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CHARACTERISTICS AND REPRODUCTIVE BIOLOGY OF GROSBEAKS (*PHEUCTICUS*) IN THE HYBRID ZONE IN SOUTH DAKOTA

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The Rose-breasted Grosbeak (*Pheucticus ludovicianus*) breeds widely in the eastern United States and the Black-headed Grosbeak (*P. melanocephalus*) in the west. The two forms are sympatric and hybridize in the Great Plains (West, 1962; Kroodsmas and Cassell, 1968), an area where several additional eastern and western bird taxa also interbreed (Sibley and West, 1959; Sibley and Short, 1959, 1964; Short, 1965; Kroodsmas and Cassell, 1968; Rising, 1970; Anderson, 1971). The characteristics of grosbeaks in the hybrid zone in South Dakota have not previously been reported, nor have such details as the kinds of pairs formed, clutch size, viability of eggs, and nesting habitat. The purpose of this report is to document hybridization in South Dakota as well as to present data on the above aspects of reproductive biology.

Grosbeaks are common breeding birds along rivers and streams supporting relatively dense vegetation in South Dakota (Fig. 1). This riparian vegetation is dominated by cottonwood (*Populus deltoides*), American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), and box elder or river maple (*Acer negundo*). This habitat connects breeding areas of grosbeaks in eastern and western South Dakota and is where hybridization occurs.

Six rivers, all of which eventually enter the Missouri River, extend from west to east in western South Dakota (Fig. 1). Riparian vegetation along them becomes less luxuriant to the westward, as the result of drier conditions and heavy grazing—the latter being especially significant in preventing the development of an understory. Perhaps largely for these reasons grosbeaks are scarce westward along these tributaries. Woodlands along the Missouri River itself were formerly important links between eastern and western populations, but reservoir construction initiated in the 1950's has greatly reduced habitat. Consequently, contact between eastern and western populations of woodland birds is now limited along that river (Anderson, 1971).



Hybrid male grosbeaks (*Pheucticus ludovicianus* X *P. melanocephalus*)
from Gregory County, southeastern South Dakota.
Painting by George Sandström.

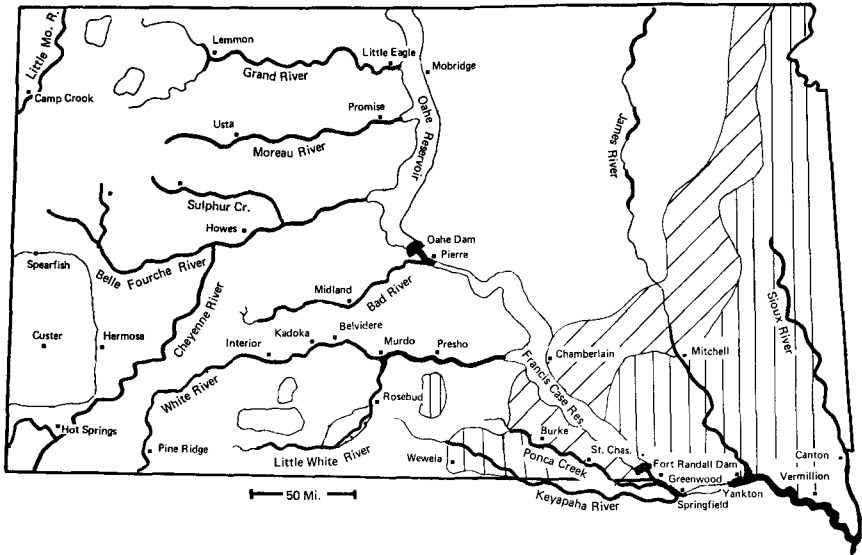


FIG. 1. Collecting localities and vegetation in South Dakota. Clear areas indicate treeless plains; irregular shaped patches, ponderosa pine (*Pinus ponderosa*); vertical lines, farm groves and shelter belts; and diagonal hatching, areas transitional between treeless plains and farm groves. Wooded portions of rivers and streams are shown by heavy lines, non-wooded portions by light lines.

CHARACTERISTICS IN THE OVERALL HYBRID AREA

This aspect of our study, based on 469 specimens (now housed at the James Ford Bell Museum of Natural History, University of Minnesota), documents the degree as well as the extent of hybridization. Preceding this analysis we collected males throughout much of the state (Fig. 1; also see Table 3) in late May, June, and early July 1965-68. An effort was made to collect all males encountered in order to obtain as nearly random a sample as possible. As some hybrid characters are rather subtle and difficult to discern in the field, the chance of an unintentional bias favoring the collecting of hybrids was further reduced. A hybrid index was established using the criteria in Table 1. In that

TABLE 1
COLOR CHARACTERS AND SCORES USED TO ASSESS THE EXTENT OF HYBRIDIZATION

Males	Score
Nape	
Black as in <i>P. ludovicianus</i>	0
Black with buffy-brown traces	1
Buffy-brown neck collar as in <i>P. melanocephalus</i>	2

TABLE 1. *Continued*

Males	Score
Back	
Black as in <i>P. ludovicianus</i>	0
Black with some brown streaks	1
Broad brown streaks as in <i>P. melanocephalus</i>	2
Rump	
White as in <i>P. ludovicianus</i>	0
Mixed brown and white	1
Brown as in <i>P. melanocephalus</i>	2
Flanks	
White as in <i>P. ludovicianus</i>	0
Mixed white and brown	1
Brown as in <i>P. melanocephalus</i>	2
Breast and underwing coverts	
Rose as in <i>P. ludovicianus</i>	0
Slightly orange or salmon pink	1
Orange	2
Salmon yellow	3
Chrome yellow as in <i>P. melanocephalus</i>	4
Total	0-12
Females	Score
Throat, breast, and side of neck	
Buffy-white as in <i>P. ludovicianus</i>	0
With traces of fawn-brown	1
Fawn-brown with traces of buffy white	2
Rich fawn-brown as in <i>P. melanocephalus</i>	3
Extent of yellow	
If present restricted to underwing coverts as in <i>P. ludovicianus</i>	0
Traces of yellow on head and/or breast	1
Yellow superciliary line and on breast as in <i>P. melanocephalus</i>	2
Streaking	
Relatively wide brown streaks over most of ventral surface as in <i>P. ludovicianus</i>	0
Similar to above but streaks fewer and somewhat narrower	1
Streaking reduced and streaks narrower	2
Streaks narrow, absent over much of ventral surface as in <i>P. melanocephalus</i>	3
Total	0-8

TABLE 2
INDEX SCORES OF BREEDING GROSBEAKS (*PHEUCTICUS*) FROM OUTSIDE THE
ZONE OF INTERGRADATION

	Males				Females			
	N	Mean	Percent scoring		N	Mean	Percent scoring	
			0 or 12	1-2 or 11			0 or 8	1-2 or 6-7
<i>P. ludovicianus</i>	72	0.2	85	15	65	0.2	78	22
<i>P. m. melanocephalus</i>	125	11.8	86	14	29	7.3	63	37

index "pure" *P. ludovicianus* scores 0 and "pure" *P. melanocephalus* 12 in males and 8 in females.

In testing this index, we also analyzed variation in grosbeaks from outside of the zone of intergradation. In 291 such specimens (Table 2), we found scores duplicating weak hybrids in 14 and 15 percent of eastern and western males, respectively, and 22 and 37 percent of eastern and western females. Because of the low scores and mosaic distribution of this "hybridity," we regard it more as an intrinsic form of variation than due to introgression. As for its bearing on indices in the area of hybridization, it simply means that low scores of hybridity are of less significance than higher ones.

In the analysis of South Dakota specimens, subadult and adult males have been combined, as they had nearly identical values. Female age classes were not evident and overall indexing of this sex was more subjective and prone to error than that of males. This may have had some slight effect on our results and conclusions. A detailed description of the two forms and an alternative method of scoring them has been presented by West (1962).

The major area of hybridization was northwest of Greenwood, Charles Mix Co., where the male hybrid scores and number of intermediate hybrids (scores 4-8) were greater than at any other locality (Table 3). In the 12 miles from that locality to the one southeast of Greenwood, the hybrid incidence decreased by nearly half and the number of intermediate hybrids to about a fourth. Another significant shift in populational (male) phenotypes occurred in the 12 miles between St. Charles and Burke, Gregory Co. The Burke population was dominately of *P. melanocephalus* (score 12), compared to the one at St. Charles being closer to *P. ludovicianus* (scores 0-2). Westward from Greenwood a marked decrease also occurred in the proportion of intermediate hybrids as the proportion of *P. melanocephalus* increased. Further study of the westerly situation was precluded as grosbeak habitat is virtually absent along the Ponca Creek and Keyapaha River west of Burke.

In a sample of 106 specimens collected along the White, Bad, Grand, and Little White Rivers (Fig. 1), 98 were "pure" *P. melanocephalus*. Only seven hybrids, all phenotypically similar to *P. melanocephalus* (scores 10-11), were

TABLE 3
CHARACTERISTICS OF MALE GROSBEAKS COLLECTED IN THE AREA OF HYBRIDIZATION
IN SOUTH DAKOTA

Localities and distances between localities	Sample size	Percentages in various phenotypic categories			
		Pure <i>P. ludovicianus</i> (score 0)	Intermediate hybrids (scores 4-8)	Other hybrids (scores 1-3, 9-11)	Pure <i>P. melanocephalus</i> (score 12)
Vermillion 30 mi.	82	87	0	13	0
Yankton 40 mi.	44	77	0	23	0
Springfield 12 mi.	53	58	6	36	0
se Greenwood 12 mi.	36	61	6	30	3
nw Greenwood 15 mi.	76	28	21	42	9
*Spencer 15 mi.	13	46	15	23	15
St. Charles 12 mi.	35	29	11	34	26
Burke	24	4	9	33	54

* Totals not equaling 100 percent resulted from rounding off.

collected: at Belvidere (1), on the White River; at Pierre (4), on the Missouri River; and at Midland (2), on the Bad River. The only "pure" *P. ludovicianus* collected was at Rosebud on the Little White River. This series of populations, formerly linked with eastern ones along the Missouri River, is now disjunct due to reservoirs that have eliminated intervening habitat.

CHARACTERISTICS AND BREEDING BIOLOGY OF MATED PAIRS

This phase of the study was based on 110 presumed mated pairs (now housed at the American Museum of Natural History). These were collected in 1969-72 in the area of greatest hybrid incidence, that is, northwest of Greenwood. Birds were presumed paired if they were both observed at or usually within 10 feet of the same nest. Because grosbeaks are highly territorial, encroachment of a "foreign" bird this close to a nest is unlikely and was not known to have occurred in this study. Thus these pairs are presumably genuine.

Randomness of pairing.—A test of the randomness of pairing was made by using a 3×2 contingency table composed of the male scores 0-2, 3, and

TABLE 4
PHENOTYPIC COMBINATIONS IN MATED PAIRS (COLLECTED)

Male index values	Female index values									Total pairs
	0	1	2	3	4	5	6	7	8	
0	10	11	7	0	0	0	0	0	0	28
1	10	8	9	2	0	0	0	0	0	29
2	6	2	3	0	1	0	1	0	0	13
3	4	4	4	0	1	0	0	0	0	13
4	3	1	2	0	0	0	0	0	0	6
5	1	2	0	0	0	0	0	0	0	3
6	2	0	0	0	0	0	0	0	0	2
7	0	2	0	0	0	1	0	0	0	3
8	0	0	0	0	0	0	0	0	0	0
9	1	1	0	0	0	0	0	0	0	2
10	0	1	0	0	0	0	0	0	0	1
11	1	0	0	0	0	0	0	0	0	1
12	1	2	3	0	1	0	0	1	1	9
Totals	39	34	28	2	3	1	1	1	1	110

4-12 and the female scores 0-1 and 2-8. These categories are the maximum number allowable when following Remington and Schork's (1970) suggestion that no expected frequency be less than 1 and not over 20 percent be less than 5. The results of analysis suggest that the sampled pairs (Table 4) approximated combinations expected in a randomly interbreeding system ($0.10 > P > 0.05$). Both members of the pair were hybrid in 64 percent of the cases. It is perhaps significant that both of the relatively pure *P. melanocephalus* females (scores 7-8) were paired with "pure" *P. melanocephalus* (score 12) males.

Clutch size and egg viability.—Data concerning clutch size and egg viability were obtained for 70 of the 110 mated pairs. In nests containing only eggs, an egg was considered viable if there was no evidence of a dead embryo or of a lack of development (when siblings did show development). The use of these procedures gave conservative estimates of mortality up to hatching.

Mean clutch size for hybrid females (scores 2-6) did not differ significantly from year to year. On the other hand "pure" females (scores 0-1 or 7-8) had significantly smaller clutches the first two years of the study ($X = 2.8$, $N = 8$) than the last two ($X = 3.8$, $N = 35$). This difference is probably misleading, as four excluded clutches found during the first two years

TABLE 5
DISTRIBUTION OF PHENOTYPES IN SUB-HABITAT TYPES (SEE TEXT)

Male index scores	Sample size	Percent in sub-habitat				Female index scores	Sample size	Percent in sub-habitat			
		I	II	III	IV			I	II	III	IV
0-3	87	45	21	18	16	0	46	46	24	17	13
4-8	12	41	25	29	9	1-2	53	51	17	20	12
9-12	11	82	0	9	9	3-8	11	45	9	18	27*

* Total less than 100 percent due to rounding off.

of the study each had at least 3 eggs and possibly 4 or 5 eggs. They were excluded because precise clutch size information could not be obtained. If one assumes that these 4 nests had a mean clutch of 3.5 eggs, the overall mean would be 3.0 and significance of the difference (at the 0.05 level) would be lost. In the absence of more convincing evidence that clutch size varied from year to year we have combined the clutch sizes from all years to facilitate comparisons of hybrids and non-hybrids.

Pairs in which the female was essentially pure (scores 0-1 or 7-8) had 3.6 eggs per nest with 9 non-viable among 153 eggs (5.9 percent). Pairs in which the female was hybrid (scores 2-6) had 3.0 eggs per nest with 8 non-viable among 81 eggs (9.9 percent). A two-tailed z-test of the mean clutch sizes reveals that the difference is statistically significant ($z = 2.35$, $0.02 > P > 0.01$), with clutch size lower in hybrids.

Subadult and adult males were associated with clutches of nearly identical size. Phenotypically, the male of pairs with clutches of 1, 2, or 3 eggs was as likely to be a pure individual as a hybrid. The two pairs with "pure" *P. ludovicianus* females (score 0) and *P. melanocephalus* males (scores 11-12) had clutches of 4 and 5 eggs.

Habitat.—We distinguished four sub-habitats in the locality northwest of Greenwood. The first (I) was more or less continuous dense woods with relatively dense understory. The second (II) included areas similar to this but which were relatively small isolated stands. The third (III) included woods in which cattle grazed, which markedly reduced the understory. The final sub-habitat (IV) was a campground in which the trees were more spaced and an understory was totally lacking.

Males indexed as *P. ludovicianus* or intermediate (scores 0-8) and all females showed an approximately similar proportional distribution among the sub-habitats (Table 5), this being an average for the males of 46, 20, 18, and 16 percent, respectively for sub-habitats I, II, III, and IV. On the other hand, 9 of 11 *P. melanocephalus*-like males (scores 9-12) were found in

TABLE 6
SUB-HABITATS (SEE TEXT) IN WHICH MATED AGE CLASSES OF MALE GROSBEAKS
WERE FOUND

Sub-habitat	Sample size	Percent	
		Adult	Sub-adult
I	53	85	15
II	21	43	57
III	20	75	25
IV	16	69	31

the denser woods with well-developed understories, and the respective percentages were 82, 0, 9, and 9 for the sub-habitats. Although this difference is statistically significant (Chi-square 4.1; $P < 0.05$), the number of such males collected is small and we have little faith in the result. Furthermore, 10 of the 11 *P. melanocephalus*-like males were adults, and this age class prefer the denser, more luxuriant areas (Table 6). Subadults were significantly more abundant in the less luxuriant areas (Chi-square 5.6; $P < 0.02$).

Trees selected for nesting.—Fifty-nine percent of the nests occurred in box elder, which constituted only 30 to 40 percent of the trees in any area. Ash, American elm, and cottonwood were about equally abundant, but these held only 8 percent of the nests. The same general preference for nesting sites seemed to be shown by all phenotypes.

Height of nest.—Nearly 70 percent of the nests were between 10 and 19 feet above the ground. Eight of the 10 nests occurring over 20 feet high were in habitats with poorly developed understories. In sub-habitats with a well developed understory (I and II) 33 percent of 55 nests were 15 feet or more above the ground, whereas in sub-habitats with a poorly developed understory (III and IV) 61 percent of 31 nests were 15 feet or more above the ground. There was no apparent association between phenotype and height of nest.

Cowbird parasitism.—Cowbird eggs and/or young were found in 16 of 70 nests (22.9 percent) with completed clutches. There was a tendency toward increased cowbird parasitism as the index value of the male of the pair increased. Three of the 6 nests in which the male of the pair was similar to *P. melanocephalus* contained at least one cowbird egg.

DISCUSSION

Although analysis suggests that pairing is random, some assortative mating cannot be entirely precluded. The fact that 78 percent of the 9 hybrid females

(scores 3–8) were mated with hybrids (scores 2–11) or *P. melanocephalus* (score 12) males, even though this group of males included only 48 percent of the sample, suggests some assortative mating. Further, both female *P. melanocephalus* (scores 7–8) were mated with “pure” *P. melanocephalus* (score 12). West (1962) also found *P. melanocephalus* females mated to males of the same species more frequently than might be expected by chance alone.

If *P. melanocephalus* females prefer males of the same species, as the data suggest, one might suppose that some females were unmated in the population northwest of Greenwood. In that locality 12 percent of the mated males were phenotypically like *P. melanocephalus* (scores 9–12), but only about two percent of the mated females were similar to *P. melanocephalus* (scores 7–8). *P. ludovicianus* females apparently accepted any male as a mate, but possibly a scarcity of acceptable mates existed for *P. melanocephalus* females.

Westward from Greenwood the hybrid incidence decreased, perhaps because more male *P. melanocephalus* were in the population and available to such females. This may have forced more of the female *P. ludovicianus* to mate with males of their own species or with hybrids. In other words, assortative mating by female *P. melanocephalus* could be operating, thus keeping the two taxa from achieving a more concerted hybridization.

West (1962) found that in Nebraska the zone of intermediacy was about 100 miles wide. His data show a gradual clinal gradation from one morphotype to the other. In South Dakota, the zone of intermediacy is less than 70 miles wide and the cline apparently much steeper. Major shifts in population structure occurred over distances as little as 12 miles (Table 3), as already explained.

West (1969) concluded that the grosbeaks should be considered conspecific in the absence of any reproductive isolation. We disagree with his conclusion because we found (1) a steep cline of intergradation, with hybrids most numerous in a narrow zone at the periphery of the ranges of the two forms, (2) some evidence of assortative mating, and (3) some evidence of reduced viability among hybrid females. Furthermore, we did not find a true zone of hybridization, that is, an area where pure parental phenotypes occur only in numbers that likely result from genetic recombination or immigration (Short, 1969). We found that hybridity was never above 63 percent, which means that one parental type or the other constituted at least a third of any population.

These lines of evidence suggest that the grosbeaks do not interbreed freely, and when they do interbreed, it is not without penalty. The steep cline within the zone of intermediacy in South Dakota suggests that the gene pools of these two morphotypes have acquired a degree of mutual incompatibility,

that is, counterselection is occurring. Taxonomically, we agree with Hubbard (1969) that where the evidence suggests both the existence of gene flow and the operation of counterselection, a semispecies designation should be applied. Semispecies have attributes of both species and conspecies (Mayr, 1963), and this term applies to the relationships of *P. ludovicianus* and *P. melanocephalus*. Together the two constitute a superspecies. This conclusion is in agreement with Short (1969) and Mayr and Short (1970). Amadon (1966), Hubbard (1969), and Short (1969) have offered suggestions concerning the nomenclatural recognition of semispecies taxa.

SUMMARY

Hybridization between *Pheucticus ludovicianus* and *P. melanocephalus* was studied in South Dakota. The greatest numbers of hybrids were found in populations along the Missouri River near the Nebraska-South Dakota border. A shift from largely *P. ludovicianus*-like male phenotypes to largely hybrid phenotypes occurred abruptly over a 12 mile distance from Springfield to Greenwood. Within another 40 miles to the west occur reductions in *P. ludovicianus* and in intermediate hybrids, with *P. melanocephalus* becoming the predominant phenotype. An analysis of mated pairs revealed that pairing did not deviate significantly from that expected in a randomly interbreeding system, but there was some evidence that *P. melanocephalus* females prefer to mate with males of the same morphotype. Hybrid females had significantly smaller clutches. We concluded from the above and from other evidence that these grosbeaks constitute semispecies and together are superspecies.

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NEW LIFE MEMBER



Thomas Henry Foster is now a Life Member of The Wilson Ornithological Society. He is a member of several nature-connected organizations and is a free-lance writer. His hobbies are nature-observing and gardening, and his travels have taken him to Eurasia and Africa. He has published many reviews in The New York Times Book Review section and his ornithological interests center on behavior. He lives in Bennington, Vermont, and is married.