SPECIES-RECOGNITION BEHAVIOR OF TERRITORIAL MALE ROSE-BREASTED AND BLACK-HEADED GROSBEAKS (*PHEUCTICUS*)

ROGER L. KROODSMA

THE evolution of two closely related, largely allopatric populations may depend on their interactions in areas of contact. Hybridization is one interaction that has been documented for many animal species. Extensive hybridization such as that occurring in orioles (Sibley and Short 1964) and flickers (Short 1965) has resulted in swamping of species-specific characters in zones of contact, and in time may result in a complete merging of the phenotypically different populations into a single monomorphic population. Less extensive hybridization has been described for buntings (Sibley and Short 1959b), towhees (Sibley and West 1959), and grosbeaks (West 1962). Other closely related species (e.g. Eastern and Western Kingbirds) apparently do not hybridize where sympatric.

Behavioral interactions between these closely related species are very critical for they may effect hybridization or conspecific mating. As behavioral interactions have been studied very little, this project was initiated to compare intra- and interspecific behavior in two hybridizing forms of birds, the Rose-breasted and Black-headed Grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*; A. O. U. Check-list 1957). The species are sexually dichromatic and differ mainly in the brightly colored plumages of the males. Females are similar, but *P. ludovicianus* (hereinafter called *ludovicianus*) has usually thick dusky streaks on a white breast, while *P. melanocephalus* (hereinafter called *melanocephalus*) has narrow or no streaks on a buffy breast. Vocalizations and behavior patterns are similar. The two grosbeak populations form eastern North American (*ludovicianus*) and western North American (*melanocephalus*) breeding populations that are complementary. Their ranges overlap slightly in the Great Plains and here hybridization occurs (West 1962). But even where hybridization is most extensive, phenotypically pure individuals of both species are present with hybrids, indicating the action of partial isolating mechanisms. This paper reports field experiments performed from 2–20 June 1969 and 5–16 June 1971 in North Dakota, where the two grosbeak species are mostly allopatric with little hybridization (Kroodsma 1970). Responses of territorial male grosbeaks to male mounted specimens and to recorded songs of their own and the other species are described.

Distribution and Study Areas in North Dakota

Grosbeaks in North Dakota breed mainly in riverine deciduous forests. *P. ludovicianus* is also common in aspen parklands in the Turtle Mountains (north central North Dakota) and upland deciduous forests in the Pembina Hills (northeastern North Dakota). The grosbeaks' main breeding ranges are separated at their closest by only 45 miles of relatively treeless prairie pothole country. This prairie lies between forests along the Souris (Mouse) River and the Missouri River where *ludovicianus* and *melanocephalus* respectively are abundant. During spring migration *ludovicianus* occurs regularly along the Missouri, but only a few remain there to breed.

Three study areas were selected to provide maximum availability of birds and sufficient understory cover to conceal me while setting up equipment within a territory. The areas are along the Sheyenne River 45 miles southwest of Fargo (*ludovicianus* range), the Souris River 16 miles southeast of Minot, and the Missouri River 9 miles south-southeast of Bismarck. Forests of elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica* var. *lanceolata*), box elder (*Acer negundo*), and basswood (*Tilia americana*) provided best conditions for experiments. I could not conduct experiments without being detected by grosbeaks in cottonwood (*Populus deltoides*) forests (in which *melanocephalus* is most abundant) along the Missouri River, because these forests typically have only a sparse short understory dominated by shrubs of *Cornus*, *Salix*, and *Rosa* spp.

Methods

Mounted specimens of adult male *ludovicianus* and *melanocephalus* were placed within the territories of singing males, which were then attracted to the mounts by playback of recorded grosbeak songs. In each trial only one mount was used, one conspecific to the territorial male or one nonconspecific to the territorial male. The mounts were attached to branches 4–7 feet above the ground. A Mercury model TR-3500 portable transistor tape recorder, wrapped in camouflaged material, was placed directly under a mount and covered sparsely with surrounding vegetation. The recorder was controlled by a remote control switch with an attached 75-foot wire. The song, on a continuous loop of tape, was played until the singing grosbeak approached the mount or as long as 5 minutes if no grosbeak approached. When a retreat followed an approach, series of songs were again played to reattract the bird. No songs were played while a bird was within about 20 feet of the mount to prevent it from discriminating between the slightly different positions of the recorder and mount.

Territorial grosbeaks were exposed to a mount only once a day, and no more than once to the conspecific and once to the nonconspecific mount during the entire period of the study. Early and late dates were equalized for the two species, so that behavioral comparisons were not affected by the progress of the breeding season. All recorded songs were of breeding North Dakota grosbeaks. The speci-

mens were mounted in a standing position with the wings folded normally over the back and sides, the tail pointing downward, and the bill closed.

Choice experiments (in which mounts of both species would be presented simultaneously in each trial to give a territorial male the choice of which to attack) were not performed because releasers in the conspecific mount do not necessarily direct attack (Tinbergen 1948). Thus once an attack is released it could be directed at both mounts, failing to show species-specific differences in response. This proved to be the case in several choice experiments attempted with *melanocephalus*, in which a *ludovicianus* mount and a *melanocephalus* mount were placed about 1 foot apart on branches. Three males attacked both mounts, one attacked the *ludovicianus* mount, and one the *melanocephalus* mount.

RESULTS

Two basic types of experiments were conducted. In the first, done in 1969, the mount and song were of the same species in each trial. In the second, performed in 1971, the mount and song were of different species in each trial. The first type was conducted to determine whether the two species of grosbeaks could distinguish each other by plumage and song. The second type was designed to determine whether plumage or song was more important in any species-discrimination that occurred.

Table 1 summarizes observed grosbeak responses to recorded songs and mounts for the first type of experiment. In 70 of 74 trials grosbeaks approached the song source. Of the 70 approaches 23 culminated in attacks. Both species attacked their conspecific mount in approximately 50% of the approaches. Attacks on the other mount occurred proportionately less. The difference is significant for both *ludovicianus* ($\chi^2 = 9.72$, 1 df, $P < 0.005$; proportion 12:13 vs. 0:14) and *melanocephalus* ($\chi^2 = 5.02$, 1 df, $P < 0.05$; proportion 9:8 vs. 2:12), and indicates that male grosbeaks distinguished specific differences in males. One of the two *melanocephalus* that attacked a *ludovicianus* mount was on a territory adjacent to that of the only *ludovicianus* I found in the Missouri River study area. I saw one encounter between these two birds, in which the *ludovicianus* chased the *melanocephalus*. This particular *melanocephalus* may therefore have been influenced by previous encounters with the *ludovicianus*. I placed mounts of both species (on different days) in the territory of this *ludovicianus*, but it attacked neither one.

The attack behavior of the two grosbeak species was different. *P. ludovicianus* was usually slow and methodical, landing on a branch near the mount, hopping closer, and then attacking by biting. *P. melanocephalus* was more aggressive, attacking swiftly, often in flight, and biting. After an initial attack in flight, birds of both species usually landed on a branch, hopped to the mount, and again attacked. During territorial encounters between live male *ludovicianus*, biting is uncommon, for Dunham (1966) observed bodily contact (with claws, bill, or

TABLE 1
BEHAVIORS OF GROSBEAKS IN THE FIRST TYPE OF EXPERIMENT

	P. ludovicianus		*P. melanocephalus*	
	Mount and song			
	Conspecific	Non.[1]	Conspecific	Non.
Number of trials	27	15	17	15
Approaches	25	14	17	14
Attacks on mount	12	0	9	2
Initial attack:				
In flight	3	—	7	1
After hopping	9	—	2	1
Hovering in attack	0	—	3	1
Increased song rates	19	14	12	12
Decreased song rates	2	0	4	0
During close proximity				
Loud (primary) song	3	6	2	5
Quiet song	9	4	6	0
Loud and quiet song	1	1	0	3
No song	3	0	2	2

[1] Non. = nonconspecific.

wings) in only 6% of 266 territorial conflicts. In 17% Dunham noted the displays wings-flicked, orient, and squawk. I observed only one of these, a vocalization similar to Dunham's description of squawk. It occurred only twice, when *ludovicianus* in flight attacked the mount.

In 11 trials I was able to note the specific body areas being attacked by grosbeaks. Five *ludovicianus* directed biting at the flank and rump areas, and one at the tail. The mount's rump feathers and portions of the secondaries and primaries partially covering the rump became quite disarranged during the course of the attacks. Five *melanocephalus* directed biting at the sides and back of the head and neck. One of these same *melanocephalus* also bit at the upper breast as well as at the neck. In one attack the skin of the mount's nape was badly ripped and had to be glued back onto the artificial neck. The two species are differently colored in rump and neck. Male *ludovicianus* have an entirely black neck and white rump, while male *melanocephalus* have a black neck with a brown collar and a brown rump. The rump of *ludovicianus* and nape of *melanocephalus* may be releasers or directors of attack, and if so, as characters affecting any species-recognition. Rumps are apparently displayed during singing, for I noticed that white rumps of singing *ludovicianus* show between the wings. One *ludovicianus*, while perched close to the *ludovicianus* mount, turned its back to it and sang, showing the rump. This agrees with Dunham's (1966) description of the phrased warble posture, which exposes "the fluffed white feathers of the lower back and rump."

TABLE 2
VOCALIZATIONS OF GROSBEAKS IN THE FIRST TYPE OF EXPERIMENT, WITH THE CONSPECIFIC MOUNT AND SONG[1]

	Attack			No attack		
	During approach	Before attack	After attack	During approach	Close proximity	After proximity
P. ludovicianus						
Quiet song	0	4 (33)	1 (13)	0	5 (56)	1 (11)
Loud song	5 (63)	2 (17)	6 (75)	3 (75)	3 (33)	5 (56)
No song	3 (38)	6 (50)	1 (13)	1 (25)	1 (11)	2 (22)
Chink	0	0	0	0	0	1 (11)
No obs.[2]	4	0	4	5	0	0
P. melanocephalus						
Quiet song	0	1 (11)	0	1 (25)	5 (71)	0
Loud song	4 (50)	2 (22)	3 (43)	1 (25)	0	3 (50)
No song	4 (50)	6 (67)	4 (57)	2 (50)	2 (29)	3 (50)
No obs.	1	0	2	3	0	1

[1] Percent occurrences of vocalizations are in parentheses.
[2] No observation recorded, but most likely no song occurred.

Females approached the song and mount in only 9 of the 75 trials. Two attacks occurred, both of these on the nonconspecific mount. A female *melanocephalus* attacked fiercely and had to be frightened away three times before I ended the trial, for it repeatedly attacked when I replayed the song to attract the male. An attack by a female *ludovicianus* occurred after its mate failed to attack during a close approach. Weston (1947) described a fierce battle between two female *melanocephalus*, which the males merely observed. To observe female behavior further I twice placed a mounted female *melanocephalus* in shrubs within a yard of *melanocephalus* nests containing nestlings. In one trial both the female and male of one pair frequented the nest, but did not respond to the mount. In the second trial involving a different nest and pair, the female did not return after seeing me place the mount.

Responses involving songs occurred in nearly all trials. Rates of repetition of songs often increased while a grosbeak was locating the mount immediately after playback, and often remained high for a few minutes after each trial (Table 2). But just as often the approaching grosbeaks gave no songs (Table 2). Grosbeaks on adjacent territories often increased their singing without approaching the mount. It was not practical to measure quantitatively and compare pre- and postplayback rates because grosbeaks usually sang only sporadically before playback of song.

While perched near the conspecific mount without attacking (close proximity, Table 2), male grosbeaks often sang quiet songs. These were similar to primary songs, but much quieter, and fit Lister's (1953)

definition of whispering song. Quiet song is often referred to as muted song (Ficken 1962), or in grosbeaks, as soft phrased warble (Dunham 1966). The proportion of loud to quiet songs while *ludovicianus* and *melanocephalus* were in close proximity was significantly different for conspecific and nonconspecific mounts ($\chi^2 = 8.06$, 1 df, $P < 0.005$; proportion 5:15 vs. 11:4). This suggests that grosbeaks recognized the conspecific plumage, and responded by singing the quiet song.

The occurrence of quiet song during or after territorial encounters has been noted before in *ludovicianus* (Dunham 1966) and in other species (Ficken 1962; Morse 1966, 1967). Ficken (1962) and Dunham (1966) feel that quiet song indicates higher escape tendency and weaker attack tendency than loud song. My data suggest that attack tendency is weaker during quiet song (Table 2), but not necessarily that escape tendency is stronger. Attack tendency seems stronger during loud song or absence of song.

Various other behaviors occurred occasionally. These were chink, preening, scratching head, fluffing feathers, stretching tail and wings and legs, quivering wings, wiping bill, and feeding. Some of these might be displacement activities, which occur in agonistic situations in many species, and also during courtship behavior (Tinbergen 1952). In five trials male *melanocephalus* were silently incubating in nests in shrubs at the beginning of playback. Two did not respond. Three began singing loudly from the nest but could not be attracted to the mount until after their mates had replaced them on the nests.

No difference in response to conspecific and nonconspecific songs was detected, even though I could distinguish the songs. Grosbeaks approached both conspecific and nonconspecific songs in almost all trials (Table 1).

In the second type of experiment the relative importance of song and plumage coloration in species-recognition was studied. A conspecific mount and nonconspecific song, or vice versa, were combined in each trial. The results (Tables 3 and 4) are similar to those of the first type of experiment. Nonconspecific (*melanocephalus*) songs attracted *ludovicianus* to their conspecific mount, which they attacked in about 50% of the approaches. Conspecific songs attracted grosbeaks to the nonconspecific mount, which was not attacked except in 1 of 29 approaches. As the switching of specific songs caused no different effects, the small differences between the songs of *ludovicianus* and *melanocephalus* are apparently unimportant in species-recognition.

In certain North American thrushes (*Hylocichla*) the roles of song and plumage in species-recognition are converse to those in grosbeaks. The species of thrushes have relatively similar plumages, but relatively

TABLE 3
BEHAVIORS OF GROSBEAKS
IN THE SECOND TYPE OF EXPERIMENT

	P. ludovicianus		*P. melanocephalus*
	Con.[1] mount Non. song	Non. mount Con. song	Non. mount Con. song
Number of trials	19	16	13
Approaches	13	16	13
Attacks on mount	6	0	1
Initial attack:			
In flight	2	—	0
After hopping	4	—	1
Hovering in attack	2	—	1
Increased song rates	10	14	9
Decreased song rates	0	0	0
During approach			
Loud song	6	9	4
No song	4	6	5
Quiet song	0	0	0
During close proximity			
Loud (primary) song	0	3	3
Quiet song	8	8	3
Loud and quiet song	1	2	2

[1] Con. = conspecific, Non. = nonconspecific.

different songs. When Dilger (1956) exposed the thrushes to songs and models species-recognition occurred, but not when models were presented without song. Songs were thus more important in species-recognition in thrushes.

Four apparent hybrid grosbeaks were encountered along the Souris River where I had collected other hybrids in previous summers. An apparent F_1 hybrid had a brown collar and an orange and brown breast. Three *ludovicianus*-like backcrosses were seen—one with an entirely pale-yellow breast, and two with salmon-pink breasts with brown on the sides. Other characters of these backcrosses were like *ludovicianus*. The responses of the three *ludovicianus*-like backcrosses were included with

TABLE 4
VOCALIZATIONS OF *P. LUDOVICIANUS* IN RESPONSE
TO THE CONSPECIFIC MOUNT AND NONCONSPECIFIC SONG[1]

	Attack			No attack		
	During approach	Before attack	After attack	During approach	Close proximity	After proximity
Quiet song	0	5 (83)	0	0	3 (50)	0
Loud song	2 (50)	0	4 (80)	4 (80)	0	4 (100)
No song	2 (50)	1 (17)	1 (20)	1 (20)	3 (50)	0
No obs.[2]	2	0	1	2	0	3

[1] Percent occurrences of vocalizations are in parentheses.
[2] No observation recorded, but most likely no song occurred.

those of apparently pure *ludovicianus* (Table 1). Of two exposed to the *ludovicianus* mount and song, one (with pale-yellow breast) attacked repeatedly. The other backcross and the F_1 hybrid, exposed to the *melanocephalus* mount and song, did not attack.

Discussion

The fact that male *ludovicianus* and *melanocephalus* visually distinguished each other suggests the action of partial isolating mechanisms between the two species, because if males distinguish males, females also would probably distinguish males during courtship and mating. The presence of reproductive isolating mechanisms in grosbeaks would probably be dependent on females' recognition of conspecific males, rather than vice versa, because female *ludovicianus* and *melanocephalus* are so similar that visual species-discrimination by males is doubtful. Also the threshold of mating readiness is generally higher in females than in males. Apparently this is true for grosbeaks as female *ludovicianus* often flee when males attempt copulation after courtship displays (Dunham 1966). Before mating and copulation occur a male would have to display appropriate species-specific stimuli to a female.

The nature of species-specific stimuli of grosbeaks can only be postulated. Such stimuli may be displayed during territorial encounters as well as during courtship (Andrew 1961). Directional biting by male grosbeaks suggests that the brown nape of *melanocephalus* and the white rump of *ludovicianus* may be species-specific releasers or directors of attack, acting complementarily to song. But during courtship females may respond to other stimuli, including vocalizations, movements, structures, and color patterns. Although songs of the two forms are slightly different, the difference appears insufficient to cause species-recognition by males.

Any reproductive isolation in grosbeaks, therefore, probably results from characteristics of the plumage and precopulatory behavior other than song. Distinguishing characteristics of the plumages involve mainly color rather than pattern. The brown nape of *melanocephalus* and the sharp demarcations between the usually black throat, rose breast, and white abdomen of *ludovicianus* form the only distinct patterns not common to both species. Color differences are white vs. brown of the rump and abdomen, and rose vs. yellow and brown of the breast. Copulatory behavior itself probably does not effect any reproductive isolation because it varies little between species (Hinde and Tinbergen 1958). Precopulatory behaviors of grosbeaks have been described by Dunham (1966), Ivor (1944), and Weston (1947), but the data are insufficient to allow detailed comparison.

As experiments were conducted only where *ludovicianus* and *melanocephalus* were largely allopatric, results of this study may have been significantly affected. For allopatric grosbeaks a nonconspecific mount would be novel. This could explain why grosbeaks did not attack the nonconspecific mount. In areas where the two species are sympatric and individuals are numerous, results might be different. Following repeated contacts between sympatric nonconspecific males, similarities of song, behavior, and overall color pattern might override differences in plumage. Male (and female) grosbeaks might then treat nonconspecific birds as conspecific. This was apparently the situation between the two male *ludovicianus* and *melanocephalus* in the Missouri River study area. Both birds apparently defended their territories from each other. Similarity of vocalization would probably be most important in reinforcing similarities. Thus greater contact between *ludovicianus* and *melanocephalus* might facilitate hybridization.

In an attempt to study interactions between sympatric nonconspecific males I visited the Platte River near Grand Island, Nebraska during the first week of June 1971, where West (1962) found a largely hybrid population of grosbeaks. But in two days I was able to find only a few singing males, and thus would not have been able to accumulate a sufficient sample size. Apparently grosbeaks are much less common here than in comparable habitats in North Dakota. This scarcity of grosbeaks in an area of sympatry may affect results of interactions between nonconspecific birds. The sexes may have a difficult time finding conspecific mates, and thus interspecific mating and hybridization may occur relatively more often, as is the case in bulbuls (Sibley and Short 1959a).

ACKNOWLEDGMENTS

I thank J. Frank Cassel, E. Charles Meslow, John J. Peterka, Robert L. Burgess, and Richard D. Frye for their help with the manuscript. 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. This paper is part of a Ph.D. thesis submitted to the Department of Zoology, North Dakota State University.

SUMMARY

To assess possible isolating mechanisms, the responses of territorial male Rose-breasted and Black-headed Grosbeaks to male mounts and songs of their own and the other species were studied. Experiments were performed during June 1969 and 1971 in North Dakota, where the species are mostly allopatric. Only one mount was placed in a territory during any one trial.

Males attacked the conspecific mount in 21 of 42 approaches, but attacked the nonconspecific mount in only 2 of 28 approaches, thus demonstrating visual discrimination. In further experiments they showed no auditory discrimination, responding equally to recorded primary songs of either species. Quiet songs occurred more often when grosbeaks perched next to the conspecific mount. Attacking grosbeaks usually sang loudly or not at all.

During attacks on conspecific mounts, Rose-breasted Grosbeaks directed biting to the rump and flank area, but Black-headed Grosbeaks to the nape area. The white rump and brown nape may be releasers or directors of attack.

Although allopatric males treated the mounts differently, sympatric nonconspecific males might treat each other conspecifically after repeated encounters elicited by their similar songs.

Literature Cited

American Ornithologists' Union. 1957. Check-list of North American birds, fifth ed. Baltimore, Amer. Ornithol. Union.

Andrew, R. J. 1961. The displays given by passerines in courtship and reproductive fighting: a review. Ibis 103a: 315–348, 549–579.

Dilger, W. C. 1956. Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. Auk 73: 313–353.

Dunham, D. W. 1966. Territorial and sexual behavior in the Rose-breasted Grosbeak, *Pheucticus ludovicianus* (L.). Z. Tierpsychol. 23: 438–451.

Ficken, M. S. 1962. Agonistic behavior and territory in the American Redstart. Auk 79: 607–632.

Hinde, R. A., and N. Tinbergen. 1958. The comparative study of species-specific behavior. Pp. 251–268 *in* Behavior and evolution (A. Roe and G. G. Simpson, Eds.). New Haven, Yale Univ. Press.

Ivor, H. R. 1944. Rose-breasted Grosbeak in semi-captivity, part 3. Aviculture 14: 179–182.

Kroodsma, R. L. 1970. North Dakota species pairs: hybridization in buntings, grosbeaks, and orioles. Unpublished Ph.D. dissertation, Fargo, North Dakota State Univ.

Lister, M. D. 1953. Secondary song: a tentative classification. Brit. Birds 46: 139–143.

Morse, D. H. 1966. The context of songs in the Yellow Warbler. Wilson Bull. 78: 444–455.

Morse, D. H. 1967. The contexts of songs in Black-throated Green and Blackburnian Warblers. Wilson Bull. 79: 64–74.

Short, L. L., Jr. 1965. Hybridization in the flickers (*Colaptes*) of North America. Bull. Amer. Mus. Nat. Hist. 129: 307–428.

Sibley, C. G., and L. L. Short, Jr. 1959a. Hybridization in some Indian bulbuls *Pycnonotus leucogenys* × *P. cafer*. Ibis 101: 177–182.

Sibley, C. G., and L. L. Short, Jr. 1959b. Hybridization in the buntings of the Great Plains. Auk 76: 443–463.

Sibley, C. G., and L. L. Short, Jr. 1964. Hybridization in the orioles of the Great Plains. Condor 66: 130–150.

SIBLEY, C. G., AND D. A. WEST. 1959. Hybridization in the Rufous-sided Towhees of the Great Plains. Auk 76: 326–338.

TINBERGEN, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull. 60: 6–51.

TINBERGEN, N. 1952. Derived activities, their causation, biological significance, origin and emancipation during evolution. Quart. Rev. Biol. 27: 1–32.

WEST, D. A. 1962. Hybridization in grosbeaks (*Pheucticus*) of the Great Plains. Auk 79: 399–424.

WESTON, H. G. 1947. Breeding behavior of the Black-headed Grosbeak. Condor 49: 54–73.

Department of Zoology, North Dakota State University, Fargo, North Dakota 58102. Present address: Biology Department, Union University, Jackson, Tennessee 38301. Accepted 19 March 1973.