HYBRIDIZATION IN GROSBEAKS (*PHEUCTICUS*) IN NORTH DAKOTA

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Rose-breasted and Black-headed grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*) are complementary species that breed in eastern and western North America, respectively. Their breeding ranges overlap in the Great Plains where hybridization occurs. West (1962) described the hybridization mainly in Nebraska, and Anderson and Daugherty (1974) in South Dakota. Because very little work had been done in the more northern Plains, I began collecting grosbeaks in 1966 in North Dakota. This paper describes grosbeak hybridization in North Dakota, and compares it with that in more southern areas and in other species in the Plains. A "hybrid" as defined in this paper is any bird that is believed to have any combination of *P. ludovicianus* and *P. melanocephalus* genes, and "hybridization" is any mating involving genes of both species.

MATERIALS AND METHODS

During June and early July of 1966–1968 I collected 21 subadult and 27 adult *P. ludovicianus*-like males, 15 subadult and 35 adult *P. melanocephalus*-like males, 2 phenotypically medial hybrid males, and 12 adult female and 9 immature *P. melanocephalus*-like birds. Birds were collected as randomly as possible at each collecting locality, so that the proportions of the different phenotypes in each sample would hopefully approximate that in each population. The specimens are housed in the North Dakota State University Vertebrate Museum.

The specimens were scored according to a hybrid index system (Table 1) that includes four pairs of colors: rose vs. brown, rose vs. yellow, black vs. brown, and white vs. brown. Scores for phenotypically pure *P. ludovicianus* are "0" $(0+0+0+0+0)$ and for *P. melanocephalus* are "20" $(4+4+4+4+4)$. Relatively invariable characters were used in the index system so that specimens from extreme eastern and western North America (here assumed to be phenotypically and genetically pure) were indexed as "pure" (i.e. scores "0" and "20"). This assumption should be valid because hybridization between grosbeaks as described by West (1962) seems to be confined to a zone about 200 miles wide in the Plains. Anderson and Daugherty (1974), with a hybrid index system different from the one used in this paper, reported "hybrid" birds in extreme eastern and western populations; however, they regarded those birds as individual variations of the typical pure grosbeak phenotypes, rather than resulting from hybridization. According to the index system in this paper, specimens having scores of 1–19 would be judged to be hybrids. Back color could have been used in the index system, with pure black representing *P. ludovicianus* and black with broad brown streaks representing *P. melanocephalus*. It was not used because the back feathers with brown streaks of the winter plumage of *P. ludovicianus* are not always molted before the breeding season (pers. obs.), and therefore some pure *P. ludovicianus* would have received scores greater

TABLE 1

HYBRID INDEX FOR MALE GROSBEAKS (*PHEUCTICUS*)

Character	Description	
Upper breast	Rose, as in Rose-breasted Grosbeak	0
	Salmon pink	1
	Intermediate between rose and brown	2
	Brown with tinge of rose	3
	Brown, as in Black-headed Grosbeak	4
Medial upper abdomen and wing linings	Rose, as in Rose-breasted Grosbeak	0
	Salmon pink	1
	Intermediate between rose and yellow (orange)	2
	Bright yellow with tinge of orange	3
	Bright yellow, as in Black-headed Grosbeak	4
Nape and crown stripes	Black, as in Rose-breasted Grosbeak	0
	Mostly black, with a few brown feathers	1
	Half black, half brown	2
	Brown with much black spotting	3
	Brown with little or no black spotting, as in Black-headed Grosbeak	4
Lateral upper abdomen; rump	White, as in Rose-breasted Grosbeak	0
	Traces of buff	1
	Half brown, half white	2
	Traces of white	3
	Brown, as in Black-headed Grosbeak	4

than "0" (see Dwight, 1900, and West, 1962, for descriptions of molt sequence in *P. ludovicianus*).

Although both adult and subadult males were scored by the same index system, some exceptions in scoring were made for subadults. Nuptial-plumaged subadult *P. ludovicianus* often have brown edges on feathers of the back, black and brown rumps, and variable amounts of buff on mostly white abdomens. Because these characters are difficult to distinguish from hybrid characters, it would seem best to place more emphasis on scores of adults. In this study the characters described above in subadult *P. ludovicianus* were given scores of "0". This probably did not significantly bias hybrid index scores toward "0", because hybridization was infrequent as indicated by the scarcity of adult male hybrids (see below).

To provide further comparison of hybrid and pure grosbeaks, several standard measurements were taken as described by Pettingill (1970); bill length was measured from the anterior edge of a nostril to the tip of the upper mandible.

RESULTS

Distribution.—The ranges of the two grosbeak species in North Dakota are separated by the prairie-pothole country between the Missouri River to the southwest and the Souris, James, and Sheyenne Rivers to the northeast

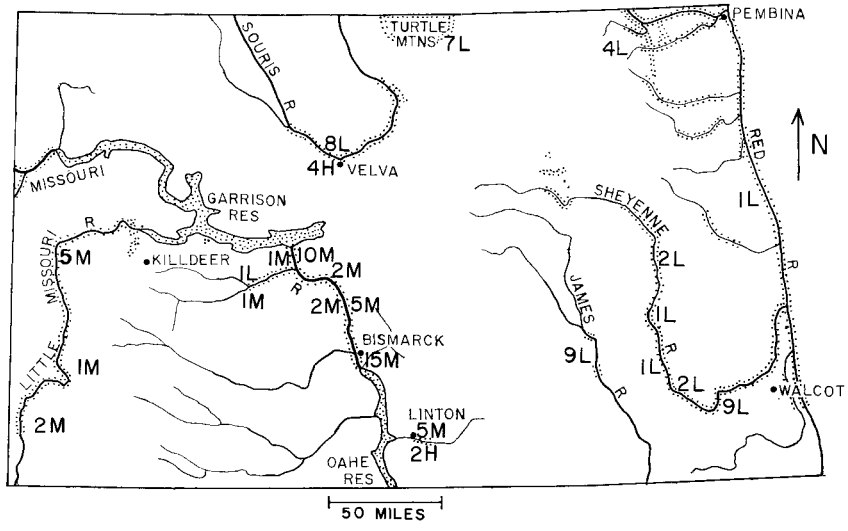

FIG. 1. Locality records of subadult and adult male grosbeaks collected in North Dakota during 1966–1968. L = *Pheucticus ludovicianus*, M = *P. melanocephalus*, and H = hybrid. The number preceding each letter is the number of specimens. Grosbeak habitat or deciduous forest is indicated by dots (except those showing reservoirs), as given by U.S. Geological Survey maps (1:250,000 series) with green forest overprint.

(Fig. 1). Upland forests and streams with riparian forests are virtually absent from this prairie country. Although some tree plantings exist in the area, grosbeaks do not utilize these appreciably as do orioles (*Icterus*) and flickers (*Colaptes*), which are forms that also hybridize in North Dakota.

Elsewhere in North Dakota, woodlands and forests along all the major streams and rivers support grosbeaks. Upland forests where grosbeaks are common are in the Killdeer Mountains (9 miles northwest of Killdeer), in the Turtle Mountains in north-central North Dakota, and in the Pembina Hills west of Pembina in the northeast. The forests consist principally of American elm (*Ulmus americana*), boxelder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and burr oak (*Quercus macrocarpa*). Plains cottonwood (*Populus sargentii*) woodlands occur along the Missouri and Little Missouri Rivers. Aspen (*Populus tremuloides*) stands predominate in the Turtle Mountains. *P. ludovicianus* were most abundant in woodlands of elm, ash, boxelder, and basswood (*Tilia americana*) along the Sheyenne River west of Walcott, and in woodlands mostly of elm along the Souris River just west of Velva. *P. melanocephalus* were most abundant in cottonwood woodlands along the Missouri River between the Garrison (Lake Sakakawea) and Oahe reservoirs.

TABLE 2

SCORES OF SUBADULT AND ADULT MALE GROSBEAKS (*PHEUCTICUS*) FROM NORTH DAKOTA[1]

	Upper breast	Medial abdomen and wing	Nape and crown	Lateral abdomen	Rump	Average total score
P. ludovicianus (45)	0	0	0	0	0	0
P. ludovicianus-like hybrids (3)	1	1	0	0	0	2
Medial hybrids (2)	2 & 3	2	2	2	2	10.5
P. melanocephalus-like hybrid (1)	4	4	4	3	4	19
P. melanocephalus (49)	4	4	4	4	4	20

[1] Numbers of birds are in parentheses.

Hybridization.—Only six of 100 males collected in North Dakota were hybrids, as judged from their hybrid index scores. These occurred only along Beaver Creek near Linton and along the Souris River (Fig. 1). Two very similar hybrids collected along Beaver Creek and the Souris River were phenotypically medial, with scores of 10 and 11 (Table 2). Three hybrids collected along the Souris River west of Velva were more similar to *P. ludovicianus* with scores of 2. One possible hybrid collected along Beaver Creek was similar to *P. melanocephalus*, with a score of 19. The 12 adult females and nine immatures were collected from the mainly *P. melanocephalus* populations from Beaver Creek to the Garrison Reservoir. One immature and three females, although generally similar to *P. melanocephalus*, had orange underwing linings. Because female and immature *P. melanocephalus* have yellow underwing linings, these four specimens are apparently hybrids. Females and immatures thus included a greater proportion of hybrids than did males, but the small sample size prohibits any generalizations. All other specimens from North Dakota, including 94 males, were phenotypically pure, with scores of 0 or 20.

During 1969 and 1971 I made additional observations on grosbeaks during behavioral experiments, in which a total of 116 territorial males were attracted to mounted specimens by recorded songs (Kroodsma, 1974). I was usually able to observe carefully each of these birds (with 8 × 30 binoculars) for a few minutes at nearly horizontal distances of 30–60 feet. I saw no obvious hybrids in 44 *P. melanocephalus* along the Missouri River south of Bismarck—where I saw one apparently pure *P. ludovicianus*, and no obvious hybrids in 47 *P. ludovicianus* along the Sheyenne River west of Walcott.

TABLE 3

MEANS ± ONE STANDARD DEVIATION OF MEASUREMENTS (IN MM) OF MALE GROSBEAKS IN NORTH DAKOTA[1]

	Rose-breasted Grosbeak		Black-headed Grosbeak	
	Subadult (21)	Adult (27)	Subadult (13)	Adult (36)
Wing	98.7 ± 1.8	101.8 ± 2.4	100.7 ± 2.2	103.1 ± 2.0
Tail	72.2 ± 2.4	73.8 ± 2.6	76.4 ± 2.3	78.2 ± 2.3
Bill	12.3 ± 0.6	12.3 ± 0.4	12.6 ± 0.4	12.8 ± 0.5
Tarsus	22.2 ± 0.6	22.6 ± 0.8	23.8 ± 0.9	23.6 ± 0.9
Total length	207.6 ± 5.1	209.4 ± 4.3	212.2 ± 4.9	214.0 ± 4.5
Weight	45.5 ± 3.6	44.6 ± 2.5	46.0 ± 1.8	46.2 ± 3.0

[1] Sample sizes are in parentheses.

Along the Souris River I saw 20 apparently pure *P. ludovicianus*, three *P. ludovicianus*-like hybrids, and one hybrid very similar to the two phenotypically medial hybrids described above. The *P. ludovicianus*-like hybrids included one with an entirely pale yellow breast and two with salmon-pink breasts with brown sides. The medial hybrid had an orange and brown breast and brown collar.

Measurements.—Subadult males were smaller than adult males in all measurements in *P. ludovicianus* except weight and in *P. melanocephalus* in tarsus (Table 3); however, only differences between wing and tail lengths in each species were significant ($P < 0.05$ by analysis of variance). Subadults and adults should therefore not be pooled during comparisons of these two size characters. For each respective age group, *P. melanocephalus* averaged larger than *P. ludovicianus* in all characters. The differences were significant ($P < 0.05$ by analysis of variance) for all except bill and weight of subadults. Thus in North Dakota the two species are distinct in size characteristics. West (1962) did not find such degrees of differences, possibly because he apparently pooled adults and subadults. Measurements of the small sample of hybrids did not show any noteworthy trend toward intermediacy.

DISCUSSION

Hybridization between grosbeaks is much less frequent in North Dakota than in South Dakota and Nebraska, and no hybrid zone or zone of overlap and hybridization (as defined by Short, 1969) exists. Hybridization in North Dakota may be less frequent because: 1, there are no rivers with riparian

woodlands to allow dispersal across the relatively treeless country between the breeding ranges of the two species; 2, relatively dense populations of grosbeaks on either side of the treeless country may quickly swamp phenotypic evidence of the infrequent hybridization; and 3, large reservoirs on the Missouri River may inhibit northwestward dispersal by *P. ludovicianus* into the range of *P. melanocephalus* along the Missouri River in North Dakota. Under these conditions contact between the two species and hybridization in North Dakota will probably not increase significantly.

Hybridization in grosbeaks is less extensive than that in the North American orioles and flickers as described by Sibley and Short (1964), Short (1965), and Anderson (1971). This may be true because the two grosbeak species: 1, have narrower habitat requirements and consequently less contact in the Plains; 2, mate assortatively—as indicated by West (1962) and Anderson and Daugherty (1974); 3, exhibit sufficiently large phenotypic differences in males that allow species-specific identification by males (Kroodsma, 1974); and 4, may have greater physiological differences. An example of the last is an apparent difference in molt, which— to my knowledge—has not been previously noted in the literature. In *P. melanocephalus* the feathers were always very worn and pointed in spring and summer specimens. In contrast, the feathers of *P. ludovicianus* had smooth unworn margins and rounded tips. Thus *P. melanocephalus* apparently lacks a prenuptial (prealternate) molt, while *P. ludovicianus*—as also stated by Dwight (1900)—has a prenuptial molt of the body feathers. Flickers (*C. auratus auratus* and *C. a. cafer*) and orioles (*I. galbula galbula* and *I. g. bullockii*) apparently show no such differences in molt (pers. obs.). A difference in molt in the two grosbeak species could indicate deep-seated physiological differences, which could in turn relate to reduced viability and fertility of hybrids. Hybrid females apparently lay more nonviable eggs than do pure females (Anderson and Daugherty, 1974).

All hybrids collected in this study showed a partial prenuptial molt of the body feathers, as indicated by the presence of both new and old feathers on the backs. In *P. ludovicianus*-like birds it would be desirable to know whether the presence of worn brown feathers on the backs results from hybridization with *P. melanocephalus* or from a delayed prenuptial molt as in *P. ludovicianus* (see methods section). This might be determined by comparing allopatric and hybridizing populations with respect to the proportion of birds that do not completely molt the body feathers of the winter plumage before the breeding season. The extent of the prenuptial molt could be inversely related to the frequency of *P. melanocephalus* genes, if the molt differences outlined above are constant in the two species.

SUMMARY

During June and July of 1966–1968, 100 male grosbeaks (*Pheucticus*) were randomly collected in North Dakota. The hybrids consisted of three *P. ludovicianus*-like, two phenotypically medial, and one *P. melanocephalus*-like hybrids, these occurring along Beaver Creek near Linton and along the Souris River. Hybridization is thus less frequent than in the more southern Great Plains. The breeding ranges of the two species in North Dakota are separated by relatively treeless country between the Missouri River and other rivers to the east. Invasion of each other's range and subsequent hybridization are apparently limited by this treeless country and large reservoirs on the Missouri River. Compared with orioles (*Icterus*) and flickers (*Colaptes*), grosbeaks hybridize less frequently, possibly because of greater phenotypic and physiological (e.g. molt) differences, narrower habitat requirements, and assortative mating. Adult males of the two species were significantly different in all six size characters measured.

ACKNOWLEDGMENTS

Field work from 1968–1969 was done as part of my Ph.D. program in the Department of Zoology at North Dakota State University. I thank J. Frank Cassel, E. Charles Meslow, John J. Peterka, Robert L. Burgess, and Richard D. Frye for their help with my thesis, of which this paper is a modified part. My research was made possible by a National Defense Education Act Fellowship (Title IV) granted by the United States Department of Health, Education, and Welfare. Collecting permits were graciously issued by the North Dakota Game and Fish Department and the United States Bureau of Sport Fisheries and Wildlife.

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