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EVIDENCE OF HYBRIDIZATION BETWEEN RED-BELLIED AND GOLDEN-FRONTED WOODPECKERS[1]

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Abstract. Golden-fronted Woodpeckers (*Melanerpes aurifrons*) and Red-bellied Woodpeckers (*M. carolinus*) are sympatric from southwestern Oklahoma to eastern Texas. Earlier studies found no evidence of hybridization (Selander and Giller 1963). However, in the recent past the area of range overlap between these two species has increased, thereby increasing the opportunity for hybridization. I investigated the possibility of hybridization by analyzing morphological and electrophoretic characteristics. Twenty-five (15.8%) individuals with intermediate morphologies were collected within the area of overlap and were identified as putative hybrids. Electrophoretic analysis of 12 liver and muscle proteins revealed a close genic affinity between the two species. Individual genic complements within the zone of overlap indicate that some individuals are intermediate. The intermediate morphology and mixed genic composition of some individuals within the zone of overlap supports the conclusion that Red-bellied and Golden-fronted woodpeckers hybridize.

Key words: *Red-bellied Woodpecker;* Melanerpes carolinus; *Golden-fronted Woodpecker;* Melanerpes aurifrons; *hybridization.*

INTRODUCTION

The purpose of my study was to investigate the possibility of hybridization between the Red-bellied Woodpecker (*Melanerpes carolinus*) and the Golden-fronted Woodpecker (*M. aurifrons*). These two woodpeckers are members of a melanerpine superspecies composed of five morphologically and behaviorally similar species: Red-bellied Woodpecker, Golden-fronted Woodpecker, Gila Woodpecker (*M. uropygialis*), Hoffmann's Woodpecker (*M. hoffmannii*), and Great Red-bellied Woodpecker (*M. superciliaris*; Short 1982). The Red-bellied Woodpecker is found throughout the south-central and eastern United States, where it inhabits mesic areas of swampy woods, open deciduous woodlands, and mixed coniferous woodlands (Bent 1939). The Golden-fronted Woodpecker ranges from southwestern Oklahoma to Honduras. In Texas and Oklahoma, Golden-fronted Woodpeckers occupy xeric habitats of mixed oak-juniper-mesquite woodlands as well as riparian woodlands of cottonwood, willow, and cypress (Selander and Giller 1963). At present, the Golden-fronted Woodpecker meets the Red-bellied Woodpecker in favorable habitats within a zone of overlap extending from southwestern Oklahoma to the Texas Gulf Coast (Fig. 1); this zone corresponds, in part, to the Western Cross Timbers of central Texas (Dyksterhuis 1948). The Cross Timbers phytogeographic region is characterized by the interdigitation of northeastern mesic oak woodlands, with southwestern semi-arid savannah (Hamilton 1962). Thus, it is a biotically intermediate zone composed of Red-bellied and Golden-fronted woodpecker habitat.

Hybridization—the crossing of individuals belonging to two unlike populations that have secondarily come into contact (Mayr 1970)—has been noted for several pairs of North American bird forms that are classified as different species (Rising 1983). Many of these pairs meet and hybridize in ecologically intermediate areas such as contact zones between two biotas (Remington 1968). In Mexico, hybridization occurs where the range of the Golden-fronted Woodpecker overlaps with the Gila Woodpecker (Short 1982). Likewise, in Honduras the Golden-fronted Woodpecker meets Hoffmann's Woodpecker and purported hybrids have been observed (Short 1982). In central Texas, however, accounts of hybridization between Golden-fronted and Red-bellied woodpeckers have not been substantiated (Selander and Giller 1963).

Selander and Giller (1963) reported that the northern breeding limit of Golden-fronted Woodpeckers in Oklahoma was near Gould.

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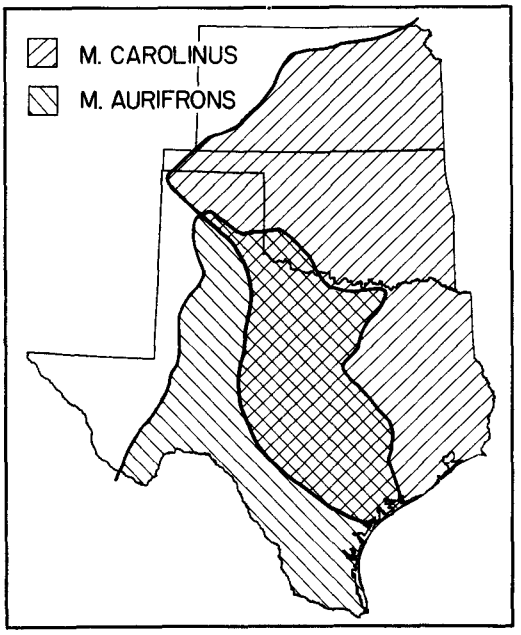

FIGURE 1. Geographic area of study, and ranges of Red-bellied and Golden-fronted woodpeckers.

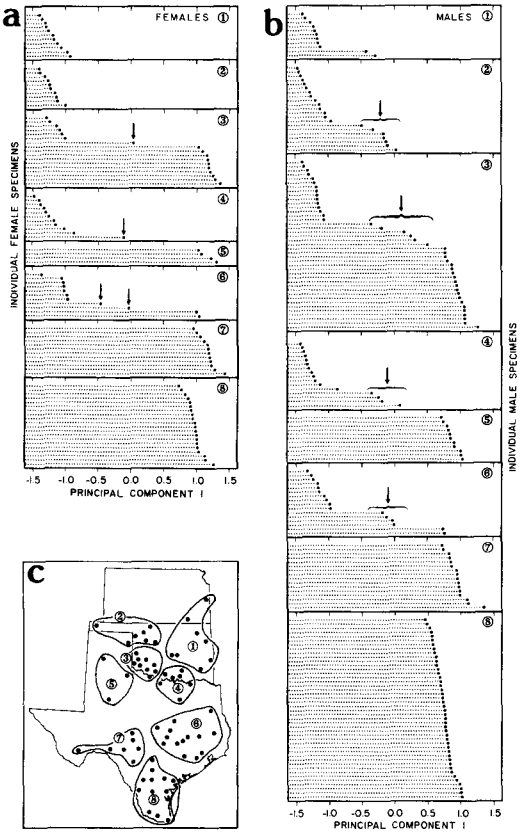

FIGURE 2. Projections of (a) female and (b) male individuals from (c) eight localities onto an adjusted principal component I. For females, scores on component I adjusted by subtracting 0.603. Similarly, male component adjusted by subtracting 0.610 from all scores. Putative hybrids designated by arrows and brackets.

However, Wood and Schnell (1984) depicted the northern limit of Golden-fronted Woodpecker permanent residency as extending beyond Gould well into southwestern Oklahoma. Similarly, in 1931 the southwestern limit of Red-bellied Woodpeckers was thought to be near Lawton, Oklahoma (Sutton 1967). However, by 1970 they were found well into southwestern Oklahoma to the Texas border (Tyler 1979). Apparently, within the recent past, both the Golden-fronted and Red-bellied woodpecker have extended their range into southwestern Oklahoma, thereby increasing the area of their sympatry. My objective was to determine whether these two woodpeckers hybridize and, if so, to estimate the frequency of hybridization. The analyses concentrated on assessing morphometric and electrophoretic characteristics of Golden-fronted and Red-bellied woodpeckers in the zone of potential hybridization, as well as beyond the overlap region.

METHODS

MORPHOLOGICAL ANALYSIS

Study skins of female (n = 96) and male (n = 176) Red-bellied and Golden-fronted woodpeckers from Oklahoma, Texas, and southern Kansas were analyzed to determine the degree and pattern of morphological variation. I examined only adult birds in breeding condition to insure that: (1) individuals were residents in the area collected; (2) plumages were not worn; and (3) age differences in plumage pattern would not confound the results. Specimen collection sites were grouped into eight physiographically homogeneous localities (Fig. 2c).

Twenty-one characters were assessed for females and 25 for males. I measured the following eight morphometric characters to the nearest 0.1 mm with dial calipers: (1) tail length on longest central rectrix from base to tip; (2) bill length from anterior edge of nostril to tip of bill; (3) bill depth from top of culmen to base of lower mandible at anterior edge of nostril; (4) length of

tarsus from tip of heel scale to base of third toe; (5) wing length of the flattened arc; (6) height of black tail bar at midpoint of tail length (if black bars not present, character scored as "no comparison"; Sneath and Sokal 1973); (7) height of white tail bar at middle of central rectrix (if white bars not present, character scored as no comparison); and (8) length of left third toe along lateral border from base of toe pad to tip of pad.

I analyzed plumage variation by assessing the color of the front, nape, belly, and cap (males only). Colors were measured by illuminating a specimen with a Standard Macbeth Artificial North Sky Daylight lamp and matching the color of the plumage to a reference color chip from the Munsell Limit Color Cascade (Munsell Color 1970). Different refractory angles can alter the structural colors of plumages; thus, I viewed each plumage region from a consistent angle while holding the specimen under the light source.

For each plumage region, Munsell Hue, Value, and Chroma were recorded. Munsell Hue indicates the position of a particular color relative to an equally spaced scale of hues from red to purple. The plumage colors I assessed ranged from red to yellow. In the Munsell Limit Color Cascade System of notation, red hues are ranked zero to 10, oranges are represented by values from 10 to 20, and yellows range from 20 to 30. In a general sense, Munsell Hue corresponds to the dominant wavelength of a color. Munsell Value indicates lightness and is related to the percent spectral reflectance of color. It ranges from zero for absolute black to 10 for absolute white. Munsell Chroma describes the degree of saturation of a color and represents excitation purity. A neutral gray would have a Munsell Chroma of zero. For a detailed description of the relationship of Munsell notations to dominant wavelength, percent spectral reflectance, and excitation purity, the reader is referred to Newhall et al. (1943).

I evaluated variation in five plumage patterns by ranking observed forms from lowest (Red-bellied Woodpecker type) to highest (Golden-fronted Woodpecker type) for the following characters. Tail pattern: white bars on central rectrices extend from central rachis to outer edge of vane (0) to no white on central rectrices (3). Back pattern: black bars on the back wider than white (0), white bars on back equal to or wider than black bars (1). Nape gap coloration (males only): no gray gap between nape and cap (0), to complete gray gap between nape and cap (2). Color of chin: red (0) to yellow (3). Subdominant color of nape: color of lateral side of nape not different from central portion (0), to lateral side orange (3).

Specimens with five or more missing values were excluded from all analyses. The missing values of the remaining damaged specimens were estimated by a linear regression onto the character that exhibited the highest correlation with the missing character (Missing Data Estimator program developed by D. M. Power; Schnell et al. 1985b). The estimated data accounted for only 3.4% (69 of 2,016) of female and 2.5% (111 of 4,440) of male measurements.

Sexual dimorphism occurs in both species (Selander 1966, Wallace 1974) so all analyses were performed separately by sex. Data matrices for both sexes were standardized, characters correlated, and principal components extracted. When more than 15% of the values for one character were estimated, I examined whether these estimated values altered the projection of individuals onto the first principal component. In each case, this treatment of missing values did not appreciably influence projections. Numerical procedures were performed using NT-SYS computer programs (Rohlf et al. 1982).

Following the suggestion of Moore and Buchanan (1985), I summarized variation between Red-bellied and Golden-fronted woodpeckers with principal component I. To center near zero the projections of individuals with intermediate morphologies, a constant was subtracted from all principal component I scores.

There are two underlying assumptions to this method of hybrid identification. First, principal component I must describe the variation relevant to the question of hybridization. Neff and Smith (1979) indicated that principal component analysis is a good way to analyze hybridization and eliminates many of the erroneous computational assumptions of other methods (e.g., discriminant function analysis). By definition, the first component is the axis that summarizes the greatest amount of variation among the elements of a data matrix. Thus, it may best represent the differences between the parental species and provide an adequate means of identifying hybrids. Specifically, hybrids would be those individuals lying between species' clusters and yet outside the limits of either species' variation.

The second assumption—that hybrids exhibit

phenotypes intermediate to the two parental forms (Neff and Smith 1979)—will hold if there is additive inheritance of traits or a combination of additivity and dominance (Rohwer 1972). For fish, hybrids are not necessarily intermediate in all characters analyzed (Smith 1973, Ross and Cavender 1981), but often are intermediate for many characters (Neff and Smith 1979, Mayhew 1983). Principal component analysis is sensitive to the covariation of many characters and relatively insensitive to unique extremes (Smith 1973). If a majority of the characters loading heavily on the first principal component are products of additive inheritance and a minority are subject to control via other genetic mechanisms, the first principal component can be expected to depict phenotypes of hybrids as intermediate. Since genetic mechanisms governing inheritance of the characters I assessed are unknown, hybrid phenotypes cannot be indisputably identified as intermediate. Thus, individuals with intermediate phenotypes are designated as putative hybrids.

ELECTROPHORETIC ANALYSIS

Red-bellied and Golden-fronted woodpeckers ($n = 93$) were collected from 20 counties in Oklahoma and Texas: Oklahoma—Cleveland ($n = 9$), Caddo (1), Woodward (3), Ellis (8), Beckham (7), Greer (5), Harmon (9), Jackson (1), Marshall (3), Love (3), and Johnston (3); Texas—Hemphill ($n = 3$), Cottle (8), Fannin (2), Williamson (4), Burleson (2), Kimble (9), Kerr (1), LaSalle (6), and McMullen (6). Specimens from Hemphill County were collected in November; all others were obtained from March to August.

Individuals from Kerr and Burleson counties could not be scored for all loci studied. Nei (1978) argued that estimates of genic variability are enhanced more by increases in the number of loci assessed than by increases in the number of individuals sampled. Consequently, rather than excluding loci that had not been scored for all individuals, I maximized the number of loci investigated by adding individuals not scored for all loci to the samples of nearby localities.

In the field, I removed pectoral muscle and liver tissue from each individual and stored them in liquid nitrogen or on dry ice until they could be transferred to a freezer and maintained at −70°C. At the Savannah River Ecology Laboratory, I analyzed samples using standard starch gel electrophoretic techniques (Selander et al. 1971) and followed the staining procedures of Harris and Hopkinson (1976). I studied six loci from muscle tissue: aconitase (ACON-1), sorbitol dehydrogenase (SDH), alpha glucophosphate dehydrogenase (AGPD), phosphoglucomutase (PGM), and leucyl-tyrosine (LT-1 and LT-2). I also analysed six loci from liver tissue: lactate dehydrogenase (LDH-1 and LDH-2), malate dehydrogenase (MDH-1 and MDH-2), glycerol dehydrogenase (GCDH), aconitase (ACON-2), naphthyl acetase (NAS), and beta naphthyl phosphotase (BNP). The LDH, MDH, and GCDH loci were applied only in an examination of possible species-specific fixed allele differences. Precise conditions of gel and buffer compositions can be obtained from the author. Mobility of alleles at a locus was judged in reference to the position of the most common allele designated "C," with slower alleles (closer to the origin) designated "D." Allele frequencies for each locality were computed using the BIOSYS-1 computer program (Swofford and Selander 1981).

I employed a Mantel test of matrix correlation (a procedure that compares the association of elements in two square difference matrices; Schnell et al. 1985a) to examine geographic trends in allele frequency for polymorphic loci. Because the number of localities ($n = 18$) compared was near the lower limit of reliability for the Mantel statistic, I confirmed the result of each Mantel test with a two-tailed permutational Mantel test (Schnell et al. 1985a) that employs a Monte Carlo simulation. The critical value of the Mantel statistic (t) is 1.96 for a positive association and −1.96 for a significant negative association. The Monte Carlo probability (P) indicates significant covariation if P is greater than 0.975 or less than 0.025.

To determine whether there are regional geographic patterns in allele frequency differences for polymorphic loci, I compared the covariation between a matrix of allele frequency differences among all localities to a corresponding matrix of Euclidean distances (kilometers) among localities. To test for local patterning of allele frequency, I compared allele frequency differences among localities to a matrix of reciprocal geographic distances. Employing reciprocals of distance results in an expansion of short distances and increases the sensitivity of the test to associations among small distances (Schnell et al. 1985a). Using the Mantel test, I also assessed the degree of covariation between genetic distances

TABLE 1. Character means, standard deviations (SD), and loadings on principal component I for females and males. Eigen values for females and males were 10.4 and 9.9, respectively.

Character	Female			Male		
	Mean	SD	Loading	Mean	SD	Loading
Tail length	79.1	4.77	0.277	81.5	5.25	0.370
Bill length	23.3	1.51	0.613	25.3	1.50	0.619
Bill depth	7.2	0.38	0.185	7.8	0.47	0.089
Tarsus	18.5	1.33	0.638	19.1	1.12	0.554
Wing length	125.7	4.78	0.343	129.3	4.12	0.384
Black tail bar	4.1	1.08	−0.927	3.6	0.86	−0.844
White tail bar	4.2	0.71	−0.916	4.3	0.68	−0.847
Toe length	15.0	0.94	0.607	15.5	0.78	0.541
Front hue	16.1	5.89	0.947	15.6	5.64	0.958
Front value	7.2	0.94	0.916	6.8	1.19	0.946
Front chroma	13.3	2.05	−0.253	15.1	1.81	−0.547
Nape hue	14.5	5.51	0.942	10.4	2.55	0.691
Nape value	6.3	1.41	0.955	5.3	0.97	0.776
Nape chroma	15.7	1.13	−0.529	16.3	0.58	0.329
Belly hue	16.3	5.87	0.961	16.0	6.17	0.952
Belly value	7.2	0.95	0.913	7.0	1.16	0.915
Belly chroma	13.4	2.57	−0.210	14.4	1.88	−0.315
Cap hue	—[a]	—	—	7.7	0.83	−0.082
Cap value	—	—	—	3.9	0.36	0.029
Cap chroma	—	—	—	15.0	1.40	−0.015
Tail pattern	1.3	1.25	0.939	1.5	1.29	0.941
Back pattern	0.4	0.49	0.372	0.4	0.49	0.333
Nape gap color	—	—	—	0.7	0.76	0.840
Chin color	1.2	0.59	−0.311	1.4	0.86	0.014
Lateral nape color	0.2	0.60	0.164	1.1	1.09	0.827

[a] Measurement not taken.

and average taxonomic distances of individuals (n = 56) assessed for both electrophoretic and morphological variation. Nei's (1978) unbiased genetic distances were estimated among individuals using the BIOSYS-1 computer program (Swofford and Selander 1981), and average taxonomic distances were computed by the NT-SYS computer program (Rohlf et al. 1982). The SDH locus was omitted from this test because it was not scored for all individuals.

RESULTS

MORPHOLOGICAL VARIATION

The characters loading most heavily (greater than 0.700) on principal component I for both females and males were: tail pattern; widths of tail bars; coloration of front, nape, and belly (Table 1). Component I summarized 47.2% of the variance for females and 41.1% for males. Descriptive statistics and character loadings on component I are summarized in Table 1.

To measure the extent of hybridization, parental populations typically are sampled away from the influence of possible hybrids and backcrosses (Johnson and Johnson 1985). I represented typical morphological variation in Red-bellied Woodpeckers as the level depicted by the range of principal component I scores in the locality farthest northeast of the overlap zone (locality 1; Fig. 2c). In this locality the morphology of female and male Red-bellied Woodpeckers is described by scores near the lower range of component I (Figs. 2a, b). Similarly, because locality 8 (Fig. 2c) is farthest south of the contact zone, I used component I scores of females and males from that region to represent morphological variation in Golden-fronted Woodpeckers (Figs. 2a, b). Golden-fronted Woodpeckers have phenotypes that project as high values on component I (Fig. 2).

Female Red-bellied and Golden-fronted woodpeckers are morphologically more readily separable than are males. There is a wide gap in female component I scores between localities 1 and 8, and only a small gap between the scores of the males (Fig. 2). I identified female putative hybrids (n = 4; Fig. 2) as those individuals of

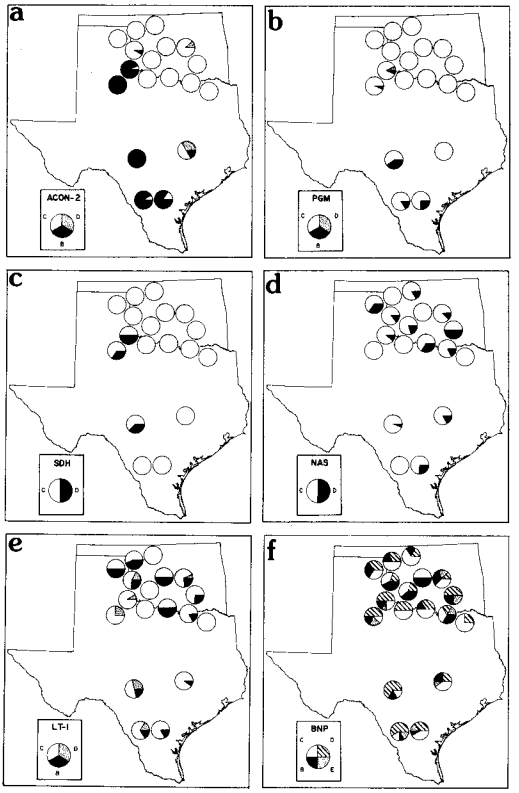

FIGURE 3. Allele frequencies at six polymorphic loci represented for 18 localities.

intermediate morphology lying within this wide gap of component I scores. These four specimens were collected from localities that are contained in part or completely within the zone of overlap (Figs. 2a, c). The hybrids represent 7.5% of the females ($n = 53$) analyzed from the area of range overlap (i.e., localities 2, 3, 4, 5, and 6). Female hybrid morphology is characterized by: large white blotches on their tails, no true tail bars; orange to yellowish-orange fronts; red napes; and orange to yellowish-orange bellies.

Males of the two species exhibit a considerable degree of morphological variation. For example, there are two Red-bellied Woodpecker specimens from locality 1 with scores near zero. Because they were collected from areas considerably beyond the suspected zone of overlap, it is unlikely that their intermediate phenotypes are a result of hybridization (Rohwer and Kilgore 1973). In particular, the individual from locality 1 with the highest score was collected in southern Kansas while the other was from east-central Oklahoma. In addition, there is less of a distinction in the nape hue character between males of the two species than females. Throughout the eight localities, male nape hue ranges from red (8.5) to orange (14.3), whereas for females, north to south, the color of the nape ranges from red (9.1) to yellow (20.2).

I identified as putative hybrids 16 intermediate males that were collected from localities 2, 3, 4, and 6. These males represent 15.2% of the males ($n = 105$) analyzed from the overlap region (i.e., localities 2, 3, 4, 5, and 6). To define more precisely the gap of component I scores between males of the two species, I incorporated an additional intralocality measure of morphological variation. For each locality, the putative hybrid range was defined as the set of intermediate component I scores clearly separate from scores of males with typical parental morphology. Employing this method, I identified five additional putative male hybrids. In all, 21 putative male hybrids were found within and near to the zone of overlap (see Fig. 2b). Thus male hybrids comprise approximately 17% of the population within the overlap zone. The estimated proportion of male hybrids ranges from a conservative 15.2% ($n = 16$) to as great as 20.0% ($n = 21$). In general, putative male hybrids resemble their female counterparts being characterized by: no tail bars, only white blotches; reddish-orange to orange fronts; orange to yellowish-orange bellies; no gray gap on nape; and no extra lateral color on nape.

GENETIC VARIATION

My electrophoretic analysis of genetic variation revealed that Red-bellied Woodpeckers and Golden-fronted Woodpeckers have a close genetic affinity. From a survey of 12 loci, I found no fixed allele differences between the two species. Seven loci were polymorphic: AGPD, BNP, NAS, SDH, ACON-2, PGM, and LT-1. The AGPD locus, while polymorphic, was only variable at two localities and, therefore, was not considered in the discussion of geographic patterns of genetic variation.

Two of the six polymorphic loci—PGM and ACON-2—demonstrated strong positive associations of allele frequency differences with geographic distances (i.e., regional patterning), indicating that for both loci the B and C allele frequencies of geographically close localities are more similar than those for distant localities (Ta-

TABLE 2. Association of allele frequency differences with geographic distances (km) and reciprocals of distances (1/km), with Mantel statistic (t), Monte Carlo probability (P), and matrix correlation (r).

Locus and alleles	Distance (km)			Reciprocal distance (1/km)		
	t	P	r	t	P	r
ACON-2						
B	4.083	0.997	0.486	−3.919	0.002	−0.403
C	4.659	0.999	0.522	−4.421	0.001	−0.435
PGM						
B	3.682	0.997	0.586	−3.654	0.000	−0.468
C	3.559	0.995	0.559	−3.504	0.000	−0.444
SDH						
C	−0.469	0.549	−0.007	−0.679	0.214	−0.085
D	−0.469	0.563	−0.007	−0.679	0.224	−0.085
NAS						
C	−0.619	0.288	−0.080	0.909	0.815	0.099
D	−0.619	0.320	−0.080	0.090	0.806	0.099
LT-1						
B	−1.030	0.122	−0.111	0.768	0.744	0.074
C	−1.260	0.064	−0.104	0.827	0.776	0.068
BNP						
B	0.111	0.561	0.001	0.395	0.633	0.041
C	0.284	0.651	0.038	−0.783	0.241	−0.087
D	1.239	0.863	0.144	−1.501	0.081	−0.152
E	1.080	0.866	0.108	−1.717	0.064	−0.158

ble 2, Fig. 3). For the B and C alleles of both ACON-2 and PGM loci, allele frequency differences are negatively associated with reciprocals of geographic distances (i.e., local patterning; Table 2 and Fig. 3). The significant regional and local patterning of B and C allele frequencies (at both the PGM and ACON-2 loci) reflects the fact that these alleles can be identified as most common for one of the two species. For example, the B allele of PGM and of ACON-2 is most common in Golden-fronted Woodpecker populations of southern Texas (Fig. 3). In contrast, the C allele at these two loci is most common in northern samples of Red-bellied Woodpeckers (Fig. 3). The four other polymorphic loci tested did not show significant local or regional patterns (Table 2).

To investigate the significant local patterning of the PGM and ACON-2 loci more fully, I examined the allelic composition of individuals within the overlap zone. The intermediate allele frequencies of localities within the overlap zone are not due simply to combining in a single sample individuals of both pure parental forms. Rather, some of the birds from these localities possess a mixed genic complement. In extreme southwestern Oklahoma and nearby north-central Texas (Harmon and Cottle counties, respectively), populations are composed of individuals with Golden-fronted Woodpecker morphology. However, the genic constitutions of individuals in these counties include alleles common for both Red-bellied and Golden-fronted woodpeckers (Table 3). For example, most individuals have the PGM allele most common for Red-bellied Woodpeckers (C), but the ACON-2 allele most common for the Golden-fronted Woodpeckers (B; Table 3). Similarly, mixed genic compositions are found near the zone of overlap in east-central Texas (Williamson County); individuals exhibited Red-bellied Woodpecker plumages, yet at the ACON-2 locus many of them possessed the B allele that is most common in Golden-fronted Woodpeckers.

The Mantel test of association between a matrix composed of Nei's unbiased genetic distances among individuals to a corresponding matrix of the average taxonomic distances among these same individuals revealed a significant positive correspondence (Fig. 4). The more dissimilar two individuals are genically the more dissimilar they are morphologically.

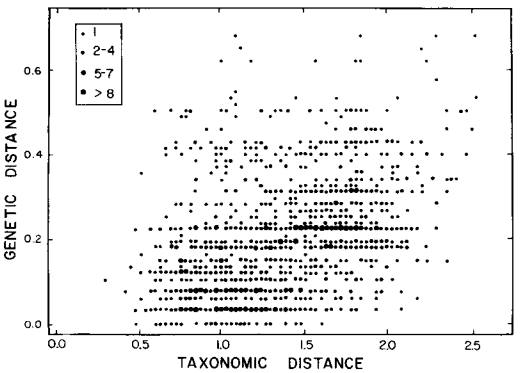

FIGURE 4. Mantel test of covariation between Nei's unbiased genetic distance and average taxonomic distances among the same individuals ($t > 6.5$, $P < 0.05$, $r = 0.415$).

DISCUSSION

My primary objective was to determine whether Red-bellied and Golden-fronted woodpeckers hybridize. On the basis of intermediate morphology there is evidence that the two species interbreed. I identified 25 putative hybrids (four females and 21 males) that were collected within or near the zone of species overlap. The frequency of hybridization is 15.8%, which is considerably greater than the level (5%) reported for hybridization between Gila and Golden-fronted woodpeckers (Selander and Giller 1963).

The analysis of genic variation also supports the identification of hybrids within the zone of overlap. In particular, the electrophoretic analysis of 12 loci revealed a close genic affinity; there are no fixed allele differences between the two woodpeckers. Prager and Wilson (1975) have reported that avian pairs with many more genic differences than Red-bellied and Golden-fronted woodpeckers can still produce viable hybrids.

The significant patterns of geographic differences in allele frequency support the conclusion that the two species are interbreeding in the contact zone. Golden-fronted Woodpeckers are most common in south Texas and Red-bellied Woodpeckers are most numerous in central Oklahoma. The significant local patterning of PGM and ACON-2 alleles indicates that geographically close south Texas populations of Golden-fronted Woodpeckers are also genically similar (Table 2, Fig. 3). Likewise, geographically close Red-bellied Woodpecker populations of central Oklahoma are genically very similar. By contrast, the significant regional patterning of these same alleles indicates that southern Texas Golden-fronted Woodpecker populations are genically most divergent from the Red-bellied Woodpecker populations of central Oklahoma. Therefore, the discovery of individuals within the zone of overlap with genic compositions that include the B allele at the ACON-2 locus (characteristic of the Golden-fronted Woodpecker) and the C allele at the PGM locus (characteristic of the Red-bellied Woodpecker) suggests that the woodpeckers are interbreeding in the zone of overlap (Table 3).

TABLE 3. Number of individuals with particular allele combinations at ACON-2 and PGM loci for counties within zone of overlap.

County	Allelic composition of ACON-2/PGM loci					
	CC/ CC	BC/ CC	BB/ CC	BB/ BC	BB/ CD	DD/ CC
Harmon		1	6	1	1	
Cottle			7	1		
Williamson	2	2				2

Initially, I identified hybrids by the *a priori* assumption that they would exhibit intermediate morphologies. There is a significant association between morphometric and genic characteristics (Fig. 4); these two character sets describe similar patterns of geographic variation, which supports the identification of the 25 putative hybrids within the zone of overlap.

Sexual selection may facilitate hybridization between the two species. In particular, female Red-bellied and Golden-fronted woodpeckers may prefer mates with red napes. The napes of male Golden-fronted Woodpeckers are more red than their female counterparts. Johnson and Johnson (1985) have noted a related condition in hybridizing sapsuckers which Howell (see Johnson and Johnson 1985) originally termed a "lust for red." Female sapsuckers are said to prefer males with red plumages. Kilham (1961) reported a comparable situation in which a female Red-bellied Woodpecker in captivity persistently solicited toward a female Pileated Woodpecker (*Dryocopus pileatus*) perhaps prompted by its extensive red crest. Similarly, female Golden-fronted Woodpeckers may preferentially select red-naped mates, resulting in the extensively red and orange napes of male Golden-fronted Woodpeckers. However, in the area of overlap the completely red napes of male Red-bellied Woodpeckers would present to female Golden-fronted Woodpeckers a "super stimulus" and could lead

to hybridization. This hypothetical female preference may promote hybridization between these two species.

If two species do not meet, they cannot hybridize. Range extension resulting in an increased area of sympatry thus increases the probability of hybridization. In the recent past Golden-fronted and Red-bellied woodpeckers appear to have extended their ranges in southwestern Oklahoma. The area of overlap between Golden-fronted and Red-bellied woodpeckers corresponds, in part, to an ecologically intermediate area where xeric southern conditions meet mesic northern habitats. The influence of the environment upon the distributions of these two species is unknown. Hamilton (1962) has argued that species distributions within ecologically intermediate areas are determined primarily by environmental limitations. He suggested that taxa become trapped within these biotically intermediate zones unable to adapt to the prevailing conditions on the other side. This implies that in southwestern Oklahoma there has been an amelioration of environmental conditions that has promoted the range extension of Golden-fronted and Red-bellied woodpeckers. In contrast, Selander and Giller (1963) have argued that the Golden-fronted Woodpecker, which has adapted to a wide variety of habitats throughout its extensive range, has the evolutionary potential to occupy much of the eastern range of the Red-bellied Woodpecker. They concluded that competition with Red-bellied Woodpeckers, rather than environmental composition, limits the extent of range overlap. This implies that for the extent of overlap between these two species to change, as it apparently has in southwestern Oklahoma, there must have been a change in their competitive interactions. Therefore, it would be of value to investigate this area of apparent range expansion for recent ecological changes, as well as modifications of woodpecker behavior that may have developed and could account for the increased sympatry in this region and subsequent increased opportunity for hybridization.

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