

Statistical Assessment of Congruence Among Phylogeographic Histories of Three Avian Species in the California Floristic Province

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CHAPTER 8

STATISTICAL ASSESSMENT OF CONGRUENCE AMONG PHYLOGEOGRAPHIC HISTORIES OF THREE AVIAN SPECIES IN THE CALIFORNIA FLORISTIC PROVINCE

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ABSTRACT.—Comparing phylogeographic histories of codistributed species can reveal how common historical events and processes have influenced lineage diversification across species. Within the California Floristic Province, the phylogeographies of a diversity of plants and animals have been studied; however, only a few bird species have been examined in this region. We compared phylogeographic histories of three species of birds—Wrentit (*Chamaea fasciata*), California Thrasher (*Toxostoma redivivum*), and White-headed Woodpecker (*Picoides albolarvatus*)—to each other as well as to the phylogeographic histories of other California taxa. Qualitatively comparing phylogeographies of these three species reveals some similarities and some differences. All three species exhibit similar levels of sequence divergence, experienced recent range expansions, and show a division between southern and northern populations in the vicinity of the Transverse Ranges. However, nested-clade phylogeographic analysis suggests that different processes have influenced current patterns of genetic structure in these three species. Other taxa within California show a similar division between northern and southern populations; however, our species did not show concordant geographic breaks elsewhere that have been identified for other species. Using a statistical assessment of concordance, our data showed more agreement across a broader regional scale than among closely spaced populations. Phylogeographic trees of the three species showing relationships among counties were not statistically congruent with each other or with a tree representing other California taxa. However, at the broader level of geomorphic province, the Wrentit and White-headed Woodpecker showed complete concordance. *Received 30 June 2006, accepted 5 February 2007.*

RESUMEN.—La comparación de la historia filogeográfica de las especies con distribuciones similares, puede revelar cómo los eventos históricos y los procesos comunes que han experimentado estas especies han influenciado la diversificación de sus linajes. Dentro de la provincia florística de California, se ha estudiado la filogeografía de diversas plantas y animales; sin embargo, sólo se han estudiado unas pocas especies de aves. En este estudio, comparamos la historia filogeográfica de tres especies de aves—*Chamaea fasciata*, *Toxostoma redivivum* y *Picoides albolarvatus*; además, comparamos la historia filogeográfica de otros taxones californianos. Las comparaciones cualitativas de la filogeografía entre las tres especies antes mencionadas, revelan algunas diferencias y similitudes. Las tres especies muestran niveles similares de divergencia genética, presentando, además, expansiones recientes en sus rangos de distribución y mostrando una división entre las poblaciones del norte y del sur en las cercanías de los rangos transversales. Sin embargo, los análisis filogeográficos de clados encajados (NCA) sugieren que los patrones de estructura genética en estas tres especies han sido determinados por procesos diferentes. Otros taxones dentro de California muestran una división similar entre las poblaciones del norte y del sur; sin embargo, nuestras especies no muestran una interrupción en otras áreas geográficas, las que han sido identificadas en especies con una misma distribución. Utilizando un análisis estadístico de correspondencia nuestras aves muestran mayor concordancia a través de una amplia escala regional que entre

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poblaciones que esten cercanamente espaciadas. Los árboles filogeográficos de las tres especies que muestran las relaciones entre condados no son estadísticamente congruentes entre ellos, como tampoco lo son con los árboles de otros taxones de California. Sin embargo, al nivel más amplio de la provincia geomórfica, existe una total congruencia entre *Chamaea fasciata* y *Picooides albolaryvatus*.

STUDIES OF GEOGRAPHIC variation in morphology (Johnson 1966, 1980; Johnson and Marten 1992) have long provided insight into the evolutionary history of species. With the advent of DNA sequencing, study of geographic variation in genetic data through phylogeographic analyses has provided additional insights into the processes responsible for diversification within species (Barrowclough et al. 2004, Cicero and Johnson 2007). Comparing the phylogeographic histories of multiple species provides a broader context for these diversification processes by identifying how geology, geography, ecology, and climatic history may have shaped population structure across codistributed species (Bermingham and Avise 1986, Zink 2002). However, comparing phylogeographic histories is difficult, partly because methods assessing statistical congruence across species have been explored only recently (Edwards and Beerli 2000, Calsbeek et al. 2003, Lapointe and Rissler 2005).

For strong inferences to be made, the phylogeographic histories of a large number of diverse taxa within the same region are necessary. Such a large data set now exists for the region known as the California Floristic Province. This region, which stretches from southwestern Oregon to northern Baja California, mostly coincides with the political boundaries of the state of California. The complex geological history of the area has led to a diversity of habitats and high levels of endemism, and the area is considered one of 34 biodiversity hotspots in the world (Mittermeier et al. 2005). In fact, more endemic taxa occur there than in any other similar-sized region in North America (Calsbeek et al. 2003). Among birds, Miller (1951) included 13 species and nearly 100 subspecies of birds within the Californian avifauna (defined by having their distributions confined to or at least centered within California).

Two recent studies have synthesized phylogeographic data for this region. Calsbeek et al. (2003) found largely congruent patterns of genetic diversity across 55 species (24 plants, 10 insects, 8 reptiles, 6 mammals, 5 birds, and 2

amphibians). Patterns of differentiation in many of these species corresponded to common past physical events. For example, most animal taxa studied showed an obvious genetic split dividing northern and southern populations around the Transverse Ranges. More recently, Lapointe and Rissler (2005) used statistical tests of congruence to compare phylogeographic histories of nine taxa. The species they studied included three amphibians, two mammals, one reptile, one bird, one insect, and one plant, each sampled from an average of 17 counties. They found significant phylogeographic signal in common across these taxa and, thus, were able to combine the data from each of these nine taxa into a single supertree representing biogeographic relationships among regions. In general, these studies show that different species have congruent phylogeographic histories within the California Floristic Province. However, only a handful of bird studies have been conducted in the area, compared with the large number of studies available for other taxa (Calsbeek et al. 2003). Here, we compare the phylogeographic histories of three different bird species and assess their congruence with each other and with other species in the region.

The three species we studied occur across the California Floristic Province and are generally sedentary, with little postbreeding dispersal (Baker et al. 1995, Garrett et al. 1996, Cody 1998). Two of the species, the Wrentit (*Chamaea fasciata*) and the California Thrasher (*Toxostoma redivivum*), are mostly restricted to California. The third species, the White-headed Woodpecker (*Picooides albolaryvatus*), has a broader distribution that also includes parts of Oregon, Washington, Idaho, and British Columbia. The Wrentit and the California Thrasher occupy similar mid- and low-elevation scrub and chaparral habitats (Cody 1998, Geupel and Ballard 2002), whereas the White-headed Woodpecker is found at higher elevations, largely confined to coniferous areas >850 m in elevation (Garrett et al. 1996). Similarities in habitat between the Wrentit and the California Thrasher may lead to more

similar phylogeographic histories, if similar climatic histories shape patterns of population structure. Alternatively, broader geographic or geological factors that transcend habitat may play a more important role, leading to congruence across all three species.

Each species was the focus of a separate phylogeographic study (Sgariglia and Burns 2003, Alexander and Burns 2006, Burns and Barhoum 2006). Thus, we do not present details of the phylogeographic history of each species. Instead, we concentrate on two main goals: (1) assessing congruence among these three species and (2) assessing congruence between each of these species and the general patterns seen in other taxa of the California Floristic Province.

Comparing phylogeographic histories among diverse organisms is often challenging because sampling designs, genetic markers, and analytical methods differ among studies, and because a rigorous methodology does not exist for identifying whether similarities and differences among species are statistically significant. We have attempted to overcome these problems by using the same genetic markers, by sampling each species from the same or nearby localities, by using the same analytical methods, and by using a statistical approach to assess congruence. We first qualitatively compared phylogeographies of each species using results of standard analyses, including analysis of molecular variation (AMOVA), mismatch distributions, haplotype networks, and nested-clade phylogeographic analysis (NCPA). Next, we used Lapointe and Rissler's (2005) method to statistically assess congruence among the different phylogeographic histories across two spatial scales.

METHODS

For each species, we sampled multiple populations throughout the distribution (Table 1) and sequenced between 1,777 and 2,148 base pairs of mitochondrial

DNA (mtDNA) per individual. Data from multiple gene regions (cytochrome *b*, ATP synthase 6, and ATP synthase 8) were combined in all analyses. An AMOVA calculation of Φ_{st} using pairwise distances (Excoffier et al. 1992) provided a measure of overall genetic structure of populations for each species. The Φ statistic indicates the proportion of nucleotide variation divided among populations and ranges from 0 to 1.0, with completely subdivided populations having a Φ statistic of 1.0. The distribution of pairwise differences among individuals (the mismatch distribution) was used to infer whether a population has undergone a sudden population expansion (Rogers 1995, Rogers and Harpending 1992). Agreement between the observed and expected distribution under a sudden-expansion model was tested following Schneider and Excoffier (1999). Evidence of a population expansion was also tested using Fu's F_s (Fu 1997) and Tajima's D (Tajima 1989). Assuming neutrality, a significantly negative value of these statistics indicates an excess of new mutations in relation to equilibrium expectations and leads to rejection of population stasis. Relationships among individuals were illustrated using parsimony-based haplotype networks constructed using TCS, version 1.13 (Clement et al. 2000). We conducted an NCPA (Templeton 1998, 2004) on the haplotype networks to infer population-level processes. The root of the intraspecific network was inferred through neutral coalescent theory (Castelloe and Templeton 1994, Crandall et al. 1994, Clement et al. 2000). In general, the haplotype with the greatest frequency and the most connections is the most likely to be identified as the ancestral haplotype. Further details on these methods of analysis as well as detailed information on sampling localities, location of voucher specimens, and molecular laboratory methods are provided elsewhere (Sgariglia and Burns 2003, Alexander and Burns 2006, Burns and Barhoum 2006).

In addition to comparing results of these methods for each species, we also statistically tested for phylogeographic congruence following the approach outlined in Lapointe and Rissler (2005). In the first step of this approach, a tree is constructed for each species that shows relationships among predefined geographic areas (e.g., counties). Trees are constructed by recoding the original data so that individuals from the same area are pooled into common units. To compare

TABLE 1. Sampling coverage and intraspecific variation in the three species compared in the present study.

Species	Number of individuals	Number of unique haplotypes	Number of populations	<i>P</i> distance ^a	Φ statistic ^b
Wrentit	61	39	20	0.41% (0–0.51%)	0.41
California Thrasher	64	37	21	0.34% (0–0.77%)	0.46
White-headed Woodpecker	78	25	24	0.25% (0–0.68%)	0.33

^a Mean and range of uncorrected distance presented.

^b Values are for comparisons among populations within each species; all are significant ($P < 0.001$).

our results with those of Lapointe and Rissler (2005), we first used counties as our geographic unit for assessing phylogeographic histories at a relatively fine spatial scale (Fig. 1). Only samples within California were used to construct these trees. The average pairwise distance based on Kimura's (1980) two-parameter model between each county was computed, and this matrix was used to draw a neighbor-joining tree (Saitou and Nei 1987) for each species using PAUP*, version 4.0b10 (Swofford 2002). Each tree then was compared to each other, and the size of the maximum agreement subtree, or MAST score, was calculated in PAUP* and used as a congruence index. The MAST score is the largest possible tree compatible with a given pair of trees, and higher MAST scores indicate more congruence between trees. For example, if two trees showed identical relationships among 20 terminals, the MAST score would equal 20. Because the same counties were not always sampled in each species, MAST scores were normalized by dividing the score by the number of counties sampled in common between the two species. Thus, pairs of trees with complete congruence have a normalized MAST score of 1.0, and complete lack of agreement would lead to a score of 0. For example, if two species were both sampled in the same 20 counties, and the relationships of 18 of those counties were the same for both species, the normalized MAST score would equal 0.9. To test whether the normalized MAST score between two trees was significantly high, we compared the observed MAST score to a null distribution of MAST scores expected by comparing two random trees. To construct the null distribution, we generated 1,000 random trees in PAUP*, with the number of terminals the same as the number of counties in common between the two trees. The agreement metric "d1" was calculated between all possible pairs of random trees (499,500 total contrasts), and the distribution of d1 was transformed into a null distribution of MAST scores. Two trees were considered significantly congruent if their observed MAST score fell within the extreme upper portion of the null distribution. If trees were significantly congruent, they could be combined into a supertree (Gordon 1986, Bininda-Emonds 2004) showing relationships among all counties sampled by either data set. Using this approach, we compared the county trees of each species to those of each other species. In addition, we compared each of the trees of our species to the county supertree of California taxa presented in Lapointe and Rissler (2005).

To look for congruence on a broader spatial scale, we repeated the analysis with our bird data by dividing populations into 12 regional areas within California (Fig. 2). The areas we used correspond to the major geographic and geological features in California. Our regions are similar to the geomorphic provinces of Hill (1984), with the exception that we divided the Coast Ranges into northern Coast Ranges

and southern Coast Ranges (Schoenherr 1992). The Wrentit and the California Thrasher occur in six of these geomorphic provinces, and the White-headed Woodpecker occurs in eight. Species were sampled from all geomorphic provinces in which they occur. Looking at the data divided into geographic provinces may be more biologically meaningful than comparing data on the basis of the political subdivision of county. In addition, the comparison among geomorphic provinces provides a broader spatial scale. Because birds are more vagile than most other organisms, widespread gene flow may prevent phylogeographic signal among closely spaced populations (among counties within geomorphic provinces), yet a pattern may be apparent across a broader regional scale (among geomorphic provinces).

RESULTS

INTRASPECIFIC VARIATION

Haplotype networks, analyses of intraspecific variation, and NCPA for each species are presented in more detail elsewhere (Sgariglia and Burns 2003, Alexander and Burns 2006, Burns and Barhoum 2006); thus, these results are summarized only briefly here. All three species showed similar levels of intraspecific sequence divergence (Table 1). For all three species, mean values of percentage of sequence divergence were <1%, typical of mitochondrial DNA for intraspecific comparisons of birds (Avice and Walker 1998, Ditchfield and Burns 1998). For each species, AMOVA indicated that this variation was significantly structured among populations, with Φ_{st} values ranging from 0.33 to 0.41. Mismatch distributions for each species did not differ significantly from the expected distribution of a growing population ($P = 0.17-0.86$), indicating that each species likely experienced a recent range expansion. Negative values of F_s and Tajima's D were obtained for each species, providing further evidence of recent range expansions.

COMPARISON OF HAPLOTYPE NETWORKS

For each species, haplotype network construction resulted in a single network in which all connections fell within a 95% plausible set of relationships. All three networks (not shown) were completely nested within four-step clades, indicating a similar temporal framework for each species. The California Thrasher network

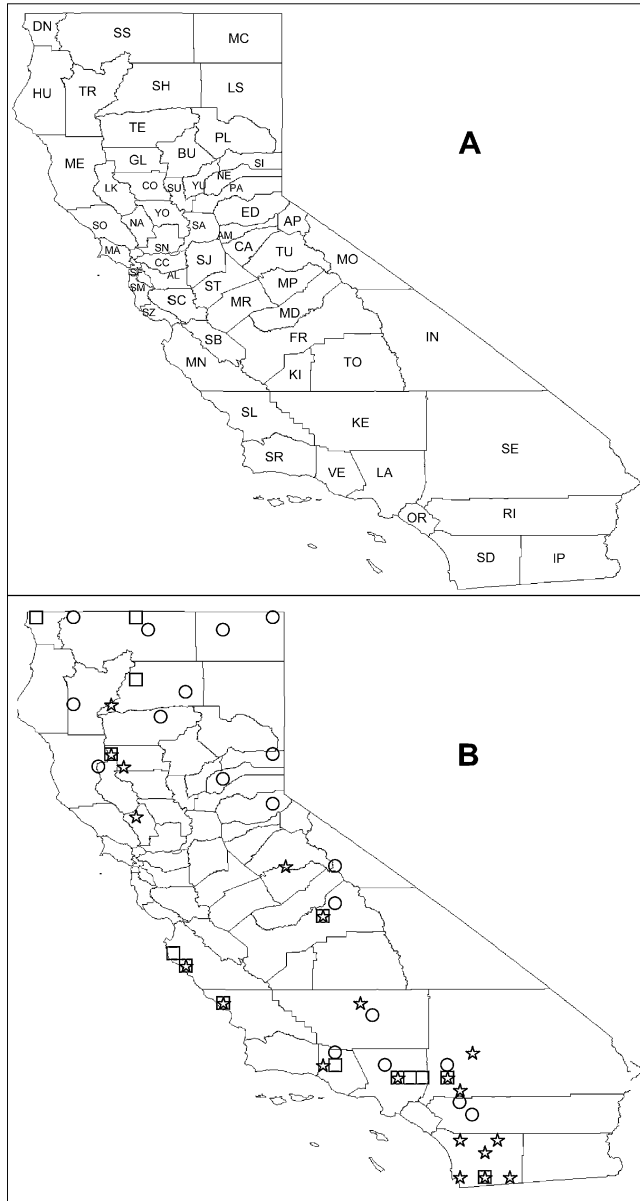


FIG. 1. (A) Map of California showing counties. Abbreviations of counties: AM = Amador, AP = Alpine, BU = Butte, CA = Calaveras, CC = Contra Costa, CO = Colusa, DN = Del Norte, ED = El Dorado, FR = Fresno, GL = Glenn, HU = Humboldt, IN = Inyo, IP = Imperial, KE = Kern, KI = Kings, LA = Los Angeles, LK = Lake, LS = Lassen, MA = Marin, MC = Modoc, MD = Madera, ME = Mendocino, MN = Monterey, MO = Mono, MP = Mariposa, MR = Merced, NA = Napa, NE = Nevada, OR = Orange, PA = Placer, PL = Plumas, RI = Riverside, SA = Sacramento, SB = San Benito, SC = Santa Clara, SD = San Diego, SE = San Bernardino, SF = San Francisco, SH = Shasta, SI = Sierra, SJ = San Joaquin, SL = San Luis Obispo, SM = San Mateo, SN = Sonoma, SO = Solano, SR = Santa Barbara, SS = Siskiyou, ST = Stanislaus, SU = Sutter, SZ = Santa Cruz, TE = Tehama, TO = Tuolumne, TR = Trinity, TU = Tulare, VE = Ventura, YO = Yola, and YU = Yuba. (B) General location of sampling sites within California for all three species. Specific locality data for each species is provided (see text). Stars indicate sites where California Thrashers were sampled, squares indicate sites where Wrentits were sampled, and circles indicate sites where White-headed Woodpeckers were sampled.

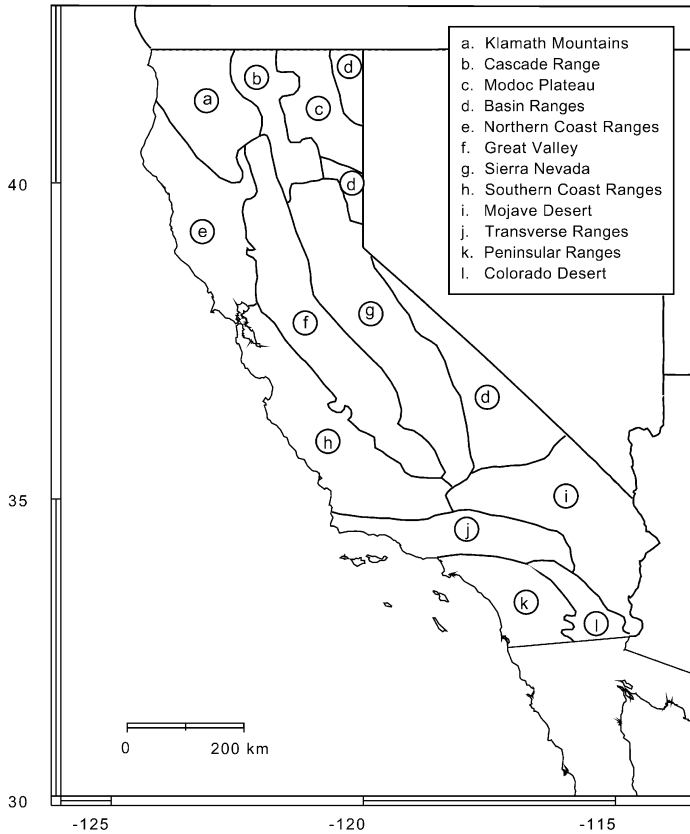


FIG. 2. Geomorphic provinces used to explore relationships among regions within the California Floristic Province.

was characterized by nine unsampled haplotypes that separated most southern haplotypes from those in the north, reflecting a comparatively greater amount of genetic divergence observed between the northern and southern populations. By contrast, sampled haplotypes in the networks of the Wrentit and White-headed Woodpecker were mostly connected to each other by other sampled haplotypes. Few geographically concordant clades are readily apparent by comparing haplotype networks of each species. However, all three species identify a separation of southern California birds from those in the rest of the network. The geographic boundaries of these southern California clades differed slightly in each of the three species. For the California Thrasher and the White-headed Woodpecker, the separation of northern and southern birds occurred just north of the Transverse Ranges, with birds found in the Peninsular and Transverse ranges

in a clade separate from other regions (Fig. 2). For the Wrentit, the separation occurred within the Transverse Ranges, with individuals in the San Bernardino Mountains (a mountain range within the Transverse Ranges) clustering with those from the Peninsular Ranges. The oldest haplotype of both the Wrentit and California Thrasher networks occurred in the same geographic area. For both networks, the oldest haplotype was found in several populations spanning the southern Coast Ranges and the Transverse Ranges. By contrast, for the White-headed Woodpecker, the oldest haplotype was found in the northern part of the distribution.

NESTED-CLADE PHYLOGEOGRAPHIC ANALYSIS

We identified, by NCPA, several clades in each species with significant values of genetic and geographic distance for which inferences about evolutionary processes could be made.

The evolutionary history of each species was complex and characterized by a diversity of processes, including range expansion, restricted gene flow with isolation by distance, and allopatric fragmentation (Table 2). These processes occurred at different times and in different regions for each species. Geographic and genetic relationships among haplotypes at the earliest branching point in the networks indicate that different processes influenced the earliest evolutionary events in each species. The inferred process at the deepest level of the haplotype network is range expansion for the Wrentit, allopatric fragmentation for the California Thrasher, and restricted gene flow for the White-headed Woodpecker. Although NCPA identified a clade of southern California birds for each species, the processes influencing this division were not the same for each species. For the California Thrasher and the Wrentit, NCPA inferred allopatric fragmentation. However, for the White-headed Woodpecker, range expansion by long-distance colonization was inferred (Table 2).

COMPARISON OF REGIONAL TREES

Trees built using pairwise distances between counties (Fig. 3) show few similarities to each other. However, all three species show a separation between northern and southern California counties. In the California Thrasher tree, a long branch connects the counties of these two regions. This corresponds to the large number of unsampled haplotypes connecting northern and southern California populations seen in the haplotype network of this species. Although the county trees of the Wrentit and the White-headed Woodpecker (Fig. 3) also show a separation between northern and southern California counties, this separation is not marked by a branch length longer than others seen in the network. Other than the separation of northern and southern counties, the three networks do not show many similarities in county relationships, and their normalized MAST scores are not significantly congruent (Table 3). Thus, the three trees are, overall, no more similar to each other than would be expected at random and cannot be combined together into a supertree. In addition, none of our avian trees shows significant congruence to the multispecies county network of Lapointe and Rissler (2005). Thus,

each species we studied shows a significantly different phylogeographic pattern in relation to each other as well as to the other California taxa at the spatial level of counties.

Constructing trees for each species on the basis of geomorphic provinces (Fig. 4) also showed a division between southern and northern California regions. For the Wrentit and the California Thrasher, the Transverse Ranges, southern Coast Ranges, and Peninsular Ranges are in a clade separate from the northern Coast Ranges, Klamath Mountains, and the Sierra Nevada. The White-headed Woodpecker does not occur in the southern Coast Ranges, but still shows a separation of Peninsular Ranges and Transverse Ranges from the geomorphic provinces of northern California. Although a north-versus-south split is shared among all three species, the trees show different relationships among regions within northern California and southern California. Different topologies within northern California prevent the California Thrasher tree from being significantly congruent with the White-headed Woodpecker tree (Fig. 4 and Table 3). Likewise, different topologies within both northern and southern California prevent significant congruence between the California Thrasher tree and the Wrentit tree (Fig. 4 and Table 3). However, both the Wrentit and the White-headed Woodpecker are completely congruent for the regions in which they both occur. Therefore, they were combined into a supertree (Fig. 5) showing relationships among eight different regions within the California Floristic Province.

DISCUSSION

QUALITATIVE ASSESSMENT OF PHYLOGEOGRAPHIC CONGRUENCE

Using standard approaches (AMOVA, mismatch distributions, haplotype networks, and NCPA) to compare phylogeographic histories across the distribution of each species indicates both similarities and differences among species. The similar level of genetic divergence found in each species suggests similar timing of diversification within each lineage, assuming equal molecular rates of evolution across these three bird lineages and a lack of error associated with ancestral polymorphism (Edwards and Beerli 2000). All have experienced recent range

TABLE 2. Inferences obtained from NCPA for clades with statistically significant distance values. Each line indicates results for a particular clade in which inferences could be made. Asterisks identify the clade and the inferred process responsible for the genetic differences observed between northern and southern populations.

Species	Step level ^a	Inferred process	Geographic region of inferred process
Wrentit	4	Range expansion (long-distance and contiguous)	Expansion from Peninsular and Southern Coast ranges to remainder of the distribution
	3*	Allopatric fragmentation*	Separation of Peninsular Ranges and San Bernardino mountains (part of the Transverse Ranges) from the rest of the Transverse and Southern Coast ranges
	3	Restricted gene flow with isolation by distance	Across Klamath Mountains, Northern Coast Ranges, and Sierra Nevada
California Thrasher	4*	Allopatric fragmentation*	Transverse and Peninsular ranges mostly separated from remainder of the distribution
	3	Range expansion (contiguous)	Expansion from southern Sierra Nevada to all other parts of the distribution
	3	Restricted gene flow with isolation by distance	Across Transverse and Peninsular ranges
	1	Allopatric fragmentation	Part of Southern Coast Ranges separated from Transverse and Peninsular ranges
White-headed Woodpecker	4	Restricted gene flow with isolation by distance	Across entire distribution
	3*	Range expansion (long-distance colonization)*	Dispersal to Transverse and Peninsular ranges from remainder of the distribution
	3	Restricted gene flow with isolation by distance	Across entire distribution except for Peninsular Ranges
	2	Restricted gene flow with isolation by distance	Across Sierra Nevada, Basin, Cascade, and Northern Coast ranges
	1	Allopatric fragmentation	Basin Ranges separated from Northern Coast and Cascade ranges

^aStep level reflects relative age of clades within each cladogram. For each species, 1-step clades are the youngest and 4-step clades are the oldest.

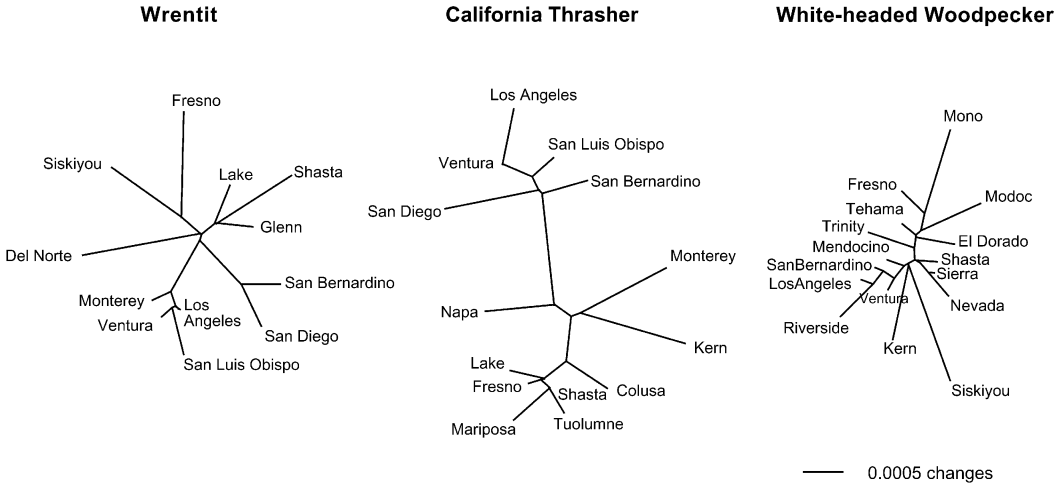


FIG. 3. Trees representing relationships among counties. Trees are unrooted, and branch lengths are proportional to amount of genetic divergence.

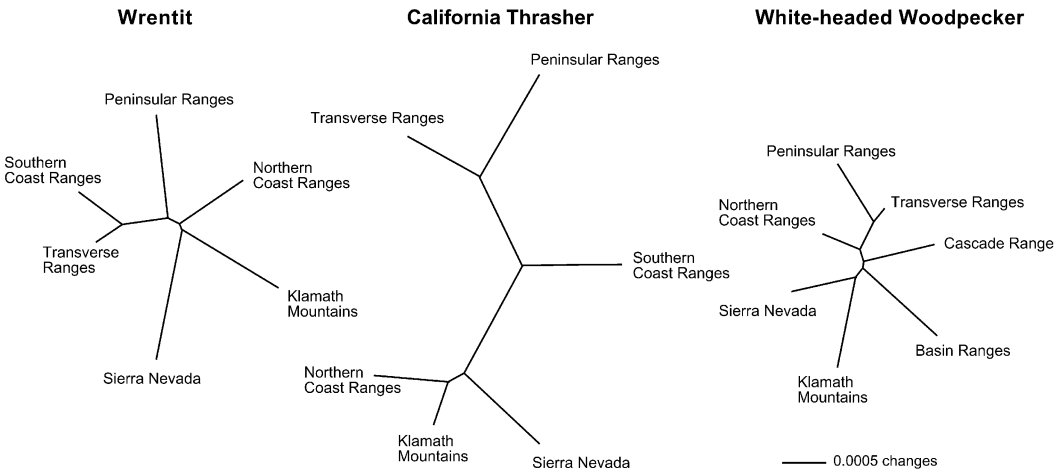


FIG. 4. Trees representing relationships among geomorphic provinces. Trees are unrooted, and branch lengths are proportional to amount of genetic divergence.

expansions, as reflected in their unimodal mismatch distributions and the NCPA inferences of range expansion for large parts of the distribution. However, other than range expansion, NCPA identified few processes that influenced the three species similarly at the same time and space. A split between northern and southern populations was identified, but the precise boundaries and processes influencing this split were different in each species. Inferred ancestral origin also showed some level of agreement across taxa. Both the Wrentit and the California

Thrasher experienced a southern ancestry followed by a northward postglacial range expansion. However, the White-headed Woodpecker likely had a more northern ancestry.

A qualitative comparison of phylogeographic histories of the species studied here and those of codistributed taxa also show similarities and differences. Calsbeek et al. (2003) analyzed genetic data from 55 species of plants and animals, and they identified several geographic barriers that seemed to influence multiple species in the same way. Most animals displayed

TABLE 3. Scores representing assessment of pairwise comparison of county-based trees and geomorphic-province-based trees.

Spatial scale of tree	Trees compared	Number of regions shared	MAST score	Normalized MAST Score	P value
County	Wrentit vs. California Thrasher	9	5	0.56	0.97
	Wrentit vs. White-headed Woodpecker	6	4	0.67	>0.99
	California Thrasher vs. White-headed Woodpecker	6	5	0.83	0.26
	Lapointe and Rissler (2005) ^a vs. Wrentit	11	6	0.55	0.70
	Lapointe and Rissler (2005) ^a vs. California Thrasher	13	6	0.46	0.95
	Lapointe and Rissler (2005) ^a vs. White-headed Woodpecker	13	7	0.54	0.35
	Wrentit vs. California Thrasher	6	4	0.67	>0.99
	Wrentit vs. White-headed Woodpecker	5	5	1.00	0.07
	California Thrasher vs. White-headed Woodpecker	5	4	0.80	0.87
	Geomorphic province				

^a Refers to county supertree for California taxa reported by Lapointe and Rissler (2005).

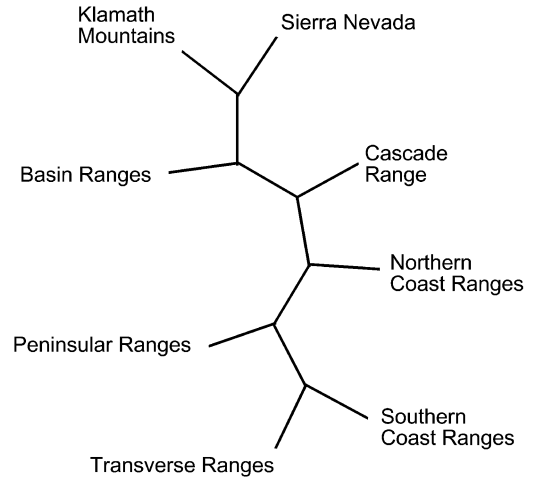


FIG. 5. Supertree showing combined relationships among geomorphic provinces for the Wrentit and the White-headed Woodpecker. Tree is unrooted, and branch lengths are constrained to be of equal length.

a genetic split dividing populations on either side of the Transverse Ranges. In addition, multiple species also were affected by population genetic breaks in the Sierra Nevada, Coast Ranges, Monterey Bay, and the Los Angeles Basin. However, Calsbeek et al. (2003) noted that the few bird species included in their study were relatively weakly differentiated and did not show breaks around any of these barriers. By contrast, our study shows that some birds have responded to the Transverse Ranges in a manner similar to that of nonavian species. All three species showed a genetic break in this region, though the process influencing this break likely differs among species (Table 2). In addition, the Oak Titmouse (*Baeolophus inornatus*), a species not included in the Calsbeek et al. (2003) study but included in the Lapointe and Rissler (2005) study, also shows a genetic break between northern and southern populations in the vicinity of the Transverse Ranges (Cicero 1996). Other than the Transverse Ranges, we did not find similar breaks in the other regions identified as important barriers by Calsbeek et al. (2003). Timing of differentiation around the Transverse Ranges appears to be generally concordant among our bird species and other species previously studied. Calsbeek et al. (2003; Table 1) provided dates of divergence for six taxa in this region. For four of these, divergence times date to within or slightly more

than 1 mya. Assuming a molecular clock rate of 1.6–2.0% divergence per million years for bird mtDNA (Shields and Wilson 1987, Fleischer et al. 1998; but see García-Moreno 2004), differentiation among our species in this region also occurred within the last million years. The pattern of southern ancestry inferred for the Wrentit and California Thrasher has also been identified in a number of other California vertebrates (Smith 1979, Tan and Wake 1995, Cicero 1996, Rodríguez-Robles et al. 1999, Maldonado et al. 2001, Matocq 2002, Richmond and Reeder 2002). However, from just the above qualitative description, strong overall conclusions about generality of phylogeographic patterns between our birds and other taxa cannot be made.

STATISTICAL ASSESSMENT OF CONGRUENCE

Using Lapointe and Rissler's (2005) method, the three species we studied showed incongruent histories when compared with each other at the relatively fine spatial scale of counties. More congruence was found at a broader regional scale. The geomorphic-province trees for the Wrentit and White-headed Woodpecker were completely congruent, despite the different habitat requirements and elevational preferences of these two species. Although the White-headed Woodpecker and the California Thrasher phylogeographies were not statistically congruent, they share relationships of four of the five regions in common. However, with only five regions in common between these two species, statistical power is low for this comparison.

Lapointe and Rissler's (2005) test of congruence among nine taxa reached a conclusion similar to that of Calsbeek et al. (2003), namely that species within the California Floristic Province are characterized by congruent phylogeographic histories. However, the three species in our study showed little agreement with the multispecies supertree of Lapointe and Rissler (2005). In general, for the counties in common between our species and those of the Lapointe and Rissler (2005) tree, only half of these counties agreed in topological arrangement between trees. This suggests that haplotypes are shared across a broader area in our bird species than in the species included in Lapointe and Rissler's (2005) supertree. Lapointe and Rissler (2005) did not include a tree based on broader regional areas; therefore, we cannot statistically compare

our geomorphic-province tree to a Lapointe and Rissler (2005) regional supertree. However, visual inspection of the Lapointe and Rissler (2005) county tree shows that counties in the Transverse Ranges, Peninsular Ranges, and southern Coast Ranges are grouped together, which is similar to our geomorphic province supertree. In addition, counties in the Sierra Nevada, Klamath Mountains, Cascade Range, and northern Coast Ranges also group together in agreement with our supertree. However, the tree of Lapointe and Rissler (2005) shows counties in the Basin Ranges grouping with the Peninsular Range counties, whereas our supertree places the Basin Ranges adjacent to regions in northern California. Our results suggest that avian species may show more congruent phylogeographic histories at regional levels than at a fine scale within the California Floristic Province. Greater dispersal abilities of birds compared with many other taxa are likely responsible for this difference. More movement among closely spaced populations would result in lower genetic differences, obscuring the ability to differentiate fine-scale geographic patterns. In addition, the ability of birds to undergo distributional shifts over hundreds of kilometers in the short period of a few decades (Johnson 1994) would also obscure phylogenetic signal. Additional studies of bird species are still needed to help clarify the extent to which the phylogeographic histories of birds comply with the congruent patterns seen in other species in this region.

The approach of Lapointe and Rissler (2005) is an improvement over previous methods of assessing congruence, in that a statistical test is employed so that common geographic associations can be identified with confidence. In addition, once regional associations are identified, these can be tested for differences in climatic or other variables (Lapointe and Rissler 2005). However, identifying congruence among areas using this approach does not reveal the evolutionary processes underlying an association. For example, a tree may indicate that two areas are grouped together, but this association could be attributable to vicariant events in the past as well as to ongoing, restricted gene flow. In addition, the congruence test does not incorporate branch lengths; thus, temporal differences and relative support for an association are ignored. For example, the California Thrasher

showed greater genetic divergence between northern and southern populations than the other two species, which suggests that events causing the split between these two regions may have occurred at different time-scales in the three species. Because this and other kinds of important information are not considered when assessing topological congruence, we advocate the continued use of traditional phylogeographic methods in conjunction with the supertree approach of Lapointe and Rissler (2005). The two approaches are complementary, with the former providing detailed information about the timing and evolutionary process of each species and the latter revealing common geographic associations across a region.

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