COMMUNICATIVE BEHAVIOUR OF THREE GRASSHOPPER SPECIES OF QUEBEC (ORTHOPTERA, ACRIDIDAE, GOMPOCERINAE)

by

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COMMUNICATIVE BEHAVIOUR OF THREE GRASSHOPPER SPECIES

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ABSTRACT

M.Sc. Paul Hunt Entomology

COMMUNICATIVE BEHAVIOUR OF THREE GRASSHOPPER SPECIES OF QUEBEC (ORTHOPTERA, ACRIDIDAE, GOMPHOCERINAE)

General taxonomy and biology of Chorthippus curtipennis curtipennis (Harris), Orphulina speciosa (Scudder) and Chloealtis conspersa (Harris) are summarized. An account of the common signals of stridulatory grasshoppers is followed by the description, occurrence and comparison of the visual and acoustical behaviour of the three species studied. Oscillogram analysis of the stridulation indicated that Chloealtis conspersa produced sound during the upstroke. A faint "tick" sound was made by Orphulina speciosa during the downstroke of stridulation. Stridulation oscillograms of Chorthippus c. curtipennis are also presented and compared with three European species of Chorthippus.

RESUME

M.Sc. Paul Hunt Entomologie

COMPORTEMENT DE COMMUNICATION DE TROIS ESPECES DE SAUTERELLES DU QUEBEC (ORTHOPTERA, ACRIDIDAE, GOMPHOCERINAE)

La position taxonomique et la biologie générale des espèces *Chorthippus curtipennis curtipennis* (Harris), *Orphulina speciosa* (Scudder) et *Chloealtis conspersa* (Harris) sont sommairement examinées. Un compte-rendu des signaux communs des sauterelles stridulantes est suivi par la description, l'occurrence et la comparison des comportements de communication visuelle et acoustique des trois espèces étudiées. Des analyses d'oscillogrammes de la stridulation ont démontré que *Chloealtis conspersa* produit un son pendant le mouvement ascendant. Un faible "tick" est produit par *Orphulina speciosa* pendant le mouvement descendant de la stridulation. Les oscillogrammes de la stridulation de *Chorthippus c. curtipennis* sont aussi présentés, et comparés avec trois espèces européennes de *Chorthippus*.

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Finally I am grateful to Ron Greendale for the French translation of the abstract, and to Alison Bentley for typing the manuscript.

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"We take an insect, we pierce it with a long pin, we fix it in a cork-bottomed box, we place under its feet a label with a Latin name and that is all there is to be said about it. This method of understanding entomological history doesn't satisfy me at all. There is no use telling me that such and such a species has so many joints in its antennae, so many wing veins ... I do not really know the animal until I comprehend its way of life, its instincts, its habits".

JULES MICHELET, l'Insecte, 1859

(after Hays, 1972).

INTRODUCTION

Stridulatory organs and other devices known to produce sound have been described for many arthropods, including practically all insect orders (Busnel, 1963) and in particular the Orthoptera (Kevan, 1955).

The present study of three gomphocerine acridid grasshoppers, Chorthippus curtipennis curtipennis (Harris), Orphulina speciosa (Scudder) and Chloealtis conspersa (Harris) describes and compares their common behavioural sequences in all possible combinations of male-female interactions. The stridulatory sounds of the three species are illustrated by means of oscillograms.

Relatively little behavioural and acoustical work of a comparative nature has been done concerning the three grasshopper species which form the basis of this study.

Since only one species from each of the three genera has been studied, generic names alone will sometimes be used in the following account in place of full species names.

LITERATURE REVIEW

Grasshoppers have interested man for centuries. Long before the times of Aristotle the song or stridulation of these insects was the subject of numerous dissertations. The second half of the nineteenth and the twentieth centuries, however, brought a more scientific approach to the writings on the topic. Several early papers, notably by Scudder (1868a, 1868b, 1897), Allard (1910, 1911, 1929) and Snodgrass (1924), gave accounts of the ecological and musical variation of numerous Northern American species of grasshoppers.

Flight stridulation or crepitation in American oedipodine acridids was studied particularly by Isely (1936). He concluded that sound was produced by the stiffened veins of the hind wings and not by the tegmina, as was previously thought. Isely showed that grasshoppers hear and react to flight stridulation.

Pumphrey and Rawdon-Smith (1936a, 1936b, 1939) published several papers dealing with sound reception in various insects, especially acridids and gryllids. They proposed (Pumphrey and Rawdon-Smith, 1939) that the sound frequency of stridulation had no significance, but rather that the temporal frequencies or impulses were of prime importance in stridulatory signalling.

The electronic recording and analysing equipment developed during and after World War II began a new era, attracting many workers into numerous aspects of the field of animal communication.

Following a symposium on orthopteran acoustics in 1954 (Busnel, 1955) studies concerning sound production and reception, stridulatory morphology and communicative behaviour were published (Jacobs, 1955; Haskell, 1956, 1957, 1958; Alexander, 1957). Again it was suggested that the ability to discriminate frequencies or pitch is less important to grasshoppers than the ability to discriminate temporal modulation sound (Haskell, 1956, 1961; Michelson, 1966; Uvarov, 1966).

By the 1960's there was a considerable accumulation of information in the field of animal acoustics and communication. Several detailed texts on the subject were released (Lanyon and Tavolga, 1960; Haskell, 1961; Busnel, 1963; Sebeock, 1968). Bioacoustic terminology was defined by Broughton (1963). Techniques in recording sound for bioacoustical studies were described by Kellogg (1960) and the analysis of sound by Borror (1960) and Andrieu (1963). The texts in which these papers appear deal with numerous sound-producing animal groups. Sound communication in orthopteroids and cicadids was discussed by Alexander (1960) and the apparatus of sound emission and the characteristics of the sound produced were described by Dumortier (1963). Communication in arthropods generally, was reviewed by Alexander (1968).

More recently, Otte (1970) published a major comparative study of communicatory behaviour in grasshoppers in which 114 North American species were examined. Subsequent to this monograph more detailed studies of individual orthopteroid species were made, both in North America and in Europe (Willey and Willey, 1971; Young, 1971; Alcock, 1972; Otte, 1972; Pickford and Gillott, 1972a, 1972b; Elsner, 1974; Hartmann and Loher, 1974; Kerr, 1974; Pickford, 1974; Steinberg and Conant, 1974; Steinberg and Willey, 1974; Willey, 1975; Samways and Broughton, 1976).

PART I. A GENERAL TAXONOMIC DESCRIPTION OF THE GRASSHOPPERS Chorthippus curtipennis curtipennis, Orphulina speciosa AND Chloealtis conspersa.

There are fourteen established species of stridulating grasshoppers which occur in Quebec and the Atlantic Provinces. (Vickery et al, 1974). All are members of the family Acrididae and are grouped in two subfamilies as follows:

Subfamily OEDIPODINAE

Chortophaga viridifasciata viridifasciata (DeGeer)
Encoptolophus sordidus sordidus (Burmester)
Camnula pellucida (Scudder)
Paradalophora apiculata (Harris)
Dissosteira carolina (Linnaeus)
Spharagemon bolli bolli (Scudder)
Spharagemon collare (Scudder)
Trimerotropis verruculatus verruculatus (Kirby)
Stethophyma lineatum (Scudder)
Stethophyma gracile (Scudder)

Subfamily GOMPHOCERINAE

Orphulina speciosa (Scudder)
Chloealtis conspersa (Harris)
Chloealtis abdominalis (Thomas)
Chorthippus curtipennis curtipennis (Harris)

Members of the Subfamily Gomphocerinae can be distinguished from the Oedipodinae by several taxonomic features, such as general size and stridulatory apparatus. Distinguishing features of the two subfamilies compiled from Dirsh (1975) are compared in Table 1.

Adult grasshoppers of the subfamily Gomphocerinae are generally smaller in size and stridulate by rubbing the hind femora, each of which bears a row of pegs on the inner surface, against toughened veins of the tegmina.

Most members of the Oedipodinae possess sharp carinulae on the inner side of the hind femora. Sound is produced by rubbing these carinulae against the serrated intercalary veins of the medial area of the tegmina. The stridulatory apparatus of some genera, notably Stethophyma, is rather similar to that of the gomphocerines, although a roughened ridge is present on the inner surface of the hind femur instead of a row of pegs, and the actual mechanism of sound production may differ.

TABLE 1

A COMPARISON OF THE TAXONOMIC FEATURES OF THE SUBFAMILIES GOMPHOCERINAE AND OEDIPODINAE

FEATURES	GOMPHOCERINAE	OEDIPODINAE
BODY SIZE	Small to medium	Small to large
BODY SHAPE	Short, cylindrical	Relatively stout, cylindrical, moderately elongate
HEAD	Obtusely conical	Subglobular to short conical
FACE (profile)	Straight or slightly outcurved; fastigium of vortex short at apex; angular or rounded; fastigial foveolae present; concave or flat	Straight, outcurved or slightly incurved; fastigium of vortex short; subglobular or angular, fastigial foveolae absent or present
ANTENNAE	Filiform, phyliform or clavate	Filiform
PRONOTUM (dorsum)	Flat, subcylindrical or slightly saddle-shaped	Tectiform
POSTERNAL PROCESS	Absent, rarely low tubercle present	Absent
TEGMINA AND WINGS	Fully developed, shortened, rarely absent; reticulation sparse; intercalary vein of medial area of tegmen absent	Fully developed or shortened, reticulatio dense, strong and mostly with serrated intercalary vein of medial area of tegmen

Ctd.

FEATURES	GOMPHOCERINAE	OEDIPODINAE
HIND WINGS	Sometimes specialized forming widened areas and speculum, thickened costal vein and inflated costal area; clear in colour	Brightly coloured to colourless and transparent; usually with some degree of colour
HIND FEMORA	Moderately widened	Short and mostly widened
HIND FEMUR-TIBIA ARTICULATION	With rounded or obtuse angular lobes	Short and mostly widened, with short rounded lobes, or rarely with angular lobes
HIND TIBIA		Sometimes with apical half slightly expanded
PHALLIC COMPLEX Endophallus		
Basal halves of penis	Strongly outcurved at proximal ends; Large and wide	Slightly curved sideways at proximal ends Small and narrow
Gonopore Process	Present	Present
Apical Valves	Relatively wide, upcurved flexure long and relatively wide	Relatively short and wide, flexure moderately short
Epiphallus	Bridge-shaped, short and narrow	Bridge-shaped, moderately narrow
STRIDULATION	Serration on inner side of hind femora consisting of a row of small pegs in a straight or regularly undulating or irregularly shaped line.	Serrated intercalary vein on medial area of tegmen and sharp carinula on inner surface of hind femur Ctd.

FEATURES	GOMPHOCERINAE	OEDIPODINAE
STRIDULATION Ctd.	Pegs articulated to femur by membraneous connections on their bases enclosed by follicles Sound is produced by rubbing row of pegs against veins of the tegmen (radial and medial)	Sound is produced by rubbing carinulae over serrations of the intercalary vein of the medial area of the tegmen

This part of the thesis is confined to the study of three of the four Quebec species of Gomphocerinae, which may be distinguished from each other as indicated below:

Orphulina speciosa (Scudder, 1862)

A species which is relatively small in size. The average adult male body length is 13.5 mm and that of the adult female 18.5 mm. Although the colour is variable, green is the most common in Quebec. This involves the head, pronotal disc and tegmina being green. The colour and size of this species make it inconspicuous in grass. The antennae are short, and are generally less than half as long as the body, the average male antenna being 5.7 and the female 5.6 mm long. The slender hind femora and clear hind wings are not distinguishing features. The tegmina are variable in length, but usually reach the ends of the hind femora. The foveolae (depressions or pits) of the front of the head are distinct but are not visible from above.

Chorthippus curtipennis curtipennis (Harris, 1841)

This is a small species with an average male body length of 15 mm, and the female 18.5 mm long. The colour is variable, from green to olive-gray or to brownish-red, with dark lines on the head and sides of the pronotum. The antennae are longer than those of O. speciosa. In the adult male they are approximately three-quarters the body length, averaging 11.35 mm. The average length of female antennae is only 6.62 mm, considerably shorter than those of the male. As in the case of O. speciosa both the slender femora and the clear hind wings are not distinguishing features. However, the hind femur-tibia articulations are black in colour, and are conspicuous when the hind legs are moved, especially when stridulating. The tegmina of the male usually reach the end of the abdomen. The foveolae of the head are visible from above as linear depressions.

Chloealtis conspersa (Harris, 1894)

This is a small species with an average male body length of 16.5 mm, that of the female being 21.3 mm. The male is dark brown in colour with the sides of the pronotum and the base of the abdomen black. The female is pale brown to gray, without black sides. The area above the antennae is black in both sexes. The average antennal length of males is approximately half that of the body length, being 9.4 mm. The average length of the female antennae is 9.2 mm. The hind tibia and undersides of the slender hind femora are dark red.

The tegmina of the male usually reach the end of the abdomen, whilst in the female only about two-thirds of the abdomen is covered. The tegmina are broadly rounded at the tips, those of the male bearing either few or no spots, whilst those of the female are conspicuously speckled.

Table 2 shows a comparison of some distinguishing features of O. speciosa, C. conspersa and C. curtipennis curtipennis. For a more detailed taxonomic discussion and for an account of the other less common Quebec gomphocerine Chloealtis abdominalis (Thomas), see Vickery et al (1974).

TABLE 2

A GENERAL TAXONOMIC COMPARISON OF Orphulina speciosa, Chloealtis conspersa and Chorthippus curtipennis curtipennis

FEATURE	Orphulina speciosa	Chloealtis conspersa	Ch. c. curtipennis
AVERAGE BODY LENGTH	Male: 13.5 mm Female: 18.5 mm	Male: 16.5 mm Female 21.3 mm	Male 15.0 mm Female: 18.5 mm
COLOUR	Variable; head, pronotal disc and tegmina green most common in Quebec	Male: dark brown with sides of pronotum and base of abdomen black. Female: pale brown to gray, without black sides. Area above the antennae black in both sexes	Variable, from green to olive-gray to brownish red. Dark lines on head and side of pronotum
AVERAGE ANTENNA LENGTH	About one-third of body length. Male: 5.7mm, Female 5.6mm	Male, over half body length 9.4mm, female 9.2mm	Male, about three quarters body length, 11.4mm Female, 6.6mm
HIND FEMORA	Slender	Slender, underside red	Slender, femur-tibia joint black
HIND WINGS	Clear	Clear	Clear
TEGMINA LENGTH	Variable, usually reaches end of hind femora. In Quebec usually green in colour	Male, usually reaches end of abdomen. Female usually covers about two thirds of abdomen Broadly rounded tips,	Male, usually reaches end of abdomen. Female usually covers about two thirds of abdomen Brown in colour

ctd.

FEATURE	Orphulina speciosa	Chloealtis conspersa	Ch. c. curtipennis
TEGMINA LENGTH Ctd.		those of male without spots or with a few dusky spots, those of female speckled	
FOVEOLAE	Distinct but not visible from above	Absent	Visible from above as linear depressions

PART II. THE GENERAL BIOLOGY OF Orphulina speciosa, Chloealtis conspersa AND Chorthippus curtipennis curtipennis

a) Range

Orphulina speciosa

O. speciosa is the only species of the predominantly Neotropical genus Orphulina which occurs in the province of Quebec. It is found over the southwestern part of the province west of Tadoussac and Quebec City (Fig. 1). It is abundant in certain eastern and central regions of Canada, but it is not very common in Quebec (Cantrall, 1943; Vickery et al, 1974; Crozier, 1977).

Chloealtis conspersa

C. conspersa is a northern species, extending from Maine to Quebec (Fig. 2) and Ontario and south in the mountains to Virgina and west to Nebraska and British Columbia (Vickery et al, 1974). It is chiefly a woodland species, found in clearings or along the edges of woodlands. Females oviposit in rotting wood (Vickery et al, 1974; Crozier, 1977).

Chorthippus curtipennis curtipennis

C. c. curtipennis is widespread in the northern United States and much of Canada. With the possible exception of Dissoteira carolina (Linnaeus), it has the widest distribution of any of the Orthoptera known from eastern Canada, where it is by far the most widely distributed species (Fig. 3).

It occurs in all provinces and territories and in the state of Alaska, in the south along the mountains it reaches Tennessee and even New Mexico; in southern California it is replaced by a different subspecies (Vickery et al, 1974).

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Figure 1. Map - Orphulina speciosa distribution in northeastern North America

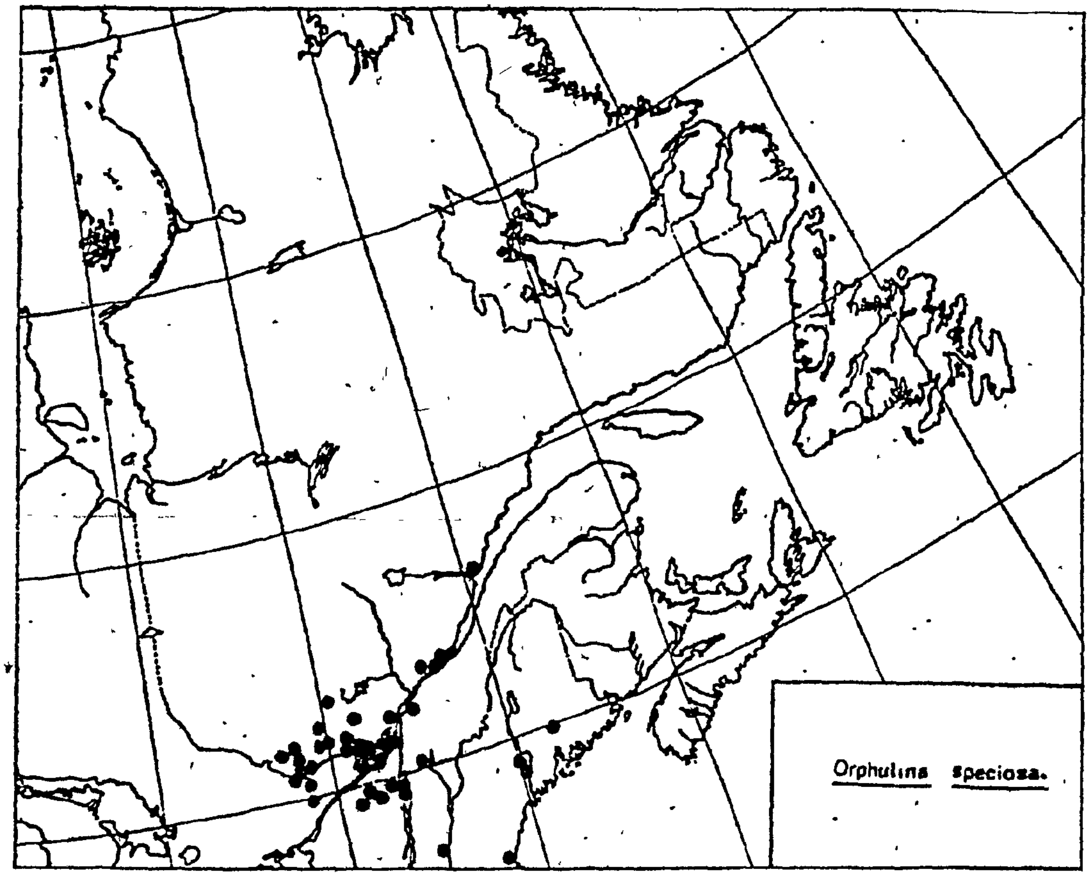
Orphulina speciosa.

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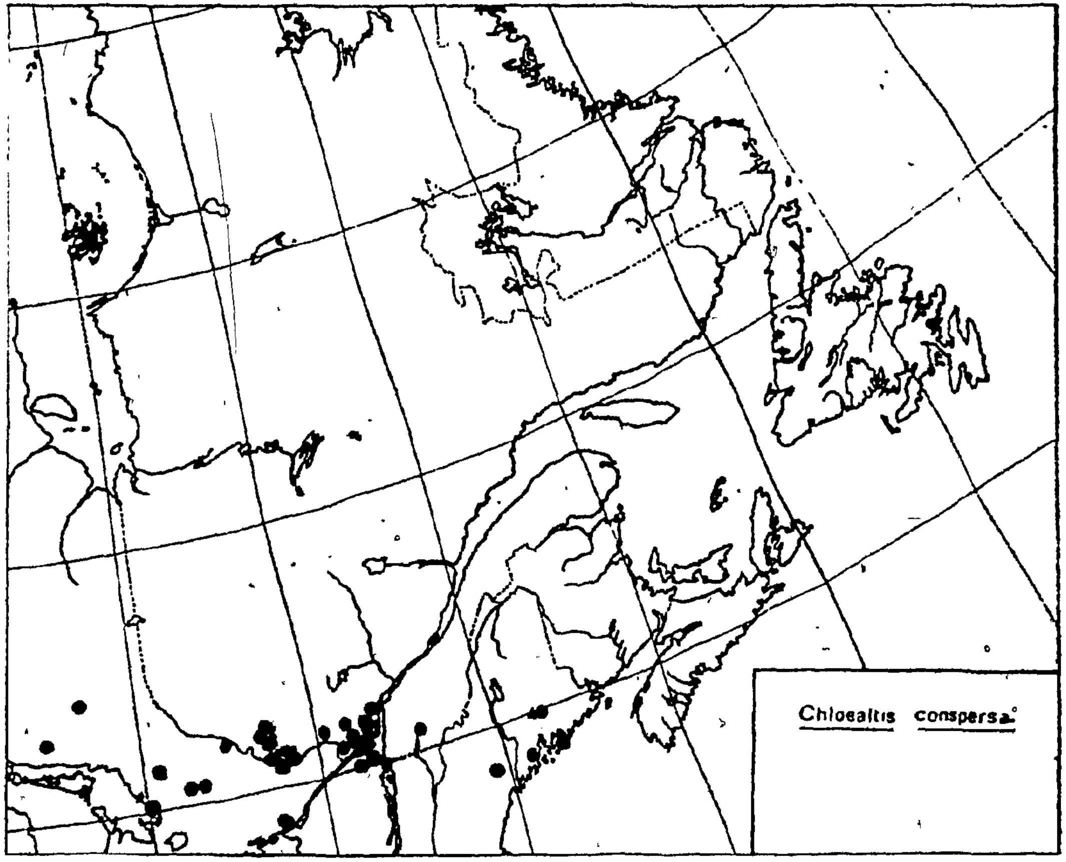
Figure 2. Map - Chloealtis conspersa distribution in northeastern North America


Chloealtis conspersa.

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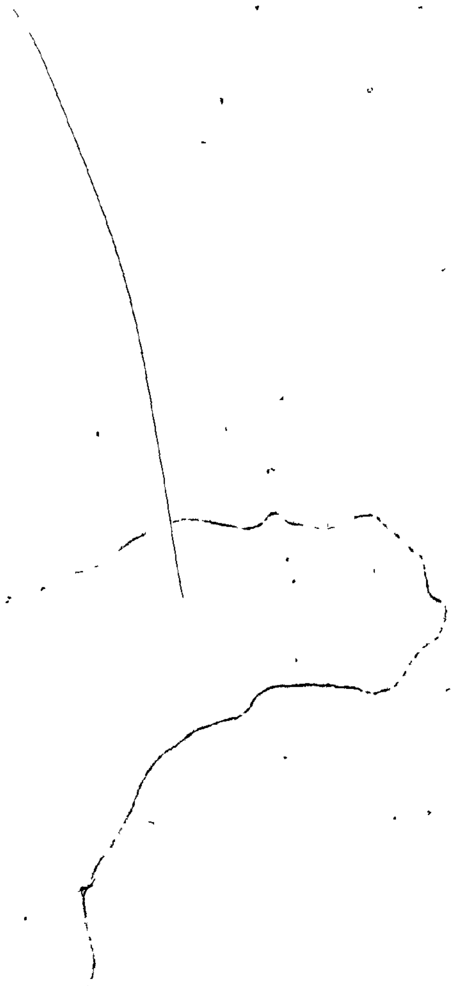
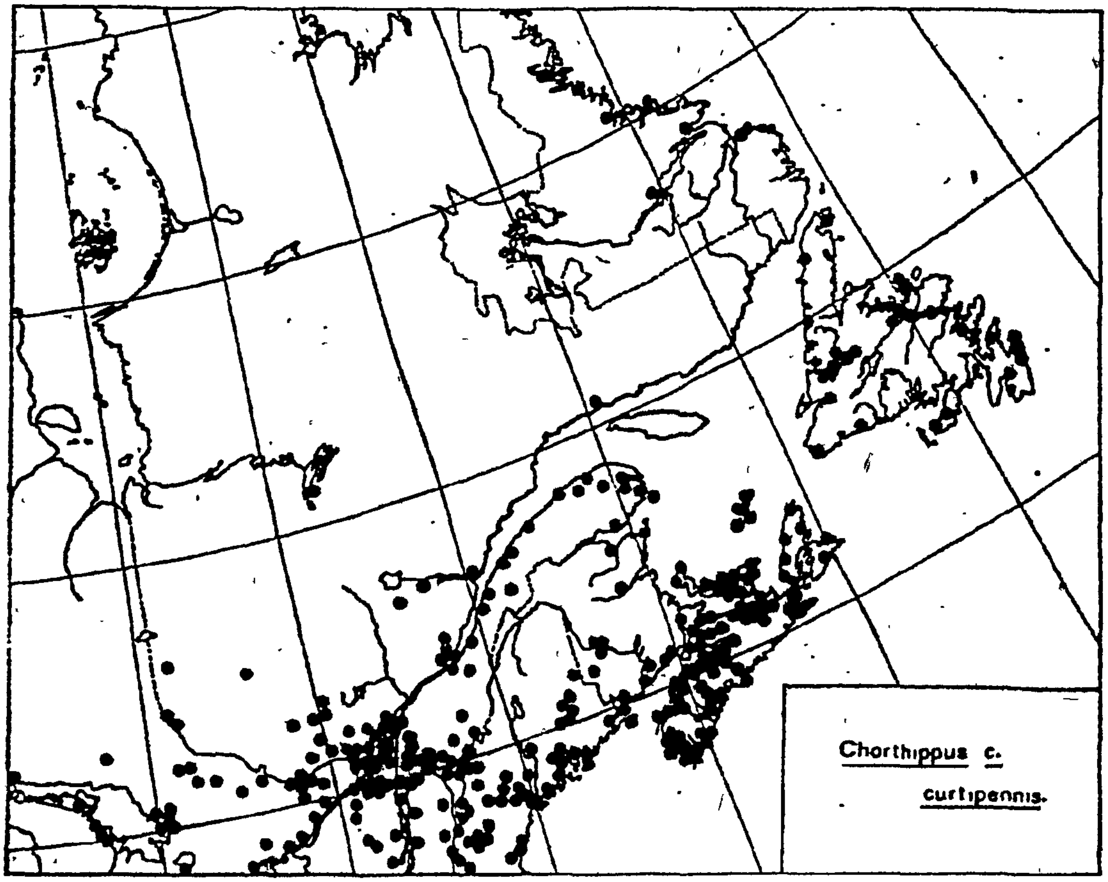


Figure 3. Map - <u>Chorthippus</u> <u>c.</u> <u>curtipennis</u> distribution in northeastern North America


Chorthippus c.
curtipennis.

b) Habitat

Orphulina speciosa occupies the more open parts of a mixed grass-herbaceous habitat with the substrate dry and sandy. Chorthippus curtipennis curtipennis, as well as inhabiting dry areas similar to those occupied by O. speciosa, also occurs in wet habitats around marshes and bogs (Cantrall, 1943). Both species appeared to be more abundant in areas having sandy soil. Chloealtis conspersa is chiefly a woodland species occurring in clearings or along the edge of woodland. The most productive collections were made along the perimeters of sand pits and nearby roadsides.

c) Food

O. speciosa, C. conspersa and C. c. curtipennis are all grass-feeders. As shown by Gangwere et al. (1976) the diet of O. speciosa consists largely of Canada Bluegrass, Poa compressa (L.), with lesser amounts of Arrowfeather, Aristida purpurescens (Poir.). The main food of C. c. curtipennis is Kentucky Bluegrass, Poa pratensis (L.) and lesser amounts of Pigeon Grass, Seteria lutescens (Weigel) Hubb, and other graminoids, but not dicotyledons. Chloealtis conspersa is a gramnivore that occasionally varies its diet with dicotyledonous material. Its preferred food is Poa spp.

d) Life Cycles

O. speciosa, C. conspersa and C. c. curtipennis all exhibit the same type of life cycle in which overwintering occurs in the egg stage. In the following spring and early summer the eggs hatch and the nymphs mature to adults after developing through five instars.

In southwestern Quebec the nymphs of O. speciosa appear from June to July. The fifth nymphal instars mature to adults during late July and these generally live until October (Crozier, 1977).

C. conspersa nymphs first appear in southwestern Quebec in mid-May, and the adults live through mid-June to September (Crozier, 1977).

The nymphs of C. c. curtipennis emerge in southwestern Quebec in early June and like O. speciosa live until October (Crozier, 1977). Low temperatures and the corresponding lack of suitable food plants both contribute to the demise of adult individuals in the autumn.

PART III. MATERIALS AND METHODS AND ASSOCIATED PROBLEMS

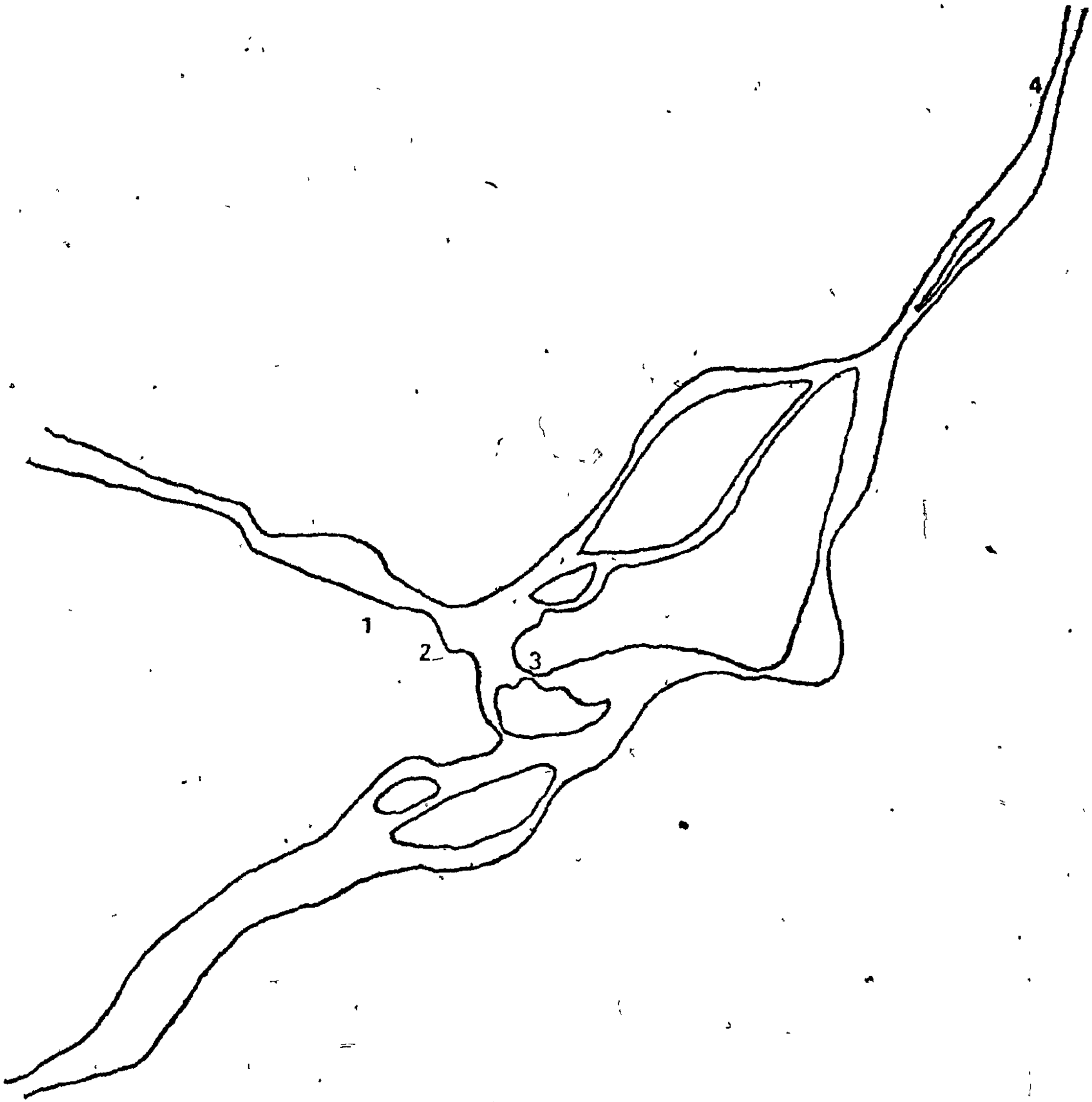
This study was started in the summer of 1976 and is based on observations of natural populations of *O. speciosa*, *C. conspersa* and *C. c. curtipennis*. Observations were also made on field-captured and reared grasshoppers kept in captivity.

Grasshoppers were observed and collected at Rigaud, Hudson, Ste. Anne de Bellevue and Lanoraie, Quebec (Fig. 4). The standard observation procedure was to walk to the edge of an area known to contain a certain population of grasshoppers, to sit down and remain still. After several minutes the grasshoppers begin to move about. Movements and interactions were noted using a miniature cassette tape-recorder. When background noise was sufficiently low, field recordings of stridulation were made using a Sennheiser MKH 815 T directional microphone, and a Uher 4000 Report IC tape-recorder with a tape speed of 19 cm/sec (system frequency response 5db at 20hz-20khz). These recordings were later analysed.

In the laboratory, the most successful observations were made by housing individuals in glass-fronted wooden cages measuring 33x33x48 cm (outside dimensions). The cages had a false floor constructed of 3 mm mesh hardware cloth positioned

[redacted]

Figure 4. Map - Montreal and surrounding area. Observation and collection sites: 1. Rigaud, 2. Hudson, 3. Ste. Anne de Bellevue, 4. Lanoraie


1
2
3
4

10 cm above the floor of the cage. Heat and light were provided by a 25-watt incandescent light bulb. A temperature of 26°C - 30°C was maintained. A 15 hour light and 9 hour dark photoperiod was used. A fresh supply of lettuce and Canada or Kentucky Bluegrass was placed in the cages daily. A supplementary mixture consisting of 200g bran, 200 g alfalfa meal, 20g Brewers' yeast and 46 ml of corn oil was fed to the grasshoppers. A cotton-stopped water vial was placed in each cage to provide moisture for the insects.

Eggs of *O. speciosa* and *C. c. curtipennis* were reared and hatched using the method described by Crozier (1977). The behaviour of the caged adults was subsequently observed. Raising of *C. conspersa* was not attempted.

Except for possible signals involving flight of *O. speciosa*, there appeared to be a close correlation between behaviour occurring in the field and that occurring in the laboratory.

Figure 5 is a photograph of the author in the field, recording stridulation. Figures 6 and 7 indicate two methods used to record and observe behavioural interactions. Cages used in the field were bottomless so as to simulate natural conditions.

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Figure 5. Recording in the field

Figure 6. Small bottomless cage and recording equipment

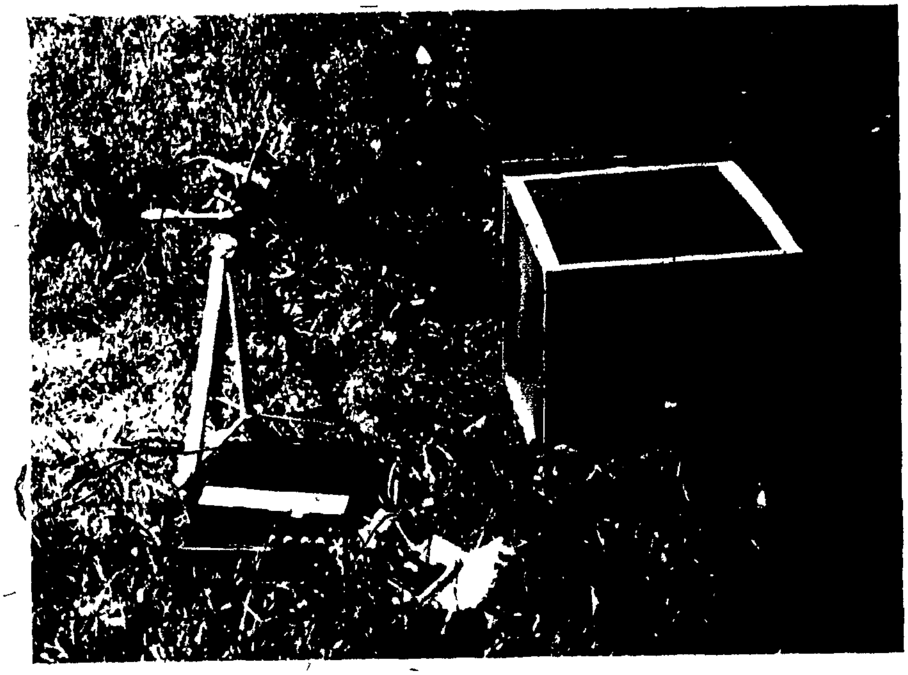

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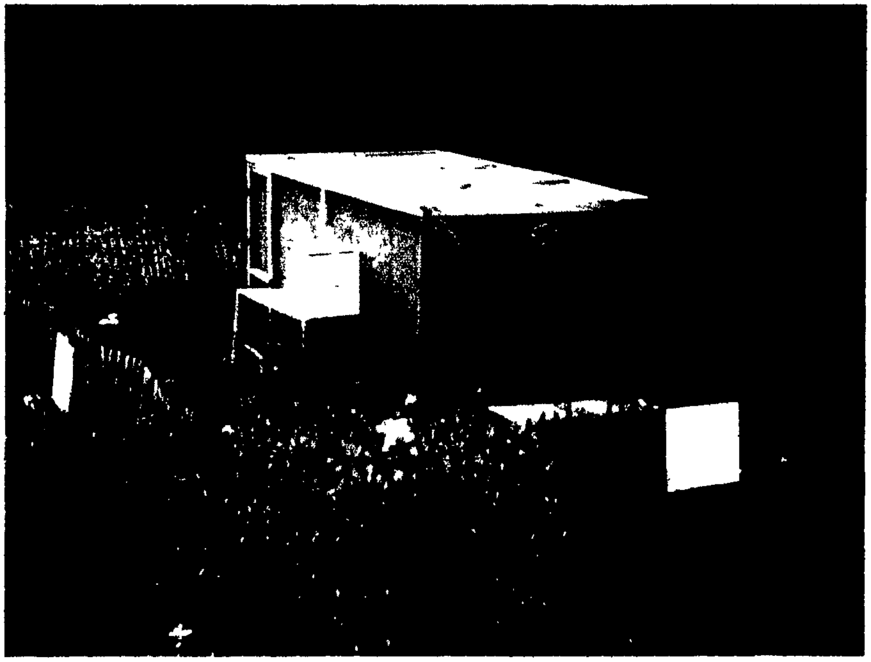
Figure 7. Large walk-in bottomless cage



The habitats where the grasshoppers were found consisted of grasses and sedges of varying lengths, which hindered accurate observations. To add to the difficulty, the grasshoppers, when alarmed or disturbed, attempted to conceal themselves in the vegetation or to leap away from the observer. Their cryptic colouration made them extremely inconspicuous. It is for these reasons that detailed observations on caged individuals were made, which were then verified by field observations.

PART IV. GENERAL GRASSHOPPER BEHAVIOUR

Acridoid grasshoppers are mostly diurnal and have relatively short antennae. However, they possess large compound eyes, which allow them to utilize many visual signals, mostly involved with sexual behaviour. Their colour, size, shape, motion, and particularly the large hind legs, all appear to be important in close range interaction, and in all cases these prelude tactile communication.

Grasshoppers have evolved an acoustic system entirely separately from that of their relatives the crickets (Grylloidea) and katydids (Tettigonioidea).The majority of the members of the latter two groups have in common an acoustic system in which the signalling device is a stridulatory apparatus on the forewings of the male and the auditory organs are tympana located within slits or foramina on the fore tibia. Acridoid grasshoppers, on the other hand, have (except for a few which lack them) tympana situated at the base of the abdomen, and, if they stridulate at all, they utilize various methods, all quite unlike those of crickets and katydids, the most common being the rubbing of the specialized inner faces of the hind femora against the outer faces of the tegmina (Fig. 8), and occasionally the sides of the abdomen. In addition or sometimes in place of this male grasshoppers of the subfamily Oedipodinae in particular, may produce sound during flight in order to attract a mate. The flapping hind wings of oedipodines produce a snapping or crackling noise usually referred to as crepitation.

Though nearly all grasshoppers possess abdominal tympana, a great many species neither stridulate or crepitate, and in those species that do so, usually only the males produce appreciable sounds by either of the two methods described above.

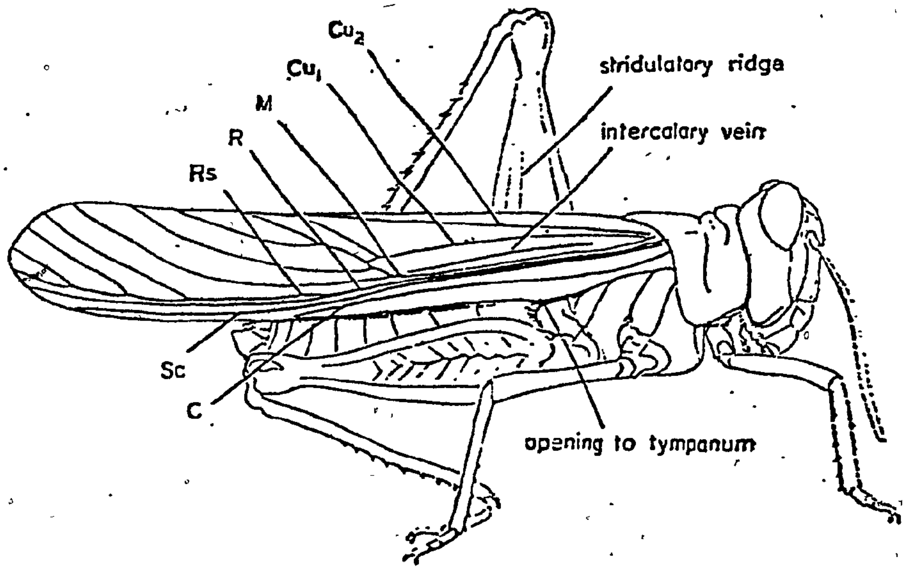
a) Stridulation and Sound

Many insects produce sound by rubbing a roughened part of the body against another part. This type of frictional mechanism for sound production is employed by a variety of insects but is particularly associated with insects of the orders Orthoptera, Hemiptera and Coleoptera (see, for example, Haskell, 1961). During the course of evolution, different body parts of these insects have become modifed to produce sound in this manner.

In orthopteroid insects, as already noted, two main methods of stridulation are used: elytral or tegminal stridulation in crickets (Grylloidea) and katydids (Tettigonioidea) of the order Grylloptera and femora-~~elytral~~ stridulation in grasshoppers (Acridoidea) of the order Orthoptera.

[redacted]

Figure 8. Diagram illustrating the sound-producing and hearing apparatus and forewing venation in a typical oedipodine grasshopper


Cu$_2$
Cu$_1$
M
R
Rs
Sc
C
stridulatory ridge
intercalary vein
opening to tympanum

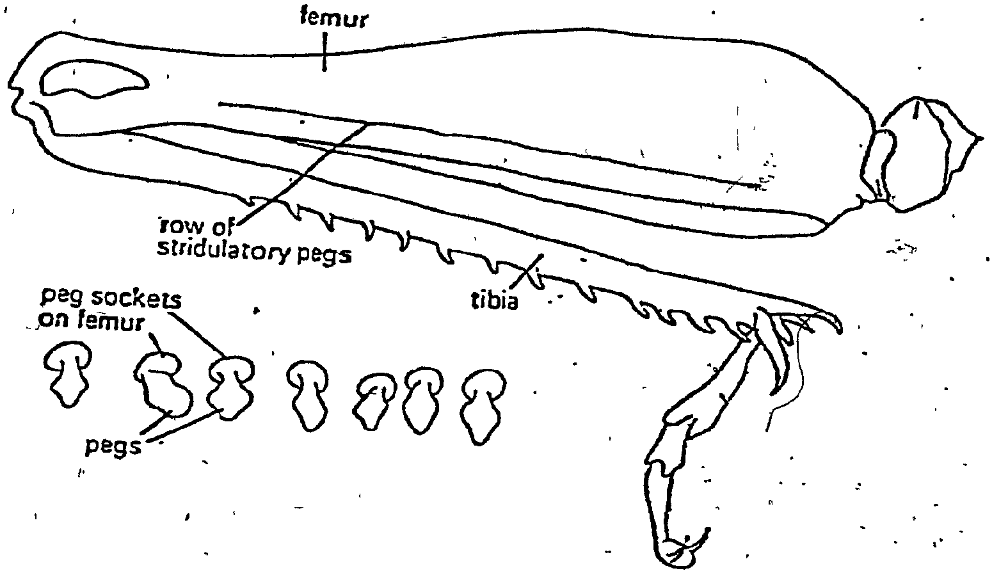
In crickets each tegmen or fore-wing of the male has a cubital vein near the base of the underside modified to form a toothed file, while on the edge of the opposite tegmen is a ridge forming a scraper. The right tegmen overlaps the left so that only the right file and the left scraper are functional. Sound is produced when the tegmina are raised at an angle of 15-40° to the body, and then opened and closed so that the scraper rasps on the file causing the tegmen to vibrate and produce a sound (Chapman, 1969). Female crickets do not possess stridulatory apparatus and therefore make no sound.

The stridulatory apparatus of the katydids is similar to that of crickets, but the left tegmen overlaps the right and in most fully-winged forms only the left file and right scraper are present. Some female katydids have stridulatory apparatus, but this is usually much less well developed than in the males and of a different nature.

Many of the stridulatory acridoid grasshoppers of the subfamilies Oedipodinae, Acridinae and Gomphocerinae produce sound by rubbing the hind femora against a pronounced sclerotized tegminal vein of the same side. Depending upon the species, the femora are moved either in unison or alternately. Sound is produced when a ridge (Oedipodinae and Acridinae) or row of pegs (Gomphocerinae) along the inner surface of the hind femora (Fig. 9), rasps against the pronounced rigid teg-

[redacted]

Figure 9. Diagram of the inside left hind leg showing the position of the stridulatory pegs


femur
row of stridulatory pegs
tibia
peg sockets on femur
pegs

minal veins. This causes the tegmina to vibrate with their natural frequency and thus produce a sound, the frequency of which varies from 2-50 Khz. To some extent the frequency of the sounds varies with the species, but even in a single insect a wide frequency spectrum results from the different resonances of different parts of the elytra. Each movement of the femur produces a single pulse of sound. Stridulatory apparatus is often present in the female as well as the male, as is found in Chorthippus species, but there are very few reports of female stridulation (Ragge, 1955). As with crickets each species has a different song and individual species may be differentiated by their pulse repetition frequencies.

b) Crepitation and Sound

In addition to, or instead of, stridulating, some acridoid grasshoppers, as previously stated, produce sound during specialized flights of the male, made in order to attract a mate. The hind wings are opened and closed, producing a snapping or crackling noise, usually referred to as crepitation.

Crepitating flight in many species is associated with the exposure of colour patterns on the hind wings when the grasshopper is in flight, for example in the case of the black and yellow colour of a flying Carolina Grasshopper, Dissoteira carolina (L.). In such cases the male becomes conspicuous in flight, and attracts a receptive conspecific female, either by the flashing of coloured wings or the production of loud flight noises or both. The fact that flash colouration is displayed by non-crepitating species and that some females also possess conspicuously coloured wings, has led to the belief that flash colouration is also a probable escape mechanism used to confuse large predators.

It is not yet known precisely how the snapping sounds are produced during flight. Cutting off fore-wings did not affect the sound produced, but crushing the thickened anal veins did suppress the sound (Isely, 1936). It was suggested that the membranes between the anal veins produced a snapping sound when they suddenly became taut. Otte (1970) investigated the possible mechanism of crepitation and found that when he extended the hind wing and lowered it at the same time, the distal half of the membranes between the thickened anal veins suddenly popped out and flattened. This was due to tension on the veins, for the membrane popped back into the folded position again when the wings were released and allowed to return to their resting position. Membranes not associated with thickened veins did not pop out in this fashion and therefore produced no sound.

A slow play-back of sound produced by these species and audiospectrographs of their sounds suggest that as the thickened veins and the membrane between them first pop into the taut position, they produce the louder snapping sounds, and as they pop out into the relaxed position they produce a softer popping sound (Otte, 1970). If this is the mechanism by which sound is produced, then it is unique in grasshoppers, but in certain respects it is quite analagous to the mechanism employed in the case of the abdominal tymbals of cicadas. In these, also, it is the vibration of a membrane which produces the sound (Haskell, 1961).

In point of fact, a very creditable imitation of oedipodine crepitation can be produced simply by means of a cheap Japanese paper fan, rapidly opened and closed whilst being jerked in the hand. It would seem that the sound thus produced is made in the same manner as that of grasshoppers during flight (D.K.McE. Kevan, personal communication).

PART V. MAJOR COMMUNICATIVE PATTERNS

The principle patterns of grasshopper behaviour involving communication are associated with pair formation and courtship, also aggression and repulsion.

Signals can be named according to the function they serve, for example, calling and male spacing, or they can be named according to the patterns of movements of the display, such as stridulating or femur-jerking. At times, however, the function of a certain display is not immediately obvious, and even if it is known for one species, it may not be the same in a different species. Therefore it is usually safer to name the display according to the pattern of movement. When the function is known, movements of displays are named according to the function they serve.

When describing the behavioural traits of any animal, it is important to systematize and give detailed accounts of behaviour currently recognized in the field, as a necessary aid to further study. Also, the names given to various types of behaviour should be used in subsequent studies, to minimize confusion.

Otte (1970) has been responsible for naming the communication signals and behaviours in grasshoppers. With use of his terminology, behavioural descriptions have been standardized, as in the publications of Willey and Willey (1969, 1971), Lohn and Chandrashekaran (1972), Kerr (1974), Steinberg and Willey (1974) and others.

a) Pair Formation and Courtship

Pair formation was described by Otte (1970), as the initial coming together of a male and a female in connection with copulation. Courtship was defined as the interaction of a male and female after the pair has been formed and before the pair copulates. The exact point at which pair formation ends and courtship begins is not always clear. In some species separation of the two phases seems quite arbitrary and is made for convenience only. However, the inability to differentiate the two is not important if the entire process of pairing and courtship is described.

b) Pair Formation

The attraction of females by the males is the first step in pair formation. In many grasshopper species solitary males produce calling signals which attract a female. Some species of Oedipodinae perform specialized flights as well. Males of the subfamilies Oedipodinae, Acridinae, Gomphocerinae and a few others stridulate. Many acridoid species, however, evidently do not utilize audible calling signals, so far as is known.

Flight displays, approaching flights and stridulation are three basic behavioural types involved in female attraction. These displays are discussed on the following pages.

1. Flight Displays

In many species of oedipodines, solitary males perform specialized flights which evidently attract sexually receptive females of their own species. In such performances males fly up from the ground and snap their hind wings (crepitate) and /or display flash colouration, then settle back to the ground again. The flight noise of crepitation is usually species-specific (Otte, 1970). A responsive female will move toward the area where the male landed. The male will then approach her.

2. Approaching Flights

Male grasshoppers may orientate themselves toward the movement of the female. Once visual contact has been made, many oedipodine males approach the females by flying, accompanied by wing flashing and/or crepitation.

3. Stridulation

Three distinct types of stridulation occur throughout the Oedipodinae, Acridinae and Gomphocerinae:

(i) the most common type, which consists of a relatively slow, high amplitude up-and-down movement of the hind femora against the tegmina (Fig. 10a).

(ii) vibratory stridulation, which consists of relatively low amplitude, rapid vibration of the hind femora against the tegmina (Fig. 10b).

(iii) "ticking", which consists of raising the femora and then kicking out with the tibia so as to strike the end of the tegmina (Fig. 10c).

Vision in pair formation and courtship is very important in all diurnal grasshopper species. Males are highly sensitive to movement and orientate toward and approach moving individuals by sight. The final stage in pair formation, even in those species where the male attracts the female, is also dependant on visual orientation and approach. Pair formation in these species can therefore occur in the absence of female attracting signals.

Male oedipodines and most acridines and gomphocerines approach the female by both flying and walking on different occasions. This approach is accompanied by visual and/or acoustical signalling by the male (Otte, 1970).

c) Courtship

As previously defined courtship is the interaction of male and female after the pair has formed and before the pair copulates. The signals which occur in a courtship context are: "ticking", presenting, flight display, approach flight stridulation and femur-tipping.

1. "Ticking"

A repetitive or non-repetitive movement in which the leg is extended so that the tibia strikes the end of the tegmina, producing a "tick" sound, as noted previously under "stridulation" (Fig. 10c).

2. Presenting

Sexually responsive females of many species lower the hind femur nearest the approaching male and spread both femora away from the abdomen (Fig. 10h). The presenting response is graded, and seems both to attract males and to render the females more accessible to males. Responsive females always allow males to mount them and to attach their genitalia. This mating posture varies in elaborateness both within and among species.

3. Flight Display

This display occurs in some but not all species. It was previously described under "Pair formation".

4. Approaching Flights

These flights occur in many species, and were previously noted under "Pair formation".

5. Stridulation

This has already been discussed under "Pair formation".

6. Femur-tipping

This is the most common femoral movement in oedipodine grasshoppers. It consists of a single quick raising and lowering of the femora (Fig. 10d), without sound production. This movement is displayed by some species in courting males, but normally occurs in male-male interactions and results in their separation. The movement is rendered conspicuous by the markings on the inside of the femur. When the femora are in the resting position these bright markings are not visible.

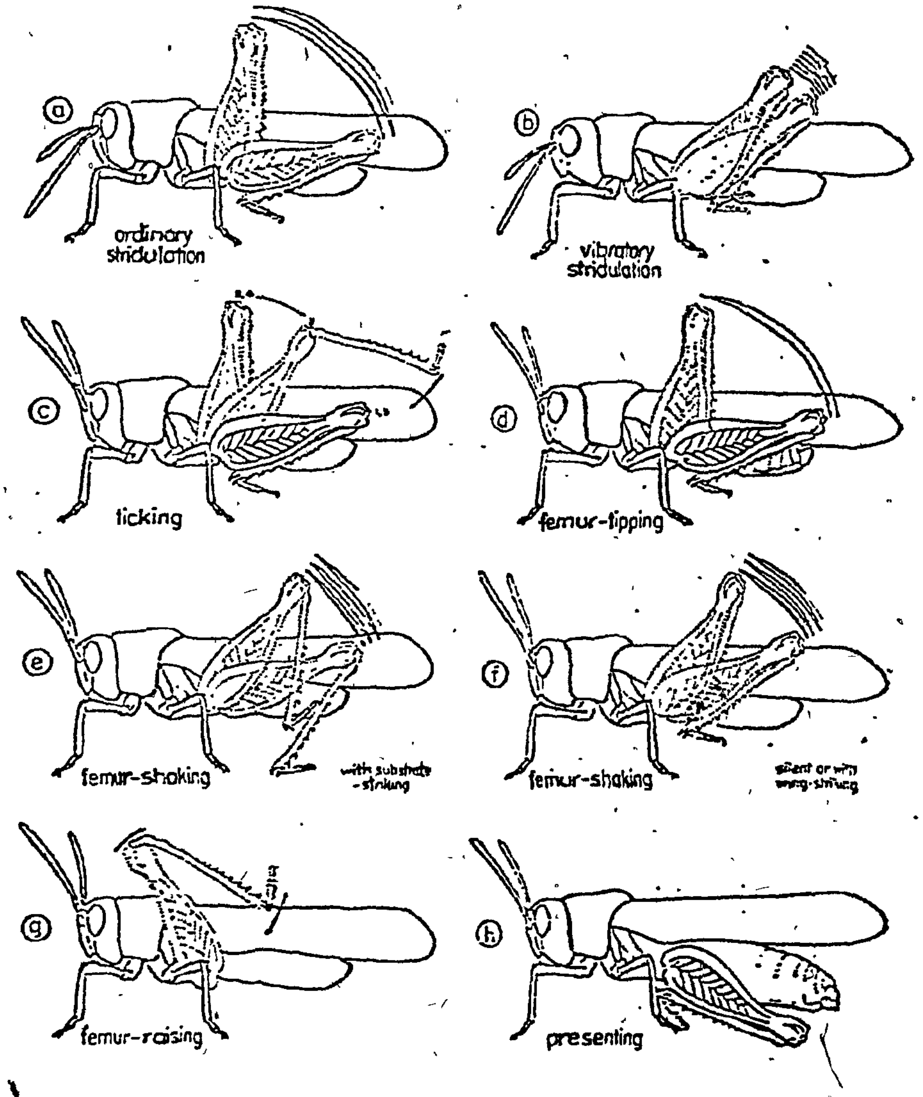
It must be pointed out that Figs. 10c,d,e and f are not restricted to courtship behaviour. See Otte (1970) and Kerr (1974).

Signals can facilitate copulation by transmitting information about the species, sex, the reproductive state, the vigor and/or motivation of the sender. This information could be coded into two categories: appropriate mate and inappropriate mate (Kerr, 1974).

[redacted]

Figure 10. Signals and postures commonly occurring in grasshoppers

From Otte (1970)


a
ordinary stridulation
b
vibratory stridulation
c
ticking
d
femur-tipping
e
femur-shaking
with substrate-striking
f
femur-shaking
silent or with wing-striking
g
femur-raising
h
presenting

The flight display and stridulation may have a dual function as courtship and calling signals. The species information would be important in both contexts, while location information would be functional in calling and extraneous in courtship. Presenting seems to function in the timing of copulation. The contribution of the other patterns is uncertain, but each of these patterns will have encoded in it information from one of the categories discussed.

d) Mounting

In all species, the male mounts the female. When on top, the male lowers the end of his abdomen beneath that of his mate and grasps her genitalia with his own. In the three subfamilies discussed in this paper (Oedipodinae, Acridinae and Gomphocerinae) the female is aware of the impending attempt of a male to mount her, because he usually signals before doing so. Sexually receptive females either remain passive or signal their receptivity in some fashion. Females that are sexually unreceptive perform movements which inhibit mounting and genitalial linking by males (Otte, 1970).

e) Copulation

After the male has attached his genitalia to those of the female, insemination occurs. This is indirected and involves the transfer of a spermatophore, produced by the male after mounting and attachment of genitalia. Its shape is determined by the opening of the male's oedeagus and by the lumen of the female's receptaculum, into which the gel-like spermatophore is pressed. After copulation the spermatophore breaks, and the female retains the tube while the male retains the sac. The presence of a spermatophore in the female makes her unreceptive to further copulations until the tube is absorbed by the receptaculum (Haskell, 1958).

f) Aggression and Repulsion

Grasshoppers do not fight. The term "aggression" is used to denote any behaviour which seems to have the function of separating individuals. Thus a display by one individual which causes an approaching individual to turn aside or to stop advancing is an aggressive display. "Repulsion" denotes any type of behaviour performed by either males or females which causes the respondent to leave. Aggression and repulsion have been used interchangeably to some extent, although the former term has usually been applied to interactions between males in which no contact was made (Otte, 1970).

Aggressive and repulsive behaviours have been categorized as follows:

1. Femur-tipping

Occurs in male-male encounters (Fig. 10d). Tipping is a visual display which usually leads to the separation of males before they touch one another (Otte, 1970).

2. Femur-shaking

This movement consists of shaking the femora, usually repetitively. There are several kinds of shaking:

(i) silent

(ii) shaking in which the tibiae strike the substrate and (iii) shaking in which the femora strike the fore-wings (Figs. 10e,f). It is performed by both males and females and causes separation of individuals. In a few species, femur-shaking is a courtship signal (Otte, 1970).

3. Femur-jerking

This is a disturbance movement produced only by individuals touched or mounted by other individuals. The intensity of the movement seems to depend on the degree of disturbance. All gradations occur, from a small upward jerk of femora through a few degrees, to an extensive upward thrust to about the vertical position accompanied by a kicking-out of the tibiae (Otte, 1970).

4. Femur-raising

Raising the femora and holding them in a nearly vertical position is a disturbance posture or a male rejection posture assumed by most species (Fig. 10g). The degree of raising and forward tilting depends on the extent of the disturbance. The posture is assumed by both males and females. If mounting is attempted, the intruder is kicked away with quick upward thrusts of the tibiae (Otte, 1970).

5. Kicking

Both sexes of all species kick out with their hind tibiae when disturbed by other individuals (Otte, 1970).

6. Femur-forward-swinging

In some species, individuals swing their femora from the resting position all the way to the head and back again in a single rapid motion, when touched from the side or the front. Usually the leg nearest the intruder is the only one that is swung (Otte, 1970).

7. Sparring

When individuals touch each other with their forequarters they often strike out at one another with their fore-legs and occasionally with their middle legs (Otte, 1970).

8. Sideways body jerking

A few species have been observed to rock their bodies from side to side when disturbed, and others do this while mounting females (Otte, 1970).

9. Regurgitation

Most grasshoppers regurgitate a brown fluid when handled. This is sometimes done when an individual is disturbed bodily by another individual (Otte, 1970). It is mainly a defence mechanism against predators.

PART VI. OCCURRENCE OF SIGNALS IN Chorthippus c. curtipennis, Orphulina speciosa AND Chloealtis conspersa.

Interactions between two grasshoppers were classified according to the sex of the participants. Male-male interactions were the most frequently observed; male-female interactions were less common, and female-female interactions were even more rare. Interactions involving more than two individuals were classified into two groups: those involving two or more males and one female and interactions between two or more females and one male. These grouping usually involved a mounted pair being confronted by another individual, either male or female.

Interactions were observed to be initiated by both males and females in all the species concerned.

The following action sequences occurred most frequently during various conspecific interactions of O. speciosa, C. conspersa and C. c. curtipennis.

a) Male-Female Interactions

Chorthippus curtipennis curtipennis (n: 132)

Sexual activity varied considerably among individuals. Interactions were usually initiated by the males, by stridulating and/or jumping or walking towards a female. Stridulating is performed both before and after sighting a female.

The rasping stridulatory sound appears to be a calling song that attracts responsive females of the same species. The males are far more active than the females and spend most of the daylight hours browsing and randomly moving about their habitat. They also appear to spend a considerable amount of time pursuing and attempting to copulate with conspecific females.

The females were never observed to stridulate. It is however a common behaviour of males. The black colour of the hind femora-tibiae joints are very noticeable when the legs are moving in unison and both this visual signal and the stridulation sounds are species and sex identification signals.

The females, if sexually receptive, move toward a stridulation sound or to the male's movement if he is visible.

In virtually all instances of observed interactions, antennal contact was made. This was followed by normal male stridulation as well as a vibratory stridulation lasting from one to three seconds, the pulsation of which increased to a climax or frenzy after which the male would pounce upon and mount the female. Mounts, when successful, that is when genitalial linking and spermatophore transfer was achieved, lasted from 20 minutes to more than an hour.

A frequent occurrence was for females to repulse the males when they attempted to mount. This was achieved by two methods, active and passive avoidance. Active avoidance involved the female either jumping away or kicking the mounting male away. The female was able passively to avoid genitalial linking with the male on top of her by either curving the end of her abdomen down or by blocking her posterior abdomen with her hind legs, thus rendering her genitalia unavailable for copulation. The repulsed male, or in the latter case, the frustrated male, usually lost interest, moved away and attempted to mate with another female. However the male sometimes persisted courting the same female, and began the courtship sequence again. On one such occasion a male was observed making mounting attempts with the same female three times in succession, being unsuccessful in all instances. See Table 3, Page 66-Page 67.

Orphulina speciosa (n: 127)

The females as well as the males are equally active in browsing and randomly moving about their habitat. The females were observed to initiate almost as many interactions as the males. Interactions were generally initiated by a walking approach. Stridulation by males, for attracting females, was not easy to observe because the resulting "tick" noise was barely audible. Stridulation, however, appeared to be used almost exclusively as an aggression or repulsion signal.

Antennal contact was made when two individuals were close enough to each other. If a female was unreceptive she would raise her femora in unison, 90° to her body, and extend her tibiae distally and/or move away from the male. If the male was not repulsed by the female after antennal contact, he would sometimes stridulate. His femora were raised and lowered in unison, with the accompanying "tick" sound, 3 to 10 times in one sequence. Attempted mounts were often shaken off by the unreceptive female.

The most frequent sequence of actions preceding mounting and copulation involved relatively few displays of the courting sequence when compared to *Chorthippus c. curtipennis* . In most cases males approached females slowly, and when sufficiently close, pounced on them, without any prior signalling. If mounting was successful, copulation lasted from 30 to 90 minutes.

Males that were repulsed never immediately attempted to remount the same female. In the field, males were observed to make short, audible flights. However no female was seen to be attracted. Flight noises seemed to be incidental to flight generally, and not comparable with oedipodine crepitation. See Table 3, Page 66-Page 67.

Chloealtis conspersa (n = 48)

Interactions were usually initiated by males, by stridulating and/or jumping or walking toward a female. Following an approach, antennae contact was generally made. If the females were strongly unreceptive they would repulse the males by kicking at them and moving away at this early stage of the interaction. More often, however, the male, after antennal contact, would either stridulate or make silent femur movements. Stridulatory movements involved the hind femora of a male individual moving simultaneously up and down. During the first two to four downstrokes no sound was produced, subsequently the femora were held closer to the body, so that the stridulatory pegs on the inner surface of the femora came in contact with the tegmina and sound was generated. It was noted that some sound was produced during the upstroke, unlike the other two species under study. Silent femur movements, also made by males only, involved the hind femora being raised at 90° to the body, with the tibiae held close to them. The femora are then dropped with a "vibratory-bounce", to a low amplitude position, almost parallel to the body. The amplitude of the vibratory-bounce decreases with time and lasts from one to two seconds.

Following stridulation or the silent vibratory-bounce movements, the male would in most instances attempt to mount the female. If the female was not receptive she would dislodge the male by jumping or kicking. This would sometimes be followed by the female making femur-raising motions. This movement usually elicited further stridulation from the rejected male and eventual separation of the two individuals. Only once was recourting and subsequent remounting by a male observed. See Table 3, Page 66-Page 67.

b) Male-Male Interactions

Chorthippus curtipennis curtipennis (n: 68)

Males usually approached each other at random by walking. Occasionally one male would be attracted by the stridulation of another. Antennal contact was made when individuals were in range of each other, after which one or both would stridulate. Stridulation was occasionally performed before antennal contact. In most cases the males moved away from each other, thus terminating the interaction. In rare instances, a sexually excited male would attempt to mount another male, if that male did not stridulate, but the mounter was quickly repulsed by kicking and/or jumping movements of the mounted male. See Table 4, Page 68.

Orphulina speciosa (n: 62)

Males usually approached each other by walking. This would occasionally be followed by one of them stridulating. Antennal contact, though, was very frequent after two males converged. This generally resulted in one or both of them moving away from the other. In other instances one or both of the males stridulated before parting. Attempted mounting between two O. speciosa males, although uncommon, occurred more frequently than with Chorthippus. It is possible that the absence of conspicuous markings and movements and the low audibility of stridulation are responsible for identification mistakes. See Table 4, Page 68.

Chloealtis conspersa (n: 18)

The initiation of male-male interactions was similar to Chorthippus curtipennis curtipennis, with the males generally approaching each other randomly by walking. Occasionally stridulation by one individual would attract another. When male individuals were close enough to each other, antennal contact was made. This resulted in either stridulation, followed by separation or immediate separation with no stridulation. See Table 4, Page 68.

c) Female-Female Interaction

Chorthippus curtipennis curtipennis (n: 34)

Approach was made by walking, followed by antennal contact, whereupon one or both of the females made repeated femur-forward swinging movements, similar to the stridulation action of the males, but less precise and with no sound being produced. The females moved away from each other after this femur movement was performed. See Table 5, Page 68.

Orphulina speciosa (n: 46)

Approach was made by walking followed by antennal contact. One or both females would then perform femur-raising movements with outstretched tibiae. It appears that this motion was a repulsive or aggressive signal, as in all instances after the signal was observed one or both females would then move away. See Table 5, Page 68.

Chloealtis conspersa (n: 7)

Interactions between females were comprised of three acts. After an approach, antennal contact was made, followed by the separation of the two individuals. See Table 5, Page 68.

d) Male-Copulating Pair Interactions

The actions observed when a solitary male approached, or was approached by, a copulatory pair, were similar to those of male-male interactions.

The following sequence of displays were performed by the three species studied (Chorthippus, n: 14; Orphulina, n: 22 and Chloealtis, n: 5). After a walking approach antennal contact was usually made, but regardless, the presence of an intruding male stimulated stridulation by the copulating male. This appeared to be a repulsive or aggressive signal, as either the solitary male and/or the mounted female moved away following the stridulation. See Table 6, Page 69.

e) Female-Copulating Pair Interactions

This interaction was observed only in the case of O. speciosa (n: 15), where a walking approach was made either by the solitary female or the copulating pair. Antennal contact was sometimes made but, regardless, repulsion or aggression movements were performed. This involved stridulation by the mounting male, or the solitary female making femur-raising movements. Either action resulted in the solitary female or the mounted female moving away. See Table 7, Page 69.

f) Copulating Pair-Copulating Pair Interactions

This behaviour was observed only in the case of O. speciosa (n: 4), where the two pairs approached each other while walking. Either antennal contact or merely the close proximity of the other individuals would cause the mounted males to stridulate. The pairs then parted. See Table 8, Page 70.

TABLE 3

COMMON BEHAVIOURAL SEQUENCES OF MALE(M)-FEMALE(F) INTERACTIONS

	Ch. c. curtipennis	*Orphulina speciosa*	*Chloealtis conspersa*
MALE INTERACTIONS WITH RECEPTIVE FEMALES	-	Crepitation flights sometimes	-
	Stridulation before sighting, by M	-	Stridulation before sighting, by M
	Approach, usually by M	Approach by M or F	Approach, usually by M
	Stridulation after approach, by M	-	-
	Antennal contact	Antennal contact, sometimes	Antennal contact
	Stridulation after antennal contact, by M	-	Stridulation after antennal contact, by M
	Vibratory stridulation by M	-	-
	M mounts F	M mounts F	M mounts F
	Copulation	Copulation	Copulation
	Copulation time: 20-60 min.	Copulation time: 30-90 min.	Copulation time: 30-60 min.

Ctd

TABLE 3. CTD.

	Ch. c. curtipennis	*Orphulina speciosa*	*Chloealtis conspersa*
MALE INTERACTIONS WITH UNRECEPTIVE FEMALES	–	Crepitation flights sometimes	–
	Stridulation before sighting, by M	–	Stridulation before sighting, by M
	Approach, by M	Approach, by M or F	Approach, usually by M
	Stridulation after approach, by M		
	Antennal contact *or* F moves away, END	Antennal contact, *or* F femur-raising *or* F moves away, END	Antennal contact
	Stridulation after antennal contact, by M *or* F moves away, END	Stridulation after antennal contact, by M *or* F moves away, END	Stridulation after antennal contact, by M *or* F repulses M (active) END
	Vibratory stridulation by M	–	–
	M mounts F	M mounts F	M mounts F
	F repulses M (active or passive), END	F repulses M (active), END	F repulses M, (active or passive), END
	Attempt to recourt and remount by M, sometimes	–	Attempt to recourt and remount by M, rare

TABLE 4

COMMON BEHAVIOURAL SEQUENCES OF MALE(M)-MALE(M) INTERACTIONS

Ch. c. curtipennis	*Orphulina speciosa*	*Chloealtis conspersa*
Stridulation before sighting, sometimes	-	-
Approach	Approach	Approach
Stridulation	Stridulation, sometimes	-
Antennal contact	Antennal contact	Antennal contact
Stridulation or Separation, END	Stridulation or Separation, END	Stridulation or Separation, END
Separation, END	Separation, END	Separation, END

TABLE 5

COMMON BEHAVIOURAL SEQUENCES OF FEMALE(F)-FEMALE(F) INTERACTIONS

Ch. c. curtipennis	*Orphulina speciosa*	*Chloealtis conspersa*
Approach	Approach	Approach
Antennal contact	Antennal contact	Antennal contact
Femur-forward swinging	Femur-raising	-
Separation, END	Separation, END	Separation, END

TABLE 6

COMMON BEHAVIOURAL SEQUENCES OF MALE(M)-COPULATING PAIR INTERACTIONS

Ch. c. curtipennis	*Orphulina speciosa*	*Chloealtis conspersa*
Approach Antennal contact Stridulation by mounted M Separation, usually solitary M moves off END	Approach – Stridulation by mounted M Separation, END	Approach Antennal contact Stridulation by mounted M Separation, usually solitary M moves off END

TABLE 7

COMMON BEHAVIOURAL SEQUENCES OF FEMALE(F)-COPULATING PAIR INTERACTIONS

Ch. c. curtipennis	*Orphulina speciosa*	*Chloealtis conspersa*
No interactions observed	Approach Antennal contact, sometimes Stridulation by mounted M <u>or</u> femur-raising by solitary F Separation, END	No interactions observed

TABLE 8

COMMON BEHAVIOURAL SEQUENCES OF TWO COPULATING PAIR INTERACTIONS

Ch. c. curtipennis	*Orphulina speciosa*	*Chloealtis conspersa*
No interactions observed	Approach Antennal contact Stridualtion by mounted M's Separation, END	No interactions observed

PART VII. A COMPARISON OF CONSPECIFIC INTERACTIONS

Conspecific interactions of Chorthippus c. curtipennis and Chloealtis conspersa were generally initiated by the males of the two species. This was due largely to the higher level of activity of the males, relative to that of the females. The more an individual moved about its habitat, the greater the oppportunity it had of interacting with other individuals.

Females of Orphulina speciosa, however, were as active as the males of their own species. Such female activity was responsible for the number of male-female interactions, which in the other species had been initiated predominantly by the males alone, either by stridulating calls or walking. The stridulation of O. speciosa is barely audible, at least to the human ear, which might explain why it is not used as a calling device.

Antennal contact was usually made when individuals were close enough. This behaviour was common to the three species under study. The frequent preening, waving, pointing and contact of the antennae suggests that these sensory appendages play a major role in sex identification and communication (Pickford and Gillott, 1972; Callahan, 1975). Perhaps even individual recognition and/or state of sexual readiness are realized through antennal contact.

Interactions where antennal contact was lacking frequently resulted in mistaken identity, especially among males, where one male would attempt to mount another. When antennal contact was made, however, this mistaken mounting seldom occurred, illustrating the importance of antennal sensory perception.

To further determine the relevance of these appendages, the antennae of five males and two females were amputated, and the individuals housed in an observation cage. It was noted that the activity of all individuals was severely reduced. I believe that the loss of sensory inputs was responsible for the decreased movement and interactions.

Antennal preening behaviour was observed periodically, even though the antennae had been removed. It is probable that when antennal sensory inputs are either unclear or non-existant preening behaviour is stimulated, in order to remedy the situation.

Aggressive signals were observed most frequently during interactions where the participants were of the same sex. In the three species studied, stridulation was used to signal aggression in male-male interactions. Stridulation indicating aggression by the males of _Chorthippus c. curtipennis_ and _Chloealtis conspersa_ was indistinguishable from the normal calling stridulation performed by the males to attract conspecific females. However the stridulation of _Orphulina speciosa_ was observed only in aggressive signalling.

Aggression by females was displayed by movements and posture. Females of *Chorthippus c. curtipennis* usually performed femur-forward-swinging movements when confronted by another female. These movements were very similar to the male stridulatory action, although no sound was produced and the performance was much slower. Females of *Orphulina speciosa* in similar female-female interactions, signalled their aggression by femur-raising movements. This involved both the hind femora being raised perpendicular to their bodies and the tibiae being extended. This posture was maintained for one to four seconds and sometimes repeated. These movements were also displayed by unreceptive females when approached by courting males. No aggressive signals were exhibited by females of *Chloealtis conspersa*.

Performance of the aforementioned aggressive signals usually resulted in the intended receiver of the signals moving away.

As stated previously, repulsion denotes any behaviour performed by males or females that causes the respondent to leave. This behaviour was commonly seen when a courting male attempted to mount an unreceptive female. In such interactions, *Chorthippus c. curtipennis* and *Chloealtis conspersa* exhibited either active or passive repulsion behaviour. Active repulsion was associated with a female ridding herself of a male by force, which usually involved kicking the mounted male off with her hind legs. Passive repulsion was achieved by the female remaining motionless, except for down-curving her genitalia, so as to prevent the male from coupling with her. This resulted in the frustrated male losing interest and eventually moving off and away from the female. Females of Orphulina speciosa did not exhibit this passive behaviour, but rather repulsed the mounted male actively by kicking.

A common behaviour to all three species was for an individual to jump suddenly if mounted by surprise. This occurred whether the mounted individual was male or female. The result of this sudden jump was to dislodge the mounted male, thereby terminating the interaction.

PART VIII. STRIDULATION AND ACOUSTICS.

Adult male gomphocerine grasshoppers produce stridulatory sound by rubbing a row of pegs located on the hind femora, across pronounced veins of the tegmina. Adult females of Chorthippus c. curtipennis and Orphulina speciosa which have not been observed to produce sound, also possess pegs, though they are of greatly reduced size.

The number of stridulatory pegs of males for the three species (n: 20, two legs, 10 specimens of each species) are as follows: Chorthippus c. curtipennis, average number 120.1 (range: 100-132), Orphulina speciosa, average number 17.6 (range: 10-27), and Chloealtis conspersa, average number 112.1 (range: 84-128).

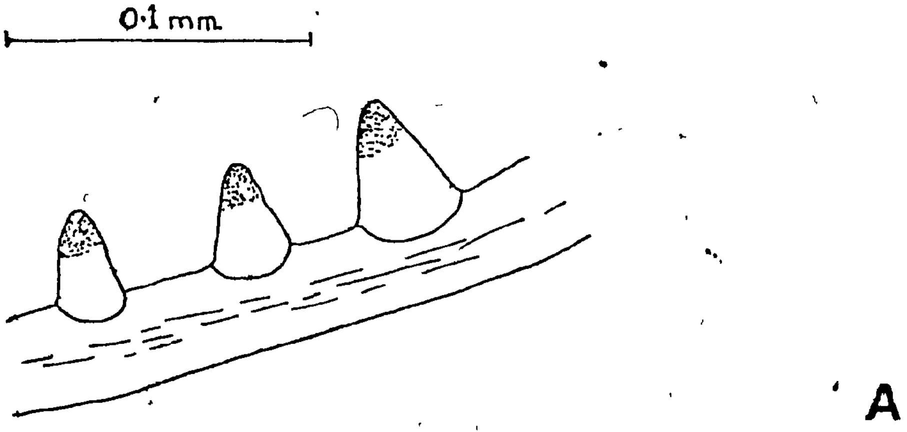
The stridulatory pegs of Chorthippus and Chloealtis are distributed along a ridge over a distance of 4 mm (Figs. 11 and 12). Orphulina have fewer pegs, which are situated along a flat surface on the inner sides of the hind femora, over a distance of 2 mm (Fig. 13).

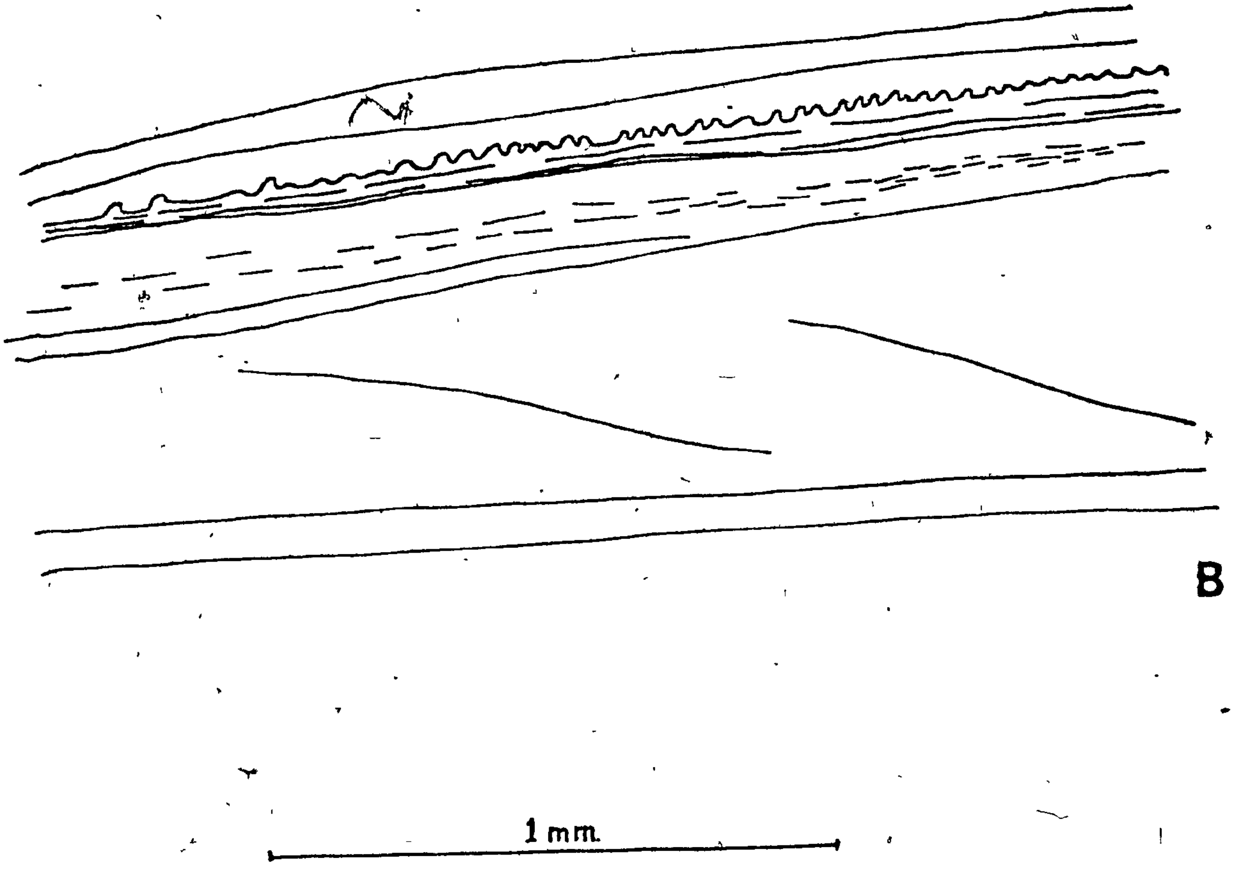
The size, height and spacing of the pegs are irregular in each of the three species.

Along the row of pegs are groups of three to six pegs which have common heights and similar spacings. These group-

[redacted]

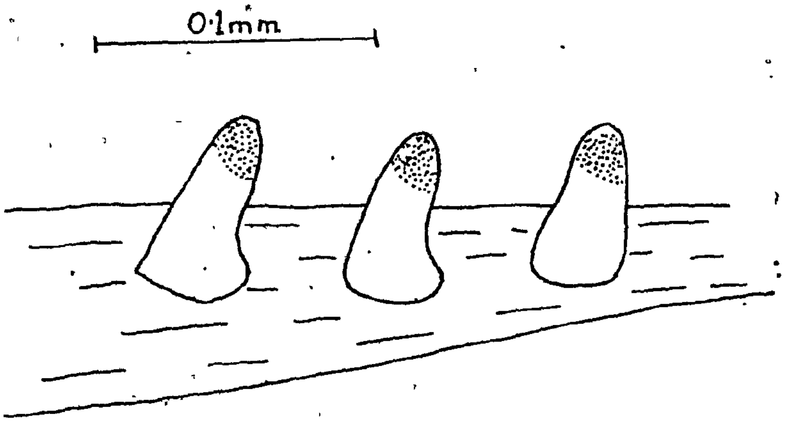
Figure 11. Diagram - Chorthippus c. curtipennis, male
(A) Stridulatory pegs
(B) A view of the inner surface of the right hind femur, showing the proximal portion of the row of stridulatory pegs


0·1 mm
A

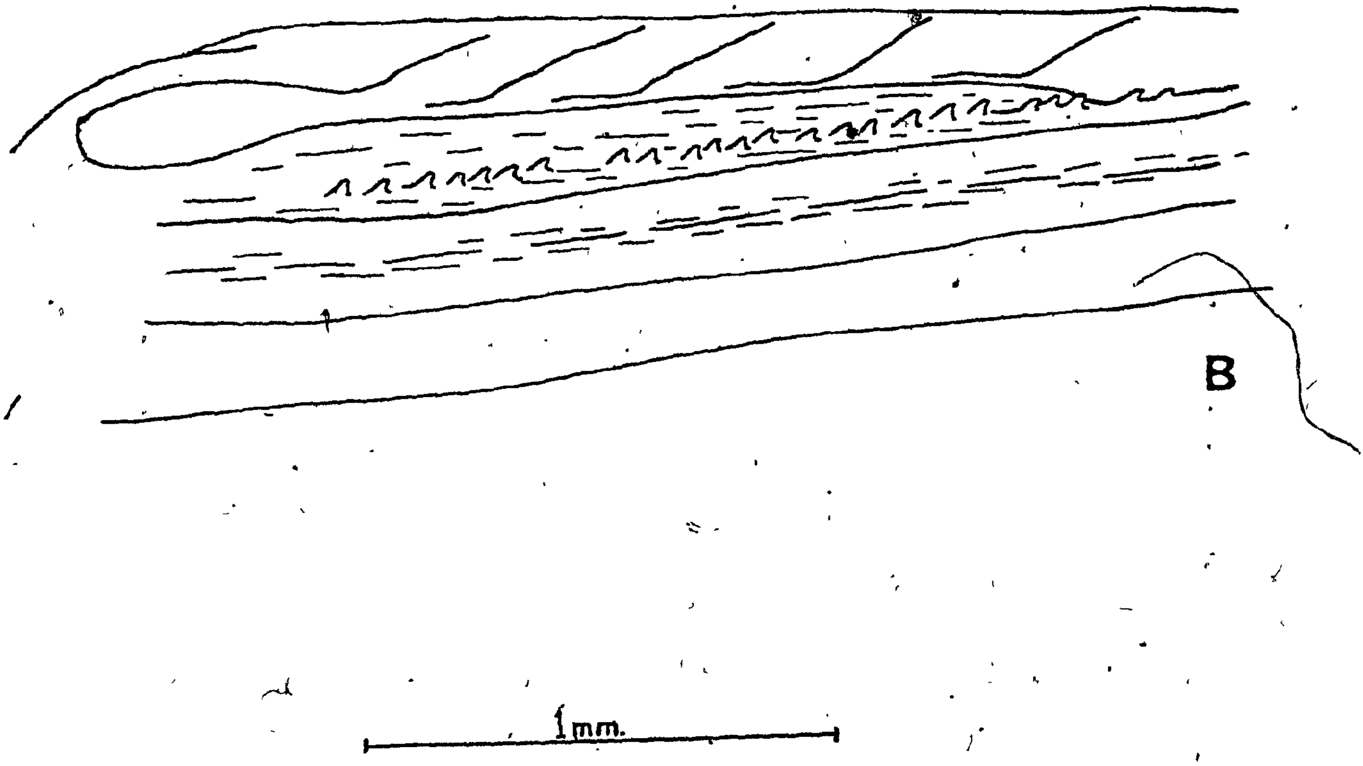

B
1 mm

[redacted]

Figure 12. Diagram - *Orphulina speciosa*, male
(A) Stridulatory pegs
(B) A view of the inner surface of the right hind femur, showing the row of stridulatory pegs



A



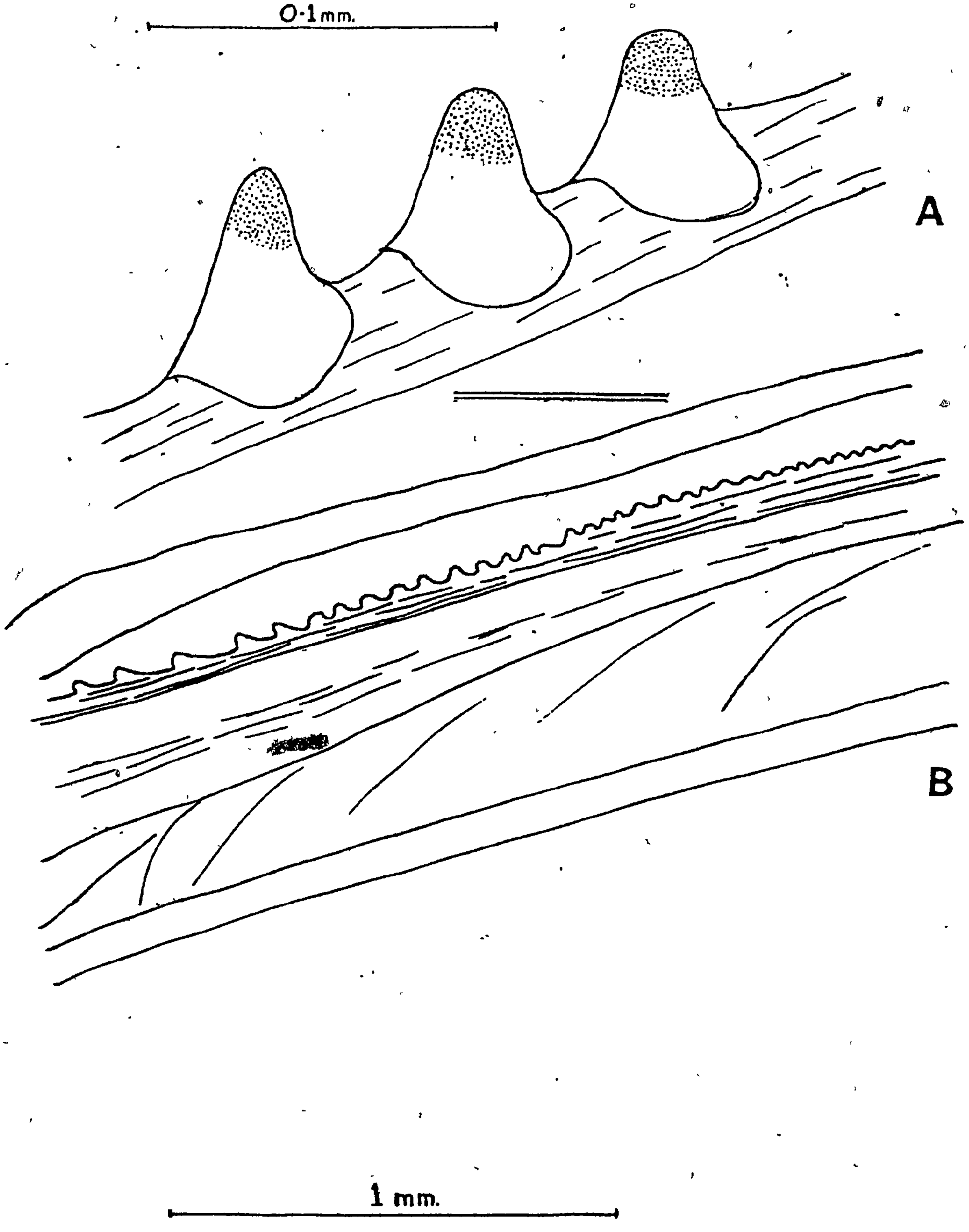
B

[redacted]

Figure 13. Diagram - Chloealtis conspersa, male

(A) Stridulatory pegs

(B) A view of the inner surface of the right hind femur, showing the proximal portion of the row of stridulatory pegs


0·1 mm.
A
B
1 mm.

ings are responsible for specific sounds produced during a downstroke of the femora, during stridulation.

Recorded sounds were analysed using a storage oscilloscope (Gould, Type Os 4000) with a memory bank (Model 4001). A 60 hz active filter was also used to reduce background noise. To make permanent records, the storage display was traced by a chart recorder (Perkin-Elmer, Model 56). By reducing the playback tape speed, it was possible to obtain individual sound impulses produced by single pegs.

a) Chorthippus c. curtipennis

The stridulatory sounds of C. c. curtipennis are reproduced through oscillograms in Figures 14 to 18. Figure 14 represents a stridulatory sequence. Each cluster of peaks averaging about 20 mm on the graphs, symbolize a single downstroke of the hind femora.

Previously the sound emitted from one downstroke of the femora was referred to as a "chirp", but Broughton (1976) proposed that the word "echeme" replace "chirp". The word "chirp" implies that the sound is unitary and undivided. Analysis has shown that a "chirp" is comprised of syllables, which in turn are composed of impulses, resulting from the impact of one stridulatory peg at the tegminal vein.

Figure 15 represents one echeme from the middle of a sequence. The echeme consists of a series of syllables which correspond to the peg-frequency of the femora. These are illustrated by the peak-groupings of the oscillogram, and are more visible in Figures 16, 17 and 18, which are enlargements of the echeme of Figure 15.

Figure 19 is an enlargement of an oscillogram by Elsner (1974) of three echemes produced by Chorthippus biguttulus (Linnaeus). When compared with Chorthippus c. curtipennis (Fig. 15) this European species appears to have a greater syllabic separation, although its stridulatory movements are faster.

Oscillograms of the two other European species Chorthippus brunneus (Thunberg) and Chorthippus parallelus (Zetterstedt) by Broughton (1963) show that they also have a greater syllabic division, even though they stridulate at a faster rate.

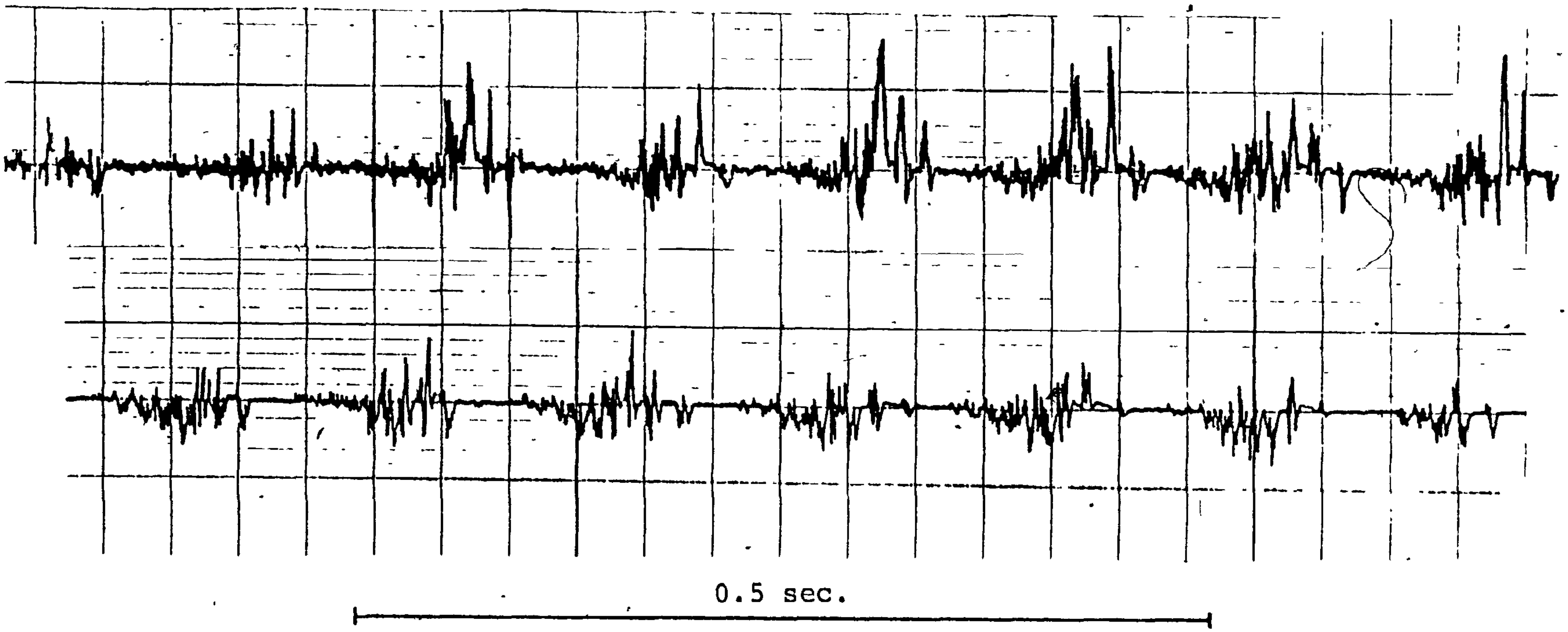
The accelerated stridulatory movements combined with an increased syllabic separation, indicate that the stridulatory pegs responsible for producing sound are probably spaced further apart than those of the North American species Chorthippus c. curtipennis.

A comparison with Chorthippus montanus (Charp.) was most desirable because of its close relationship to Chorthippus c.

curtipennis, but unfortunately no stridulatory oscillograms for this European species could be obtained.

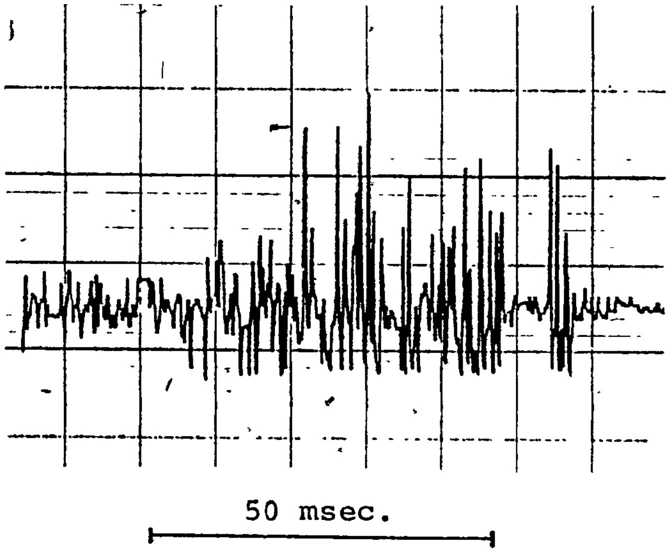
[redacted]

Figure 14. Oscillogram - Chorthippus c. curtipennis
A Stridulatory sequence


0.5 sec.

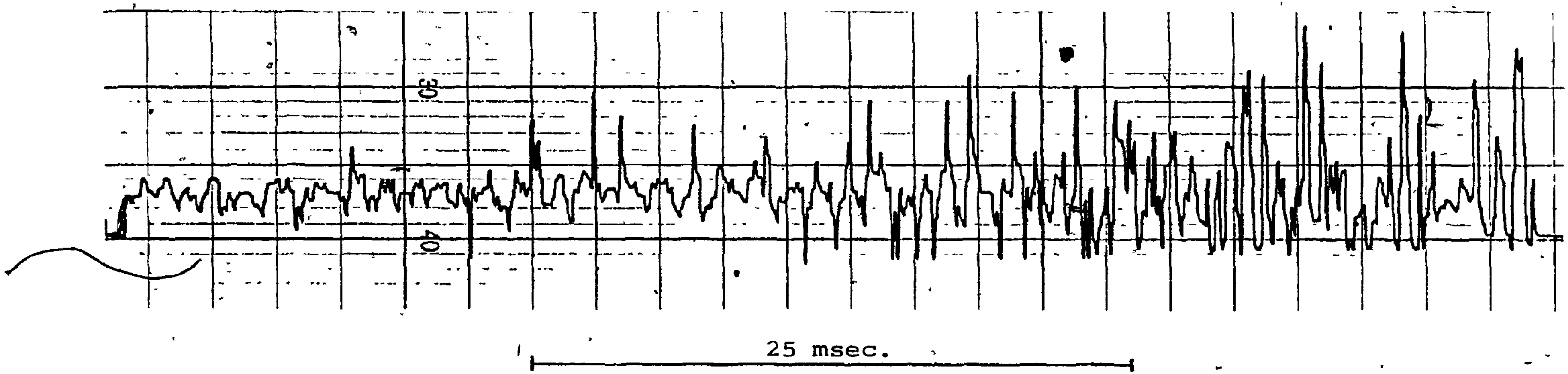
[redacted]

Figure 15. Oscillogram - *Chorthippus c. curtipennis* An echeme from the middle of a stridulatory sequence


50 msec.

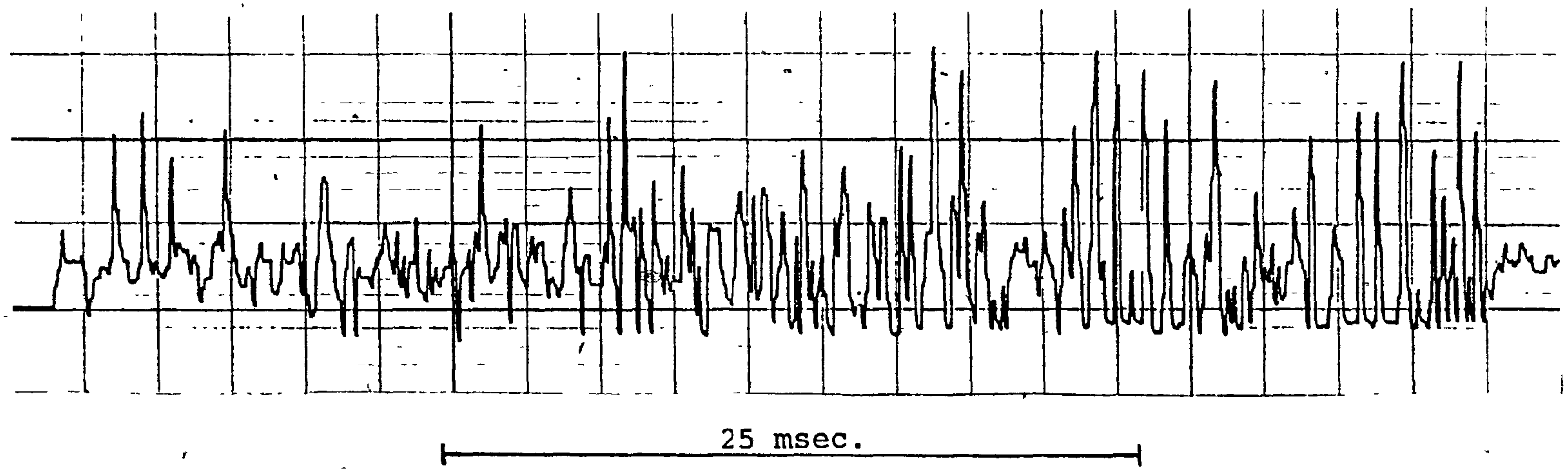
[redacted]

Figure 16. Oscillogram - *Chorthippus c. curtipennis*
Syllables from the first part of the
echeme in Figure 15


30
40
25 msec.

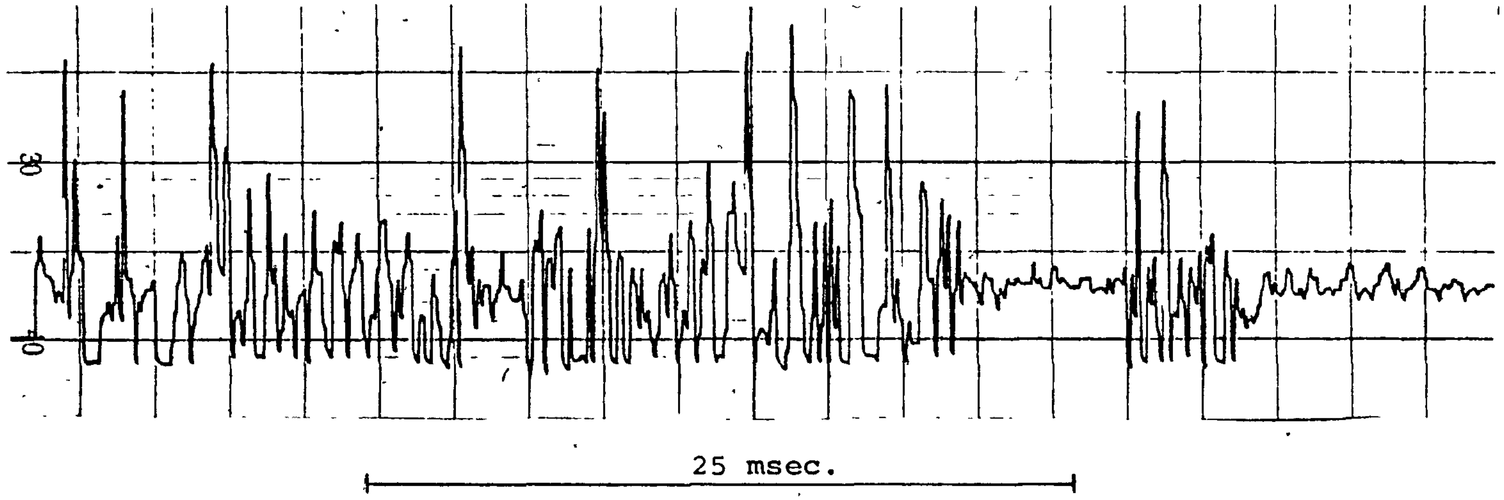
[redacted]

Figure 17. Oscillogram - *Chorthippus* *c.* *curtipennis*
Syllables from the middle part of the
echeme in Figure 15


25 msec.

[redacted]

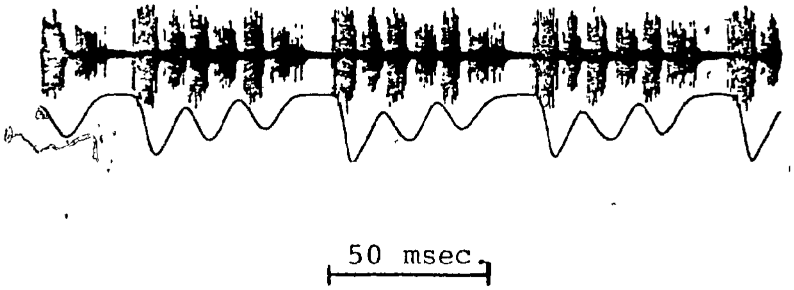
Figure 18. Oscillogram - _Chorthippus_ _c._ _curtipennis_
Syllables from the last part of the
echeme in Figure 15


30
40
25 msec.

[redacted]

Figure 19. Oscillogram - <u>Chorthippus biguttulus</u>
Three echemes <u>from a stridulatory</u>
sequence.

Fron Elsner (1974)


50 msec

b) Orphulina speciosa

The stridulation of O. speciosa is barely audible. Rather than the loud pulsating hissing sounds made by Chorthippus and Chloealtis during stridulation, O. speciosa produces only a "tick" sound with each downstroke of the hind femora. This is due to only a few pegs striking the tegmina. The raised hind femora are held slightly away from the body, and during the downward movement of the femora are adducted so that only a few stridulatory pegs make contact with the tegmina and produce the "tick" sound.

Figures 20, 21 and 22 are oscillograms of O. speciosa stridulation.

Figure 20 represents an echeme from the middle of a stridulatory sequence. The peak clusters representing syllables are clearly evident even though background noise was present and is responsible for the undulating base line of the trace.

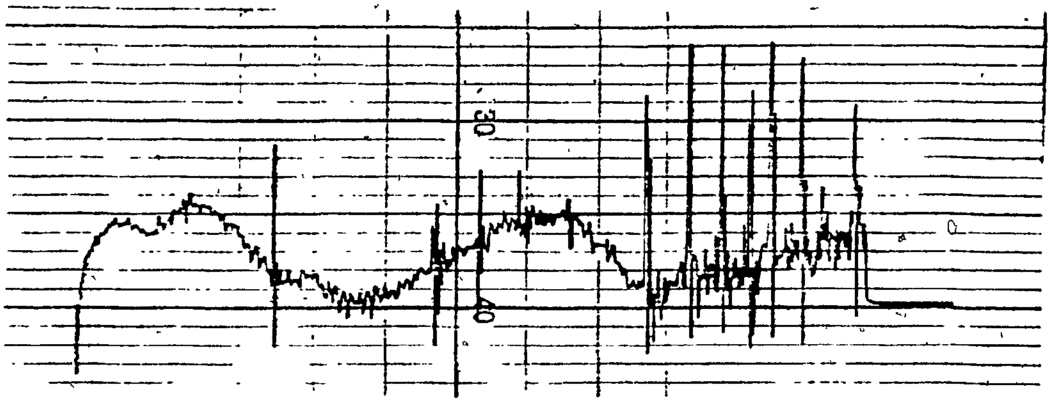
Figures 21 and 22 illustrate individual syllables within an echeme, Each peak of the trace represents the sound produced by a single peg striking the tegmina. Figure 22 represents the syllables which are formed by three stridulatory pegs striking the tegmina.

[redacted]

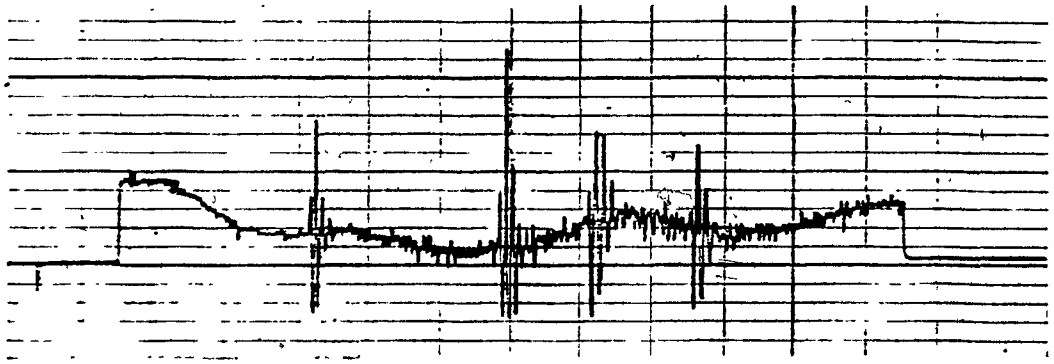
Figure 20. Oscillogram - <u>Orphulina</u> <u>speciosa</u>
An echeme from the middle of a
stridulatory sequence

Figure 21. Oscillogram - <u>Orphulina</u> <u>speciosa</u>
Four syllables from the echeme
in Figure 20

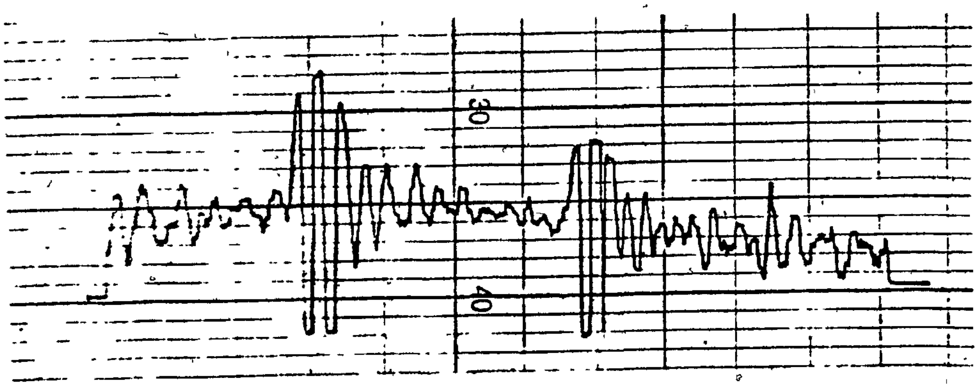
Figure 22. Oscillogram - <u>Orphulina</u> <u>speciosa</u>
Two syllables from the echeme in
Figure 20



7.5 msec.



2.5 msec.



0.5 msec.

c) Chloealtis conspersa

Stridulation of C. conspersa is slower than that of Chorthippus by approximately a half. The first two to four downstrokes of the hind femora are silent. The hind legs are then brought closer to the body of the individual, so that the stridulatory pegs rub against the tegminal veins and produce sound.

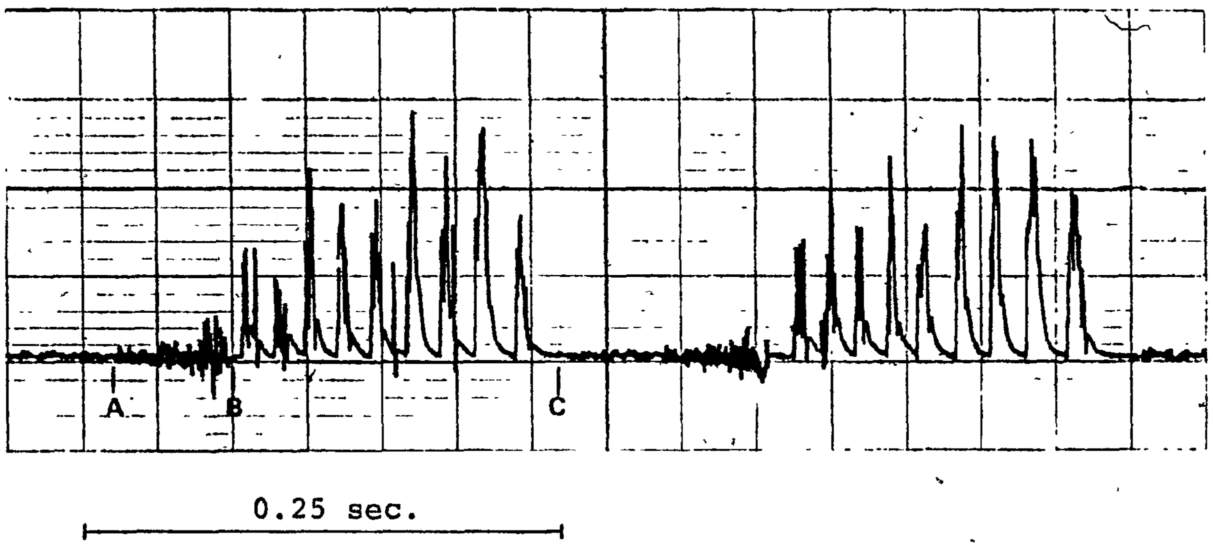
Figure 23 shows two complete echemes. Some sound is produced during the upstroke of the femora, A to B, as well as the downstroke, B to C. Figure 24 is an enlargement of the first part of the echeme. Included is the upstroke sound from A to B and the first four syllables of the downstroke from B to C.

Nine syllables comprise the downstroke portion of an echeme. Isolation of separate syllables is possible due to an increased temporal separation. This distinctness is due to the reduced speed of stridulatory movements and the increased spacing between the stridulatory pegs, relative to Chorthippus.

Figures 25 and 26 represent the fourth and last (ninth) syllables of an echeme from the middle of a stridulatory sequence.

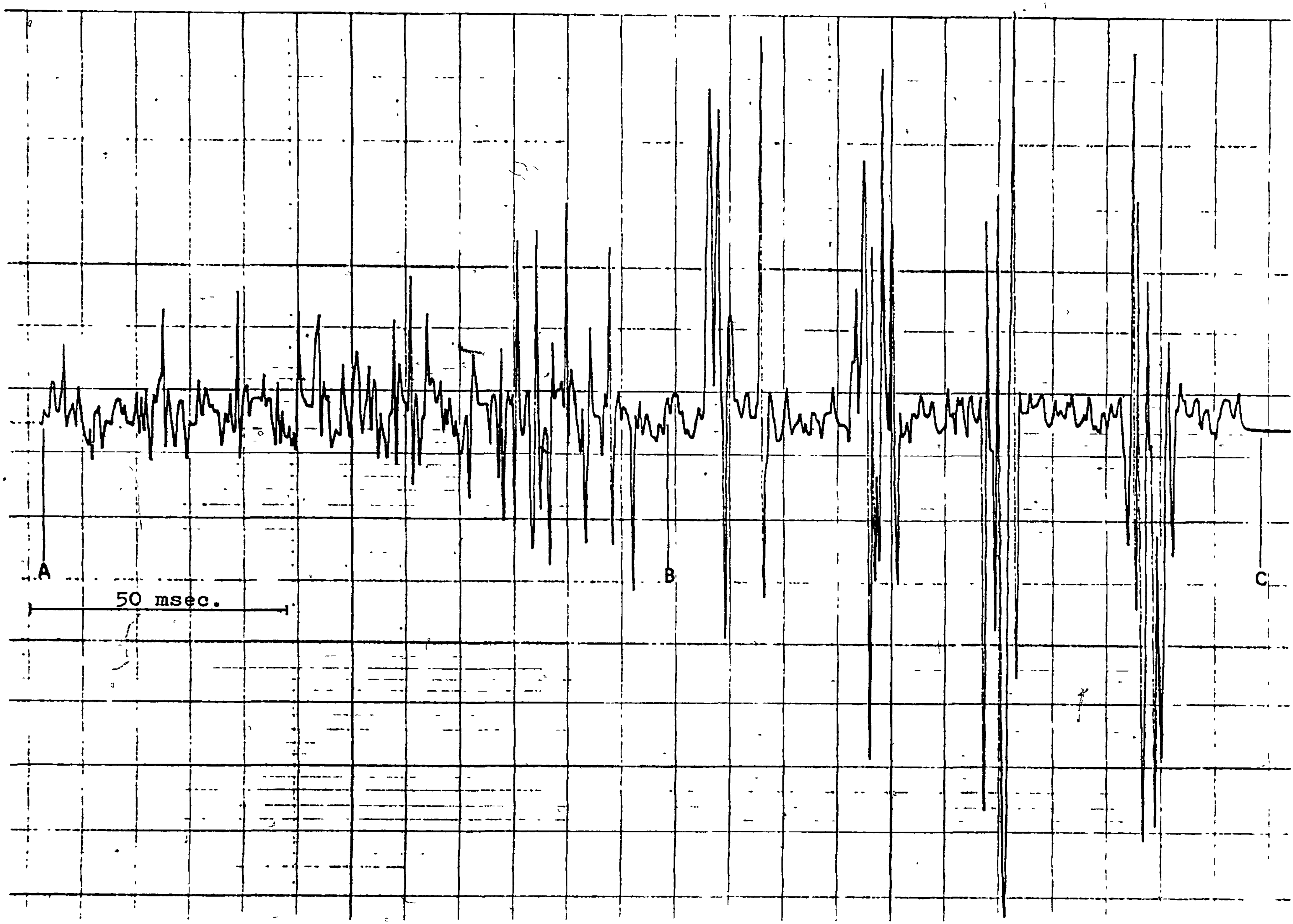
[redacted]

Figure 23. Oscillogram - <u>Chloealtis conspersa</u>
Two echemes from the middle of a
stridulatory sequence


A
B
C
0.25 sec.

[redacted]

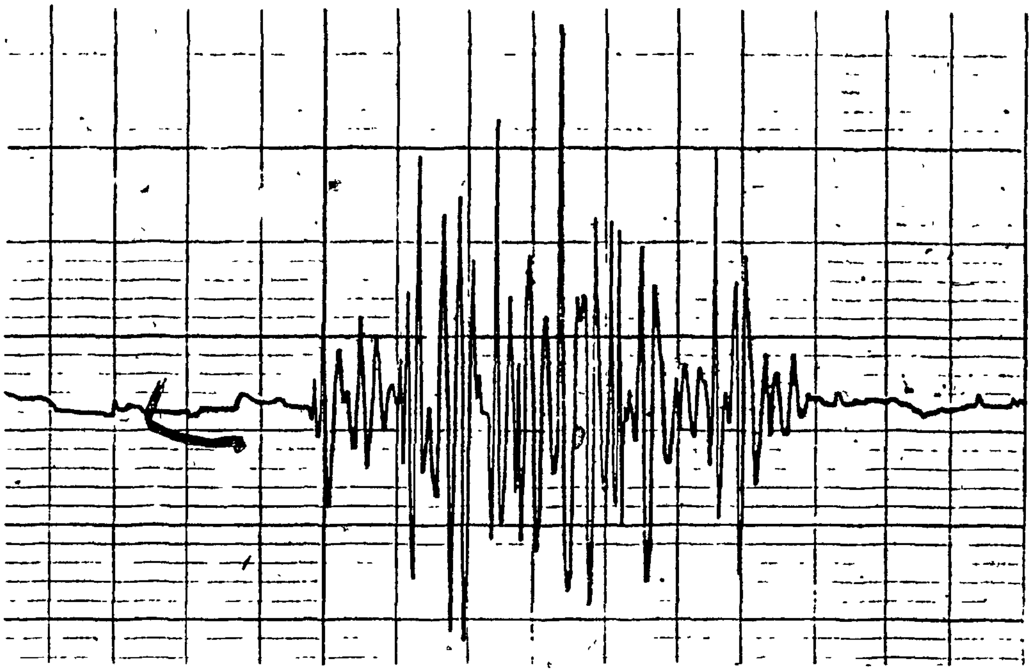
Figure 24. Oscillogram - Chloealtis conspersa
An enlargement of the first part
of an echeme


A
B
C
50 msec.

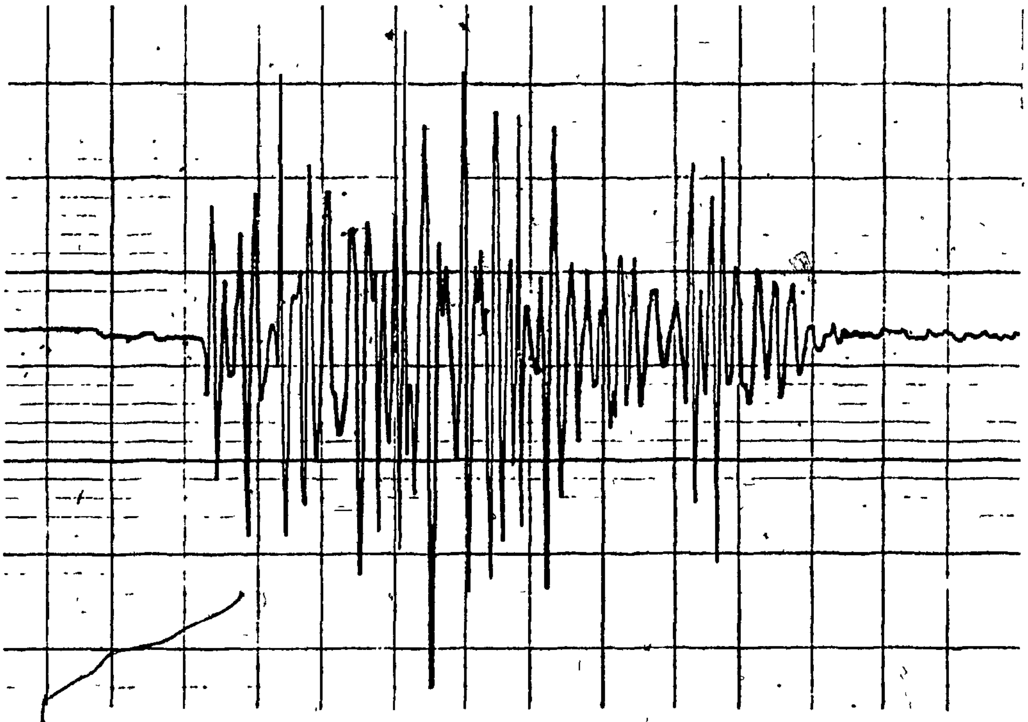
[redacted]

Figure 25. Oscillogram - *Chloealtis conspersa*. The fourth syllable of the first echeme in Figure 23.

Figure 26. Oscillogram - *Chloealtis conspersa* The last (ninth) syllable of the first echeme in Figure 23.



18.5 msec.



20 msec.

SUMMARY AND CONCLUSIONS

Although studies of grasshoppers have increased during the past few decades, only a limited amount of work has been done that relates especially to comparative studies concerning North American species of the subfamily Gomphocerinae, such as Chorthippus c. curtipennis, Orphulina speciosa and Chloealtis conspersa. Individuals of the three species of grasshoppers were observed and recorded from 1976 to 1978, and a comparison of their communicative behaviours has been made.

Conspecific interactions were usually initiated by the males of Chorthippus c. curtipennis and Chloelatis conspersa, which were more active than the females. Males also stridulated to attract females. Since males and females of Orphulina speciosa are equally active, females began as many interactions as did the males. The males stridulated only to signal aggression, not to attract females, as did the other two species. This is probably due to the low volume of the stridulation, making it inaudible at distances greater than a metre.

The general behaviour of Chorthippus c. curtipennis and Chloealtis conspersa was similar, although the latter did not stridulate as often nor as fast as the former. This was because Chorthippus c. curtipennis is generally more active and aggressive than the other two species.

Individuals of the three species usually initiated conspecific interactions through antennal contact. Information regarding the sex and possibly the state of sexual readiness of the participants of an interaction appeared to be sensed by this contact. It is clear that studies of both antennal detection capabilities and cuticular wax composition of the grasshoppers concerned is necessary to confirm or refute this hypothesis.

Aggression by males was signalled by stridulation and usually occurred during male-male interactions. This type of signalling by Chorthippus and Chloealtis was indistinguishable from their normal calling or female-attracting stridulation. It is probable that this aggressive stridulation merely asserts the fact that an individual is a male.

Females of Chorthippus and Orphulina displayed aggression by hind leg movements and posture. No aggressive signals were exhibited by females of Chloealtis conspersa.

Recordings of stridulation by the three species were analysed by means of oscillogram traces. By reducing the playback speed of a stridulatory sequence, individual echemes and syllables were isolated and compared.

Syllables of an echeme from Chloealtis conspersa were more separated and distinct when compared with those of Chor-

thippus c. curtipennis. This was owing to both an increased spacing of stridulatory pegs and to slower movements of the hind femora during stridulation.

Oscillogram analysis of stridulation by *Chloealtis conspersa* confirmed observations that sound was produced during the upstroke of the hind femora, as well as on the downstroke. This discovery contradicts Otte (1970) who stated that sound appeared to be made exclusively on the downstroke in this species.

A faint "tick" sound was found to be produced with each downstroke when *Orphulina speciosa* made stridulatory movements. This consisted of several syllables which in turn were composed of groups of three stridulatory pegs striking the tegmina in close succession. I believe this to be due to the abduct-adduct -abduct movement of the hind femora in the course of a downstroke during stridulation.

A comparison of stridulation oscillograms of the three European species of *Chorthippis* (*Ch. biguttulus*, *Ch. brunneus* and *Ch. parallelus*) with those of the North American species *Chorthippus c. curtipennis* show that all three European species stridulate at a faster rate and have greater syllabic separation than the North American *Chorthippus* species. This indicates that the stridulatory pegs of the European species which are responsible for producing sound, are spaced further apart than those of *Chorthippus c. curtipennis*.

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