SONG CATEGORIES AND THEIR FUNCTIONS IN THE FIELD SPARROW (*SPIZELLA PUSILLA*)

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ABSTRACT.—Two song categories, distinguished by their acoustic structure, contextual usage, and potency in provoking responses from territorial males, are found in repertoires of individual male Field Sparrows (*Spizella pusilla*). Simple songs are sung spontaneously throughout the day and in long-distance countersinging by territorial males. Complex songs are sung most frequently during the dawn chorus and during territorial boundary chases. Most males sing one simple and one complex song type. Males responded more strongly to playback of complex songs than to simple songs. Our experiment supports the hypothesis that male songbirds respond differently to songs that are sung in different contexts. *Received 13 November 1989, accepted 11 July 1990.*

IN MANY species of passerine birds, males sing two or more acoustically distinct song types (reviews in Krebs and Kroodsma 1980, Kroodsma 1982). Many hypotheses have been proposed to explain the proliferation of song types within repertoires. One class of hypotheses assumes that all songs within a species' repertoire contain the same information. Repertoires of redundant song types may be favored by both intra- and intersexual selection. Large repertoires could function as effective "keep-out" signals by decreasing habituation in listening males (Krebs 1976), or by appearing to represent the presence of several singers (Krebs 1977). Large repertoires might also be favored by females during mate choice (Howard 1974, Catchpole 1980). Accordingly, songs should be used interchangeably and should provoke indistinguishable responses from listeners.

A second class of hypotheses assumes that different song types within a repertoire provide different information to listeners. Different song types are sung in different behavioral contexts, and thus appear to provide different information to listeners (Morse 1970, Ficken and Ficken 1970, Lein 1978, Smith et al. 1978, Payne 1979, Järvi et al. 1980, Sossinka and Böhner 1980, Catchpole 1983, Gaddis 1983, Nelson 1985, Derrickson 1987, Trainer 1987). In some warblers, males share different temporal patterns of song delivery in different contexts (MacNally and Lemon 1985, Staicer 1989). In species where song usage varies with behavioral context, different songs may provide information on the singer's intentions or motivation (Lein 1978) and fighting ability (Lemon et al. 1987). In some species it has been suggested that some songs are directed primarily at females, while others within the repertoire are used primarily in male-male interactions (Morse 1966, 1967; Kroodsma et al. 1989). According to these hypotheses, which are not mutually exclusive, different song types should provoke different responses from recipients.

To distinguish between these two forms of repertoire organization, we refer to song types that have different behavioral or contextual correlates as different song categories. In a similar way, Schroeder and Wiley (1983) grouped song types of the Tufted Titmouse (*Parus bicolor*) into "classes" based on usage and structure, and others have referred to song "groups" (Nolan 1978) or "modes" (MacNally and Lemon 1985). We suggest that three criteria must be met for song types to be separated into distinct categories: the song types must differ acoustically, they must be used in different behavioral contexts or reliably predict different subsequent behaviors, and they must elicit different responses from listeners in playback tests. If these criteria are met, a strong case is made that the songs serve different functions and convey different messages. Although we are concerned here with song-type variation, other aspects of song, such as the pattern of song delivery, could vary across contexts and so cause songs to be grouped into different categories.

We documented the occurrence of two song types in male Field Sparrows (*Spizella pusilla*), a species in which males were previously re-

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ported to sing a single song type (Goldman 1973, Heckenlively 1976, Morrison-Parker 1977, Searcy 1983). Most studies of song repertoires have identified song types by subjective visual examination of sonograms. In Part 1 we present a quantitative acoustic analysis of song variation that supports the classification of songs into discrete acoustic categories, and we also estimate the size of individuals' song repertoires. In Part 2 we present observations of the contexts of singing. In Part 3 we describe an experiment to support the hypothesis that the two song types convey different messages, thus constituting distinct song categories.

STUDY LOCATION AND OBSERVATIONAL METHODS

Territorial male Field Sparrows were observed from 1984-1989 at The Rockefeller University Field Research Center, Mary Flagler Cary Arboretum, and Dutchess County Infirmary, Dutchess County, New York. The most intensive work was in 1986 (140 territories) and 1987 (146 territories). Songs of all males were tape-recorded and analyzed (see below). We identified birds on the basis of their songs, which are retained from year to year (Nelson unpubl. data). Color bands on some birds also aided identification. Two banded males were in the study area when the study began, and 36 other resident males were banded with unique color-band combinations in June and July of 1985 and 1986.

We used focal-animal and *ad libitum* sampling (Altmann 1974) to observe singing behavior. Focal samples are described in Part 2. From 1984 through 1987 we sampled singing behavior *ad libitum*. Territories were visited periodically from April through July (1986 median: 3.5 visits, range = 1-15; 1987: 5.0, range = 1-16). During each visit, whenever we were certain that only one bird was singing, we noted the number of acoustically distinct songs heard (see below). Most of the results were drawn from the 109 males that were visited four or more times or tested with playback two or more times in 1987.

1. SONG CLASSIFICATION

METHODS

Songs were recorded with a Nagra III tape recorder (19 cm/s) and Sennheiser MKH816 microphone. Recordings were digitized at 20.8 kHz using a PDP-11/23 minicomputer and stored as disk files.

Following Isaac and Marler (1963) we defined a *song* as a series of notes in which the quiet intervals between notes are much shorter (40-200 ms) than the quiet intervals between songs (5-15 s). A *note* was defined as a continuous tracing on a sonogram. Notes were composed of one or more elements, where an *element* was a note sub-unit with a nearly constant rate of frequency modulation (FM). In this study, note types were distinguished subjectively on the basis of note shape on a sonogram. All Field Sparrow songs were composed of at least 2—and usually 3–5—different note types. Notes were grouped into phrases of trills of repeated identical notes or a sequence of different note types. All complete songs had at least two phrases. This distinguished songs from several calls in the repertoire in which a single note is trilled (Morrison-Parker 1977, Nelson pers. obs.).

We based initial classification of songs into types on visual inspection of sonograms. A song type was a consistently sung song pattern that differed noticeably from other types either in the repertoire of one male or from those of other males. "Noticeably different" is subjective, but our criteria excluded the occasional addition or deletion of notes in a song. The substitution of different note types in one or more phrases was sufficient to classify a song as a different type. Variation in simple song (see below) structure is very low within individuals (Nelson 1989a).

To determine whether the songs grouped into discrete categories, we used principal components (PC) analysis (Sneath and Sokal 1973, Frey and Pimentel 1978) on songs recorded from 27 different males in 1986 and 1987. These males were chosen because we had good-quality recordings of two different song types in their repertoires. Presumably we recorded their entire repertoires because each was sampled a median of 6 times in one breeding season. Samples included both spontaneous singing and song induced by tape playback. We used PC analysis instead of canonical discriminant analysis, because the latter technique assumes the song categories are known a priori. A PC analysis was well-suited for our goal, which was to discover whether, and how many, natural categories of song existed.

Song sonograms were displayed on a computer terminal and measurements were made with a graphics cursor driven by an analytical software program (Engineering Design 1987). We made temporal measurements on plots produced with a 128-point digital Fourier transform (DFT, resolution = 6 ms), while frequency measures were derived from a 512-point DFT (resolution = 41 Hz). We measured eight variables on one note sampled from the middle of each of the first three phrases as described in Nelson (1989b). The variables were as follows: (1) Maximal and (2) minimal frequencies, (3, 4) durations of each of the first two elements, (5) note duration, (6, 7) the FM rate and direction (upsweep or downsweep) of each of the first two elements, and (8) the internote interval. We also measured song duration, total number of phrases, total number of notes in a song, and number of notes in each of the first three phrases. Our measurements yielded a total of 30 variables.
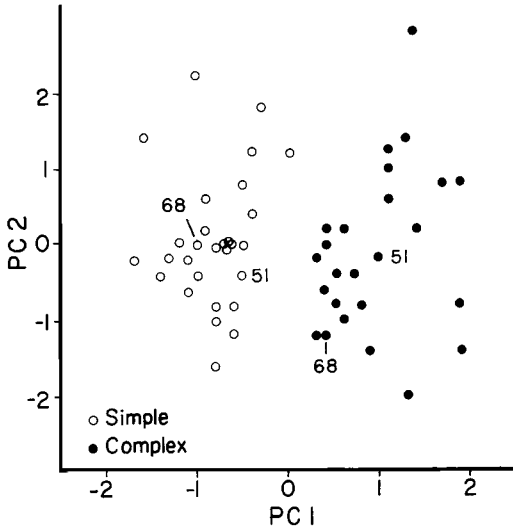
Fig. 1. Scatterplot of 54 songs in two song categories on the first two principal components derived from 22 song variables. Statistics describing variation in song structure are in Table 1; PC1 accounted for 27%, and PC2 13%, of the total variation among the 22 variables. The four numbered points are the songs used as playback stimuli in Part 3 (see Fig. 2).

For the final PC analysis, we eliminated 8 of the 30 variables because they correlated highly with other variables that remained in the analysis. The PC analysis reduced the set of 22 intercorrelated variables into a smaller set of orthogonal PCs that efficiently summarized the variation in the original data. We examined a scatterplot of the 54 songs on the first two PCs to see if songs clustered into two or more groups. Correlation coefficients between the original variables and the PCs identified variables along which songs varied.

RESULTS

Song categories.—Based on principal component analysis of Field Sparrow song structure, we identified two major song categories (Fig. 1). Of the 27 males, 25 had one song type in each category. All of the two song types from each of the two remaining males fell within the category on the left side of the plot. We refer to songs clustered on the left side of the plot as simple songs, and those on the right as complex songs. (See Fig. 2 for examples of the two categories).

Simple songs have been described previously (Davis 1964, Goldman 1973, Heckenlively 1976, Morrison-Parker 1977). They began with long notes with slow frequency modulation and long inter-note intervals, followed by a steady, faster trill of shorter notes (Table 1). The long introductory notes usually consisted of one or two elements, and the trill notes consisted of one, rarely two, elements.

Complex songs differed from simple songs in both syntactical and note structures so as to make them sound more complex to our ears. Complex songs had the reverse syntactical order of simple songs. For example, complex songs began with a steady trill of short notes followed by longer notes. Complex songs frequently alternated between phrases of short and long notes (Fig. 2: songs 19-C, 124-C). Also, the short notes in complex songs were shorter and had more elements than short simple-song notes.

Song repertoire sizes.—Most males (106 of 109 or 97% in 1987) sang simple songs. Three birds sang only complex songs in spontaneous sing-

TABLE 1. Statistics describing variation in two categories of Field Sparrow song. Values are acoustic variables ($\bar{x} \pm$ SE) correlated (r) with PC1 plotted in Figure 1.

Variable[a]	r	Simple ($n = 29$)	Complex ($n = 25$)
N1 duration	−0.77	322.0 ± 22.76	109.9 ± 10.38
Notes in phrase 1	0.74	2.1 ± 0.30	6.8 ± 0.70
N2 duration	−0.73	201.4 ± 11.23	134.0 ± 11.30
N3 inter-note interval	0.71	32.5 ± 1.32	61.1 ± 5.15
Notes in phrase 2	0.70	2.9 ± 0.21	5.2 ± 0.40
Elements in N1	0.67	1.3 ± 0.09	2.4 ± 0.14
N1 inter-note interval	−0.64	89.1 ± 4.58	60.2 ± 4.23
N3 maximal frequency	−0.63	4,335 ± 50.00	3,975 ± 46.09
N1 element 1 FMI[b]	−0.60	−2.1 ± 0.66	−13.9 ± 2.72
N3 element 2 FMI	0.54	−21.3 ± 2.36	−0.4 ± 4.45
Song duration	0.53	2,806 ± 106.9	3,714 ± 276.9
N2 element 1 FMI	−0.44	−2.7 ± 0.93	−8.5 ± 2.44

[a] N = note, number = phrase in song. Temporal measures are in ms, frequency in Hz.

[b] FMI = frequency modulation index. Frequency upsweeps were coded as positive, downsweeps as negative (Nelson 1989).
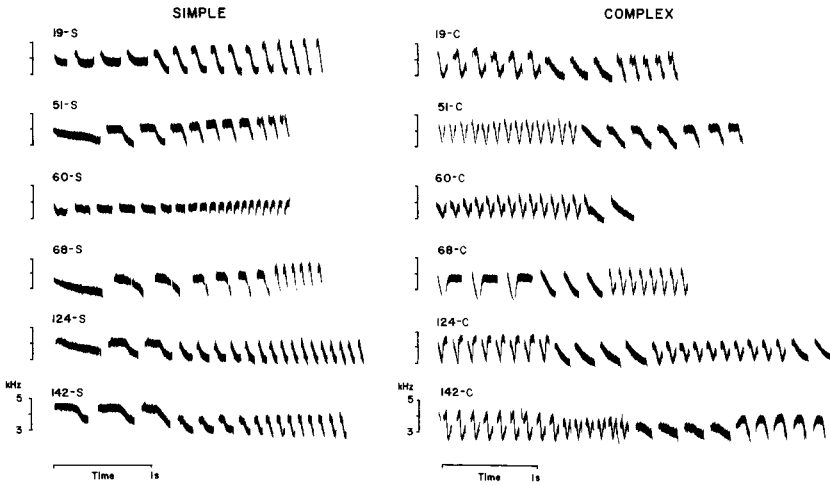
Fig. 2.   Sonograms (300 Hz analyzing filter) of simple and complex songs of six male Field Sparrows. See text for description of features separating the two song categories.

ing. Two of these birds were observed on 5 and 10 occasions in 1987, and on 3 and 5 visits in 1989, so it is unlikely we missed any simple songs. We lack observations of these birds at dawn.

Most birds sang complex songs as well. We heard complex songs from 20/29 (69%) of the banded males studied in 1986 and 1987. Eight of 11 (73%) focal males observed at dawn (see Part 2) sang complex songs, along with 13 of 18 (72%) of their neighbors that sang. Repeated samples of the same individuals would likely increase these estimates.

From 1985 to 1988 we tape-recorded two or, rarely, three or four simple-song types in one observation period from 20 birds. Four of the 109 (3.6%) birds that we visited at least 4 times or tested twice in 1987 sang 2 or more simple song types. Males repeated one simple type a median of two times (range = 1–11, $n = 15$ males) before switching to another simple type. No bird sang more than one complex song type.

In summary, most—perhaps all—male Field Sparrows sang two acoustically distinct song types. The two song types share similarities across males such that they can be grouped into larger categories, thereby meeting the first prerequisite for establishing the existence of song categories. In the next section we describe the behavioral contexts in which songs occur and show that the two song categories are used distinctively.

2. CONTEXTUAL ASSOCIATIONS OF SONG CATEGORIES

In 1988 we conducted two sets of focal-animal watches. One was conducted during the dawn chorus, the most intense period of singing in the day (e.g. Kacelnik and Krebs 1983). The other sampled singing before and after a simulated territorial intrusion staged in midmorning. Singing behavior in the focal observations was compared to that observed during territorial chasing observed during *ad libitum* observations.

METHODS

Dawn chorus watches.—Eleven birds were observed singly during the dawn chorus (0430–0515) from 14 June to 9 July. We counted numbers of simple and complex songs for 15 min.

Midmorning watches.—From 26 April through 3 May we observed 12 males in midmorning (0630–1030). Of the 12 males, 9 were on territories also used in the dawn chorus samples. Based on song similarities, the 9 males were probably the same individuals observed later in the year. We chose males in advance and began watches as soon as we reached the center of the male's territory. We did not wait for males to sing before beginning the sample. Before each watch we placed a Nagra DH loudspeaker on the ground near the center of the male's territory. A stuffed Field Sparrow, held in a vertical position by a thin wire, was placed atop the speaker. Both mount and speaker were covered with a brown cloth. After retreating to a po-
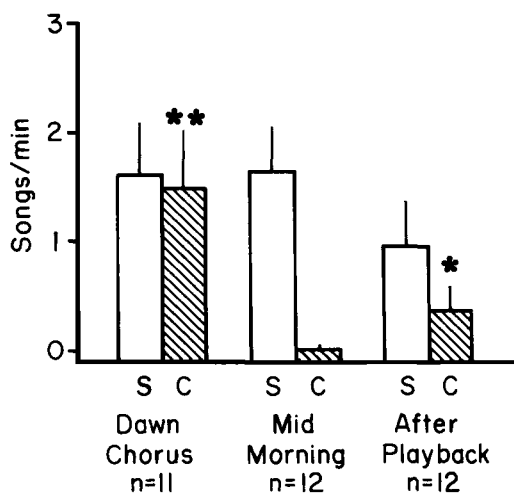
Fig. 3. Rates ($\bar{x} \pm$ SE) of simple (open bars) and complex (hatched bars) songs sung in three contexts. Asterisks denote statistically significant differences relative to midmorning (* = $P < 0.05$, ** = $P < 0.01$, see text).

sition 10–15 m away, the observer then counted the numbers of simple and complex songs during a 15-min preplayback period. The mount—but not the speaker—was then uncovered, and after a 3-min wait, song playback began. Songs were played for 3 min, followed by 3 min of silence, then 3 min more of song, terminated by 3 min of silence. We alternated playback and silence because many males do not sing during playback. Twelve songs, at 15-s intervals, were played in each 3-min playback period. One of two simple songs (51-S or 68-S in Fig. 2) was chosen randomly and played to a male. The numbers of simple and complex songs given by the subject were counted over the entire 12 min of alternating playback and silence. Song rates (songs/min) were compared between preplayback and playback periods by a Wilcoxon matched-pairs signed-ranks test. Mann-Whitney U-tests were used to compare song rates at different times of the day.

Territorial interactions.—During the *ad libitum* samples we observed 22 instances of chasing between two Field Sparrows. All of the chases occurred in April of 1986 and 1988, before females were common in the area.

RESULTS

Song rates during dawn chorus watches.—Males sang a total of 3.1 ± 0.49 ($\bar{x} \pm$ SE) songs/min during the dawn chorus (Fig. 3). Forty-eight percent were complex songs, and 8 of 11 males (73%) sang complex songs at dawn. Males alternated between simple and complex songs.

They repeated one category a median of 4 times (range = 1–13 among 7 males) before switching to the other category. Males frequently gave trill calls between songs and flew about their territories every 5–10 songs. Some males gave trill calls and moved to their territory boundaries, apparently in response to a neighbor's approach.

Song rates during mid-morning watches.—Males sang 1.7 ± 0.39 songs/min during undisturbed singing in midmorning (Fig. 3). Only 1 of 12 males (8%) sang complex songs. Total song rates were significantly lower in midmorning than at dawn (Mann-Whitney $z = -1.94$, $P < 0.05$), primarily because complex song rates decreased significantly ($z = -3.15$, $P < 0.01$) (Fig. 3). Simple song rates did not differ between dawn and midmorning ($z = -0.34$, $P > 0.10$). Simple song rates declined slightly after song playback. Complex song rates increased significantly after playback as 6 of 12 males sang complex songs (Wilcoxon matched-pairs signed-ranks test, $z = -2.02$, $P < 0.05$, $n = 12$). In midmorning, males usually restricted their activity to sitting and singing on a few perches and were quiet between songs.

Territorial interactions.—In 18 of 22 (82%) instances of chasing, complex songs were sung by at least one bird. No singing occurred in four cases. In 6 cases only the resident or chasing male sang complex songs. In 4 of these 6 cases the bird being chased sang simple songs. In 6 additional cases only one bird sang complex songs, while the other sang simple songs, but we were uncertain of the roles played by each bird in the dispute. In 3 cases we heard both birds sing complex songs, while in the 3 remaining cases we heard complex songs, but could not distinguish the singer(s). Males also exchanged high-pitched trill calls during chases. Birds were usually silent while flying in a chase or moving together on the ground. Complex songs, frequently muted, occurred when the birds were perched between chases. The intruder bird usually initiated flights, followed by the resident.

Complex songs were generally restricted to two contexts typified by high levels of agonistic stimulation. These were actual or simulated territorial interactions and the dawn chorus. We assume the dawn chorus is an agonistic context because it shares several behavioral features (high song rates, trill calls, increased locomotory activity) with territorial interactions. Sim-

ple songs were most commonly sung by undisturbed males in midmorning and in the dawn chorus.

Our observations in midmorning were conducted 6–8 weeks before those at dawn, which suggests that a seasonal factor may explain the differences in song usage. However, complex songs are rarely heard in midmorning at any time of year and are common at dawn after mid-May (we lack dawn observations before then). Simple song rates in midmorning are lower in June and July than in early May, but are higher than complex song rates (Nelson unpubl. obs.). Therefore, the contrast in singing behavior between dawn and midmorning holds at least after mid-May.

3. MALE RESPONSES TO PLAYBACK OF SIMPLE AND COMPLEX SONGS

The contextual differences in song usage suggested that complex songs may convey stronger aggressive tendencies to other males than do simple songs. Therefore territorial males would be expected to respond more strongly to playback of complex songs than to simple songs. We conducted a playback test in 1987 to test this prediction.

METHODS

Stimuli.—We selected simple and complex songs sung by two different males recorded in 1986. The recordings were of high quality, and all songs were of approximately the same duration (Fig. 2: males 51 and 68). Kroodsma (1989) recommended that many song stimuli be used to represent complex stimulus distributions. The positions of the four stimuli are plotted in the "acoustic space" defined by principal components in Fig. 1. We assume that these stimuli represent the variation in the two song categories.

Each song was digitized and stored in a PDP 11/23 minicomputer using a high-pass filter to remove noise below 1 kHz and a brickwall low-pass filter at 8.3 kHz to prevent aliasing. Each song was then copied 12 times, with 13-s intersong intervals (3-min total playback) onto a Sony TC-D5M cassette recorder using a software program (Engineering Design 1987). The song rate was thus 4 songs/min, which is the average rate for actively singing birds.

Experimental procedure.—We tested 10 males between 20 and 28 June 1987. None resided within 500 m of either bird that sang the stimulus songs in 1986. All trials occurred between 0545 and 1030 on days of little wind and no rain. We used a single-speaker design in which each male was presented with a different song category in two trials, one or two days apart. Stimulus exemplars were assigned randomly

from each song category, and the two songs were presented in random order to each subject. Thus there were four possible combinations of stimuli (51-S and 51-C, 68-S and 68-C, 51-S and 68-C, 51-C and 68-S).

A Nagra DH loudspeaker, covered with brown speaker-grille cloth, was placed face up on the ground near the center of a subject's territory. To facilitate measuring approach distance, we used poles placed in the ground at 4-m intervals out to 16 m in three directions from the speaker. We kneeled 15–20 m away and operated the playback recorder and dictated observations into a second cassette recorder.

A trial consisted of a 3-min playback period and a 5-min postplayback period. In both periods we recorded seven variables: the numbers of (1) songs, (2) chip calls, (3) trill calls, and (4) flights; the numbers of seconds spent (5) 0–4 m from the speaker, and (6) 4–16 m; and (7) the distance of closest approach. We used principal components analysis to reduce the 14 response variables to 2 orthogonal principal components. The PC scores were then used as variables in Wilcoxon matched-pairs signed-ranks tests of the hypothesis that birds would respond differently to the two song categories.

RESULTS

Of 14 response variables, 9 were strongly correlated (nominally significant at $P < 0.05$) with the first PC (Table 2). Positive values of PC1 represented stronger responses, and males gave significantly stronger responses to playback of complex song than to simple song (Table 2, $z = -2.3$, $n = 10$, $P = 0.01$, one-tailed). Males flew, chipped, and trilled more often, spent more time near the speaker, and approached closer to playback of complex song than to simple song. Although there was broad overlap between categories on univariate measures, PC1 represented the weighted contribution of all response variables and provided a more sensitive measure of differences; PC2 did not differ between treatments. Of the 10 males, 3 sang complex songs after complex playback, and a fourth male sang complex songs after playback of both song categories. Thus, as predicted, males gave stronger responses to the song category (i.e. complex song) that contextual evidence suggested conveyed strong aggressive tendencies. This result supports our recognition of functionally distinct song categories.

DISCUSSION

Male Field Sparrows sing two acoustically distinct song types from simple and complex

TABLE 2. Experimental playback of two song categories to male Field Sparrows ($n = 10$). Values ($\bar{x} \pm$ SE) are PC1, and 9 of 14 variables strongly correlated with PC1.

Variable	Period	r^a	Stimulus song	
			Simple	Complex
PC1[b]		—	-0.41 ± 0.28	0.41 ± 0.30
Songs/min	Quiet	-0.78	3.02 ± 0.61	2.46 ± 0.66
Flights	Playback	0.70	5.20 ± 0.95	6.90 ± 0.76
Trills	Quiet	0.62	0.20 ± 0.13	3.60 ± 2.03
Closest approach (m)	Playback	-0.60	5.10 ± 1.68	3.40 ± 1.17
Time (s) < 12m	Playback	0.55	57.2 ± 15.3	71.9 ± 11.1
Time (s) < 4m	Playback	0.54	24.5 ± 13.3	53.1 ± 14.4
Chips	Quiet	0.48	1.2 ± 0.51	5.3 ± 2.02
Flights	Quiet	0.47	4.9 ± 0.97	6.3 ± 0.96
Songs/min	Playback	0.45	1.83 ± 0.43	2.27 ± 0.67

[a] r is the Pearson correlation coefficient between each variable and PC1.

[b] Means differ significantly by Wilcoxon matched-pairs signed-ranks test, $P = 0.01$. The nine original variables were not tested because they were correlated.

song categories, and they use them in different contexts. Simple songs are sung by males in spontaneous undisturbed singing and in long-distance countersinging among neighbors. In contrast, complex songs are generally restricted to contexts characterized by high levels of agonistic interaction: male-male territorial boundary conflicts and the dawn chorus. In a playback experiment, the two song types provoke different responses from listeners. We assigned simple and complex songs to different categories because they met three criteria. They differed acoustically, they were used in different contexts, and they evoked different responses from listeners. These results support the general hypothesis that different song types provide different information to listeners. The results are inconsistent with the hypotheses that assume song types are redundant.

The two song categories within a male Field Sparrow's repertoire appear to have different functions. However, we can draw only indirect inferences on function from our contextual data. Simple songs probably have the dual function of repelling males and attracting females. Simple songs are the most common song in midmorning early in the breeding season (Fig. 3). Approximately half the males share part of their simple song with a neighbor (Nelson unpubl. data). Shared songs possibly facilitate distance estimation during countersinging between distant neighbors (Morton 1982, McGregor and Krebs 1984).

A mate attraction function is suggested because males stop singing after they acquire mates. Singing resumes, but is less frequent,

about the time females begin incubation. In males that sing two or more simple-song types, the different types appear to be redundant because males switch between song types rapidly within the same context.

Complex songs, in contrast, appear to function primarily in male-male interactions by communicating increased tendencies to interact or aggress. A mate attraction function for complex songs seems unlikely because they are rarely sung outside of male-male interactions before pair formation. Neighboring males rarely share complex songs.

The acoustic differences between song categories in syntax and note structure identified by the principal components analysis are not arbitrary measurements, but the differences are meaningful to male Field Sparrows in field playback tests. When territorial males were given a choice between a control song with simple-song notes in simple-song syntax, and a "hybrid" experimental song with simple-song notes in complex-song syntax (i.e. reversed order), they approached closest to the control song (Nelson 1988). In another experiment, males responded more strongly to the control song than to a "hybrid" song with a terminal trill of complex-song notes (simple song syntax, complex note structure). Thus, songs that combined attributes from the two song categories elicited lower responses than "pure" simple songs. This indicates that at least two acoustic dimensions used to define song categories in the PC analysis, or other features correlated with them, are used by the birds to distinguish songs.

Playback experiments have been performed

TABLE 3. Species in which song types are grouped into categories based on statistical associations with contexts or behaviors.

Species	Song categories	Repertoire total	Reference
Northern Mockingbird (*Mimus polyglottos*)	2	100+	Derrickson 1987
Aquatic Warbler (*Acrocephalus paludicola*)	2	3	Catchpole and Leisler 1989
Great Reed Warbler (*A. arundinaceus*)[a]	2	2	Catchpole 1983, Catchpole et al. 1989
Willow Warbler (*Phylloscopus trochilus*)[a,b]	2	2	Järvi et al. 1980
Wood Warbler (*P. sibilatrix*)	2	2	Temrin 1986
Black-capped Chickadee (*Parus atricapillus*)	2	2	Ratcliffe and Weisman 1985, Hill and Lein 1987
Bridled Titmouse (*P. wollweberi*)	3	3	Gaddis 1983
Plain Titmouse (*P. inornatus*)	3	9	Gaddis 1983, Johnson 1987
Tufted Titmouse (*P. bicolor*)	3–5	9–12	Schroeder and Wiley 1983
Field Sparrow (*Spizella pusilla*)[a,b]	2	2	This study
Cuban Grassquit (*Tiaris canora*)[b]	2	2	Baptista 1978
Golden-winged Warbler (*Vermivora chrysoptera*)	2	2	Ficken and Ficken 1967, Highsmith 1989
Blue-winged Warbler (*V. pinus*)	2	2	Ficken and Ficken 1967, Kroodsma 1981
Yellow Warbler (*Dendroica petechia*)	2	4+	Morse 1966, Bankwitz and Thompson 1979
Chestnut-sided Warbler (*D. pensylvanica*)	3	5	Lein 1978, Kroodsma et al. 1989
Black-throated Green Warbler (*D. virens*)[a]	2	2	Morse 1967, Ficken and Ficken 1970, Lein 1972
Grace's Warbler (*D. graciae*)[c]	2	5–9	Staicer 1989
Prairie Warbler (*D. discolor*)	2	4+	Nolan 1978
Blackburnian Warbler (*D. fusca*)	2	2	Morse 1967
American Redstart (*Setophaga ruticilla*)[c]	2	4	Ficken and Ficken 1970, MacNally and Lemon 1985
Yellow-throated Vireo (*Vireo flavifrons*)	4+	8	Smith et al. 1978
Yellow-rumped Cacique (*Cacicus cela*)	5	7	Trainer 1987
Yellow-headed Blackbird (*X. xanthocephalus*)[b]	2	2	Cosens and Falls 1984
Zebra Finch (*Poephila guttata*)[b]	2	2	Sossinka and Böhner 1980
Village Indigobird (*Vidua chalybeata*)	4	18	Payne 1979

[a] Denotes species where experimental evidence indicated birds respond differently to different categories.

[b] Denotes species where quantitative acoustic differences between song categories have been described.

[c] In these warblers, the pattern of song delivery differs among contexts. Within males, different song types are sung in different contexts, but there may not be common acoustic differences among males.

on six other species to determine whether males distinguish between song types sung in different contexts. Comparisons to our results must be made cautiously because all studies have used different methods. Results from the Black-throated Green Warbler (*Dendroica virens*) agree with those reported here for the Field Sparrow. Males approached significantly closer to the type A song that is sung in male-male interactions than to the type B sung in spontaneous advertising (Ficken and Ficken 1970). Aquatic Warblers (*Acrocephalus paludicola*) sing three different song "structures" (Catchpole and Leisler 1989). Song structures B and C are sung in spontaneous singing, and A songs (the initial part of B songs) were elicited by tape playback (a simulated territorial interaction). Playback of a series of A and B songs elicited significantly more A songs (interpreted as a strong response)

from subjects than did a tape of C songs alone. Mean approach distances did not differ between the two treatments. In contrast, male Willow Warblers (*Phylloscopus trochilus*) withdrew more often after playback of the song type (A song) that correlates with attack in territorial interactions (Järvi et al. 1980). Similarly, Great Reed Warblers (*Acrocephalus arundinaceus*) made weaker responses to songs (short) associated with aggressive contexts than to "sexual songs" (long) (Catchpole 1983). Captive males had a similar response pattern, and estradiol-implanted captive females responded to long song but not to short song (Catchpole et al. 1986).

Interpretation of results from the two remaining species is problematic. In the American Redstart (*Setophaga ruticilla*) and Chestnut-sided Warbler (*Dendroica pensylvanica*), males made significantly weaker responses to unaccented-

ending songs typically sung in male-male encounters (Ficken and Ficken 1970). In these experiments the unaccented-ending songs were always played first, followed 6 min later by the accented-ending songs. A randomized design, as was used in the experiments with *D. virens* (Ficken and Ficken 1970), would minimize sensitization and "carry-over" effects (Brenowitz 1981, MacNally and Lemon 1985). The evidence from five species (Field Sparrow, Black-throated Green Warbler, Aquatic Warbler, Willow Warbler, and Great Reed Warbler) supports the conclusion that male songbirds perceive differences between song categories (song types that are characteristically sung in different contexts).

For species in which behavioral evidence suggests that different song types convey similar messages, males respond similarly to different songs sampled from the local population (Indigo Bunting, *Passerina cyanea*, Emlen 1972; Fox Sparrow, *Passerella iliaca*, Martin 1980; Swamp Sparrow, *Melospiza georgiana*, Searcy et al. 1982; Carolina Wren, *Thryothorus ludovicianus*, Simpson 1985).

Song category repertoires identified to date are generally small (Table 3). Nine song types distributed among 4 or 5 categories is the largest number yet identified statistically within any songbird repertoire. Experimental evidence that songs elicit different responses is only available for species with two song categories (Table 3). If songs are specialized for inter- and intrasexual functions, as hypothesized (e.g. Morse 1966, Catchpole 1980), then only two categories would be necessary. If song categories are associated with different behavioral messages, then more categories may be expected, but an upper limit of a dozen or so seems to be placed by the small number of messages that animals use in social communication (Smith 1977).

The occurrence of song categories may be widespread among songbirds (Gaddis 1983). Repertoires of redundant song types, delivered particularly during spontaneous singing, are also common. In contrast to song categories, repertoires of redundant song types may number in the dozens or even hundreds (Kroodsma 1982), and are likely to be subject to selective forces that differ from those that operate on categories of song. Some form of sexual selection is usually invoked to explain the proliferation of redundant song types (Kroodsma 1976, Payne 1979, Searcy and Andersson 1986).

An upper limit on the number of redundant song types may be placed by the abilities of listeners to distinguish and remember different song types. Additional constraints may result from the need for songs to be species-specific (Nelson and Marler 1990) and individually identifiable (Falls 1982). The severity of these constraints and their importance in explaining variation in repertoire sizes remains to be determined.

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