

THE STABILITY OF THE ORIOLE HYBRID ZONE
IN WESTERN KANSAS¹

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INTRODUCTION

In the Great Plains of North America a number of species of birds that breed in woodland edge in the east are replaced by western counterparts (Rising 1983a). In many instances (*Colaptes*, *Passerina*, *Pheucticus*, *Pipilo*, and *Icterus*) the counterpart congeners apparently hybridize, often rather commonly, where their ranges are in contact. It is widely postulated that these eastern and western counterpart taxa differentiated in allopatry during the Pleistocene (Mengel 1970), and today are interbreeding following rather recent secondary contact (Rising 1983a). The consequences of this hybridization are not clear, but may be clarified by long-term studies (Selander 1965, Yang and Selander 1968, Rising 1983b, Moore and Buchanan 1985).

The eastern Baltimore Oriole (*Icterus galbula*) and the western Bullock's Oriole (*I. bullockii*) are among the best studied of these east-west species pairs (Rising 1983a, 1983b). They hybridize in a zone of apparent secondary contact that runs from southwestern Alberta south through northeastern Montana and western North and South Dakota, Nebraska, Kansas, and Oklahoma. In 1965 and 1966 I collected orioles in riparian woodlands (principally cottonwoods [*Populus*]) from 14 sites along four river systems in western Kansas, the Republican, Smoky Hill, Arkansas, and Cimarron, that run essentially west to east through the oriole hybrid zone (Rising 1970). In 1976 and 1978, I recollected orioles from six of the sites that I had previously collected in the 1960s, along the Cimarron and Smoky Hill rivers, as well as a sample of Bullock's Orioles from along the Cimarron River near Kenton, Oklahoma, on the Oklahoma-New Mexico border (Rising 1983b) to serve as a western reference sample. Here I report on orioles that I collected in 1992 and 1993 from the same sites, shown in Figure 1, that I had collected in the 1970s; in 1992, I also collected a sample of Baltimore Orioles from central (Rice Co.) Kansas, to serve as an eastern reference sample. These three sets of collections, taken over a nearly 30-year span, allow me to directly assess the changes of oriole hybridization in western Kansas.

METHODS

Baltimore and Bullock's orioles are strikingly dichromatic in plumage color. Males have a bright display plumage, which they do not obtain until their second summer. Although there is little interindividual variation in plumage coloration of ASY (after second year) males, breeding females are highly variable in coloration, probably becoming more brightly colored with age; second year males resemble breeding females. In previous studies, I and others have relied heavily on a character index analysis of features of the plumage of ASY males. The index that I have used (Rising 1970) scores 14 plumage features from the head, wing and tail, and ranges from 0 (typical Baltimore plumage) to 29 (typical Bullock's plumage). For this study, I scored each of the 128 male specimens collected in the 1990s, rescored the 165 specimens collected in the 1970s, and tested the significance of differences in the distributions of the scores among years with the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf 1995).

The samples examined are listed in Table 1. Although I have no quantitative information on changes in abundance of orioles in western Kansas, it was my impression that their numbers were substantially lower at most sites in the 1990s than I had found on earlier occasions, making it difficult in some cases to obtain a reasonable sample from the site where I had previously collected. This was particularly true for the Sitka sample. In June 1978, collecting alone, I was able to obtain a large sample there in a single morning, whereas in 1992–1993 an assistant and I were able to collect only nine individuals in two full days, forcing us to augment the Sitka sample with birds collected near Protection, Comanche County (Table 1). As well, the site in Scott County where I collected most of my birds in the 1960s and 1970s is now a state park, and consequently it was necessary for me to collect the 1990s sample from several sites near the park. Similarly, I was unable to obtain permission to collect at the same site near Kenton as in 1976, but collected nearby (Table 1). Thus, these samples, unlike the others, are not directly comparable to those taken previously, but were collected in nearby areas.

RESULTS AND DISCUSSION

The character index scores from the samples from along the Cimarron River are illustrated in Figure 2a, and those from the along the Smoky Hill River in Figure 2b. The east-to-west clines in plumage coloration are clear along both river systems, but none of the differ-

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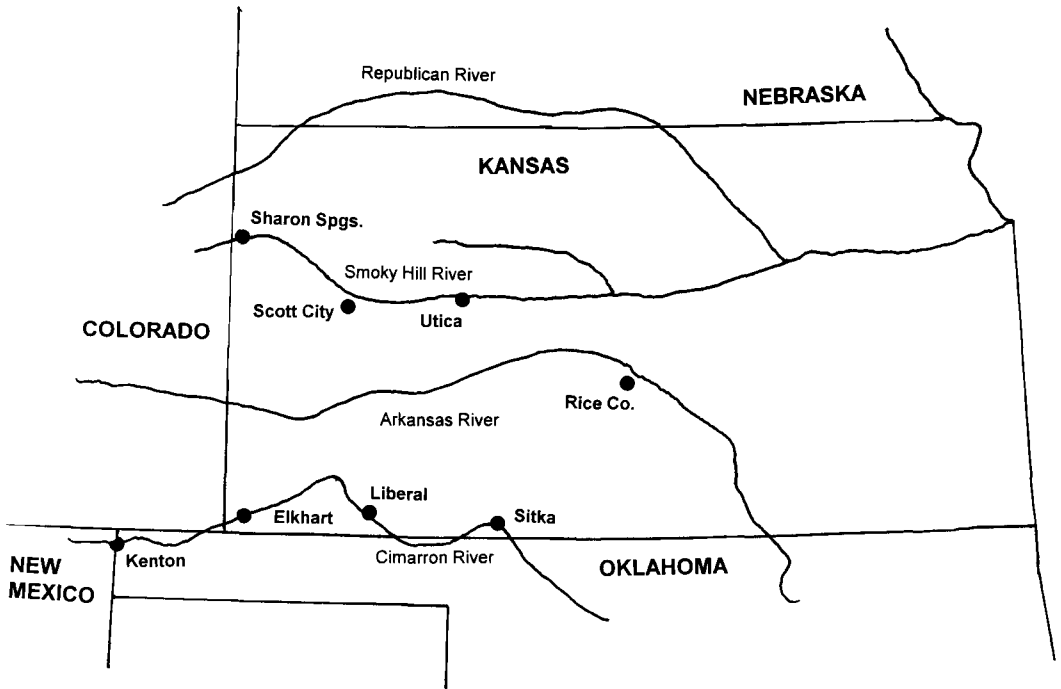


FIGURE 1. Oriole collection sites in the 1970s and 1990s for this study.

ences in distribution among years are significant ($P > 0.05$, e.g., there is no significant difference among the scores for the three samples of birds from Scott City). Also, a substantial number of individuals, even in the center of the hybrid zone (Scott City, Liberal) are apparently non-hybrids, and this has remained true for the nearly 30 years of this study.

Historically, it was commonly argued that hybrid zones, though perhaps apparently stable, were ephemeral on a time scale of hundreds or perhaps thousands of years, and would become wider as interbreeding and backcrossing progressed. Alternatively, a zone stable through time either may be dynamically maintained by the interaction between selection and gene flow, or

TABLE 1. Samples of Orioles Examined.

Locality	1960s	1970s	1990s	Dates specimens collected
Rice Co: 7 km S, 5 km W Silica, Rice Co., KS	—	—	3	7 June 1992
2 km S, 1 km E Silica, Rice Co., KS	—	—	3	7 June 1992
3 km W Raymond, Rice Co., KS	—	—	3	7 June 1992
4 km W Raymond, Rice Co., KS	—	—	2	8 June 1992
Sitka: 13 km S Sitka, Clark Co., KS	25	23	9	30 May 1992, 24 June 1993
1 km N Protection, Comanche Co., KS	—	—	9	25 June 1993
Liberal: 18 km NE Liberal, Seward Co., KS	26	23	20	5–6 June 1992
Elkhart: 12 km N Elkhart, Morton Co., KS	26	21	20	2 June 1992
Kenton: 4 km W Kenton, Cimarron Co., OK	—	26	3	31 May 1992
4 km W, 3 km S Kenton, in Union Co., NM	—	—	5	31 May 1992
8 km E Kenton, Cimarron Co., OK	—	—	4	1 June 1992
Utica: 16 km N, 3 km E Utica, Trego Co., KS	23	21	18	26 June 1993
Scott City: 17 km N, 1 km W Scott City, Scott Co., KS	28	26	3	28 June 1993
12 km N, 2 km W Scott City	—	—	2	28 June 1993
29 km N Scott City, in Logan Co., KS	—	—	8	28 June 1993
29 km N, 2 km W Scott City, Scott Co.	—	—	5	28 June 1993
Sharon Springs: 8 km N, 2 km W Sharon Spgs., Wallace Co., KS	28	25	11	30 June 1993

Cimarron River Transect

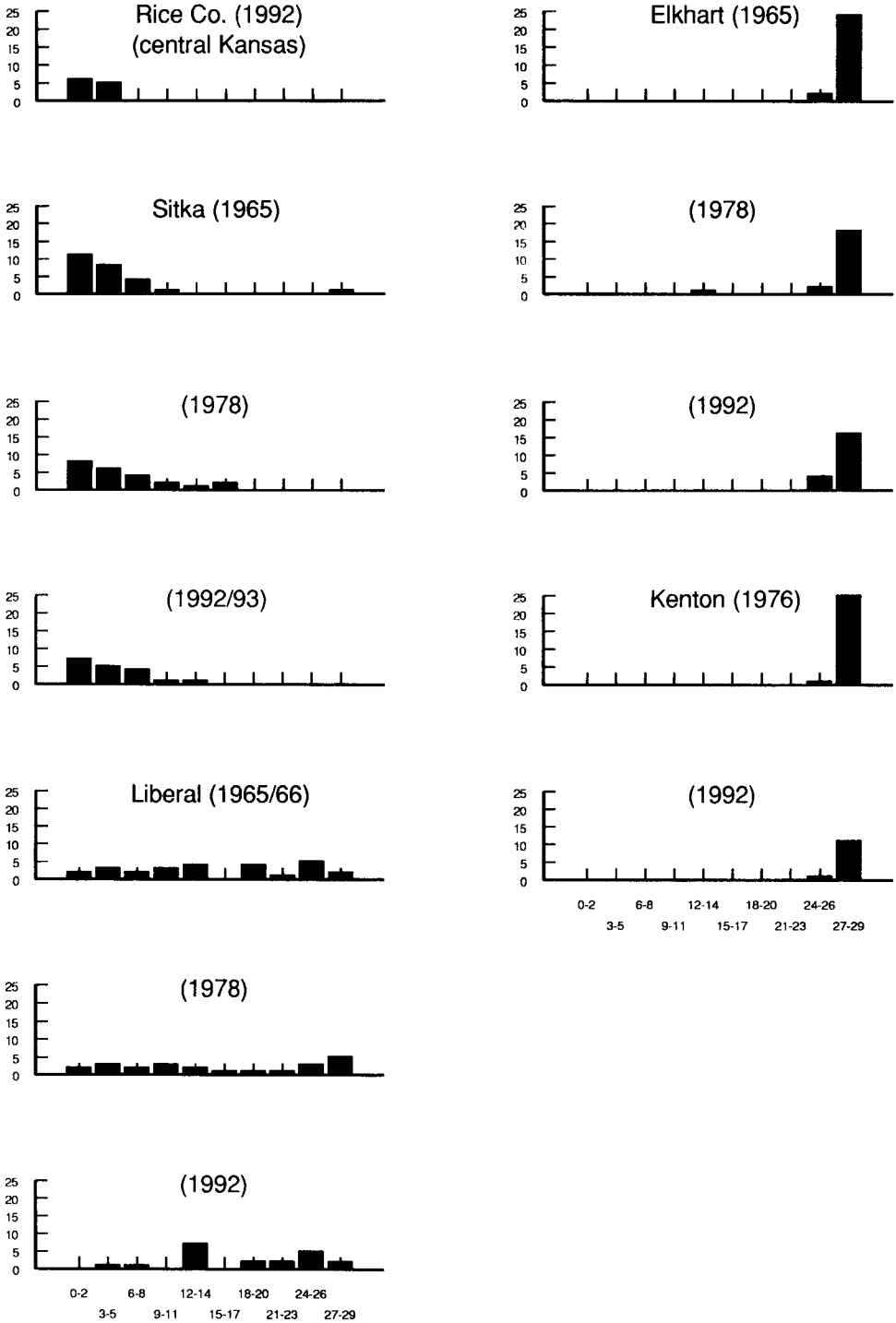
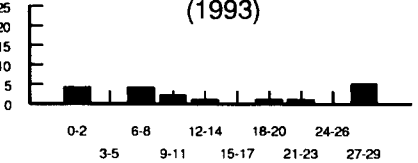
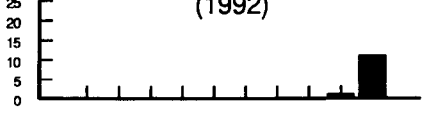
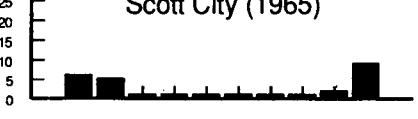
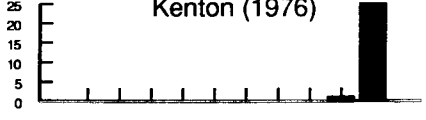
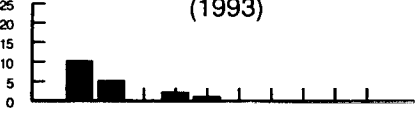
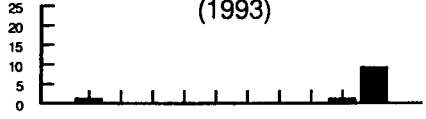
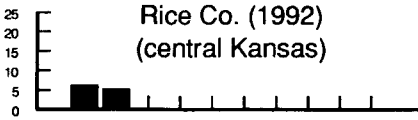


FIGURE 2. Character index scores of adult male orioles collects in the Great Plains in the 1960s, 1970s and 1990s. The index scores range from 0 (typical Baltimore Oriole) to 29 (typical Bullock's Oriole). Scores are grouped into 10 groups of three adjacent scores, 0-2, 3-5, etc. with the lowest (most Baltimore-like) scores to

Smoky Hill River Transect



0-2 6-8 12-14 18-20 24-26
3-5 9-11 15-17 21-23 27-29

the left. In 2a, scores for the Cimarron River Transect, with samples from Rice Co., Ks and Kenton, OK/NM included for reference. 2b, scores for the Smoky Hill River Transect, with reference samples.

form in troughs of low population density (Barton and Hewitt 1985, Hewitt 1989).

Here I see no evidence of any change either in the center of the zone or in its width in western Kansas, and this can be taken as supporting one of the stable zone hypotheses. Inasmuch as the oriole hybrid zone follows a zone of climatic transition from Alberta to Texas, separating the relatively humid low plains from the dryer high plains, I have argued (Rising 1970, Rising 1983b) the zone is maintained by selection against Bullock's Orioles east of the zone and Baltimore Orioles west of it, and there is evidence that the Bullock's Orioles tolerate higher temperatures than Baltimore Orioles (Rising 1969). Along the Smoky Hill River, vegetation suitable for orioles extends only a few kilometers west of the site where I collected the Sharon Springs sample, and to the east of there Baltimore Orioles become increasingly prominent (Fig. 2b). Therefore, the number of Bullock's Orioles living along that river must be small; the nearest other population of Bullock's Orioles is along the Arkansas River, over 100 km to the south, and there is no suitable habitat to the west or northwest for over 250 km. Thus, immigration into the western Smoky Hill area must be predominantly of Baltimore or hybrid orioles. There is, however, a small and stable population of Bullock's Orioles there, with only a few Baltimore phenotypes present, suggesting that Bullock's are selectively favored along the western-most areas of the Smoky Hill River. If the zone were forming in a density trough (Hewitt 1989), it would seem that Bullock's Orioles would be extirpated along the Smoky Hill River.

As noted above, in the absence of selection we would expect the hybrid zone to increase in width. The rate at which this would happen, however, would depend on dispersal rates. Barrowclough (1978, 1980) calculated dispersal distances for eight songbird species; these ranged from about 0.34 to 1.7 km/year. Given the latter figure, we could expect the zone to have increased in width by less than 0.5 km since the mid-1960s if there were no selection. This is a distance that would not be detectable by the methods used here. Thus, if Barrowclough's estimates of dispersal rates are appropriate for plains orioles, the absence of any detectable change in the width of the zone in approximately 30 years is not compelling evidence for selection against hybridization. On the other hand, we do know of cases where the location of hybrid zones have changed markedly in this amount of time (*Vermivora* in New England [Gill 1979]; *Corvus* in Scotland [Sharrock 1976]).

Edinger (1985) found mating to be significantly non-random and assortative in a mixed population of orioles near Crook, Colorado, and all mixed pairs involved Baltimore males with Bullock's females, and usually SY (second year) Baltimore males with Bullock's females. He also found that Baltimore pairs fledged significantly more young than did either Bullock's pairs or mixed pairs, but that there was no significant difference in the fledging success of Bullock's pairs and mixed pairs. To the human eye, the males of the two species are more similar in color in their SY (second year) plumage than in their ASY plumage. If female orioles discriminate between males on the

basis of their appearance, they would be more likely to mistake a male of one species for the other in the SY plumage. Also, female Bullock's Orioles nested later than female Baltimore Orioles at Crook, leaving fewer unmated males available for Bullock's females to mate with, and because SY males nest later than ASY ones (Flood 1984), proportionally more of the males available for Bullock's females would be SY. The assortative mating described by Edinger may explain the rather large number of apparently non-hybrid individuals found at all sites in western Kansas.

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