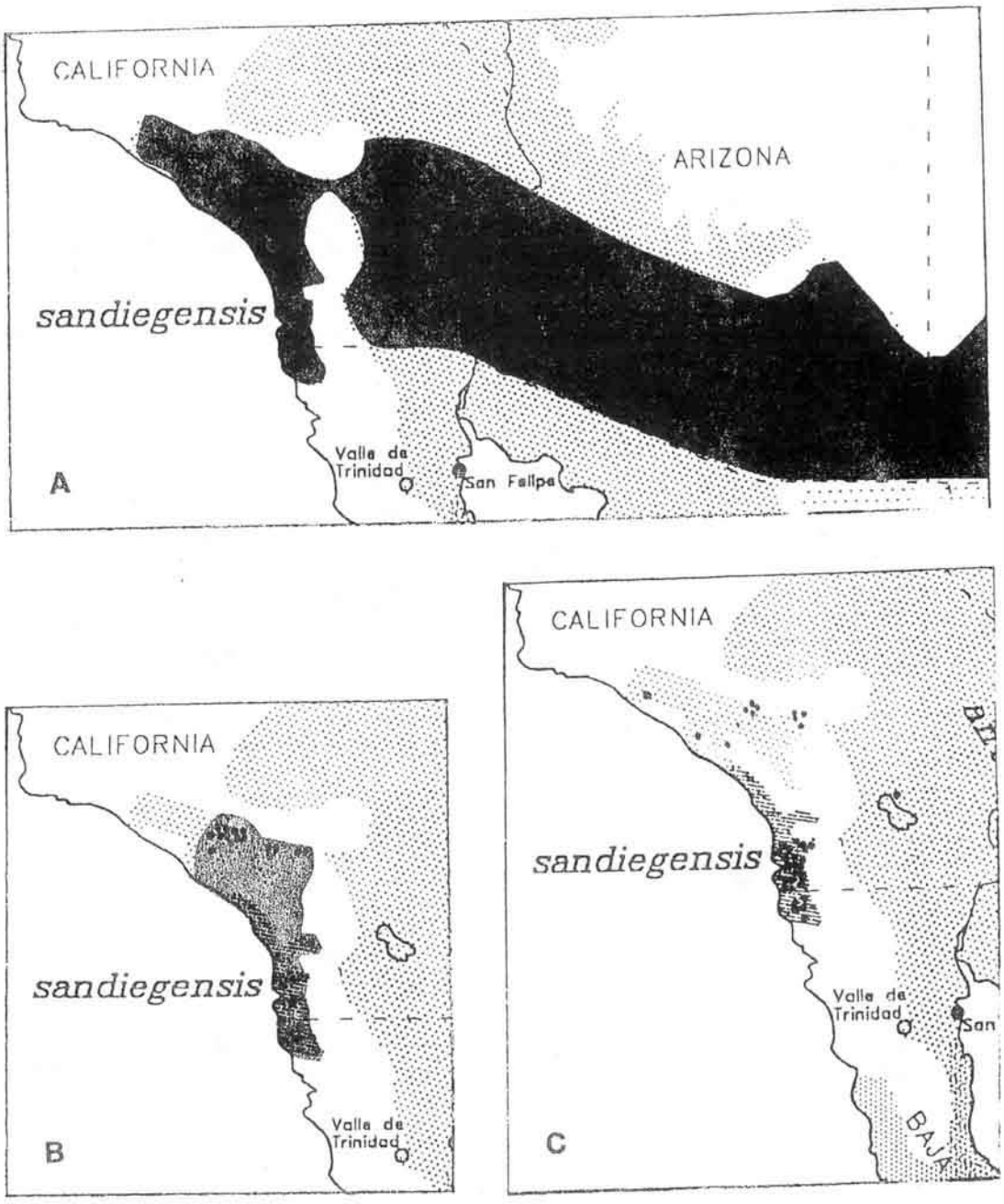


*Figure 5. Geographic distribution of clade 1 (**A**), clade 2 (**B**), and clade 3 (**C**) of the majority-rule consensus tree based on seven morphological characters designated by Rea and Weaver (1990) to distinguish* Campylorhynchus brunneicapillus sandiegensis.

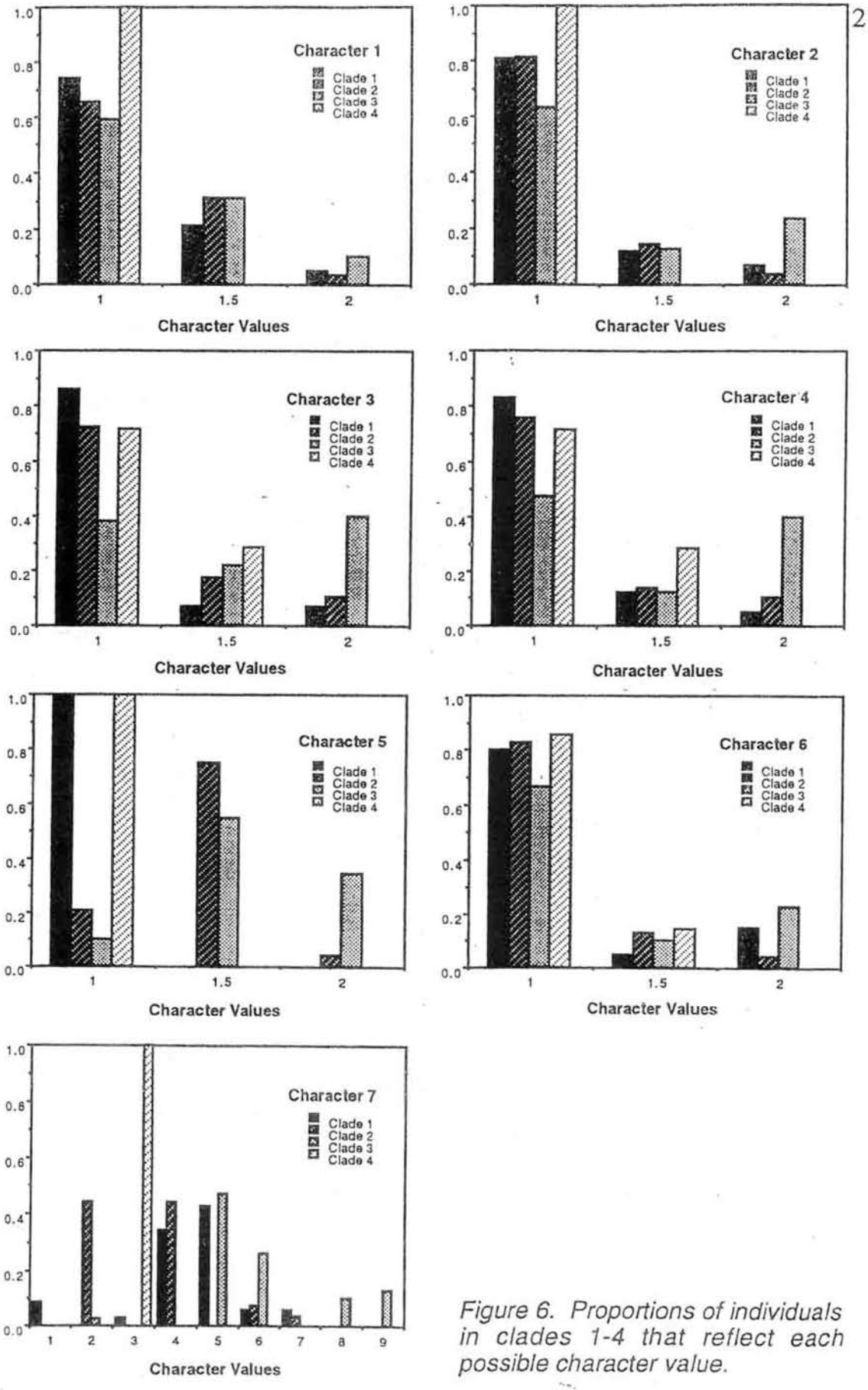


Figure 6. Proportions of individuals in clades 1-4 that reflect each possible character value.

only cactus wren feathers, the possibility of including erroneous samples exists when identification is made from a by-product without an animal being present. Sequences were compared to CBA for similarity and alignment. Any sequence that was more different from CBA than the sequence of CR (a closely related congener) was rejected and another feather was extracted and sequenced. If the supply of feathers for a sample was exhausted without obtaining a sample that met this test, the sample was dropped from the analysis. Fifteen samples were eliminated using this criterion (Anaheim Hills = 3, Borrego Springs = 2, Camp Pendleton = 1, Lake Hodges = 1, Lake Jennings = 3, Palm Desert = 1, San Pasqual = 2, Sweetwater Reservoir = 2). Samples that passed this test and were used in the analysis are shown in Table 4 (Appendix).

The fragment amplified was 307 base pairs and 280 base pairs of sequence were determined for all birds (Figure 7). There were 58 variable sites within the data set, of these 33 bases differed at the outgroup level. Within cactus wrens, there were 25 base pairs that were variable, four of these were transitions found in single samples. Twenty (84%) of the 25 base changes were transistions, and six were transversions. One base (#258, a third position base) shows a transition in 29 samples and a transversion in five samples. The pairwise distances between taxa are shown in Table 5 (Appendix) as both number of nucleotides that differ and the mean sequence difference. No single cactus wren differed from *C. b. affinis* at more than ten sites.

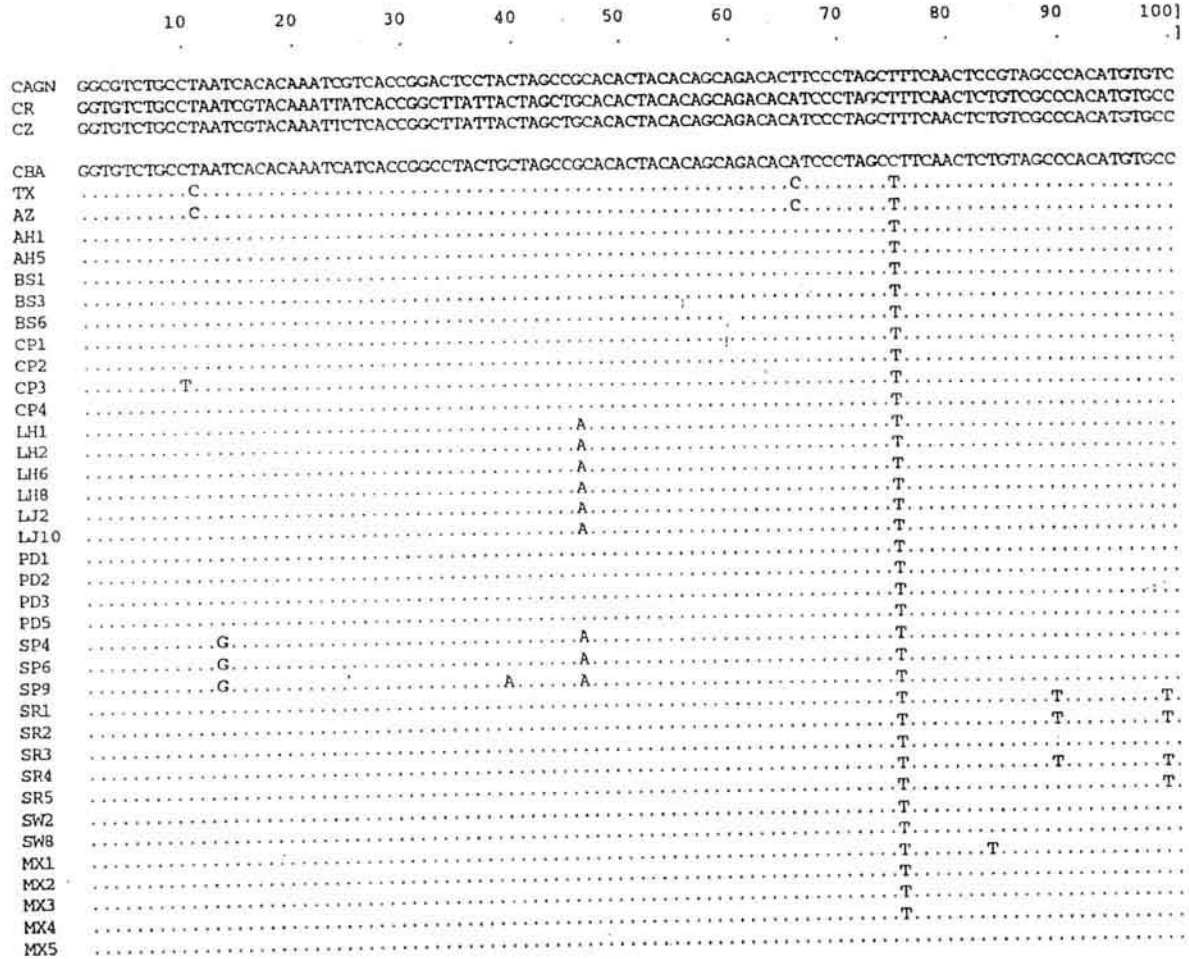
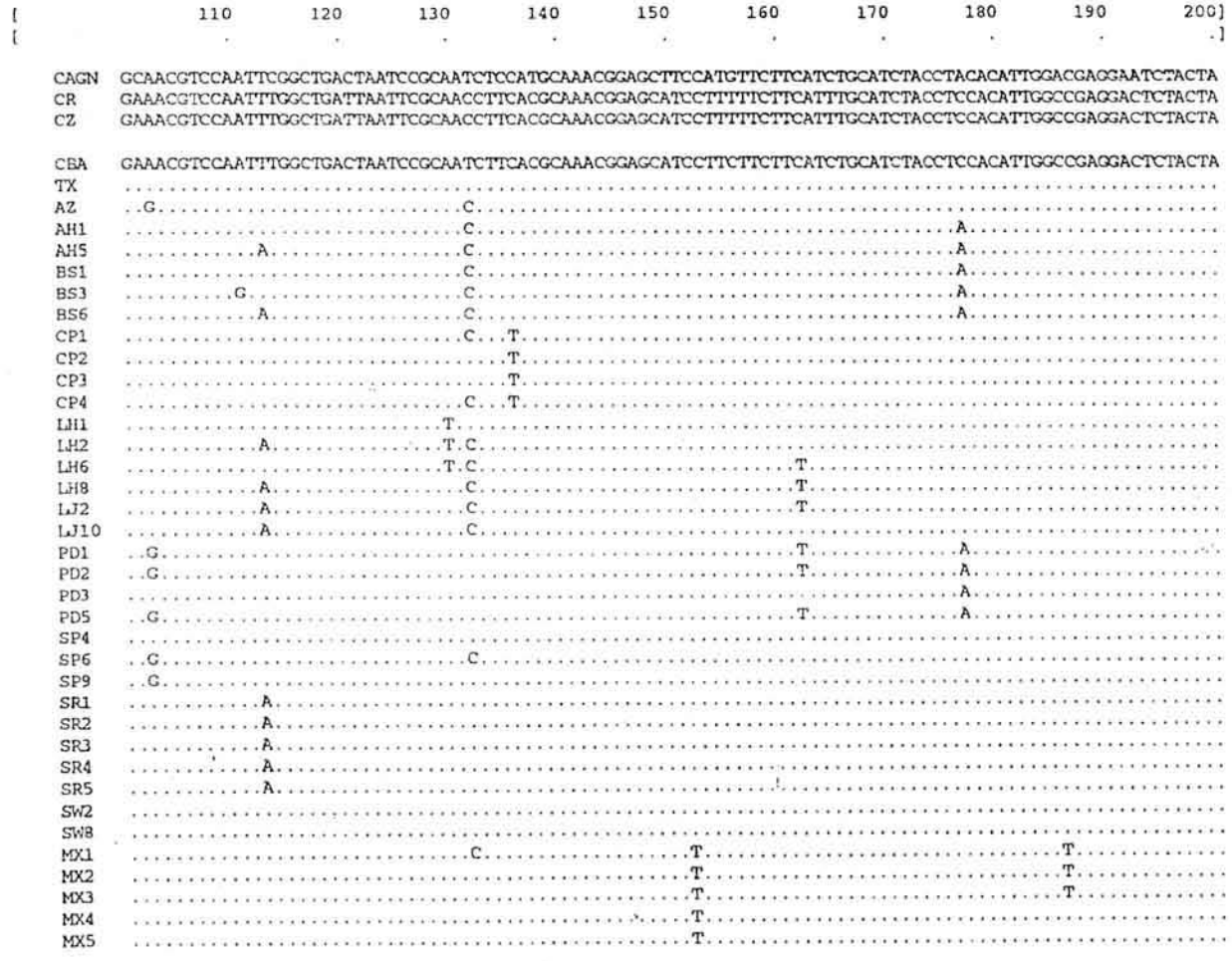
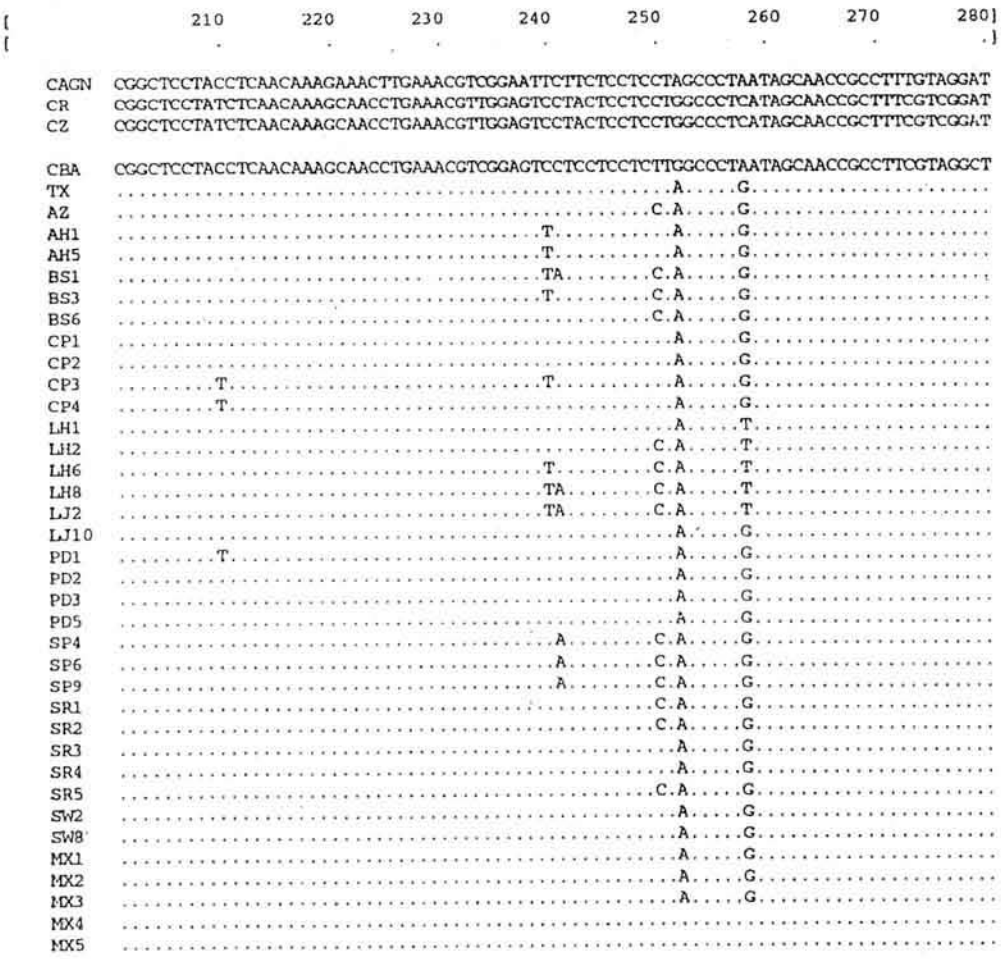


Figure 7. Variable positions in a 280 base pair segment of the mitochondrial cytochrome b gene. Dots signify identity to the sequence of Campylorhynchus brunneicapillus affinis (CBA).


110 120 130 140 150 160 170 180 190 200
CAGN GCAACGTCCAATTCGGCTGACTAATCCGCAATCTCCATGCAAACGGAGCTTCCATGTTCTTCATCTGCATCTACCTACACATTGGACGAGGAATCTACTA
CR GAAACGTCCAATTTGGCTGATTAATTCGCAACCTTCACGCAAACGGAGCATCCTTTTTCTTCATTTGCATCTACCTCCACATTGGCCGAGGACTCTACTA
CZ GAAACGTCCAATTTGGCTGATTAATTCGCAACCTTCACGCAAACGGAGCATCCTTTTTCTTCATTTGCATCTACCTCCACATTGGCCGAGGACTCTACTA
CBA GAAACGTCCAATTTGGCTGACTAATCCGCAATCTTCACGCAAACGGAGCATCCTTCTTCTTCATCTGCATCTACCTCCACATTGGCCGAGGACTCTACTA
TX
AZ
AH1
AH5
BS1
BS3
BS6
CP1
CP2
CP3
CP4
LH1
LH2
LH6
LH8
LJ2
LJ10
PD1
PD2
PD3
PD5
SP4
SP6
SP9
SR1
SR2
SR3
SR4
SR5
SW2
SW8
MX1
MX2
MX3
MX4
MX5


210 220 230 240 250 260 270 280
CAGN CGGCTCCTACCTCAACAAAGAAACTTGAAACGTCGGAATTCTTCTCCTCCTAGCCCTAATAGCAACCGCCTTTGTAGGAT
CR CGGCTCCTATCTCAACAAAGCAACCTGAAACGTTGGAGTCCTACTCCTCCTGGCCCTCATAGCAACCGCTTTCGTCGGAT
CZ CGGCTCCTATCTCAACAAAGCAACCTGAAACGTTGGAGTCCTACTCCTCCTGGCCCTCATAGCAACCGCTTTCGTCGGAT
CBA CGGCTCCTACCTCAACAAAGCAACCTGAAACGTCGGAGTCCTCCTCCTCTTGGCCCTAATAGCAACCGCCTTCGTAGGCT
TX
AZ
AH1
AH5
BS1
BS3
BS6
CP1
CP2
CP3
CP4
LH1
LH2
LH6
LH8
LJ2
LJ10
PD1
PD2
PD3
PD5
SP4
SP6
SP9
SR1
SR2
SR3
SR4
SR5
SW2
SW8
MX1
MX2
MX3
MX4
MX5

Analysis of Cytochrome b Data

For the molecular analyses, three outgroups were used: the California gnatcatcher (*Polioptila californica californica*) is a member of a closely related family (Sibley and Ahlquist 1990), the band-backed wren (*C. zonatus*) is a congeneric species, and the rufous-naped wren (*C. rufinucha*) is a closely related congener (Selander 1964). The cytochrome b relationships among the outgroup species and three recognized subspecies of cactus wren (*C. b. couesi* as represented by TX and AZ, *C. b. bryanti* as represented by samples MX1-3, and *C. b. affinis* as represented by CBA) are shown in Figure 8. The single tree produced by a branch and bound search had 59 steps and a consistency index of 0.932.

Parsimony analysis of the complete cytochrome b data set was performed using PAUP (Swofford 1993). The majority-rule consensus tree (Figure 9) contains 105 steps and has a consistency index of 0.657. The groupings suggested by this tree are plotted geographically in Figure 10. The Texas and Arizona specimens group together separately from other cactus wrens, although the bootstrap support for this grouping is not strong. The specimens from Baja California Norte and Baja California Sur group together separately from the California birds. These birds divide further into two groups, one from Baja California Sur and the Pacific side of Baja California Norte (CBA, MX4, MX5), and one from the Sea of Cortez side of Baja California Norte (MX1-MX3). This clade was well-supported by the bootstrap at all levels. The birds from Anaheim Hills grouped with the birds from Borrego Springs in a clade that showed weak support in the bootstrap analysis. Three of the four Camp Pendleton specimens grouped together in a

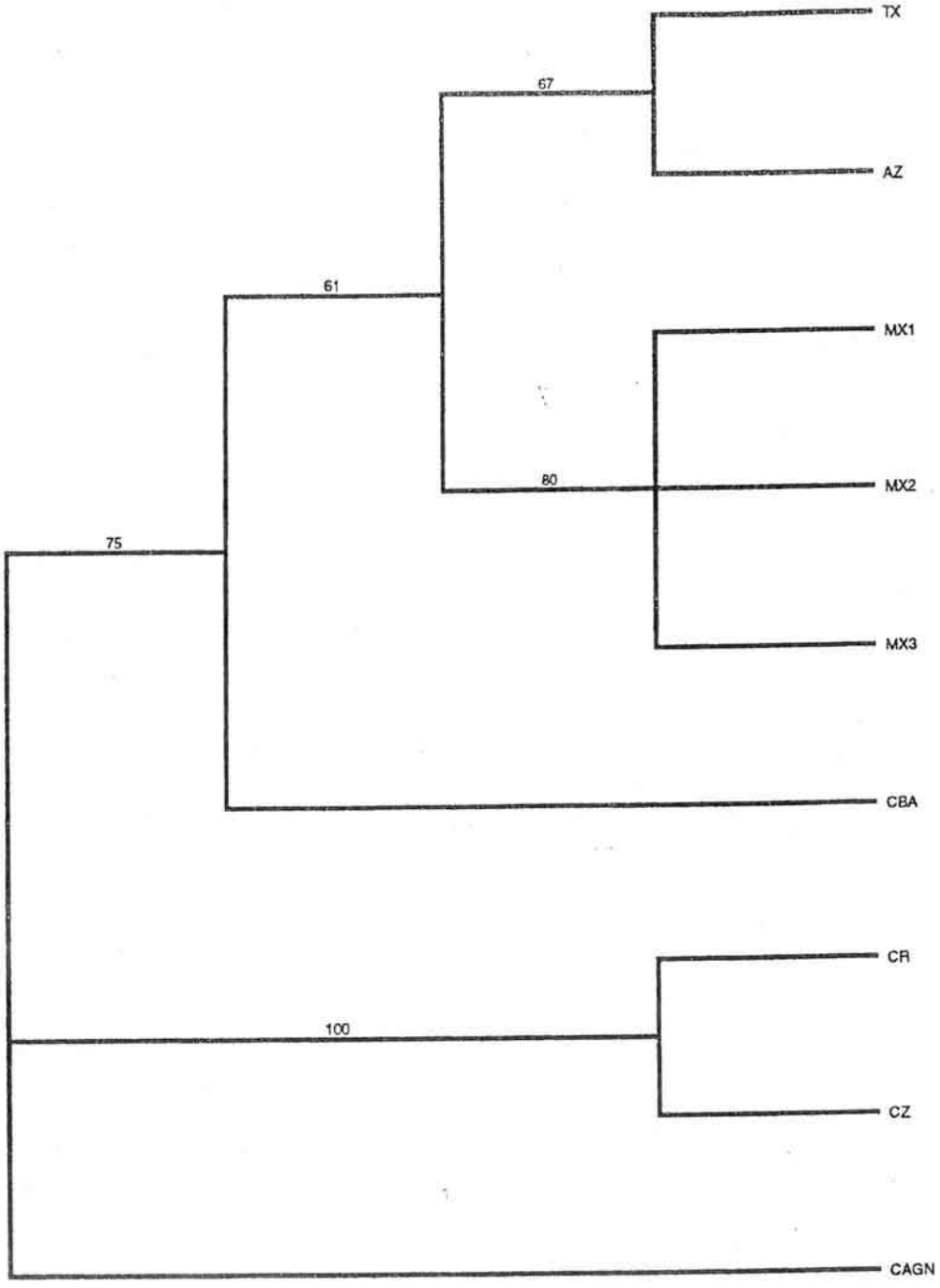


Figure 8. Genetic relationships between the outgroups used in this study and three recognized subspecies of cactus wren, Campylorhynchus brunneicapillus couesi *(TX and AZ),* C. b. bryanti *(MX1-3), and* C. b. affinis *(CBA), as inferred by sequencing of a 280 base pair segment of cytochrome b. Outgroups shown are* C. rufinucha *(CR),* C. zonatus *(CZ) and* Polioptila californica californica *(CAGN). The tree length is 59 steps (CI = 0.932); percentages of 100 bootstrap replications that support each node are shown.*

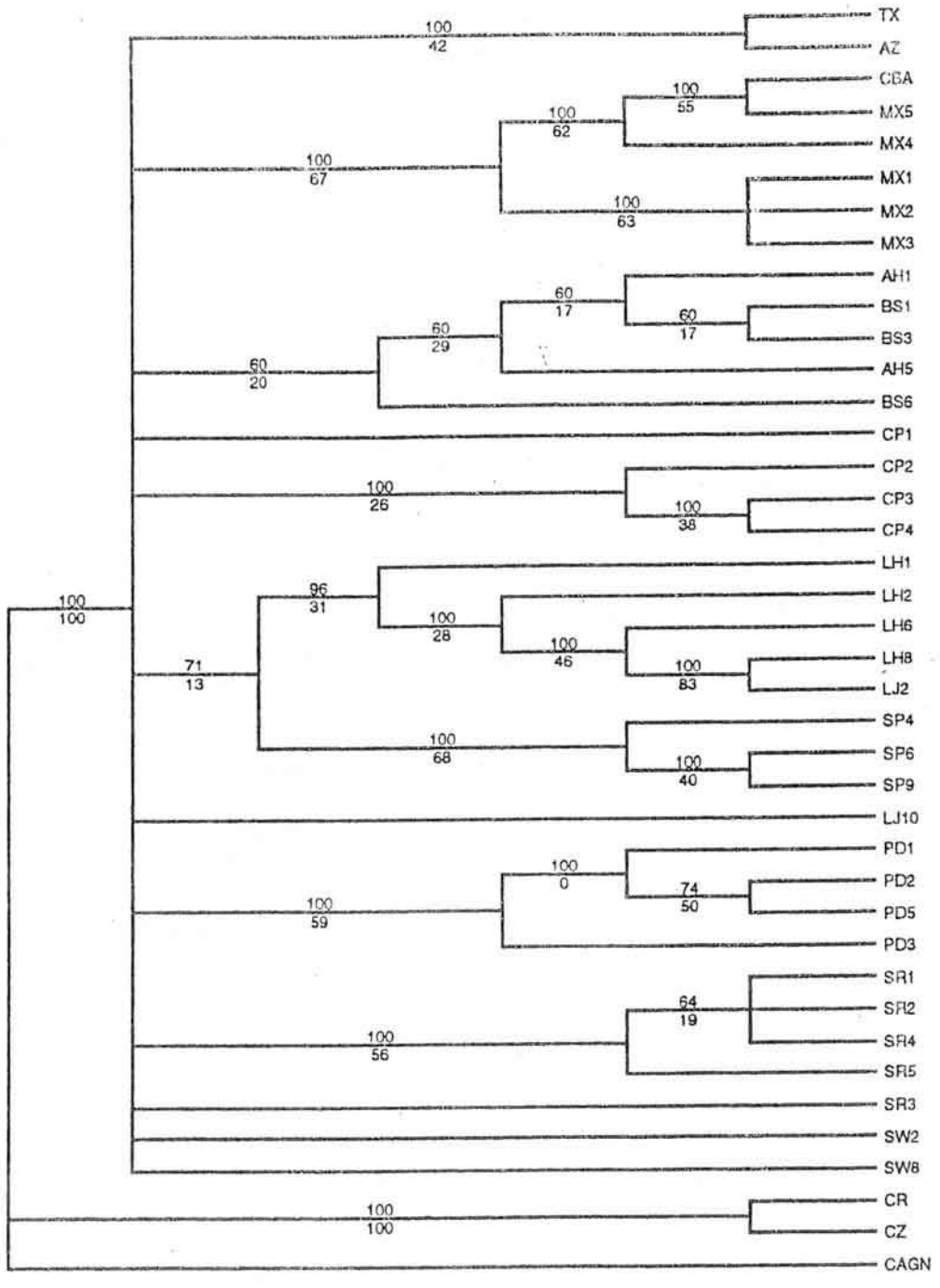


Figure 9. Majority-rule consensus tree of 100 equally parsimonious trees produced using the heuristic search option of PAUP (Swofford 1993) on 280 base pairs of cytochrome b sequence (Tree length = 105 steps, consistency index = 0.657). Values shown above the nodes are majority rule consensus values (percent of 100 equally parsimonious trees) that support the node. The value below the node is the bootstrap value for 100 bootstrap replications.

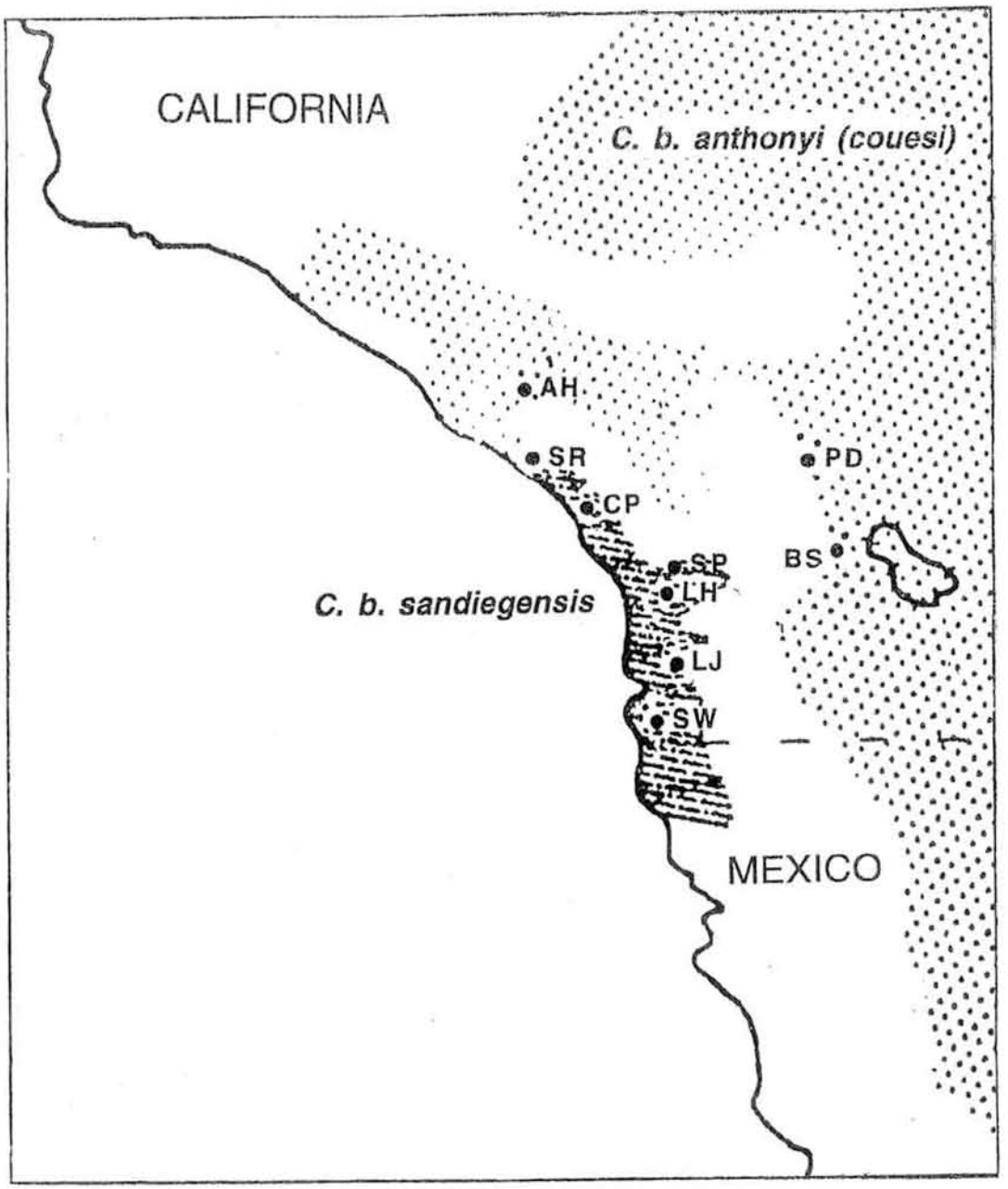


Figure 10. The geographic distribution of groupings of coastal California cactus wrens inferred by the majority-rule consensus tree based on 280 base pairs of cytochrome b sequence. For location key, see Figure 1.

clade with weak bootstrap support. A larger grouping includes all three San Pasqual specimens, all four Lake Hodges specimens, and one of the two Lake Jennings specimens. The bootstrap analysis shows little support for the deep branches of this clade, but moderate to strong support for the population level grouping. The four specimens from Palm Desert group together, as do four of the five specimens from Starr Ranch. Each of these clades received good support from the bootstrap analysis. Five specimens (CP1, LJ10, SR3, SW2, and SW8) are unresolved.

DISCUSSION

When the four clades that emerge from the analysis of the morphological data set are plotted geographically (Figure 5), the patterns are not indicative of complete geographic subdivision. Clade one includes all of the Texas and Arizona specimens (n=4), all but one of the birds from the California desert (n=8), and 22 of the 63 birds from Los Angeles and Ventura counties (54 of these were resolved, and 9 were unresolved). Only eight birds are included from the area of Orange county and south. If the proposed subspecies distribution map (Figure 1) is correct, the eastern, Los Angeles and Ventura county, and California desert birds should belong to the subspecies *C. b. anthonyi*. The scoring system of Rea and Weaver (1990, see Table 1) would predict that birds of this subspecies would be scored at 1,1,1,1,1,1,1-3 for characters 1-7, respectively. For characters 1-6, these predicted values agreed well with the observed values for birds in Clade 1 (Figure 6). For character 7, the predicted values were 1-3, while the observed values for Clade 1 birds were 4-5, which was within the range of values that would be predicted for *C. b. sandiegensis*.

Clade 2 has a geographic distribution limited to the California coast, ranging from Los Angeles county in the north to just below the United States/ Mexico border in the south. This distribution does not coincide with any one of the proposed subspecies' distributions. The observed values for characters 1-4 and 6 were predominantly those predicted for *C. b. anthonyi,* but the

predominant value for character 5 was the value predicted for *C. b. sandiegensis*. Character 7 in this clade has a value of 2 (n=12) or 4 (n=12). A value of 2 would be predicted for *C. b. anthonyi*, while a value of 4 would be predicted for *C. b. sandiegensis*.

The third clade contains primarily birds from Orange county , San Diego county and Baja California, but also includes birds from Los Angeles, Riverside and Ventura counties. Using the subspecies distribution map (Figure 1), the birds collected from southern Orange county south to just below the US/Mexico border would be expected to be of the subspecies *C. b. sandiegensis*, while those from Baja California would be expected to be of the subspecies *C. b. bryanti*. The expected values for characters 1-7 for *C. b. sandiegensis* would be 1,1,1.5, 1.5, 1.5, 1.5, 4-6, and the expected values for *C. b. bryanti* would be 2, 2, 2, 2, 2, 2, 7-9. The values that predominate in this clade were 1,1,1-2, 1 & 2, 1.5, 1, 5-6 & 8-9. These values were not a perfect match for either subspecies, but approximated the values expected for both.

Clade 4, however, with observed values of 1,1,1,1,1,1,3, were in agreement with the character values expected for *C. b. anthonyi*. These 7 birds were collected from the California coast, from Ventura county in the north to San Diego county in the south. There is no obvious pattern to their geographic distribution.

Phylogenetic analysis of the seven morphological characters presents a picture of incomplete geographic subdivision. There was a tendency for birds collected in Los Angeles county and from the north and east to group into Clade 1, while birds from southern Orange county and south largely grouped into Clade 3. One possible explanation for this incomplete

subdivision might be that 122 of the 130 specimens were collected by 1941, which was before southern California had been heavily developed and habitats had been severely fragmented. Contiguous habitat may have been more conducive to cactus wren dispersal over the approximately 150 miles of southern California coast. Today, the San Fernando and San Fernando Valley populations exist only as a remnant population at Tujunga Wash; if the Claremont population exists it has been severely reduced; and the largest Los Angeles County population may consist of 50-100 pairs in the Chino Hills area and to the east (Kimball Garrett, Los Angeles County Natural History Museum, pers. comm). The large populations represented in the Rea and Weaver study no longer exist. If the specimens used by Rea and Weaver (1990) represent earlier steps along the path of divergence, a modern-day set of specimens may show more complete morphological differentiation.

It is also possible that seven morphological characters may not be enough to do an adequate phylogenetic analysis of these subspecies. In his monograph of wrens of the genus *Campylorhynchus*, Selander (1964) considered nine characters of size and six characters of plumage pattern and color. Many of these characters were highly variable, allowing him to resolve relationships within the genus. Atwood (1988) considered 19 linear measurements of body elements (e. g. bill length, bill depth, tarsus length), 12 characters of color measured using a spectrophotometer, and quantified differences in calls and responses to call playbacks. Additional morphological characters such as those used by Selander and Atwood may be required to more clearly distinguish the variation among the subspecies of *C. brunneicapillus*.

Selander (1964) suggested that the ancestral cactus wren is most closely represented by *C. b. affinis* of Baja California Sur. Analysis of cytochrome b sequence (Figure 8) supports his hypothesis. With respect to the outgroup species *C. rufinucha* (CR), *C. zonatus* (CZ) and *Polioptila californica californica* (CAGN), *C. brunneicapillus* forms a monophyletic group with *C. b. affinis* (CBA) in a position basal to *C. b. bryanti* and *C. b. couesi.*

Within the genus *Campylorhynchus*, sequence divergence varies from 0.004 (between CR and CZ) to 0.082 (between CZ and CBA). The very small genetic divergence between CR and CZ was unexpected, but the distance between CZ or CR and CBA is in agreement with the cytochrome b sequence divergence previously observed within bird genera (Cicero and Johnson 1995) which ranges from 0.033 (*Anthropoides*) to 0.114 (*Phylloscopus*). There is 0.143 cytochrome b sequence divergence between CAGN and CR, while the divergence between CAGN and CBA is 0.100. While this may indicate that the cytochrome b sequence of *C. brunneicapillus* is closer to the ancestral genotype than either CR or CZ, it might also be attributable to saturation at first and third positions in amino acid codons. The 40 nucleotide differences between CAGN and CR are made up of 25 transitions and 15 transversions (63% transitions), while the 28 differences between CAGN and CBA are made up of 15 transitions and 13 transversions (54% transversions), indicating that saturation is a possibility. While this caused no problems with the heuristic searches, it caused problems with the bootstrap analysis of the entire data set as the position of CAGN became unstable. Constraint of CAGN to a basal position was necessary when analyzing the entire data set.

While the mtDNA variation within coastal cactus wrens is large for a bird species at approximately 0.021 (an average of 6.4 ± 2.1 differences in 280 bases), much of this variation is not phylogenetically informative. What emerges is a set of genetically distinct populations with little, if any, gene flow. The populations found in Baja California are large and the close genetic relationships of these populations either through gene flow or sufficient population size to maintain ancestral genetic lines is well supported. There is some indication that the populations of Anaheim Hills and Borrego Springs, which are widely separated geographically, are more closely related to each other than to other populations of cactus wrens, lending support to the hypothesis that they may belong to a different subspecies than the coastal birds, *C. b. anthonyi (couesi)*. The population at Palm Desert shares relatively few substitutions with any other population. These birds would be predicted to belong to the subspecies *C. b. anthonyi*, along with the birds of Anaheim Hills and Borrego Springs. The population at Palm Desert, however, may suffer as much from isolation as many of the coastal populations. Palm Desert is a rapidly growing area, and the population sampled was bounded by mountains to the west, suburbs to the north, and agriculture to the south and east.

The only close genetic relationship among the coastal populations suggested in this analysis was between Lake Hodges, San Pasqual, and Lake Jennings. The genetic relationship between Lake Hodges and San Pasqual makes sense given that they are the two closest collection sites in this study and are connected by a valley used for agriculture. The inclusion of one of the Lake Jennings birds in this clade is harder to explain. While it is

possible that there has been recent dispersal between the two sites, there is no obvious dispersal route connecting them. It may be that this represents the retention of a mitochondrial lineage that existed prior to the recent isolation of these populations.

Three of the birds from Camp Pendleton and four of the birds from Starr Ranch form their own clades and do not appear to be closely related to any other population. Each of these populations contains one bird whose affiliation was unresolved in the analysis. Neither of the birds from Sweetwater Reservoir were resolved, nor was one of the Lake Jennings birds.

The pattern that emerges from the cytochrome b data is one of population-level genetic differentiation, likely due to genetic drift in small geographically isolated populations. These populations have been isolated over a short period of evolutionary time (less than 100 years), but if we assume a generation time of one to two years, a significant number of generations have elapsed since former widespread populations were fragmented. If populations were fragmented gradually, we might expect to see a number of isolated populations (refugia) that contain much of the former genetic diversity and are very similar genetically (Dinerstein and McCracken 1990). If these populations were isolated more rapidly, it might be expected that there would be insufficient time for animals in the peripheral populations to move into the refugia and what we would observe would be regionally unique populations with a reduced amount of genetic variability (Dinerstein and McCracken 1990).

Although it is unclear how complete fragmentation of the habitat must be to isolate a species with the dispersal capabilities of a bird, cactus wrens

have been observed to be a sedentary species (Anderson and Anderson 1973). Fragmentation of habitat in southern California has been rapid and the sizes of the coastal populations are now very small. All of these may have been factors that contributed to the isolation of today's genetically distinct, geographically isolated coastal populations.

When interpreting the results of this study, it is important to note that cytochrome b is not considered to be a hypervariable locus, although it is a mitochondrial gene, and would be expected to mutate five to ten times faster than a nuclear gene. While this study revealed population level differences, a hypervariable region of the mitochondrial genome might be able to provide more phylogenetically informative information to better define the population level genetic relationships. Now that primers have been developed for the mitochondrial control region in cactus wrens (Zink pers. comm.), this study should be repeated using the more variable region.

The results of the reanalysis of the morphological data and the genetic study do not support the designation of the subspecies *C. b. sandiegensis* as proposed by Rea and Weaver (1990). They also do not support the decision of the U. S. Fish and Wildlife Service not to list these populations for protection under the Endangered Species Act. Under section 3(15) of the Act "the term 'species' includes any distinct population segment of any species of vertebrate fish and wildlife which interbreeds when mature" (Department of the Interior 1994). The populations are geographically isolated, and this study shows that the populations at Camp Pendleton and Starr Ranch contain unique genotypes, while the genotypes found in populations at Lake Hodges, Lake Jennings, and San Pasqual show that these birds are more closely

related to each other than to cactus wrens in other populations. By both geographic and genetic criteria, these are distinct populations.

A management plan for these populations should recognize the fact that the birds are genetically distinct from the populations in Mexico, as well as those in the California desert. The analysis indicates that the populations at Lake Hodges, San Pasqual and Lake Jennings are more closely related to each other than to other populations, and might be included in a multi-population management plan. The support for grouping these populations, however, is much weaker than the support for within population groupings, and care should be taken to maintain the genetic variation present at each location. Translocations between these sites might be considered if suitable habitat that has no resident cactus wren population cannot be found. Combining birds from genetically distinct populations such as those at Camp Pendleton and Starr Ranch could result in outbreeding depression and should not be considered.

If a management plan for a coastal population of cactus wrens includes a translocation, ecological as well as genetic factors should be considered. The proposed translocation site must contain sufficient tall *Opuntia* cacti (four feet or taller, Rea and Weaver 1990) to allow the birds to select sites for roosting and breeding nests. In one instance, tall (10') and wide (15') cacti were moved from one location to another and are still alive after two years, although changes in their structure resulted from the move. For reasons that are as yet unknown, cactus wrens have not yet nested in these cacti (V. Marquez, pers. comm.). Additional research into the moving of cactus will be required before it can be considered a valid mitigation or management option

for cactus wrens. Further, cactus wrens are primarily insectivorous, and translocations to areas that are subject to agricultural pesticides would likely be unsuccessful.

The results of this study support the conclusion of Anderson and Anderson (1973) that cactus wrens are sedentary. However, no banding studies have been done on a regional scale to determine actual dispersal patterns and distances, other than the current two-year U. S. Marine Corps funded study of John and Jane Griffiths at Camp Pendleton. To understand the dispersal patterns of coastal cactus wrens, a regional study of three to five years should be done. Careful observation of dispersal times and patterns will be important in planning for reserve size and possible corridors.

Each of the coastal populations included in this study survives on protected land. The Anaheim Hills population survives in a City of Anaheim nature reserve known as the Oak Canyon Nature Center. This reserve is surrounded by homes and a golf course and contains habitat for other native species. Starr Ranch is a large, well-managed National Audubon Society reserve with habitat ranging from coastal sage scrub to oak woodland and streams. This reserve harbors not only avian species, but an array of native mammals. Aside from its military population, Camp Pendleton is the home of many native species and is the site of a multi-year cactus wren study. The San Diego Wild Animal Park has a large and relatively undisturbed area of coastal sage scrub around its off-exhibit breeding and veterinary facilities. Within this area, I observed at least 10 breeding pairs of cactus wrens. Lake Hodges currently has protected areas where wrens nest near hiking and bicycle trails. Lake Jennings is a County of San Diego park with fishing and

camping accommodations. Sweetwater Reservoir is protected by the water district.

These protected areas probably contain the last viable populations of coastal cactus wrens. Their importance to the survival of these birds cannot be underestimated; the loss of any of these areas of habitat would clearly diminish the existing genetic variation of *C. brunneicapillus*. Isolated, genetically distinct populations often house the genetic diversity that is crucial in allowing a species to adapt to changing environments (Lesica and Allendorf 1995). Coastal cactus wrens are adapted to coastal sage scrub, habitat that is very different than that found in the deserts of California, Arizona and parts of Baja California. Populations that are highly isolated (as evidenced by genetic differentiation) and are adapted to very different environments are often disproportionately important to the future of a species and should be given high conservation priority (Lesica and Allendorf 1995). Coastal cactus wrens are tolerant of a low level of human intrusion into their habitat, as evidenced by their willingness to nest near camping grounds at Lake Jennings and bicycle trails at Lake Hodges, but will be unable to survive if the cactus is destroyed during conversion of these areas to residential or agricultural uses.

The secondary goal of this study was to investigate the possibility of using non-invasive sampling techniques for population level studies. In this study, all but 9 of the California and Baja California specimens were collected non-invasively, using shed feathers found in nests. This form of sample collection reduces stress for study organism, but presents special problems for the investigator.

When collecting non-invasively, one cannot assume that a single feather or hair from a specimen will provide amplifiable DNA. Often several feathers or hairs must be extracted before one of them yields DNA that can be amplified and sequenced. When collecting samples, it is important to collect several feathers or hairs from each sample. It is tempting to extract several feathers or hairs together to increase the yield of DNA. Unless these are collected directly from the animal, however, there is no way to be sure that multiple feathers or hairs are from the same animal. Cactus wrens line their nests with feathers: their own, those found in old cactus wren nests, and those of other species. To avoid mixing the DNA from multiple animals and possibly multiple species, each sample must be extracted individually.

The number of samples that were excluded due to the sequence similarity test was greater than expected. This indicates that several things should be considered when planning studies using non-invasively collected specimens. First, an a-priori method of determining that the specimen is from the target species must be established. This will be especially important for studies that do not include sequencing for comparison to a closely related specimen, such as those using microsatellites or randomly amplified polymorphic DNA (RAPD). The inclusion of a non-homologous sequence (microsatellite allele pattern, RAPD profile) could have a serious impact on the results of a study.

In this study, the similarity test suggested that one-third of the samples collected were misidentified. Although the most likely explanation for this problem was the misidentification of feathers, an alternative explanation may be the existence of nuclear analogs of mitochondrial genes (Hu and Thilly

1995; vanderKuyl et al. 1995; Lopez et al. 1994; Zullo et al. 1991). In the PCR, the copy number of mtDNA is much greater than that of nuclear DNA, and amplification products should be dominated by those copied from mtDNA template. However, some samples in this study required a second PCR amplification to produce sufficient DNA for sequencing. If a nuclear copy of the cytochrome b gene exists in this species, the first amplification would have increased its copy number and, by chance, these copies could be reamplified such that they dominated the amplification products of the second PCR. The nuclear copy would be expected to be quite different from the mitochondrial copy. If the "pseudogene" no longer codes for a functional protein, it would be free to mutate in such a way that termination codons or frameshift mutations could be found in the sequence (Lopez et al. 1994). Only one of the eliminated sequences contained a termination codon, and no frameshift mutations were detected in the 280 base pairs of sequence.

To avoid having to reduce sample size due to this problem, my results indicate that 1/3 to 1/2 more samples should be collected than is projected to be needed for the study. When collecting non-invasively, animals are not marked and often the researcher cannot identify which animal has been included in the study. Collecting samples non-invasively for more than one season increases the possibility that the same animal is being included at more than one location (i.e. has moved to a new nest or territory between years). If having multiple independent samples is important, a study using non-invasive sampling (shed feathers, shed hairs, excrement) should be designed to collect all samples within a single field season.

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Amadeo Rea made available to me the data on which he based his History Museum helped me to locate samples of cactus wrens and the appropriate outgroups, as well as providing a few feathers from a California gnatcatcher. I will always appreciate Phil's willingness to answer "one more quick question" about locations from which specimens were collected, current status of populations, holdings of the Museum, or whatever else I could think of to bother him with.

The Anaheim Hills field site was a nature center owned by the City of Anaheim. Manager Kathy Glasco arranged for permission to collect feathers from their off-exhibit Tri-Canyon parcel, and naturalist "just Shelly" was a pleasure to have along during my visit.

The National Audubon Society's Starr Ranch preserve was an excellent collecting site, with habitat for many sensitive species. I appreciate

the help of Pete DeSimone, manager, in obtaining permission to collect and in locating nesting sites. At the San Diego Wild Animal Park (San Pasqual), Dr. J. E. Oosterhuis and Sandy Walton, his administrative assistant, helped me obtain permission to collect and Mike Mace pointed out nesting sites. At Sweetwater Reservoir, Robin Church helped me to locate nests. At Camp Pendleton, John and Jane Griffiths collected feathers from juvenile cactus wrens during banding. At Lake Jennings, Karen Miller helped me to scout for new nests and collect feathers. At Borrego Springs and Palm Desert, Jennie McNeill scouted for nests and birds while I mapped the sites and collected feathers.

During the laboratory portion of this study, Leona Chemnick, Ann Oakenfull, and Yaping Zhang of CRES helped me design and optimize my procedures to obtain the best results. CRES volunteers Sandy Vissman and Jessica Bessler assisted me with the lab work. Discussion of the results with Michael Purugganan and Nick Mundy at UCSD helped me to make sense of the results. Consultation with Mike Simpson at SDSU helped me to understand the implications of, and justification for, phylogenetic analysis.

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By giving me the opportunity to help him with the 1993 Przewalski Horse Masterplan meeting, Oliver Ryder gave me my first opportunity to deal with the issues of management of endangered species. He allowed me to do

this study in his lab and actively contributed to its planning and execution. He and the research staff at CRES made me a part of their family, and I will always be grateful.

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APPENDIX

TABLES

Table 2. Numbers and locations of San Diego cactus wrens (from Rea and Weaver 1990).

Location	Count	Territorial Males
San Juan Creek[d]		
1. Rancho Mission Viejo	—	64
2. Rancho Mission Viejo	—	32
3. Rancho Mission Viejo	—	15
4. Caspers Park[e]	—	3
5. Caspers Park	19	13
6. Starr Ranch[e]	—	1
7. Starr Ranch[e]	—	2
Segunda Deshecha Cañada		
8. San Clemente	1	1
San Mateo/San Onofre Creeks		
9. Rancho Mission Viejo	—	13
10. Camp Pendleton	—	5
Unnamed creek		
11. Camp Pendleton	—	1
Aliso Creek		
12. Camp Pendleton	—	2
Santa Margarita River		
13. Camp Pendleton	—	1
14. Camp Pendleton	0	0
15. Camp Pendleton	—	5
16. Camp Pendleton	—	3
17. Camp Pendleton	—	1
18. Camp Pendleton	1	1
19. Naval Weapons Station	17	—
20. Naval Weapons Station	2	—
San Luis Rey River		
21. Camp Pendleton	ON	—
22. Camp Pendleton	—	1
23. Camp Pendleton	—	3
24. Camp Pendleton	—	2
25. Camp Pendleton/ Naval Weapons Station	11	—
26. Naval Weapons Station	1	—
27. Bonsall	5	2
28. Lilac	0	0
29. Pala	0	0
30. Pala	0	0
31. Pauma Valley	0	0
Agua Hedionda Creek		
32. Agua Hedionda Lagoon	0	0
San Marcos Creek		
33. Batiquitos Lagoon	0	0
Escondido Creek		
34. San Elijo Lagoon	0	0
San Dieguito River		
35. Rancho Santa Fe	0	0
36. Rancho Sante Fe	ON	—
37. Rancho Bernardo	—	1
38. Rancho Bernardo	0	0
39. Rancho Bernardo	0	0
40. Rancho Bernardo	5	1
41. Rancho Bernardo	0	0
42. Escondido	21	12
43. Escondido	0	0
44. Escondido	0	0
45. Escondido	20	13
46. Escondido	1	1
47. Escondido	2	1
48. Escondido	4	3
49. San Pasqual Valley	0	0
50. San Pasqual Valley	0	0
51. San Pasqual Valley	0	0
52. San Pasqual Valley	2	2
53. San Pasqual Valley	54	38
54. San Pasqual Valley	0	0
55. San Pasqual Valley	2	1
56. San Pasqual Valley	6	4
57. San Pasqual Valley	0	0
58. San Pasqual Valley	2	1
Los Peñasquitos Creek		
59. Torrey Pines State Res.	0	0
60. Poway	0	0
61. Poway	0	0
San Diego River		
62. San Diego	1	1
63. Santee	3	2
64. Spring Valley	—	1
65. El Cajon	1	1
66. Lakeside	0	0
67. Lakeside	33	18
68. Lakeside	0	0
Sweetwater River		
69. Chula Vista	5	—
70. Chula Vista	2	1
71. Sunnyside	1	—
72. San Diego	N	—
73. Sweetwater Reservoir	13	8
74. Sunnyside	3	2
75. Mother Miguel Mt.	—	3
76. Mother Miguel Mt.	2	2
77. S of Mother Miguel Mt.	—	1
78. S of Mother Miguel Mt.	2	1
79. S of Mother Miguel Mt.	1	1
Otay River		
80. Dennery Canyon	6	3
81. Rancho Otay	6	—
82. Rancho Otay	27	—
83. Rancho Otay	16	—
84. Proctor Valley	1	—
Tijuana River		
85. Otay Mesa	2	1
86. Spring Canyon	2	1
87. Valle de las Palmas	5	1

[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.

Table 2 continued.

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).

Table 2 continued.

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 Jamal 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 Jamal 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).

Table 3. Specimens used in the morphological study. All specimens from Baja California Norte, Los Angeles County, Orange County, Riverside and San Bernardino Counties, San Diego County, and Ventura County are those used by Rea and Weaver (1990). The three specimens designated by * are type specimens of the San Diego cactus wren. Specimens from Baja California Sur, Texas, and Arizona were scored and added for comparison of cactus wren subspecies. A representative specimen of the rufous-naped wren and the California gnatcatcher were scored and added as outgroups.

			CHARACTER SCORES						
Specimen number	Collection location	Collection date	1	2	3	4	5	6	7
BAJA CALIFORNIA NORTE									
8682	15 mi. east of Tijuana	4/6/1923	1.5	1.5	1	1	1.5	1	6
8683	15 mi. east of Tijuana	4/6/1923	1.5	1.5	1.5	1.5	1	1	6
8684	15 mi. east of Tijuana	4/6/1923	1.5	2	1	2	2	1	6
17196	Aguajito Spg, Valle de la Trinidad	3/23/1936	1.5	2	1.5	1	1.5	1.5	4
17197	Aguajito Spg, Valle de la Trinidad	3/23/1936	1	1	1.5	2	1.5	1.5	5
17785	Carriso Valley	3/30/1894	1	1	1.5	1	2	1	5
17786	Carriso Valley	4/03/1894	1	1	2	1	2	1	4
17787	Carriso Valley	4/03/1894	1	1.5	2	2	2	1	4.5
17788	15 mi S. Tecate, Valle de las Palmas	4/05/1894	1	2	1.5	2	2	1	9
BAJA CALIFORNIA SUR									
18302	San Bartolo	1941	1.5	2	2	2	2	2	8
18371	Los Barriles	1941	1	2	2	2	2	2	8
18401	La Paz	1941	1	2	2	2	2	2	8
18425	Buena Vista	1941	1.5	2	2	2	2	2	9
18455	Santo Domingo	1941	1.5	2	2	2	2	2	8
LOS ANGELES COUNTY									
xxx	Claremont	7/29/1894	1	1	1	1	1	1	5
"Clare"	Claremont	10/2/1914	1	1	1	1	1.5	2	4.5
122	Claremont	12/10/1915	1	1	1	1	1.5	1	4
184	Claremont	11/25/1907	1	1	1	1	2	1	4.5
253	Claremont	4/26/1909	1	1	1	1	1	1	4
254	Claremont	4/10/1909	1	1	1	1	1	1	2
282	San Fernando	12/31/1913	1	1	1	1	1.5	1	2
286	Los Angeles	11/27/191x	1.5	1	1	1	1.5	1	2
294	Claremont	11/25/1907	1	1	1	1	2	1	4.5
494	Claremont	3/31/1909	1	1	1	1	1	1	5

Table 3 continued.

530	Claremont	4/3/1909	1	1	1	1	1.5	1	5
A-595	Sunland	3/2/1917	1	1	1.5	1			1.5
2061	San Fernando	9/25/1907	1	1	1	1	1	1	4.5
2188	Lankershim	11/3/1917	1	1	1	1	1	1	3.5
9944	San Fernando	10/14/1895	1	1	1	1	1	1	2
12021	San Fernando Valley	9/12/1903	1.5	1	1	1	1	1	
12022	Garnsey, San Fernando Valley	10/31/1903	1	1	1	1	1	1	5
12024	Garnsey, San Fernando Valley	11/01/1902	1.5		1		1	1	1
12026	Pasadena	9/05/1903	1.5	1	2	1	1	1	4.5
12027	Pasadena	8/22/1902	1.5	1	1	1	1	1	
12029	Pasadena	9/06/1902	1	1	1.5	1	1	1	
12032	Pasadena	9/09/1901	1.5	1	1	1	1.5	1	
12033	Garnsey, San Fernando Valley	10/31/1903	1	1	1	1	1	1.5	4.5
12034	Pasadena	1/24/1903	1.5	1	1	1	1.5	1	5
12035	Pasadena	8/22/1902	1	1	1	1	1.5	1	
12036	San Fernando Valley	9/12/1903	1	1	1	1	1	1	3
12039	San Fernando	9/12/1903	1	1	1.5	1	1.5	1	3
12040	San Fernando Valley	12/21/1913	1.5	1	1	1		1	3
12041	San Fernando Valley	6/13/1899	2	1	1	2		1	5
12042	San Fernando	6/13/1899	2		1	1.5			4
12045	Garnsey, San Fernando Valley	10/31/1903	1	1	1	1	1	1	3
12046	San Fernando Valley	9/12/1903	1	1	1	1	1	1	
12047	San Fernando Valley	4/18/1897	1	1	1	1		1	1
12049	San Fernando	9/12/1903	1	1	1.5	1	1.5	1	
12050	San Fernando	9/12/1903	1	1	1	1	1	1	
12052	San Fernando	9/12/1903	1	1	1	1	1	1	
12054	San Fernando	6/13/1899	1.5		1	1.5			2
12055	San Fernando	9/12/1903	1	1	1.5	1	1.5	1.5	
12056	Pasadena	9/06/1902	1.5	1	1	1	1.5	1	3
12057	Pasadena	11/26/1900	1	1	1	1	1	1	
12059	San Fernando Valley	9/12/1903	1	1	1	1	1	1	2
12060	San Fernando	4/18/1897	1	1	1	1			4
12063	Burbank	4/09/1890		1	1	1			3
13775	Taluca	2/13/1908	1	1	1	1	1.5	1	2
13776	San Fernando Valley	10/31/1903	1	1	1	1			3
24614	Culver City	5/26/1928	1	1	1	1	1	1	4.5
24615	Culver City	5/26/1928	1	1	1	1	1	1	6
38052	Tujunga Wash, San Fernando Valley	4/23/1896	1	1	1	1	1.5	1	3
38054	Tujunga Wash, San Fernando Valley	6/17/1904	1	1	1	1	1.5		2

Table 3 continued.

38062	Tujunga Wash, San Fernando Valley	9/13/1903	1	1	1	1	1	1	2
38063	Tujunga Wash, San Fernando Valley	9/13/1903	1	1	1	1	1	1	2
38064	Pasadena, Los Angeles Co.	2/15/1896	1.5	1	1	1	1.5	1	4
38065	Pasadena, Los Angeles Co.	10/07/1896	1	1	1	1	1.5	1	5
38066	Pasadena, Los Angeles Co.	11/14/1903	1	1	1	1	1.5	1	3
38068	Pasadena, Los Angeles Co.	9/16/1904	1	1	1	1	1.5	1	3
38069	Pasadena, Los Angeles Co.	4/5/1905	1	1	1	1	1.5	1	4
38071	Pasadena, Los Angeles Co.	9/20/1904	1	1	1	1	1	1	4
38072	Pasadena, Los Angeles Co.	9/14/1906	1	1	1	1	1	1	4
46038	San Fernando Valley	2/19/1988	1	1	1	1	1	1	3
417756	Lankershim	8/28/1914	1	1	1	1	1	1	4
ORANGE COUNTY									
3372	Santa Ana Canyon	9/21/1908	1	1	1	1	1	1	3
3373	Santa Ana Canyon	9/22/1908	1	1	1	1	1	1	4.5
3374	Santa Ana Canyon	9/21/1908	1	1	1	1	1	1	6
RIVERSIDE AND SAN BERNARDINO COUNTIES									
1530	San Bernardino	1/09/1887	1	1	1	1	1	1	4
1536	Salton Sea Area	1/05/1898	1	1	1	1	1	1	6
1538	Salton Sea Area	10/18/1899	1.5	1	1	1	1	1	4
11744	Mecca, Riverside Co.	12/27/1908	1.5	1	1	1.5	1	1	7
11745	Mecca, Riverside Co.	12/27/1908	1	1	1.5	1	1	1	1
12058	Riverside	4/1891	1	1	1	1		1	4.5
24612	Mecca, Riverside Co.	1/11/1911	1	1	1	1	1	1	4
24613	Mecca, Riverside Co.	3/21/1911	1	1	1	1	1	1	5
204295	Cabezon	9/14/1907	1	1	1	1	1.5	1	3
523004	San Bernardino Co.	1/21/1895	1	1	1	1	1	1	4
SAN DIEGO COUNTY									
C.112	San Diego	4/24/1915	1	1	1	1	1.5	1	6
1930	San Diego	12/17/1916	1	1	2	2	1.5	1	5.5
2579	San Diego	12/17/1916	2	1	1.5	1	1.5	1	5
3656	San Diego	6/13/1908			2	2	2	1	6
3660	San Diego	6/15/1908	1.5		2	2	1.5	1	9
4275	San Diego	3/02/1862	1.5	2	2	1.5	2	1.5	2
4276	San Diego	3/02/1862	1.5	1	1	1.5	1	1	2
10838	National City	12/31/1913	1.5	1	2	1.5	1.5	1	6.5
17771	Lakeside	3/16/1894	2	1	2	1	1.5	2	6
17773	San Diego	9/16/1889	1.5	1.5	1	1	1.5	1	
17776	San Diego	10/04/1893	2	1.5	1.5	1.5	1.5	1	5

Table 3 continued.

17780	San Diego	9/14/1894	2	1	1.5	2	1.5		5
17781	San Diego	9/18/1894	1	1	1	1	1	1	4.5
17782	San Diego	5/20/1895	1.5	1.5	1	2	1	1	5
17783	San Diego	5/20/1895	1.5	1	1	2	1	1	6
17784	San Diego	12/17/1895	1	1	2	1.5	1.5	1	5
24618	Paradise Valey	1/6/1930	1	1.5	1.5	1	1.5	1	4.5
32644	Bonita	4/7/1918	1	1	1.5	1	1.5	1	4
32645	Bonita	12/9/1919	1	1	1.5	1.5	1	1	3
32646	Chula Vista	4/18/1918	1.5	1	1	2	1.5	1	5
32647	Mission Valley, San Diego	2/18/1930	1.5	1	2	1	1.5	1.5	3
32648	National City	4/7/1918	1	1.5	1	2	1.5	1.5	6
32654	National City	9/1/1918	1	1	1	2	1.5		4
32655	National City	11/8/1922	1	1.5	1	2	1.5	1	4
32656	National City	12/24/1922	1	1	1.5	1	1.5	2	5
32657	National City	12/24/1922	1	1	2	1	1.5	2	6
41152	Bonita	10/31/1980	1	1.5	1.5	1.5	1	1.5	4
41242	Bonita	12/1/1980	1	1	1	1.5	1.5	1	3
43986*	Bonita	1/7/1986	2	1	2	1	1.5	2	3.5
44253*	Bonita	1/12/1986	1.5	1	1	1.5	1	2	3.5
44256*	Bonita	14/12/1986	1	1	1.5	1.5	1	1.5	3
757795	San Diego	11/4/1917	2	1.5	2	2	1	2	6
757796	San Diego	11/4/1917	1	1	1	1	1	1	6.5
757797	San Diego	2/18/1893	1	1.5	2	1	1.5	1.5	9
757798	San Diego	11/09/1893	1.5	2	2	2	1.5	1.5	9
757800	Lakeside	6/13/1894	1.5	1.5	2	1.5	1.5	1	4.5
TEXAS and ARIZONA									
24609	Sanderson, Tx.	1930	1	1.5	1	1	1	2	3
24611	Sierra Blanca, Tx.	1930	1	2	1	1	1	2	4
40836	Maricopa Co., Az.	1980	1	2	1	1	1	2	4
40902	Maricopa Co., Az.	1979	1	2	1	1	1	2	5
VENTURA COUNTY									
44455	Ventura Co.	19xx	1	1	1		1	1	5
44691	Ventura Co.	19xx	1	1	1	1	1	1	3
45699	Ventura Co.	19xx	1	1	1.5	1.5	2	1	4.5
OUTGROUPS									
Rufous-naped wren			1	0	0	0	2	3	8
California gnatcatcher	San Diego	1994	0	0	0	0	2	2	1

Table 4. Samples used in cytochrome b sequencing and analysis.

Sample	Date collected	Location	Sample type	Collector
Polioptila californica californica	1994	San Diego , Ca.	Feather	S.D. Museum of Nat. History
Campylorhynchus rufinucha	After 1987	Puntarenas Province, Costa Rica	Tissue	Donna Dittmann (LSUMNS)
Campylorhynchus zonatus	1987	Esmeraldas Province, Ecuador	Tissue	Mark B. Robbins (LSUMNS)
Campylorhynchus brunneicapillus affinus	2/85	Area Todos Santos, Baja Ca. Sur	Tissue	J. M. Bates (LSUMNS)
Campylorhynchus brunneicapillus couesi	7/25/92	Falcon, Zapata Co., Tx	Tissue	Tom Huels (U. of Az.)
Campylorhynchus brunneicapillus couesi	12/9/83	Tucson, Az	Museum skin	Tom Huels (U. of Az.)
Campylorhynchyus brunneicapillus (coastal California):				
AH1	7/14/94	Anaheim Hills	Shed feather	LE
AH5	7/14/94	Anaheim Hills	Shed feather	LE
BS1	7/21/94	Borrego Springs	Shed feather	LE
BS3	7/21/94	Borrego Springs	Shed feather	LE
BS6	7/21/94	Borrego Springs	Shed feather	LE
CP1	8/94	Camp Pendleton	Pulled feather	John Griffiths
CP2	8/94	Camp Pendleton	Pulled feather	John Griffiths
CP3	8/94	Camp Pendleton	Pulled feather	John Griffiths
CP4	8/94	Camp Pendleton	Pulled feather	John Griffiths
LH1	5/94	Lake Hodges	Shed feather	LE
LH2	5/28/94	Lake Hodges	Shed feather	LE
LH6	6/1/94	Lake Hodges	Shed feather	LE
LH8	2/12/95	Lake Hodges	Shed feather	LE
LJ2	4/24/94	Lake Jennings	Shed feather	LE
LJ10	2/18/95	Lake Jennings	Shed feather	LE
PD1	7/22/94	Palm Desert	Shed feather	LE
PD2	7/22/94	Palm Desert	Shed feather	LE
PD3	7/22/94	Palm Desert	Shed feather	LE
PD5	7/22/94	Palm Desert	Shed feather	LE
SP4	5/13/94	San Pasqual	Shed feather	LE
SP6	5/13/94	San Pasqual	Shed feather	LE
SP9	10/1/94	San Pasqual	Shed feather	LE
SR1	7/10/94	Starr Ranch	Shed feather	LE
SR2	7/10/94	Starr Ranch	Shed feather	LE
SR3	7/17/94	Starr Ranch	Shed feather	LE
SR4	7/17/94	Starr Ranch	Shed feather	LE
SR5	7/17/94	Starr Ranch	Shed feather	LE
SW2	5/17/94	Sweetwater Reservoir	Shed feather	LE
SW8	5/17/94	Sweetwater Reservoir	Shed feather	LE
Campylorhynchus brunneicapillus (Baja California):				
MX1	11/12/94	N. of San Felipe, Baja Ca.	Tissue	Robert Zink (U. of Minn.)
MX2	11/12/94	N. of San Felipe, Baja Ca.	Tissue	Robert Zink (U. of Minn.)
MX3	11/12/94	N. of San Felipe, Baja Ca.	Tissue	Robert Zink (U. of Minn.)
MX4	11/15/94	Calamu, Baja Ca.	Tissue	Robert Zink (U. of Minn.)
MX5	11/15/94	Calamu, Baja Ca.	Tissue	Robert Zink (U. of Minn.)

Table 5. Pairwise distances between taxa. Below the diagonal are shown absolute distances (number of variable sites). Above the diagonal are mean distances.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 TX	-	0.011	0.018	0.086	0.089	0.100	0.018	0.021	0.025	0.025	0.021	0.018	0.011	0.021	0.021	0.018
2 AZ	3	-	0.029	0.082	0.086	0.104	0.021	0.025	0.021	0.021	0.018	0.021	0.021	0.032	0.025	0.029
3 CBA	5	8	-	0.079	0.082	0.100	0.021	0.025	0.029	0.029	0.025	0.021	0.014	0.025	0.025	0.018
4 CR	24	23	22	-	0.004	0.143	0.082	0.086	0.082	0.082	0.079	0.082	0.082	0.086	0.079	0.086
5 CZ	25	24	23	1	-	0.143	0.086	0.089	0.086	0.086	0.082	0.086	0.086	0.089	0.082	0.089
6 CAGN	28	29	28	40	40	-	0.093	0.096	0.093	0.093	0.096	0.107	0.100	0.104	0.111	0.104
7 AH1	5	6	6	23	24	26	-	0.004	0.007	0.007	0.011	0.014	0.014	0.018	0.018	0.021
8 AH5	6	7	7	24	25	27	1	-	0.011	0.011	0.007	0.011	0.018	0.021	0.021	0.025
9 BS1	7	6	8	23	24	26	2	3	-	0.007	0.011	0.021	0.021	0.025	0.025	0.029
10 BS3	7	6	8	23	24	26	2	3	2	-	0.011	0.021	0.021	0.025	0.025	0.029
11 BS6	6	5	7	22	23	27	3	2	3	3	-	0.011	0.018	0.029	0.021	0.025
12 CP1	5	6	6	23	24	30	4	3	6	6	3	-	0.007	0.018	0.011	0.021
13 CP2	3	6	4	23	24	28	4	5	6	6	5	2	-	0.011	0.011	0.014
14 CP3	6	9	7	24	25	29	5	6	7	7	8	5	3	-	0.014	0.025
15 CP4	6	7	7	22	23	31	5	6	7	7	6	3	3	4	-	0.025
16 LH1	5	8	5	24	25	29	6	7	8	8	7	6	4	7	7	-
17 LH2	8	7	8	23	24	30	7	6	7	7	4	5	7	10	8	3
18 LH6	9	8	9	24	25	29	6	7	6	6	7	8	8	9	9	4
19 LH8	10	9	10	25	26	30	7	6	5	7	6	7	9	10	10	7
20 LJ2	10	9	10	25	26	30	7	6	5	7	6	7	9	10	10	7
21 LJ10	5	6	6	23	24	30	4	3	6	6	3	2	4	7	5	4
22 PD1	6	7	7	24	25	29	5	6	7	7	6	7	5	6	6	7
23 PD2	6	7	7	26	27	28	5	6	7	7	6	7	5	8	8	7
24 PD3	4	7	5	24	25	26	3	4	5	5	4	5	3	6	6	5
25 PD5	6	7	7	26	27	28	5	6	7	7	6	7	5	8	8	7
26 SP4	6	7	7	24	25	29	7	8	5	7	6	7	5	8	8	5
27 SP6	8	5	9	24	25	31	7	8	5	7	6	7	7	10	8	7
28 SP9	8	7	9	24	25	29	9	10	7	9	8	9	7	10	10	7
29 SR1	7	8	8	25	26	28	8	7	8	8	5	6	6	9	9	8
30 SR2	6	7	7	24	25	27	7	6	7	7	4	5	5	8	8	7
31 SR3	3	6	4	23	24	28	4	3	6	6	3	2	2	5	5	4
32 SR4	5	8	6	25	26	28	6	5	8	8	5	4	4	7	7	6
33 SR5	5	6	6	23	24	26	6	5	6	6	3	4	4	7	7	6
34 SW2	2	5	3	22	23	27	3	4	5	5	4	3	1	4	4	3
35 SW8	2	5	3	22	23	27	3	4	5	5	4	3	1	4	4	3
36 MX1	6	7	7	24	25	30	5	6	7	7	6	5	5	8	6	7
37 MX2	4	7	5	24	25	28	5	6	7	7	6	5	3	6	6	5
38 MX3	5	8	6	25	26	29	6	7	8	8	7	6	4	7	7	6
39 MX4	5	8	2	22	23	28	6	7	8	8	7	6	4	7	7	5
40 MX5	6	9	1	23	24	29	7	8	9	9	8	7	5	8	8	6

Table 5 continued.

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1 TX	0.029	0.032	0.036	0.036	0.018	0.021	0.021	0.014	0.021	0.021	0.029	0.029	0.025	0.021	0.011	0.018
2 AZ	0.025	0.029	0.032	0.032	0.021	0.025	0.025	0.025	0.025	0.025	0.018	0.025	0.029	0.025	0.021	0.029
3 CBA	0.029	0.032	0.036	0.036	0.021	0.025	0.025	0.018	0.025	0.025	0.032	0.032	0.029	0.025	0.014	0.021
4 CR	0.082	0.086	0.089	0.089	0.082	0.086	0.093	0.086	0.093	0.086	0.086	0.086	0.089	0.086	0.082	0.089
5 CZ	0.086	0.089	0.093	0.093	0.086	0.089	0.096	0.089	0.096	0.089	0.089	0.089	0.093	0.089	0.086	0.093
6 CAGN	0.107	0.104	0.107	0.107	0.107	0.104	0.100	0.093	0.100	0.104	0.111	0.104	0.100	0.096	0.100	0.100
7 AH1	0.025	0.021	0.025	0.025	0.014	0.018	0.018	0.011	0.018	0.025	0.025	0.032	0.029	0.025	0.014	0.021
8 AH5	0.021	0.025	0.021	0.021	0.011	0.021	0.021	0.014	0.021	0.029	0.029	0.036	0.025	0.021	0.011	0.018
9 BS1	0.025	0.021	0.018	0.018	0.021	0.025	0.025	0.018	0.025	0.018	0.018	0.025	0.029	0.025	0.021	0.029
10 BS3	0.025	0.021	0.025	0.025	0.021	0.025	0.025	0.018	0.025	0.025	0.025	0.032	0.029	0.025	0.021	0.029
11 BS6	0.014	0.025	0.021	0.021	0.011	0.021	0.021	0.014	0.021	0.021	0.021	0.029	0.018	0.014	0.011	0.018
12 CP1	0.018	0.029	0.025	0.025	0.007	0.025	0.025	0.018	0.025	0.025	0.025	0.032	0.021	0.018	0.007	0.014
13 CP2	0.025	0.029	0.032	0.032	0.014	0.018	0.018	0.011	0.018	0.018	0.025	0.025	0.021	0.018	0.007	0.014
14 CP3	0.036	0.032	0.036	0.036	0.025	0.021	0.029	0.021	0.029	0.029	0.036	0.036	0.032	0.029	0.018	0.025
15 CP4	0.029	0.032	0.036	0.036	0.018	0.021	0.029	0.021	0.029	0.029	0.029	0.036	0.032	0.029	0.018	0.025
16 LH1	0.011	0.014	0.025	0.025	0.014	0.025	0.025	0.018	0.025	0.018	0.025	0.025	0.029	0.025	0.014	0.021
17 LH2	-	0.011	0.014	0.014	0.011	0.036	0.036	0.029	0.036	0.021	0.021	0.029	0.025	0.021	0.018	0.025
18 LH6	3	-	0.011	0.011	0.021	0.032	0.032	0.032	0.032	0.025	0.025	0.032	0.036	0.032	0.029	0.036
19 LH8	4	3	-	0.000	0.018	0.036	0.036	0.036	0.036	0.021	0.021	0.029	0.032	0.029	0.025	0.032
20 LJ2	4	3	0	-	0.018	0.036	0.036	0.036	0.036	0.021	0.021	0.029	0.032	0.029	0.025	0.032
21 LJ10	3	6	5	5	-	0.025	0.025	0.018	0.025	0.018	0.018	0.025	0.021	0.018	0.007	0.014
22 PD1	10	9	10	10	7	-	0.007	0.014	0.007	0.029	0.029	0.029	0.032	0.029	0.018	0.025
23 PD2	10	9	10	10	7	2	-	0.007	0.000	0.029	0.029	0.029	0.032	0.029	0.018	0.025
24 PD3	8	9	10	10	5	4	2	-	0.007	0.021	0.029	0.029	0.025	0.021	0.011	0.018
25 PD5	10	9	10	10	7	2	0	2	-	0.029	0.029	0.029	0.032	0.029	0.018	0.025
26 SP4	6	7	6	6	5	8	8	6	8	-	0.007	0.007	0.025	0.021	0.018	0.025
27 SP6	6	7	6	6	5	8	8	8	8	2	-	0.007	0.032	0.029	0.025	0.032
28 SP9	8	9	8	8	7	8	8	8	8	2	2	-	0.032	0.029	0.025	0.032
29 SR1	7	10	9	9	6	9	9	7	9	7	9	9	-	0.004	0.014	0.007
30 SR2	6	9	8	8	5	8	8	6	8	6	8	8	1	-	0.011	0.004
31 SR3	5	8	7	7	2	5	5	3	5	5	7	7	4	3	-	0.007
32 SR4	7	10	9	9	4	7	7	5	7	7	9	9	2	1	2	-
33 SR5	5	8	7	7	4	7	7	5	7	5	7	7	2	1	2	2
34 SW2	6	7	8	8	3	4	4	2	4	4	6	6	5	4	1	3
35 SW8	6	7	8	8	3	4	4	2	4	4	6	6	5	4	1	3
36 MX1	8	9	10	10	5	8	8	6	8	8	8	10	9	8	5	7
37 MX2	8	9	10	10	5	6	6	4	6	6	8	8	7	6	3	5
38 MX3	9	10	11	11	6	7	7	5	7	7	9	9	8	7	4	6
39 MX4	8	9	10	10	6	7	7	5	7	7	9	9	8	7	4	6
40 MX5	9	10	11	11	7	8	8	6	8	8	10	10	9	8	5	7

Table 5 continued.

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1 TX	0.029	0.032	0.036	0.036	0.018	0.021	0.021	0.014	0.021	0.021	0.029	0.029	0.025	0.021	0.011	0.018
2 AZ	0.025	0.029	0.032	0.032	0.021	0.025	0.025	0.025	0.025	0.025	0.018	0.025	0.029	0.025	0.021	0.029
3 CBA	0.029	0.032	0.036	0.036	0.021	0.025	0.025	0.018	0.025	0.025	0.032	0.032	0.029	0.025	0.014	0.021
4 CR	0.082	0.086	0.089	0.089	0.082	0.086	0.093	0.086	0.093	0.086	0.086	0.086	0.089	0.086	0.082	0.089
5 CZ	0.086	0.089	0.093	0.093	0.086	0.089	0.096	0.089	0.096	0.089	0.089	0.089	0.093	0.089	0.086	0.093
6 CAGN	0.107	0.104	0.107	0.107	0.107	0.104	0.100	0.093	0.100	0.104	0.111	0.104	0.100	0.096	0.100	0.100
7 AH1	0.025	0.021	0.025	0.025	0.014	0.018	0.018	0.011	0.018	0.025	0.025	0.032	0.029	0.025	0.014	0.021
8 AH5	0.021	0.025	0.021	0.021	0.011	0.021	0.021	0.014	0.021	0.029	0.029	0.036	0.025	0.021	0.011	0.018
9 BS1	0.025	0.021	0.018	0.018	0.021	0.025	0.025	0.018	0.025	0.018	0.018	0.025	0.029	0.025	0.021	0.029
10 BS3	0.025	0.021	0.025	0.025	0.021	0.025	0.025	0.018	0.025	0.025	0.025	0.032	0.029	0.025	0.021	0.029
11 BS6	0.014	0.025	0.021	0.021	0.011	0.021	0.021	0.014	0.021	0.021	0.021	0.029	0.018	0.014	0.011	0.018
12 CP1	0.018	0.029	0.025	0.025	0.007	0.025	0.025	0.018	0.025	0.025	0.025	0.032	0.021	0.018	0.007	0.014
13 CP2	0.025	0.029	0.032	0.032	0.014	0.018	0.018	0.011	0.018	0.018	0.025	0.025	0.021	0.018	0.007	0.014
14 CP3	0.036	0.032	0.036	0.036	0.025	0.021	0.029	0.021	0.029	0.029	0.036	0.036	0.032	0.029	0.018	0.025
15 CP4	0.029	0.032	0.036	0.036	0.018	0.021	0.029	0.021	0.029	0.029	0.029	0.036	0.032	0.029	0.018	0.025
16 LH1	0.011	0.014	0.025	0.025	0.014	0.025	0.025	0.018	0.025	0.018	0.025	0.025	0.029	0.025	0.014	0.021
17 LH2	-	0.011	0.014	0.014	0.011	0.036	0.036	0.029	0.036	0.021	0.021	0.029	0.025	0.021	0.018	0.025
18 LH6	3	-	0.011	0.011	0.021	0.032	0.032	0.032	0.032	0.025	0.025	0.032	0.036	0.032	0.029	0.036
19 LH8	4	3	-	0.000	0.018	0.036	0.036	0.036	0.036	0.021	0.021	0.029	0.032	0.029	0.025	0.032
20 LJ2	4	3	0	-	0.018	0.036	0.036	0.036	0.036	0.021	0.021	0.029	0.032	0.029	0.025	0.032
21 LJ10	3	6	5	5	-	0.025	0.025	0.018	0.025	0.018	0.018	0.025	0.021	0.018	0.007	0.014
22 PD1	10	9	10	10	7	-	0.007	0.014	0.007	0.029	0.029	0.029	0.032	0.029	0.018	0.025
23 PD2	10	9	10	10	7	2	-	0.007	0.000	0.029	0.029	0.029	0.032	0.029	0.018	0.025
24 PD3	8	9	10	10	5	4	2	-	0.007	0.021	0.029	0.029	0.025	0.021	0.011	0.018
25 PD5	10	9	10	10	7	2	0	2	-	0.029	0.029	0.029	0.032	0.029	0.018	0.025
26 SP4	6	7	6	6	5	8	8	6	8	-	0.007	0.007	0.025	0.021	0.018	0.025
27 SP6	6	7	6	6	5	8	8	8	8	2	-	0.007	0.032	0.029	0.025	0.032
28 SP9	8	9	8	8	7	8	8	8	8	2	2	-	0.032	0.029	0.025	0.032
29 SR1	7	10	9	9	6	9	9	7	9	7	9	9	-	0.004	0.014	0.007
30 SR2	6	9	8	8	5	8	8	6	8	6	8	8	1	-	0.011	0.004
31 SR3	5	8	7	7	2	5	5	3	5	5	7	7	4	3	-	0.007
32 SR4	7	10	9	9	4	7	7	5	7	7	9	9	2	1	2	-
33 SR5	5	8	7	7	4	7	7	5	7	5	7	7	2	1	2	2
34 SW2	6	7	8	8	3	4	4	2	4	4	6	6	5	4	1	3
35 SW8	6	7	8	8	3	4	4	2	4	4	6	6	5	4	1	3
36 MX1	8	9	10	10	5	8	8	6	8	8	8	10	9	8	5	7
37 MX2	8	9	10	10	5	6	6	4	6	6	8	8	7	6	3	5
38 MX3	9	10	11	11	6	7	7	5	7	7	9	9	8	7	4	6
39 MX4	8	9	10	10	6	7	7	5	7	7	9	9	8	7	4	6
40 MX5	9	10	11	11	7	8	8	6	8	8	10	10	9	8	5	7

Table 5 continued.

		33	34	35	36	37	38	39	40
1	TX	0.018	0.007	0.007	0.021	0.014	0.018	0.018	0.021
2	AZ	0.021	0.018	0.018	0.025	0.025	0.029	0.029	0.032
3	CBA	0.021	0.011	0.011	0.025	0.018	0.021	0.007	0.004
4	CR	0.082	0.079	0.079	0.086	0.086	0.089	0.079	0.082
5	CZ	0.086	0.082	0.082	0.089	0.089	0.093	0.082	0.086
6	CAGN	0.093	0.096	0.096	0.107	0.100	0.104	0.100	0.104
7	AH1	0.021	0.011	0.011	0.018	0.018	0.021	0.021	0.025
8	AH5	0.018	0.014	0.014	0.021	0.021	0.025	0.025	0.029
9	BS1	0.021	0.018	0.018	0.025	0.025	0.029	0.029	0.032
10	BS3	0.021	0.018	0.018	0.025	0.025	0.029	0.029	0.032
11	BS6	0.011	0.014	0.014	0.021	0.021	0.025	0.025	0.029
12	CP1	0.014	0.011	0.011	0.018	0.018	0.021	0.021	0.025
13	CP2	0.014	0.004	0.004	0.018	0.011	0.014	0.014	0.018
14	CP3	0.025	0.014	0.014	0.029	0.021	0.025	0.025	0.029
15	CP4	0.025	0.014	0.014	0.021	0.021	0.025	0.025	0.029
16	LH1	0.021	0.011	0.011	0.025	0.018	0.021	0.018	0.021
17	LH2	0.018	0.021	0.021	0.029	0.029	0.032	0.029	0.032
18	LH6	0.029	0.025	0.025	0.032	0.032	0.036	0.032	0.036
19	LH8	0.025	0.029	0.029	0.036	0.036	0.039	0.036	0.039
20	LJ2	0.025	0.029	0.029	0.036	0.036	0.039	0.036	0.039
21	LJ10	0.014	0.011	0.011	0.018	0.018	0.021	0.021	0.025
22	PD1	0.025	0.014	0.014	0.029	0.021	0.025	0.025	0.029
23	PD2	0.025	0.014	0.014	0.029	0.021	0.025	0.025	0.029
24	PD3	0.018	0.007	0.007	0.021	0.014	0.018	0.018	0.021
25	PD5	0.025	0.014	0.014	0.029	0.021	0.025	0.025	0.029
26	SP4	0.018	0.014	0.014	0.029	0.021	0.025	0.025	0.029
27	SP6	0.025	0.021	0.021	0.029	0.029	0.032	0.032	0.036
28	SP9	0.025	0.021	0.021	0.036	0.029	0.032	0.032	0.036
29	SR1	0.007	0.018	0.018	0.032	0.025	0.029	0.029	0.032
30	SR2	0.004	0.014	0.014	0.029	0.021	0.025	0.025	0.029
31	SR3	0.007	0.004	0.004	0.018	0.011	0.014	0.014	0.018
32	SR4	0.007	0.011	0.011	0.025	0.018	0.021	0.021	0.025
33	SR5	-	0.011	0.011	0.025	0.018	0.021	0.021	0.025
34	SW2	3	-	0.000	0.014	0.007	0.011	0.011	0.014
35	SW8	3	0	-	0.014	0.007	0.011	0.011	0.014
36	MX1	7	4	4	-	0.007	0.011	0.018	0.021
37	MX2	5	2	2	2	-	0.004	0.011	0.014
38	MX3	6	3	3	3	1	-	0.014	0.018
39	MX4	6	3	3	5	3	4	-	0.004
40	MX5	7	4	4	6	4	5	1	-

ABSTRACT