

I have been able to detect a reedy quality in the songs of other individuals, but this never proved to be a reliable means of distinguishing the individual from neighboring Grasshopper Sparrows.

The males sing the Grasshopper Song from a grass stalk, low bush, fence post, 10 to 30 feet up in a tree, or from electric power lines. During the height of territorial establishment this song may be sung up to 220 times an hour.

The Sustained Song.—The second vocalization of the Grasshopper Sparrow is more elaborate and more musical than the Grasshopper Song and is subject to more individual variation. The Sustained Song, which may vary from five to 15 seconds in length may be represented as follows:



Tip tup a zeeeeeeee zeedle zeee zeedle zeedle zeeee

At times the "grasshopper" introduction is omitted and the song then consists of the last phrase only.

The Sustained Song is not confined to perch singing alone. The male often sings it in flight, either alone or while pursuing the female. The male rises out of the grass on quivering wings, delivers this song in a low, fluttering flight and then drops down into the grass again.

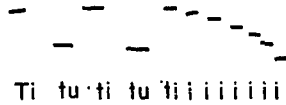
Even though this song can be heard frequently during the mating and nesting season and during summer evenings, it is surprising how much confusion has developed regarding it. Saunders (1951:254) considered what obviously is the Sustained Song as a post-season elaboration of the typical Grasshopper Song. Todd (1940:630) stated that it probably was a mating song. Eaton (1914:292) stated that Gerald Thayer considered this the true song of the species. Jouy (1881:58), apparently on mistaken identification, attributed this song to Henslow's Sparrow (*Passerherbulus henslowii*). He wrote:

"Besides their characteristic note of *te-wick*, they have quite a song which may be fairly represented by the syllables *sis-r-r-rit-srit-srit*, with the accent on the first and last parts. This song is often uttered while the bird takes a short flight upward; it then drops down again in the tangled weeds and grasses where it is almost impossible to follow it."

This is an adequate description of the Sustained Song of the Grasshopper Sparrow which is often given in flight. Fortunately both the Grasshopper and Henslow's sparrows nested in the study area. Not once in five years of observations of both species have I heard a Henslow's Sparrow sing a song that even remotely resembled the Sustained Song of the Grasshopper Sparrow. A similar view was given by Sutton (1928:179-182).

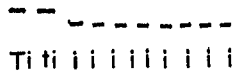
The Trill.—The male possesses still another vocal performance, the Trill, which seems to be confined to mated birds. It is the least common of the vocalizations and, unless one is frequently afield, it is apt to be missed entirely.

Saunders (1951:254) gives a graphic description of the Trill, although he does not seem to recognize it as a distinct type of vocalization. Walkinshaw (1940: 59) described it as a nesting song. It consists of a series of moderately loud notes on two tones, rapidly given:



It may be delivered either from a perch or in the grass.

The Trill of the Female.—The female Grasshopper Sparrow possesses a vocalization quite similar to the Trill of the male but it is weaker, suggestive of the Chipping Sparrow's (*Spizella passerina*) song and lacks the downward trill:



It is difficult to observe the female singing because, except in courtship flights, she delivers this song while concealed in the grass. On May 21, 1945, I had an excellent opportunity to observe the female uttering the Trill. She appeared in a small bare area in some rather sparse grass near the boundary of a hay and wheat field. Flirting her tail and hopping slowly about in a circle she delivered the Trill. Then she flew into the wheat where she sang it again.

The female may sing this trill in answer to the Sustained Song or the Trill of the male, or she may give it without the stimulus of the song of the male.

PERIODS OF SONG

Singing falls into seasonal and daily patterns (Fig. 1). The seasonal distribution of song is influenced by the reproductive cycle of the bird; the daily pattern is influenced by the seasonal pattern and by daily weather conditions.

Grasshopper Sparrows are in song when they return to their breeding areas in mid-April. The average date over a 5-year period for their arrival on the study area was April 16. The earliest arrival was March 31, 1945, the earliest ever recorded for western Pennsylvania, and the latest arrival was April 21, 1946. The entire population on the study area did not arrive at once, but built up over a period of a week. During the first days following their arrival the males sang only the Grasshopper Song and confined their singing to the morning hours. As the population increased during the succeeding days, the males sang the Grasshopper Song more and more frequently, until they were heard throughout the day.

Within 10 to 14 days after their arrival, the males introduced the Sustained Song. At first each male may sing this song no more than two or three times a day, but within a week he almost replaces the Grasshopper with the Sustained Song for a few days. In general, however, it is given interchangeably with the

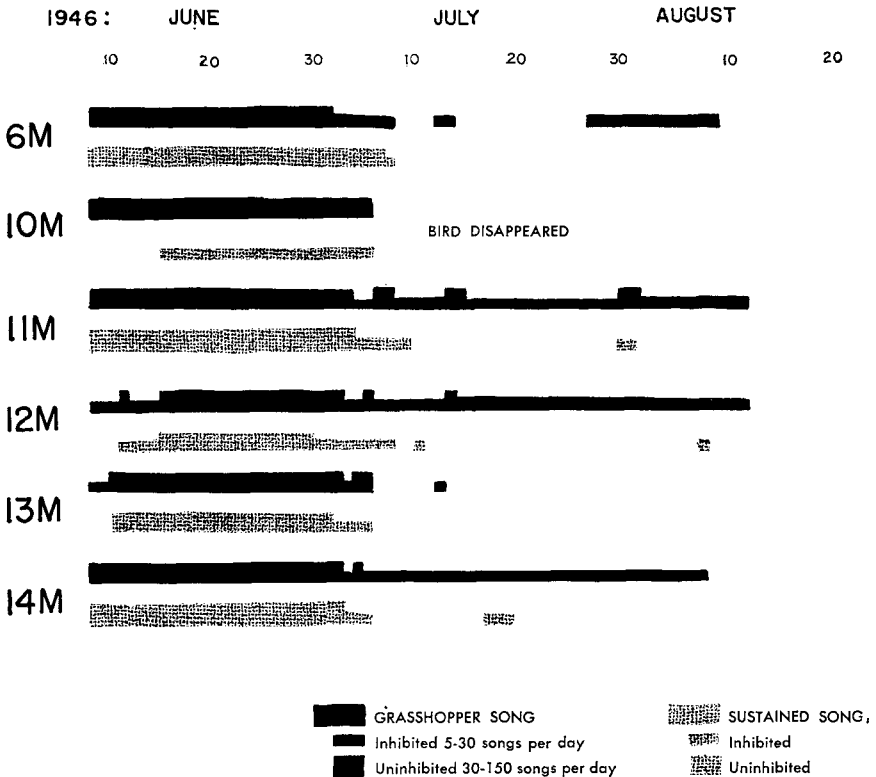


FIG. 1. Frequency of song among Grasshopper Sparrows during summer, 1946.

Grasshopper Song and is rarely sung for any length of time without interruption by the Grasshopper Song.

After pairing all song appears to be inhibited for a few days, but the birds I observed never ceased singing entirely. During the period of egg-laying and incubation, the male sings both songs frequently, especially in the early morning and evening, continuing until darkness. Occasionally a bird may sing sporadically throughout moonlight nights.

During June, when most Grasshopper Sparrows are feeding young, song wanes. The Sustained Song is heard less frequently during the day and more or less assumes the status of a twilight song. The Grasshopper Song is again the common daytime song; but prior to reneating the Sustained Song becomes conspicuous for several days, then wanes again. By mid-July the Sustained Song has all but disappeared and is sung only occasionally from then until the cessation of song in mid-August. The Grasshopper Song, however, is retained

and is sung with diminished vigor and frequency as the summer wears on (Fig. 1).

After pair formation in late April the male introduces the Trill. He gives this infrequently and only on specific occasions. After nesting is completed and the young are on the wing, the male drops the song.

The Trill of the female is heard from the time of pair formation to the cessation of nesting.

The Grasshopper Sparrow does not have an extended morning awakening song. Upon awakening the bird may remain silent and start to feed, it may utter the *chi-ip* call note or it may sing the Sustained or Grasshopper Songs. Once the bird commences singing, it interrupts the song sequence frequently with feeding.

By mid-July the daily pattern gradually assumes a different character. The Sustained Song is dropped except for a few occasional days when it may be given several times in the very early morning or at evening twilight. Morning song has nearly ceased and daytime song is rarely heard. The cooler temperatures of evening and the suspension of feeding activity bring in the twilight song which lasts until darkness comes. At this period the Sustained Song, with its greater carrying power, seems to be the most conspicuous and for this reason has been erroneously described as a post-season elaboration of the regular song of the species.

Song may be inhibited by adverse weather conditions. For example, in 1945 spring came exceptionally early. In late March temperatures were in the high 70's and low 80's, leaves were opening and the grass was three inches high. As might be expected, the Grasshopper Sparrows returned very early, on March 31. Song increased in volume up to May 1, when cold, wet weather set in. Song nearly ceased. On May 9 the weather cleared, and although the temperature was 30°F., all Grasshopper Sparrows broke into song. Hot, humid weather also has an inhibiting effect on song, but not to the extent of cold, wet weather.

FUNCTIONS OF SONG

The objective study of the function of bird song has suffered from the lack of a suitable definition of bird song. Howard (1920) in his pioneer work on territorialism in birds emphasized the advertising function of song. Tinbergen (1939:73) regarded bird song as an utterance "that serves to attract a sex partner, to warn off a bird of the same sex or both." Nice (1943:144-149) and Lack (1943:28-33) also considered song from this viewpoint. More recently, Moynihan and Hall (1954:50) suggested that the term "song" be confined to those vocalizations with the dual functions of warning rivals and attracting mates. On the other hand, Armstrong (1947:294) stated that from a functional point of view no distinction can be drawn between songs and calls.

For the purposes of this paper, and of attempting more clearly to distinguish song from other vocalizations of a bird, song is regarded as a vocal utterance, long or short, simple or complex and species specific, which is given by either sex or both and which functions primarily to repel rivals of the same species, to attract a mate, or both.

This definition is exclusive to the point that it eliminates any vocalizations, however complex, which do not serve primarily to attract or repel. At the same time it does not assume that song is exclusively the function of the male. It thus includes the rarer instances of song in female birds. The words "functions primarily" do not eliminate the post or pre-breeding season songs of many birds. Other musical utterances not serving to attract or repel should be considered sub-songs and all other vocalizations as calls.

The Grasshopper Song.—Its peak occurrence early in the season and its consistent appearance in daytime and evening singing up to the complete cessation of song suggest that the Grasshopper Song is territorial in function.

The behavior of the bird itself, however, is even stronger evidence that the song is hostile. During territorial establishment the male alternates song with display. In a crouched position with his head lowered between his shoulders (Fig. 2, A), the male raises and flutters one or both wings (Fig. 2, B). The primaries and secondaries are not extended, but the wing is fluttered quickly above the back at the humerus. Then, after hearing the song of his neighbor, the bird stands erect and sings back (Fig. 2, C). The song completed, the male again assumes the crouched position and flutters his wings. The sequence is as follows: (1) The male stands erect and sings the Grasshopper Song. (2) Song completed, he assumes the crouched position. (3) He flutters one wing or both simultaneously. (4) He hears rival's song, and rises to a singing position. (5) He sings Grasshopper Song.

The wing-fluttering of the Grasshopper Sparrow is never accompanied by a song or a call, but is confined to that interval between songs, and is conspicuous only during the period of territorial establishment.

It seems unusual that this behavior has not been reported by other writers. The only comment on wing-fluttering by the Grasshopper Sparrow that I have found was made by William Brewster (1874) in his unpublished Nantucket journal for July 3, 1874: "... I have a new one, namely that the bird frequently quivers its wings like a Bluebird."

Wing-fluttering is closely associated with territorial establishment. Some manner of wing-fluttering occurs in the mating and territorial behavior of a number of passerine species, for example, the Snow Bunting, *Plectrophenax nivalis* (Tinbergen, 1939:17); the Song Sparrow, *Melospiza melodia* (Nice, 1943:154); the House Wren, *Troglodytes aedon* (Kendeigh, 1941:21); the European Wren, *Troglodytes troglodytes* (Armstrong, 1954:47, 114-117); the European Goldfinch, *Carduelis carduelis* (Hinde, 1955:720); the Canary,

Serinus sp. (Hinde, 1955:713-715); and the Greenfinch, *Chloris chloris* (Hinde, 1955:719). The stimuli for these displays differ from those of the Grasshopper Sparrow. One male has actually invaded or is threatening to invade the territory of another; the birds see one another; or often they are face to face. The Grasshopper Sparrows in most instances do not see one another. The males may be hidden from one another by the vegetation or the topography of the field. They do not erect the body feathers. The attitude, however, of the male between songs, the crouched posture with the bill pointed forward, the fluttering of the wings, the apparent readiness of the bird to move forward to meet a threat, all strongly indicate that this is a hostile display. During the period of territorial establishment the song of a rival is a sufficient stimulus to release this display. The bird senses the presence of a rival by the sound of his song and manifests this by a hostile display, as if the rival were nearby in the grass. Marler (1956:497) has observed a similar reaction in the Chaffinch (*Fringilla coelebs*). The song of the Chaffinch played through a loud speaker induced fierce aggressive display in males.

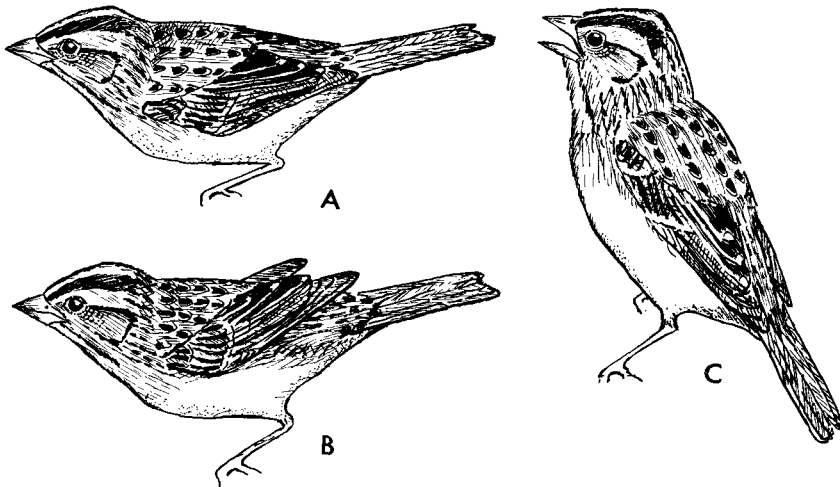


FIG. 2. Attitudes of male during the Grasshopper Song sequence. (A) crouched position. (B) Wing-fluttering. (C) Delivering song.

Unfortunately I have never observed among Grasshopper Sparrows a territorial dispute that elicited a high intensity intimidation display. If any occurred it happened out of sight in the grass. The only physical encounters I have observed during hundreds of hours spent with the species were those after a bird saw another invade its aerial territory. In each instance the bird chased the intruder, then retired to a singing perch, fluttered his wings and sang the

Grasshopper Song. I have witnessed a number of aerial clashes at disputed territorial boundaries. In fact, this mode of defense could be the most important, because the deep grass would generally conceal territorial infringement on the ground. Perhaps the Grasshopper Sparrow recognizes the limits of its territory only from a grass-top point of view.

The Grasshopper Song, then, serves primarily as an advertising or territorial song. The distribution and occurrence of this song during the season, its timing, and the response it elicits from neighboring males emphasizes this function. It is the first song given by the male in the spring and is delivered from the highest perch in the territory. It is sung when one male is chasing another from his territory, and is delivered by both when the two retire to their singing posts.

At times the Grasshopper Sparrow will deliver the Grasshopper Song while protesting other animal or human intrusion. On occasions male Grasshopper Sparrows protested my presence in their territories. As soon as I left they would return to their singing perches and deliver the Grasshopper Song.

The Sustained Song.—The Sustained Song attracts a mate. Its occurrence in the seasonal song cycle, its loudness, and the response it elicits from the female indicate this function. Upon hearing the Sustained Song, the female will answer the male with a Trill (Fig. 3). In turn, the male will respond to the female's vocalization by answering her with the Sustained Song again, or by flying to her.

The function of the Sustained Song cannot be limited to attracting a mate. If that were its sole purpose it should cease upon the arrival of a female, as in the case of the Snow Bunting (Tinbergen, 1939:77). The song, however, is delivered through the periods of nesting and caring for the young. Furthermore, it is given with increased frequency just prior to the second nesting. Apparently this song is quite important in maintaining the pair bond throughout the season.

The complete Sustained Song with the "grasshopper" introduction is hostile to other males. The first phrase of the song is identical to the Grasshopper Song. This is necessary in the early period of courtship because the territories have been newly settled by the males and the warning function still is of prime importance. The second phrase of the song, however, serves to attract and hold a mate. Later in the season, when territories are well established and the warning is not so imperative, the majority of Sustained Songs lack the "grasshopper" introduction. When one male hears another singing the Sustained Song, he responds not with the Sustained Song but with the Grasshopper Song. Then both birds launch into a song duel of Grasshopper Songs.

The Trill.—The Trill generally is not given by the male until the pair is formed and even then it is usually uttered only in the vicinity of the nest, and only from a perch or in the grass. It may follow one of the other two songs or it may be given alone, often in answer to the female (Fig. 3). It is also given by the male when he is in close proximity to the nest.

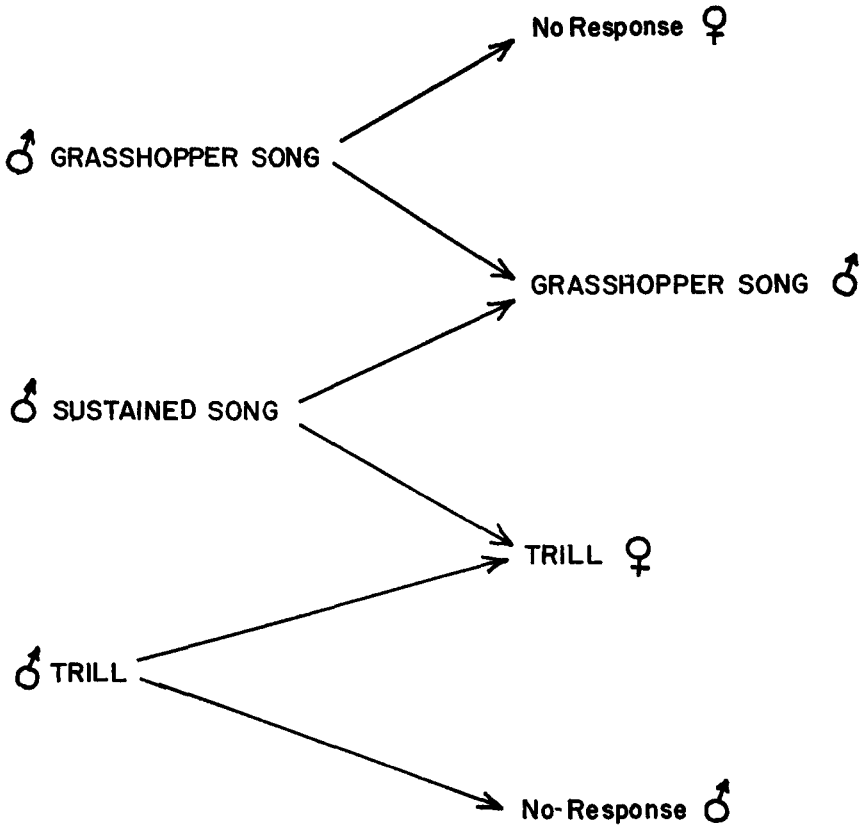


FIG. 3. Responses of male and female Grasshopper Sparrows to the several songs.

The Trill apparently serves as a bond to hold the pair together, and as a signal to both the female and the young that the male is approaching the nest. The fact that the Trill usually is given only by the mated male seems further to support this function. Only once did I hear the Trill given by an unmated male, several of which I have followed through a season.

The Trill of the Female.—The Trill is a distinctive vocalization of the female which may or may not be given under the stimulus of the song of the male. The fact that the female Grasshopper Sparrow vocalizes should not be regarded as unusual, but the problem is whether or not this vocalization can be regarded as true song.

The manner and circumstances under which the Trill of the female is sung, and its function, indicate that it can be. Just as the male Grasshopper Sparrow can detect the presence of a rival in his territory by the rival's song, so can he

detect the presence of a female by some distinctive signal. Herein lies the significance and the biological importance of the female's song. When the male sings the Sustained Song, he proclaims his availability to a female. A female bird present on his territory answers with a vocal performance which is loud, species specific, and which advertises her presence to the male. In fact she sings this Trill independent of any song from the male. Hearing the female, the male flies to her.

The importance of the female's song as an attracting mechanism is apparent. The male does not have to see by chance a strange bird in his territory and then challenge it to determine its sex. Because of the nature of the habitat this might be difficult and time consuming. Instead, the song of the female assures that the male will be led to a potential mate, that this potential mate is of the male's own species and that the male will have the opportunity to find a mate at the proper time in the breeding cycle.

The female also gives the Trill when she is approaching, or is in the vicinity of the nest.

The primary function of the Trill of the female Grasshopper Sparrow is to declare her presence to the male, to announce her location, to maintain the pair bond, and to signal both the male and the young that she is approaching the nest.

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SUMMARY

The male Grasshopper Sparrow possesses three primary forms of vocalizations, the Grasshopper and Sustained Songs and the Trill, and the female Grasshopper Sparrow one, the Trill.

The male sings the Grasshopper Song from mid-April to mid-August. The Sustained Song is introduced approximately at the time the females arrive. It is sung with diminished vigor until mid-July and only sporadically from then on until the cessation of song in mid-August. The Trill is given from the period of pair formation to the completion of nesting, as is the Trill of the female.

Early in the season song is heard throughout the day. After mating, song is inhibited but does not cease entirely. During the periods of nest-building, incubation and care of the young, song is confined primarily to morning and late evening. Song is inhibited by adverse weather.

The Grasshopper Song is the familiar song of the species. It is used primarily to proclaim and defend territory. During the period of territorial establishment the male assumes a crouched, bill-forward position and flutters his

wing or wings between songs. This is regarded as a hostile display released by the song of the rival.

The Sustained Song in its entirety consists of a "grasshopper" introduction and a sustained series of melodious notes. After the territories are well established, the "grasshopper" introduction is usually dropped. The primary function of the Sustained Song is to attract a mate, but the "grasshopper" introduction is hostile in character. A secondary function of the song is to maintain the pair bond.

The Trill serves to maintain the pair bond and to signal the mate and the young of the male's approach to the nest. It apparently is given only by mated males.

The Trill of the female advertises the presence of a potential mate in the male's territory and identifies her species and sex. The Trill also serves to maintain the pair bond and to signal the male and the young that she is approaching the nest.

The male Grasshopper Sparrow responds to the Grasshopper and Sustained Songs with a Grasshopper Song, to the female's Trill with a Sustained Song or a Trill. There is no response by the male to the Trill of another male. The female responds to the Sustained Song and the Trill of the male with her Trill, but shows no apparent response to the Grasshopper Song.

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