

GEOGRAPHIC VARIATION AND GENETIC STRUCTURE IN THE STREAK-BACKED ORIOLE: LOW MITOCHONDRIAL DNA DIFFERENTIATION REVEALS RECENT DIVERGENCE

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Abstract. Many avian species from the temperate zone show low levels of genetic diversity when compared with species from the tropics, although there are some interesting exceptions, and species whose ranges occur across the temperate–tropical boundary could have characteristics of either or both zones. The distribution of the Streak-backed Oriole (*Icterus pustulatus*) extends from northwestern Sonora in Mexico south along the Pacific coast to Costa Rica. In addition, there is a population on the Tres Mariás Islands. Northern populations are migratory and dichromatic (sexes different), whereas southern populations are nonmigratory and monochromatic (sexes alike). We sequenced mtDNA (control region domain I) from 102 individuals across the range of this species. Maximum parsimony and maximum likelihood analyses did not support the existence of multiple species within *Icterus pustulatus* based on mtDNA. However, populations from the Tres Mariás Islands seem to have been isolated long enough to have fixed differences from populations on the mainland. The species complex shows an uncommon phylogeographic pattern, with shallow haplotype trees and weak geographic structure, suggesting that it has undergone recent population expansion. We recommend that the insular populations be considered a separate species, *Icterus graysonii*, given the fixed differences from mainland birds in multiple characteristics, including mtDNA and plumage patterns.

Key words: *Icterus pustulatus*, mitochondrial DNA, phylogeography, population genetics, speciation.

Variación Geográfica y Estructura Genética de *Icterus pustulatus*: Poca Diferenciación en el DNA mitocondrial Revela una Divergencia Reciente

Resumen. Muchas especies de aves de zonas templadas muestran niveles bajos de diferenciación genética en comparación con especies de las zonas tropicales. Sin embargo, hay algunas excepciones interesantes y especies cuyos rangos de distribución se encuentran a través del límite tropical-templado podrían tener características de cualquiera o ambas zonas. La distribución de *Icterus pustulatus* va de Sonora en el noroeste de México, al sur a lo largo de la costa del pacífico hasta Costa Rica. Además, existe una población en las islas de Tres Mariás. Las poblaciones norteñas son migratorias y dicromáticas (sexos diferentes), mientras que las poblaciones sureñas no son migratorias y monocromáticas (sexos iguales). Se secuenció el primer dominio de la Región Control (DNA mitocondrial) para un total de 102 individuos a lo largo de su distribución. Los análisis de parsimonia y de máxima verosimilitud no apoyaron la existencia de más de una especie al interior del complejo *Icterus pustulatus*, sin embargo, las poblaciones de las islas de Tres Mariás pudieran haber estado aisladas por un período bastante largo para acumular diferencias fijadas entre las islas y el continente. El complejo presenta un patrón filogeográfico poco común, con árboles que muestran baja resolución y una estructura geográfica débil, sugiriendo que la especie ha experimentado una reciente expansión poblacional. Recomendamos que las poblaciones insulares se consideren como una especie separada, *Icterus graysonii*, debido las diferencias fijas que la diferencian de los individuos del continente y utilizando múltiples caracteres incluyendo patrones del mtDNA y del plumaje.

INTRODUCTION

Many studies of geographic variation in temperate-zone birds have shown low levels of genetic variation (Ball et al. 1988, Milá et al. 2000, Baker et al. 2003, Kondo et al. 2004). In contrast, many tropical species show relatively high levels of variation in mitochondrial DNA (mtDNA; Peterson 1992, Hackett

1993, Bates et al. 1999, García-Moreno et al. 2004, Tobias et al. 2008; see also Weir and Schluter 2007). In many tropical species, molecular variation coincides with phenotypic variation, e.g., in the Common Bush-Tanager (*Chlorospingus ophthalmicus*; García-Moreno et al. 2004). However, there are exceptions to these general trends, and several temperate species also show marked genetic divergences that correspond

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with morphology (Drovetski et al 2004, Spellman and Klicka 2007, Spellman et al. 2007). Other temperate species do not show substantial morphological variation, yet show deep molecular splits (e.g., Carolina Chickadee [*Poecile carolinensis*], Gill et al. 1999; Common Raven [*Corvus corax*], Omland et al. 2000). Furthermore, there are cases such as the Orchard Oriole group (*Icterus spurius spurius* vs. *Icterus spurius fuer-testi*; Baker et al. 2003), in which morphology shows variation without differences in mtDNA. Further studies with intensive geographic sampling are needed to test for correspondence between genes and morphology in temperate versus tropical regions.

A well-known example of within-species geographic variation among Mexican birds is the Streak-backed Oriole (*Icterus pustulatus*) complex. This polytypic species has an extensive range, from Sonora in northwestern Mexico south along the Pacific coast to Costa Rica, as well as an insular population on the Tres Mariás Islands (Friedmann et al. 1950, Howell and Webb 1995, AOU 1998, Jaramillo and Burke 1999). Thus, this species' range includes both tropical and temperate regions. Despite its generally continuous distribution, populations show differences in plumage coloration patterns and in morphometric traits. Northern temperate breeding populations (race *microstictus*) are winter migrants and are sexually dichromatic. Males are bright orange with a reddish-orange head, small black streaks on the back, and black wings with white edges; females are similar to males in pattern, but much duller and with the back, nape, and crown

olive-green (Jaramillo and Burke 1999). Males from the Tres Mariás Islands (race *graysonii*) tend to be a yellowish orange and usually lack the streaks on the back (or have only a few streaks on the scapulars), while females are similar but with a more olive coloration (Howell and Webb 1995, Jaramillo and Burke 1999). More southern tropical populations (El Salvador to Costa Rica, race *sclateri*) are not migratory and are monochromatic (sexes alike, both sexes elaborate). Additionally, in specimens from Guatemala to Honduras (race *alticola*), the streaking is much wider so that birds' backs are almost completely black (Miller and Griscom 1925).

The general plumage variation and some of the morphometric measurements reported by Jaramillo and Burke (1999) might show a general clinal pattern, since male specimens show more black coloration on their backs and females become more male-like farther south; in addition, southernmost specimens (*sclateri* and *alticola*) show longer wing measurements on average (although no rigorous morphometric analysis has been conducted). Specimens from the Tres Mariás Islands are not substantially bigger; however, these populations show the largest average culmen measurements.

Given all this geographic variation, many authors (Table 1) have proposed that the Streak-backed Oriole is a superspecies composed of several groups or distinct species. Howell and Webb (1995) proposed four groups: *microstictus* (breeds from Sonora to Jalisco in Mexico), *graysonii* (resident in the Tres Mariás Islands), *pustulatus* (including *formosus*, resident from Jalisco in Mexico to Honduras), and *alticola* (resident

TABLE 1. Summary of all the taxonomic proposals made for the Streak-backed Oriole (*Icterus pustulatus*) complex, since the description of the species. Three major proposals for species limits that we tested using mtDNA and AMOVA are marked with a dagger (†).

Reference	Main conclusions
Wagler (1829)	Describes the Streak-backed Oriole (<i>Icterus pustulatus</i>)
Cassin (1867)	Describes <i>I. sclateri</i> and <i>I. graysonii</i> (Tres Mariás Islands)
Lawrence (1872)	Describes <i>Icterus formosus</i>
Ridgway (1911)	Recognizes several species of <i>Icterus</i> , particularly <i>I. pustulatus</i> , <i>I. sclateri</i> , and <i>I. graysonii</i> . Proposes that the specimens from Nicaragua should be treated as <i>I. s. formosus</i>
Van Rossem (1927)	Proposes <i>I. sclateri</i> and <i>I. pustulatus</i> as conspecific
Friedman et al. (1950)	Recognize <i>I. p. microstictus</i> , <i>I. p. graysonii</i> , <i>I. p. pustulatus</i> , and <i>I. p. formosus</i> (southern Mexico and northwestern Guatemala)
Peters (1968)	Recognizes <i>I. p. microstictus</i> from Sonora and Chihuahua to Jalisco and Guerrero, <i>I. p. graysonii</i> from Tres Mariás Islands (México), <i>I. p. pustulatus</i> from Colima to Guatemala, <i>I. p. formosus</i> from southeast Mexico to northern Guatemala, <i>I. p. alticola</i> on the Atlantic slope of Guatemala, and <i>I. p. sclateri</i> from Guatemala to Nicaragua
Howell and Webb (1995)†	Recognize four groups: <i>microstictus</i> (breeds from Sonora to Jalisco), <i>graysonii</i> (Tres Mariás Islands), <i>pustulatus</i> (including <i>formosus</i> , breeds from Jalisco to Honduras), and <i>alticola</i> (breeds in Costa Rica valley)
Phillips (1995)	Proposes three new forms: <i>I. p. yaegeri</i> (southern Sinaloa to southern Nayarit), <i>I. p. dickermani</i> (southwestern Jalisco to southern Guerrero), and <i>I. p. interior</i> (central-south Mexico)
AOU (1998)	Recognizes three groups: <i>pustulatus</i> , <i>graysonii</i> , and <i>sclateri</i>
Jaramillo and Burke (1999)†	Propose three groups: <i>pustulatus</i> (from Sonora to north Oaxaca), <i>graysonii</i> (from Tres Mariás Islands), and <i>sclateri</i> (from north Oaxaca to Costa Rica)
Navarro-Sigüenza and Peterson (2004)†	Recognize three distinct species: <i>I. sclateri</i> (includes <i>I. s. formosus</i>) from Chiapas to Honduras, <i>I. pustulatus</i> (includes <i>I. p. microstictus</i>) in Western Mexico from Sonora to Chiapas, and <i>I. graysonii</i> on the Tres Mariás Islands (Mexico)

in the interior valleys of Central America). Later, Jaramillo and Burke (1999) proposed three groups: *pustulatus* (from Sonora to northern Oaxaca in Mexico), *graysonii* (on the Tres Mariás Islands), and *sclateri* (from southern Oaxaca and Chiapas in Mexico to Costa Rica). Recently, Navarro-Sigüenza and Peterson (2004) proposed full species status for the same groups as Jaramillo and Burke (1999); however, their proposed group boundaries are different. Navarro-Sigüenza and Peterson (2004) suggest that *pustulatus* occurs from Sonora to Chiapas in Mexico, *sclateri* occurs from Chiapas in Mexico to Honduras, and *graysonii* is found on the Tres Mariás Islands. The AOU (1998) also recognizes the three groups proposed by Jaramillo and Burke (1999), although, again, the proposed boundaries between them are slightly different.

It is important to emphasize that even though these morphologically based species descriptions agree on the probable existence of more than one species within *Icterus pustulatus*, the boundaries between them are not clear. Also, no rigorous morphological or molecular study has been conducted. Therefore, we set out to accomplish several goals: (1) to determine if the degree of genetic variation among Streak-backed

Oriole populations corresponds to the degree of morphological variation, (2) to evaluate whether the recognition of multiple species would be supported by mtDNA, and (3) to report the overall patterns of genetic variation within and among populations of the Streak-backed Oriole complex. Our results give important insights into the evolutionary history and taxonomic status of this interesting temperate-tropical species.

METHODS

LABORATORY PROCEDURES

We obtained tissue samples (muscle, heart, and liver) from 102 individuals (Appendix) of the Streak-backed Oriole complex collected from across the species' range (38 localities; Fig. 1). We used the Bullock's Oriole (*Icterus bullockii*) and Baltimore Oriole (*Icterus galbula*) as outgroups for phylogenetic analyses (Omland et al. 1999, Allen and Omland 2003). DNA was extracted from tissue samples using the DNeasy Tissue Kit (Quiagen, Valencia, California). We amplified the mitochondrial control region (CR-Domain I) using two primers spanning 344 base pairs: LGL2 (CGCCACATCAGACAGTCCAT)

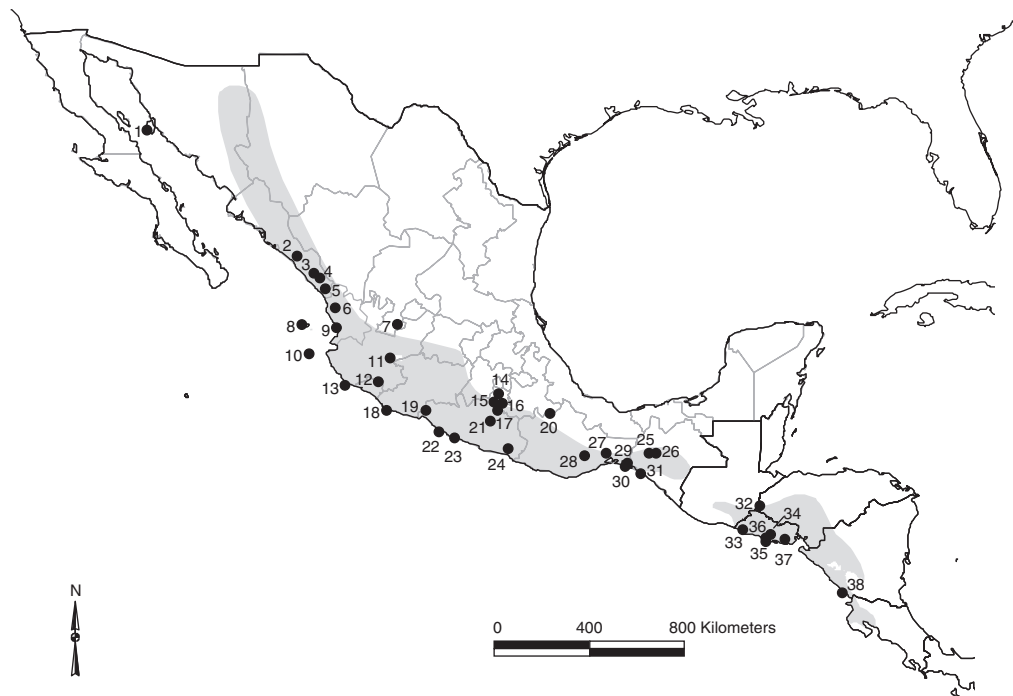


FIGURE 1. Map summarizing the approximate geographic range (gray shadow) of the Streak-backed Oriole (*Icterus pustulatus*), and sampling localities surveyed for this study (circles). Localities are: 1. Isla Tiburón, Sonora; 2. Cosalá, Sinaloa; 3. El Magistral, Sinaloa; 4. Copala, Sinaloa; 5. El Limón, Sinaloa; 6. Tierra Generosa, Nayarit; 7. Jalpa, Zacatecas; 8. Isla María Magdalena, Nayarit; 9. San Blas, Nayarit; 10. Isla Maria Madre, Nayarit; 11. Chapala, Jalisco; 12. Laguna la María, Colima; 13. Emiliano Zapata, Jalisco; 14. Yauatepec, Morelos; 15. Puente de Ixtla, Morelos; 16. Limón, Morelos; 17. Huautla, Morelos; 18. Las Haciendas, Michoacán; 19. Presa Infiernillo, Michoacán; 20. Venta Salada, Puebla; 21. San Miguel Tecuiciapan, Guerrero; 22. Los Cirilos, Guerrero; 23. Laguna Nuxco, Guerrero; 24. El Carmen, Guerrero; 25. Ocozocuaula, Chiapas; 26. Tuxtla Gutierrez, Chiapas; 27. Nizanda, Oaxaca; 28. Cerro Piedra Larga, Oaxaca; 29. Rancho las Minas, Oaxaca; 30. San Pedro Tapanatepec, Oaxaca; 31. Rancho Bellavista, Chiapas; 32. Copán, Honduras; 33. Cruz Grande, El Salvador; 34. San Vicente, El Salvador; 35. Zacatecoluca, El Salvador; 36. Volcán San Miguel, El Salvador; 37. Cantón Animas Abajo, El Salvador; and 38. La Flor, Nicaragua.

and H417 (CTCACGAGAACCGAGCTACT; Tarr 1995). A typical control region amplification involved an initial cycle of 4 min at 95°C, 1 min at 50°C, and 45 sec at 72°C, followed by 35 cycles of 1 min at 95°C, 1 min at 50°C, 45 sec at 72°C, and a final elongation step of 10 min at 72°C. PCR was carried out on the Gene Amp PCR System 9700 (Applied Biosystems, Foster City, California) and products were verified on a 1% agarose gel, revealed by staining ethidium bromide, and cleaned using QIAquick PCR purification kits (Qiagen). We sequenced these products using ABI's BigDye v.3 Terminator Cycle Sequencing Kit on the Gene Amp PCR system 2400 (Applied Biosystems). Excess dye terminators were removed by the EDTA-ethanol precipitation protocol recommended by Applied Biosystems, and sequences were run out on an ABI 3100 DNA sequencer (Applied Biosystems).

PHYLOGENETIC ANALYSES

Once we obtained the mtDNA sequences, we edited and aligned them using Sequencher 4.1 (Genecodes Corporation, Ann Arbor, Michigan). Maximum parsimony trees were constructed for the control region sequences using heuristic searches in PAUP* (version 4.0b8; Swofford 1999). We conducted 1000 bootstrap pseudoreplications to determine support values for various nodes on the phylogenies. We tested for the nucleotide substitution model that best fit our data using Modeltest 3.7 (Posada and Crandall 1998). We then performed maximum likelihood analysis in PAUP* with

a heuristic search of 1000 random additions. We also constructed a haplotype network using Network 4.1.1.2 (Bandelt et al. 1999; <www.fluxus-engineering.com>, MJ algorithm).

POPULATION GENETIC ANALYSES

We performed an analysis of molecular variance (AMOVA) to test which of the three major taxonomic proposals (Table 1) best fit the mtDNA (Howell and Webb 1995, Jaramillo and Burke 1999, Navarro-Sigüenza and Peterson 2004). We also conducted an additional AMOVA separating the northern populations into two groups: individuals from the Tres Marías Islands (*graysonii* group) versus individuals from the mainland. Significance values for the AMOVA took into account the number of mutations among haplotypes (Φ -statistics) and were performed with 1000 permutations. We used mismatch distributions to determine whether the Streak-backed Oriole complex is in mutational-drift equilibrium or undergoing demographic expansion. These analyses were performed in Arlequin version 3.01 (Excoffier et al. 2005).

RESULTS

SEQUENCE DATA

Of the 344 base pairs of mtDNA sequence obtained from the control region, only 13 were variable (3.8%) and eight were parsimony informative (2.3%). We found a total of 16 haplotypes (Table 2). The most common haplotype (A1) was found

TABLE 2. MtDNA haplotypes and sampling sites of the Streak-backed Oriole (*Icterus pustulatus*) throughout its range. The numbers in parentheses correspond to the number of individuals in the population containing that specific haplotype.

Haplotype	No. of individuals	Sampled state, locality, and number of samples
A1	34	Chiapas: Rancho Bellavista (3), Tuxtla Gutierrez (2), Ocozocautla (2); Guerrero: El Carmen (3); Oaxaca: San Pedro Teapanatepec (3), Nizanda (3), Cerro Piedra Larga (3); Morelos: Yautepec (1); El Salvador: Cantón Cruz Grande (2), San Vicente (2), Cantón Animas Abajo (2) Volcán de San Miguel (1), Zacatecoluca (2); Honduras: Cópán (5)
A2	1	Guerrero: Los Cirulos (1)
A3	1	Oaxaca: Cerro Piedra Larga (1)
B1	29	Sonora: Isla Tiburón (1); Colima: Laguna la María (2); Jalisco: Emiliano Zapata (2), Chapala (2); Michoacán: Presa Infiernillo (1), Las Haciendas (1); Nayarit: San Blas (4), Tierra Generosa (1); Chiapas: Rancho Bellavista (1); Zacatecas: Jalpa (1); Puebla: Venta Salada (1); Sinaloa: Copala (4), El Magistral (1), Cosálá (3), El Limón (4)
B2	1	Jalisco: Emiliano Zapata (1)
B3	1	Michoacan: Presa Infiernillo (1)
B4	15	Nayarit: Isla María Magdalena (6), Isla María Madre (2)
B5	2	Nayarit: San Blas (2)
B6	1	Sinaloa: Cosálá (1)
B7	1	Sinaloa: Cosálá (1)
B8	1	Sinaloa: El Limón (1)
C1	14	Guerrero: San Miguel Tecuiciapan (5); Michoacán: Laguna Nuxco (1), Presa Infiernillo (2); Morelos: Puente de Ixtla (1), Limon (1); Nicaragua: La Flor (1); Oaxaca: Cerro Piedra Larga (1); Puebla: Venta Salada (2)
C2	3	Guerrero: San Miguel Tecuiciapan (1); Morelos: Huautla (1), Yautepec (1)
C3	2	Guerrero: Los Cirulos (1); Michoacán: Presa Infiernillo (1)
C4	2	Morelos: Limon (2)
C5	1	Oaxaca: Cerro Piedra Larga (1)

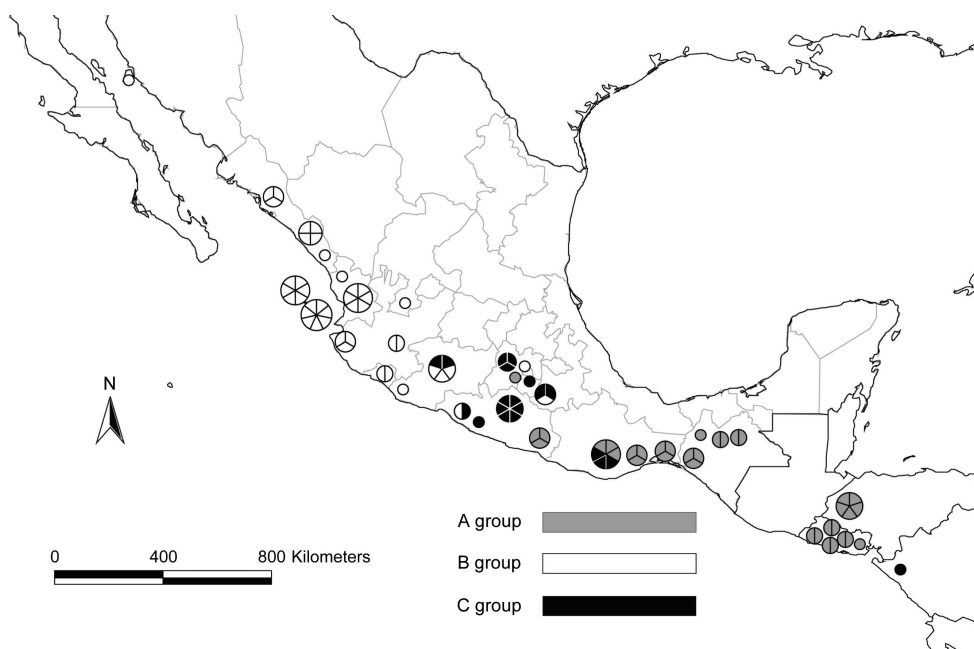


FIGURE 2. Map showing the distribution of the three major groups of mtDNA haplotypes of Streak-backed Orioles (*Icterus pustulatus*) found in this study. Most of the individuals from the north of Mexico belong to the B group, while most of the individuals in the south belong to the A group. Wedges inside each circle represent the number of individuals sampled from that specific locality.

predominantly in southern populations (15 populations from Guerrero, Morelos, Oaxaca, Chiapas, El Salvador, and Honduras). The second most common haplotype (B1) was generally found in northern populations (Sonora, Sinaloa, Zacatecas, Nayarit, Jalisco, Michoacan, Colima, Puebla, and Oaxaca). Haplotype C1 was generally restricted to birds from central Mexico, except for a single individual from Nicaragua. Individuals from the Tres Mariás Islands all shared one unique haplotype (B4); there were no haplotypes shared between these islands and the mainland. However, on the mainland, haplotypes were roughly divided into three groups—one each in the north, south, and central parts of the range—although there were not strong geographic breaks between haplotype groups (Fig. 2). Haplotype diversity was greatest in central Mexico, especially in the states of Guerrero, Morelos, and Puebla. There were few differences among haplotypes, with only one base change separating most haplotypes. Nucleotide diversity (π) for the whole species was 0.0041 ± 0.0028 , while haplotype diversity (h) was 0.80 ± 0.02 , with a maximum pairwise divergence of 1.7%.

NETWORKS AND TREES

The median joining network (Fig. 3) showed the distribution of haplotypes and their relationships to geography. As mentioned previously, haplotype A1 was the most common. Haplotype B7 from Sinaloa appeared as an alternative connection between haplotype B1 and C1. The individuals from the Tres Mariás Islands had a unique haplotype (B4); one fixed mutational step separated them from the common northern

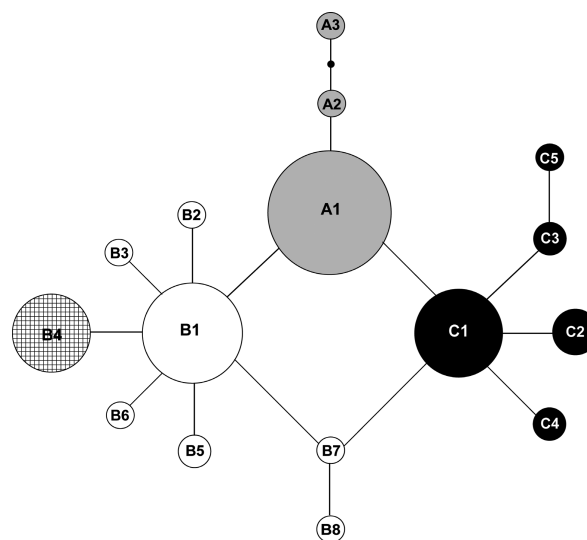


FIGURE 3. Haplotype median joining network of the Streak-backed Oriole (*Icterus pustulatus*) as computed in Networks 4.1.1.1 using mitochondrial DNA sequenced from individuals sampled throughout the species' range. The size of each circle is proportional to the number of individuals with that specific haplotype. Three different haplotype groups were distinguished: gray shaded circles represent haplotype group A, generally found in southern Mexico and Central America; white circles represent haplotype group B, found in northern and central Mexico; and black circles represent haplotype group C, generally found in central Mexico and with an outlier individual from Nicaragua. Text inside the circle represents each haplotype's unique designation. An unsampled haplotype is shown as a solid dot. Note the distinct Tres Mariás Islands haplotype (B4).

TABLE 3. Results of AMOVAs testing hypotheses regarding the Streak-backed Oriole (*Icterus pustulatus*) complex. We tested the hypothesis of Howell and Webb (1995), who proposed that populations were divided into four main groups, and an alternative hypothesis that populations were divided into two groups, one containing the Tres Mariás Islands individuals, and the other containing mainland northern individuals.

Hypothesis Source of variation	df	Sum of squares	Variance components	Percent of variation	P-value
Howell and Webb (1995): $\Phi_{ST} = 0.75$					
Among groups	3	30.6	0.53	55.67	< 0.001
Among populations within groups	34	24.3	0.18	18.75	< 0.001
Within populations	64	15.8	0.24	25.58	< 0.001
Total	101	70.7	0.96		
Tres Mariás Islands vs. mainland: $\Phi_{ST} = 0.68$					
Among groups	1	6.2	0.47	60.27	< 0.001
Among populations within groups	9	3.7	0.06	7.57	< 0.001
Within populations	21	5.3	0.25	32.15	< 0.001
Total	31	15.2	0.79		

haplotype (B1). Each of the three most common haplotypes had a group of less-common haplotypes likely derived from it (e.g., B1 had B2 to B6).

The model of evolution that best fit our data according to Akaike's information criterion (AIC) was the HKY + I model, with the following parameter values: A = 0.30, C = 0.30, G = 0.16, T = 0.22, Ti:Tv ratio = 4.59, and I = 0.81. Maximum likelihood searches produced only one tree (not shown) with a $-\text{Log}(n) = 679$, which showed the nonmonophyly of haplotypes within each of the geographic areas. The Tres Mariás Islands appeared nested within the same group containing all northern samples.

We obtained six parsimonious trees of 32 steps, with a consistency index = 0.87, retention index = 0.95, and homoplasy index = 0.12. A majority rule consensus was made for the six trees. We found three major groups, but we did not find support for the reciprocal monophyly of geographic areas, as many haplotypes were shared between populations in different regions.

POPULATION GENETIC ANALYSES

Of the three major taxonomic proposals that we tested, that of Howell and Webb (1995) explained the largest percentage of variation (56%; Table 3). Thus, the majority of variation was accounted for by among-group divergence (*I. p. microstictus*, *I. p. pustulatus*, *I. p. graysonii*, and *I. p. alticola*), but, because of haplotype sharing, a lot of the variation was still not accounted for by Howell and Webb's (1995) proposal. Jaramillo and Burke's (1999) proposal explained the second-largest percentage of genetic variation, but their three proposed groups explained only 45% of the among-group variation. Finally, Navarro-Sigüenza and Peterson's (2004) proposal explained only 42% of the variation among their three suggested groups. In contrast, the AMOVA analysis comparing mainland northern populations to the Tres Mariás Islands populations accounted for a higher percentage of the total genetic

variation (60%; Table 3). The Φ_{ST} value was 0.68 ($P < 0.001$), even though there was only one fixed nucleotide difference between the two groups.

Differentiation index (Φ_{ST}) values among populations generally revealed low levels of genetic differentiation. These low Φ_{ST} values could be due to recent ancestry or gene flow. For calculation purposes we assumed that these values were due to gene flow, and computed the number of migrants per generation following Slatkin (1991). Many of the values suggested more than one migrant per generation or an infinite number of migrants. However, values for the Tres Mariás Islands suggested these populations had less than one migrant per generation, with an average of 0.55 migrants per generation and a Φ_{ST} of 0.75, meaning that even though they shared no haplotypes with mainland populations, we cannot exclude some low level of gene flow.

The mismatch distribution for the whole species complex resulted in τ (number of generations) = 1.27, θ_0 (population size before demographic expansion) = 0, and θ_1 (population size after demographic expansion) = 2239 (Fig. 4). These values show a unimodal distribution consistent with a population that has undergone a sudden demographic expansion (Rogers and Harpending 1992). The raggedness index was 0.08 ($P = 0.13$).

DISCUSSION

Low amounts of genetic variability in the control region sequences and the intermixing of haplotypes among *Icterus pustulatus* populations suggest a very recent origin of the different subspecies. The average sequence divergence among individuals was only 0.4%; similar amounts of divergence have been observed in other species of the genus *Icterus* (Baker et al. 2003, Kondo et al. 2004).

Geographic groupings of Streak-backed Oriole individuals did not show reciprocal monophyly, a pattern that has been reported in the early stages of speciation in other species of birds (Avice et al. 1990, Baker et al. 2003, Funk and

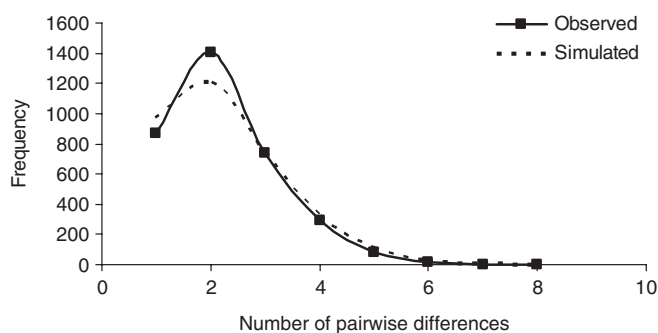


FIGURE 4. Mismatch distribution of the observed number of pairwise differences among haplotypes of the Streak-backed Oriole (*Icterus pustulatus*) complex. The solid line indicates the observed distribution of pairwise differences, and the dotted line indicates the simulated distribution under a model of population expansion. The observed Poisson-like distribution is consistent with a population that has undergone demographic expansion.

Omland 2003). This mtDNA polyphyly could be a consequence of incomplete lineage sorting due to insufficient time since separation or high amounts of gene flow (Seutin et al. 1993, Baker et al. 2003). Conversely, the lack of reciprocally monophyletic groups may be a result of most of the sampled subspecies not corresponding to independent histories and being only arbitrary divisions of morphological clines (Avisé 1994, Zink et al. 2002).

Mitochondrial gene trees of several avian species have shown intermixing of haplotypes among populations (e.g., Song Sparrow [*Melospiza melodia*], Zink and Dittman 1993; Savannah Sparrow [*Passerculus sandwichensis*], Zink et al. 2005), suggesting many species are going through the early stages of divergence (Funk and Omland 2003). Given the low mitochondrial variation in *Icterus pustulatus*, the obvious plumage differences among populations may reflect different ecological and social selection pressures across the different environments in Mexico and Central America. Omland and Lanyon (2000) reported that plumage characters can evolve rapidly in orioles, which could help explain the high diversity of plumage forms found in this species. Many species of birds show variation in plumage coloration, in spite of little or no molecular variation (Greenberg et al. 1998, Baker et al. 2003, Zink et al. 2005).

POPULATION HISTORY

The distribution of Streak-backed Oriole haplotypes is consistent with a process of isolation by distance; however, the haplotypes from the B group in the median joining network are directly interconnected with haplotypes from the A group, rather than with those from the center (C group). This species has an uncommon phylogeographic pattern (Type III), with shallow haplotype trees showing weak geographic structure associated with recent population expansion and a lack of isolating barriers (Zink et al. 2001). Thus, the observed geographic distribution of haplotypes may be the result of

recent colonization from a less widespread common ancestor without sufficient time for geographic differentiation, involving incomplete lineage sorting or reasonable amounts of gene flow. The sharing of internal ancestral haplotypes among geographically disparate localities (e.g., Nicaragua and Michoacan) strongly suggests incomplete lineage sorting due to recent divergence and range expansion (Omland et al. 2006). However, there is still uncertainty about the location of the ancestral range for this species. The mismatch analysis was consistent with a recent range and population expansion, but it is unclear whether the direction of colonization was from the north to the south or vice versa.

TRES MARÍAS ISLANDS POPULATIONS

The Tres Marías Islands populations of *Icterus pustulatus* (*I. p. graysonii*) have long been known for their morphological distinctiveness (Cassin 1867, Ridgway 1911, Howell and Webb 1995, AOU 1998, Jaramillo and Burke 1999, Navarro-Sigüenza and Peterson 2004). They are paler than individuals from the continent, almost lack streaking on the back, and seem to differ in some morphometric measurements (Jaramillo and Burke 1999). This pattern of plumage coloration, in which the continental counterpart is brighter than individuals from the islands, has been found in other birds endemic to the Tres Marías Islands (e.g., Happy Wren [*Thryothorus felix*], Blue Mockingbird [*Melanotis caerulescens*], Broad-billed Hummingbird [*Cyananthus latirostris*], and Cinnamon Hummingbird [*Amazilia rutila*]; Grant 1965). Individuals we sampled from the islands showed one fixed nucleotide substitution that separated them from all sampled continental haplotypes. This fixed difference suggests that populations from the islands have been isolated for a relatively long period of time, especially considering the low levels of mtDNA differentiation among the mainland subspecies. We did not find the island haplotype on the mainland, which is consistent with in situ mutation since island colonization; however, a recent founder event with fixation of a rare or now extinct mainland allele is also possible.

I. p. graysonii differs in multiple characters from the rest of the species, which argues that it could be considered a distinct unit. There are differences in mtDNA, plumage, and perhaps morphometrics and vocalizations. The phylogenetic species concept of Cracraft (1983), or the diagnosable approach, holds that a species can be recognized based on at least one diagnostic character. Based on the distinctiveness of the plumage coloration and the fixed differences in mitochondrial DNA, we recommend recognizing this taxon as a distinct species, *Icterus graysonii*, as proposed recently by Navarro-Sigüenza and Peterson (2004).

GEOGRAPHIC PATTERN

The most interesting result of this study is that even though the distribution of *Icterus pustulatus* is mostly tropical (northern Mexico to Costa Rica), the geographic pattern and haplotype

diversity is similar to that of some temperate species (Ball et al. 1988, Greenberg et al. 1998, Milá et al. 2000, Baker et al. 2003, Kondo et al. 2004). Phenotypically, this species complex shows characteristics of a tropical species, given its geographically structured plumage variation (even though this may be clinal). The low amounts of genetic variation observed and other signatures of intermediate divergence are consistent with the earliest stages of speciation (Omland et al. 2006). It is important to emphasize that two protein coding genes (ND2 and cytochrome *b*) showed no variation at all when we sequenced ten of the most variable haplotypes, supporting the recent divergence of this species complex (NC-R, unpubl. data). Given that there were no definite genetic breaks in mtDNA, it is possible that the subspecies described earlier may represent only a morphological and mitochondrial DNA cline. The only fixed geographical difference we found was for the Tres Mariás Islands populations. Additional morphological and behavioral work should be done to further elucidate the evolutionary history of the Tres Mariás Islands populations.

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APPENDIX. Specimens of *Icterus pustulatus* ($n = 102$) sequenced for the mtDNA control region gene in this project, showing country, state (or department, abbreviated as “Dpto.”), and locality of sampling, and catalog number. Acronyms are: FMNH = Field Museum of Natural History; KU = Museum of Natural History, University of Kansas; MBM = Marjory Barrick Museum, University of Nevada, Las Vegas; MZFC = Museo de Zoología “Alfonso Herrera” Facultad de Ciencias, Universidad Nacional Autónoma de México; UWBM = University of Washington Burke Museum of Natural History and Culture; and YPM = Yale Peabody Museum. Tissues without a voucher skin specimen show only the field reference number.

Country	State or Department	Locality	Voucher Catalog Number	GenBank Number
El Salvador	La Paz	Cantón Animas Abajo	KU 9274	FJ410878
El Salvador	La Paz	Cantón Animas Abajo	KU 9277	FJ410879
El Salvador	La Paz	Zacatecoluca	KU 9275	FJ410873
El Salvador	La Paz	Zacatecoluca	KU 9524	FJ410874
El Salvador	El Sonsonate	Cruz Grande	KU 6005	FJ410875
El Salvador	El Sonsonate	Cruz Grande	KU 6001	FJ410872
El Salvador	San Vicente	San Vicente	KU 7691	FJ410876
El Salvador	San Vicente	San Vicente	KU 7693	FJ410877
El Salvador	San Miguel	Volcán de San Miguel	YPM 100371	FJ410871
Honduras	Copán	Copan, Ruinas	MBM 7147	FJ410824
Honduras	Copán	Copan, Ruinas	MBM 7146	FJ410823
Honduras	Copán	Copan, Ruinas	MBM 7737	FJ410825
Honduras	Copán	Copan, Ruinas	MBM 7762	FJ410826
Honduras	Copán	Copan, Ruinas	MBM 7763	FJ410827
Nicaragua	De Rivas	La Flor	UWBM 69072	FJ410854
México	Chiapas	Ocozocuaula	UWBM 52129	FJ410807
México	Chiapas	Ocozocuaula	UWBM 52133	FJ410808
México	Chiapas	Rancho Bellavista Tonalá	MZFC 19431	FJ410802
México	Chiapas	Rancho Bellavista Tonalá	MZFC 19430	FJ410804
México	Chiapas	Rancho Bellavista Tonalá	MZFC 19432	FJ410803
México	Chiapas	Tuxtla Gutiérrez	KEO 10	FJ410806
México	Chiapas	Tuxtla Gutiérrez	MZFC 13569	FJ410805
México	Colima	Laguna la María	MZFC 16347	FJ410810
México	Colima	Laguna la María	MZFC 16346	FJ410809
México	Guerrero	2km NE of El Carmen	MZFC 16535	FJ410821
México	Guerrero	2km NE of El Carmen	MZFC 16536	FJ410822
México	Guerrero	2km NE of El Carmen	MZFC 16534	FJ410820
México	Guerrero	Laguna Nuxco	MZFC 16352	FJ410819
México	Guerrero	Los Cirulos Petatlan	MZFC 19426	FJ410818
México	Guerrero	Los Cirulos Petatlan	MZFC 19425	FJ410817
México	Guerrero	San Miguel Tecuiciapan	MZFC 18969	FJ410815
México	Guerrero	San Miguel Tecuiciapan	MZFC 18968	FJ410813
México	Guerrero	San Miguel Tecuiciapan	MZFC 18998	FJ410811
México	Guerrero	San Miguel Tecuiciapan	MZFC 18970	FJ410812
México	Guerrero	San Miguel Tecuiciapan	MZFC 19005	FJ410814
México	Guerrero	San Miguel Tecuiciapan	MZFC 18974	FJ410816
México	Jalisco	3km E of Chapala	MZFC 15558	FJ410834
México	Jalisco	3km E of Chapala	MZFC 15559	FJ410833
México	Jalisco	Emiliano Zapata	JAL 2	FJ410830
México	Jalisco	Emiliano Zapata	JAL 3	FJ410831
México	Jalisco	Emiliano Zapata	JAL 4	FJ410832
México	Michoacán	Las Haciendas	MZFC 16353	FJ410840
México	Michoacán	Presa Infiernillo	MZFC 16483	FJ410838
México	Michoacán	Presa Infiernillo	MZFC 16485	FJ410836
México	Michoacán	Presa Infiernillo	MZFC 16482	FJ410835
México	Michoacán	Presa Infiernillo	MZFC 16486	FJ410839
México	Michoacán	Presa Infiernillo	MZFC 16484	FJ410837
México	Morelos	Huautla	MZFC 13560	FJ410842
México	Morelos	Limón	P 01	FJ410843
México	Morelos	Limón	P 02	FJ410844
México	Morelos	Limón	P 03	FJ410845
México	Morelos	Puente de Ixtla	MZFC 13744	FJ410841

(Continued)

APPENDIX. (Continued).

Country	State or Department	Locality	Voucher Catalog Number	GenBank Number
México	Morelos	Yautepec	PEP 1485	FJ410847
México	Morelos	Yautepec	MZFC 6797	FJ410846
México	Nayarit	Isla María Madre	MZFC 19224	FJ410891
México	Nayarit	Isla María Madre	MZFC 19225	FJ410890
México	Nayarit	Isla María Madre	MZFC 19226	FJ410896
México	Nayarit	Isla María Madre	MZFC 19227	FJ410897
México	Nayarit	Isla María Madre	MZFC 19228	FJ410898
México	Nayarit	Isla María Madre	MZFC 19229	FJ410899
México	Nayarit	Isla María Magdalena	MZFC 19221	FJ410888
México	Nayarit	Isla María Magdalena	MZFC 19222	FJ410895
México	Nayarit	Isla María Magdalena	MZFC 19232	FJ410892
México	Nayarit	Isla María Magdalena	MZFC 19223	FJ410894
México	Nayarit	Isla María Magdalena	MZFC 19233	FJ410893
México	Nayarit	Isla María Magdalena	MZFC 19234	FJ410887
México	Nayarit	Isla María Magdalena	MZFC 19235	FJ410889
México	Nayarit	San Blas	MZFC 15546	FJ410853
México	Nayarit	San Blas	MZFC 15557	FJ410848
México	Nayarit	San Blas	MZFC 15545	FJ410852
México	Nayarit	San Blas	MZFC 15556	FJ410849
México	Nayarit	San Blas	MZFC 15555	FJ410850
México	Nayarit	San Blas	MZFC 15544	FJ410851
México	Nayarit	Tepic	MZFC 19660	FJ410905
México	Oaxaca	Cerro Piedra Larga	MZFC 12406	FJ410864
México	Oaxaca	Cerro Piedra Larga	MZFC 12408	FJ410863
México	Oaxaca	Cerro Piedra Larga	MZFC 18696	FJ410861
México	Oaxaca	Cerro Piedra Larga	MZFC 18706	FJ410860
México	Oaxaca	Cerro Piedra Larga	MZFC 18702	FJ410859
México	Oaxaca	Cerro Piedra Larga	MZFC 18704	FJ410862
México	Oaxaca	Nizanda, C. al Aguaje	MZFC 16906	FJ410857
México	Oaxaca	Nizanda, Enclave1	Conacyt 1265	FJ410855
México	Oaxaca	Nizanda, Enclave1	Conacyt 1293	FJ410856
México	Oaxaca	Rancho Las Minas	MZFC 19433	FJ410858
México	Oaxaca	San Pedro Tepanatepec	UWBM 52181	FJ410865
México	Oaxaca	San Pedro Tepanatepec	UWBM 52182	FJ410866
México	Oaxaca	San Pedro Tepanatepec	UWBM 52193	FJ410867
México	Puebla	Venta Salada	MZFC 11132	FJ410868
México	Puebla	Venta Salada	MZFC 11131	FJ410869
México	Puebla	Venta Salada	MZFC 11134	FJ410870
México	Sinaloa	Copala	MZFC 15392	FJ410881
México	Sinaloa	Copala	MZFC 15393	FJ410884
México	Sinaloa	Copala	MZFC 15391	FJ410883
México	Sinaloa	Copala	MZFC 15394	FJ410882
México	Sinaloa	Cosalá	UWBM 81439	FJ410902
México	Sinaloa	Cosalá	MZFC 19712	FJ410904
México	Sinaloa	Cosalá	MZFC 19719	FJ410903
México	Sinaloa	El Limón	MZFC 19710	FJ410900
México	Sinaloa	El Limón	UWBM 81433	FJ410901
México	Sinaloa	2km W of El Magistral	MZFC 15395	FJ410880
México	Sonora	Isla Tiburón, El Caracol	MZFC 14967	FJ410885
México	Zacatecas	Jalpa	MZFC 15818	FJ410886