# VARIATION IN CADENCE OF FIELD SPARROW SONGS

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Over 10 years ago, Reynard (1963) showed that different species of song birds sing at different rates. Since that time singing rates have received little attention, although they have occasionally been used as one measure of the response of birds to playback of recorded songs (e.g., Goldman 1973). The purpose of this study was to examine intra-population variation in singing rates of Field Sparrows (*Spizella pusilla*) in a variety of contexts, taking an initial hypothesis that rate of singing reflects male responsiveness to exogenous conditions. Consideration of population variation in song morphology has also been included in the report, since previous descriptions (Saunders 1922, Brand 1938) antedated the development of sound spectrography.

## METHODS

Breeding populations of Field Sparrows were studied in the summers of 1967–1971, inclusive, at the University of Michigan, Matthaei Botanical Gardens, Dixboro, Washtenaw Co., Michigan. Additional observations were made in 1971 at Island Lake State Recreation Area, Livingston Co., Michigan. Field work started in late May in 1967, in mid-June in 1968 and 1969, and in early April in 1970 and 1971.

Territorial limits of the males were estimated from the areas encompassed by their singing sites. Males were identified by their songs, which were generally unique within populations (Saunders 1922, pers. observ.). Recordings were made in the field with a Uher 4000 Report-L tape recorder at 19.05 cm/sec. A 61 cm aluminum parabola was used in the first several years; in 1971 a 30.5 cm parabola with pistol grip, fashioned from a photoflood reflector, was used interchangably with the larger reflector. While obtaining recordings, I often induced the birds to continue singing by playback of their own songs; this was done using the Uher speaker.

Singing rate was measured as the cadence, i.e., the time interval between successive songs in a bout. The average cadence was then calculated for each bout, except for the data in Table 5, which involved comparisons of rates within bouts. It should be noted that this criterion of singing rate does not include the number of bouts of singing in which an individual bird might engage, which could also be a key factor in the overall daily rate of singing. Cadences were measured both directly in the field and from tape recordings. Timing was done with the second hand of a watch, to an estimated accuracy of ± 0.5 sec. Cadences were measured simultaneously from adjacent birds whenever possible.

About 500 songs were recorded from the 8 birds on the study area in 1967, averaging 62 songs (range 6–263) from each. About 110 songs from the 1967 population were chosen for sound spectrography, forming the basis for most of the analysis of population characteristics. In subsequent years an additional 400 songs were recorded, primarily for identification of individuals. Sound spectrograms were done on a Kay Elemetric Corp. Vibralyzer, using a wide-band filter setting; a Sony TC-106A recorder was used for laboratory playback.
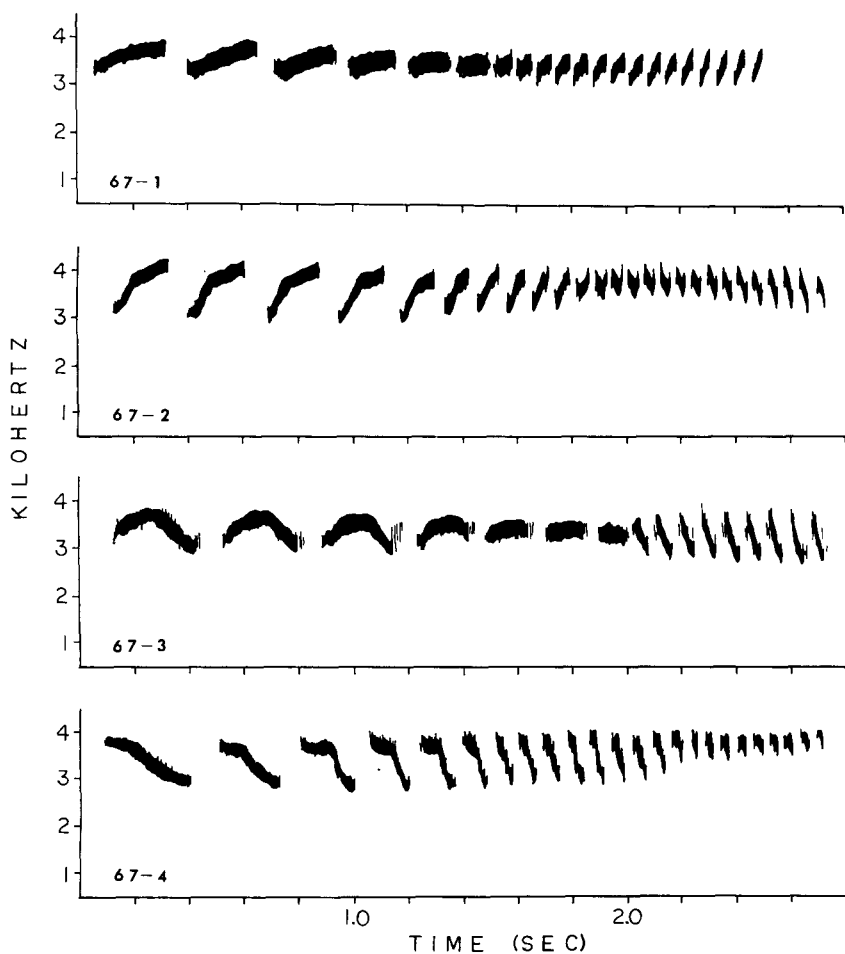
FIG. 1. Typical songs from four individuals in the 1967 population of Field Sparrows at Matthaei Botanical Gardens.

Unless otherwise stated, parameter estimates are given as the mean ± 1 standard deviation. Statistical notation generally follows Simpson, et al. (1960).

## SONG MORPHOLOGY

Each male in the 1967 population had 1 distinctive song-type, unique within the population. Typical songs of 6 individuals are shown in Fig. 1 and Fig. 2. These differences were readily distinguishable by ear and formed the basis by which I identified individuals. Characteristically, Field Sparrow
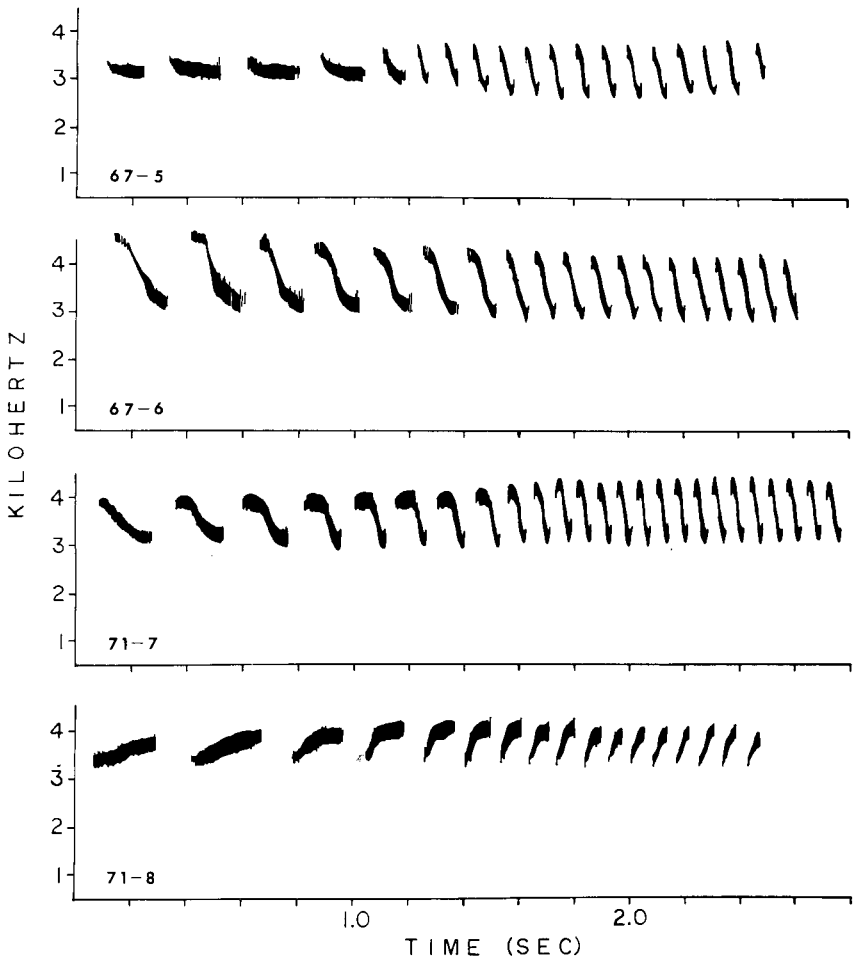
Fig. 2. Typical songs from four individuals in the 1967 population of Field Sparrows at Matthaei Botanical Gardens (67-5 and 67-6) and the 1971 population at Island Lake State Recreation Area (71-7 and 71-8).

song starts with several notes of relatively long duration, with subsequent notes of progressively shorter duration to form a final trill, so that the overall effect is one of acceleration of the notes in the song. The initial notes may be of rising pitch (Fig. 1, 67-1, 67-2), dropping pitch (Fig. 1, 67-4), straight pitch (Fig. 2, 67-5), or a rising then falling pitch (Fig. 1, 67-3). Similarly, the more rapid notes in the final trill may be either of rising or falling pitch. In some song-types notes in the final trill continued the rising or falling pat-
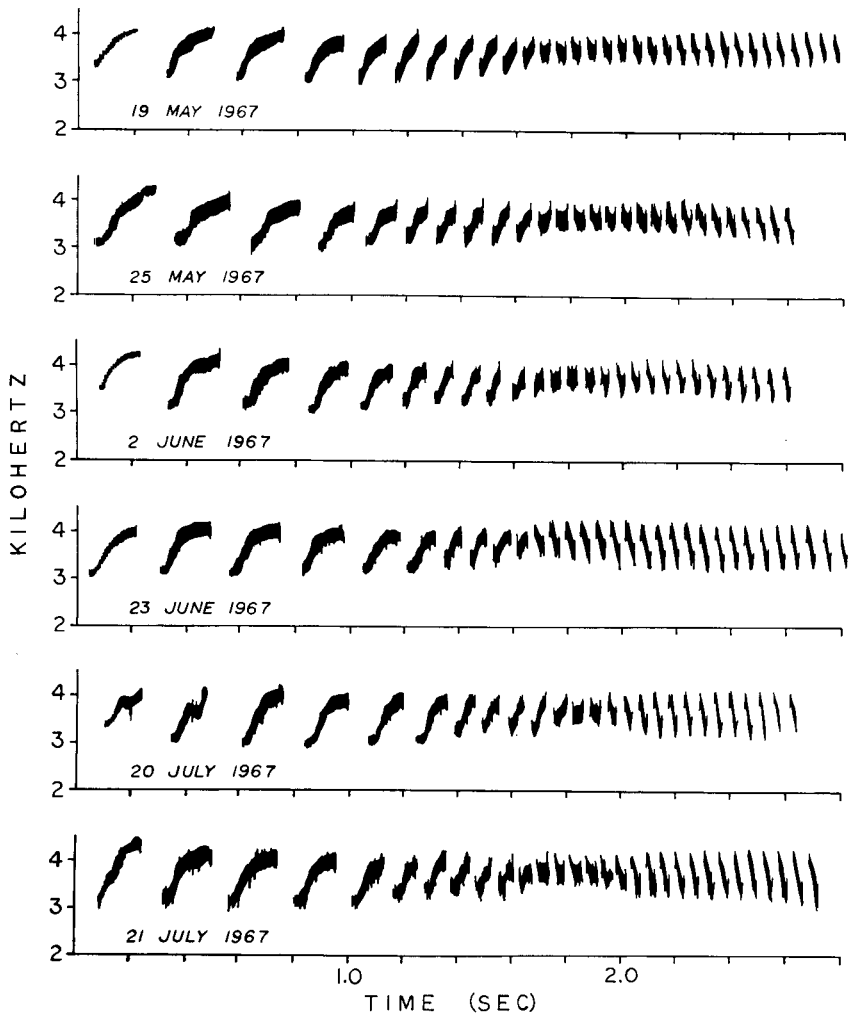
FIG. 3. Songs of individual 67-2, over the 1967 season.

tern of the earlier part of the song (e.g., Fig. 2, 67-6) ; in others the notes in the final trill took a form distinct from the opening notes (e.g., Fig. 1, 67-3).

Variation within individuals primarily took the form of adding or omitting notes, resulting in variation in the overall duration of the song as well. Notes were omitted both from the early portion of the song and from the final trill. Nonetheless, the basic, overall pattern of any one individual's song-type remained essentially the same throughout the season. Fig. 3 shows samples

TABLE 1

CHARACTERISTICS OF THE SONGS OF 8 FIELD SPARROWS

| Birds | Sample Size (N) | No. of Notes Mean ± SD | Song Duration (sec) Mean ± SD | Max. Frequency (kHz) Mean ± SD | Min. Frequency (kHz) Mean ± SD |
|---|---|---|---|---|---|
| 67-1 | 4 | 22.25 ± 1.89 | 2.55 ± 0.16 | 4.06 ± 0.06 | 3.01 ± 0.08 |
| 67-2 | 4 | 30.25 ± 3.10 | 2.74 ± 0.12 | 4.25 ± 0.07 | 2.96 ± 0.08 |
| 67-3 | 2 | 19.00 ± 4.24 | 2.79 ± 0.28 | 3.98 ± 0.04 | 2.72 ± 0.04 |
| 67-4 | 4 | 23.00 ± 0.82 | 2.75 ± 0.12 | 4.08 ± 0.10 | 2.60 ± 0.08 |
| 67-5 | 3 | 21.00 ± 6.00 | 2.46 ± 0.52 | 4.05 ± 0.23 | 2.53 ± 0.06 |
| 67-6 | 2 | 18.00 ± 1.41 | 2.49 ± 0.04 | 4.72 ± 0.04 | 2.75 ± 0.07 |
| 71-7[1] | 3 | 26.00 ± 1.00 | 2.86 ± 0.17 | 4.52 ± 0.08 | 2.92 ± 0.03 |
| 71-8[1] | 3 | 17.00 ± 0.0 | 2.48 ± 0.08 | 4.25 ± 0.0 | 3.13 ± 0.06 |
| Overall | 25 | 22.72 ± 4.92 | 2.65 ± 0.21 | 4.22 ± 0.24 | 2.84 ± 0.21 |

[1] From the Island Lake population, 1971.

taken from individual 67-2 over the season. Out of a sample of 263 songs from this individual, 44 of which were spectrographed, the slight inflection in the opening notes of the song illustrated from 20 July 1967 was the only observed departure from the basic pattern of rising initial notes that graded into a final trill of dropping pitch.

Since individual variation was slight, a sample of songs, averaging 3 per bird, was used for measurements to summarize population characteristics in song morphology (Table 1). The average song duration in the population was 2.65 sec, with an average of 22.72 notes per song. Maximum frequency was 4.22 kHz and minimum frequency was 2.84 kHz.

*Acceleration.*—One of the most obvious characteristics of Field Sparrow song is the progressive shortening, or "acceleration," of the notes in the song. To examine this aspect of the song, note and interval durations in the songs of the individuals in Table 1 were plotted as a function of successive order in
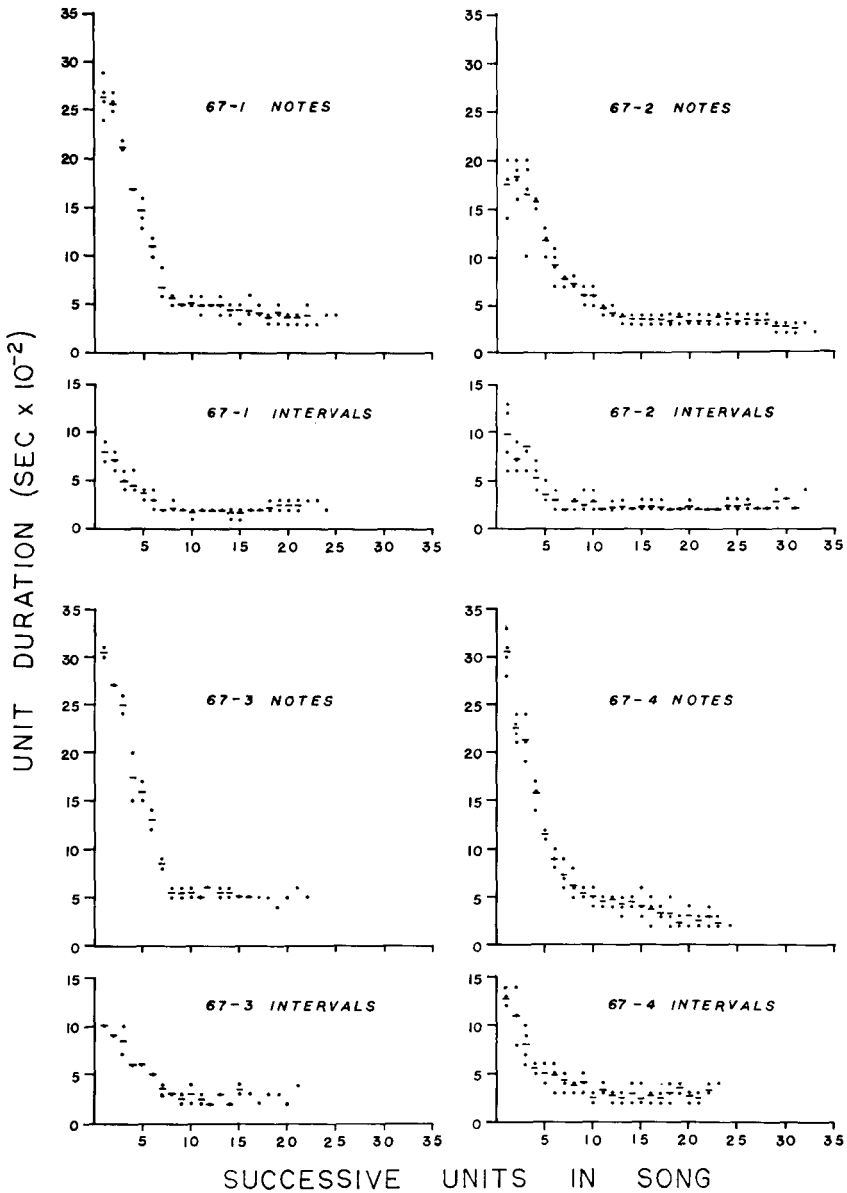
FIG. 4.   Duration of song units as a function of order of occurrence in the song. Dots represent individual data points; horizontal lines show the mean for each unit. Designation of songs the same as in Fig. 1.
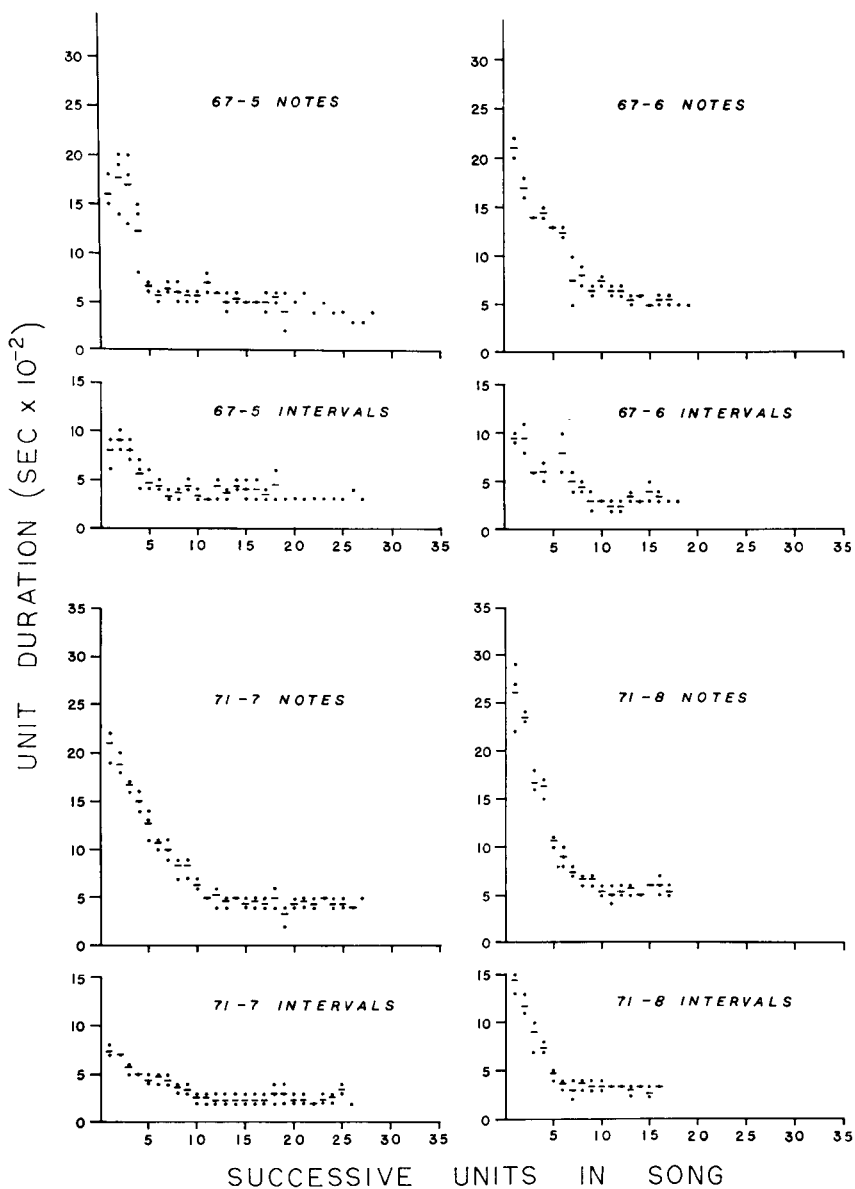
FIG. 5. Duration of song units as a function of order of occurrence in the song. Symbols the same as in Fig. 4 and designation of songs the same as in Fig. 2.

TABLE 2

ACCELERATION PATTERN IN THE NOTES AND INTERVALS OF FIELD SPARROW SONGS[1]

| Birds | Initial Shortening Rate | | Transition Point (%) | Final Shortening Rate of Notes[2] (sec/note) |
| | Notes[2] (sec/note) | Intervals[2] (sec/int.) | | |
|---|---|---|---|---|
| 67-1 | −2.69 | −0.83 | 40.9 | −0.04 |
| 67-2 | −1.40 | −0.60 | 46.7 | −0.13 |
| 67-3 | −3.71 | −0.94 | 42.1 | −0.04 |
| 67-4 | −3.88 | −1.95 | 39.1 | −0.21 |
| 67-5 | −3.00 | −1.13 | 23.8 | −0.08 |
| 67-6 | −1.81 | −0.72 | 50.0 | −0.15 |
| 71-7 | −1.60 | −0.52 | 42.3 | −0.05 |
| 71-8 | −3.40 | −2.13 | 52.9 | −0.15 |
| Overall: ($N = 8$) | | | | |
| x̄ | −2.69 | −1.10 | 42.2 | −0.11 |
| s | 0.98 | 0.61 | 8.8 | 0.06 |

[1] Rates estimated graphically from Figs. 4 and 5.
[2] Values x $10^{-2}$.

the song (Fig. 4 and 5). Several curvilinear transformations were attempted to fit regression lines to the observed patterns. It was found that the simplest, and perhaps most straight-forward, fit was obtained by plotting separate linear regression lines by eye through early and late portions of the curves.

All of the songs examined showed the same pattern of acceleration (Table 2). There was a rapid initial rate of shortening of the notes, averaging −2.69 ± 0.98 × $10^{-2}$ sec/note, to an inflection point midway in the song. At the inflection the rate of shortening decreased to an average of −0.11 ± 0.06 × $10^{-2}$ sec/note. The average inflection point for the transition in rate of shortening came after 42.2 ± 8.8% of the song was completed. The intervals between notes showed the same trends, with an initial shortening rate of −1.10 ± 0.61 × $10^{-2}$ sec/interval. Interval duration became virtually constant after the inflection point, which tended to be slightly earlier in the intervals than in the notes.

### CADENCES

*Individual variation.*—Table 3 summarizes the observed variations in cadence in the 1967 population at the Botanical Gardens. Analysis of variance indicated that there were significant differences in cadence among individuals in the population ($F = 6.32$, $P < .05$). The Student-Newman-Keuls test of Least Significant Range (Snedecor 1956) was used to test differences between individuals. Differences ($P < .05$) were found between the cadences of individuals 67-4 and 67-6, 67-3 and 67-6, and 67-5 and all others.

TABLE 3

INDIVIDUAL VARIATION IN CADENCES OF FIELD SPARROW SONGS

| Bird | Sample Size[1] (N) | Mean (sec) | SD |
|------|------|------|------|
| 67-1 | 5 | 12.47 | 2.41 |
| 67-2 | 16 | 11.86 | 1.87 |
| 67-3 | 10 | 13.80 | 1.39 |
| 67-4 | 7 | 13.42 | 1.55 |
| 67-5 | 3 | 17.63 | 7.62 |
| 67-6 | 9 | 9.99 | 0.88 |

[1] Number of bouts per individual.

*Seasonal changes and circumstances.*—Cadences from 1967 through 1970 were categorized in several ways to attempt to isolate the sources of the observed variation in the population. One possible source was the circumstance in which the bird was singing, i.e., if he was singing alone or if a neighboring bird was singing at the same time. Playback of recordings of an individual's own song was included as a third possible circumstance affecting singing rate, since differential response of an individual to his own song is one possible criterion for demonstrating individual recognition by song (e.g., Falls 1963, Hinde 1958).

Another source of variation might be the time in the breeding season. In fact, it would be reasonable to expect an increased singing rate assuming that most of the singers were unmated individuals and that one of the functions of singing is to advertise mating availability.

A 2-way comparison of seasonality and singing circumstances (Table 4) showed significant trends in cadences ($F = 3.39, P < .01$). Cadences were generally faster later in the season than earlier ($P < .01$). Comparing singing circumstances in this regard, cadences were significantly faster late in the season only when individuals were singing at the same time as a neighbor ($P < .02$); similar trends were seen when an individual was singing alone or after playback, but neither was significantly different between early and late in the season ($P > .20$ and $P > .60$, respectively). Differences were negligible between cadences of individuals singing alone and those that were singing at the same time as a neighbor ($t = 0.58, P > .50$). Birds singing in response to tape playback sang significantly faster than those singing alone ($t = 2.89, P < .01$) or at the same time as a neighbor ($t = 2.42, P < .05$).

*Response to neighbors.*—During field work, neighboring birds frequently were observed to sing at the same time. Often, one bird would start singing and nearby males would commence to sing shortly thereafter, so that onset of singing appeared to move as a sporadic wave across the study area. This

TABLE 4

CADENCES AS A FUNCTION OF TIME IN THE BREEDING SEASON
AND CIRCUMSTANCES OF SINGING

| Circumstances of Singing | Early in Season (April–May) $\bar{x} \pm s$ sec (N)[1] | Late in Season (June–July) $\bar{x} \pm s$ sec (N) |
|---|---|---|
| Singing alone | 15.51 ± 2.51 (15) | 13.80 ± 4.20 (13) |
| Singing when neighbors are | 15.60 ± 3.70 (17) | 13.86 ± 2.44 (16) |
| Singing after tape playback | 12.29 ± 2.95 (5) | 11.79 ± 1.78 (10) |

[1] N = Number of bouts in each category.

phenomenon suggested another possible source of cadence variation, that neighboring birds were singing in response to each other. Without definite knowledge of response latencies or memory capacities of Field Sparrows, it would be most parsimonious to expect response to neighbors to be on a song-for-song basis, rather than on a basis of bout-for-bout. If males were responding to neighbors in this way, one observable effect should be that at any given encounter, neighbors should have more similar cadences than non-neighbors. Data were not collected with this question in mind, but it was possible to approach the problem by comparing cadences of birds singing alone and at the same time as neighbors (Table 5). Responsiveness to a neighbor's singing appeared to be sensitive to the distance between individuals. Birds 67-5 and 67-6 had adjacent territories with a common boundary, and 67-5 showed a strong shift in cadences, from 21.9 sec when singing alone to 9.0 sec when singing at the same time as 67-6. There were also subtler shifts in the cadences of the adjacent individuals 67-1 and 67-3, so that cadences were more similar when singing at the same time. Individual 67-2 was also a neighbor of 67-1, but there was an area of about 100 m between their territories that was unoccupied by either bird. The changes in cadence did not appear to indicate that these neighboring, but non-adjacent, birds were singing in response to each other.

Another test of whether neighboring birds were answering each other was to assume that they were singing simultaneously but independently. On that assumption, one would expect that a song of one bird could occur anywhere in the time interval between successive songs of a neighbor who was singing at the same time. This model was tested by examining 11 instances from

TABLE 5

CADENCES WHEN SINGING ALONE AND AT THE SAME TIME AS A NEIGHBOR

| | Bird #1 | | | Bird #2 | | | Differences |
|---|---|---|---|---|---|---|---|
| | Mean[1] | SD | N[2] | Mean | SD | N | (Mean #1–Mean #2) |
| Bird #1 = 67-5 | | | | | | | |
| Bird #2 = 67-6 | | | | | | | |
| Alone | 21.9 | 13.1 | 18 | 9.8 | 1.7 | 42 | 12.11 |
| Together | 9.0 | 2.9 | 8 | 9.4 | 4.0 | 8 | 0.38 |
| Bird #1 = 67-1 | | | | | | | |
| Bird #2 = 67-3 | | | | | | | |
| Alone | 13.5 | 2.3 | 30 | 15.3 | 2.3 | 10 | 1.83 |
| Together | 14.5 | 5.0 | 13 | 13.2 | 3.7 | 14 | 1.33 |
| Bird #1 = 67-1 | | | | | | | |
| Bird #2 = 67-2 | | | | | | | |
| Alone | 13.5 | 2.3 | 30 | 11.1 | 1.6 | 36 | 2.39 |
| Together | 15.6 | 4.9 | 7 | 11.7 | 4.4 | 7 | 3.89 |

[1] Time in seconds.
[2] N = Number of cadences in bout.

1967 and 1970 in which cadences were recorded for an individual and his singing neighbor for at least 6 songs each; most commonly 7 to 9 cadences were measured for each. In each encounter, every time interval between successive songs of an individual was divided into 3 equal intervals, and the "answering" song of the neighbor was added as a count in one of the 3 intervals. This procedure was followed for every cadence interval in the song bout and for both birds in each encounter. In all instances, one bird seemed to be the initiator of the exchange and was observed at least to be the first singer in the encounter; the other seemed to be responding, or "following," so that separate tallies of songs were kept for initiating and following birds. This represents some *a priori* selection of data, but it does not seem directly related to the underlying assumption of the test, that a neighboring bird's songs should occur with equal probability in any of the 3 equal time intervals between songs if the birds are singing independently.

The tally over all such encounters resulted in strongly disproportionate distributions among the 3 time intervals. Among followers' songs, 39 were in the first, 30 in the second, and 9 in the third interval between initiators' songs ($\chi^2 = 18.24$, $P < .001$). For initiators' songs, 10 were in the first, 33 in the second, and 37 in the third interval between followers' songs ($\chi^2 = 16.96$, $P < .001$). Thus, the hypothesis for the model, that neighboring birds were singing independently, was rejected.

TABLE 6

CADENCE AS A FUNCTION OF TIME OF DAY

| Time | Sample Size (N)[1] | Mean (sec) | SD | V[2] |
|---|---|---|---|---|
| Before 08:00 | 10 | 14.42 | 1.14 | 8.0 |
| 08:00–09:00 | 19 | 14.69 | 2.84 | 19.3 |
| 09:00–10:00 | 22 | 12.38 | 3.04 | 24.6 |
| 10:00–11:00 | 12 | 14.32 | 3.88 | 27.1 |

[1] N= Number of bouts.
[2] $V$ = Coefficient of variation, $(SD/Mean) \times 100$.

*Time of day.*—A comparison of cadences according to time of day that they were observed (Table 6) showed no particular trends in average cadence, although the variability in the samples increased as the day progressed. Observations before 08:00 were significantly less variable ($F = 6.13$, $P < .01$) than observations later in the day.

*Matedness.*—Walkinshaw (1968) stated that mated Field Sparrows markedly reduce their singing. From early season records where matedness was specifically noted, I found unmated males to have a cadence of $16.09 \pm 2.33$ sec ($N = 10$) and mated birds a cadence of $16.17 \pm 4.87$ sec ($N = 7$). The rate of singing as measured by cadences, then, was about the same ($t = 0.04$, $P > .50$). However, the cadences of mated birds were much more variable ($F = 4.39$, $P < .05$), indicating, perhaps, less attentiveness to singing during a bout by mated males.

## DISCUSSION

Information about the manner in which messages are coded in communication signals has been obtained from experimental playback studies with altered song. Two studies have been outstanding in this regard, Emlen's (1972) work with Indigo Buntings (*Passerina cyanea*) and Falls's (1969) studies of White-throated Sparrows (*Zonotrichia albicollis*). They have generally confirmed earlier hypotheses of Marler (1959, 1960) that individual and species identification messages are coded in different parameters of the song.

Descriptive summaries of population characteristics of song, such as presented here, are a necessary prerequisite to experimental studies of message encoding. As such, they represent a first approximation to species specific characters of the song, providing an initial estimate of the limits of variation still recognized by the members of the population as a species specific signal. For instance, on the basis of the summary characteristics (Table 1), normal

Field Sparrow song is given between 2.8 kHz and 4.2 kHz with a duration between 2 and 3 sec. Progressive shortening of song units, or an "accelerating" tempo, appears to be a species specific characteristic. The rate of shortening does not appear to be critical, however, since it varied 3-fold (−1.4 to −3.9 × 10⁻² sec/note) within the population. Similarly, the number of notes varied 2-fold, between 16 and 33 notes, suggesting that this is not a critical factor in species identification.

The structure of Field Sparrow song is relatively simple, suggesting that experimental playback studies could profitably use electronically produced synthetic songs, after the manner of Falls (1963, 1969) with White-throated Sparrows. Goldman (1973) played synthetic songs to territorial male Field Sparrows, comparing songs with accelerating tempo to songs with notes of equal duration and tempo. Synthetic accelerating songs produced a weaker response than actual recorded songs; non-accelerating synthetic songs produced no measurable responses. Beyond confirming the general importance of accelerating tempo, the significance of Goldman's observations cannot be assessed without more information about the criteria used to construct the synthetic song.

Other questions about specific *vs.* individual identification messages must await experimental analysis. Particular questions include: (1) Is the shortening pattern, with an initially rapid rate and a later, slower rate, a necessary specific character? (2) How long does the song have to be—either in number of notes or in duration? (3) How much variation in frequency is permissible? (4) How does the tonal quality of the notes affect species recognition? The amount of redundancy, and how it might be coded, also remains to be found.

Singing cadences were remarkably stereotypic in Field Sparrows, remaining essentially unchanged under a variety of circumstances. Aside from a slight increase in rate as the season progressed, experimental manipulations were required to produce significant changes in cadence. Even mated males appear to conform to a species specific singing rate while singing, albeit more variably than unmated individuals.

Walkinshaw's (1968) observations on the reduction in singing by mated males appear to refer to changes in the overall daily rates of singing, due to fewer bouts of singing by mated birds. I have unpublished data on captive Field Sparrows that confirm Walkinshaw's observations; in captivity male Field Sparrows stop singing almost entirely upon pair formation. This raises the interesting possibility that the faster cadences observed late in the season were primarily from unmated males, although I have no confirming evidence.

Several criteria have been used to demonstrate individual recognition of songs. One criterion has been to show differential responses of territorial

males to the songs of neighbors and non-neighbors (Weeden and Falls 1959, Falls 1969, Emlen 1971). Goldman (1973) has shown that territorial male Field Sparrows respond more strongly to songs of non-neighbors than to those of neighbors.

Another criterion of individual recognition is based on differential response by a bird to his own song. Hinde (1958) found that Chaffinches (*Fringilla coelebs*) respond more strongly to songs resembling their own; and Falls (1963, 1969) has shown that Ovenbirds (*Seiurus aurocapillus*) and White-throated Sparrows tend to treat their own songs as unfamiliar, i.e., responses were intermediate between those given familiar songs and songs of a stranger. Data on cadences in the present study show differential responses to playback of a bird's own songs, confirming individual recognition by song in Field Sparrows.

## SUMMARY

Descriptions are given for variations in song morphology in a population of Field Sparrows and for variations in singing cadences in a variety of circumstances. Each male Field Sparrow had a single song-type that was distinctive within the study population. Intra-individual variation consisted of adding or omitting notes, without alteration of the basic song-type morphology. Accelerating tempo within the song, due to progressive shortening of the notes, was characteristic of all songs.

Cadences, i.e., the time interval between successive songs in a bout, varied 2-fold within the population. Cadences were shorter later in the season, but cadence rates were unaltered by time of day or matedness of the singer. Neighboring birds appear to sing in response to each other. Differential responses of individuals to taped playback of their own songs confirm individual recognition by song in Field Sparrows.

## ACKNOWLEDGMENTS

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