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DISPLAY BEHAVIOR OF OVENBIRDS (*SEIURUS AUROCAPILLUS*) II. SONG VARIATION AND SINGING BEHAVIOR

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Song of the Ovenbird (*Seiurus aurocapillus*) is a characteristic sound of late spring and early summer in woodlands over much of North America. John Burroughs (1871) first used the onomatopoeic phrase teacher to describe its apparently double-syllabled phrases, characterizing it as a series of repetitions of this phrase, beginning softly and building in a crescendo. Although the Ovenbird was the subject of an intensive life-history study (Hann 1937) and of experimental investigations of song recognition (Weeden and Falls 1959, Falls 1963), there has been no detailed examination of song variation within local populations, or of the role of song in behavioral interactions.

In addition, the Ovenbird has a second song, often referred to as the "flight song," heard far less frequently than the normal teacher song. Many authors have commented on this display (Burroughs 1871, Gibbs 1885, Wright 1913, Allen 1919, Hann 1937, Kendeigh 1945), but it has not been described carefully on the basis of tape recordings and its significance has been largely a matter of speculation.

I previously have described the nature and use of non-song vocalizations of breeding Ovenbirds (Lein 1980). This paper describes the song variation of local populations, and documents singing behavior in detail.

METHODS

The study areas and methods are described in a previous paper (Lein 1980) and are summarized only briefly here. Fieldwork was conducted in 1970, 1971 and 1972 in Bedford, Middlesex Co., Massachusetts and in South Lyndeboro, Hillsboro Co., New Hampshire. The habitat consisted of second-growth mixed forest in both areas.

Detailed behavioral observations were made on 5–10 pairs of Ovenbirds each season, including 9 individually color-banded males. More casual observations were made on numerous other males. Individual males are identified by a 2-letter species designation (OB), plus a suffix designating the individual (OB-A, OB-B, etc.). Behavior was recorded on a cassette recorder and subsequently transcribed for analysis. Short-term singing rates (songs per min) were calculated from the time required for a bird to sing 10 complete songs, and were normally made only during regular singing not interrupted by other activity. Long-term singing rates (songs per h) during different phases of the breeding cycle were calculated from the number of songs males sang during entire observation periods. High-fidelity recordings of songs for audiospectrographic analysis were made with a Nagra IIIB tape recorder and a Norelco D-119ES cardioid dynamic microphone and analysed with a Kay Elemetrics 6061B audiospectrograph. Because of background noise and echos in recordings, I use trac-

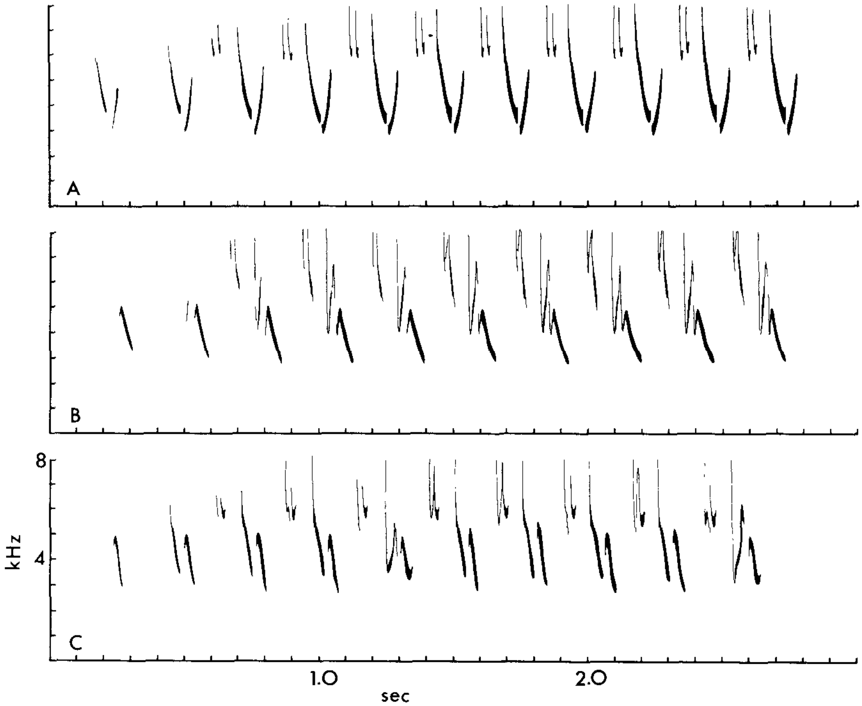

FIG. 1. Complete "primary songs" of male Ovenbirds: (A) song of OB-A; (B) song of OB-C; (C) song of an unbanded male. Note that the fifth and tenth phrases differ from the others; only 5 songs by this male, out of all songs recorded in this study, showed this phenomenon.

ings for illustration, rather than the actual sonagrams themselves. Terms describing the structure of the songs are used in the manner proposed by Shiovitz (1975).

RESULTS

Song variation

Male Ovenbirds have 2 vocalizations referred to as song: the normal "primary" or "territorial song" (Thorpe 1961), and the song referred to in the literature as the "flight song." This latter name is inappropriate because the vocalization is often given when the bird is not in flight. Therefore, I refer to this song as "attenuated song" and restrict the term "flight song" to those performed during a stereotyped aerial display (see below).

Primary Song

Description.—The "primary song" consists of a series of repetitions of a single phrase (Fig. 1A, B). Each phrase consists of 3–5 separate notes.

Most notes sweep rapidly downward in frequency with a concentration of energy between 3.0 and 5.0 kHz. The highest-pitched notes start at about 9.0 kHz and some notes may fall as low as 2.5 kHz. The phrases range in duration from 0.16–0.25 sec in different birds. The phrase is usually repeated from 8–13 times in complete songs. Songs longer than 14 phrases were heard only rarely, although once a song of 26 phrases was recorded. The phrases are separated by silent periods of about 0.05–0.1 sec. Complete songs vary in length from about 2.5–4.0 sec. Songs of an individual can vary considerably in length, however, depending on how many repetitions of the phrase are involved.

Although the first phrase of a song may be separated from the second by an interval longer than those occurring later in the song, the rate of delivery is usually constant after the second phrase. However, the amplitude increases for at least the first 5 or 6 phrases, producing the crescendo effect. The song is harsh and certainly could not be called musical, but it is delivered at such a loud volume that it carries long distances in the woods.

Intra-individual variation.—Each male Ovenbird sings a single phrase type. I recorded songs of 15 males repeatedly during this study (some over several years), and approximately 30 other males were recorded less regularly. Only once did a male sing more than 1 phrase pattern. On 24 May 1971, an unbanded male at Bedford sang 5 songs which included 1 or 2 phrases of a type other than the predominant one (Fig. 1C). This occurred about 5 min after a territorial encounter on the first day that the male was on territory. The significance of these circumstances is uncertain. All other songs of this male consisted of a single phrase type.

Complete songs of individuals showed minor variation in the number of phrases. For example, during 4 bouts of singing on 28 May 1971, OB-I sang 82 songs. These included songs with the following numbers of phrases: 7 phrases—1 song; 8 phrases—11 songs; 9 phrases—56 songs; 10 phrases—14 songs. Such variation was typical of all males, although the modal song length differed between birds.

Incomplete songs (arbitrarily defined as songs of less than 8 phrases) and muted songs were sung in a variety of situations described and analyzed in detail below. By definition, incomplete songs can vary from 1–7 phrases in length, but songs of 4 or 5 phrases predominated. Muted songs were delivered at a much lower volume than normal. Most incomplete songs are also muted since they are not long enough to develop the crescendo.

Inter-individual variation.—There is much inter-individual variation in the form of the phrases (Fig. 2). I did not attempt to sample all males over wide areas, but the samples from both Bedford (Fig. 2A-L) and South

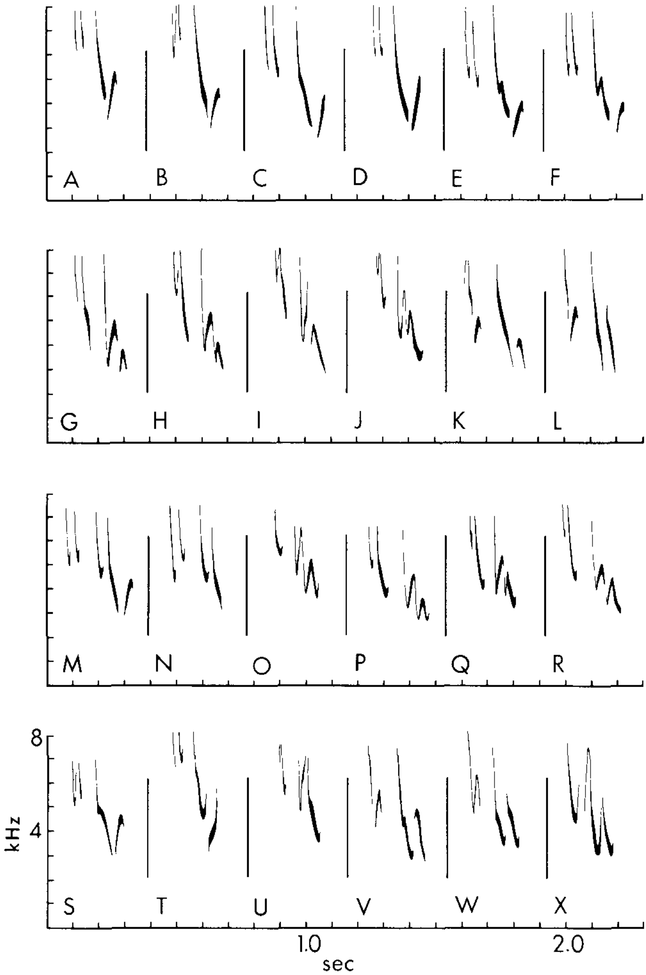

FIG. 2. Individual phrases from the "primary songs" of male Ovenbirds: (A–L) phrases from the songs of 12 males recorded at Bedford, Massachusetts; (M–X) phrases from the songs of 12 males recorded at South Lyndeboro, New Hampshire.

Lyndeboro (Fig. 2M-X) probably indicate the extent of variation within local populations.

In some cases, aural recognition of individuals was possible on the basis of the rate of delivery of the phrases or the quality of the phrases themselves. For example, OB-G (Fig. 2J) sang a recognizably more rapid song than did his neighbors. Similarly, OB-I's song (Fig. 2L) was distinguishable to the ear by the squeaky quality of the phrases. Such aural discrimination could be made with certainty only for individuals with extremes of variation in these song characters.

The situation differs for audiospectrographic analysis. With a recording of reasonable quality I could always identify the singer by comparison with sonagrams of known individuals, even with males sharing a similar phrase structure and whose songs could not be distinguished reliably by ear. For example, OB-D (Fig. 2F) and OB-F (Fig. 2E) occupied neighboring territories. Their song phrases are very similar, but are characterized by a number of minor differences. The first 2 notes of OB-F's phrase terminate at a lower frequency than those of OB-D. The down-up-down inflection of the third note is more pronounced in OB-D's phrase. Finally, the terminal note of OB-F's phrase begins at a lower frequency than that of OB-D. Repeated recordings of these color-banded males established that these minor differences were constant and could be used to identify them. Similar consistent differences exist for other pairs of males with similar phrases (see OB-K and OB-J, Fig. 2Q, R).

Attenuated song

Description.—"Attenuated song" is a highly variable vocalization. Characteristically it is introduced by a series of *whink* notes and a *ple-bleep* vocalization (for a description of these calls see Lein 1980). Several normal song phrases occur immediately or shortly after the *ple-bleep.* This initial part of the song is followed by a rambling succession of other notes, many possessing a large amount of gradual frequency modulation (see Figs. 3 and 4). This "rambling" section of the song includes 1 or more *chip* notes and, in some examples, additional "primary song" phrases or *ple-bleep* notes. "Attenuated songs" are variable in length, ranging from 4–7 sec.

"Attenuated song" is frequently given as part of an aerial display, variously referred to as "love-song" (Burroughs 1871, Gross 1953), "passion song" (Jones 1900) and most frequently "flight song" (Chapman 1907, Hann 1937, Saunders 1951, Gross 1953, Gunn and Borror 1957). I use the last term to avoid the subjective implication of motivation.

"Flight song" was heard frequently and was recorded on a number of occasions. Because it was given irregularly, and most commonly at twilight, the performance was rarely seen. The male was initially perched in a tree, usually at the height of the subcanopy. The male gave a series of "soft sip" calls (Lein 1980) while perched. The rate of delivery of these calls accelerated until the bird took flight and climbed to 3–15 m above the treetops. He then flew in a hovering flight with spread wings and tail while delivering the song. The flight appeared labored and the bird sometimes circled as it sang. Immediately upon completion of the song the bird dropped back into the woods.

"Attenuated song" was also frequently given by perched males during encounters with conspecifics. While the songs in such situations were often incomplete, they were frequently as long as those of the "flight song" display, and match the latter in form (Fig. 4B).

Intra-individual variation.—The "attenuated songs" of individuals vary within the constraints of the above description. In several cases, "flight songs" of the same individual recorded on different dates can be matched note by note throughout their entire length, indicating that there is some stereotypy in the form of the song. However, other examples of "flight songs" of the same male show differences in the rambling terminal portion, including variation in the ordering of the elements, repetition of some elements, or inclusion of a second series of phrases from "primary song" (Fig. 3A, B).

Inter-individual variation.—"Attenuated song" always includes 2 individually-distinctive elements: the *ple-bleep* vocalization (Lein 1980) and the "primary song" phrases. It is perhaps significant that both these elements occur together during the more stereotyped initial portion of the display. The terminal part of the song is more variable both within and between birds, but has the same quality and form in different males and there is much overlap in elements between birds (Figs. 3, 4).

Singing behavior

Primary song

General pattern of singing.—Singing is almost the only feature of Ovenbird biology that uses the vertical aspects of the territories. The Ovenbird is a ground-nesting, ground-foraging species and seldom perches in trees, except when singing or when alarmed. Prior to female arrival, undisturbed males sing regularly while sitting still on perches near the bottom of the canopy. Bouts of singing range from 1 or 2 to more than 20 min in length. The mean height (estimated within 1 m) of 95 Ovenbird song perches was 8.8 m (SE = ±0.23 m, range = 1.8–15.2 m), while the mean height of the trees in which they were perched was 15.5 m (SE = ±0.42 m, range = 3.0–24.5 m). Bouts of song are interspersed with bouts of feeding on the ground, during which males are silent, or sing very sporadically. Males feeding on the forest floor frequently would hop or flit up to a rock, stump or twig before singing one of these sporadic "ground" songs; then they would hop down and continue foraging. Several reasons may be suggested for the obvious reluctance of males to sing from the ground. First, singing

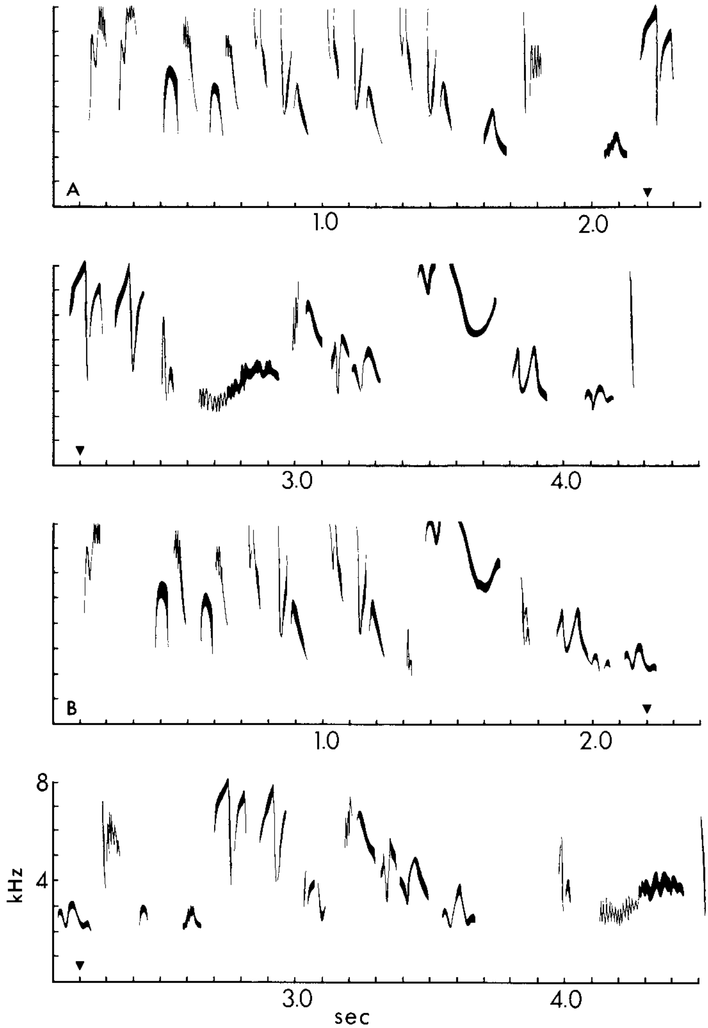

FIG. 3. "Attenuated songs" of male Ovenbirds, because of their length, have been broken for the illustrations. The solid triangles on the time axis indicate the point of overlap of the upper and lower portions of each song. (A–B) "Flight songs" of OB-C. Note the similar introduction of the 2 examples, consisting in A, of 2 *whink* calls, 1 *ple-bleep* call and 3 "primary song" phrases. Also note the occurrence of the same elements in different sequences in the terminal parts of the 2 examples.

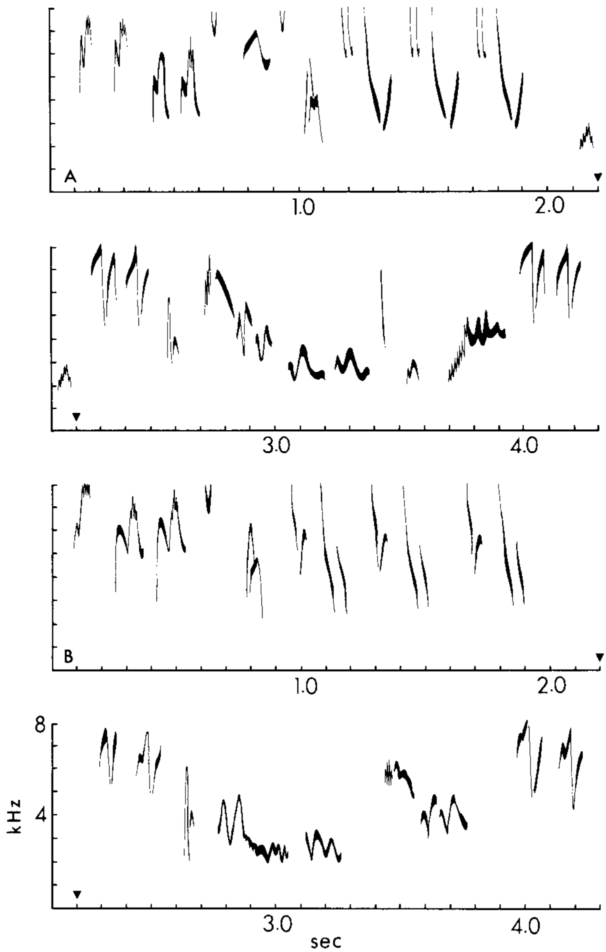

FIG. 4. "Attenuated Songs" of male Ovenbirds, because of their length, have been broken for the illustrations. ▼ on the time axis indicate the point of overlap of the upper and lower portions of each song. (A) "Flight song" of OB-A. Note the similarity of the elements to those of the "flight songs" of OB-C, shown in Fig. 3. (B) "Attenuated song" of OB-I given from the ground. Note the similarity in form to the "flight songs" illustrated in Fig. 3 and Fig. 4A.

on the ground may attract predators to an inconspicuously colored bird on the forest floor. Second, songs delivered from the ground may not carry well because of ground attenuation and interference by dense vegetation with sound transmission (Wiley and Richards 1978). Song perches are at a level of the vegetation profile which has an open structure, consisting

TABLE 1

SONG RATES OF MALE OVENBIRDS DURING STEADY SINGING IN RELATION TO OTHER FEATURES OF THE SITUATION[a]

Situation	Mean song rate[b] (songs/min ± SE)	Range (songs/min)	No. observations
Steady singing with no disturbance	3.20 ± 0.06	1.09–4.44	73
Steady singing with preening activity	2.80 ± 0.11	2.20–3.33	16
Counter-singing with another male	3.71 ± 0.12	2.98–4.41	12
Rapid singing in first morning bout[c]	4.24 ± 0.33	2.51–5.40	8
Rapid singing during territorial encounters[c]	6.36 ± 0.93	4.05–10.34	6

[a] Short-term song rates were calculated from the times required for 10-song intervals.

[b] Song rates differ significantly between situations (Model 1 one-way ANOVA, $P < 0.001$); rate for steady singing with no disturbance differs significantly from those for the other situations (Student-Newman-Keuls multiple range test, $P < 0.05$).

[c] Both these situations involve many incomplete and/or muted songs.

only of trunks and dead branches, with very few leaves and little shrubbery.

During the bouts of steady singing, Ovenbirds sing at a rate of about 3 or 4 songs per min (Table 1). Several features of the external situation influence the song rate. Bouts of intense preening activity result in a slightly slower rate, while several other factors, such as counter-singing with another male, increase the song rate (Table 1). In 2 situations in particular, during bouts of song at dawn, and during mild territorial encounters (and at the beginning and ending of more intense encounters), Ovenbirds may sing very rapidly. The highest rate recorded, 10.34 songs per min, occurred in such an encounter. However, in both of these situations, most of the songs given were incomplete and many were muted.

Counter-singing (Armstrong 1963) was noted frequently. Two neighboring males would sing in phase, the songs of 1 male following immediately after, or overlapping with, the songs of the leading male. Several facts suggest that this is not merely the fortuitous result of 2 males singing at approximately the same rate. First, the singing rate of such birds was higher than during normal singing (Table 1). Second, the relationship of "song a—song b—pause—song a—song b—pause . . ." could continue for 30–40 songs. When the relationship changed it was not due to the 2 birds drifting out of phase, as would be expected if it were fortuitous, but in many instances by the "b" bird not "waiting" for "song a," but rather singing his own song toward the end of the pause. In such cases, the birds would sometimes continue to counter-sing with the lead reversed. This demonstrates that the males are "paying attention" to the songs of neighboring males and responding to them, even at a considerable distance.

TABLE 2

LONG-TERM SINGING RATES OF MALE OVENBIRDS IN RELATION TO THE PHASE OF THE BREEDING CYCLE

Phase in cycle	No. observations[a]	Singing rate[b] (songs/h ± SE)	Observation time (min)
Unmated	21	139.4 ± 9.7	633
Courtship period	18	65.9 ± 10.2	692
Incubation period	13	85.4 ± 12.6	456
Nestling period	9	87.9 ± 13.7	299
Fledgling period and later	8	26.9 ± 5.8	296

[a] All observations during morning activity period.

[b] Singing rates differ significantly between phases of the breeding cycle (Model 1 one-way ANOVA, $P < 0.001$); rates for unmated and fledgling periods differ from those of other periods (Student-Newman-Keuls multiple range test, $P < 0.05$); rates for courtship, incubation and nestling period do not differ significantly.

Daily pattern of singing.—The effects of daily activity rhythms on singing behavior have been well-described (Thorpe 1961, Armstrong 1963). As in other birds, Ovenbirds show an activity peak in early morning and a second, smaller peak in the evening. The morning peak is more pronounced early in the breeding season, when the birds are very active until noon. Later in the season strong singing becomes more restricted to early hours. Extremely hot or cold weather inhibits singing, as does heavy rain. Early in the season, however, birds sing strongly during light rain.

Many workers have shown that the beginning of song at dawn, and to a lesser extent its cessation at dusk, is closely correlated with the light intensity (Armstrong 1963). The times of first songs of Ovenbirds gradually became earlier until the longest days of June, then became later as the summer progressed. A comparable relationship in the time of the last song of the evening was also noted.

Light intensity appears to influence singing in other ways as well. The songs at the beginning of the initial bouts of the morning were characteristically incomplete and/or muted. This was also true of late evening singing. Light level is also important in determining the occurrence of "flight song" (see below).

Seasonal pattern of singing.—A seasonal decline in singing is known for many species (Thorpe 1961, Armstrong 1963). Many studies have demonstrated that the long-term singing rates of a male bird are related not to the calendar date per se, but rather to the stage of the breeding cycle (see summary in Armstrong 1963:152–156). Since the breeding cycles of individual males are usually out of phase with one another, studies which report only population averages in relation to calendar date may miss important and abrupt changes.

The long-term singing rates of male Ovenbirds at various phases in the nesting cycle are shown in Table 2. All figures are based on observations made during the morning activity period (04:30–10:00 EDT). Unmated males sing an average of 139.4 songs per h. If they were singing at the mean rate calculated for undisturbed birds, 3.2 songs per min (Table 1), this would represent steady singing for about 75% of the time.

Upon arrival of females, however, singing rate drops significantly to 65.9 songs per h, a decrease of over 50%. The decline is related to the male's close association with the female at this time. During such activity he sings only sporadically and many of the songs are incomplete or muted, a feature rarely observed prior to female arrival.

Once incubation begins, the singing rate may increase slightly, but it never regains the level reached prior to mating. Song bouts are much more irregular during incubation and feeding of young. By early July regular singing is heard only for a short period at dawn.

Incomplete song.—The situations in which incomplete songs were used range from the occurrence of 1 or 2 incomplete songs during bouts of regular singing, to periods of up to 1 h when a male sang incomplete songs repeatedly while moving with his mate (Table 3). Half the observations involved association of paired males and females. Most of these were during courtship; contact between mates during the incubation or nestling periods is similar to that during courtship, although much less frequent or prolonged. Males used incomplete songs when at intermediate distances from their mates. When within 7 m or less of females, males rarely sang at all (with the exception of "attenuated song," see below). When more than 25–30 m from their mates, males usually sang full songs. Males changed from incomplete to full song (11 cases) as they moved away from their mates. Switching from full to incomplete song (7 cases), and from incomplete song to silence (9 cases), occurred as mates moved closer together. Males gave incomplete songs on 4 occasions in association with chases of their mates.

Incomplete songs were a regular feature of territorial encounters between males. Males gave incomplete songs at either a normal or a reduced and irregular rate during male-female interactions; during male-male encounters there frequently was an elevated rate of singing (Table 1). In some encounters, males sang incomplete songs almost continuously, with very short pauses between them. Incomplete songs were not used during intense interactions involving vigorous or prolonged chasing; these were characterized by silence or by the use of non-song vocalizations such as *chep, whink, ple-bleep* and *pink* (Lein 1980). Incomplete song was used during mild encounters, or at the beginning or end of encounters, or during pauses between bouts of active chasing.

TABLE 3
SUMMARY OF SITUATIONS IN WHICH MALE OVENBIRDS USED INCOMPLETE SONGS

Situation	No. cases	
	Major category	Subcategory[a]
Male-female interactions	49	
During association		49
During male-female chasing		4
Male-male interactions	15	
During territorial encounter		14
During male-male chasing		3
Response to approach of male		2
At territorial boundary		1
Non-encounter situations	34	
During dawn or dusk singing		27
While carrying food to young		2
During vigorous preening		3
At end of singing bout		2
Total	98	

[a] Total for subcategories may be greater than number of cases in major category since 1 observation may fall into several subcategories.

Birds also switched from full to incomplete songs in other circumstances. Several times a male began to sing incomplete songs when a neighbor, who had been silent or singing at a distance, suddenly approached the mutual territory boundary. Encounters did not ensue in these instances and the males resumed singing full songs when they separated. Once, a male switched to incomplete song when he moved near a known territorial boundary. The neighbor was not singing at the time although I had previously observed several territorial encounters in the same area. The bird resumed full song again when he moved away from the boundary.

Incomplete song was noted on 34 occasions not involving interactions. Twenty-seven cases occurred during the first bouts of song in the morning or during late evening singing. In view of the influence of light level on the onset or cessation of daily song, it is not surprising that the birds should show a transition from silence to incomplete song to full song during the morning twilight, or vice versa in the evening. An important difference was that the morning performance usually involved incomplete songs given very rapidly and regularly (Table 1), whereas the singing in the evening was typically slow and sporadic.

Other non-encounter circumstances in which incomplete song was used suggest that they were correlated with a conflict between a tendency to

TABLE 4
SUMMARY OF SITUATIONS IN WHICH MALE OVENBIRDS USED MUTED SONGS

Situation	No. cases	
	Major category	Subcategory[a]
Male-female interactions	19	
During association		19
During male-female chasing		2
Male-male interactions	10	
During territorial encounter		8
At territorial boundary		2
Non-encounter situations	4	
During dawn singing		2
While carrying food to young		1
Response to playback of song		1
Total	33	

[a] Total for subcategories may be greater than number of cases in major category since 1 observation may fall into several subcategories.

sing and a tendency to carry out some other activity. In 3 cases, males sang incomplete songs during vigorous preening while on a song perch; when the preening ceased, full song was resumed. Twice incomplete songs came at the end of a bout of full songs, just before the male ceased singing and began to forage. In 2 other instances, a male sang incomplete songs while foraging and carrying food to its young. Males were typically silent during this activity.

Muted songs.—Incomplete songs frequently sound muted, but since normal songs increase in volume for the first 4 or 5 phrases it is impossible to determine this with certainty. Therefore, only songs of 5 or more phrases are considered here. The situations in which muted songs were recorded (Table 4) are similar to those in which incomplete songs were employed (Table 3). Therefore, I will not consider the uses of muted song in detail. I believe that muted song is intermediate in motivation between incomplete song and full song, or that it represents a "less inhibited" variation of full song than does incomplete song. On several occasions, the first morning bout of singing of a male began with a series of incomplete (and certainly muted) songs. These gradually lengthened until they were recognizable as complete, but still muted, songs. Then there was a gradual increase in volume until the male was singing normal volume, full songs. I believe that this represents the usual pattern of onset of song in the morning, but I was rarely close enough to a singing male to ascertain that

TABLE 5
DISTRIBUTION OF OVENBIRD FLIGHT SONGS BY TIME OF DAY

Beginning h[a]	No. displays[b]	Beginning h	No. displays
01:00	0	13:00	6
02:00	1	14:00	6
03:00	0	15:00	2
04:00	23	16:00	5
05:00	0	17:00	10
06:00	1	18:00	8
07:00	3	19:00	53
08:00	0	20:00	102
09:00	3	21:00	0
10:00	1	22:00	0
11:00	0	23:00	1
12:00	0	24:00	0

[a] All times are Eastern Daylight Time.
[b] Total of 225 displays recorded.

the intermediate songs were really muted. Similar transitions from full to muted to incomplete songs were occasionally noted at the beginning of male-male or male-female interactions; switching in these situations was often abrupt and frequently omitted 1 or more of the intermediate steps from full song to silence.

Attenuated song

Flight song.—I observed or heard 225 performances of the Ovenbird "flight song" display. There is a major concentration of displays at dusk (Table 5), with 155 (68.9%) occurring between 19:00 and 21:00. Most "flight songs" heard in an evening occurred in a 15–20 min interval when it was quite dark in the woods, although the sky was fairly bright and visibility was good in open areas. A second, smaller peak occurs at sunrise. Similar daily patterns of distribution of Ovenbird "flight songs" have been reported by Hann (1937) and Eaton (1957).

Because "flight songs" were noted in the course of other activities and there were no controlled observation periods, it is difficult to assess the remainder of the distribution pattern. The twilight peaks are so pronounced as to leave no question as to their reality. The rarity of "flight songs" during the morning is also real, since the majority of my fieldwork was between 05:00 and 11:00. "Flight songs" may occur at night (21:00–03:00) more frequently than recorded since almost no observations were made during this period.

TABLE 6
SUMMARY OF SITUATIONS IN WHICH MALE OVENBIRDS USED "ATTENUATED SONG" (EXCLUDING FLIGHT SONG)

Situation	No. cases: Major category	No. cases: Subcategory[a]
Male-female interactions	17	
During association		17
During male-female chasing		6
During attack by male		2
During flight toward female		1
During copulation attempts		4
Male-male interactions	13	
During territorial encounter		13
During male-male chasing		6
After chasing		1
At end of encounter		1
Non-encounter situations	3	
At dawn or dusk		2
Late in breeding season		2
Total	33	

[a] Total for subcategories may be greater than number of cases in major category since 1 observation may fall into several subcategories.

The predisposing influence of low light intensity on the performance of "flight song" is evident from the twilight peaks. This is also suggested by the occurrence of "flight songs" during the middle of drizzly and heavily-overcast days. At least 9 (20%) of the 45 "flight songs" recorded between 06:00 and 19:00 occurred during such weather. On a dark afternoon, during light rain, I sometimes heard several "flight songs" in an hour. This never occurred during more clement weather.

Attenuated song during encounters.—Incomplete "attenuated songs" are often given, but all cases considered here included some of the "rambling" terminal portion of the song and may thus be considered to be complete. Of the 33 instances when "attenuated song" was recorded (excluding "flight song" performances), 30 involved interactions between conspecifics (Table 6). Its use in these situations is similar to those of incomplete and muted song, but with one difference. Twelve of 17 records during male-female interactions involved chases, aggressive (?) attacks by the male, or copulation attempts. This is a much higher association with very intense interaction than was recorded for incomplete or muted song (see Tables 3 and 4).

This association of "attenuated song" with high activity was also noted during male-male encounters. Almost half (6 of 13) of the records in territorial encounters were during aerial chases. This is in contrast to incomplete or muted songs which were rarely used during chases.

Attenuated song during non-encounter situations.—On 3 occasions, male Ovenbirds sang 1 or more "attenuated songs" from a perch, or from the ground, in the apparent absence of conspecifics (Table 6). Twice it occurred during the twilight of dusk or dawn when one might expect to hear "flight songs." The third record was somewhat different and warrants an extensive description.

On 7 July 1971, I was observing OB-I, who had been singing irregularly for at least 20 min. At 07:05 he flew down to the ground and in the next 4 min sang at least 16 "attenuated songs." All were muted in volume, but were full-length and had the form of other "attenuated songs" (Fig. 4B). Several times 2 or more of the songs were run together, so that the bird was singing the soft, rambling song for periods of 10–30 sec. This performance of "attenuated song" resembles what has been called "sub-song" (Thorpe 1961:64–70, Thorpe and Pilcher 1958, Armstrong 1963:58–69). Sub-song in other species is a low-volume, rambling vocalization, usually bearing little resemblance to the typical song, although it frequently contains call notes and isolated elements of "primary song." It may be produced almost continuously for extended periods of time. The similarity to the performance of OB-I is striking and suggests that a relationship may be involved.

DISCUSSION

Song variation.—The Ovenbird's pattern of song variation is a relatively simple one which is exhibited by many passerines (Borror 1961, Thielcke 1969). Each male possesses 1 "primary song" pattern, and the song patterns of different males in a local population show considerable variation. This is in contrast to the pattern shown by the Chestnut-sided Warbler (*Dendroica pensylvanica*) (Lein 1978) and some other members of that genus (Lein 1972; Morse 1966, 1967, 1970), in which each male possesses 2 or more song patterns shared by all males in a local population.

This type of individual song variation may facilitate individual recognition of neighbors' songs by male Ovenbirds. The experiments of Weeden and Falls (1959) clearly demonstrated that males discriminate between the songs of familiar and strange birds. The aggressive responses of males were more prompt and pronounced toward the songs of strangers. This implies that territorial establishment in this species results in a relatively stable relationship between neighbors. The outcome is that males are more tolerant toward neighbors, who presumably pose less of a threat to their territorial security, than they are to strangers, who are likely to be newly-arrived birds searching for a territory. Subsequent work by Falls (1963) demonstrated that the pitch, form and arrangement of the component sounds of the song, and the length of the sounds and the intervals between them, are important in eliciting normal responses from male Ovenbirds during playback experiments. These are the features that vary between the songs of different individuals and they probably form the basis of individual discrimination.

The wide range of variation in phrase structure within a local population (Fig. 2), and the similarity of the phrases of some individuals in different populations (compare Fig. 2H and Q, and Fig. 2L and V), suggest that a system of "dialects" (Marler and Tamura 1962, Baptista 1975) is unlikely.

Little can be said regarding the pattern of variation in "attenuated song" because of the small sample of recordings. However, since it contains individually-distinctive "primary song" phrases and *ple-bleep* notes, it probably shows patterns of variation comparable to those of "primary song."

Singing behavior.—Several features of the singing behavior of Ovenbirds deserve comment, especially in relation to the differences found in a parallel study of the Chestnut-sided Warbler (Lein 1978). First, Ovenbirds rarely sing while foraging on the ground; Chestnut-sided Warblers commonly sing while foraging in foliage. Whatever the reasons for the Ovenbird's reluctance to sing from the ground, simultaneous singing and foraging are largely incompatible in this species. In contrast, the Chestnut-sided Warbler combines singing and foraging with only a slight decline in song rate (Lein 1978) and with little apparent interference with foraging. This difference has interesting consequences for time and energy budgets. If we assume, for the sake of argument, that males of both species require the same time and expend the same energy in acquiring the food necessary for subsistence, then it follows that Ovenbirds will have less time available for territorial proclamation than will Chestnut-sided Warblers. Although it is improbable that this assumption is strictly true, it suggests a manner in which the features of the foraging niche of the species could influence territorial advertisement. Species that can combine singing and foraging may be better suited to situations of intense territorial competition, or to conditions which require extended and continuous advertisement for other reasons.

The second difference is in the influence of pair formation on singing behavior. The large decline in singing of Ovenbirds at pairing is due to the almost continuous association of mates at this time, and its inhibitory effect on song. In contrast, pairing seems to have little influence on the singing of the Chestnut-sided Warbler, and perhaps on the singing of sexually dimorphic warblers in general (Lein 1978, Morse 1966, Ficken and Ficken 1969). Chestnut-sided Warbler pairs spend relatively little time in association in the period between female arrival and the start of incubation (16.4% of 373 min of observations on birds whose exact breeding status was known) in contrast to the Ovenbird (83.4% of 452 min).

This sharp decline suggests that song functions in attracting females to unmated males. This is supported by the observation that males who lose their mates resume singing in a manner similar to that of newly-arrived males. However, because new males may be arriving and establishing territories after the first males are already mated, song probably continues to function in territorial proclamation and defense after pairing. The amount of time that a male Ovenbird devotes to pair-related activities during the courtship period possibly decreases his efficiency in territorial defense. Other males frequently intrude on a territory during the courtship period, but this may be due to the attractiveness of the highly vocal females to neighboring males at this time (pers. obs.) rather than to a decline in the efficiency of defense.

Communicative function of song.—The broad range of circumstances in which "primary song" is used indicates that, as with other Ovenbird vocalizations (Lein 1980), it encodes rather general behavioral messages (Smith 1969, 1977). It is rich in identifying messages, indicating that the singer is a male Ovenbird, in breeding condition and on his territory. In addition, a recipient with previous experience may be able to identify the singer as a specific individual. By monitoring singing rate over a period of time, the listener may also be able to determine the mating status of the singing male.

It is difficult to suggest which behavioral selection messages (Smith 1977) the signal encodes. Probably the message is one relating to interactional behavior, indicating that the singer is prepared to interact in any of the ways typical of territorial male Ovenbirds. This is perhaps the only behavioral selection message encoded. It could still have a variety of meanings to different recipients. To a male who was a potential intruder it could signify a threat; to an unmated female it could mean the presence of a potential mate.

Additional messages for muted or incomplete songs are equally difficult to determine. Although both variants are used in clearly agonistic situations, they also occur in circumstances not involving attack or escape, and hence these agonistic messages probably are not encoded. The only general feature of their use is that the bird is experiencing some type of inhibition of, or conflict with, his tendency to sing. Hence they may encode a message of indecisive behavior. This may provide information regarding the communicator's probable future behavior, although the meanings of the signals are certainly dependent upon the class of recipient and the context. The frequent association of these variants with interactions suggests that they may encode a supplemental message indicating a greater probability of interaction than that of full "primary song."

"Attenuated song" used during interactions probably encodes information similar to that borne by incomplete or muted "primary song," since all these vocalizations are used in similar circumstances. In encounter situations "attenuated song" frequently accompanies chasing and attack. However, its use in other situations, such as copulation attempts and "flight song," argues against the encoding of a specific attack message. An attack meaning may be available to the recipient from the context of the signal. The main difference between the messages of "attenuated song" and muted or incomplete songs probably relates to differences in the supplemental messages of probability and intensity of the behavioral selection. "Attenuated song" may indicate a higher probability of a more intense interaction, either aggressive or sexual.

It seems impossible to assess the communicatory function of the "flight song," regardless of how dramatic it is. Its rare occurrence and peculiar situation of use, plus the obvious influence of low light level in its elicitation, make it difficult to suggest its function.

SUMMARY

Song variation and singing behavior of Ovenbirds were studied at 2 locations in New England. Each male possesses a single, distinctive "primary song," which may also be given in muted or incomplete forms. Males also possess a second type of song, "attenuated song," often used as part of an aerial display ("flight song").

Prior to pair formation, male Ovenbirds sing strongly from perches near the bottom of the forest canopy. Few songs are given from the ground, where the majority of foraging occurs. There is a sharp decline in singing at pairing, the result of the inhibitory effect of the female's presence on her mate's singing. Muted and incomplete "primary songs" are associated with both male-male and male-female interactions, but are used in other situations as well. "Flight song" is given primarily at dusk and dawn but may occur at other times, particularly during heavy overcast. Other performances of "attenuated song" are associated almost entirely with very intense interactions.

The relatively simple pattern of song variation described may facilitate individual recognition of neighbors' songs by males. The incompatibility of singing and foraging in this species suggests that features of the foraging niche may influence the ability of birds to advertise territories. Similarly, the reduction in singing produced by the extensive courtship interactions may affect the efficiency of territorial defense at this time.

The songs of Ovenbirds appear to be rich in the identifying messages they encode, but their message regarding future behavioral selections is probably very general, indicating only that the singer is prepared to interact in any manner typical of territorial male Ovenbirds. Muted and incomplete songs, and "attenuated songs," probably encode different supplemental messages about the probability and intensity of interaction.

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MEANDARRA ORNITHOLOGICAL FIELD STUDY UNIT

In December 1980 the Meandarra Ornithological Field Study Unit (MOFSU) was formally established as a research group of the University of Queensland, Australia. Active in field research mainly near Meandarra, 300 km west of Brisbane, MOFSU's major interest is in aspects of the behavior and ecology of communally breeding species. Visitors and volunteer field assistants are welcomed, and although no funding is available, students are accepted to work on field projects towards an M.Sc. or Ph.D. For further information write to: Dr. Douglas Dow, Director, MOFSU, Dept. Zoology, University of Queensland, Brisbane, Australia, 4067.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following opinion has been published by the ICZN in the Bulletin of Zoological Nomenclature, Vol. 38, Pt. 1, 26 Feb. 1981: Opinion No. 1168 (p. 69) "*Cacatua ducorpsii* Pucheran, 1853 (Aves): conserved." The Commission cannot supply separates of Opinions.