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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.

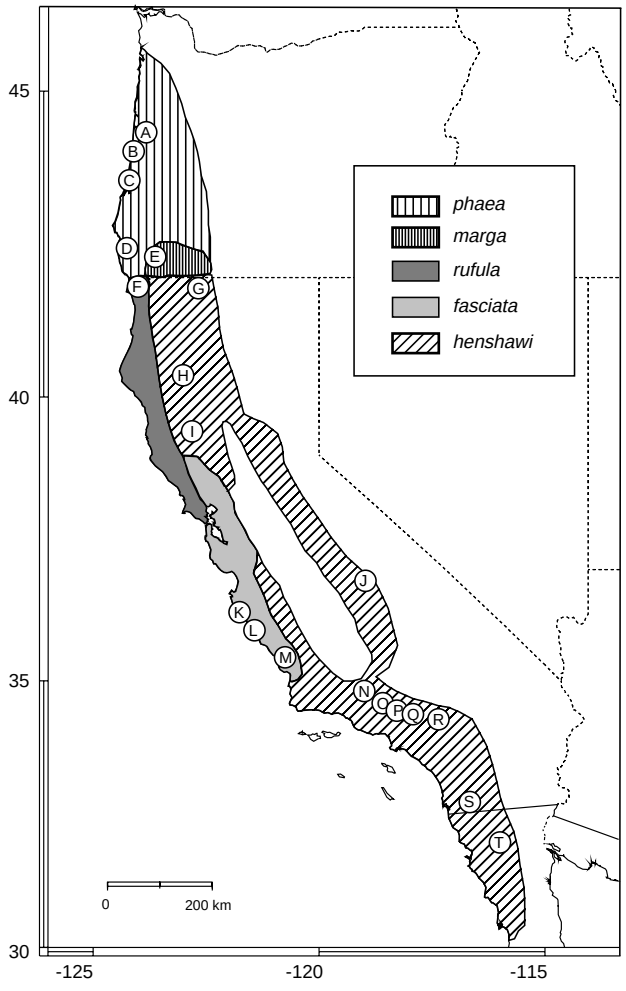

Fig. 1. Geographic distribution of wrentit subspecies. Letters indicate locations of sampled populations as indicated in Table 1. Geographic features of the California Floristic Province encompassed within our sampling include the Klamath Mountains (populations F, G, and H), the Coast Ranges (I, K, L, 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