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# GENETIC STRUCTURE OF GALÁPAGOS POPULATIONS OF THE YELLOW WARBLER

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*Abstract.* Sequence variation of control region mitochondrial DNA, phylogenetic reconstruction, and analysis of molecular variance (AMOVA) were used to determine the degree of genetic structure of Yellow Warblers (*Dendroica petechia*) in the Galápagos Archipelago. When the Galápagos population was partitioned into subpopulations (by island), AMOVA indicated a nonsignificant level of genetic structure. The presence of the same haplotype on more than one island also indicated low genetic divergence among subpopulations. Using these sequences and those available in Genbank, we also determined the degree of divergence between the Galápagos Yellow Warbler population and other New World populations. Mean sequence divergence between the Galápagos population and Latin American populations was 3.7%, and between the Galápagos population and North American populations was 6.7%.

*Key words*: Dendroica petechia*, Galápagos Islands, mitochondrial DNA, population structure, Yellow Warbler.*

## Estructura Genética de las Poblaciones de *Dendroica petechia* de Galápagos

*Resumen*. Determinamos el grado de estructura genética de *Dendroica petechia* en el archipiélago de Galápagos usando la variación en una región de control del ADN mitocondrial, una reconstrucción filogenética y un análisis de varianza molecular (AMOVA). Cuando la población de Galápagos fue separadas en subpoblaciones (una en cada isla), el AMOVA presentó un nivel no significativo de estructura genética. La presencia del mismo haplotipo en más de una isla también indicó una baja divergencia genética entre subpoblaciones. Utilizando estas secuencias y las que están disponibles en Genbank, también determinamos el grado de divergencia entre la población de *D. petechia* de Galápagos y otras poblaciones del Nuevo Mundo. El promedio de la divergencia de las secuencias entre la población de Galápagos y las de América Latina fue de 3.7%, y entre la población de Galápagos y las poblaciones de Norte America fue de 6.7%.

The Galápagos Archipelago is located approximately 1100 km southwest of Central America, 1000 km from continental South America, and 720 km from Cocos Island. Potassium-argon aging indicates a maximum age for extant islands of less than six million years (Bailey 1976, Geist 1996), although a series of now-submerged islands in this region could have supported terrestrial life more than 10 million years ago (Cox 1983, Christie et al. 1992, Geist 1996).

Yellow Warblers (*Dendroica petechia*) are found on all major Galápagos Islands and many of the islets. Yellow Warblers from the Galápagos Islands and Cocos Island have been recognized as an endemic subspecies, *D. p. aureola* (Lowther et al. 1999), based on the rusty crowns of mature males (Harris 1974, Castro and Phillips 2000). This trait is usually absent or is muted in Yellow Warblers in other locations, consistent with divergence of these populations from the remainder of the range. Some investigators have hypothesized, based on the absence of Yellow Warbler fossils in lava tubes, that the species has colonized the Galápagos relatively recently, perhaps in conjunction with human colonization (Snow 1966, Steadman 1986). Despite its widespread distribution throughout the islands, we lack morphological or genetic studies on the Galápagos population beyond casual observations.

The geographic range of Yellow Warblers extends from Canada to the middle of South America. Based on geographical variation in plumage color and pattern (Browning 1994), nine subspecies are assigned to the *aestiva* group, eighteen to the *petechia* group, and sixteen to the *erithachorides* group. In the *erithachorides* group, subspecies inhabit the coasts of Mexico, Central America, northern South America, Cocos Island, and the Galápagos Archipelago (Browning 1994). Previous work using mitochondrial DNA (mtDNA) restriction sites examined populations throughout North America, Central America, South America, and the West Indies (Klein and Brown 1994). The phylogenetic relationships among subspecies in the eastern Pacific, including the Galápagos and Cocos Island populations, have not been clearly established. These populations (collectively, *D. p. aureola*) are similar to other members of the *erithachorides* group in size, but have chestnut crowns (like the *petechia* group) rather than chestnut heads as do other members of the *erithachorides* (Klein and Brown 1994).

In this study, we used mtDNA sequences, analysis of molecular variance (AMOVA), and phylogenetic reconstruction to determine the degree of genetic structure of the Yellow Warbler population in the Galápagos Archipelago. We also used sequences available in Genbank to estimate the degree of divergence between the Galápagos *D. petechia* populations and other New World populations.

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## METHODS

Blood samples from the brachial vein were collected on filter paper from 44 Yellow Warblers caught in May 2001 in mist nets on six islands (Fig. 1) of the Galápagos Archipelago at the following locations: Punta Cevallos, Española (samples 1–8), 01°23′S, 89°37′W; Darwin Bay, Genovesa (samples 9–13), 00°19′N, 89°57′W; Punta Pitt, San Cristóbal (samples 14–21), 01°42′S, 89°15′W; Puerto Ayora, Santa Cruz (samples 22–31), 00°40′S, 90°10′W; Post Office Bay, Floreana (samples 32–38), 01°13′S, 90°27′W; Espumilla Beach, Santiago (samples 40–44), 00°10′S, 90°30′W. After drying, samples were stored at ambient temperature in Galápagos until our return to Wake Forest University when they were stored at –70°C prior to analysis.

Total DNA extractions were performed using phenol chloroform: isoamyl alcohol (Hillis et al. 1996). A 348–base pair fragment of the control region of mtDNA was amplified using the polymerase chain reaction (PCR). We used the primers DPdl-L5 (5′ TTCTTGCTTTAAGGGTATGT) and DPdl-H4 (5′ TCAATAGATAAC CATGTCCT), located 86 base pairs upstream of the 3′ end of L16743 and 9 base pairs downstream of the 3′ end of H417, respectively (Milot et al. 2000). Amplification using PCR protocols followed standard procedures, which are described in detail by Collins (2003). Sequencing was performed on an ABI Prism 377 automated sequencer (Perkin-Elmer, Boston, Massachusetts). Primers used in DNA sequencing were the same primers used in PCR amplification. Sequences were deposited in GenBank under accession numbers AY124884–AY124933. After sequencing, amplified fragments were manually aligned using program BioEdit (Version 5.0.6; Hall 1999) and compared to previously published Yellow Warbler sequences from Pennsylvania ($n = 5$), western Canada or Alaska ($n = 6$), eastern Canada ($n = 44$), Costa Rica ($n = 1$), Venezuela ($n = 1$), and Puerto Rico ($n = 1$), as well as two species in the sister clade (Blackpoll Warbler [*Dendroica striata*] and Chestnut-sided Warbler [*Dendroica pennsylvanica*]), deposited in GenBank under Accession numbers AF205953–AF206016 (Milot et al. 2000).

## STATISTICAL ANALYSES

Using previously published Yellow Warbler mtDNA sequences (Milot et al. 2000), we calculated the average number of pairwise differences, based on the distance method of Tajima and Nei (1984), for Yellow Warblers from the Galápagos Islands (consisting of six subpopulations), from North America (consisting of eastern Canada, western Canada or Alaska, and Pennsylvania populations), and from Latin America (consisting of Puerto Rico, Venezuela, and Costa Rica populations). Calculations were based on 348 base pairs. Sequence divergence estimates among phylogenetic groups were corrected for within-group variation with a formula from Wilson et al. (1985).

Average pairwise differences between populations and subpopulations, total number of haplotypes, haplotype grouping in all subpopulations, and AMOVA results were all calculated using program Arlequin (Version 2.000; Schneider et al. 2000). Kimura (1981) two-parameter distances were used. This approach requires a priori considerations that are used to group sets of populations together to form defined hierarchical levels. For comparative purposes, samples can be hierarchically sorted into seven sampling units composed of Yellow Warblers from three North American sites (Pennsylvania, eastern Canada, and western Canada or Alaska), three Latin American sites (Puerto Rico, Venezuela, and Costa Rica), and the Galápagos Islands sites, representing six subpopulations (six islands). We used $\varphi_{ST}$, an analog of Wright's fixation index ($F_{ST}$; Wright 1921), to quantify the inbreeding effects of population structure. Pairwise $\varphi_{ST}$ values were calculated in Arlequin for all combinations of sites sampled. The null distribution of values under a hypothesis of no difference among sites was obtained by permuting haplotypes among sites. *P*-values were determined as the proportion of permutations leading to $\varphi_{ST}$ values larger than or equal to the value observed. Attempts to obtain maximum likelihood estimates of *Nm* (the number of migrants successfully exchanged between a pair of populations per generation) for the Galápagos samples using program MIGRATE 1.6.7 (Beerli and Felsenstein 2001), which employs a coalescent-theory approach to estimate past migration rates with an asymmetric matrix model, were inconsistent, probably due to the relatively small sample size and single mitochondrial locus employed. We used Mantel's test (Mantel 1967) to examine the relationship between genetic distance versus geographical distance among populations of Yellow Warblers within the Galápagos archipelago. Historical demography of populations was investigated with Fu's *F* statistic (Fu 1997). Mismatch distributions of pairwise distances between haloptypes (Rogers and Harpending 1992) were plotted using DNASP 3.53 (Rozas and Rozas 1999). Mismatch distributions were compared to Poisson distributions (Slatkin and Hudson 1991), and the associated raggedness indices were interpreted using the generalizable simulation results of Harpending (1994).

We used statistical parsimony (Templeton et al. 1995, Templeton 1998) to construct a haplotype network for the Galápagos samples and to infer phylogenies among haplotypes. This technique assesses the limits of parsimony and connects operational taxonomic units within the calculated 95% probability limit. Whereas traditional methods of phylogenetic reconstruction have greater statistical power when sequences are more divergent (Huelsenbeck and Hillis 1993), statistical parsimony has been found to outperform parsimony bootstrapping when the number of shared characters is large (Crandall 1996). The limits of probability were assessed for Yellow Warbler data sets, matrices of absolute pairwise differences were calculated considering gaps as an additional character state, and matrices were used to construct statistical parsimony cladograms in TCS 1.13 (Clement et al. 2000). Multifurcations in the generalized network were resolved using the criteria of Templeton and Sing (1993). For all analyses, we considered results with $P < 0.05$ to be significant.

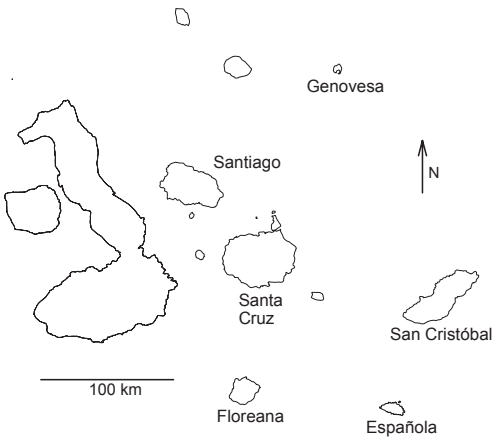


FIGURE 1. The Galápagos Archipelago. Islands where Yellow Warblers were obtained in 2001 for mitochondrial DNA analysis are labeled.

## RESULTS

We found 24 haplotypes in 44 individuals examined from the Galápagos Islands. Several haplotypes were shared among Galápagos subpopulations (islands). No shared haplotypes were found among the Galápagos, North America, and Latin America. For Yellow Warblers in the Galápagos, nucleotide substitutions were observed at 72 of 348 (20.7%) loci. Diversity indices (reported as mean ± SD) for Galápagos Yellow Warblers are as follows: $\pi$, pairwise differences between haplotypes (Tajima 1983), was 17.4 ± 8.2; *H*, gene diversity (Nei 1987), was 0.973 ± 0.021; and nucleotide diversity, *h* (Nei 1987), was 0.033 ± 0.017.

As determined via AMOVA, within-subpopulation sequence variation of Yellow Warblers for the six Galápagos sites was 1.7% for Española, 3.1% for Genovesa, 2.2% for San Cristóbal, 1.2% for Santa Cruz, 0.5% for Floreana, and 1.2% for Santiago. Within-population sequence variation for the three continental sites where *n* (the number of individual sequences) > 1 was 2.4% for Pennsylvania, 1.2% for eastern Canada, and 0.7% for western Canada. The mean within-subpopulation value (1.7%) for sequence variation from the six Galápagos sites and the mean within-site value (1.4%) from the three continental sites were not significantly different from each other (independent $t_{107} = 0.3$, $P > 0.75$).

For the Galápagos samples, Fu's *F* test produced a value of $F_S = -16.2$, $P < 0.001$). Significant negative $F_S$ values are associated with a demographic model indicative of an expanding population.

Statistical parsimony analysis depicted a haplotype network (Fig. 2) that was largely in agreement with results obtained using traditional parsimony, but which showed much greater resolution. Due to the strict statistical nature of this analysis, four separate networks more distant than ten mutational steps from one another (the distance calculated by the 95% probability for this dataset) were recovered for Yellow Warblers from the Galápagos Archipelago. One network consisted of a single individual from San Cristóbal. The remaining networks each contained haplotypes from four or more islands.

Percent sequence differences among all Yellow Warbler sampling units are listed in Table 1. Mean sequence divergence between the Galápagos Archipelago population and Yellow Warblers from the three Latin America sites was 3.7%, and between the Galápagos population and the three North American sites was 6.7%. Mean sequence divergence between the six Galápagos subpopulations and the six continental sites was 5.2 %. When the Galápagos population was compared to Yellow Warblers from all other sites, the smallest sequence divergence, 3.4%, was for Venezuela, and the largest value, 6.9%, was for western Canada.

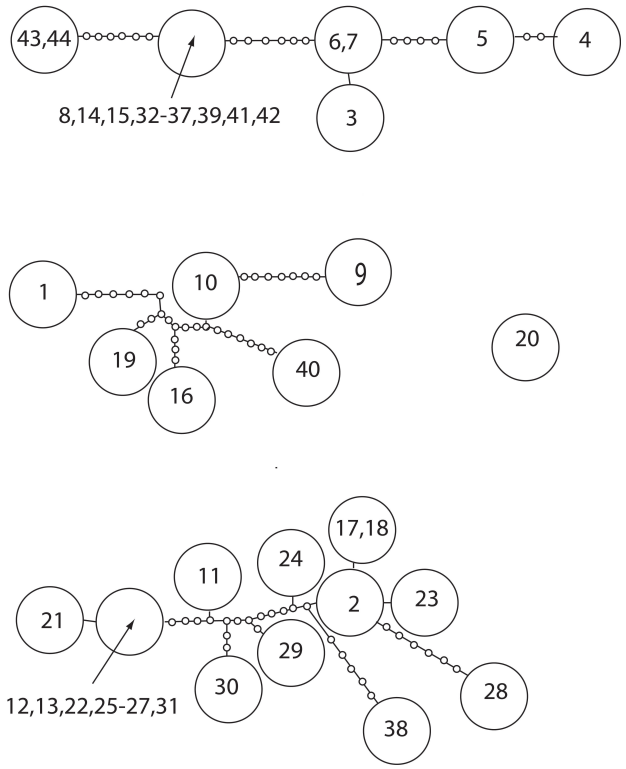


FIGURE 2. Haplotype networks of 44 Yellow Warbler mitochondrial DNA sequences, estimated under the parsimony criterion, with ambiguities resolved using the method of Templeton and Sing (1993). Four separate networks not within ten mutational steps of one another (the cutoff for 95% probability for this dataset) were recovered. Haplotype numbers represent individuals from the following Galápagos Islands: 1–8, Española; 9–13, Genovesa; 14–21, San Cristóbal; 22–31, Santa Cruz; 32–39, Floreana; 40–44, Santiago.

TABLE 1. Percent mitochondrial DNA nucleotide sequence differences among all Yellow Warbler populations sampled, based on Tajima and Nei's distance method (Tajima and Nei 1978). Samples from the Galápagos Islands (Española, Genovesa, San Cristóbal, Santa Cruz, and Floreana) were collected in 2001. Sequence data from Yellow Warblers from the remaining locations were taken from Milot et al. (2000).

| | Genovesa | San Cristóbal | Santa Cruz | Floreana | Santiago | Venezuela | Puerto Rico | Costa Rica | Pennsylvania | Eastern Canada | Western Canada or Alaska |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Española | 0.5 | 0.4 | 1.4 | 0.5 | 0.4 | 5.0 | 5.5 | 5.0 | 7.0 | 7.5 | 7.8 |
| Genovesa | | 0.1 | 0.2 | 1.0 | 0.6 | 3.2 | 3.2 | 3.2 | 5.4 | 5.7 | 5.9 |
| San Cristóbal | | | 0.8 | 0.4 | 0.01 | 4.1 | 4.1 | 4.0 | 6.2 | 6.6 | 6.6 |
| Santa Cruz | | | | 2.0 | 1.6 | 2.7 | 2.7 | 2.7 | 5.3 | 5.2 | 5.6 |
| Floreana | | | | | 0.2 | 5.6 | 5.6 | 5.6 | 7.5 | 8.0 | 8.0 |
| Santiago | | | | | | 5.3 | 5.0 | 5.3 | 7.2 | 7.7 | 7.6 |
| Venezuela | | | | | | | 1.7 | 1.7 | 6.1 | 5.0 | 5.2 |
| Puerto Rico | | | | | | | | 1.2 | 5.4 | 4.9 | 5.5 |
| Costa Rica | | | | | | | | | 5.0 | 4.7 | 5.2 |
| Pennsylvania | | | | | | | | | | 5.7 | 6.8 |
| Eastern Canada | | | | | | | | | | | 1.8 |

When the Galápagos population was partitioned into subpopulations (islands), genetic structure was not detected (AMOVA, $\varphi_{ST} = 0.14$, $P = 0.25$). Genetic distances among Galápagos subpopulations were not correlated with genetic distances among islands ($r = -0.11$, $P = 0.40$, Mantel's test). At a higher hierarchical level, genetic structure was found for the partitioning of samples into three components representing individuals from North America, Latin America, and the Galápagos Islands $\varphi_{ST} = 0.60$, $P = 0.001$; among group variation = 60%, within group variation = 22%). Map distance and percent sequence difference among the seven sampling units were correlated ($r = 0.62$, $P = 0.004$, Mantel's test).

## DISCUSSION

The data from this study indicate little genetic divergence of Yellow Warblers within the Galápagos among the six islands sampled. Numerous haplotypes are found on more than one island, and AMOVA results indicate that islands do not constitute structured genetic units. The existence of identical haplotypes on multiple islands suggests a high level of gene flow among islands or incomplete lineage sorting. Given the limited power associated with single-locus data, we cannot adequately discriminate among these possibilities.

Haplotype diversity within the Galápagos archipelago was robust, with the proportion of individuals sampled to total haplotypes > 0.5 for all locations except Floreana, for which the value was 0.3. Similar levels of variation over small geographic distances have been reported for Song Sparrows (*Melospiza melodia*) and MacGillivray's Warblers (*Oporornis tolmiei*), for which values range from 0.3–1.0, with most locations sampled yielding values >0.5 (Zink et al. 1991, Milá et al. 2000).

Darwin's finches (Freeland and Boag 1999), iguanas (Rassman 1997), giant tortoises (Caccone et al. 1999, 2002), and *Opuntia* cactus (Browne et al. 2003, Helsen et al. in press) also have distinct morphological phenotypes among islands with shallow levels of genetic divergence. In other organisms (e.g., Galápagos Mockingbirds; Arbogast et al. 2006; land snails; Parent and Crespi 2006), distinct morphological differences among islands have been accompanied by more pronounced genetic differences.

The mtDNA data indicate little genetic structuring among island populations of Yellow Warblers within the Galápagos, yet significant genetic divergence between the Galápagos population and birds from Latin America and North America. The presence of rusty crown plumage for Galápagos individuals also suggests some degree of separation between the Galápagos population and the remaining Yellow Warbler populations.

The calibration of molecular clock data for the passerine mtDNA control region is an area of ongoing research and discussion (Shields and Wilson 1987, Avise and Walker 1998, Klicka and Zink 1999, Arbogast et al. 2002), with estimates especially problematic when based on a single molecular marker. For mtDNA, different parts of the control region also evolve at different rates, with the 5′ end evolving more rapidly than remaining portions. For Snow Geese, nucleotide substitution rates for the 5′ end (which was used in our study) are estimated to be 10%–20% per million years (Quinn 1992), suggesting divergence of 185 000 to 370 000 years between Galápagos and Latin American Yellow Warblers. Lambert et al. (2002) estimate that substitution rates may be as high as 40% to 140% in the HVR1 region of mtDNA, based on ancient DNA from Adélie Penguins (*Pygoscelis adeliae*). Applying even this estimate of divergence time to Yellow Warblers suggests divergence of 37 000 to 92 000 years, and would not support the hypothesis that Yellow Warblers colonized the Galápagos in modern historical times (Snow 1966, Steadman 1986). Additional studies will be necessary before robust conclusions can be made for interisland variation or differences between Galápagos and continental populations of Yellow Warblers, and additional molecular markers are needed to clarify divergence time estimates.

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