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Nicholas S. Thompson

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Departments of Biology and Psychology, Clark University, Worcester

Levels of Organization in the Song of the Bobolink (Icteridae: Dolichonyginae)

By ANKE BAKKER, KAREN WITHROW and NICHOLAS S. THOMPSON

With 2 figures

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Abstract and Summary

By comparison with other icterids, the bobolink (*Dolichonyx orizivorus*) sings an unusually long and complex song. The songs of four male bobolinks were analysed in terms of units at four different levels of analysis: the figure, the figure-sequence, the song-pattern, and the song. The different levels of analysis show different degrees of stereotypy and variation. Individual males in the study area differed in the frequency of use of the different song-patterns and in the way they assembled them into songs. Immediate repetition of song patterns within a song was unusual. Songs sung from fixed perches were shorter than songs sung in flight. The results suggest that the length of bobolink song is in part a consequence of its use of the song as a part of an elaborate flight display, and that the unit we called the "song-pattern" was closest to the unit designated "song" in most other species.

Introduction

In many respects, the bobolink appears to be an altogether typical North American blackbird (ORIANS and CHRISTMAN 1968). Like many of the other open country Icteridae, it is polygamous and dimorphic. Like them it has a variety of flight displays, perch displays and calls which it deploys in social situations (WITHROW 1980). The bobolink's song, however, seems to be strikingly different. Most blackbirds have songs which are short and simple. The song of the bobolink, on the other hand, is long and melodious and appears to consist of dozens of different notes strung together (AVERY and ORING 1977). Given all the similarities between the other blackbirds and the bobolink, the differences in the structure of their song are remarkable. In this context, the extraordinary complexity of bobolink song seemed a phenomenon worth investigating. This study was designed to elucidate the structure of bobolink song.

Method

More than 1000 complete songs from four territorial male bobolinks (*Dolichonyx oryzivorus*) were recorded through one breeding season in May and June, 1979. Recordings were made with a tripod-mounted AKG C451 E/CK9 shotgun microphone connected to a Sony portable reel-to-reel TC 800B recorder operated at 2.4 cm/s. Field observations were spoken simultaneously into the recorder as events occurred.

Study Area

The study area was a hayfield, 2.84 ha in area, located in the township of Barre, Massachusetts. A grid system was used to identify locations within the field with stakes placed at 20-m intervals to locate intersecting gradlines. Subjects were 6 male bobolinks identified by their frequent and exclusive use of one or more stakes in the grid (WITHROW 1980).

Song Analysis

Sound spectrograms were made of high quality recordings of each male's songs using a Kay Sonagraph set on the wide band and linear setting. The sound analysis was based on a song unit, the "figure", which was defined as the minimum temporally discrete unit of sound. Marks on the sound spectrograph 1 mm or less (= 0.008 s) apart were considered connected and were treated as a single figure.

A "figure-type" was defined as a morphological category of figures. Any two figures were recognized as being the same type if the figures were essentially identical in shape, frequency and duration. A catalogué of spectrograms of 66 figure-types was assembled and each type was assigned a number (BAKKER 1981). 40 to 70 different sound spectrograms of each territorial male were examined, figure by figure, comparing each with the types in the catalogue. Each song was then rendered for purposes of further analysis as a list of figures. The sequencing of figures in bobolink song was analyzed with the aid of sequence circles.

The sequence circle method was suggested by a similar diagram appearing in VERNER (1975). Like the VERNER diagram, the sequence circles are designed to make the song's organization apparent at a glance. The novelty of the sequence circles is that each song element type appears only once in the diagram and always in the same position, so that the circles make apparent the similarities and differences in complexity among individuals.

Each circle depicts the sequence of figures sung in a sample of 25 songs from one of the males in the study population. The circumference of a circle was divided equally into 66 positions and one of the figure-types was assigned to each position. The order of assignment was determined by the most frequent order of occurrence of the figures in the songs of the four birds collectively. Transitions between figure-types in the song of an individual were represented by connecting the two figure positions on the circle with a semi-circular loop. Where a transition violates the usual order of singing, the loops between figures will go anticlockwise. Such anticlockwise loops were indicated by arrows. Transitions greater than 7 figures on the circle were represented by straight lines, the number of arrowheads indicating the number of such transitions. Song beginnings are indicated by arrows pointing *toward* the sequence circle at the initial figure of the song; song terminations are indicated by arrows pointing *away* from the circle at the terminating figure.

Results

Description of Bobolink Song

The analysis confirms that bobolinks sing a long and complex song. The average duration of a song was 3.5 s, while individual songs were as long as 11 s or as short as 0.5 s. 66 different figure-types were sung by the birds in the

study population. Each figure was a complex sound consisting of 1 to 8 marks on the sonagram. Figures can vary rapidly in pitch, so that a wide frequency range was often covered by a single figure (Fig. 1). Figures ranged in pitch from 1.15 to 7.45 kHz excluding harmonics. Figures varied in duration from 0.02 to 0.40 s. The average figure length was 0.11 s. The duration of the intervals between the figures varied from 0.15 s to 0.21 s and averaged 0.07 s.

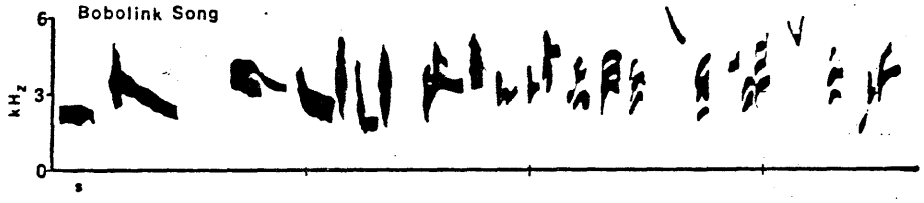


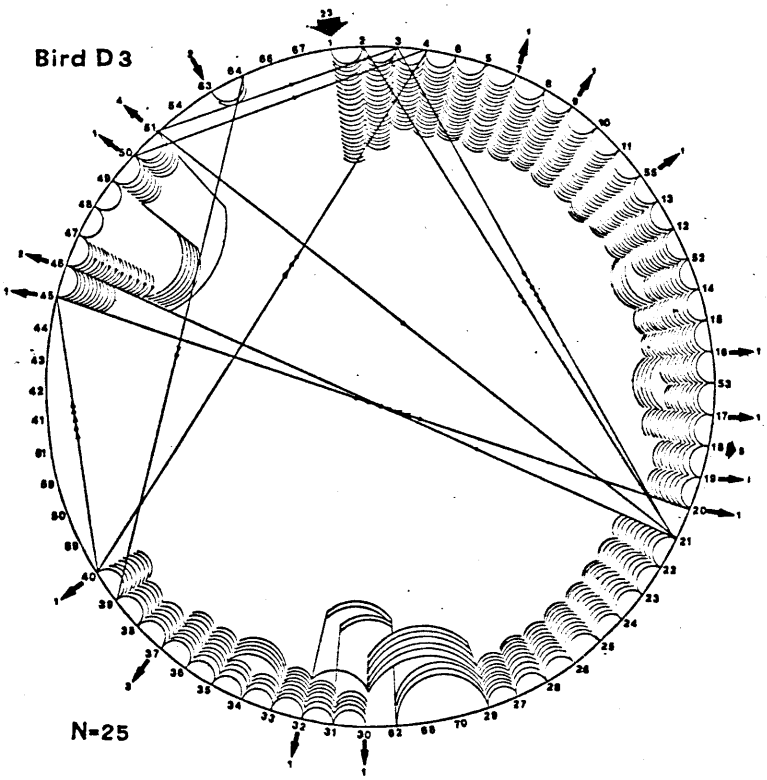
Fig. 1: A sample bobolink song. Each mark on the abscissa denotes 1 s

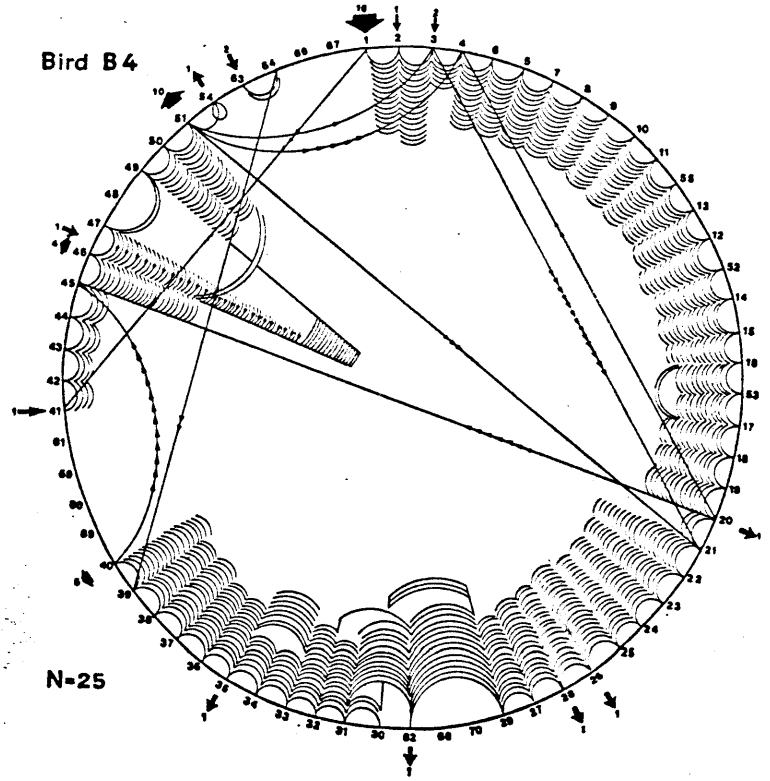
Bobolink song performances were found to be organized at three levels of analysis above the figure: the figure-sequence, the song-pattern and the song. The figures were used by the birds as building blocks to form *figure-sequences.* There were two kinds of figure-sequences: figure-chains and variable regions. Figure-chains varied in length from 1 to 20 figures; variable regions varied in length from 2 to 8 figures (Table 1, Fig. 2).

A *figure-chain* is defined as a particular sequence of figure-types distinguished by the fact that in almost every rendition of the sequence each figure was preceded by a figure of a particular type. For instance, in the figure-chain, 21, 22, 23, 24, 25, in all renditions by all 4 singers examined, the figure-type designated by the number 25 was always preceded by a figure of the type designated by the number 24 and type 24 as always preceded by type 23 and so forth (see the lower right of each circle in Fig. 2). The converse does not

Table 1: The figure-types contained in figure-sequences (figure-chains and variable regions) sung by the four territorial males

Designation in text	Figure-chains
4-20	4, 6, 5, 7, 8, 9, 10, 11, 55, 13, 12, 52, 14, 15, 16, 53, 17, 18, 19, 20
21-25	21, 22, 23, 24, 25
26-29	26, 28, 27, 29
32-38	32, 33, 34, 35, 36, 37, 38
41-44	41, 42, 43, 44
63-64	63, 64
66-67	66, 67
	Variable regions
1-3	1, 2, 3
(62 or 30) - 31	(62 or 30), 31
70-70	70, 68, 70
39-40	39, 60, 40
39-61	39, 69, 60, 59, 61, 61, 61
45-51	45, 46, 47, 46, 48, 49, 50, 51
54-60	54, 54, 60


Bird D3
N=25


Bird B4
N=25

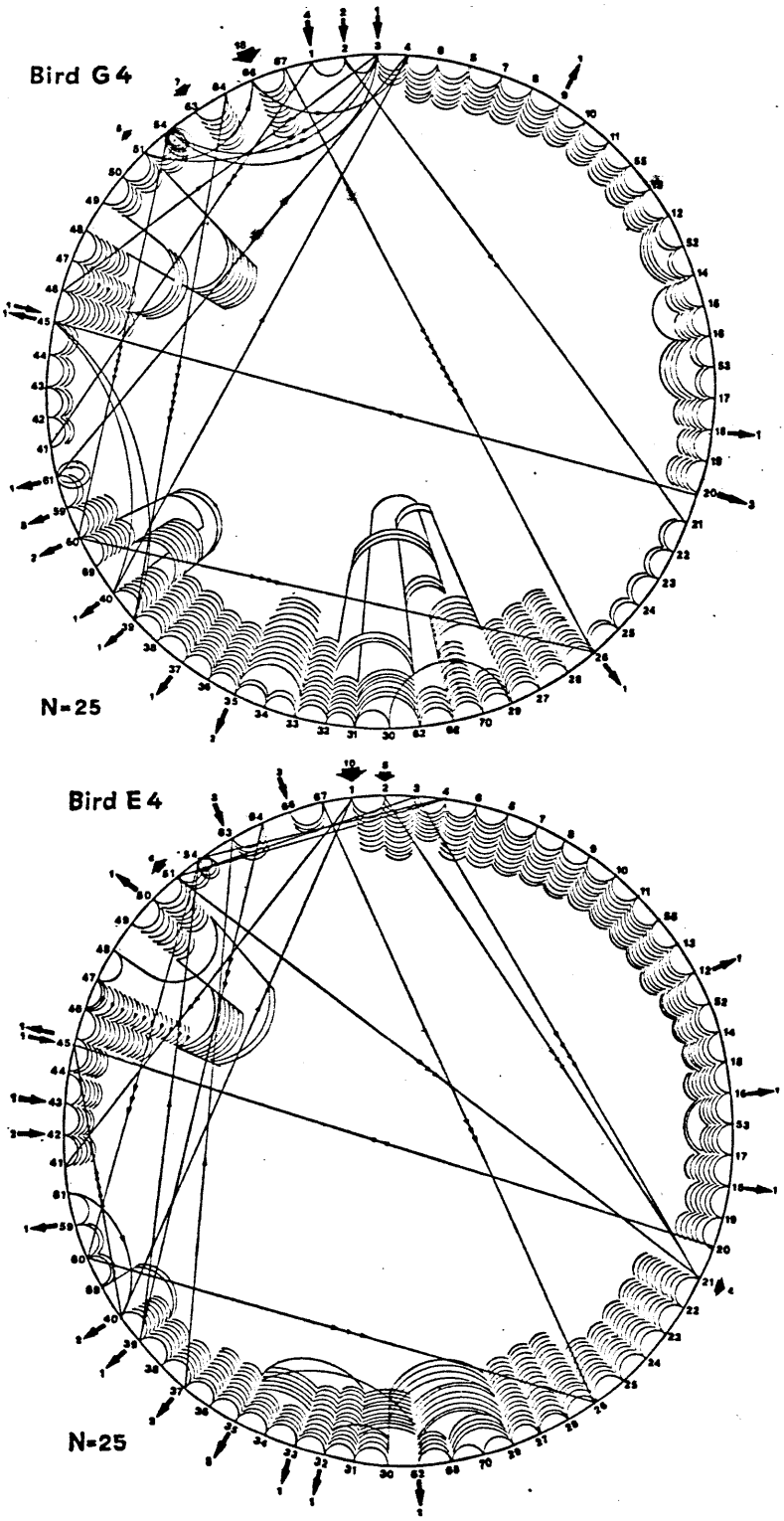


Fig. 2: Sequence circles: Each circle represents the transitions observed in a sample of 25 songs from a single bobolink, Bird D3, Bird B4, Bird G4, and Bird E4

apply; each type of the chain was not necessarily succeeded by the next type, since the chain could be broken off at any point. In such case however, the song itself was terminated and no other figure occurred in the succeeding place.

The preceding figure rule was applied normally to identify figure-chains with only one kind of exception: if a figure-type was missing from a chain, but the space ordinarily allocated for that figure was unoccupied and all other figure-types of the chain were in their usual positions, *then the chain was still considered to have been sung in its entirety*. For example, in figure-chain 4—20 the figure of the type designated number 52 appears between types 12 and 14 (see the upper right of each circle in Fig. 2). However, in several cases figure-type 52 was not apparent on the sonagram while the distance between figure 12 and 14 was the same as if figure 52 had been sung. In such instances the figure-chain 4—20 was considered to have been sung.

Variable regions consisted of less rigid sequences of figures (Fig. 2). Because their order varied they appear in Fig. 2 as regions of the circle where the line marking transitions are visually more congested: i.e., lines cross more often and the arcs intrude more toward the center of the circle. There were three possibilities of variation: (1) a figure or figures could be substituted as in variable region (62 or 30)—31; (2) a figure could be added or left out as in variable region *70—70* which was sometimes rendered 70—68—70 or (3) an individual figure could be repeated within the same sequence as in variable region *45—51*. Immediate repetitions were rare and occurred only at the end of a song. The variation within the variable regions in each of the different song-patterns were variations between birds with only occasionally a minor variation in the same bird.

Figure-chains and variable regions were strung together by the birds into longer units which were called *song-patterns* (Table 2). A song-pattern is built up of one or more figure-chains and/or one or more variable regions, in a precisely designated order. That is, the occurrence of a novel figure-sequence in a song-pattern or the occurrence of a novel order of sequences in a song-pattern required the designation of a new song-pattern. Thus, the same figure sequence could occur in different song-patterns (Table 2). As with figure-chains, the birds did not always sing a song-pattern all the way through, thus some songs consisted only of the first part of a song-pattern.

A *song* consisted of a continuous performance of one or more song-patterns preceded by an introduction. The introduction consisted of one or

Table 2: The figure-chains and variable regions (in italics) which comprised each of the five song-patterns

	Song-pattern
A	*2-3*, 4-20
B	*2-3*, 21-25, 26-29, *(62 or 30)-31*, 32-38, *39-40*
C	41-44, 45-51
D	26-29, *70-70*, *(62 or 30)-31*, 32-38, *39-61*
E	*39-40*, *45-51*, *54-60*

two figures sung only at the beginning of a song. Each introduction was associated with one or at most a few particular song-patterns. Note that a song-pattern is not always preceded by its introduction. When the song-pattern occurs in the middle of a song preceded by other song-patterns the introduction is usually omitted.

The length of a bobolink song varied from an introduction plus part of a variable region or figure-chain to several song-patterns strung together into longer songs. The length of the song depended on the behavior which accompanied the song. Songs sung from a perch were shorter than songs sung during flight. 78.7 % of flight songs consisted of more than one song-pattern, whereas only 15.8 % of perch songs exceeded one song pattern (Table 3).

Table 3: The number of long and short songs sung in flight and from perches

	In flight	From perches	Total
More than one song-pattern	54	14	68
One song-pattern	15	78	93
Total	69	92	161

Note: $\chi^2 = 61.67$, $df = 1$, $p \leq 0.001$.

Table 4: Number of renditions of each song-pattern attributed to each of the birds in the study population

Birds	Song-patterns A	B	C	D	E	Total
D3	61	56	46	0	2	165
B4	21	17	22	0	2	62
E4	15	14	12	8	8	57
G4	9	7	8	13	9	46
Total	106	94	88	21	21	330

Note: χ^2 (A vs. B vs. C vs. D + E) = 89.73, $df = 9$, $p < 0.001$.

A total of five different song-patterns, A—E, were recorded for the four territorial birds studied (Table 4). Each male had a song repertoire consisting of 4 or 5 song-patterns. Four of the 5 song-patterns were thus shared by all 4 males, while one song-pattern, song-pattern D, was shared by birds E4 and G4 but did not occur in the song repertoires of bird D3 and bird B4.

The frequency with which each bird sang each song-pattern differed among the 4 birds. For instance, bird D3 sang mostly song-patterns A, B, and C, while bird G4 emphasized song-patterns D and E.

The order of song-patterns within songs varied widely. All song-patterns with the exception of song-pattern E were sung both as first song-patterns and as subsequent song-patterns within the song. Song-pattern E was sung only in the first position. The song-patterns differed in the frequency with which they were sung in the various positions. Song-patterns A, B, D, and E were sung predominantly in the first position, whereas song-pattern C was sung about equally in first and subsequent positions (Table 5). The order of songs maximized the variety in song-patterns within a song. Table 6 illustrates

40 multi-pattern songs, listed by pattern-type. Note that among these 40 songs, a song-pattern in the first position is never followed by the same song-pattern in the second position. In fact, the only immediate repetitions of song patterns within a song occur at the ends of songs with more than three song patterns. Note also, that in 23 songs long enough to include three patterns, only once does the pattern in the third position constitute a repetition of the patterns in the first or second position.

Table 5: The positions in which the birds placed song-patterns in songs

	Song-patterns					
	A	B	C	D	E	Total
First position	78	68	41	20	21	228
Subsequent positions	28	26	47	1	0	112
Total	106	94	88	21	21	330

Note: $\chi^2 = 38.44$, $df = 4$, $p < 0.001$.

Table 6: Examples of 40 sequences of song-patterns in bobolink songs

Bird D3	Bird B4	Bird E4	Bird G4
BAC	ACBA	ACB	AC
AC	BC	ACBC	ACDA
BCAC	AC	CA	CA
AC	ACBA	BCA	CBB
BAC	ACB	CAB	CBA
ACB	BCAAB	CB	EB
BACB	BCAA	CB	BCA
ACBA	ACB	DC	BCAB
AC	BCA	CB	EB
BCABAC	AC	CB	EB

Discussion

The song of the bobolink is striking for its multilevel hierarchical structure. The song is composed of units that are assembled in successively higher and higher levels of organization. At the lowest level of organization is the figure, which is a discrete repeatable sound. A figure may sometimes be organized into precisely repeated chains but also sometimes they occur in variable regions where one figure may be substituted for another. Even though there is variability at the level of the figure, song-patterns can be described as particular sequences of figure-chains and variable regions. Songs, in turn, are built up of different song-patterns strung together in various ways. The organization of the performance is most flexible at the level of the song since the song-patterns in the song do not follow a rigid order.

The great complexity of bobolink song is anomalous. Among songbirds, these performances are unusual for the length of their repeatable units. Many birds perform songs which are as complex and long as bobolinks, but few bird songs are composed of precisely repeated complex units as long as the figure

chains of bobolink song. Figure chain 4—20, including pauses, was almost 4 s long when sung in its entirety. The bobolink's song is more similar to the songs of certain wren species studied by VERNER (1975) and KROODSMA (1980), that it is to the songs of any other blackbird. No other icterid has a song which approaches the bobolink song in complexity and length, despite the fact that many Icterids are similar to bobolinks in a great many respects. The bobolink's behavior repertoire corresponds in a great many particulars with that of the other open country blackbirds (ORIANS and CHRISTMAN 1968; WITHROW 1980). Only the song is strikingly aberrant. The contrast in the length and complexity of the song is especially striking with the redwing blackbirds, because of the large area of sympatry between the two species and their habit of nesting on neighboring or even overlapping territories. Bobolinks are different from redwings in having a long migration, a short breeding season, and a habitat with relatively few prominent perches. Any or all of these differences in the bobolink's natural history may account for its elaboration of a complex song.

KROODSMA (pers. comm.) has suggested a way of looking at bobolink song which doesn't diminish its remarkableness within blackbird vocalizations but which helps considerably to fit it within the context of the vocalizations of other songbirds. He suggests simply that what we and other bobolink researchers have called a song pattern is equivalent to what is called a song in many other songbirds. Song usually refers to a temporally discrete unit of sound, and we were not led to call the song patterns songs because they were often performed without any break between them. Hence, we used the term song to refer to a chain of song patterns separated in time from other chains of song patterns. While terminologically correct, this practice may obscure important similarities between the "song patterns" of bobolinks and the "songs" of other species. Like the songs of other oscines, the bobolink's song patterns are composed of elements which are both shared with other neighboring males (figure chains) and elements which are more or less distinct to the singer (variable regions). Comparison of our sonagrams with those of other authors suggests that these song elements like those of many species are given to geographic variation, as well. Finally, like the songs of many species (HARTSHORNE 1973), bobolink song patterns are sung together in a manner which emphasizes their distinctness. That is, each bird rarely follows a song pattern immediately with the performance of the same song pattern.

This terminological adjustment in turn raises the question why bobolinks should on some occasions string their songs together without pause. The answer may lie in the fact that the bobolink's song is often a flight song. A perched bird, not engaged in an elaborate display may alternate his songs with periods of listening, looking for predators, or in some cases even, feeding. The organization of a bobolink's song, however, may be dictated by the requirements of the performance of which the song is a part. Our data provide some support for this notion — as does the data of WITTENBERGER (1982) — because it shows that songs sung in flight usually contain more than one song pattern in tandem, songs sung from perches usually contain one song pattern or less. Thus, the long, continuous song performances of the bobolink appear to be an adapta-

tion to the performance of flight displays. These, in turn, seem particularly well suited to the comparatively open and perchless habitat in which the bird breeds.

Zusammenfassung

Dolichonyx orizivorus hat einen für Stärlinge ungewöhnlich langen und komplexen Gesang (song). Er besteht aus Strophen (song-pattern), die aus Folgen (figure-sequence) einzelner Elemente (figure) aufgebaut sind. Variation und Stereotypie sind auf diesen vier Ebenen ganz verschieden. Jedes der untersuchten Männchen benutzte die verschiedenen Strophen verschieden oft und setzte sie zu eigenen Gesängen zusammen. Unmittelbare Wiederholungen von Strophen sind selten. Von einer Warte vorgetragene Gesänge sind kürzer als im Flug vorgetragene. Die Länge des Gesanges scheint damit zusammenzuhängen, daß Gesang ein Teil der Flugbalz ist. Was hier „Strophe" heißt, entspricht dem „Gesang" der meisten anderen Arten.

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Authors' addresses: N. S. THOMPSON, Rm 322 Jonas Clark Hall, Clark University, Worcester, Massachusetts 01610, U.S.A.; A. BAKKER, 31 Hudson Street, Worcester, Massachusetts 01609, U.S.A.; K. WITHROW, P. O. Box 753, Estacada, Oregon 97023, U.S.A.