

THE PROGRESS OF ORIOLE HYBRIDIZATION IN KANSAS

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ABSTRACT.—Specimens of Northern (“Baltimore” and “Bullock’s”) orioles collected at six sites in western Kansas in 1976 and 1978 are compared with specimens collected at the same sites in the mid-1960’s. No changes in the location or size of the step-cline (“hybrid zone”) between the two taxa are indicated by comparisons of the plumage features of the male specimens; the distribution of phenotypes of birds from sites where both Baltimore and Bullock’s orioles occur is not bimodal, and, therefore, there is no indication of selection against intermediate birds. Female Bullock’s-like orioles, however, are found farther east along the Cimarron River in southwestern Kansas than they were in the 1960’s. The correlations between the amount of precipitation at a locality in western Kansas and the phenotype of oriole that occurs there are high (about 0.90). This suggests that precipitation *per se* is a factor that determines the distributional limits of these birds relative to each other. There are no recent changes, however, in the average climatic conditions in western Kansas. Perhaps the orioles present at a site in any given season are a reflection of the conditions there the previous season or two.

The analyses of size variation among samples collected in the 1970’s show an east-west cline that is more-or-less congruent with that found for plumage features; at any given site, the variability in size is positively correlated with the variability in plumage. Where a diversity of oriole phenotypes occurs, there is no tendency for females to associate with males of the “same type” (i.e. Bullock’s with Bullock’s or vice versa); this suggests that assortative mating does not occur. Received 25 January 1982, resubmitted 6 May 1982, accepted 18 April 1983.

THE ranges of Baltimore and Bullock’s orioles (*Icterus galbula* and *I. bullockii*)¹ meet in the Great Plains. In regions of contact, from southern Alberta to central Texas, variability in plumage color and pattern exists, and in the most variable populations the majority of individuals (70–90%) are variously intermediate between the two nominal forms. Throughout this region there is an abrupt step-cline in plumage pattern, from Baltimore-like orioles in the east to Bullock’s-like orioles in the west (Sibley and Short 1964, Rising 1970, Corbin and Sibley 1977).

On the prairies, orioles most commonly are

found in open riparian woodlands along the trans-Plains rivers, which run essentially southeastwards from the Rocky Mountains to the Mississippi River. At different times, the oriole plumage step-cline has been described along several of these trans-Plains rivers. Sutton (1938) collected “hybrid” orioles from along the Canadian River in western Oklahoma in the 1930’s; Sibley and Short (1964) described the step-cline in the plumages of male orioles collected from along the Platte and Niobrara rivers in Nebraska and Colorado in the 1950’s; Rising (1970) described the clines both for males and females taken from along the Republican, Smoky Hill, Arkansas, and Cimarron rivers in Kansas; and Anderson (1971) described the orioles from along tributaries of the Missouri River in South Dakota in the 1960’s. As early as 1908, Bent described “hybrid” orioles from the Cypress Hills region in the southern Canadian prairies, and Rising (1973) described additional hybrids from Montana, Alberta, and Saskatchewan. The north to south correspondence of the step-cline in male plumages from along the different rivers is indirect evidence that this is a stable step-cline, like those described be-

¹ At present, the A.O.U. (1982) combines these two as the Northern Oriole, *Icterus galbula* (this presumably includes a third well-marked form from Mexico, Abeille’s Oriole). It has been argued that the status of these orioles is uncertain (Rising 1970, 1973; Corbin and Sibley 1977), so, for the sake of clarity, I use the well-established and unambiguous English common names “Baltimore” and “Bullock’s” orioles in this paper. For the Great Plains orioles, appropriate trinomials are *I. g. galbula* and *I. g. bullockii*, respectively.

tween morphologically and geographically distinctive populations of Rufous-naped Wrens (*Campylorhynchus rufinucha*; Selander 1964, 1965), Carrion Crows (*Corvus corone*; Mayr 1963), Common Grackles (*Quiscalus quiscula*; Yang and Selander 1968), and house mice (*Mus musculus*; Hunt and Selander 1973).

A step-cline can be stable through time if there is gene flow among populations and selection favors one morph or genotype on one side of the step and another on the other side whether or not intermediate or heterozygous individuals are favored at intermediate sites (in the region of the step) (Endler 1977, Slatkin 1978). If intermediate individuals were selected against, the step-cline would disappear. If intermediate individuals were selectively equivalent (i.e. no selection) or superior in all regions, the steps would become obscure through time. Thus, if temporally repeated collections show a flattening of step-clines for characters that vary geographically, we can infer that those characteristics are selectively neutral and that there is no "hybrid" advantage. On the other hand, a stable step-cline indicates selective maintenance. Nevertheless, in practice it can be difficult to differentiate between stable and transient clines, because, unless samples are taken at closely adjacent sites along a cline over several generations, a cline that is in fact transient may appear to be stable (Endler 1977). If a step-cline shifts in geographic position without flattening, however, it is highly probable that selection is maintaining the step.

Although the differences in plumage pattern between Baltimore and Bullock's orioles are of no obvious adaptive significance, some of the physiological responses of Bullock's Orioles would seem to give them a selective edge over Baltimore Orioles in hot, dry areas (Rising 1969), and, presumably, Baltimore Orioles have an adaptive edge in mesic conditions. Rising (1970) noted that the plumage step was correlated with a zone of climatic transition in the Plains and argued that the step-cline between Baltimore and Bullock's orioles was stable.

Corbin and Sibley (1977) describe changes in the plumages of orioles at several sites along the Platte River in Nebraska and Colorado that were examined first in the mid-1950's. They found that Baltimore-like orioles had extended their range westward along the Platte. At Big Springs, in western Nebraska, a mixed popu-

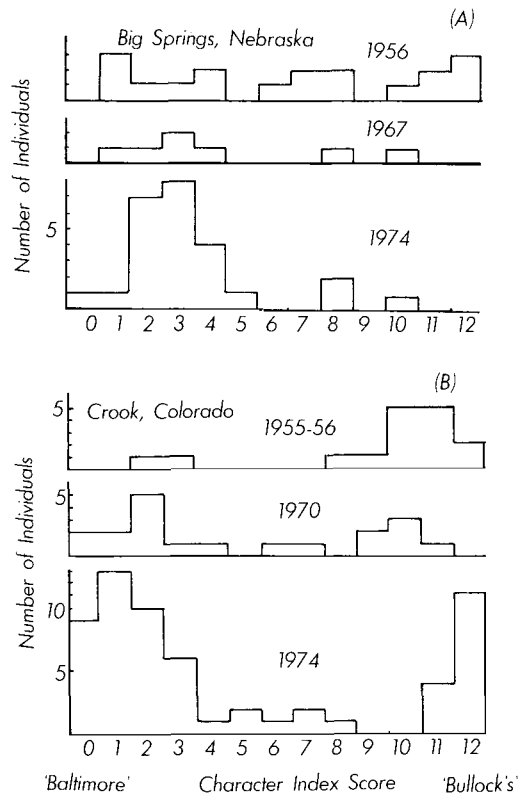


Fig. 1. Histograms of character index scores for male orioles from along the Platte River. The scores used for this figure are from the Character Index of Sibley and Short (1964), and they range from 0 ("Baltimore") to 12 ("Bullock's"). (A) shows the shift toward Baltimore-like orioles that has occurred at Big Springs, Nebraska (data for 1956 and 1974 from Corbin and Sibley 1977, for 1967 from Rising 1970); the 1956 and 1974 distributions are significantly different (Kolmogorov-Smirnov test; $P < 0.01$), but the 1967 distribution is not significantly different from either the 1956 or 1974 ones; (B) shows the shift from Bullock's-like orioles to a bimodal population at Crook, Colorado (data from Corbin and Sibley 1977); the 1955-1956 and 1970, and 1955-1956 and 1974 distributions are significantly different ($P < 0.01$), but the 1970 and 1974 distributions are not significantly different.

lation occurred in the 1950's; in the 1970's orioles at that site were predominately Baltimore-like (Fig. 1A). At Crook, in northeastern Colorado, Bullock's Orioles predominated in 1955-1956, with no "pure" Baltimore Orioles present; by 1974, there was a distinctly bimodal distribution of orioles, with Baltimore and Baltimore-like orioles predominating (Fig. 1B). This

TABLE 1. Specimens examined.

Locality	Sex	Skins		Skeletons 1970's	Dates collected
		1960's	1970's		
Ontario	M	—	12 ^a	38 ^b	Various
	F	30	9 ^a	15 ^b	Various
Oklahoma/New Mexico (4 km N, 6 km W Kenton)	M	—	26	33	15-16 June 1976
	F	—	20	19	15-16 June 1976
Kansas					
Morton County (13 km N Elkhart)	M	26	22	39	5-6 June 1976
	F	16	18	20	5-6 June 1976
Seward County (13 km NE Liberal)	M	26	23	39	2-3 June 1978
	F	15	12	12	2-3 June 1978
Clark County (13 km S Sitka)	M	26 ^c	22	34	11 June 1978
	F	22 ^c	13	12	11 June 1978
Wallace County, 3 km N, 5 km W Sharon Springs)	M	28	26	38	6-8 June 1978
	F	21	12	11	6-8 June 1978
Logan/Scott counties (29 km N Scott City)	M	28	27 ^d	30	10-13 June 1976
	F	14	22 ^e	21	10-13 June 1976
Trego County (16 km N, 3 km E Utica)	M	24	21	27	9-10 June 1978
	F	22	16	14	9-10 June 1978
Douglas County (Lawrence vicinity)	M	22	—	0	Various
	F	14	—	0	Various

^a Ontario only (collected for this study).

^b Includes some birds collected in several northeastern states.

^c Specimens collected in Comanche (1.5 km E Protection, 17.7 km S Protection).

^d Includes 12 specimens collected 13 km N, 1.5 km W Scott City.

^e Includes 7 specimens from 13 km N, 1.5 km W Scott City.

is evidence of a westward shift in the zone. The bimodality at Crook could be the consequence of a rejection of hybridization (either by assortative mating or selection against hybrids) or of a recent recolonization of that locality following a catastrophe of some sort. Anderson (1971) and Rising (1973) suggest that Baltimore Orioles are moving westward, at the expense of Bullock's Orioles, in South Dakota and the southern Canadian prairies, although there are few "old records" from those places to form the basis of rigorous temporal comparisons.

The purposes of this study are (1) to assess directly the stability of the hybrid zone in western Kansas by comparing samples taken in the 1960's with those taken in the 1970's, (2) to ascertain whether or not the step-cline has fluctuated in accordance with any climatic changes in western Kansas, (3) to describe morphometric variation across the region where there is a plumage step-cline in order to find whether or not morphometric variation parallels plumage variation, and (4) to seek evidence of assortative mating.

METHODS

In the summers of 1976 and 1978, I collected samples of orioles from six sites selected from among those at which I had obtained samples in the mid-1960's (Rising 1970) and from near Kenton, Oklahoma; the precise localities, numbers of birds taken, and dates of collection are given in Table 1. The approximate locations of the collecting sites in the Plains are illustrated in Fig. 2. Although the birds collected in the 1960's were prepared as conventional study skins, those collected in the 1970's were made as skin-and-skeleton specimens (a study skin and skeleton saved from each individual). The specimens from the 1960's are in the University of Kansas Museum of Natural History, Lawrence; those from the 1970's are in the Royal Ontario Museum, Toronto.

Plumage differences.—The clines in plumage-color pattern for both sexes (adult females and "after second year" males, aged by plumage and skull ossification) were quantified using the Character Index (CI) described by Rising (1970); this differs in minor details from that used by Sibley and Short (1964) and Corbin and Sibley (1977). These papers give detailed descriptions of the character-index method and the plumages of these orioles. Although the character

scores are subjectively determined, most of the differences between "Baltimore" and "Bullock's" orioles are so striking that the results are repeatable. For the present study, I first assessed the 1970's samples, then the 1960's, then scored the 1970's birds a second time. The two assessments of the latter sample gave nearly identical results; hence, variability in my subjective scoring of the birds probably did not influence the results. To compare the 1960's scores with those of the 1970's, I plotted the distributions of the scores from the various localities as histograms and then compared the distributions of the two samples from each site (e.g. Utica 1965 with Utica 1978) using a Kolmogorov-Smirnov two-sample test of the differences between two independent sample distributions (Gibbons 1976).

Morphometric differences.—I measured 26 variables (Tables 2 and 3) on the skeletons available from the specimens collected in the 1970's. In each case, the longest dimension of a bone or element was measured; hence, "ulna length" is the maximum length of the ulna, and so on. Values for missing or broken features were estimated by regression analysis (BMD two-step method, Dixon and Brown 1979); if a specimen was missing more than three features, it was omitted from multivariate analyses. Specimens from Ontario and northeastern states were taken as a "reference" sample of Baltimore Orioles; those from Kenton were taken as "reference" Bullock's Orioles. I used the MANOVA in discriminant functions analysis (DFA) (SPSS, release 8, subprogram DISCRIMINANT, method DIRECT, Nie et al. 1975) to ascertain that there were significant differences between the reference samples and then repeated the DFA using the 8 groups (6 from the "hybrid zone" and the 2 reference samples). First-year males were included in these analyses.

To avoid overdetermination of a matrix in DFA there must be more individuals in the smallest sample than there are characters in the analysis. The smallest sample of males available was 27, so in the DFA of males I used the entire set of 26 characters. The position of each of the 278 male specimens available was calculated on the discriminant function 1 (DF1) axis and then these DF scores were used to calculate means and variances for each of the eight samples.

For the females, sample sizes were as small as 11 birds. I ran a DFA between the female reference samples, using all 26 variables, and then selected the 10 variables that maximized the separation of these groups. Inasmuch as these reference samples contained fewer than 26 individuals, this DFA is valid only as a variable-selecting technique. I subsequently used the 10 variables selected to discriminate among the eight groups and to determine the positions of the 124 females on the DF1 axis. (I also discriminated among the female samples using two other sets of

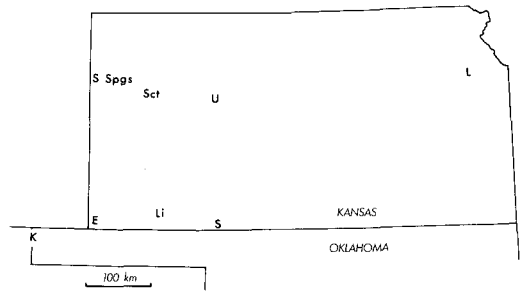


Fig. 2. Map of localities in the central Great Plains from which orioles were taken for this study. The letters are abbreviations for site names: K = Kenton, Oklahoma and New Mexico; E = Elkhart, Kansas; Li = Liberal, Kansas; S = Sitka, Kansas; S Spgs = Sharon Springs, Kansas; Sct = Scott City, Kansas; U = Utica, Kansas; L = Lawrence, Kansas.

variables that I had selected on the basis of their univariate F values and their value in discriminating among the male samples. These other sets of variables gave similar results, so I have not included data from them.)

For both sexes, the ANOVA of the DF1 scores of the birds from the eight sites (which are normally distributed) was followed by an *a posteriori* SNK test (Sokal and Rohlf 1969) to determine which localities were significantly different from others on the DF1 axis.

I used nonparametric analysis (Kendall's rank correlation) to assess the correlation between color pattern (CI score) and size and shape (DF1 score); many of the specimens had the same CI scores, and Kendall's test is preferred when there are many ties in the data (Nie et al. 1975). These correlations were calculated for the birds (of both sexes) from each locality and for all localities pooled.

Climatic correlations.—I used multiple regression (SPSS program REGRESSION, Nie et al. 1975) to describe the relationship between the climate and the distribution of Baltimore and Bullock's orioles. In four different analyses, the average CI scores and DF1 scores for males and females for each of the six western Kansas samples, and for the Kenton, Oklahoma/New Mexico sample, were regressed against 10 measures of climate, namely average annual May and June precipitation; average May, June, and July temperatures; the average highest temperature recorded in July (the hottest month); the average lowest temperature recorded in May (the coolest "summer" month); the highest summer temperatures (May through August); and the lowest summer temperature. (Orioles arrive in western Kansas in late April and leave by mid-September.) Climate values used

TABLE 2. Statistics for skeletons of male orioles.

Variable	Group means		Significance ^a	SDFC ^b
	Baltimore (n = 38)	Bullock's (n = 33)		
Skull length	36.8	37.6	***	0.003
Skull width	17.3	17.6	***	-0.002
Premaxilla length	9.4	9.6	n.s.	
Premaxilla depth	5.6	5.7	n.s.	
Nasal bone width	8.9	8.7	0.06	0.424
Premaxilla width	6.2	6.3	n.s.	
Interorbital width	5.0	5.0	n.s.	
Mandible length	29.1	29.9	***	0.068
Gonys length	7.7	7.7	n.s.	
Mandible depth	3.0	2.9	n.s.	
Coracoid length	20.8	21.5	***	0.121
Scapula length	22.9	23.5	***	0.050
Femur length	20.5	21.3	***	0.041
Femur width	1.6	1.8	***	-0.250
Tibiotarsus length	34.8	36.2	***	-0.276
Tarsometatarsus length	23.6	24.6	***	0.051
Humerus length	22.0	23.0	***	-0.308
Ulna length	27.0	28.1	***	0.120
Carpometacarpus length	15.5	16.0	***	0.097
Hallux length	9.4	9.9	***	-0.294
Sternum length	23.4	24.9	***	-0.364
Sternum depth	9.9	10.4	***	-0.116
Keel length	22.6	24.3	***	-0.316
Synsacrum width	13.0	13.3	n.s.	
Phalanx length	7.1	7.5	***	-0.289
Synsacrum length	20.1	20.4	***	0.194

^a n.s. = not significant; *** = $P < 0.01$.

^b SDFC = standardized discriminant function coefficient for function 1; Baltimore Orioles have positive scores; Bullock's Orioles have negative scores.

were averages from U.S. National Oceanic and Atmospheric Administration data (NOAA 1978a, 1978b).

To assess recent climatic changes in western Kansas, I used weather data from Dodge City (NOAA 1978a) and Goodland (NOAA 1978b), in western Kansas. The annual average temperature and amount of rainfall for each of the months, April through August, for the 11-yr period preceding the first collection (1954 through 1964) were compared by ANOVA to the corresponding data for the 11-yr interval between collections (1965 through 1975).

Assortative mating.—Time did not allow me to ascertain which birds were mated to which when the specimens were collected. Nonetheless, during the breeding season mated birds commonly are closely associated (pers. obs., N. J. Flood pers. comm.), and, whenever I collected such a closely associated "pair," I noted it. I calculated Spearman's Rank Correlations (r_s) between the CI scores and between the DF scores of birds in such "pairs" using only orioles from localities where there is great phenotypic variability (Scott City and Liberal); at other sites, for the most part, birds had the opportunity to mate only with a like bird. This tests two questions: does, say, a female that looks like a Bullock's Oriole consort with a male

that looks like a Bullock's Oriole, and does, say, a female that is shaped like a Bullock's Oriole consort with a male that is shaped like a Bullock's Oriole? Spearman's Rank Correlation Coefficient is an appropriate test, because the CI scores are not normal deviates and because there are few ties in the ranked observations.

RESULTS

Plumage analyses.—Histograms of the CI scores for male orioles are shown in Fig. 3. The east-to-west clines in plumage characteristics are clear along both the Smoky Hill and Cimarron river transects, with Baltimore-like orioles at Lawrence (eastern Kansas) and Bullock's-like orioles at Kenton (Oklahoma and New Mexico). Comparisons of the distributions (Kolmogorov-Smirnov tests) show that none of the mid-1960's distributions differ significantly from those from the same localities in the late 1970's (e.g. Scott City 1965 is not significantly different from Scott City 1976). Rising (1970)

TABLE 3. Statistics for skeletons of female orioles.

Variable	Group means		Significance ^a	SDFC ^b
	Baltimore (<i>n</i> = 15)	Bullock's (<i>n</i> = 19)		
Skull length	36.9	37.2	n.s.	
Skull width	17.0	17.3	***	
Premaxilla length	9.6	9.6	n.s.	
Premaxilla depth	5.5	5.6	n.s.	
Nasal Bone Width	8.6	8.7	n.s.	-0.667
Premaxilla width	6.3	6.2	n.s.	
Interorbital width	4.8	4.9	n.s.	
Mandible length	29.2	29.4	n.s.	
Gonys length	7.9	7.7	n.s.	0.722
Mandible depth	2.9	2.9	n.s.	
Coracoid length	20.3	20.7	*	
Scapula length	22.4	23.0	*	
Femur length	20.6	21.1	*	
Femur width	1.6	1.6	n.s.	
Tibiotarsus length	34.6	35.7	*	0.838
Tarsometatarsus length	23.4	24.6	***	-1.030
Humerus length	21.7	22.5	***	-1.630
Ulna length	26.2	27.1	***	1.641
Carpometacarpus length	15.0	15.4	n.s.	
Hallux length	9.3	9.9	***	-1.497
Sternum length	22.6	23.8	***	
Sternum depth	9.4	9.7	***	
Keel length	21.2	22.2	***	
Synsacrum width	12.9	13.0	n.s.	-0.687
Phalanx length	6.9	7.2	***	0.970
Synsacrum length	19.6	19.9	n.s.	0.644

^a n.s. = not significant; * = $P < 0.05$; *** = $P < 0.01$.

^b SDFC = standardized discriminant function coefficient for function 1; Baltimore Orioles have negative scores, Bullock's positive scores.

noted the apparent bimodality at Scott City in 1965 (Fig. 3A) and suggested that at this site selection might be against individuals that hybridize—as it apparently is at Crook, Colorado (Corbin and Sibley 1977; Fig. 1B). The present data certainly do not indicate that such is the case: the 1976 birds, though not significantly different from the 1965 ones, are, if anything, less bimodal in distribution. Likewise, there is no indication of increased bimodality at Liberal, the other "hybrid locality" in the 1965 data (Fig. 3B).

The data for the females (Fig. 4) present a somewhat different picture. Along the Cimarron River (Fig. 4B) the females taken at Sitka in 1978 are like those at Liberal (100 km to the west) in 1965, and the females from Liberal in 1978 are like Bullock's Orioles that occurred 100 km to the west in the 1960's. Thus, there has been an eastward shift of approximately 100 km by Bullock's-like orioles from the 1960's to the 1970's. The difference between the 1960's and 1970's is significant (Kolmogorov-Smirnov

test) at Liberal ($D = 0.51$, $n = 8$, $P < 0.05$) and at Sitka ($D = 0.45$, $n = 8$, $P = 0.05$). [Most of the 1965 "Sitka" sample was collected along Bluff Creek, ca. 13 km east of the site where the 1978 Sitka sample was collected (Table 1).] No differences, however, are suggested by the data for the birds from along the Smoky Hill River.

Size differences.—Univariately, male Baltimore and Bullock's orioles (reference samples) differ significantly with regard to 18 of the 26 variables measured (Table 2). Bullock's Orioles are slightly larger than Baltimore Orioles, except in bill measurements.

In the DFA of the eight samples of males, there are three significant discriminant functions. The first of these (i.e. the one that explains the greatest amount of the among-group variation, in this case 49.4% of it) discriminates between Baltimore-like and Bullock's-like birds; 46.0% of the males are correctly identified as to locality by this discriminant function. (The 46.0% compares with a figure of approximately 12.5%— $1/8$ —for random placement of the spec-

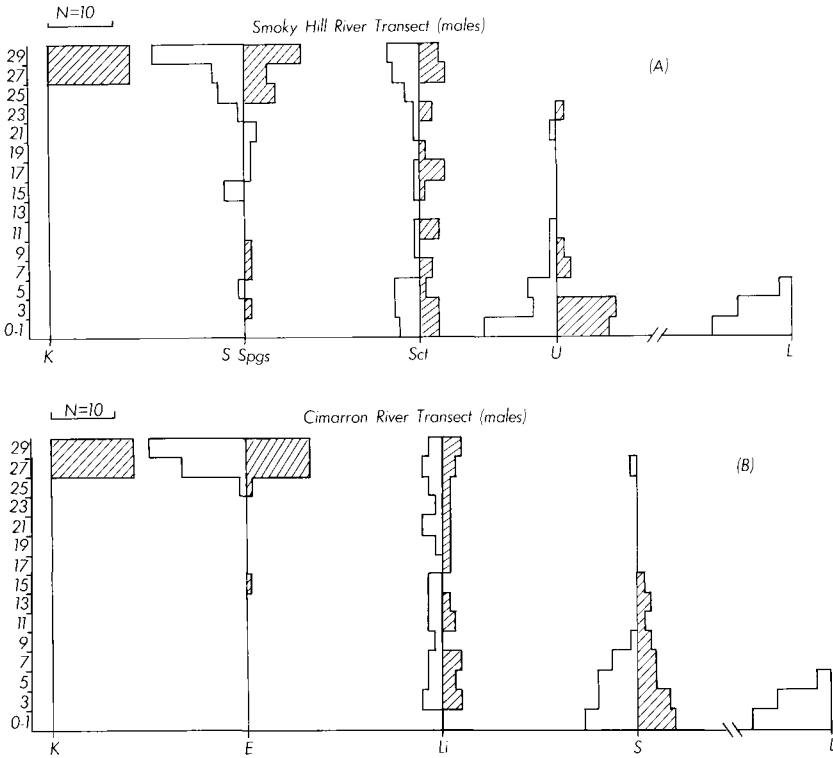


Fig. 3. Histograms of the character index scores of male orioles collected in the mid-1960's (open) contrasted with those collected in the late 1970's (hatched). The vertical axes show the character index scores, which range from 0 (Baltimore-like) to 29 (Bullock's-like); the horizontal axes are west-to-east transects, with the site names indicated at a distance that is proportional to geographical distance. The site name abbreviations are the same as those used in Fig. 2. (A) illustrates the males from the Smoky Hill River transect; for scale, Sharon Springs is approximately 100 km west of Scott City; (B) illustrates the males from the Cimarron River transect; for scale, Liberal is about 105 km east of Elkhart.

imens; this figure is not exactly 12.5%, because prior probabilities are adjusted for unequal sample sizes.) The variables that load most strongly on DF1 (i.e. those with the highest standardized discriminant function coefficients), and hence are the most useful for discriminating between the taxa in multivariate space, are indicated in Table 2. An ANOVA of the DF1 scores of the 278 males from the eight samples shows a significant difference among localities, and an *a posteriori* SNK test identifies the following statistically homogeneous groups: (1) Ontario, (2) Kenton, (3) Elkhart + Sharon Springs + Liberal, and (4) Liberal + Scott City + Sitka + Utica, in other words "Baltimore," "Bullock's," "western hybrid zone," and "eastern hybrid zone." [Discriminant functions 2 and 3, although statistically significant, do not separate the taxa and therefore are of no interest

to us here. DF2, in a phrase, separates southwestern Kansas from the other localities; DF3 discriminates between the "eastern hybrid-zone localities" (Sitka, Liberal, Scott City, Utica) and the others.]

The means and variances of the DF1 scores are in Table 4. *F*-tests show that the variance of the Elkhart males is significantly greater than that of either reference sample and, additionally, is greater than those of the Sitka, Sharon Springs, and Utica males (all samples on the edge of the step-cline defined by the plumages); the males from Scott City are significantly more variable than are those from the Baltimore reference, Sitka, or Utica samples.

Using the 10 selected variables, I found one significant discriminant function among the eight samples of females; it explains 55.7% of the among-group variance and identifies 46.8%

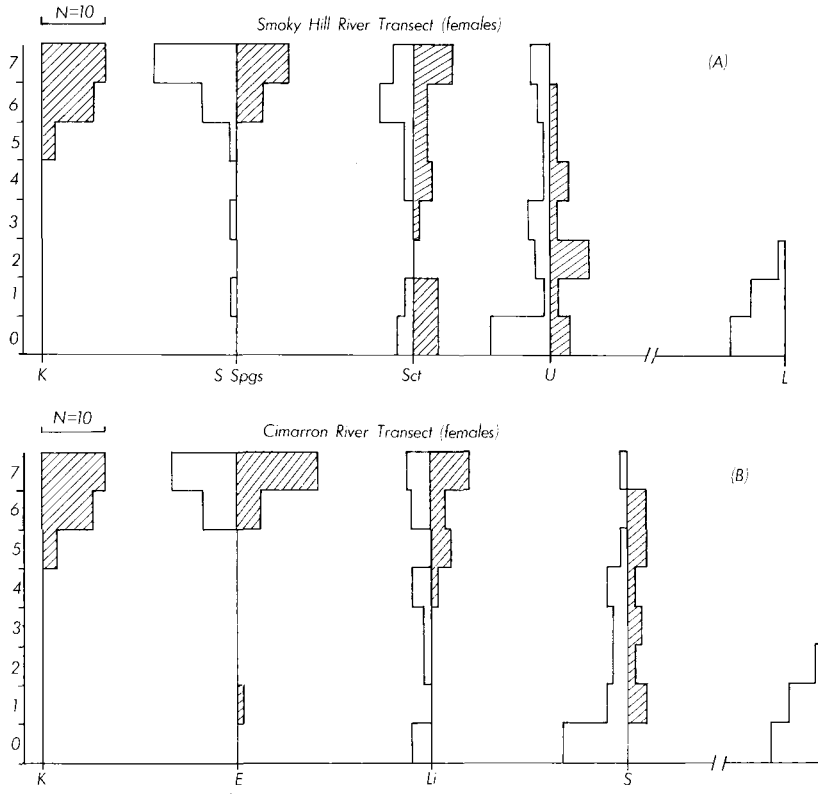


Fig. 4. Histograms of the character index scores of female orioles collected in the mid-1960's (open) contrasted with those collected in the late 1970's (hatched). The vertical axes show the character index scores, which range from 0 (Baltimore-like) to 7 (Bullock's-like). For an explanation of horizontal axes, see the legend to Fig. 3. (A) illustrates the females from the Smoky Hill River transect; (B) illustrates the females from the Cimarron River transect.

of the individuals correctly as to locality. Univariate (ANOVA, followed by an SNK test) analysis of the DF1 scores of the females from the eight localities identifies the following statistically homogeneous sets: (1) Ontario + Sitka + Utica, (2) Sharon Springs + Scott City + Liberal + Elkhart, and (3) Kenton.

As with the males, the female Bullock's Orioles are equal to or larger than Baltimore females for all 26 variables (Table 3). The means and variances of the female DF1 scores are given in Table 4. The females from Sitka and Scott City are significantly more variable than those from the Baltimore reference or Elkhart. The females from the Bullock's reference sample are more variable than those from either the Baltimore reference sample or some of the other "hybrid zone" samples (e.g. Elkhart, Liberal, Sharon Springs), though not significantly more variable.

The clines of both plumage and size variation of both sexes and river systems are plotted in Fig. 5. Both character sets change greatly in the relatively restricted area of western Kansas, though the patterns differ sufficiently to suggest that there is not a tight genetic linkage between the size- and color-pattern features. The size variation in males is nearly ramp-clinal (recall the left-most sample for size variation is Ontario and New York, not eastern Kansas), and the most variable samples (Scott City and Elkhart) are thus samples from along a clinal pattern. As a consequence of gene flow among localities, we would expect such samples to have higher variances than samples from regions where there is little geographic variation (e.g. the eastern reference sample in this case). Size variation for the females shows step-clinal variation, with the most variable populations at either end of the step (e.g. Sitka, Kenton)

TABLE 4. Statistics for discriminant function 1 scores.

Sample	Males			Females		
	<i>n</i>	Mean	Variance	<i>n</i>	Mean	Variance
Baltimore reference ^a	38	1.85	0.689	15	-1.12	0.539
Bullock's reference ^b	33	-1.32	0.798	19	1.22	1.207
Elkhart, Kansas	39	-0.69	1.650	20	0.48	0.574
Liberal, Kansas	39	-0.16	1.051	12	0.24	0.660
Sitka, Kansas	34	0.39	0.715	12	-1.08	1.512
Sharon Springs, Kansas	38	-0.57	0.970	11	0.16	0.697
Scott City, Kansas	30	0.11	1.390	21	0.20	1.578
Utica, Kansas	27	0.43	0.655	14	-0.84	1.031

^a Ontario and northeastern states.

^b Kenton, Oklahoma and adjacent New Mexico.

along the Cimarron River but in the middle on the Smoky Hill River. Spearman's Rank Correlation Coefficient between the variance of the DF scores and the variance of the CI scores was calculated for males ($r_s = 0.38$, $n = 8$, n.s.), for females ($r_s = 0.71$, $n = 8$, $P = 0.02$), and for the sexes combined ($r_s = 0.45$, $n = 16$, $P = 0.04$). On the whole, where variance in plumage (CI scores) is high, variance in size and shape (DF scores) is high; females from Elkhart are an exception, and the trend in males is not significant.

There is a significant correlation between the CI and the DF1 scores for all males pooled ($\tau = -0.37$, $n = 158$, $P < 0.001$) and for all females pooled ($\tau = 0.26$, $n = 103$, $P < 0.001$). (The correlation for males is negative, because Bullock's Orioles have large CI values and small DF values, and Baltimore Orioles the reverse.) Within localities, however, none of the correlations for females is significant, and only those of the males from the "hybrid" localities are significant (Liberal, $\tau = -0.36$, $n = 23$, $P = 0.009$; Scott City, $\tau = -0.30$, $n = 23$, $P = 0.03$; Liberal + Scott City, $\tau = -0.37$, $n = 46$, $P = 0.001$). (Within "non-hybrid" localities correlations are nearly zero.)

Assortative mating.—The Spearman's Rank Correlation Coefficient between the CI scores of females and those of their apparent mates is not significant ($r_s = 0.10$, $n = 23$, $P = 0.64$); similarly, the DF1 scores of females and those of their mates are not significantly correlated ($r_s = -0.10$, $n = 20$, $P = 0.68$). (Inasmuch as female Baltimore Orioles have negative DF scores and male Baltimore Orioles have positive ones, this value is "in the right direction" but clearly not significant.) Hence, there is no evidence of nonrandom association in these data.

Weather analysis.—The stepwise multiple regression analyses of male and female CI and DF1 scores with 10 weather variables all show that the best climatic predictor of oriole "type" is average annual precipitation. Univariate Pearson's correlations between DF and CI scores and average annual precipitation are all high (range from 0.88 to 0.94). In other words, about 85% of the interpopulational variation in phenotype is "explained" by interlocality variation in precipitation.

There are no significant differences in the average weather conditions (summer rainfall or temperature) at either Goodland or Dodge City between the two 11-yr periods, 1954-1964 and 1965-1975. In fact, the 11-yr means are quite similar. There is a great deal of year-to-year variation, however. For example, the early summers in southwestern Kansas were particularly dry in both 1976 and 1977 and particularly wet in 1978; the spring of 1978 was unusually cold, with snow falling in early May (after the return of many orioles). Many may have perished in Kansas as a consequence of the snow that year (Flood in press). It may be the "unusual" years, rather than average ones, that select for one oriole relative to the other. Indeed, N. J. Flood and L. L. Short (pers. comm.) have noted year-to-year fluctuations in numbers of orioles along some trans-Plains rivers. Perhaps orioles are periodically decimated by catastrophes in this area with subsequent recolonization (possibly of necessity mostly by "pure" types), followed again by hybridization and backcrossing.

DISCUSSION

There is geographic variation in plumage pattern as well as in size among orioles in west-

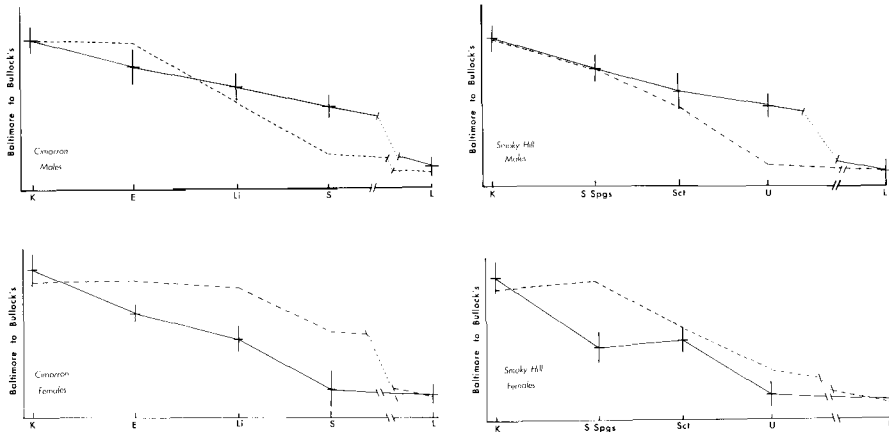


Fig. 5. Comparisons of the clines for character index scores (dashed lines) and DF scores ("size") (lines) for male and female orioles from the Cimarron and Smoky Hill River transects. The vertical scales are scaled to range from Bullock's-like (high values) to Baltimore-like (low values); on the horizontal axes, the localities (Fig. 2) are ordered west to east, with the distances proportional to geographic distance. For the DF scores, the easternmost sample is not L (Lawrence, Kansas), but rather the Baltimore reference sample from Ontario and New York, ca. 1,500 km northeast of western Kansas.

ern Kansas. Within single populations, however, the correlations between plumage pattern and size are not great, suggesting that these are genetically and developmentally independent. The geographical variation in the plumage features is step-clinal, there being a step between populations comprised of birds with Baltimore Oriole plumage and populations comprised of birds with Bullock's Oriole plumage. The geographical variation in size, at least in females, is step-clinal as well and in both sexes more or less parallels the pattern of plumage variation.

Two hypotheses explain the origin of step-clines in general and, by inference, of the oriole step-cline in the Great Plains: (1) the two taxa differentiated in allopatry and are at present hybridizing in a zone of secondary contact (Mayr 1963, Sibley and Short 1964); and (2) there is clinal (i.e. ramp-clinal) geographic variation, the step resulting from the interaction of a few genetic loci and modifiers that differentially affect the fitness of different genotypes (Clarke 1966, Endler 1977). Without series of samples taken through time, it is difficult—perhaps impossible—to differentiate between "hybridization" and "geographic variation." The congruence of the size- and plumage-pattern clines suggests that these forms are interbreeding in a zone of secondary contact, merely because it is otherwise unlikely that independent patterns of character varia-

tion would correspond geographically. On the other hand, the absence of assortative mating is most easily explained if differentiation had occurred along a cline, without a period of geographical isolation.

There is no evidence of any change in the distributions of the males in western Kansas from the mid-1960's to the late 1970's. If the features that differ between Baltimore and Bullock's orioles were selectively neutral, we would find a broadening and flattening of the character step-clines; the rate of change in the clines would be influenced only by the rate of gene flow. Given such neutrality, however, these clines might change so slowly that differences would be imperceptible after only 11–13 yr (in these birds, that would be approximately 11–13 generations). Endler (1977) calculated the rate at which a step in a cline will broaden, assuming no selection (passive diffusion of "genes"). Given a single locus and uniform gene flow, the formula $w = 1.68l\sqrt{T}$ calculates the width of a cline at any time (T), where w is the width of the cline, l is the root-mean-square distance of gene flow each generation, and T is the number of years since secondary contact. [The differences in plumage pattern between Baltimore and Bullock's orioles (CI scores) are probably determined by only a few loci, and therefore the single-locus model is a good approximation of this system.] The width of the

oriole morph-clines in western Kansas is approximately 250 km (Figs. 3 and 4); unfortunately, the rate of gene flow among populations of orioles is not known. Barrowclough (1978, 1980) calculated root-mean-square dispersal distances for eight songbird species; these range from ca. 0.34 km/yr (Song Sparrows, *Melospiza melodia*, in Ohio) to ca. 1.7 km/yr (Bewick's Wrens, *Thryomanes bewickii*, in Oregon). If we assume that $l = 1.7$ km/yr for a Great Plains oriole, that $w = 250$ km, and selective neutrality, we calculate that the age of the (presumed) secondary contact is ca. 7,700 BP; the current rate of increase in the width of the step-cline is ca. 0.21 km in 13 yr. If we assume that the contact is only 100 yr old, l is 14.9 km/yr; the zone would increase in width by about 16 km in 13 yr. With the samples at hand, a change of even 16 km would not be detected with certainty, and therefore the lack of any demonstrable change in the step-clines for males does not constitute evidence of selective maintenance of the steps, unless we are considerably underestimating the rate of gene flow among these populations.

The situation with the females, however, differs. Along the Cimarron River, but not along the Smoky Hill River, the distribution of plumage phenotypes is shifting toward Bullock's-like orioles in the easternmost localities. This eastward shift suggests not only selective maintenance of the zone but also an eastward shift of conditions that favor female Bullock's Orioles. As mentioned above, about 85% of the inter-populational variation in either plumage characteristics or size can be "explained" as a function of variation in average precipitation among localities. The magnitude of these correlations, in fact, suggests that the ecological consequences of precipitation are a direct selective factor in the maintenance of the step-cline. The relatively paler colors of Bullocks' Orioles may increase their crypsis at the relatively arid western edge of the Plains; the differences in size may be directly adaptive as well. This, of course, remains to be tested, but we know of differences in response to high temperatures in laboratory situations (Rising 1969). The eastward shift of Bullock's Orioles along the Cimarron River would thus be expected if there had been a recent decrease in rainfall in that sector, but my analyses of the weather show no such changes, at least in 11-yr averages. It was particularly dry in southwestern Kansas during June of both 1976 and 1977 (I collected there

in June of 1978), however, and this might have caused a shift toward Bullock's-like orioles there.

The eastward extension of Bullock's Orioles along the Cimarron River in southwestern Kansas, coupled with the westward shift of Baltimore Orioles in the central and northern Plains (Fig. 1), indicates that the zone is "tipping" northwestward to southeastward, and doing so rather rapidly. We would expect this if Baltimore Orioles were selectively favored in the relatively mesic northern Plains and Bullock's Orioles in the relatively xeric southern Plains and if these birds had only recently colonized these parts of the Great Plains and their distributions had not yet stabilized. There are three reasons to suspect that Baltimore and Bullock's orioles are not adaptively equivalent in all environments of the Great Plains: (1) the laboratory indication of physiological differences, (2) the recent distributional changes along the Platte and Cimarron rivers, and (3) the nearly uniform width of the hybrid zone along each river system in the Plains. To expand a bit on the last point, Rising (1970, 1973) argued that the contact along the Cimarron River (unlike that along the Arkansas, Platte, and Missouri rivers) might have been of recent occurrence (less than 100 BP). In southwestern Kansas and the Oklahoma Panhandle the Cimarron carries little surface water (in many years it is dry for much of the summer), and until recently tree growth was considerably inhibited by the activities of bison (*Bison bison*) and prairie fires. Whereas flowing water would have protected small stands of trees along other watercourses, providing nesting sites and a route for the dispersal of orioles, such areas were scarce along the Cimarron (Rising 1974). Indirectly, this suggests that the contact along the Cimarron is considerably more recent than along most of the other transplains rivers, yet the hybrid zone there is comparable in width to that along other rivers (Rising 1970). A diffusion model (adaptive neutrality and gene flow) predicts that the width should be proportional to the age of contact. The only "new" evidence against a diffusion model that is presented here is the change in the distribution of the females along the Cimarron River. The changes manifested there in 13 yr suggest both rapid dispersal and selection; as discussed above, we would not expect to see a change in 13 generations in the absence of selection. Also, the fact that the zone has shifted, but not

apparently changed in width, along both the Cimarron and Platte rivers also is evidence of selection, not passive diffusion.

CONCLUSIONS

On the basis of male specimens, there is evidence neither of any change in the relative distributions of Baltimore and Bullock's orioles in western Kansas from the mid-1960's to the mid-1970's nor of selection against "hybridization" (if hybridization is occurring) or against males that are intermediate between these two orioles in plumage pattern. This is somewhat unexpected, as Rising (1970) saw some indication of bimodality in the character index scores of males collected near Scott City, Kansas in the 1960's, and Corbin and Sibley (1977) found a shift toward bimodality in orioles at Crook, Colorado (Fig. 1B). Nonetheless, the males collected at Scott City in 1976 are, if anything, less bimodal than those previously collected at that locality. Because of the lack of information about dispersal rates, however, this lack of change in itself cannot be taken yet as strong evidence for a stable step cline, maintained by a balance between gene flow and natural selection.

There has been a change in the distribution of females along the Cimarron River, however. In the 1970's, Bullock's-like females occurred approximately 100 km farther east than they did in the mid-1960's. The close correspondence between the distributions of the orioles and the quantity of precipitation suggests that this change in range is in response to a change in climate, but there has been no such change, at least in 11-yr averages, during this time. Alternatively, Bullock's Orioles may have moved eastward along the Cimarron during the dry years of 1976 and 1977 or disproportionately survived the cold snowy spring of 1978. I suggested above that orioles might be locally decimated by natural catastrophes from time to time. When a population in the "hybrid zone" is affected, recolonization of necessity would be from populations of either Baltimore or Bullock's orioles. Soon after recolonization, such a population would be bimodal, reflecting the phenotypes of the founders. Later, after a few generations of random mating, a mixed population occurs. This model explains in part what has been observed in males in Kansas and in Nebraska and Colorado, but other than some indication of catastrophes, there is no direct

evidence for it. The changes along the Platte and Cimarron rivers are similar at adjacent localities: along the Platte, male Baltimore Orioles are replacing Bullock's both at Big Springs and to the west at Crook; along the Cimarron, female Bullock's Orioles are replacing Baltimore Orioles both at Liberal and to the east at Sitka. If the catastrophe theory is correct, it implies that decimation occurred in an entire region (e.g. southwestern Kansas). Alternatively, these changes might reflect ongoing changes in distribution, but, in the absence of any long-term climatic changes, it is not clear why this should be occurring. One possibility is that there has been a recent (within the last 100 generations?) secondary contact and the relative ranges of the two have not yet stabilized; inference from historical evidence makes such a recent contact, at least along the Platte, unlikely.

In any case, there does not appear to be selection against intermediate individuals in the "hybrid zone." If there is selection against at least some of the features of Baltimore Orioles at the western edge of the zone and against some of those of Bullock's Orioles at the eastern edge, we can expect the hybrid zone to persist—perhaps even to shift in geographic position if the environment shifts—without changing in width.

The patterns of geographic variation in plumage pattern and size are similar in western Kansas for both sexes. The low correlations between size and pattern within populations, however, indicates that these are nearly independent sets of characters in a genetic sense. It has been generally assumed that these two orioles diverged both in size and color pattern in allopatry (Sibley and Short 1964) and are now hybridizing in a zone of secondary contact, but it is also possible that the differences between them evolved without extrinsic isolation (Rising 1970). The congruence in the patterns of geographic variation of size and color is most easily explained if secondary contact has occurred, but the apparent random mating is most easily explained if divergence was along a cline.

ACKNOWLEDGMENTS

I thank George Barrowclough, Kendall Corbin, Francis Cook, Nancy Flood, David MacKenzie, Trudy Rising, Fred Schueler, Lester Short, and Richard Snell for reading and making many constructive comments on the manuscript and the game and fish com-

missions of the states of Kansas, Oklahoma, and New Mexico for granting me collecting permits. I appreciate the help and hospitality of many ranchers, as well, especially Maurice Barr, Vaughan Chisum, L. L. Lashell, and Delano Schwindt. This research was financed by a grant from the Natural Science and Engineering Research Council of Canada.

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