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Population-level history of the wrentit (*Chamaea fasciata*): Implications for comparative phylogeography in the California Floristic Province

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Abstract

The phylogeography of a variety of species has been studied within the California Floristic Province; however, few studies have examined genetic variation in bird species across the entire region. This study uses mitochondrial DNA data to investigate the phylogeography of the wrentit (*Chamaea fasciata*), a sedentary bird native to scrub and chaparral habitats of this region. Analysis of molecular variance shows geographic structure, and maximum likelihood, Bayesian, and parsimony analyses consistently identify six main clades that are each restricted geographically. Nested clade phylogeographic analyses infer an overall range expansion for the entire cladogram, and a range expansion is also inferred from the mismatch distribution. Thus, our results suggest that the wrentit was isolated into southern refugia during the Pleistocene and has undergone a recent range expansion. Southern refugia and a range expansion were also identified in a previous study of the California thrasher (*Toxostoma redivivum*). The wrentit did not show marked divergence between northern and southern California defined by the Transverse Ranges, a pattern seen in a variety of other taxa within this region, including some birds.

Keywords: Phylogeography; Wrentit; *Chamaea fasciata*; California Floristic Province; Subspecies; Nested clade analysis

1. Introduction

By comparing the phylogeographic histories of co-distributed taxa, the influence of common historical events on lineage diversification can be revealed (Bermingham and Avise, 1986; Zink, 2002). Alternatively, incongruent patterns can indicate that some species respond uniquely to particular events due to characteristics of their ecology (Ditchfield, 2000). For such inferences to be made, large data sets consisting of diverse taxa from the same region are necessary. Within the California Floristic Province, the phylogeography of a wide array of organisms has now been studied. Calsbeek et al. (2003) recently analyzed and compared data from 55 such studies and reported broad similarities across taxa. However, these authors noted that only a few avian species have been examined in this region. Because birds in general have greater dispersal abilities than other organisms, they might be expected to show unique phylogeographic patterns. In this study, we describe the phylogeography of a species of bird native to the California Floristic Province, the wrentit (*Chamaea fasciata*), and compare it to the phylogeography of other taxa in this region. In addition, we discuss the phylogeography of another avian species, the California thrasher (*Toxostoma redivivum*; Sgariglia and Burns, 2003), whose data were not available at the time of the Calsbeek et al. (2003) study.

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The wrentit is a common year-round resident North American bird distributed from coastal Oregon through California and into northern Baja California (Fig. 1). Its distribution mostly excludes the Central Valley of California, creating a ring-like distribution also displayed in a number of co-distributed taxa (e.g., *Ensatina eschscholtzii* species complex, California mountain kingsnake (*Lampropeltis zonata*), California newt (*Taricha torosa*), *Eumeces skiltonianus* species complex, rubber boa (*Charina bottae*), and California thrasher (*Toxostoma redivivum*). The wrentit prefers scrub and chaparral habitats (from sea level to 2300 m) that also follow the same general ring distribution (Geupel and Ballard, 2002). Several factors indicate that, among birds, the wrentit may be a suitable candidate for the study of intraspecific genetic variation. Wrentits are sedentary and form lifelong pair bonds with relatively limited dispersal abilities. Adults spend their lifetime on 1–2.5 acre territories and typically travel less than 400 m from their natal site to their first breeding site (Baker et al., 1995). Thus, gene flow between populations should be relatively low, favoring the accumulation of local variation. The presence of geographic variation in morphology indicates that such local variation may be present. Despite the relatively small range of the wrentit compared to other avian species, five subspecies are currently recognized (Dickinson, 2003; Geupel and Ballard, 2002) on the basis of plumage color and other morphological features.

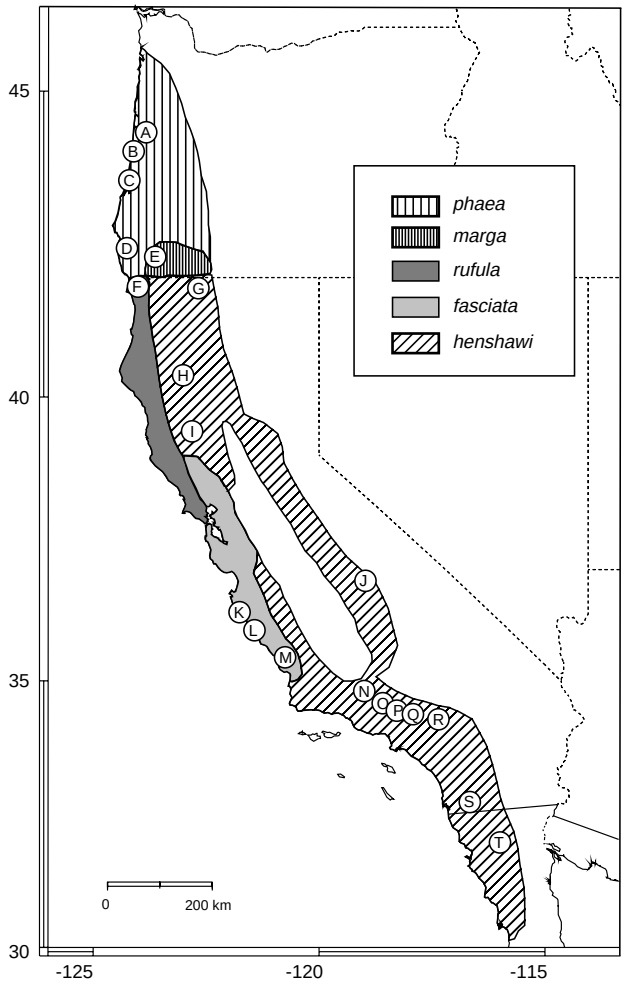

Fig. 1. Geographic distribution of wrentit subspecies. Letters indicate locations of sampled populations as indicated in Table 1. Geographic features of the California Floristic Province encompassed within our sampling include the Klamath Mountains (populations F, G, and H), the Coast Ranges (I, K, L, and M), the Sierra Nevada (J), the Transverse Ranges (N, O, P, Q, and R), and the Peninsular Ranges (S and T).

In this study, we use mitochondrial DNA markers to study the phylogeography of the wrentit. Several methodological approaches (e.g., phylogenetic trees, nested clade analysis, mismatch distributions, and AMOVA) are used to infer population-level history. Our results are compared to described subspecies to elucidate how patterns in morphological variation compare to evolutionary units as identified by mitochondrial data. In addition, the phylogeography of the wrentit is compared to that of other species in the region. In particular, we compare our data to that of the California thrasher and discuss general patterns observed for birds versus other taxa in the region.

2. Materials and methods

2.1. Taxon and character sampling

A total of 61 individuals from 20 populations were sampled for this study (Fig. 1, Table 1), including representatives of all five subspecies. Major geographic features of the California Floristic Province were encompassed within our sampling including the Klamath Mountains (populations F, G, and H), the Coast Ranges (populations I, K, L, and M), the Sierra Nevada (population J), the Transverse Ranges (populations N, O, P, Q, and R), and the Peninsular Ranges (populations S and T). DNA was extracted using a 5% Chelex solution, incubated for 20 min at 95.0 °C (Walsh et al., 1991) from fresh liver, heart, or breast muscle stored at −80 °C. Template DNA was amplified using avian-specific primers for fragments of cytochrome *b* (cyt *b*); 1143 bp, and a continuous strand containing ATP synthase 6 (ATPase6; 684 bp), ATPase8 (158 bp), transfer RNA-lysine (tRNA-Lys; 71 bp), and small portions of cytochrome oxidase subunit 2 (COII; 68 bp) and subunit III (COIII; 23 bp). Cyt *b* was sequenced in three overlapping segments using primer pairs L14851/H15297, L15206/H15710, and L15656/H16058 (Groth, 1998). Primers A8PWL (Hunt et al., 2001) and H9906 (Sgariglia and Burns, 2003) were used for ATPase6, and primers H9481 (Sgariglia and Burns, 2003) and CO2QL (Hunt et al., 2001) for the COII-tRNA-ATPase8 segment. Cyt *b* has

Table 1
Locality and voucher information for wrentits

Site	Individual	Voucher number	Locality
A	1	SDSU 2220	Oregon: Lincoln Co., 9 miles southeast Tidewater, N 44° 20.928′, W 123° 44.510′
	2	SDSU 2224	Oregon: Lincoln Co., 9 miles southeast Tidewater, N 44° 20.928′, W 123° 44.510′
	3	SDSU 2225	Oregon: Lincoln Co., 6 miles southeast Tidewater, N 44° 21.490′, W 123° 48.226′
	4	SDSU 2226	Oregon: Lincoln Co., 5 miles southwest Tidewater, N44° 20.607′, W 123° 56.901′
	5	SDSU 2222	Oregon: Lincoln Co., 8 miles southeast Tidewater, N 44° 20.743′, W 123° 46.072′
	6	SDSU 2221	Oregon: Lincoln Co., 4.5 miles southwest Tidewater, N 44° 21.153′, W 123° 57.965′
B	1	SDSU 2228	Oregon: Lane Co., 4.5 miles north of Florence, N 44° 03.364′, W 124° 06.799′
C	1	SDSU 2231	Oregon: Coos Co., 0.25 mile west of Lakeside, N 43° 34.946′ W 124°, 11.132′
D	1	SDSU 2233	Oregon: Curry Co., 11 miles northeast of Gold Beach, N 42°29.130′, W 124° 14.433′
	2	SDSU 2235	Oregon: Curry Co., 11 miles northeast of Gold Beach, N 42°28.423′, W 124° 14.234′
	3	SDSU 2236	Oregon: Curry Co., 11 miles northeast of Gold Beach, N 42°28.445′, W 124° 14.163′
E	1	SDSU 2241	Oregon: Josephine Co., 3 miles east of Squaw Mt., N 42° 20.459′, W 123° 37.091′
F	1	SDSU 2239	California: Del Norte Co., 2 miles northwest Gasquet, N 41° 51.749′, W 123° 59.924
	2	SDSU 2240	California: Del Norte Co., 2 miles northwest Gasquet, N 41° 51.692′, W 123° 59.816′
	3	SDSU 2237	California: Del Norte Co., 2 miles northwest Gasquet, N 41° 51.788′, W 124° 0.033′
	4	SDSU 2238	California: Del Norte Co., 2 miles northwest Gasquet, N 41° 51.610′, W 124° 0.082′
G	1	SDSU 2218	California: Siskiyou Co., 2.5 miles east of China Peak, N 41° 50.004, W 122° 40.005′
	2	SDSU 2219	California: Siskiyou Co., 2.5 miles east of China Peak, N 41° 49.951′, W 122° 40.118′
	3	SDSU 2217	California: Siskiyou Co., 2.5 miles east of China Peak, N 41° 49.951′, W 122° 40.118′
H	1	MVZ 167898	California: Shasta Co., 0.5 miles south and 1 mile east Goods Mt.
	2	MVZ 167906	California: Shasta Co., 0.5 miles south and 1 mile east Goods Mt.
	3	MVZ 167909	California: Shasta Co., 0.5 miles south and 1 mile east Goods Mt.
I	1	MVZ 167029	California: Lake Co., 1 mile north and 2.5 miles west Crockett Peak
	2	MVZ 167034	California: Lake Co., 1 mile north and 2.5 miles west Crockett Peak
	3	MVZ 170431	California: Lake Co., 4 miles south and 1 mile east Hull Mt.
	4	MVZ 178264	California: Lake Co., 4.5 miles south and 1 mile east Hull Mt.
	5	MVZ 167041	California: Lake Co., Deer Creek, 3.5 miles south and 5 miles west Crockett Peak
	6	MVZ 178263	California: Lake Co., 2 miles south and 1.25 miles east Poges Peak
	7	MVZ 167046	California: Glenn Co., Black Diamond Ridge, 2 miles north and 4 miles west Stonyford
	8	MVZ 167049	California: Glenn Co., Black Diamond Ridge, 2 miles north and 4 miles west Stonyford
J	1	SDSU 2214	California: Fresno Co., 4 miles west of Hume Lake, N 36° 48.276′, W 118° 58.794′
	2	SDSU 2215	California: Fresno Co., 4 miles west of Hume Lake, N 36° 47.262′, W 118° 58.531′
	3	SDSU 2216	California: Fresno Co., 4 miles west of Hume Lake, N 36° 46.824′, W 118° 57.868′
K	1	SDSU 2203	California: Monterey Co., 0.5 miles SW Manuel Peak, N 36° 15.086′, W 121° 46.198′
	2	SDSU 2198	California: Monterey Co., 0.5 miles SW Manuel Peak, N 36° 15.086′, W 121° 46.198′
L	1	SDSU 2201	California: Monterey Co., 1 mile northwest of Mount Mars, N 35° 48.888′, W 121° 21.712′
	2	SDSU 2195	California: Monterey Co., 1 mile northwest of Mount Mars, N 35° 48.888′, W 121° 21.712′
	3	SDSU 2196	California: Monterey Co., 3 miles W of Chalk Peak, N 35° 59.239′, W 121° 29.034′
	4	SDSU 2202	California: Monterey Co., 3 miles W of Chalk Peak, N 35° 59.302′, W 121° 29.034′
M	1	SDSU 2190	California: San Luis Obispo Co., 6 miles NW of Morro Bay, N 35° 25.274′, W 120° 43.634′
	2	SDSU 2191	California: San Luis Obispo Co., 6 miles NW of Morro Bay, N 35° 25.247′, W 120° 44.012′
	3	SDSU 2192	California: San Luis Obispo Co., 6 miles NW of Morro Bay, N 35° 24.947′, W 120° 44.230′
	4	SDSU 2193	California: San Luis Obispo Co., 6 miles NW of Morro Bay, N 35° 24.732′, W 120° 44.231′
N	1	MVZ 168267	California: Ventura Co., 1.5 miles north and 1.5 miles W Frazier Mt.
	2	MVZ 168268	California: Ventura Co., 1.5 miles north and 1.5 miles W Frazier Mt.
	3	MVZ 168269	California: Ventura Co., 1.5 miles north and 1.5 miles W Frazier Mt.
O	1	MVZ 168270	California: Los Angeles Co., 0.75 miles north and 0.125 miles east Red Mt.
	2	MVZ 168277	California: Los Angeles Co., 0.75 miles north and 0.125 miles east Red Mt.
P	1	MVZ 168285	California: Los Angeles Co., 1mile north and 0.5 miles west Snow Mt.
Q	1	MVZ 168288	California: Los Angeles Co., 1.5 miles west and 1.5 miles north Mt. Gleason
R	1	MVZ 168292	California: San Bernardino Co., 3 miles east Cleghorn Mt.
	2	MVZ 168296	California: San Bernardino Co., 3 miles east Cleghorn Mt.
S	1	SDSU 2189	California: San Diego Co., 4 miles west Corte Madera Mt.
	2	SDSU 2187	California: San Diego Co., 4 miles west Corte Madera Mt.
	3	SDSU 2184	California: San Diego Co., 4 miles west Corte Madera Mt.
	4	SDSU 2185	California: San Diego Co., 4 miles west Corte Madera Mt.
	5	SDSU 2188	California: San Diego Co., 4 miles west Corte Madera Mt.
	6	SDSU 2183	California: San Diego Co., 4 miles west Corte Madera Mt.
	7	SDSU 2186	California: San Diego Co., 4 miles west Corte Madera Mt.
T	1	AMNH MGL188	Mexico: Baja California, Sierra Juarez
	2	AMNH MGL189	Mexico: Baja California, Sierra Juarez

Each individual is labeled according to its population (site), and population letters (A through T) correspond to Fig. 1. For example, the six individuals from population A are labeled A1, A2, A3, A4, A5, and A6. SDSU = Vertebrate Collections, San Diego State University, MVZ = Museum of Vertebrate Zoology, University of California (Berkeley), and AMNH = American Museum of Natural History.

been used extensively in avian phylogenetic studies and has been demonstrated to be a useful phylogenetic marker at the population level. ATPase6 and ATPase8 have relatively high rates of evolution (Russo et al., 1996; Zardoya and Meyer, 1996) and are also good markers at the population level (Sgariglia and Burns, 2003). Importantly, these same gene regions were used in the earlier study of California thrasher; thus, they allow direct comparison of the phylogeography of these two species without the confounding effects of variable rates of evolution between different markers.

Initial amplification was performed in 10 μl reactions in capillary tubes for 40 cycles (94 °C for 3 s, 43 °C for 1 s, and 71 °C for 30 s) in a Rapid Cycler (Idaho Technology, Inc.). Desired PCR products were verified on 2.3% agarose gels and excised using 750 μl pasteur pipets. Reamplification of melted plugs (74 °C for 20 min in 250 μl H_2O) was also performed in capillary tubes in a Rapid Cycler but in larger reaction volumes for longer denaturing and annealing times and at a higher annealing temperature (40 μl reactions, 94 °C for 12 s, 52 °C for 4 s, 71 °C for 30 s). Final PCR product was purified using the GeneClean Kit (Bio101) and cycle sequenced (96 °C for 1 min, 96 °C for 30 s, 50 °C for 15 s, 60 °C for 4 min—28 cycles) using Big Dye terminator reaction mix from Applied Biosystems. Samples were passed through spin columns containing Sephadex beads before being sequenced on an ABI 377 DNA sequencer (Applied Biosystems). DNA sequences were edited and linked using Sequencher 3.0 (Gene Codes Corp.) and completed target gene sequences were aligned and translated using Seal v1.0a1 (Rambaut, 1995). Support for mitochondrial authenticity of sequence data comes from unambiguous alignment of overlapping sequence fragments, sequencing both heavy and light strands of all PCR fragments, appropriate fit to avian sequence template, absence of inappropriate stop codons, and lack of heterozygosity during editing. All sequences were deposited into GenBank (Accession Nos. AY124547, AY124546, DQ109818–DQ109876, DQ110951–DQ111011).

2.2. Intraspecific analyses

Overall genetic structure of populations was represented in an analysis of molecular variation (AMOVA) calculation of Φ_{st} using pairwise distances (Excoffier et al., 1992) as calculated in Arlequin 2.0 (Schneider et al., 2000). We also used Arlequin to construct plots of the distribution of pairwise differences among individuals, also known as the mismatch distribution. The shape of mismatch distributions can be used to infer whether a population has undergone a sudden population expansion (Rogers, 1995; Rogers and Harpending, 1992). Unimodal distributions tend to indicate a population expansion, whereas more ragged distributions indicate the population is in stable equilibrium. Agreement between the observed distributions and expected distributions under a sudden-expansion model was tested following Schneider and Excoffier (1999). In addition, we calculated the raggedness index (Harpending, 1994) which has larger values for stable populations than for expanding populations. Assuming neutrality, evidence of a population expansion was also tested using Fu's (1997) F_s as implemented in Arlequin. A significantly negative value indicates an excess of new mutations relative to equilibrium expectations based on number of observed alleles (Fu's F_s).

Relationships among wrentit haplotypes were explored using maximum likelihood, Bayesian, and parsimony approaches as well as through reconstruction of a haplotype network. To choose our maximum likelihood model and parameters, we used MrModeltest, vers. 1.1b (Nylander, 2002) to choose the best fit model for the combined data. Using a starting tree constructed using neighbor joining and Kimura 2-parameter distances, we chose the best fit model by a likelihood ratio test. The chosen model (HKY85 + I + Γ) and parameters were then used in a maximum likelihood analysis with 10 random addition replicates as implemented in PAUP* 4.0b10 (Swofford, 2002). Support for nodes was obtained through 100 bootstrap replicates of the data set. Parsimony analyses were also implemented using PAUP* 4.0b10 (Swofford, 2002). Each site was given equal weight, and we used the heuristic search option with 1000 random addition replicates and the tree-bisection–reconnection branch swapping algorithm.

Bayesian analyses were performed with data partitioned by each gene region (the cyt *b* segment and the ATPase segment). We used MrModelest, v. 1.1b (Nylander, 2002) to choose the best fit model via a likelihood ratio test for each gene region separately, in case different models were optimal for the different gene regions. We then used the chosen models (HKY85 + I + Γ was identified for cyt *b*; GTR + Γ was identified for the ATPases) in conjunction with MrBayes 3.0b3 (Huelsenbeck and Ronquist, 2001) to perform Bayesian analyses on the data set. Our analyses did not specify values for specific nucleotide substitution model parameters. Thus, parameters were treated as unknown variables with uniform prior values and estimated as part of the analysis. We partitioned the data separately by gene and allowed the parameters to be determined separately for each gene by unlinking them prior to analysis. This was done to account for potential differences in optimal model parameters for the two genes. This analysis was run for five million generations and sampled every 100 generations, resulting in 50,000 samples. Four Markov Chain Monte Carlo chains were run for each analysis. Resulting log-likelihood scores were plotted against generation time to identify the point at which log-likelihood values reached a stable equilibrium value. Sample points prior to this point of stationarity were

discarded as "burn-in" samples. The remaining samples were used to produce a majority rule consensus tree, with the percentage values indicating the percentage of samples that identified a particular clade (the clade's posterior probability). We repeated the analysis five times to ensure that results were not dependent on the initial random starting tree used. For these repeated analyses, we compared log-likelihood values and posterior probabilities of each repeated analysis to confirm that using a different starting tree did not alter our results significantly.

In addition to the tree-building methods described above, we also performed a Nested clade phylogeographical analysis (NCPA, Templeton, 1998; Templeton, 2004). A haplotype network was generated according to the parsimony-based algorithm developed by Templeton et al. (1992), as implemented in the program TCS v.1.13 (Clement et al., 2000). Inferred relationships of the haplotype network were nested by hand following rules described in Templeton et al. (1987) and Templeton and Sing (1993). Nesting design in conjunction with genetic data and locality data (in the form of latitude and longitude coordinates) was used in random permutational analysis as implemented by GeoDis v. 2.0 (Posada et al., 2000). For each nested clade, both clade distance and nested clade distance were calculated. Clade distance (D_c) is the average distance of a clade's haplotypes from the geographical center of those haplotypes. Nested clade distance (D_n) measures how far the geographic center of a particular clade is to the geographic center of all clades nested at the same level. Clades with statistically significant values (0.05 level) for either of the two measures of geographical distance (D_c and D_n) were taken through an inference key (Templeton, 2004) in order to infer population-level evolutionary processes.

2.3. Rooting

Two methods were used to infer the root of our intraspecific trees and network. First, a traditional method was used in which outgroup taxa were used to infer polarity and root ingroup taxa. The wrentit is the only North American representative of a large clade of babblers (Timaliidae). This clade contains more than 200 species, but two recent studies have identified potential close relatives of the wrentit within this clade. Of the species sampled by Barhoum and Burns (2002), species in the genus *Sylvia* were identified as the most closely related species to the wrentit. Cibois (2003) had more extensive sampling of babblers and placed the wrentit within a clade that included species in the genera *Sylvia*, *Paradoxornis*, *Pseudoalcippe*, *Chrysomma*, and some species of *Alcippe*. We used cyt *b* sequences from a variety of species in these genera to root our tree (GenBank Accession Nos. Z73494, AF135052, AF484843, AF484872, AF484873, AF484874, AF484875, AF484878, AJ534542, AY124540, AY128549, AY128552). These sequences and the cyt *b* portions of the wrentit sequences were subjected to Bayesian analyses following the protocol described above.

We also inferred root placement using neutral coalescent theory by calculating root probabilities using TCS v.1.13 (Clement et al., 2000). This method uses haplotype frequency (common/rare) and topology of the unrooted tree (tip/interior distinction and connectedness) to assign outgroup weights or root probabilities to haplotypes (Castelloe and Templeton, 1994; Crandall et al., 1994). In general, haplotypes occurring in a greater frequency and having more connections are more likely to be identified as the ancestral haplotype.

3. Results

3.1. Sequence variation and population structure

Thirty-nine unique haplotypes were found among the 61 individuals sequenced. Of the 2148 total base pairs, 2102 (98%) characters were constant, 24 (1%) were variable but uninformative, and 22 (1%) were parsimony informative. Transition and transversion variation by codon position for protein-coding portions of ATPase6, ATPase8, COII, COIII, and cyt *b* were as follows: position one—10 transitions and 2 transversions, codon position two—4 transitions, and codon position three—24 transitions and 6 transversions. Uncorrected *p*-distance averaged 0.14% (range 0–0. 51%) among wrentit individuals.

Overall geographic structure among localities was indicated by an AMOVA in which individuals were categorized into populations ($\Phi_{st} = 0.41$; Table 2). Although populations were structured, more variation was explained by within population differences rather than among population differences. Results of the AMOVA in which populations were divided into subspecies (Table 2) indicate that little of the variation (14.6%) can be attributed to subspecies. Again, most of the variation is due to differences within populations. A mismatch distribution of all individuals was unimodal and not significantly different for the expected distribution of a growing population ($p = 0.17$, mean = 4.35, raggedness index = 0.33). We obtained a significantly negative value for Fu's F_s ($F_s = -11.82$, $p = 0.0003$), indicating a possible recent expansion in population size.

3.2. Rooting

In agreement with Cibois (2003), our Bayesian analyses that included potential outgroups placed the wrentit samples in a clade with representatives of the genera *Alcippe*, *Chrysomma*, and *Paradoxornis* (posterior probability = 100%). However, support for nodes among

Table 2
Analysis of molecular variance in the wrentit

Groups	Source of variation	Percentage of variation	Φ statistic	p
None specified	Among populations	41.3	0.41	<0.0001
	Within populations	58.7		
Subspecies	Among subspecies	14.6	0.15	0.0068
	Among populations within subspecies	29.7	0.35	<0.0001
	Within populations of species	55.7		

Results are shown first for an analysis in which populations were not divided into groups and then for an analysis in which populations were divided into subspecies.

these genera was too low to distinguish which of these taxa was most closely related to the wrentit. Among wrentit samples, a clade containing individuals labeled I1 and H3 was identified as being the most basal clade. In contrast, the coalescent-based method identified a haplotype shared by nine individuals (labeled K1, L1, M1, N1, N3, O1, O2, P1, and Q1) as being the most probable ancestral haplotype (outgroup weight of 0.15).

3.3. Relationships among haplotypes

Maximum likelihood analysis of haplotype relationships resulted in a tree (−ln likelihood = 3330.063, Fig. 2) which recognizes six major clades. Each of these clades is restricted geographically, although most clades have overlapping distributions (Fig. 3). In general, relatively few substitutions define each clade. Clade I includes all individuals from the central Coast Ranges (populations K, L, and M) and all individuals from the Transverse Ranges with the exception of the San Bernardino Mountains (populations N, O, P, and Q). Clade II is comprised of all northern-most samples (populations A and B) as well as one individual from northern California (population F). Clade III consists of northern California populations (populations F, H, and I). Clade IV has all southern Oregon populations (populations C, D, and E) as well as two northern California populations (populations F and G). Clade V contains individuals from the Sierra Nevada (population J) as well as northern California (populations G, H, and I). Clade VI consists of all individuals from the Peninsular Ranges (southern California and Baja California, populations S and T) as well as the San Bernardino Mountains (population R) which are part of the Transverse Ranges. In addition to these six clades, one individual from population I did not show a close relationship to any of these clades (I5, Fig. 2). Relationships among the six clades could not be resolved and most relationships within the clades are also ambiguous.

For the Bayesian analyses, log-likelihood values reached a stable equilibrium well before 500,000 generations. Thus, we chose a burn-in value of 5000 samples for each analysis. The five repeated analyses converged on similar posterior probabilities and likelihood values, indicating insensitivity to initial starting tree. The majority-rule consensus tree of the 45,000 trees shows broad agreement with the maximum likelihood tree (Fig. 2). The Bayesian analyses identified the same six clades identified in the maximum likelihood analyses.

Equal weights maximum parsimony analysis yielded 6300 most-parsimonious trees (length = 60 steps, consistency index = 0.783). All of these trees identified clades II, III, IV, and VI. Clade I was identified in 67% of the most-parsimonious trees and clade V was identified in 81% of the most-parsimonious trees (Fig. 2).

3.4. Nested clade phylogeographical analysis

Haplotype network construction resulted in a single network in which all connections (<20 steps) fall within a 95% plausible set of relationships (Fig. 4). A total of 62 haplotypes (39 sampled and 23 unsampled) make up the network which was nested into a single 4-step clade. Ambiguities or loops where multiple mutational pathways are equally probable were left unbroken and nested accordingly. Only clades that displayed both geographic and genetic variation were used in permutational analysis. Of the twenty-seven 1-step clades, eight contained both genetic and geographical variation of which none showed significant geographical association (no significant D_c or D_n values). Of the eleven 2-step clades, eight contained both genetic and geographical variation, but only clade 2-3 showed a significant geographical association. Of the four 3-step clades, all contained both genetic and geographical variation of which three showed significant geographical association, and the one 4-step (total cladogram) clade also showed significant geographical association. Evolutionary patterns identified from permutational analysis were as follows (Table 3, Fig. 5):

Clade 2-3 (inconclusive outcome)—both 1-4 and 1-9 are interior clades and make up clade 2-3. Clade 1-4 has significantly small D_c and D_n values. Although significant D_c and D_n values were generated, no inferences can be made about the significant geographical associations within the clade because tip/interior status cannot be determined.

Clade 3-1 (past fragmentation)—clade 3-1 contains all individuals from the Coast, Transverse, and Peninsular Ranges (populations K through T). Clade 2-1 (Coast

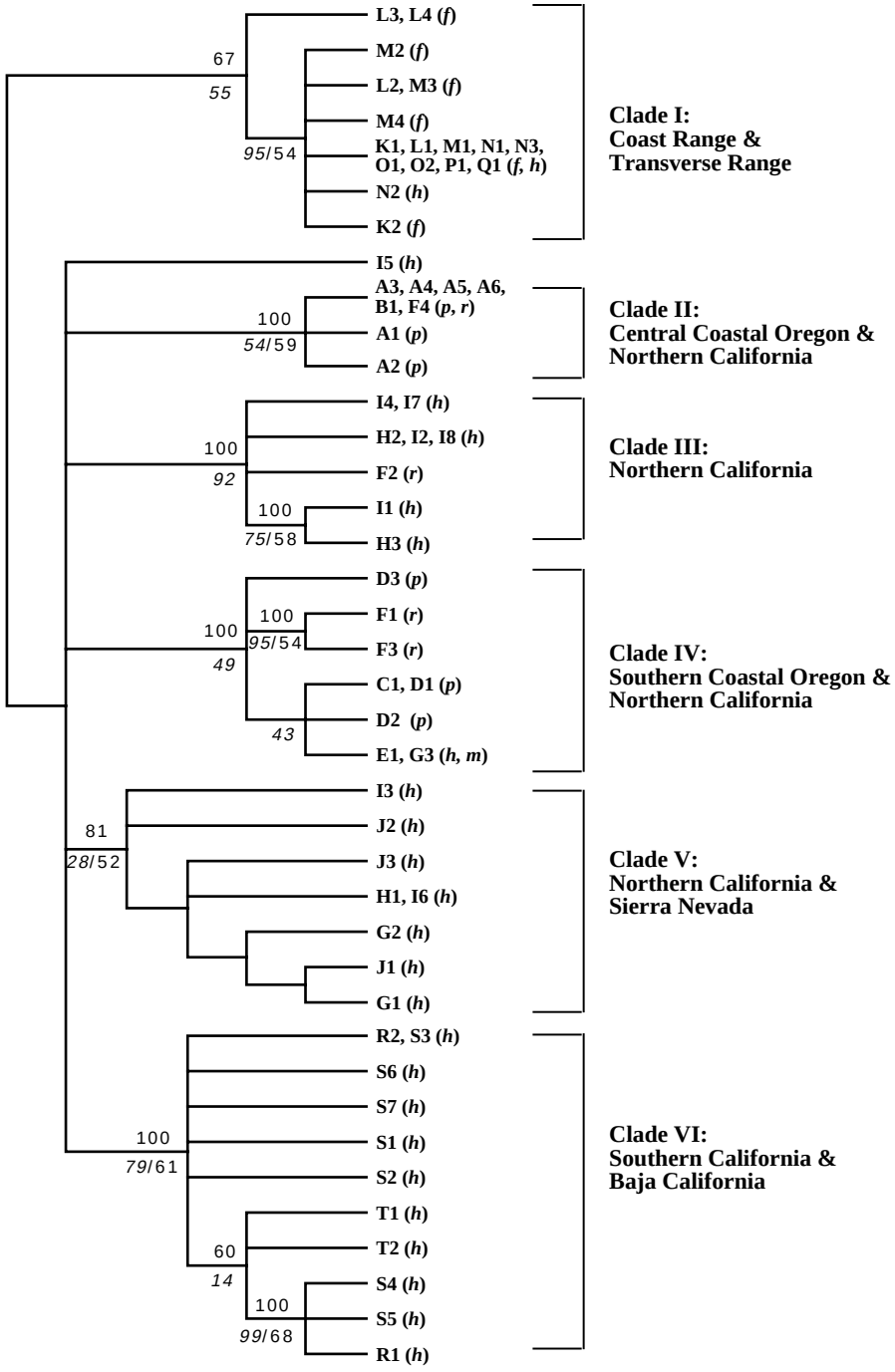

Fig. 2. Maximum likelihood tree of wrentit haplotypes. Terminal haplotypes are coded by population and individual according to Table 1. Therefore, haplotypes shared by more than one individual are represented by multiple letter and number combinations. Lowercase letters following terminal haplotypes indicate subspecies represented by the haplotype (*f* = *fasciata*, *h* = *henshawi*, *p* = *phaea*, *r* = *rufula*, and *m* = *marga*). The branch lengths are not proportional and the tree is unrooted. Numbers above the nodes indicate the percentage of equally weighted parsimony trees that recovered the clade, italicized numbers below the nodes indicate Bayesian posterior probabilities, and non-italicized numbers below the node indicate the number of maximum likelihood bootstrap replicates that retained the clade.

Ranges and the Transverse Ranges excluding San Bernardino Mountains) has a significantly small D_c value and its geographic distribution is mostly non-overlapping with those of clades 2-2 and 2-3 (mostly Peninsular Ranges and San Bernardino Mountains). Thus, an allopatric fragmentation event is inferred for 3-1. According to the geographic distributions of these clades, this event occurred within the Transverse Ranges at the gap separating the San Bernardino Mountains from the rest of the Transverse Ranges (Fig. 5). These two geographic

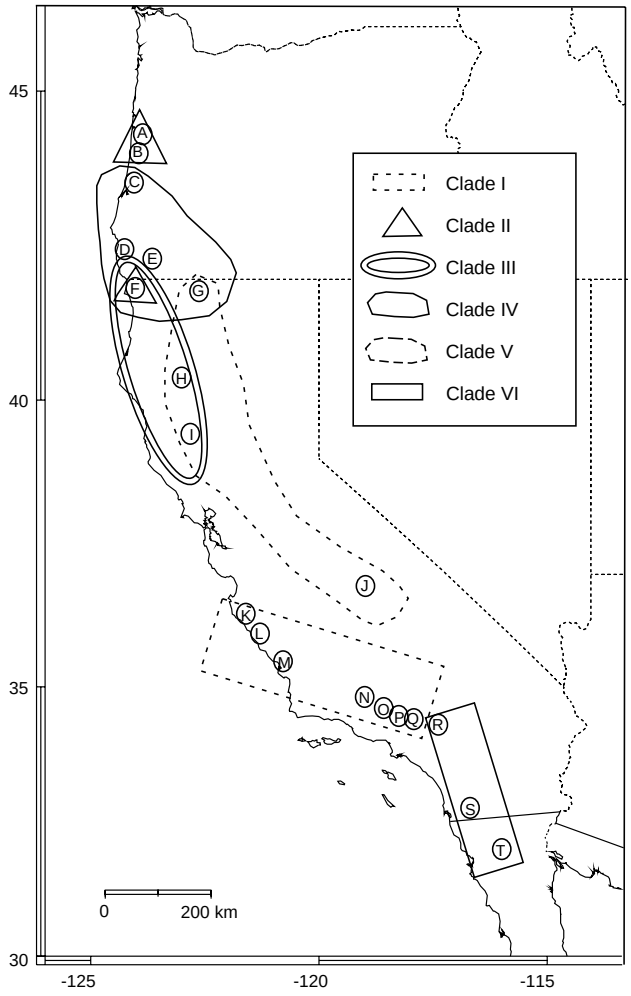

Fig. 3. Geographic distribution of the six major clades identified by parsimony, maximum likelihood, and Bayesian analyses.

regions also formed separated clades in the maximum likelihood, parsimony, and Bayesian analyses (clade I and clade VI, Figs. 2 and 3).

Clade 3-3 (restricted gene flow with isolation by distance)—members of clade 3-3 are found in the Sierra Nevada, near the California and Oregon border, and northwest of the Central Valley. Members of interior clade 2-11 are significantly far from other 3-3 members (significantly large D_n). In addition, the ranges of members of the 2-step clades within clade 3-3 are mostly overlapping. Thus, restricted gene flow with isolation by distance is inferred.

Clade 3-4 (inconclusive outcome)—all individuals from the Oregon populations and two of the northernmost California populations make up clade 3-4. Geographic distance analysis shows that individuals from clade 2-7 are significantly underdispersed. That is, the average distance of this clade's haplotypes from the geographical center is significantly small (significantly small D_c). However, the D_c and D_n values of the remaining clades within 3-4 are such that no conclusions about evolutionary processes can be made from the inference key.

Total cladogram 4-1 (range expansion—contiguous and through long distance colonization)—four 3-step clades make up the total cladogram (Figs. 4 and 5). The interior or ancestral clade (3-1) is made up of populations from the southern end of the wrentit's distribution as well as a more northern individual from population I. A significantly small D_c value for this interior clade leads to an inference of range expansion. Relationships between the interior clade 3-1, and tip clades 3-2 and 3-3 infer patterns of contiguous range expansion from clade 3-1 to clades 3-2 and 3-3. Due to significantly reversed D_c and D_n values for clade 3-4, two possible inferences can be made for 3-4. One possibility is that a long distance colonization event occurred in the past from the southern clade 3-1 to the northernmost part of the distribution occupied by clade 3-4. Alternatively, the pattern observed could have been produced by fragmentation followed by a subsequent contiguous range expansion. Under either scenario, range expansion is inferred. Because outgroup rooting infers that I3 and H3 are the oldest haplotypes, we also considered the possibility that 3-2 is the interior clade in the network for the NCPA analyses. Even under this scenario, we still obtain the inference of recent range expansion for the entire cladogram.

4. Discussion

4.1. Subspecific taxonomy

Since the early 1900s, ornithologists have described morphological variation in the wrentit (Bowers, 1960; Bowles, 1911; Grinnell, 1913, 1915). This morphological variation, in particular plumage color and tail length, is currently used to divide the wrentit into five subspecies (Browning, 1992; Dickinson, 2003; Geupel and Ballard, 2002; Phillips, 1986). In at least some parts of the range, plumage variation follows ecomorphological trends with darker individuals found in more humid environments (Bowers, 1960). The most northern subspecies, *C. f. phaea*, is the darkest subspecies and occurs from humid coastal Oregon south to the California/Oregon border (Fig. 1; populations A–D). The subspecies with the most restricted distribution, *C. f. marga*, is confined to interior southern Oregon (population E). *C. f. rufula* is distributed along the north coast of California (population F). *C. f. fasciata* is distributed along the central coast of California (populations K–M). The subspecies with the most widespread distribution, *C. f. henshawi*, is also the palest and is found from northern California south through the west slope of the Sierra Nevada and southern California to northern Baja California (populations G–J and N–T).

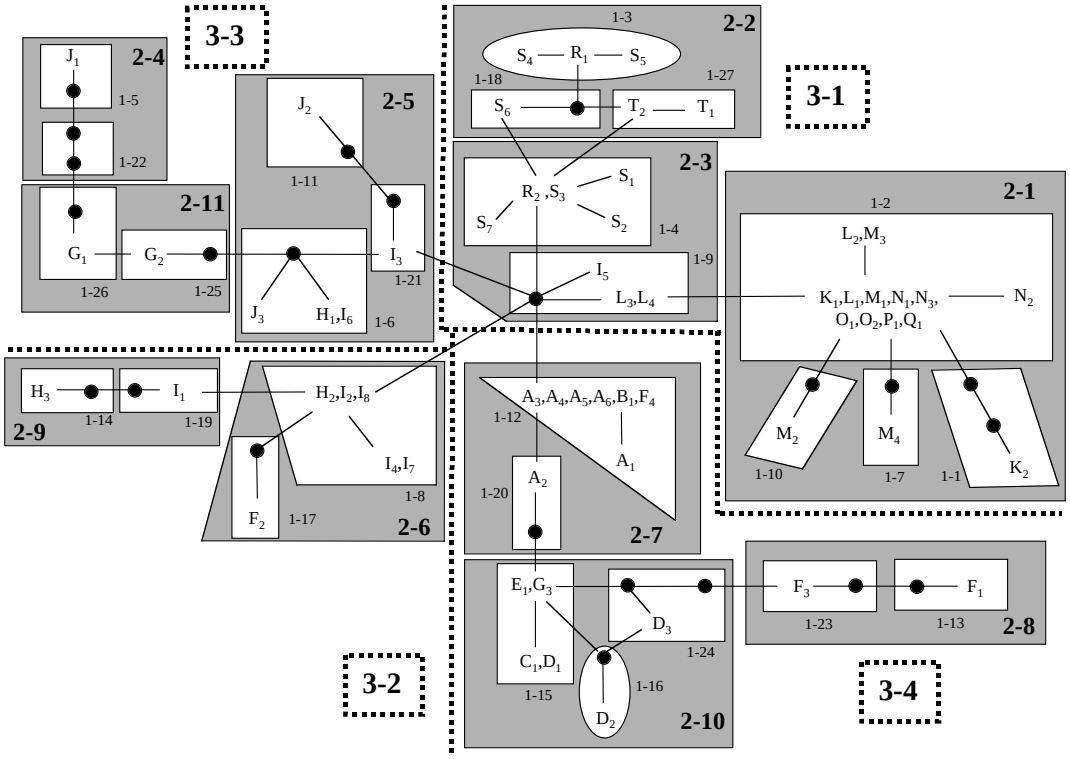

Fig. 4. Nested haplotype network. Each branch represents a single base pair mutation. Black circular nodes represent unsampled haplotypes; lettered nodes represent sampled haplotypes. Each letter with subscript number is one individual from its corresponding locality (Fig. 1, Table 1). 1-step clades are contained within white boxes, 2-step clades are contained within larger shaded boxes, and 3-step clades are delineated by dashed lines. The overall cladogram is a single 4-step clade.

Table 3
Chains of inference of clades with significant D_c or D_n values

Clade	Inference Chain	Inferred pattern or demographic event
2-3	1-19-20-2	Inclusive
3-1	1-2-3-4-9	Past fragmentation
3-3	1-2-11-17-4	Restricted gene flow with isolation by distance
3-4	1-2-11-17	Inconclusive
4-1	1-2-11-12-13-21	Range expansion (long distance colonization or fragmentation followed by continuous range expansion)

Analyses of mtDNA variation within the wrentit do not support this current subspecific taxonomy. Parsimony, Bayesian, and maximum likelihood analyses consistently identified six clades that were restricted geographically (clades I–VI; Figs. 2 and 3). However, this geographic structure does not match the subspecific taxonomy of the wrentit. In the trees produced in this study (Fig. 2), none of the subspecies forms a monophyletic group and each of the major clades identified includes a mix of different subspecies. Representatives of one of the subspecies (*C. f. henshawi*) is found in five of the six major clades. In addition, some individuals from different subspecies have identical haplotypes. For example, the haplotype shared by K1, L1, M1, N1, N3, O1, O2, P1, and Q1 spans the geographic range of two different subspecies (*C. f. fasciata* and *C. f. henshawi*). Likewise, the haplotype shared by A3, A4, A5, A6, B1, and F4 includes representatives of *C. f. phaea* and *C. f. rufula*, and the haplotype shared by E1 and G3 includes representatives of *C. f. henshawi* and *C. f. marga*. The AMOVA also indicates that population structure does not reflect subspecific taxonomy. When genetic data were partitioned by subspecies, only a small amount of variation could be explained by subspecific boundaries, and Φ_{st} actually decreased when subspecific boundaries were taken into account (Table 2). Our results for the wrentit add to the growing body of literature (Zink, 2004) demonstrating that recognized avian subspecies do not match evolutionary units as defined solely by mtDNA.

The lack of concordance in the wrentit between mtDNA variation and subspecific taxonomy does not necessarily indicate that the morphological variation apparent among localities is insignificant. The plumage color differences, for example, may have an underlying genetic basis and may spread more rapidly through a population than neutral mtDNA alleles if they are subject to strong selection. Recent studies (e.g., Hoekstra and Nachman, 2003; Mundy et al., 2004) have indicated that DNA sequence differences in the melanocortin-1 receptor (MC1R) gene are directly related to observed color differences similar to that observed in the wrentit.

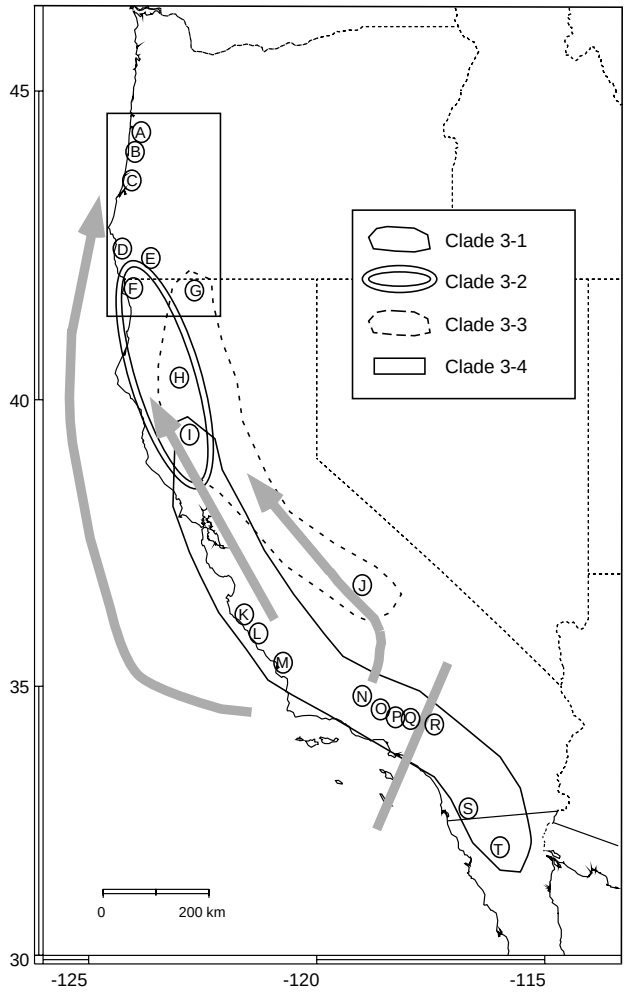

Fig. 5. Diagrammatic representation of biogeographic conclusions. Three-step clades are outlined. Arrows indicate directions of proposed range expansions, both contiguous and long-distance colonization. The thick grey line between populations Q and R indicates the location of the proposed fragmentation event.

If plumage color does have a genetic basis, it may represent adaptation to local conditions, an important trait that may warrant preservation in some cases (Crandall et al., 2000). Nevertheless, the monophyletic units reflected by the mtDNA data are likely older and thus reflect more fundamental evolutionary divisions within this species (Zink, 2004).

4.2. Phylogeography of the wrentit

The wrentit has no close relatives in North America and is genetically distant from any of its potential close relatives in Asia. Based on our Bayesian analyses of outgroup relationships, and in agreement with Cibois (2003), members of the genera *Alcippe*, *Chrysomma*, and *Paradoxornis* were most closely related to the wrentit, with average uncorrected sequence divergence around 13%. Assignment of a molecular clock rate of 1.6–2.0% divergence per million years for bird mtDNA (Fleischer et al., 1998; Shields and Wilson, 1987) indicates that the wrentit diverged from its ancestors 6.5–8.1 million years ago. Our data are unable to elucidate when or how a wrentit ancestor arrived in North America (through over-water dispersal or via the Beringia land bridge). However, inferences can be made about more recent history within the wrentit, given that the maximum divergence observed among wrentit individuals is 0.51%. Our two methods of rooting arrived at different interpretations for the location of the oldest wrentit populations within this time frame. Because the wrentit is so divergent from its close relatives, the use of traditional outgroup methods for identifying older haplotypes is problematic (Castelloe and Templeton, 1994). With this method, one is attempting to polarize a group of sequences that may differ slightly by using outgroups that usually differ considerably from the ingroup. Wrentit sequences are relatively weakly differentiated from each other compared to levels of divergence observed between wrentit individuals and potential close relatives. Thus, the long branch connecting the genera *Alcippe*, *Chrysomma*, and *Paradoxornis* to the wrentit may contain numerous homoplasies obscuring phylogenetic signal. Although Bayesian analyses indicated that the haplotypes I1 and H3 are the oldest wrentit haplotypes, these individuals are some of the most divergent wrentit samples. Furthermore, the posterior probability of this relationship is extremely small (17%). Thus, results of the outgroup rooting are probably best interpreted as inconclusive. Neutral coalescent theory (Castelloe and Templeton, 1994) inferred the haplotype shared by K1, L1, M1, N1, N3, O1, O2, P1, and Q1 as being the most probable ancestral haplotype. This method uses haplotype frequency for making inferences; thus, it can be influenced by overall sampling design. However, our sampling was roughly equivalent in the northern ($n = 29$) versus the southern ($n = 32$) parts of the wrentit's range. Therefore, it is unlikely that sampling is driving the conclusion that a southern haplotype is the oldest haplotype in the network. A southern ancestry also agrees with the fact that cooler temperatures during the Pleistocene (over 200,000 years ago) probably restricted the range of the wrentit to the southern end of its current distribution (populations K–T).

Given the results of the analyses of this study, we propose the following biogeographic scenario for the recent history of the wrentit (Fig. 5). The wrentit was initially isolated into the southern parts of the distribution. As temperatures warmed and aridity increased during the Pleistocene/Holocene transition (Cicero, 1996), a contiguous northward expansion of the wrentit followed. Members from this southern ancestral population likely used the foothills of the Coast Ranges to establish the northern clade 3-2. In the same fashion, southern ancestral members could have used the Sierra Nevada foothills to establish clade 3-3. A long distance colonization

event could have occurred as a result of the post-glacial expansion of chaparral into Oregon (Detling, 1961), resulting in the pattern of reversed D_c and D_n values seen in clade 3-4. Several lines of evidence support a recent range expansion in the wrentit described above. NCPA inferred range expansion for the entire cladogram. In addition, the mismatch distribution was unimodal and Fu's F_s was significantly negative; both are indications of recent population growth. More recently, patterns of differentiation within clade 3-3 are driven by restricted gene flow with isolation by distance. Within clade 3-1 a vicariant event was inferred within the Transverse Ranges between the San Gabriel and San Bernardino Mountains (populations Q and R; Fig. 5). The two areas may represent two separate southern refugia in which the wrentit was isolated during the Pleistocene.

4.3. Comparative phylogeography

California is a complex geographic region with more climatic and topographic variation than any other region of comparable size in the United States (Schoenher, 1992). By comparing the phylogeography of co-distributed taxa, the influence of common historical events on lineage diversification in this region can be evaluated. Of all the species that have been studied in this region, the most relevant species to compare to the wrentit is the California thrasher (*Toxostoma redivivum*) (Sgariglia and Burns, 2003). Both taxa are avian species that co-exist in the same community, have a similar distribution, occupy similar habitat, and have similar life history traits (non-migratory residents with short natal dispersal). Also, the same molecular markers and sampling sites were used in both studies and both birds exhibited similar levels of intraspecific sequence divergence. Thus, if biogeographic events commonly result in similar patterns across species, one would expect the same inferences to be made for both species. While the two species do show many similarities, several important differences were also identified. For both species, a southern ancestry was inferred with the ancestral haplotype for both species occurring in both the Transverse and Coast Ranges (populations K–R). A northward post-glacial range expansion was also inferred for both species. However, a division between northern populations and southern populations was identified for the California thrasher in the vicinity of the Transverse Ranges. In contrast, wrentit populations show little divergence between populations north and south of the Transverse Ranges. For example, populations on the southern slope of the Transverse Ranges (clade I, populations N–Q) are no more similar to other southern California populations in clade VI (populations R–T) than they are similar to northern California and Oregon populations (clades II, III, IV, and V). Another difference between the wrentit and California thrasher involves the break between populations Q and R within the Transverse Ranges that was observed for the Wrentit but not found for the California thrasher. The wrentit also differs from the California thrasher in that the wrentit has colonized large areas of Oregon, probably during the post-glacial expansion of chaparral into this area. However, the California thrasher does not occur in this area, despite the presence of suitable habitat into this region.

In addition to the California thrasher, the phylogeography of many other species has been studied in the California Floristic Province in recent years. Calsbeek et al. (2003) analyzed data from 55 of these studies including studies of plants, insects, mammals, birds, reptiles, and amphibians, and they identified concordant patterns seen among many species. Most animal taxa showed reciprocal monophyly between two or more geographically restricted clades. Calsbeek et al. (2003) noted the lack of bird studies in this region, but were able to include data from five studies: large-billed fox sparrow (*Passerella megarhyncha*; Zink, 1994); spotted owl (*Strix occidentalis*; Barrowclough et al., 1999); California gnatcatcher (*Polioptila californica*; Zink et al., 2000), clapper rail (*Rallus longirostris*; Fleischer et al., 1995), and loggerhead shrike (*Lanius ludovicianus*; Mundy et al., 1997). Data from the avian studies contrasted with those seen in other animals in that the bird studies showed extensive polytomies and lack of population-specific haplotypes. Thus, the phylogeographic patterns described here for the wrentit and the California thrasher contrast somewhat with those of other avian studies. Although some lack of resolution is present in the trees of both the wrentit and California thrasher, more geographic structure was identified for the California thrasher and the wrentit than for most of the other bird studies. This result probably reflects different population-level histories of these species. However, differences in sampling design, markers used, or methods of analyses between previous work and the thrasher and wrentit studies could also be driving the dissimilarity in degree of population structure recovered.

The most obvious concordant pattern seen in the non-bird studies involved a genetic break in the vicinity of the Transverse Ranges. Most animal taxa had an obvious genetic split in this region, dividing populations in southern California from those in northern California. Most of the five bird species available to Calsbeek et al. (2003) do not occur in both northern and southern California on both sides of the Transverse Ranges. Thus, these species cannot be used to test the significance of this barrier to avian population differentiation. However, one of these (the large-billed fox sparrow) does occur on both sides of the Transverse Ranges, and the populations studied did not show major genetic differences across this area (Zink, 1994). The large-billed fox sparrow is a migrant; therefore, its lack of congruence may be explained by greater dispersal abilities. However,

the wrentit and California thrasher are both sedentary taxa with limited dispersal abilities. Although the break at the Transverse Ranges was detected in the California thrasher, it was not seen in the wrentit. In addition to the above-mentioned studies, we are aware of only one other bird study that can be used to look for phylogeographic concordance in this region, a study of the oak titmouse (*Baelophus inornatus*; Cicero, 1996). This study also revealed a genetic break between northern and southern populations in the vicinity of the Transverse Ranges. Although a distinct genetic break was not revealed in the wrentit at the site of the Transverse Ranges, this break clearly influenced the evolution of a variety of species, including some birds. In addition to a break at the Transverse Ranges, many vertebrate taxa also show a general pattern of southern ancestry or southern refugia, similar to those seen in both the wrentit and California thrasher. Taxa that exhibit this pattern include the California mountain kingsnake (*Lampropeltis zonata*; Rodriguez-Robles et al., 1999), dusky-footed woodrat (*Neotoma fuscipes*; Matocq, 2002), California newt (*Taricha torosa*; Tan and Wake, 1995), *Eumeces skiltonianus* species complex (Richmond and Reeder, 2000), California mouse (*Peromyscus californicus*; Smith, 1979), ornate shrew (*Sorex ornatus*; Maldonado et al., 2001), and the oak titmouse (*Baelophus inornatus*; Cicero, 1996).

Comparative phylogeography of diverse organisms can reveal how the ecological characteristics of a species influence its ability to respond to particular biogeographic events. For example, Ditchfield (2000) showed that Neotropical bats have lower levels of geographic structuring than non-volant mammals in the same region. For birds, similar conclusions can be made within the California Floristic Province. Phylogenies of some avian taxa show less resolution overall than those of non-volant taxa in this region, suggesting that different life histories have effected patterns of differentiation. However, some species such as the California thrasher and wrentit show geographic structure and some of the phylogeographic patterns correspond to those seen in non-avian species. Further studies of avian taxa are still needed to help clarify the extent to which birds comply with the evolutionary patterns seen in other species in this region. Studies focusing on other non-migratory avian species that occur across the region like the wrentit and the California thrasher will be particularly useful.

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