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Tufted and Black-crested Titmouse (Paridae) Hybrid Zone in  
the Southern Great Plains**

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# Current and Historical Extent of Phenotypic Variation in the Tufted and Black-crested Titmouse (Paridae) Hybrid Zone in the Southern Great Plains

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**ABSTRACT.**—Hybrid zones, where phenotypically distinct populations interbreed, should expand or contract until reaching a balance between selection and dispersal. Few studies examine multiple contacts within one species complex to compare how their extent changes over time. Black-crested and Tufted Titmice (*Baeolophus atricristatus* and *B. bicolor*) hybridize extensively within a narrow zone in Texas and southwestern Oklahoma. In Texas, hybridization has been occurring for several thousands of years, while evidence suggests the southwestern Oklahoma contact is more recent, beginning within the past century. We quantify plumage and morphology of the two species across both the younger and older hybrid zones and compare the current and historical extent of phenotypic variation in the older Texas contact with that in the younger Oklahoma contact. Variation in plumage between species is similar in the younger and older contacts, while overlap in morphological characters is broader in the older contact. Recently and historically surveyed transects in the older zone have similar cline widths, indicating selection, at least on crest and forehead plumage, has reached equilibrium with dispersal over the time periods involved (comparing both the historically surveyed data from 1955 vs. the recently surveyed data from the 2000s in Texas). In the recently surveyed younger Oklahoma contact, cline width is narrower, indicating potential for expansion if it follows the course of the older contact. This temporal complexity should make this species complex a productive system for future work, using plumage and additional traits such as song and genetics, on the relative influences of both natural and sexual selection on the evolution of reproductive isolation.

## INTRODUCTION

Hybrid zones form where phenotypically distinct populations meet and interbreed at secondary contact (Harrison, 1990; Arnold, 1997). These populations, which are partially reproductively isolated, provide important tests of the relative contributions of natural and sexual selection to speciation (Labonne and Hendry, 2010; Moriarty Lemmon and Lemmon, 2010). Hybrid zones are most commonly maintained by a balance of selection for, or against, hybrids with dispersal (Moore, 1977; Barton and Hewitt, 1985, 1989; Arnold, 1997). These conditions often result in a zone that is narrow when compared to the parental ranges. Studying hybrid zones of differing ages is useful to understand what isolating barriers arise as speciation progresses. Zones with repeated sampling over time (Reudink *et al.*, 2007; Brelsford and Irwin, 2009; Mettler and Spellman, 2009; Carling and Zuckerberg, 2011; Roy *et al.*, 2012; Smith *et al.*, 2013) or containing contacts of different ages (Haavie

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TABLE 1.—Predicted changes in relative cline width over time under varying scenarios. Bars represent relative cline width

Scenario	Most time since contact <—————>Least time since contact		
	Modern old (TX)	Historical old (1950s)	Young (SW OK)
1. Equilibrium.	—	—	—
2a. Expansion over time.	—	—	—
2b. Expansion over time, with no change between modern and historical sampling.	—	—	—
3a. Narrowing over time.	—	—	—
3b. Narrowing over time, with no change between modern and historical sampling.	—	—	—
3c. Narrowing over time, with no change between historical and young sampling.	—	—	—
4a. Temporal variation, one possibility.	—	—	—
4b. Temporal variation, potential alternative scenario.	—	—	—

*et al.*, 2004; Rohwer and Martin, 2007) are particularly enlightening because we can examine selective forces over time within the same species complex.

When sampling transects of differing ages and, for the moment ignoring the possibility of movement, four patterns of variation in hybrid zone width are possible (Table 1). First, dispersal and selection (Moore, 1977; Barton and Hewitt, 1985) have reached equilibrium, resulting in stable clines of similar widths at each transect or time period (Moore and Buchanan, 1985; Smith *et al.*, 2013). Second, expansion in width of transects over time is expected when ongoing dispersal and introgression have not been balanced by selection either against hybrids within the zone or against hybrids dispersing out of suitable intermediate habitat. Mechanisms for such a pattern might include sexual selection on hybrids (Rosenfield and Kodric-Brown, 2003) and ecological adaptation (Donovan *et al.*, 2010), both of which could allow the spread of hybrids. Neutral gene flow could also allow transects to continue widening over time (Table 1; scenario 2a). Third, narrowing of a zone over time should occur when the balance of dispersal and introgression has shifted to reduce the suitable area for hybridization. Hybrid unfitness can result from phenomena such as genetic incompatibilities resulting in inviability (Barton and Hewitt, 1981) or reduced fertility (Alatalo *et al.*, 1990), ecological disadvantages of hybrids (Tobler *et al.*, 2009), preference for parental phenotypes (Merrill *et al.*, 2011), or a combination of multiple factors (Patten *et al.*, 2004). Hybrid disadvantages can then cause narrowing of the zone (Carling and Zuckerman, 2011) by shifts in population density (Barton and Hewitt, 1989), reinforcement (Howard, 1993), or shifts in environmental regimes (Swenson, 2006). Fourth, a lack of consistent temporal pattern is expected to occur when selection pressures have changed direction over time (Roy *et al.*, 2012). Such a pattern could be caused by large-scale changes (anthropogenic or natural) within or between regions in habitat (Grant and Grant, 2002; Arnold and Martin, 2010) or in population density (Barton and Hewitt, 1989). Additionally, a zone can move while remaining the same width (Smith *et al.*, 2013); this is expected to occur with shifts in population density (Barton and Hewitt, 1989).

Many avian hybrid zones have demonstrated intrinsic selection against hybrids (Sætre *et al.*, 1999; Bronson *et al.*, 2003; Haavie *et al.*, 2004), extrinsic selection for hybrids

(Flockhart and Wiebe, 2008), or a combination of both (Good *et al.*, 2000; Gay *et al.*, 2008); yet, few of these studies have examined more than one hybrid zone within the same species complex. Where multiple zones have been examined, such as for the Hermit/Townsend's Warbler (*Setophaga occidentalis* and *S. townsendi*) (Rohwer and Martin, 2007) and Pied/Collared Flycatchers (*Ficedula hypoleuca* and *F. albicollis*) (Sætre *et al.*, 1999; Haavie *et al.*, 2004; Vallin *et al.*, 2012) complexes, differences in gene flow (Sætre *et al.*, 1999), phenotypic introgression (Rohwer and Martin, 2007), and song characteristics (Haavie *et al.*, 2004) have been found. One species pair with hybrid zones of different ages is the Black-crested Titmouse (*Baeolophus atricristatus*) and Tufted Titmouse (*B. bicolor*) complex. The older contact zone in central and north-central Texas (TX) (Dixon, 1955, 1978, 1990) likely formed no later than 4000 years ago based on climatic data (Dixon, 1978). An apparently younger contact zone in southwestern Oklahoma (OK) (Dixon, 1955, 1978; Sutton, 1967; Patten and Smith-Patten, 2008) likely formed as a result of shrub, chiefly honey mesquite (*Prosopis glandulosa*) (Callahan, 2002), invasion in response to fire suppression and overgrazing within the past century (Van Auken, 2000).

The main margins of the TX hybrid zone appear to be phenotypically stable in previously studied areas of the TX coast, central TX, and north-central TX (Dixon, 1990), and climatic evidence suggests that it has remained in the same region since the original putative secondary contact (Dixon, 1955). However, the exact extent of the hybrid zone is poorly known outside of central TX (Dixon, 1955). Additionally, some maps (*i.e.*, Oberholser, 1974) do not distinguish phenotypically intermediate individuals (Dixon, 1990) and Pulich (1988) noted that many observers attempt to categorize all individuals as one of the parental species, even in areas of hybridization, making it difficult to map the hybrid zone using survey data not aimed explicitly at these species and their hybrids. Dixon's (1955, 1978, 1990) studies focusing on TX are the most recent works aimed specifically at the distribution of this hybrid zone. In the southwestern OK contact zone, the extent of interbreeding has not been studied. Thus, an update is warranted on the status of hybridization in this species complex.

The two titmouse forms diverged during the Pleistocene glaciations (Dixon, 1978; Klicka and Zink, 1997; Patten and Smith-Patten, 2008) and currently are considered two species (Banks *et al.*, 2002) on the basis of mitochondrial DNA sequences and DNA-DNA hybridization (Braun *et al.*, 1984; Avise and Zink, 1988; Sheldon *et al.*, 1992) and vocalizations (Dixon, 1955; Coldren, 1992). The two species occupy different habitats, the Tufted wetter deciduous forest and the Black-crested a variety of arid, more open woodlands; interbreeding occurs across this ecological transition in TX (Dixon, 1955). The species can be distinguished by crest and forehead color (Dixon, 1955) and differ on average in song characteristics such as frequency, duration and spacing of phrases, spacing of notes and phrases, and number of phrases per song (Coldren, 1992; C.M. Curry, pers. obs.). These phenotypic differences provide multiple avenues to observe the relative effects of natural and sexual selection on introgression in the younger and older zones (Vallin *et al.*, 2012).

Our study compares both plumage and morphology in north-central TX and southwestern OK, including the first quantitative analysis of plumage for these species. Further, our study compares the current extent of hybridization to previous records, yielding three time periods in which to compare cline width in two regions: historical (1955) and recent (2000s) for the older north-central TX and recent for the younger southwestern OK zone. We also evaluate the use of Dixon's (1955) hybrid index, developed for specimens, on live birds in the field.

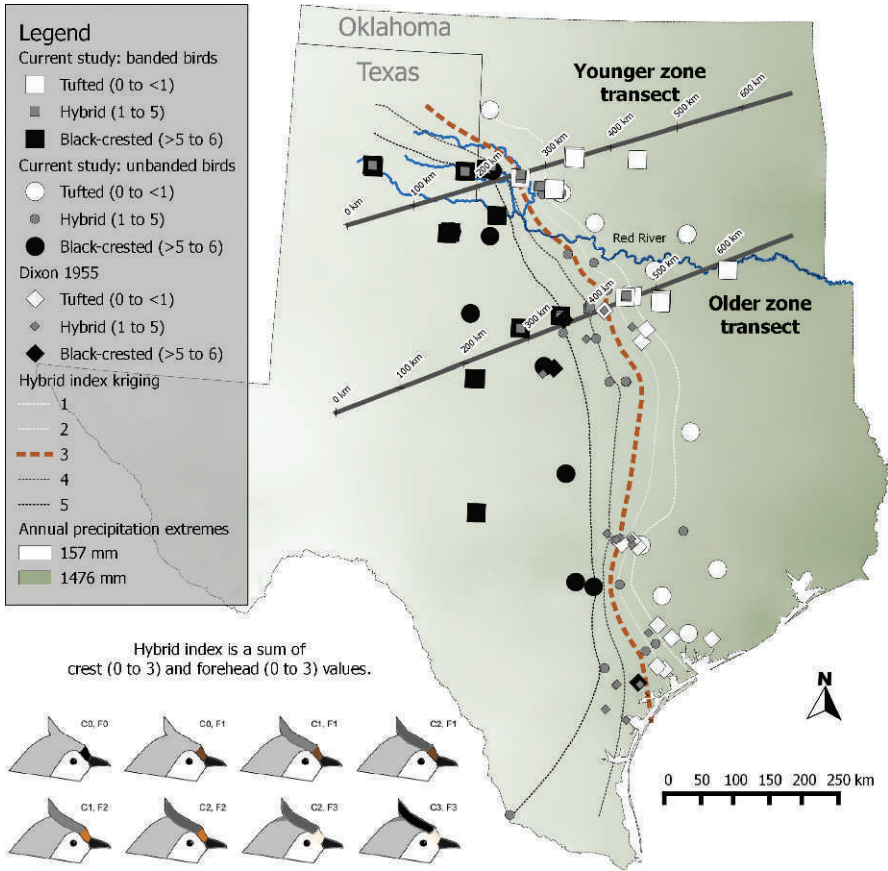


FIG. 1.—Recent (2007–2012) and historical (Dixon, 1955) distribution of hybrid index values across the hybrid zones in TX and OK. Tick marks on transects represent 100 km intervals for comparison with Fig. 3. Annual precipitation gradient is a 30 arc-second grid from WorldClim (Hijmans *et al.*, 2005). Contour lines for the hybrid zone were created using empirical Bayesian kriging in ArcGIS 10.1 via the Geostatistical Analyst extension (subset size 100, overlap factor 1, 100 simulations, no transformation, standard circular neighborhood, 10–15 neighbors, 4 sectors, 0 angle, and radius 5) (ESRI, 1999). Inset: Color interpretation of Dixon’s hybrid index, based on black-and-white illustrations in Dixon (1955). Crest values: 0 = Gray, similar color as neck and back; 1 = Dark gray, obviously different from neck and back although color may blend at edges; 2 = Dull black or very dark gray, blackish color can blend at edges; 3 = Shiny black or black crest with crisply defined border, may extend down back of crest into back of neck. Forehead values: 0 = Black or only small amounts of brown at the edge of the forehead; 1 = Dark chestnut or dark brown; 2 = Light brown or chestnut color that is distinct from facial color; 3 = White or pale color that blends into facial area, not a distinct patch of color

METHODS

STUDY AREA

This study was conducted in TX and OK, with banding at 20 public and private sites (Fig. 1; Table 2). One banding site (Llano River Field Station) in central TX is excluded from the cline analyses because of its long distance from the main older transect. Banding

TABLE 2.—Main study sites with transect (older or younger contact zone), sample size (n), average hybrid index scores  $\pm$  standard deviation (range), and GPS coordinates in decimal degrees

Site	Transect	n	Forehead hybrid index	Crest hybrid index	Total hybrid index
Texas Tech University Llano River Field Station, TX (30.474 N, -99.783 W)	Older (but see Methods)	2	3.0 $\pm$ 0 (3)	3.0 $\pm$ 0 (3)	6.0 $\pm$ 0 (6)
Abilene State Park, TX (32.235 N, -99.886 W)	Older	7	3.0 $\pm$ 0 (3)	3.0 $\pm$ 0 (3)	6.0 $\pm$ 0 (6)
Fort Griffin State Historic Site, TX (32.924 N, -99.216 W)	Older	5	3.0 $\pm$ 0 (3)	2.4 $\pm$ 0.55 (2-3)	5.4 $\pm$ 0.55 (5-6)
City of Graham sewage treatment plant, TX (33.098 N, -98.599 W)	Older	4	2.5 $\pm$ 0.58 (2-3)	2.8 $\pm$ 0.5 (2-3)	5.3 $\pm$ 0.96 (4-6)
City of Graham Fireman's Park, TX (33.115 N, -98.595 W)	Older	1	2.0	3.0	5.0
Fort Richardson State Park, TX (33.225 N, -98.152 W)	Older	4	2.0 $\pm$ 0 (2)	2.0 $\pm$ 0.81 (1-3)	4.0 $\pm$ 0.82 (3-5)
Lyndon B. Johnson National Grasslands, TX (33.379 N, -97.579 W)	Older	5	0.8 $\pm$ 0.45 (0-1)	0.2 $\pm$ 0.45 (0-1)	1.0 $\pm$ 0.71 (0-2)
Private land near Greenwood, TX (33.388 N, -97.488 W)	Older	1	0.0	0.0	0.0
Ray Roberts State Park, TX (33.328 N, -97.034 W)	Older	10	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)
Caddo National Grasslands, TX (33.745 N, -95.991 W)	Older	7	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)
Palo Duro Canyon State Park, TX (34.960 N, -101.669 W)	Younger	5	3.0 $\pm$ 0 (3)	2.8 $\pm$ 0.45 (2-3)	5.8 $\pm$ 0.45 (5-6)
Matador Wildlife Management Area, TX (34.137 N, -100.387 W)	Younger	4	3.0 $\pm$ 0 (3)	3.0 $\pm$ 0 (3)	6.0 $\pm$ 0 (6)
Private land near Eldorado, OK (34.389 N, -99.652 W)	Younger	3	3.0 $\pm$ 0 (3)	3.0 $\pm$ 0 (3)	6.0 $\pm$ 0 (6)
Private land near Wellington, TX (34.951 N, -100.191 W)	Younger	5	2.6 $\pm$ 0.55 (2-3)	2.8 $\pm$ 0.45 (2-3)	5.4 $\pm$ 0.89 (4-6)
Sandy Sanders Wildlife Management Area, OK (35.013 N, -99.818 W)	Younger	4	2.3 $\pm$ 0.58 (2-3)	2.3 $\pm$ 0.58 (2-3)	4.7 $\pm$ 1.15 (4-6)
Quartz Mountain Nature Park, OK (34.911 N, -99.300 W)	Younger	9	1.7 $\pm$ 0.71 (0-2)	1.1 $\pm$ 0.60 (0-2)	2.8 $\pm$ 1.09 (0-4)
Mountain Park Wildlife Management Area, OK (34.797 N, -98.998 W)	Younger	2	1.5 $\pm$ 0.71 (1-2)	1.0 $\pm$ 0 (1)	2.5 $\pm$ 0.71 (2-3)
Wichita Mountains Wildlife Refuge, OK (34.763 N, -98.763 W)	Younger	8	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)
Fort Cobb State Park, OK (35.190 N, -98.455 W)	Younger	5	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)
Oliver's Woods Preserve, OK (35.180 N, -97.446 W)	Younger	3	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)	0.0 $\pm$ 0 (0)

sites are located in the following USGS Level III ecoregions in TX (Griffith *et al.*, 2004) and OK (Woods *et al.*, 2005): Cross Timbers (all TX hybrid sites), Central Great Plains, Edwards Plateau, Southwestern Tablelands, and East Central Texas Plains and occur across a gradient in precipitation. Additional sight records were gathered at locations throughout the two states near previously reported areas of hybridization (Dixon, 1955; Patten and Smith-Patten, 2008).

#### SAMPLING AND MEASUREMENTS

We observed titmice in 2007, 2008, and Mar.–Jun. 2009 near the reported hybrid zone throughout TX and in southwestern OK. We observed and banded additional titmice from 2010–2012 in north TX and southwestern and central OK.

The original hybrid index for these species (Dixon, 1955) classifies the range of crest and forehead plumage on a scale from 0 (pure Tufted) to 6 (pure Black-crested) by combining crest (0 to 3) and forehead (0 to 3) values. Outside of the hybrid zone birds are typically 0–1 (Tufted) or 5–6 (Black-crested), so hybrids show a large range of intermediate plumage within the narrow zone of contact (Dixon, 1955). It was developed from and used on museum specimens, but we used the hybrid index to score live birds (Fig. 1). Most observations of unbanded birds were made with  $8 \times 32$  Leica Rangefinder binoculars. To compare hybrid index values to a quantitative measurement of plumage color, we scored the hybrid index and then used a Konica-Minolta CR-400 colorimeter to quantify forehead and crest colors on in-hand birds using the  $L^*a^*b^*$  color scale (CIE, 2004) with light-dark, red-green, and blue-yellow axes. The colorimeter was calibrated on a white standard before each use.

As female Black-crested Titmice can have paler crests (Dixon, 1955), only males are included. We counted all singing birds for sight records as males. All singing banded birds for which blood samples have been analyzed were males (genetically sexed following Griffiths *et al.*, 1998). Dixon (1955) included female titmice in the hybrid index site average, so those site averages are lowered (Fig. 1).

To compare body plumage and morphology between the species and between TX and OK, we quantified color on the dorsum, flanks, breast, and side of head using the colorimeter to compare with verbal descriptions given in Dixon (1955). Each banded bird was measured by one author (CMC) for wing chord, tail length, tarsus length, bill length, bill width, and bill depth following Pyle (1997) and crest length (Dixon, 1955).

These methods were approved by the University of Oklahoma Institutional Animal Care and Use Committee (R09-004, R12-009). Banding was conducted under U.S. Fish and Wildlife Service permit 23215-H, Oklahoma Department of Wildlife Conservation scientific collecting permits 4716, 4955, and 5210, and Texas Parks and Wildlife Department scientific collecting permit SPR-0310-019.

#### DATA ANALYSES

We estimated measurement error for all plumage and morphology data (Bailey and Byrnes, 1990; Marantz and Patten, 2010) using SAS 9.2 (SAS Institute Inc., 2002). Repeated measures were taken on randomly selected birds ( $n = 14$ ) in 2010 and 2011. Tarsus was excluded from analyses due to high measurement error (20.3%). Instead, we used wing chord for a size proxy. Forehead (measurement errors: light-dark 1.8%, red-green 3.8%, blue-yellow 11.8%) and crest (measurement errors: light-dark 10.5%, red-green 5.08%, 11.8%), likely due to their easily observed fixed locations, were just above or well below a 10% cut-off for measurement error, as were wing chord (3.0%) and tail length (3.7%). Because of measurement error  $>10\%$  for bill measurements and many colorimeter

measurements in 2010–2011, we began to average three replicates for the bill and all colorimeter measurements in 2012. Bailey and Byrnes (1990) suggested this as an acceptable approach for using variables with high measurement error, as averaging multiple measurements and increasing the sample size allows for sound inference from such variables.

Birds are grouped in two ways in the following analyses: by using the hybrid index directly and by using the hybrid index to categorize birds with scores of  $\geq 1$  but  $\leq 5$  as hybrids; though occasional birds far from the hybrid zone (Fig. 1) can also display specific hybrid-like variations. [These variations are always a paler crest (crest scored as 2) in Black-crested and a hint of brown forehead (forehead scored as 1) on a Tufted; (C.M. Curry, pers. obs.). On some species feather wear reveals colors (*e.g.*, Johnson and Johnson, 1985), and this may be the cause of hybrid-like variations on the titmouse crest and foreheads outside of the hybrid zone.] Although this is an arbitrary cut-off, it allows for convenient grouping of birds for illustrative purposes and for a few categorical tests.

To compare colorimeter values with the visually estimated hybrid index values, we performed canonical correlation analysis (CCA) in SAS 9.2 (SAS Institute Inc., 2002). The six crest and forehead colorimeter values (three color axes for each region) were one canonical axis; crest and forehead hybrid index values were the other canonical axis.

To test for spatial autocorrelation indicative of geographic variation within each parental species, we performed Mantel tests (Sokal, 1979) using the R package ‘ade4’ (Dray and Dufour, 2007). Tufted Titmouse is monotypic (Grubb and Pravasudov, 2008), whereas the Black-crested Titmouse has several weakly marked subspecies (Patten and Smith-Patten, 2008). The Black-crested Titmouse in this study include mostly *B. a. sennetti* with five individuals of *B. a. paloduro* from Palo Duro Canyon, all identified by geographic range (Dixon, 1955; Patten and Smith-Patten, 2008). Hence, variation is not likely to be the result of subspecific identity, especially for Tufted Titmouse. We tested for significance after using the Dunn-Sidak correction for family-wise error rates for morphology (six comparisons,  $P < 0.0085$ ) and plumage (18 comparisons,  $P < 0.0028$ ). For both the young and old zones combined, we described plumage and morphology using principal components analysis (PCA) with a correlation matrix in R 2.15.0 (R Development Core Team, 2012), with axis loadings (Pearson correlations between components and raw variables)  $> 0.33$  interpreted; this corresponds to roughly 10% of variation explained (Comrey and Lee, 1992). We illustrate these results for each species with the centroid of the first two principal components and 68% data concentration ellipses in the R package ‘car’ (Fox and Weisberg, 2011); these ellipses are equivalent to approximately one standard deviation around the average assuming bivariate normality.

We used ArcGIS to create shape files of historical sightings (figures 9 and 12 in Dixon, 1955). All additional mapping was done in Quantum GIS (QGIS) 1.8.0 (Quantum GIS Development Team, 2012). Sightings from this study are identified as individuals. Dixon’s sightings are identified by their hybrid index values as site averages (tables 14–16 in Dixon, 1955).

To compare recent and historically surveyed cline widths and centers for hybrid index, we first created standardized transects through the main OK and TX banding sites (excluding one site far to the south of the main study areas) using standard (reduced) major axis regression in the R package lmodel2 (Legendre, 2011) to determine the slope and intercept of each transect. Each transect starts at  $-102^\circ\text{W}$  and ends at  $-95^\circ\text{W}$  to allow for approximate comparison of the cline center from east to west, although the transect slopes differ. We transformed coordinates into the Universal Transverse Mercator (UTM)

projection in QGIS and calculated the distance of each individual's GPS points along the transect.

We then fit clines using the R package 'hzar' (Derryberry, 2012) and CFit-8 (Gay *et al.*, 2008). Both programs fit three-part cline equations to the data using maximum likelihood (Szymura and Barton, 1986; Brumfield *et al.*, 2001; Gay *et al.*, 2008). However, the sigmoidal curves were a poor fit to the data. Instead, clines were described using loess smoothing, a type of local polynomial regression fitting, as implemented with the "loess" function in R 2.15 (R Development Core Team, 2012). Loess smoothing is a type of local polynomial regression fitting with its shape dictated by a polynomial degree and a spanning parameter, which adjusts how many local points are used in the fit (Cleveland, 1979). These values were adjusted for each cline but are comparable with 84% confidence intervals. As the historically surveyed data mainly covers hybrid values and lacks the parental asymptotic tails that are present in recently surveyed data, using span  $f = 0.5$  (older) and  $f = 0.6$  (younger) for the recently surveyed transects (degree = 1 for both), and span  $f = 1$  and degree = 2 for historically surveyed data produced appropriate fits. Recently surveyed data included plumage and morphology PCAs, so the first principal component for each was also plotted using this method.

Cline center was defined as the location where maximum slope was located. We calculated cline width in two ways: first as the absolute value of  $1/(\text{maximum slope})$  (Szymura and Barton, 1986) and second as a range of minimum and maximum width. Because cline width, as estimated by the slope, does not generate a confidence interval, we calculated the minimum and maximum range where birds with hybrid index values between one and five are found using the cline confidence intervals (*see* Appendix 1 for an illustration of the calculations). Cline positions were compared by overlap of 84% confidence intervals generated by the "predict" function in R. Confidence intervals of this width overlap 95% of the time and thus are approximately equivalent to a significance test at  $\alpha = 0.05$  (Payton *et al.*, 2003).

Dispersal estimates for our titmouse species were not available, so to estimate selection within each hybrid zone, we used dispersal distances from the sister group (Gill *et al.*, 2005) to Tufted and Black-crested Titmice: the Juniper/Oak Titmouse complex (*B. ridgwayi* and *B. inornatus*; natal dispersal distances reported of 0.091–1.097 km, with an average of 0.343 km) (Cicero, 2000a; Cicero, 2000b); and from the related Carolina Chickadee (*Poecile carolinensis*; Mostrom *et al.*, 2002) (8 km) and Black-capped Chickadee (*P. atricapillus*; Weise and Meyer, 1979) (11.2 km). We calculated selection strength with the equation  $w = \sqrt{(8 \sigma^2)/s}$  (Szymura and Barton, 1986; Moore and Price, 1993; Brelsford and Irwin, 2009), where  $w$  = width of the cline,  $s$  = selection, and  $\sigma$  = dispersal. We also calculated the length of time that would result in the widths for each contact under neutral gene flow (Barton and Hewitt, 1985) using  $1/T = 2\pi(\sigma/w^2)$ , where  $T$  = number of generations, to determine the number of generations. We converted this time to years using this equation to calculate generation time:  $G = \alpha + u/(\lambda - u)$  where  $u$  = survivorship,  $\alpha$  = age at first breeding, and  $\lambda$  = population growth rate (Lande *et al.*, 2002; Milá *et al.*, 2007). We assumed  $\alpha = 1$  and  $\lambda = 1$  (one year of age at first breeding in a stable population) and survivorship was 0.54 (Grubb and Pravasudov, 2008); this resulted in a generation time of 3.35 y.

## RESULTS

### HYBRID INDEX

Crest and forehead colorimeter values were correlated strongly with variance in crest and forehead hybrid index values ( $n = 89$ , Wilks'  $\Lambda = 0.091$ ,  $P < 0.0001$ ; Appendix 2).

TABLE 3.—PCA loadings for plumage. Loadings  $r > 0.33$  are in bold

Plumage character	Both zones combined (n = 89)	
	PC1	PC2
Crest light-dark	<b>0.370</b>	0.113
Crest red-green	<b>-0.395</b>	0
Crest blue-yellow	-0.215	0.289
Forehead light-dark	<b>-0.360</b>	-0.162
Forehead red-green	-0.183	0
Forehead blue-yellow	<b>-0.369</b>	-0.176
Dorsum light-dark	0	<b>-0.383</b>
Dorsum red-green	-0.158	<b>0.399</b>
Dorsum blue-yellow	-0.106	0
Side of head light-dark	-0.116	<b>-0.368</b>
Side of head red-green	-0.250	<b>0.359</b>
Side of head blue-yellow	<b>-0.332</b>	0.160
Flank light-dark	-0.237	-0.205
Flank red-green	0.222	0
Flank blue-yellow	0	-0.148
Breast light-dark	0.101	-0.306
Breast red-green	0.113	0.274
Breast blue-yellow	0	-0.102

## PLUMAGE AND MORPHOLOGY

The Black-crested Titmouse showed no significant spatial autocorrelation in plumage or morphology. The Tufted Titmouse showed significant spatial autocorrelation for crest color on the red-green axis (Mantel's  $r = 0.242$ ,  $P < 0.001$ ). The crest is redder to the north ( $r = 0.47$ ,  $t = 3.06$ ,  $df = 34$ ,  $P = 0.004$ ) and west ( $r = -0.59$ ,  $t = -4.25$ ,  $df = 34$ ,  $P = 0.0002$ ). The difference in crest color is not obvious to the author in the field or from photos. The range in variation is also small (*see* Appendix 3).

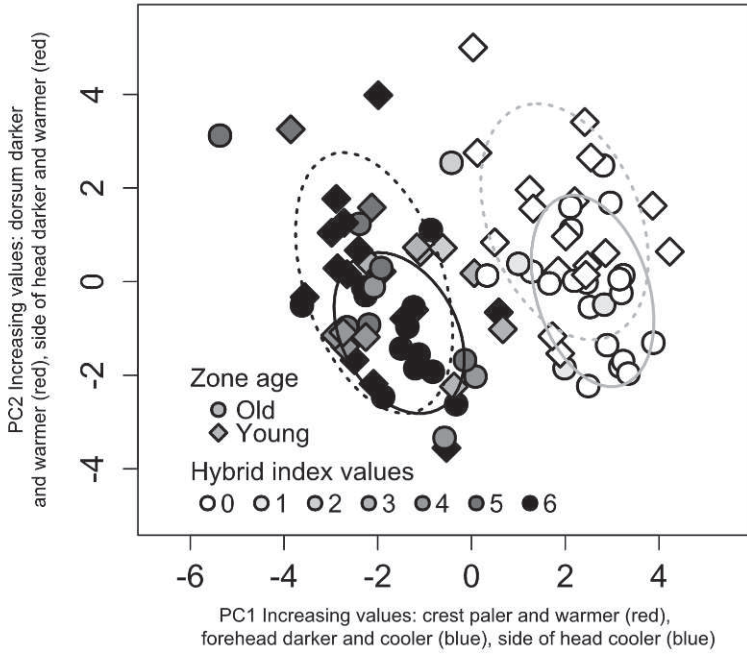
The main variation in plumage for recently surveyed data (Table 3; Fig. 2A; Appendix 4) is in the light-dark and red-green axes for crest and in the light-dark and blue-yellow axes for forehead colors, along with the blue-yellow axis on the side of the head. PC2, which captures mainly individual variation in both recently surveyed regions, shows additional variation in the light-dark and red-green axes on both the dorsum and side of head, which is usually a similar color to the dorsum (C. M. Curry pers. obs.). In general, Tufted Titmice have paler, greener crests, darker, bluer foreheads.

In both the younger and older zones for recently surveyed data, Black-crested Titmice are smaller with a longer crest and shorter, shallower bill ( $n = 91$ ; Table 4; Fig. 2B; Appendix 4). Additional individual variation in these features, plus bill width and excepting crest length, occurs on PC2.

## DISTRIBUTION AND CLINES

The current extent of hybridization between Tufted and Black-crested Titmice in TX generally matches previous records (Fig. 1). New sightings of hybrids follow in similar areas north and south of past sightings for central TX. The cline centers are similar for the recently surveyed and historically surveyed older zone in north-central TX (Fig. 3) but widths are 23 and 17 km, respectively. The 84% confidence intervals for the loess smooths

A



B

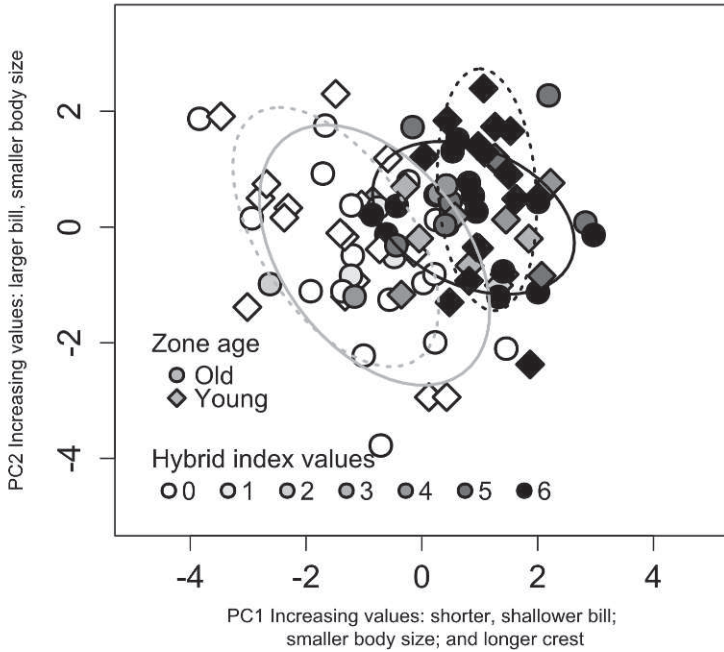


TABLE 4.—PCA loadings for morphology. Loadings  $r > 0.33$  are in bold

Morphological character	Both zones combined (n = 91)	
	PC1	PC2
Bill length	<b>-0.418</b>	<b>0.525</b>
Bill depth	<b>-0.455</b>	<b>0.402</b>
Bill width	-0.187	<b>0.359</b>
Wing chord	<b>-0.500</b>	<b>-0.459</b>
Tail	<b>-0.469</b>	<b>-0.469</b>
Crest length	<b>0.336</b>	0

do not overlap from approximately 410–470 km, indicating a slight shift in traits towards Black-crested in that region. However, the shift occurs within the same region (between 310 and 500 km), indicating the overall location and width of the hybrid zone is similar despite a shift in characters towards Black-crested within it and a potential widening. Compared to the recently surveyed older zone, the recently surveyed younger zone is located farther west (as one would expect from Fig. 1) and is 16 km wide. When using the ranges for the hybrid index clines calculated using 84% confidence intervals, the recently surveyed younger zone is generally narrower at 18–23 km than the historically surveyed older zone (18–31 km) but overlaps with the recently surveyed older zone (10–29 km). The historically and recently surveyed older zone width ranges also overlap. Using hybrid index values of 2–4 as the range of the hybrid zone gives qualitatively similar ranges in width, with the recently surveyed younger transect being narrower than the historically surveyed older transect.

Using those width values and a range of potential dispersal distances to estimate selection strength, values range from almost zero in the recently surveyed older zone to over 10 in the recently surveyed older zone, depending on the parameters (Appendix 5).

#### DISCUSSION

The recently and historically surveyed older zone phenotypic clines did not differ in width while the recently surveyed younger zone cline was narrower. Our current distributional data for north-central TX show a region of intermediate individuals (Fig. 1) that is similar both in extent to previous reports (Dixon, 1955) and to previous estimates of a zone 24–40 km (Lockwood and Freeman, 2004) or 50–100 km wide (Dixon, 1990) in north-central TX. Expansion of a zone over time is expected when ongoing dispersal and introgression has not been balanced by selection against hybrids (Barton and Hewitt, 1985; Barton and Hewitt, 1989) balanced with dispersal of parental individuals into the zone (Barton and Hewitt, 1989) or selection for hybrids within a narrow zone (Moore, 1977). The narrower width for only the recently surveyed younger zone, which is the area with least time since presumed secondary contact, suggests that the recently surveyed younger zone is likely to become wider but then stabilize as a result of selection as appears to have happened with the

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FIG. 2.—PCA averages and 68% data concentration ellipses for (A) plumage and (B) morphology. Ellipses represent birds with a hybrid index of  $<1$  as Tufted, 1–5 as hybrids, and  $>5$  as Black-crested, although slight variation within parental species is possible (see Methods). Symbols: black = Black-crested Titmouse, gray = hybrid, white = Tufted

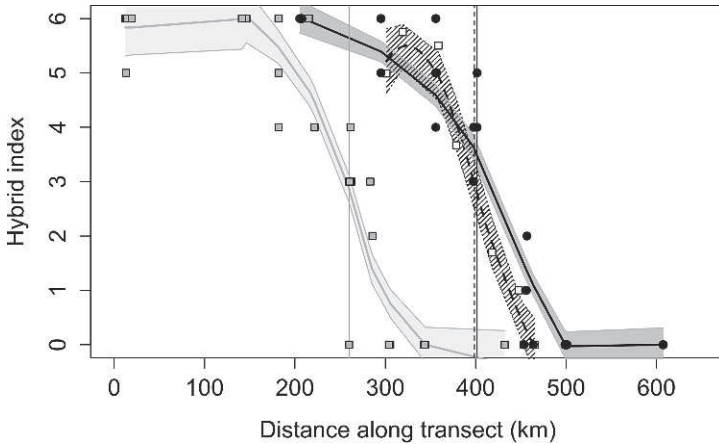


FIG. 3.—Historical and modern older (north-central TX) and younger (southwestern OK) hybrid zone clines. The leftmost cline is the younger hybrid zone (gray lines, symbols, and fill). The remaining clines are the modern older zone (black line and circles, dark gray fill) and the historical older zone (white squares, dashed line, and hatched fill). Fill areas represent 84% confidence intervals, while each symbol is an individual bird (recently surveyed data) or a population (historically surveyed data). Vertical lines are placed at the cline center (location of maximum slope). Clines were fit as described in Methods

recent and historical transects through the older zone (Table 1, scenario 2b). Additional evidence for selection is the amount of time estimated for the cline to reach its current width assuming neutral introgression. Either the younger zone is wider than it should be for its age (for titmouse values of dispersal) or narrower (for chickadee values of dispersal), indicating selection could, respectively, either be favoring introgression or preventing further expansion of the zone. The time to current width under neutrality for the older zone (both historical and recent data) for the maximum titmouse and chickadee dispersal distances also suggest that selection is constraining expansion of the older contact zone. Additional work with genetic data in our system should allow better estimates of dispersal and selection; experimental work with male agonistic responses and female mate choice will clarify what processes may be exerting selection pressure.

The lack of expansion and small center shift (3 km) in the older north-central TX zone over the 60 y historical and recent resurveying periods matches results from other avian hybrid zones in the Great Plains and western North America that have been stable, such as Rose-breasted and Black-headed Grosbeaks (Mettler and Spellman, 2009) and Yellow-rumped Warblers (Brelsford and Irwin, 2009) or shifted only slightly, such as the “Red-shafted” and “Yellow-shafted” Northern Flickers (Moore and Buchanan, 1985). A contact zone in Australia between two species of frogs, resurveyed after 60 y, also showed no change in width but a small change in cline center, possibly in response to changes in local population density (Smith *et al.*, 2013). A similar process could be occurring in the titmouse zones; additional possible reasons for movement are discussed below. That the zone has not narrowed, as has occurred with Lazuli and Indigo Buntings (Carling and Zuckerberg, 2011), indicates that selection, such as by reinforcement (Howard, 1993) or by other natural or sexual selection (Barton and Hewitt, 1981; Alatalo *et al.*, 1990; Patten *et al.*, 2004; Tobler

*et al.*, 2009; Merrill *et al.*, 2011) is at least not overcoming dispersal into the zone. Another resampled zone, that of Townsend's and Hermit Warblers, has continued to move over recent resampling (Krosby and Rohwer, 2010) consistent with past genetic evidence of its movement (Krosby and Rohwer, 2009). The related Carolina and Black-capped Chickadees have also shown obvious movement in their hybrid zone (Reudink *et al.*, 2007).

Although there was no overall difference in width for the recently surveyed and historically surveyed data, a small local shift (as in Moore and Buchanan, 1985) in the north-central TX zone has occurred since Dixon's (1989, 1990) work in the region; the cline center has moved by about 3 km to the east, matching with a shift towards Black-crested Titmouse on the hybrid index at any given hybrid locality for the older zone (Fig. 3). Lockwood and Freeman (2004) described the Black-crested Titmouse as occurring east to Clay County, TX; we found hybrids occurring west to at least Wichita County, TX and a Tufted or near-Tufted hybrid in Clay County. Pulich (1988) noted the two forms interbreed freely west of Tarrant County, TX and north to the Red River. Dixon (1955) speculated the north-central TX zone may have expanded in response to changes in oak distributions; Dixon (1990) discussed slight distributional shifts on the basis of local weather events, such as drought and vegetation changes along coastal TX, but concluded the main area of the hybrid zone had not changed despite small details of movement. Slight movements in climatic gradients (Dixon, 1955, 1989; Swenson, 2006) or in population density (Barton and Hewitt, 1989; Smith *et al.*, 2013) could also be a causal factor. Genetic work should aid in determining any potential shifts in the extent (Sattler and Braun, 2000) and rate of introgression of neutral markers (Krosby and Rohwer, 2009; Mettler and Spellman, 2009) and also determine if phenotypic and genetic clines coincide (Sattler and Braun, 2000; Gay *et al.*, 2008; Toews *et al.*, 2011; Seneviratne *et al.*, 2012).

We present herein the first detailed description of the younger southwestern OK contact zone, where the Black-crested Titmouse has expanded its range into southwestern OK likely in response to woody shrub encroachment (Van Auken, 2000; Callahan, 2002). Parids prefer not to cross large open areas (Desrochers and Bélisle, 2007) so this is a reasonable cause for the range expansion. We posit east-west contact between the two forms; though, another possibility is that all titmouse populations (parental and hybrids) have moved north and westward together into southwestern OK. However, after a fairly smooth curve north along the Edwards Plateau, the contact orientation (Fig. 1) jogs abruptly westward at the Red River, as evidenced by hybrids just south of the Red River and Tufted Titmouse present north of it in south-central OK. This is consistent with a new east-west contact in southwestern OK. Dixon (1955) reported neither titmouse nor appropriate habitat along the Red River in TX (Hardeman and Hall Counties); isolating a population of the Black-crested in the TX panhandle (*B. a. paloduro*) from those in north-central TX. A break is still possible between the TX and OK contact zones in the present day, but it is more likely to be continuous along the riparian woodlands of the Red River despite sparse titmouse habitat in southwestern OK and western north TX, as both the Black-crested and hybrids are now found in counties where formerly absent (*see* references in Patten and Smith-Patten, 2008 and sight records in the current study). Ongoing genetic work may clarify the route of the range expansion.

We present the first quantitative analysis of plumage within this species complex. Plumage variation across both contact zones (Fig. 2A; Appendix 4A) is similar with minor differences between zones in coloration on the side of the head and breast. Otherwise, excepting the obvious change in crest and forehead coloration between the species, most variation in plumage was individual scatter within species. Despite the individual scatter, however, the

Black-crested Titmouse [which is comprised of four weakly marked subspecies (Patten and Smith-Patten, 2008)], does not show any spatial autocorrelation in plumage, while the monotypic Tufted Titmouse (Grubb and Pravasudov, 2008) shows only slight clinal variation in one plumage character. The larger sampling range in latitude for the Black-crested Titmouse (Fig. 1) should result in easier detection of any potential clinal variation compared to the shorter expanse sampled for the Tufted Titmouse. The recent range expansion in the Black-crested Titmouse could result in the lack of clinal variation observed in the populations we sampled, which included approximately equal numbers of birds from the younger and older zones.

For morphology, we found no significant spatial autocorrelation in size over the range of either species (Table 2); but we sampled a much smaller range in latitude, particularly for the Tufted Titmouse, than did Dixon (1955). He noted a distinct size difference between populations of the Black-crested and Tufted Titmice at similar latitudes and clinal variation in size, with northern birds being larger. Tufted Titmice tend to have larger bills in both the TX and OK contacts; Dixon (1955) speculated the prevalence of “oaks and other mast-producing trees” in the Tufted range during winter might result in these slightly larger bills for handling these larger foods. In the recently surveyed younger zone, the species show less overlap along PC1 (Fig. 2B). Perhaps continued introgression in the older zone has blunted body size differences (Appendix 4B) and left only potentially ecologically important differences despite the widths of the plumage clines being similar in both regions for both recent and historical data.

Future work on this temporally complex hybrid zone should focus on forces acting to hold the older clines in equilibrium and monitoring the younger cline for potential expansion and movement. Plumage may be under sexual selection at least in the Black-crested Titmouse (Dixon, 1955), preventing the clines from spreading in the older zones. In the future, we will compare mitochondrial and nuclear genetic markers for concordance of clines (Barton and Hewitt, 1985), as they are expected to be coincident where selection against hybrids is balanced against dispersal into the zone (Barton and Hewitt, 1985). Additionally, if the younger hybrid zone is a new secondary contact as we postulate and not a northwestward range expansion of both parental and hybrid titmouse populations, neutral genetic clines should also be narrower in the younger hybrid zone, reflecting a shorter time for introgression. Finally, differences in song between the two species (Coldren, 1992; C. M. Curry, pers. obs.) provide an additional avenue for exploration. If hybrids have reduced fitness, whether it is intrinsic or extrinsic, conspecific song preferences may have not yet evolved (Labonne and Hendry, 2010) in response to selection pressures in the younger zone, allowing it to potentially spread to a width comparable to those in the older zone. Our study describing the size of and phenotypic variation across this temporally complex hybrid zone provides a baseline for such further studies of behavioral, ecological, and genetic processes shaping its maintenance (Harrison, 1990).

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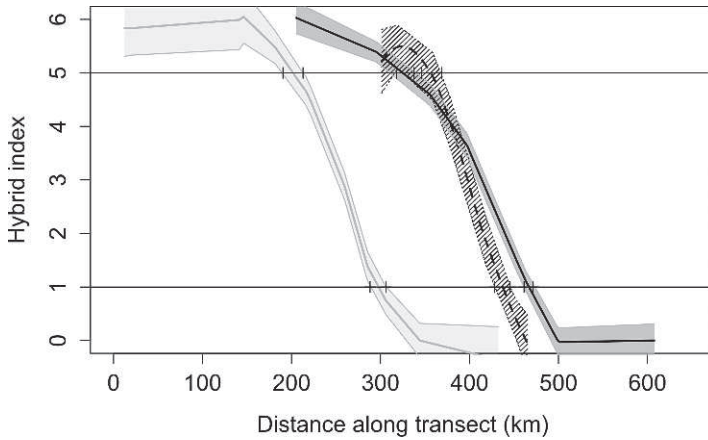
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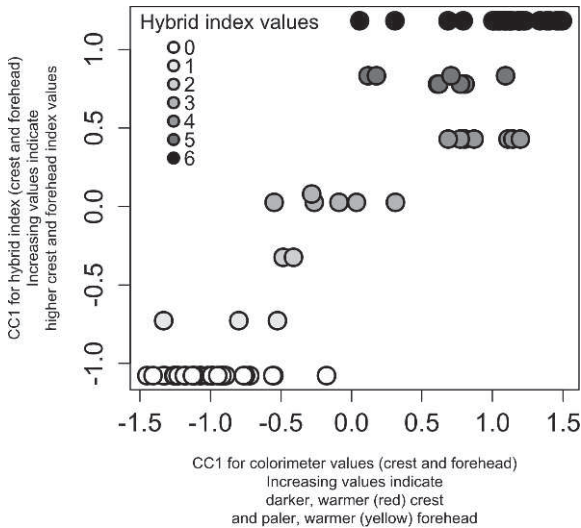
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APPENDIX 1.—Cline width figure showing how cline width ranges were calculated using upper and lower 84% confidence intervals. The distance between each cut-off line (1 and 5) to the loess smoothing prediction was minimized to find the point closest to the intersection of the cut-off line and the loess smoothing predicted values. The point does not always match the visual of the smoothing line for the smoothing because the graph interpolates between the predicted loess smoothing values, but the estimate is repeatable. For each of the three transects, the two closest values were subtracted to find the minimum width, while the two most distance values were subtracted to find the maximum width



APPENDIX 2.—Canonical correlation between hybrid index and colorimeter values for CC1 ( $F_{12,162} = 31.4, P < 0.0001$ ). The hybrid index CC1 variate accounts for 97.4% of variance in the hybrid index values; the colorimeter CC1 variate accounts for 55.9% of variance in colorimeter values. Variance in colorimeter values for crest and forehead explain 86.9% of variance in the hybrid index. While CC2 is significant ( $F_{5,82} = 3.1, P = 0.04$ ), very little (0.4%) variance in the hybrid index values are explained by variance in colorimeter values on the CC2 variates and so is not illustrated further. Actual hybrid index values (crest and forehead values summed) are shown for each individual

APPENDIX 3.—Average  $\pm 1$  sd (range), and sample size for birds at each site. Tarsus is included here for comparison with Dixon (1955), despite  $>>10\%$  measurement error in our study (see Methods)

	Texas Tech University Llano River Field Station, TX "LLANO"	Abilene State Park, TX "ABILENE"	Fort Griffin State Historic Site, TX "FTGRIFFIN"	City of Graham sewage treatment plant, TX "GRAHAM"	City of Graham Fireman's Park, TX "FIREMAN"
Bill length	8.3 $\pm$ 0.5 (8.0–8.7) n = 2	9.1 $\pm$ 0.4 (8.4–9.5) n = 7	9.1 $\pm$ 0.6 (8.3–9.6) n = 5	9.1 $\pm$ 0.3 (8.6–9.3) n = 4	9.1 (9.1) n = 1
Bill depth	5.0 $\pm$ 0.02 (5.0–5.03) n = 2	5.2 $\pm$ 0.2 (4.9–5.5) n = 7	5.3 $\pm$ 0.1 (5.2–5.4) n = 5	5.2 $\pm$ 0.2 (5.0–5.4) n = 4	5.2 (5.2) n = 1
Bill width	4.9 $\pm$ 0 (4.9) n = 2	5.0 $\pm$ 0.3 (4.6–5.6) n = 7	5.0 $\pm$ 0.3 (4.5–5.3) n = 5	5.1 $\pm$ 0.3 (4.7–5.3) n = 4	4.9 (4.9) n = 1
Tarsus (left)	21.2 $\pm$ 0.3 (21.0–21.4) n = 2	21.4 $\pm$ 0.5 (20.5–21.8) n = 7	20.4 $\pm$ 0.6 (19.9–21.4) n = 5	21.0 $\pm$ 0.8 (20.1–21.9) n = 4	20.9 (20.9) n = 1
Wing chord (right)	73.8 $\pm$ 0.2 (73.7–74) n = 2	78.5 $\pm$ 1.5 (77–81) n = 7	73.9 $\pm$ 3.0 (69.3–77) n = 5	77.0 $\pm$ 2.0 (76–80) n = 4	79 (79) n = 1
Tail	63.5 $\pm$ 0.7 (63–64) n = 2	70.4 $\pm$ 2.3 (68–73) n = 7	66.1 $\pm$ 1.9 (64–68) n = 5	69.3 $\pm$ 3.4 (65.3–73) n = 4	67 (67) n = 1
Crest length	18.3 $\pm$ 0.9 (17.7–19) n = 2	21.3 $\pm$ 0.6 (20.3–22) n = 7	19.9 $\pm$ 0.9 (19–21) n = 5	20.0 $\pm$ 1.4 (18–21) n = 4	19 (19) n = 1
Crest light–dark	14.9 $\pm$ 4.7 (11.6–18.2) n = 2	13.7 $\pm$ 1.7 (12.3–16.8) n = 7	17.3 $\pm$ 3.1 (13.4–21.4) n = 5	19.1 $\pm$ 2.7 (16.6–22.9) n = 4	19.0 (19.0) n = 1
Crest red–green	1.7 $\pm$ 0.4 (1.5–2.0) n = 2	1.8 $\pm$ 0.2 (1.7–2.2) n = 7	2.0 $\pm$ 0.5 (1.5–2.8) n = 5	1.7 $\pm$ 0.4 (1.3–2.2) n = 4	1.4 (1.4) n = 1
Crest blue–yellow	2.8 $\pm$ 0.1 (2.7–2.9) n = 2	2.7 $\pm$ 0.5 (1.9–3.4) n = 7	3.7 $\pm$ 1.3 (2.8–6.0) n = 5	2.9 $\pm$ 0.5 (2.6–3.6) n = 4	4.5 (4.5) n = 1
Forehead light–dark	39.3 $\pm$ 3.0 (37.1–41.4) n = 2	37.3 $\pm$ 3.8 (31.7–41.1) n = 7	37.5 $\pm$ 4.5 (31.7–42.8) n = 5	33.6 $\pm$ 3.3 (28.9–36.3) n = 4	28.7 (28.7) n = 1
Forehead red–green	1.8 $\pm$ 0.1 (1.75–1.9) n = 2	2.9 $\pm$ 0.8 (2.3–4.5) n = 7	2.1 $\pm$ 0.4 (1.6–2.5) n = 5	2.5 $\pm$ 0.3 (2.2–2.8) n = 4	4.5 (4.5) n = 1
Forehead blue– yellow	11.5 $\pm$ 0.5 (7.4–10.4) n = 2	12.5 $\pm$ 2.4 (10.0–16.8) n = 7	11.1 $\pm$ 1.1 (10.0–12.6) n = 5	10.8 $\pm$ 1.5 (9.3–12.4) n = 4	14.1 (14.1) n = 1
Dorsum light–dark	37.2 $\pm$ 0.8 (36.7–37.7) n = 2	35.4 $\pm$ 2.2 (32.2–38.1) n = 7	34.9 $\pm$ 1.3 (32.8–36.0) n = 5	37.6 $\pm$ 1.4 (36.4–39.4) n = 4	35.0 (35.0) n = 1
Dorsum red–green	0.7 $\pm$ 0.1 (0.6–0.7) n = 2	0.5 $\pm$ 0.4 (0.2–1.1) n = 7	0.9 $\pm$ 0.2 (0.6–1.2) n = 5	0.6 $\pm$ 0.1 (0.57–0.7) n = 4	0.8 (0.8) n = 1

## APPENDIX 3.—Extended

	Fort Richardson State Park, TX "FTRICHARDSON"	Lyndon B. Johnson National Grasslands, TX "LBJNG"	Private land near Greenwood, TX "CURRY"	Ray Roberts State Park, TX "GREENBELT"	Caddo National Grasslands, TX "CADDO"
Bill length	9.2 ± 0.2 (9.0–9.3) n = 4	8.9 ± 0.5 (8.1–9.3) n = 5	9.5 (9.5) n = 1	9.1 ± 0.8 (8.0–10.7) n = 10	9.1 ± 0.5 (8.4–9.7) n = 7
Bill depth	5.2 ± 0.2 (5.0–5.3) n = 4	5.3 ± 0.3 (4.9–5.5) n = 5	5.4 (5.4) n = 1	5.4 ± 0.3 (5.0–5.9) n = 10	5.3 ± 0.3 (5.0–5.7) n = 7
Bill width	5.0 ± 0.3 (4.6–5.2) n = 4	5.0 ± 0.3 (4.6–5.4) n = 5	4.9 (4.9) n = 1	5.0 ± 0.2 (4.6–5.3) n = 10	5.0 ± 0.3 (4.5–5.4) n = 7
Tarsus (left)	20.2 ± 0.7 (19.2–20.8) n = 4	21.5 ± 0.8 (20.2–22.5) n = 5	22.0 (22.0) n = 1	21.3 ± 0.9 (19.8–22.8) n = 10	21.1 ± 0.7 (19.9–21.8) n = 7
Wing chord (right)	78.2 ± 3.3 (75.6–82) n = 4	81.9 ± 2.9 (78–86) n = 5	75 (75) n = 1	79.3 ± 2.1 (76–83) n = 10	80.7 ± 2.8 (76–85) n = 7
Tail	70.0 ± 3.6 (67–74) n = 4	73.4 ± 4.2 (69–79) n = 5	71 (71) n = 1	72.2 ± 2.9 (67.7–76) n = 10	71.1 ± 2.4 (68–74) n = 7
Crest length	18.9 ± 0.8 (18–19.7) n = 4	18.4 ± 2.2 (17–22) n = 5	19 (19) n = 1	19.1 ± 1.5 (17–21) n = 10	17.5 ± 0.8 (17–19) n = 7
Crest light- dark	17.7 ± 3.0 (15.1–21.1) n = 4	30.9 ± 3.7 (26.1–35.9) n = 5	33.1 (33.1) n = 1	32.0 ± 1.7 (29.9–34.7) n = 10	30.7 ± 1.5 (29.2–33.2) n = 7
Crest red-green	1.8 ± 0.3 (1.5–2.0) n = 4	0.9 ± 0.3 (0.6–1.3) n = 5	0.7 (0.7) n = 1	0.6 ± 0.2 (0.4–0.9) n = 10	0.7 ± 0.2 (0.3–0.8) n = 7
Crest blue- yellow	3.4 ± 0.4 (3.1–3.6) n = 4	3.0 ± 0.8 (2.3–4.3) n = 5	2.2 (2.2) n = 1	2.8 ± 0.6 (1.8–3.5) n = 10	2.5 ± 0.3 (2.2–3.0) n = 7
Forehead light- dark	29.7 ± 3.2 (26.6–32.9) n = 4	22.9 ± 6.3 (13.7–30.7) n = 5	18.7 (18.7) n = 1	16.6 ± 4.0 (11.2–23.7) n = 10	14.8 ± 6.0 (6.8–24.4) n = 7
Forehead red- green	4.2 ± 1.0 (3.1–5.2) n = 4	2.7 ± 0.8 (2.0–3.9) n = 5	2.2 (2.2) n = 1	2.1 ± 0.3 (1.3–2.4) n = 10	1.9 ± 0.7 (1.0–3.0) n = 7
Forehead blue- yellow	12.4 ± 2.0 (10.9–14.7) n = 4	8.2 ± 1.2 (7.4–10.4) n = 5	4.0 (4.0) n = 1	6.5 ± 0.6 (5.6–7.5) n = 10	5.0 ± 1.3 (3.1–6.7) n = 7
Dorsum light- dark	38.7 ± 0.2 (38.6–38.9) n = 4	34.9 ± 2.5 (33.0–38.8) n = 5	41.3 (41.3) n = 1	35.2 ± 2.2 (29.5–37.4) n = 10	34.7 ± 1.9 (32.6–38.0) n = 7
Dorsum red- green	0.5 ± 0.5 (–0.1–0.8) n = 4	0.7 ± 0.3 (0.2–1.0) n = 5	0.4 (0.4) n = 1	0.5 ± 0.2 (0.2–0.9) n = 10	0.6 ± 0.3 (–0.01–1.0) n = 7

## APPENDIX 3.—Continued

	Palo Duro Canyon State Park, TX "PALODURO"	Matador Wildlife Management Area, TX "MATADORWMA"	Private land near Eldorado, OK "OSBORNE"	Private land near Wellington, TX "HENARD"	Sandy Sanders Wildlife Management Area, OK "SSWMA"
Bill length	9.1 ± 0.4 (8.7–9.6) n = 5	9.0 ± 0.4 (8.4–9.4) n = 4	8.2 ± 0.4 (7.8–8.5) n = 3	8.9 ± 0.5 (8.3–9.4) n = 5	8.5 ± 0.4 (8.1–8.9) n = 3
Bill depth	5.3 ± 0.1 (5.2–5.4) n = 5	5.3 ± 0.1 (5.2–5.4) n = 4	5.2 ± 0.2 (5.1–5.4) n = 3	5.3 ± 0.1 (5.2–5.4) n = 5	5.0 ± 0.1 (4.9–5.1) n = 3
Bill width	4.9 ± 0.2 (4.6–5.2) n = 5	5.2 ± 0.3 (4.8–5.4) n = 4	5.2 ± 0.6 (4.8–5.9) n =	5.0 ± 0.6 (4.4–5.8) n = 5	5.1 ± 0.7 (4.3–5.5) n = 3
Tarsus (left)	21.1 ± 0.5 (20.3–21.7) n = 5	21.2 ± 0.2 (20.9–21.3) n = 4	20.7 ± 0.8 (19.8–21.2) n = 3	20.7 ± 1.2 (19.0–22.1) n = 5	19.7 ± 0.8 (18.7–20.3) n = 3
Wing chord (right)	74.5 ± 1.1 (73–76) n =	75.8 ± 1.7 (74–78) n = 4	77.7 ± 0.6 (77–7) n = 3	75.0 ± 2.4 (72–78) n = 5	74.4 ± 4.7 (69–77.3) n = 3
Tail	65.4 ± 1.1 (64–67) n = 5	66.5 ± 1.0 (65–67) n = 4	71.6 ± 2.5 (68.7–73) n = 3	66.7 ± 3.3 (63.7–72) n = 5	69.7 ± 2.3 (67–71) n = 3
Crest length	20.5 ± 0.8 (19.3–21) n = 5	20.5 ± 1.3 (19–22) n = 4	20.3 ± 0.6 (20–21) n = 3	19.2 ± 1.4 (17–20.8) n = 5	20.1 ± 1.0 (19–21) n = 3
Crest light–dark	16.6 ± 3.0 (13.1–20.9) n = 5	15.7 ± 3.0 (13.4–20.0) n = 4	14.5 ± 1.1 (13.7–15.8) n = 3	17.0 ± 5.0 (13.0–25.3) n = 5	14.7 ± 0.9 (13.6–15.2) n = 3
Crest red–green	2.1 ± 0.3 (1.8–2.7) n = 5	2.0 ± 0.4 (1.5–2.3) n = 4	1.9 ± 0.2 (1.7–2.1) n = 3	1.8 ± 0.3 (1.4–2.1) n = 5	2.0 ± 0.2 (1.9–2.2) n = 3
Crest blue– yellow	3.9 ± 0.8 (3.0–5.0) n = 5	3.3 ± 0.6 (2.6–3.9) n = 4	3.1 ± 0.6 (2.6–3.7) n = 3	2.9 ± 0.6 (2.1–3.7) n = 5	3.4 ± 0.3 (3.2–3.7) n = 3
Forehead light– dark	40.5 ± 5.2 (31.9–46.2) n = 5	35.2 ± 5.2 (29.9–42.1) n = 4	38.2 ± 2.9 (35.0–40.8) n = 3	33.3 ± 4.7 (26.9–39.2) n = 5	36.5 ± 4.5 (33.3–41.7) n = 3
Forehead red– green	2.9 ± 0.5 (2.2–3.7) n = 5	1.9 ± 0.2 (1.7–2.0) n = 4	2.8 ± 0.1 (2.7–2.9) n = 3	2.7 ± 0.8 (1.6–3.5) n = 5	3.2 ± 1.1 (2.5–4.5) n = 3
Forehead blue– yellow	13.1 ± 2.5 (9.6–15.8) n = 5	9.5 ± 2.5 (5.8–10.8) n = 4	12.7 ± 2.1 (11.3–15.1) n = 3	11.9 ± 3.2 (7.4–16.4) n = 5	14.8 ± 1.7 (12.9–16.0) n = 3
Dorsum light– dark	36.5 ± 3.7 (31.6–40.1) n = 5	34.4 ± 2.4 (31.7–37.1) n = 4	36.3 ± 1.6 (34.9–38.0) n = 3	35.8 ± 2.7 (32.9–38.6) n = 5	37.1 ± 1.7 (35.2–38.5) n = 3
Dorsum red– green	1.0 ± 0.3 (0.7–1.3) n = 5	0.9 ± 0.2 (0.8–1.3) n = 4	0.7 ± 0.4 (0.3–1.1) n = 3	0.8 ± 0.4 (0.4–1.4) n = 5	0.9 ± 0.2 (0.6–1.0) n = 3

## APPENDIX 3.—Extended Continued

	Quartz Mountain Nature Park, OK "QUARTZMTN"	Mountain Park Wildlife Management Area, OK "MTNPARKWMA"	Wichita Mountains Wildlife Refuge, OK "WITCHITAMTNS"	Fort Cobb State Park, OK "FTCOBB"	Oliver's Woods Preserve, OK "OWP"
Bill length	9.1 ± 0.4 (8.3–9.6) n = 9	8.7 ± 0.1 (8.6–8.7) n = 2	9.2 ± 0.7 (8.0–10.1) n = 8	9.7 ± 0.4 (9.2–10.5) n = 5	9.0 ± 0.6 (8.5–9.7) n = 3
Bill depth	5.2 ± 0.2 (4.9–5.4) n = 9	5.0 ± 0.1 (4.9–5.0) n = 2	5.4 ± 0.3 (4.9–6.1) n = 8	5.5 ± 0.1 (5.4–5.7) n = 5	5.4 ± 0.2 (4.8–5.8) n = 3
Bill width	5.0 ± 0.3 (4.6–5.2) n = 9	4.9 ± 0.3 (4.7–5.1) n = 2	5.3 ± 0.3 (4.8–5.9) n = 8	5.1 ± 0.3 (4.8–5.4) n = 5	5.1 ± 0.5 (4.5–5.5) n = 3
Tarsus (left)	21.4 ± 1.6 (18.8–23.4) n = 9	20.3 ± 0.3 (20.1–20.5) n = 2	22.0 ± 0.6 (21.0–22.8) n = 8	22.1 ± 0.8 (20.8–22.7) n = 5	21.7 ± 0.1 (21.7–21.8) n = 3
Wing chord (right)	77.3 ± 1.6 (74.3–79) n = 9	77.0 ± 0 (77) n = 2	81.0 ± 1.5 (79–83) n = 8	82.1 ± 1.3 (81–84) n = 5	80.5 ± 3.0 (77–82.5) n = 3
Tail	70.5 ± 1.5 (68–72) n = 9	67.5 ± 2.1 (66–69) n = 2	71.5 ± 2.1 (68–74) n = 8	73.6 ± 3.0 (72–79) n = 5	71 ± 2.6 (68–73) n = 3
Crest length	19.5 ± 1.5 (17.3–22) n = 9	19.5 ± 0.7 (19–20) n = 2	18.2 ± 1.4 (16–20) n = 8	17.7 ± 1.1 (16–19) n = 5	17.7 ± 1.3 (16.5–19) n = 3
Crest light- dark	26.7 ± 7.2 (14.4–34.1) n = 9	23.6 ± 3.2 (21.3–25.8) n = 2	29.7 ± 1.8 (26.7–32.3) n = 8	32.1 ± 0.9 (31.2–33.5) n = 5	31.2 ± 2.7 (28.2–33.6) n = 3
Crest red-green	1.4 ± 0.6 (0.7–2.5) n = 9	1.4 ± 0.2 (1.3–1.6) n = 2	1.0 ± 0.2 (0.7–1.4) n = 8	0.9 ± 0.1 (0.7–1.0) n = 5	0.6 ± 0.2 (0.4–0.7) n = 3
Crest blue- yellow	3.6 ± 0.7 (2.7–4.8) n = 9	4.4 ± 0.4 (4.1–4.7) n = 2	3.1 ± 0.5 (2.5–3.9) n = 8	3.2 ± 0.7 (2.3–4.0) n = 5	3.1 ± 0.3 (2.8–3.4) n = 3
Forehead light- dark	26.5 ± 5.5 (15.5–32.1) n = 9	24.3 ± 1.5 (23.3–25.3) n = 2	19.0 ± 7.5 (10.8–30.9) n = 8	18.5 ± 8.5 (8.8–31.2) n = 5	13.7 ± 1.9 (11.6–15.4) n = 3
Forehead red- green	4.7 ± 1.4 (1.7–6.7) n = 9	3.9 ± 0.7 (3.4–4.3) n = 2	2.2 ± 0.5 (1.5–3.2) n = 8	2.1 ± 0.4 (1.7–2.5) n = 5	2.0 ± 0.7 (1.4–2.8) n = 3
Forehead blue- yellow	12.0 ± 3.6 (5.5–18.1) n = 9	10.7 ± 1.4 (9.8–11.7) n = 2	6.0 ± 0.9 (4.5–7.0) n = 8	6.2 ± 2.3 (3.7–10.0) n = 5	3.8 ± 1.1 (2.8–5.0) n = 3
Dorsum light- dark	36.2 ± 2.6 (31.8–41.1) n = 9	34.2 ± 0.3 (34.0–34.4) n = 2	35.2 ± 2.6 (30.8–37.7) n = 8	34.0 ± 1.6 (31.9–35.6) n = 5	33.8 ± 1.1 (32.7–34.7) n = 3
Dorsum red- green	0.6 ± 0.2 (0.3–0.9) n = 9	0.8 ± 0.03 (0.79–0.84) n = 2	0.8 ± 0.3 (0.4–1.2) n = 8	0.8 ± 0.2 (0.5–1.1) n = 5	0.7 ± 0.3 (0.5–1.0) n = 3

## APPENDIX 3.—Continued

	Texas Tech University Llano River Field Station, TX "LLANO"	Abilene State Park, TX "ABILENE"	Fort Griffin State Historic Site, TX "FTGRIFFIN"	City of Graham sewage treatment plant, TX "GRAHAM"	City of Graham Fireman's Park, TX "FIREMAN"
Dorsum blue-yellow	3.5 ± 0.3 (3.3–3.7) n = 2	3.8 ± 1.9 (0.6–5.3) n = 7	4.2 ± 0.8 (3.3–5.4) n = 5	3.9 ± 0.8 (2.8–4.7) n = 4	5.4 (5.4) n = 1
Side of head light- dark	42.3 ± 1.7 (41.2–43.5) n = 2	38.5 ± 2.4 (35.3–41.6) n = 7	39.0 ± 3.8 (34.2–44.6) n = 5	38.9 ± 3.6 (35.4–42.6) n = 4	41.2 (41.2) n = 1
Side of head red- green	0.6 ± 0.1 (0.5–0.7) n = 2	0.7 ± 0.2 (0.5–1.0) n = 7	1.0 ± 0.4 (0.7–1.6) n = 5	0.6 ± 0.1 (0.4–0.8) n = 4	0.6 (0.6) n = 1
Side of head blue- yellow	3.0 ± 0.03 (2.99–3.03) n = 2	3.6 ± 0.7 (2.9–4.8) n = 7	4.6 ± 1.3 (3.2–6.6) n = 5	3.0 ± 0.2 (2.7–3.3) n = 4	4.3 (4.3) n = 1
Flank light-dark	61.8 ± 6.4 (57.3–66.4) n = 2	54.5 ± 2.9 (49.1–57.8) n = 7	60.0 ± 2.9 (57.4–64.9) n = 5	62.9 ± 18.2 (47.5–63.7) n = 4	56.2 (56.2) n = 1
Flank red-green	4.5 ± 4.0 (1.6–7.3) n = 2	7.4 ± 1.6 (5.4–10.1) n = 7	4.3 ± 1.4 (3.1–6.6) n = 5	7.1 ± 1.8 (5.2–8.9) n = 4	6.5 (6.5) n = 1
Flank blue-yellow	19.6 ± 8.3 (13.8–25.5) n = 2	25.3 ± 1.6 (23.6–27.3) n = 7	20.4 ± 3.2 (17.6–24.2) n = 5	24.0 ± 3.7 (19.7–28.1) n = 4	24.8 (24.8) n = 1
Breast light-dark	68.9 ± 3.4 (66.6–71.3) n = 2	67.2 ± 4.4 (63.0–74.2) n = 7	67.3 ± 3.7 (61.7–70.9) n = 5	72.1 ± 3.4 (67.3–74.6) n = 4	68.0 (68.0) n = 1
Breast red-green	-0.3 ± 0.5 (-0.7–0.03) n = 2	-0.2 ± 0.4 (-0.9–0.3) n = 7	-0.3 ± 0.2 (-0.5–0.1) n = 5	-0.3 ± 0.2 (-0.5–0.1) n = 4	0.7 (0.7) n = 1
Breast blue-yellow	8.2 ± 1.8 (7.0–9.5) n = 2	6.7 ± 1.6 (5.4–9.3) n = 7	7.0 ± 1.3 (5.0–8.3) n = 5	7.5 ± 1.3 (5.6–8.6) n = 4	12.2 (12.2) n = 1

## APPENDIX 2.—Extended Continued

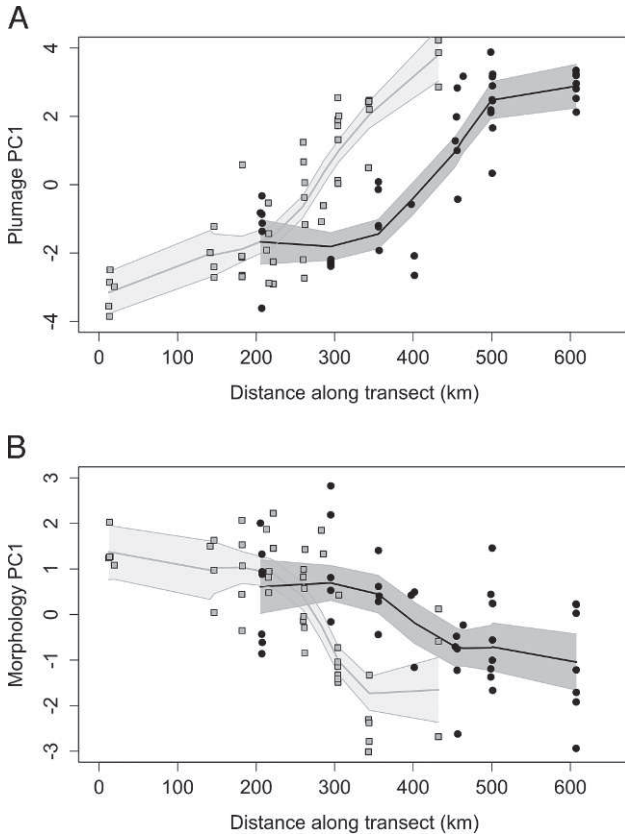
	Fort Richardson State Park, TX "FTRICHARDSON"	Lyndon B. Johnson National Grasslands, TX "LBJNG"	Private land near Greenwood, TX "CURRY"	Ray Roberts State Park, TX "GREENBELT"	Caddo National Grasslands, TX "CADDO"
Dorsum blue- yellow	5.5 ± 0.9 (4.5–6.1) n = 4	3.3 ± 0.6 (2.3–3.8) n = 5	4.0 (4.0) n = 1	3.7 ± 1.2 (1.6–5.3) n = 10	3.4 ± 0.6 (2.6–4.1) n = 7
Side of head light-dark	37.2 ± 6.0 (30.4–40.8) n = 4	38.1 ± 3.5 (34.3–42.0) n = 5	38.1 (38.1) n = 1	36.7 ± 2.3 (32.1–39.2) n = 10	34.7 ± 4.0 (29.0–40.5) n = 7
Side of head red-green	0.7 ± -/2 (0.5–0.9) n = 4	0.7 ± 0.1 (0.6–0.9) n = 5	0.6 (0.6) n = 1	0.5 ± 0.2 (0.3–0.9) n = 10	0.6 ± 0.2 (0.2–0.7) n = 7
Side of head blue-yellow	3.0 ± 0.8 (2.3–3.8) n = 4	2.7 ± 0.6 (2.0–3.3) n = 5	2.4 (2.4) n = 1	2.0 ± 0.5 (1.3–3.0) n = 10	2.1 ± 0.2 (1.9–2.3) n = 7
Flank light- dark	59.1 ± 3.3 (56.5–62.8) n = 4	53.7 ± 3.0 (48.9–56.1) n = 5	46.4 (46.4) n = 1	54.0 ± 7.0 (43.9–67.1) n = 10	51.5 ± 4.9 (44.0–56.9) n = 7
Flank red- green	5.8 ± 3.0 (2.4–7.8) n = 4	7.4 ± 1.9 (5.6–10.3) n = 5	10.1 (10.1) n = 1	6.3 ± 3.1 (0.9–11.8) n = 10	8.3 ± 1.6 (6.6–10.6) n = 7
Flank blue- yellow	23.2 ± 7.1 (15.0–27.8) n = 4	23.1 ± 2.4 (19.7–25.9) n = 5	24.0 (24.0) n = 1	20.9 ± 4.5 (11.9–27.2) n = 10	24.0 ± 2.6 (19.6–27.4) n = 7
Breast light- dark	70.1 ± 4.6 (65.5–74.8) n = 4	68.1 ± 6.1 (61.2–76.3) n = 5	74.3 (74.3) n = 1	71.3 ± 4.3 (66.8–78.2) n = 10	67.8 ± 7.5 (58.3–76.7) n = 7
Breast red- green	-0.4 ± 0.04 (-0.5–-0.4) n = 4	0.04 ± 0.1 (-0.2–0.1) n = 5	-0.2 (-0.2) n = 1	-0.2 ± 0.2 (-0.6–0.2) n = 10	-0.1 ± 0.3 (-0.9–0.1) n = 7
Breast blue- yellow	6.2 ± 0.8 (5.3–6.7) n = 4	7.0 ± 2.8 (3.6–9.9) n = 5	8.1 (8.1) n = 1	8.1 ± 1.8 (5.3–10.4) n = 10	5.8 ± 1.2 (4.0–7.4) n = 7

## APPENDIX 3.—Continued

	Palo Duro Canyon State Park, TX "PALODURO"	Matador Wildlife Management Area, TX "MATADORWMA"	Private land near Eldorado, OK "OSBORNE"	Private land near Wellington, TX "HENARD"	Sandy Sanders Wildlife Management Area, OK "SSWMA"
Dorsum blue- yellow	4.3 ± 0.7 (3.4–5.1) n = 5	4.6 ± 0.3 (4.2–4.9) n = 4	2.5 ± 2.1 (0.1–4.1) n = 3	3.7 ± 1.1 (2.3–5.3) n = 5	3.9 ± 0.4 (3.4–4.1) n = 3
Side of head light-dark	37.7 ± 2.3 (34.5–40.0) n = 5	34.6 ± 4.5 (30.7–40.5) n = 4	39.9 ± 3.5 (36.5–43.6) n = 3	37.9 ± 3.8 (31.3–40.6) n = 5	38.9 ± 0.8 (38.1–39.6) n = 3
Side of head red-green	1.0 ± 0.2 (0.8–1.3) n = 5	1.2 ± 0.5 (0.6–1.9) n = 4	0.9 ± 0.5 (0.5–1.5) n = 3	0.8 ± 0.1 (0.6–0.9) n = 5	0.7 ± 0.2 (0.6–0.9) n = 3
Side of head blue-yellow	3.9 ± 0.7 (3.4–5.0) n = 5	3.7 ± 0.9 (2.9–4.9) n = 4	3.8 ± 1.8 (2.2–5.8) n = 3	3.0 ± 0.6 (2.4–3.8) n = 5	2.6 ± 0.9 (1.6–3.3) n = 3
Flank light-dark	58.0 ± 4.4 (51.8–63.3) n = 5	57.9 ± 1.0 (56.9–59.3) n = 4	54.8 ± 0.7 (54.0–55.3) n = 3	58.8 ± 3.9 (54.3–64.2) n = 5	58.7 ± 2.0 (57.4–61.0) n = 3
Flank red-green	4.8 ± 2.5 (0.8–6.7) n = 5	6.1 ± 0.7 (5.3–6.8) n = 4	7.1 ± 0.3 (6.8–7.4) n = 3	2.9 ± 1.2 (1.8–4.2) n = 5	4.8 ± 1.7 (3.0–6.4) n = 3
Flank blue- yellow	20.9 ± 5.6 (12.5–26.7) n = 5	24.0 ± 1.9 (22.2–26.6) n = 4	24.6 ± 0.5 (24.3–25.1) n = 3	17.8 ± 2.9 (14.1–21.6) n = 5	21.7 ± 4.4 (17.3–26.2) n = 3
Breast light-dark	68.3 ± 6.6 (58.1–73.7) n = 5	64.9 ± 3.1 (60.5–67.6) n = 4	74.3 ± 1.7 (72.4–75.5) n = 3	69.3 ± 3.1 (65.4–73.7) n = 5	68.2 ± 4.5 (63.9–73.5) n = 3
Breast red-green	-0.1 ± 0.7 (-1.0–0.7) n = 5	-0.5 ± 0.5 (-1.0–0.1) n = 4	0.2 ± 0.5 (-0.2–0.7) n = 3	-0.4 ± 0.3 (-0.7–0) n = 5	-0.1 ± 0.03 (-0.2–-0.1) n = 3
Breast blue- yellow	7.7 ± 2.1 (5.2–10.4) n = 5	5.8 ± 1.0 (4.4–6.7) n = 4	8.9 ± 0.4 (8.4–9.1) n = 3	6.4 ± 1.4 (4.6–8.5) n = 5	5.6 ± 1.9 (3.4–7.0) n = 3

## APPENDIX 3.—Extended Continued

	Quartz Mountain Nature Park, OK "QUARTZMTN"	Mountain Park Wildlife Management Area, OK "MTNPARKWMA"	Wichita Mountains Wildlife Refuge, OK "WITCHITAMTNS"	Fort Cobb State Park, OK "FTCOBB"	Oliver's Woods Preserve, OK "OWP"
Dorsum blue- yellow	4.7 ± 1.1 (3.5–6.7) n = 9	3.1 ± 0.6 (2.6–3.5) n = 2	2.8 ± 0.8 (1.1–3.6) n = 8	4.1 ± 1.0 (2.6–5.5) n = 5	4.1 ± 1.3 (2.9–5.5) n = 3
Side of head light-dark	38.5 ± 2.5 (35.3–41.9) n = 9	38.2 ± 0.8 (37.7–38.8) n = 4	34.9 ± 3.7 (30.3–41.2) n = 8	34.6 ± 1.9 (32.1–37.4) n = 5	34.5 ± 2.3 (32.0–36.6) n = 3
Side of head red-green	0.6 ± 0.1 (0.4–0.8) n = 9	0.7 ± 0.2 (0.6–0.8) n = 2	0.8 ± 0.2 (0.6–1.1) n = 8	0.7 ± 0.2 (0.3–1.0) n = 5	0.5 ± 0.1 (0.4–0.6) n = 3
Side of head blue-yellow	2.9 ± 0.4 (2.3–3.6) n = 9	2.8 ± 0.5 (2.5–3.2) n = 2	2.5 ± 0.6 (1.7–3.4) n = 8	2.5 ± 0.6 (1.7–3.4) n = 5	1.6 ± 0.6 (1.1–2.2) n = 3
Flank light- dark	55.3 ± 5.4 (48.1–66.1) n = 9	56.2 ± 0.9 (55.5–56.8) n = 2	52.9 ± 5.2 (46.5–62.6) n = 8	50.0 ± 6.7 (42.9–56.7) n = 5	49.2 ± 7.2 (42.7–57.0) n = 3
Flank red- green	5.2 ± 2.8 (1.5–8.8) n = 9	4.3 ± 2.9 (2.3–6.3) n = 2	6.0 ± 2.6 (0.9–9.4) n = 8	7.4 ± 1.3 (5.4–8.5) n = 5	9.4 ± 1.6 (7.6–10.7) n = 3
Flank blue- yellow	19.8 ± 5.8 (10.1–25.0) n = 9	19.9 ± 3.9 (17.2–22.6) n = 2	19.7 ± 6.4 (5.3–26.7) n = 8	21.2 ± 1.5 (19.5–22.7) n = 5	24.8 ± 0.9 (24.0–25.7) n = 3
Breast light- dark	69.1 ± 4.5 (60.0–74.2) n = 9	68.5 ± 0.6 (68.1–68.9) n = 2	66.7 ± 7.1 (50.4–72.6) n = 8	70.2 ± 3.0 (67.8–75.4) n = 5	72.7 ± 4.4 (67.9–76.6) n = 3
Breast red- green	0.1 ± 0.3 (–0.2–0.7) n = 9	–0.03 ± 0.1 (–0.1–0.1) n = 2	0.1 ± 0.2 (–0.3–0.5) n = 8	0.04 ± 0.4 (–0.3–0.8) n = 5	0.5 ± 0.6 (0.2–1.2) n = 3
Breast blue- yellow	6.8 ± 2.6 (3.3–10.6) n = 9	7.6 ± 0.1 (7.5–7.6) n = 2	5.5 ± 1.3 (3.2–7.3) n = 8	6.9 ± 2.7 (3.5–10.9) n = 5	7.1 ± 1.2 (6.4–8.7) n = 3



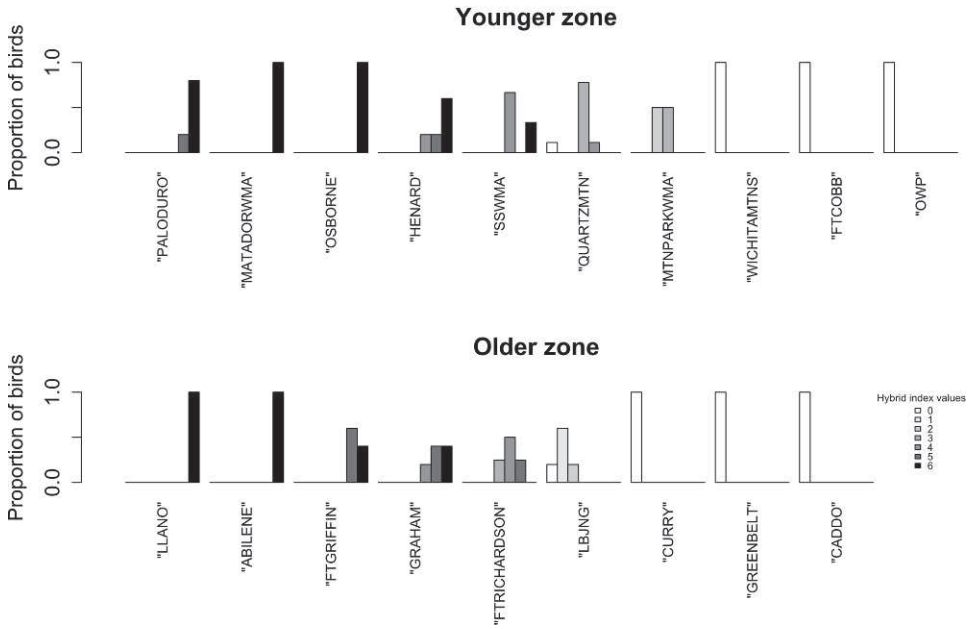
APPENDIX 4.—Phenotypic clines fit with loess smoothing. (A) plumage PC1 and (B) morphology PC1. These data are the same as in Fig. 2, but are instead PC1 is shown across the hybrid zone. The leftmost cline is the younger hybrid zone (gray lines, symbols, and fill). The recently surveyed older zone (black line and circles, dark gray fill) is to the right. Fill areas represent 84% confidence intervals, while each symbol is an individual bird. Clines were fit as described in Methods

APPENDIX 5.—(A) Selection strength and neutral generation time estimates for 15 ranges of dispersal and width. Estimates are shown as selection range, neutral time for this width in generations (years with generation time as 3.35 y; generations and years are rounded after calculations). (B) Histogram showing proportion of birds with a given hybrid index value at each site. [For this figure, Graham and Fireman’s Park have been merged into one site (Graham) for ease of visualization. The site codes are shown in Appendix 3.] Despite potential selection pressure as shown in (A), no parental forms are found at the center of the older contact zone; more potential mixing occurs in the younger contact zone

A

	Low titmouse (0.0091 km)	Average titmouse (0.343 km)	Max. titmouse (1.097 km)	Carolina chickadee (8 km)	Black-capped chickadee (11.2 km)
Historically surveyed older zone (18–31 km width)	0.00000069–0.0000020 5667–16,807 generations 18,983–56,305	0.00098–0.0029 150–446 generations 503–1494 y	0.010–0.030 47–139 generations 157–467 y	0.53–1.58 6–19 generations 22–64 y	1.04–3.10 5–14 generations 15–46 y
Recently surveyed older zone (10–29 km width)	0.00000079–0.0000066 1749–14,709 generations 5859–49,274	0.0011–0.0094 45–390 generations 155–1307 y	0.011–0.096 15–122 generations 49–56 y	0.76–5.12 2–17 generations 7–56 y	1.19–10.04 1–12 generations 5–40 y
Recently surveyed younger zone (18–23 km width)	0.0000013–0.0000020 5667–9252 generations 18,983–30,994	0.0018–0.0029 150–245 generations 504–822 y	0.018–0.030 47–77 generations 157–257 y	0.97–1.58 6–11 generations 25–35 y	1.90–3.10 5–8 generations 15–25 y

**B**



APPENDIX 5.—Continued