MAN'S INFLUENCE ON HYBRIDIZATION IN TWO AVIAN SPECIES IN SOUTH DAKOTA

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Numerous studies of hybridization on the Great Plains have been published within the last four decades (Swenk 1936; Sutton 1938; Dixon 1955; Sibley and Short 1959, 1964; Sibley and West 1959; West 1962; Short 1965; Rising 1968; Sutton 1968). These authors have primarily documented the occurrence of hybridization in various contact situations and discussed its taxonomic significance. Some have also commented on man's impact on the vegetation of the Great Plains and its significance to hybridization (e.g., West 1962; Short 1965). Recent changes in the vegetation of South Dakota and possible effects of these changes on hybridization of flickers (*Colaptes auratus auratus* and *C. a. cafer*) and orioles (*Icterus galbula galbula* and *I. g. bullockii*) are considered here. Nomenclature used conforms to the guidelines established by Short (1969) for hybridizing forms.

Flickers and orioles occur throughout much of South Dakota. Hybrids are common in the western half of the state and both hybridizing pairs form zones of hybridization, areas in which parental phenotypes make up 5 per cent or less of the population (Short 1969). Both species occur wherever there are tall or moderately tall trees (towns, farm groves, shelter belts, and along streams and rivers). Dominant trees occurring naturally in such areas include cottonwood (*Populus deltoides*), American elm (*Ulmus americanus*), ash (*Fraxinus* spp.), and river maple (*Acer negundo*). Orioles were found more frequently than flickers in burr oak (*Quercus macrocarpa*). Flickers, but not orioles, were found in ponderosa pine (*Pinus ponderosa*). The requirements of flickers for trees in which they can make holes differ somewhat from the nesting requirements of orioles and help to understand the above observations.

FLICKER AND ORIOLE HABITAT IN SOUTH DAKOTA

Present distribution of flicker and oriole habitat was determined through travel, primarily during summers 1965–1969, and by studying aerial photographs of the state. Based on this, I distinguished five types of vegetation (fig. 1) which are characterized as follows: Type 1, essentially treeless plain, flicker and oriole habitat primarily restricted to towns; Type 2, farm groves and other stands of oriole and flicker habitat interspersed with cropland and treeless plain, transitional between types 1 and 3; Type 3, cropland with shelter belts or farm groves in nearly every square mile; Type 4, woodland along streams and rivers; and Type 5, woods with ponderosa pine as the dominant.

Man has been a primary force acting upon the vegetation of South Dakota within the last century. He has planted trees in towns for shade and ornamentation. In rural areas, shelter belts and farm groves provide shelter from winds, help reduce wind erosion, and provide habitat for wildlife. This type of habitat composes the corridor of more or less continuous flicker and oriole habitat from northeastern South Dakota southwestward to the Missouri River and west of the Missouri for about 75 miles (fig. 1). Much of the rest of the area west of the Missouri River is open plain with woods confined to rivers and some creeks. Some of these woods are in contact with habitat occupied by the western subspecies of flickers and orioles.

Six rivers enter the Missouri from the west. Flood plain vegetation along these rivers becomes less luxuriant westward where trees are stunted due to the drier conditions. Heavy grazing often eliminates the understory.

Former woodlands along the Missouri River were an important link between eastern and western populations, but dam-building initiated in the 1950s has resulted in large reservoirs which have flooded much of the river valley and killed most of the trees. These reservoirs have greatly reduced contact between eastern and western populations of flickers, orioles, and other birds (fig. 1).

ANALYSIS OF FLICKER AND ORIOLE HYBRIDIZATION

Interbreeding between the eastern and western subspecies of flickers and orioles in South Dakota was documented through collections of adults made during late May, June, and early July 1965–1968. A hybrid index score

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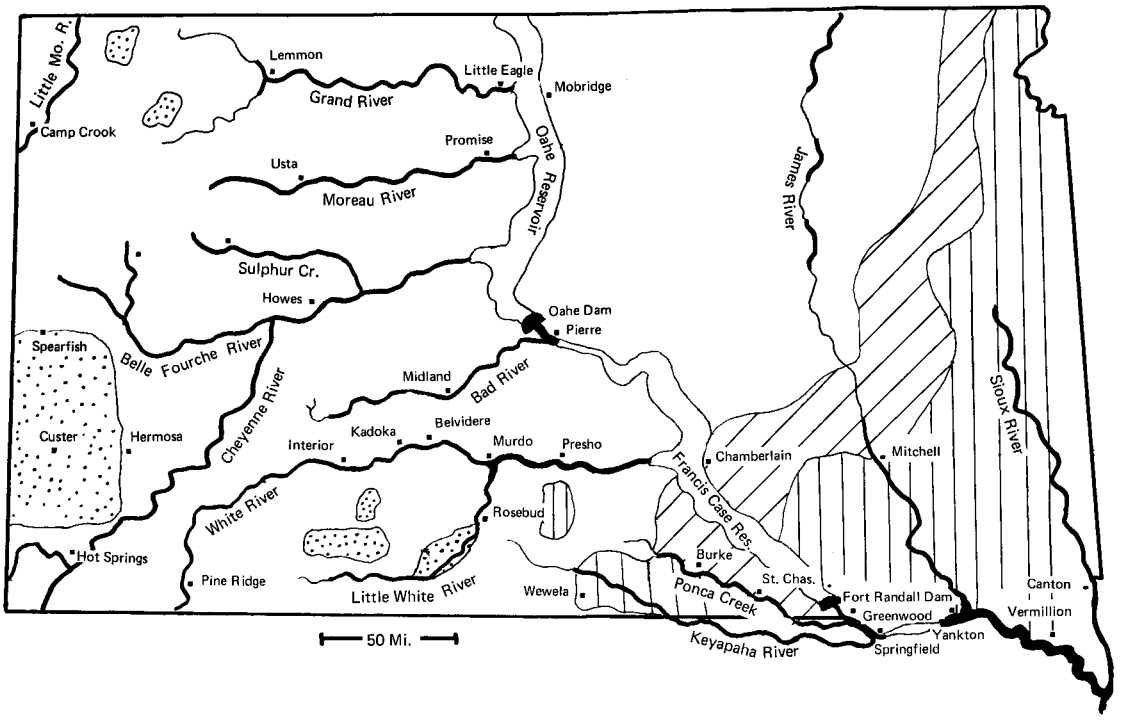

FIGURE 1. Collecting localities and vegetation in South Dakota. Clear spaces indicate treeless plains; dotted areas, ponderosa pine; vertical lines, farm groves and shelter belts; and diagonal hatching, areas transitional between treeless plains and farm groves. Wooded portions of rivers and streams are shown by heavy lines, non-wooded portions by light lines.

was established for each specimen, using the technique developed by Sibley and Short (1964) for orioles and by Short (1965) for flickers. In both species the score of 0 refers to the "pure" eastern subspecies; scores of 12 in adult male orioles, 20 in female flickers, and 24 in males refer to the "pure" western subspecies. Analysis of these samples is presented in tables 1 and 2. Data on pertinent samples collected in South Dakota prior to this study are presented in table 3. Localities are shown in fig. 1.

In order to test whether my index scores were similar to scores obtained for flicker and oriole samples collected and scored by other investigators, I indexed samples of about 100 flickers and orioles which had been indexed by L. L. Short. The difference in mean scores varied by only a few hundredths of an index point, although individual scores occasionally varied as much as two index points. Because my scores were very similar to Short's, I used scores originally reported for earlier samples from South Dakota.

INITIAL EFFECTS OF TREE PLANTING AND FLOODING

Prior to the tree planting in southeastern South Dakota the region had been prairie for several thousand years (Wright 1968). Gene flow from the east was probably restricted to the Missouri River Valley. Tree planting has undoubtedly increased gene flow from the east, probably resulting in a further shift toward *C. a. auratus* and *I. g. galbula*, especially in populations along the Keyapaha River and Ponca Creek (fig. 1). Introgression of western genes into southeastern South Dakota through Missouri River Valley populations was greatly reduced subsequent to flooding of the valley. Introgression into the region is now restricted mainly to the Niobrara River Valley and this applies only to flickers. The west end of the Niobrara has either no trees or primarily ponderosa pine, thus allowing no contact for orioles (L. L. Short, Jr., pers. comm.). Some exchange must also occur across the narrow gap of treeless plain separating the southeastern populations from those along the White River.

Before the Missouri River Valley was flooded, flicker and oriole populations inhabiting it were probably larger than populations along the tributaries to the west. Three lines of evidence support this idea. First, habitat along the Missouri River, as judged from aerial photographs taken before flooding, was formerly more substantial and probably sustained larger populations. Second, flickers and orioles

TABLE 1. Hybrid indices of flickers from South Dakota.

Locality	♂ Hybrid index				♀ Hybrid index			
	n	$\bar{x}$	SD	range	*n*	$\bar{x}$	SD	range
Missouri River system, SE S. Dak.								
Vermillion	34	0.74	0.91	0– 4	24	0.71	1.02	0– 4
Mitchell	4	1.33		1– 2	5	1.00		0– 3
St. Charles	29	1.31	1.29	0– 5	39	1.00	1.02	0– 6
Wewela	23	1.41	1.76	0– 8	11	1.09	0.67	0– 2
White River								
Presho	10	2.90	2.83	0– 8	12	2.41	1.78	0– 6
Murdo	19	3.00	2.24	0– 9	14	3.08	2.74	0–10
Rosebud	4	3.25		2– 5	1			4
Belvidere	22	4.58	2.68	2–11	18	4.22	3.20	0–10
Kadoka	10	8.80	5.34	1–17	4	4.50		1–12
Pine Ridge	10	13.60	3.51	7–18	10	10.50	2.92	5–15
Missouri–Bad River								
Pierre	16	2.20	1.70	0– 6	16	1.38	1.41	0– 4
Midland	8	6.38	4.20	1–16	4	4.40		1–12
Cheyenne River system								
Howes	9	9.22	5.50	0–17	10	9.30	3.96	0–14
Sulphur Creek	2	14.00		14	3	11.67		11–16
Union Center	1	11.00		11	2	10.50		9–12
Hermosa	6	13.33	5.16	6–21	3	13.00		11–16
Custer	10	15.80	3.00	8–19	8	12.00		8–15
Spearfish	4	16.75		15–18	2	11.50		11–12
Moreau River								
Usta					3	6.00		3–11
Promise	3	4.67		4– 6				
Grand River								
Little Eagle	18	6.10	3.60	2–14	17	4.94	2.64	1–12
Lemmon	14	8.21	2.98	3–12	11	6.00	2.94	1–11
Little Missouri River								
Camp Crook	21	15.95	1.62	12–19	27	12.31	2.61	6–16

were easier to collect at existing Missouri River localities for this study, even though an equal amount of time was spent searching for orioles and flickers at other localities, suggesting larger population sizes there. Third, habitat is less extensive and orioles and flickers are less abundant in western than in eastern portions of the tributaries.

In addition to being larger, Missouri River populations were also probably phenotypically most similar to the eastern forms, *C. a. auratus* and *I. g. galbula*. The 15 specimens collected in 1955 along the Missouri River (table 3), all more similar to eastern than to western forms, support this idea. In addition, 32 flickers and 19 of 22 orioles collected south of Pierre on the Missouri River for this study are phenotypically most like the eastern subspecies.

As habitat in the Missouri River Valley was eliminated, segments of flicker and oriole populations must have moved westward along the tributaries that join the Missouri River from the west. This is especially likely north of the White River where eastward emigration is hampered by 100 miles of treeless plain separating the Missouri River from the closest habitat to the east (James River and farm groves east of there). Evidence of re-establishment of dislocated populations might be most apparent in relatively small neighboring populations which differed significantly in average phenotype.

Immigration seems to be most apparent along the Cheyenne River. At Howes, orioles indexed 3–12 in this study, and three of the seven specimens indexed less than the three orioles collected there before flooding (table 3). Among 19 flickers collected for this study at Howes, the range spanned 18 index points, but the span was only eight index points among seven flickers collected there earlier. Six of the 19 flickers collected for this study had an index lower than the lowest index of specimens collected at Howes prior to flooding.

Low-indexed flickers and orioles were also collected at Lemmon (Grand River). Immi-

TABLE 2. Hybrid indices of orioles from South Dakota.

Locality	n	Hybrid index $\bar{x}$	SD	range
Missouri River system, SE S. Dak.				
Canton	8	1.13	0.85	0– 3
Vermillion	54	2.00	0.91	0– 4
Yankton	44	2.11	0.89	0– 5
Springfield	23	2.60	1.13	1– 6
Mitchell	11	2.20	0.72	1– 3
Greenwood	29	2.24	1.25	0– 5
St. Charles	25	2.60	1.13	1– 5
Burke	26	2.73	1.13	1– 6
Wewela	81	3.04	1.47	0– 7
White River				
Presho	16	3.75	1.45	1– 6
Murdo	19	4.21	1.53	2– 8
Rosebud	31	4.20	1.51	1– 9
Belvidere	16	4.31	2.06	2–11
Kadoka	2	6.50	—	3–10
Interior	2	11.00	—	11
Pine Ridge	18	10.80	1.26	8–12
Missouri–Bad River				
Pierre	22	3.91	1.41	2– 7
Midland	7	5.37	2.62	3–12
Cheyenne River system				
Howes	7	8.00	3.14	3–11
Hot Springs	18	10.90	0.76	9–12
Grand River				
Little Eagle	28	4.00	1.40	2– 6
Lemmon	11	6.00	2.52	1–10
Little Missouri River				
Camp Crook	8	10.13	2.60	5–12

TABLE 3. Orioles and flickers collected in South Dakota prior to this study (selected data from Sibley and Short 1964, and Short 1965).

Locality	n	Hybrid index $\bar{x}$	range
Orioles			
Missouri River, Chamberlain	6	2.83	1– 5
Missouri River, Mobridge	2	3.00	3
White River, Kadoka	2	8.50	7–10
Cheyenne River, Midland	3	10.00	9–11
Cheyenne River, Howes	3	11.00	9–12
Grand River, Lemmon	1	—	3
Flickers			
Missouri River, Chamberlain			
♂	1	—	2
♀	2	0.00	0
Missouri River, Mobridge			
♂	3	4.30	1– 7
♀	1	—	1
White River, Murdo			
♂	2	3.00	2– 4
♀	1	—	3
White River, Kadoka			
♂	3	12.30	9–16
♀	3	6.70	1–13
Cheyenne River, Midland			
♀	5	5.00	0– 9
Cheyenne River, Howes			
♂	3	7.70	6– 9
♀	4	9.75	6–13
Grand River, Lemmon			
♀	2	4.00	3– 5

gration must have occurred westward from the Missouri River Valley along the Grand River, but the low scoring individuals do not necessarily reflect this. Grand River populations were in contact with populations of *C. a. auratus* and *I. g. galbula* but not with *C. a. cafer* or *I. g. bullockii* prior to flooding, thus low-scoring individuals were perhaps found as far west as Lemmon at that time. In fact, flicker and oriole indices were probably lower along the Grand River formerly than now. Evidence from earlier collections, although scant and not statistically significant, seems to support this thesis: three of four flickers collected northeast of Mobridge (only a few miles east of Little Eagle), both flickers collected south of Lemmon, and three of four flickers from southwestern Montana indexed less than the respective means nearest these localities in this study.

It is likely that the Moreau and Bad River histories are similar to that of the Grand River, although this is not confirmed by existing data.

Westward movement along the White River extended perhaps as far as Kodoka (fig. 1). This is suggested by the wide range in flicker scores there, as well as by the oriole specimen index of 3. White River samples collected earlier indexed higher than those in this study, although there has probably always been some movement and the lack of low-scoring individuals could be the result of the very small sample sizes.

PROJECTIONS FOR THE FUTURE

Barring unforseen developments there will be significant genetic changes in the flicker and oriole populations in South Dakota in years to come. Contact between eastern and western forms is not likely to be re-established in the near future because the dry hilly land adjacent to the reservoirs is not suited for establishment of trees. In general there is lack of information concerning dispersal potential in these species, but it is possible that the western populations, occupying a more arid and perhaps more changing environment (historically), might have a greater dispersal capability than the eastern populations. The following state-

ments, made with this possibility in mind, summarize the probable genetic consequences of the break in contact.

Grand River. Grand River flicker and oriole populations are not in contact with eastern or western populations. Immigration from western populations is more likely because they are closer (fig. 1), and hybrid indices are likely to reflect this in the future. Flicker indices will probably increase faster than oriole indices because open plain is probably a less effective barrier to the former. We often saw flickers, but never orioles, several miles onto treeless plain, and on three occasions we found flickers with nests in fence posts well out in treeless plain. I suspect that immigration from the relatively large flicker populations to the west occurs more frequently than from the relatively small oriole populations.

Little Missouri River and Black Hills. These populations are in direct contact with populations with higher indices to the west, and it is likely that they will become phenotypically even more similar to *C. a. cafer* and *I. g. bullockii.*

Cheyenne River. The mean hybrid indices of eastern Cheyenne River populations are increasing faster than any others in South Dakota because they are in direct contact with higher indexing populations to the west, but contact with the east has been broken. This partly explains the differences between the Howes and Lemmon (Grand River) mean indices (see fig. 1 and tables 1–2). Introgression from the west will cause hybrid indices in Cheyenne River populations to continue to rise.

Bad and Moreau Rivers. Flicker and oriole populations along these rivers are relatively small because habitat is sparse. They are not in direct contact with any populations to the east or west. Hybrid indices will probably increase in populations along the Moreau because of their proximity to the Cheyenne River populations (fig. 1). Bad River populations will probably reflect whatever happens on the White River.

White River. While these populations are in direct contact with western populations, this contact is very slight from Interior to north of Pine Ridge because habitat in that region is very sparse. Only a narrow zone of open plain separates the White River from the large populations of flickers and orioles in southeastern South Dakota. However, because contact with the east has been reduced, hybrid indices along the White River will probably reflect a greater influence from western populations in the future.

The above statements may not apply if immigration rates are low. That is, if gene flow is very slow, local selection might cause shifts in index values other than those expected by simply noting the nearest sources of immigrants. This could result in phenotypic stabilization of local populations.

It should also be emphasized that the results of analysis of interbreeding are precisely those to be expected by random mating. The close correlation between enhancement and interruption of habitat on the one hand, and index values on the other shows that the hybrid zones are literally being "manipulated" by external factors because intrinsic isolating mechanisms patently are lacking. This reinforces Short's (1969) conclusions concerning the conspecific status of the forms involved.

SUMMARY

Man's tree-planting activities have greatly increased flicker and oriole habitat in southeastern South Dakota in the last century. Man-made reservoirs in the Missouri River Valley have nearly eliminated habitat which formerly united eastern flicker and oriole populations with those along five major tributaries in South Dakota. As Missouri River habitat was eliminated, many flickers and orioles probably were displaced along the tributaries, temporarily extending eastern influence farther west. Presently, populations along the tributaries north of the White River are being influenced more by introgression from the west. This is particularly true of Cheyenne River populations which are in direct contact with western populations. The White River is in loose contact with western and eastern populations, but the eastern contact has been reduced by the reservoirs. Greater western influence will probably be evident in future White River populations.

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