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MITOCHONDRIAL DNA AND MORPHOLOGICAL VARIATION OF WHITE-WINGED DOVES IN TEXAS[1]

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Abstract. White-winged Doves (*Zenaida asiatica*) in Texas are separated into four subspecies primarily based on morphological variation. However, problems differentiating the subspecies by morphological measurements alone and a recent range expansion have led to questions about their systematic status and population structure. We evaluated both morphological characters and a 289 base-pair segment of the mitochondrial control region from 183 White-winged Doves taken from 31 locations in Texas, New Mexico, and Arizona. Twenty-seven variable base changes were observed, which resulted in 44 haplotypes. An analysis of haplotypes yielded little phylogenetic signal; however, analyses of haplotype frequencies indicated geographic heterogeneity between doves collected in the four historic subspecies ranges. Doves from the range expansion areas were intermediate in size and genetically homogenous. Morphological analyses suggested congruency between control region variation and body size. Our data support the recognition of two subspecies of White-winged Doves with a zone of intergradation in the range expansion areas. The dispersal of White-winged Doves into the expansion areas appears to be a congruent process by both subspecies.

Key words: control region, mitochondrial DNA, morphology, range expansion, subspecies, White-winged Dove, Zenaida asiatica.

INTRODUCTION

Twelve subspecies of White-winged Doves (*Zenaida asiatica*) have been described that range from the southwestern portion of the United States, throughout Mexico, Central America, and western South America (Saunders 1968). Four subspecies have ranges that extend into the United States where they are primarily found in Texas, New Mexico, Arizona, and California (Saunders 1968, Brown et al. 1977, George et al. 1994). In Texas, where all four subspecies are thought to occur, White-winged Doves are an important migratory game bird that has undergone large population fluctuations over the last 75 years (Kiel and Harris 1956, Cottam and Trefethan 1968, Waggerman 1992). Recent population increases in Texas have been attributed to a northward range expansion out of both the western Chihuahuan desert and the semi-tropical southeast (Gallucci 1978, West 1993).

Before 1968, there were two recognized subspecies of White-winged Doves in the United States that were separated into eastern (*Zenaida asiatica asiatica*) and western (*Z. a. mearnsi*) races (Ridgway 1915, AOU 1957). Saunders (1968) conducted a morphometric study and determined that there were four subspecies in the United States; two new subspecies (*Z. a. grandis* and *Z. a. monticola*) were depicted as occurring between the ranges of the eastern and western races. The four ranges were described in the United States as (1) *Z. a. asiatica* found in the

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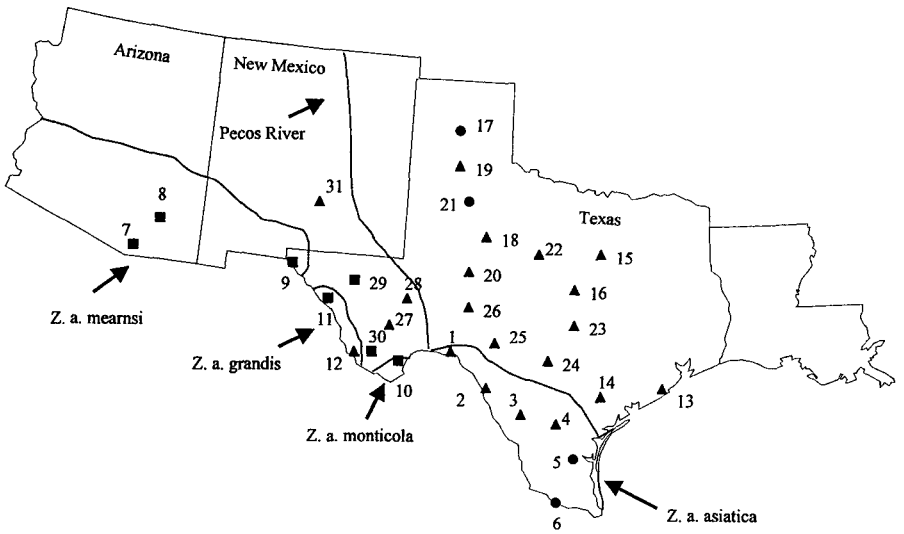

FIGURE 1. Collection locations and Saunders' (1968) subspecies ranges for White-winged Doves in Texas, New Mexico, and Arizona. Squares are locations that are fixed for thymine at position 23, circles are locations fixed for adenine, and triangles are non-fixed locations. Location numbers correspond to those given in Table 1.

Tamaulipan Biotic Province, primarily restricted to areas along the Rio Grande River, (2) *Z. a. mearnsi* found in Arizona, New Mexico, and El Paso county in Texas, (3) *Z. a. monticola* found in the Chihuahuan Biotic Province, restricted to areas in and adjoining Big Bend National Park, and (4) *Z. a. grandis* also found in the Chihuahuan Biotic Province, restricted to areas west of Big Bend National Park along the Rio Grande River (Blair 1950, Cottam and Trefethan 1968, Saunders 1968; Fig. 1). However, based on a reexamination of Saunders' (1968) specimens, Browning (1990) concluded that *Z. a. grandis* and *Z. a. monticola* were synonymous with *Z. a. mearnsi.*

Disagreement about the subspecies status of White-winged Doves in the United States has increased as the birds have expanded into areas north of their historic ranges along the Rio Grande River (Cottam and Trefethan 1968, George et al. 1994). Based on morphological characters, Gallucci (1978) and Jenks (1983) both concluded that *Z. a. monticola* was the primary subspecies expanding in the western portions of Texas. These findings led George et al. (1994) to construct a new map of the subspecies that eliminated *Z. a. mearnsi* from Texas and greatly expanded the ranges of *Z. a. monticola* and *Z. a. asiatica.* Therefore, to clarify the systematic status and expansion ranges of White-winged Doves in Texas, we analyzed a segment of the mitochondrial control region because it is useful in identifying organisms at the subspecies level (Baker and Marshall 1997).

Previous studies that used mtDNA to evaluate the differences between morphologically distinct avian subspecies have found mixed results (Ball et al. 1988, Ball and Avise 1992, Wood and Krajewski 1996). Fry and Zink (1998) found discordance between mtDNA control region and morphological data sets for Song Sparrows (*Melospiza melodia*), whereas Wenick et al. (1996) and Barrowclough et al. (1999) found that their mtDNA groups were related to morphometrically described subspecies. In an effort to determine whether White-winged Doves exhibit similar patterns of congruence or discordance between mtDNA control region sequences and morphological subspecies, we measured all adult doves we collected.

METHODS

COLLECTION, STORAGE, AND MORPHOLOGICAL MEASUREMENT

White-winged Doves were collected between April and September 1997 and in March 1998 from 31 locations in Texas, New Mexico, and Arizona (Table 1, Fig. 1). To increase the likelihood of tracking changes at the subspecies level, we collected birds during the breeding season

TABLE 1. Distributions of 44 haplotypes of White-winged Doves (n = 183) collected from 31 locations in Texas, New Mexico, and Arizona. Numbers correspond to locations in Figure 1. Abbreviations: WMA—Wildlife Management Area, SP—State Park, NF—National Forest.

Location	Haplotype (n)
1. Del Rio, Val Verde Co., Texas	A(2), B(1)
2. Eagle Pass, Maverick Co., Texas	A(4), B(1), D(1), K(1), R(1), W(1)
3. Cotulla, La Salle Co., Texas	A(2), E(1)
4. Beeville, Bee Co., Texas	A(3), B(1), LL(1)
5. Kingsville, Kleberg Co., Texas	A(4)
6. McAllen, Hidalgo Co., Texas	A(6), C(1), N(2)
7. Coronado NF, Santa Cruz Co., Arizona	B(3), JJ(1)
8. Sierra Vista, Cochise Co., Arizona	B(3)
9. El Paso, El Paso Co., Texas	B(2), G(1)
10. Black Gap WMA, Brewster Co., Texas	B(3), H(1), Q(1)
11. Esperanza, Hudspeth Co., Texas	B(1), H(1)
12. Ocotillo WMA, Presidio Co., Texas	A(2), B(3), D(2), E(1), I(1), II(1)
13. Galveston, Galveston Co., Texas	A(3), C(1), D(1), L(1), M(1), DD(1) OO(1)
14. Victoria, Victoria Co., Texas	A(1), C(1), E(1), J(2), V(1), Z(1)
15. Waco, McLennan Co., Texas	B(1), C(1), D(2)
16. Killeen, Bell Co., Texas	A(7), B(3), C(1), M(1)
17. Plainview, Hale Co., Texas	A(2)
18. Abilene, Taylor Co., Texas	A(2), B(2), C(1), QQ(1)
19. Lubbock, Lubbock Co., Texas	A(4), D(1), 1(1)
20. San Angelo, Tom Green Co., Texas	A(3), B(1), C(2), D(1), F(1)
21. Snyder, Scurry Co., Texas	D(1), X(1), Y(1), FF(1)
22. Brownwood, Brown Co., Texas	A(6), B(1), C(1), D(1)
23. Austin, Travis Co., Texas	A(1), C(1), I(1)
24. San Antonio, Bexar Co., Texas	A(1), C(2), D(1), BB(1), EE(1), HH(1), KK(1), PP(1)
25. Uvalde, Uvalde Co., Texas	A(2), B(4), C(1), K(1), P(1), MM(1)
26. Sonora, Sutton Co., Texas	A(1), B(1), D(1), F(1), O(1)
27. Alpine, Brewster Co., Texas	A(1), B(1), H(1), L(1), CC(1)
28. Fort Stockton, Pecos Co., Texas	A(2), B(1), G(1), O(1), S(1)
29. Sierra Diablo WMA, Culberson Co., Texas	B(5), H(1), T(1), GG(1), OO(1)
30. Big Bend Ranch SP, Presidio Co., Texas	B(2), G(1), T(1), U(1)
31. Alamogordo, Otero Co., New Mexico	A(1), F(1), AA(1), RR(1)

(end of March to beginning of September; Cottam and Trefethan 1968), and used only adult birds found with enlarged gonads or juveniles for the mtDNA analysis to limit error due to the collection of non-resident birds. For some of the analyses, individuals were categorized according to whether they were collected in the ranges depicted by Saunders (1968) or in the expansion ranges—west or east of the Pecos River (Fig. 1).

Heart tissue, blood, or feather pulp were collected and stored under cryogenic conditions using liquid nitrogen. Morphological measurements of wing chord, tail length, and exposed culmen were taken following the methods of Pyle et al. (1987). These three measurements were used because previous studies have shown them to be useful in identifying subspecies in White-winged Doves (Saunders 1968, Gallucci 1978, Jenks 1983). Only adult birds that had little flight feather wear were used in the morphological analyses. Voucher specimens were placed in the collections of Texas A&M University-College Station or at Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville.

mtDNA ANALYSIS

Whole genomic DNA was extracted from heart tissue, blood, or feathers. All extractions were performed using phenol–chloroform–isoamyl alcohol methods (Sambrook et al. 1989, Hillis et al. 1996). A 289 base-pair (bp) segment of the first domain of mtDNA control region was amplified using standard polymerase chain reaction (PCR) protocols (Palumbi 1996). Initially, the primers developed for the Plain Pigeon (*Columba inornata*) by Miyamoto et al. (1994) were used. However, these primers did not reliably

amplify White-winged Dove mtDNA, so a new set of nested primers (5′-CCCAGACCAAAG-CCACAGT-3′ and 5′-GCAAGTTATGGCCCT-GACAT-3′) was developed. Amplified fragments were cycle sequenced (Hillis et al. 1996) and run on an automated sequencer (ABI 377, Perkin Elmer, Foster City, California). For outgroup comparisons, a Mourning Dove (*Zenaida macroura*; GenBank accession number AF141860) also was sequenced using the newly developed primers. All sequences were compared to the Plain Pigeon sequences deposited in GenBank to confirm that we had correctly amplified mtDNA control region sequences.

GENETIC ANALYSES

Sequences were aligned manually against the previously published Plain Pigeon sequence. Individuals were separated into haplotypes by the possession of at least one variable base change using MacClade 3.04 (Maddison and Maddison 1992).

For population structure analyses, collection locations were placed into one of four groups based on Saunders' (1968) subspecies ranges (*Z. a. asiatica, mearnsi, grandis,* or *monticola*; Fig. 1) or one of two expansion ranges (east or west of the Pecos River; Fig. 1). Haplotype frequencies of these groupings were then evaluated using the analysis of molecular variance (AMOVA) procedure in Arlequin 1.1 (Schneider et al. 1997). Population pairwise differentiation tests also were conducted using Arlequin 1.1. Because so many singlets (haplotypes unique to one individual) were found in our data set, we also used a randomized Chi-square test of independence using the Monte Carlo method in REAP to test for heterogeneity between haplotype frequencies (McElroy et al. 1992). Ten thousand simulations were compared to the original matrix to minimize the effect of small sample size caused by singlets (Roff and Bentzen 1989).

We also analyzed our data using a hierarchical analysis of nucleotide diversity to evaluate which subspecies were the source populations for the range expansion in Texas (Holsinger and Mason-Gamer 1996). This test has the advantage that hierarchical structure need not be imposed prior to analysis. Therefore *a priori* groupings are not needed to determine population structure. Instead, any structure present is allowed to emerge naturally. However, we did group locations within Saunders' (1968) historical subspecies ranges to determine which areas were sources for the range expansion.

PHYLOGENETIC ANALYSIS

To determine the phylogeographic structure of haplotypes and to assess whether base changes that appear to track subspecific limits were homoplastic, we used maximum likelihood methods (PAUP 4.0b2; Swofford 1999). We chose maximum likelihood because no arbitrary weighting is needed, it takes into account differences in the rate of evolution across sites, and with very short sequences it tends to outperform alternative methods (Swofford et al. 1996). To obtain the most likely topology using the model with the least number of parameters, we followed the methods described by Sullivan et al. (1997) with a few modifications. We used a neighbor-joining tree to begin our analyses using the heuristic search option in PAUP 4.0b2 (Saitou and Nei 1987, Swofford 1999). After multiple runs to determine the best likelihood score, we determined that the General Time Reversal model with among-site rate variation following a discrete approximation of the gamma distribution (GTR+Γ) was the most appropriate model. Maximum likelihood settings for empirical nucleotide frequencies were A = 0.295, C = 0.294, G = 0.160, and T = 0.251. The gamma distribution setting used was 0.371. The negative log-likelihood score obtained was 1,162.48. We estimated nodal support using 100 bootstrap replicates (Felsenstein 1985).

MORPHOLOGICAL ANALYSIS

Groupings of individuals and locations based on mtDNA sequence variation were examined by ANOVA for differences in morphology. Multiple comparisons were made using Duncan's Multiple Range test when a significant *F*-test was noted (SAS 1996).

RESULTS

SEQUENCE AND HAPLOTYPE ANALYSIS

Two hundred eighty-nine base pairs of the mitochondrial control region were sequenced for 183 White-winged Doves from 31 locations. Twenty-seven variable base changes were observed. An A-T transversion at position 23 was fixed for thymine in the *Z. a. mearnsi* (n = 13) and *monticola* (n = 5) populations, whereas adenine was found in 89% (n = 33) of doves from

TABLE 2. Results of AMOVA and randomized chi-square tests of 183 White-winged Doves collected in Texas, New Mexico, and Arizona during April–September 1997 and March 1998.

Population groups	Among-groups variation	Within-populations variation	χ^2
Four subspecies	29.0**	72.9**	45.8**
Four subspecies + total expansion area	7.8**	89.3**	169.0
Four subspecies + two expansion areas	9.9**	89.9**	211.3*

* $P < 0.05$, ** $P < 0.001$.

the range of *Z. a. asiatica*. A mixture of this base change was found in the expansion areas and in the range of *Z. a. grandis* (Fig. 1).

Forty-four haplotypes were described (GenBank accession AF141862, AF263948–263990; Table 1), 15 had more than one individual, which accounted for 84% of all doves sequenced; all other haplotypes were singlets. The two most common haplotypes were A and B, which described 32% and 22%, respectively, of all birds sequenced. Haplotype A was most frequently found in the range of *Z. a. asiatica* and in the east of the Pecos expansion area, whereas haplotype B was most common in all areas west of the Pecos River (Table 1).

POPULATION STRUCTURE

AMOVA was run for several different groupings to determine the level of among-group and within-population variation (Table 2). When only the four subspecies were analyzed, 29% of the variation was among groups; however, when the expansion range is treated as one large area or two areas separated by the Pecos River, only 7.8–9.9% of the variation was among groups. Chi-square analyses were run on the same groupings and indicated that geographic heterogeneity was found between the four subspecies, yet when the range expansion was treated as one large group, heterogeneity was not evident (Table 2).

To evaluate among-group variation, population pairwise differentiation tests were used. These analyses found that the *Z. a. asiatica* group was different from all other groups except for the range expansion area east of the Pecos River (Table 3). *Z. a. mearnsi, Z. a. monticola, Z. a. grandis,* and west of the Pecos expansion areas were not different.

The hierarchical analysis of nucleotide diversity separated the historical subspecies and range expansion locations into two clades (Fig. 2). The lower clade includes *Z. a. grandis, Z. a. monticola, Z. a. mearnsi,* and various locations east and west of the Pecos expansion areas. The upper clade includes *Z. a. asiatica* and locations found only in the east expansion area.

PHYLOGENETIC ANALYSIS

All White-winged Dove haplotypes formed a single clade with very short branch lengths (Fig. 3). Most bootstrap scores were low except for the branch that separated all haplotypes from the Mourning Dove outgroup. The weakly supported clade 1 comprised all haplotypes that possessed thymine at position 23.

MORPHOLOGICAL ANALYSIS

Individual birds were assigned to one of two groups based on whether they possessed the A or T substitution at position 23. Doves also were separated into males and females to avoid bias due to sexual dimorphism. Groups were significantly different for both sexes and all morphometric measurements (Table 4). Locations also were separated into three groups by whether the substitution at position 23 was fixed (fixed T, fixed A, or non-fixed). Morphometric measurements of doves grouped as fixed T, A, or non-fixed groups were significantly different from one another for both males and females (Table 4). The fixed groupings were always different at every measurement for both males and females; birds with fixed A were smaller than birds with fixed T (Table 5). Depending upon sex and morphological measurement, birds in the non-fixed group ranged from being different from both fixed groups (i.e., male and female wing length) to not being different from the fixed A group (i.e., male and female tail length).

TABLE 3. Population pairwise differentiation tests to evaluate the among group variation of 183 White-winged Doves collected in Texas, New Mexico, and Arizona during April–September 1997 and March 1998. Plus signs indicate significant differences between groups.

	ZAAS	ZAMO	ZAGR	ZAME	WP	EP
Z. a. asiatica (ZAAS)	—	+	+	+	+	—
Z. a. monticola (ZAMO)	0.004 ± 0.006	—	—	—	—	—
Z. a. grandis (ZAGR)	0.012 ± 0.008	0.190 ± 0.010	—	—	—	—
Z. a. mearnsi (ZAME)	0.000 ± 0.000	0.402 ± 0.012	0.094 ± 0.001	—	—	—
West of Pecos (WP)	<0.001 ± <0.001	0.461 ± 0.050	0.237 ± 0.024	0.461 ± 0.050	—	+
East of Pecos (EP)	0.299 ± 0.044	0.076 ± 0.022	0.328 ± 0.038	0.065 ± 0.021	<0.001 ± <0.001	—

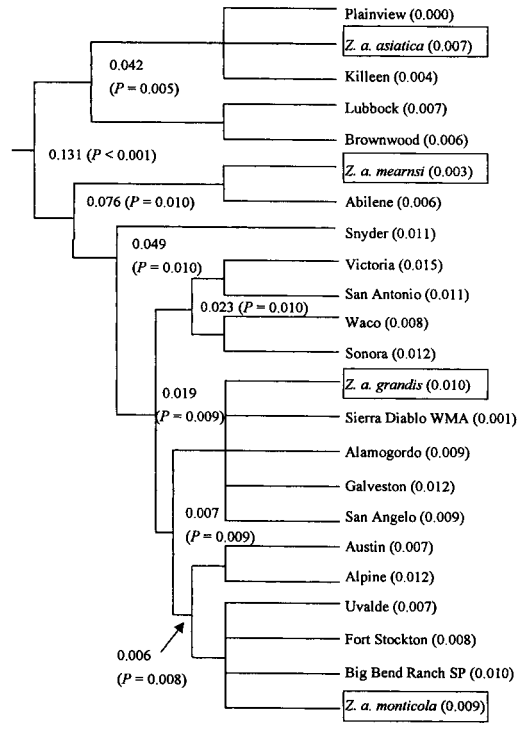

FIGURE 2. Tree of relationships of White-winged Dove collection locations determined from the hierarchical analysis of nucleotide diversity. Genetic distances between the two daughter nodes are indicated at branch nodes. *P*-values within parenthesis are the probability of getting a larger distance value under the hypothesis that there is no differentiation between daughter nodes using 10,000 random resamplings. Locations correspond to those in Table 1 and Figure 1; values in parenthesis are the nucleotide sequence diversity within each location.

DISCUSSION

By grouping locations and conducting population structure analyses, two complementary hypotheses about the past and current composition of White-winged Dove populations emerged. The first hypothesis is that before the range expansion there was a separation of White-winged Doves into two discrete subspecific units in Texas. By removing the range expansion areas from the AMOVA, we found that a substantial amount of variation was among groups (Table 2). However, when the range expansions were included in the analysis, less among-group variation was found. This indicated that most among-group variation was found between Saunders' (1968) four subspecies groupings. When the same grouping schemes were used in

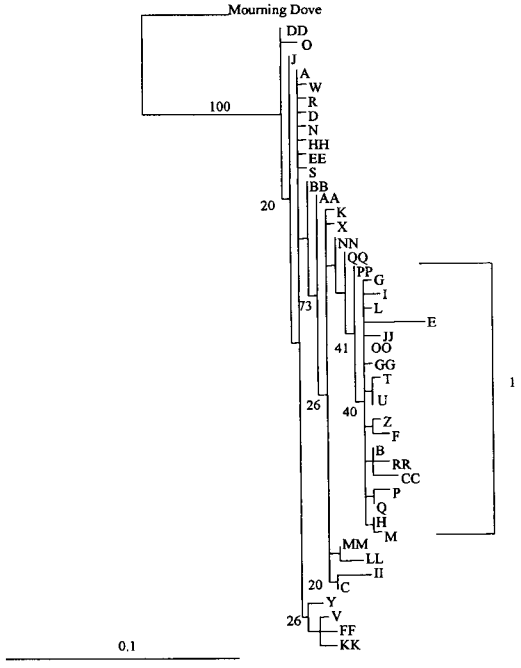

FIGURE 3. Maximum likelihood tree of 44 White-winged Dove control region haplotypes. Bootstrap values based on 100 replicates are given at branches. Letters at branch tips correspond to haplotypes in Table 1. Corrected pairwise sequence divergence is indicated by bar.

the chi-square analysis, significant population structure was apparent between the four subspecies, but when the range expansion was included population structure was not evident (Table 2). A third analysis that supported this hypothesis and indicated where among-group variation and population structure were found was the population pairwise differentiation test. Between Saunders' (1968) subspecies, significant variation was found between *Z. a. asiatica* and the other three races (Table 3). These findings support Browning's (1990) conclusion that White-winged Doves in Texas were separated into two subspecies—*Z. a. asiatica* and *Z. a. mearnsi*. Our results do not preclude the existence of *Z. a. grandis* and *Z. a. monticola* in Mexico, but indicate that these subspecies are not found in Texas.

The second hypothesis about White-winged Dove population structure is that the range expansion area is a "melting pot" supplied by several source populations. When the range expansion areas were included in the above analyses, within-population variation increased and little population structure was found (Table 2). Both of these findings indicate that high levels of gene flow were occurring within the expansion areas. However, this hypothesis must be qualified by the fact that some population structure was found between the range expansion areas east and west of the Pecos River. The population pairwise differentiation test showed that there was a significant difference between areas east and west of the Pecos River (Table 3). This analysis indicated that *Z. a. asiatica* was contributing primarily to the eastern expansion area, whereas *Z. a. mearnsi* was expanding into all areas. These findings also are supported by the hierarchy analysis, which indicated that *Z. a. asiatica* was only contributing to populations (Plainview, Killeen, Lubbock, and Brownwood) in the

TABLE 4. Differences between haplotype groupings for lengths of wing chord, tail, and exposed culmen of White-winged Doves collected in Texas, New Mexico, and Arizona during April–September 1997 and March 1998. Doves are separated by the possession of either the thymine or adenine at position 23 in the individual group. Collection locations are separated into either fixed thymine, fixed adenine, or non-fixed groups in the location group.

	Females			Males		
Measurement	*F*	df	*P*	*F*	df	*P*
Individual Group						
Wing	4.1	1, 60	<0.05	16.0	1, 76	<0.001
Tail	9.8	1, 60	<0.005	8.5	1, 76	<0.005
Culmen	8.0	1, 60	<0.01	6.9	1, 76	<0.05
Location Group						
Wing	5.4	2, 59	<0.01	18.7	2, 75	<0.001
Tail	12.7	2, 59	<0.001	22.7	2, 75	<0.001
Culmen	4.7	2, 59	<0.01	10.1	2, 75	<0.001

TABLE 5. Comparison of haplotype groupings for lengths of wing chord, tail, and exposed culmen of White-winged Doves collected in Texas, New Mexico, and Arizona during April–September 1997 and March 1998. Mean lengths (mm; $\bar{x} \pm$ SE) of morphometric characteristics for male and female White-winged Doves grouped by fixation of mtDNA control region location 23.

	Females			Males		
Grouping[a]	Wing	Tail	Culmen	Wing	Tail	Culmen
Fixed T	162 ± 3 A[b]	113 ± 7 A	20.8 ± 1.0 A	169 ± 4 A	120 ± 6 A	21.4 ± 1.5 A
Non-fixed	157 ± 5 B	104 ± 6 B	19.9 ± 1.0 B	163 ± 4 B	111 ± 5 B	20.3 ± 1.3 B
Fixed A	154 ± 3 C	102 ± 4 B	19.9 ± 1.0 B	159 ± 4 C	109 ± 4 B	20.2 ± 1.3 B

[a] Significant main effect ($P \leq 0.01$) due to grouping.
[b] Means within columns with the same letter are not different ($P > 0.05$).

eastern area, whereas *Z. a. mearnsi* was expanding into areas both west (Alpine and Fort Stockton) and east (Abilene and Galveston) of the Pecos River (Fig. 2). The easy availability of water, food, and nesting sites provided by the growth of cities is the most probable cause for the congruent nature of the range expansion (Scudday et al. 1980, West 1993). If this is true, then White-winged Doves should continue to expand as human development provides suitable habitat throughout the southwestern United States. As expansion and intergradation continue, the eventual loss of population structure is likely.

Although population structure was evident when haplotype frequencies were analyzed, our maximum likelihood analysis of haplotypes yielded little phylogenetic signal (Fig. 3). The two most prevalent haplotypes (A and B) were separated by only a single base pair. Recently, several other studies have found low variability in morphologically described subspecies (Mundy et al. 1997, Grapputo et al. 1998, Questiau et al. 1998). Questiau et al. (1998) also had significant differences in haplotype frequencies but little variation (a single base pair out of 1,725 bp). They argued that recent divergence between the morphs accounted for the poor resolution of their tree. This could be but one explanation for the small amount of divergence between morphologically different White-winged Dove populations. Other explanations include low levels of gene flow, secondary contact between isolated populations, and strong selection on morphology. The two most likely scenarios for our data set are the recent divergence of two allopatric White-winged Dove populations in Texas and then secondary contact between these two populations. These conclusions are supported by both the significant differences in haplotype frequencies between the *Z. a. mearnsi* group (including *Z. a. monticola* and *Z. a. grandis*) and *Z. a. asiatica,* and the low levels of variation between haplotypes.

To test the idea that secondary contact is occurring between White-winged Dove subspecies and to determine whether morphological and molecular variation was congruent, we decided to group our morphological data based on control region variation. We believed that if an intergradation zone or "melting pot" was occurring in the range expansion areas, then the birds from these areas would be intermediate in size. We decided to group our populations according to whether they possessed thymine or adenine at position 23. Based on our phylogenetic analyses and the geographic structure (Fig. 1) of this base change, we decided that the probability of homoplasy for this character was low. Our results strongly support the idea that an intergradation zone exists between the ranges of *Z. a. asiatica* and *Z. a. mearnsi.* Every character we analyzed was intermediate in size for the populations that were not fixed between the groups that had a fixed T (found in the range of the *Z. a. mearnsi* grouping) or a fixed A (primarily found in the range of *Z. a. asiatica*; Table 5). We also grouped the morphological data set into two groups—those who had the A and those that had the T. For every character, the two groups were significantly different (Table 4). Although phenotypic plasticity might account for some of the size differences we observed, the congruency between mtDNA and morphology and the recent origins of intermediate size populations in the expansion zones indicates secondary contact and subsequent intergradation. These findings support the idea that morphological measurements might be useful in determining which subspecies were sources for individual doves.

We support Browning's (1990) conclusion

that *Z. a. asiatica* and *Z. a. mearnsi* are found in Texas. Although *Z. a. grandis* and *Z. a. monticola* might occur in Mexico, we found no evidence supporting their existence in the areas we sampled. The current range expansion of White-winged Doves appears to be a congruent process with colonization from both subspecies' ranges. Our morphological and molecular data support the idea of secondary contact and intergradation within this expansion area. Because morphology and mtDNA appear to be congruent, the use of both techniques might be useful in identifying source populations and the subspecies status of individual White-winged Doves.

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