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CONTACT ZONES OF AVIAN CONGENERS ON THE SOUTHERN GREAT PLAINS[1]

KEITH L. DIXON
Department of Biology and the Ecology Center, Utah State University, Logan, UT 84322-5305

Abstract. This paper examines the contacts of hybridizing taxa and potentially interacting congeners on the southern portion of the Great Plains. Environmental differences between the northern and southern (Oklahoma, Texas) Great Plains include increasing evaporation southward, extensive scarp woodlands, mesquite savanna, and discontinuous riparian timber in the south. Four of the five pairs of taxa that hybridize prominently on the northern plains have disjunct ranges south of the Red River. Only the Golden-fronted (*Melanerpes aurifrons*) and Red-bellied (*M. carolinus*) woodpeckers, and the forms of the Tufted Titmouse (*Parus bicolor*) and Northern Oriole (*Icterus galbula*) are known to interbreed in Texas. Sympatry of Western (*Otus kennicottii*) and Eastern (*O. asio*) screech-owls on the western Edwards Plateau has been reported, but interbreeding has not been documented there. Reported displacement of eastern populations of the Tufted Titmouse by the western (black-crested) form appears unfounded. Both upland and riparian timber of the southern and eastern Edwards Plateau provide a corridor for interchange of eastern and western avifaunal elements that is more extensive than that in either the discontinuous woodlands in north-central Texas or the Niobrara drainage in Nebraska. In the northern plains congeners meet along ribbons of streamcourse timber that are isolated from one another by intervening grasslands. In the southern Great Plains the western taxa of hybridizing or potentially interacting pairs occupy diverse woodlands. Many of their eastern counterparts have restricted access across prairies and meet their congeners on a broad front.

Key words: Avian distribution; hybridization; ecological counterparts; Great Plains; Texas.

INTRODUCTION

The replacement of avian taxa of eastern affinities by their western counterparts on the Great Plains of North America has been appreciated for at least a century (e.g., Coues 1892, p. 390–391). Such pairs of taxa reflect separate evolutionary histories and divergent ecological adaptations. The term "contact zone" was introduced by Short (1970) for the meeting ground of such pairs of taxa, implying a degree of congruence in their separate distributions. He stated that "These zones are characterized by diverse levels of interaction, including primary intergradation . . . intraspecific secondary intergradation (hybrid zones) . . . interspecific hybridization . . . and various overlap and non-overlap situations involving species-pairs that are reproductively isolated." For the most part, such contacts have been dealt with case by case (e.g., Sutton 1938, Short 1965), although more general reviews were presented by Sibley (1961), Bock et al. (1977), and Rising (1983a), the last based on the author's intensive studies of orioles, buntings, and flycatchers (Rising 1983b and antecedent papers, Rising and Schueler 1980). Rising's approach was comparative and was extended to include the range of phenomena included in Short's concept of contact zones.

On the central and northern Great Plains the contact zones of arboreal birds are confined to timber and brush along streams that traverse treeless expanses (originally grasslands, presently cultivated fields and rangelands). Southward from 37°N (Fig. 1) the vegetation of the plains is more diverse, and the range of habitats utilized by individuals of some taxa is greater. Therefore, an examination of the contact zones of eastern and western arboreal taxa on the southern plains seems warranted. Since the distributions of some pairs of taxa extend to the southern perimeter of the Great Plains physiographic province (the Balcones Escarpment), I follow Rising (1983a) in his inclusion of the Edwards Plateau in the Great Plains, even though the vegetation is not typical of the plains to the north.

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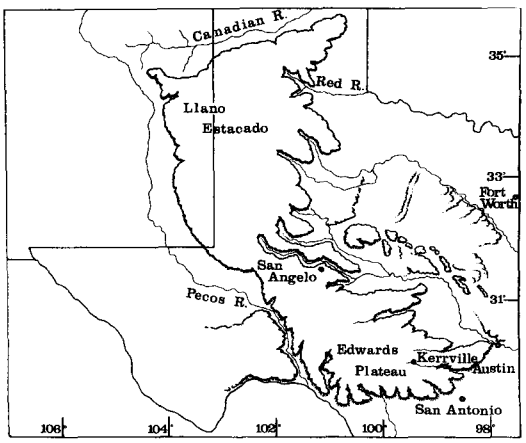

FIGURE 1. Major physiographic features of the southern Great Plains (after Fenneman 1931).

METHODS

In addition to searching the current literature, I corresponded with resident naturalists and consulted personal notes from extensive travel in central and western Texas in the 1950s (Dixon 1955, 1959) and in 1987 and 1988.

THE ENVIRONMENTAL SETTING

Environmental conditions are altered increasingly southward from the 37th parallel. Although lines connecting stations of equal precipitation (isohyets) generally trend north and south (e.g., Wells 1970: fig. 1), annual evaporation increases southward in the Great Plains (Rising 1974). Stream courses south of the Canadian River originate on the High Plains rather than draining the Rocky Mountains. Their volume accordingly is diminished, and stream flow may be intermittent in the upper reaches (Oberholser 1974, p. 10). Streamside timber in the southern High Plains is confined closely to the banks (references in Rising 1974), and may be discontinuous and lacking in mature trees for cavity-nesting birds (Short 1965, p. 343; Marshall 1967, p. 9). Scarp-restricted nonriparian timber mapped by Wells (1970) assumes greater importance, in some cases bridging the uplands between stream courses. Woody vegetation on the escarpment at the eastern edge of the Llano Estacado (Fig. 1) provides for north-south dispersal of sedentary birds. Edaphic factors play a greater role in determining whether a particular upland site is occupied by woody vegetation or grasses (Bray 1901), and honey mesquite (*Prosopis juliflora*) is prominent in plains landscapes from the Oklahoma Panhandle southward. Former grasslands have become mesquite savannas ". . . due to increased population densities [of mesquite] in areas in which *Prosopis* has always been found . . ." (Fisher 1977).

DISJUNCTIONS OF TAXA HYBRIDIZING ON THE NORTHERN PLAINS

On the northern Great Plains hybridization between western and eastern members of the following pairs of taxa occurs principally in floodplain timber and associated shrubbery: Northern (Red-shafted and Yellow-shafted) Flickers (*Colaptes auratus*), Black-headed (*Pheucticus melanocephalus*) and Rose-breasted (*P. ludovicianus*) grosbeaks, Lazuli (*Passerina amoena*) and Indigo (*P. cyanea*) buntings, Rufous-sided ("Spotted" and Eastern) Towhees (*Pipilo erythrophthalmus*) and Northern (Bullock's and Baltimore) Orioles (*Icterus galbula*). Insofar as I am aware, populations of western and eastern flickers, grosbeaks, buntings, and towhees do not meet at present south of 34°N, since suitable timber does not extend across the plains there (Marshall 1967, p. 9). The western populations of flicker, grosbeak, and towhee breed in Texas only in montane forests (Wauer and Ligon 1978). The Lazuli Bunting is confined to higher elevations in New Mexico (Ligon 1961), and is not known to nest in the Texas Panhandle (Williams 1985b). In the latitude of Texas the eastern populations of grosbeak and towhee do not nest regularly west of the Mississippi River. Interbreeding of the orioles is discussed in the next section.

TAXA INTERBREEDING ON THE SOUTHERN PLAINS

The only taxa listed by Rising (1983a) that are known to interbreed south of the Canadian River are the *Melanerpes* woodpeckers, crested titmice, and orioles.

Melanerpes *complex.* The Golden-fronted (*Melanerpes aurifrons*) and Red-bellied (*M. carolinus*) woodpeckers exhibit narrow overlap from the central coast of Texas into southwestern Oklahoma (Selander and Giller 1963, Sutton 1967). Selander and Giller (1963) characterized the two species as ecologically incompatible, and (p. 260) stated that ". . . heterospecific pairing is unknown." Evidence of hybridization between the two species was detected by Smith (1987) by

means of both morphologic and electrophoretic criteria. She estimated the frequency of hybridization to be 15.8% of the specimens examined, representing several sectors of the zone of overlap. Selander and Giller's map (fig. 15) suggests the importance of floodplain timber (e.g., Colorado River drainage, Canadian River) in the westward penetration of *M. carolinus*. Mesquite savanna is an important component in the distribution of *M. aurifrons* in Texas (Hamilton 1962, Oberholser 1974).

Parus bicolor *complex.* Although the crested titmice were said by Rising (1983a) to show a northeast-southwest replacement, the points of contact of black- and gray-crested populations in central Texas deviate little from a north-south line (Dixon 1955:fig. 15). However, the black-crested populations extend well southward into Mexico. Rising's inference that the ancestral form was the more easterly one agrees with the conclusion of Dixon (1978) who suggested that morphological divergence followed a north-south disjunction in eastern Mexico at the close of a glacial episode.

Comments by Rising (1983a), based upon statements in Oberholser (1974), imply an eastward extension of the range limits of the black-crested populations, with consequent "displacement" of the gray-crested or Eastern Tufted Titmouse in central Texas. That "movement" (Oberholser 1974, p. 609), said to have occurred chiefly prior to 1940, was considered to have been the result of a warmer and drier climate of the early 1900s and a thinning of woodlands occupied by the eastern form (*Parus bicolor,* s.s.). In considerable measure, Rising's interpretation derives from the colorful terminology (e.g., "eastward trek") and generalizations of the late E. B. Kincaid, Jr. (editor of the Oberholser volumes). It would appear that Kincaid misinterpreted a shift in character-index values in a local population that consisted of intermediate individuals 100 years ago (Dixon 1955:fig. 13) as constituting an extension of the range limits of one "species" with concurrent "retreat" of the other.

Evidence for the eastward "advance" of the black-crested *populations* and/or "replacement" of the gray-crested ones is tenuous. Kincaid (in Oberholser 1974, p. 610) stated, "From 1950 into the 1970's . . . the line of contact and interbreeding between the two tits has remained about the same, at least in central Texas, according to the observations of E. B. Kincaid, Jr., and others." Pulich's account (1979, p. 98) indicates no "retreat" of the eastern form in the vicinity of Fort Worth in the past 100 years. This topic will be developed in detail elsewhere (Dixon, unpubl.).

Icterus *complex.* At the eastern margin of the plains province, in the vicinity of Fort Worth, both races of orioles nest ". . . and some hybridize . . ." (Pulich 1988, p. 388). In that region the Baltimore Oriole nests principally in riparian cottonwoods, whereas the Bullock's Oriole associates with mature mesquites. The breeding range of the western form extends south through the Edwards Plateau and locally on the Coastal Plain (Rappole and Blacklock 1985).

POTENTIALLY INTERACTING CONGENERS

This discussion considers closely related congeners that are not known to interbreed, but which might interact ecologically. It is hoped that ornithologists will direct attention to these situations.

Otus *complex.* The screech-owls, *Otus kennicottii* and *O. asio,* were discussed as hybridizing taxa by Rising (1983a, p. 134). However, Marshall had cautioned earlier (1967, p. 29) that, along the Rio Grande, "we have not a zone of hybridization or intergrading, but a single file of individuals whose potential mates are few and far between, and who pair up as best they can." He reported (pers. comm.) that, in discontinuous habitat, the eastern species extended upstream to 104°W, and the western *O. kennicottii* east to 101° at Juno, Val Verde County on the Devil's River. Along the Rio Grande he located fledged young from one mixed pair, as well as scattered phenotypically "pure" pairs, and attributed the infrequently encountered mixed pairs to long-distance dispersal. That interpretation is strengthened by Marshall's discovery of a duetting pair of Western Screech-Owls in Kerr County, Texas, in May 1985 (Williams 1985a), a range extension of 190 km eastward. Recent field studies have shown that ". . . the zone of sympatry and locations of actual syntopy . . . of the two screech-owls on the central and western Edwards Plateau are considerable" (Terry C. Maxwell, letter, 14 January 1988).

Archilochus *complex.* In the Coastal Bend region of Texas the Black-chinned Hummingbird (*Archilochus alexandri*) nests in vegetation that is more xeric than that utilized by the Ruby-

throated Hummingbird (*A. colubris*) (Rappole and Blacklock 1985). The two species were similarly segregated in the Austin Region (Simmons 1925), an observation supported by Kutac (1982, p. 29). Referring to the Fort Worth area, Pulich (1988, p. 191) stated "I find today that both species nest in Tarrant County and that they tend to separate into distinct niches. The Ruby-throated Hummingbird prefers shaded woods along riparian areas, while the Black-chinned Hummingbird prefers the drier habitats—areas of post oak and blackjack oak." The ecological relationships of these species are difficult to resolve since the females are indistinguishable in the field (Sutton 1967, p. 286). Pulich (1988) reported an adult male hummingbird, found dead in Grayson County, Texas, 2 May 1975, and identified as a hybrid between these species.

Picoides *complex.* Differences in the foraging substrates of the *Picoides* woodpeckers in western Oklahoma were discerned by Sutton (1967, p. 298, 315). He noted that the Ladder-backed Woodpecker (*P. scalaris*) frequently utilized cholla cactus (*Opuntia* sp.) and mesquite both of which the sympatric Downy Woodpecker (*P. pubescens*) avoided. In the Austin region (Simmons 1925) the habitat distribution of the Ladder-backed Woodpecker is more generalized (xeric), whereas the Downy Woodpecker is more prevalent along streams and in orchards. In the Fort Worth area Downy Woodpeckers nest in riparian softwoods whereas the Ladder-backed Woodpecker is found in ". . . prairies with scattered hackberry trees" (Pulich 1979). The report of Downy Woodpeckers nesting in Potter and Hemphill counties in the Texas Panhandle (Williams 1977) extends the area of geographic overlap. Short (1971:fig. 27) considered the Ladder-backed Woodpecker to be the closest relative of the Downy Woodpecker, and (p. 62) predicted that hybrids would be found eventually where the two species are in contact.

Contopus *complex.* Rising and Schueler (1980) found ". . . no good evidence of hybridization" between the Western (*Contopus sordidulus*) and Eastern (*C. virens*) wood-pewees. They reported a male specimen of *C. virens* taken on 13 June 1969, in the Pecos River Valley in Texas (ca. 600 m elevation) ". . . within the range of *C. sordidulus*." Presumably this represented a breeding locality for *C. virens. Contopus sordidulus* was described as a "rare to common resident in the Trans-Pecos; reported from . . . the western edge of the Edwards Plateau . . ." and *C. virens* as a "Common summer resident . . . west through . . . the Edwards Plateau . . ." (Texas Ornithological Society 1984). Oberholser's map (1974, p. 563) indicates a breeding record of the Western Wood-Pewee for Kerr County, on the Edwards Plateau, although Lacey (1911) did not include the species in his list for Kerrville. Pulich (1988) considered the Western Wood-Pewee a "casual visitor" in north-central Texas, and rejected the report of its nesting in Bosque County (ca. 98°W) cited by Oberholser (1974). "Short- and long-term wet-dry cycles" (discussed by Rappole and Blacklock 1985, p. 59, 77) may influence the range limits of these species. Further study of their distributions supported by specimens is needed. Conceivably they may not be sympatric in central Texas.

Myiarchus *complex.* At the western margin of its range in Texas the Great Crested Flycatcher (*Myiarchus crinitus*) appears confined to stream courses or to denser timber (Simmons 1925, Rappole and Blacklock 1985), whereas the Ash-throated Flycatcher (*M. cinerascens*) ". . . the desert *Myiarchus* . . ." (Oberholser 1974, p. 544) occupies a variety of more open woody plant formations in central Texas. However, at low densities in riparian stands along the Cimarron River in extreme southern Kansas (Rising 1974, p. 374) and ". . . to a limited extent . . . in some areas of southwestern Oklahoma" (Tyler 1979) the two species are sympatric. The geographic overlap of the two species on the southern Edwards Plateau is more extensive (Texas Ornithological Society 1984). Hybrids apparently are unknown. Detailed study of the two species in sympatry is needed.

On the coastal plain in Texas the range of the more southerly Brown-crested Flycatcher (*M. tyrannulus*) overlaps those of the two species discussed above. The Brown-crested Flycatcher, ecologically equivalent to the Great Crested Flycatcher, occupies larger trees than does the Ash-throated Flycatcher where two (or three) *Myiarchus* species occur in the same vicinity (e.g., Beeville, Oberholser 1974).

DISCUSSION

The breeding ranges of several pairs of taxa that interbreed prominently along major streams of the central and northern plains become disjoined southward, presumably in response to the progressive climatic changes detailed by Rising

(1974). (The probable influence of moisture regimes on both the abundances of resident birds and location of hybrid zones was discussed by Bock et al. 1977.) A group of taxa associated with arid climates and xeric vegetation extends northward on the Great Plains into the area vacated by these disjunctions. These taxa constitute a "southwestern" element (Rising 1974) or "southern" element (Johnsgard 1978) of the Great Plains avifauna. Several of the arid-southwestern taxa meet eastern counterparts, and the ecological consequences may be sharpened by diminution of preferred conditions at the peripheries of their respective ranges. Included are Black-chinned and Ruby-throated hummingbirds, Golden-fronted and Red-bellied woodpeckers, Ladder-backed and Downy woodpeckers, Ash-throated and Great Crested flycatchers, and the Black-crested and Eastern Tufted titmice. In each case, the ranges of the eastern counterparts (mapped by Johnsgard 1979) extend well northward from the respective southwestern contacts. Bock et al. (1977) listed several avian species of eastern hardwood forest affinities whose patterns of abundance dropped sharply across the plains ". . . without being replaced by any obvious western counterparts." Thus, east–west (or east–southwest) replacement patterns reflect individual histories, and not all result from straightforward vicariance events. It may be worth noting that affinities of the Great Crested Flycatcher within *Myiarchus* are not certain (AOU 1983, p. 464).

EAST–WEST DISTRIBUTION CORRIDORS

Only two bands of essentially unbroken scarp-restricted nonriparian timber extend across the Great Plains according to Wells' (1970) map. One is the Pine Ridge, parallel to the Niobrara River at 42°N, where coniferous forest extending eastward meets floodplain deciduous timber (Kaul 1986). The other is the Balcones Escarpment, bordering the Edwards Plateau (Fig. 1), marking the southern perimeter of the Great Plains province. Prior to settlement the level uplands of the Edwards Plateau were grass covered, and the woodlands of junipers and oaks were restricted to deeply eroded slopes and canyon walls (Bray 1904). The replacement of prairies by woody plants, associated with intensive grazing by livestock in the latter 1800s and the cessation of range fires, was detailed by Buechner (1944) and Pulich (1976, p. 64). Although the Edwards Plateau proper was mapped by Küchler (1964) as "Juniper-oak Savanna," the vegetation is diverse. According to Ford and Van Auken (1982) the vegetation of the southern and eastern portions, the "cedar breaks," is a scrub forest of juniper, evergreen oak, and Mexican persimmon (*Diospyros texana*). Other upland woodlands include liveoak-shinoak (Buechner 1944) and a deciduous forest association on northeast-facing slopes (Van Auken et al. 1981).

Many of the western bird taxa range widely through this juniper-oak woodland complex (Fig. 2), and reach the eastern margin of the Edwards Plateau as at Austin. Among those extending to that well-known biogeographic boundary (Blair 1950, p. 96) are the Black-chinned Hummingbird, Golden-fronted and Ladder-backed woodpeckers, Ash-throated Flycatcher, "Black-crested" Titmouse, and "Bullock's" Oriole. The ranges of the hummingbird, woodpeckers, and titmouse abut those of their eastern counterparts which also are halted at or near the Balcones Escarpment, and which appear limited to denser timber or to floodplain situations. Only the titmice interbreed there.

Floodplain forests provide corridors for dispersal of several Neotropical migrants of eastern hardwood forest affinities westward into Kerr County. The streamside baldcypress (*Taxodium*), pecans, and sycamores of the Guadalupe River represent outliers of the Southern Floodplain Forest (Ford and Van Auken 1982), and were suggested as a dispersal route for such birds by Simmons (1925, p. 267). Included are the Acadian Flycatcher (*Empidonax virescens*), Yellow-throated (*Vireo flavifrons*) and Red-eyed (*V. olivaceus*) vireos, Northern Parula (*Parula americana*), Yellow-throated (*Dendroica dominica*), Black-and-white (*Mniotilta varia*), and Kentucky (*Oporornis formosus*) warblers. Lacey (1911) cited certain of these species as well as *Sayornis phoebe* as reaching their southwestern limits there. None meets a western counterpart regionally, and none extends as far west elsewhere in Texas. Several mammal and urodele species that exhibited a similar extension onto the Edwards Plateau were listed by Blair (1950). A possible correlate is found in Orton's maps (1969, p. 12, 42) which show the southern and eastern Edwards Plateau receiving more total annual precipitation and experiencing lower maximum temperatures for July than other Texas stations of the same longtitude. Thus, the juxtaposition of upland evergreen

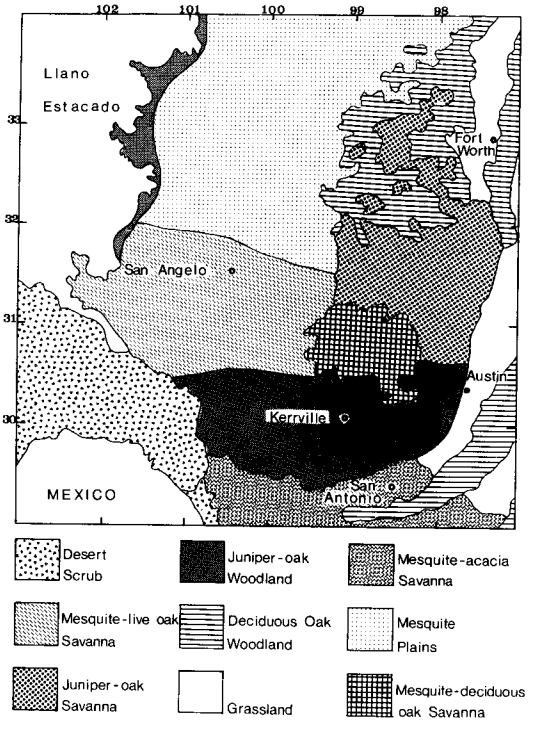

FIGURE 2. Generalized vegetation of central Texas with reference to the distribution of arboreal birds (modified from Küchler 1964 and Riskind and Diamond 1988).

woodland and riparian timber of eastward-flowing rivers of the southern Edwards Plateau facilitates the reciprocal penetration of eastern and western bird taxa to a greater extent than does the conifer timber and riparian growth of the Pine Ridge and Niobrara drainage (see Short 1961).

To the north of the Edwards Plateau where the original limestone surface is eroded and discontinuous, woodlands of several types are inhabited by birds of western distributional patterns. Hamilton (1962) recognized "... a mosaic of plant communities ..." in north-central Texas (west of 98°30'W), including variants of mesquite savanna on the rolling prairies, and juniper and/or oak woodland of the limestone-capped mesa tops in addition to riparian woodland. This mosaic permitted interdigitation of the distribution of eastern and western taxa such as Red-bellied and Golden-fronted woodpeckers. The variety of woody vegetation types in that sector recognized and mapped by Küchler (1964) and Riskind and Diamond (1988), and the vastly increased acreage of mesquite spreading from local stands (Fisher 1977) have favored the increase and spread of many of the western taxa, which as a group are more euryoecious (Hamilton 1962). The list of western taxa reaching their eastern limits on the Mesquite Plains includes most of the timber-dependent forms of the southern Edwards Plateau. However, the eastern species at their limits in Hamilton's study area include only *V. olivaceus* and *M. varia* among those listed from Kerr County. Lower diversity of floodplain timber may be responsible for such differences.

In the northern Great Plains the populations of arboreal birds that hybridize have extended eastward and westward along ribbons of riparian timber that are isolated from one another by intervening grasslands. The isolation is underscored by longitudinal differences in the midpoints of the "zones," as between Rufous-sided Towhees of the Platte and Niobrara drainages (Sibley and West 1959), and orioles of the Platte and Cimarron rivers (Rising 1983b). In the southernmost reaches of the Great Plains the interstream uplands often are bridged by woody vegetation types (scarp-restricted nonriparian timber) suitable for dispersal if not occupancy by many of the taxa discussed above. As noted by Selander and Giller (1963, p. 260) for *Melanerpes,* the eastern forms whose ranges transcend the Blackland Prairie of central Texas via stream-associated timber meet their western counterparts that occupy the woodlands on a broad front. Yet the faunistic boundary is fairly stable, in part a consequence of the transition from semi-arid to subhumid environments.

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