

but not in the appropriate direction). Behavior was noted in 508 sightings of Common Loons; 111 were sitting, 366 were migrating, and 31 were flying. The frequency of sightings of migrating loons was greatest in early morning hours (05:00–08:00) and low throughout the rest of the day (Fig. 5). In spring Williams (Wilson Bull. 85:230, 1973) rarely noted Common Loons migrating after 09:30 at a coastal location along the Gulf of Mexico. Kerlinger (Condor 84:97–100, 1982) observed Common Loons migrating from 2–9 h after sunrise in central New York state. The behavioral data for offshore sightings of Red-throated Loons were insufficient to reveal any conclusive pattern of daily timing. The near-shore data from Manomet Point were not analyzed, since observation effort was biased toward morning hours.

Discussion.—Our data show a substantial offshore migration of Common Loons in both spring and autumn, while Red-throated Loons occur with less frequency away from the coast. The proportions of Red-throated to Common loons at a coastal site in Massachusetts during autumn, when compared to their abundance offshore, indicate that substantial numbers of Red-throated Loons migrate near shore (cf. Ward, Records of New Jersey Birds 6:2–4, 1980). The offshore distribution of both species conforms to waters over the continental shelf (shoreward of the 200-m isobath); thus, sightings off the mid-Atlantic states are closer to shore and less dispersed than in waters northeast of Long Island (Figs. 1–4).

Forbush (1925) and Hill (1965) indicated that Common Loons principally migrate over Cape Cod, but another flight remains at sea outside of Cape Cod. Our offshore data confirm the latter flight since we found Common Loons passing south of the Cape Cod islands of Nantucket and Martha's Vineyard. These loons probably cross the southern Gulf of Maine to or from Nova Scotia. The timing of this movement in autumn (mid-November), which differs from peak flights at Manomet Point (late October), suggests that different populations of Common Loons are using different migration routes. The offshore component may be breeders from Nova Scotia and Newfoundland, whereas the coastal movement may originate from the mainland of eastern Canada. Such an hypothesis may explain why there is no substantial migration of Red-throated Loons away from the coast, since their breeding range does not extend as far east along the Atlantic coast as that of Common Loons.

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Responses of Black-headed Grosbeaks to songs of conspecifics.—Bird song may communicate several kinds of information, including the species, sex, reproductive status, aggressiveness, location, and individual identity of the singer. Birds recognize songs of their own species and usually respond exclusively to them (Marler, *Behaviour* 11:13–39, 1957; Lanyon, *Am. Mus. Novit.*, No. 2126:1–16, 1963; and others). Such recognition appears to depend on song features that are relatively constant among all individuals of a given species (Falls, pp. 259–271 in *Proc. 13th Int. Ornithol. Congr.*, Ithaca, New York, 1963; Emlen, *Behaviour* 41:130–171, 1972; Wunderle, *Anim. Behav.* 27:982–996, 1979).

TABLE 1
RESPONSES OF TERRITORIAL MALES TO SONGS OF NEIGHBORING MALES AT TERRITORIAL BOUNDARY^a

	Closest approach (m)	No. songs	Syllables per song	No. "chips"	No. flights
Pre-test period (PTP)	9.4	0	0	0.4	0.5
Test period (P)	10.1	1.9	6.1	0.4	0.7
Post-test period (PP)	10.2	1.7	5.0	0	0.5
PTP vs P	NS ^b	NS	NS	NS	NS
PTP vs PP	NS	NS	NS	NS	NS
P vs PP	NS	NS	NS	NS	NS

^a Values for responses are averages for all tests; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed, N = 5.

^b P < number given, NS = not significant.

However, there is often considerable intraspecific variation in bird song, and songs are frequently characteristic for each individual. This variation suggests the probability of individual recognition. Such recognition has been demonstrated for the White-throated Sparrow (*Zonotrichia albicollis*) (Brooks and Falls, Can. J. Zool. 53:879-888, 1975), Stripe-backed Wren (*Campylorhynchus nuchalis*) (Wiley and Wiley, Behaviour 41:10-34, 1976), and Common Yellowthroat (*Geothlypis trichas*) (Wunderle, Auk 95:389-395, 1978).

The songs of male and female Black-headed Grosbeaks (*Pheucticus melanocephalus*) exhibit considerable intraspecific variation (Ritchison, Ph.D. diss., Utah State Univ., Logan, Utah, 1980). Such variation probably provides ample information for individual recognition. The objective of this study was to determine if male and female Black-headed Grosbeaks can discriminate between the songs of neighboring and non-neighboring male and female conspecifics.

Materials and methods.—Fieldwork was conducted during the breeding season of 1978 at

TABLE 2
RESPONSES OF TERRITORIAL MALES TO SONGS OF NON-NEIGHBORING MALES AT TERRITORIAL BOUNDARY^a

	Closest approach (m)	No. songs	Syllables per song	No. "chips"	No. flights
Pre-test period (PTP)	9.30	0.90	4.00	0.40	0.20
Test period (P)	3.30	22.10	6.70	2.60	5.20
Post-test period (PP)	8.40	8.00	8.70	0.10	0.80
PTP vs P	0.005 ^b	0.005	0.005	0.025	0.005
PTP vs PP	NS	0.005	0.01	NS	NS
P vs PP	0.01	0.01	NS	0.01	0.025

^a Values and significance levels derived as in Table 1, N = 6.

^b P < number given, NS = not significant.

TABLE 3
RESPONSES OF TERRITORIAL MALES TO SONGS OF NEIGHBORING MALES WITHIN
TERRITORY^a

	Closest approach (m)	No. songs	Syllables per song	No. "chips"	No. flights
Pre-test period (PTP)	5.30	1.60	9.00	0	1.40
Test period (P)	4.70	10.10	11.90	0.40	4.60
Post-test period (PP)	6.70	4.60	11.30	0	1.00
PTP vs P	NS ^b	0.005	NS	NS	NS
PTP vs PP	NS	NS	NS	NS	NS
P vs PP	0.01	0.01	NS	NS	NS

^a Values and significance levels derived as in Table 1, N = 5.

^b $P <$ number given, NS = not significant.

Malibu-Guinavah Campground in Cache National Forest, 10 km east of Logan, Cache Co., Utah. Experiments began on 24 May and continued until 8 July. Throughout this period playback experiments were conducted to determine if the birds could discriminate among songs of different individuals. All experimental birds were captured in mist nets and color banded to facilitate identification.

Birds with common territorial boundaries were referred to as neighbors and those from areas at least 8 km distant were designated strangers. Because birds were exposed to songs of neighboring males daily, it was assumed they had little or no previous contact with songs of strangers.

Each experiment consisted of three 5-min segments. During the first 5 min (pre-test period), undisturbed, ongoing behavior was observed. During the second 5 min (test period) songs were played every 15 sec, an interval characteristic of an undisturbed singing bout (Ritchison, pers. obs.). The final 5 min (post-test period) was used again for observation. Throughout each test all sounds and non-vocal behavior were noted.

TABLE 4
RESPONSES OF TERRITORIAL MALES TO SONGS OF NON-NEIGHBORING MALES WITHIN
TERRITORY^a

	Closest approach (m)	No. songs	Syllables per song	No. "chips"	No. flights
Pre-test period (PTP)	6.90	4.20	6.40	0.70	0.60
Test period (P)	2.30	27.30	7.70	2.20	6.20
Post-test period (PP)	5.80	16.60	10.10	0.10	2.80
PTP vs P	0.005 ^b	0.005	0.005	0.025	0.005
PTP vs PP	NS	0.005	0.005	NS	0.005
P vs PP	0.005	0.005	NS	0.01	0.01

^a Values and significance levels derived as in Table 1, N = 6.

^b $P <$ number given, NS = not significant.

TABLE 5
COMPARISON OF RESPONSES OF TERRITORIAL MALES TO PLAYBACK OF SONGS OF
NEIGHBORING AND NON-NEIGHBORING MALES AT TERRITORIAL BOUNDARY^a

	Closest approach (m)	No. songs	Syllables per song	No. "chips"	No. flights
Pre-test period (PTP)	NS ^b	NS	NS	NS	NS
Test period (P)	0.01	0.005	0.005	NS	0.025
Post-test period (PP)	0.01	0.005	0.01	NS	NS

^a Values compared are listed in Tables 1 and 2, respectively; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed, $N = 5$.

^b $P <$ number given, NS = not significant.

Each bird was tested twice with each of the following: (1) the mate's song; (2) the neighboring male's song; (3) the songs of non-neighboring males; and (4) the songs of non-neighboring females. Different trials with the same bird, using either male or female song, occurred at least 2 days apart, i.e., tests with the songs of males were at least 2 days apart; however, tests with the songs of one sex were conducted 1 day before or after tests with the songs of the other sex. The sequence of test songs played to each bird and the order in which birds were tested each day were random. All experiments were conducted between 05:00 and 11:00 MDT.

Speaker locations for the respective tests were: (1) at the approximate center of the territory for songs of mates and strange females and (2) at both the territorial boundary and at the center of the territory for songs of neighboring and non-neighboring males. At the boundaries the speaker was directed toward the center of the territory to minimize the neighbor's responses. At the center, speaker orientation was not standardized. Boundaries were established for each territory by observation of encounters and by preliminary experiments using playback of the songs of non-neighbors (different from those used later).

Recordings were made using an Altec 633A microphone mounted in a 62-cm parabolic reflector with a Nagra IIIB recorder at a tape speed of 19 cm per sec (7½ ips). Experimental tapes were prepared using previously recorded songs of mates, neighbors, and non-neigh-

TABLE 6
COMPARISON OF RESPONSES OF TERRITORIAL MALES TO PLAYBACK OF SONGS OF
NEIGHBORING AND NON-NEIGHBORING MALES WITHIN TERRITORY^a

	Closest approach (m)	No. songs	Syllables per song	No. "chips"	No. flights
Pre-test period (PTP)	NS ^b	NS	NS	NS	NS
Test period (P)	0.005	0.005	0.005	0.005	0.01
Post-test period (PP)	0.01	0.005	0.01	NS	NS

^a Values compared are listed in Tables 3 and 4, respectively; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed, $N = 5$.

^b $P <$ number given, NS = not significant.

TABLE 7
RESPONSES OF INCUBATING/BROODING FEMALES TO SONGS OF THEIR MATES^a

	No. songs	No. "chips"
Pre-test period (PTP)	0	0
Test period (P)	0	6.80
Post-test period (PP)	0	0
PTP vs P	— ^b	0.005
PTP vs PP	—	—
P vs PP	—	0.005

^a Values for responses are averages for all tests; the significance levels are according to Wilcoxon matched-pairs tests, one-tailed, $N = 6$.

^b $P <$ number given.

bors. Each tape was 5 min in duration with songs spaced at 15-sec intervals. For playback a portable speaker was connected to an amplifier and the Nagra and placed in a bush or small tree 2–3 m above ground.

Criteria of response.—To obtain a quantitative measure of a bird's reaction to playback the following features of response were used. (1) Number of songs and syllables per song. Grosbeak songs vary considerably in the number of syllables per song and observations indicated a relationship between the number per song and a bird's level of excitement (Ritchison, pers. obs.). Therefore, the number of syllables in each song was counted as well as the total number of songs uttered by the experimental bird. Syllables were uttered by the grosbeaks at a rate that allowed me to count them individually. (2) Latency to the first song. The time from the beginning of the experiment (the start of the test tape song) to the time when the experimental bird first sang was noted. (3) Distance of closest approach. The distance of the experimental bird's closest approach to the speaker during the playback was noted. (4) Number of flights. Short flights (i.e., less than 50 cm) and non-flight movements were not counted. If it was obvious from the relative location of consecutive vocalizations that the bird had made an unobserved flight, this movement was counted. Since some flights were missed, this number was a minimum value. (5) Number of "chips." Grosbeaks gave these calls in a number of situations. At times these calls appeared to indicate anxiety or distress and at other times they appeared to function as location calls between mates. The total number of these vocalizations given during each 5-min segment of the experiment was counted.

The above measures were compared for the same birds responding to different songs at the same locations and to the same songs in different locations. The Wilcoxon matched-pairs signed-ranks test was used for all statistical comparisons (Siegel, *Nonparametric Statistics for the Behavioral Sciences*, McGraw-Hill, New York, New York, 1956).

Results.—Males responded to the songs of non-neighbors in a significantly different fashion than they did to the songs of neighbors at both the territorial boundary and the center of the territory (Tables 1–6). This was true for all measures of response during playback (with the exception of number of flights at the center of the territory). In the post-playback period at the boundary, there were significant differences in response for three of the five categories of response and, at the center of the territory, in one of the five categories (number of songs). Thus, it is clear that neighbor/non-neighbor discrimination by song occurred at the boundary and at the center of the territory.

Differences in male response to the same type of song given at the different locations are less clear. Comparisons of responses to the songs of non-neighbors at the territorial boundary and at the center of the territory revealed but one significant difference ($P < 0.01$): playback of the songs of non-neighbors at the center of the territory elicited more singing in the post-playback period. In general, however, responses to the songs of non-neighbors at the territorial boundary and at the center of the territory were similar.

Two measures of response (approach distance and numbers of songs) revealed significantly different reactions ($P < 0.025$) by males to the songs of neighbors at the center of the territory than at the territorial boundary. Females showed no responses to the songs of either neighboring or non-neighboring males. They did, however, respond significantly to the songs of their mates (Table 7). Neither males nor females responded to the songs of non-neighboring females. In addition, territorial males showed no significant responses to the songs of their mates ($P > 0.025$).

Discussion.—The results of the playback experiments indicate that territorial male Black-headed Grosbeaks responded with different intensity to the songs of different males of their own species. More precisely, they distinguish between familiar songs of neighbors and unfamiliar songs of non-neighbors.

Discrimination between the songs of neighbors and non-neighbors was achieved very quickly. Latency to the first song generally was less when a strange song was played, and at times only one rendition of the song was necessary to elicit singing by the test bird.

Weeden and Falls (Auk 76:343–351, 1959), Goldman (Auk 90:106–113, 1973), and Brooks and Falls (1975) found that Ovenbirds (*Seiurus aurocapillus*), Field Sparrows (*Spizella pusilla*), and White-throated Sparrows, respectively, could distinguish between songs of neighbors and non-neighbors and that in these species the reactions to the songs of non-neighbors were stronger. In each of these species, as well as in the Black-headed Grosbeak (Ritchison 1980), each individual possesses a distinctive song (or syllable repertoire) which remains more or less constant throughout the breeding cycle. Therefore, males of these species have ample opportunity to learn the distinctive songs of their neighbors. Presumably, such learning accounts for the differential strength of response to songs of neighbors and non-neighbors.

Evidence suggests that decreased response to a neighbor's songs results from habituation. For example, Falls (1963) found that Black-backed Magpies (*Gymnorhina tibicen*) habituated to playback of recorded songs as well as to the location from which they were broadcast. Petrinovich and Peeke (Behav. Biol. 8:743–748, 1973) reported habituation in the response of White-crowned Sparrows (*Zonotrichia leucophrys*) to playback and found that response decrement was specific to the particular song played.

What is the function of such habituation? Reduced responses to neighbors, which do not pose as great a threat as do strangers to the integrity of the territory, may diminish risks and save energy for other activities (Brooks and Falls 1975). Further, any behavior which increases the probability of a male's detecting significant changes from the status quo should have survival value. Ability to recognize the songs of each neighbor would allow the detection of new birds and/or the displacement of existing neighbors, situations that could easily pose a threat to a bird's territory. The importance of detecting such changes becomes apparent upon examination of the results of removal experiments reported by Brooks and Falls (1975).

In contrast to the responses shown by territorial males to the songs of other males, they showed no response to the playback of songs of strange females. In other words, singing by female Black-headed Grosbeaks appears to have no territorial function. Other species have been reported in which the females' songs apparently have no territorial function, e.g., Bullfinches (*Pyrrhula pyrrhula*) (Nicolai, Z. Tierpsychol. 13:93–132, 1956) and Northern Orioles (*Icterus galbula*) (Pugsley, News from Bird Banders 21:32–36, 1946). Armstrong (A Study of Bird Song, Oxford Univ. Press, London, England, 1963) divided passerine species

into two broad groups: (1) species in which the female sings and defends territory with the male and (2) species in which the female sings as well, or nearly as well, as the male, but the singing is concerned with pair-bond and/or family-group maintenance and not with the defense of territory. The results of the present study indicate that Black-headed Grosbeaks are another "group 2" species, since the singing of females has no territorial function. Previous studies indicate that such singing is important in the maintenance of the pair bond and of the family-group after fledging (Ritchison 1980).

Although females failed to respond to the songs of either neighboring or non-neighboring males, they did show a response when the songs of their mates were played back. Such a response indicates that female Black-headed Grosbeaks are able to recognize the songs of their mate. There have been several reports of such mate recognition in colonial seabirds (White, *Anim. Behav.* 19:125–131, 1971; Wooller, *Z. Tierpsychol.* 48:68–86, 1978; and others). However, mate recognition has rarely been documented in passerines.

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Vocal learning in the Parulinae.—Vocal learning is the ability to use auditory information, including feedback, to modify or enhance vocal development (Nottebohm, *Am. Nat.* 106:116–140, 1972). This learning is well documented in both humans and birds (e.g., Marler, *Am. Sci.* 58:669–673, 1970), and suspected in cetaceans (e.g., Payne and Payne, *Z. Tierpsychol.*, in press) and perhaps non-human primates (Green, *Z. Tierpsychol.* 38:304–314, 1975). Among birds, evidence for vocal learning now exists for over 300 bird species (Kroodsma and Baylis, in *Acoustic Communication in Birds*, Kroodsma and Miller, eds., Academic Press, New York, New York, in press) from the Psittaciformes, Apodiformes, Passeriformes, and perhaps even the Piciformes (Wagner, *Wilson Bull.* 56:65–76, 1944) and the Galliformes (Sparling, *Wilson Bull.* 91:618–621, 1979).

Most documented examples of avian vocal learning are from the oscines, however, and in this group the Parulinae (wood warblers) is one of the largest subfamilies for which solid evidence of vocal learning is still lacking. Evidence from micro-geographical variation suggests that some song types among warblers are learned (Kroodsma, *Auk* 98:743–751, 1981). Herein we verify through both experiment and observation that males of the Common Yellowthroat (*Geothlypis trichas*) and Chestnut-sided Warbler (*Dendroica pensylvanica*) are capable of vocal learning.

One male Chestnut-sided Warbler nestling at about 10 days of age was taken into the laboratory and then tutored from day 25 to day 100 with a Common Yellowthroat *witchity* song type (see Fig. 1A) and nine different song types of Yellow Warblers (*Dendroica petechia*). Yellow and Chestnut-sided warbler songs are rather similar and often confused by field biologists; hence, it was reasoned that, if Chestnut-sided Warblers do develop songs through imitation, then Yellow Warbler songs would be likely hetero-specific songs that would be learned. The Common Yellowthroat song was used both to tutor a male Common Yellowthroat in an adjacent cage and as an additional song model for the Chestnut-sided