

HYBRIDIZATION IN GROSBEAKS (*PHEUCTICUS*) OF THE GREAT PLAINS

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IN bisexual, cross-fertilizing organisms a species may be defined as a group of populations that shows intrinsic reproductive isolation (actual or potential) from other such groups of populations (Mayr, 1942). Sympatric populations are easily accommodated by this definition, but in allopatric groups the existence of potential reproductive isolation is more difficult to determine. It is widely believed that spatial isolation is necessary for species formation (Mayr, 1942; Dobzhansky, 1951: 205). Once a population is divided and gene flow between the isolates ceases, differential selection and the occurrence of mutation and recombination lead to divergence. This is classical theory of speciation and needs no further elaboration. A later rejunction of these populations will provide a natural test of the degree of intrinsic reproductive isolation that they have acquired. For this reason such rejunctions, or secondary contacts, are of interest to the student of evolution.

There are two basic outcomes of a secondary contact: the populations are reproductively isolated, or they hybridize. Actually a continuous series of possibilities exists. Since the evolution of species is a gradual process, its interruption at any given time will result in something between hybridization and lack of it. In addition, the ecological compatibility of the two populations will modify this simplified dichotomy.

Hybridization is of common occurrence in secondary contacts. Among birds the studies of Meise (1936), Sibley (1950, 1954, and 1958), Dixon (1955), and Mayr and Gilliard (1952) may be mentioned. A distinction should be made between the occasional hybridization between sympatric species (*e.g.*, ducks of the genus *Anas*), in which reduced success of the hybrids preserves the integrity of the species, and hybridization between allopatric populations in recent secondary contact. In this paper the latter case is considered.

An example of a secondary contact with hybridization is found in two North American grosbeaks, the Rose-breasted Grosbeak, *Pheucticus ludovicianus*, and the Black-headed Grosbeak, *P. melanocephalus*. These birds, hereinafter referred to as *ludovicianus* and *melanocephalus*, are the North American representatives of a small genus that also includes *P. chrysopheplus* and *P. aureoventris* of Central and South America. They are more closely related than either is to the Latin American species. They occupy complementary ranges, *ludovicianus* east of the Great Plains, *melanocephalus* to the west. They are primarily woodland birds and do not breed widely in the Plains. They do occur in the riparian woodlands of the Plains

rivers, however, and there they interbreed. It has rarely been doubted that the two forms are good species, despite the evidence of hybridization reported by Swenk (1936). The similarities of nests, eggs, and habits have often been noted, however, and it appears that the differences in male plumage have convinced taxonomists of their specific status.

This paper is a reevaluation of the status of the two grosbeaks. Specimens from the Great Plains will be described, and evidence from hybridization will be considered in relation to the specific status of the two forms. The paper describes the biological situation, but a taxonomic judgment will be made.

The investigation is part of a study of avian hybridization in the Great Plains initiated by Charles G. Sibley under grant G-1832 of the National Science Foundation. Other studies in this project include the following: Indigo and Lazuli buntings, *Passerina* (Sibley and Short, 1960); Rufous-sided Towhees, *Pipilo* (Sibley and West, 1958); Flickers, *Colaptes* (Short, 1959); orioles, *Icterus galbula* and *bullockii* (Short, in prep.). This paper is modified from a thesis presented to the Graduate Faculty of Cornell University in partial fulfillment of the degree of Doctor of Philosophy.

METHODS AND MATERIALS

Between 1955 and 1957 field parties from Cornell University collected 308 specimens of *Phœucticus* in Nebraska, South Dakota, and Colorado. Material was borrowed from other museums for additional information. Most specimens were males, and little information was gathered on females. All specimens were taken between mid-May and late July.

Standard measurements are in millimeters. The length of the black throat of adult males from the chin to the posterior edge of the black area was also measured. In specimens with an indefinite posterior margin the measurement extended to the point where black and the breast color were equally mixed. The lengths of terminal white spots on rectrices were also taken.

Hybrid index. Two color characters are sufficiently different in the two grosbeaks to be used in a hybrid index scheme of the sort commonly employed (Anderson, 1949). The characters are:

1. Breast, belly, and underwing color: rose-red in *ludovicianus*, yellow in *melanocephalus*.

2. Extent of brown in plumage: present on underparts, rump, hind neck, and other areas of *melanocephalus*, absent and usually replaced by white in *ludovicianus*.

Five gradations of each character could be derived from specimens, using only males. These are scored as follows:

Belly color

"0" rose, as in *ludovicianus*

"1" slightly orange or salmon-pink

"2" orange

- "3" yellow with slight salmon tinge
- "4" rich yellow, as in *melanocephalus*

Brown extent

- "0" no brown in areas noted, as *ludovicianus*
- "1" trace of hind neck collar; tinge of brown on rump and underparts
- "2" collar obvious; other areas about half of maximum
- "3" only slightly less than *melanocephalus*, especially in collar and underparts
- "4" brown as in *melanocephalus*

Thus a male specimen is indexed on a scale of "0" to "8" when the two characters are summed. When given separately (as "1" + "3"), the first number refers to belly color. Intermediacy in underwing color of males is expressed either as a uniform color or as a mixture of pinker and yellower feathers. Because of the individual variation in brown head striping of *melanocephalus*, that area is not included in the scoring of brown.

Correlation of hybrid index characters. Ideally each character of a hybrid index should be independent. That is, it should not be linked with the other characters. If single genes, or gene complexes, are the bases of the characters, then independent assortment is desired, although differential survival of some combinations might mask it. Lacking knowledge of the genetics of the characters, a correlation coefficient between the two characters will give some indication of the degree of linkage. If, in a scheme with three characters, two are closely linked, any summed index will be biased in favor of the two linked characters. Using 67 specimens of obviously hybrid origin, a correlation coefficient of 0.484 was calculated for the two characters of the hybrid index. The hypothesis of no correlation is rejected at the 0.001 level. Despite the close correlation there are two reasons for retaining the two characters. There are many specimens that do not fall into the category of perfect correlation. It would be difficult to compress all the variation of the hybrids into a more simple scheme. In addition, since only two characters are used, there is no danger of introducing a bias into the summed index.

Male plumage. Comparisons of male plumage are given in Table 1. Descriptions are modified from Ridgway (1901), and they refer to typical specimens. There is considerable variation, however, and several points concerning such variation should be noted.

1. Several adult male *ludovicianus* in nuptial plumage have partly obscured supra- and postocular stripes and capital stripes. These are identical in placement to the brown marks in *melanocephalus* although lacking the brown pigment of the latter.

2. All adult male *ludovicianus* examined have a concealed hind neck collar of subterminal white bars on the otherwise black feathers. *Melanocephalus* commonly has several black-tipped feathers in its brown collar.

3. Many adult male *ludovicianus* have partly concealed, white subterminal bars on the black interscapulars. *Melanocephalus* feathers are brown-barred on rather lanceolate interscapulars. Some individuals of *ludovicianus* have similar lanceolate interscapulars though lacking the brown pigment.

4. The extent of black on the throat of *ludovicianus* is variable. Some individuals

TABLE 1
PLUMAGE OF ADULT MALES

Plumage area	<i>ludovicianus</i>	<i>melanocephalus</i>
Throat	black, sometimes mixed with rose (note 4)	black for about 5 mm, rest brown
Breast	rose	brown, some with partly concealed yellow
Belly	center streak rose, sides white	brown with yellow center streak
Undertail coverts	white	pale brown
Head and neck	black (note 1)	black with brown collar (some have head stripes, note 2)
Back	black (note 3)	black and brown striped
Rump	white, with some black tips	brown, with some black tips
Underwing coverts and axillars	rose	yellow
Tail	black, outer three pairs of rectrices with white tips (note 5)	black with outer two pairs of rectrices white-tipped (note 5)

have the black restricted to a narrow band at the chin, as is typical of *melanocephalus*, while others have the black extending onto the breast. Data are given in Table 2.

5. The number of white-tipped rectrices varies in each form. Typical *melanocephalus* has two pairs of rectrices with large white tips, while *ludovicianus* usually has three such pairs. Table 3 summarizes variations among "pure" samples of each form.

Female plumage. *Ludovicianus* females usually have salmon-yellow underwing feathers, while in *melanocephalus* this area is pure yellow. There is great variation in *ludovicianus*, however, as has often been noted. Ridgway (1901: 614) says: ". . . underwing coverts and axillars yellow (maize yellow, chrome yellow or light orange yellow) . . ." Of adult females from northeastern United States only two have yellow underwings. The others range from slightly pinkish-orange to rose-red, as in males. A female with rose-red underwings was collected near O'Neill, Holt County, Nebraska, on 26 June 1955 and had an enlarged ovary. Moyer (1930) described two similar

TABLE 2
LENGTH OF BLACK THROAT IN MM WITH VARIANCES OF SOME SAMPLES

Locality	3-9	10-14	15-19	20-24	25-29	30-34	35-39	s ²
Appalachian Region (<i>ludovicianus</i>)	-	2	10	16	8	4	-	23.4
Mich. and Minn. (<i>ludovicianus</i>)	2	-	10	12	14	9	2	42.4
Platte Transect (hybrid zone)								
Blair	-	2	3	4	4	-	-	
Schuyler	1	1	1	5	9	12	1	
Silver Creek	3	1	1	8	7	4	1	
Grand Island	8	3	3	5	7	6	1	96.0
Elm Creek	11	2	-	2	-	-	-	
Gothenburg	12	3	2	-	1	-	-	
Western U.S. (<i>melanocephalus</i>)	63	20	4	-	-	-	-	6.5
Southern Mexico (<i>melanocephalus</i>)	13	4	-	-	-	-	-	

TABLE 3
TAIL SPOT LENGTH, IN MM

Locality	Rectrix	0	+0	10-19	20-29	30 up mm
Appalachian Region (<i>ludovicianus</i>)	6	-	-	-	9	29
	5	-	-	-	14	24
	4	2	-	-	22	14
	3	19	14	1	4	-
	2	32	5	-	-	-
	1	36	1	-	-	-
Western U.S. (<i>melanocephalus</i>)	6	-	-	-	27	6
	5	-	-	3	28	2
	4	-	25	-	7	-
	3	5	25	-	-	-
	2	13	17	-	-	-
	1	25	3	-	-	-

The white spot on the inner web is measured from the tip to the basal end of the spot about 3 mm from the rachis. An isolated spot is indicated by +.

specimens from near Chicago. Rand (1948) reports one from Medicine Hat, Alberta. There is no lack of such individuals, and their occurrence away from the zone of hybridization in Nebraska excludes hybridization as the responsible factor.

Females differ in two other ways: breast of *ludovicianus* is usually heavily streaked; that of *melanocephalus* usually clear buffy-yellow. The amount of yellow in the plumage differs. *Melanocephalus* has yellow in the belly streak, head stripes, etc., while *ludovicianus* does not.

GENERAL BIOLOGY OF THE GROSBEEKS

Plumage sequence and molts. Dwight (1900) described the molts and plumages of *ludovicianus*. His sequence includes partial postjuvenile and prenuptial molts, as well as a complete postnuptial molt. The only part of his sequence requiring modification is the first prenuptial molt.

First nuptial plumage is acquired through a partial prenuptial molt, including body feathers, tertiaries, and most wing coverts. Some secondaries and a few rectrices are replaced. All primaries are retained. Dwight incorrectly states that the tail is replaced at this time and is black (not brownish as in juvenile plumage) in first nuptial plumage. A first-year *ludovicianus* retains most of his juvenile rectrices until the following fall. Among nine first-year males taken in May and June (after completion of the molt) the following variation was found:

- 7 May. Pairs 1 and 2 and right 6 replaced; the rest not.
- 10 May. Pairs 1 and 6 replaced; right 2 emerging.
- 11, 12, 15 May. Pair 1 replaced.
- 22 May. Right 1-6 and left 1-2 replaced.
- 25 May. Pair 1 and right 3 replaced.
- 27 May. Right 1-6 and left 1-3 replaced.
- 5 June. Pair 1 dropped; right 2-6 replaced; left 2-3 emerging.

Apparently most individuals molt the central rectrices first (the usual

passerine pattern). The remainder are molted, however, with considerable irregularity. Ivor (1944) described the molt of *ludovicianus* in captivity as lasting from early January to late April. He found that while first-year birds replace a few remiges and rectrices in the prenuptial molt, adults retain all these feathers, molting them only in their postnuptial molt. This is confirmed by specimens.

There is a distinct winter plumage in adult male *ludovicianus*, the head acquiring stripes similar to those of first-year males and of adult *melanocephalus*. The rose breast is well veiled with buff and spotted with black.

Adult nuptial plumage is acquired by a partial prenuptial molt, in which the body feathers alone are involved. At this time the rose breast reaches full expression, and, with few exceptions, the back and head become completely black. The tips of the secondaries retained from the previous fall become worn and have small notches where there were buffy spots before.

The plumage sequence of *melanocephalus* is much like that of *ludovicianus*, although there is no distinctive winter plumage in males, the feathers being only slightly buffy-edged.

Distribution and migration. Generalized ranges are shown in Figure 1. Two banding recoveries of *ludovicianus* in its wintering range suggest that the more eastern populations winter farther south and hence farther east. Two hybrids, presumably reared in the Great Plains, were taken from the area where the winter ranges overlap, in southern Mexico. These specimens are described below.

Habitat preference. *Ludovicianus* is found in deciduous and mixed deciduous-coniferous woodland throughout its range. At the northern end of the breeding range (northern British Columbia) it is restricted to the area designated by Munro and Cowan (1947) as Peace River Parkland. The habitat is characterized by ". . . predominance of mature aspens growing in semi-open stands with occasional dense groves of smaller aspens, scattered white spruces, white birch and, in depressions along seepage courses, groves of willows." Ground cover is dense. The distribution of aspen forest north of the Canadian prairies delimits grosbeak distribution in the area, with the exception of the river valleys of southern Manitoba, Saskatchewan, and Alberta.

In northeastern United States deciduous woods with dense undergrowth are a common habitat. At Ithaca, New York, *ludovicianus* is abundant in wet woods at the head of Cayuga Lake. Elms (*Ulmus americana*), Cottonwood (*Populus deltoides*), Silver Maple (*Acer saccharinum*), and Basswood (*Tilia americana*) are common trees, and there is a dense understory of shrubs, especially Spicebush (*Lindera benzoin*) and Elderberry (*Sambucus canadensis*), and vines.

In the southern Appalachians *ludovicianus* breeds at elevations above

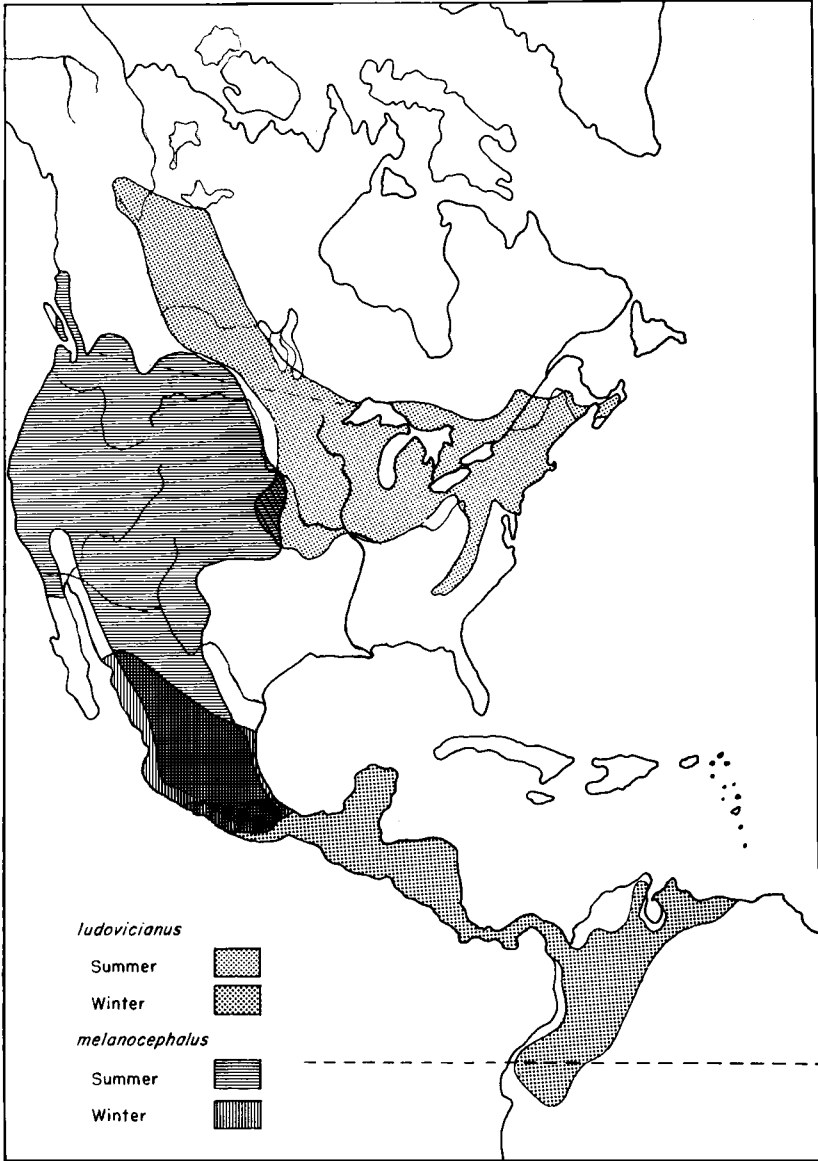


Figure 1. Approximate breeding and winter ranges of the two North American *Pheucticus*. Data from Dr. E. M. Reilly, unpublished.

about 1,000 meters (3,000 feet). In northern Georgia (Burleigh, 1958) it is restricted to areas of scattered rhododendron thickets, and nests were found here and in yellow birches and chestnuts. Perrygo (1936,

unpubl. journal in USNM) reports its breeding in birch-spruce associations (Cranberry Glades) in West Virginia.

Along the Platte and Missouri rivers in Nebraska this grosbeak breeds most commonly in groves of mature cottonwoods, with understory vegetation two to three meters high. This formation is similar to that found at Ithaca, New York, and seems to be the one favored throughout the range.

Melanocephalus is reported from a greater diversity of habitats, although riparian woodland is most frequently mentioned. Munro and Cowan (1947) report it in coastal British Columbia in "mixed and second growth forest in the Puget Sound Lowlands." In California Grinnell and Miller (1944) state that willow-cottonwood associations are especially favored, and that grosbeaks occur in montane forest also, especially where intermixed with deciduous oaks. They conclude (p. 444): "Perhaps an important factor is local diversity of plant growth and extensive 'edge' conditions."

Although primarily a bird of mountains and foothills in the West, *melanocephalus* breeds on the western edge of the Plains and along the rivers to eastern Nebraska and Kansas. Here it occupies habitat similar to that of *ludovicianus*. Breeding birds often wander to open fields and dry, sparsely wooded areas of river bottom land along the Platte River to feed, but they apparently require dense vegetation nearby for nesting.

Nests and eggs. Many authors have commented on the similarity of the nests and eggs of the two grosbeaks. Reed (1904) described the eggs of *ludovicianus* as greenish-blue, spotted especially at the larger end with reddish-brown. The eggs of *melanocephalus*, he says, are a paler blue, the spots being less distinct. Coues (1874) states, concerning the eggs of *melanocephalus*: "In nearly a dozen specimens I can find no reliable differences from the eggs of the Rose-breasted Grosbeak." The nests of the two are extremely similar, being built of twigs and rootlets and so frail that the eggs are usually visible from below.

Vocalizations. Recordings of the songs and calls of both forms are available and indicate the similarities better than descriptions can. *Melanocephalus* has more mewing and slurred notes in its primary song. In addition the common call note (a sharp *chink*) is a little less sharp in *melanocephalus*. The songs and calls appear to serve similar functions in the two, however, and they are no more different than those of many geographic races.

Plumage pigments. The grosbeaks differ in two types of pigments. The brown color prevalent in *melanocephalus* is probably a melanin, while the reds and yellows are carotenoids, most likely xanthophylls, which are common in red and yellow feathers (Fox, 1953). Several subspecies or closely related species are known in which the differences in red and

yellow feathers involve simple differences in carotenoids. Test (1942) has investigated the pigments of the flickers, *Colaptes*, and Kritzler (1943) those of certain African weavers, *Euplectes*. Among other examples not as yet studied at the pigment level are two South American tanagers, *Ramphocelus* (Sibley, 1958), the two North American tanagers, *Piranga olivacea* and *ludoviciana*, and two Indian bulbuls, *Pycnonotus* (Sibley and Short, 1959). In all these cases there is some hybridization between the forms, and it seems likely that these will prove to involve quantitative differences in carotenoids. There is no reason to believe that the grosbeaks are different from *Euplectes* and *Colaptes* in this regard either.

Evolution of plumage differences. It is important to ask what sources of selection have operated in the evolution of the plumages of the two grosbeaks. Once the original division of the ancestral populations occurred, differences in selection would be expected to alter the genetic characteristics of the isolates. Although chance events may have been important when the original division took place, it is unlikely that they would continue to be important. It is probable that selection is responsible for the present plumage patterns of the grosbeaks. In this connection interaction between the ancestral grosbeaks and sympatric, but perhaps unrelated, species may have played a part. Such interactions, although they may be theoretically important, are difficult to demonstrate. A logical extension of the idea of reinforcement of isolating mechanisms through selection against hybridization is that interaction, however slight, can effect similar results. Sibley (1957) has discussed this possibility more fully.

Ludovicianus is strongly sexually dimorphic compared with *melanocephalus*. It has been suggested since Darwin that sexual selection is at least partly responsible for the more brightly colored males of sexually dimorphic species through the greater success of those individuals in stimulating and attracting mates. On the other hand the dull-colored females have evolved under the impact of selection by predators. In *ludovicianus* it is difficult to fit the facts to this theory. Males of both the grosbeaks incubate part of each day while females alone incubate at night. In addition males assist in brood care, and both sexes sing while on the nest. Thus it would seem that any selective advantage accruing to the concealingly colored females would be cancelled by the presence of a brightly colored male around the nest when predators (small accipitrid hawks, jays, etc.) could eliminate a whole generation of birds.

The occurrence of hybridization suggests that whatever it is in male plumage of the two forms to which females respond in pair formation it is not the details of plumage, including a particular color, red or yellow. It may be instead the over-all appearance of the males, including the white

wing and tail patches, which are the same in the two forms and which are displayed prominently by courting males (Ivor, 1944). The great individual variation that both forms show in certain aspects of plumage further suggests that details of plumage are not important in reproductive success of males.

HYBRIDIZATION

Previous studies. Swenk (1936) summarized the knowledge of grosbeak hybridization in the Missouri Valley region, particularly Nebraska, and described the hybrid specimens known to him. The first hybrid collected in Nebraska was taken in 1920 east of Hastings, in Clay County, and others were seen during the following 15 years. These were all adult males and were nearly intermediate in breast color. In June 1930 two male *melanocephalus* were seen in Lincoln, Lancaster County, and appeared to be mated to female phenotypic *ludovicianus*. They were seen feeding young out of the nest. Several of the local grosbeaks were banded at the end of summer, and the following year a hybrid, although unbanded, returned with them. Swenk described the bird, and it closely resembled a first-generation hybrid raised in captivity by Ivor (see below). Other hybrids have been reported since 1936 (Brooking, 1936; Nebr. Orn. Union Report, 1938). Unfortunately, very few specimens have been taken in Nebraska, and most sight records are of intermediate individuals. Slight traces of hybridization are not evident in the field. Specimens are often labeled as one or the other species and are thus buried unreported in collections. In addition hybrid females are difficult to identify.

Other hybrids collected outside Nebraska before 1955 include the following:

1. Ad. male. Jalapa, Veracruz, Mexico. January 1888. F. D. Godman Collection, in the British Museum (N.H.). This and the following are the only wintering hybrids known to me.
2. Sex? San Agustin, 5,700', Michoacán, Mexico. 23 February year? R. T. Moore Collection. I have not seen the specimen, which is reported by Friedmann, Griscom, *et al.*, 1957 as "hybrid." It is presumably a male.
3. "Young" male. Stump Lake, Nelson County, North Dakota. 29 July 1902. L. B. Bishop (reported by Swenk, 1939). This bird had "the general color of the Black-headed Grosbeak but with underwing coverts and axillars salmon pink."
4. Adult male. Rawlins County, Kansas. 28 July 1936. KUMNH 21523. This specimen scores "2" + "2" and is the only one known to me from Kansas. Tiemeier (1937) called it "*ludovicianus*."
5. Two adult males. Wheeler, Charles Mix County, South Dakota. 9 June 1937. UMMZ 128894 and 128896. The former specimen scores "2" + "2," the latter "4" + "3." These are among the very few hybrids known from South Dakota.

Up to 1955 at least nine hybrids had been collected and another half dozen seen. The earliest known specimen was taken in Mexico in 1888,

while the majority were collected in Nebraska from 1920 to 1940. Paucity of specimens from the Great Plains accounts for lack of knowledge of hybridization.

Changes in distribution in historic times. Swenk mapped the ranges of the grosbeaks and documented an apparent invasion of eastern Nebraska by *melanocephalus* between 1915 and 1930. He also discussed a similar westward expansion of *ludovicianus* a little earlier. His evidence was largely anecdotal, consisting of personal observations of residents and a few specimens. He recorded that *melanocephalus* had appeared for the first time in a number of localities in eastern Nebraska during the period mentioned. He was certain that this form had invaded eastern Nebraska, since competent observers had been in the area before the invasion and had reported no breeding records of *melanocephalus* before about 1915.

At Hastings, Adams County, *melanocephalus* was not reported until 1914, but by 1924 it was common. These records may in part refer to hybrids, as no specimens were collected until 1920. At Crete, 120 km (70 miles) to the east, it was first reported about 1930. At Lincoln presumed migrants were seen as early as 1911, but it was not until 1930 that breeding *melanocephalus* (a hybrid pair) were reported. It is probable that this was a true invasion, as the appearance of *melanocephalus* fairly recently agrees somewhat with the increase in numbers of hybrids, a result, presumably, of greater reproductive contact between the forms. Unfortunately, there were few observers or collectors in the Platte Valley, where grosbeaks are now commonest in Nebraska. Thus evidence from that critical area is lacking.

Regarding *ludovicianus* Swenk (1936: 28) states: "It seems quite certain that the species has extended its range westward in the past seventy-five years" (that is, since about 1860). The evidence for this assertion is scanty. In 1900 *ludovicianus* seems to have bred (or hybridized) nearly as far west as it now does along the Platte. A specimen was collected near Kearney in June 1901, and at Elm Creek, a few miles west of Kearney, very few pure *ludovicianus* are now found. Along the Republican River in northwestern Kansas a hybrid was collected in 1936 (listed above) nearly 200 km (130 miles) west of the nearest locality (Red Cloud, Nebraska) where *ludovicianus* was reported by Swenk the same year.

There are several recent records of *ludovicianus* in breeding season from the Nebraska-Colorado border along the South Platte River (near Brule, Nebraska; Nebr. Orn. Union Report, 1950 and 1951). The information does not reveal whether these were breeding, or whether they were mated to female *ludovicianus*, but their presence there in mid-June is suggestive of breeding, and most likely with female *melanocephalus*. There are earlier reports of breeding *ludovicianus* in northern Colorado (Burnett, 1902), but there is no evidence of a general increase of that form in the western Plains.

In South Dakota Hayden collected both forms on the Missouri River at the Bijou Hills on 16 May 1856 (Baird, 1858), but these in part may have been migrants. A female *ludovicianus* and several *melanocephalus* were taken. This is the easternmost part of the Missouri Valley in which Hayden encountered *melanocephalus*. At the present time the influence of *ludovicianus* does not extend far beyond this point. The hybrids collected in 1937 were taken just south of the Bijou Hills.

Present study. In 1955 a grid of collecting localities was visited in the central Plains (Nebraska and South Dakota) to learn something of the distribution and extent of hybridization of grosbeaks and other bird popu-

TABLE 4
SAMPLING GRID, 1955, WITH HYBRID INDEX SCORES OF MALES

Locality	Number		Index scores of males									
	♂♂	♀♀	0	1	2	3	4	5	6	7	8	
Nebraska												
Crete	1	—	—	—	1	—	—	—	—	—	—	
Hastings	3	—	1	1	—	—	1	—	—	—	—	
St. Paul	2	2	—	—	—	1	—	—	—	—	1	
Burwell	2	—	1	—	—	—	—	—	—	—	1	
Halsey	1	—	—	—	—	—	—	—	—	—	1	
O'Neill	2	1	—	1	—	—	1	—	—	—	—	
Spencer	2	—	1	—	—	—	1*	—	—	—	—	
Bassett	2	—	—	—	—	—	—	—	—	—	2	
Chadron	11	1	—	—	—	—	—	—	—	—	11	
South Dakota												
Chamberlain	3	1	—	—	—	—	—	—	—	—	3	
Murdo	1	—	—	—	—	—	—	—	—	—	1	
Kadoka	6	4	—	—	—	—	—	—	—	—	6	
Midland	3	1	—	—	—	—	1*	—	—	—	2	
Howes	11	3	—	—	—	—	—	—	1	—	11	
Rapid City	7	2	—	—	—	—	—	—	—	—	7	
Promise	—	1	—	—	—	—	—	—	—	—	—	
Mobridge	5	1	—	—	—	—	—	—	—	—	5	

* Sight records; approximate index.

lations in secondary contact. It then seemed desirable to run a transect across the Plains through the zone of hybridization. This was done in 1956 and 1957, and camps were established at 80-km (50-mile) intervals from the Missouri River, near Omaha, to the base of the Rocky Mountains in northern Colorado. This river system was chosen for its direct route across the Plains and because of its fine riparian woodland nearly all the way. In the transect most of the grosbeak hybrids were collected.

The localities visited in the three years are shown in Figure 2, the town nearest the collecting station being indicated. In Figure 3 is shown the distribution of grosbeaks in the Plains. Records from North Dakota are largely derived from unpublished notes at the North Dakota State University, Fargo, supplied by J. F. Cassel. Table 4 lists the localities of the 1955 sampling grid together with the numbers of specimens and the hybrid indices of the males.

Platte Transect, 1955-1957. Eleven localities were visited along the Platte and South Platte rivers, with one camp on the Missouri River at Blair, Nebraska, north of Omaha. At each locality collecting was done along several kilometers of river bottom land. The sampling technique consisted simply of collecting all grosbeaks possible, with equal effort spent on each specimen and no special attempt to collect hybrids. In the time available (three days) this seemed the best system. The Grand Island locality was visited in all three years; others in 1956 and/or 1957. Histo-

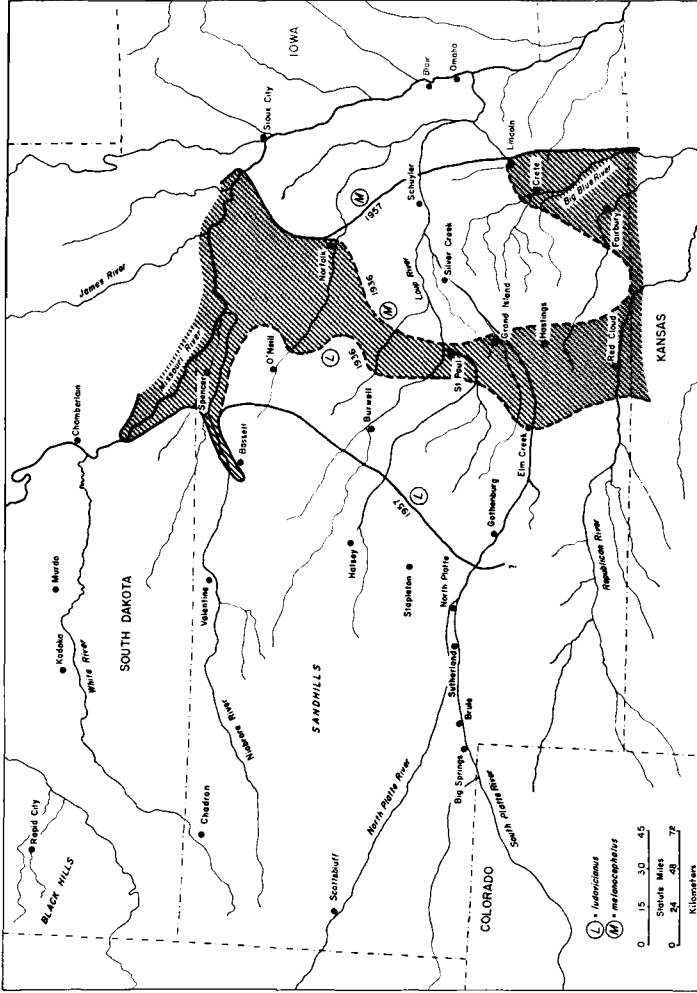


Figure 2. Localities in Nebraska and surroundings and zone of hybridization in 1936 (Swenk) and 1957.

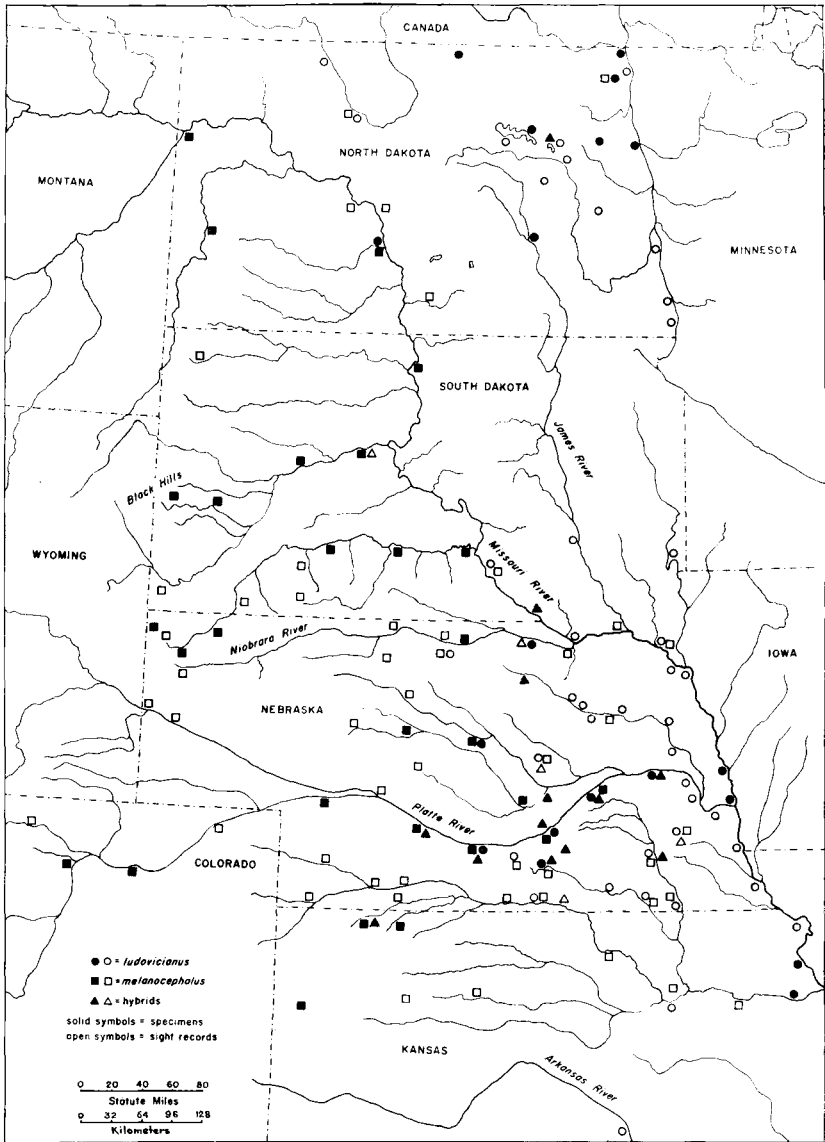


Figure 3. Distribution of grosbeaks in the central Great Plains.

grams of hybrid index scores of specimens taken in the Transect are given in Figure 4.

The South Platte River rises in the Rocky Mountains of central Colorado and flows northeastward across the Plains to its junction with the North Platte in western Nebraska. From this point the Platte runs east-

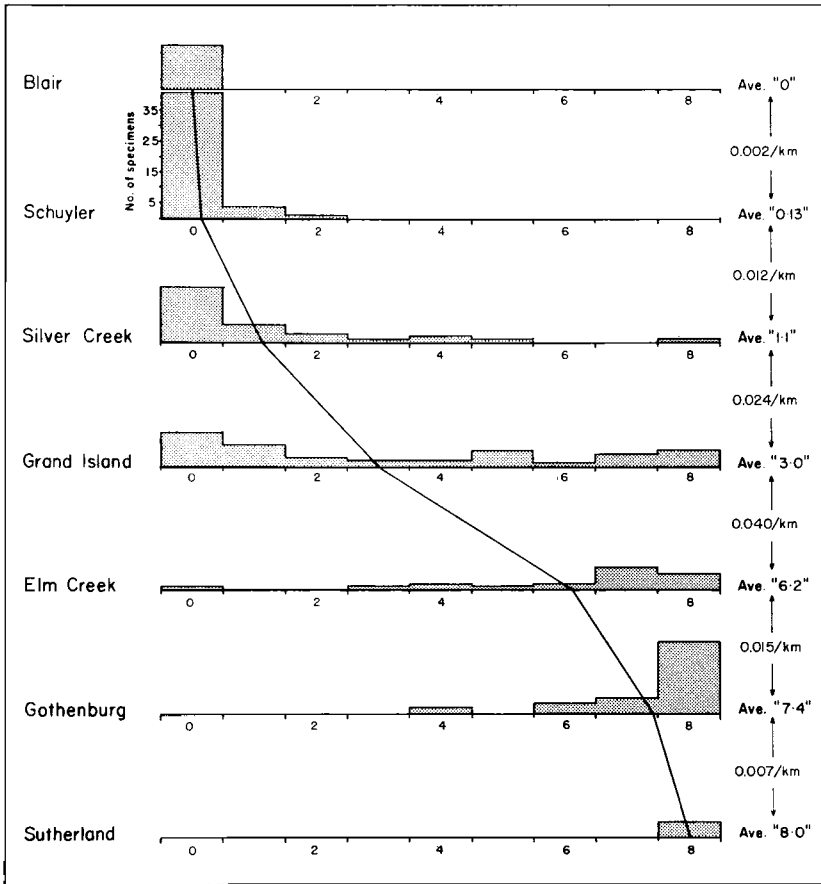


Figure 4. Histograms of hybrid index scores for samples from the Platte Transect. The shift per kilometer in average index is given. Localities are about 80 kilometers (50 miles) apart.

ward to enter the Missouri south of Omaha. There is a continuous riparian woodland along this river system that spans the grassland of the Great Plains and provides a dispersal route for woodland birds from the Missouri River to the mountains. It also provides habitat for some western species, including some mammals, although birds have taken a greater advantage of it. In parts of the Plains (western Kansas for example) the rivers have their watershed well east of the mountains, leaving a wide gap between their western ends and the western edge of the Plains. In other areas (Nebraska for example) there is a continuous woodland connection across the grassland.

Several writers, especially Fremont (1848), were consulted for information on the state of riparian timber in the Plains before white man had changed it drastically. For more details on this point see West (1959). Two points seem valid concerning woodland along the rivers of the Plains during the last 150 years.

1. There has been at least a scattering of woodland nearly throughout the length of the Platte and South Platte rivers since before white man arrived there. Islands were more thickly wooded than river banks, but there was undoubtedly suitable grosbeak habitat at least as far west as the present Nebraska-Colorado border, although perhaps not so continuously distributed.

2. There was reduction through lumbering in the original amount of riparian woodland during the 19th century. The already narrow belt of trees was reduced to a sparser condition, while trees were being planted around towns and on the flood plain. Since the turn of the century, however, there has been an increase in riparian timber, until at the present time there is undoubtedly more such woodland along the Platte than there was 150 years ago. The increase may be accounted for by several factors.

The reduction in water volume in the Platte, through increased diversion for irrigation in the western Plains, has apparently substantially reduced the scouring of banks and subsidiary channels downstream. Near Grand Island, in central Nebraska, it seems that old channels are being overgrown faster than new ones are being cut by the river. Local residents report that the river is dry in many years in early summer; this is confirmed by personal experience. The annual floods that ravaged the channels during the spring in the last century are reported to have filled the river from bank to bank. The Platte River is no longer subject to such devastation throughout most of its course.

Fire, which is believed by many to have contributed to the prevention of natural forests on the prairie (Bessey, 1914; Gleason, 1923), is no longer a factor along the rivers. Bessey (1897), speaking of the tributaries of the Loup, Blue, and Missouri rivers in eastern and central Nebraska, said: "No one who has seen and studied the forest areas of eastern Nebraska will be able to doubt that they are spreading where they are given a fair opportunity and are not prevented by man or his domestic animals." By now man had replaced fire.

Tree planting has contributed many shelterbelts and timber claims to the Platte Valley. Because of their sparse undergrowth these are not usually suitable habitat for grosbeaks. In some areas the plantings have been closer to the river, and undergrowth has been allowed to develop. There is now little lumbering along the Platte. Hence natural regeneration is not seriously impeded, except sometimes by grazing.

Although the river channels may be dry for months, there is underground water in the bed, and this provides moisture for trees along the banks. One often finds pools of cold water where underground water comes to the surface in an otherwise dry, sandy river bed.

Grosbeaks were among the common birds at all localities on the Platte River. The braided channels provide much suitable habitat in the islands that lie between them. These have a characteristic vegetational structure including much "edge." The sides of the islands usually have a wall of understory two to three meters high with mature cottonwoods above. Behind the wall is a clearing or area of scrubby vegetation. If the island is cut by a disused channel there will be another wall on either side of it, and it will often have a thicket of willows in its bed. The effect of all this is to provide local diversity in plant cover, a condition that attracts grosbeaks.

Hybrid zone. The zone of hybridization is shown in Figure 2. In Nebraska hybrids were collected at five localities on the Platte Transect, from Schuyler to Gothenburg. It can be seen that at no locality were hybrids alone collected. The zone, which here is about 320 km (200 miles) wide, is actually an overlap zone with hybridization. Since it seems that ecological factors are not keeping the grosbeaks separated, other reasons must be sought to explain the broad overlap without complete breakdown. Three such reasons were considered: reduced success of hybrids, assortative mating, and differential immigration. Data on success of hybrids are quite inadequate, and only a little information was gathered on assortative mating. Five mated pairs were collected on the Platte and two more near Hastings. The mated pair taken near Silver Creek suggests assortative mating, since both birds appeared to be *melanocephalus*, while the rest of the sample collected there was close to *ludovicianus* (index of "4" or less). The remainder of the mated pairs, however, shows commonest classes paired, not classes most similar. The information is meager.

If there is a tendency toward assortative mating it would be strengthened if immigration into new parts of the range were accomplished by both sexes. Several extralimital records of *ludovicianus* in the western states have apparently involved mated pairs, with both birds *ludovicianus*. The most recent is reported by Rickard (1960). Females are difficult to distinguish from those of *melanocephalus*, but it is possible that small groups of *ludovicianus* may migrate together and lead to intragroup matings. The pair of *melanocephalus* at Silver Creek could be explained this way. The methods of range expansion in birds are not well known, but it is presumably first-year birds that do the pioneering, remaining where they go for successive breeding seasons. Michener and Michener

(1951) found that *melanocephalus* males wandered more than females within the local area.

Factors influencing the width of the hybrid zone. Although the zone of hybridization extends from Kansas to southern Canada, it is not of equal width everywhere. Some of the factors responsible for this variation are discussed below.

In Kansas and Nebraska there are several large rivers that cross the Plains and provide relatively broad areas in which contacts can occur. In southern Nebraska the zone is about 300 km wide, in northeastern Nebraska about 200 km. Beginning in South Dakota and extending into Canada there is a gap between the eastern river systems, flowing into the James, Red, and Souris rivers, and the western streams flowing into the Missouri. Many rivers cross the area west of the Missouri River in the Dakotas and provide habitat for *melanocephalus*, but east of the Missouri the habitat is unsuitable, being mostly treeless country, and not spanned by rivers. The ranges of the grosbeaks are effectively separated here. There is hybridization along the Missouri River in southern South Dakota, but the influence of *ludovicianus* can reach western South Dakota only by this route, and not directly across the eastern part of the state. There is a record of a hybrid in eastern North Dakota (Bishop, in Swenk, 1939), but there is no evidence of more than sporadic occurrence of *melanocephalus* genes east of the Missouri River in the northern Plains.

The same gap extends across southern Saskatchewan, but in the Cypress Hills, in southwestern Saskatchewan, both grosbeaks have been found breeding (Godfrey, 1950). Although no hybrids are reported, it would be surprising if none were there. A hybridizing population could flourish in the Cypress Hills, where there is suitable habitat, even though the surrounding country is open grassland. West of the Cypress Hills the ranges of the two grosbeaks finally separate, *ludovicianus* extending north along the western edge of the Plains and *melanocephalus* south into the foothills of the Rocky Mountains of Montana. *Melanocephalus* is unreported from Alberta, even in the western edge of the Cypress Hills, but it must surely occur there and perhaps along the rivers of the area.

Measurements. Statistical summaries of mensural data are given in Tables 6-9 and 11 of West (1959). Average lengths of wing samples east and west of the Plains are not significantly different, although within the zone there is a gradual shift toward longer wing in the western samples. Differences in tail length are more consistent between the two forms. Data on tail and tarsal length are given in Figure 5. In general the two grosbeaks differ only slightly in measurements, *melanocephalus* in the western Plains being a little larger and having a deeper bill.

Hybrid index. Histograms of hybrid index for the Platte Transect are

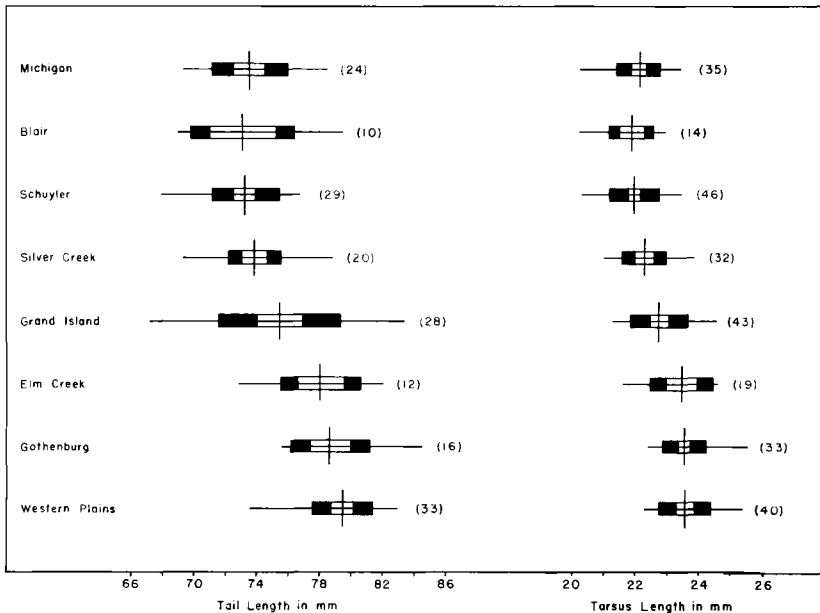


Figure 5. Statistical summaries of tail length and tarsal length. Horizontal lines show range; vertical line marks the mean; open rectangle shows one standard deviation either side of the mean; solid rectangle shows two standard errors of the mean either side. Numbers of specimens are given in parentheses.

given in Figure 4, the shift in average index per kilometer being indicated. The figure is self-explanatory. The greater variation in hybrid populations toward the center of the zone should be noted.

EXPERIMENTAL HYBRIDIZATION AND GENETICS

The genetics of wild birds are poorly known, largely because of the difficulties of making large-scale crosses. As Danforth pointed out (1950), however, this should not deter one from investigating the genetics of wild species. In several studies of polymorphism (Southern, 1945; Cooch and Beardmore, 1959), counts of phenotypes derived from field work have been used, and in those species commonly kept by aviculturists (estrildines, ducks, pheasants) the results of aviary crosses have been used as well.

The genetic basis of polymorphism is often one or two pairs of alleles (Huxley, 1955). Likewise, major gene differences often characterize domestic breeds of fowls and ducks (Danforth, 1950). The investigation of genetic differences between species or geographic races is not so easy. Danforth believes that the first differences to develop between isolated forms are of major genes, but that these are modified and reinforced to

form multiple-factor systems. Sheppard (1954) finds that the genetic differences between species are of such multifactorial systems, but he believes that differences develop gradually through the accumulation of small changes. Miller (1941) suggested both major genes and multiple factors in the genus *Junco*, a group of allopatric populations showing more or less complete interfertility. Hinde (1956) found considerable variation in plumage of offspring between two sympatric European finches and concluded that the genetic differences between them are multiple-factor systems. He remarks: "... with some exceptions those characters of plumage which the ethologist would expect to have significance as social signals depend upon multiple factor differences. The fact is circumstantial evidence that they have survival value."

One cross has been made in captivity between the grosbeaks. H. R. Ivor hybridized them in his aviaries in 1943, using a male *melanocephalus* from Vancouver, B. C., and a female *ludovicianus* from southern Ontario. Since the cross is unreported, I am grateful to Mr. Ivor for allowing me to use his journals and report it here. The following account and quotations are from his notes.

The male parent came into full song on 30 April 1943 and mated about 20 May. Nest building was in progress on 25 May, and eggs were laid on 28, 29, and 30 May. The nestlings hatched 8, 9, and 10 June. The youngest died two days later; the oldest left the nest at 12 days. By 3 July both surviving young showed rosy-orange feathers on their breasts, indicating that they were both males. By mid-February 1944 their heads were getting "quite black, a much better black than one sees on the Rose-breast in the first winter . . . breast buff with apricot showing through and a small streak of apricot extending towards the abdomen; abdomen white with tinge of buff towards flanks; primaries seem to be the old ones, brown with whitish patches . . . greater wing coverts black and white . . . secondaries with two new black feathers (one each wing)." In early May the more advanced hybrid was described:

"Head fairly good black, with a few buff feathers; nape same; back black and rich buff striping; rump light cinnamon; tail same black as head, three outer rectrices on each side with pure white on ventral surface; chin black with a few buff feathers; breast very rich mahogany brown, covered by apricot tinging the feathers; apricot pure on lower breast, forming a fairly wide streak; abdomen white tinged with cinnamon. . . ." The younger hybrid died on 13 June 1944 and was preserved (skin and partial skeleton, ROMZ 71002). This specimen resembles in nearly every detail a first-year male collected at Grand Island, Nebraska, on 17 June 1957 (CU 27792). The specimen was scored "1" + "3," or just intermediate in summed index.

The surviving hybrid lived until 18 November 1947. Ivor described the bird in detail, and it was evidently much like its sibling. These birds are similar to one of the common classes of hybrids collected in Nebraska, although there is considerable variation in the color of breast and underwing feathers of the presumed first-generation hybrids. In addition the hybrids cannot be divided into discrete categories; rather, a gradual series can be demonstrated between the parental types. This suggests that the two grosbeaks differ in a small number of genetic factors, but that these are part of a multiple-factor system. It appears further that there is some

dominance of factors controlling rose breast (as against yellow) and brown (against lack of brown). The hybrid index was devised before Ivor's hybrid was seen and was based on the assumption of no dominance. Although this may be invalid, the index was retained until more evidence could be gathered.

DISCUSSION AND CONCLUSIONS

Several authors (Chapman, 1924, and Mayr, 1942, among them) have stressed that the use of allopatry as a species criterion is unrealistic and tends to mask the evolutionary history of such forms, even when they have diverged considerably in external morphology or ecology. These authors feel that allopatric relatives are often best considered members of polytypic species. This opinion has received support from several recent studies of avian hybridization between allopatric populations in secondary contact. Among many examples may be mentioned Sibley (1950, 1954, and 1958), Mayr and Gilliard (1952), and Short (1959). On the other hand, Vaurie (1955) has stressed the importance of careful studies of allopatric forms and has pointed out that they are sometimes species ("pseudosubspecies"). Selander and Giller (1961) have recently described such a case in a North American pair of grackles.

It is apparent that difference per se is not important in effecting reproductive isolation between species, but that differences in particular aspects of structure and physiology are needed to accomplish this. The differences in plumage that have evolved in the spatially isolated grosbeaks are not effective in preventing hybridization between them when the two have come into contact. This is reasonable, since these differences did not evolve under selection against interaction between the two forms. The differences are fortuitous in relation to the two grosbeaks.

The breeding range of the common ancestor of the grosbeaks was split at some time in the recent geological past, probably not earlier than the Pleistocene. Since it is not known when *Pheucticus* first entered North America from the New World tropics, any discussion of the time of the split must remain highly speculative. If the ancestor was in North America before the last glacial maximum (about 17,000 years ago according to Martin, 1958), it would have been driven south by the advancing ice sheet (see Martin, 1958 for recent summary). For the ancestor of *melanocephalus* suitable habitat would probably have existed in Mexico; the population from which *ludovicianus* evolved might have been pushed into the southeastern part of North America or the West Indies. Alternatively, the eastern populations might have been founded by a small offshoot of *melanocephalus* stock into the West Indies or northern South America. The retreat of the ice sheet and amelioration of climate across North America would have permitted the northward expansion of woodland and with it the populations, now partly differentiated, into their

present ranges and eventually secondary contact. The openness of the Great Plains has existed since this time and would have prevented gene exchange between the two expanding populations. The founding of *ludovicianus* by a small offshoot of the larger *melanocephalus* ancestral population could have provided the conditions necessary for a rapid evolution of the eastern form (Mayr, 1954), if one assumes that *ludovicianus* is more changed from the ancestor than is *melanocephalus*. *Ludovicianus* shows far more sexual dimorphism, a condition most probably derived from the monomorphism common in many tropical finches at the present time. It is also much less a tropical or subtropical form than is *melanocephalus*.

It is difficult to predict the future of the contact in *Pheucticus*. There are at least three possibilities:

1. Swamping, by which the borders of the zone of hybridization would expand, and the populations in the zone and to either side of it would become blurred through increased gene flow.

2. Stabilization of the zone, through selection against hybrids outside it, while hybridization would continue within it. This could result in a situation like that of certain European crows (*Corvus corone* and *cornix*; Mayr, 1942).

3. Reinforcement of isolating mechanisms, by which selection against the hybrids would lead to divergence in those aspects of plumage, behavior, etc. that are effective as isolating mechanisms. This would produce a reverse cline with the two forms more different where they come into contact than where they are allopatric. (See Sibley, 1957, for further discussion of this possibility.)

At the moment the development of something between swamping and stabilization seems most probable. The zone of hybridization will probably expand, as it apparently has in the recent past, while in the center of the zone there may still be "pure" individuals, at least for a time. These may be recombination products that resemble the parental forms, but if the genetic differences between the grosbeaks are multifactorial this seems unlikely.

It does not seem likely that better mate choice or the development of isolating mechanisms through selection against the hybrids will cause hybridization to cease as the zone of overlap widens. Gene flow from *ludovicianus* populations to the east, where reinforcement would have no selective basis, would tend to prevent the populations in the zone of overlap from evolving intrinsic isolation. In addition there seem to be insufficient ecological differences between the grosbeaks to allow them to become sympatric.

Whatever may be the future of the zone of hybridization in *Pheucticus*,

it is evident that there is no well-developed barrier to gene exchange at the moment. The level of species evolution of the two grosbeaks seems best described biologically by regarding them as members of a polytypic species. I choose to disregard the Pacific coast race of *melanocephalus* (*maculatus*) in view of the doubtful position of the populations in Mexico and until a full study of variation there can be done. The grosbeaks then become: *Pheucticus ludovicianus ludovicianus* (Linnaeus), Rose-breasted Grosbeak, and *P. l. melanocephalus* (Swainson), Black-headed Grosbeak.

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SUMMARY

A collection of 308 grosbeaks from the Great Plains, representing *Pheucticus ludovicianus*, *melanocephalus*, and hybrids between them, is

described. The two forms come into secondary contact along many of the river valleys of the central and northern Plains. The zone of overlap and hybridization is about 320 km (200 miles) wide across its widest point in Nebraska.

The grosbeaks are geographically complementary forms. Habitat preference, nests, eggs, and vocalizations are very similar. Although the males differ in certain aspects of plumage colors, there is a great similarity in plumage pattern. Some aspects of males of *melanocephalus* are represented in many adults of *ludovicianus* in less-developed form. Female plumages are almost identical. There is overlap in mensural characters investigated.

Where their ranges overlap in the Plains the two forms interbreed, and variation found in hybrids suggests that backcrossing and production of second generation hybrids is occurring. Two hybrids reared in captivity by H. R. Ivor closely resemble one of the classes of hybrids collected in the hybrid zone in Nebraska.

There is some evidence of increased range overlap during this century.

The two grosbeaks act as members of a polytypic species; they are not more different than members of a number of geographically variable species, and they interbreed where their ranges come into contact.

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