# HYBRIDIZATION IN THE ORIOLES OF THE GREAT PLAINS

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The Baltimore Oriole (*Icterus galbula galbula*) breeds in deciduous woodland in eastern North America from southern Canada to northern Georgia, northern Louisiana and southern Texas. The Bullock Oriole (*Icterus g. bullockii*) occupies a similar habitat in western North America. The ranges of the two forms meet in the Great Plains from Saskatchewan to central Texas. In the Great Plains, orioles are common in the riparian woodland along all of the rivers and creeks and in arboreal vegetation of other types. They occur as nesting birds in shade trees in towns, in woodlots and shelterbelt plantings, in small groups of trees and even in single, relatively isolated trees. Evidence of extensive hybridization between the two forms is found throughout the Great Plains. The purpose of the present paper is to present an analysis of this hybridization based primarily upon specimens collected by Cornell University field parties from 1954 to 1957, inclusive.

This paper is one of a series concerned with hybridization in birds. Others reporting upon hybridization in the Great Plains are Sibley and West (1959), Sibley and Short (1959*a*), West (1962), and Short (MS). These papers present additional discussions of the ecology and other aspects of the area. The evolutionary and taxonomic implications of hybridization, especially pertaining to birds, have been discussed by Sibley (1957, 1959, 1961). Other studies in the series include Sibley (1950, 1954, 1958), Sibley and West (1958), Sibley and Short (1959*b*), and Sibley and Sibley (in press).

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## MATERIALS

This study is based on 623 adult orioles collected in the Great Plains in the breeding seasons of 1954 through 1957, plus eight adults taken by George M. Sutton in Oklahoma in 1936, and three specimens from Texas in the Texas Natural History Collection. The total (634) is composed of 602 adult males from 39 localities and 32 females from 17 localities. Young birds and males not in fully adult plumage were excluded from the study. Localities represented are listed in table 1 (see also fig. 1). Field work at the localities listed generally occupied a three-day period. Several localities were visited both in 1956 and 1957, and one locality, Grand Island, was visited

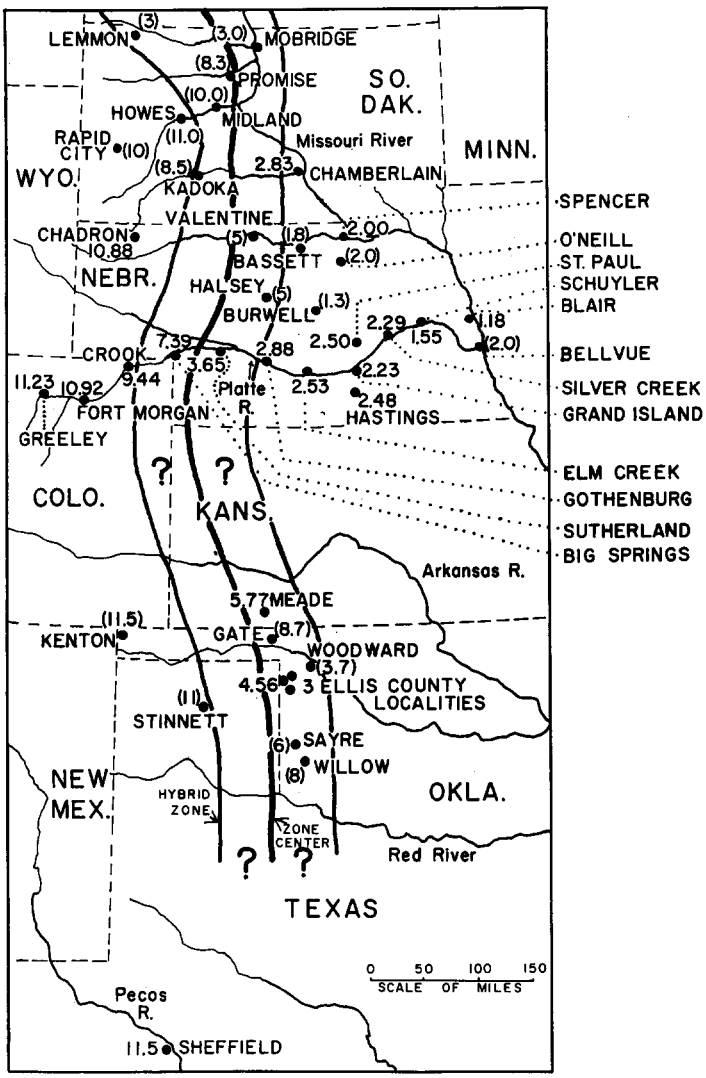


Fig. 1. Zone of hybridization in the orioles of the Great Plains. Numbers indicate the average hybrid index for male specimens; parentheses enclose values based on fewer than five specimens.

in the course of three breeding seasons (1955, 1956, 1957). Additional specimens of *Icterus g. bullockii* from California and Arizona, and of *I. g. galbula* from various eastern localities were available for comparison in the Cornell University collection.

## METHODS

### Mensural Characters

Weights were available for all specimens taken by Cornell field parties. Standard measurements, including wing length (chord), tail length, bill length (from nostril) and tarsal length, were obtained from all specimens.

TABLE 1

LIST OF LOCALITIES REPRESENTED BY SPECIMENS

| State | General locality | Locality description | Number of specimens ♂♂ | ♀♀ |
|---|---|---|---|---|
| Texas | Sheffield | 13 mi. W Sheffield, Terrill County | 2 | 0 |
| | Stinnett | 9 mi. E Stinnett, Hutchinson County | 1 | 0 |
| Oklahoma | Arnett | Arnett, Ellis County | 12* | 1 |
| | Gage | Gage, Ellis County | 5 | 2 |
| | Shattuck | Shattuck, Ellis County | 1 | 0 |
| | Gate | Gate, Beaver County | 3 | 2 |
| | Sayre | Sayre, Beckham County | 1 | 0 |
| | Woodward | Woodward, Woodward County | 3 | 1 |
| | Willow | Willow, Greer County | 1 | 0 |
| | Kenton | 4 mi. SE Kenton, Cimarron County | 2 | 0 |
| Kansas | Meade | Gyp Creek, 12 mi. E Meade, Meade County | 9 | 6 |
| Colorado | Crook | 5 mi. ESE Crook, South Platte River, 3700 ft., Logan County | 16 | 0 |
| | Fort Morgan | 8 mi. WNW Fort Morgan, South Platte River, 430 ft., Morgan County | 12 | 0 |
| | Greeley | 7 mi. SW Greeley, South Platte River, 4800 ft., Weld County | 26 | 0 |
| Nebraska | Blair | 4 mi. SE Blair, Missouri River, 1000 ft., Washington County | 45 | 0 |
| | Schuyler | 2½ mi. ESE Schuyler, Platte River, 1300 ft., Colfax County | 51 | 0 |
| | Silver Creek | 3 mi. SSW Silver Creek, Platte River, 1550 ft., in Polk County | 62 | 1 |
| | Grand Island | 7 mi. SSW Grand Island, Platte River, 1900 ft., Hall County | 56 | 5 |
| | Elm Creek | 3 mi. SE Elm Creek, Platte River, 2300 ft., in Phelps County | 56 | 0 |
| | Gothenburg | 2 mi. SE Gothenburg, Platte River, 2500 ft., Dawson County | 49 | 1 |
| | Sutherland | 1 mi. SE Sutherland, South Platte River, 2950 ft., Lincoln County | 54 | 0 |
| | Big Springs | 8 mi. SW Big Springs, South Platte River, 3500 ft., Deuel County | 18 | 0 |
| | Bellvue | Bellvue, Sarpy County | 4 | 0 |
| | O'Neill | 1 mi. W O'Neill, Holt County | 3 | 0 |
| | Halsey | 2 mi. W Halsey, Thomas County | 1 | 0 |
| | Burwell | 8 mi. W Burwell, Garfield County | 3 | 1 |
| | Bassett | 13 mi. N Bassett, Niobrara River in Keyapaha County | 4 | 0 |
| | Valentine | 16 mi. SSW Valentine, Cherry County | 1 | 1 |
| | Hastings | 7 mi. S Hastings, Little Blue River, Adams County | 23 | 4 |
| | St. Paul | 3 mi. S St. Paul, Howard County | 40 | 2 |
| | Spencer | 5 mi. SSE Spencer, Niobrara River, Holt County | 6 | 1 |
| | Chadron | 2 mi. NE Chadron, Dawes County | 8 | 1 |
| South Dakota | Midland | 45 mi. N Midland, Cheyenne River, Haakon County | 4 | 0 |
| | Howes | 9 mi. SSE Howes, Cheyenne River, Haakon County | 3 | 1 |
| | Rapid City | 6½ mi. N Rapid City, in Meade County | 1 | 1 |
| | Mobridge | 9 mi. NNE Mobridge, Missouri River, in Campbell County | 3 | 0 |
| | Lemmon | 15½ mi. SW Lemmon, Grand River, Perkins County | 1 | 0 |
| | Kadoka | 6 mi. S Kadoka, White River, Jackson County | 2 | 0 |
| | Chamberlain | 10 mi. SE Chamberlain, in Lyman County | 6 | 0 |
| | Promise | 15 mi. WSW Promise, Cheyenne River, Dewey County | 4 | 1 |

* Six of these collected by Sutton in 1936, six by a Cornell party in 1954.

TABLE 2

SYNOPTIC LIST OF CHARACTERS AND SCORES USED IN THE HYBRID INDEX*

| Character | Description | Score |
|---|---|---|
| | **HEAD PATTERN** | |
| Superciliary line | Absent (head all black) as in *galbula*. | 0 |
| | Orange flecks in black feathers. | 1 |
| | Broken, obscure orange superciliary. | 2 |
| | Orange line, but with black traces and/or encroachment of black above and below it. | 3 |
| | Broad, complete orange line to end of ear coverts, as in *bullockii*. | 4 |
| Forehead color | Black as in *galbula*. | 0 |
| | Black with some orange. | 1 |
| | Narrow orange patch as in *bullockii*. | 2 |
| Sides of neck | Black as in *galbula*. | 0 |
| | Black and orange. | 1 |
| | Orange as in *bullockii*. | 2 |
| Ear covert color | Black as in *galbula*. | 0 |
| | Orange traces. | 1 |
| | About half orange, half black. | 2 |
| | Black traces. | 3 |
| | Orange as in *bullockii*. | 4 |
| Throat color | Black. Orange at sides of throat never forward beyond rear of ear coverts. As in *galbula*. | 0 |
| | Orange traces forward to level of ear coverts. | 1 |
| | Orange forward to rear half of orbit. | 2 |
| | Orange forward to between center of orbit and a millimeter from the bill. | 3 |
| | Orange reaching the bill, or within a millimeter of it, separating black of throat from that of the mandibular area. As in *bullockii*. | 4 |
| | **WING PATTERN** | |
| Bar (greater primary coverts) | Narrow white bar as in *galbula*. | 0 |
| | Bar expanded, may be traces of second bar. | 1 |
| | Two white bars separated by broad black area. | 2 |
| | Bars merging, narrow black edges between bars. | 3 |
| | Single broad white bar. | 4 |
| Coverts (lesser primary coverts) | Orange-yellow as in *galbula*. | 0 |
| | Pale orange-yellow, white traces. | 1 |
| | Mixed white and orange-yellow. | 2 |
| | White with orange-yellow traces. | 3 |
| | White as in *bullockii*. | 4 |
| | **TAIL PATTERN** | |
| Tail base | Bases of outer rectrices with large, black rectangular or oval patches. As in *galbula*. | 0 |
| | Patches oval, restricted. | 1 |
| | Patches small, oval. | 2 |
| | Only traces of patches visible. | 3 |
| | Bases of outer rectrices yellow as in *bullockii* | 4 |
| Tail tip | Tips of outer rectrices yellow as in *galbula*. | 0 |
| | Dusky edges on tips of outer one or two rectrices. | 1 |
| | Narrow dusky edges on all three outer rectrices. | 2 |
| | Edges broader, usually with dark brown traces. | 3 |
| | Outer rectrices with broad, brown tips. These may be faded or naturally dusky, but are always broader than above. As in *bullockii*. | 4 |

* Character complex indicated at top of each group.

## Color Characters

*Icterus g. galbula* and *I. g. bullockii* differ markedly in color pattern, especially in the adult male plumage. Males which had acquired the adult tail pattern were considered adults for the purposes of this study. The adult male Baltimore Oriole differs from the Bullock Oriole in possessing a completely black head rather than a patterned orange and black head, in being more orange and less yellow generally over the body, in having narrow white wing bars rather than broad white wing bars, and in showing a tail pattern broadly black at the base and yellow at the outer tips, rather than one with yellow at both sides of a black base and dark outer tips. Most of these differences are utilized in a hybrid index system formulated to facilitate color analysis of hybrids. A hybrid index is simply a synoptic method of dealing quantitatively with color characters. The method has been used frequently in recent studies of avian hybridization (see Sibley and Short, 1959*a*; and Sibley and West, 1959) and requires no further description. In this instance the various characters were grouped into character complexes, that is, head pattern, wing pattern and tail pattern, and then into characters within each complex, such as throat color, neck color, ear covert color, superciliary line color and forehead color (all grouped in the head pattern complex). Scores were assigned to gradations of each character, a 0 being given a specimen with a character expressed as in *galbula*, scores of 1, 2, and so forth being assigned to specimens exhibiting intermediate gradations of the character, and the highest score for the character (either a 2 or 4) given to a specimen showing the condition of the character as expressed in *bullockii*. Scores for the various characters were totaled within each character complex (see tables 2, 3). This gives a combined score range for each character complex as follows: head pattern, 0 to 16; wing pattern, 0 to 8; and tail pattern, 0 to 8. Each character complex was then assigned an equal range of values from 0 to 4, giving five gradations per complex. The character complex score for a specimen is obtained by

Table 3

Component Scores of the Hybrid Index* in Male Orioles

| Character complex | Character | Total score | Score breakdown | | Index score |
|---|---|---|---|---|---|
| I. Head pattern | Superciliary | 0 – 4 | 0 – 1 | = | 0 |
| | Forehead | 0 – 2 | 2 – 5 | = | 1 |
| | Sides of neck | 0 – 2 | 6 –10 | = | 2 |
| | Ear coverts | 0 – 4 | 11 –14 | = | 3 |
| | Throat | 0 – 4 | 15 –16 | = | 4 |
| | Total | 0 –16 | | | |
| II. Wing pattern | Bar | 0 – 4 | 0 | = | 0 |
| | Coverts | 0 – 4 | 1 – 2 | = | 1 |
| | Total | 0 – 8 | 3 – 5 | = | 2 |
| | | | 6 – 7 | = | 3 |
| | | | 8 | = | 4 |
| III. Tail pattern | Base | 0 – 4 | 0 | = | 0 |
| | Tip | 0 – 4 | 1 – 2 | = | 1 |
| | Total | 0 – 8 | 3 – 5 | = | 2 |
| | | | 6 – 7 | = | 3 |
| | | | 8 | = | 4 |

* Hybrid index = sum of an individual's index scores for head pattern, wing pattern and tail pattern = 0–12.

assigning a value of from 0 to 4 equivalent to the combined character score of the specimen (see table 3). For example, a specimen with character scores of 0 for superciliary line, 1 for forehead color, 2 for neck color, 0 for ear covert color, 1 for throat color, 2 for wing bar, 1 for wing covert, 1 for tail base and 2 for tail tip would be assigned character complex scores of 1 for head pattern ($0 + 1 + 2 + 0 + 1 = 4$, equivalent value = 1), 2 for wing pattern ($2 + 1 = 3$, equivalent value = 2) and 2 for tail pattern ($1 + 2 = 3$, equivalent value = 2). The hybrid index is the sum of the character complex values, which for this specimen would be $1 + 2 + 2 = 5$. Hybrid index values thus range from 0 for a phenotypically pure *galbula* individual to 12 for an individual phenotypically like *bullockii*. The justification for the use of this rather complicated system lies in the fact that it permits the utilization of a maximum number of characters, while reducing bias in favor of groups of characters which may be closely related genetically.

Adult females of the two forms differ in several characters. Only back color and color of the underparts were utilized in formulating the female hybrid index. The various gradations and scores for the two characters are indicated in table 4. Hybrid index

TABLE 4

SYNOPTIC LIST OF CHARACTERS COMPOSING FEMALE HYBRID INDEX

| Character | Description | Score |
|---|---|---|
| Back color | Golden-olive, noticeable spotting, as in *galbula*. | 0 |
| | Golden-olive, gray traces in neck and rump regions. | 1 |
| | Yellow-olive in middle, gray toward neck and rump. | 2 |
| | Olive gray with yellow traces in center of back. | 3 |
| | Olive gray to gray, spots absent or a few traces only, as in *bullockii*. | 4 |
| Color of underparts | Yellow-olive to yellow-orange from vent to bill, as in *galbula*. | 0 |
| | Traces of white on lower abdomen, rest of underparts yellow-olive to yellow-orange. | 1 |
| | Abdomen white, lower breast to bill yellowish. | 2 |
| | Yellowish extending from throat back into lower breast region, abdomen and part of lower breast white. | 3 |
| | Throat and upper breast yellowish, lower breast and abdomen white, as in *bullockii*. | 4 |

values for females range from 0 for specimens phenotypically like *galbula* in both characters to 8 for those like *bullockii*.

The considerable variation in *bullockii* in the West has been stressed by van Rossem (1945:238–239). One factor probably at least partly responsible for this variation is gene exchange between *bullockii* and two well-differentiated oriole populations (*galbula* in the East, *abeillei* in México) which have secondary contacts with *bullockii*. The present study deals primarily with orioles from the Great Plains which were used in setting up the hybrid index system just discussed, but examination of specimens of *galbula* from eastern North America and *bullockii* from western North America indicates that variation in color pattern is extensive in both. For example, many eastern *galbula* show traces of *bullockii* color characters. A large-scale investigation of variation in populations of *galbula, bullockii,* and *abeillei* may well demonstrate that introgression among them is as extensive as among the three well-differentiated North American flicker (*Colaptes*) populations (Short, MS).

## HISTORY OF THE SITUATION

Possible hybridization between *Icterus g. galbula* and *I. g. bullockii* was noted by Sutton in 1938. This paper, containing a fine color plate depicting several hybrids, was responsible for the hybrid oriole situation becoming widely known among ornithologists. Earlier papers mentioning hybrids or possible hybrids are cited by Sutton. Baird, Brewer and Ridgway (1875) described variants of *Icterus galbula,* of which those from Kansas and Nebraska were probably hybrids. These authors also described variants from farther east, some of which may have been introgressants resembling *bullockii* in one or more respects. Bent (1908:29) gave a description of a hybrid from southwestern Saskatchewan, the northernmost area in which they are known to occur. Cooke (1888) and Cary (1901) had indicated still earlier that both forms bred together in certain areas of the Plains (Gainesville, Texas, and Edgemont, South Dakota, respectively). The occurrence of considerable hybridization between the two forms has been corroborated by several workers since Sutton, especially Graber and Graber (1951:168) and Tordoff (1956:347).

It seems likely that *galbula* and *bullockii* were interbreeding to some extent in the Great Plains before white men entered the area. Audubon's party collecting along the upper Missouri River in 1843 found timber all along that river. The party encountered hybrid flickers in the woods along the Missouri. There is no reason to doubt that orioles occupied these same wooded areas, as they do now, and that the two forms were in contact and hybridizing at that time. It is apparent also that, following white man's entry into the Plains, tree-planting activity has increased oriole habitat in the area, thus providing more opportunities for the two forms to come into contact. Actually, only a minimum amount of arboreal vegetation is necessary to provide a nesting site, as orioles have been observed nesting in a scraggly 30-foot cottonwood situated a half mile or more from other trees (in southwestern Kansas). The birds are able to make use of such isolated trees and small, poorly developed shelterbelts apparently because they are able to feed in open areas and in shrubs along ravines and streambeds lacking taller trees. Where trees are few orioles may be observed feeding in fields, moving about in low grass, or hawking insects from fence rows, often far from any tree. The oriole population of the Plains has also increased following the planting of shade trees about ranches and along village streets.

The present interbreeding between the two orioles is the result of a secondary contact between previously isolated, well-differentiated populations. In view of the considerable divergence in plumage patterns it is suspected that initial separation of the original populations occurred during, or, more probably, before the last glacial maximum. A detailed discussion of historical aspects of hybrid situations in the Plains may be found in Short's (MS) report on hybridization in flickers.

## THE PLATTE VALLEY TRANSECT

### General

In the breeding seasons of 1956 and 1957 a special effort was made to obtain specimens from avian populations known or suspected to be interbreeding in the Plains by collecting at intervals along an east-west transect. The Platte-South Platte River valley from the Missouri River to central Colorado was selected for this transect because the river appeared large enough to provide sufficient woodland habitat across the Plains to permit contacts between eastern and western woodland birds. Eleven camps were established at intervals of approximately 50 miles along this valley. These camps were in the vicinity of Blair, Schuyler, Silver Creek, Grand Island, Elm Creek, Gothenburg, Suth-

erland and Big Springs, Nebraska, and Crook, Fort Morgan and Greeley, Colorado (actual localities are listed in table 1; see also fig. 1). Big Springs, Nebraska, and the three Colorado localities were visited for three days each in 1956. Grand Island, Nebraska, was visited during the breeding seasons of 1955, 1956 and 1957, for three days each season. The other six localities were sites of three-day camps in 1956 and 1957. A total of 445 adult male orioles was secured from these eleven localities, an average of 40.4 specimens per locality.

Along the Platte River orioles ranked with House Wrens (*Troglodytes aedon*) and Mourning Doves (*Zenaidura macroura*) as the commonest avian species (for an account of the distribution of these and other species along the Platte, and elsewhere in the Central Plains, see Short, 1961). Plains river valleys with trees spaced moderately far apart seem to provide the optimum habitat for orioles in North America. These birds were seen feeding in the trees, in brush along the river, and in grasses and low shrubs of the valley floor and surrounding plains. Songs of both forms and of hybrids were variable, with no constant differences among the males of various phenotypes. Generalized oriole songs imitated by members of the field parties served to bring territorial males within hearing range, thus facilitating collecting. Males were highly aggressive, defending territories with vigor whenever other males intruded. Observations of encounters between males of different phenotypes indicated that there are no apparent differences in territorial behavior between *galbula* and *bullockii*.

## Hybrid Index Analysis

The hybrid indexes of all males which could be scored for all color characters are indicated in a histogram (fig. 2). Results of the statistical analysis of the hybrid indexes for the Platte samples are contained in table 5. Samples from the eastern localities

Table 5

Statistical Analysis of Hybrid Indexes of Platte Transect Male Orioles

| Locality | N | Mean | Two standard errors | One standard deviation | Per cent of shift to *bullockii* | Range |
|---|---|---|---|---|---|---|
| Blair | 45 | 1.18 | 0.32 | 1.05 | | 0 – 4 |
| | | | | | 3 | |
| Schuyler | 51 | 1.55 | 0.30 | 1.08 | | 0 – 4 |
| | | | | | 6 | |
| Silver Creek | 52 | 2.29 | 0.34 | 1.24 | | 0 – 5 |
| | | | | | —1 | |
| Grand Island | 56 | 2.23 | 0.28 | 1.08 | | 0 – 5 |
| | | | | | 3 | |
| Elm Creek | 55 | 2.53 | 0.30 | 1.14 | | 1 – 5 |
| | | | | | 3 | |
| Gothenburg | 49 | 2.88 | 0.40 | 1.42 | | 1 – 7 |
| | | | | | 6 | |
| Sutherland | 54 | 3.65 | 0.48 | 1.79 | | 1 –11 |
| | | | | | 31 | |
| Big Springs | 18 | 7.39 | 1.36 | 2.87 | | 4 –12 |
| | | | | | 17 | |
| Crook | 16 | 9.44 | 1.44 | 2.90 | | 2 –12 |
| | | | | | 12 | |
| Fort Morgan | 12 | 10.92 | 0.96 | 1.68 | | 9 –12 |
| | | | | | 3 | |
| Greeley | 26 | 11.23 | 0.34 | 0.86 | | 9 –12 |

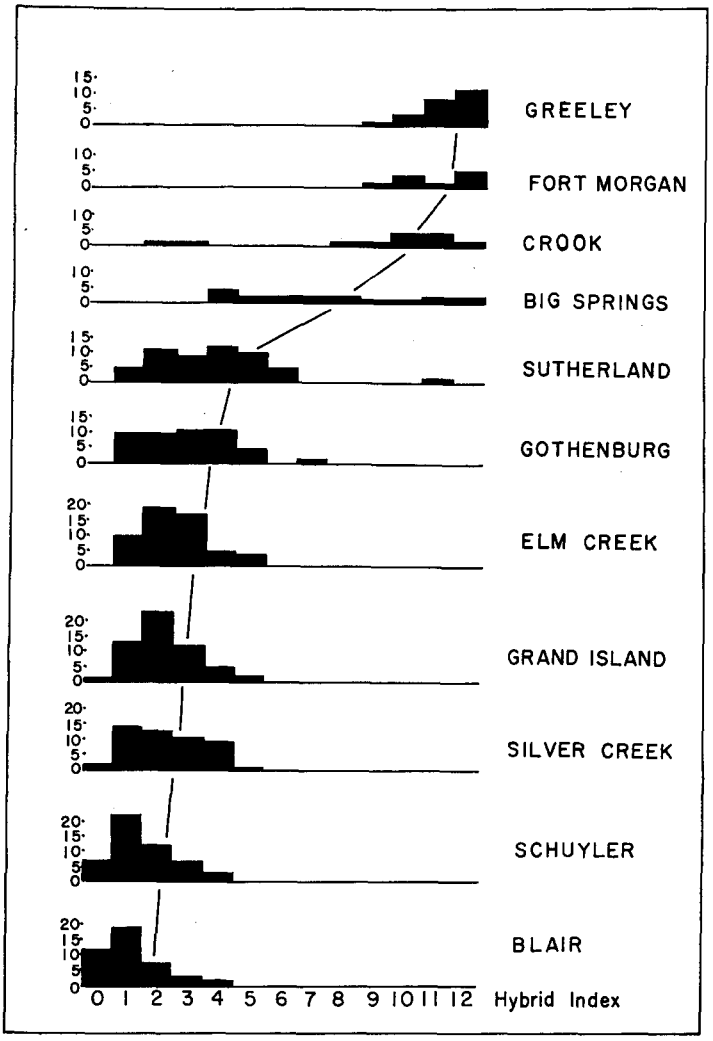


Fig. 2. Histograms of the hybrid indexes of male orioles from the Platte Valley transect. Number of specimens is indicated at the left.

(Blair, Schuyler) show a low incidence of *bullockii* color character traces, although the majority (69 per cent at Blair, 57 per cent at Schuyler) are phenotypically pure or nearly pure *galbula* (indexed 0, 1). An index value of 2 or more is considered indicative of the effect of *bullockii* influence in an individual. (Likewise an index of 10 or less is indicative of definite *galbula* influence in an otherwise *bullockii*-like individual). West of Schuyler the mean hybrid index gradually rises as more individuals exhibit *bullockii* traces and fewer are phenotypically like *galbula*. In the Platte Valley east of Elm Creek (roughly the eastern half of Nebraska) most of the specimens (127 of 204 or 62 per cent) showed evidence of the influence of *bullockii* genes. Actually, only 22, or 11 per cent had indexes of 0 while 55 were scored 1. The latter, as well as the other 127, probably indicate the influence of gene flow from the western *bullockii* pop-

ulation. Even at Blair, on the Nebraska-Iowa border, phenotypically pure *galbula* individuals comprised less than a third (27 per cent) of the sample. West of Elm Creek more nearly intermediate individuals become more numerous than 0 and 1 indexed individuals in the samples. The first specimen having an index value of 6 or more (6 being exactly intermediate) was obtained at Gothenburg, 50 miles west of Elm Creek and 250 miles west of Blair. No phenotypically pure specimens of either parental form were taken from three localities along the Platte-South Platte River in the 200 miles of continuous oriole habitat between Grand Island and Big Springs, Nebraska. The number of specimens, all hybrids, taken from the three localities (Elm Creek, Gothenburg and Sutherland) was 159. Thus, the eastern *galbula* and western *bullockii* populations are in genetic contact through a hybrid population in a zone through the Plains of 150 to 200 miles in width. Since phenotypically pure individuals of the two forms are absent from this zone, or are at least very uncommon, primary hybridization resulting in $F_1$ individuals being produced is undoubtedly a very rare event, if indeed it occurs at all.

The major shift in hybrid index from near *galbula* to near *bullockii* takes place between Gothenburg and Fort Morgan over a distance of 200 miles. The greatest change occurs between Sutherland and Big Springs (see table 5); within a 50-mile area a 31 per cent shift in hybrid index is found in the samples. The "hybrid zone" may now be defined for the purpose of this study. The simplest definition would be the area inhabited by hybrids, in which phenotypically pure individuals of the parental forms are absent, or rare. Such a zone for the orioles would be in the Platte-South Platte Valley extending from just west of Grand Island to just east of Big Springs. The center of the hybrid zone with a population having a mean hybrid index of 6.00 lies between Sutherland and Big Springs; its position may be predicted as being about 15 miles east of Big Springs (calculated using the index shift from the Sutherland sample to the Big Springs sample and the distance between the two localities). Using the above definition of the hybrid zone, the center of the zone would actually be located at or near the western boundary of the zone. In addition, the largely hybrid Crook sample would be far beyond the limits of the hybrid zone. Another method of defining the zone will be used in this report, namely: the hybrid zone is that area inhabited by populations having mean hybrid indexes of from 3.00 to 9.00. This zone, including localities between Gothenburg and Crook, is represented by 72 specimens, 21 of which (29 per cent) are intermediate or nearly so (indexed 5, 6, and 7). No intermediate hybrids were taken west of the zone at localities represented by 54 specimens, while east of the zone only 13 of 319 specimens (4 per cent) indexed at 5, 6, or 7.

The sample from Sutherland, in the hybrid zone about 30 miles east of its center, contains five specimens indexed at 1. All but one of the remaining 49 specimens indexed from 2 to 6, tending toward *galbula*. The other individual was taken in a cottonwood tree near a lone house in open country away from the riparian timber in which the others were taken. This oriole was near *bullockii* in its color characters, indexing at 11. It is not known whether this bird was a wanderer from the west, or merely represents the *bullockii* extreme of variation in the Sutherland population. Phenotypically pure *bullockii* were obtained at the Big Springs camp, 50 miles west of Sutherland and 20 miles west of the center of the hybrid zone. Indeed, the majority of specimens from Big Springs tended toward *bullockii*. It is noteworthy that phenotypically pure individuals of one form occur close to the center of the hybrid zone, while the nearest "pure" *galbula* was secured some 150 miles away.

West of Big Springs at Crook, Colorado, most individuals indexed close to *bullockii*.

Two specimens, however, indexed close to *galbula* (2 and 3). This situation is almost the reverse of that at Sutherland just discussed. West of Crook the hybrid index gradient tapers off as most individuals closely approach *bullockii*. Only three specimens at Fort Morgan and three at Greeley are intermediate (scoring 2) in any one of the nine characters.

Thus, in a transect of one of the major Great Plains river valleys a phenotypic shift from *galbula* to *bullockii* takes place, mostly within a 200-mile area. Only 22 of the 214 adult male orioles from the eastern 150 miles of the Platte Valley could be considered phenotypically pure *galbula* (and four of these showed slight indications of *bullockii* influence in one character). Phenotypically pure *bullockii* individuals from four localities in the western 150 miles of the Platte-South Platte Valley numbered only 21 individuals out of 72 (again, ten of the 21 showed indications of *galbula* influence in one or two characters). A total of 402 (or 416, counting the above mentioned deviants from the parental types) of 445 adult male orioles collected along the Platte River are hybrids ranging in appearance from nearly pure *galbula* through every stage of intermediacy to nearly pure *bullockii*. The hybrid zone in the Platte Valley is approximately 150 miles wide extending from just west of Gothenburg to just east of Crook, with the center of the zone located about 20 miles east of the Nebraska-Colorado border (see fig. 1). The shift in hybrid index is generally rapid west of the center of the zone, going from 6.00 to 11.23 in about 170 miles. The shift in index toward *galbula* east of the center of the zone is more gradual, changing from 6.00 to 1.18 in about 330 miles. The *galbula* population east of the zone appears to show more evidence of introgression from *bullockii* than vice versa.

## Analysis of Individual Color Characters

The mean scores for the nine color characters of male orioles from eleven localities in the Platte Valley are indicated in table 6. Gradients for the individual characters differ from each other in various ways, although the major shifts of all occur in about the same area.

The several characters of the head pattern complex show considerable variation in their gradients. Forehead color and ear covert color are most similar. Both exhibit low mean scores for the eastern samples. The gradients for both increase between Grand

Table 6

Mean Color Character Scores for Samples of Male Orioles from the Platte Valley

| | Character | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locality | Super-ciliary | Fore-head* | Neck color* | Ear coverts | Throat color | Wing bar | Wing coverts | Tail base | Tail tip |
| Blair | 0.13 | 0.00 | 0.18 | 0.04 | 0.29 | 0.56 | 0.31 | 0.29 | 0.13 |
| Schuyler | 0.10 | 0.00 | 0.12 | 0.00 | 0.29 | 0.86 | 0.61 | 0.33 | 0.31 |
| Silver Creek | 0.15 | 0.04 | 0.44 | 0.05 | 0.38 | 1.20 | 1.00 | 0.58 | 0.38 |
| Grand Island | 0.07 | 0.04 | 0.36 | 0.02 | 0.52 | 1.00 | 1.06 | 0.77 | 0.45 |
| Elm Creek | 0.25 | 0.10 | 0.78 | 0.07 | 0.68 | 1.02 | 1.34 | 0.61 | 0.56 |
| Gothenburg | 0.24 | 0.24 | 0.82 | 0.12 | 0.94 | 1.14 | 1.43 | 0.61 | 0.69 |
| Sutherland | 0.61 | 0.40 | 1.04 | 0.19 | 1.18 | 1.28 | 1.81 | 0.93 | 1.15 |
| Big Springs | 2.11 | 1.66 | 2.34 | 1.72 | 2.61 | 2.89 | 2.84 | 2.39 | 2.45 |
| Crook | 3.19 | 2.76 | 3.12 | 3.38 | 3.56 | 3.44 | 3.56 | 3.06 | 3.31 |
| Fort Morgan | 3.75 | 3.66 | 3.66 | 3.92 | 3.75 | 3.92 | 3.92 | 3.42 | 3.67 |
| Greeley | 3.96 | 3.46 | 3.92 | 3.96 | 3.84 | 3.76 | 3.88 | 3.65 | 3.84 |

* Since scores for color of forehead and neck ranged only from 0 to 2 whereas other characters ranged in score from 0 to 4, mean scores for the two characters were doubled for use in this table to facilitate comparison with other characters.

Island and Elm Creek, with abrupt upward shifts commencing at Sutherland and continuing west to Fort Morgan. The major shift from a mean score of 1.0 to 3.0 was accomplished in 90 miles (east of Big Springs to west of Crook) for forehead color, and in 60 miles (just east of Big Springs to just east of Crook) in the case of ear covert color. The sample from Greeley exhibits about the same degree of *galbula* influence in both characters as the sample from Sutherland shows of *bullockii* influence for forehead color and the sample from Elm Creek for ear covert color. A low level of *bullockii* superciliary traces occurs in the samples from eastern Platte. This character shows a gradient somewhat similar to the above two. There is a noticeable rise west of Gothenburg, continuing steadily to Fort Morgan. The major shift occurs between Big Springs and Crook, over a distance of 60 miles. The incidence of *galbula* influence at Greeley is about equal to that of *bullockii* at Grand Island. Evidence of *bullockii* neck color is apparent in the populations at Blair and Schuyler. There is a gradual rise westward from Grand Island to Sutherland, beyond which the major shift takes place (from a mean score of 1.0 to 3.0) in about 95 miles (vicinity of Crook). The incidence of *bullockii* characters in the eastern samples is greater than that of *galbula* at Greeley, suggesting greater introgression eastward from *bullockii* than vice versa. Traces of *bullockii* throat color also occur in the eastern samples. There is a steady increase in the slope of the gradient from Blair west to a mean score above 1.0 at Gothenburg. From Sutherland to Crook there is an abrupt rise. The major shift occurs over a distance of 108 miles from Gothenburg to west of Big Springs. The incidence of *bullockii* throat color traces at Blair is about equal to the incidence of *galbula* traces at Greeley. Thus, in three head pattern characters the change from *galbula* to *bullockii* is abrupt and virtually complete in the Platte populations, taking place within 150 to 200 miles. The change in the other two characters is gradual and incomplete, that is, the incidence of *bullockii* and *galbula* traces is sufficiently high in the eastern and western Platte Valley samples, respectively, to prevent the mean scores from reaching 0 or 4.

The gradient for the two characters in the wing pattern complex is similar. Evidence of *bullockii* colors is frequent in males from Blair, 56 per cent of the individuals exhibiting this influence in wing bar color and 31 per cent in wing covert color. This suggests considerable introgression of *bullockii* genes into the *galbula* populations east of Nebraska. The mean scores for both characters rise to 1.0 or more at Silver Creek. West of that locality the wing bar gradient rises gradually across the central part of the transect all the way to Fort Morgan, while the wing covert gradient is generally gradual, but with a somewhat abrupt rise between Sutherland and Fort Morgan. The major shifts occur in 288 miles (Schuyler to west of Big Springs) for wing bar color and in 263 miles (Silver Creek to west of Big Springs) for wing covert color. The incidence of *galbula* characteristics at Greeley is in both cases much less than the incidence of *bullockii* traces at Blair. As in the case of neck color, it appears that introgression responsible for the wing pattern characters is proceeding from west to east to a greater extent than from east to west.

The two tail complex characters are as similar to each other as are the wing complex characters. The incidence of *bullockii* tail base color traces at eastern localities is high (see table 6), while that of tail tip color is lower. Both rise gradually westward. The most rapid change from mean scores of 1.0 to 3.0 takes place over 96 miles (Sutherland to Crook) for both tail base color and tail tip color. For both characters the samples from Blair and Greeley show about equal incidences of color characteristics of the opposite forms, *bullockii* at Blair and *galbula* at Greeley.

While the gradients of the characters vary somewhat, all undergo shifts from low mean scores (*galbula*) to high mean scores (*bullockii*) within a 200-mile area, which in

every instance includes the area between Sutherland and Big Springs. The east-west gradient is steep in some characters and gradual in others. The best single character for determining whether or not a sample is from within the hybrid zone is ear covert color, while superciliary color is also useful. Virtually no specimens from localities outside the hybrid zone show indications of hybridization in this character.

## Mensural Characters

The results of the analysis of mensural characters of the male orioles from the Platte transect are summarized in figure 3 and tables 7 and 8.

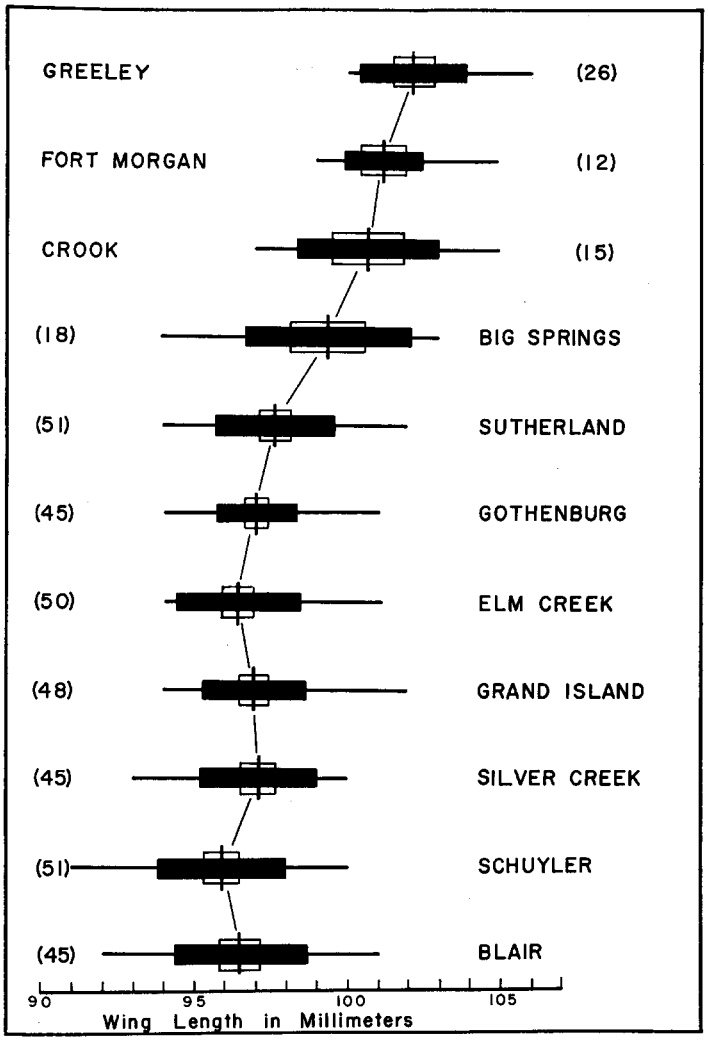


Fig. 3. Statistical analysis of variation in wing length in male orioles from the Platte Valley transect. Numbers of specimens are in parentheses. Means are indicated by vertical lines; ranges by horizontal lines; open rectangles indicate twice the standard error of the mean; solid black rectangles indicate one standard deviation from the mean.

TABLE 7

ANALYSIS OF TAIL LENGTH OF MALE ORIOLES FROM THE PLATTE VALLEY

| Locality | N | Mean (mm.) | Two standard errors | One standard deviation | Coefficient of variability (per cent) | Range (mm.) |
|---|---|---|---|---|---|---|
| Blair | 44 | 77.53 | 0.72 | 2.36 | 3.1 | 70.3–79.7 |
| Schuyler | 48 | 75.08 | 0.70 | 2.43 | 3.2 | 71.0–81.8 |
| Silver Creek | 39 | 76.52 | 0.58 | 1.83 | 2.4 | 72.6–80.0 |
| Grand Island | 44 | 76.54 | 0.56 | 1.85 | 2.4 | 72.5–81.0 |
| Elm Creek | 45 | 76.66 | 0.64 | 2.18 | 2.8 | 72.5–80.4 |
| Gothenburg | 37 | 77.08 | 0.70 | 2.13 | 2.8 | 73.6–81.8 |
| Sutherland | 46 | 77.68 | 0.50 | 1.67 | 2.2 | 72.1–82.3 |
| Big Springs | 18 | 78.63 | 1.22 | 2.59 | 3.3 | 73.7–83.7 |
| Crook | 15 | 80.62 | 1.24 | 2.41 | 3.0 | 76.2–84.7 |
| Fort Morgan | 11 | 81.15 | 0.76 | 1.27 | 1.6 | 79.0–83.2 |
| Greeley | 24 | 81.54 | 0.72 | 1.78 | 2.2 | 79.0–86.4 |

Differences between the Greeley and Blair populations were observed in all four measurements (wing length, tail length, bill length, and tarsal length) and in weight. Only the weight difference and differences in two measurements were great enough to warrant analysis.

The wing length of *galbula* at Blair averaged 96.49 mm. while that of *bullockii* at Greeley averaged 102.08 mm. Wing length in the eastern six samples (west of Gothenburg) is fairly constant, generally averaging 96 to 97 mm. (see fig. 3). Within the 250 miles from Gothenburg to Greeley there is a steep, though fairly even, cline, reaching a mean of over 102 mm. The major shift takes place between Sutherland and Big Springs, the average wing length changing from 97.63 to 99.39 mm. in 50 miles. The greatest wing length shift thus occurs between the same two localities where the major shifts in most color characters take place.

The Blair sample exhibited a mean tail length of 75.53 mm., while that of the Greeley sample was 81.54 mm. The tail length gradient is somewhat similar to that for wing length, but it is slightly more complicated. There is a small decrease in mean tail length between Blair and Schuyler (see table 7), followed by a rise to 76.52 mm. at Silver Creek. West of that locality tail length is nearly constant to Elm Creek (between 76.52 and 76.66 mm.), beyond which there is a gradual increase in mean values to Big

TABLE 8

ANALYSIS OF WEIGHTS OF MALE ORIOLES FROM PLATTE VALLEY

| Locality | N | Mean (gm.) | Two standard errors | One standard deviation | Coefficient of variability (per cent) | Range (gm.) |
|---|---|---|---|---|---|---|
| Blair | 45 | 35.61 | 0.52 | 1.76 | 5.0 | 31.9–40.0 |
| Schuyler | 51 | 37.13 | 0.48 | 1.68 | 4.5 | 32.6–40.4 |
| Silver Creek | 62 | 37.25 | 0.60 | 2.35 | 6.3 | 33.1–45.0 |
| Grand Island | 44 | 76.54 | 0.60 | 2.23 | 5.9 | 34.1–43.8 |
| Elm Creek | 56 | 35.52 | 0.54 | 2.03 | 5.7 | 31.4–40.6 |
| Gothenburg | 49 | 36.75 | 0.38 | 1.31 | 3.6 | 33.2–41.0 |
| Sutherland | 54 | 37.02 | 0.52 | 1.93 | 5.2 | 33.4–41.7 |
| Big Springs | 18 | 38.39 | 0.96 | 2.03 | 5.3 | 34.0–41.9 |
| Crook | 16 | 37.73 | 1.22 | 2.45 | 6.5 | 33.8–41.8 |
| Fort Morgan | 12 | 38.23 | 2.70 | 4.69 | 12.2 | 35.9–41.1 |
| Greeley | 26 | 36.16 | 0.70 | 1.79 | 5.0 | 32.9–39.8 |

Springs, 150 miles to the west. The greatest increase in tail length occurs between Big Springs and Crook, the mean shifting from 78.63 to 80.62 mm. in 50 miles. The tail length shift occurs west of the major wing length shift. From Crook to Greeley a slight increase in tail length is evident. Although the region of the greatest shift in tail length lies west of the area in which major changes in wing length and color characters take place, the pattern of the gradient is similar and the overall difference between the extreme means is small.

Table 8 contains an analysis of weights of adult males from the Platte localities. The difference in weight between the extreme samples is small (0.55 gm.). The western samples usually have higher mean weights than eastern ones, but the pattern is unclear due to the small difference between the extreme populations. The four lowest averages are from the ends of the transect at Blair and Greeley and from Elm Creek and Gothenburg near the center. Three of the five greatest weight averages are of samples from Big Spring, Crook and Fort Morgan, west of the center of hybridization, but the remaining two are of samples from Silver Creek and Grand Island to the east of it. This character is thus of no value in the analysis of the effects of hybridization.

The mean bill length of the Blair sample is 12.79 mm. and the mean tarsal length 23.32 mm. The means of the Greeley sample for the same characters are 13.32 and 23.54 mm., respectively. Since the differences are small (0.53 mm. difference in bill length; 0.22 mm. difference in tarsal length) and the overlap among the various samples great, these two characters do not merit further attention in regard to hybridization.

Study of the wing and tail lengths in the Platte transect orioles indicates that hybridization between the two forms is affecting these characters as well as the color characters. The clines in these mensural characters correspond closely with the color character gradients. Other measurements (bill length, tarsal length, and weight) are so similar in all of the populations that they shed no light on the hybrid situation.

## THE HYBRID SITUATION IN OTHER LOCALITIES

### NEBRASKA

Ninety-three adult male orioles were collected from ten Nebraska localities other than those discussed in the above section. (The total number of adult males from Nebraska localities was 466.) Results of the study of these additional specimens are summarized in table 9 (see also fig. 1).

TABLE 9

ANALYSIS OF COLOR AND TWO MENSURAL CHARACTERS OF MALE ORIOLES FROM NEBRASKA*

| Locality | N | Mean hybrid index | Hybrid index range | N | Mean wing length (mm.) | N | Mean tail length (mm.) |
|---|---|---|---|---|---|---|---|
| Bellvue | 4 | (2.0)** | 0 – 4 | 4 | (97.0) | 3 | (76.8) |
| O'Neill | 3 | (2.0) | 1 – 3 | 2 | (96.5) | 2 | (77.6) |
| Halsey | 1 | (5) | ..... | 1 | (95) | 0 | ..... |
| Burwell | 3 | (1.3) | 1 – 2 | 3 | (97.0) | 3 | (76.4) |
| Bassett | 4 | (1.8) | 1 – 3 | 4 | (96.0) | 2 | (74.3) |
| Valentine | 1 | (5) | ..... | 1 | (97) | 1 | (77.2) |
| Hastings | 23 | 2.48 | 0 – 5 | 23 | 96.61 | 22 | 76.90 |
| St. Paul | 40 | 2.50 | 0 – 6 | 37 | 97.03 | 30 | 76.72 |
| Spencer | 5 | 2.00 | 0 – 4 | 5 | 96.40 | 4 | (77.1) |
| Chadron | 8 | 10.88 | 10 –12 | 8 | 101.38 | 6 | 82.25 |

* Except those from the Platte transect.
** To facilitate comparison parentheses enclose values from samples of fewer than five individuals.

Four adult male orioles were obtained near Bellvue, Nebraska, not far from Blair. The mean index of the four specimens was 2.0 (see table 9), slightly greater than the value of 1.18 for the Blair sample. The range was 0 to 4 in both samples.

Eastern Nebraska samples from Hastings, St. Paul and Spencer exhibit mean hybrid indexes close to that of the Grand Island sample, which is as expected, since these localities are about on the same longitude. The most eastern specimen having an intermediate (6) score was secured at St. Paul. Specimens indexed 5 were taken east as far as Hastings, Halsey, Valentine, St. Paul, and Silver Creek. The samples from Burwell, Bassett, and O'Neill showed low mean indexes, as expected on the basis of comparison with means of larger samples from localities about as far east as these. Single specimens from Halsey and Valentine indexed at 5.

A series collected at Chadron in northwestern Nebraska (see fig. 1) shows that this region is inhabited by an oriole population phenotypically very close to *bullockii*. The hybrid index range was from 10 to 12. The mean hybrid index is 10.88, about the same as that of the Fort Morgan, Colorado, sample (index = 10.92). Chadron is thus west of the hybrid zone. The western edge of the zone must enter Nebraska from South Dakota somewhat east of Chadron, then extend southward across the Sand Hills toward Colorado. The Niobrara River valley is well wooded and probably affords a good contact with more *galbula*-like populations farther east toward Valentine.

Wing lengths and tail lengths of eastern Nebraska males (see table 9) are well within the range of those of eastern Platte Valley birds. As in the case of the hybrid index, the Chadron and Fort Morgan samples showed a close similarity in wing length (means, 101.38 and 101.25 mm., respectively). The mean tail length in Chadron orioles was 82.25 mm., exceeding even those of Greeley. The northwestern Nebraska orioles are thus strongly *bullockii* in mensural and color characters.

The hybrid zone in Nebraska is approximately 150 miles wide, extending from a point east of Chadron on the Niobrara River, the Sand Hills and, probably, the North Platte River in the vicinity of Oshkosh and Lisco, east about to Meadville or Riverview on the Niobrara, Brewster in the central part of the state, and just west of Gothenburg along the Platte River. The center of the hybrid zone extends from an undetermined point on the Niobrara, probably just west of Valentine, south and west to the South Platte River approximately 15 miles east of Big Springs. Within this zone (see fig. 1) it is probable that phenotypically pure individuals of *galbula* and *bullockii* either do not occur or are uncommon; the chance of such individuals meeting is decidedly poor. West of the zone in northwestern Nebraska "pure" *bullockii* individuals occur, although most should show some *galbula* traces when examined in the hand. Phenotypically pure *galbula* individuals occur only in the eastern one-third of the state. Even along the eastern border of Nebraska, however, a majority of individuals exhibit traces of *bullockii* in color characters. It is apparent that most of the breeding orioles in Nebraska are affected to some degree by hybridization and introgression.

### South Dakota

Only 24 adult male orioles were secured at eight localities in this state. The results of the examination of these specimens are contained in table 10. The samples were too small for detailed analysis. Only two of the males were phenotypically pure *bullockii* in all characters, these being from Howes. No phenotypically pure *galbula* individuals were taken, although one male from Chamberlain closely approaches that form. The hybrid zone in South Dakota probably extends from the Missouri River in the southeast north and west to the edge of the Black Hills. It is presumed that the Black Hills

TABLE 10

ANALYSIS OF COLOR AND TWO MENSURAL CHARACTERS IN MALE ORIOLES FROM SOUTH DAKOTA

| Locality | N | Mean hybrid index | Hybrid index range | N | Mean wing length (mm.) | N | Mean tail length (mm.) |
|---|---|---|---|---|---|---|---|
| Chamberlain | 6 | 2.83 | 1 – 5 | 5 | 96.80 | 4 | (75.65)* |
| Mobridge | 2** | (3.0) | 3 | 3 | (98.3) | 2 | (77.9) |
| Promise | 4 | (6.25) | 4 –10 | 2 | (100.5) | 1 | (81) |
| Midland | 3** | (10.0) | 9 –11 | 4 | (100.75) | 4 | (79.60) |
| Lemmon | 1 | (3) | ..... | 1 | (100) | 0 | ..... |
| Kadoka | 2 | (8.5) | 7 –10 | 2 | (99.5) | 1 | (81.3) |
| Howes | 3 | (11.00) | 9 –12 | 3 | (100.33) | 2 | (80.0) |
| Rapid City | 1 | (10) | ..... | 1 | (102) | 1 | (78.2) |

* Parentheses are used where samples are comprised of fewer than five birds.

** One other male at each locality could not be indexed due to disruption of tail pattern. In each case the specimen indexed otherwise at 4.

population is similar to that of the Pine Ridge of northwestern Nebraska in being predominantly *bullockii,* but with many individuals exhibiting traces of *galbula.* Measurements of the South Dakota specimens are intermediate between eastern Nebraska *galbula* and central Colorado *bullockii* (generally), or tend toward *bullockii,* except for the Chamberlain sample, which is similar to those of eastern Nebraska in mean wing and tail lengths.

Two abnormally plumaged individuals were noted. A male (Cornell Univ. no. 25646) from Kadoka exhibited the tail pattern of *bullockii,* but the area normally yellow in that form was white. The yellow rump of a Chamberlain male (Cornell Univ. no. 25643) was moderately spotted with black.

## KANSAS, OKLAHOMA, AND TEXAS

Results of the analysis of 28 adult males from eight localities in Oklahoma, nine males from Meade in southwestern Kansas and three from two localities in Texas are summarized in table 11. While the number of specimens and localities represented by specimens is insufficient to permit the accurate determination of the limits of the hybrid

TABLE 11

ANALYSIS OF COLOR AND TWO MENSURAL CHARACTERS OF MALE ORIOLES FROM KANSAS, OKLAHOMA, AND TEXAS

| Locality | N | Mean hybrid index | Hybrid index range | N | Mean wing length (mm.) | N | Mean tail length (mm.) |
|---|---|---|---|---|---|---|---|
| Meade, Kansas | 9 | 5.77 | 3 – 8 | 9 | 98.22 | 7 | 77.09 |
| Ellis County, Okla.* | 18 | 4.56 | 2 – 9 | 17 | 99.06 | 13 | 78.57 |
| Gate, Okla. | 3 | (5.6)** | 4 – 9 | 3 | (97.3) | 2 | (78.6) |
| Sayre, Okla. | 1 | (6) | ..... | 1 | (97) | 1 | (77.3) |
| Woodward, Okla. | 3 | (3.6) | 3 – 4 | 3 | (99.3) | 3 | (79.2) |
| Willow, Okla. | 1 | (8) | ..... | 1 | (103) | 1 | (84.5) |
| Kenton, Okla. | 2 | (11.5) | 11–12 | 2 | (99.5) | 2 | (79.2) |
| Stinnett, Texas | 1 | (11) | ..... | 1 | (102) | 1 | (82.3) |
| Sheffield, Texas | 2 | (11.5) | 11–12 | 2 | (99.0) | 2 | (78.3) |

* Three Ellis County localities represented. The three, Arnett, Gage and Shattuck, are within 12 miles of each other.

** Parentheses enclose values for localities represented by samples of fewer than five birds.

zone in these states, it is evident that the zone passes through western Oklahoma, western Kansas, and central Texas. The limits of the hybrid zone and the location of its center in the southern Plains, as suggested by analysis of the specimens available, are indicated on the map (fig. 1). It should be kept in mind that the zone limits are only approximate and may be subject to modification when larger series are available from additional localities.

The oriole situation is unclear in central Texas. The Baltimore Oriole reaches its southern and western limits in eastern and central Texas. The Bullock Oriole breeds in southern Texas, almost to the Gulf coast (observed breeding in Laredo by the junior author), and in central and western Texas (American Ornithologists' Union Check-list, 1957). Both occur in central Texas, presumably interbreeding there. The specimens from Texas are phenotypically like *bullockii,* although two show evidence of *galbula* influence. Additional specimens from north-central and central Texas are needed to clarify the situation.

The center of the hybrid zone in western Oklahoma probably lies in the eastern Panhandle, between Kenton and Ellis counties, perhaps crossing the state from the vicinity of Liberal, Kansas, south near Beaver, Oklahoma, and then into Texas. The fact that specimens indexed at 4 or more were secured at the eastern-most localities represented by more than a single specimen indicates that the zone extends east at least into west-central Oklahoma. The western limit of the zone must be in the western Panhandle (Boise City-Griggs area?).

The eastern and western limits of the hybrid zone in Kansas are not known. The situations in adjacent Nebraska, Colorado, and Oklahoma suggest that the center of the zone may extend from the northwestern corner of Kansas southward and slightly eastward to the Oklahoma border near Liberal.

If the large series from Meade, Kansas, and Ellis County, Oklahoma, is compared (using tables 5, 7, and 11 and fig. 3) with those from the Platte Valley, it will be seen that in mean hybrid index, wing length and tail length (Ellis County only for this character) the Meade and Ellis County samples generally approach the conditions to be expected in populations from near the center of the hybrid zone similar to that between Sutherland and Big Springs in the Platte Valley transect.

## ANALYSIS OF FEMALE COLOR CHARACTERS

In the effort to secure as many male orioles as possible from the Plains populations, little time could be spent seeking out and collecting the less obvious females. As a result, only 32 females were taken, representing 17 localities. Only three of these localities, Hastings and Grand Island, Nebraska, and Meade, Kansas, are represented by more than three specimens. The other localities, with number of specimens and hybrid indexes, are indicated in table 12.

Generally, the specimens from eastern Nebraska indexed close to *galbula,* the female from Silver Creek scored at 6 and the one from St. Paul scored at 5 being notable exceptions. As expected on the basis of the situation indicated by the males, the Chadron female resembles *bullockii.* The three females from South Dakota show *bullockii* influence to the same extent as the males from the same localities. The females from Oklahoma appear rather closer to *bullockii* than one would expect from the male color character study, although the range of variation in the males is sufficient to include males having hybrid index values comparable to these females.

A small series of six females from Meade, Kansas, has a range in index from 2 to 6 with a mean of 3.67. Comparison of the mean female and male indexes is facilitated by

TABLE 12

ANALYSIS OF SPECIMENS OF FEMALE ORIOLES

| State | Locality | N | Hybrid indexes |
|---|---|---|---|
| Nebraska | Silver Creek | 1 | 6 |
| | St. Paul | 2 | 0, 5 |
| | Burwell | 1 | 0 |
| | Spencer | 1 | 1 |
| | Gothenburg | 1 | 1 |
| | Valentine | 1 | 0 |
| | Chadron | 1 | 8 |
| South Dakota | Promise | 1 | 3 |
| | Howes | 1 | 7 |
| | Rapid City | 1 | 5 |
| Oklahoma | Gage | 2 | 3, 7 |
| | Arnett | 1 | 7 |
| | Woodward | 1 | 4 |
| | Gate | 2 | 6, 7 |

converting the separate indexes into percentages by dividing sample means by the maximum possible index scores (female, 8; male, 12). The resulting figures represent the mean percentages of *bullockii* characteristics in the samples. The female mean index when converted gives a value of 46 per cent, whereas the male index value converts to 48 per cent.

The mean hybrid index of four females from Hastings, Nebraska, with an index range of 0 to 4 was 1.75. This converts to 22 per cent, approximating the converted male value of 20 per cent (mean hybrid index = 2.48). Five females from Grand Island, Nebraska, have an index range of 0 to 3. The sample mean is 0.80 or 10 per cent of *bullockii* characteristics, somewhat less than the male converted mean of 18 per cent (mean hybrid index, 2.23). The female sample is insufficient for any significance to be attached to the difference, however.

The sample sizes of females are too small to permit mensural analysis. The results of the color character analysis of females generally support the results of the study of adult males.

## DISCUSSION

Several of the papers cited in the introduction contain discussions, definitions and examples of various aspects of avian hybridization. We prefer to define hybridization as interbreeding between populations in secondary contact, regardless of their taxonomic rank. This avoids the fruitless argument as to whether or not interbreeding between species is somehow qualitatively different from interbreeding between subspecies. This argument is fruitless because the results of such interbreeding may determine whether the two forms will evolve more effective mutual isolating mechanisms and eventually become unable to interbreed or merge and become one freely interbreeding population. Which way the balance swings depends upon many factors but the taxonomic problem may be solved by answering a single question. Is natural selection acting more strongly against the offspring of mixed matings than against those of pure matings or is it not? If selection is removing a higher percentage of hybrid offspring than of nonhybrid offspring the result will be an increase in the incidence of those genotypes that avoid pairing with a member of the other form. This process will gradually reinforce the partly formed isolating mechanisms to the point where hybridization ceases

and the two forms will become good species by any reasonable definition. However, if selection is not greater against the hybrids and if they are just as successful as the offspring of pure matings, they will form a genetic bridge between the two rejoined populations. The variation of both forms will increase through recombination and, for a time, a zone of hybridization will be detectable. Gradually the variability will decrease as the characters best fitted for each geographic area are selected. The ultimate result will be a cline between two geographically complementary populations of a single species.

The answer to the question posed above, as it relates to the present problem, seems clear. There is ample evidence that the hybrids are fully as successful as the offspring of pure matings and introgression is extending far beyond the area of the secondary contact or "hybrid zone." Because the widespread breakdown of the extrinsic barrier is recent, selection has not yet had time to reduce the variability of the recombinant populations in the "hybrid zone" and we are able to detect what has happened and is happening there. It is also possible to predict how this situation will change in the future. If present conditions in the Great Plains continue, or if even more trees are planted, the orioles will continue to increase in numbers, selection will fashion populations adapted to local conditions from the variable hybrid gene pools, and gradually the variability will be reduced to normal. At present the Baltimore and Bullock orioles are treated as separate species (A.O.U. Check-list, 1957). The evidence presented here proves that they are conspecific. We therefore propose that they be merged as subspecies of a single species.

## SUMMARY

Hybridization between the Baltimore and Bullock orioles in the Great Plains is documented by an analysis of the coloration and mensural characters of 634 breeding birds. Color character analysis, utilizing the hybrid index technique, indicates that only 39 of 620 adults exhibit pure *galbula* or *bullockii* characteristics, the remaining 581 birds being hybrids. The composite hybrid index gradient and those of nine individual color characters are described. The major shift from Baltimore to Bullock oriole characters in Great Plains populations occurs over a 150- to 200-mile wide area, the gradients being more gradual east and west of this region. The "hybrid zone" is defined as that area which includes populations with mean hybrid indexes of from 3.0 to 9.0 in an index scheme with values ranging from 0 (phenotypically like *galbula*) to 12 (phenotypically like *bullockii*). All but three of 138 individuals taken within the hybrid zone (indicated in fig. 1) were hybrids. In a transect along the Platte River, phenotypically pure individuals of the two parental types were absent in samples containing 110 birds from localities within a 150-mile area between localities where "pure" specimens were secured. Color character analysis of samples east and west of the hybrid zone indicates that considerable introgression is occurring through the zone and into both parental populations.

Mensural character analysis corroborates the evidence of extensive hybridization obtained from the study of color characters. Samples from localities in the western Plains show greater mean wing length and tail length than those from the eastern Plains. Populations in the intervening area are intermediate, samples grading clinally between the extremes from shorter wings and tails in the east to longer wings and tails in the west. Weight, bill length, and tarsal length differences between eastern and western Plains orioles are minute.

The importance of increased variability through interbreeding is stressed. On the basis of the extensive hybridization and introgression between the Baltimore Oriole

and the Bullock Oriole, and evidence that hybrids are not at a selective disadvantage in comparison with the offspring of unmixed matings, it is proposed that the two forms be considered conspecific.

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