

## SHORT-RANGE AND LONG-RANGE SONGS: USE OF TWO ACOUSTICALLY DISTINCT SONG CLASSES BY DARK-EYED JUNCOS

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**ABSTRACT.**—Communication signals can be divided into two functional classes: long-range signals and short-range signals. The study of bird song has concentrated almost exclusively on long-range songs. Because bird song often is used as a model system for studying learning, mate choice, and territoriality, this lack of attention to short-range songs may have misrepresented our understanding of communication systems. Short-range songs are expected to differ acoustically and functionally from those broadcast over long distances. Male Dark-eyed Juncos (*Junco hyemalis*) produce two classes of song that appear to function as long-range and short-range signals, respectively. These two classes differ markedly in frequency and syntax as well as in repertoire size. In terms of use, rates of short-range song production were highest in conjunction with courtship displays, when males were within close proximity to fertile mates, and during interactions with other males. In contrast, production of long-range song was not associated with courtship displays, did not vary significantly with the reproductive state of females, and was produced when males were relatively far from conspecifics. Received 5 May 1997, accepted 8 September 1997.

THE TYPES OF SIGNALS USED in communication can be separated into two classes: those used over long distances and those used over short distances. These two classes represent ends of a continuum of signals that function over many different distances. Long-range signals are conspicuous, broadcast signals that often function as advertisements of territorial and reproductive status (Krebs et al. 1978, Clutton-Brock and Albon 1979). In contrast, short-range signals often are inconspicuous and characteristically are directed at specific individuals that are within close proximity to the signaler (Wiley and Richards 1982, Smith 1991, McGregor and Dabelsteen 1996).

The structure and function of avian vocalizations have been well studied. In particular, bird song has been categorized extensively and is thought to function mainly in territorial defense, mate attraction, and pair-bond maintenance (Kroodsma and Byers 1991). The study of bird song in turn has contributed greatly to our understanding of development and reproductive biology (Slater 1989, Marler 1990, Baptista and Gaunt 1994). A key factor in the success of these studies is the conspicuous nature of the signals involved. Some types of short-

distance vocalizations, such as those used in parent-offspring communication, have been well studied (Beecher 1990), but most of the work on avian vocalizations has focused on high-amplitude, long-range songs (LRS; Catchpole 1982, Wiley and Richards 1982, Smith 1996). Although many workers recognize that birds produce short-range songs (SRS) that function over shorter distances, the emphasis on LRS may under-represent the importance of vocal communication by only partially addressing the range of songs produced.

The structure of LRS is constrained by environmental degradation, which limits the variety of sounds used to those that can be effectively transmitted across territories (Wiley and Richards 1982, Brown and Handford 1996, McGregor and Dabelsteen 1996). Songs transmitted over short distances should be less constrained by environmental degradation (Wiley and Richards 1982). The more complex structure of some SRS may facilitate their transmission specifically to intended receivers (McGregor and Dabelsteen 1996). A few studies have found components within the same songs that appear to be adapted for long- and short-range functions. Among Brown-headed Cowbirds (*Molothrus ater*), King et al. (1981) found that a small reduction (3 dB) in the signal-to-noise ratio decreased female response to playback by 50%. Other song components were

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thought to retain their effectiveness in communication with more distant individuals. Among Eurasian Blackbirds (*Turdus merula*), Dabelsteen and Pedersen (1988) found that females responded to both long- and short-range components of song. Such systems provide a partial separation of song classes, but the linkage of two functional components within one song complicates investigations of function.

Less conspicuous SRS have been largely ignored, yet they may be a key to understanding song systems. Short-range songs can be defined as those that are effectively transmitted over short distances relative to LRS. They may be structurally distinct from ordinary (i.e. loud) songs in the repertoire, or they may be ordinary songs produced at lower amplitude (Smith 1996). Early workers (e.g. Chapman 1907, Saunders 1929) realized the existence of these "whisper" songs, but difficulty in observing and recording them seems to have prevented further research. Because SRS are expected to degrade rapidly with distance (Wiley and Richards 1982), recordings made at typical distances (e.g. >4 m in field studies) from birds are likely to be of poor quality. The reluctance to categorize these vocalizations as songs also seems to have hindered research. Smith (1996) argued that such reluctance may arise from the popular idea that each species has just one "song," and Spector (1994) noted that using the criterion of high amplitude to define song would exclude these low-amplitude vocalizations. Finally, SRS sometimes are labeled as a transitional stage in song development. Indeed, Hartshorne (1973) considered most quiet songs to be "subsong," in effect implying that they have no communicative function.

I investigated the structure and use of LRS and SRS by Dark-eyed Juncos (*Junco hyemalis*). From 1991 to 1993, I studied 47 territorial pairs of juncos belonging to a color-banded population at Mountain Lake Biological Station in southwestern Virginia (see Wolf et al. 1990, Chandler et al. 1994). Juncos are socially monogamous, territorial passerines and in the study population occupy mixed woodlands that often are dense and hilly (Ketterson et al. 1991). Females typically lay three or four eggs and incubate for 12 days. Males help protect eggs and young and feed nestlings (Wolf et al. 1990). Development and individual variation of LRS in juncos have been studied by Marler et

al. (1962), Konishi (1964a, b), and Williams and MacRoberts (1977, 1978). Earlier accounts mention SRS and their use in courtship (Tanner 1958, Hostetter 1961; also noted in captives by Marler et al. 1962), but researchers have not studied the function of either song class. I describe the two song classes structurally using recordings obtained in the field. Focal observations were conducted to begin to understand how both classes function. I present results showing contextual differences in song use and behavioral correlates of the two song classes.

#### METHODS

*Recordings and song analysis.*—During the 1991 breeding season (May to July), I recorded LRS from 13 male juncos with a Sennheiser ME30 microphone mounted in a 34.3-cm Sony parabola attached to a Marantz 316 cassette recorder. Females were never heard singing LRS. All recordings were made of males that were singing spontaneously (i.e. I did not use playback to attract them). Distance from microphone to singer varied from 3 to 13 m. I attempted to record each male several times to increase the number of song types recorded. Recordings were made throughout the day.

Recordings of SRS were obtained by presenting caged conspecifics to 11 territorial pairs during June and July 1992 (none of which were recorded in 1991). Equipment was identical to that used in 1991 except that the microphone was not mounted in a parabola. Because males were attracted to a stimulus (i.e. the caged bird) near the microphone, most recordings were from distances of 0.3 to 3 m, which facilitated the capture of these low-amplitude songs. Although females occasionally sing SRS (Titus unpubl. data), none did so during this study. Recordings of four males that were considered to be of high quality (i.e. songs clearly heard over background noise) were used for analyses.

I analyzed tapes using a Uniscan II sound spectrum analyzer set at 10 or 20 kHz with a time base of 1.6 or 3.2 s. Although both song classes are composed of identifiable syllables (i.e. the largest repeated units within the song; Konishi 1964b), they differ greatly in syntax and timing (see Fig. 1). LRS most often are composed of one syllable repeated 10 to 20 times over a period of 1 to 2 s. The song is followed after several seconds by another nearly identical song (i.e. of the same song type). Only after many songs are produced is a new type introduced (Konishi 1964b, Williams and MacRoberts 1977). In contrast, SRS are composed of syllables that are not repeated until much later during the song bout. Song syntax is variable (i.e. syllables are not organized into readily identifiable song types). The number of

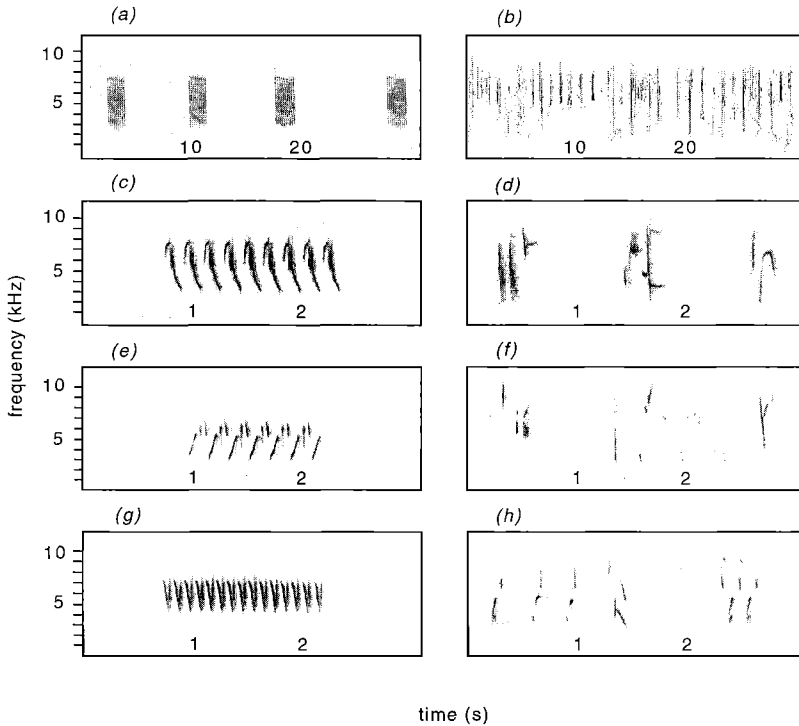


FIG. 1. Typical examples of two song classes of Dark-eyed Juncos, long-range songs (LRS) on the left and short-range songs (SRS) on the right. (A, B) Thirty-second sonagrams. LRS are produced in discrete units, with several seconds between songs, whereas SRS are more continuous. (C, D) Three-second segments of the above. Each LRS is composed of a single syllable repeated many times, whereas SRS show more complex structure and fewer repetitions of syllables. (E, F) LRS and SRS recorded from a wild-caught, captive male on the same day in June. (G, H) LRS and SRS of a different wild-caught captive male. (Captive males were not part of the study, but their sonagrams are used here for illustrative purposes.)

distinct syllables within each male's repertoire was counted for both song classes. Konishi (1964b) and Williams and MacRoberts (1977, 1978) used shapes to categorize syllables and found that temporal and frequency measures showed less variation within than among these groups. I considered syllables to be the same type if sonagram tracings had similar shapes and were within  $\pm 400$  Hz in overall frequency (Konishi [1964b] found that high and low frequencies varied by an average SD of  $\pm 384$  Hz within syllable types). To compare repertoire sizes, for each male I measured all LRS recorded ( $\bar{x} = 24.8$  songs, or ca. 3.2 min of singing) and the first 2 min of SRS (the average duration of high-quality recordings; 116 to 157 syllables) recorded. Although these estimates allow comparisons between the two song classes, longer recordings likely would reveal larger repertoire sizes (Williams and MacRoberts 1977, 1978). Because each LRS type was repeated many times before a new song type was given, the number of songs recorded during one session was insufficient to determine "eventual variety" (i.e. the average number

of songs before changing to a new song type; Hartshorne 1973). For this measure, I used song counts obtained during the focal observations (see below), using only males for which more than 20 songs were heard in succession.

*Focal observations.*—To determine whether use of the two song classes was affected by reproductive status, from April to June 1993 I conducted focal observations of 22 males (none of which had participated in the 1991 or 1992 studies) after they had acquired territories. Observations were made opportunistically as birds were encountered on their territories; no schedule was followed. Because SRS normally were audible only at distances of less than 20 m, I recorded behavior only when I was less than this distance from the focal bird and only on calm days. During the 15-min observations, I noted: (1) the class of song produced, (2) nonvocal behaviors (including two typically used during courtship: a feather-erection display in which body feathers are elevated, and a tail-spreading display in which the white outer rectrices and darker inner ones are

TABLE 1. Measurements ( $\bar{x} \pm SE$ , range in parentheses) of long-range (LRS) and short-range (SRS) songs of male Dark-eyed Juncos ( $n = 13$  males for LRS and 4 males for SRS).

	Long-range songs	Short-range songs
Highest frequency (kHz)	6.5 $\pm$ 0.6 (5.4 to 8.2)	8.7 $\pm$ 1.4 (3.3 to 11.4)
Lowest frequency (kHz)	3.4 $\pm$ 0.4 (2.4 to 4.1)	4.4 $\pm$ 1.8 (1.1 to 9.4)
Frequency range (kHz)	3.1 $\pm$ 0.7 (2.1 to 4.4)	2.8 $\pm$ 0.7 (0.2 to 8.8)
Repetitions per syllable	13.4 $\pm$ 4.0 (9 to 21) <sup>a</sup>	1.0 $\pm$ 0.0 (1 to 4)
Song duration (s)	1.5 $\pm$ 0.2 (1.2 to 1.6)	continuous
Bout duration (s) <sup>b</sup>	152.9 $\pm$ 32.9 (42 to 295)	164.5 $\pm$ 53.9 (60 to 840)
Time between syllables (s)	0.04 $\pm$ 0.01 (0.02 to 0.10)	1.6 $\pm$ 1.0 (0.04 to 8.40)
Time between songs (s)	6.3 $\pm$ 1.5 (4 to 11)	continuous
Syllable types per song	1.1 $\pm$ 0.3 (1 to 2)	not defined

<sup>a</sup> Within songs.

<sup>b</sup> Data from focal observations. Bouts are defined as songs (for LRS) or syllables (for SRS) separated by  $\leq 30$  s. Observations include some that began singing before or stopped singing after the focal period.

spread apart), and (3) the distance between the focal male and other males and females. Because focal "points" were 8 s long, more than one behavior could be expressed during each point, so cumulative totals could exceed 100%.

Observations were assigned to one of three reproductive periods: (1) the fertile period (seven days prior to laying of the penultimate egg; Birkhead and Møller 1992; the exact onset of fertility is unknown in this species); (2) the courtship period (before the fertile period); and (3) the nonfertile period (during incubation or brood rearing). Because not all males were observed during all periods, pairwise comparisons could not be made. Therefore, I assigned individual males to one of these three periods. For nine randomly chosen males, I included in analyses only

observations from the fertile period, for six males only observations during the courtship period, and for the remaining seven males only observations during the nonfertile period. Males in all groups were followed for an average of 2.7 separate focal watches (total of ca. 40 min/male). Mean time of day did not differ among observations of the three groups of males (11.2, 11.8, and 11.8 h EST for courtship, fertile, and nonfertile observations, respectively; Kruskal-Wallis test,  $H = 37$ ,  $P = 0.681$ ). Because of nesting phenology, dates of courtship-period observations (5 to 21 April) preceded those during fertile and nonfertile periods, which did not differ significantly from each other (mean dates of 21 May versus 13 May for fertile and nonfertile periods, respectively; Mann-Whitney  $U$ -test,  $U = 50.5$ ,  $P = 0.129$ ).

*Statistical methods.*—SYSTAT software (Wilkinson 1990) was used to analyze data. For most comparisons, nonparametric statistics were used because of small sample sizes and nonnormal distributions. Tests are two-tailed unless indicated otherwise. All values are presented as  $\bar{x} \pm 1 SE$ .

TABLE 2. Syllable repertoire size for long-range and short-range songs of male Dark-eyed Juncos. Males for which fewer than 15 long-range songs were recorded are not included.

Bird no.	No. songs analyzed	No. unique syllables
<b>Long-range songs</b>		
1	16	1
2	20	2
3	20	2
4	48	1
5	70	3
6	60	1
7	21	1
8	35	1
Mean	36.3	1.5 <sup>a</sup>
<b>Short-range songs</b>		
9	137	25
10	116	17
11	157	25
12	126	27
Mean	134	24

<sup>a</sup> Eleven wild-caught captive males recorded more extensively ( $\bar{x} = 99.1$  songs per male) had produced an average of 2.7 syllable types.

RESULTS

*Structure of the two song classes.*—Long-range songs typically were composed of a single syllable repeated in a trill (Fig. 1). Each LRS type was repeated an average of  $24.9 \pm 5.6$  times before a new song type was produced ( $n = 10$  males). Frequency, syntax, and temporal measures of LRS are presented in Table 1. Short-range songs were more variable in syntax than were LRS (Fig. 1), and their frequency range was wider (Table 1). Syllables seldom were repeated until much later in the song bout (Table 1). Syllable repertoire sizes for both song classes are presented in Table 2. All four males included typical junco calls (see Ralph 1977) into their SRS. Half (2 of 4) also included in their

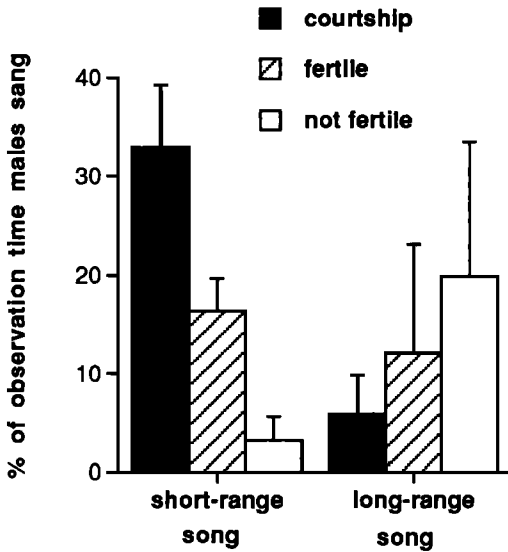


FIG. 2. Percentage of time during focal observations that males spent singing long-range versus short-range songs. Amount of short-range song differed significantly ( $P < 0.05$ ) among courtship ( $n = 6$ ), presumed fertile ( $n = 9$ ), and presumed nonfertile ( $n = 7$ ) periods. The amount of long-range song did not vary significantly among periods. Values are  $\bar{x} \pm$  SE.

SRS some syllables identical to those used in their LRS.

*Focal observations.*—Rates of singing LRS did not differ significantly among the three reproductive stages (Kruskal-Wallis test,  $H = 3.6$ ,  $P = 0.163$ ; Fig. 2). Males produced SRS more frequently during courtship than during the fertile (Mann-Whitney  $U$ -test,  $U = 42$ ,  $P = 0.020$ ) or nonfertile ( $U = 42$ ,  $P < 0.005$ ) stages, and more frequently during the fertile stage than during the nonfertile stage ( $U = 51.5$ ,  $P = 0.031$ ; Fig. 2).

Long-range songs usually were given while males were perched in trees (97.6%) and rarely while they foraged (0.3%). In addition, LRS seldom were accompanied by feather-erection (0.4%) or tail-spreading (0.2%) displays. Short-range songs were produced while males were sitting on the ground or perched in low vegetation (60.5%) or foraging (50.7%). They were accompanied by feather-erection or by tail-spreading displays during 51.4% and 31.4% of observations, respectively. Males sang LRS from an average of  $8.5 \pm 1.3$  m (range 3 to 13 m) above the ground and SRS from an average

of  $2.0 \pm 0.9$  m (range 0 to 8 m) above the ground (paired  $t$ -test,  $t = 3.78$ ,  $df = 7$ ,  $P < 0.01$ ).

During focal observations, the distance between pair members affected which class of song males produced. SRS were produced from an average of  $4.3 \pm 0.6$  m (range 0.5 to 9.5 m) from females, whereas LRS were produced from  $9.5 \pm 0.7$  m (range 2 to 11 m; sign test,  $P = 0.016$ ). The value for LRS is probably an underestimate, because the highest distance category ( $>10$  m) was conservatively scored as 11 m during analyses. All males that countersang LRS during observations ( $n = 7$ ) spaced songs so that they did not overlap temporally with those of other singing males, and did so with distant, out-of-sight males. Production of SRS by two males during the same focal observation ( $n = 3$  males) involved males that were from 3 to 10 m apart. In each case, songs of the two males overlapped in time. Countersinging of LRS occurred throughout the study (19 April to 7 June), whereas overlapping production of SRS occurred only early in the season (13 to 14 April).

## DISCUSSION

Males produced SRS during a variety of interactions with nearby conspecifics. High rates of production of SRS in conjunction with courtship displays (e.g. feather-erection and tail-spreading) and when males accompanied females during the fertile period point to the function of SRS in male-female communication. The use of SRS during male-male chases supports that idea that SRS are used during intense interactions with nearby conspecifics (Dabelsteen and McGregor 1996, Dabelsteen et al. 1997). Later in the season, the use of SRS during the females' fertile periods suggests that SRS also function in the stimulation of female reproductive condition or in pairbond maintenance. Whether SRS differ in structure in these different contexts remains to be explored.

In contrast, production of LRS did not vary with the reproductive state of females and was not associated with courtship displays or close-range interactions with other males. Countersinging of LRS involved distant males and occurred throughout the season (i.e. during many stages of the nesting cycle), suggesting that the continued defense of territories is an important function of LRS. Unmated males sing more

during the breeding season than do mated males (Ketterson et al. 1992), suggesting that LRS also function as advertisement for mates. Together, these findings suggest that LRS function primarily in communication over long distances.

Song use by juncos is similar to other systems in which different LRS types are associated with reproductive stages. In some paruline warblers, for example, song types that differ in structure are associated with inter- and intrasexual contexts (Spector 1992). Differences in syntax within two types of LRS also have been detected in Swamp Sparrows (*Melospiza georgiana*; Nowicki et al. 1991). After pairing, Grasshopper Sparrows (*Ammodramus saviannarum*) produce complex, rapid songs that appear more prone to degradation than do their shorter, simpler songs (Vickery 1996). These structural differences among song types may help to direct songs to different intended audiences. Galapagos finches (Geospizinae) use whistle songs as high as 16 kHz during short-range interactions with mates (Bowman 1983). These songs probably do not carry far due to their high frequencies, yet limited measurements have shown that their amplitude is actually greater than that of the finches' other song type (Bowman 1983). Although this may seem paradoxical, it illustrates the importance of both amplitude and structure in determining a song's range of transmission. Using a functional definition, these songs should be categorized as SRS.

Other songs are more readily categorized as SRS because both their structure and amplitude differ from LRS. Baptista (1978) found that songs of Cuban Grassquits (*Tiaris canora*) used in interactions between pair members were more complex in structure and sometimes lower in amplitude than were other songs. Eurasian Blackbirds produce twitter songs that are faster, lower in frequency, and quieter than songs used in long-range interactions (Dabelsteen and McGregor 1996). Other songs in their repertoire contain a mixture of twitter and long-range syllable types (Dabelsteen et al. 1993, Dabelsteen and McGregor 1996). Juncos appear to differ from previously reported species in the extent to which the two song classes differ in structure as well as in amplitude. In these systems, the opportunity exists to ex-

amine the role that each feature plays in determining the range of song transmission.

Why have the two song classes of Dark-eyed Juncos diverged so greatly? A simpler solution would be to produce songs with the structure of ordinary LRS at low amplitudes, as do many species (e.g. Nolan 1978, Payne 1992, Webb and Bock 1996, Bowen 1997). The specialized structure of other SRS may provide another means to confine transmission to specific ranges (i.e. those that contain the intended audience). Richards and Wiley (1980) describe acoustical characteristics of songs that are adapted for different environments. The frequencies of LRS (2.4 to 8.2 kHz) correspond well to those proposed by Richards and Wiley as optimal for long-range communication in wooded habitats (i.e. 2 to 8 kHz). The repetition of syllables also is thought to enhance reception of such songs in this type of habitat. Short-range song, on the other hand, covers a broader range of frequencies (1.1 to 11.4 kHz) and includes rapid frequency modulations (e.g. buzzes) that should degrade quickly over long distances (Richards and Wiley 1980). The lack of immediate repetition of syllables also suggests that the song would lose considerable information in transmission through dense habitat (i.e. whole syllables may not be heard by distant receivers). Thus, the structure of SRS seems prone to rapid environmental degradation over long distances, contributing to the already low amplitude in rendering it useful for communication targeted at nearby individuals.

The conspicuous nature of long-range signals makes them perceptible to unintended receivers such as predators and conspecifics (Otte 1974, Krebs and Dawkins 1984). For example, conspicuous courtship displays may attract conspecifics that are seeking extrapair fertilizations (Birkhead and Møller 1992). Because short-range signals are likely to be inconspicuous, they may be thought of as more "secretive" or "private" forms of communication (Krebs 1991). Such signals might be used during courtship to conceal from conspecifics the fact that a potentially fertile individual is being courted (Krebs 1991). They also could be used in the stimulation of female reproductive condition without alerting conspecifics to the presence of a fertile female.

Although it is recognized that different messages are encoded within the LRS repertoires

of many species, and that many species employ two or more types of LRS, the importance of SRS seldom has been examined. Recognizing that SRS may function in some of the contexts traditionally proposed for LRS may lead to a more accurate understanding of avian vocal systems. For example, songs of corvids appear to be used primarily at close range (Goodwin 1986) but have been understudied. In species for which studies of LRS fail to find anticipated relationships between song and behavior, investigators might examine SRS for such functions.

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