THE FUNCTION OF SINGING IN FEMALE BLACK-HEADED GROSBEAKS (*PHEUCTICUS MELANOCEPHALUS*): FAMILY-GROUP MAINTENANCE

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ABSTRACT.—The responses of young Black-headed Grosbeaks (*Pheucticus melanocephalus*) to playback of the songs of parents and strangers were examined. I found that young grosbeaks moved about more, called more, and were more often oriented toward speakers in response to parental song (both male and female) than in response to the songs of strangers. I suggest that such a response is part of a system used by Black-headed Grosbeaks to maintain family groups after the young fledge. In this system, an adult with food, but unaware of the location of its young, sings to elicit begging from its young. The parent bird is then able to locate and feed its young. *Received 31 August 1981, accepted 26 May 1982.*

AMONG passerines, song is typically the function of the male. There is also much evidence, however, of regular, occasional, and artificially induced song by females. It has long been recognized, for instance, that females of many species can be induced to sing by injection of testosterone (Baldwin et al. 1940, Kern and King 1972). There are also many reports of species in which the female sings only in exceptional cases, e.g. the Western Meadowlark (*Sturnella neglecta*; Lanyon 1957), Indigo Bunting (*Passerina cyanea*; Nolan 1958), Song Sparrow (*Melospiza melodia*; Van Tyne and Berger 1976), Eastern Phoebe (*Sayornis phoebe*; Smith 1969), Eastern Bluebird (*Sialia sialis*; Morton et al. 1978), and White-crowned Sparrow (*Zonotrichia leucophrys*; Kern and King 1972). In other species, singing appears to be a regular feature of female behavior, i.e. many species have been reported in which females commonly sing in a variety of situations (Table 1).

Despite these many observations, the significance of singing in females remains obscure. Possible functions, however, have been postulated. Armstrong (1963) suggested that antiphonal singing is a "means whereby contact, *rapport*, and the social bond are maintained." Duetting is believed to be important in the synchronization of breeding behavior and in the reinforcement of the pair bond (e.g. Thorpe and North 1965, Thorpe 1966, Hooker and Hooker 1969, Bertram 1970, Payne 1971). Concerning instances of female singing other than antiphonal singing or duetting, Kern and King (1972) have suggested a number of functions, including stimulating the breeding activities of the male. Nottebohm (1975) suggested that singing by females may influence a bird's socialization and choice of partner and, in some cases, aid in territorial defense.

Among the species of birds in which singing by females has been reported is the Black-headed Grosbeak (*Pheucticus melanocephalus*; see Fig. 1). Weston (1947), in a general study of the breeding behavior of the grosbeak, reported that females sang "while incubating or brooding, usually as the male comes to take his place on the eggs or young. Several times during nest-building, the female uttered songs in the vicinity of the nest and always in the presence of the male. The female will also occasionally sing while foraging in the peripheral foliage of trees, but only when the male is close by." Armstrong (1963) stated that singing by females tends to be characteristic of cardueline finches. Van Tyne and Berger (1976: 249), in a general discussion of female song, suggested that the songs of the female Black-headed Grosbeak are nearly as elaborate as those of the male.

Despite these observations, the function of female song in the Black-headed Grosbeak, as in other species, is unclear. The present study is an attempt to ascertain the function(s) of this song. The initial year of this 2-yr study was devoted to extensive field observation and re-

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TABLE 1. Reports of singing in females among various avian species.

Species	Situations in which female sings[a]					Suggested function(s)[a]				Source
	NB	NR	I	B	FY	TD	PB-M	C	F-GM	
Greenshank *Tringa nebularia*					X					Simms 1958
European Nightjar *Caprimulgus europaeus*		X								Selous 1905
Gray-capped Flycatcher *Myiozetetes granadensis*			X		X					Skutch 1953
Loggerhead Shrike *Lanius ludovicianus*						X				Armstrong 1963
European Dipper *Cinclus cinclus*							X	X		Van Tyne and Berger 1976
American Dipper *Cinclus mexicanus*			X			X				Bakus 1959a, b
House Wren *Troglodytes aedon*			X		X				X	Armstrong 1955
Wrentit *Chamaea fasciata*						X				Armstrong 1963
Blue Wren *Malurus cyaneus*								X		Robinson 1949
Paradise Flycatcher *Terpsiphone viridis*			X							Moreau 1949
Elepaio *Chasiempis sandwichensis*	X		X	X				X		Conant 1977
Willie Wagtail *Rhipidura leucophrys*						X				Robinson 1949
White-crowned Sparrow *Zonotrichia leucophrys*							X	X		Blanchard 1941, Kern and King 1972
Grasshopper Sparrow *Ammodramus savannarum*		X					X	X		Smith 1959
Variable Seedeater *Sporaphila aurita*					X					Gross 1952
Cuban Grassquit *Tiaris canora*		X					X			Baptista 1978
Gray Catbird *Dumetella carolinensis*			X							Palmer 1949
Mockingbird *Mimus polyglottos*						X				Armstrong 1963
Brown Thrasher *Toxostoma rufum*		X	X	X						Thomas 1952
European Robin *Erithacus rubecula*						X				Lack 1939, 1943
Eastern Bluebird *Sialia sialis*								X		Thomas 1946
Russet Nightingale Thrush *Catharus occidentalis*		X		X	X					Skutch 1958
Gray-cheeked Thrush *Catharus minimus*							X	X		Van Tyne and Berger 1976
European Blackbird *Turdus merula*					X					Messmer and Messmer 1956
American Robin *Turdus migratorius*						X				Armstrong 1963
Brown Towhee *Pipilo fuscus*							X	X		Marshall 1960

TABLE 1. Continued.

Species	Situations in which female sings[a]					Suggested function(s)[a]				Source
	NB	NR	I	B	FY	TD	PB-M	C	F-GM	
Abert's Towhee *Pipilo aberti*							X	X		Marshall 1960
Orange-billed Sparrow *Arremon aurantiirostris*			X							Skutch 1954
Rose-breasted Grosbeak *Pheucticus ludovicianus*	X	X	X	X						Ivor 1944, Dunham 1964
Northern Cardinal *Cardinalis cardinalis*			X	X		X	X	X		Laskey 1944
Common Grackle *Quiscalus quiscula*							X			Wiley 1976
Greenfinch *Carduelis chloris*					X					Ferguson-Lees 1943
American Goldfinch *Carduelis tristis*	X									Berger 1953
Lawrence's Goldfinch *Carduelis lawrencei*	X									Linsdale 1950
Red Crossbill *Loxia curvirostra*							X			Lawrence 1949
White-winged Crossbill *Loxia leucoptera*								X		Bent 1968
Magpie Lark *Grallina cyanoleuca*							X	X		Robinson 1949
Butcherbird *Cracticus* sp.						X				Robinson 1949
Black-backed Magpie *Gymnorhina tibicen*						X				Robinson 1949

[a] NB = nest-building; NR = nest-relief; I = incubation; B = brooding; FY = feeding young; TD = territorial defense; PB-M = pair-bond maintenance; C = courtship; F-GM = family-group maintenance.

cording. During this period the situations in which females sang were noted, and hypotheses concerning the function(s) of this song were derived. During the second year of the study, these hypotheses were tested experimentally.

SYNOPSIS OF THE BLACK-HEADED GROSBEAK BREEDING CYCLE

The first birds arrived in the study area (Malibu-Guinavah Campground, in Cache National Forest 10 km east of Logan, Cache County, Utah) about the first week in May. Observations indicated that some birds were paired upon arrival. Such pairs may have been formed on the wintering grounds or during migration. During the early part of the breeding season, paired birds foraged together within their territories. The female usually followed the male as he moved through the territory feeding and singing. Such singing apparently serves a territorial function and, in addition, probably enables the female to maintain contact with the male. Females infrequently sang while foraging near the male (Weston 1947, pers. obs.).

Singing, alone, is not sufficient to maintain a territory, at least early in the breeding season, and agonistic encounters involving chasing and even physical contact occurred. Nearly all chases involved males, although several female-female chases were observed, and, on three occasions, females were observed chasing males. On one of these occasions, a female was observed chasing a male, and, upon landing, she sang one loud song. On another occasion a female appeared to engage in a brief singing duel with a neighboring male.

Following territory establishment, Black-headed Grosbeaks become progressively less aggressive. This change in behavior was quantified in two ways: (1) male singing rates de-

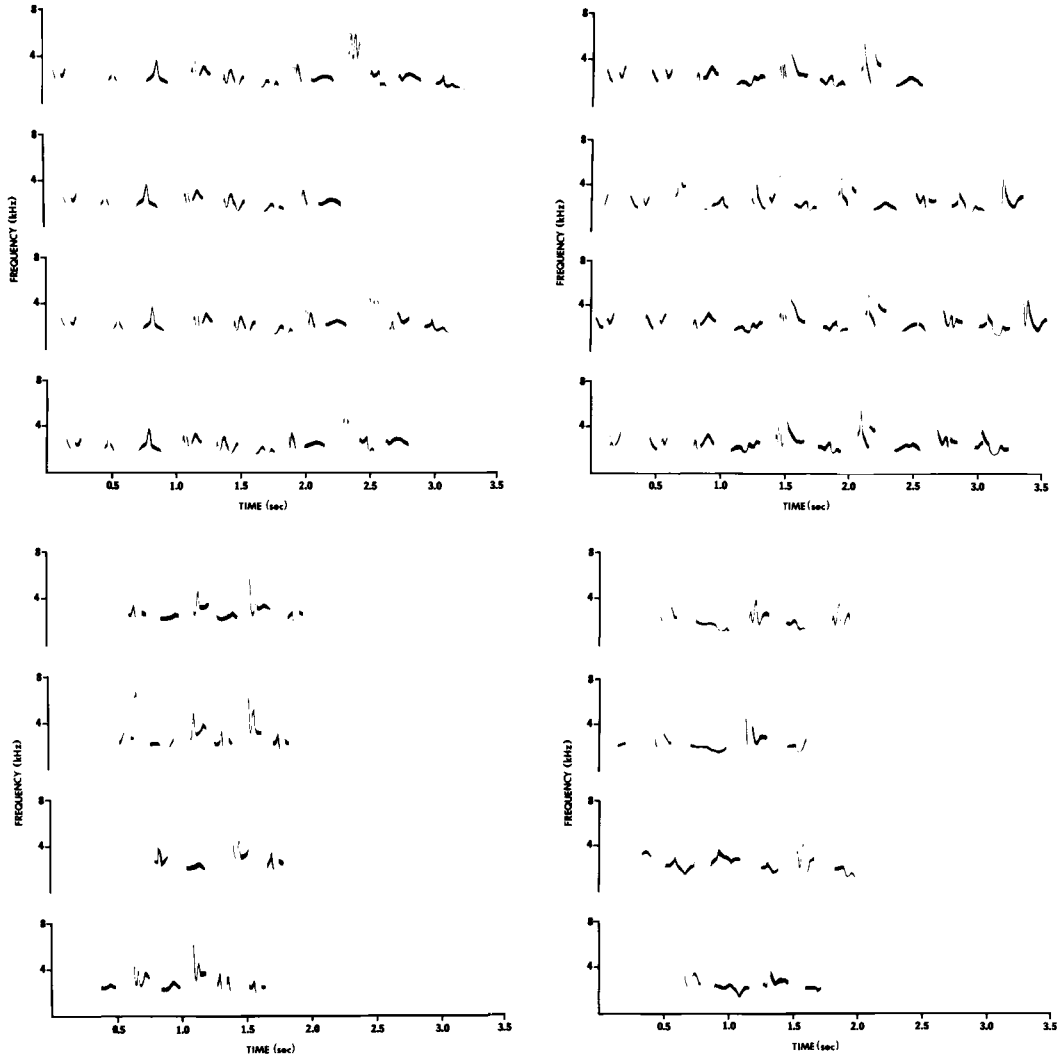

Fig. 1. Representative sonograms of the songs of male (above) and female (below) Black-headed Grosbeaks.

clined as the season progressed, and (2) the frequency of intraspecific agonistic encounters (i.e. chases and/or actual physical encounters) decreased (Fig. 2).

Nest building.—The female normally builds the nest, and I observed three instances in which females sang while involved in such construction. Twice, females sang while gathering nest materials, and, on another occasion, a female was observed singing while sitting in a partially constructed nest. On each of these occasions a male was within a few meters of the singing female.

Incubation.—Both sexes are surprisingly vocal on and around the nest. Males frequently sang while incubating. At times this song appeared to be in response to the singing of neighboring males, i.e. a male would be quietly incubating when, upon hearing a neighboring male singing, the incubating bird began to sing. At other times the male's singing appeared to be a signal to the female that he was about to leave the nest.

Females rarely sing while incubating. On two occasions incubating females sang in apparent response to the singing of neighboring males.

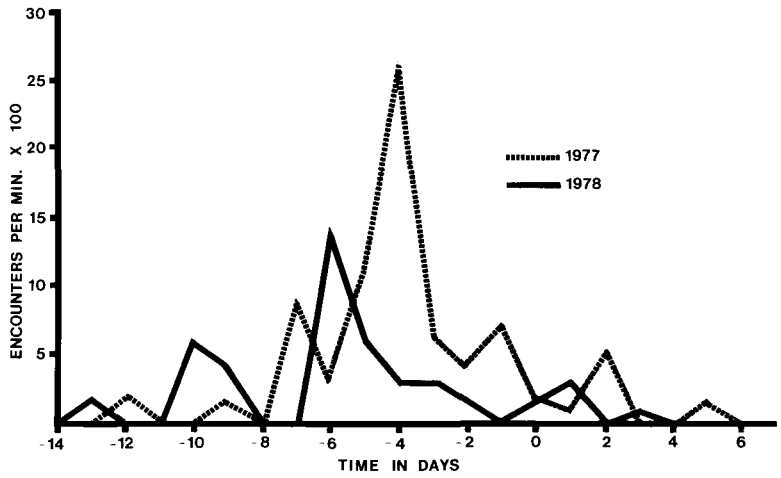

Fig. 2. Distribution of intraspecific agonistic encounters (chases and/or actual physical encounters) among male and female Black-headed Grosbeaks (Day 0 = first egg laid).

In most cases, however, females showed no response to the singing of neighboring males.

On many occasions a male or female would approach the nest and find its mate quietly incubating. At these times, males and females frequently uttered "chip" calls or sang. The incubating bird, upon hearing its mate, would then leave the nest.

Parental care.—During the first few days post-hatching, the adults maintained the same schedule as when incubating. Both adults fed and brooded the young, and their behavior when changing places on the nest was similar to that during incubation, with one significant difference. As the brooding period progressed, the females began to sing more frequently (Fig. 3).

By the eighth day post-hatching the young

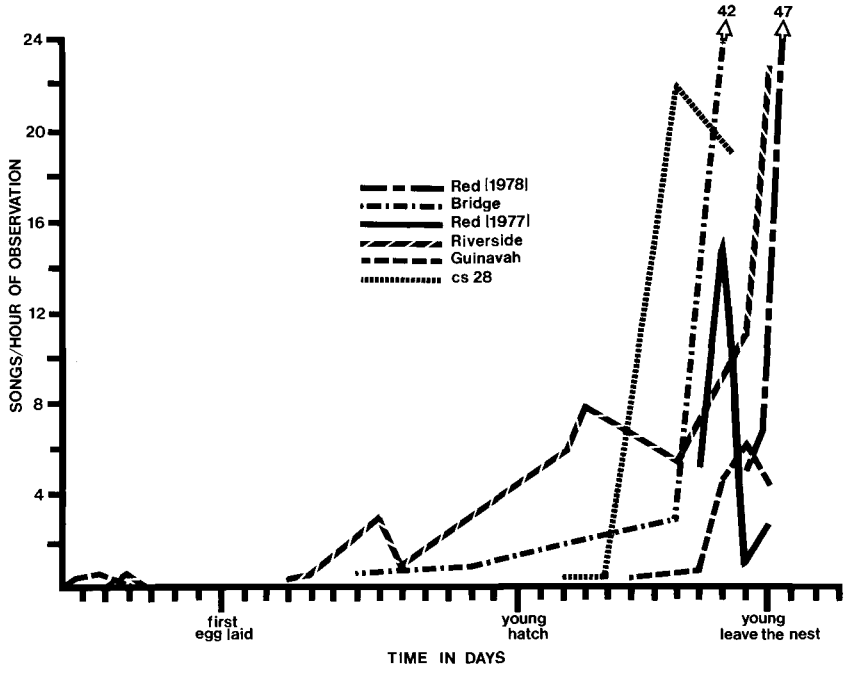

Fig. 3. Singing rates of selected females during the 1977 and 1978 breeding seasons.

were brooded infrequently. Adults approaching the nest to feed the young frequently vocalized. These vocalizations were either "chip" calls or songs. Upon the arrival of the adult at the nest, the young grosbeaks immediately began calling. At times the young began calling upon hearing the calls or songs of their parents.

The young may leave the nest as early as the ninth day post-hatching, although departure at 10–14 days post-hatching was more common ($n = 21$, $\bar{x} = 11.5$). After leaving the nest they scatter among the shrubs near the nest, perching on low branches. During the first few days, the young are rather quiet. As they are unable to fly at this time, they remain within a restricted area, and the adults generally have little trouble locating and feeding them (Weston 1947, pers. obs.). If, however, a parent is unable to locate a young bird, the parent will begin to utter "chip" calls and/or songs. Upon hearing their parents' vocalizations, young grosbeaks respond by uttering "phee-oo" and/or "hunger-distress" calls. In this manner the parents and young are able to maintain contact.

Maintaining contact between the parents and their young obviously becomes more difficult after the young attain flight (approximately 15 days post-hatching). To maintain contact, grosbeaks appear to use the same system described above. When parents have food for the young, but are unsure of the location of the young, the parents begin to utter "chip" calls or, more frequently, songs. Upon hearing a parent, young grosbeaks utter "phee-oo" and/or "hunger-distress" calls. The parent then flies to the young bird and feeds it. Occasionally, after hearing a parent sing, a young grosbeak will fly to within a few meters or less of the adult and, if not fed immediately, will begin calling.

At this stage (2–3 weeks post-hatching), family groups begin to wander and no longer stay within their territories. Because of this wandering, it is difficult to observe specific family groups over long periods, and, therefore, the duration of such groups remains a question. Weston (1947) reported seeing young grosbeaks being fed by adults in early August, but he was unable to determine the actual length of the dependent period.

Summarizing the above observations, I found that both male and female Black-headed Grosbeaks sing in the following situations: (1) as they forage with their mates before nesting, (2) after chasing neighboring males from their territory, (3) during nest building, (4) during incubation, (5) during change-overs at the nest (both during incubation and brooding), (6) when coming to the nest to feed the young, (7) when attempting to locate and feed fledged young.

These observations, along with those of Head (1902, 1904) and Weston (1947), suggested the following generalized functions of female song in the Black-headed Grosbeak: (1) maintenance of the pair bond, (2) territorial defense, (3) family-group maintenance.

Other reports (Ritchison in prep.) have revealed that female song in the Black-headed Grosbeak does appear to be important in the maintenance of the pair bond, although it plays no role in territorial defense. The main objective of the present study was to examine the possible role of singing by female Black-headed Grosbeaks in family-group maintenance.

MATERIALS AND METHODS

Fieldwork was conducted during the breeding season of 1978 at Malibu-Guinavah Campground. Eight young grosbeaks from five different nests were tested in these experiments. All birds tested were between 10 and 17 days of age.

Apparatus.—Testing was conducted in an automobile from which the birds had no contact (visual or vocal) with their parents or other grosbeaks. The test apparatus consisted of a testing arena and a portable tape recorder (Nagra IIIB) connected by cable to a portable loudspeaker.

The arena was a box with floor dimensions of 125 × 28.8 cm and walls 28.8 cm high. The floor and long walls of the box were made of wood while the short walls consisted of cheesecloth. To provide a reference grid for the purpose of scoring a bird's position in the arena, the floor was marked out into 25 5-cm cells. In addition, the top of the apparatus was covered with a wire screen.

During tests the observer sat in the front seat of the automobile and viewed the floor of the arena by means of a mirror suspended at an angle above it. For the playback of recorded songs the portable loudspeaker was placed against the cheesecloth at one end or the other of the arena, and the tape recorder was controlled by the observer from the front seat.

Playback recordings.—The songs of parents and strangers were recorded using a Nagra IIIB tape recorder with an Altec 633A microphone, which was

housed in a 62-cm parabolic reflector. All recordings were made at a tape speed of 19 cm/s (7½ ips). From these recordings were made 3-min test tapes, with songs spaced at 15-s intervals.

Testing procedure.—Each bird was tested alone. Initially, the young bird was placed at the central position on the floor grid of the arena, and its behavior during the next 3 min was observed and scored without playback of any sound through the speaker. Such a period will be referred to as a "pre-test." At the end of a pre-test, the young grosbeak was replaced at the central position of the floor grid. For the next 3 min songs were played, and again the behavior of the bird was observed and scored. Such a period with playback will be referred to as a "test." Immediately after the test period, the young bird was again replaced at the central position of the floor grid. Its behavior during the next 3 min was again observed and scored. Such a period without playback after the test period will be referred to as a "post-test."

Each bird was exposed to four types of test in this way: two parental tests, in which the songs of its mother and father were played, and two "stranger" tests, in which the songs of strange males and females were played. The young birds experienced each of the four types of pre-test/test/post-test sequences twice, once with the speaker at one end of the arena and once with the speaker at the other end. The sequence of presentation was either parental-stranger-parental-stranger or stranger-parental-stranger-parental; as many birds experienced the one as the other. The sequence in which the ends of the arena were used was also varied among birds, and the order of ends was independent of the order of test types. The complete sequence of testing for a young grosbeak thus consisted of 8 pre-test/test/post-test runs, each 9 min in duration. I allowed 5 min between each run for rewinding and changing test tapes on the tape recorder. The young bird remained in the arena during this time.

For the tests the volume controls of the tape recorder were adjusted so that modulometer readings were similar for each tape used. No precise measurements of sound intensity levels in the arena were made, however.

Scoring.—For the purposes of scoring the behavior of the young grosbeaks, each pre-test, test, and post-test was divided into 12 15-s intervals. At the end of each 15-s interval, a bird's position, orientation, and the types and numbers of calls were noted. Details of the conventions used for scoring the behavior of the young grosbeaks are as follows:

(i) Orientation. Two scores for orientation were accumulated: one for orientation toward the speaker end of the arena and one for orientation toward the other end. A bird was judged as oriented to one end or the other if it was pointed directly toward that end or in a direction within 20° to either side of the direct line from it to the end. In each 15-s interval the bird was thus scored as oriented toward the speaker end, or as oriented toward the other end, or as unoriented. By counting up the intervals in which orientation was one way and the intervals in which it was the other way I obtained the two scores. In a 3-min pre-test, test, or post-test, therefore, the maximum possible score for one end, and for the two ends taken together, was 12.

(ii) Position. As in the procedure for orientation, two scores were obtained: one for the speaker end of the arena and one for the other end. The central position in the arena, from which a bird started out in each pre-test, test, and post-test, carried a position value of 0. The 5-cm transverse divisions of the floor carried position values, which increased from 1 to 12, reading from the central position to one side or the other. At the end of each 15-s interval, a bird's position on the floor grid, determined by the location of its feet, was noted and scored. Summing the scores for the two sides separately gave the two position scores. The maximum possible score in a 3-min pre-test, test, or post-test, for one side or for the two sides taken together, was therefore 144 (12 × 12). The maximum score would result if a bird spent all 12 intervals of a pre-test, test, or post-test within 5-cm of one or other of the end-walls of the arena.

(iii) Position Change. A 15-s interval was scored as positive for position change if the bird's position on the floor grid at the end of that interval was different from what it had been at the end of the preceding interval, regardless of direction. The maximum score for position change in a 3-min pre-test, test, or post-test was therefore 12.

(iv) Calling. The types and numbers of calls given by a bird during the pre-test, test, and post-test periods were noted.

Playback experiments with free-living young.—In addition to tests in the apparatus, a series of experiments were performed with young grosbeaks in a natural setting, i.e. while the birds were perched in a bush or small tree. Each experiment consisted of three 5-min segments (pre-test, test, post-test), and throughout each test all sounds and nonvocal behavior were noted. Each bird was tested twice with its mother's songs, and trials were at least 1 day apart. The speaker was placed 5–10 m from the young grosbeaks in these experiments.

Playback experiments with adult females.—The responses of females to playback of the "phee-oo" calls of their young were also examined in the field. The procedures followed in these tests were the same as those used in the playback experiments with the young. Each experiment consisted of three 5-min segments (pre-test, test, and post-test). Throughout each test all sounds and non-vocal behavior were noted. Each female was tested twice with the "phee-oo" calls of one of her young. Different trials were at least 1 day apart.

TABLE 2. Responses of young grosbeaks to playback of female song in the test apparatus.

	Mean scores[a,c]						Significance levels[b,c]				
	PPT	SPT	PT	ST	PAT	SAT	PPT vs. SPT	SPT vs. ST	PPT vs. PT	PT vs. ST	PAT vs. SAT
Orientation to speaker	2.4	1.7	5.4	2.4	5.1	2.5	NS	NS	NS	0.05	NS
Orientation to other end	1.3	1.9	1.3	2.0	1.2	2.8	NS	NS	NS	NS	NS
Position score, speaker end	18.1	8.6	33.6	17.9	13.5	17.0	NS	NS	NS	NS	NS
Position score, other end	31.0	37.1	28.8	32.4	32.0	25.0	NS	NS	NS	NS	NS
Position change	2.2	4.5	2.4	2.0	0.6	1.2	NS	NS	0.02	0.02	NS
Number of "phee-oo" calls	17.4	15.7	54.2	27.0	37.6	26.8	NS	0.05	0.01	0.01	0.05
Number of "hunger-distress" calls	0.3	0.3	10.5	2.2	0	0	NS	NS	0.01	0.02	NS

[a] The mean scores were derived from two sets of experiments on each of eight birds. The significance levels are according to Wilcoxon matched-pairs tests, two-tailed.
[b] $P <$ number given: NS = not significant.
[c] PPT = parental pre-test; SPT = stranger pre-test; PT = parental test; ST = stranger test; PAT = parental post-test; SAT = stranger post-test.

RESULTS

Responses of young grosbeaks to parental song in the test apparatus.—The results are summarized in Tables 2 and 3, together with significance levels, given by Wilcoxon comparisons, for the differences among all pre-tests, tests, and post-tests. As these figures and comparisons clearly show, the young grosbeaks moved about more, called more, and were more often oriented toward the speaker in response to parental song than to the songs of strangers. The effects on a young grosbeak's behavior of playing the parental songs were spectacular in most cases. Typically a bird's behavior in the pre-tests consisted of standing or sitting near the center of the arena and giving occasional "phee-oo" calls. At the sound of the parental song, however, there was usually an immediate and sudden change: the young grosbeak raised its head and started calling (often beginning by uttering a series of "hunger-distress" calls followed by nearly continuous "phee-oo" calls). In general, then, there was incessant calling and locomotion (i.e. position change) in the parental tests.

Responses of young grosbeaks to the songs of strangers in the test apparatus.—Although the responses of the young grosbeaks to playback of the songs of strangers were less pronounced, they were still significant in several categories of response (Tables 2, 3). As in the parental tests, the young grosbeaks' first response to the songs of strangers was often a series of "hunger-distress" calls followed by nearly continuous "phee-oo" calls. This vocal response to the songs of strangers, however, was significantly less pronounced than the response to parental song (Tables 2, 3). In addition, strangers' songs elicited no significant locomotory responses. Finally, young grosbeaks showed a significant orientation away from the speaker in response to the playback of the songs of strange males (Table 3).

Playback experiments with free-living young.—In the test apparatus, as well as under natural conditions, young grosbeaks responded to parental song by uttering "phee-oo" calls and/or "hunger-distress" calls. A comparison of the responses of young birds in the apparatus and in a natural setting, however, revealed differences with respect to orientation and approach. Under natural conditions young grosbeaks showed a significant tendency to approach the speaker (Table 4); birds in the test apparatus, however, showed no such tendency (Tables 2 and 3). Young grosbeaks in the apparatus did, however, show increased locomotion. These results, although not predicted initially, might be explained as follows. In precocial species, such as the Laughing Gull (*Larus atricilla*; Beer 1970a, b) and Ring-billed Gull

TABLE 3. Responses of young grosbeaks to playback of male song in the test apparatus.

	Mean scores[a,b]						Significance levels[a,b]				
	PPT	SPT	PT	ST	PAT	SAT	PPT vs. SPT	SPT vs. ST	PPT vs. PT	PT vs. ST	PAT vs. SAT
Orientation to speaker	2.8	2.4	3.2	1.5	2.3	2.4	NS	NS	NS	0.05	NS
Orientation to other end	1.5	1.8	2.1	3.4	2.5	2.4	NS	0.02	NS	NS	NS
Position score, speaker end	13.1	11.8	18.2	11.5	27.2	31.9	NS	NS	NS	NS	NS
Position score, other end	12.3	23.6	37.0	36.4	19.8	36.6	NS	NS	NS	NS	NS
Position change	0.6	0.7	5.2	1.7	1.7	1.1	NS	NS	0.01	0.01	NS
Number of "phee-oo" calls	17.9	23.0	62.9	44.1	37.4	28.7	NS	0.01	0.01	0.01	0.01
Number of "hunger-distress" calls	0	0.1	7.9	9.3	2.7	0	NS	0.02	0.02	NS	NS

[a] Mean scores and significance levels as in Table 2.
[b] PPT = parental pre-test; SPT = stranger pre-test; PT = parental test; ST = stranger test; PAT = parental post-test; SAT = stranger post-test.

(*L. delawarensis*; Evans 1970b), chicks have been found to show orientation and approach responses to the played-back calls of their parents. Because precocial chicks normally approach their parents by walking or running, the quickest route to a "calling parent" (i.e. the speaker) is to orient toward and approach the sound source. In the grosbeak, on the other hand, young birds come in contact with their parents by flying toward them or, if they are not yet capable of flight, by remaining motionless and calling the adults toward them. In the apparatus, therefore, young grosbeaks would not be expected to walk or run toward the sound source (speaker), but instead (depending on the age of the young) would either remain motionless and call or attempt to "fly" out of the apparatus to locate and approach their unseen parent. Such reasoning might explain the absence of significant orientation or approach behavior by young grosbeaks in the test apparatus.

Playback experiments with adult females.—The responses of females to the playback of the begging calls ("phee-oo" calls) of their young were significant in several categories, i.e. distance of closest approach, number of songs, and syllables per song (Table 5). Because only the calls of their own young were played to individual females, these results do not constitute proof of individual vocal recognition of young by females. As will be discussed later, how-

TABLE 4. Responses of free-living young Black-headed Grosbeaks to playback of their mother's song.

	Closest approach (m)	Number of flights	Number of "phee-oos"	Number of "hunger-distress"	Number of "chips"
Responses[a]					
Pre-test period (PTP)	7.00	0	0.20	0	0.10
Test period (P)	3.30	0.80	2.50	1.60	0.40
Post-test period (PP)	3.50	0.30	0	0	0.30
Significance levels[b]					
PTP vs. P	0.05	0.05	0.05	NS	0.05
PTP vs. PP	0.05	NS	NS	NS	0.05
P vs. PP	NS	0.05	0.05	NS	NS

[a] Values for responses are averages for all tests. The significance levels are according to paired *t*-tests ($n = 6$).
[b] $P <$ number given; NS = not significant.

TABLE 5. Responses of females to playback of the "phee-oo" calls of their young.

	Closest approach (m)	Number of songs	Syllables per song	Number of "chips"	Number of "wheets"	Number of "distress"	Number of flights
Responses[a]							
Pre-test period (PTP)	7.00	0	0	5.70	0	0	5.70
Test period (P)	3.00	1.70	5.60	23.20	10.40	0.20	7.20
Post-test period (PP)	4.80	3.80	4.70	13.90	1.20	0	3.20
Significance levels[b]							
PTP vs. P	0.01	NS	NS	0.05	NS	NS	NS
PTP vs. PP	0.05	0.05	0.001	NS	NS	NS	NS
P vs. PP	0.05	0.05	0.05	NS	NS	NS	0.01

[a] Values for response are averages for all tests. The significance levels are according to paired t-tests ($n = 4$).
[b] $P <$ number given; NS = not significant.

ever, these results do lend support to the conclusion that singing by females is important in family-group maintenance.

DISCUSSION

Recent studies involving the recognition of parents by their young have concentrated on colonial species, e.g. Common Murres (*Uria aalge*; Tschanz 1965, 1968), Black-billed Gulls (*Larus bulleri*; Evans 1970a), Laughing Gulls (Beer 1970a, b), Ring-billed Gulls (Evans 1970b), and Black-Legged Kittiwakes (*Rissa tridactyla*; Cullen 1957). Evidence of individual recognition between parents and young has been found in every colonial species in which it has been sought, with the exception of the Black-legged Kittiwake. The survival value of this recognition in colonial species seems quite apparent. Because a young bird is surrounded by adults who are not its parents, who are unlikely to feed it, and who may even attack it, individuals who beg only from their own parents should conserve energy and have a selective advantage over indiscriminating young. The case of the Black-legged Kittiwake may be regarded as an exception that proves this rule, for in that species the young remain confined to the nest until they fledge (Cullen 1957), so that up to that time the young do not normally encounter adults other than their parents.

In contrast to the situation described for colonial species, there is little information available concerning the recognition of parents by their young in noncolonial, altricial species. Only a few observations suggesting the possibility of such recognition have been reported. For example, Michener and Michener (1935) stated that a young Mockingbird (*Mimus polyglottos*) recognized the voice of the parent who fed it and started to beg on hearing it. Nestling European Blackbirds (*Turdus merula*) are reported to know their mother by her food call (Messmer and Messmer 1956), and fledged young apparently recognize their fathers' vocalizations (Thielcke-Poltz and Thielcke 1960). Young Ring Doves (*Streptopelia risoria*) and Chiffchaffs (*Phylloscopus collybita*) are also reported to recognize the calls of their mother (Craig 1908, Gwinner 1961). Other authors have reported observations suggesting that altricial young may recognize parental song. For example, Saunders (1929) referred to young House Wrens (*Troglodytes aedon*) being stimulated to open their bills by the males' song. Young Snow Buntings (*Plectrophenax nivalis*) may also be able to distinguish their father's song from the song of other males (Armstrong 1963). The present study provides clear evidence that young Black-headed Grosbeaks are able to recognize the songs of their parents.

Grosbeak family groups begin to wander 2–3 weeks after hatching and no longer stay within their breeding territories. Because the birds are moving through thick vegetation in unfamiliar areas, maintaining contact becomes more difficult. Under such conditions individual vocal recognition is essential. Without such recognition, the maintenance of family groups would probably be impossible. The need for the recognition of parental song by young grosbeaks, therefore, is apparent. Even with such recognition, however, it would certainly be possible for young grosbeaks to stray from the family groups. Given that possibility, a positive response to the songs of other adult

grosbeaks would be advantageous. Such a response to strange adults would presumably tend to enhance the chances of "adoption" by foster parents. This, in fact, appears to be the "strategy" used by young grosbeaks. Although fledglings respond more strongly to the songs of their own parents, they also show significant responses to the songs of strange males and females (Tables 2, 3).

The responses of young grosbeaks to parental song represent but one side of the parent-young relationship. The responses of parents to the vocalizations (or absence of vocalizations) of their young are equally important. Among older fledglings, contact with parents generally results from these fledglings flying to the parents in response to parental song. Younger fledglings, however, as well as young birds that have left the nest but are not yet capable of flight, maintain contact with parents by means of the mutual recognition system discussed previously, i.e. an adult with a food item, but unaware of the location of its young, will often begin singing to elicit begging ("phee-oo" and/or "hunger-distress" calls) from its young. In this way a parent is able to locate its young. The responses of females to the playback of the "phee-oo" calls of their young appear to verify the existence of such a system. Upon hearing the playback, females showed a significant approach response, as well as significant increases in the number of flights and number of "chip" calls (Table 5). Such responses would, under natural conditions, enable a parent to locate a young grosbeak quickly. On the other hand, once playback ended, females showed significant increases in singing rates. Under natural conditions this would elicit calling by young grosbeaks and, thus, allow a parent to locate its offspring.

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