

RAPID EVOLUTION IN ORIOLES OF THE GENUS *ICTERUS*

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Hybridization involving orioles of the genus *Icterus* has been extensive throughout the Great Plains of North America, from southern North Dakota to north central Texas. The first specimens to be recognized as hybrids were described by Sutton (1938), and the zone of hybridization has been studied by Sibley and Short (1964), Rising (1968, 1969, 1970, 1973), Anderson (1971), and Misra and Short (1974). The specimens collected during the 1950's by Sibley and Short (1964) indicated that the parental forms were behaving biologically as subspecies. As clarified by Short (1969), the parental types were allopatric and separated by a hybrid zone. At that time *there was no zone of overlap and hybridization, within which both parental types existed in sympatry* and in a combined frequency greater than 5% of the total population. That is, there was no apparent reinforcement of isolating mechanisms. In 1973 the A.O.U. Check-list Committee accepted the recommendation by Sibley and Short (1964) that the western forms (*bullockii*) be treated as subspecies of *I. galbula*. This decision was based primarily on birds collected along the Platte River, extending from Greeley, Colorado to Blair, Nebraska. However, Rising (1968, 1970) believed that the "Bullock's Oriole" and "Baltimore Oriole" should not be treated as conspecific until the extent of introgression was better known.

During the breeding seasons of 1970, 1971 and 1974, we collected additional orioles to measure the extent of introgression by means of an electrophoretic analysis of protein polymorphism. The results of that analysis, to be discussed elsewhere, showed that a smooth cline in allelic frequencies existed over much of the range sampled except for the population at Crook, Colorado. Further analysis of the birds collected in 1970, 1971 and 1974 indicates that reproductive isolating mechanisms are being reinforced at some localities and that the "Bullock's Oriole" and "Baltimore Oriole" are sympatric, although hybridizing, over an area extending for at least 80 km along the Platte River in eastern Colorado and western Nebraska. The analysis and dis-

ussion of these data are presented in this paper.

MATERIALS AND METHODS

Two collections of adult orioles provide the data for this paper. The first consists of 271 birds collected during the 1950's by Sibley and Short (1964) from the following localities: Nebraska: Blair, Schuyler, Gothenburg, Sutherland, and Big Springs; Colorado: Crook, Fort Morgan, and Greeley. The data for these birds are presented in Table 5 and Figure 2 of Sibley and Short (1964) and in Tables 1 and 2 of Misra and Short (1974). The second group of birds includes 231 adult males collected during the breeding seasons of 1970, 1971 and 1974 (these specimens are now in the collection of the Peabody Museum of Natural History, Yale University). The localities sampled are given in Figure 1 and Table 1. The hybrid index technique used by Sibley and Short (1964: Table 2) was used to analyze the birds collected in 1970-1974.

To determine if we were assigning comparable scores to character states recognized by Sibley and Short (1964), the birds they collected at Big Springs, Nebraska and Crook, Colorado were analyzed independently (Corbin and Barrowclough 1977). Each specimen was rescored and the two data sets then compared by an analysis of variance. The differences in scores between the two sets of measurements (raw data of Sibley and Short are unpublished), either for individual character scores or for the resulting hybrid indices, were not significant.

RESULTS

HYBRID INDEX ANALYSIS

The frequency distribution of the hybrid indices for each of the localities we sampled is shown in Figure 1. The means and the standard errors of the means for the individual character index values and for the hybrid indices for all birds collected in 1970, 1971 and 1974 are given in Table 1.

The mean hybrid indices of birds collected in 1955-1956 were compared to those of 1970 and 1974 using the *t* test (Table 2) after showing that the hybrid indices within localities were normally distributed. In cases where the same locality was not sampled in both the 1950's and the 1970's, localities closest to one another were chosen for the comparison; in all instances the two collecting localities of a pair were within 60 km of one another. The distributions and means for three of these pairs of localities are signifi-

TABLE 1. Character and hybrid indices for 1970-74 birds.

	Connecticut		Pennsylvania		Missouri		Nebraska					
	Madison (15)*		Clearfield (15)		Columbia (18)		Venice (20)		Cozad (14)		Big Springs (25)	
	\bar{x}	S.E.	\bar{x}	S.E.	\bar{x}	S.E.	\bar{x}	S.E.	\bar{x}	S.E.	\bar{x}	S.E.
Superciliary	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.071	.071	.800	.265
Forehead	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.280	.136
Side of neck	0.00	0.00	.267	.118	.111	0.76	.250	.099	.071	.071	.600	.129
Ear coverts	0.00	0.00	.333	.126	.222	.101	.150	.109	.286	.125	.320	.198
Throat	.400	.190	.400	.163	.667	.181	.550	.170	.500	.174	1.280	.204
Wing bar	0.00	0.00	.067	.067	.111	.076	.400	.152	.071	.071	1.040	.204
Wing coverts	.733	.206	.333	.159	.111	.076	.250	.099	.357	.169	1.200	.200
Tail base	.067	.067	.533	.215	.500	.167	.450	.135	.357	.169	1.120	.307
Tail tip	.200	.145	.400	.131	.111	.076	.600	.184	.286	.125	1.080	.182
Hybrid index	.800	.200	1.267	.284	.944	.235	1.500	1.99	1.214	.214	3.440	.451

	Colorado									
	Crook, 1970 (19)		Crook, 1974 (61)		Fort Morgan (12)		Fort Collins (16)		Glenwood Spgs (16)	
	\bar{x}	S.E.	\bar{x}	S.E.	\bar{x}	S.E.	\bar{x}	S.E.	\bar{x}	S.E.
Superciliary	1.579	.428	1.279	.214	3.583	.149	3.750	.112	3.563	.128
Forehead	.526	.177	.607	.105	1.250	.131	1.688	.120	1.500	.158
Side of neck	.895	.215	.623	.110	2.000	0.00	1.938	.063	1.938	.063
Ear coverts	1.526	.393	1.131	.222	4.000	0.00	3.938	.063	3.938	.063
Throat	1.842	.299	1.279	.174	4.000	0.00	3.813	.101	3.813	.101
Wing bar	1.474	.400	1.311	.212	4.000	0.00	4.000	0.00	3.938	.063
Wing coverts	1.632	.344	1.770	.206	4.000	0.00	3.938	.063	3.875	.085
Tail base	1.474	.362	1.475	.207	3.833	.167	3.563	.157	3.563	.157
Tail tip	1.579	.392	1.016	.189	3.500	.195	3.438	.223	3.438	.182
Hybrid index	4.789	.903	4.443	.582	11.056	.221	11.188	.209	10.813	.187

* Numbers in parentheses indicate sample size.

cantly different for the two sampling periods although only two of these are indicated in Table 2. The 1970 and 1974 distributions of hybrid indices for Crook, Colorado are significantly different from those obtained in 1955-1956. However, the distributions cannot be compared by means of the t test because the 1970-1974 distributions are bimodal as discussed below. The t values for the comparisons involving Gothenburg-Cozad and Big Springs are significantly different at the .001 level. These changes in time are indicated in Figure 2.

COMPARISON AMONG SAMPLING PERIODS

The population sample taken in 1974 from Crook, Colorado appears to be bimodally distributed (Fig. 1). To test this, the 1974 distribution was first compared to a normal distribution having an identical mean (4.442) and standard deviation (4.544). Using the Kolmogorov-Smirnov one-sample test, the observed distribution is significantly different from a normal distribution (maximum $\alpha = .263$, $P < .01$). Secondly, the 1974 distribution at Crook was compared, by means of the Kolmogorov-Smirnov two-sample test, to the combined distributions of Madison, Connecticut (*galbula* phenotype) and Glenwood

Springs, Colorado (*bullockii* phenotype). In this instance the distribution at Crook was not significantly different from the bimodal distribution of the two parental phenotypes (maximum $\alpha = .229$, $P > .05$). Finally, to compare the distributions at Crook, Colorado in 1955-1956, 1970, and 1974, the Kolmogorov-Smirnov two-sample test was again used. The distribution in 1955-1956 was significantly different ($P < .01$) from those of both 1970 and 1974 (Table 3).

Changes in the average hybrid index value of the population may be effected in one of several ways depending upon the net changes in the composition of the individual morphological types making up the population. Figure 3 illustrates the ways in which the composition of the populations at Crook, Colorado and Big Springs, Nebraska have changed relative to the percentages of the hybrid and parental phenotypes present in the populations as a function of time. At Crook, Colorado, the predominant phenotype present in the 1950's was that of *I. g. bullockii* whereas in the 1970's it was *I. g. galbula*. The combined frequency of the parental phenotypes was higher at all times than that of the hybrids; over that time the frequency of hybrids declined somewhat. For the population at Big Springs, Nebraska the relative frequen-

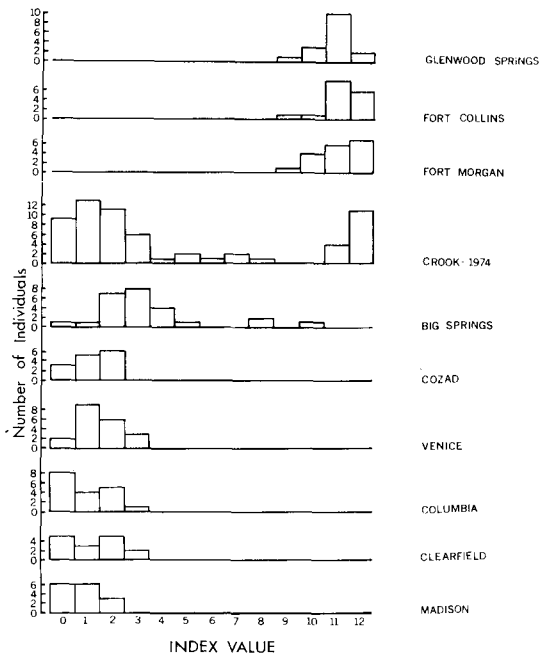


FIGURE 1. Distribution of hybrid indices assigned to individual birds collected at 10 localities in 1970, 1971 or 1974. Values range from 0 for *Icterus galbula galbula* to 12 for *I. g. bullockii*.

cies of the two parental phenotypes also reversed between 1955–1956 and 1974. However, at that locality hybrids were more frequent than parental phenotypes throughout the two decades. The frequency of hybrids decreased slightly from 1955–1956 to 1974.

DISCUSSION

The history of the hybridization between the “Baltimore” and “Bullock’s” orioles has been dealt with by Sibley and Short (1964), Sutton (1968), Rising (1970, 1973), and Anderson (1971). These authors also documented the extent of hybridization during the decade between 1955 and 1965. At that time a hybrid zone (as defined by Short 1969) approxi-

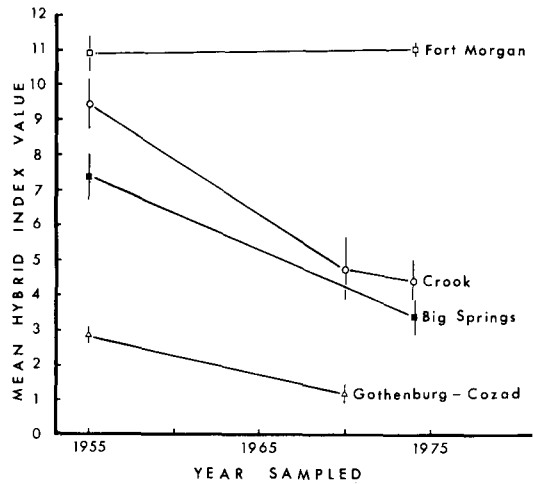


FIGURE 2. Changes in the mean hybrid indices at localities sampled in 1955–1956, 1970, and 1974. The vertical lines indicate \pm one standard error of the mean values.

mately 320 km wide extended from southern North Dakota through central South Dakota, central and western Nebraska, eastern Colorado, western Kansas, western Oklahoma and into the north central area of Texas. In 1955–1956 the transition of morphological types along the Platte River transect proceeded from pure “Baltimore” orioles in eastern Nebraska through a hybrid zone which began near Gothenburg, Nebraska, on the east and extended westward to Crook, Colorado, and then to the pure “Bullock’s” type. At no point in this distribution were the two parental types sympatric at combined frequencies greater than 5% of the total population (Sibley and Short 1964). As discussed by Short (1969), there was evidence of introgression immediately adjacent to the hybrid zone, parental populations were allopatric to one another, and the parental types were most appropriately dealt with as subspecies of *Icterus galbula*. The re-examination of these data by Misra and Short (1974) did not alter the con-

TABLE 2. Comparison of mean hybrid indices of birds collected in 1955–56 and 1970–74.

Locality	Mean Hybrid Indices				d.f.	t
	1955–1956		1970–1974			
	\bar{x}	S.E.	\bar{x}	S.E.		
Schuyler-Venice	1.549	.152	1.500	.199	69	.196
Gothenburg-Cozad	2.878	.203	1.214	.214	61	5.679***
Big Springs	7.389	.677	3.440	.451	41	4.857***
Crook	9.438	.724	4.442	.581		a
Fort Morgan	10.917	.313	11.056	.221	28	.363
Greeley-Fort Collins	11.231	.169	11.188	.209	40	.159

*** Significant at the .001 level.
 a A t value for Crook is omitted because the distribution of hybrid indices for 1955–1956 is significantly different from that for 1970–74. The former is unimodal whereas the latter is bimodal as discussed in the text.

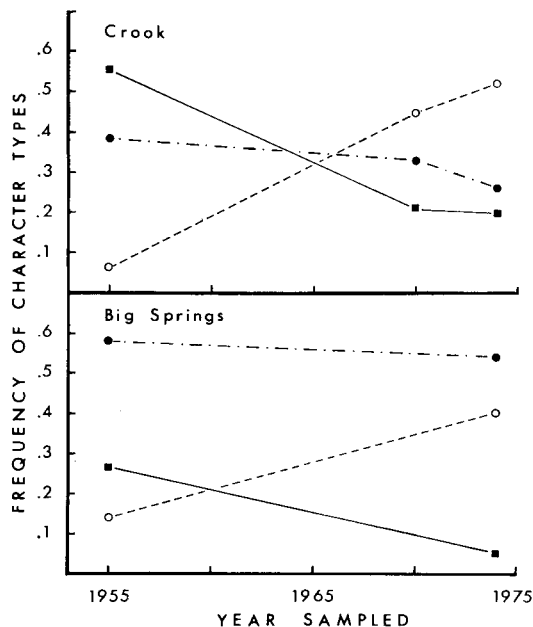


FIGURE 3. Changes in the frequencies of individual plumage character phenotypes as a function of the year in which the respective localities were sampled. White dots indicate the frequency of plumage characters assigned the value of 0 and equivalent in appearance to *Icterus galbula galbula*. Squares indicate the frequency of plumage characters assigned values of 4 (or 2 for forehead and side of neck patterns) and equivalent in appearance to *I. g. bullockii*. Black dots indicate the frequency of characters assigned intermediate values of 1, 2 or 3 (or 1 for forehead and side of neck patterns) and equivalent in appearance to hybrids between *I. g. galbula* and *I. g. bullockii*.

clusions of the earlier study by Sibley and Short (1964).

Ideally, the assignment of index scores to the individual plumage characters is done so as to include all the variation within the "pure" parental populations. That is, a hybrid index value of 0 theoretically accounts for the total individual variation found in a sample of pure "Baltimore" orioles; the value 12 accounts for the total variation in a sample of pure "Bullock's" orioles. Consequently, in the analysis of hybrid populations, a bird having an intermediate hybrid index value of 1 through 11 would be a hybrid by definition. The degree of correspondence between theory and application will depend on how well the variation in parental populations can be measured at the time the hybrid index is constructed.

When hybrid indices were first assigned to the orioles, it was recognized that the easternmost and westernmost populations sampled might not provide adequate measures of the

pure parental types. Sibley and Short (1964: 138) stated that "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)." That is, individuals in a pure "Baltimore" population might be indexed as either 0 or 1 whereas those in a pure "Bullock's" population might be indexed as either 11 or 12. Figure 1 shows that this was a fair estimate if we assume that the variation found in the populations of Madison, Connecticut and Glenwood Springs, Colorado is not due to introgression of alleles from the alternate parental types. The hybrid indices 0 and 1 encompass 80% of the sample from Madison, Connecticut; the values 11 and 12 encompass 75% of the sample from Glenwood Springs, Colorado. To be consistent with the previous analyses of orioles, we adhere to the former interpretation of the hybrid indices. However, we recognize that hybrid indices of 2 and 10 are encompassed by the normal variation within the pure parental populations collected in 1970-1974.

The distribution of the morphological types collected by Rising (1968, 1970) differed in several ways from that observed for birds collected a decade earlier. Transects of the Cimarron, Arkansas, Smoky Hill, and Republican rivers of Kansas each had developed zones of overlap and hybridization. In no case was there a clear-cut hybrid zone where parental types were either absent or existed at combined frequencies of less than 5% of the population (Rising 1970). Parental phenotypes in a zone of overlap along the Cimarron River transect were present at frequencies of about 40%. Their frequency in the zone of overlap and hybridization along the Arkansas River was approximately 60%. Along the Smoky Hill River transect, in the zone of overlap and hybridization, the frequency of parental types was approximately 70%, and it was about 60% in a zone of overlap along the Republican River transect. We obtained these percentages by reanalyzing the principal components analysis data in Figures 12, 15, 17, and 19 of Rising (1970).

Following secondary contact and hybridization between the "Bullock's Oriole" and "Baltimore Oriole", changes in the frequencies of the morphological types (parental types and hybrids) may be expected to have proceeded in one of several ways. (1) A permanent hybrid zone may have formed, serving as a buffer between two allopatric subspecies, as is apparently true for *Corvus corone* and *C.*

TABLE 3. Kolmogorov-Smirnov two-sample test of differences between cumulative frequency distributions of hybrid indices of birds collected at Crook, Colorado in 1955-56, 1970 and 1974.

Hybrid Index	Cumulative Frequency Distributions			Absolute Differences		
	1955-56 (N = 16)	1970 (N = 19)	1974 (N = 61)	1955 vs 1970 ^a	1955 vs 1974 ^b	1970 vs 1974 ^c
0	.000	.105	.148	.105	.148	.043
1	.000	.210	.361	.210	.361	.151
2	.063	.473	.541	.410	.478**	.068
3	.126	.526	.639	.400	.513**	.113
4	.126	.579	.655	.453	.529**	.076
5	.126	.579	.688	.453	.562**	.109
6	.126	.632	.704	.506**	.578**	.072
7	.126	.685	.739	.559**	.613**	.054
8	.189	.685	.753	.496*	.564**	.068
9	.252	.790	.753	.538*	.501**	.037
10	.565	.948	.753	.383	.188	.195
11	.878	1.001	.819	.123	.059	.185
12	1.003	1.001	.999	.002	.004	.002

^a Value for $\alpha_{.05} = .461$ and $\alpha_{.01} = .553$.

^b Value for $\alpha_{.05} = .382$ and $\alpha_{.01} = .458$.

^c Value for $\alpha_{.05} = .357$.

* Significant at the .05 level.

** Significant at the .01 level.

"*cornix*" (Meise 1928, Vaurie 1954). (2) The hybrids may have been selectively inferior, resulting in the selection for premating reproductive isolating mechanisms and the eventual formation of "good" species. (3) Introgression of parental gene pools may have been extensive, ultimately resulting in the elimination of step clines in the various character systems and the reduction of variation at any one locality.

In the first case, changes in the frequencies of the morphological types would not occur within zones, although the geographic boundaries of the zones might change through time. The majority of cases of the second type would be inferred a posteriori. However, we believe that the present situation is a transitional stage of the type predicted by alternative (2) and that we are observing a portion of the process of species formation. The third case also would be manifest by changes in the frequencies of the morphological types through time. In this case, however, our ability to distinguish zones should diminish as each population within a transect gradually approached a normal distribution and variation was reduced. This is not what is happening; the zones are becoming more distinct, and a new zone of sympatry has developed.

If we consider how changes may occur in populations undergoing speciation, we can make two predictions. First, the hybrid phenotypes may gradually disappear throughout the hybrid zone with concurrent increases in the frequencies of sympatric parental phenotypes. In those cases where hybridiza-

tion has been relatively frequent prior to the reinforcement of isolating mechanisms, the introgression of alleles from one parental phenotype into the other may alter the genetic background of the parental phenotypes. This may enable them to expand their former geographical ranges. That is, in spite of selection against hybrids, hybridization may result in the infusion of new genetic material into each parental population so as to increase the relative fitness of parental phenotypes in these marginal populations. There is no reason to suppose that this process should be bi-directional because the ecological adaptations of the parental forms should differ. If, in fact, it were uni-directional, one of the parental phenotypes might expand its range whereas the other would not.

Second, hybrid phenotypes may gradually disappear while only one of the parental phenotypes became established in a given area. This would result in allopatry or parapatry of the parental phenotypes due either to competitive exclusion or to physiological and/or ecological limitations.

Considering the changes that have taken place during the last 20 years in the oriole populations of the Great Plains, it is clear that a stable hybrid zone (alternative 1 above) has not been established. Along the Platte River transect the mean hybrid indices have changed significantly at localities located within what was previously recognized as the hybrid zone (Tables 2, 3). For localities outside the previous hybrid zone but within the zone of overlap and hybridization, the varia-

tion has diminished with the easternmost and westernmost localities within the zone of overlap now having mean hybrid indices significantly more like those of the geographically closest parental type (Tables 1, 2; Fig. 2).

The most striking change within the previous hybrid zone has been the establishment of sympatry of the parental types at Crook, Colorado for a distance of about 80 km along the Platte River. Even in the collections of 1955-1956, there was a hint of bimodality in the Crook population (Sibley and Short 1964). By 1970 only 34% of the birds collected at Crook showed evidence of intermediacy in individual plumage characters, and this value dropped to 26% in 1974 (Fig. 3). At the same time the frequency of pure *I. g. galbula* phenotypes in the population at Crook, Colorado increased from 6.5% in 1955 to 53% in 1974 (Fig. 3). As shown in Figure 1, the frequency of birds having hybrid indices presumably similar to those of F_1 hybrids (i.e., a hybrid index value of 5, 6, or 7) was much lower than that of either of the parental extremes in 1974.

The formation of the zone of sympatry between the two parental types has not occurred simultaneously with the elimination of the hybrid zone to the east, nor does the zone of sympatry exist in an area behind the moving front of secondary contacts. Either of these two alternatives might have been expected on the basis of our knowledge of the history of previous hybrid contacts. The distribution of morphological types of orioles along the Platte River transect in 1970-1974 is thus unique among examples of avian hybridization. Populations of essentially pure parental types exist on the eastern and western edges of the Great Plains, a hybrid zone exists in central Nebraska, and sympatric populations of phenotypically "pure" parental types exist to the west of the hybrid zone. The latter exists in an area that was at the western boundary of the previous hybrid zone. This situation is compatible with changes predicted by alternative (2), but not with alternatives (1) or (3) above. Seemingly pure parental types are in secondary contact, but apparently seldom enter into hybridization. Some hybrid phenotypes are present in the zone of sympatry (i.e. birds scored as 3-8). Although they make up about 20% of the total population, their origin is unknown. Some may be the result of recombination following matings between individuals of only one of the parental types. Others may indeed

be intermediate because of continued cross mating between the two parental types.

The present case involving hybridization between "Bullock's" and "Baltimore" orioles is thus unlike any previously described. The establishment of premating isolating mechanisms apparently has occurred within the zone of overlap and hybridization, *without* the simultaneous elimination of the hybrid zone. The changes that have taken place along the Platte River are most probably the results of directional selection. The "Baltimore" phenotype is increasing in frequency, the hybrid phenotype is decreasing in frequency, and the "Bullock's" phenotype is becoming stabilized at a frequency lower than that of the "Baltimore" oriole.

The population at Crook, Colorado is clearly bimodal and cannot be distinguished statistically from a combined sample of parental phenotypes taken from Madison, Connecticut and Glenwood Springs, Colorado (Table 3). Although we do not know why these changes have taken place, some evidence allows us to speculate about the kinds of selection pressures that have brought them about.

In addition to the striking differences in plumage pattern and color that distinguish the "Baltimore Oriole" from the "Bullock's Oriole", differences exist in mensural characteristics (Sibley and Short 1964), in ability to thermoregulate (as measured by O_2 consumption at various temperatures, Rising 1969), in the degree to which individuals aggregate during the nesting season (Rising 1970), and in call notes and songs (Saunders 1951).

Habitat along the Platte River has changed during the past 20 years, but the changes are not well documented. Cottonwoods have been cleared for gravel extraction, road construction and farming. Whether these changes have modified the dispersal patterns of orioles along the western Platte River cannot easily be determined. It is likely, however, that relatively limited disturbance of the riparian vegetation would have a major effect on the distribution and abundance of orioles along the Platte River, comparable at least to that observed along several rivers in South Dakota (Anderson 1971).

It is plausible that several mechanisms have acted together to produce the rapid change in the composition of the oriole populations in the vicinity of Crook, Colorado. Directional selection appears to be accentuating and reinforcing the differences between the parental

types. The potential modes of action may be summarized as follows: (1) The introgression of alleles from the *bullockii* gene pools into those of *galbula* may be allowing *galbula* to expand its range westward. For example, this could be due to the elevation of the temperature tolerance threshold of *galbula*. (2) Dispersal rates and patterns may be such that the influx of *galbula* phenotypes into the Crook population is greater than that of *bullockii* phenotypes. If so, however, the absence of *galbula* phenotypes within the hybrid zone to the east of Crook, must be explained. (3) The reinforcement of those aspects of communication that enable an individual to discriminate between its own morph and another may be acting to reduce the frequency of cross matings between parental types.

Whatever the reasons may be that have resulted in the establishment of sympatry of *galbula* and *bullockii* phenotypes in the vicinity of Crook, Colorado, it is clear that other aspects of the biology of the "Bullock's" and "Baltimore" orioles must be studied in much greater detail and at frequent intervals to document this rapidly changing situation.

SUMMARY

Hybrid indices and character indices are presented for a series of "Baltimore" and "Bullock's" orioles and their hybrids collected during the breeding seasons of 1970, 1971, and 1974 along an east-west transect extending from Madison, Connecticut to Glenwood Springs, Colorado. The mean values and the frequency distributions of hybrid indices for some of the localities differ significantly from those obtained from specimens collected during 1955-1956. Within that portion of the transect extending along the Platte River of Nebraska and Colorado, a hybrid zone that separated allopatric populations of the parental types existed previously. A hybrid zone still appears in central Nebraska, but now a zone of sympatry of the two parental types exists within the zone of overlap and hybridization. Within this zone of sympatry in western Nebraska and eastern Colorado, the frequency distribution of the morphological types is now bimodal, with the hybrids comprising only about 20% of the population. Those populations lying to the west of this zone of sympatry are now characterized as being more like the "Bullock's" type than they were in the 1950's. Conversely, those populations lying to the east of the zone of sympatry are now significantly more like the "Baltimore" type than they were in 1955-1956. It

therefore appears that in some areas at least the hybrid genotype is less fit than are the parental genotypes. Because little is known about certain critical aspects of the biology of these birds, it is impossible at present to determine the selective pressures that have resulted in the observed changes. The net results, however, appear to be the reinforcement of isolating mechanisms and an increase in the frequency of the "Baltimore" phenotype in certain areas of western Nebraska and eastern Colorado that were previously dominated by the "Bullock's Oriole."

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