

# THE RELATION OF SONG STRUCTURE TO TEGMINAL MOVEMENT IN *METRIOPTERA SPHAGNORUM* (ORTHOPTERA: TETTIGONIIDAE)

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## Abstract

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Flash photography of the wings of a decticine katydid, *Metriopectera sphagnorum* (F. Walker), during stridulation, indicates that major trains of sound pulses of both song modes coincide with wing closures. The song mode characterized by intense ultrasonics is generated by tooth-scraper interactions over an interval of approximately 60 teeth at the lateral end of the file. A more medial file region is employed for the audio-dominated mode. Tooth removal confirms the role of different file regions in mode generation. Each pulse of the ultrasonic mode closure is a wave train of 10-15 waves of uniform amplitude, approximating a pure tone frequency of 33 kHz.

## Introduction

The songs of male katydids result from opening and closing movements of the overlapped tegmina. File teeth project downward from the second cubitus of the left forewing; a scraper, the anal edge of the underlying right forewing, moves back and forth along this file, generating sound pulses.<sup>1</sup> Though many species make both to and fro sounds, it appears that the most intense and sustained components of katydid songs are produced only on wing closure.

Pierce (1948) compared the duration of sound "pulses" (pulse trains) with the time required for wing closure and for opening in three tettigoniid species: *Scudderia curvicauda* (DeGeer), *S. texensis* Saussure and Pictet, and *Pterophylla camellifolia* (F.). He determined that the sounds of these insects were produced as the tegmina moved together. Suga (1966) removed teeth from the files of *Conocephalus saltator* (Saussure), *Drepanoxiphus modestus* (Bruner), and two species of *Phlugis*. These four species were shown to generate major components of their songs on tegminal closure.

Pasquinelly and Busnel (1955) used high speed photography to demonstrate that *Ephippiger bitterensis* Fieb. produces a major pulse train (la phase principale) on tegminal closure and a minor pulse train (la phase préparatoire) on tegminal opening. Thomas and Alexander (1962) report the same result for *Orchelimum vulgare* Harris. *C. saltator* also has a minor (short-duration) pulse train that coincides with wing opening (Suga 1966).

The present paper concerns a study relating wing movements in a decticine, *Metriopectera sphagnorum* (F. Walker), to the pulse pattern of the emitted sound. Results support the generalization that major song components coincide with wing closures. The pulse train pattern of this species is complex (Morris 1970). Two stridulation modes (pulse train groups) alternate, each characterized by a unique pair of major and minor pulse trains. Each mode has a different frequency spectrum. In one mode audio frequencies predominate, in the other, ultrasonics.

<sup>1</sup>The case for a definition of the term pulse based on physical wave forms has been well argued by Broughton (1963). In the present study pulse means a wave train that is isolated or nearly isolated in time (discrete) when viewed with an oscilloscope.

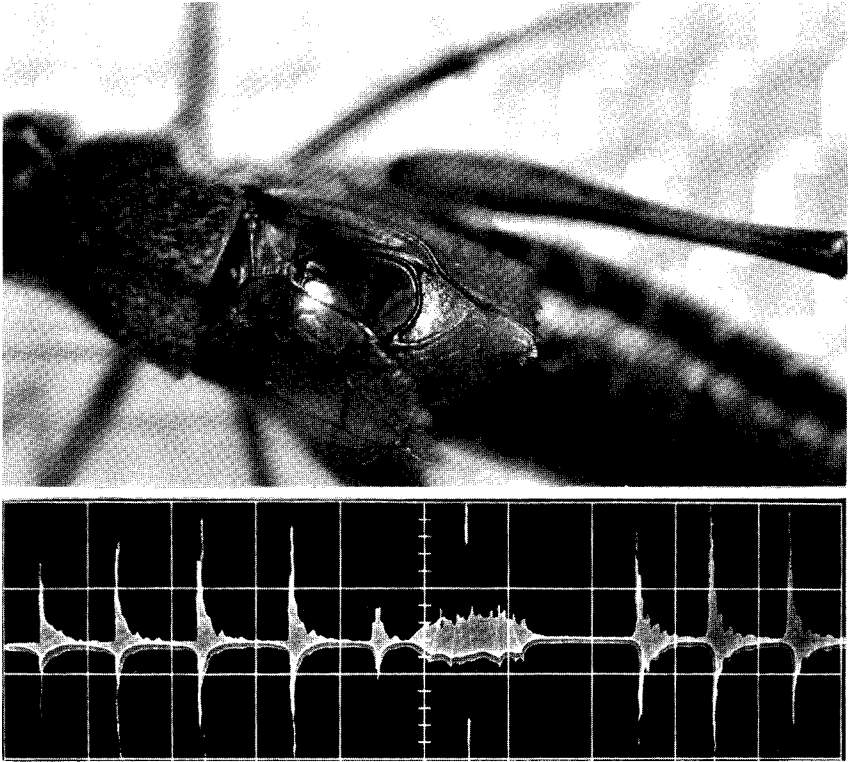


FIG. 1.

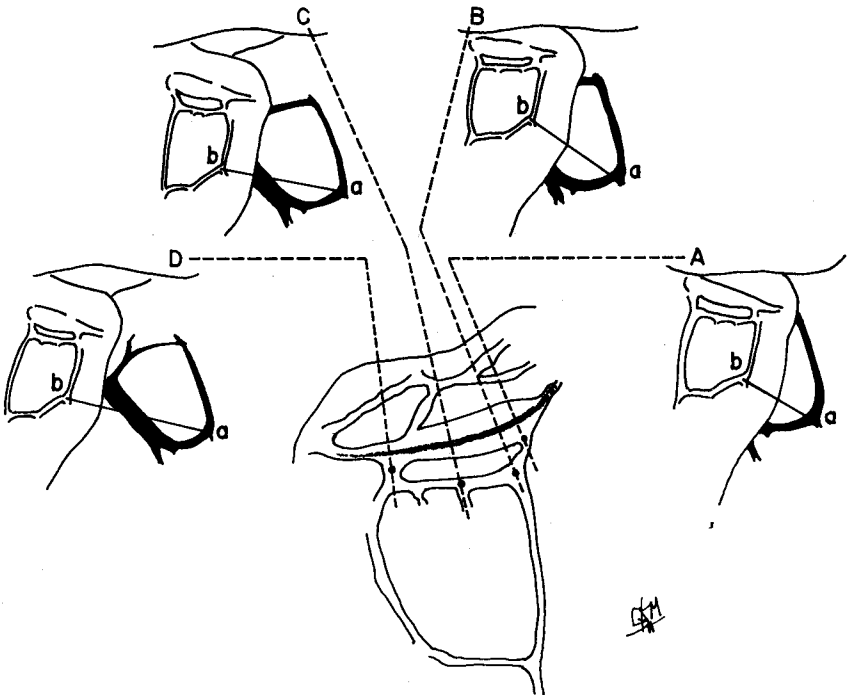


FIG. 2.

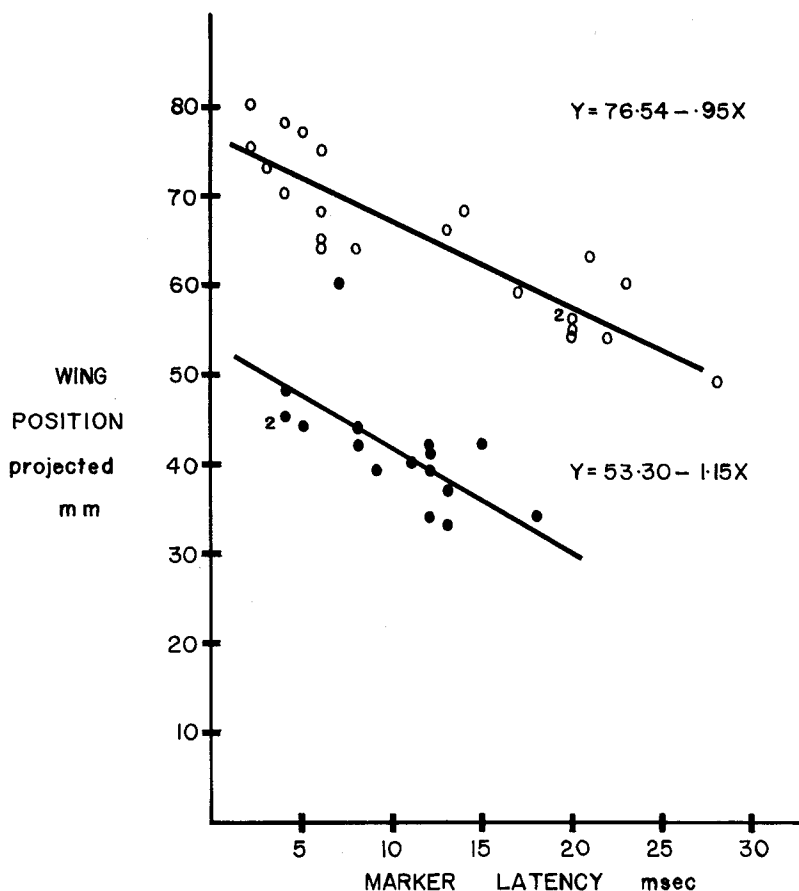


FIG. 3. Regression analyses of wing position (distance *ab* of Fig. 2 in projected mm) as a function of marker latency (msec). Each plotted point represents a single record (flash photograph and oscilloscope trace) for which the marker fell within a major pulse train of either mode. Records obtained during the ultrasonic mode are plotted as closed circles; audio mode records are represented by open circles.

### Materials and Methods

Specimens of *M. sphagnorum* were collected from bog near the junction of highway 17 and the Firesteel River in northwestern Ontario. Photographs of tegminal displacement during stridulation were paired with oscilloscope time-amplitude traces of the emitted sound.

A sheet of plexiglas (23 × 25 cm) formed one side of a narrow cage; the opposite side, 5 cm distant, was of screen. Males were placed in this cage in lots of one, two, or three. A camera was directed at their tegmina through the plexiglas. A Bruel and Kjaer ¼ in. condenser microphone, type 4135, received

FIG. 1. A stored oscilloscope trace obtained at 5 msec/division and a flash photo of the tegmina of *M. sphagnorum*. The marker visible above the minor pulse train indicates when the wing photo was taken.

FIG. 2. Camera lucida drawings of tegminal overlap for several locations of the scraper on the file.

the insect's song on the screened side and conveyed this signal to a Tektronix storage oscilloscope, type 564. A General Radio stroboscope, type 1531-AB, illuminated the singer from the plexiglas side.

To photograph the moving wings, the camera shutter was held open manually and a specially constructed delay circuit was activated by closing a switch. The delay circuit triggered a single stored sweep of the oscilloscope beam. This trace recorded the singer's pulse train sequence at a sweep rate of 5 msec/division. As the beam neared mid-screen, the delay circuit automatically caused a single flash of the stroboscope, providing a photograph of the tegmina. A photocell, aimed at the stroboscope, produced a marker pulse which was superimposed on the oscilloscope trace at the moment of the flash. In Fig. 1, a typical record, the trace shows the insect's song in its ultrasonic mode with the marker midway through a minor pulse train.

Linear regression analyses were carried out to examine tegminal displacement as a function of marker latency. Marker latency is defined as the time in milliseconds from the start of the major pulse train to the occurrence of the marker. Only those records in which the marker fell within the major pulse train were used. Slides of the wing photos were projected on a screen from a fixed distance. The displacement of the tegmina in each photograph was obtained by measuring, on the projected image, the distance between two tegminal landmarks. These landmarks were the vein junctions labelled *a* and *b* in Fig. 2.

The actual point of engagement of scraper and file was related to the dorsal views of wing overlap by examining freshly killed specimens with a microscope. The scraper was positioned at selected points along the file, and the tegmina were drawn in dorsal view with the aid of a camera lucida. These drawings are reproduced in Fig. 2.

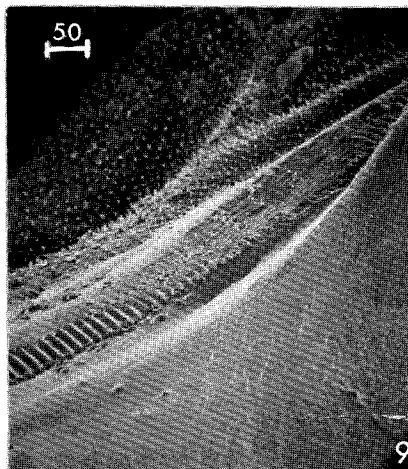
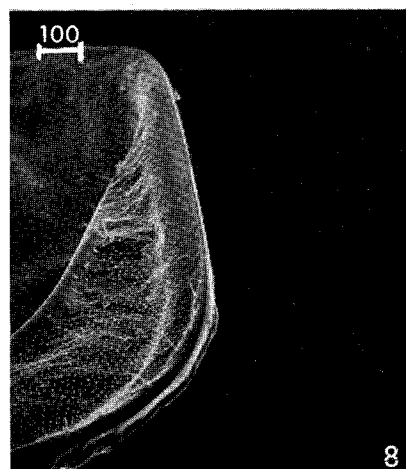
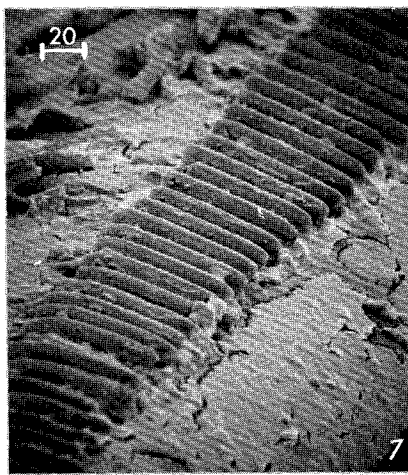
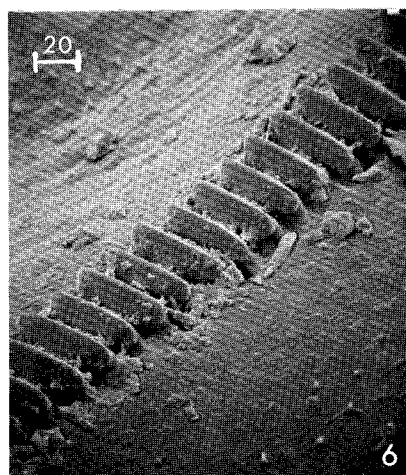
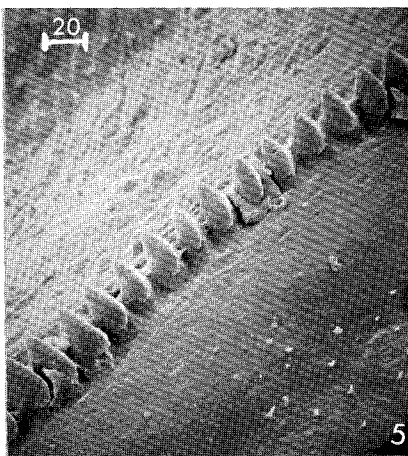
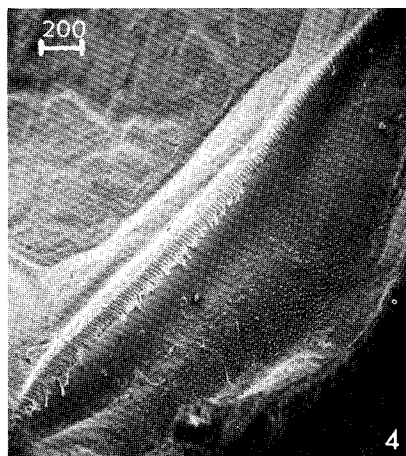
Eccentric tooth removal was carried out on two specimens. Each insect was restrained on the stage of a dissection microscope and with a sharp scalpel several teeth were removed from the lateral end of the file. Before and after this mutilation a song sample was recorded on a Philips Ana-log 7 tape recorder, type EL 1020. The signal from the Bruel and Kjaer 1/4 in. condenser microphone was directed through either a Keithley amplifier, type 102 B, or the amplifier of a Bruel and Kjaer sound level meter, type 2204. Recordings were made at 24°C with a tape speed of 30 in./sec. The microphone was directed at the insect's dorsum over a distance of 5 cm. The oscilloscope records of Figs. 10-14 were generated at slower playback speeds to permit trace storage; however, the sweep rates cited have been adjusted to real time values.

## Results

When wing position is plotted as a function of marker latency (Fig. 3) the points fall into two groups corresponding to the two stridulation modes. With the exception of one record, the maximum distance observed between the landmarks *a* and *b* during the ultrasonic-dominated mode is less than the minimum *ab* distance observed during the audio. Thus the tegmina are always farther apart during the audio than during the ultrasonic. From this we conclude that different non-

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FIGS. 4-9. Scanning electron micrographs of the file and scraper of *M. sphagnorum*. 4, entire file; 5, 6, 7, teeth from medial, intermediate, and lateral file regions respectively; 8, dorsoanterior aspect of scraper showing upturned rim; 9, mutilated lateral end of the file of specimen 71-2. Scale in  $\mu\text{m}$ .



overlapping file regions are employed in generating the major pulse trains of each mode.

These file regions were delimited more precisely with the aid of the camera lucida drawings of Fig. 2. The flash photographs of the wings in dorsal view were 'translated' into scraper-tooth locations. The file bears 150-180 teeth (Fig. 4). The major pulse train of the audio mode is produced over the medial file region near *C* and *D* of Fig. 2; the major pulse train of the ultrasonic mode is generated by a region of about 60 teeth near *A* and *B* of Fig. 2, at the lateral end of the file.

There is no sudden change in tooth structure reflecting the use of different file regions for the two modes. But laterally, where the ultrasonic is generated, the teeth do become broader and the number per unit of file length increases (compare Figs. 5, 6, 7).

A regression line was determined for the records of each mode. The slope of the regression line is the rate of change in wing displacement. A negative slope means that displacement will always be less for the larger of any two latencies. In other words, the wings are closer together as the latency time increases. Both regression lines in Fig. 3 have a negative slope, therefore the major pulse trains of both modes are produced on wing closure.

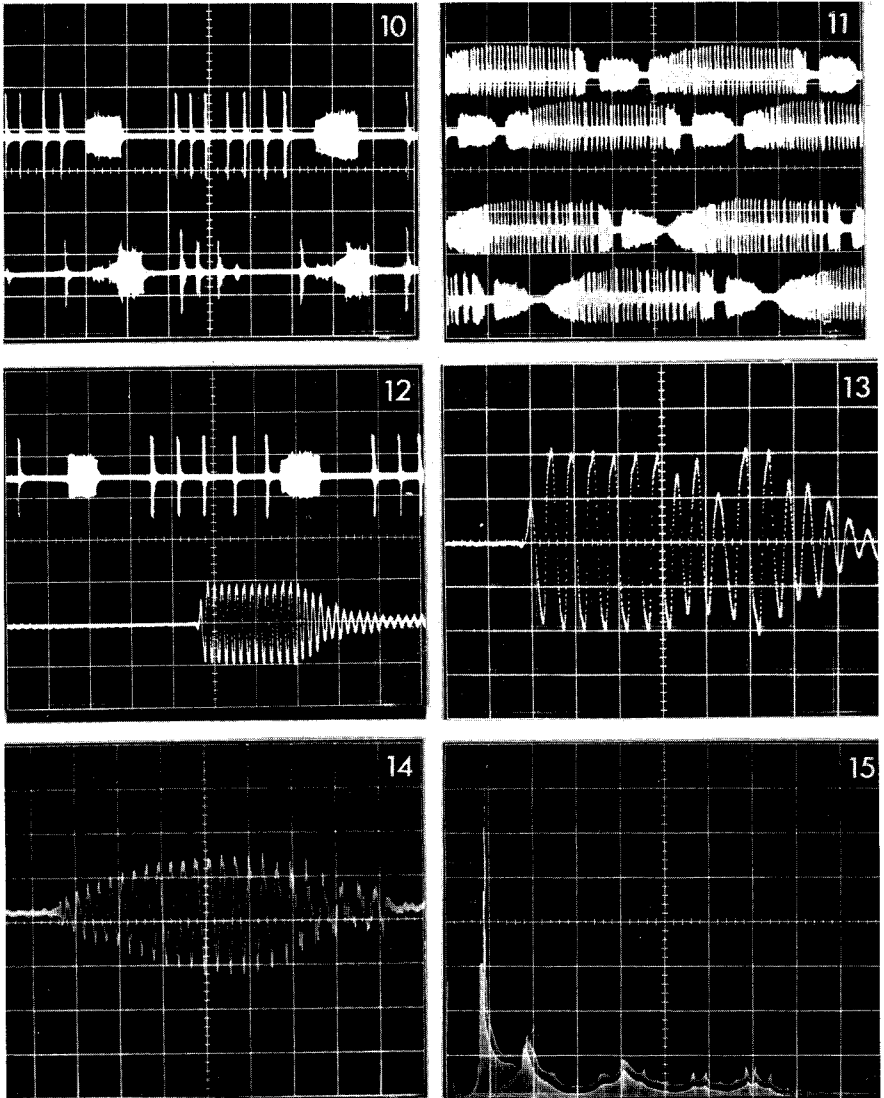
The role of the lateral file region in ultrasonic mode closures was confirmed by tooth removal. Figure 9 shows this file region in specimen 71-2 after mutilation. The normal song of this individual is displayed in the upper traces of Figs. 10 and 11. Following tooth removal, the ultrasonic mode pulses (lower trace Fig. 10) are altered considerably toward the end of the major pulse train. By contrast, the two lower traces of Fig. 11 show no change in the audio mode following mutilation. This result confirms that the production of the major pulse train of the ultrasonic mode occurs on wing closure and that the two modes are generated over different file regions. Identical results were obtained in a second mutilation experiment.

In Fig. 10 a reduced intensity is evident on the leading edge of post-mutilation minor pulse trains. This indicates that the minor pulse train of the ultrasonic mode is the result of an opening of the tegmina.

### Discussion

The direction of wing movement has been related to the pulse pattern of the emitted sound in surprisingly few species of Tettigoniidae and the generalization that the most intense and prolonged song components are produced on closure should be accepted cautiously. Although small, the sample is drawn from seven subfamilies (Decticinae, Phaneropterinae, Pseudophyllinae, Conocephalinae, Litroscelinae, Ehippigerinae, and Copiphorinae) and without exception the results support the generalization. - It seems likely that closure holds some mechanical advantage over opening in the generation of katydid sounds.

Two pulse types are common in the stridulations of tettigoniids. One is a rapid-decay pulse, characteristic of Conocephalinae. The other is a prolonged pulse which crudely approaches a pure tone signal. Figure 14 shows the prolonged pulse of the copiphorine *Neoconocephalus robustus* (Scudder) ('buzzer' sibling) in which the wave train approximates a pure tone frequency near 10 kHz, seen as a prominent narrow peak in the frequency spectrogram (Fig. 15) (G. K. Morris, unpub.). This prolonged pulse is the product of a tegminal closure (T. J. Walker, pers. comm.). Similar prolonged pulses have been documented in *D. modestus*



FIGS. 10-13. Oscilloscope traces of *M. sphagnorum* song. 10, ultrasonic mode traces of specimen 71-2 at 6.25 msec/division, upper trace prior to mutilation, lower trace after mutilation; 11, audio mode traces of 71-2 at 6.25 msec/division, upper two traces before mutilation and lower two after mutilation; 12, upper trace of ultrasonic mode at 6.25 msec/division, lower trace a single ultrasonic closure pulse (prolonged pulse) at 156  $\mu$ sec/division; 13, a single ultrasonic mode closure pulse (prolonged pulse) at 62.5  $\mu$ sec/division.

FIGS. 14, 15. *N. robustus* 'buzzer' oscilloscope records. 14, a trace at 312.5  $\mu$ sec/division showing a single prolonged pulse; 15, a frequency spectrogram, each division on the horizontal axis represents 10 kHz running from 0 to 100 kHz.

by Suga (1966) and in *Homorocoryphus nitidulus vicinus* (Walker) by Bailey and Broughton (1970).

Whereas one wing closure of *N. robustus* generates a single pulse, one closure of a conocephaline such as *C. saltator* (Suga 1966) generates a whole series of pulses. The audio mode closure of *M. sphagnorum* is a train of rapid-decay pulses resembling those of a conocephaline; but closures during the decticine's ultrasonic mode generate prolonged pulses. It is of interest that both pulse types should be present in the same species and it may be significant that different file regions are employed.

Before observing *M. sphagnorum* song at a reduced playback speed on the Philips analog recorder, the ultrasonic closure pulses were assumed by the authors to have a rapid-decay wave structure. This led to the erroneous interpretation that since only 5-8 pulses resulted from travel along a 60-tooth interval, and assuming one pulse per tooth interaction, the insect must be skipping teeth. Once the detailed structure of the ultrasonic closure pulse was known, the skipping hypothesis (Morris 1971) was abandoned.

Each of the prolonged pulses of *M. sphagnorum* approximates a pure tone frequency of 33 kHz (Fig. 13). This frequency is a narrow peak in the frequency spectrogram (Morris 1970). Each pulse consists of 10-15 waves of uniform amplitude followed by a gradual decay. The mechanism by which such prolonged pulses are believed to be generated is described by Pasquinely and Busnel (1955) and by Bailey and Broughton (1970).

When scraper and file interactions occur at a rate which permits complete or nearly complete damping of the vibrating areas of the tegmina between energy inputs, a train of rapid-decay, discrete pulses results. If the scraper travels along the file at a rate which allows time for the completion of only one wave between energy inputs, the result is a continuous train of waves with relatively constant amplitude or at least very gradual amplitude change. Each wave is "reinforced by the next before any decay can set in" (Bailey and Broughton 1970). In this latter situation the wing is being driven at a frequency corresponding to the rate of tooth-scraper interactions. This is the method which crickets use and it is presumably the method used by *M. sphagnorum*. The number of waves of uniform amplitude summed across the pulses of one major pulse train of the ultrasonic mode corresponds approximately with the number of teeth available.

Compare the prolonged pulses of *M. sphagnorum* (Figs. 12, 13) with those of *N. robustus* 'buzzer' (Fig. 14). *N. robustus* generates only one pulse per closure whereas *M. sphagnorum* produces several, each separated from the next by a substantial interval of silence. Instead of a gradual increase to maximum pulse amplitude as in *N. robustus*, the decticine begins its pulse abruptly at maximum amplitude. What is happening to the scraper during the silence between pulses? If it continued to move, surely it would generate sound. Pauses in the travel of the scraper along the file seem a reasonable possibility. The following model is suggested.

As the wings move together, the scraper is pushed into the teeth of the file. The actual point of scraper engagement is an upward projecting ridge (Fig. 8) located on the scraper lobe margin. This ridge lodges behind a tooth while the wings continue to move past each other. The scraper lobe becomes ventrally more convex. Energy is stored in the bent lobe and the scraper ridge is gradually rotated within the intertooth space until no longer restrained by the tooth edge. Slipping free, the scraper moves suddenly along the file and passes over 10-15



teeth. The right tegmen is driven into vibration at the rate of tooth contact. As the stored energy is exhausted, the lobe returns to its original plane. This, plus the ventrally concave shape of the file, causes the scraper to lodge once again behind a file tooth. A process of energy storage and sudden release continues at locations along the file separated by 10–15 teeth.

The prolonged pulses of *M. sphagnorum* approximate a 33,000 cycle/sec pure tone. This is a substantially higher frequency than occurs in *N. robustus* 'buzzer' (10 kHz), *H. nitidulus vicinus* (15 kHz), and *D. modestus* (24 kHz). The pauses in the scraper advance of *M. sphagnorum*, if they occur, may provide a means of achieving the very high driven frequency of this species.

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