

THE MODULATED SOUNDS MADE BY THE TSETSE FLY *GLOSSINA BREVIPALPIS* NEWSTEAD

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ABSTRACT

The modulated sounds made by *Glossina brevipalpis* are physiologically and reflexly induced phenomena, produced by muscular vibrations in the pterothorax. The patterns and physical nature of the calls and songs were investigated acoustically, spectrographically and oscilloscopically to explore the possibility of a syntactical content. The findings are compatible with a concept of sound-motivated behaviour, which offers a new approach to the study of tsetse fly behaviour.

INTRODUCTION

Tsetse flies produce modulated sounds, variously described as singing, buzzing, squeaking or ping-pong. The calls are closely related to the vital functions of the community namely hunting, feeding, mating and larviposition. The ecological significance of this faculty, therefore, needs further investigation. The flight sounds described by Kartman *et al.* (1946) have not been heard by the author and are not considered here.

One of the first questions that needs answering is how do they produce and perceive the calls? The next is, why do they stridulate on special occasions? Lastly, does the stridulation have any meaning to them?

As early as 1924 Carpenter suggested that the flies are in acoustic contact with each other (Buxton 1955: 210). Do these calls perhaps represent the "social factor" suggested by Buxton (1955: 486) which is responsible for the dispersal or aggregation of the community? Do they conform to the principles of Wynne-Edwards' concept (1962: 15) of dispersion in relation to social behaviour?

Vanderplank (1948) first demonstrated the significance of the "mating" call. The fact that the mating calls stimulate copulation proves that they do hear each other, according to Pumphrey's criteria (Haskell 1961: 2). "Hearing", by definition therefore, implies a response. Dethier and Stellar (1961: 72) consider that any "releasing stimulus"—in this case a call—provides an innate basis for social interaction and organization in the community.

Two community phases can be recognized, namely an active hunting, and a static, resting or hiding phase. The first involves mostly males, the second predominantly females. Initially there are only males surrounding the host in "the following swarm of Swynnerton". The females arrive later. The question is, how do they locate the host if they are more sedentary?

Sound-motivation and -location is apparently fairly common in the insect world (Frings & Frings 1958: 87-106). The purpose of the present investigation was to ascertain whether it is also the case in tsetse flies. In other contributions (Kolbe 1971, 1972) certain aspects of the ecological significance of sound production are discussed in rather speculative vein. This was unavoidable at that time. More factual evidence is available now.

The syntactical correlations of sound emission were explored by trying to prove that the

flies do hear each other; that the song patterns are related to specific activities; and lastly, that predictable responses can sometimes be elicited by certain calls and songs. As most glossinologists are aware, the tsetse flies are very refractory to behavioural manipulation (Bursell 1968: 11), but by conditioning them beforehand the response was improved.

Since the acoustic time-constant of insects is considerably shorter than ours, more critical and objective methods for investigation were employed. Besides the normal acoustic analyses, electronic apparatus viz. a tape-recorder, a wave analyzer and an oscilloscope were needed to explore the sound patterns beyond the human range of acoustic discrimination.

MATERIALS, METHODS AND APPARATUS

For obvious reasons the biggest available species of tsetse fly was used. A tape recorder, an audio-frequency generator, a modified oscilloscope and a 35 mm Asahi Pentax Spotmatic camera were also necessary. (Details in appendix.)

For record purposes, ease of handling and better sound recordings suitable for oscillography, the flies were isolated in 14 G mono-pill-boxes of which the tops and bottoms were cut out and replaced by dacron gauze glued on securely with clear Bostik household adhesive. The serial number, sex, date of emergence and feeding particulars of the fly were given on each box. This provided a direct and immediate reference to record on the tape with every call. Keeping the flies separately behind gauze also facilitated direct examination under the stereo-microscope for studying the possible sound-producing mechanisms, and provided a convenient way of keeping a constant distance between the fly and the microphone for standardizing the input volume at a comparable level. It is essential that all the relevant data should accompany every recording and be shown on every oscillogram. These details have been omitted in Figures 8–15.

To reduce static hum in a hand-held microphone, it was covered with a 1 cm thick plastic sponge. To eliminate scratching noises when the pill-box was held in front of the microphone a plastic cuff projected 0.5 cm beyond the head. The box containing the singing fly was held firmly on this rubber cuff. In this way many extraneous sounds which would spoil the quality of the oscillographic image on the screen were excluded.

DEFINITIONS

“Stridulation” is modulated insect sound-production irrespective of the mechanism.

A “pulse” is a basic unit of the oscillographic wave pattern.

A “phrase” consists of a short continuous series of pulses.

A “call” is a series of phrases in interrupted form, in which the duration of the sounds and intervals vary in temporal alignment.

A “song” is a continuous pattern of modulated sound.

“Chitter” is the soft calling sound made in the early phases of arousal when a number of flies sit together.

OBSERVATIONS

Call and song patterns

A tsetse fly of whichever sex or whatever age emits modulated sounds, in solo or in concert. The "call" or "song" is a distinct vibrato, formed by the pulses with an average repeat frequency (P.R.F.) of between 350–475 cycles per second. During this performance the greatest vibration of the thorax occurs over the pterothorax. The wingbase and tegula on the active side rock synchronously in the coronal plane. Usually only the overlapping wing, but occasionally both wings, can be seen to vibrate slightly.

Some flies are more prone to sing than others. From observations of 140 captive flies it was found that the females sing more readily, particularly after meals. A few can be coaxed to sing almost any time. Males "call" rather than "sing", but on a few occasions after a meal one sang as well as any female.

Distension of the abdomen seems to render the flies more prone to sing because they not only sang more frequently after a meal but also for longer periods. That it need not necessarily be blood that causes the distension was seen in a female with a very bloated abdomen. She never

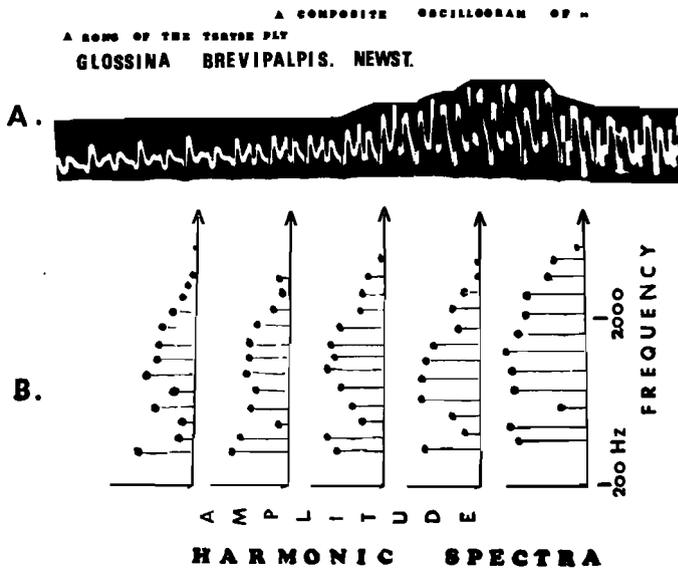


FIGURE 1

A. A composite oscillogram of a female song to show the amplitude and frequency modulation in the pulse patterns from the beginning to the end. Single pulses from each of 14 oscillograms taken at regular intervals of $\pm 3\frac{1}{2}$ seconds are arrayed in sequence.

B. A series of harmonic spectra of the same song taken every 5 seconds as shown by the arrows. The harmonic patterns seem fairly consistent, the dominant one either the first, second, fifth or sixth.

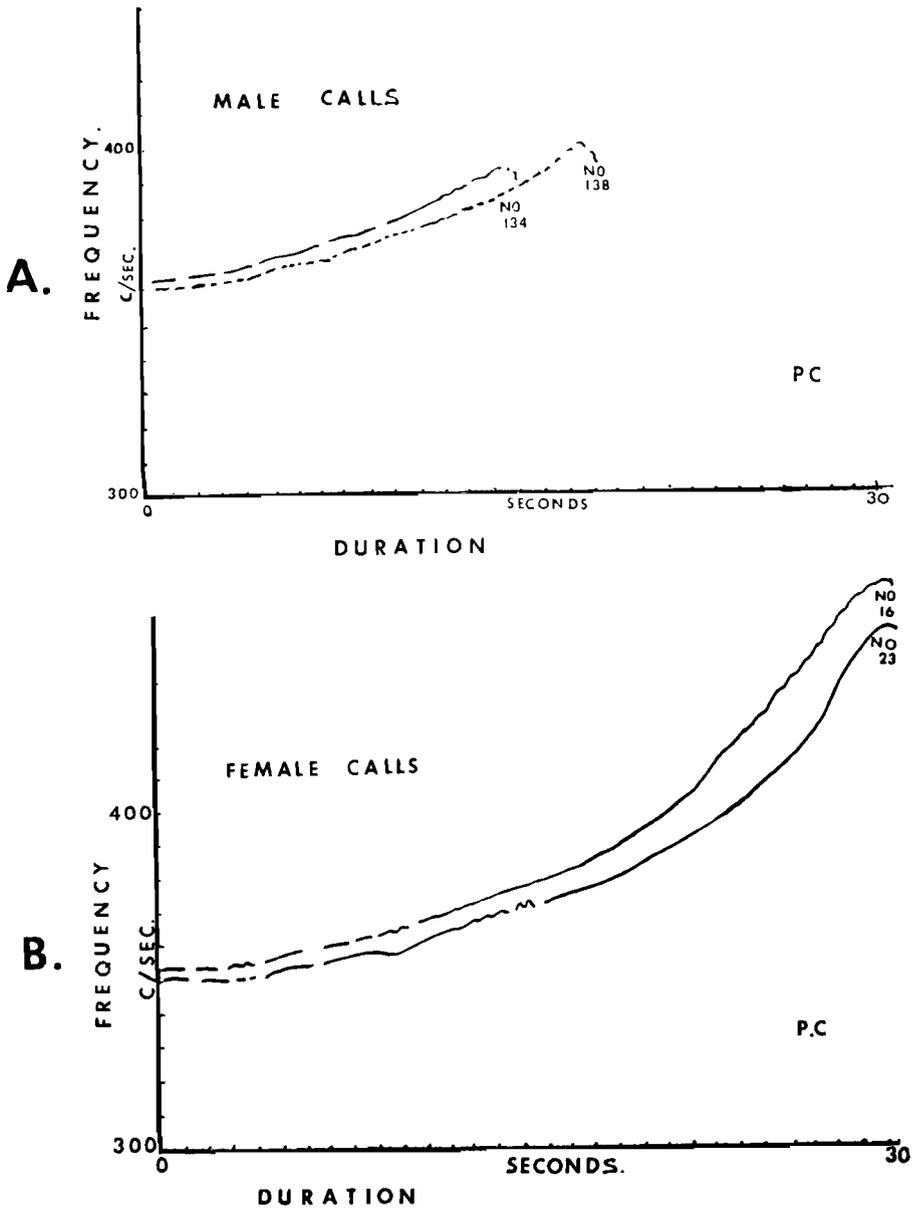


FIGURE 2

A and B. Graphic presentations of male and female calls and songs to show the temporal alignment of the phrases, the wavering notes, the rise in pitch and terminal decline of the post-feeding (P.C.) calls and songs. These graphs were prepared from specific numbered flies, but they approximate the average call and song patterns fairly closely. (See Table I.).

had a meal, the abdomen was transparent and therefore contained only air. She only lived four days but was the second-best singer in the collection.

Although singing seems to be a spontaneous activity, there is evidence of a periodic rhythm (Fig. 3). In responsive flies it can be elicited by external movements, rotary movement of their boxes, movement to and from an electric light, bringing them near one's body or by the calling of other flies.

On warm days they sing more readily. Complete darkness inhibits the singing reflex, which is again released as soon as the surroundings are faintly illuminated. As soon as the light is put off the song stops abruptly. Localized heat also seems to inhibit singing because it stimulates the probing reflex instead.

Sound is primarily produced by muscular contraction. The fly first changes to the "aroused" stance, then begins to call. Singing represents a phase of activity which, according to the amount of energy involved, borders on flying. Although it can be evoked reflexly, other factors, e.g. an endogenous rhythm, appetitive states (hunger and sex), ambient temperature and illumination, etc., seem to affect their responsiveness or phase of arousal.

Basically two sound patterns can be recognized, namely an interrupted "call" and a continuous "song". Three calls can be distinguished, namely the "chitter" of early arousal, the "common" and the "distress" call.

GLOSSINA BREVIPALPIS.

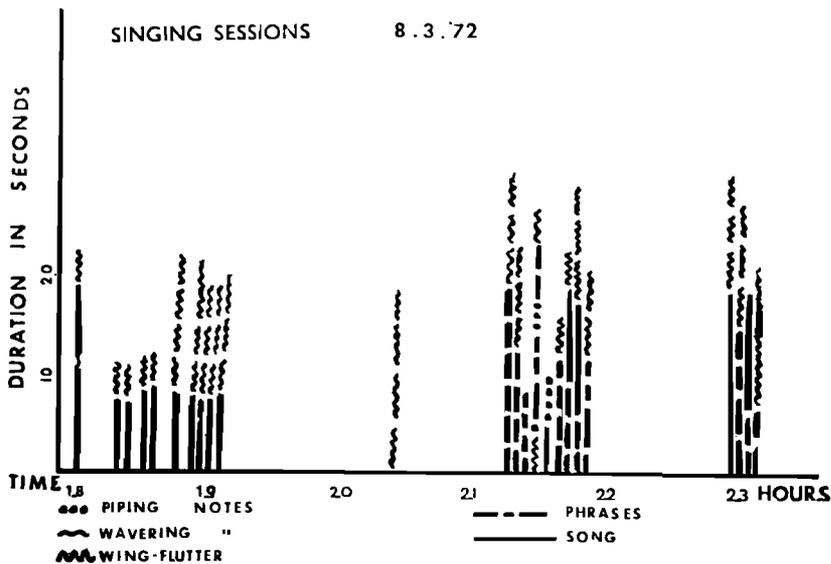


FIGURE 3

The periodicity, duration, and types of calls and songs of flies kept separately in boxes near to each other. Note the single or multiple bursts of wing fluttering after every call.

In the early stages of arousal a faint chittering can usually be heard in a group. The sounds vary in pitch and amplitude, while those of a teneral female have a warbling quality and seem to attract the older males or cause them to move about or call in their boxes. The common call varies considerably in pitch, tone, pattern and duration. Sometimes it is merely a monotonous repetition of phrases, but occasionally a lively morse-like call develops, followed by one or more bursts of wing-fluttering (Fig. 3). The "distress" call is heard whenever the fly is handled or when the female resists the male's copulatory efforts. It is always followed by violent wing-fluttering.

A song usually develops from a call (Fig. 2B). The call begins on a lower note, rises gradually, though not evenly, and ends on a higher note (Fig. 2A). While in the "calling" stage the pitch rises slowly, but once the singing stage is reached it rises more evenly and rapidly near the end (Fig. 2B). Before a meal the song usually ends in a decided lilt or piping note, followed by a wing-flutter. After a meal the call develops into a song sooner, usually lasts longer and invariably terminates on a few desultory notes without any wing-fluttering (Fig. 2A, B). The female song usually lasts longer than the average male's, and generally reaches a higher note (Fig. 2B).

TABLE 1

THE DURATION AND FREQUENCY OF MALE AND FEMALE SONGS

<i>No of Flies</i>		<i>Duration of Song</i>		<i>Rise of frequency</i>		<i>Limits of frequency</i>	
<i>Male</i>	<i>Female</i>	<i>Maximum</i>	<i>Average</i>	<i>Maximum</i>	<i>Average</i>	<i>Low</i>	<i>High</i>
26		40 sec.	13 sec.	150 c/s	43 c/s	250 c/s	520 c/s
	49	55 sec.	24 sec.	190 c/s	89 c/s	270 c/s	510 c/s

Apart from the ones mentioned above, no other calling patterns could be recognized amongst the flies reared in captivity. Amongst the recently caught ones at Ndumu, recurrent patterns could sometimes be detected, but these were too elusive and transient to recall.

Normally the calling phrases are short and set so closely that it is difficult to plot them graphically. Recording them at $3\frac{1}{2}$ i.p.s. and playing them back at $1\frac{1}{2}$ i.p.s., made it easier to distinguish the various characteristics of a call, namely the temporal alignment of the phrases and intervals between them, the rise in pitch and the termination of the songs (Fig. 2).

Electronic analyses

Electronic apparatus is required for highspeed analyses of sound records, and for a more sensitive evaluation of the various physical parameters of the sound patterns.

From the observations of Haskell (1961: 165-168) and Frings and Frings (1958: 99) there are several acoustic parameters which seem to evoke behavioural responses in the Orthoptera and Homoptera, namely frequency, intensity, temporal alignment of the sound unit and wave form.

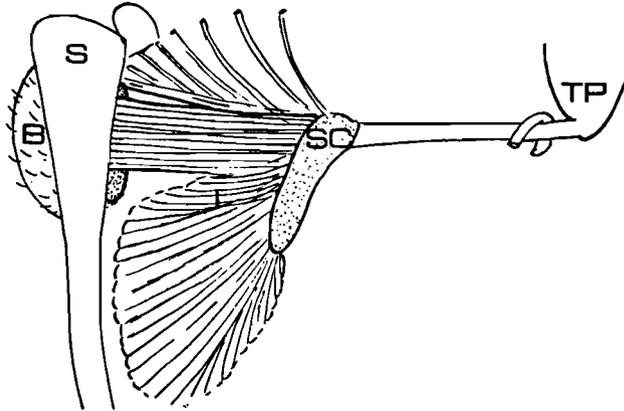


FIGURE 4

The tergal muscle of the pleural wing process (1). It originates on the pleural wing process, on the inside of the posterior half of the infra-alar bulla (B) and, by means of a few muscle strands, from the bottom of the tegula. The three heads insert on a small sclerite (SC) which is connected by a round tendon to the lateral process (TP) of the transverse suture. A tendinous sling from the basalare encircles this tendon near its insertion. (See also Figure 5.).

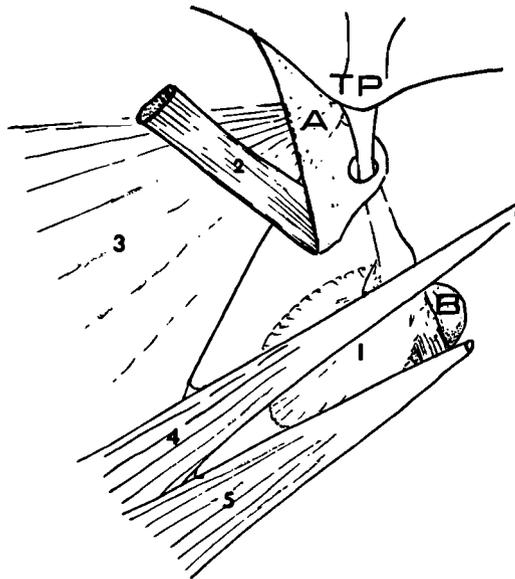


FIGURE 5

A medio-ventral view of the right tergal muscle of the pleural wing process (1) to show its relationship to the other structures and infra-alar bulla (B). An unusual condition of the basalare (A) is shown with the posterior part enlarged, sclerotized and perforated. Normally only a tendinous sling from the posterior surface of the basalare encircles the tendon of the tergal muscle of the pleural wing process (see Figure 4). The insertions of the anterior tergal muscle (2) and the pleural muscle (3) of the basalare (A) are shown. The pleural muscle of the first axillary sclerite (4) and the pleural muscle of the third axillary sclerite (5) are shown passing below the tendon of the tergal muscle of the pleural wing process.

Wave analyzer

Only one series of harmonic spectra is available (Fig. 1), prepared from the same song as the composite oscillogram shown above them. The patterns seem to be fairly characteristic in that the dominant harmonic is either the 1st or 2nd, 5th or 6th. No more can be said at this stage except that this aspect needs further investigation.

Oscilloscopic analyses

In the present series the sweep-frequencies remained fairly constant and the amplitude was adjusted so that all the oscillograms, except Fig. 13, are directly comparable. The sweep-frequencies were adjusted so that at least three pulses appeared on the screen, to avoid distortion of the central one. To familiarize oneself with the sound-image relationship, it is desirable to monitor oscilloscopy audio-visually. An oscillogram is a time-amplitude display of transduced sound impulses on a cathode ray screen. It consists of a steady linear pattern, synchronizing with a particular sweep-frequency. By increasing the input volume of sound to be explored the vertical aspect is enlarged. By increasing the sweep-frequency the horizontal aspect is enlarged so that fewer pulses appear on the screen. A slower sweep-frequency results in a condensed array of pulses on the screen.

Normally the frequency, intensity, and tone of a song change all the time. These parameters are reflected on the oscillogram by the width of the pulses, amplitude of the phases, and by the modification of the pulse configurations, respectively. As these changes occur independently of each other, an almost infinite variety of pulse patterns results, complicating the task of determining the basic one. From a study of a great many songs on the oscilloscope certain variations seem to be fairly constant and the modulation of the pulse patterns consistent enough to warrant description.

Every pulse is divided into two parts by an N-shaped coupling ("C" in Fig. 10). The wavy line on either side, at the beginning and end of a pulse, is produced by harmonics or sounds probably caused by the wings or other thoracic structures. Very often there is a double ripple superimposed on one or other side of the coupling disfiguring the pulse pattern (Fig. 15). When these harmonic ripples cycle faster or slower in relation to the basic pattern, they move to the left or right on the phases of the pulse pattern, augmenting or obliterating the existing wave lines. If the ripples occur on the left side, the ascending phase of the coupling becomes shorter or obliterated resulting in a notch (V) (Fig. 9B and 10A). Should they occur on the right side, a peak (A) results. Sometimes a superimposed ripple occurs on both sides, then both the ascending phases are affected (Fig. 10B). When there is a big phase difference between the left and right halves of the pulse only a single oblique line represents the coupling (Fig. 8B, 9A, 12).

There are indications that each half of the pulse is affected by one or other side of the thorax of the fly. In the distress call both wings are used and on the oscillogram the halves of the pulse are fairly equal (Fig. 13). The pattern of a fly without wings is fairly simple, except for the superimposed ripple seen in Fig. 15A, B. In a fly with a congenitally twisted right wing, the left half of the pulse is more pronounced (Fig. 12).

As the tone frequency and amplitude of the songs vary considerably, it is not surprising that the oscillograms of the same fly on different occasions vary as much as those of different flies. Even in the same song the pulse patterns vary markedly in the various stages (Fig. 1A). For this

reason only oscillograms of fully developed songs should be used for comparative oscillography.

So far oscilloscopy has not proved very helpful in the elucidation of consistent song patterns for syntactical correlation. Further research is indicated, particularly comparative oscillography of the songs of the different species of tsetse flies.

The mechanism of sound production

Several mechanisms for sound production have been described. (Pierce 1948; Haskell 1961: 26–61), e.g. frictional, vibrating or pulsed air mechanisms. Little is known about the mechanisms in Diptera, as most of the investigations have been confined to the Orthoptera and Homoptera.

In the tsetse fly muscular contractions cause rapid vibratory movements of the pteropleural area, peri-alar membranes and one, or sometimes both, wings. Amputation of both wings and halteres only changes tone slightly. Blocking the thoracic spiracles with vaseline does not inhibit sound emission. Several attempts have been made to watch the operculum of the metathoracic spiracle while the fly is singing, but synchronous vibrations were not observed.

Dissection of the thorax revealed a short stout tricipital muscle originating on the inside of the posterior half of the infra-alar bulla, from the sclerites of the tegula by means of a few tenuous fibres and from the pleural apodeme below the bulla. It inserts on to a small sclerite

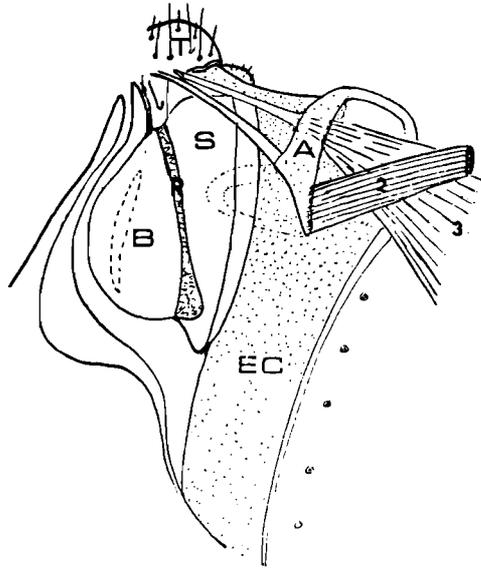


FIGURE 6

A medial view of the left infra-alar bulla (B) to show its sclerotized posterior rim and tendinous anterior rim (R) behind the subalifer (S) and below the tegula (T). The anterior tergal muscle (2), and the pleural muscle (3) of the basalare (A) are shown with two tendinous bands connecting it to the tegula. The membranous folds covering these two structures have been omitted, but are the reflections of the same membrane covering the epimeron-episclelerite cleft (E.C.). The outline of the muscular origin in the infra-alar bulla is shown by a broken line. The tendinous sling which encircles the tendon of the muscle arising in the infra-alar bulla is faintly indicated behind the basalare.

which is attached by a stout tendinous ligament to the lateral process of the transverse suture (Fig. 4). The infra-alar bulla is drawn antero-medially towards the lateral process of the transverse suture and at the same time downwards, pulling the posterior half of the bulla inwards and downwards, probably slackening the tendinous anterior rim of the bulla (Fig. 6). The posterior edge of the bulla is fairly rigid. The sound could be produced by clicking of the denting bullar wall or by the twanging of the anterior edge as it snaps taut when the pull is suddenly relaxed. These movements, as well as the contraction of the thin fibres attached to the tegula, cause the slight rocking motion of the wing-base and the vibration in the overlapping wing. Sounds may emanate from one or both sides of the thorax since vibrations are formed in one or both sides.

Posteriorly, the basalare is connected to the base of the tegula by two tendons (Fig. 6). From the postero-inferior edge a tendinous sling encircles the tendon of the muscle originating in the infra-alar bulla (Fig. 4, 5). A cord-like muscle from the humeral callus inserts on the anterior, lower edge of the basalare, while a fan-shaped muscle from the anterior edge of the episternum 2 inserts on the middle, anterior surface (Fig. 5, 6). An exceptional formation of the basalare is shown in Fig. 5. The posterior side is enlarged, sclerotised and perforated. The tendon of the muscle of the infra-alar bulla passes through this hole.

As the basalare will be pulled downward and forward by the two muscles, more or less perpendicularly to the axis of the muscle from the infra-alar bulla, a plucking effect or modulating action may result. Is it responsible for the superimposed ripple described above and seen in Figs. 11 and 15(?).

The anatomical arrangement is very reminiscent of the homopteral tymbal mechanism (Haskell 1961: 53, Fig. 34). It was decided to test this mode of action in the tsetse fly and to decapitate the tops of the infra-alar bullae. This procedure altered the tone of the sound but did not abolish it. It was discovered later that the muscle originates on the posterior half of the infra-alar bulla and that in the experiment the muscle was not destroyed. By that time the experiment could not be repeated as all the flies had died.

DISCUSSION

The following questions need answering and discussion:

1. *Can the tsetse flies "hear" each other?*

No organs of "hearing" have been described so far, but the following observations suggest that they do "hear":

- i Vanderplank (1948) succeeded in effecting inter-specific breeding by reproducing the mating calls.
- ii In the flexor angle of the tibio-tarsal joints of a fly the vascular pulsations stop as soon as an object is brought near it. This has also been observed when parts of a song were played back, or sometimes when other flies started singing or chattering nearby.
- iii When a recorded song was played back to a number of flies in separate boxes they could be heard to move about after a refractory period varying from 9–30 seconds. This experiment

was conducted in absolute darkness. As soon as the room was illuminated faintly they also started and one or more began to sing.

- iv Older males usually sit up from the "resting" to the "aroused" stance when a teneral female chitters. Later they begin to move about restlessly in their separate boxes.
- v Captive flies usually start moving about in their boxes after others have started calling.
- vi According to the observations on endogenous rhythm (Fig. 3) the flies were only in acoustic contact with each other as they were isolated in separate boxes, yet they soon began to sing one after the other.
- vii How does one explain the fact that there are more males in "the following swarm of Swynerton" near the host, while the female percentage increases as soon as feeding and singing has started? How do the females locate the host so readily when they are supposed to be sedentary and therefore unlikely to be in visual contact? Is it because they are attracted by the "pre-, and post-feeding call" of the early feeders?
- viii When singing in concert the flies often start and stop together.

2. How do the tsetse flies react to the calls of others in the community?

Several phonokinetic responses have already been described in captivity, e.g. stopping of vascular pulsations for a few seconds; changing the sitting stance from a more relaxed to the "aroused" one; orienting to the stimulus; starting to perform grooming motions; flying in response to the call of the teneral female. This does not imply that all the flies respond to a stimulus every time. By conditioning them beforehand and selecting the right types the number of responding flies can be increased and the refractory period decreased.

Under feral conditions it is very difficult to observe and record the motions and movements of members of *Glossina brevipalpis*, for the following reasons: When they sit, they do not move about, and when they fly it is difficult to keep them in sight in their usual environment. In the day they hide away and the males only emerge shortly before sunset, leaving only 30–45 minutes to observe their activity in the bush. In several hundreds of specimens caught at this time, not a single female was found. This was also the experience of Dr. F. A. Pires (personal communication) who did extensive observations on this species in the valley of the Maputo river a short distance from Ndumu. Here the flies were more abundant along the edge of the Shokwe and Niamiti floodpans where the hippos emerge and bushbuck and nyala drink at dusk. It was suspected that the females only emerge after the feeding calls started. To ascertain whether or not it was the case pre-recorded "pre- and post-feeding" calls were played at these sites and all the flies which arrived were caught. No females were found before it became too dark to see. With a small parabolic reflector and using a pre-amplifier the calls of the males were recorded as they arrived, but the numerous bird, bat, cricket and frog calls rendered it impossible to obtain clear, continuous calls of the males.

It should be very interesting to repeat these observations under more favourable circumstances in complete darkness, away from the water. The use of two bait animals, one to feed, another to catch flies by a covering of hessian treated with a sticky substance, should be very interesting. By recording the sexes of the flies, the time of arrival of the females in relation to the feeding ritual can be determined and may supply useful information.

CONCLUSIONS

Sound production is associated with structures in the ptero-thorax. The exact mechanism has not been proved conclusively but it seems to be related to the tymbal mechanism of the Homoptera. The pulse pattern appears to be source-generated. The indications for a bilateral origin of the two halves of a pulse suggest the possibility of separating the two sonic components by using sharply cutting band-pass filters, a method masterfully developed by Greenewalt (1968) for demonstrating the two voices of a bird.

While the mechanism of sound production and mode of hearing is only of academic interest, the reactions to the calls and songs may have practical significance.

The acoustic patterns of the calls and songs are constant enough, and the correlation with the activities sufficiently consistent in such an unco-operative subject, to regard the calls and songs as conventionally coded, physiologically induced and reflexly emitted signals.

In such an intensively studied, well-documented and economically important insect, the significance of sound in the social organization and functional integration of the tsetse fly community may be well worth further investigation.

ACKNOWLEDGEMENTS

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The modification of the oscilloscope was done by Mr. J. Human of Senekal who also lent me another one for comparative purposes, while Mr. J. J. Seymore of the Technical Services, S.A.B.C., prepared the harmonic spectra.

My wife corrected and typed the manuscript. To her my appreciation and thanks.

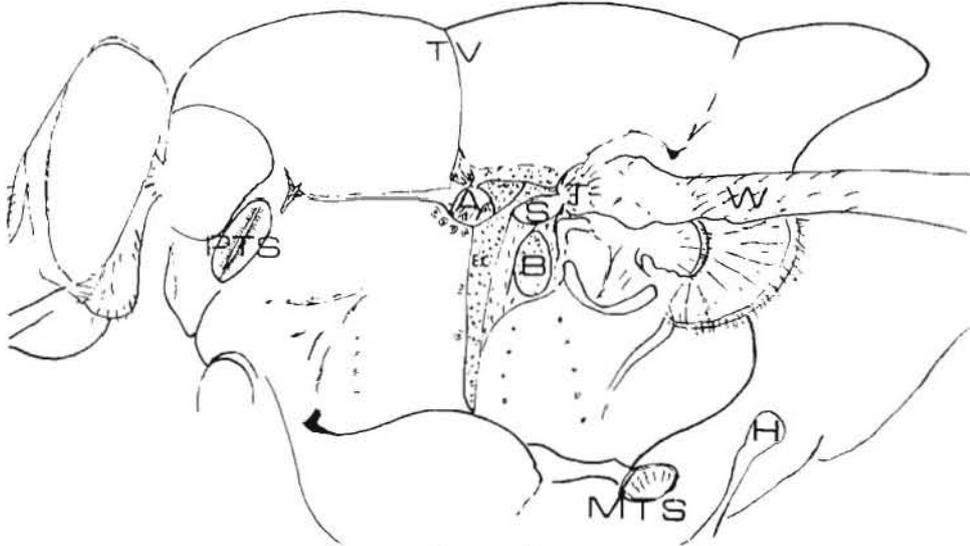


FIGURE 7

A lateral view of the wing-base area to show the infra-alar bulla (B) between the anterior and posterior wing processes; the epimeron-episternal cleft with membranous covering (EC) and the basalare (A). The position of the transverse suture (TV) is slightly anteromedial to the infra-alar bulla. PTS = Pro-thoracic spiracle; MTS = Metathoracic spiracle; H = Haltere.

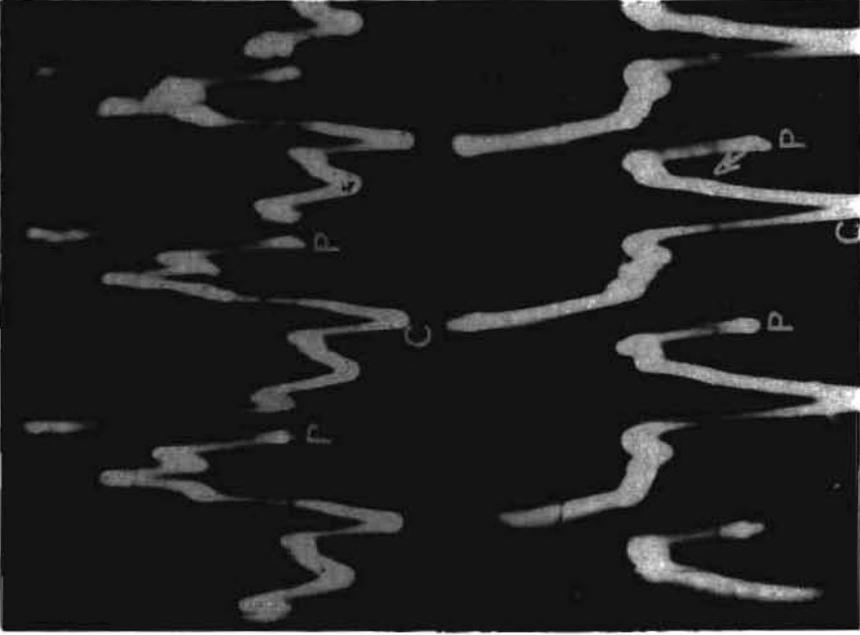


FIGURE 9

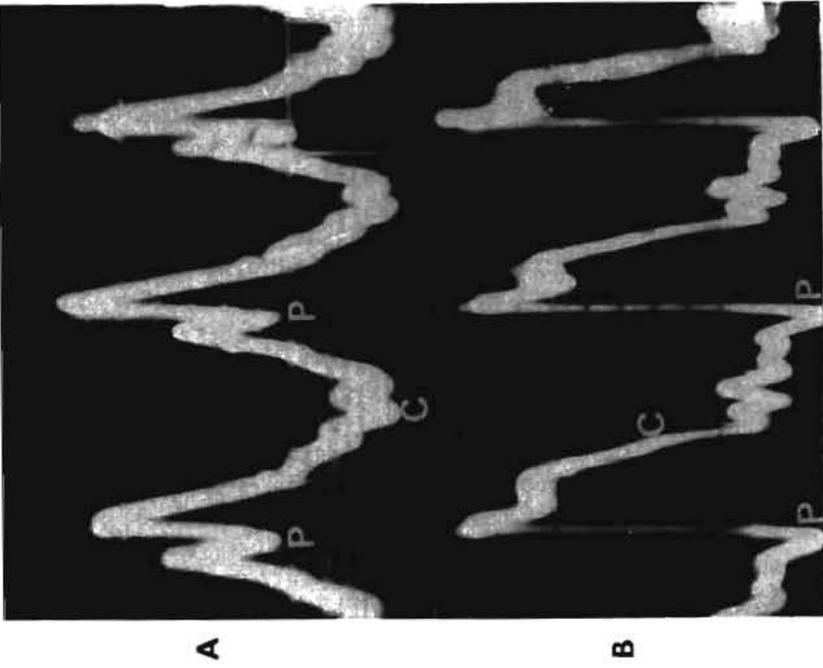


FIGURE 8

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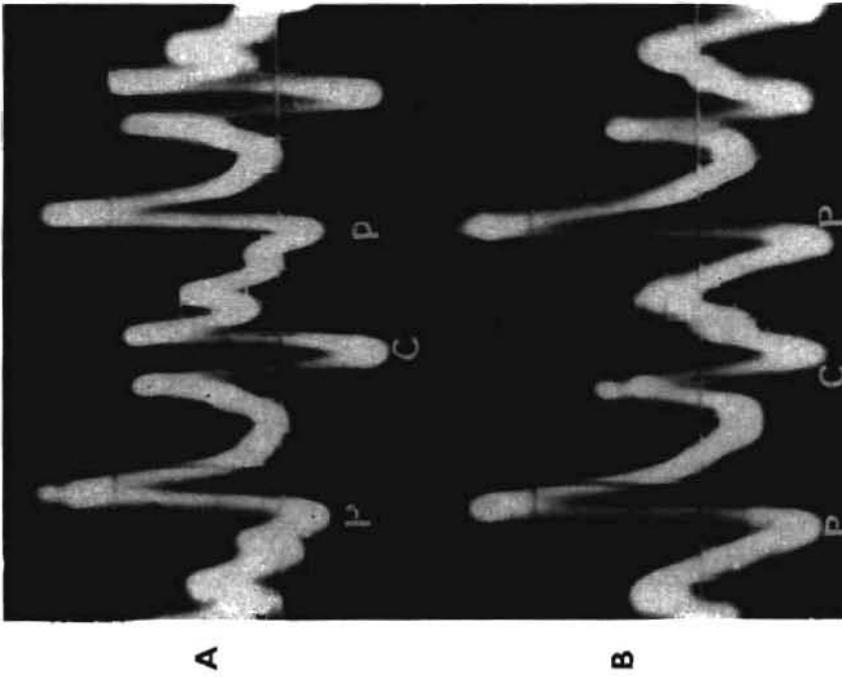


FIGURE 10

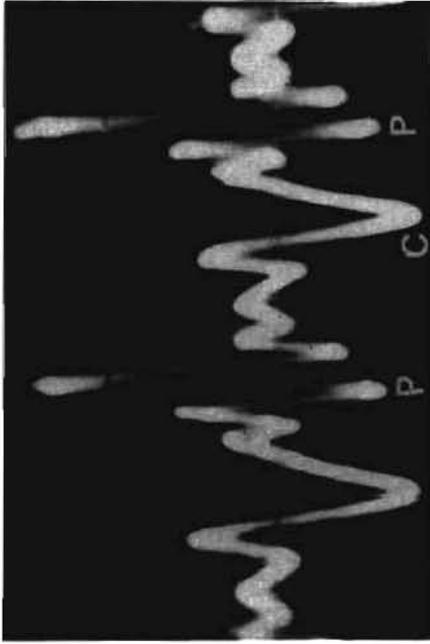


FIGURE 11

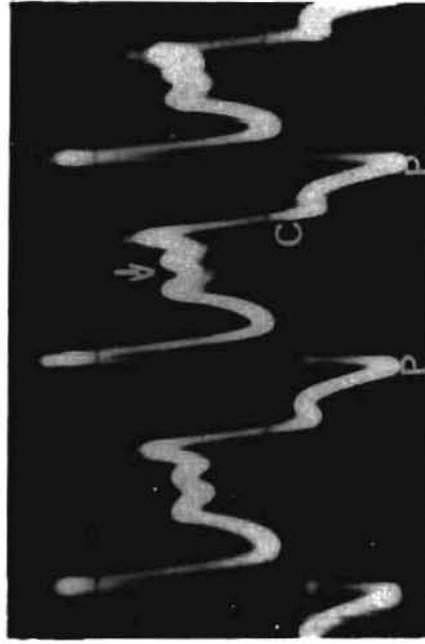


FIGURE 12

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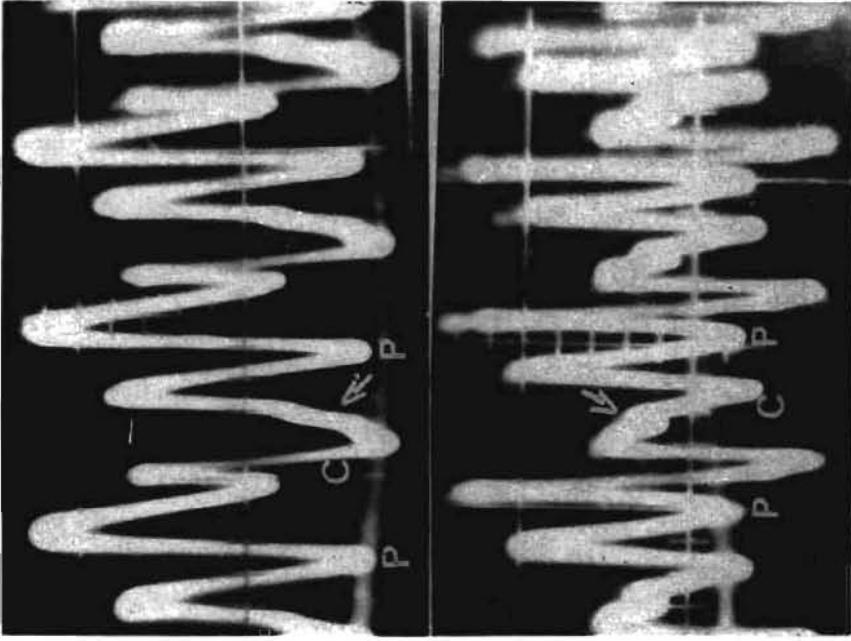


FIGURE 15

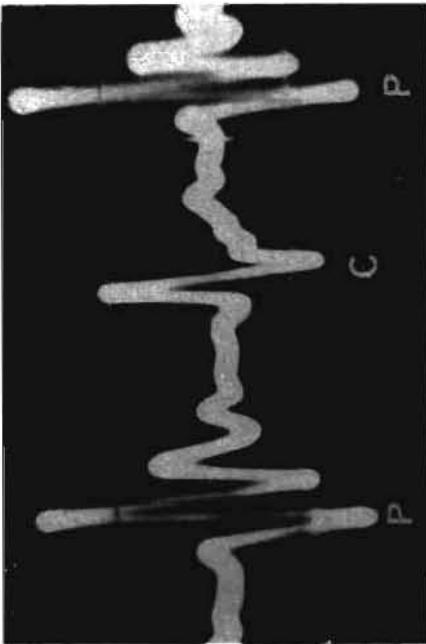


FIGURE 13

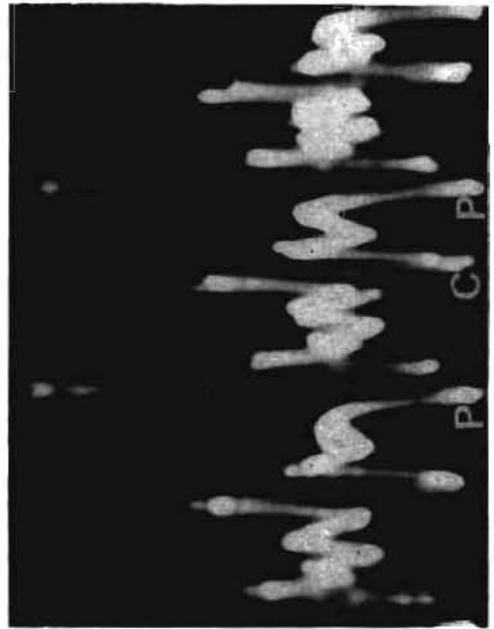


FIGURE 14

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CAPTIONS TO FIGURES 8-15

FIGURE 8

Oscillograms of the song of a male fly immediately after a meal. The repetition of the pulse patterns can be seen. A early in the song and B in the fully developed stage. P indicates the beginning of each pulse and C the coupling between the two halves of the pulse. When the harmonics of the two halves lie on the same level the coupling is basically N-shaped (cf. Figures 13-14), but when widely separated the coupling is virtually a straight line as in Figures 8B, 9A and 12.

FIGURE 9

Oscillograms to show the variation in pulse patterns taken one minute (A) and two hours (B) after a meal. In A the harmonics in the two halves of the pulse lie at different levels and the coupling is rectilinear. In B the coupling is exaggerated possibly by a superimposed harmonic (arrow) in the same phase. The initial ascending phase of the N-coupling has been cancelled by the harmonics on the left half.

FIGURE 10

Oscillograms of the pulse patterns of two males taken two (A) and five (B) hours after a meal to show the deformation of the coupling by the harmonics in the first and second halves of the pulse.

FIGURE 11

An oscillogram to show the pulse pattern of a female five days after a meal vibrating her right wing only. Note the greater number of harmonics in the left half deforming the initial ascending phase of the N-coupling (C).

FIGURE 12

An oscillogram to show the pulse pattern of a female with a congenitally twisted right wing. Again the active right wing causes a dominant half on the left side of the pulse. (See Figure 11).

FIGURE 13

An oscillogram using a faster sweep frequency to increase the pulse length of the 'distress' call in which both wings are vibrating vigorously. In this pattern the halves are very similar, the harmonics on the same level, with the left side slightly more dominant, probably caused by the overlapping wing. The N-shaped coupling (C) is hardly deformed due to the equality of the two sides.

FIGURE 14

An oscillogram of the 'chitter' of a female using both wings. Again there is near equality of the two halves of the pulse and little deformity of the N-shaped coupling (C). The difficulty in synchronizing the signal is due to the fact that the sound was very soft and a stronger 'take-up volume' used with the result that extraneous sounds were also recorded. These sounds adversely affect the oscilloscope quality of the main signal.

FIGURE 15

The oscillogram of a fly with both wings and halteres amputated, showing the comparatively simple patterns of the pulses with a superimposed harmonic ripple (arrow) moving from the right to the left side of the coupling (C). The relatively featureless pattern may be due to the absence of wings which seems to affect the modulation of sound pattern and oscilloscope image.

APPENDIX

Apparatus

1. National Automatic Reverse, Model RQ-158 S, Tape Recorder. Tape speed $3\frac{1}{2}$ or $1\frac{1}{2}$ i.p.s. Double track. Automatic Reverse Recording system: AC bias 35 K c/s. Batteries 6 X UM-1. Frequency response 130 8000 c/s at $3\frac{1}{2}$ i.p.s. Input impedance Mic. 8 K. Aux. 80 K. Output impedance Ext. Speaker. 8. Dynamic microphone.
2. Mini-A.F. Generator Mod. 6803. 10 c/s-100 K c/s. in 4 bands. Sine and square wave.
3. Tech-Model TO-2. Oscilloscope. Time-base (modified) 3 bands: 40-60 c/s; 160-600 c/s, and 400-1800 c/s.
4. Photo-oscillography: Camera: Asahi Pentax Spotmatic. Exposure 1/60 sec. Film: Tri-X Pan. Develop. D.76, undiluted for 20 min. at 70° F.

REFERENCES

- BRADY, J. 1970. Characteristics of spontaneous activity of tsetse flies. *Nature* 228: 286-287.
- BRADY, J. 1971. Laboratory observations on the visual responses of tsetse flies. *Trans. R. Soc. trop. Med. Hyg.* 65: 226-227.
- BURSELL, E. 1968. *A prospect of tsetse flies*. Inaugural lecture, University College of Rhodesia, Salisbury.
- BUXTON, P. A. 1955. *The natural history of tsetse flies*. London, Lewis.
- DETHIER, V. G. and STELLAR, E. 1961. *Animal behaviour* (2nd Edit.). Foundations of modern Biology Series, Prentis Hall.
- FRINGS, H. and M. 1958. Uses of sounds by insects. *A. Rev. Ent.* 3: 87-106.
- GREENEWALT, C. H. 1968. *Bird Song: acoustics and physiology*. Smithsonian Institution Press, Washington.
- HASKELL, P. T. 1961. *Insect sounds*. London, Witherby.
- KARTMAN, L. *et al.* 1946. A note on the noise-making ability of the tsetse fly, *Glossina palpalis* Rob.-Desv. (Diptera, Glossinidae) while in flight. *J. Parasit.* 32:91.
- KOLBE, F. F. 1971. The significance of an intercommunicating system in a tsetse fly community (read at 2nd Rhodes Scient. Congr.).
- KOLBE, F. F. 1972. The social organisation and functional integration of a tsetse fly community. *Rhodes. Sci. News*, 6: 28-30.
- PIERCE, G. W. 1948. *The Songs of Insects*. Cambridge Harvard University Press, Mass.
- SCHLEIN, Y. 1970. A comparative study of the thoracic skeleton and musculature of the Pupipara and the Glossinidae (Diptera). *Parasitology*, 60: 327-373.
- VANDERPLANK, F. L. 1948. Experiments in cross-breeding tsetse flies (*Glossina* species). *Ann. trop. Med. Parasit.* 42: 131-153.
- WYNNE-EDWARDS, V. C. 1962. *Animal dispersion in relation to social behaviour*. Edinburgh, Oliver and Boyd.