SHORT COMMUNICATIONS

Constancy of Margins of the Hybrid Zone in Titmice of the *Parus bicolor* Complex in Coastal Texas

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Statements of historical changes in the distribution of populations presently grouped under *Parus bicolor* (see Oberholser 1974: 608) have led to questionable ecological interpretations, such as displacement of one taxon by another (e.g. Rising 1983). Hence, a review of the distribution of the two taxa since the time of settlement of Texas is in order.

The Eastern Tufted Titmouse (the *bicolor* group of the AOU check-list [1983]) is replaced westward in central Texas and southwestern Oklahoma by black-crested titmice of the *atricristatus* group. The parental forms are connected by populations of intermediates in a belt 50–100 km wide. Apparently Ridgway (1887: 561) was the first to recognize the interbreeding of these forms. He suggested that the "subspecies" (*Parus b. texensis* and *P. a. castaneifrons*) described from Bee County in south-central Texas by Sennett (1887) represented hybridism. Allen (1907) reviewed the available specimens and concurred. Both men retained the two taxa as distinct species, as did Oberholser (1974) who listed them in the long-abandoned genus *Baeolophus*.

Mayr and Short (1970: 93) included this hybrid complex in their category of "intraspecific hybridization" reflecting "indiscriminate pairing and massive introgression." That conclusion was based in part on the field investigations and systematic review of Dixon (1955).

H. C. Oberholser's lifelong investigation of "The Bird Life of Texas" appeared posthumously in 1974, edited by the late Edgar B. Kincaid Jr. Distributional data were reduced to symbols on maps of Texas, representing seasons of occurrence by counties, and specimen records were distinguished from sight records. According to Kincaid (Oberholser 1974: xx), "Detailed" (i.e. subspecies) accounts were retained essentially unedited from Oberholser's original manuscript (cited hereafter as "Oberholser MS"). These were grouped under "Species accounts," prepared by Kincaid as Senior Editor. Thus, authorship for statements of distribution and systematic treatment can be assigned.

Oberholser's volumes include distributions of the two titmice that are at variance with those published earlier (i.e. Allen 1907, Dixon 1955, AOU 1957). The species account for *Baeolophus bicolor*, written by Kincaid, (p. 608) reads: "*Resident*: Breeds . . . throughout the eastern third, west to Gainesville, Fort Worth, Waco, Bastrop and Refugio. Formerly west to San Angelo and San Antonio, and south to Corpus Christi." ("Formerly" was defined (p. 609) as ". . . the late 1800's and early 1900's.") For *B. atricristatus*, ". . . Increasingly rare and irregular east of the 97th meridian to Tarant, Ellis, Limestone, Grimes and Lavaca cos. . . ." The last four counties lie east of a line that connects Fort Worth, Waco, and Bastrop (Fig. 1), and are within the range of "*B. bicolor*" as described above. In addition, ". . . The Tufted Titmouse has been retreating eastward during the first half of the twentieth century . . ." and ". . . during this period the Black-crested Titmouse . . . has been invading the Tufted's original range from the southwest."

To reconcile conflicting statements of distribution, and to ascertain the basis for reports of "displacement," I investigated historical and contemporary records of titmice in central Texas. I reviewed available specimens from selected localities in central Texas, and personal notes on some 470 specimens that were reported earlier (Dixon 1955). Individuals and populations were evaluated by means of the same hybrid index (HI) used earlier (Dixon 1955: 128). Specimens were compared to a reference series used previously. I recognized four categories of crest color and four of forehead color. At the extremes, I scored the gray crest and black forehead of the eastern form as 0, and the shiny black crest and whitish forehead of the western form each received a value of 3. Thus, the HI of a phenotypically pure Eastern Tufted Titmouse equals 0.0. The HI for a pure Black-crested titmouse is 6. The crests of some individuals (especially females) of the black-crested form are dull black (index value = 2). Therefore, values for males are listed separately (Table 1). I also examined locality data reported on maps in Oberholser (1974: 608–610) and I studied the original Oberholser manuscript for the titmice (courtesy of R. C. Banks and M. R. Browning). In addition, I visited selected localities in coastal Texas and obtained specimens in March of 1987, 1988, and 1989.

In the Oberholser-Kincaid text (1974: xx) the terms "Resident or Breeding" were used in contradistinction to "Migration and/or Winter" as major headings for seasonal status. Oberholser (MS) used the phrase "permanent range" for titmice. The relevance of "resident" may be examined by reviewing specimens from San Antonio. That city, at 98°28'W, lies within

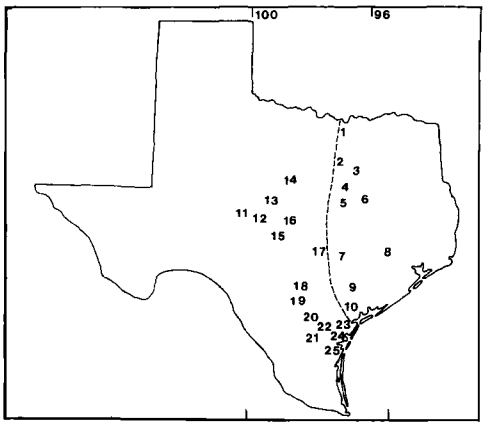

Fig. 1. Map of localities mentioned in the text. According to E. B. Kincaid Jr. (Oberholser 1974: 608), a majority of post-1940 records of *Parus b. bicolor* are from stations located east of the dashed line. Key: Atascosa County (19), Austin (17), Bastrop (7), Bee County (22), Concho County (12), Coleman County (13), Corpus Christi (25), Eastland County (14), Ellis County (3), Fort Worth (2), Gainesville (1), Grimes County (8), Hill County (4), Lavaca County (9), Limestone County (6), Live Oak County (20), Mason County (15), Navasota (8), Nueces River (21), Refugio (23), San Angelo (11), San Antonio (18), San Patricio County (24), San Saba (16), Tarrant County (2), Victoria (10), and Waco (5).

Thornthwaite's (1941: pl. 3) Dry Subhumid Zone. (The dashed line in Figure 1 approximates the boundary between that zone and the Moist Subhumid.) Titmice from that vicinity have been listed as the Black-crested form since early in the 20th century (Quillin and Holleman 1918, Kirn and Quillin 1927). However, 8 of 10 specimens taken in the winter and spring of 1886–1887 at San Antonio by C. W. Beckham were "pure" *P. bicolor;* the other two were Black-crested Titmice (HI = 6). That occupancy of San Antonio by the Eastern Tufted Titmouse was transitory because the HI for a series of 18 titmice taken there in the winter and spring of 1890–1891 (discussed by Dixon 1955: 167) is 4.3; the majority approach *P. atricristatus* in head markings. The crest of one female was gray, but no specimen had a black forehead. Most were taken by H. P. Attwater, who listed the Tufted Titmouse (1892: 343) as "Common in winter" and the Black-crested as "Common resident." That appraisal was based upon his field experience over five breeding seasons (1884, 1885, 1889–1891). Evidently some Eastern Tufted Titmice remained in San Antonio to nest in 1887, and their genetic contribution was diminished through the repeated back-crossing of their progeny to black-crested birds. Ridgway (1904: 386) referred to two pairs of intermediate character from

TABLE 1. Hybrid index values[a] for selected titmouse samples from Texas for the interval 1880–1896. Sample sizes are in parentheses.

	Males only		Sexes combined
	$\bar{x}$	Range	$\bar{x}$
Parus b. bicolor			
Fort Worth	0.0 (4)		0.0 (5)
Victoria Co.	0.0 (4)		0.2 (5)
P. b. sennetti			
Eastland Co.	5.1 (9)	4–6	5.0 (11)
Concho Co.	5.2 (5)	5–6	5.2 (10)
San Antonio[b]	4.6 (10)	3–6	4.3 (18)
Nueces River[c]	4.9 (8)	4–6	4.5 (10)
Corpus Christi	4.9 (8)	4–6	4.9 (8)
P. b. atricristatus			
Lower Rio Grande Valley	5.9 (18)	5–6	5.9 (27)

[a] Total score of 0 denotes gray crest and black forehead typical of the Eastern Tufted Titmouse; 6 denotes black crest and white forehead of the Black-crested Titmouse (see text).

[b] 1890–1891 only.

[c] Am. Mus. Nat. Hist., March 1886, stated by Oberholser (MS) to be Live Oak County.

Attwater's series from 1891 in support of his view that hybridization had occurred at San Antonio. The only other specimen of *P. b. bicolor* from San Antonio known to me (Texas Cooperative Wildlife Collection [TCWC] 7954) was found dead by K. T. Knight on 15 March 1969.

I am aware of no locality where phenotypically pure individuals of both parental forms meet and interbreed. At San Antonio, both parental forms were found in 1887. In subsequent years, intermediates (but not *both* parental forms) were found there. This statement represents a temporal qualification of Ridgway's assertion (1904: 386) that "... hybrids ... occur together in the same localities along with the two hypothetical parent species ...."

The exceptionally severe drought in Texas in 1886 was documented by Stewart (1936) and by Dyksterhuis (1948). Dixon (1955) suggested that the westward influx of Eastern Tufted Titmice may have been linked to that widespread drought. Source populations could have been from the vicinity of Bastrop (110 km northeast). Although Elder (1985) found no evidence of long-distance movements of titmice in Missouri, a conspicuous autumn irruption occurred in the New York City area (Post 1979). Similar irruptive movements at the periphery of a major community type (oak-hickory forest) are postulated for San Antonio in 1886.

The *P. b. bicolor* specimens from San Antonio in the 1880s represent an unusual occurrence. The characterization, "resident" (synonymous with sedentary),

is not supported. Rather, individual titmice or small flocks may be found outside the breeding range irregularly during exceptional winters. Kincaid (in Oberholser 1974: 608) acknowledged that the Eastern Tufted Titmouse was a ". . . highly irregular winter visitor to Coleman [225 km southwest of Fort Worth] and San Patricio cos., where rare." Simmons (1925: 306) reported that form as a "Scarce winter resident, fairly common at rare intervals; extremely rare summer resident . . ." in Austin. Thus, winter records of titmice should not be equated with breeding status at a particular locality.

In the late 1800s, titmice were taken from three localities of purported (Oberholser 1974: 609) former occurrence of the Eastern Tufted Titmouse. Concho (immediately east of San Angelo; HI = 5.2) and Eastland (HI = 5.1) counties, and Corpus Christi (HI = 4.9). The HI values clearly represent black-crested titmice (Table 1). Lloyd's (1887) list from the vicinity of San Angelo included as "abundant" or "common" the Ladder-backed and Golden-fronted woodpeckers (*Picoides scalaris* and *Melanerpes aurifrons*) and the Scrub Jay (*Aphelocoma coerulescens*). None is characteristic of ". . . the humid woodland range . . ." attributed to the Tufted Titmouse by Kincaid (Oberholser 1974: 610). Documented western outposts of the latter in the 1880s were Fort Worth and Victoria (Table 1) and Waco (300 km east of San Angelo). Allen (1907: 481) noted that two of Lloyd's specimens from Concho County were of "mixed character" with chestnut foreheads and gray-tipped crest feathers. At most, those individuals would have been descendants of gray-crested vagrants from an earlier winter influx. San Antonio and the other three localities listed as probable breeding stations of the Eastern Tufted Titmouse do not represent outposts of a regularly inhabited distributional range. Rather, they are localities of highly irregular, unexpected occurrences after which any vagrants that remained apparently were assimilated into black-crested populations by repeated back-crossing, selective removal of their progeny, or both.

Although Oberholser (MS) recognized that hybridization in these titmice occurred ". . . on an extensive scale . . . ," he apparently assigned every specimen to either *B. bicolor* or *B. atricristatus*. Oberholser (MS) listed under *B. b. "floridanus"* several specimens that I find to be unquestionably Black-crested Titmice. One is an individual (HI = 5), taken 2 miles north of Pleasanton, Atascosa County, Texas, 29 December 1937, by W. B. Davis (TCWC no. 1446). Another (TCWC no. 1121), collected at San Saba, San Saba County, 24 March 1938, by W. P. Taylor, had a hybrid index of 6. Several localities are listed as within the "permanent and breeding range" of both *B. b. floridanus* and *B. a. sennetti*. What is apparently the same specimen (Mason County, 26 April 1878, G. H. Ragsdale) is listed under both taxa.

Localities east of the Fort Worth–Bastrop–Victoria line (Fig. 1) that were attributed to the Black-crested Titmouse by Oberholser (MS) include sets of eggs from Lavaca County ". . . secured March 8, 1886, March 14, and 16, 1887 for S. B. Ladd, . . ." and a set of eggs from Navasota, Grimes County, collected by A. D. Doerge, 5 April 1905. A specimen (14 December 1904), reported from Grimes County by Vernon Bailey, has not been verified. Sight records for Ellis, Hill, and Limestone counties plotted on p. 610 of the 1974 volume are not listed in the Oberholser manuscript (for which the last entry is June 1941). Thus, they were added by Kincaid. None of these localities represents the perimeter of a continuously inhabited range.

Egg sets are of dubious value as sources of distributional information in a hybridizing complex. Sizes of eggs vary within sets and, if egg size is proportional to body size, one would expect intermediacy in measurements of the eggs. Similarly, sight records must be viewed with caution in the analysis of distribution in a hybrid complex of this sort.

Kincaid's text (Oberholser, pp. 609–610) creates the impression of a progressive advance of black-crested populations eastward in recent decades at the expense of gray-crested titmice, an advance associated with postulated concurrent changes in climate and vegetation (some by human agency). However, all the *specimen* records cited above are for the interval before 1910.

Conceivably, Kincaid interpreted phenotypic changes in the Bee County population (already intermediate in the 1880s) as the displacement of one species by the other. Hybrid index values (sexes combined) were 2.9 for 1886 and 1887, 3.6 for 1910, and 4.6 for 1951 (Dixon 1955: fig. 12). The Bee County titmice were found at the terminus of a peninsula of oak woodland extending southwestward from oak-hickory forests, restricted to porous soils, and bordered originally by prairies growing on clay soils. Presumably, as range fires became infrequent following settlement (ca. 1870), woody plants invaded the prairies rapidly from previously isolated mottes. Those vegetational changes were documented (Johnston 1963, Inglis 1964). Thus, the influence of black-crested phenotypes would have been enhanced, whereas introgression from "pure" gray-crested populations (some 95 km to the northeast) was limited presumably to the woodland peninsula.

Although nominate *bicolor* did not form a stabilized population at San Antonio in the late 1880s, its subsequent disappearance constituted a "retreat," with replacement by Black-crested Titmice. Kincaid may have envisioned a similar process at other localities from which "Specimens of Mixed Character" were noted by Allen (1907: 479). These included Eastland and Concho counties and Corpus Christi (as discussed above), which were alluded to (Kincaid *in* Oberholser 1974: 609) as ". . . the Tufted's original range . . ." being invaded by the Black-crested Titmouse. The "retreat and replacement" did not transcend the western outposts of the breeding range of "pure" *bicolor*

as documented by specimens from the 1880s (Table 1, Fig. 1).

Edgar Kincaid was deeply concerned with environmental changes as they affected the bird life of his native state. Chief among these were drought (see account for *Vireo atricapillus*, Oberholser 1974: 701), brush-eradication programs (e.g. 1974: 513) and pesticide use. A revealing comment in the account of *Sturnella magna* (1974: 804) reads "all the destruction of this terrible twentieth century." Certainly the impact of drought on bird populations was overstated. Oscillations in annual rainfall about a long-term median are expected in semiarid climates (Norwine 1978). Intervals of severe drought are followed by years of ample rainfall. The responses of birds may include local fluctuations in abundance (Rappole and Blacklock 1985: 57–59), but not permanent recessions 100–300 km in extent. The ". . . thinning of woodlands by drought and man . . ." that Kincaid considered coincident with the ". . . eastward trek . . ." of the Tufted Titmouse was not supported by the investigations of Dyksterhuis (1948) and Allred (1949).

I believe that both the eastern and western margins of the hybrid zone on the coastal plain have remained essentially unchanged in the past 100 years. Five males from the Nueces River in Live Oak County taken in 1989 differ only slightly from the Nueces River males from 1886 (Table 1). In some, the black of the crest is less intense and the foreheads are tinged faintly with chestnut; their HI is 4.6 compared with 4.9 for the males from 1886.

On the eastern margin of the hybrid zone, specimens from Inez (25 km northeast of Victoria) represent "pure" *bicolor* (HI = 0.0), as does one taken there in 1891. The HI (sexes combined) for five taken from Mission Valley (22 km northwest of Victoria) in 1987–1989 is 2.0, identical to that for four specimens from that locality in 1951. (The other Victoria County specimens in Table 1 are from southwest of Victoria; recent specimens from those localities are not available.) Two of three specimens from Fort Worth (dating from 1955 and 1963) have brown foreheads. The HI for the sample is 0.7, a slight weakening of "pure" *bicolor* traits in comparison with 1886 (Table 1). Frederick R. Gehlbach (letter 5 May 1989) stated that the location of the hybrid zone at two study sites 13 km apart across the Balcones Escarpment at Waco had not changed in detail since 1963. Thus, the eastern and western margins of the hybrid zone have remained essentially constant for many decades. This suggests selection against intermediates at those margins.

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Multiple Functions of Courtship Displays in Dabbling Ducks (Anatini)

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The displays of courting ducks have been described, analyzed, and compared by ornithologists and ethologists for a variety of reasons. Early comparative studies showed that stereotyped displays can be used as taxonomic characters and therefore behavioral evidence was used extensively to deduce relationships within the Anatidae (Lorenz 1941, Delacour and Mayr 1945, Johnsgard 1965). Ethological analyses of the form, contexts, sequences, and spatial orientation of duck displays have been used to infer motivation of the performer and signal functions of individual displays (e.g. Dane and van der Kloot 1964, Weidmann and Darley 1971, Simmons and Weidmann 1973, McKinney 1975, Standen 1980). Other authors have explored how ecological and social factors have influenced the evolution of display repertoires (McKinney 1965a, McKinney et al. 1978) or have used displays to test predictions from sexual conflict theory (Anderson 1984). In spite of the diverse objectives of these various lines of research, all depend on the gathering of accurate descriptive information on displays.

Most of the displays performed by male dabbling ducks (genus *Anas*) during social courtship have distinct orientation components that can be used to identify the target bird. Movie film analyses have shown that male displays may be categorized into three types: (Type a) displays that are directed at a specific female, (Type b) displays that are directed at rival males, and (Type c) displays that appear to be directed simultaneously at the female and at another male. Evidence of many kinds indicates that displays aimed at females function in pair formation (courtship displays) or pair-bond maintenance; those aimed at other males are agonistic and function in competition for mates or mate defense. Film analyses of courtship groups of Mallard (*Anas platyrhynchos*; Weidmann and Darley 1971), Green-winged Teal (*A. crecca*; McKinney 1965b), Chilean Teal (*A. flavirostris*; Standen 1976, 1980), Gadwall (*A. strepera*; Schommer 1977), and American Wigeon (*A. americana*; Wishart 1983) indicated that each major male display can be placed in only one of these three categories. Recent studies of White-cheeked Pintail (*A. bahamensis*) and Chilean Teal, however, have convinced us that some frequently used displays of these two species cannot be assigned uniquely to one category. We have found that major displays are used in *both* courtship (male-female) and agonistic (male-male) contexts, and apparently they serve multiple signal functions. We draw attention to this phenomenon because it has not been reported previously, and we stress the need to reexamine *Anas* signaling systems with special attention to the orientation components of displays.

In most male-female (type a) displays (e.g. grunt-whistle, bridling, head-up-tail-up; terminology for displays follows Johnsgard 1965), the long axis of the male's body is broadside to the female; in others (facing the female, turn-back-of-head), the male's bill is pointed directly at, or away from, the female. Lorenz (1941) noted that these displays often feature conspicuous plumage, and most are accompanied by loud whistles or grunting noises. During the grunt-whistle display, males direct a spray of water sideways, always aimed at the target female (von de Wall 1963). Simmons and Weidmann (1973) showed that similar directional bias is present also in three shaking movements that precede major displays. Such displays are thought to have evolved as signals that indicate the male's interest in a specific female and are designed to attract that female's attention to the performing male.

Male-male (type b) displays are presumed to serve threat or appeasement functions, and to allow assessment of potential competitors. In Mallards, bill-up postures with "rabrab" calls occur when males approach one another. Threatening with open bill or chasing often follows. The males face more or less