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LATIMER W.

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CITY OF LONDON POLY.

ASPECTS OF SONG INTERACTION BETWEEN THE CLOSELY RELATED BUSH CRICKET GENERA PLATYCLEIS AND METRIOPTERA.

A thesis submitted for the degree of
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by

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ABSTRACT.

This study is concerned with the behavioural and ecological aspects of the acoustic interaction that occurs when two bush cricket species, Platycleis albopunctata and Metrioptera roeselii, sing together. The effects of the interaction are predominantly one-way and result in inhibition of singing activity by albopunctata, or a change in its song pattern. This behaviour was initially described by Broughton in 1965 who also described song changes in other species resulting from interactions with singing allospecifics. The present study continues this research into song modification in insects.

The extent of natural variation is examined in detail in the song of P. albopunctata. The acoustic behaviour of this species when singing with conspecifics is also examined in detail. The songs and singing behaviour of some other bush cricket species are analysed and tested for susceptibility to modification. These latter studies, though less detailed than the study on the albopunctata/roeselii interaction, have contributed to the formation of hypotheses as to the causation of song modification.

The results indicate that insects with songs of similar frequency content are liable to interact acoustically. Species which show slight readjustments in song output when singing with conspecifics are also liable to song modification especially when the song of the influencing insect is more continuous in nature than the song of the influenced insect. The results of the detailed analysis of the albopunctata/roeselii interaction reveal a complex interplay between endogenous rhythms of motivation displayed

in the singing activity of albopunctata, and parallel inhibitory and excitatory factors from the song of the roeselii.

Much of the fieldwork has been undertaken in France where, in many localities, albopunctata and roeselii are sympatric. Song modification in the wild is usually prevented by a negative phonotactic response by albopunctata to the song of roeselii. This response may be derived from pre-existing behavioural patterns that result in 'territorial' spacing between males in grassland populations. In habitats where populations overlap, interspecific spacing develops with the onset of singing activity by the adults. In this way albopunctata is excluded from certain localities by high-density roeselii populations due to the acoustic competition between these two species.

CONTENTS.

INTRODUCTION.

Sound production and its reception as a means of communication has assumed great importance in the biology of many animal groups. Insects are one such group in which, particularly in the Orthoptera, sounds of various patterns (e.g. long trills or discrete chirps), frequencies, and intensities are produced. The 'message' (Smith 1968) of the song is radiated through the vegetation while the singer remains visually concealed; a prime advantage of acoustic communication.

The continuous calling or <u>proclamation</u> song (Broughton 1963) of the male identifies the species and advertises its position. The message of the song may vary, depending on the sex or status of the receiver. Females moving randomly through the vegetation are likely to move towards the sound source, thus locating the male (see Autrum 1940, Murphy & Zaretsky 1972, Lewis 1974b, Nocke 1974,1975, Hill & Boyan 1977, Bailey & Thompson 1977 for studies on directional localization). Proclamation song therefore acts as a releaser for positive phonotaxis by the female (Regen 1913, Baier 1930, Zippelius 1949, Busnel, Dumortier & Busnel 1956b, 1959, Walker 1957, Busnel, Dumortier & Pasquinelly 1959; more recent studies will be mentioned in the Discussion). The message of proclamation song may, in some species, be different for the males which, as a result, tend to space themselves territorially (Alexander 1960, Morris 1967, 1971, Young 1971, Otte & Joern 1975) This aspect of male acoustic behaviour is a prime reason for referring to the song as proclamation song (in preference to calling song).

A close encounter with another male may result in a song change to rivalry or aggressive singing (Weih 1951, Haskell 1957, Alexander 1961, Jones 1966, Samways 1976b). The close proximity of a receptive female, however, results in the male changing from proclamation singing to courtship singing (see Busnel & Loher 1953 1954, Faber 1953, Jacobs 1953, Haskell 1958, Alexander 1961, Loher & Chandrashekaran 1970, 1972, Young 1971 for data on song types and associated behaviour). In many bush-cricket species, however, including those species studied here, only two song types are recognizable, proclamation song and "aggressive" or close-contact calls (Samways 1975, 1976b).

Sound in many insect species is produced by frictional mechanisms (Dumortier 1963, Sales & Pye 1974, Lewis & Broughton, in press). In the crickets and bush crickets, passage of a toothed 'file' on one tegmen across a plectrum on the other results in the rapid vibration of a specialized area of tegmen adjacent to the plectrum. In the crickets, and certain bush crickets (Morris & Pipher 1972), the frequency of vibration of the tegmen varies according to the tooth-strike rate (Walker 1962c). In most bush crickets the frequency band of the song is constant. In these species the specialized structure of the right tegmen, the mirror frame, vibrates at its natural frequency of free vibration (Broughton 1964). Frequency modulation of the tegminal vibration is therefore not available as a means of information coding.

The frequency of the song of different species varies from a few hundred cycles/second to around 100 kilocycles/second, a great range of variation (see Sales & Pye 1974). The song spectrum may consist of a single pure frequency, pitched relatively low, as in most of the true crickets, whose songs fall in the range from 2 kHz to around 6 kHz (Walker 1956, 1957, 1962, Alexander 1956, Hill, Loftus-Hills & Gartside 1972). The songs of bush crickets are generally higher in pitch and frequently contain ultrasonic components. They may similarly consist of a single, more-or-less pure frequency as in Homorocoryphus nitidulus vicinus (Bailey & Broughton 1970), or contain many frequencies producing a broad-band song spectrum, as in, for example, Platycleis albopunctata (see p. 47). Often, closely related species have very similar frequency spectra (see Dubrovin & Zhantiev 1970, Bailey & Robinson 1971, Samways 1976a). The other temporal parameters of the song (or amplitude modulation patterns) are therefore of prime importance in species-specific communication (Pumphrey 1940).

The relatively simple songs of these insects, being an integral component of the reproductive process, are therefore under heavy selection pressure for clarity and species-specificity, particularly in habitats rich in singing orthoptera. In most habitats in the temperate regions adult bush crickets do not survive over the winter. Eggs are laid in late summer and autumn to hatch in the following spring. Thus the nymphs are never exposed to the song of the adult, yet the stability of the song is preserved in each generation. Studies by Leroy 1964, Bentley 1971, Bentley & Hoy 1972, Hoy 1974 and Helversen & Helversen 1975, have shown that the song is, in at least certain aspects, under direct genetic control. The selective advantage of this 'system' (as opposed to that in many birds where proclamation songs are very much influenced by learning) is clear, given that the life cycle is univoltine and the young are never exposed to adult influences. A learning facility might indeed be disadvantageous, especially in orthoptera-rich habitats where species emerging later in the spring may be exposed for many weeks to the songs of other species. It is therefore, perhaps, not surprising that as yet no song-learning ability has been satisfactorily demonstrated in the orthoptera.

Nevertheless, it is clear that song is not entirely independent of extraneous influences (see p. 7). Moreover, studies on intraspecific chorusing behaviour have shown that, in some species, the acoustic output of a singing individual can be altered by the song of a nearby singer. In such cases however, the changes in the song are such that the clarity of those parameters of the song that attract the female are maintained, and often enhanced. For example, colonies of snowy tree-cricket males synchronize their chirps, so maintaining the clarity of the chirp rate (see p. 25 for details of song terminology). In this species the chirp rate is the principal parameter for female phonotaxis (Walker 1957, 1969c). Females of other species may use different parameters; some respond primarily to the syllable (see p. 25) content of the chirp (Zaretsky 1972, Hill 1974, Popov & Shuvalov 1977). Therefore in some species syllable synchrony is maintained (Samways 1976c), or chirps are sung in alternation by neighbouring males (Regen 1908, 1914, 1926, Baier 1930, Fulton 1934, Busnel et al 1956, Jones 1966, Shaw 1968). Both of these chorusing strategies (reviewed by Alexander 1975) preserve the pattern of the song and therefore its species specificity; despite the implied potential for modification, they operate as stabilizing agencies.

Against this background of song stability it seems at first surprising that Pierce, in 1948 (later confirmed by Alexander 1960) was able to induce a change in the number of syllables in the chirp of Pterophylla camellifolia. Here the number of syllables produced by the insect was statistically equivalent to the number of artificially broadcast sound "pulses" (a human voice in Pierce's experiments, typewriter taps in Alexander's). However, the song of this species varies between populations, two or three syllables *per* chirp being typical of northern populations in the U.S.A., while southern populations have five to seven syllables in the chirp (Alexander 1968). While the changes of song noted by Pierce and Alexander were atypical of the *population* from which the insect was taken, they were nevertheless within the *species'* repertoire.

These remarkable responses of Pterophylla prompted Broughton (1965) to check Pierce's observations, using various European bush-cricket species. Heterospecific male couples were caged together and allowed to sing together. In many species, songs were extensively modified during the interspecific duets that took place. The songs produced under these circumstances were sometimes completely novel, unlike the Pterophylla modification. Some of the most interesting interactions occurred between species with continuous 'buzzing' songs and those whose songs, by contrast, consisted of regularly produced, discrete chirps. These discontinuous songs usually suffered the greatest modification. McHugh (1971), studying song modification and behaviour within the genus Metrioptera found no consistent behavioural pattern to be associated with these interactions. He recorded instances of both aggressive behaviour and homosexual courtship, but simple passive behaviour accompanied many interactions, suggesting that song change is largely a result of acoustic input. Samways (1975,1976,1977) carried out an intensive investigation of interactions within the genus Platycleis and showed that such interactions also occurred in the field. Thus, song modification may have maladaptive ecological repercussions. Samways suggested that the similarity of the song frequency spectra within the group resulted in species (that normally adjust their song output during intraspecific chorusing) adjusting their songs, now to an inappropriate stimulus, during inter-specific interactions. He suggested furthermore that the interspecific similarity of syllable durations and intervals might also be responsible for the reactivity shown to songs of allospecifics in this group.

The present research concerns an even more extreme situation: intergeneric interactions in which the syllable parameters are dissimilar. The study concentrates on the interaction between Metrioptera roeselii and Platycleis albopunctata in which, as Broughton (1965) showed, the discontinuous (chirping) song of the albopunctata is modified by the continuous song of the roeselii. Other species with discontinuous songs are also tested for susceptibility (see p.142). M. roeselii and P. albopunctata are sympatric in many areas in France (though not yet found so in England). Extensive fieldwork has therefore been undertaken to ascertain if song modification occurs in the wild, and what (if any) are the results of this interaction.

The results of this study are arranged in three sections. The first examines in detail the normal songs of the species concerned, and the range of individual variation. The song of albopunctata has been examined in the greatest detail using material from over thirty individuals. Generally, data from the songs of four or five individuals have been selected to show the extent of variation. Data on variation of song for the remaining species are derived from small samples of not more than five individuals. Knowledge of natural song variation is clearly a prerequisite for the study of that which results from interspecific interactions. So too, is a detailed consideration of the 'influenced' species' normal reaction to the song of a conspecific. Therefore, section 2 of the results examines intraspecific song interactions both in the laboratory and in the field. Finally, section 3 deals with interspecific interactions and the ecological repercussions.

Most of the data are derived from my own recordings of song: both of solo singing and intra- and interspecific interactions. Some recordings made by Broughton (1965) have also been analysed. A large number of intra- and interspecific interactions have been analysed; again, data from a selection of these have been illustrated in the results to show the range of behaviour encountered.

It has unfortunately not been possible to use techniques of artificial acoustic stimulation for the equipment necessary for the synthesis of these complex, ultrasonic songs has not, until very recently (Taylor 1978), been available. The brief working time with live adult insects (at most, from mid-June to mid-October) has also imposed limitations on this study. For example, no neurophysiological work has been attempted, though, in any case, the small size of these insects might preclude such studies until refined techniques are developed. This is in a way unfortunate for it would be most interesting to monitor the peripheral (tympanic nerve) and especially the central (auditory neurone) responses of the influenced insect to the influencing song. Studies relevent to this problem are at present being undertaken at the City of London Polytechnic.

Nevertheless, despite these limitations, much can be inferred from behavioural work of the type undertaken here. Where relevant, the results of this study will be discussed in relation to previously published work on topics such as hearing and frequency discrimination (see p. 159). There is, fortunately, a good deal of information on these topics.

The earliest workers, noting the linear arrangement of sensory cells in the orthopteran ear, thought that frequency analysis might therefore be possible, as in the human cochlea (see Pumphrey 1940). The work of Wever & Bray (1933) and Pumphrey & Rawdon-Smith (1939) led Pumphrey (1940) to discount this hypothesis. Though he contended that the insect ear was incapable of frequency analysis, he noted that the three groups of sensory cells attached to different points of the tympanic membrane in acridids might enable some degree of frequency discrimination by an averaging process similar to that of colour vision (see also Broughton, Samways & Lewis 1975). Other species, particularly those with those with songs consisting of a single frequency (i.e. resonant singers) have narrow auditory threshold curves that closely match the song spectra (Suga & Katsuki 1961, Suga 1963, Mckay 1969, Hill 1974) suggesting that hearing in these species is sharply tuned to the frequency of the song. However, Mckay (1969, 1970) showed in Homorocoryphus that certain auditory neurones were maximally sensitive to frequencies much higher than those present in the song. Recent research has shown that in crickets there are low-frequency neurones responding to the proclamation song, and broad-band, high-frequency neurones that respond to the courtship song (Popov 1971, Nocke 1972, Rheinlander, Kalmring, Popov & Rehbein 1976). These latter neurones may also respond to the ultrasonic calls of predators (e.g. bats, rodents, see Sales & Pye 1974) or the broad-band noise of disturbed vegetation (Samways 1976). Popov, Shuvalov & Markovich (1975) and Popov & Shuvalov (1977) have demonstrated negative phonotaxis to frequencies of 10 kHz and over, in Gryllus bimaculatus (frequency of proclamation song - 5 kHz), though this seems more properly described as an evasion response rather than a phonotaxis (see Lewis & Broughton, in press). Nevertheless, it is clear that crickets are at least able to differentiate high and low frequencies within their hearing compass.

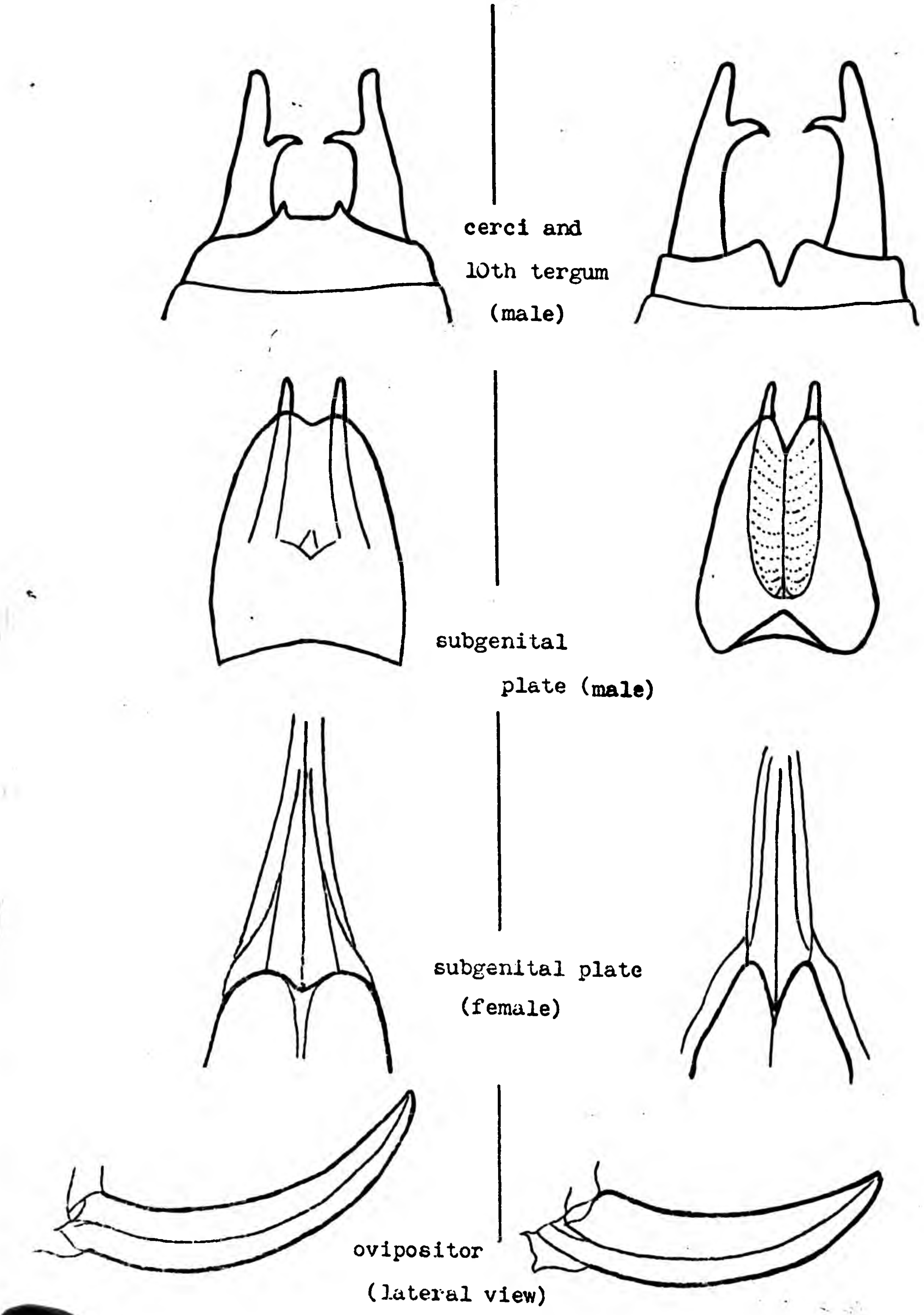
Acridids seem to have a similar capability for this broad type of frequency discrimination (Horridge 1960, 1961, Michelson 1966, 1968, 1971, Kalmring 1975).

Bush crickets with broad-band songs, e.g. Decticus verrucivorus appear to have a highly refined auditory system (Rheinlaender 1975, Kalmring, Lewis & Eickendorf, in press). In this species many auditory units have been detected, each one responding maximally to a different frequency or frequency compass. This work and its relevance to the problems of song modification will be examined in the Discussion (p. 159).

Thus, as research progresses on the subjects of hearing and frequency discrimination it is becoming apparent that many species have the capability to analyse a wide range of sounds encountered in their environment. The advantages of predator detection have been mentioned; that such a capability can potentially result in acoustic interference and song modification, may be an occasional, disadvantageous side-effect.

Fig. 1. **COMPARATIVE MORPHOLOGY OF**

P. ALBOPUNCTATA AND M. ROESELII.



MATERIALS AND METHODS.

1. The Insects and their Localities.

The two principal localities for the study and collection of the insects were the Causse du Larzac and the Causse Noir, two of a number of high limestone plateaux that form part of the Cévennes mountains in the south of France. Here, *Platycleis albopunctata* (Goeze), *Metrioptera roeselii* (Hagenbach) and *Gampsocleis glabra* (Herbst) are to be found in the calcareous grasslands, the former two species also extending into the hedgerows. The adults are easily distinguished from each other by colouring and gross morphology, and by the distinctive songs of the males. Immature *P. albopunctata* and *M. roeselii* are difficult to differentiate until the later instars when details of the subgenital plate, cerci, ovipositor and tegminal development can be compared, (fig. 1, and see Zeuner 1941, Ander 1948, Chopard 1951, Cejchan 1960 and Harz 1969).

Other localities in France where *P. albopunctata* and *M. roeselii* occur together were visited, in particular the area around the town of Les Eyzies in the Dordogne. Here, the two species occur in the hedgerows and grass verges in the river valleys; *albopunctata* extends into shrublands on the limestone slopes.

Platycleis sabulosa (Azam) occurs in the *Salicornia*/*Agropyron* community of the coastal salt marsh in the south of France. In certain areas it penetrates inland, along river valleys and in agricultural land where it can be found in the *Arrhenatherum*/*Dactylis* grasslands and in the hedgerows bordering fields and woods. As this species is nocturnal, studies were made just after sunset when singing activity commenced. All other species studied were diurnal and heliophile.

Sites in England were visited in order to collect P. albopunctata, M. roeselii and Metrioptera brachyptera (L.). These species are not known to be sympatric in England, P. albopunctata being restricted to certain localities on the south coast, M. roeselii to the alluvial grasslands of the Thames estuary and sea-wall areas of the Essex coast. P. albopunctata has also been recorded from Essex but seems most uncommon in this area. M. brachyptera is found in the damp Calluna/Erica tetralix community of the New Forest and similar areas (see Ragge 1965 for data on distribution).

Most of the data in this thesis are derived from studies on French populations. Individuals from British populations have at times been studied as indicated in the text.

2. Fieldwork, Collecting and Transport.

Behavioural and ecological observations were made by moving carefully through the vegetation, locating singing males aurally, then, if possible, visually. Gentle, cautious movements enabled close observations to be made. Population estimates of singing males were made by marking their positions with canes; this also allowed the measurement of nearest-neighbour distances. Marking individuals on the pronotum and hind femora using coloured enamel paint facilitated the study of dispersion. Three captive individuals marked in this way retained these marks throughout their adult life. Absolute estimates of the population could be made by flushing out (by repeatedly trampling the vegetation) and capturing the insects within a fairly small sample area, e.g. up to 9 m^2. The most accurate counts were from areas with natural boundaries, e.g. a small area of dense growth surrounded by open vegetation where escapes would be noticed. Such vegetational patterns are common in the Causses (see fig. 27, p. 85).

The accuracy of this method of population estimation was checked by cropping approximately 3 square metres of grass within the sample area to search for crickets that might have remained immobile deep down in the grass stems. On three occasions throughout the season small areas were cropped down to the level of the soil surface; on no occasion were any crickets found remaining in these areas. It must be stressed however, that all field ecological and behavioural work was carried out during warm, sunny weather when the insects are most active. Bush crickets are rarely evident in the habitat during dull or cold weather, tending to remain inactive deep in the vegetation.

Further behavioural studies were made in the field by enclosing the insect, or insects, in a 'tent' of nylon mesh placed over the vegetation and supported by canes. The size and shape of the enclosure could be varied up to a maximum area of 4 square metres. This arrangement ensured the most natural environment for the insect whilst confining it for repeated studies.

Collecting tongs designed by Samways (1973) were used to capture the insects. The addition of circular strips of foam plastic to the edges of the cups that meet to enclose the insect reduced the possibility of damaging a specimen. The insects were then introduced into 'Hartley' boxes (see Samways 1975) for easy transportation in the field. For long term storage large cages made of nylon gauze glued onto a stiff wire frame were used; the use of a fine mesh prevented the entry of ants. Mortality was low in these cages in comparison to closed plastic cages in which adverse microclimates may develop. Small Petri dishes were glued to the floor of the cage to contain food and water. Food consisted of wheat grains and wheat germ

('Bemax'); fresh vegetation was added whenever possible to serve as a food source and to give cover. The addition of sticks increased the 'standing room' and provided anchorage for the insects during the moult. In the cages containing Platycleis, 'Oasis' blocks were introduced (see Samways 1975) in order that oviposition in the blocks might commence as soon as possible. The blocks had to be kept moist to prevent desiccation of the eggs; this was facilitated by allowing each block to stand in a shallow container full of water.

The cages were always stored in open shade as these species cannot tolerate continuous, direct insolation, particularly around mid-day, when death can result after two or three hours of exposure. When being transported in the car, windows were opened slightly to provide a throughflow of air and the car was never allowed to stand in the sun for more than a few minutes. Transportation was clearly a source of stress, resulting in higher mortality. Therefore whenever possible insects for lab. study were not collected until a few days before the return journey so as to subject them to the minimum travelling time.

3. Laboratory Maintenance and Culture.

In the laboratory it was possible to keep the insects in conditions of controlled humidity and temperature (between 60% and 70% R.H., and 20° to 26° C.). As in the field, net cages were used; the floor of these cages, however, consisted of a sand substratum contained in a tray into which the five-sided mesh cage was placed. New 'Oasis' blocks were provided though it was found that the Platycleis readily laid in the dry sand; in order to prevent desiccation the sand was kept moist. Egg-laying would continue until mid-October; after this the insects became senescent. The eggs were recovered from the sand by sieving, placed on moist tissue paper in Petri dishes, and covered. Eggs in Oasis blocks were allowed to remain there and the damp blocks were put into a polythene bag to prevent water loss. Diapause and subsequent maturation of the eggs was induced by incubating the eggs at various temperatures for set periods following the schedule given by Hartley and Warne (1972). This resulted in eggs hatching some two months earlier than in the wild (Pesson 1940).

The nymphs were transferred to the net cages and reared on a diet of wheat germ and fresh Agrostis tenuis. This grass was grown from insecticide-free seed in small shallow trays (Samways 1975), and the tray then put in the cage. When the adults emerged, these trays were removed to prevent eggs from being laid in the turf, from which they are difficult to recover. Again, sticks were introduced to facilitate moulting.

4. Song Recording and Behavioural Observations.

The songs and interactions to be analysed in terms of their temporal components were recorded using portable Akai X-IV tape-recorders with the standard dynamic microphone, (frequency range: - 40 Hz to 20 kHz at 7½ i.p.s.). The insects to be recorded were kept in clear plastic cylindrical cages of the type used by Broughton (1965) and Samways (1975). Twigs were introduced as singing posts. Signal/noise ratios in these cages were good while sound transmission between them was reduced in comparison with net cages. Thus, more interacting pairs of insects could be set up in a given area without the songs of one pair appearing to affect the behaviour of others. (For details of terminology see page 25). For recordings where fine analysis was required the insects were recorded in small net cages to reduce echo anomalies. The dimensions of all types of cage were such that the interacting insects were no more than 15cm apart.

Observations on behaviour could be made with both types of cage. As the net cages did not impair sound transmission these were used to separate influencing and influenced insects by confining each species to its own cage. When required, the two cages were placed on either side of an opaque screen, so eliminating the visual and tactile modes of communication. The degree of song modification could be tested over varying distances by moving the cages apart. When G. glabra was used in interspecific interactions such separation was particularly necessary because this species may prey upon smaller bush crickets when confined with them.

Recordings intended for accurate frequency analysis were made using a Phillips Analog-7 Instrumentation tape-recorder in conjunction with a Bruel & Kjaer ¼ inch condenser microphone. The microphone amplifier section of a B & K Frequency Analyser (Type 2017) was used, without the frequency analysis section, to amplify the signal. The fastest tape speed of 32 i.p.s. was used. This combination of equipment gave a flat response from 250 Hz up to 80 kHz. The quality of the signal was monitored at the time of recording using a Tektronix (Type 502 A) dual beam oscilloscope, the upper beam displaying the signal output from the B & K before it entered the tape-recorder while the lower beam showed the monitor output of the tape-recorder. The insects, in net cages, were placed in the centre of a large recording arena (1.5 x 1.5 m) with all its surfaces thickly padded (15 cm) with layers of plastic foam and a product made from rubberized horse hair. The bench surface was built up to a height of 25 cm with these materials. With these precautions no echos were detected. The microphone was placed within eight centimetres of the singing insect and whenever possible in a position behind and slightly above the insect in the area of the greatest sound intensity.

The air temperature was measured at the time of each recording using a thermistor probe. The use of small thermistors is preferred in conditions of radiant energy when mercury thermometers become most inaccurate. It must be remembered, however, that the internal temperature of an insect is not always related to the air temperature. Their relatively dark colouration results in absorption of radiant energy. Therefore, when temperature was varied experimentally no radiant energy was allowed to fall on the singing insect.

5. Preservation of Specimens and Morphology Studies.

Several specimens of each species were preserved in liquid ethyl acetate. One of the principal advantages of this preservative is that it prevents the specimens from becoming brittle (Samways 1974).

In addition to conventional specific morphological characteristics, the sound-producing structures of the tegmina were examined. Counts were made of the teeth on the stridulatory file and the dimensions of the file and the mirror frame measured using a standard binocular microscope with a graticule slide. As it was not necessary to keep the specimens intact, the file and the mirror frame were cut out of the tegmina to facilitate their measurement.

6. Analysis of the Songs.

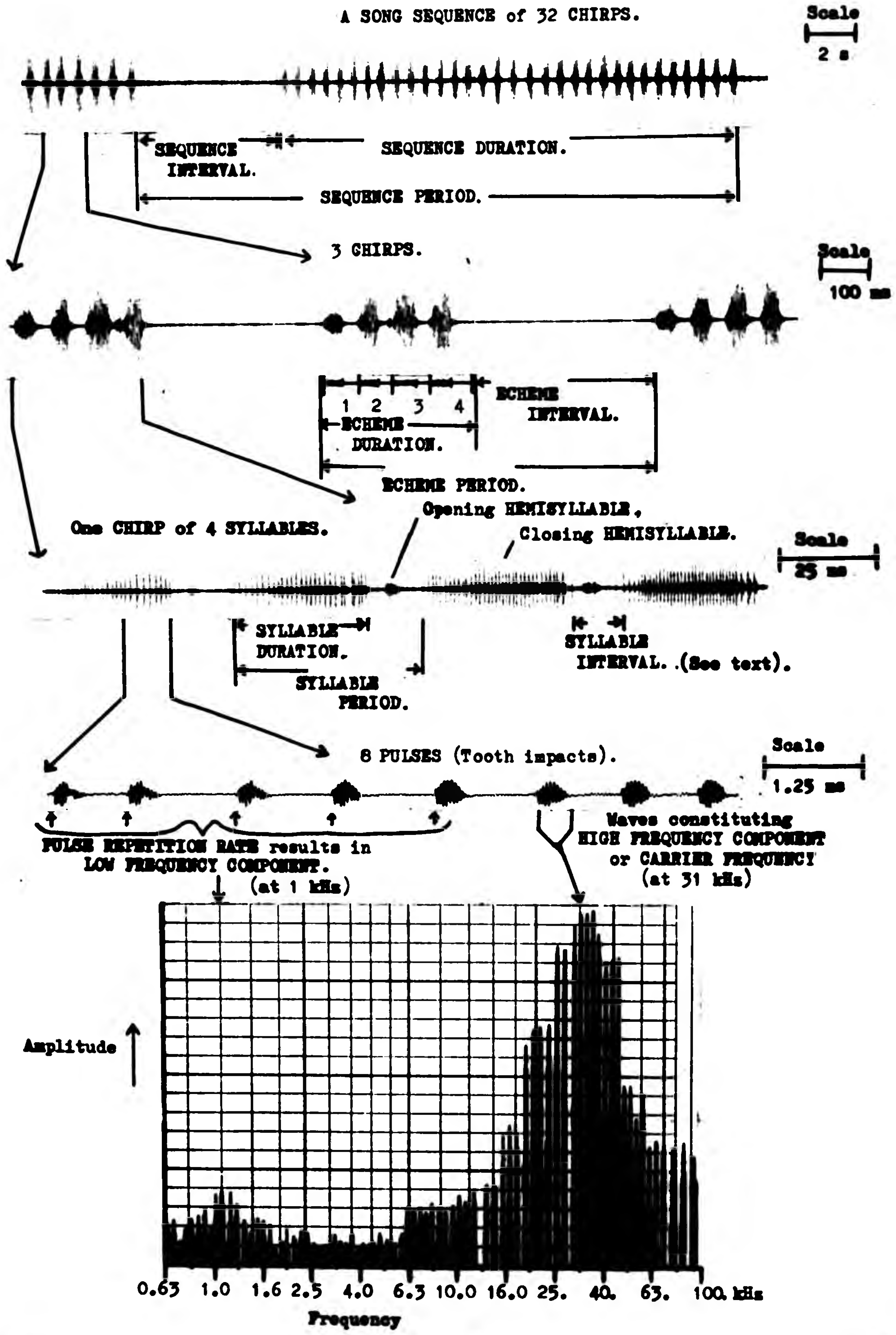
Analysis of many of the interactions was done on a B & K Level Recorder (Type 2305). The signal was fed via the microphone amplifier section of the B & K Frequency Analyser into the level recorder which prints out a rectified trace of amplitude with time. When two insects were singing simultaneously the song of one was usually raised above that of the other on the trace. When desired, the frequency selection and rejection facilities on the analyser could be tuned to enhance this differentiation. Thus, singing activity of both insects could readily be measured. One disadvantage, however, is the inherent inertia of the mechanically operated stylus which prints the trace. For accurate measurements of shorter components, such as syllable durations, oscillography is necessary.

A Mingograph 800 Multi-Channel Recorder was used to print oscillograms directly on paper. The tape-recorders providing the input were set to their lowest playing speeds, ⅛th of the recording speed of the Akai and 1/32nd for the Philips. This ensured that the normally high frequencies recorded on the tape were reduced to within the acceptance range of the Mingograph (upper frequency limit, 4 kHz). Slowing the tape speed also improved the quality of the trace and enabled correlation with heard components.

Frequency analysis was performed on the B & K Analyser, (see below), on the Kay Sonagraph, type 6061 A, (see below), and by careful measurement of expanded traces produced by the high speed print-out of the Mingograph. The B & K Frequency Analyser was used in conjunction with the B & K external filters (type 1612, frequency range 22 Hz - 40 kHz) and the Level Recorder, to print amplitude/frequency spectra. Halving the tape speed enabled analyses to be made to an upper frequency limit of 80 kHz.

The Sonagraph produces frequency/time spectra and frequency/amplitude spectra at any point along the time axis. The wide bandwidth analysing filter (200 Hz) provides better time discrimination and emphasises the tooth impacts of the songs of these

Fig. 2. TERMINOLOGY OF THE SONG OF P. ALBOPUNCTATA.



bush crickets. The narrow band filter (20 Hz) produces a more accurate frequency plot. Similarly, by successively reducing the tape speed, high frequencies are brought within the range of the Sonagraph (frequency range 85 Hz to 8 kHz). Thus with the tape speed reduced to $\frac{1}{8}$ of the recording speed the Sonagraph will analyse from 680 Hz to 64 kHz.

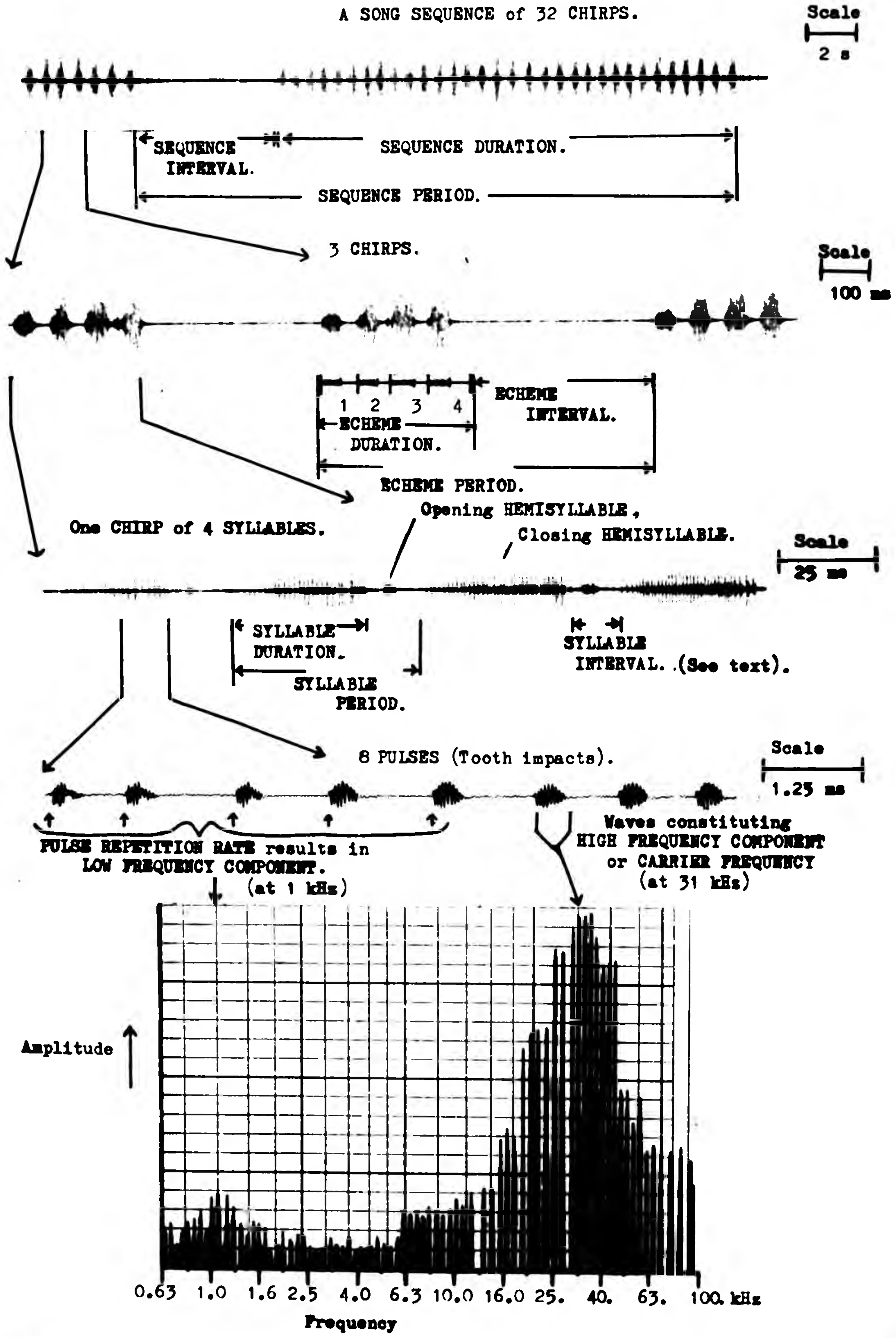
7. Terminology.

The terminology used to describe bush-cricket songs is illustrated with reference to the song of P. albopunctata in fig. 2. The song of this species is often delivered in short sequences, each sequence comprising about thirty echemes (Broughton 1976). The echeme is defined as a first-order assemblage of syllables (see below); its duration is the sum of the syllable durations and the same number of syllable intervals.

The term chirp (defined as a sound unitary to the unaided human ear, see Broughton 1963) can, when referring to the song of albopunctata produced at normal singing temperatures, be used synonymously with the term echeme except that the duration of the chirp is measured from the beginning of the first syllable to the end of the last syllable. The chirp interval is therefore measured from the end of the last syllable of one chirp to the beginning of the first syllable of the succeeding chirp. These terms have been used advisedly at various points in the text (e.g. throughout section 2 of the Results) where it is felt that these particular parameters are of relevance to the acoustic behaviour of the insect.

Each syllable (Broughton 1963) results from an opening and closing movement of the tegmina. On the closing stroke the plectrum on the upper surface of the right tegmen is drawn

Fig. 2. TERMINOLOGY OF THE SONG OF *P. ALBOPUNCTATA*.



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The terminology used to describe bush-cricket songs is illustrated with reference to the song of *P. albopunctata* in fig. 2. The song of this species is often delivered in short *sequences*, each sequence comprising about thirty *echemes* (Broughton 1976). The echeme is defined as a first-order assemblage of syllables (see below); its duration is the sum of the syllable durations and the same number of syllable intervals.

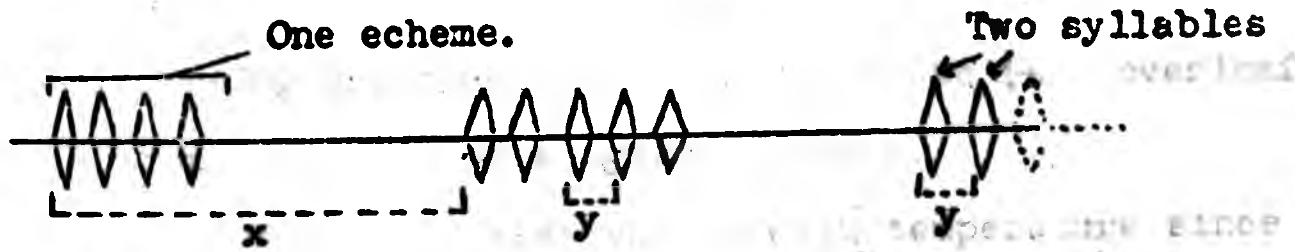
The term *chirp* (defined as a sound unitary to the unaided human ear, see Broughton 1963) can, when referring to the song of *albopunctata* produced at normal singing temperatures, be used synonymously with the term echeme except that the duration of the chirp is measured from the beginning of the first syllable to the end of the last syllable. The *chirp interval* is therefore measured from the end of the last syllable of one chirp to the beginning of the first syllable of the succeeding chirp. These terms have been used advisedly at various points in the text (e.g. throughout section 2 of the Results) where it is felt that these particular parameters are of relevance to the acoustic behaviour of the insect.

Each *syllable* (Broughton 1963) results from an opening and closing movement of the tegmina. On the closing stroke the plectrum on the upper surface of the right tegmen is drawn across the stridulatory file on the lower surface of the left tegmen. As each tooth in the file (see fig. 10, p.43) is struck, the mirror frame (Broughton 1964, Bailey & Broughton 1970) vibrates briefly at a high frequency, the *carrier* frequency (see also Pierce 1948, Broughton 1955, Dumortier 1963). Thus the syllable consists of a series of damped *pulses* (Broughton 1963). The repetition rate of these tooth-impact pulses produces a lower-frequency component in the song spectrum (see fig. 2). This component, being a product of muscular movement, varies with temperature and the internal excitatory state of the insect. The high-frequency components do not vary in this manner as they are produced by vibration of tegminal structures, the sonorous properties of which do not change with temperature.

Often the file and plectrum also engage on the fast opening stroke of the tegmina. The syllable then comprises a very short opening *hemi-syllable* and a closing hemisyllable. Unless otherwise indicated, the parameters of the syllable (e.g. duration, period, see fig. 2) refer to the closing hemisyllable, since the opening hemisyllable is usually of very short duration and low amplitude, and is often absent entirely.

Some special rate parameters have been used in the Results to describe songs and quantify changes in singing behaviour.

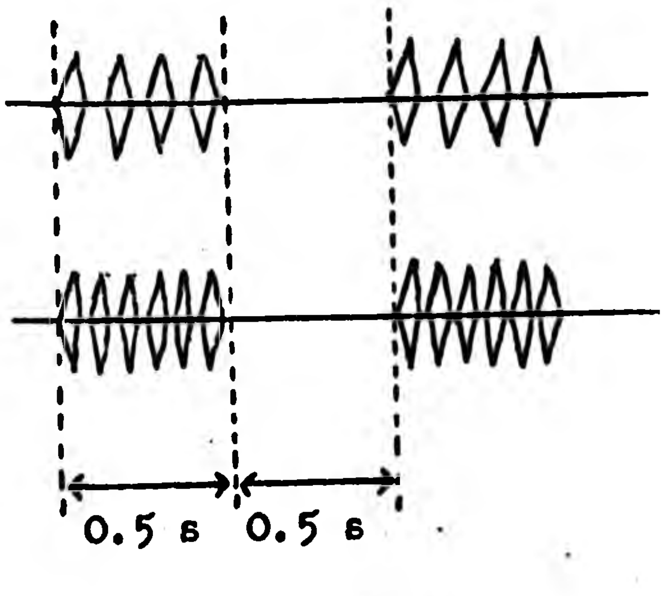
The *echeme rate* is the reciprocal of echeme period (see fig. 2), i.e. the time period measured is from the beginning of one echeme to the beginning of the next. Similarly the *syllable rate* is the reciprocal of syllable period.



Echeme rate = 1/x, Syllable rate = 1/y

The rate of singing is also calculated using the echeme period (x) as the denominator, but uses the number of syllables sung in the echeme period as the numerator, i.e. the rate of singing in the time period x in the above diagram is 4/x. If this parameter is plotted on a graph, values for two or three successive echeme periods are averaged to reduce the fluctuations that would occur in the curve when values for four- and five-syllable echemes are plotted separately.

The rate of singing measurement has been used extensively in the section on interspecific interactions. It is directly comparable to the measurement of percentage time spent singing as used by Broughton (in Lewis & Broughton, in press); this compares the chirp duration with the chirp period (see fig. 2). The advantage of using the rate of singing is that in addition to recording changes in the echeme rate and changes in the ratio of chirp duration to chirp interval, it also records changes in the syllable rate. This would not be recorded by measuring the percentage singing time if the ratio of chirp duration/chirp interval remained the same.



Rate of singing - 4 syllables/s
Percentage singing time - 50%

Rate of singing - 6 syllables/s
Percentage singing time - 50%

The syllable, being a product of one wing stroke (see overleaf), seems an appropriate unit of singing activity.

The rate of singing also varies with temperature since muscular movement is temperature-dependent in insects. For this reason, temperature was kept constant during any experiment involving intra- and interspecific interactions.

RESULTS.

SONG AND VARIATION.

The songs of many of the species to be considered have been analysed previously (Dubrovin & Zhantiev 1970, McHugh 1971, Sales & Pye 1974, Samways 1976a). For the purposes of this study it is necessary to present more detailed analyses of these songs along with new data on individual variation.

1. Variation with Temperature.

Generally, in ectothermic animals (see Schmidt-Nielsen 1975) rates of motor output vary in a predictable manner with short-term fluctuations in temperature. Rates of singing in crickets and bush crickets usually increase linearly with rising temperature (Dolbear 1897, Walker 1962, 1975, Jones 1967, Alexander 1968) though Frings & Frings, 1957, 1962 have suggested that these data may represent only the middle ranges of logarithmic relationships between rate of singing and temperature.

Various parameters of the song of P. albopunctata have been measured to see if they vary with temperature changes in the same way. If so, one could expect the relative pattern of the song to remain constant at all temperatures. Since both chirp (see p. 25) and interval duration decrease with rising temperature the ratio shows no appreciable change, e.g. in one individual :-

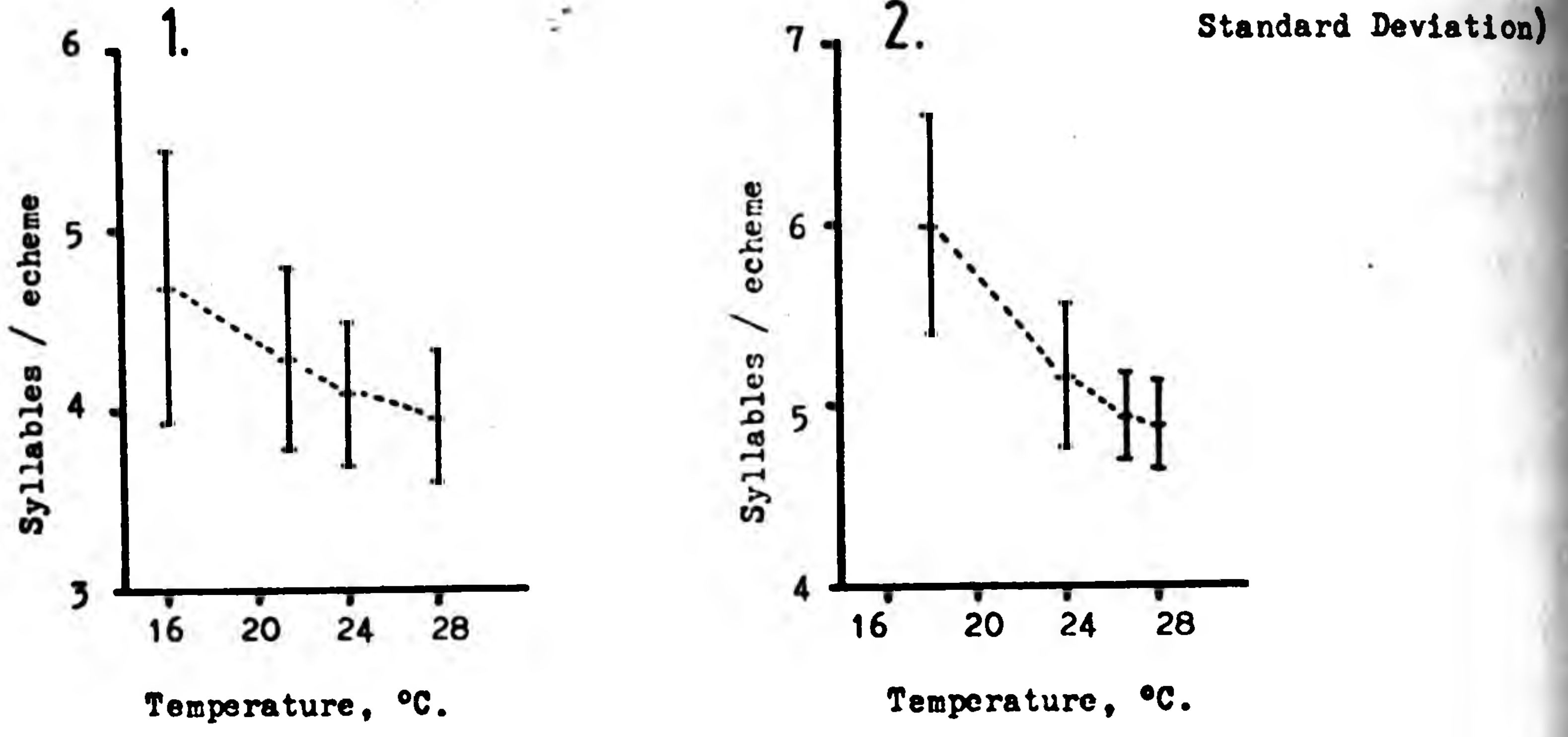
Temperature -	18°	24°	34° Centigrade.
Interval/chirp duration -	1.14	1.07	1.11

Four other individuals tested similarly showed no change in this ratio.

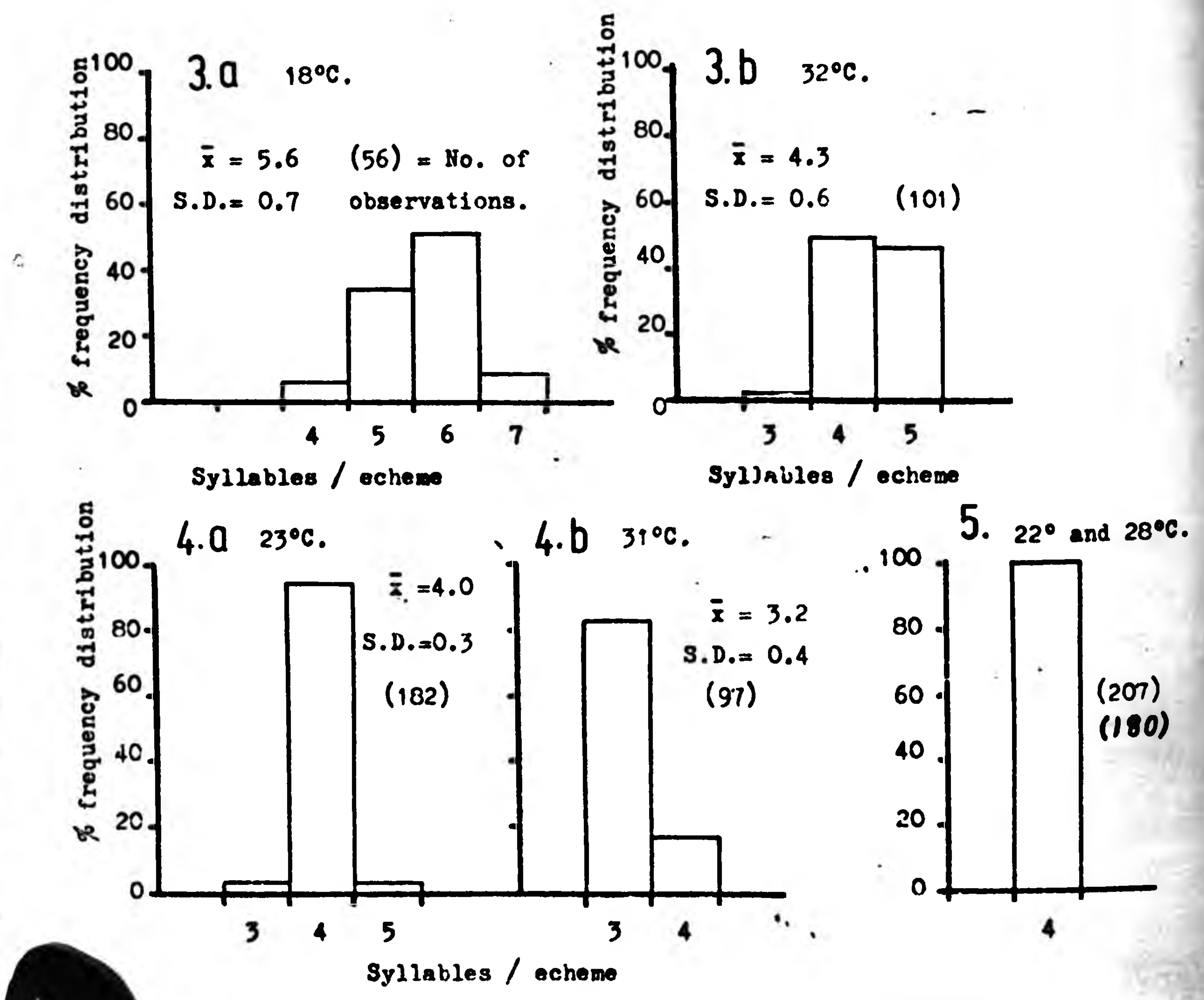
The number of syllables produced in each echeme does,

Fig. 3 EFFECTS OF TEMPERATURE ON THE SONG OF P. ALBOPUNCTATA.

Graphs 1 and 2:- Decrease in average syllables/echeme with rising temperature for two individuals. (Values + and - one Standard Deviation)



Below:- % frequency distribution of syllables/echeme for 3 individuals tested at two different temperatures (a and b).

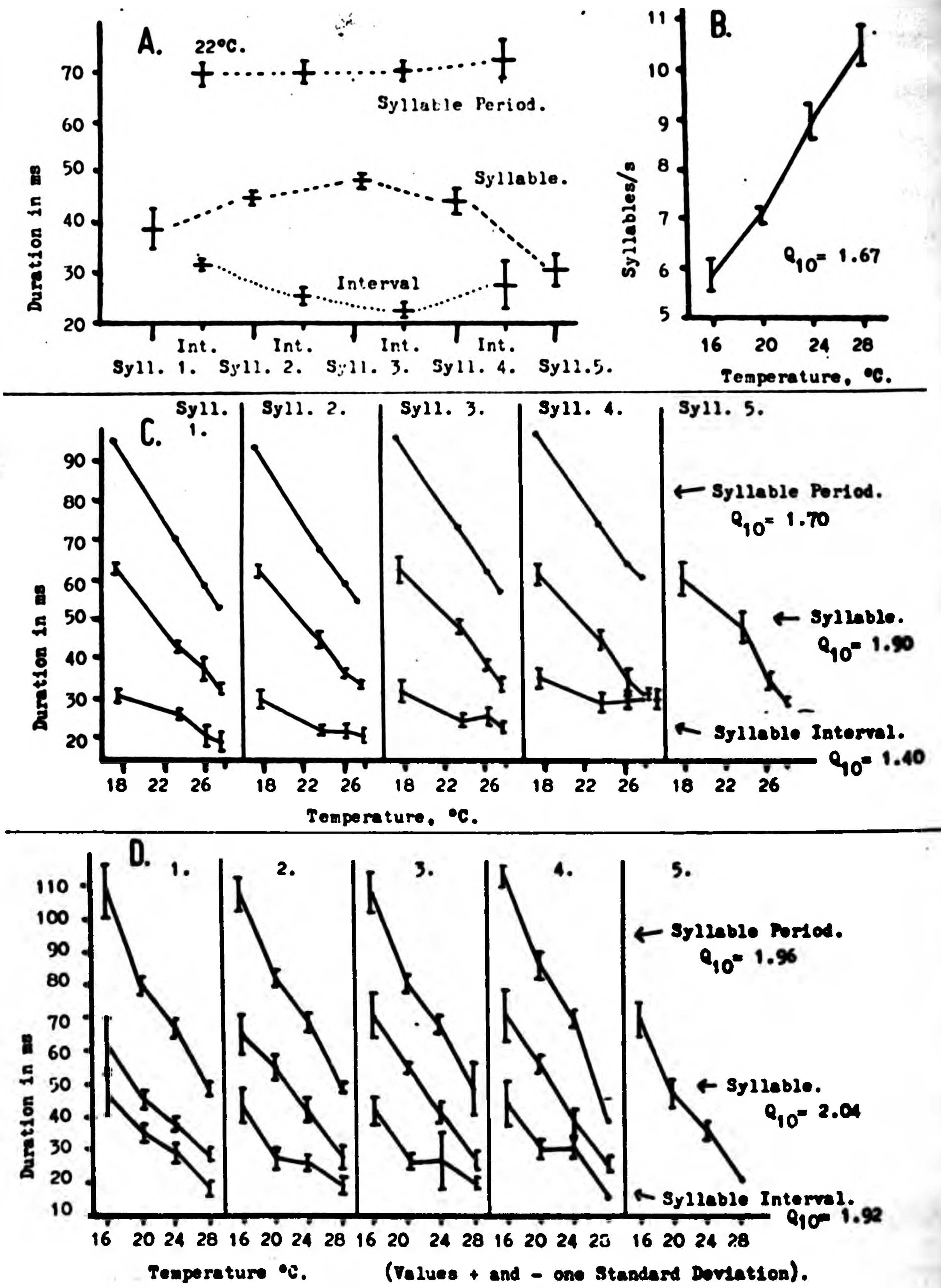


however, change with temperature. Individuals generally decrease the syllable content of the echeme as temperature increases (see fig. 3). Graphs 1 and 2 show mean syllables/echeme ± 1 standard deviation (S.D.) at various temperatures. The difference between the means at highest and lowest temperatures for both insects are highly significant ($t = 10.06$, $p \ll 0.001$, $N = 100$, 170 for graph 1; $t = 21.2$, $p \ll 0.001$, $N = 200$, 160 for graph 2). Two other insects tested showed similarly significant differences (histograms 3a and b; 4a and b). However, one individual from a British population near Portsmouth, which sang only 4- syllable echemes, remained unaffected by temperature in this respect (histogram 5).

The temperature variations of syllable period, syllable duration and syllable interval are illustrated in fig. 4. Each successive syllable and interval in the echeme has been considered separately as they show characteristic duration differences depending on their position in the echeme. Data for ten echemes from an insect singing at a steady temperature of 22° C. have been displayed in this manner in graph A, which shows mean durations ±1 S.D. (As the songs of these insects are extremely regular, a representative mean and standard deviation can be produced from a relatively low number of measurements). Generally the first and particularly the last syllables are shortest with corresponding intervals longest. This produces a fairly stable syllable period throughout the echeme, i.e. the syllable "on" switch remains constant.

The temperature curves for two other individual insects (graphs C and D) show generally linear decreases in all syllable durations with rising temperature (no. of echemes analysed = 10). Syllable intervals however, show anomalous

Fig. 4 EFFECTS OF TEMPERATURE ON THE SONG OF P. ALBOPUNCTATA.
Changes in durations of syllable parameters.



(Values + and - one Standard Deviation).

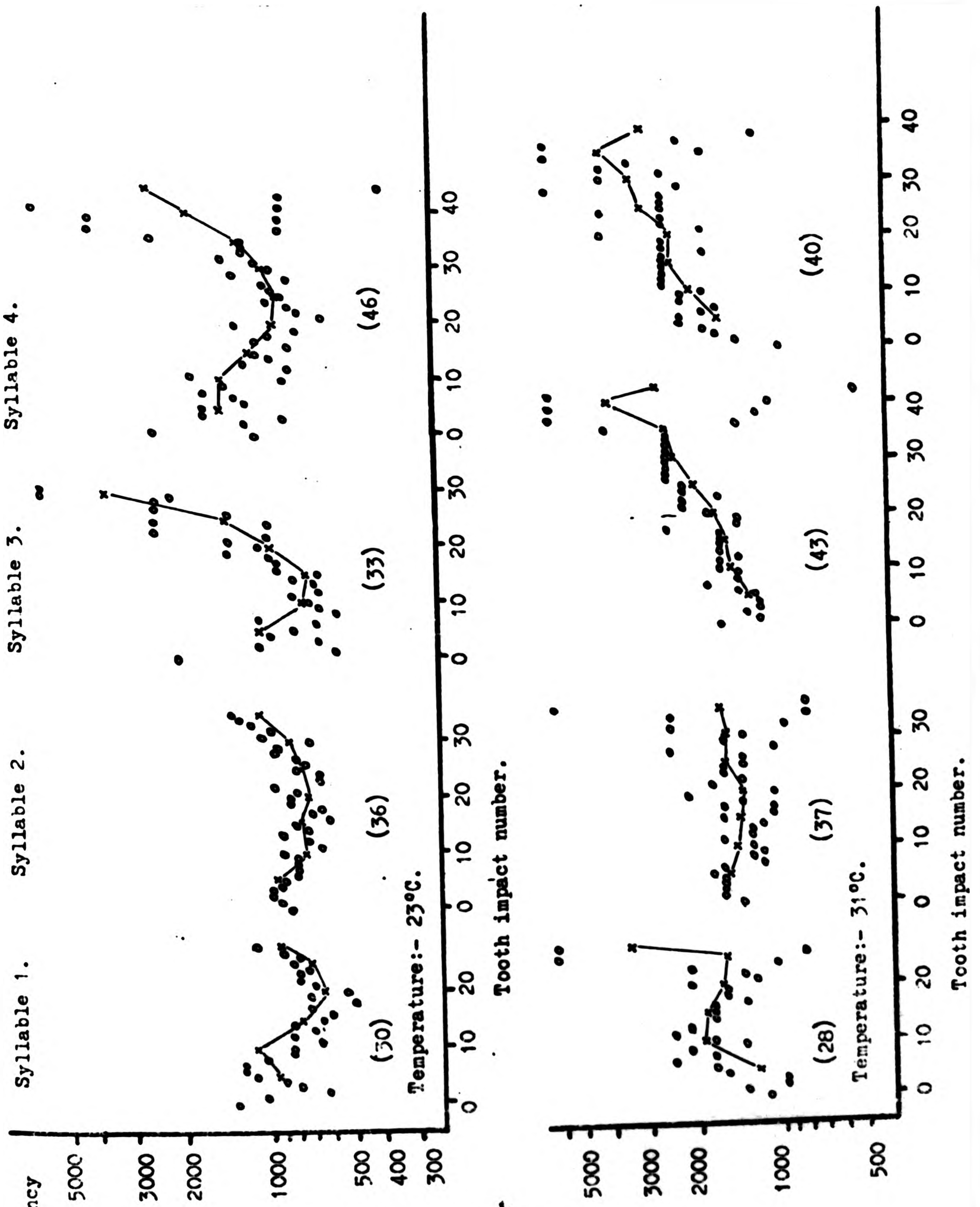
changes with temperature, sometimes showing no change or actually increasing in duration in parts of the 20° to 26° range. Syllable period shows the most constant rate of change in graph C but in graph D a reduction in the rate of decrease from 20° to 24° is evident.

Average Q_{10} values (for 18° to 28°) for the syllable parameters are also shown in fig. 4 (derived from the sum of Q_{10} values for each syllable parameter/no. of parameters). The rate of singing plotted against temperature (graph B) shows a lower Q_{10} value than the syllable parameters. This is a result of the tendency to produce more syllables/echeme at lower temperatures. Q_{10} values for crickets and bush crickets range from 1.5 to 2.3 (calculated from the results of Dolbear 1897, Walker 1962, Nielsen & Dreisig 1970). Jones (1967) shows values between 2.1 and 2.3 for some British tettigoniids.

The change in the low-frequency (tooth-impact) component with temperature is illustrated for one individual in fig.5. Here successive tooth-impacts have been plotted as scatter points on a frequency scale. The solid lines join up mean pulse repetition rates for each successive group of five pulses within the syllable. The number in brackets indicates the number of discrete pulses corresponding to the tooth impacts (see p.41). The increase in speed of the wing stroke with rising temperature is reflected by the mean tooth-impact rate's increasing from 1115 Hz (S.D. 592) at 23° C. to 2130 Hz (S.D. 865) at 31° C. (5 echemes analysed). Thus the rate approximately doubles for a 10° rise in temperature (i.e. a Q_{10} value of 2). The syllable duration approximately halves for the same rise, and there appears to be no consistent change with temperature in the number of tooth impacts.

Fig. 5 EFFECTS OF TEMPERATURE ON THE LOW-FREQUENCY COMPONENTS OF THE SONG OF *P. ALBOPUNCTATA*.

Explanation in text.



This last observation suggests that there is no change in the length of the wing stroke when temperature varies, i.e. the same number of teeth are swept by the plectrum.

The carrier and other emphasized frequencies of the song do not change with temperature. This is as would be expected from the theoretical consideration of a parameter that depends on structural features.

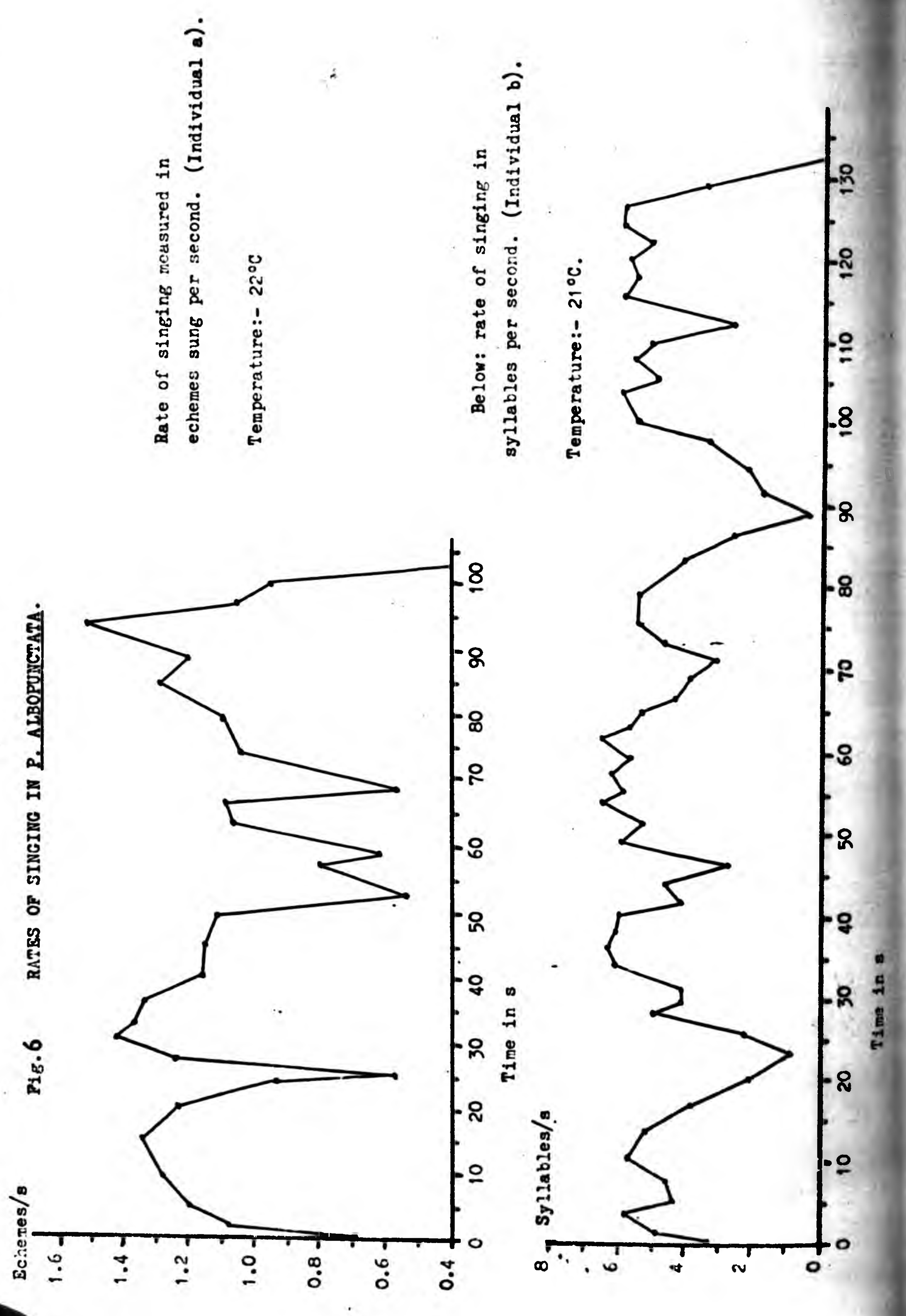


Fig.6 RATES OF SINGING IN *P. ALBOPUNCTATA*.

2. Variation between Individuals.

Little is known about the range of individual variation in the songs of insects, though data are available in the works of some authors (Walker 1962c, Spooner 1968, Sales & Pye 1974). Such data are clearly important when song is used as a taxonomic character (Walker 1956, 1962a,b, 1969a,b, Alexander 1957, 1967, Bailey & Robinson 1971), or when song modification phenomena are being examined (Broughton 1965, McHugh 1970, Samways 1975, 1976). Therefore, individual variation is here examined in detail in the song of *P. albopunctata*. Songs of other species are then analysed and show further examples of individual variation in various song parameters. Unless otherwise indicated, individuals compared were collected from the same locality.

(i) Variation in the song of *P. albopunctata*.

As mentioned previously, some *albopunctata* individuals apparently only sing in short sequences as the following small sample indicates (durations measured in seconds).

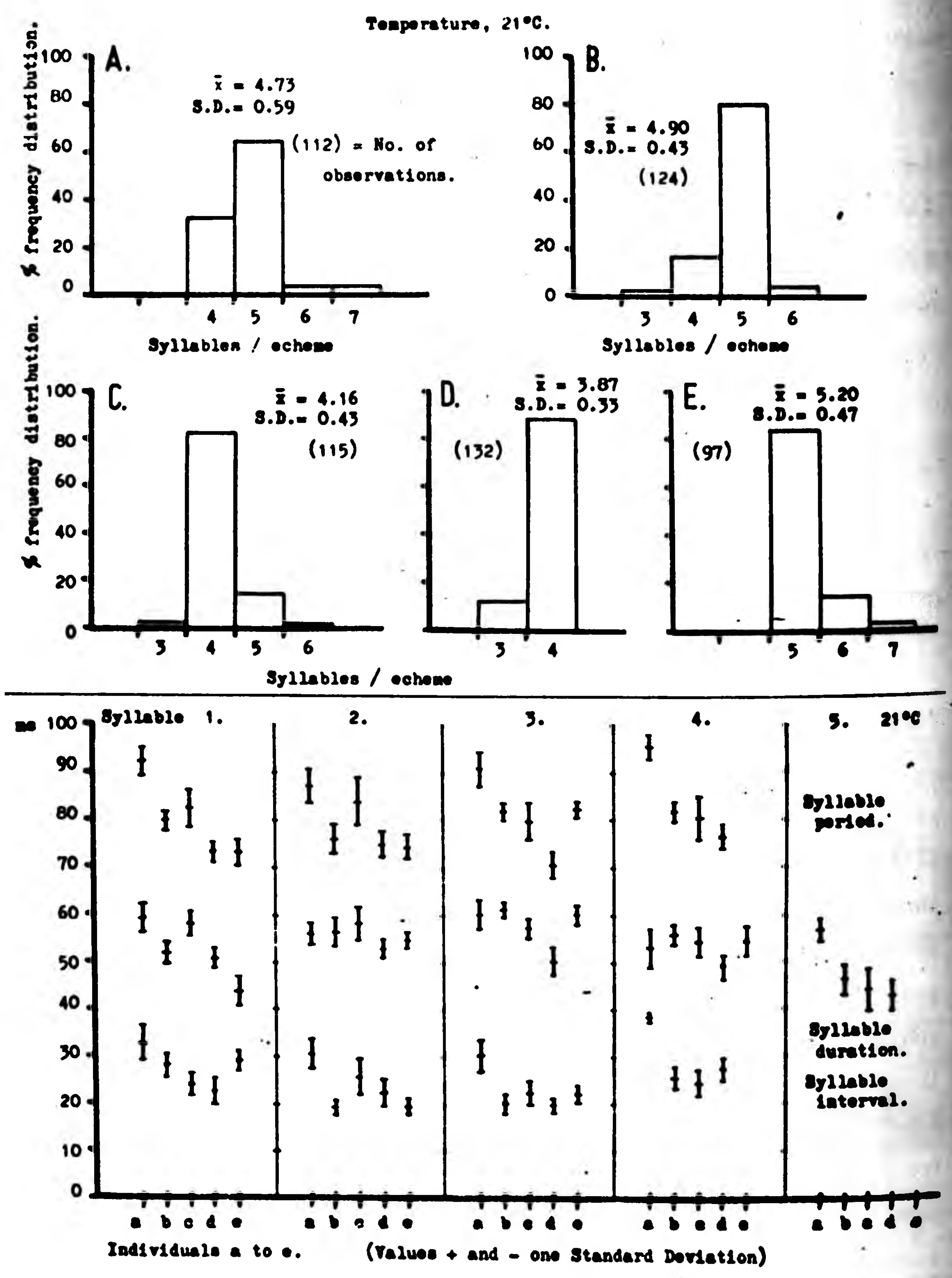
Sequence duration	$\bar{x}$ = 21.71	S.D. = 5.67	N = 18
Sequence interval	$\bar{x}$ = 21.62	S.D. = 8.59	N = 14

(Grouped data from three individuals).

It has not been possible to ascertain if this behaviour persists throughout the singing life of the insect. The delivery of song in short sequences seems more prevalent in young animals, though old animals have also been heard to sing in this manner. Other individuals sing in sequences of variable duration, some lasting many minutes. When a measure of singing activity (e.g. echeme rate, rate of singing) is plotted against time for these longer song sequences, a regular periodicity is seen in the resulting curve (fig. 6). The duration of these cycles (measured from minima to minima) varies between 15 and 30 s ($\bar{x}$ = 22.1, S.D. = 4.89). In some individuals, however, such a regular oscillation is difficult to detect.

Chirp interval to *chirp* duration ratios calculated at maximum rates of singing generally vary around unity. Values

Fig. 7 INDIVIDUAL VARIATION IN THE SONG OF P. ALBOPUNCTATA.



recorded for three individuals are as follows:- 0.94, 1.15 and 0.70. When the rate of singing falls this ratio increases, i.e. it is the chirp interval which increases. The syllable rate within the echeme remains constant at any give temperature even when echeme parameters are varying.

Each individual has a characteristic frequency distribution of syllables/echeme. Histograms A to E in fig. 7 show distributions for five individuals singing at the same temperature. Average syllables/echeme ranges from 3.87 to 5.20 with modal values of either 4 or 5. If variation due to temperature is included, modal values can range from 3 to 6 (see fig. 3, p. 30).

Variation in the syllable parameters is shown in the last graph at the bottom of fig. 7 where each syllable's period, duration and interval (N = 10) are plotted for five individuals (a to e). Here inter-individual variation can be as much as 21 ms for the syllable period, 16 ms for the syllable duration and 10 ms for the syllable interval. In addition to the straightforward variation in these values, individuals also vary in the relative pattern of successive syllable and interval durations. For example, animals b and e show a common pattern where the first and last syllables are relatively shorter than the rest, while their intervals are correspondingly longer (as illustrated in graph A, fig. 4). In other words the syllable pattern is Short, Long, Long, Short (SLLS). Animal a, however, has alternately longer and shorter syllables in the echeme (LSLSL), while animal c exhibits the pattern LLSSS. Pearson's Coefficient of Variation, (100 x S.D.)/ $\bar{x}$ has been calculated for each of the syllable parameters and averaged for the echeme (N = 10) of each individual (table 1, p. 41). The table shows the song of some individuals to be more variable than in others. In each individual in this sample, the syllable interval is the most variable parameter, while the syllable

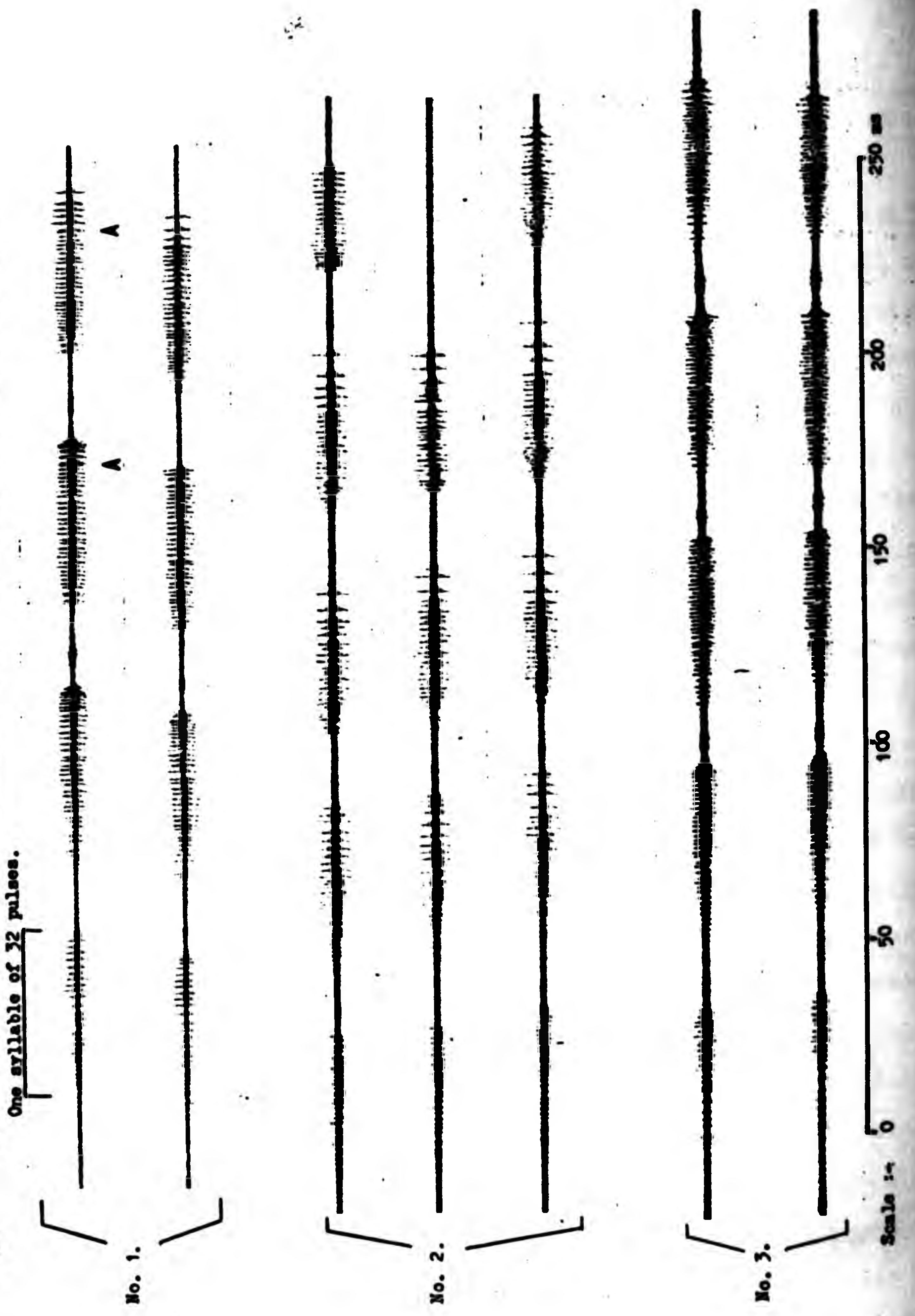


Fig. 8 SYLLABLE STRUCTURE OF THREE P. ALBOPUNCTATA INDIVIDUALS. Note variation in pulse spacing.
One syllable of 32 pulses.

period is the most stable, (see Discussion, p.156).

Table 1. P. albopunctata: coefficients of variation for the syllable parameters of individuals a to e.

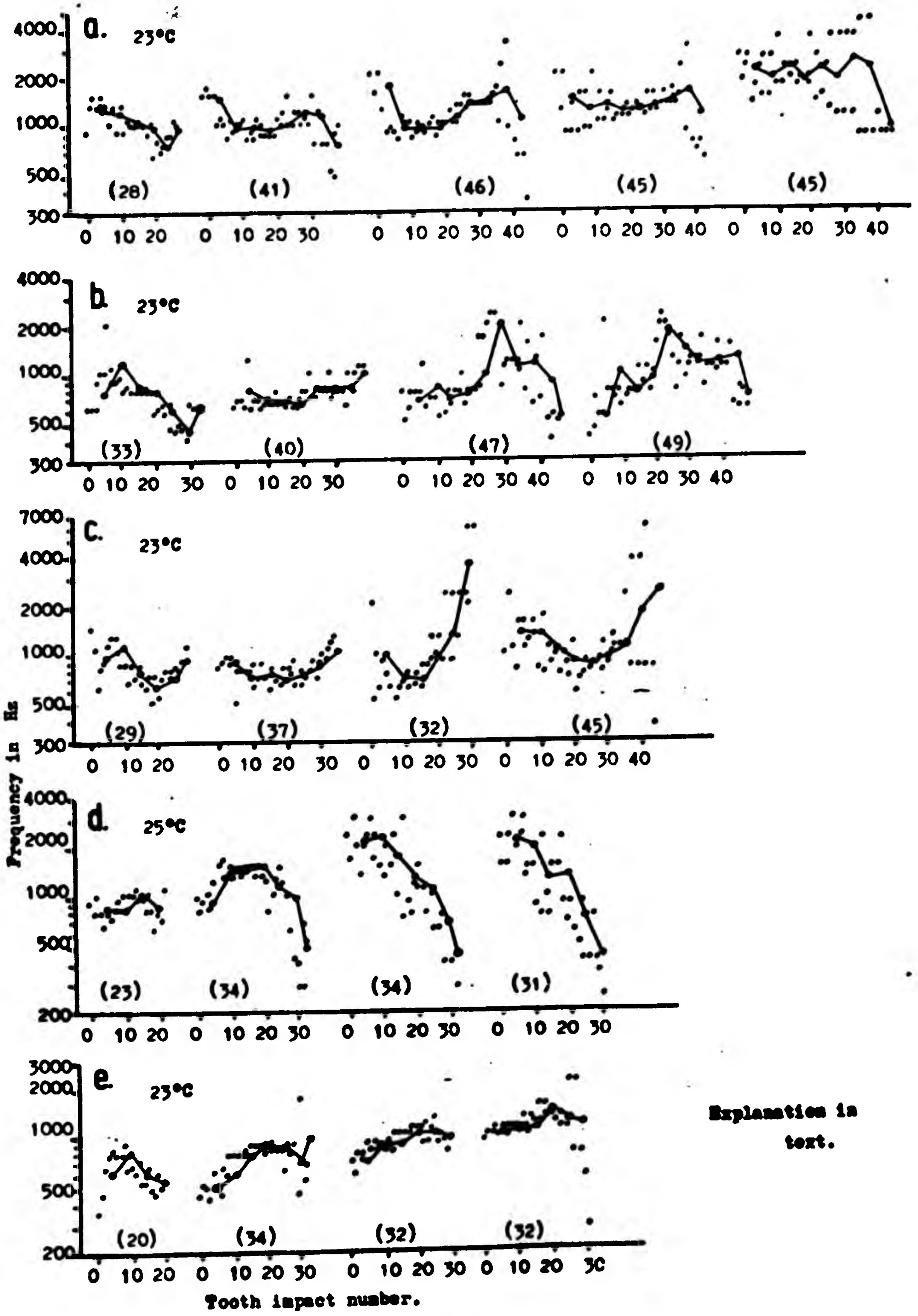
Individual -	a	b	c	d	e	
Syllable period	3.37	2.83	5.25	3.33	3.15	%
Syllable duration	4.61	4.76	5.96	5.37	4.91	%
Syllable interval	8.44	8.90	11.73	9.87	6.67	%

Maximum rates of singing for each of these five individuals have been measured for a ten-second section of the song sequence. These are as follows:- a, 4.44, b, 5.96, c, 6.20, d, 4.00, and e, 5.76 syllables/s (temperature - 21°C.).

The pattern of the tooth impacts is also characteristic in each individual (see fig. 8). When successive tooth-impact rates are plotted on a frequency scale this pattern is resolved into a spectral pattern of frequency sweeps as shown in fig. 9. These low-frequency sweeps are shown for each syllable in one echeme of each of the same five individuals a to e. The oscillograms for insects c and d are illustrated in traces 1 and 2 of fig. 8. The number in brackets under each syllable in fig. 9 indicates the number of tooth impacts, (this equals the number of points plus one because the rate is derived from the measurement of pulse periods). As in fig. 5, the solid lines on the graph join up points representing mean pulse repetition rates for each successive group of five pulses.

As fig. 9 shows, the low-frequency component varies slightly between syllables of the same individual, but varies much more between individuals. Within the echeme, the first syllable is typically the shortest in duration and has the fewest

Fig. 9 LOW-FREQUENCY COMPONENTS IN THE SONGS OF FIVE P. ALBOPUNCTATA INDIVIDUALS.

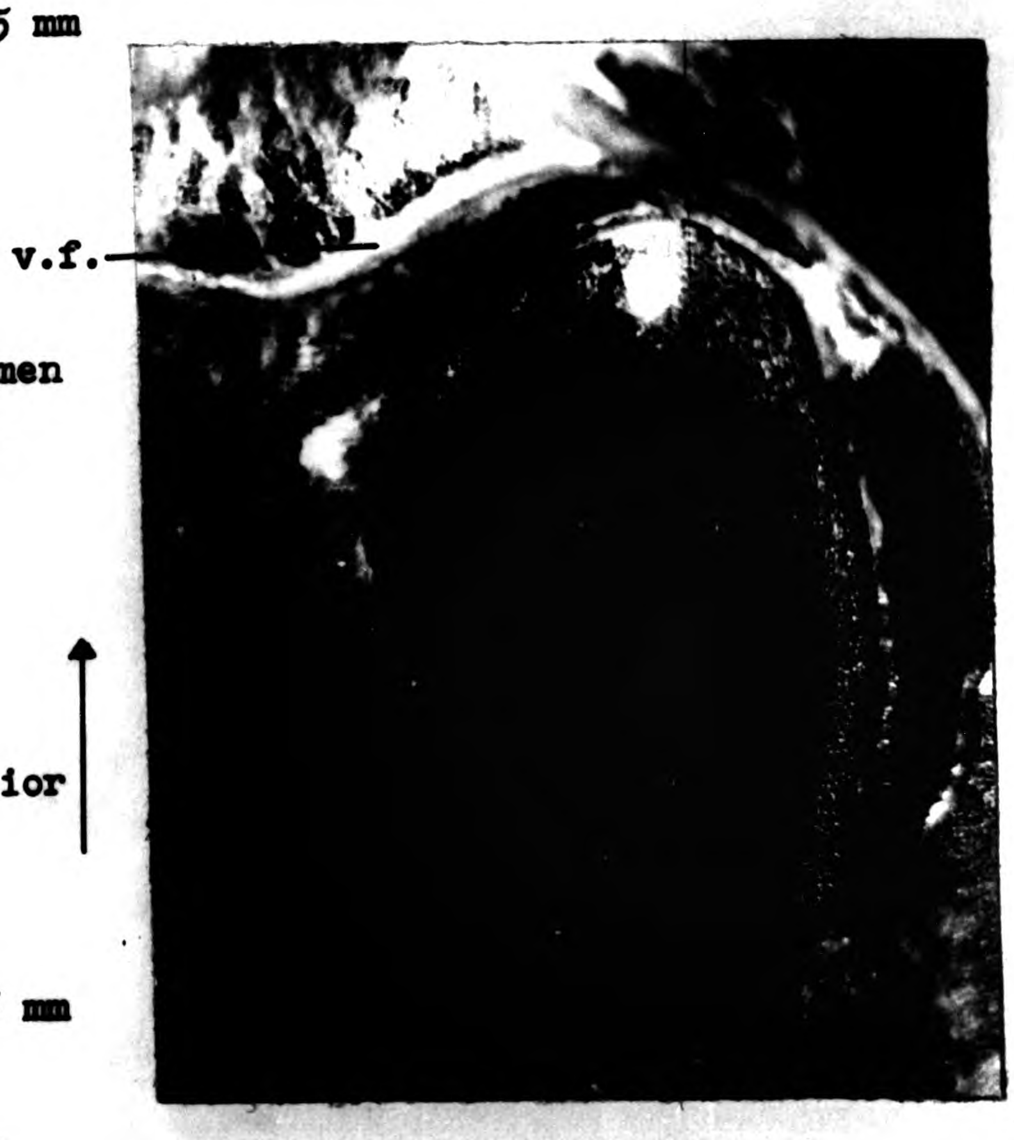


Explanation in text.

Fig.10. **THE FILE AND MIRROR OF <u>P. ALBOPUNCTATA</u>.**

Underside of left tegmen showing detail of the stridulatory file

Scale - 0 0.5 mm



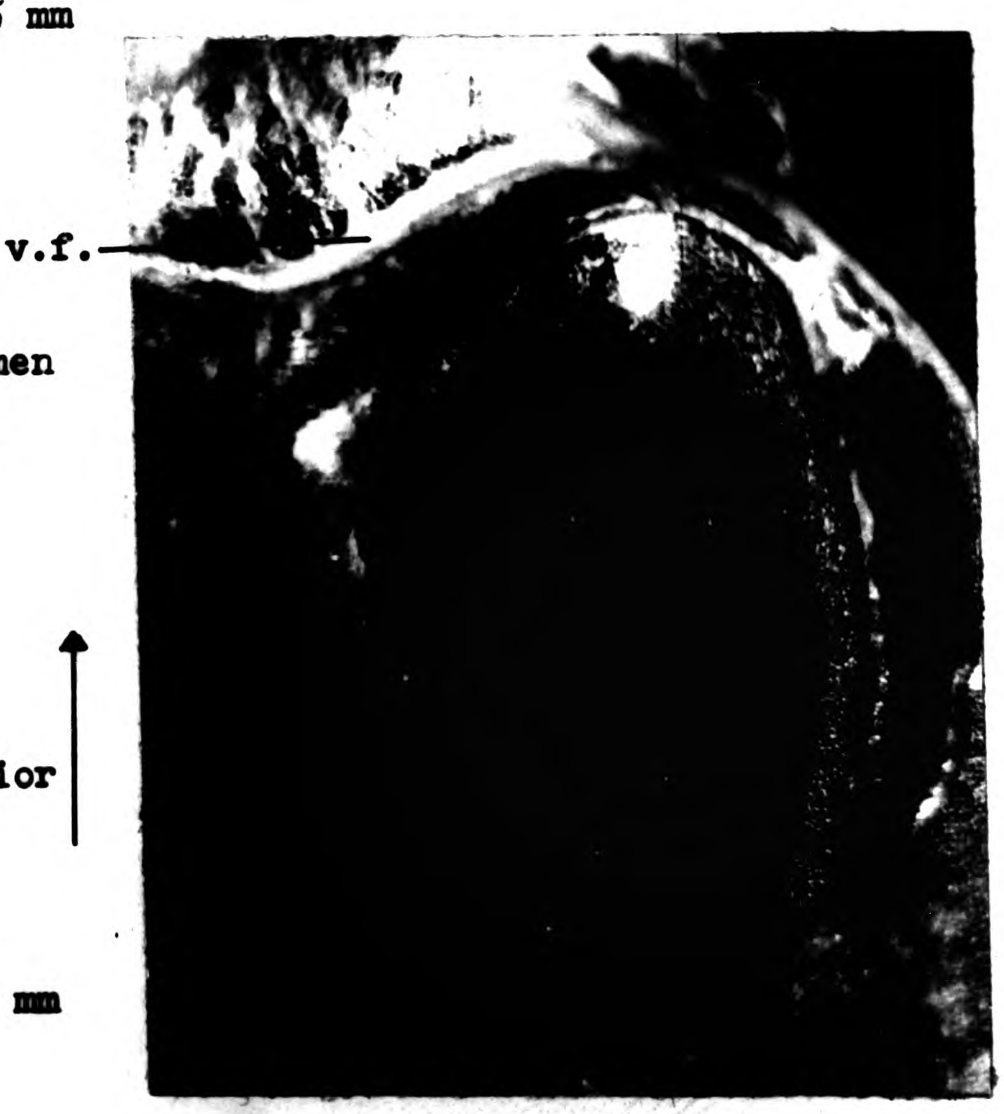
Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.)

Scale - 0 0.5 mm

Fig.10. THE FILE AND MIRROR OF P. ALBOPUNCTATA.

Underside of left tegmen showing detail of the stridulatory file

Scale - 0 0.5 mm



Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.)

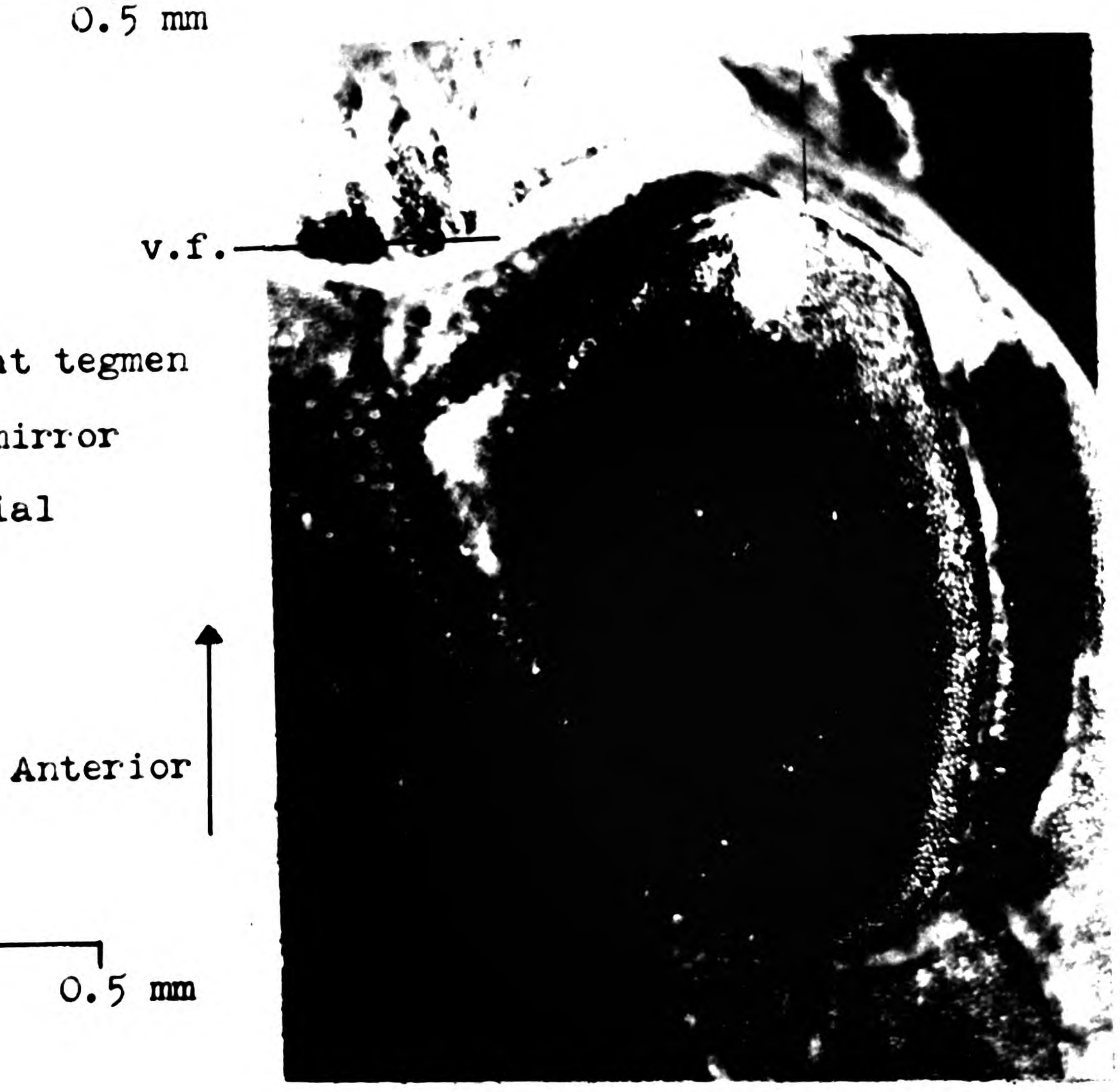
Anterior

Scale - 0 0.5 mm

Fig. 10. THE FILE AND MIRROR OF P. ALBOPUNCTATA.

Underside of left tegmen showing detail of the stridulatory file

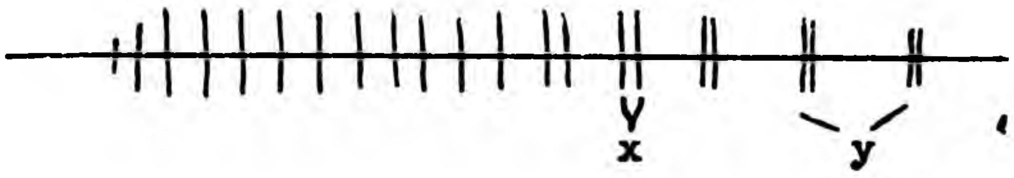
Scale - 0 0.5 mm



Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.)

Scale - 0 0.5 mm

tooth impacts. In successive syllables there is often an increase in both the number of tooth impacts and the tooth-impact rate, i.e. the pulse repetition rate. In some individuals, towards the end of the syllables, teeth appear to be struck in pairs (see fig. 8, arrowed), thus:-



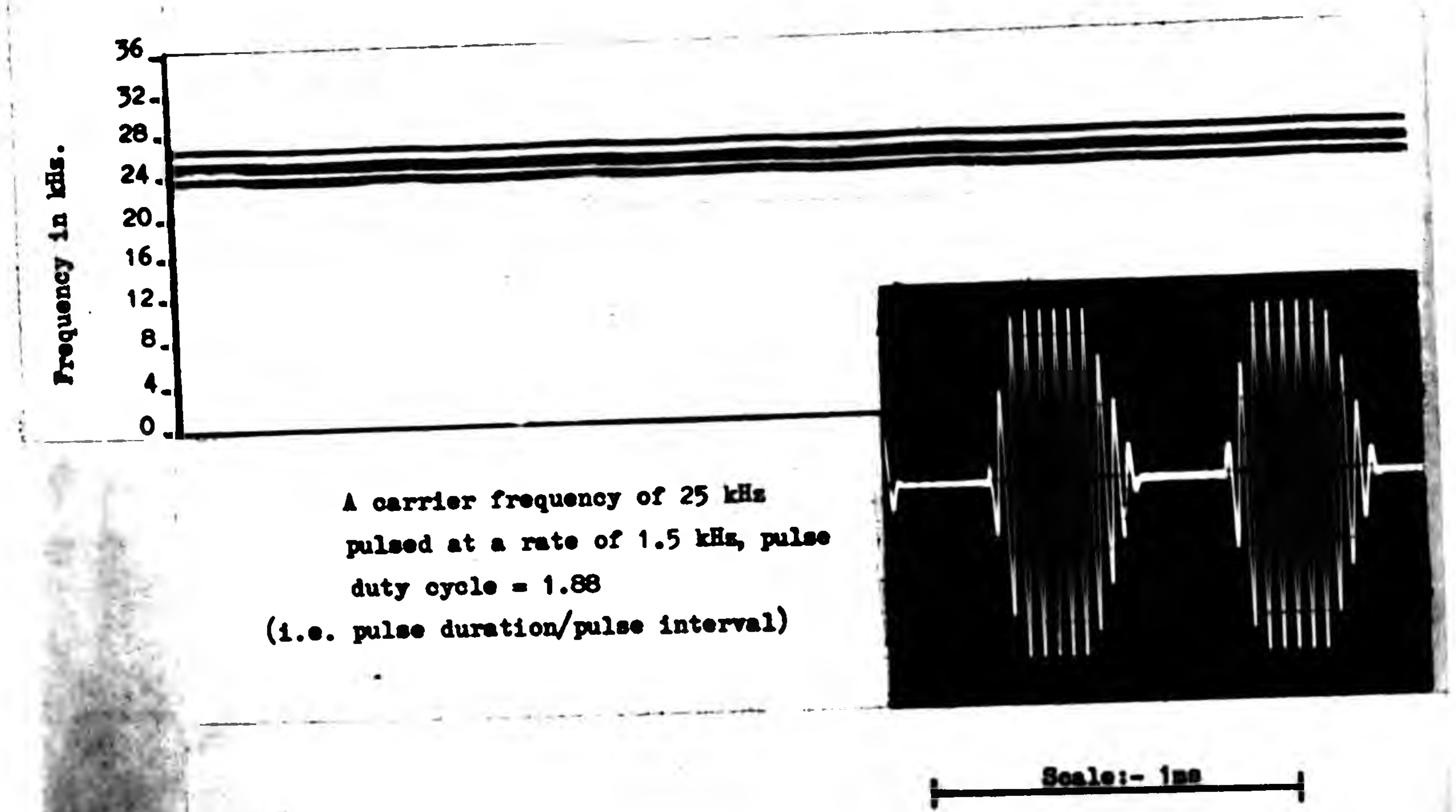
This produces diverging pulse repetition rates; one rate increases in accordance with the decreasing period between the two pulses in the pair (x); the other rate decreases as a result of the increasing period between pairs. This is seen in fig.9, in the last three syllables of animal a. The Sonagraph appears to analyse this phenomenon in the same way, producing a similar, though rather indistinct, sound spectrum.

The general pattern of the low-frequency sweep is repeated in each echeme and does not appear to change as the insect matures, (however, very young and very old individuals have not been compared). It is not known to what extent the individual variation in the low-frequency sweep can be attributed to morphological variation in the file (see fig.10) or to variation in the rate of tegminal closure. As was shown in fig.5, p. 34, temperature extremes can begin to modify the shape of the sweep.

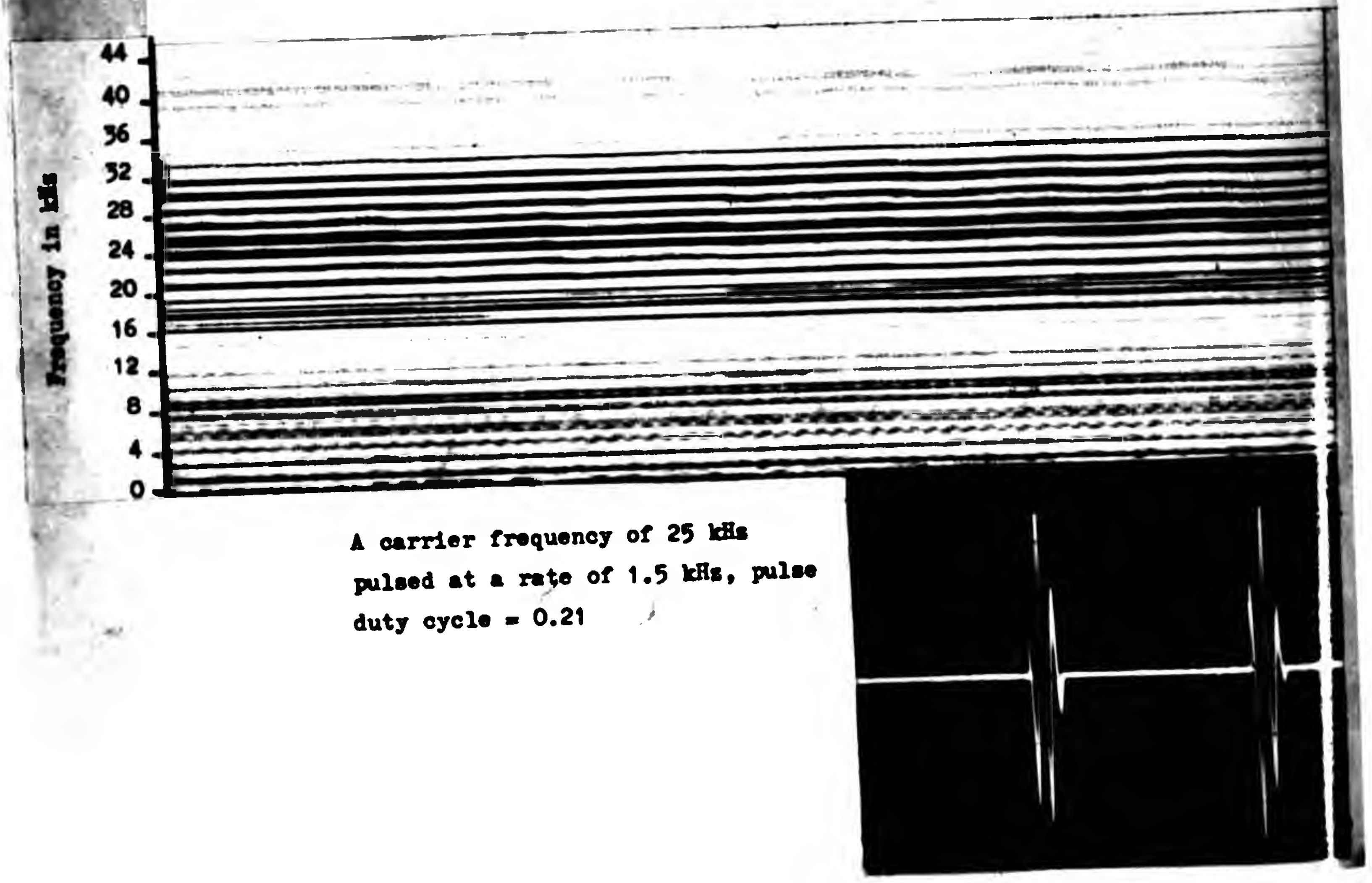
The high-frequency components also show a similar range of variation between individuals. This can be ascribed to both variation in the dimensions of the mirror frame, (see p.63) and to variation of the low-frequency sweeps. A brief explanation of the structure of the ultrasonic sound spectrum of these insects should serve to clarify the following analyses.

If, for example, a continuous sine wave at a frequency of 25 kHz

Fig. 11. EFFECT OF PULSE DURATION ON THE SOUND SPECTRUM.



A carrier frequency of 25 kHz
pulsed at a rate of 1.5 kHz, pulse
duty cycle = 1.88
(i.e. pulse duration/pulse interval)



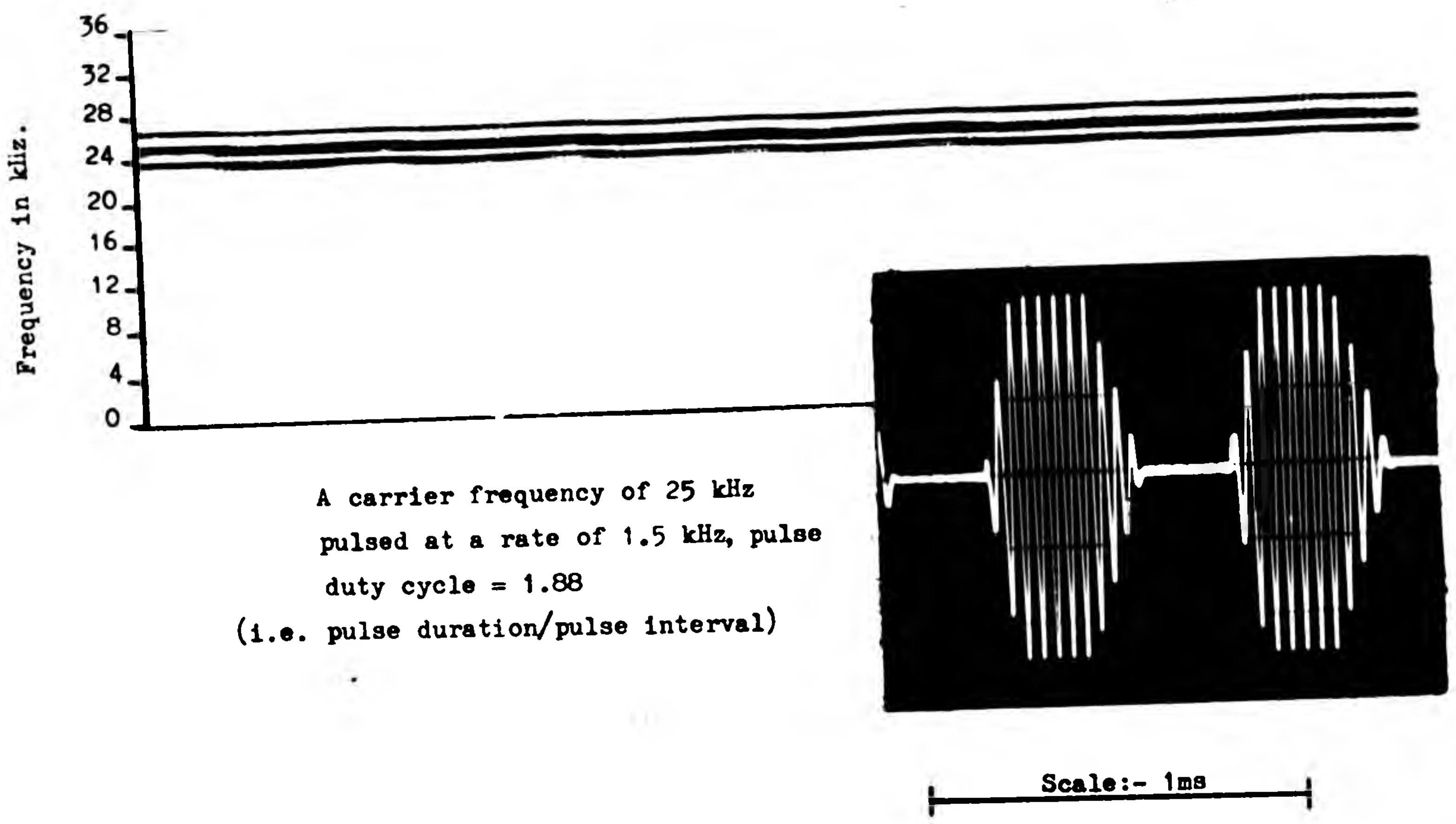
A carrier frequency of 25 kHz
pulsed at a rate of 1.5 kHz, pulse
duty cycle = 0.21

is analysed by the sonagraph, a thin, horizontal line is produced on the sonagram. When a periodic modulation is imposed on this carrier frequency other, side-band frequencies related to the periodicity are introduced. Thus, when a 25 kHz sine wave is pulsed at, for example, a rate of 1.5 kHz, side-band frequencies are produced symmetrically above and below the carrier frequency (fig.11, top). The spacing between each band and the next corresponds to 1.5 kHz on the vertical frequency scale, and their intensity progressively decreases the farther from the carrier frequency. The shorter the pulses in relation to their intervals, the more side bands are produced and the greater the frequency compass (fig. 11, bottom). The pulse repetition rate of 1.5 kHz is also now evident. (See Watkins 1967, Sales & Pye 1974, Lewis & Broughton, in press, for further discussion on this topic).

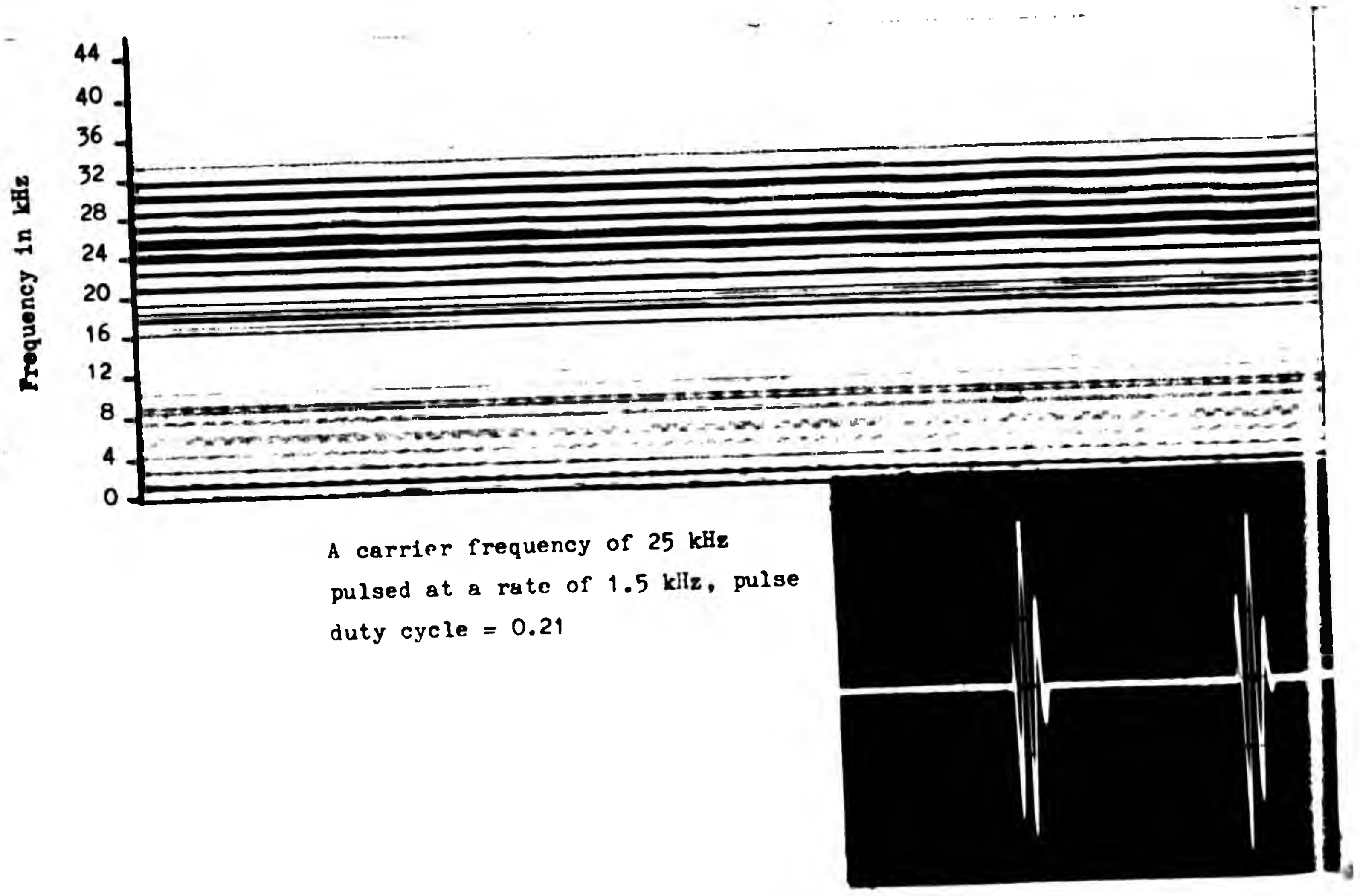
In the song of P. albopunctata side bands are produced around the carrier frequency with a spacing corresponding to the tooth impact rate. This averages out on the sonagram at around 1 kHz. The mirror frame (see fig.10) is generally assumed to produce the carrier frequency (Broughton 1964, Morris and Pipher 1967, Bailey 1967,1970). Other regions of the tegmina may also vibrate, for other emphasised ultrasonic frequencies can often be identified on the sonagram and they do not appear to be a function of the carrier frequency or the pulse repetition rate (see also Dumortier 1963, Bailey and Broughton 1970).

Ultrasonic components in the songs of six P. albopunctata individuals, A to F, are shown in fig.12; the data on these songs are presented in table 2. The histogram in fig.12 shows the variation in the peak carrier frequency in a sample of 31 individuals. In some animals the carrier frequency changes during the duration of the syllable, e.g. in animal C where the carrier changes from 25 to 22.5 kHz, and animal D where the

Fig. 11. EFFECT OF PULSE DURATION ON THE SOUND SPECTRUM.



A carrier frequency of 25 kHz pulsed at a rate of 1.5 kHz, pulse duty cycle = 1.88 (i.e. pulse duration/pulse interval)



A carrier frequency of 25 kHz pulsed at a rate of 1.5 kHz, pulse duty cycle = 0.21

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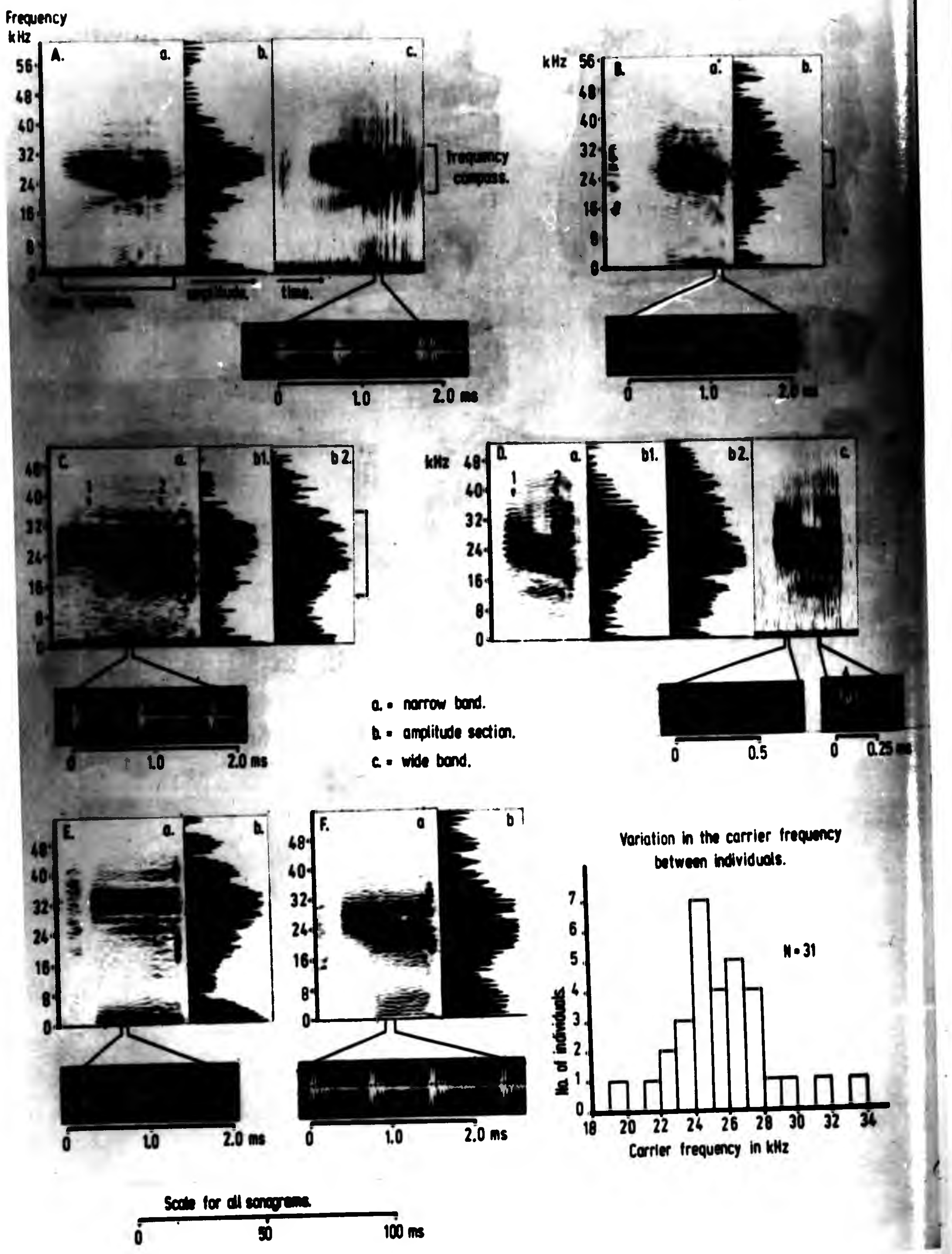
Fig. 12. VARIATION IN THE SONG OF P. ALBOPUNCTATA.



carrier changes from 24 to 21 kHz. The amplitude sections nos. 1 and 2 taken at the points indicated on sonagram D (a) show this shift in the peak frequency. (The carrier frequency for D is plotted as an average of its two extremes, i.e. 22.5 kHz in the histogram on individual variation in the carrier). The oscillograms beneath sonagram D (c) show the pulse structure at the points indicated in the syllable. There is a consistent change in the pulse structure towards the end of every syllable in this individual. The position of this phase shift is arrowed in fig. 12.

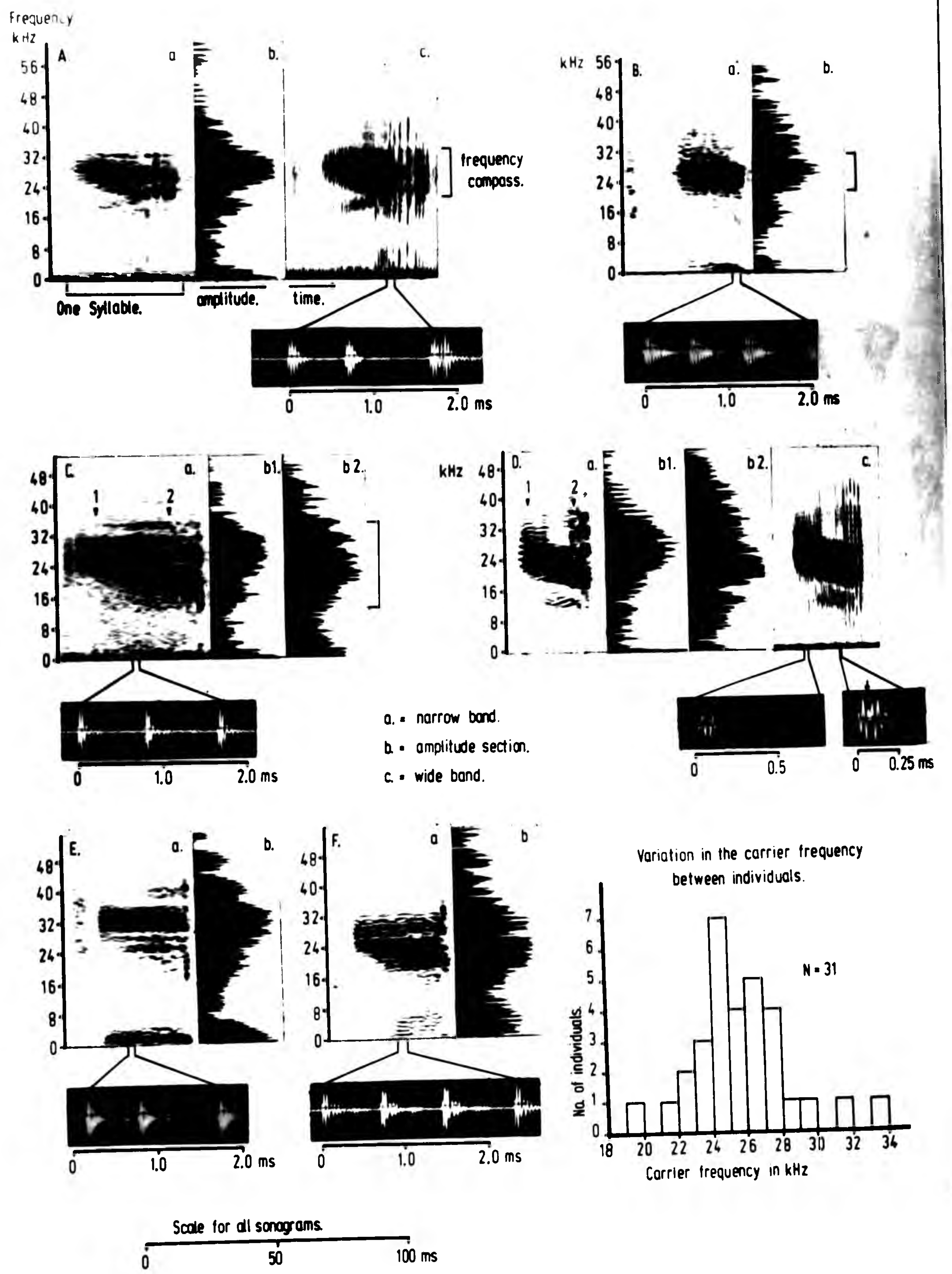
The effect of pulse duration in relation to the pulse interval (duty cycle) is seen by comparing animals A and B with animal C. In A and B, where the pulse is relatively long in duration, the frequency compass is small. Animal C, however, has short pulses with a long interval between; here the frequency compass is large, (see fig. 12).

Two distinct peaks are discernible in the song spectrum of animal F, one being the carrier at a frequency of 23.5 kHz, the second band at 29 kHz; this interferes with the carrier, producing a difference tone of 5.5 kHz which shows as a slight peak at this value on the frequency scale. The interference pattern is also seen in the waveform of the pulses in the form of a phase shift between the third and fourth waves of the pulse.

Table 2. P. albopunctata: high-frequency components in the songs individuals A to F

Insect.	Carrier frequency.	Other peaks.	Frequency compass.
A	27 kHz		21 - 33 kHz
B	25.5 kHz		21 - 31 kHz
C	25 — 22.5 kHz	30, 34 kHz	13 - 36 kHz
D	24 — 21 kHz	13 kHz	17.5 - 37 kHz
E	33 kHz	26, 39 kHz	24 - 40 kHz
F	23.5 kHz	29 kHz	18 - 33 kHz

Fig. 12. VARIATION IN THE SONG OF P. ALBOPUNCTATA.



carrier changes from 24 to 21 kHz. The amplitude sections nos. 1 and 2 taken at the points indicated on sonagram D (a) show this shift in the peak frequency. (The carrier frequency for D is plotted as an average of its two extremes, i.e. 22.5 kHz in the histogram on individual variation in the carrier). The oscillograms beneath sonagram D (c) show the pulse structure at the points indicated in the syllable. There is a consistent change in the pulse structure towards the end of every syllable in this individual. The position of this phase shift is arrowed in fig. 12.

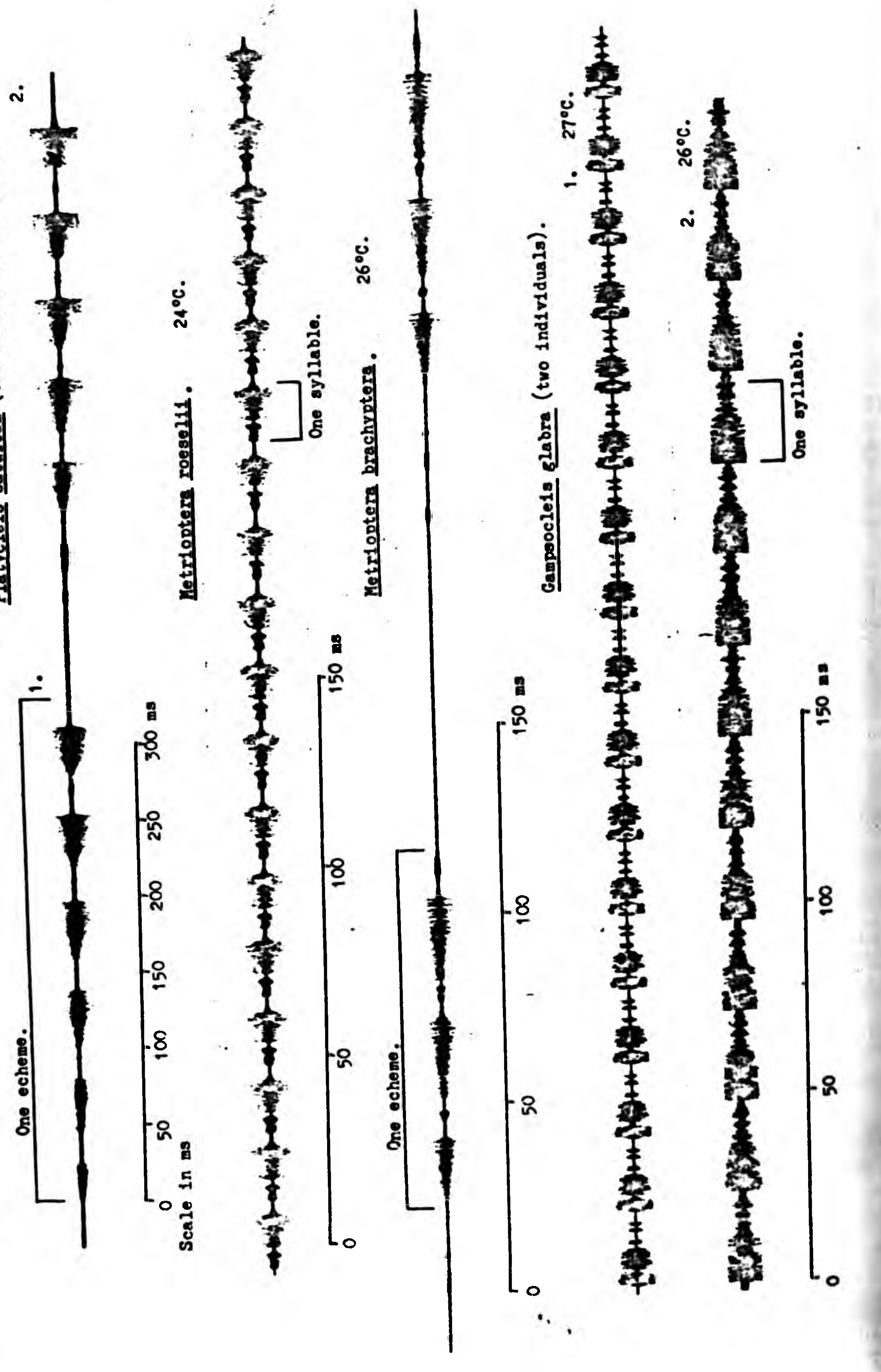
The effect of pulse duration in relation to the pulse interval (duty cycle) is seen by comparing animals A and B with animal C. In A and B, where the pulse is relatively long in duration, the frequency compass is small. Animal C, however, has short pulses with a long interval between; here the frequency compass is large, (see fig.12).

Two distinct peaks are discernible in the song spectrum of animal F, one being the carrier at a frequency of 23.5 kHz, the second band at 29 kHz; this interferes with the carrier, producing a difference tone of 5.5 kHz which shows as a slight peak at this value on the frequency scale. The interference pattern is also seen in the waveform of the pulses in the form of a phase shift between the third and fourth waves of the pulse.

Table 2. P. albopunctata: high-frequency components in the songs individuals A to F

Insect.	Carrier frequency.	Other peaks.	Frequency compass.
A	27 kHz		21 - 33 kHz
B	25.5 kHz		21 - 31 kHz
C	25 — 22.5 kHz	30, 34 kHz	13 - 36 kHz
D	24 — 21 kHz	13 kHz	17.5 - 37 kHz
E	33 kHz	26, 39 kHz	24 - 40 kHz
F	23.5 kHz	29 kHz	18 - 33 kHz

Fig. 13 SONGS OF FOUR TETTIGONIID SPECIES.



(ii) Songs of other Tettigoniid Species.

Oscillograms of the songs of the other species to be considered are shown in fig.13.

The song of P. sabulosa is similar to that of P. albopunctata in many respects. Some individuals have been heard to sing in short sequences, others sing continuously for longer periods of time. At maximum rates of singing the chirp interval is approximately equal to the chirp duration. This species, however, has more syllables/echeme; common modal values are 7 and 8 (see fig.14). Syllable parameters are presented for two individuals in fig.14, graph D, which shows mean values ± one S.D. (N = 12, 7). Each dotted line connects points representing mean syllable durations for a given individual. Syllable duration and interval tend to be slightly shorter than those of albopunctata (p. 38). The syllable intervals may equal or exceed syllable durations, particularly during the first and last syllable periods in the echeme. The songs of the two individuals analysed show a progressively increasing syllable period throughout the echeme. Thus, once again, the period tends to be the least variable parameter, as table 3 indicates.

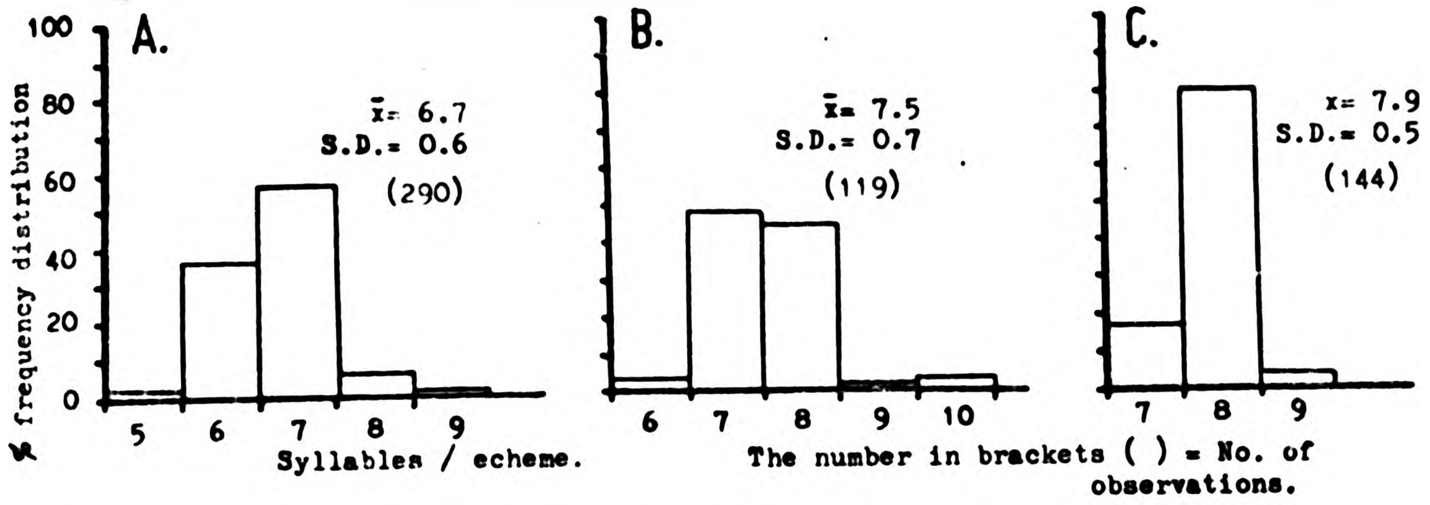
Table 3. P. sabulosa: coefficients of variation for the syllable parameters of the two individuals a and b.

	Syllable No.	1.	2.	3.	4.	5.	6.	7.
a.	Syllable period	2.88	2.81	1.49	1.03	4.49	1.96 %	
	duration	7.02	3.26	4.42	4.75	3.87	9.77	11.33 %
	interval	3.71	3.23	4.63	9.04	9.64	9.53 %	
b.	Syllable period	3.86	1.41	1.29	2.67	7.49 %		
	duration	2.71	2.13	1.79	3.91	6.23	7.41 %	
	interval	6.39	2.75	5.13	5.35	3.15 %		

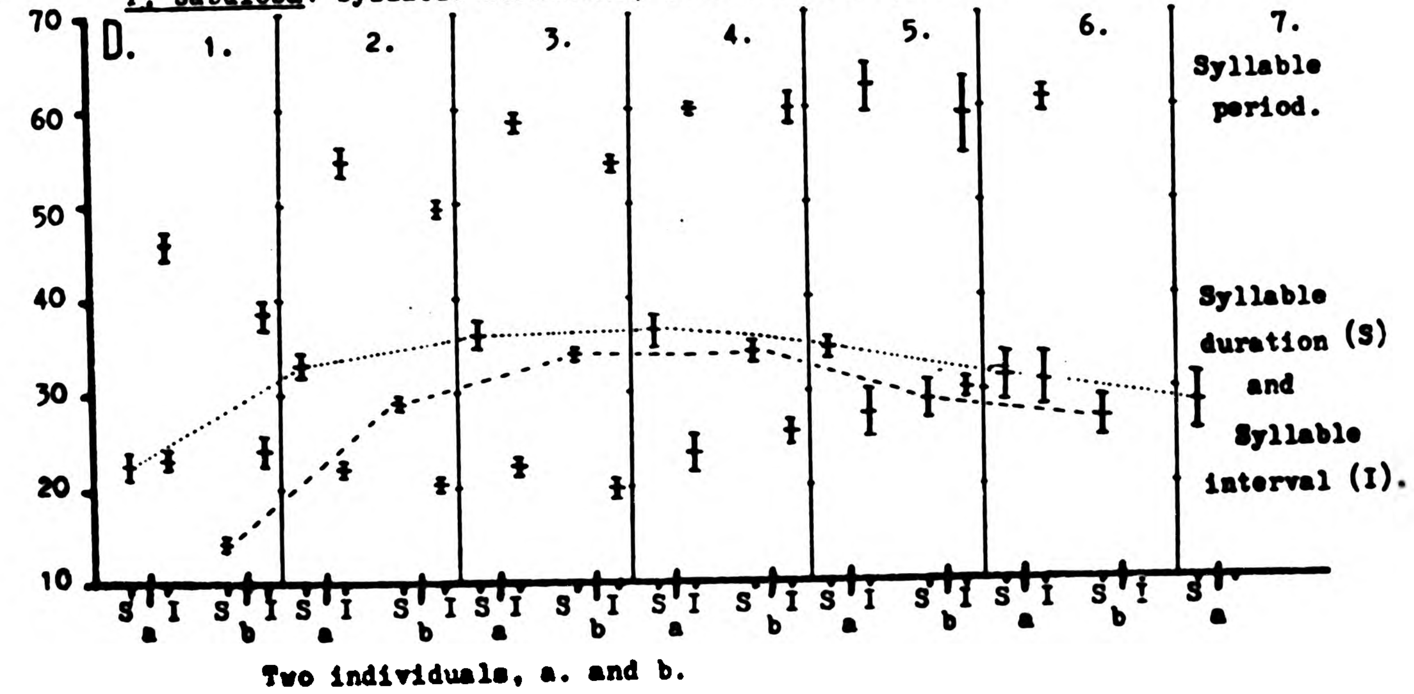
Insect a, N = 12. Insect b, N = 7.

Fig.14. SYLLABLE PARAMETERS OF P. SABULOSA AND M. BRACHYPTERA.

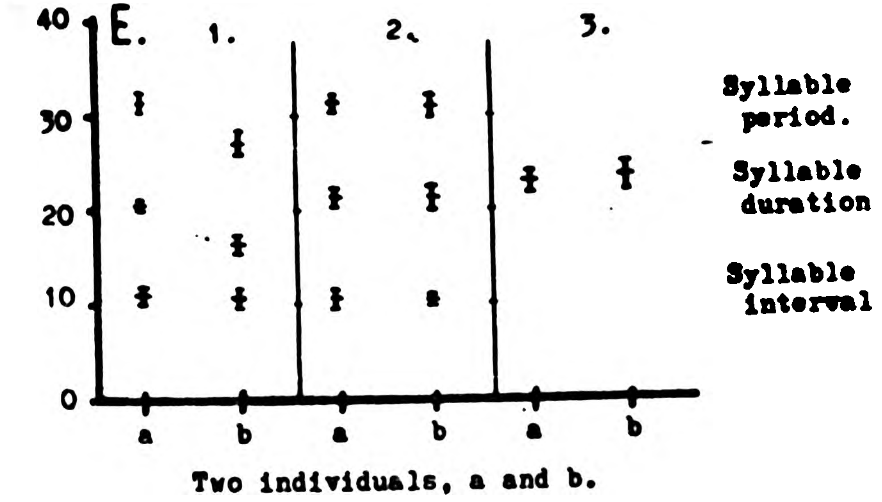
P. sabulosa: syllables/echeme of three individuals. Temperature - 22°C.



ms P. sabulosa: syllable durations, intervals and periods. 22°C.



ms M. brachyptera: syllable durations, intervals and periods. 26°C.



It is worth noting that, in species having a variable number of syllables in the echeme, the last two syllables are usually the most variable in duration. This is also true for *P. albopunctata* as can be surmised from graph A, fig.4. Rates of singing for two *sabulosa* individuals tested were slightly faster than for *albopunctata*, e.g. 7.14 syllables/s at 22°C. (individual *s*).

The song of *M. roeselii* consists of a continuous syllable train, (see fig.13). These sequences may be short, e.g. 0.5 to 2.0 s when the animal first starts to sing; or long, lasting many minutes when the animal is under radiant heat and motivation to sing is high. Syllable parameters for this species are shown in table 4. Once again, syllable period tends to be the most constant parameter. A longer-than-average syllable is usually followed by a shorter-than-average syllable interval, thus maintaining a constant period. Frequently, as in the song illustrated in fig.13, "opening" hemisyllables are present.

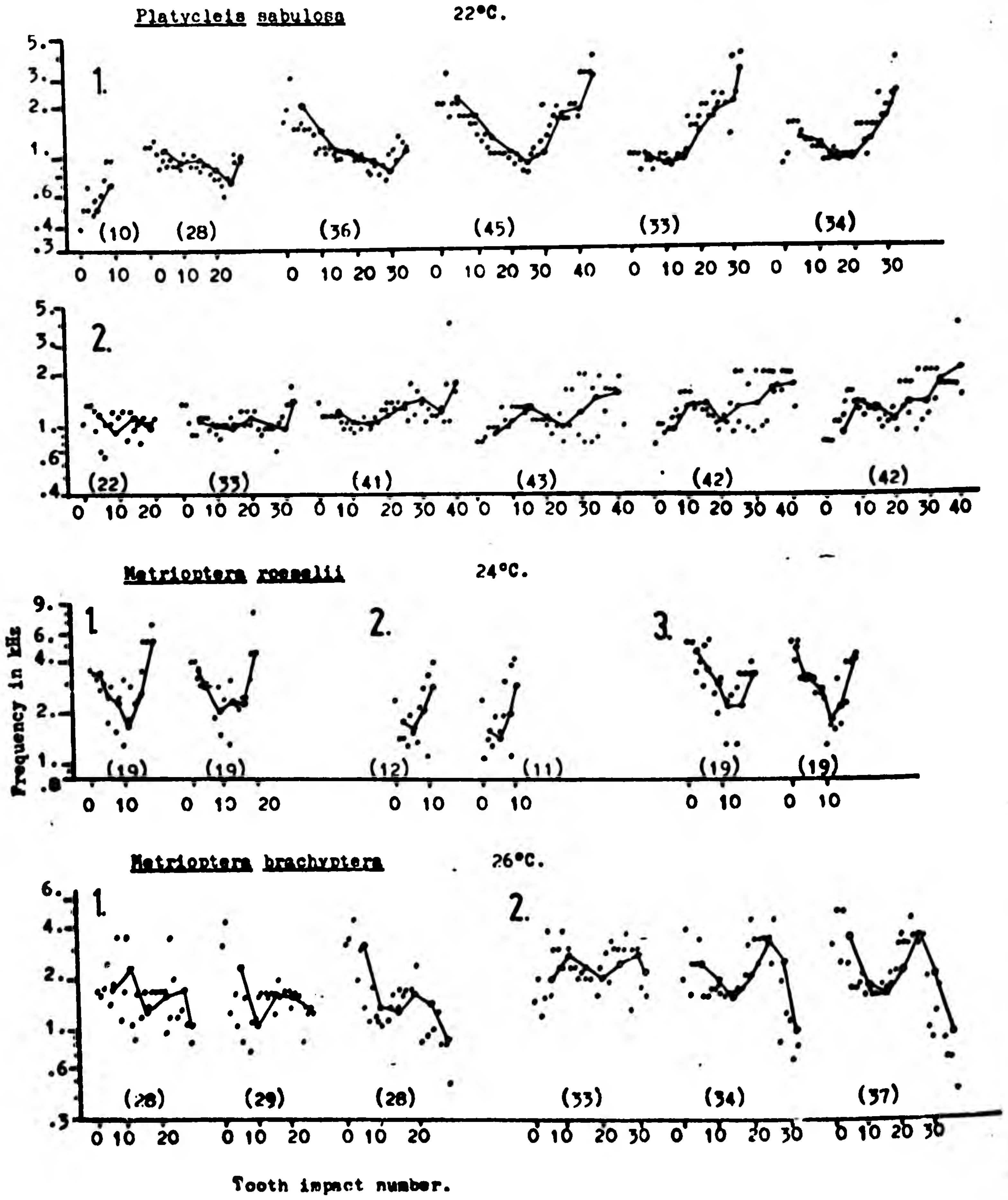
Table 4. *M. roeselii*: syllable parameters of two individuals. Durations in ms. Temperature - 24°C.

	Insect a. (N = 10)			Insect b. (N = 10)		
	Syllable period,	duration,	interval.	Period,	duration,	interval.
Mean ($\bar{x}$)	17.02	8.22	8.79	18.45	9.44	8.91
S.D.	0.32	0.41	0.51	0.45	0.78	0.52
Coeff. of variation (%)	1.88	4.99	5.80	2.44	8.26	5.84

Syllable rate - 58.5 syllables/s - - 53.8 syllables/s

Syllable parameters of two *M. brachyptera* individuals, *a* and *b*, are shown in graph E, fig.14. The points show means ± 2 S.D. (as variation is low). The song is not unlike that of *P. albopunctata* except that the syllable parameters are approximately halved in their durations and the echemes are composed of three syllables only.

Fig.15. LOW-FREQUENCY COMPONENTS IN THE SONGS OF THREE TETTIGONIIDS.



No variation was detected in the number of syllables/echeme, though McHugh (1971), in a detailed study, reports the occasional occurrence of two- and four-syllable echemes. It is clear from the oscillogram in fig.13 that the individual illustrated makes four wing strokes for each echeme. The first stroke, however, engages very few teeth and is of very low amplitude so that only three syllables are audible to the human ear.

The song of G. glabra is similar to that of M. roeselii in consisting of a continuous syllable train. It is not known at this stage whether the syllables are the product of both "opening" and "closing" strokes of the tegmina, or one stroke only. Whatever the method of producing the song, the temporal characteristics are nevertheless very similar to those of M. roeselii as the following table indicates.

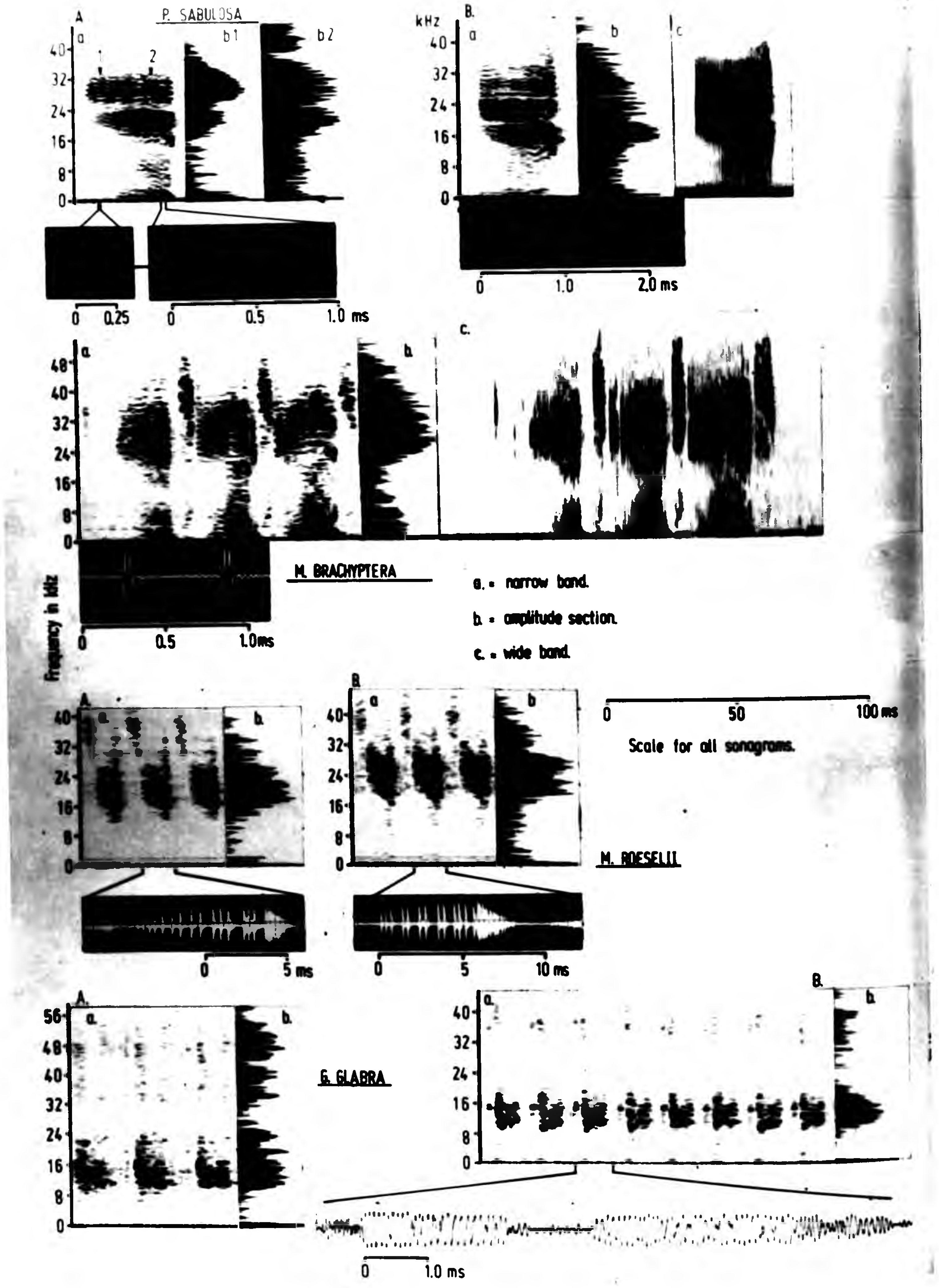
Table 5. G. glabra: syllable parameters of two individuals.
Durations in ms. Temperature - 26°C.

	Insect a. (N = 10)			Insect b. (N = 10)		
	Syllable period,	duration,	interval.	Period,	duration,	interval
Mean ($\bar{x}$)	24.43	12.71	11.71	17.23	9.50	7.73
S.D.	0.17	0.25	0.34	0.30	0.28	0.23
Coeff. of variation (%)	0.70	1.97	2.9	1.74	2.95	2.98
Syllable rate -	42.0 syllables/s			57.0 syllables/s		

The low-frequency components of the songs of P. sabulosa, M. roeselii and M. brachyptera are shown in fig.15. Tooth-impact rates of P. sabulosa are very similar to those of albopunctata (p.42). The shape of the low-frequency sweep is similarly quite variable between individuals (compare insects 1 and 2 in fig.15).

The low-frequency sweep of M. roeselii generally assumes a V shape in the sound spectrum. The exact shape of the V and its

Fig. 16. HIGH-FREQUENCY COMPONENTS IN THE SONGS OF FOUR TETTIGONIIDS.



frequency compass varies between individuals (two syllables each from three individuals are shown in the figure). The tooth-impact rate for this species is higher than that of the *Platycleis* species, varying from 1.3 to 6.0 kHz.

The low-frequency sweep of *M. brachyptera* may also assume a species-specific shape though this statement carries some reserve as only two specimens have been analysed (fig. 15). The tooth-impact rate of this species is higher than that of the *Platycleis* species but lower than that of *M. roeselii*.

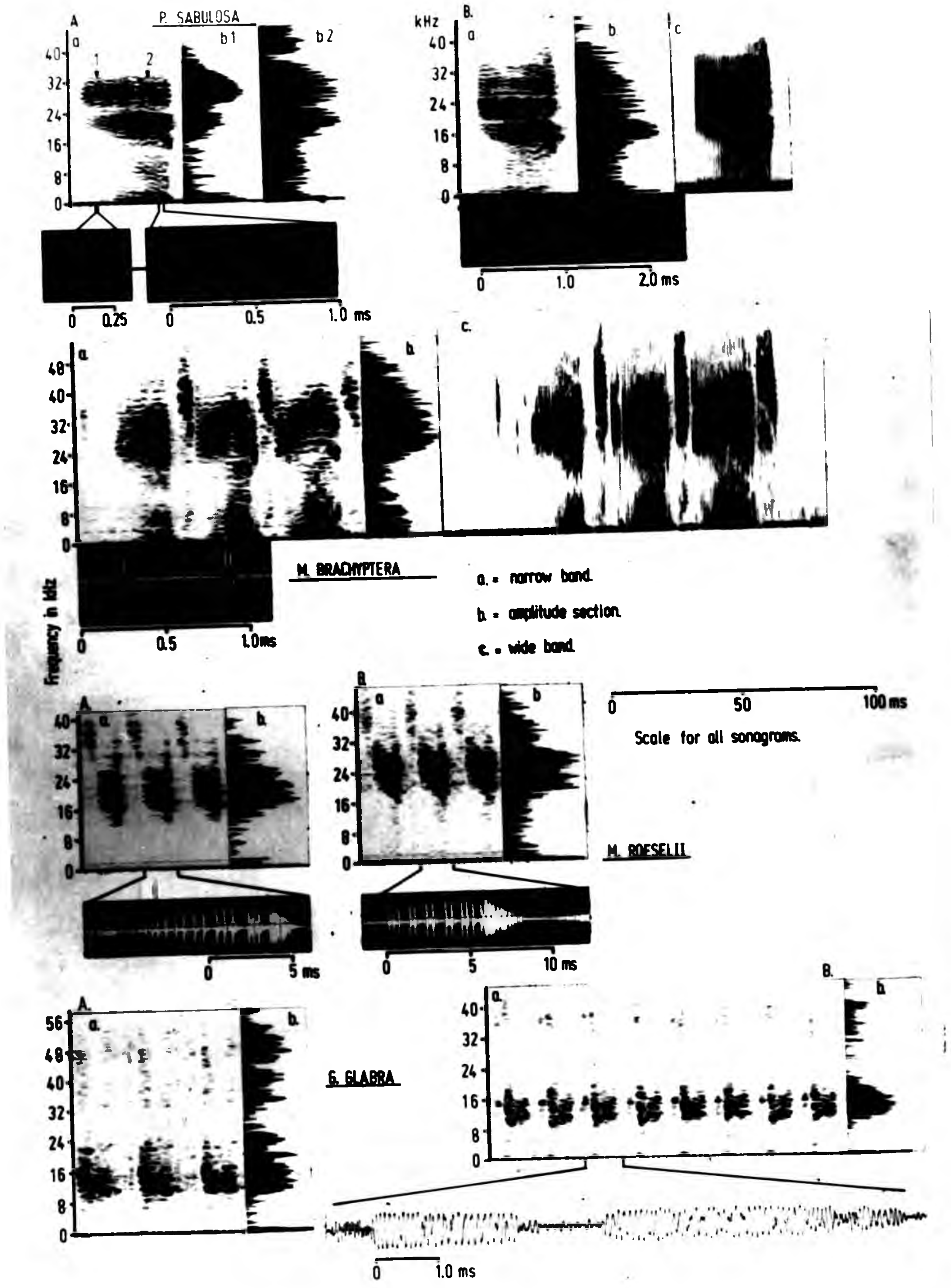
The high-frequency components in the songs of these species are illustrated in fig. 16. Data for these songs are presented in table 6, p. 59.

The song spectrum of *P. sabulosa* is very similar to that of *albopunctata* and it is probable that a similar range of variation exists in this species also. The carrier frequency of both individuals shown in fig. 16 changes during the duration of the syllable. In animal A, pulses at the beginning of the syllable contain six waves while pulses of equal duration at the end of the syllable contain five waves. A phase shift is observed halfway through the syllable (see fig. 16).

The ultrasonic song spectrum of *M. brachyptera* is similar to that of the *Platycleis* species with respect to the frequency compass and the peak frequency (see fig. 16 and table 6).

Detailed analysis of many expanded oscillograms has shown that the carrier frequency of the song of *M. roeselii* changes in each syllable, first sweeping downwards then rising again. Sales & Pye (1974) also noted this characteristic sweep. The frequencies of the sweep vary between individuals as does the frequency compass. The frequency compass and the frequencies of the carrier are similar to those of the species considered so far (see table 6). It is worth noting that in both the *Metrioptera*

Fig. 16. HIGH-FREQUENCY COMPONENTS IN THE SONGS OF FOUR TETTIGONIIDS.



frequency compass varies between individuals (two syllables each from three individuals are shown in the figure). The tooth-impact rate for this species is higher than that of the Platycleis species, varying from 1.3 to 6.0 kHz.

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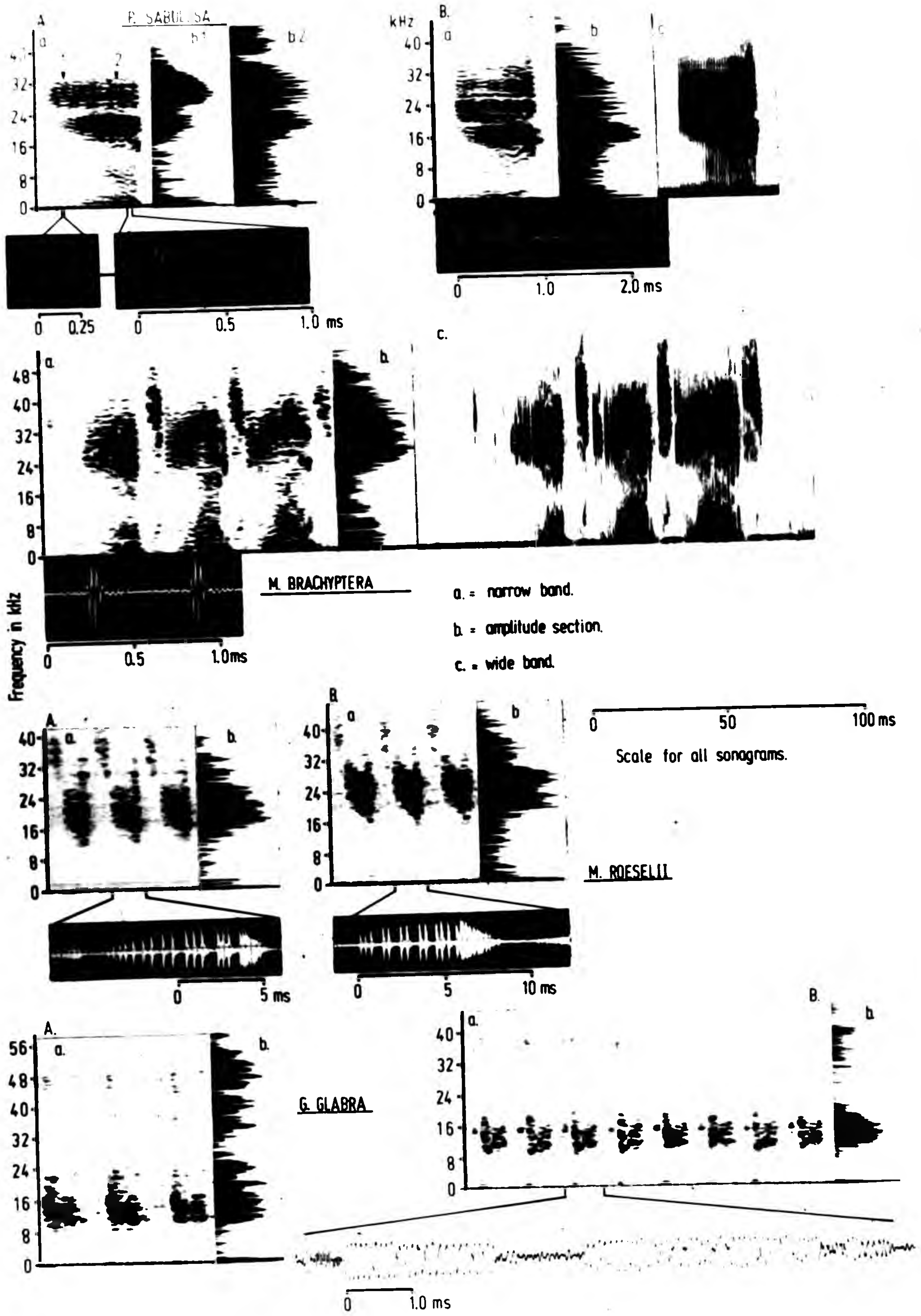
Fig. 16. HIGH-FREQUENCY COMPONENTS IN THE SONGS OF FOUR TETTIGONIIDS.



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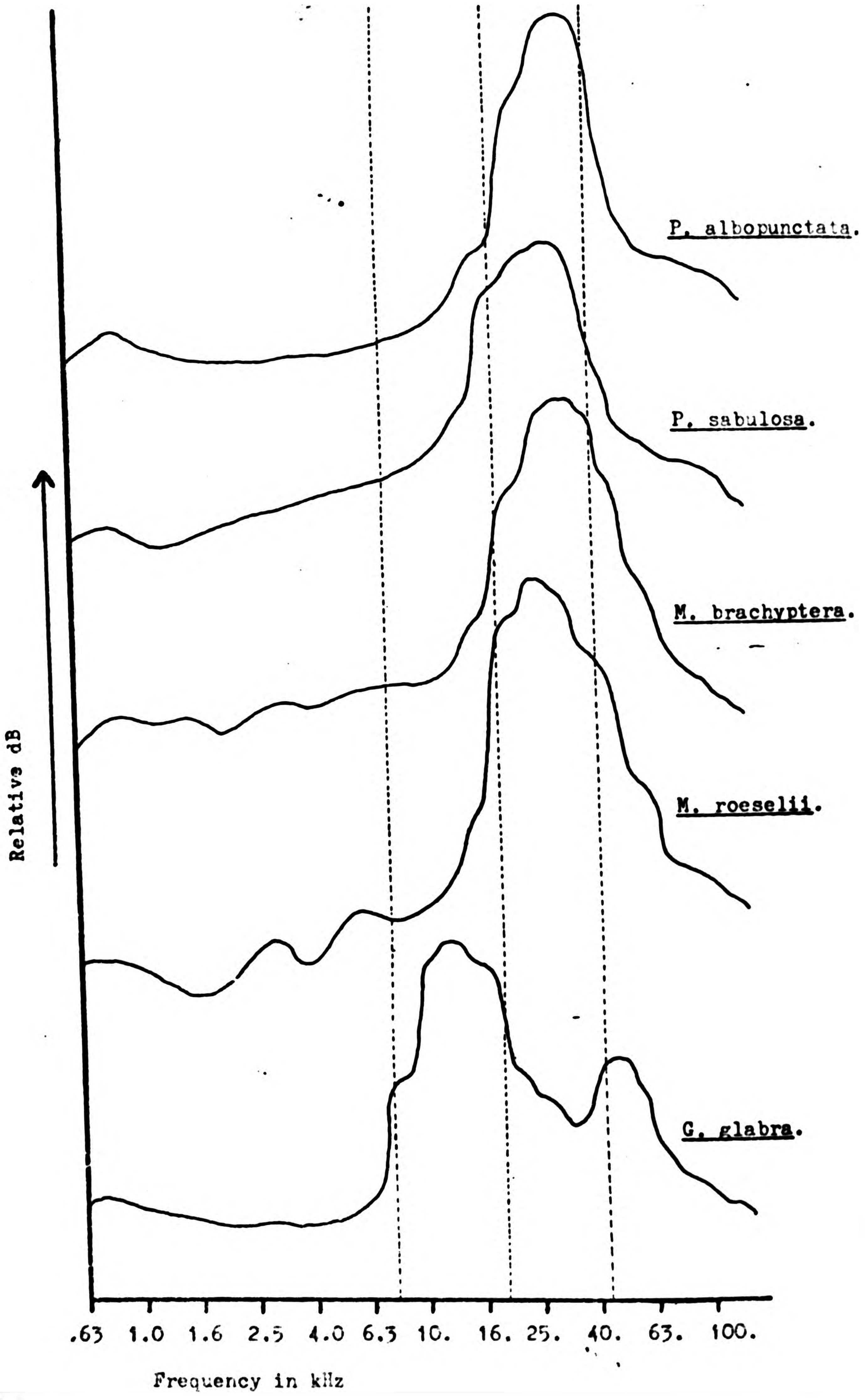
Detailed analysis of many expanded oscillograms has shown that the carrier frequency of the song of M. roeselii changes in each syllable, first sweeping downwards then rising again. Sales & Pye (1974) also noted this characteristic sweep. The frequencies of the sweep vary between individuals as does the frequency compass. The frequency compass and the frequencies of the carrier are similar to those of the species considered so far (see table 6). It is worth noting that in both the Metrioptera

Fig. 17 FREQUENCY SPECTRA OF THE FIVE TETTIGONIID SPECIES.



species the "opening" hemisyllables produce a band of energy with higher frequencies than those of the "closing" hemisyllable. This phenomenon will be referred to in the Discussion (p. 163).

G. glabra, though sounding similar to M. roeselii to the human ear, has a distinctly different frequency spectrum as can be seen in fig. 16. The tooth-impact rate of this species is difficult to determine from acoustic analyses alone. Analysis using wide-band sonagrams (not shown, since the salient features are indistinct) suggests a pulse repetition rate of around 5 to 6 kHz. It seems therefore that a tooth impact generates two waves before reinforcement by the next tooth strike, so producing a carrier frequency of around 11 to 12 kHz resonating to the second harmonic of the tooth-impact rate. The oscillogram in fig. 16 shows that the waveform produced is not entirely sinusoidal but the relative smoothness of its envelope strongly suggests some resonance. Any roughness may be due to the tooth-impact rate varying about the value required to produce resonance. Thus, at times resonance is impaired, a pulsed waveform develops and side-band frequencies are produced. A similar phenomenon is seen in the song of Homorocoryphus nitidulus vicinus (see Bailey & Broughton 1970). In Gampsocleis, these side-band frequencies occupy a band from approximately 9 to 20 kHz (see fig. 16). In addition to this there is a second band of sound energy at around 40 to 50 kHz. The intensity and frequency compass of this band vary between individuals (see table 6). Those frequencies, which do not appear to be related to the carrier (12 kHz), may, by interference, contribute to loss of resonance in the carrier.

Frequency spectra of all the species discussed so far are compared in fig. 17. The curves are derived from frequency spectra produced by the B & K Frequency Analyser and Level Recorder. As each species was recorded on separate occasions, absolute amplitude is not comparable between species. The curves show that the closely related Platycleis and Metrioptera species have very similar song spectra. The difference between these species and G. glabra is also demonstrated.

Table 6. High-frequency components in the songs of the four tettigoniid species. (Data from fig. 16)

Species.		Carrier frequency.	Other peaks.	Frequency compass.
P. sabulosa.	A.	28 ↘ 20 kHz	-	14 - 34 kHz
	B.	24 ↘ 22 "	16, 28 kHz	13 - 36 "
M. brachyptera.	A.	28 kHz	-	19 - 38 kHz
	B.	26 "	-	20 - 39 "
(Individual B not shown in fig.16)				
M. roeselii.	A.	21 ↘ 17 ↗ 22 kHz		13 - 31 kHz
	B.	25 ↘ 20 ↗ 24 "		17 - 32 "
G. glabra	A.	11.5 kHz	46 kHz	9-22 and 40-50 kHz
	B.	12.5 "	37 "	9-20 and 32-40 "

(iii) Studies of Stridulatory Morphology

Some preliminary studies have been made on variation in the morphology of the sound-producing structures. Table 7 shows the mean, standard deviation and range of measurements recorded for various morphological features of the species P. albopunctata, P. sabulosa and M. roeselii. Photographs of the file and mirror of these species are shown in figs. 10 (p. 43), 18 and 19 respectively. Two P. albopunctata populations have been referred to in the table, one French from the Causse Noir, the other British from a locality near Portsmouth.

In all the species, differences in body length (not tabulated) between preserved specimens can exceed 4 mm between individuals. The tegmina vary within species, both in absolute length and in relation to body length. There appears to be an allometric relationship between body size and tegminal length. Individuals from the Portsmouth population were all quite small in size, with tegmina that did not project

Fig.18. THE FILE AND MIRROR OF P. SABULOSA.

Underside of left tegmen showing detail of the stridulatory file.

Anterior

Scale 0 0.5 mm

v.f.

Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.)

Anterior

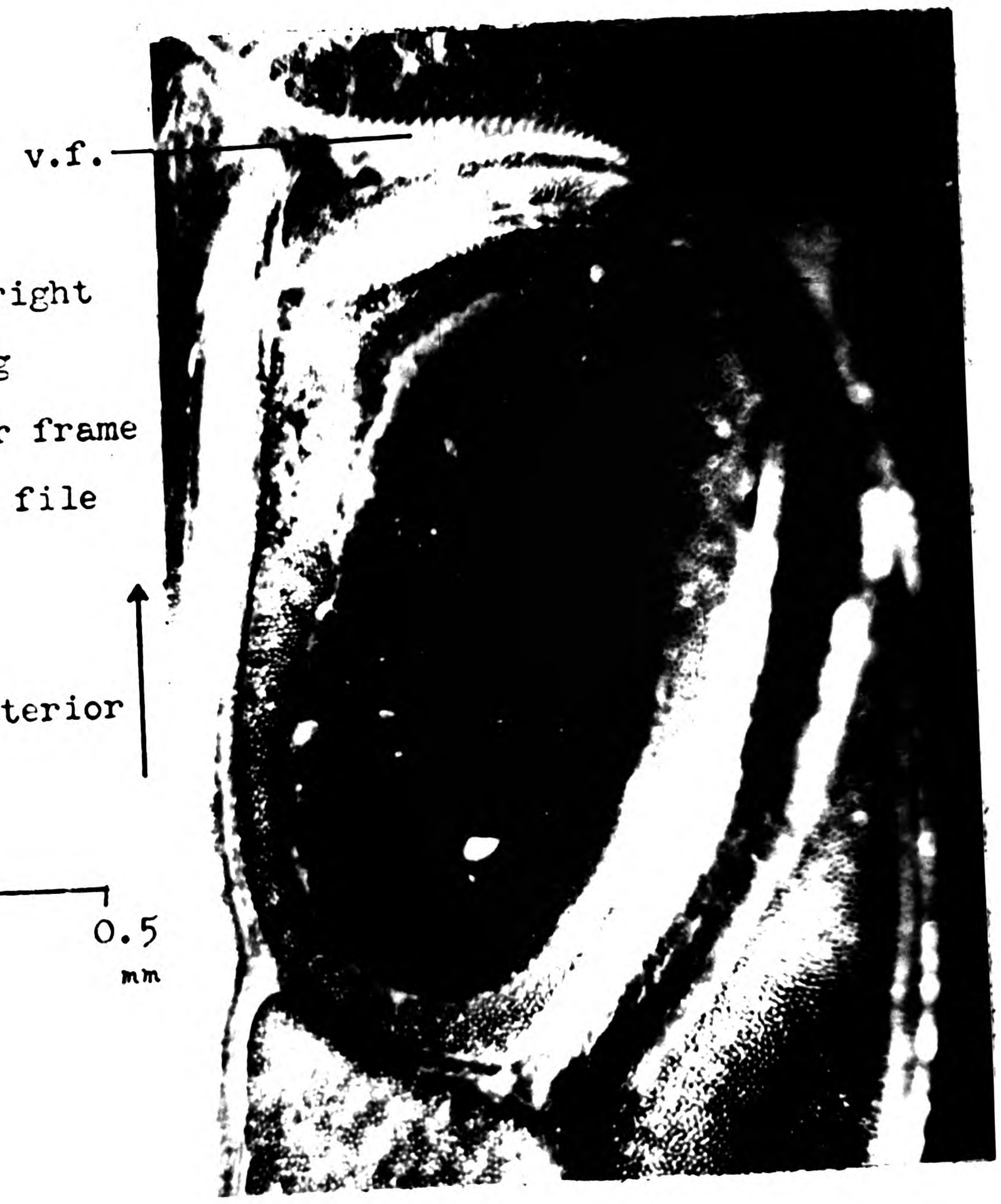
Scale 0 0.5 mm

Fig.18. THE FILE AND MIRROR OF P. SABULOSA.

Underside of left tegmen showing detail of the stridulatory file.

Anterior

Scale 0 0.5 mm



Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.)

Anterior

Scale 0 0.5 mm

Fig.19. THE FILE AND MIRROR OF M. ROESELII.

Underside of left tegmen showing detail of the stridulatory file.

Anterior

Scale 0 0.25 mm

Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.).

Anterior

0 0.5 mm

Scale .

Fig.19. THE FILE AND MIRROR OF *M. ROESELII*.

Underside of left tegmen showing detail of the stridulatory file.

Anterior

Scale 0 0.25 mm

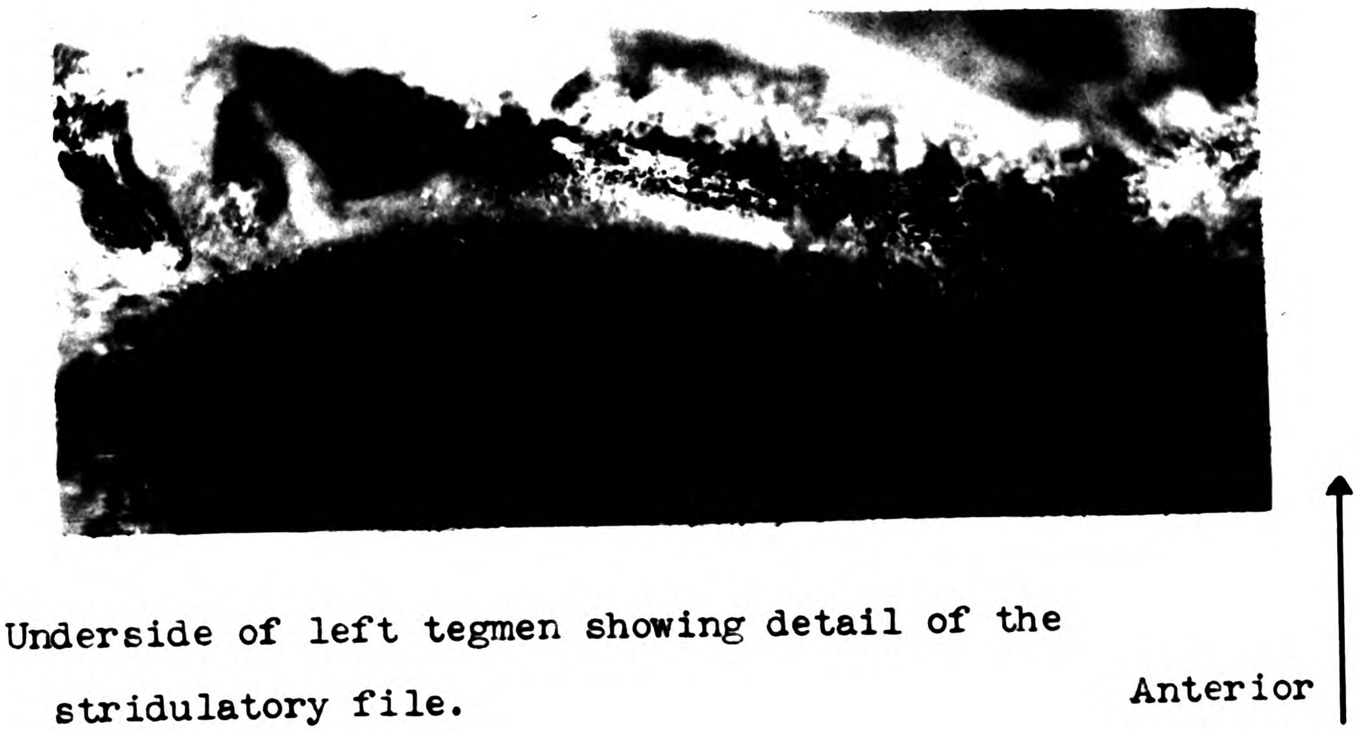
Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.).

Anterior

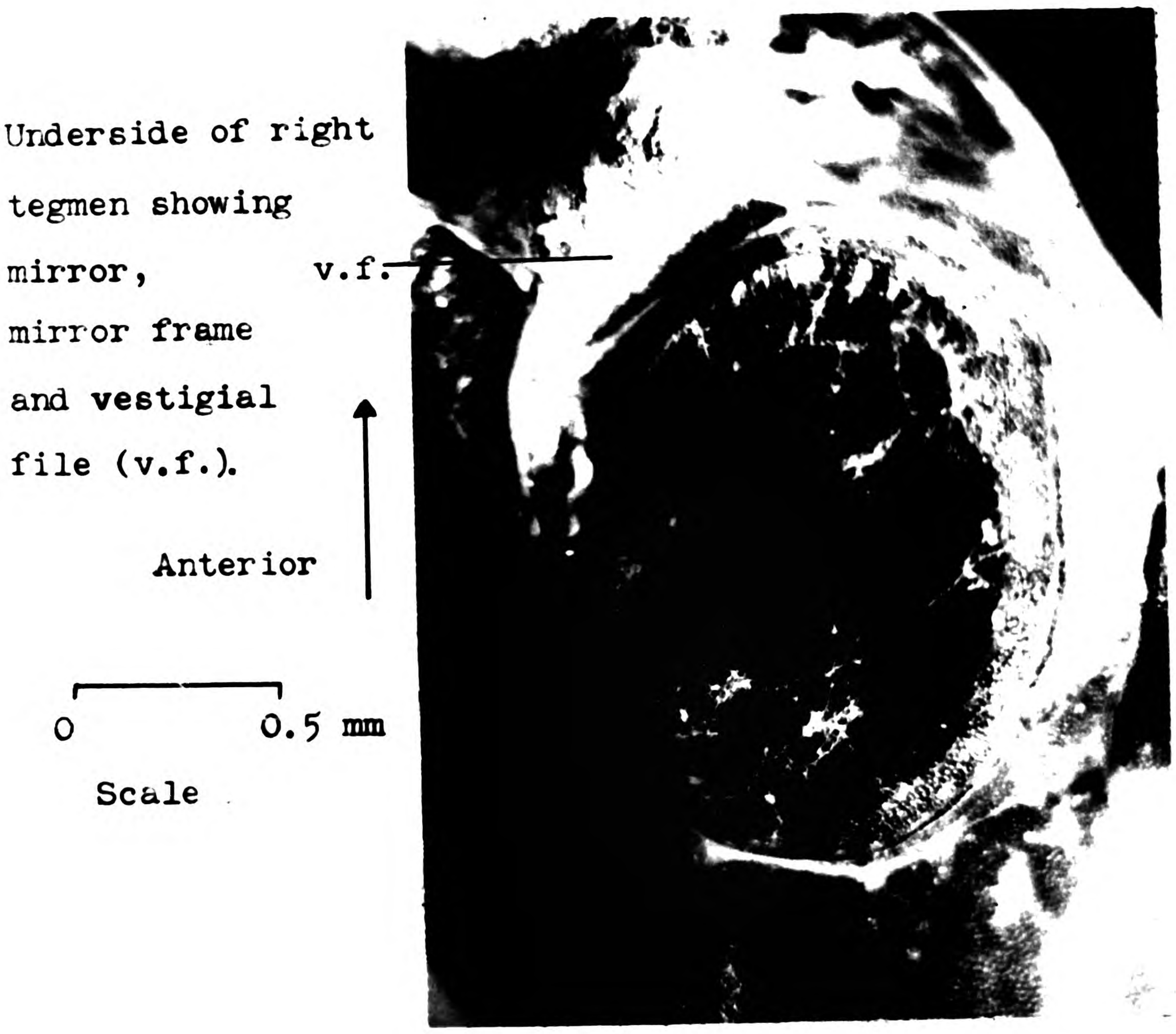
0 0.5 mm

Scale

Fig.19. THE FILE AND MIRROR OF M. ROESELII.



Underside of left tegmen showing detail of the stridulatory file.



Underside of right tegmen showing mirror, mirror frame and vestigial file (v.f.).

Table 7. Individual variation of various morphological characteristics. Linear dimensions in mm.

Species.		Wing length	Wing length / Body length.	Mirror dimensions p	q	File length	No. of teeth	Teeth/mm
P. albopunctata. (French population).	x̄	22.40	1.05	1.13	1.72	1.93	74.20	38.20
	S.D.	1.10	0.10	0.06	0.07	0.10	4.60	1.84
	Range.	21.1-23.8	0.88-1.16	1.05-1.22	1.60-1.82	1.82-2.1	70-82	35.3-40.1
P. albopunctata. (Portsmouth population).	x̄	17.70	0.90	1.08	1.51	1.76	72.00	40.50
	S.D.	1.10	0.08	0.09	0.09	0.09	4.30	0.82
	Range.	16.4-19.0	0.82-0.97	1.05-1.22	1.60-1.82	1.64-1.83	66-74	39.8-41.7
P. sabulosa.	x̄	28.20	1.18	1.21	1.91	1.93	65.00	33.80
	S.D.	2.80	0.07	0.10	0.09	0.20	1.80	3.59
	Range.	25.6-31.2	1.08-1.26	1.07-1.32	1.80-2.00	1.75-2.20	63-67	29.1-37.7
M. roeselii. (brachypterous).	x̄	8.40	0.49	1.30	1.52	1.02	46.0	46.30
	S.D.	0.10	0.06	0.11	0.10	0.09	4.1	2.22
	Range.	7.1-9.8	0.4-0.55	1.15-1.39	1.42-1.65	0.9-1.10	42-50	43.6-49.0

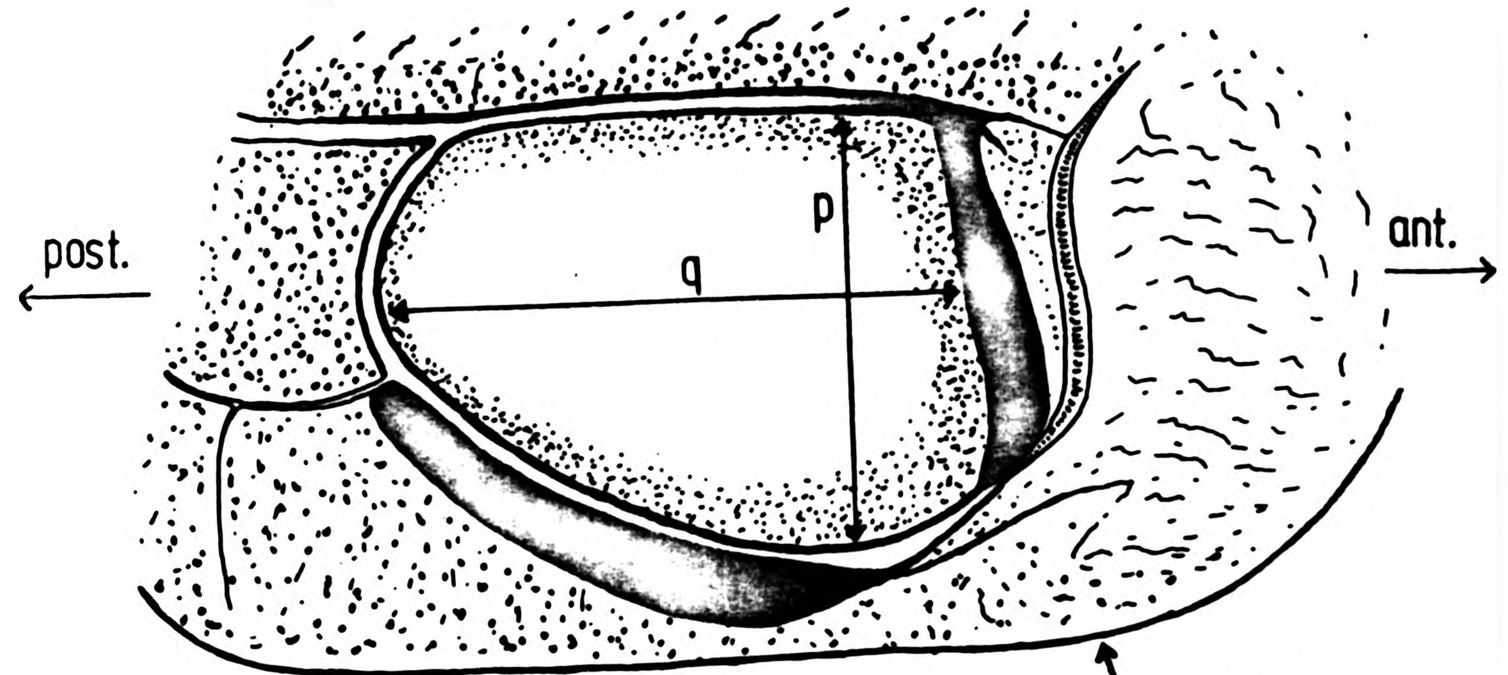
N = 7 (French P. albopunctata), 5 (British P. albopunctata), 5 (P. sabulosa), 7 (M. roeselii).

beyond the tips of the cerci. Other British populations sampled, however, resembled the French populations with more of the larger individuals, having also relatively longer tegmina that usually project beyond the cerci.

The variation in the number of discrete teeth in the file and their linear density reflect the variation in the low-frequency components of the song. However, the number of observed tooth impacts (see fig.9, p.42) is less than the number of teeth: it appears that approximately 60% of the teeth in the file are struck by the plectrum. The file of M. roeselii (fig.19) has a characteristic structure that correlates with the pattern of the low-frequency sweep: the density of distribution of the teeth is reduced in the central region of the file, thus producing a lower pulse repetition rate halfway through the syllable.

Mirror dimensions vary by 0.2 or 0.3 mm. In fig.20 the carrier frequency of 18 P. albopunctata individuals has been plotted against their mirror dimensions. The solid line shows the relationship between the carrier and the length of the mirror frame (dimension q in the upper figure). The correlation coefficient (r) is 0.67 ($p < 0.01$). A similar parameter has been correlated with peak frequency in various species by Morris and Pipher 1967, Bailey 1970, and Sales and Pye 1974. These authors have measured the length of the frame to be the distance from the posterior edge to the vestigial file. The dotted line shows the relationship of the carrier with q x p, (these two dimensions can vary independently but obviously their product is related to the area enclosed by the frame). For this plot $r = 0.84$ ($p < 0.001$). Points have been added for other species but have not been included in the regression equations. In general, the results indicate that the larger the mirror dimensions, the lower the carrier frequency of the song. This topic is pursued in the Discussion (p.162).

Fig.20. HIGH FREQUENCY COMPONENTS AND THE MIRROR REGION.



Mirror region of P. albopunctata showing dimensions measured (p,q).

Approximate point of contact with the stridulatory file.

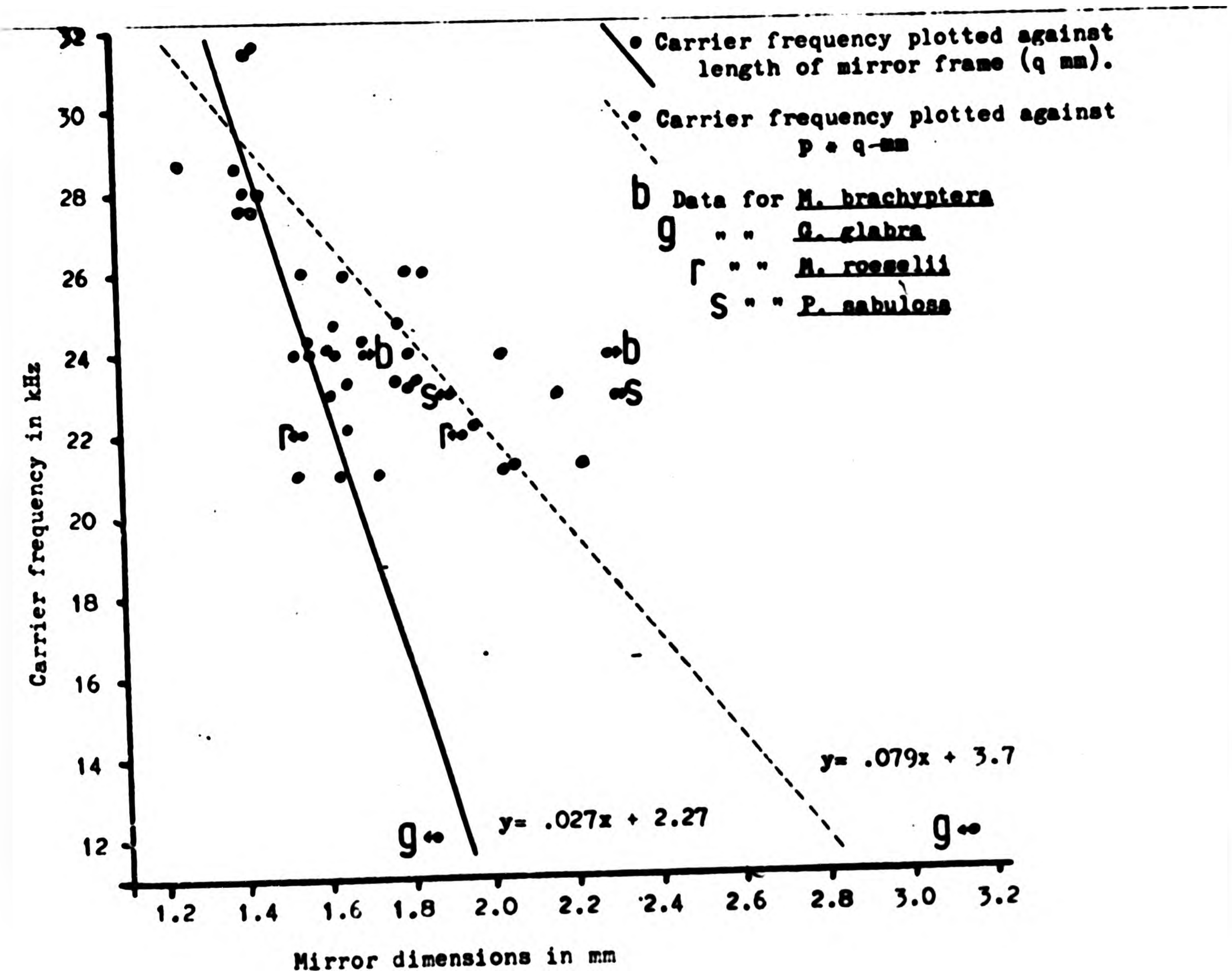
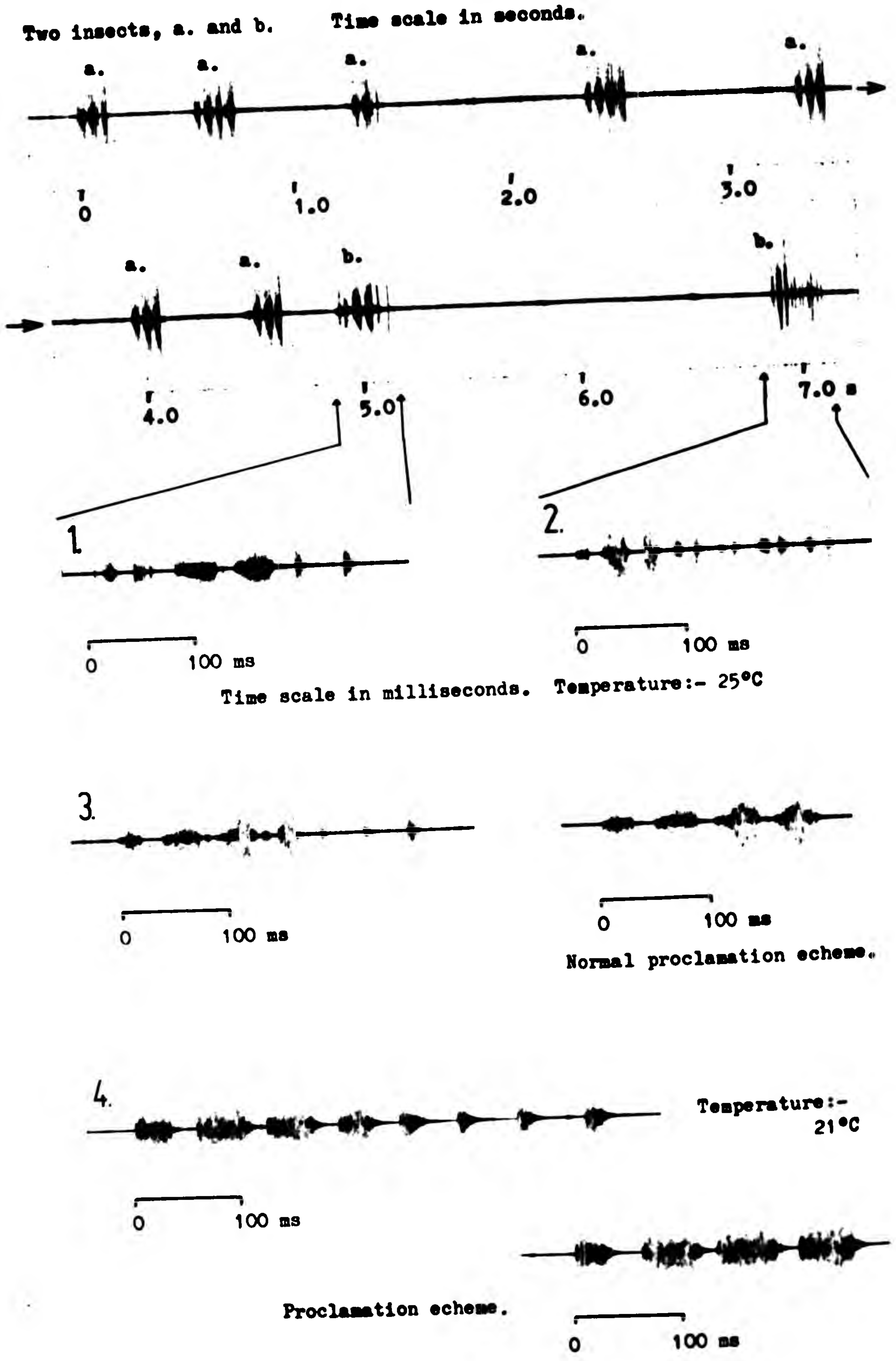


Fig.21 MICROSYLLABIC ECHEMES OF *P. ALBOPUNCTATA*.



3. Microsyllable-containing Echemes.

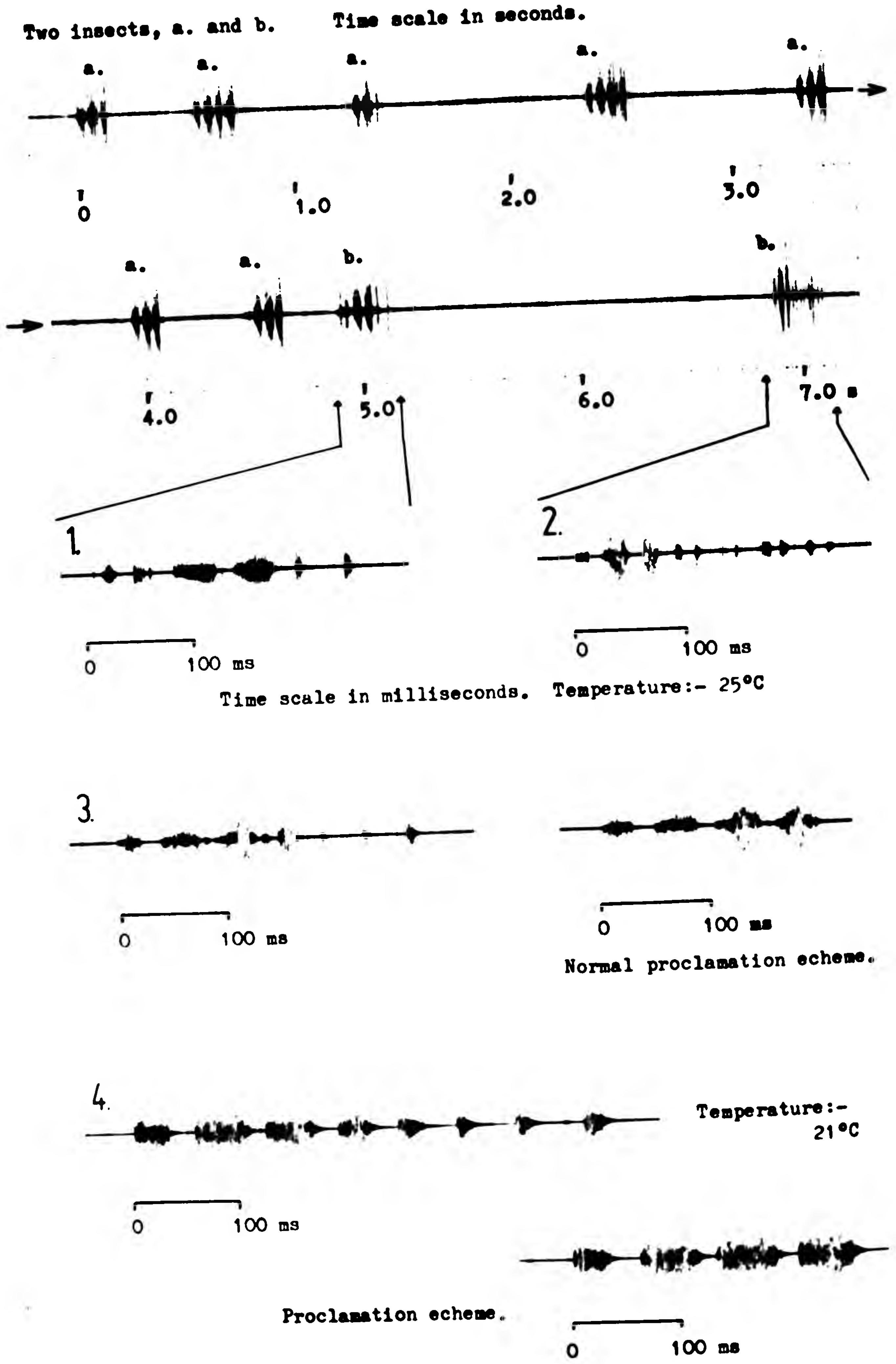
These echemes have been described for some *Platycleis* species by Samways (1975, 1976*b*). They contain syllables very much shorter in duration than those of proclamation song and are normally produced when males come into physical contact, particularly if they have been interacting acoustically prior to making contact. Associated behaviour sometimes appears aggressive in nature. Common movements are the rapid approach of one or both insects, followed by antennal lashing, grappling and occasionally biting. At other times little overt aggression can be detected, though rapid antennal movements are usually evident as the insects approach.

The microsyllabic echemes of *P. albopunctata* generally consist of an assemblage of short syllables. Both syllable duration and echeme duration are extremely variable. The echeme period of these calls is also quite irregular; they lack the strict temporal rhythmicity characteristic of proclamation song. Microsyllabic echemes therefore sound distinctly different from the normal proclamation song.

Oscillograms of some microsyllabic echemes are shown in fig.21. The first trace shows the terminal portion of a song sequence by insect *a* as it approaches and grapples with insect *b*. Insect *b* responds by producing echemes 1 and 2. Echeme 3 was later produced by insect *a*. The normal proclamation echeme of this insect is also shown. Echeme type 2 is normally only heard in association with rapid antennal lashing and rough physical contact and therefore seems indicative of a high level of excitation. All the syllables in this echeme are of high amplitude and very short duration, and have unusually steep transients. The opening hemisyllables are also easily audible in a slowed-down tape replay.

Echemes 3 and 4 (echeme 4 being from a third individual in

Fig.21 MICROSYLLABIC ECHEMES OF P. ALBOPUNCTATA.



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3. Microsyllable-containing Echemes.

These echemes have been described for some Platycleis species by Samways (1975,1976b). They contain syllables very much shorter in duration than those of proclamation song and are normally produced when males come into physical contact, particularly if they have been interacting acoustically prior to making contact. Associated behaviour sometimes appears aggressive in nature. Common movements are the rapid approach of one or both insects, followed by antennal lashing, grappling and occasionally biting. At other times little overt aggression can be detected, though rapid antennal movements are usually evident as the insects approach.

The microsyllabic echemes of P. albopunctata generally consist of an assemblage of short syllables. Both syllable duration and echeme duration are extremely variable. The echeme period of these calls is also quite irregular; they lack the strict temporal rhythmicity characteristic of proclamation song. Microsyllabic echemes therefore sound distinctly different from the normal proclamation song.

Oscillograms of some microsyllabic echemes are shown in fig.21. The first trace shows the terminal portion of a song sequence by insect a as it approaches and grapples with insect b. Insect b responds by producing echemes 1 and 2. Echeme 3 was later produced by insect a. The normal proclamation echeme of this insect is also shown. Echeme type 2 is normally only heard in association with rapid antennal lashing and rough physical contact and therefore seems indicative of a high level of excitation. All the syllables in this echeme are of high amplitude and very short duration, and have unusually steep transients. The opening hemisyllables are also easily audible in a slowed-down tape replay.

Echemes 3 and 4 (echeme 4 being from a third individual in

Table 8. P. albopunctata: syllable parameters of microsyllabic and amphimorphic echemes.

Durations in ms, temperature - 25°C.

Syllable no.	1	2	3	4	5	6	7
Echeme 1.							
Syllable duration,	13.0	16.5	38.0	36.0	7.0	7.0	
" interval,	16.0	21.5	16.0	21.0	38.0		
" period,	29.0	38.0	54.0	57.0	45.0		
Pulse repetition rate (P.R.R.),	1150	480	1000	1170	1710	1570 Hz	
No. of pulses,	15	8	38	42	12	11	
Echeme 2.							
Syllable duration,	12.0	18.75	11.25	2.5	1.0	5.5	1.0
" interval,	14.5	16.75	33.25	32.75	38.75	38.25	
" period,	26.5	35.5	44.5	35.25	39.75	43.75	
P.R.R. (in Hz),	1000	1479	1775	2800	2000	1270	2000
No of pulses,	12	28	20	7	2	7	2
Echeme 3, (amphimorphic, i.e. having normal and micro-syllables).							
Syllable duration,	21.25	33.5	40.0	17.0	1.25	3.25	5.75
" interval,	19.25	15.5	20.0	21.75	36.25	36.25	
" period,	40.5	49.0	60.0	38.75	37.5	42.0	
P.R.R. (in Hz),	900	1045	1100	2100	4000	2770	2800
No. of pulses,	19	35	44	36	5	9	15
Proclamation echeme (N = 3).							
Syllable duration,	34.4	38.9	33.6	24.9			
" interval,	16.25	16.8	21.5				
" period	50.7	55.45	51.5				
P.R.R. (in Hz),	826	975	1028	1182			
No. of pulses	28.0	37.6	34.6	29.5			

another interaction) have four almost normal syllables followed by four microsyllables. They are typically produced in the transition between normal singing and the singing of completely microsyllabic echemes. They may be initiated by the first, rather tentative antennal contact. It seems, therefore, that progressively more syllables are shortened as the insects' level of excitation is increased. It is worth noting at this point that echemes 3 and 4 are very similar to the short amphimorphic echemes (i.e. echemes comprising two groups of syllables, the syllables of one group being recognizably different from those of the other) of P. affinis (see Samways 1975, 1976a).

Measurements of various parameters of echemes 1, 2 and 3 are presented in table 8. The tables show that syllable duration can be reduced by as much as 97%. Such microsyllables consist of two to seven pulses and have a duration of one to three milliseconds. The corresponding intervals are extended to over twice their normal duration: thus the syllable period tends to be more constant than the other parameters: it can be reduced by as much as 47% though the reduction is usually less, at around 27%. Pulse repetition rates are usually two or three times faster than in normal proclamation song, indicating a very rapid but short wing stroke. The tables show all these parameters to be extremely variable; no two microsyllabic echemes are alike. This contrasts with the proclamation echemes which are all very similar in the same individual. It is therefore probable that the microsyllabic echemes illustrated do not represent the whole range of variation of this type of echeme.

Many tettigoniid species produce microsyllabic echemes. During the present study P. sabulosa, M. roeselii and G. glabra have all been heard to produce microsyllabic echemes similar in pattern to echeme 2 in the figure.

INTRASPECIFIC INTERACTIONS.

This section on intraspecific duetting behaviour in P. albopunctata, P. sabulosa and M. roeselii examines the way that these species react to the conspecific song. With regard to this reaction an initial broad generalization on acoustic behaviour of tettigoniids can be proposed. Either males respond to the song of a neighbour by adjusting their own song output; this leads to synchrony or alternation of chirps: or there is no apparent change in acoustical output; this results in unison chorusing, (see review by Dumortier 1964 and Alexander 1975).

In insects which alternate or synchronize chirps with those of their neighbours, there exist mechanisms which maintain accurate alternation or synchrony between singers (Jones 1966, Walker 1969c Samways 1975, 1976a). Thus the specific characteristics of the song, e.g. syllable or echeme pattern, are maintained (Walker 1957). Where insects live in cohesive groups, any given insect can be alternating with one neighbour and synchronizing with another (Alexander 1960). However, in insects that chorus in unison, though the bouts of singing may be synchronized, chirps and syllables need not be; so that the temporal pattern of the song is indistinct, at least for the human listener, (personal observation; and see Samways 1976c).

In the following analyses various terms have been used as defined below:-

Duet: Two insects engaged in singing activity at the same time. The echeme interval is not considered as a cessation of singing activity. The insect is regarded as having ceased to sing after a silent period of over three seconds has elapsed. Such a period suggests the end of a song sequence, for the echeme interval is never over three seconds in duration.

Alternation: A duet where echemes are sung alternately by each singer without overlapping, (see fig.22, trace 1).

Synchrony: Echemes sung together so that the species-specific syllable pattern is clearly maintained (i.e. in P. albopunctata, four or five syllables, see trace 3).

Unison: Echemes sung together without synchrony, thus resulting in the loss of the syllable pattern either by complete interference (see fig.22, trace 4), or by echemes overlapping thus giving the impression of a lengthened echeme with more syllables than normal, (see traces 5 and 6).

1. The Duetting Behaviour of P. albopunctata.

The duetting behaviour of this species seems at first to present an enigma. At times perfect alternation takes place, and occasionally synchrony occurs. However, the duet often develops into a form of unison singing where any mechanisms that may have operated to maintain alternation appear to break down. This type of interaction, termed "unison duetting" is that shown in traces 5 and 6 in fig. 22.

Six duets from different pairs of insects have been analysed to show the proportion of total time spent singing in alternation or synchrony, or in unison duetting where alternation and synchrony are absent. Two or more successive synchronized echemes are counted as synchronous singing, and similarly four or more alternated echemes are regarded as a sequence of alternation. The results are shown in table 9 overleaf.

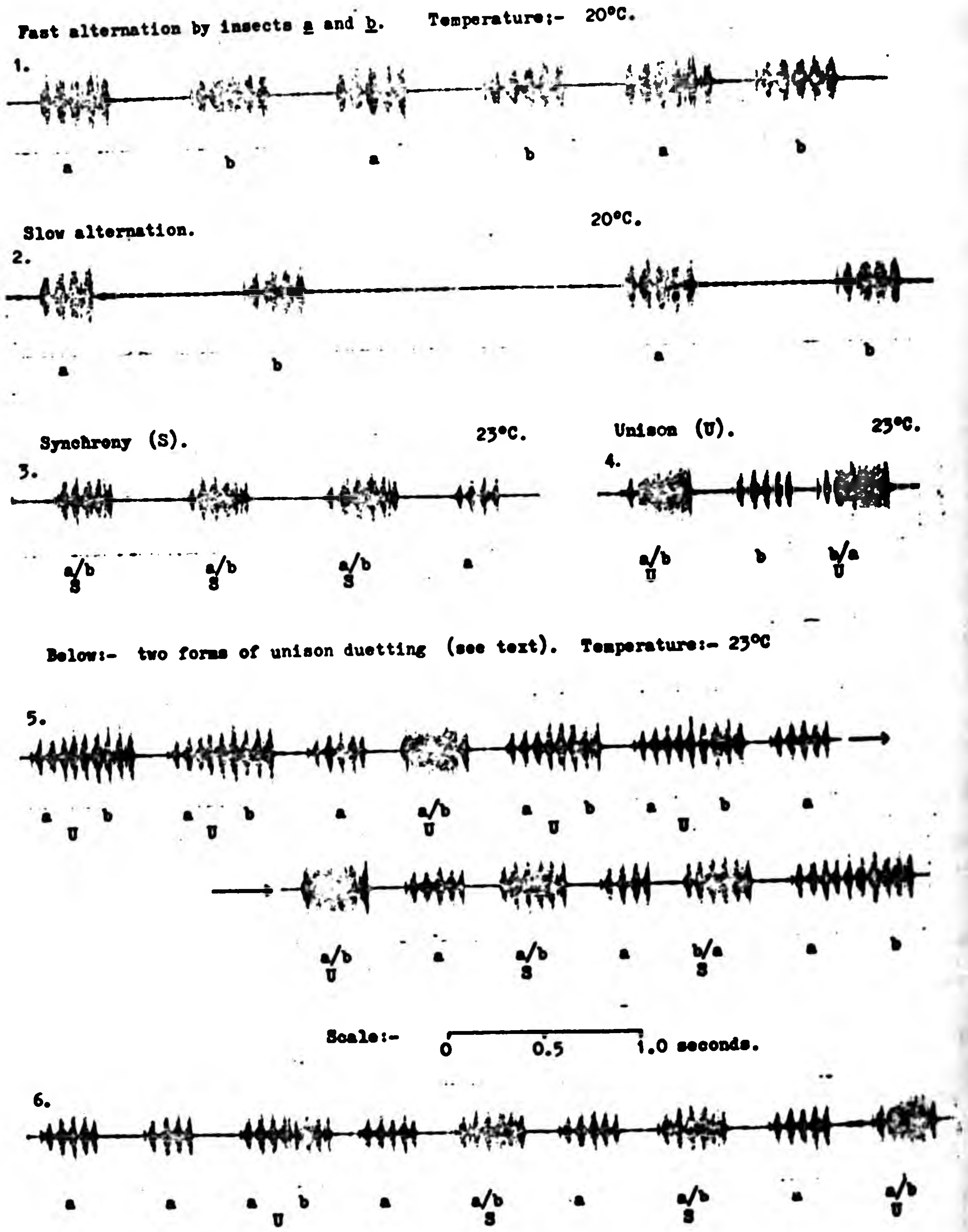


Fig. 22. DUETTING BEHAVIOUR OF P. ALBOPUNCTATA

Table 9. P. albopunctata: percentage time spent singing in alternation, synchrony or unison duetting.

Pair no.	Alternation (%)	Synchrony (%)	Unison duetting (%)	Total time in seconds
1.	4.72	0.00	95.28	185
2.	52.0	0.00	48.00	55
3.	10.5	0.00	89.40	64
4.	73.3	0.00	26.66	150
5.	7.85	1.77	90.38	260
6.	2.20	3.00	94.80	192

It can be seen that every pair engages in unison duetting, most pairs doing so for about 90% of the time. Two pairs spend over half the time alternating; the remainder alternate echemes infrequently. Synchrony is never common.

The three categories of duetting behaviour will now be examined in turn.

Alternation.

In normal solo singing the echeme duration is usually equal to, or greater than the echeme interval (see p. 39). If two insects were to alternate without modifying their songs, clearly echemes would overlap and the species-specific pattern of the song would be lost. However, when these insects alternate, as shown in trace 1, fig.22, the echeme period of each insect is approximately doubled. Thus, the echeme rate (or the rate of singing) is halved, and the echeme interval is extended with the result that alternated echemes do not overlap. In fact, the echeme rate of the combined songs is very similar to that of normal solo singing. This behaviour is comparable to the alternation singing in certain Ephippiger species studied by Busnel et al (1956 a,b). Durations for the normal, solo interval and the extended, alternation interval are shown in the next table.

Table 10.	Solo chirp interval.	Alternation chirp interval
$\bar{x}$	316.43 ms	805.00 ms
S.D.	47.00 ms	120.42 ms
Range	280 - 475 ms	575 - 975 ms

(Data from one of the insects of pair no. 2 in table 9). Here the alternation interval is more than double the solo interval. The chirp interval/chirp duration ratio is now 2.46.

The following table shows the chirp interval of insect 'a' when singing alone compared with the interval between chirps of 'a' and 'b' when the insects are alternating.

Table 11.	'a' - 'a', solo song.	'a' - 'b', alternating.
$\bar{x}$	355.5 ms	290.8 ms
Maximum	380.0 ms	348.0 ms
Minimum	333.0 ms	260.0 ms

(Data from pair no. 4)

Therefore, on average the chirp of 'b' is sounded 65 ms before the chirp of 'a' would normally have begun. This situation seems analogous to the alternation singing of *Pholidoptera griseoaptera* by mutual reciprocating inhibition (Jones 1966). Insect 'a' is inhibited from chirping on hearing the chirp of 'b'; a slightly shorter alternation interval ensues, then 'a' chirps, inhibiting 'b' and so on.

Occasionally mutual stimulation rather than mutual inhibition seems to operate to produce "slow alternation" (see trace 2, fig.22). Here the slow chirping of 'a' appears to stimulate 'b'. When 'a' ceases chirping so too does 'b'. The motivation of both singers seems too low for fast alternation to take place.

Synchrony.

Exact synchronization of echemes is infrequent. Very rarely three successive echemes are synchronized; usually only one or two are synchronized before the echemes overlap and move out of phase. This again is similar to the duetting of Pholidoptera griseoaptera (Jones 1966). There appears to be no mechanism to maintain synchrony as there is in Platycleis intermedia for example, where phase shifts result in a rapid retiming of echemes so that synchrony is re-established (Samways 1975, 1976a). However, insects from the Portsmouth population seemed to synchronize echemes more often than insects from the French or other British populations studied. It should be remembered that where populations are relatively isolated slight or even major changes in singing behaviour may evolve.

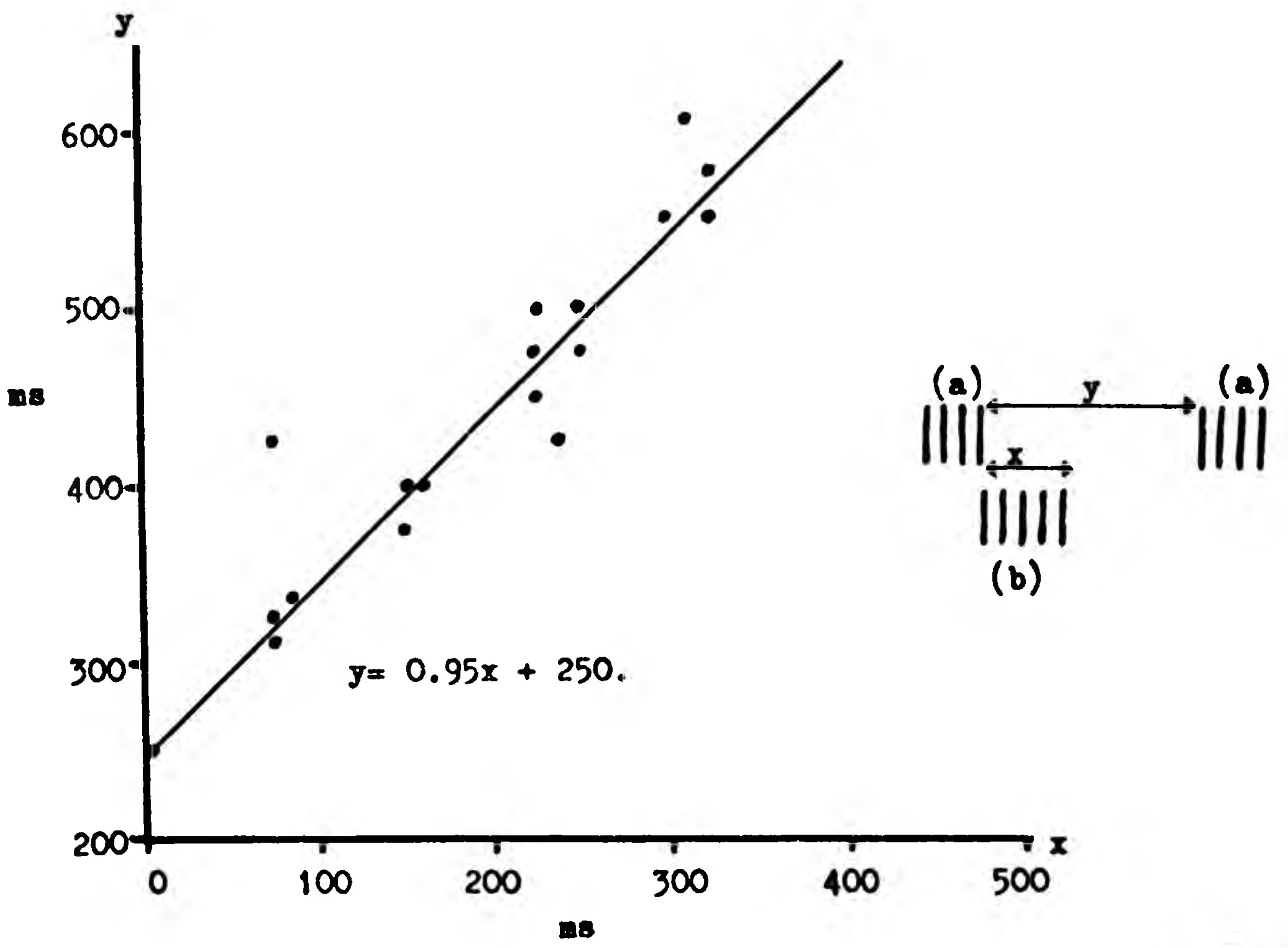
Unison Singing

As a duet where insects are alternating proceeds, one insect will often cease to alternate, and will commence singing at the solo rate (see fig. 22, trace 6). Here insect 'a' is singing the solo rate while 'b' sings the alternating rate. Thus every second echeme of 'a' is sung in unison or occasionally synchrony with the echemes of 'b'. At other times both insects ''attempt'' to sing the solo rhythm. As a result most echemes of one insect clash or interfere with those of the other (fig.22, trace 5). Usually in such duets one insect (a) sings at the solo rate continuously while the other (b) often reverts to the alternating rate. Thus one insect spends more time singing; this insect is referred to as insect 'a' throughout this section.

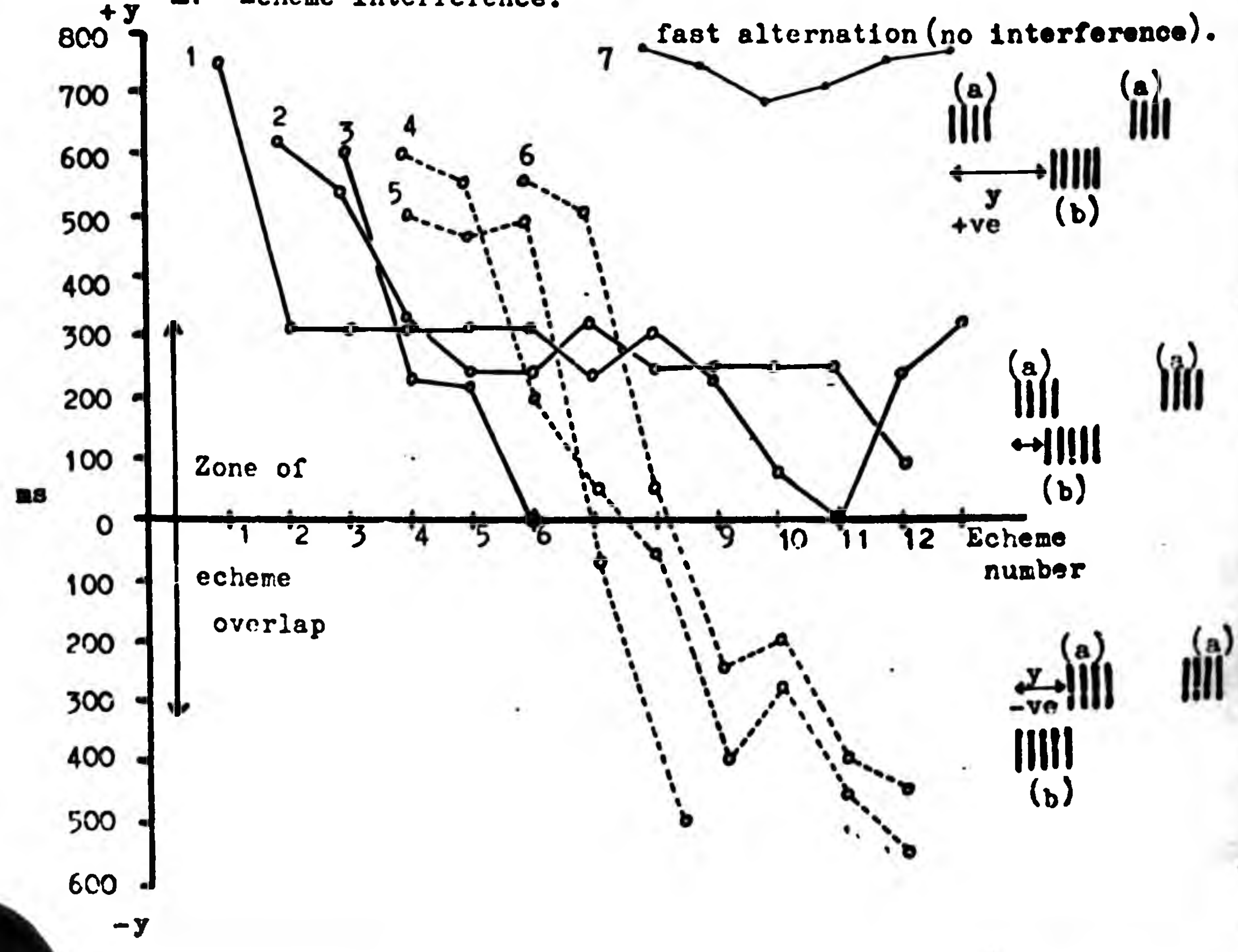
In addition to being the dominant singer insect 'a' also appears to be the leader chronologically, i.e. where echemes are sung in unison, the echeme of 'a' precedes that of 'b'. Interruptions by 'b' are particularly numerous when insect 'a' is singing close to the normal solo echeme rate (see fig. 22, traces 5 and 6). Where 'b' interrupts the echeme of 'a' the next echeme of 'a' may be delayed. The delay is in proportion

Fig. 23. DUETTING BEHAVIOUR OF P. ALBOPUNCTATA.

1. Extension of the echeme interval.



2. Echeme interference.

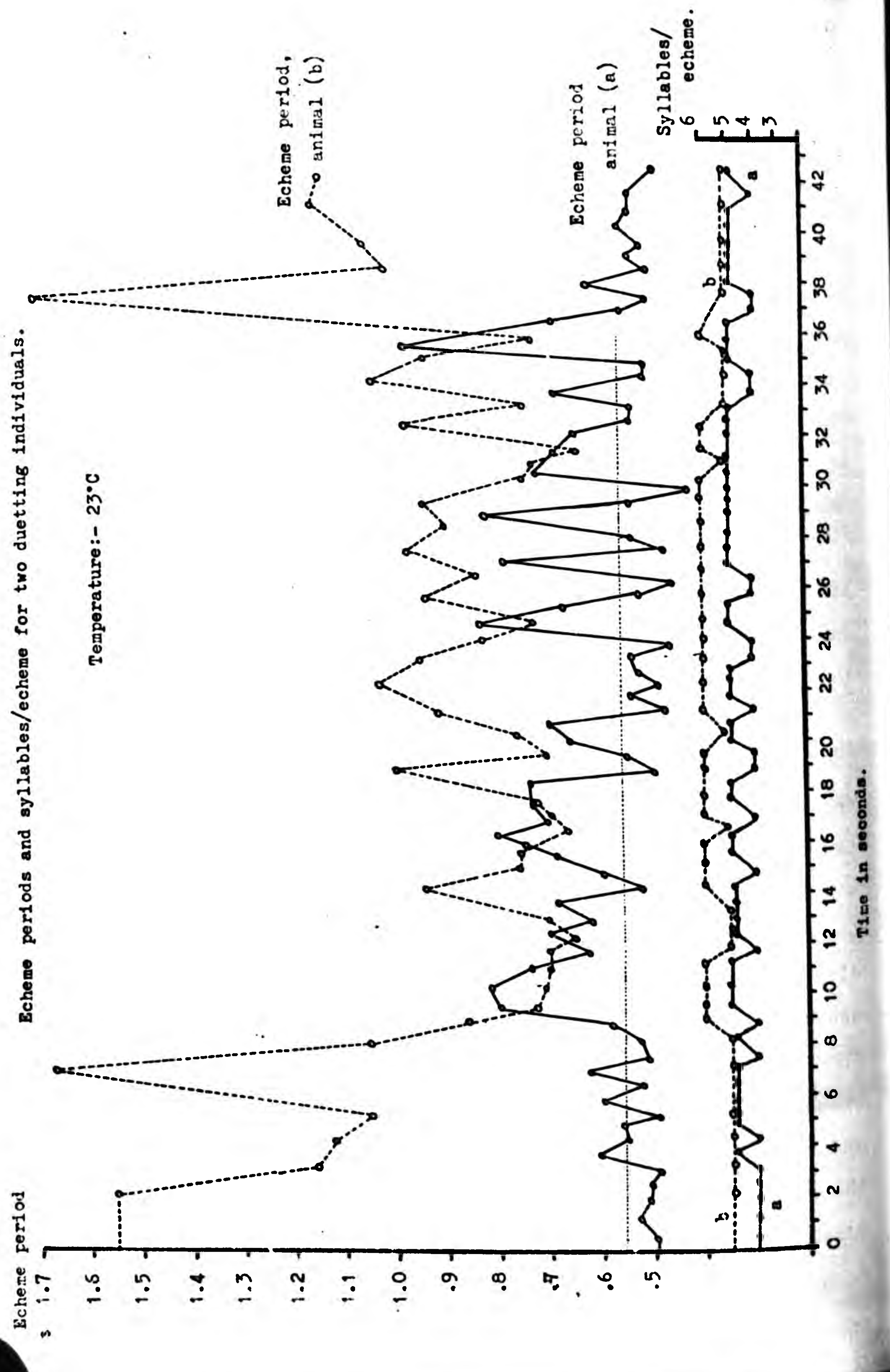


to the extent to which the echeme of 'b' overlaps into the echeme interval of 'a'. This relationship is shown in fig. 23, graph 1. Here, x represents the extent of overlap, and y the chirp interval of 'a'. Thus, insect 'a' appears to be inhibited from chirping until (y-x) ms after the end of the chirp of 'b'. As read from the graph, this inhibition period has a duration of approximately 250 ms. However, as this duet progresses, (pair no. 5 in table 9, p. 72) either 'a' becomes habituated to the song of 'b', or its motivation to sing increases. Consequently, the inhibition period is reduced until 'a' begins to interrupt the echeme of 'b'. Insect 'b' is apparently already habituated to the continuous singing of 'a' for it frequently interrupts the echemes of 'a' (see graph 2, fig. 23).

In graph 2, successive echeme periods between 'a' and 'b' are plotted on the y-axis. It is arranged that this period differential has a positive value when the echeme of 'a' precedes that of 'b'. When echemes are synchronous the value is zero and when 'b' precedes 'a' the period differential is negative. Seven samples of consecutive period differentials taken from the recording of pair no. 5 (p. 72) are plotted on the graph and show the before-mentioned decrease in the inhibition period and the consequent interference of echemes.

During fast alternation between the two singers, the period differential maintains a positive value of around 700 ms, as shown by curve 7 on the graph. The other solid lines (curves 1-3) show instances where the period differential is successively reduced until echemes interfere (i.e. where the curves meet the "zone of overlap"). At this stage insect 'b' may interrupt the echeme of 'a' for up to twelve successive echemes; then 'b' misses a chirp and commences to sing at the alternation rate as shown in fig. 22, trace 6 (p. 71). This type of intense

Fig. 24. DUETTING BEHAVIOUR OF P. ALBOPUNCTATA.



interaction may then be repeated. The dotted lines on the graph (curves 4-6) indicate occasions where the echeme of 'b' successively advances relative to the echeme of 'a' until it precedes the echeme of 'a' (i.e. the curve falls below the x axis). This phase-shift process has never been observed to continue for more than nine successive echemes, during which the phase alters by 180° (i.e. a shift from +550 ms to -550 ms on the y-axis of the graph). Insect 'b' then begins to sing once more at the alternation rate.

Such phase shifts are possibly the result of the slight retardation imposed on the rate of singing of 'a' by the increase in the rate of singing of 'b'. This effect is shown in the graph in fig. 24 where the echeme period of both individuals (pair 5) is plotted. The mean solo echeme period (derived from periods of around twenty seconds of continuous solo singing) of animal 'a' is shown by the faint dotted line. As the rate of singing by 'b' increases (i.e. its echeme period decreases) the echeme period of 'a' fluctuates and many periods are extended. The period of 'b' can be similarly affected by the singing of 'a'. The peaks at around 0.95 to 1.05 s (on the y-axis) indicate points where 'b' is singing the alternating rhythm (with a chirp interval of 675-775 ms, c.f. table 10, p.73). The lower points in this curve show where 'b' is "attempting" to sing the solo rhythm (e.g. from 9 s to 14 s on the time axis).

Throughout the intense phase of this section of the duet (i.e. from 9 s to 37 s in fig. 24) 'a' still produced more echemes than 'b', 48 to 35 respectively. If the number of echemes sung by 'a' is defined as 100% then the value for 'b' is 72%. The percentage for 'b' for the whole duet is clearly much lower.

The two lower traces in fig. 24 show the number of syllables/ echeme for each insect. As the rate of singing by 'b' increases, its echemic syllable number increases by one extra syllable. As 'a' sang for most of the time throughout the duet, very little data on solo singing by 'b' are available. Hence it is difficult to determine if the observed increase in echemic syllable number is due to the intensifying interaction with 'a' or whether it is merely associated with the increased echeme rate and might occur naturally in solo singing by 'b'. (During solo singing, longer echemes are associated with higher echeme rates and vice versa.) However, the large number of six-syllable echemes sung by 'b' during this phase of the duet would be considered unusual for solo singing at the given temperature (23°C.)

The total number of syllables sung by 'a' and 'b' during this intense phase (9-37 s, fig. 24) is 215 and 195 respectively. Again, if the number of syllables sung by 'a' is 100%, then the value for 'b' is now 90.7%. Such echeme extension is not seen in every duet; it may result from high singing activity by both insects.

Figs. 25 and 26 examine in detail at what point in the echeme period of each insect, the other insect is likely to commence its echeme. For clarity the echeme and its interval are treated separately. Graph 1 in fig. 25 shows the number of times 'b' interrupts the echeme of 'a', x milliseconds after the beginning of the echeme. The distribution indicates that 'b' can interrupt at any point in the echeme of 'a'. The pattern of the distribution suggests that 'b' may be "trying" to synchronize the onset of its echeme with any one of the five syllables in the echeme of 'a'. As some of the peaks in the distribution are not aligned with the syllables of 'a', and because 'b' often chirps in the syllable intervals of 'a', synchronized echemes are much less frequent than unison echemes.

Fig. 25. DUETTING BEHAVIOUR OF P. ALBOPUNCTATA.

Echeme interference between insects a and b.

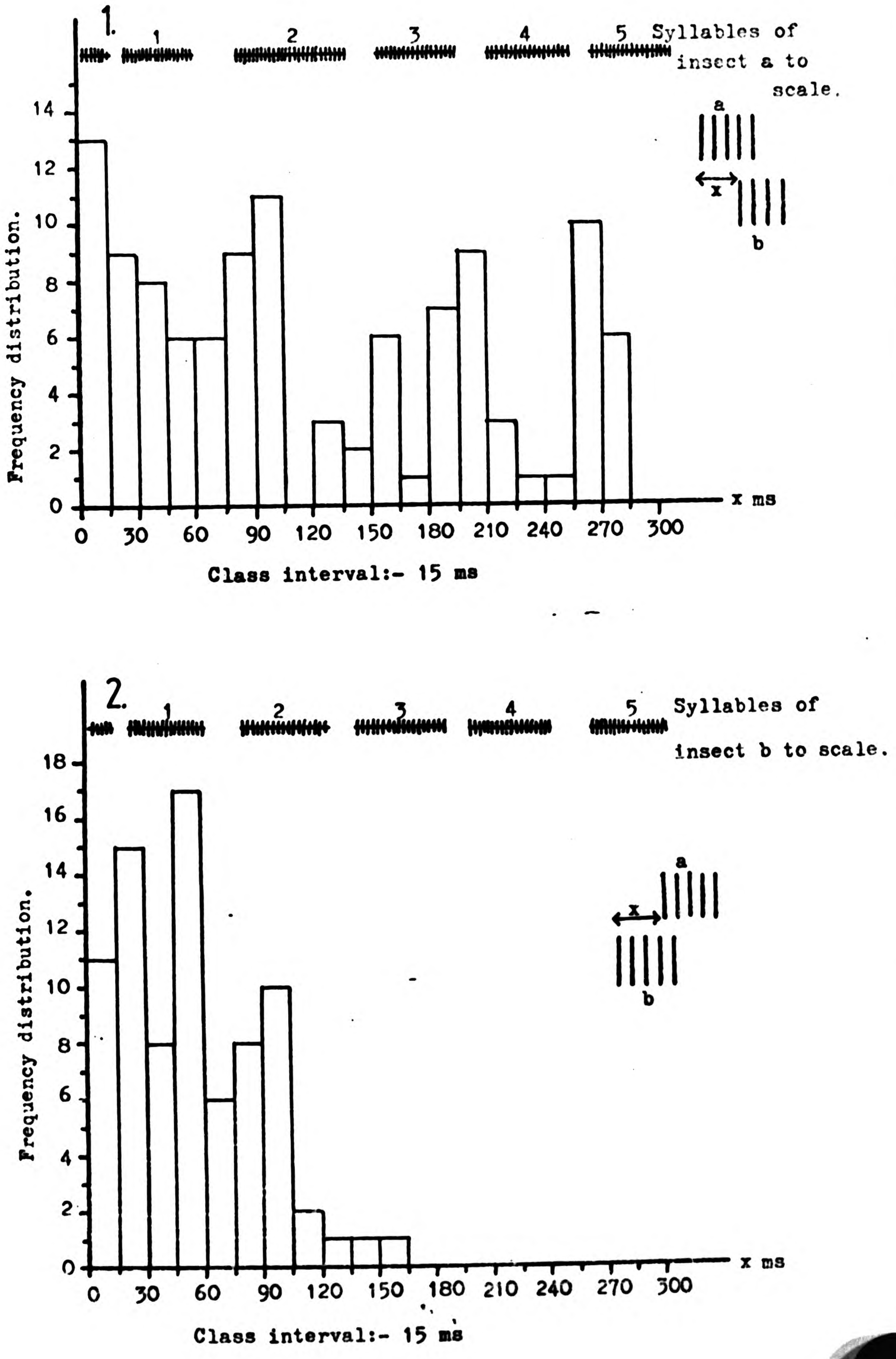
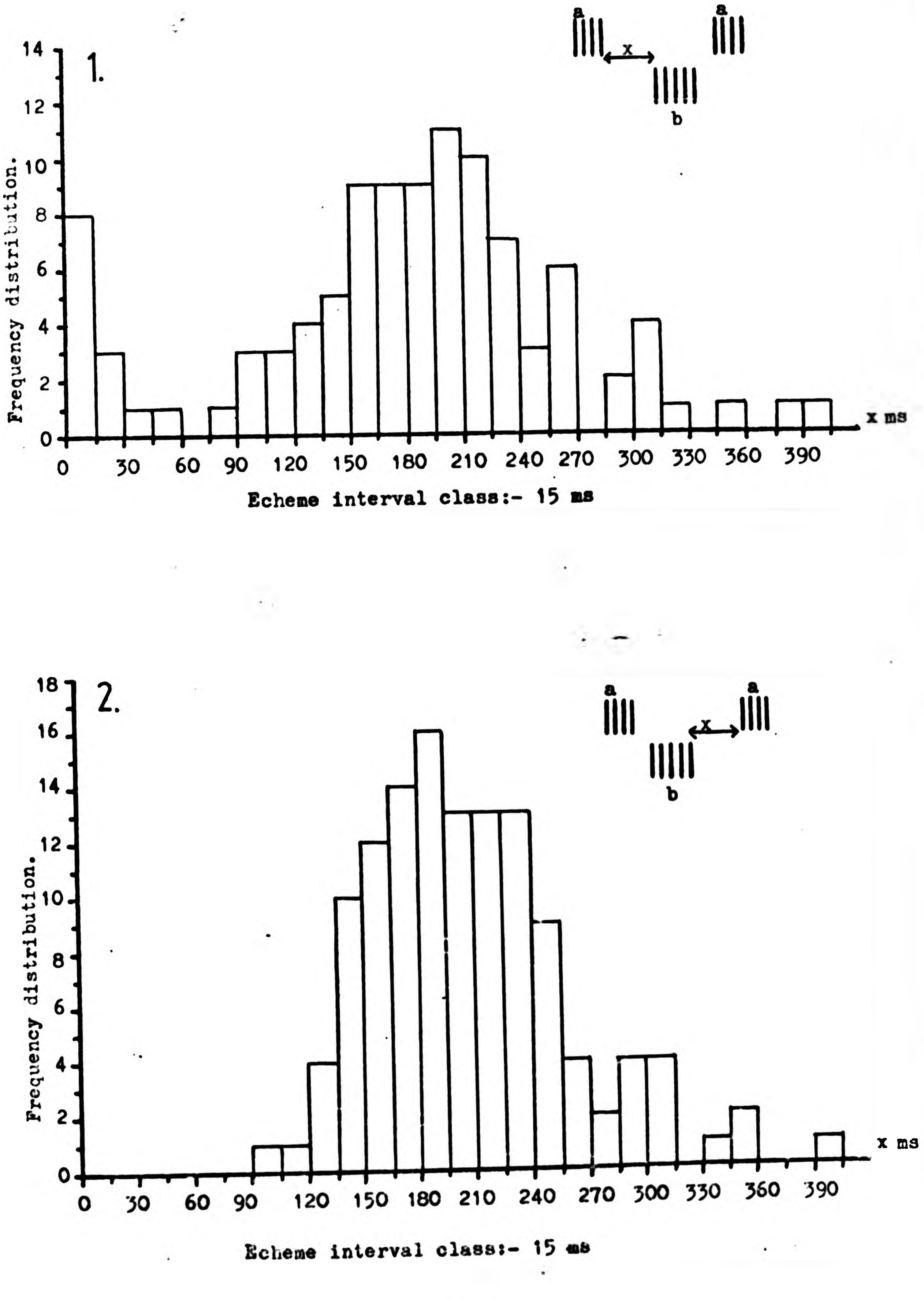


Fig. 26. DUETTING BEHAVIOUR OF *P. ALBOPUNCTATA.*

Variation in echeme interval (x) between insects a and b.



The second graph in the figure shows the reverse situation, i.e. the interruption of the echeme of 'b' by insect 'a'. This distribution exhibits a large reduction in interruptions 60 ms after the onset of the echeme of 'b', with most interruptions ceasing after 105 ms. The data in figs. 25 and 26 are derived from the duet of pair no. 5. Analysis of the duet of pair no. 6 produces very similar results. Interruptions by 'a' cease 60 ms after the onset of the echeme of 'b', while interruptions by 'b' continue throughout the echeme of 'a'.

Graph 1 in fig.26 shows at what point in the chirp interval of 'a' insect 'b' is likely to commence its echeme. Again, 'b' is able to chirp at almost any point, though there is a large reduction in the number of interruptions from 30 to 90 ms after the termination of the echeme of 'a'. The second graph shows that 'a' does not commence chirping until 90 ms after the end of the chirp of 'b'. These figures, i.e. 60 to 90 ms, recall the reaction time for a response to an auditory input proposed by Jones 1966, Spooner 1968 and Walker 1969. This will be referred to in more detail in the Discussion.

Insect 'a' has been described as the dominant singer for the reasons given (p. 74). True behavioural dominance has been well established in the Orthoptera (Kato & Hayasaka 1958, Alexander 1961, Busnel 1967, Young 1971, Ewing 1972, Rivault 1974, Otte & Joern 1975). It was therefore decided to make brief observations of the behaviour accompanying the duet in P. albopunctata. These observations reveal that insect 'a' generally sings steadily from a secure perch usually high up in the cage. Insect 'b', in contrast, sings intermittently, often moving around and falling from potential singing perches. McHugh (1971) observed very similar behaviour in M. roeselii

In a simple test, ten marked males were caged singly and left for 24 hours. Using collecting tongs, five individuals were then removed from their cages and paired with the other five males. The pairs were then observed for ten minutes and any differences in singing behaviour between the "cage owner" and the "intruder" noted. The insects were then separated and after 24 hours the test was repeated the other way around, i.e. previous "cage owners" were now "intruders" and vice versa. As males that are caged alone sing infrequently, very few were singing prior to being paired. Those that were doing so are indicated in the following table, thus:- (s).

Table 12. P. albopunctata: singing behaviour of newly paired males.

Trial no.	"Cage owner".	"Intruder".
1.	Continuous singing.	Intermittent singing.
2.	" "	" " (s)
3.	" "	" "
4.	" "	Not singing.
5.	Little singing activity.	Intermittent singing developing into continuous singing.
6.	Continuous singing.	Not singing.
7.	" "	Intermittent singing.
8.	" "	" "
9.	" " (s)	" " (s)
10.	" "	Not singing.

As the table shows, in nine out of the ten trials, the "cage owner" sang continously upon the introduction of the second insect. The word 'continuous' however, should be qualified. A few "cage owners" sang in sequences as described previously (p.37). Singing activity of this type was continuous as compared to that of the "intruder" which usually consisted of brief, intermittent interruptions during the ongoing song sequence. "Cage owners" therefore usually initiated song sequences, as do dominant Ephippiger individuals (Busnel 1967), and continued to sing at the solo rate. Thus the singing behaviour of the "cage owner" seems to correspond to that of insect 'a' of the previous analyses. It was interesting to observe that the individual which showed dominance both as a "cage owner" and "intruder" (trials 5 and 10) was a particularly large and vociferous specimen. Other factors apart from acoustic ones may have a rôle in deciding dominance, e.g. size.

The singing behaviour observed in the field seems similar to that studied in the laboratory. As mentioned previously, this species was studied in the Causses, where it is found in areas with a good grass cover, usually patches of Brachypodium pinnatum and Bromus erectus. Fig. 27 is a diagram of a belt transect starting in the open, xerophytic herb community and running through a patch of B. pinnatum. Percentage cover values and mean height of principal plant species 'a' to 'k' are shown. The adverse effects of direct insolation, as well as predation pressure, are probably the chief factors in restricting the distribution of these bush crickets to the areas of maximum cover (see also Uvarov 1928, 1932, 1933). P. albopunctata can be found in the more open community, but only where loose rocks or crevices in the limestone afford cover.

Dispersal was investigated by marking individuals as described in the Methods (p. 17). Samples of both juveniles and adults were marked, and recaptures attempted 48 hours later within a radius of ten metres from the original point of capture. Individuals were only marked if they were caught on the first attempt. Thus, disturbance in the community was kept to a minimum. Of the adults, only singing males were marked.

From a sample of nineteen marked juveniles (last two instars) nine were recaptured. Of these, one had moved 2.1 metres from the point of capture; two had moved 1.5 m, while the remainder had moved less than a metre. Moulting or predation may have eliminated the other marked individuals, or they may simply have remained well hidden within or without the search

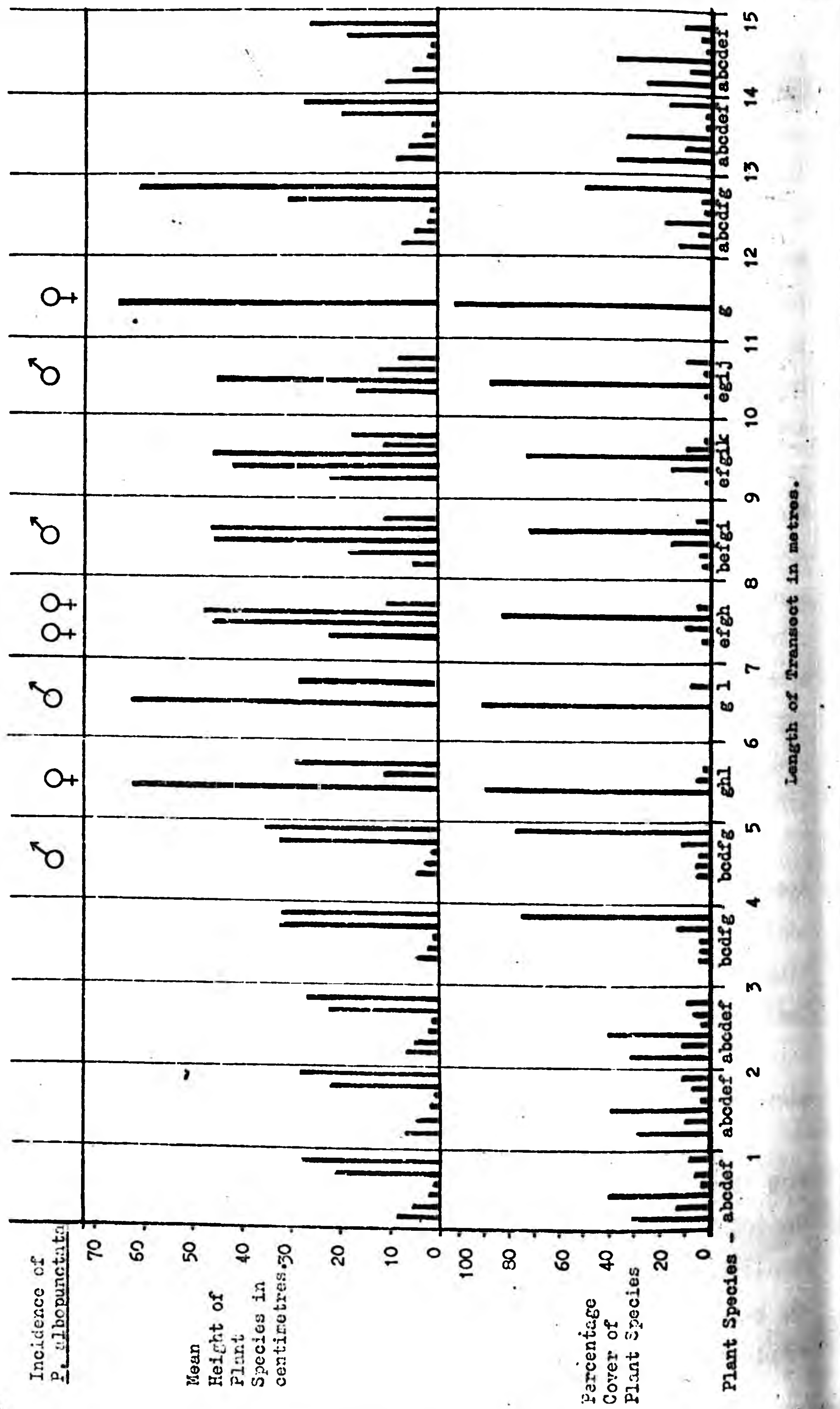


Fig. 27. P. ALBOPUNCTATA: HABITAT PREFERENCE IN LIMESTONE GRASSLAND.

The diagram opposite shows data recorded from a belt transect, one metre wide and fifteen metres long, running through a clump of Brachypodium pinnatum in the Causse du Larzac.

The percentage cover value of 12 plant species was estimated visually in each metre square quadrat and the mean height of those species measured. The incidence of P. albopunctata in each quadrat was recorded.

The plant species in the diagram are as follows:-

a. - Thymus serpyllum.
b. - Anthyllis hermaniae.
c. - Ononis striata.
d. - Bryophyte spp.
e. - Echinops ritro.
f. - Bromus erectus.
g. - Brachypodium pinnatum.
h. - Trifolium campestre.
i. - Genista hispanica.
j. - Astralagus sp.
k. - Galium sterni.
l. - Cirsium sp.

radius.

Only one adult male was recaptured from a sample of fourteen in a trial that took place approximately ten days after emergence of the adults. Other unmarked males were singing in place of the marked males at the original capture sites. Two weeks after this trial, ten singing males were marked and three recaptured. All recaptured males were found within one metre from the point of capture.

Distribution patterns of juvenile and adult males were determined using the nearest-neighbour technique (Clark and Evans 1956). A parameter R is calculated from the mean nearest-neighbour distance ($\bar{r}_a$) and the population density (d).

$$R = 2\bar{r}_a\sqrt{d}$$

The value of R can range from 0 when insects are maximally aggregated, through 1 when the distribution is random, to 2.149 indicating absolute regularity of dispersion. Areas of homogeneous vegetation were chosen for these tests so as to avoid discontinuities in the distribution of the insects resulting from the vegetational pattern. The results are summarized below.

Table 13. *P. albopunctata*: nearest-neighbour (n.n.) data.

	Mean n.n. ($\bar{r}_a$)	Insects/m^2 (d)	R	p (see below)	Habitat type.
Juveniles Site 1.	1.01	0.27	1.03	>0.1	*Brachypodium*/ *Bromus* community.
Site 2.	0.85	0.49	1.18	>0.1	*Brachypodium*.
Adults Site 1.	3.89	0.07	2.06	<0.001	Open *Bromus* community.
Site 2.	1.29	0.47	1.77	<0.001	Dense *Brachypodium*.
Site 3.	1.78	0.21	1.72	<0.001	*Brachypodium*/ *Bromus* community.
Site 4.	1.64	0.21	1.51	<0.001	*Brachypodium*/ *Bromus* community.

The probability, p assesses the significance of the departure of $\bar{r}_a$ (the actual mean nearest neighbour distance) from $\bar{r}_e$ (the mean nearest neighbour distance expected if the distribution were completely random: $\bar{r}_e = \frac{1}{2\sqrt{d}}$). It can be seen therefore, that there is no significant difference between a theoretical random distribution and that observed for the juvenile populations. The adult populations however, show distribution patterns that are significantly different from random. As the ratio R has a value larger than 1.0, it can be deduced that these distributions are regular. The results also suggest that adult males are spaced farther apart where the vegetation is less dense (as in site 1).

A further technique for assessing the departure from randomness was employed (Svedberg 1922). Fifty 1-metre quadrats were placed at random in an area of homogeneous grassland and the incidence of P. albopunctata in the quadrat was recorded. By applying the Poisson distribution to the data an 'expected' random distribution can be calculated. The deviation of the observed distribution from the theoretical random distribution can then be assessed (see table 14).

Table 14. The observed and expected number of quadrats containing 0, 1,2 and 3 P. albopunctata individuals.

	Male				Female			
Number of insects per quadrat.	0	1	2	3	0	1	2	3
Observed number of quadrats.	29	20	1	0	30	16	2	2
Expected number of quadrats.	32.22	14.18	3.12	0.45	29.72	15.45	4.02	0.69
Ratio of variance to mean (for observed distribution).	0.66				1.12			

The variance/mean ratios of these distributions indicates the type of distribution pattern of the population (Svedberg 1922). A value of 1 indicates a random distribution, less than 1 suggests regularity while values over 1 indicate aggregation of individuals. The value of 0.66 suggests that males are regularly distributed. The significance of this departure from randomness can be tested by comparing the 'observed' and 'expected' distributions using the chi-square statistic. The result ($p < 0.05$) suggests males to be significantly non-random in their distribution. The apparent departure from randomness in the females is not statistically significant ($p > 0.1$).

In certain sites, e.g. very dense clumps of grass, males can be found very close together. In these situations singing behaviour resembles that heard in the laboratory. Generally one male sings continuously while one or more peripheral males sing intermittently. The acoustic behaviour of these peripheral males seems to correspond to the behaviour of insect 'b' of the previous analyses. These same sites were revisited about sixteen days later (approximately one month after the emergence of the adult population). The number of males present in the grass clumps was much reduced; often only one male remained and no intraspecific interactions were heard.

2. The Duetting Behaviour of P. sabulosa

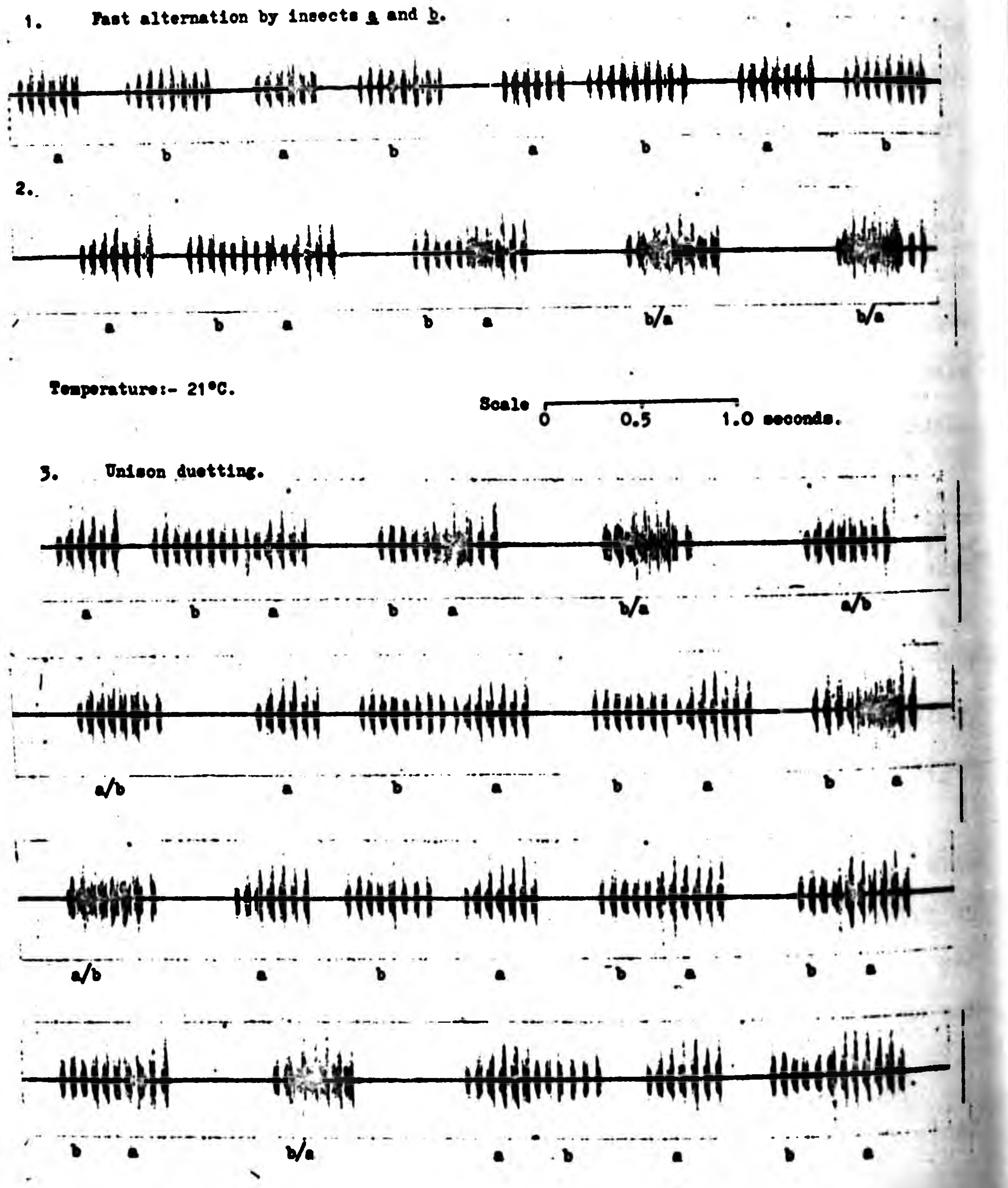
The intraspecific duetting behaviour of this species seems very similar to that of P. albopunctata and has therefore been analysed in the same way. P. sabulosa may tend to alternate echemes more frequently than P. albopunctata though the data on duetting in sabulosa are probably insufficient to enable rigorous comparisons to be made.

Four duets from different pairs have been recorded. In the first, lasting 12 minutes, the individuals alternate echemes throughout most of the recording, (see fig.28, trace 1). The recording begins with one individual (b) singing continuously without pausing (not shown). After 90 seconds insect 'a' commences singing with the result that both insects now alternate echemes. It is interesting that the singing of insect 'b' now becomes cyclical (not illustrated); each cycle of exactly alternated echemes is around 25 seconds in duration ($\bar{x}$ = 25.20, S.D. = 7.40, N = 8). At the end of each cycle 'b' pauses ($\bar{x}$ = 13.10 s, S.D. = 7.40 s, N = 7) before resuming alternation. No such cycles are seen in the song of 'a' which continues singing during the pauses of 'b'.

The mechanism maintaining alternation appears to be the same as in P. albopunctata. Table 15 shows the duration (in ms) of the normal solo chirp interval (a - a), the interval between the chirps of the two insects when alternating (a - b) and the extended chirp interval of 'a' when alternating with 'b' (a - $_b$ - a).

Table 15.	Solo interval. (a - a)	Alternation. (a - b)	Alternation interval. (a - $_b$ - a)
$\bar{x}$	851.5	535.6	1,673.0
S.D.	81.2	188.5	155.0
Range	712 - 960	125 - 815	1,340 - 1,900

Fig. 28 DUETTING BEHAVIOUR OF P. SABULOSA.



1\. Fast alternation by insects a and b.

3\. Unison duetting.

Temperature:- 21°C.

Scale 0 0.5 1.0 seconds.

The table shows that during alternation, insect 'b' chirps well before 'a' would normally have done so; as a result 'a's echeme is delayed until well after the chirp of 'b' has ended. Thus, the chirp interval of 'a' is approximately doubled in duration. As in P. albopunctata, this species seems to alternate echemes by the process of mutual acoustic inhibition.

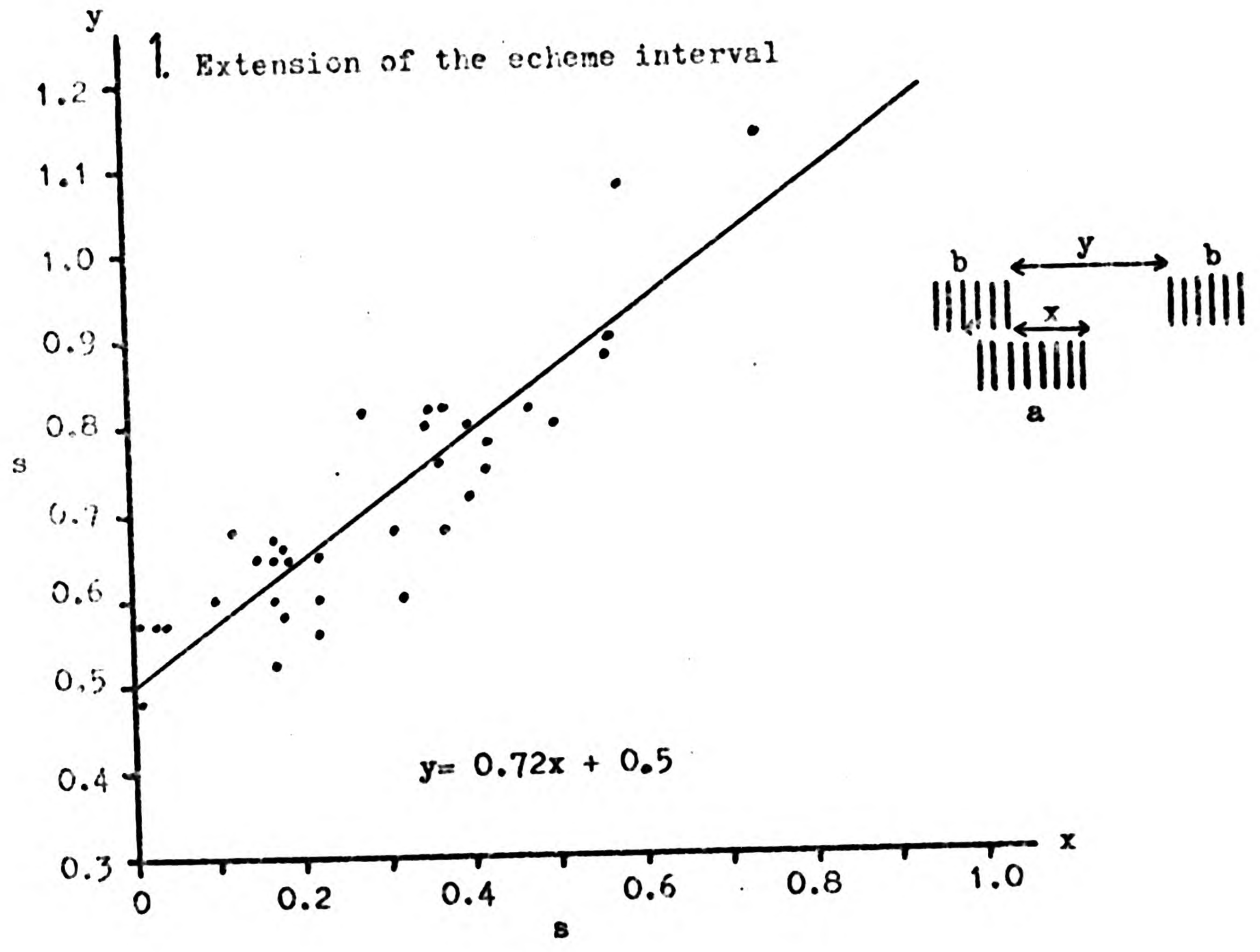
In two of the remaining three recordings, alternation between insects occurs but is never maintained as in the first recording. Generally in these recordings one insect sings continuously with only sporadic interruptions from the other individual. During these brief duets the insects may alternate or sing in unison. (Durations of the two recordings are 8 minutes and 4.5 minutes respectively).

In the last recording, the insects engage in unison duetting (see trace 3, fig.28). (Again, the individual that sings the most is referred to as insect 'a'). Brief sequences of alternation occur infrequently; usually this type of duetting changes rapidly to unison duetting as shown in traces 1 and 2, fig 28. In the initial stages of the duet the process of acoustic inhibition operates on one of the singers at least. Graph 1 in fig.29 illustrates the situation where the echeme of 'a' interrupts that of 'b'. The next echeme of 'b' is delayed; the length of the delay is proportional to the extent to which the echeme of 'a' overlaps into the echeme interval of 'b'. This is an identical situation to that described for P. albopunctata where the echeme of one insect exerts an inhibitory effect on the other. The inhibition period lasts throughout the duration of the echeme and for a brief period after its termination.

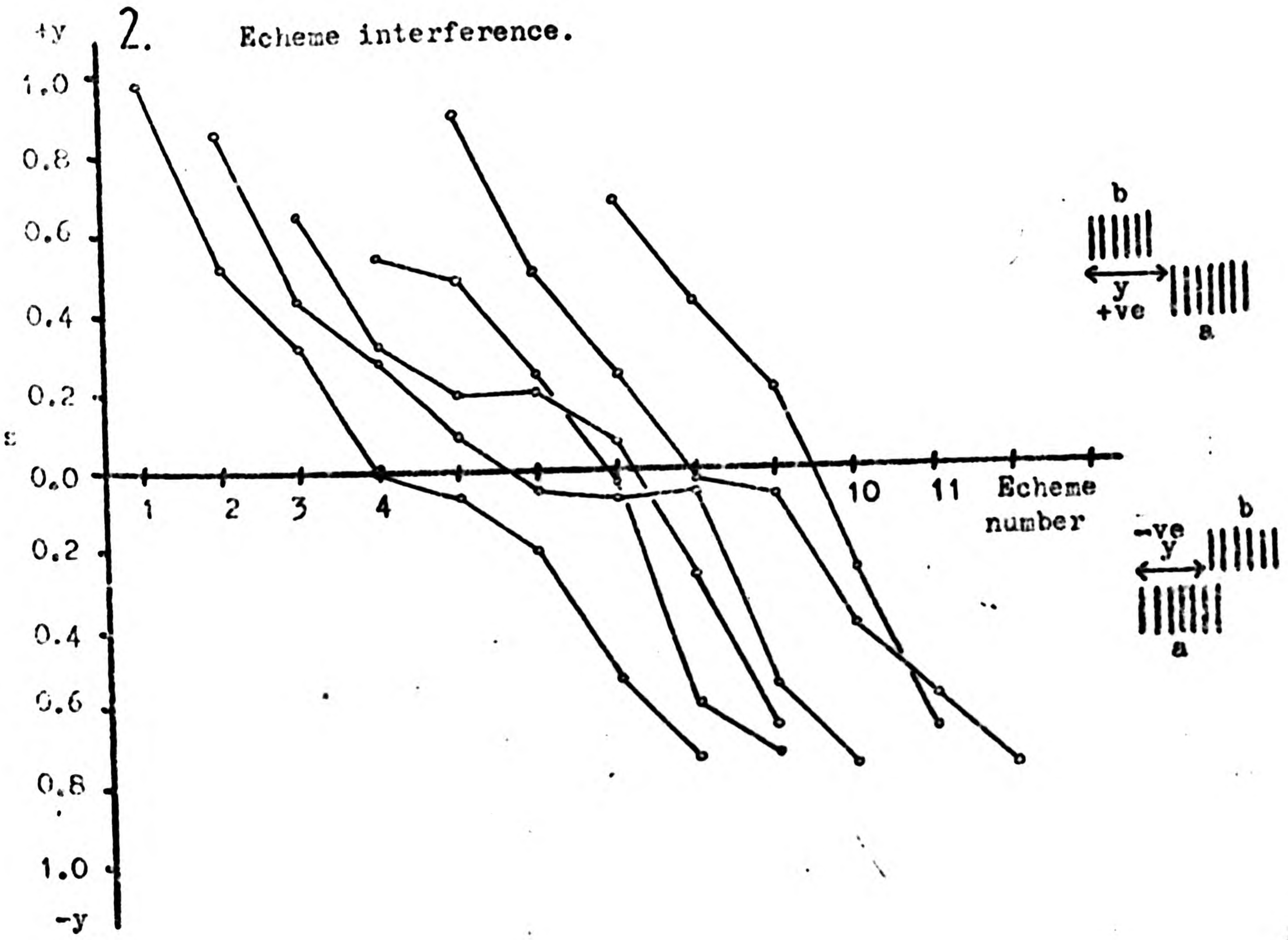
However, again as in albopunctata, this inhibition period is reduced as the duet progresses, until both insects begin to interrupt each other's echemes. Graph 2, in fig. 29,

Fig.29. DUETTING BEHAVIOUR OF P. SABULOSA

1. Extension of the echeme interval



2. Echeme interference.



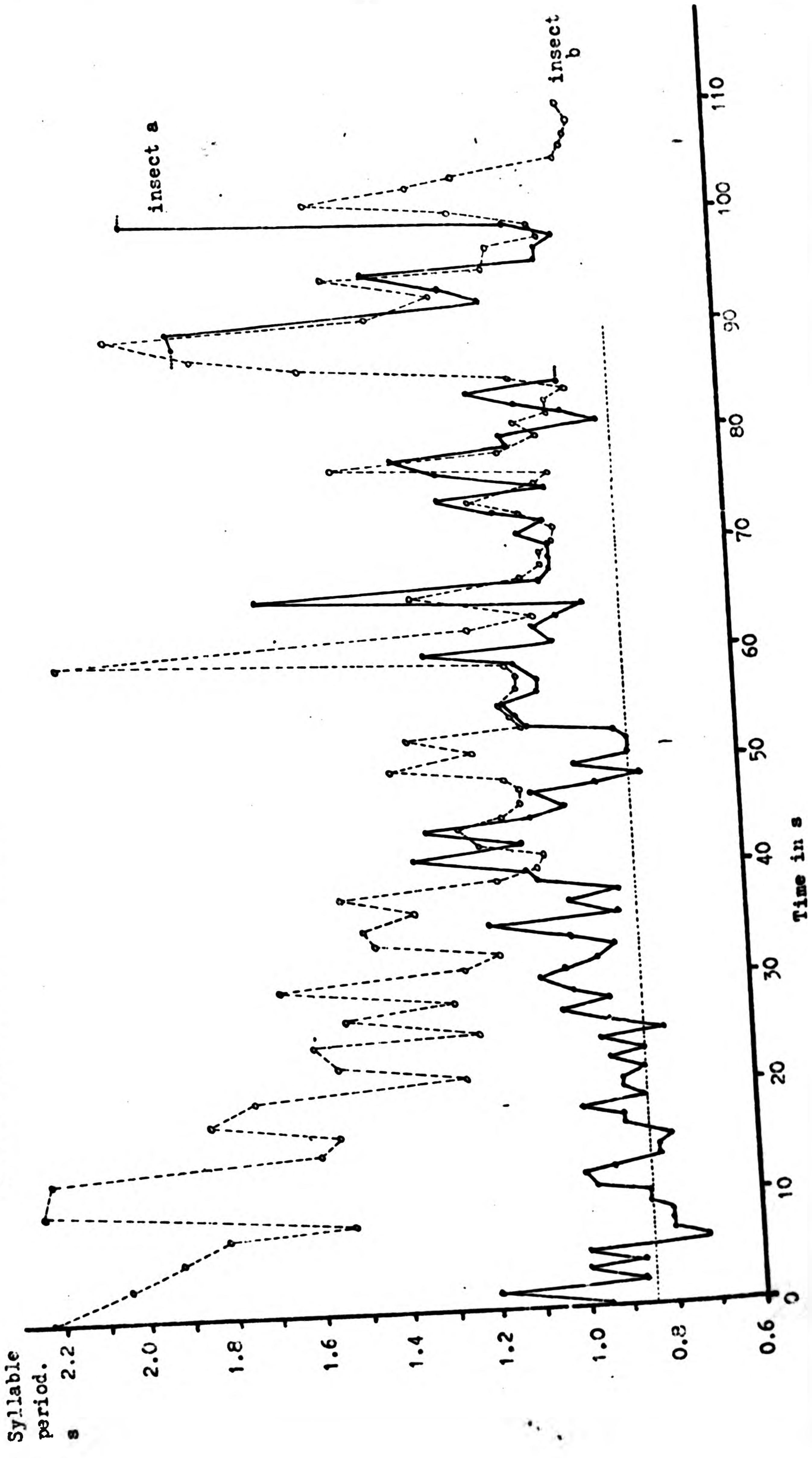


Fig.30. DUETTING BEHAVIOUR OF *P. SABULOSA*.

Syllable periods of two duetting individuals.

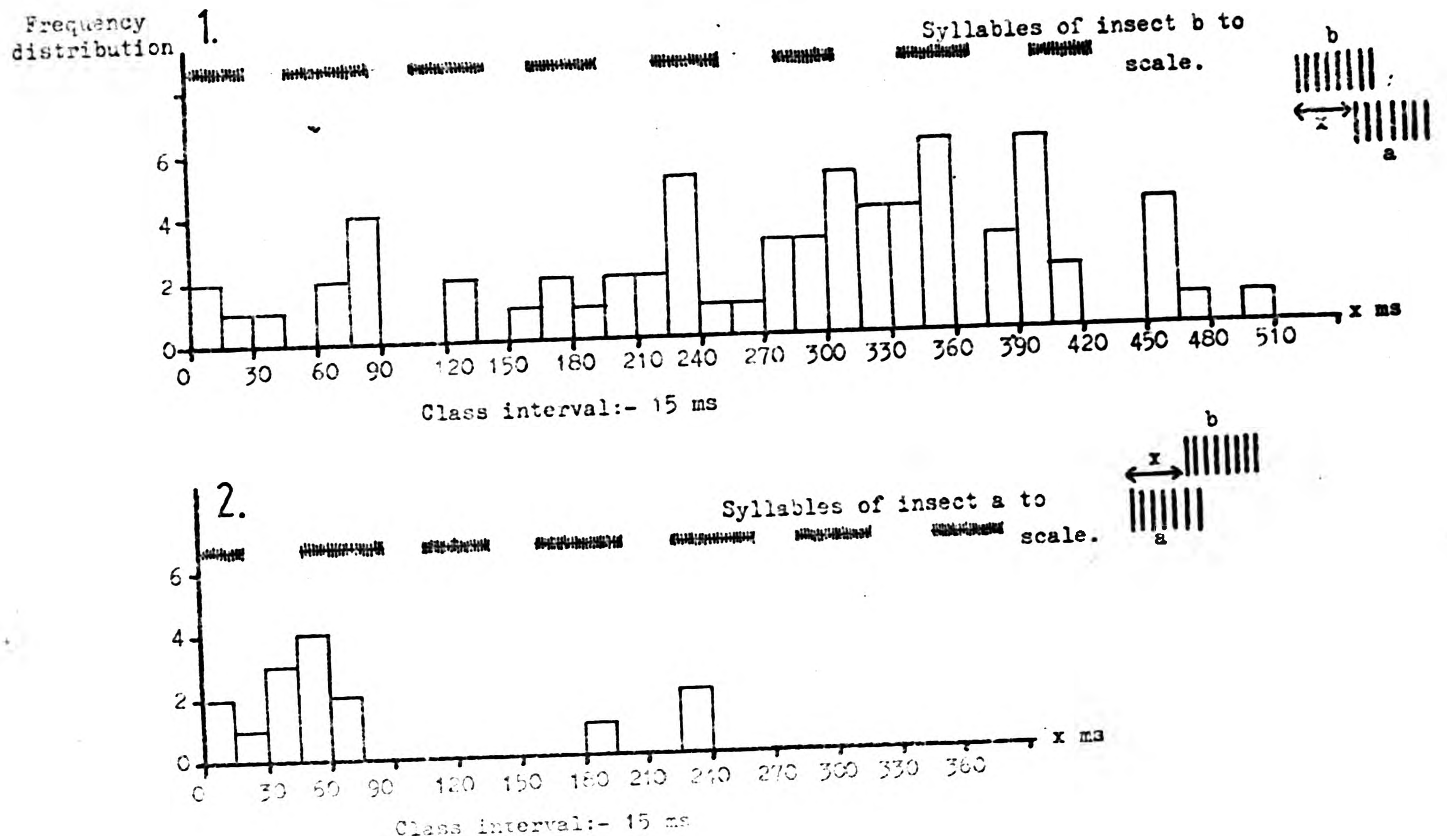
similar to graph 2, fig. 23 (p.75), shows plots of successive period differentials between the echemes of the two insects. The values of successive period differentials are reduced until echemes begin to interfere; at a value of zero echemes are synchronized exactly. Period differentials become negative as 'a', originally chirping after 'b', now chirps before. The graph shows six sequences where such phase shifts occur.

This process of phase shifting starts after 40 seconds of the interaction shown in graphical form in fig.30. During the first 40 s the echeme rate of 'b' gradually increases (i.e. the period decreases) while insect 'a' sings at around the solo rate (the average period for 'a' is shown by the faint dotted line). From 30 to 40 s, many echeme periods of 'a' are extended as 'b' interrupts its song more frequently, i.e. the increase in the echeme rate of 'b' reduces the echeme rate of 'a' until, at times, the echeme rate of 'b' equals or exceeds that of 'a'. At approximately 90 s there is a long pause by 'a'; at 100 s 'a' ceases to sing leaving 'b' singing at the solo rate. About ten seconds later (not shown in the graph) 'a' resumes singing and the interaction is repeated with 'a' on average singing more than 'b'

Figs.31 and 32 correspond to figs.25 and 26 for *P. albopunctata*; they show at what point in the echeme period of one insect, the other insect is likely to commence its echeme. Fig.31 shows that insect 'a' can interrupt at any point during the echeme of 'b' (graph 1) while 'b' interrupts 'a' much less frequently and usually only during the first 75 ms of 'a's echeme. Insect 'a' also interrupts at any point during the chirp interval of 'b' though over half the interruptions recorded take place within the first 60 ms after the end of 'b's chirp, (see graph 1, fig.32). Individual 'b', however, usually

Fig. 31. DUETTING BEHAVIOUR OF P. SABULOSA.

Echeme interference between insects a and b.



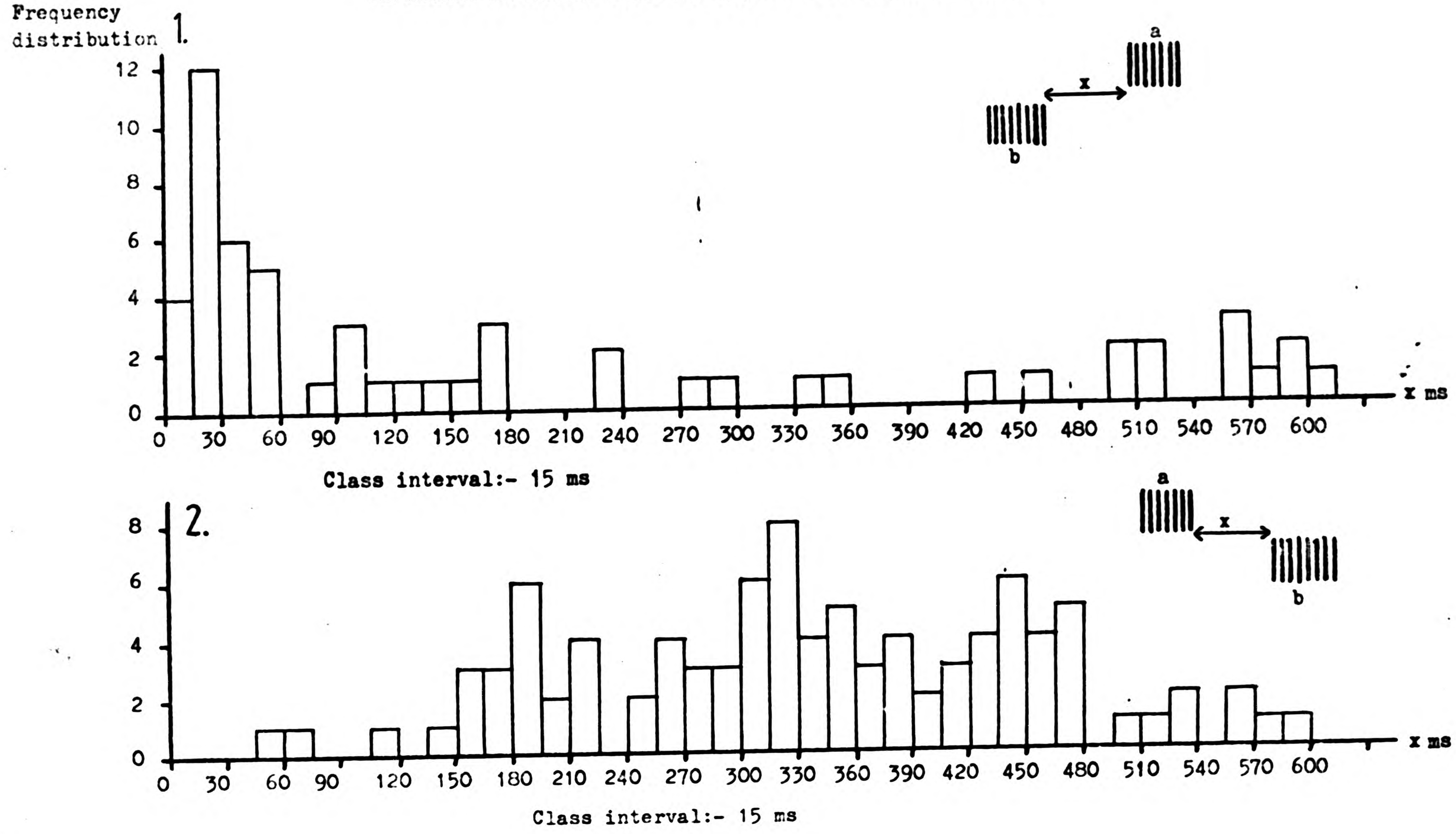
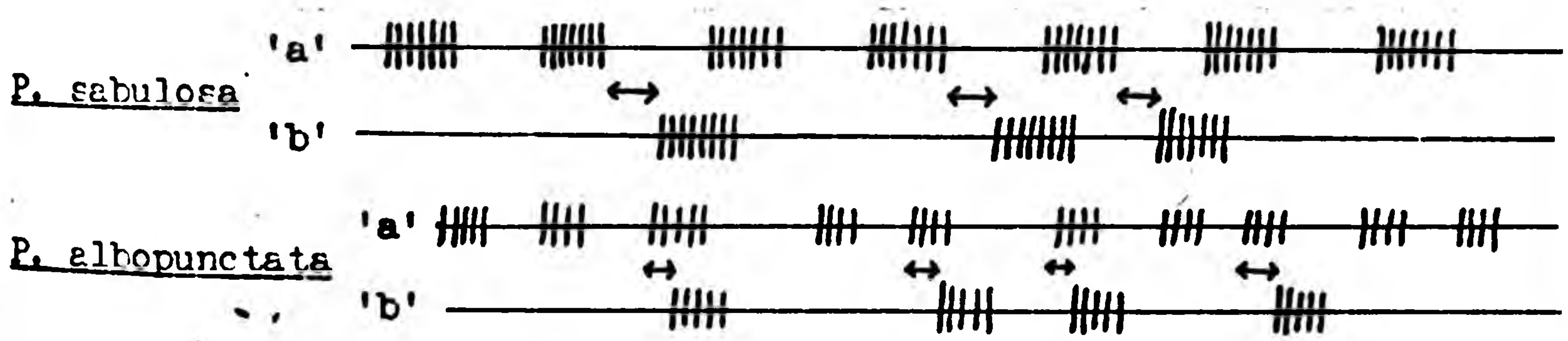


Fig.32. DUETTING BEHAVIOUR OF P. SABULOSA

Variation in echeme interval (x) between insects a and b.

commences chirping at least 150 ms after the end of the chirp of 'a', (see graph 2). It can be seen from figs. 31 and 32 that the majority of interruptions by 'a' occur during the echeme of 'b'. Individual 'b', however, usually chirps during the chirp interval of 'a'. Thus as in albopunctata, each individual reacts to the song of the other in a different way.

If analogous figures for these two species are compared, it is seen that in P. sabulosa the behaviour of individual 'b' corresponds to the behaviour of 'a' in the P. albopunctata duets. For example, in fig.25 (P. albopunctata) individual 'b' interrupts throughout the echeme of 'a', while 'a' only interrupts at the beginning of 'b's echeme. In P. sabulosa the converse is true, (see fig.31). At the beginning of the P. sabulosa duet (as plotted in fig.30) insect 'b' usually chirps after the chirp of 'a' has ended. Insect 'a', singing at the solo rate then interrupts the echeme of 'b'. In albopunctata, 'b' also chirps after 'a' but usually interrupts in doing so. The following diagram illustrates this difference.



It is not clear at this stage whether or not this is a species-specific difference. It may be a result of individual variation for in duets 2 and 3 (p. 92) the only interruptions are by insect 'b'; but these are too few to enable statistical comparisons to be made. This topic is considered briefly in the Discussion(p.170).

Unison duetting has been heard from male P. sabulosa individuals in close proximity in the field. However, most males in the Salicornia salt marsh vegetation appear to be spaced out in an even distribution. A single plot was made, measuring nearest neighbours of thirty singing males in an area of 111.6 square metres. The mean nearest-neighbour distance was 1.8 metres and the Clark-Evans parameter R = 1.40. It is extremely improbable that this figure represents a random distribution ($p < 0.001$); as its value is greater than 1.0, a regular distribution is indicated. Thus this species seems very similar to P. albopunctata with respect to its song and acoustic behaviour.

3. Duetting Behaviour of M. roeselii

The acoustic behaviour of this species has not been analysed in as much detail as in the previous two species. Observations and preliminary analyses suggest that, unlike the Platycleis species, individuals can interrupt songs of other individuals with apparently no resulting change in any of the song parameters, (e.g. syllable rate, echeme duration). Therefore, as syllable rates in two individuals are usually unequal (due to individual variation or slight temperature differences) syllable synchrony is not maintained. Syllables of two duetting individuals move in and out of phase. When more than two singers are present discrete syllables are difficult to distinguish on an oscillographic trace of the chorus.

Again, no detailed study has here been made of the field behaviour of roeselii. The distribution of singing males in a colony seems regular, but this has not been tested. Morris (1968) and McHugh (1971) have observed aggressive behaviour in roeselii males and have suggested that this might result in regular spacing between males. However, gaps are often present in the overall distribution (this was also noted by McHugh 1971). For example, M. roeselii is often found along roadside verges where the vegetation shows little change along the length of the verge, yet certain stretches are devoid of males (see fig. 44, p. 134). Population densities are therefore quite variable; maxima of 1.75 and 2.08 males *per* square metre have been recorded for a roadside strip of vegetation, one metre in width, adjacent to a low wall. Mean nearest-neighbour distances for these sites were 0.57m and 0.48m respectively. This species is also found in the *Brachypodium pinnatum* associations on the Causses. Mean densities of 0.71 and 0.90 males/m^2 have been recorded for two such sites in the Causse du Larzac. The density of males of this species is therefore generally greater than the density of *P. albopunctata* males.

INTERSPECIFIC INTERACTIONS

This section examines in detail both behavioural and ecological aspects of the acoustic interaction between *P. albopunctata* and *M. roeselii*. Interactions between other bush cricket species are examined briefly to assist in formulating hypotheses on the causation of song modification in the *Platycleis* and *Metrioptera* genera.

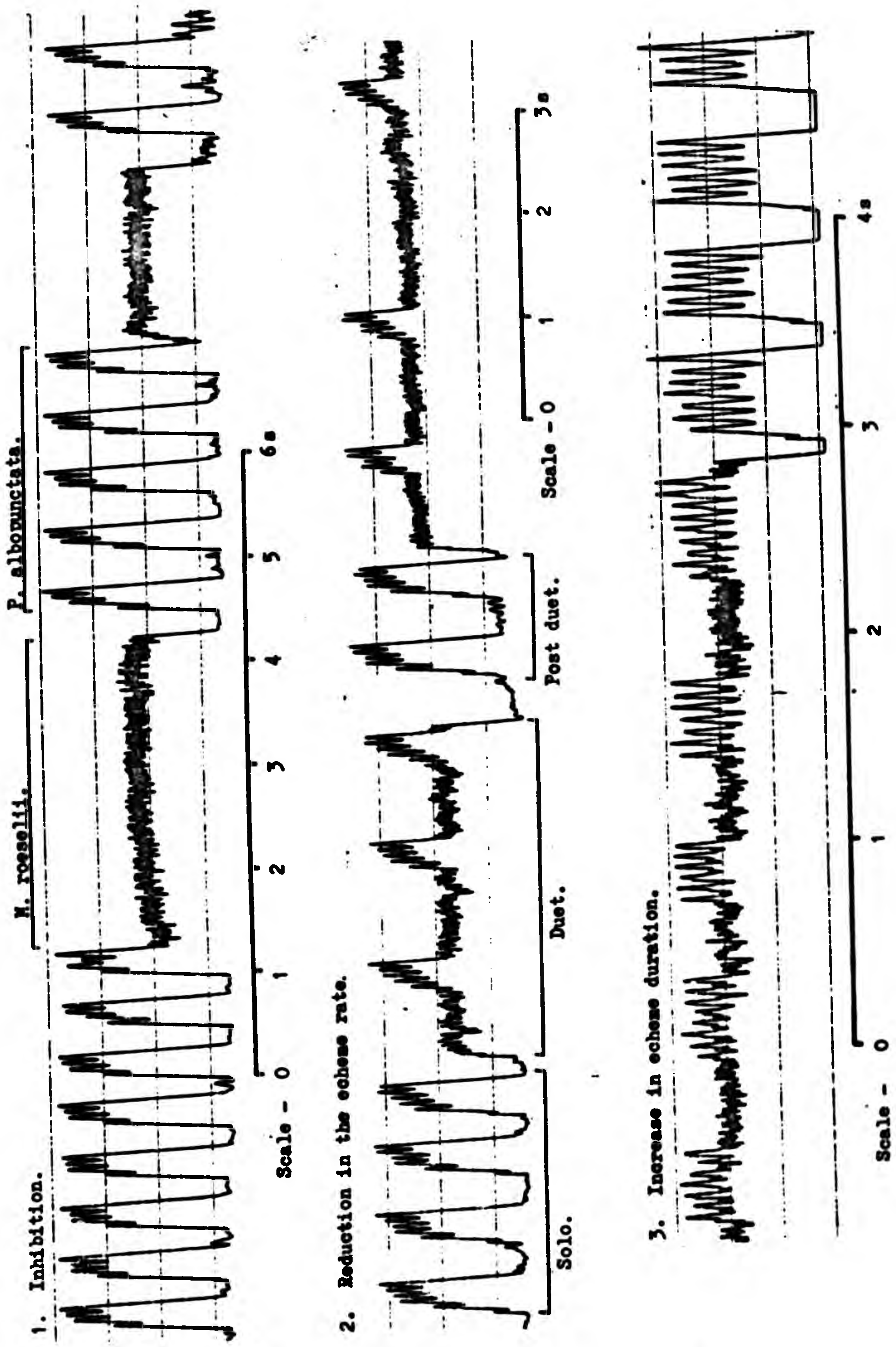
1. The *P. albopunctata*/*M. roeselii* Interaction.

(i) Changes in echeme duration, rate and rate of singing.

Many interactions between these two species fall naturally into three phases. These are (1), the Duet where both species are singing at the same time; (2), the Post-duet, the phase immediately after *M. roeselii* (i.e. the influencing insect) ceases singing whereas *P. albopunctata* (the influenced insect) continues to sing. In both these phases, modified singing by the *albopunctata* can be observed. For the purposes of analysis the first three seconds after the duet is defined as the post-duet. (3) After three or four seconds of post-duet singing the song enters the third phase which is usually found to be indistinguishable from normal solo singing.

Broughton has analysed a recording of an interaction between these two species (Broughton 1965, Lewis and Broughton, in press) and shown an increased chirp duration and lower percentage time spent singing by the *albopunctata* during the duet. The post-duet was also characterized by longer-than-normal chirps and frequently a rebound effect occurred in the time spent singing (i.e. a sudden swing to a value above that of normal solo singing). The following analyses support these observations

Fig. 33. RESPONSES OF *P. ALBOPUNCTATA* TO THE SONG OF *M. ROESELII*.



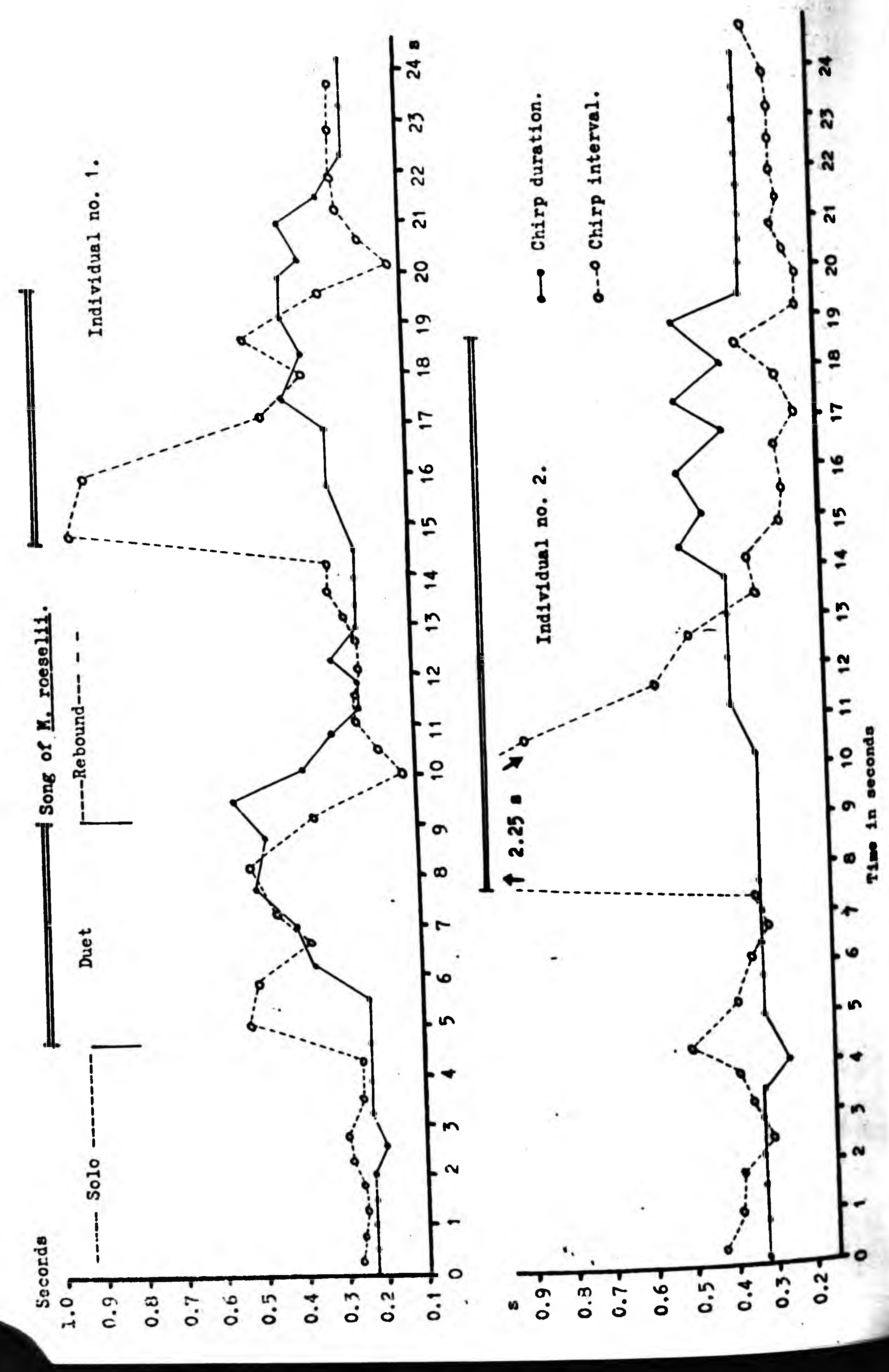
and indicate some further abnormal effects on the song of *P. albopunctata* through hearing the song of *M. roeselii*. The singing behaviour of the *roeselii* seems in no way to be affected by the acoustical output of the *albopunctata*.

The reaction by *P. albopunctata* to the song of the *Metrioptera* varies from individual to individual and also varies in accordance with the apparent internal motivation to sing. These reactions can be broadly divided into three types. These are:- (a) Inhibition, i.e. complete cessation of singing by the *albopunctata* whenever the *roeselii* sings; the individual never duets with the *roeselii*. No significant rebound effect is observed during the post-inhibition phase; the *albopunctata* merely resumes singing at a rate similar to, or lower than that of normal solo singing (see fig. 33, trace 1). This type of reaction is quite common, occurring in approximately 30% of the interactions studied. Young males seem particularly susceptible to inhibition. Pre-singing males caged with singing *roeselii* males made no attempt to engage in singing activity until three weeks after regular singing was heard from the control group. A few individuals continued to be inhibited by the song of the *roeselii* throughout the experimental period (approximately six weeks from the final moult).

(b) Duetting, resulting in quantitative changes in the song parameters e.g. echeme duration and rate (fig 33 traces 2 and 3). Individuals that duet with the *roeselii* may also at times be inhibited. Such inhibitions are usually brief and are often followed by a rebound in singing activity during the post-duet phase.

(c) Duets and inhibitions resulting in qualitative changes to the

Fig. 34. EFFECT OF M. ROESELII ON CHIRP DURATION AND INTERVAL.



song, namely the production of amphimorphic echemes. Though this is obviously the result of a quantitative change in syllable duration, the result is a distinct modification of the song timbre. Such responses seem fairly uncommon. Four insects out of twenty-two gave this reaction.

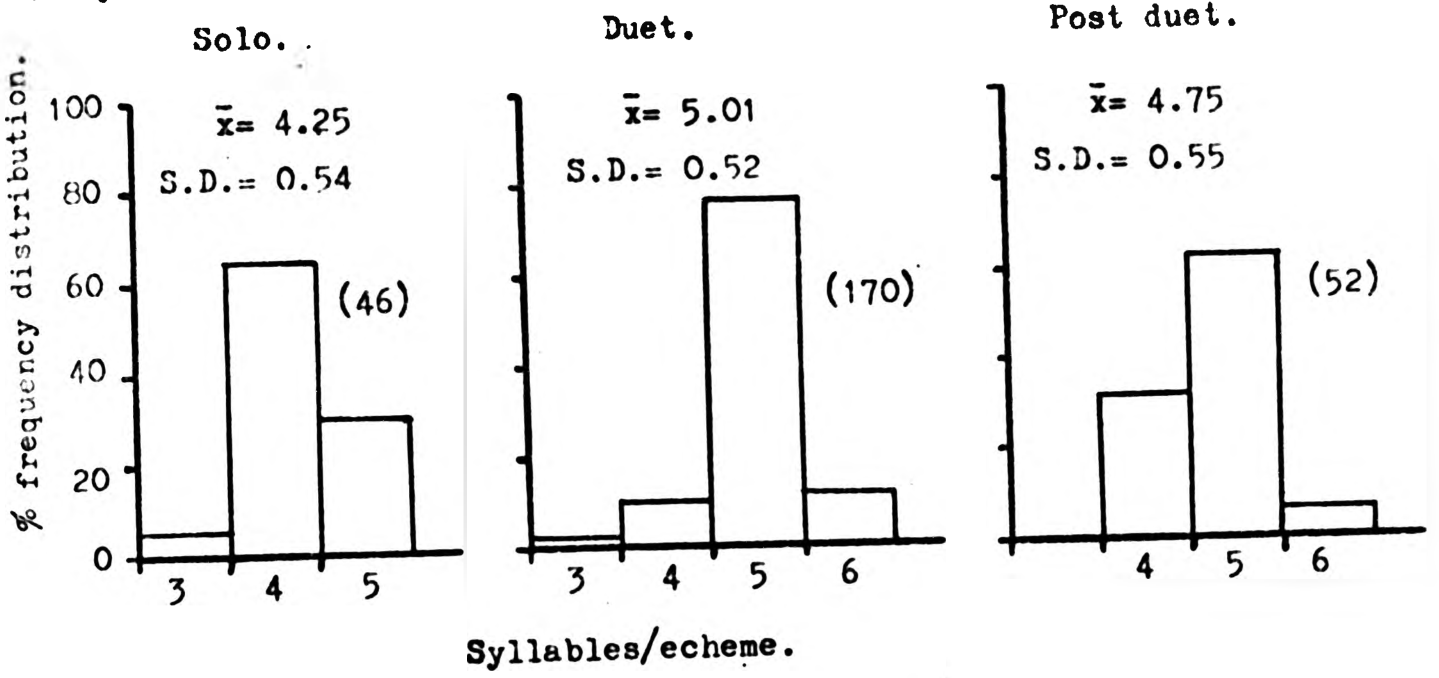
In those individuals which duet with *M. roeselii* there also exists a range of variation in the type of response. For example, some individuals show a large reduction in the echeme rate during the duet (see fig.33, trace 2). Echeme duration may or may not be increased. Other individuals show a consistent increase in the echeme duration (trace 3).

Many individuals show a marked reduction in the echeme rate at the beginning of the duet, as shown in fig. 34 (i.e. the echeme interval is greatly extended). As the duet progresses the echeme interval is often reduced and the echeme duration extended. The echeme interval can, at times, be less than in normal solo singing. At the post-duet the echeme interval is usually very much reduced. The echeme duration may still be extended but is gradually reduced in each successive echeme. At the same time the echeme interval increases until normal solo singing is regained. These responses are shown for two individuals in fig. 34 where *chirp* (see p. 25) intervals and durations have been measured.

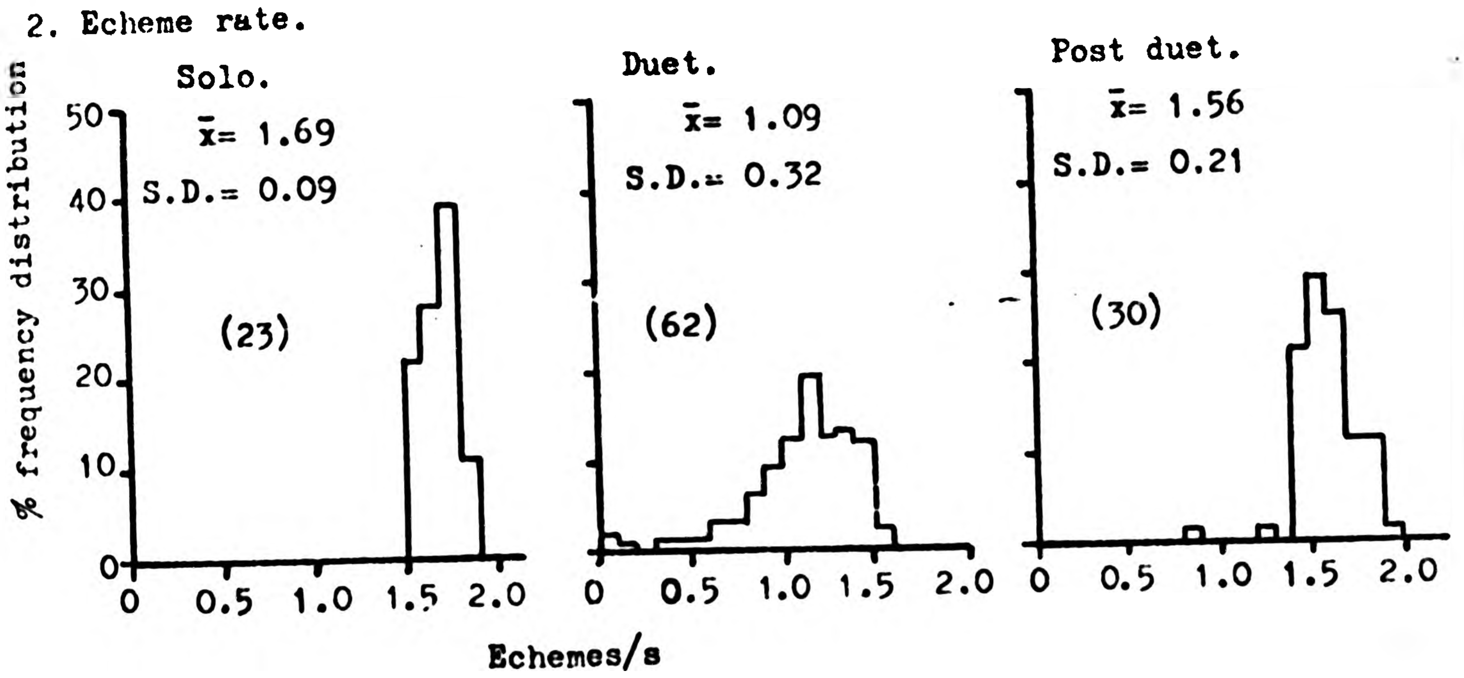
Fig. 35, 36 and 37 summarize data on interactions from three *albopunctata* individuals (*a*, *b* and *c*). Solo singing is compared with that during the duet and post-duet. Table 16 shows the results of statistical tests applied to the data in these figures. The echeme content has been analysed in terms of the number of syllables present. Echeme rate (i.e. the reciprocal of echeme period) is compared between the three phases of singing.

Fig. 35 EFFECT OF M. ROESELII ON THE SONG OF P. ALBOPUNCTATA.
(Individual a)

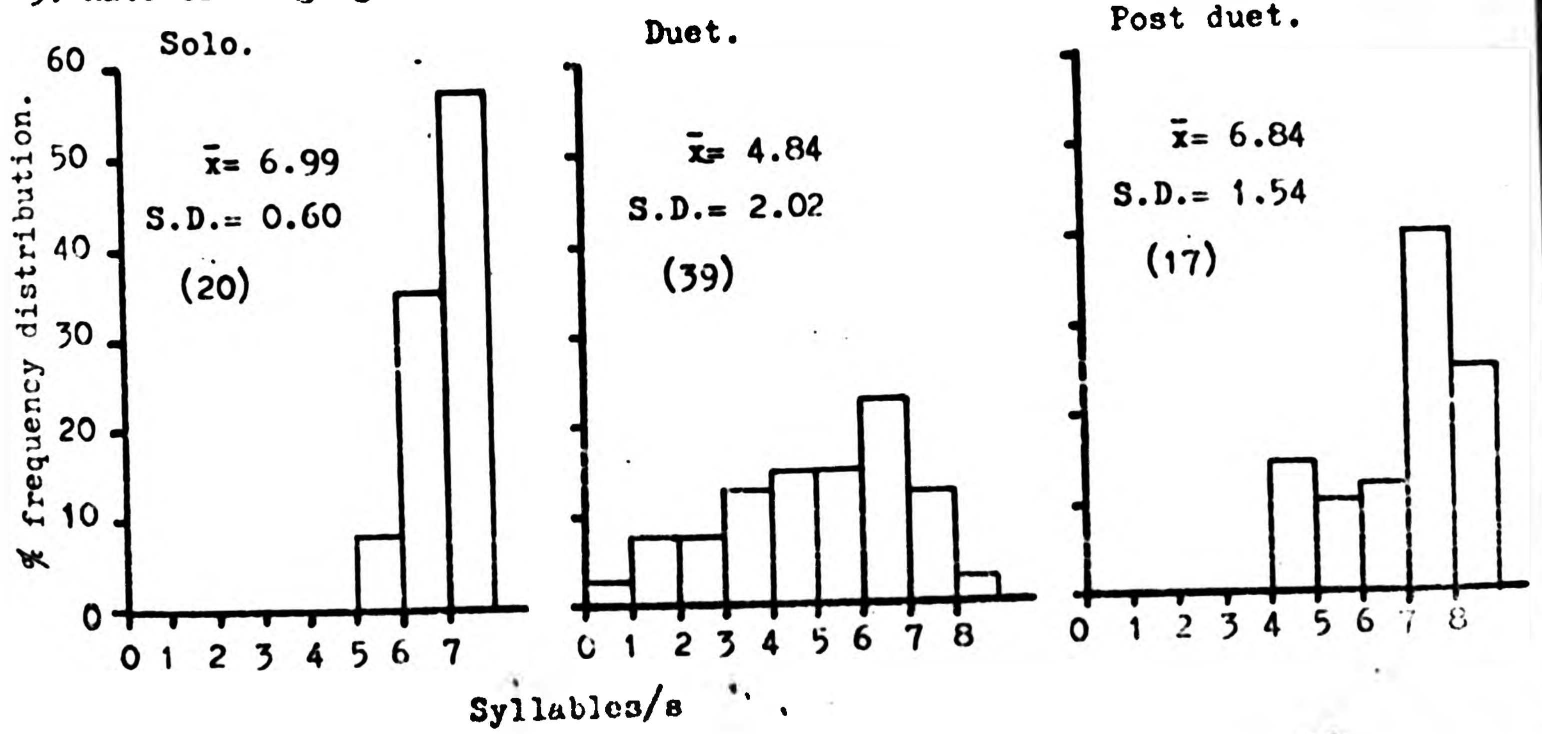
1. Syllables/echeme.



2. Echeme rate.



3. Rate of singing.



The number in brackets ( ) = No. of observations. See also Table 16

Fig.36. EFFECT OF M.ROESELII ON THE SONG OF P. ALBOPUNCTATA.

(Individual b)

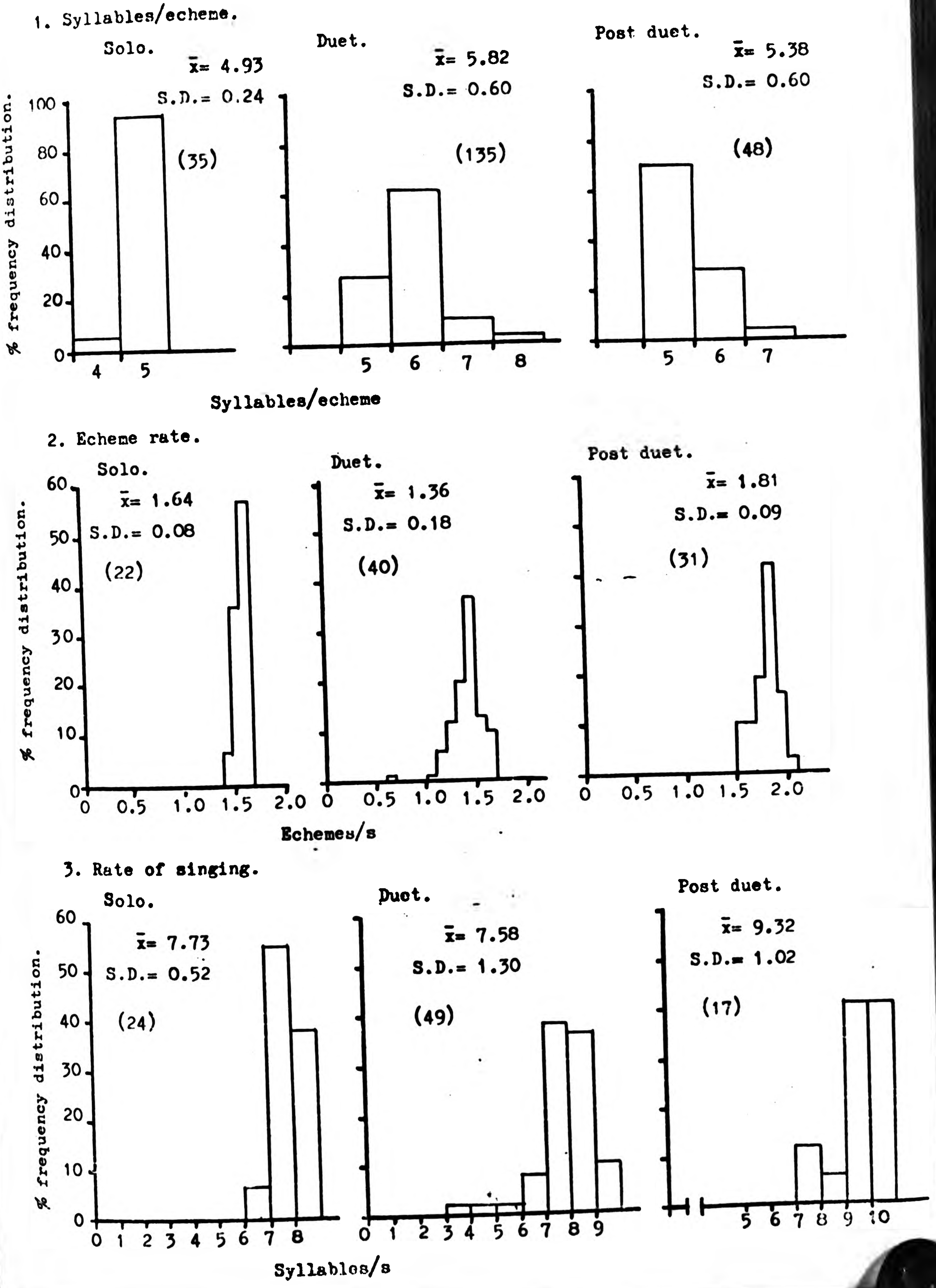


Fig. 36. EFFECT OF M.ROESELII ON THE SONG OF P. ALBOPUNCTATA.

(Individual b)

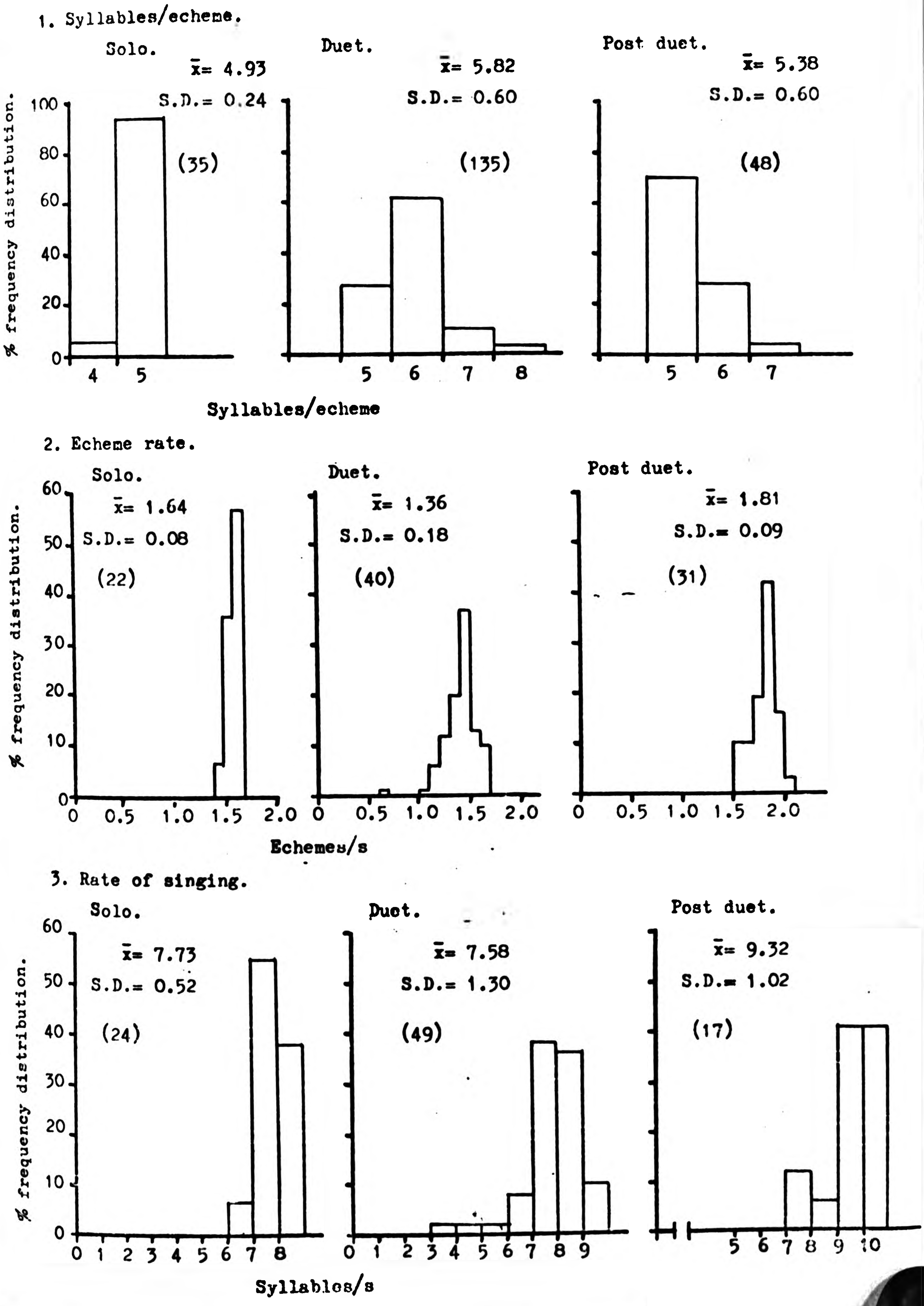


Fig. 37 EFFECT OF M. ROESELII ON THE SONG OF P. ALBOPUNCTATA.
(Individual c)

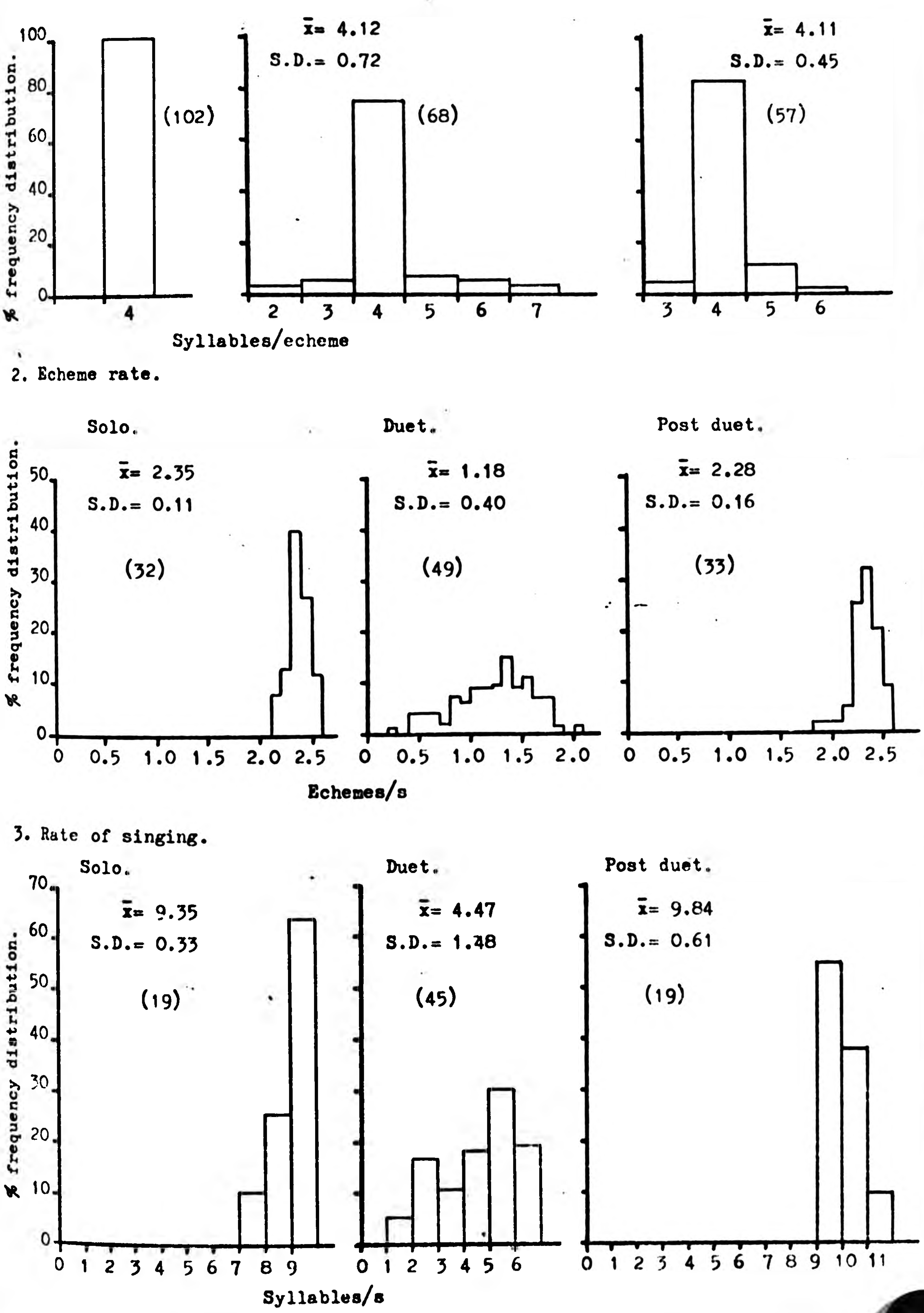


Table 16. Differences between variances and means for the data presented in figs. 35, 36 and 37.

		Comparing Solo and Duet	Comparing Solo and Post-duet.
Individual a. (Fig. 34) Syllables/echeme.	Var.	$p > 0.05$ (n.s.)	$p > 0.05$ (n.s.)
	$\bar{x}$	$p < 0.001$	$p < 0.001$
Echeme rate.	Var.	$p < 0.001$	$p < 0.001$
	$\bar{x}$	$p < 0.001$	$p < 0.01$
Syllable rate.	Var.	$p < 0.001$	$p < 0.001$
	$\bar{x}$	$p < 0.001$	$p > 0.1$ (n.s.)
Individual b. (35) Syllables/echeme.	Var.	$p < 0.001$	$p < 0.001$
	$\bar{x}$	$p \ll 0.001$	$p < 0.001$
Echeme rate.	Var.	$p < 0.001$	$p > 0.05$ (n.s.)
	$\bar{x}$	$p < 0.001$	$p < 0.001$
Syllable rate.	Var.	$p < 0.001$	$p < 0.001$
	$\bar{x}$	$p > 0.1$ (n.s.)	$p < 0.001$
Individual c. (36) Syllables/echeme.	Var.	-	-
	$\bar{x}$	$p > 0.1$ (n.s.)	$p > 0.1$ (n.s.)
Echeme rate.	Var.	$p < 0.001$	$p > 0.05$ (n.s.)
	$\bar{x}$	$p \ll 0.001$	$p > 0.1$ (n.s.)
Syllable rate.	Var.	$p < 0.001$	$p < 0.025$
	$\bar{x}$	$p < 0.001$	$p < 0.05$

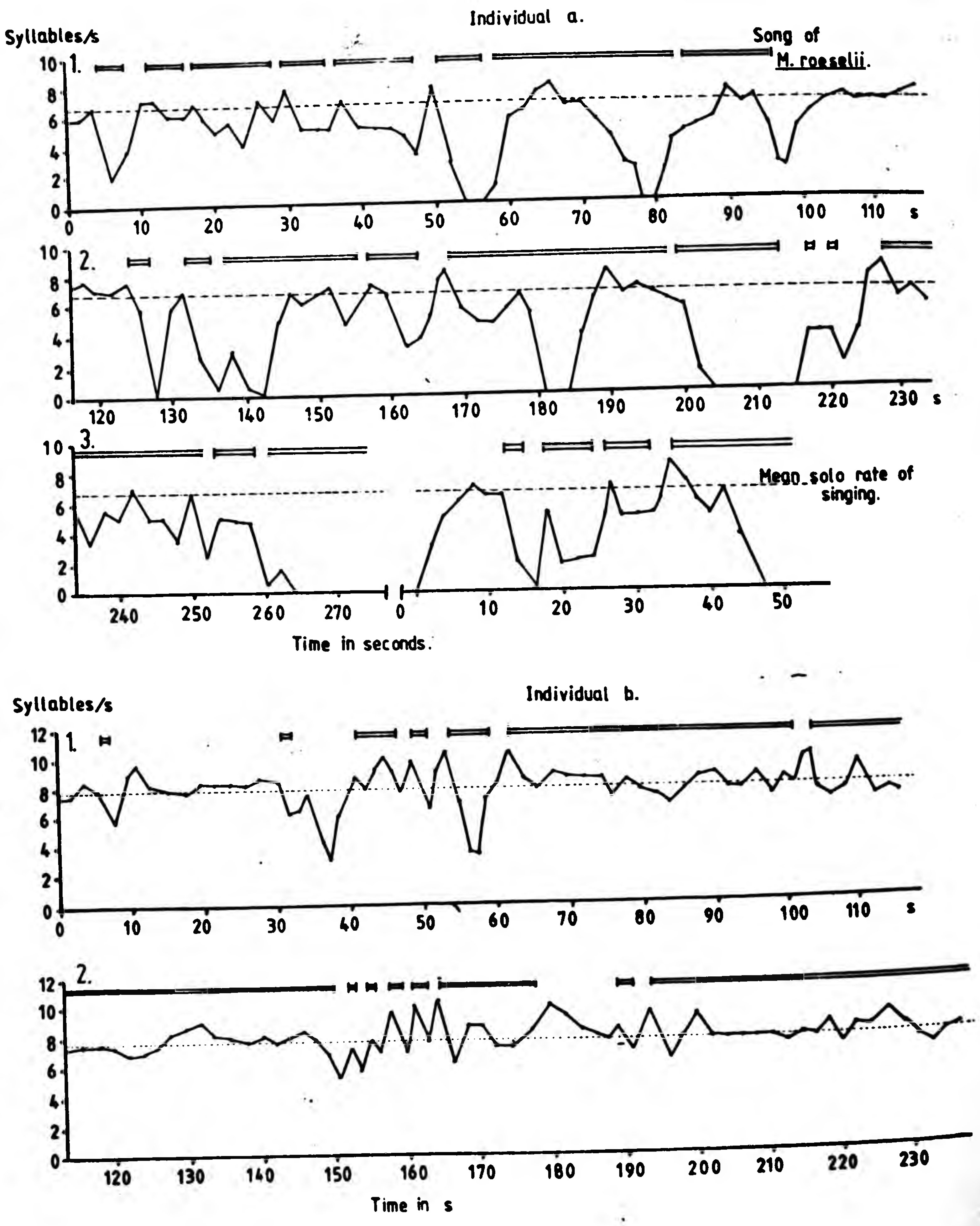
p = the probability level that data are from identical distributions. Comparisons that show no significant difference are marked thus - (n.s.). Other comparisons can be regarded as significantly different.

The product of syllables/echeme and echemes sung per second is the rate of singing in syllables sung per second.

Individual a (fig 35) reacts to the song of *M. roeselii* by generally increasing the echeme content by one syllable, sometimes two, during the duet and post-duet. The means of both these distributions differ significantly from the mean value for solo singing but there is no significant change in the variation about the means (see table 16). The echeme rate is significantly reduced, and is much more variable during the duet, as is the rate of singing. During the post-duet no rebound occurs in the echeme rate, though the rate of singing shows some high values not found in solo singing. This is due to echemes being extended in duration and content while their period remains the same (thus the echeme interval is often much reduced during the post-duet as can be seen in fig.33, trace 3). On average, both the rate parameters show slightly lower values for post-duet singing than for solo singing.

Individual b (fig 36) also tends to increase the echeme content during the duet and post-duet with a significant increase in variability (see table 16). As with insect a, the the mean value for post-duet singing lies between those for the duet and the solo song. There is a small but significant reduction in the echeme rate during the duet. However, because this reduction is small and because echemes are extended during the duet, the average rate of singing is not significantly reduced, though it is more variable. During the post-duet there is a large and significant rebound for both the echeme rate and the rate of singing, i.e. the values of these parameters are now greater than the values for solo singing.

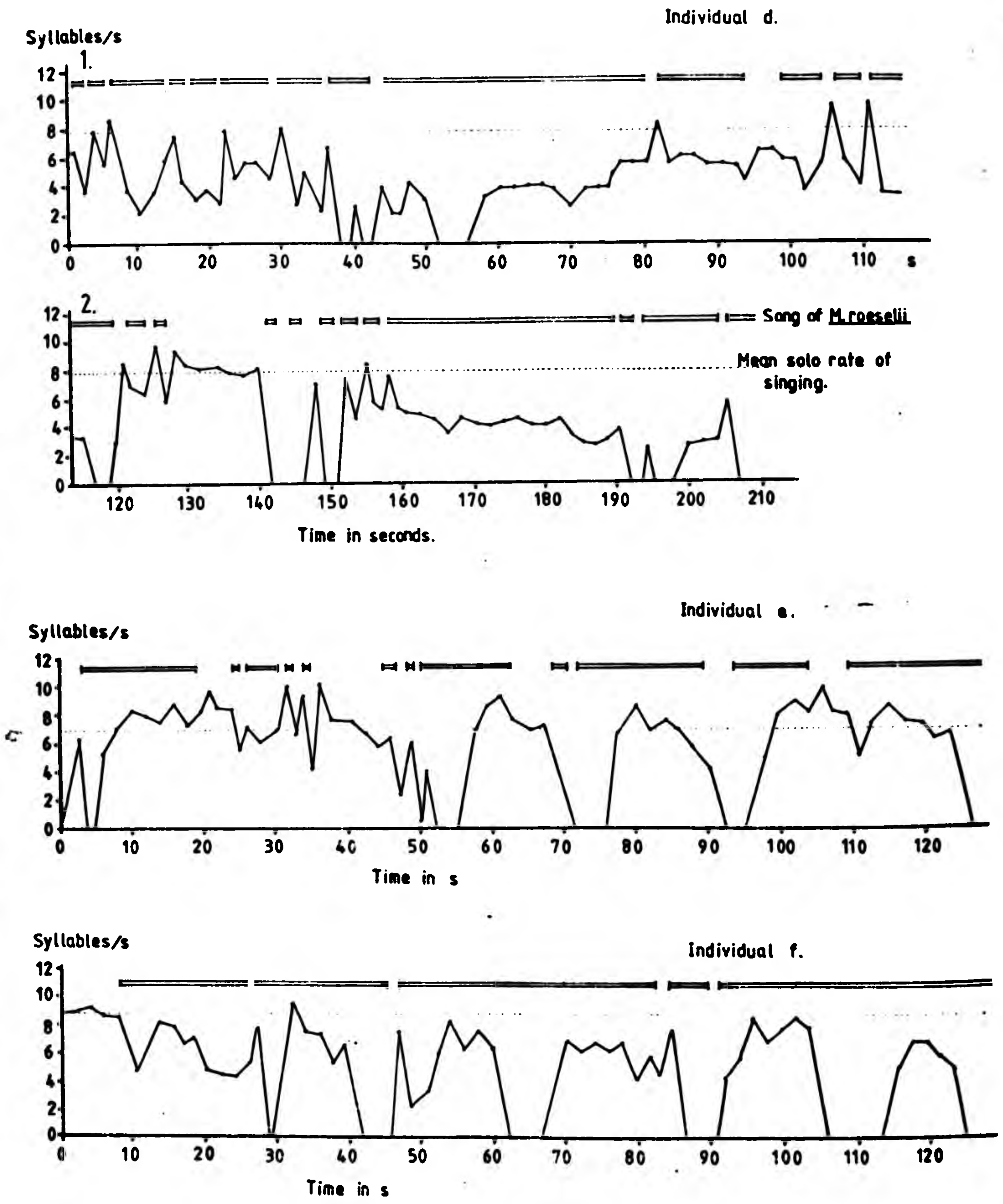
Fig. 38. EFFECT OF *M. ROESELII* ON THE RATE OF SINGING.



Individual *c*, (fig.37) collected from the Portsmouth locality (insects *a* and *b* are from a French population) shows no change in the modal value for *syllables/echeme* during the interaction, though clearly this parameter is much more *variable* during the duet and post-duet. The *echeme rate* is more than halved during the duet with many very low values. No rebound effect is observed at the post-duet phase. The rate of singing is also halved during the duet. A slight rebound occurs at the post-duet due to the slightly larger percentage of five-syllable echemes sung during this phase. This type of response seems typical for this *particular* British population. Usually the rate of singing is greatly reduced and the average echeme duration increases only slightly during the duet, e.g. in another individual from the same population the mean value for syllables/echeme increased from 4.88 (S.D. = 0.27) to 5.25 (S.D. = 0.65).

Some of the interactions have been analysed by plotting the rate of singing of *P. albopunctata* against time, with the song of *M. roeselii* diagrammatically represented on the time scale also. Fig.38 shows in this way the singing behaviour of individuals *a* and *b*. The rapid reduction in the rate of singing is seen when the *roeselii* starts singing. When the *roeselii* stops singing the rate of singing of *P. albopunctata* recovers, often showing a rebound. Peaks in the rate of singing also occur during the duet, where extended echemes are produced (see discussion, p.178). Individual *a*, after interacting for 200s is finally inhibited from singing until the next pause in the song of *M. roeselii*. Inhibition occurs again at 260s with the animal remaining silent for over a minute. Another brief (45s) duet ensues before total inhibition. Fig.38

Fig. 39. EFFECT OF *M. ROESELII* ON THE RATE OF SINGING.



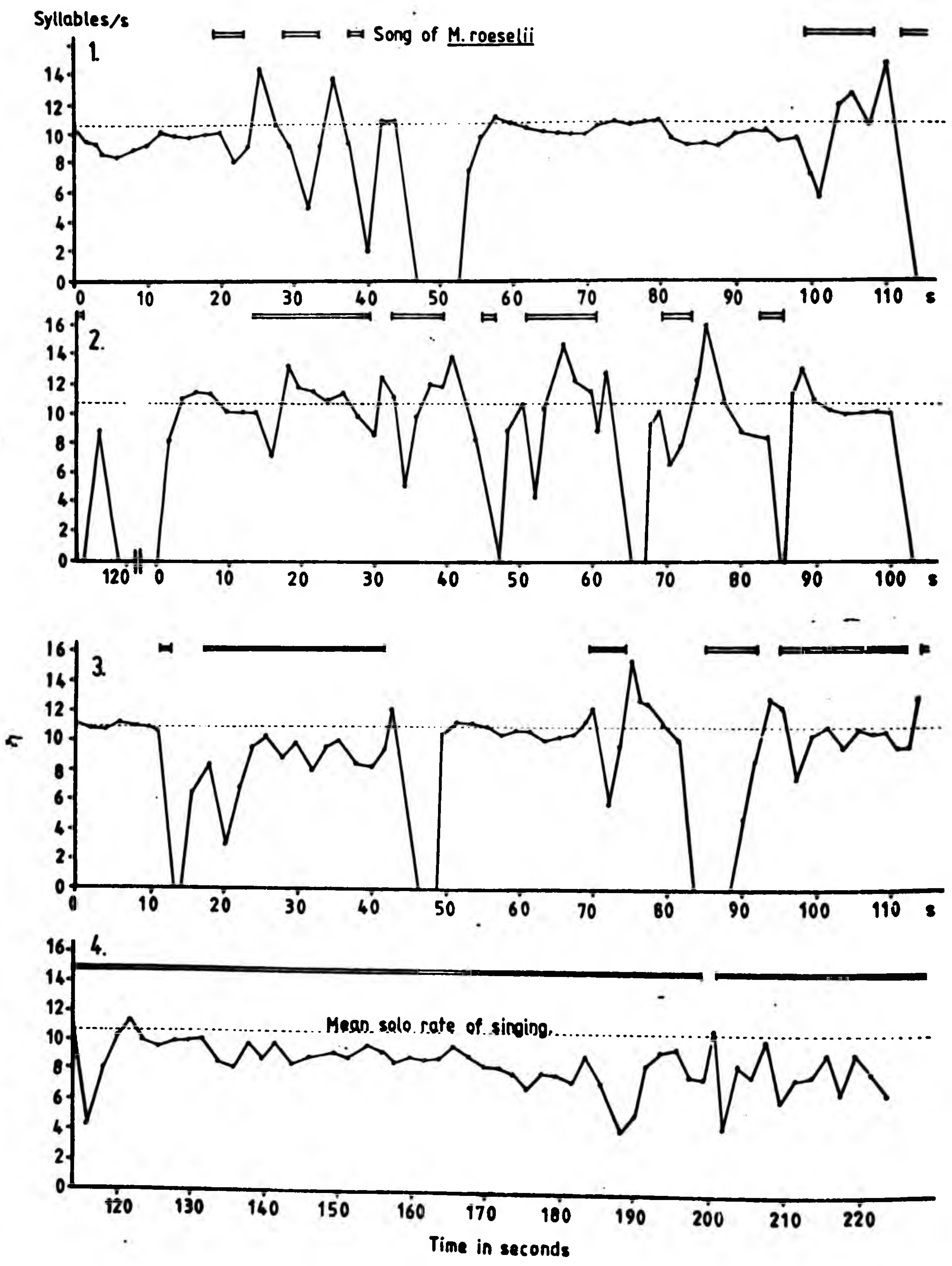
(lower 2 graphs) also shows the behaviour of individual *b*. Here it is seen that by singing longer echemes during the duet, the insect maintains the rate of singing at a value comparable to that of solo singing. Short emissions by the *roeselii* induce large fluctuations in the rate of singing; depressions followed by rebounds. Again, peaks during the duet correspond to the production of long, seven- and eight-syllable echemes.

Another individual from the Portsmouth population (individual *d*) is shown in fig.39, where, again, very large depressions in the rate of singing are seen during the duets. After 210s the insect is totally inhibited from singing.

Fig.39 also shows brief sections of interactions of two more French individuals. Individual *e* exhibits large peaks in the rate of singing as seven- and eight-syllable echemes are produced. The second insect (individual *f*) tends not to increase its echeme duration as much. Thus its rate of singing during the duet is usually well below the average solo value, as it suffers the usual reduction in the echeme rate. Also evident in these graphs is the tendency for the rate of singing at the onset of the duet to be deeply depressed, and then to increase rapidly to a value close to, or exceeding that of normal solo singing. Often this is followed by an oscillation in the rate of singing, e.g. at 10s in the upper graph (individual *e*) and at 55s in the lower graph (individual *f*). Both insects also show a tendency to develop a cyclical pattern in the *rate of singing* curve as the duet progresses.

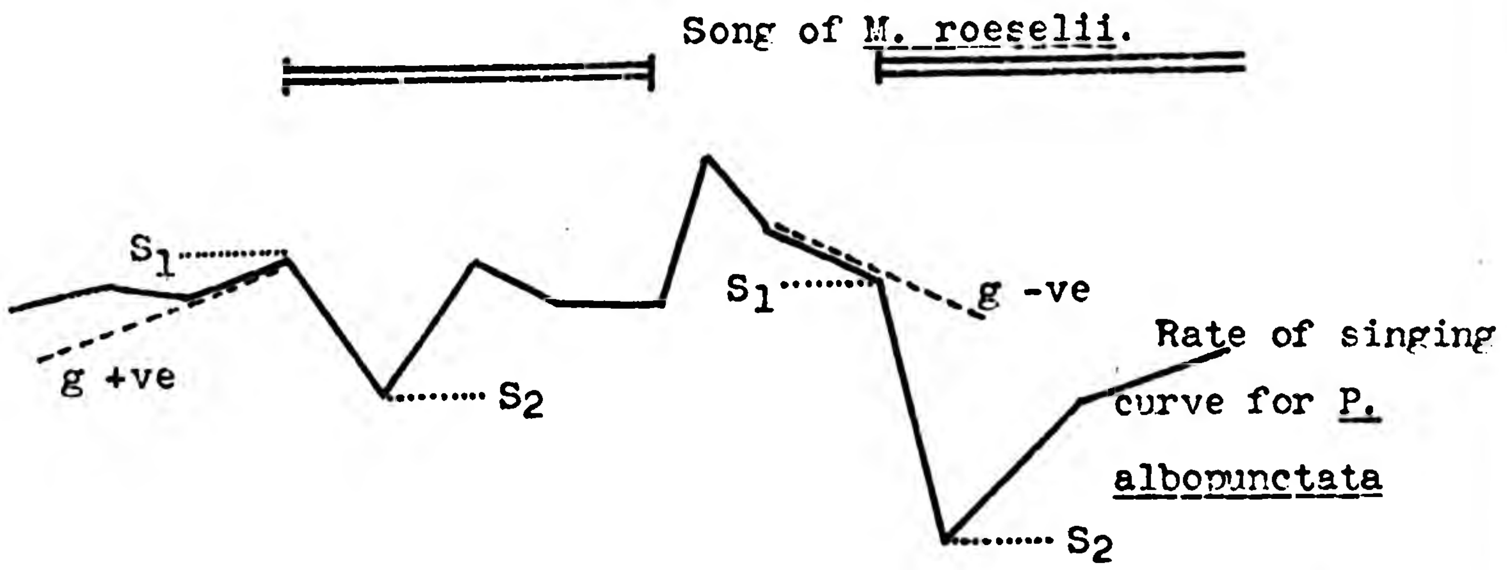
The recording by Broughton has also been analysed in this way. Fig.40 shows four sequences from this interaction. The initial response by this individual is the production of very long echemes (see Broughton 1965) so producing the large peaks

Fig. 40. EFFECT OF *M. ROESELII* ON THE RATE OF SINGING.



in the rate of singing in graphs 1 and 2. As the duet proceeds these long polysyllabic echemes become more infrequent. In graph 4, for example, echemes are generally five, six or seven syllables in length (x = 6.39, S.D. = 0.74).

By examining all the graphs of rate of singing, in particular those of Broughton's recording, it is seen that generally the initial depression in the rate of singing, due to the onset of the *roeselii* song, is large where the singing rate of the *albopunctata* immediately prior to the duet is already low or decreasing (i.e. the slope of the curve is negative). If the initial solo singing rate is high or increasing (positive slope) and the *roeselii* interrupts, the subsequent depression in the rate of singing is usually not so great. This relationship is illustrated diagrammatically using the same graphical format as shown in figs. 38 to 40.



S_1 - Solo rate of singing.

S_2 - Duet rate of singing.

g - Gradient of the rate of singing curve.

Table 17 shows data for 14 interruptions by <u>roeselii</u> arranged in chronological order. The gradient (g) is measured over a two-second period immediately prior to the interruption. S_1 is the solo rate of singing at the point of interruption, and S_2 is the rate of singing two seconds later during the duet. The data are derived from the interaction recorded by Broughton.

Table 17.	g	S_1 (Syllables/s).	S_2 (Syllables/s).
1.	+ 0.07	9.8	8.0
2.	- 0.97	9.2	5.2
3.	- 2.22	11.8	3.4
4.	- 1.67	8.8	5.6
5.	-10.50	5.0	0.0
6.	+ 0.01	10.0	7.2
7.	- 0.80	11.2	5.4
8.	- 3.00	5.0	1.8
9.	+ 1.00	10.4	8.8
10.	+ 0.72	10.0	7.6
11.	- 0.07	8.2	0.5
12.	- 0.20	10.6	0.5
13.	+ 0.72	8.2	3.0
14.	+ 1.06	12.4	7.4

Mean solo rate
of singing -
10.4 syllables/s

The degree of correlation between singing behaviour before interruption (i.e. g and S_1) and after interruption (S_2) was ascertained using Multiple Linear Regression Analysis for which various computer programmes exist. In this case the REGRE programme was used, written in FORTRAN. The programme uses four sub-routines from the IBM, system/360, Scientific Subroutine Package. These subroutines, CORRE, ORDER, MINV and MULTR are used in sequence (see appendix).

The programme prints out means and standard deviations of the variables, correlation coefficients, regression coefficients, the intercept of the multiple regression line on the y (S_2) axis, the multiple correlation coefficient and an analysis of variance for the regression. An estimate of significance is therefore available for the data by the use of the F statistic. The programme also prints a Table of Residuals showing the deviations of the actual y (S_2) values from those predicted by the regression line. The data from table 17 were subjected to this analysis and produced the following results.

Table 18. Results of Multiple Linear Regression Analysis.

Variable.	Mean,	S.D.	Correlation x versus y	Regression coefficient.
x				
1. g	-1.13	2.96	0.56	0.34
2. S_1	9.33	2.21	0.57	0.48
y				
1. S_2	4.60	3.06		

Intercept = 0.51

Multiple Correlation = 0.62

Analysis of Variance F value - 3.41 for 2 and 11 degrees of freedom.

Table of Residuals

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
2.7	0.6	-2.0	1.4	0.6	1.9	-0.2	-0.8	2.9	2.0	-3.9	-5.0	-1.7	0.6

The multiple correlation coefficient shows the conventional range of values where 0 indicates no correlation and 1.0 maximum correlation. The above data however do not achieve the required level of statistical significance ($F = 3.41$, $p > 0.05$) for any firm conclusions to be drawn. The Table of Residuals indicates that points 11 and 12 show large negative deviations from the regression line. At these points therefore, the rate of singing of the *albopunctata* was depressed more than usual by the song of the *roeselii*. As these points represent interruptions in the later stages of the interaction it is possible that they indicate an increasing susceptibility by *albopunctata*; the insect may be more easily inhibited towards the end of the interaction. Broughton, in his primary analysis of this interaction noted that the motivation to sing was reduced in *albopunctata* in the later stages of the duet (personal communication).

If, therefore, the last four points are deleted as representing a change in behaviour, and points 1 to 10 analysed, the following results are produced.

Table 18a.

Variable.	Mean.	S.D.	Correlation x versus y.	Regression coefficient.
x				
1. g	-1.73	3.33	0.88	0.68
2. S_1	9.12	2.34	0.69	0.14
y				
1. S_2	5.30	2.83		

Intercept = 5.22

Multiple Correlation = 0.89

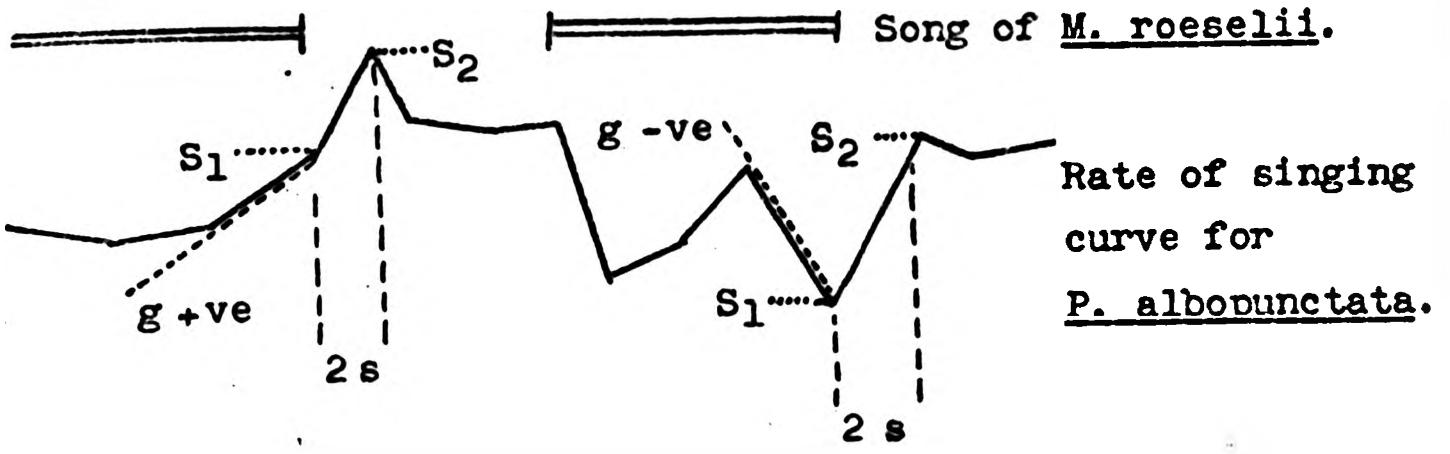
Analysis of Variance F value - 13.00 for 2 and 7 degrees of freedom.

Table of Residuals.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1.3	-0.6	-1.9	0.3	1.2	0.6	-0.8	-2.1	1.4	0.5

These results now show a high positive correlation ($p < 0.01$) between the rate of singing parameters before the duet and the rate of singing two seconds later during the duet. Smaller deviations in the table of residuals indicates a tighter grouping of points.

The change in singing behaviour from the duet to post-duet can be analysed in the same way (see diagram overleaf).



Here S_1 represents the rate of singing at the point where *M. roeselii* ceases singing, and S_2 the rate of singing two seconds later during the post-duet. Values for these parameters for fourteen points are shown in the table below.

Table 19.	g.	S_1 (Syllables/s)	S_2 (Syllables/s)
1.	+ 0.50	8.8	14.2
2.	+ 2.50	9.0	13.8
3.	- 2.50	1.6	10.8
4.	+ 1.38	11.6	14.6
5.	- 0.75	8.4	12.2
6.	- 0.13	11.7	13.6
7.	- 2.36	8.4	12.6
8.	+ 2.00	11.3	15.8
9.	+ 0.58	9.4	12.3
10.	+ 2.75	12.8	15.7
11.	+ 1.50	11.0	13.2
12.	- 0.01	9.7	12.9
13.	- 0.14	7.8	10.8
14.	+ 2.13	8.2	12.6

Mean solo rate of singing - 10.4 syllables/s

Here it seems that if, prior to the end of the duet, the rate of singing is high and increasing, the rebound during the post-duet is large in magnitude. Conversely if the rate of singing is low and decreasing the rebound is of a smaller magnitude. Multiple linear regression analysis on these data produced the following results.

Table 20. Results of Multiple Linear Regression Analysis on data from table 19.

Variable.	Mean.	S.D.	Correlation x versus y.	Regression coefficient.
x				
1. g	0.53	1.65	0.68	0.28
2. S_1	9.25	2.71	0.77	0.33
y				
1. S_2	13.22	1.53		

Intercept = 10.06

Multiple Correlation = 0.81

Analysis of Variance F value - 10.33 for 2 and 11 degrees of freedom.

Table of Residuals

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
1.1	0.1	0.9	0.4	-0.4	-0.2	0.5	1.5	-1.0	0.7	-0.9	-0.3	-1.7	-0.7

A significant correlation is again achieved ($p < 0.01$). It is interesting to note that the multiple correlation of g and S_1 versus S_2 produces a higher correlation coefficient than either of the x variables alone, (i.e. g versus S_2, or S_1 versus S_2). This is also true of the analyses shown in tables 18 and 18a.

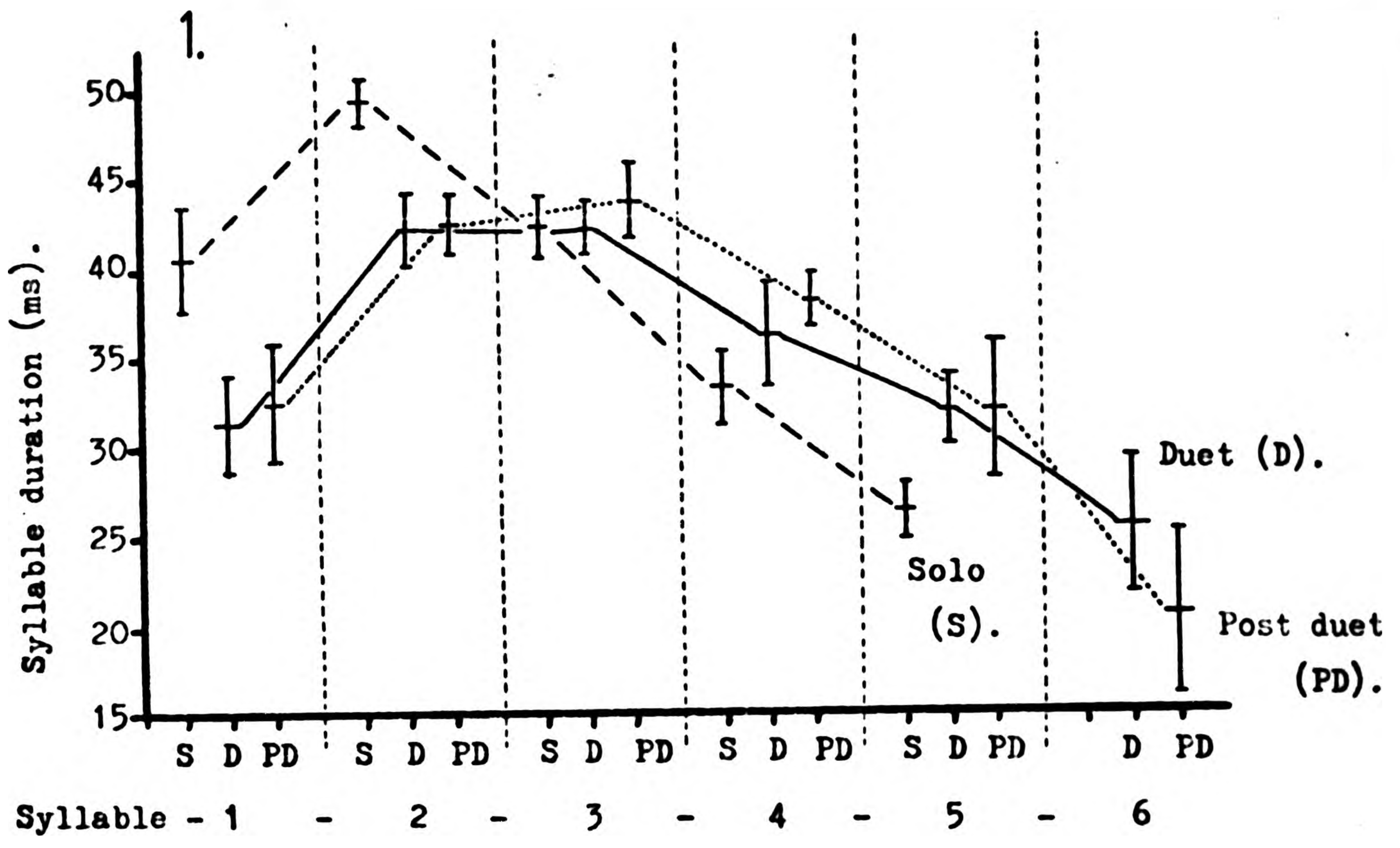
Thus the singing behaviour of P. albopunctata during the first few seconds of the duet and post-duet is usually a reflection of the singing behaviour immediately prior to these phases. A large reduction in the rate of singing during the duet is generally a result of a low and decreasing rate of singing prior to the interruption by roeselii. This reduction is less if the rate of singing is high and increasing before the duet. There may then follow a large peak in the rate of singing during the duet (see for example, graph 2, fig.40 at 50 seconds on the time axis). A large rebound is produced during the post-duet when the rate of singing is relatively high and increasing at the end of the duet. If M. roeselii stops singing while the rate of singing of albopunctata is low and decreasing, the rebound will be of low magnitude. As was mentioned previously, the rate of singing at the beginning of the duet is depressed, then rises rapidly, often overshooting the value for solo singing. If, during this overshoot, the roeselii stops singing, the resulting rebound can be very large, e.g. in fig. 40, at 70s in graph 2, and again at 70s in graph 3.

(ii). Changes in Syllable Duration

In order to ascertain if any song modification occurs at the syllable level, special recordings of the interactions must be made so as to reduce the recorded amplitude of the roeselii song. Only then is it possible to define accurately the beginning and end of each syllable of the albopunctata on an expanded oscillographic trace. Such recordings were made with the roeselii in a separate cage situated behind the microphone which was directed at the albopunctata. This arrangement produced the desired effect whereby the roeselii syllables were only just detectable on the oscillographic trace.

In some individuals no difference could be detected between solo syllables and syllables sung during the interaction. Other individuals, however, sang syllables of slightly shorter duration during the interaction (i.e. duet and post-duet). Fig. 41, graph 1 compares the syllable durations for solo singing with those of the duet and post-duet, (points represent the mean ± 1 standard deviation). Both first and second syllables are significantly shorter during the duet and post-duet. Conversely, the fourth and fifth syllables tend to be of greater duration during the interaction. This difference is significant

Fig. 41. EFFECT OF M. ROESELII ON SYLLABLE DURATION OF P. ALBOPUNCTATA.



Difference between solo syllable durations and interaction syllable durations.

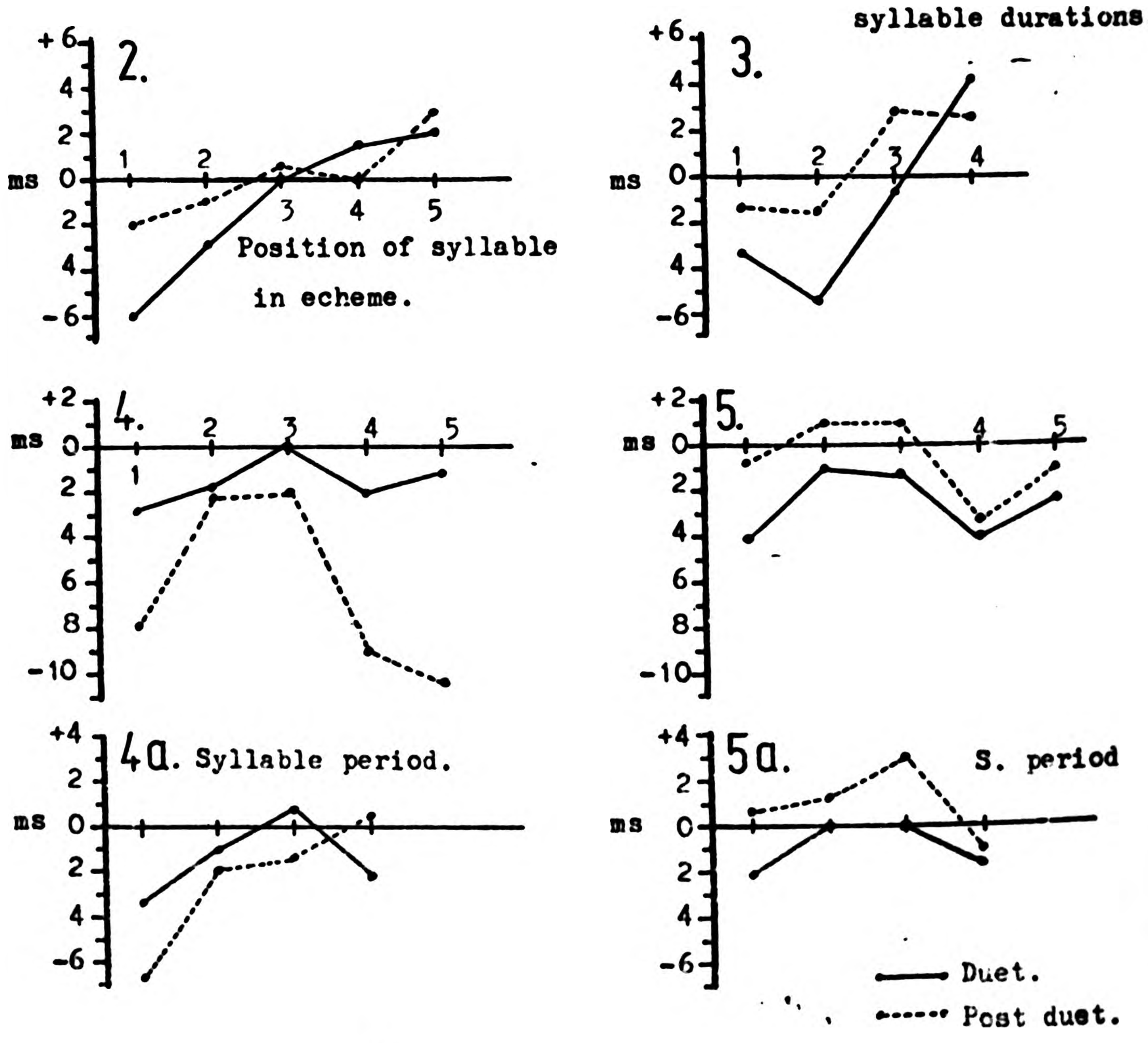


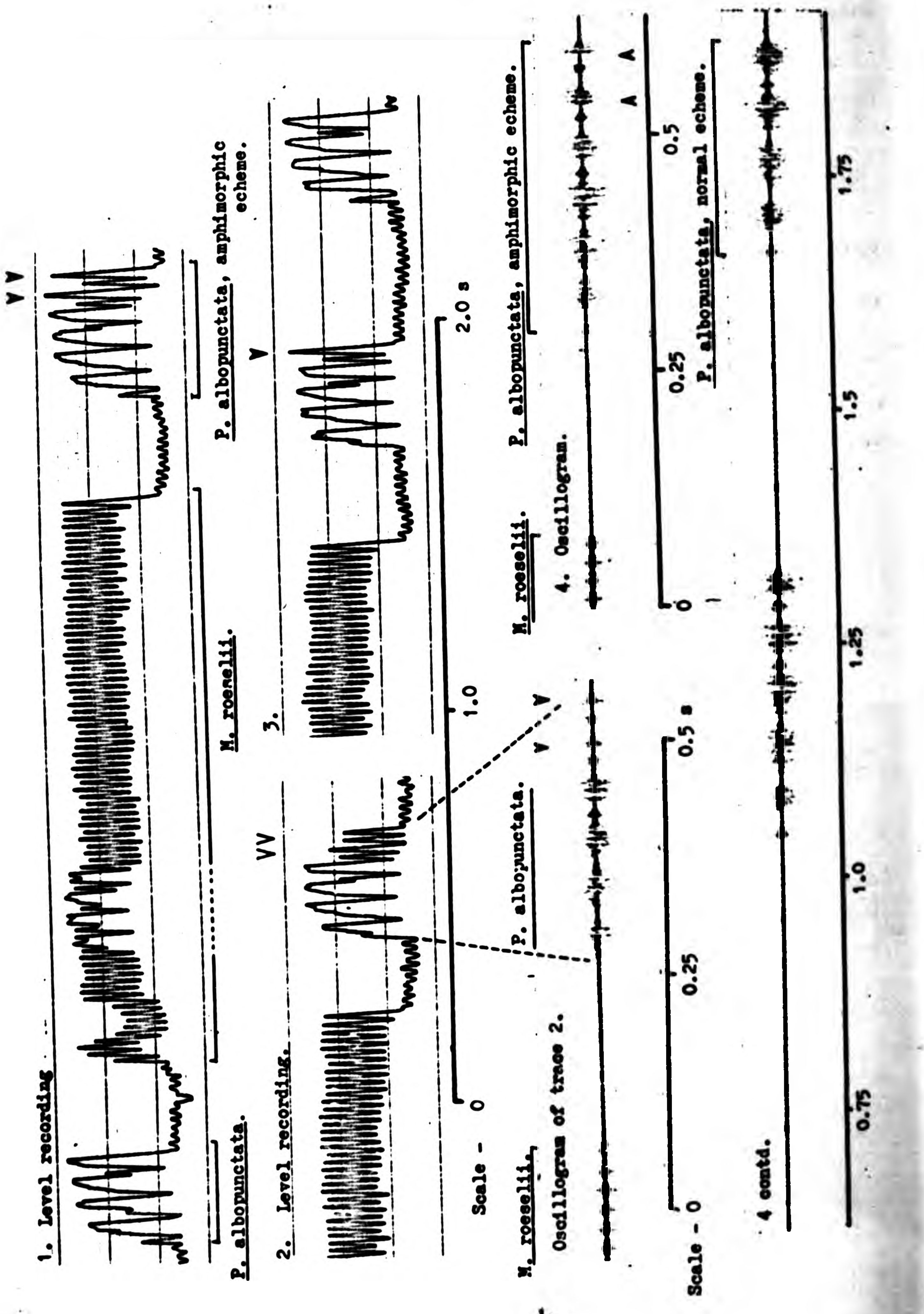
Table 21. Differences between means for the data presented in fig. 41.

Syllable No. -	1.	2.	3.	4.	5.
Graph 1.					
Comparing Solo and Duet.	p< 0.001	p< 0.001	p> 0.1	p> 0.1	p< 0.001
Solo and Post-duet.	p< 0.002	p< 0.001	p> 0.1	p< 0.01	p< 0.01
Graph 2.					
Comparing Solo and Duet.	p< 0.001	p< 0.05	p> 0.1	p< 0.1	p> 0.1
Solo and Post-duet.	p< 0.05	p> 0.1	p> 0.1	p> 0.1	p> 0.1
Graph 3.					
Comparing Solo and Duet.	p< 0.1	p< 0.001	p> 0.1	p< 0.001	
Solo and Post-duet.	p> 0.1	p> 0.1	p< 0.05	p= 0.05	
Graph 4.					
Comparing Solo and Duet.	p< 0.05	p< 0.01	p 0.1	p> 0.1	p> 0.1
Solo and Post-duet.	p< 0.02	p< 0.1	p> 0.1	p> 0.1	p> 0.1
Graph 5.					
Comparing Solo and Duet.	p= 0.05	p> 0.1	p> 0.1	p> 0.1	p> 0.1
Solo and Post-duet	p> 0.1	p> 0.1	p> 0.1	p> 0.1	p> 0.1

p= the probability level that data are from identical distributions. Comparisons that show a significant difference are underlined. Other comparisons can be regarded as showing no significant difference.

(N= 14 for solo and duet, 10 for post-duet).

Fig. 42. AMPHIMORPHIC ECHEMES PRODUCED IN RESPONSE TO THE SONG OF M. ROESELII.



for both these syllables during the post-duet, but only for the fifth syllable during the duet (see table 21). The sixth syllable, present during the duet and post-duet, is quite short and variable in duration. The largest difference is at the first syllable which, during the duet, is on average, 9.2 ms shorter than in normal solo singing.

The remaining graphs in fig. 41 show the difference between the interaction syllable durations and those of solo song for four more individuals. The y-axis indicates whether syllables are shorter (-ve value) or longer (+ve value) than normal. Individuals 2 and 3 show a similar pattern to individual 1 with first and second syllables tending to be shorter during the interaction. In individual 3 the last syllable is significantly longer in duration during the duet; the last two syllables are longer during the post-duet.

Individuals 4 and 5 also show a significant reduction in the duration of the first syllable during the duet (see table 21). The fourth and fifth syllables are, on average, shorter during the interaction. Statistical significance is not achieved, however, because of the extreme variability in the durations of these syllables. Some syllables are normal in duration while others resemble microsyllables. The syllable period seems to be more stable during the interaction as the slight differences recorded were not statistically significant (see graphs 4a and 5a).

Fig. 42 shows four instances during an interaction where amphimorphic echemes are produced by <u>P. albopunctata</u>. These echemes resemble those normally produced as a result of tactile contact between singing conspecifics (cf. fig. 21, p. 65). However, in this experiment the insects were kept singly in individual net cages. Therefore it seem that in some individuals these amphimorphic echemes can be evoked by the broadcast song of

M. roeselii. Syllable durations of such an echeme are shown in the table below.

Table 22. Syllable parameters measured in ms. Temperature - 23°C.

Syllable No. -	1.	2.	3.	4.	5.	6.	7.	8.
Syllable duration.	33.7	45.0	43.7	28.7	18.2	9.5	12.0	14.2
Syllable interval.	22.5	17.5	22.5	26.2	33.7	42.5	46.5	
Syllable period.	56.2	62.5	66.5	55.0	52.0	52.0	58.5	

The following tables show the number of amphimorphic echemes sung by two *albopunctata* individuals during separate interactions with *roeselii.* The number of echemes sung during the solo, duet and post-duet is expressed as a percentage of the total number of echemes sung during that phase

Table 23. Individual No. 1. Temperature - 24°C.

Solo.		Duet.	Post-duet.	
During song sequence.	After pause		After inhibition.	After duet.
0.00%	0.29%	2.79%	8.63%	2.25%

This individual produced two amphimorphic echemes during solo singing. It is not uncommon for a few sequences to commence with an amphimorphic echeme, particularly after a long pause.

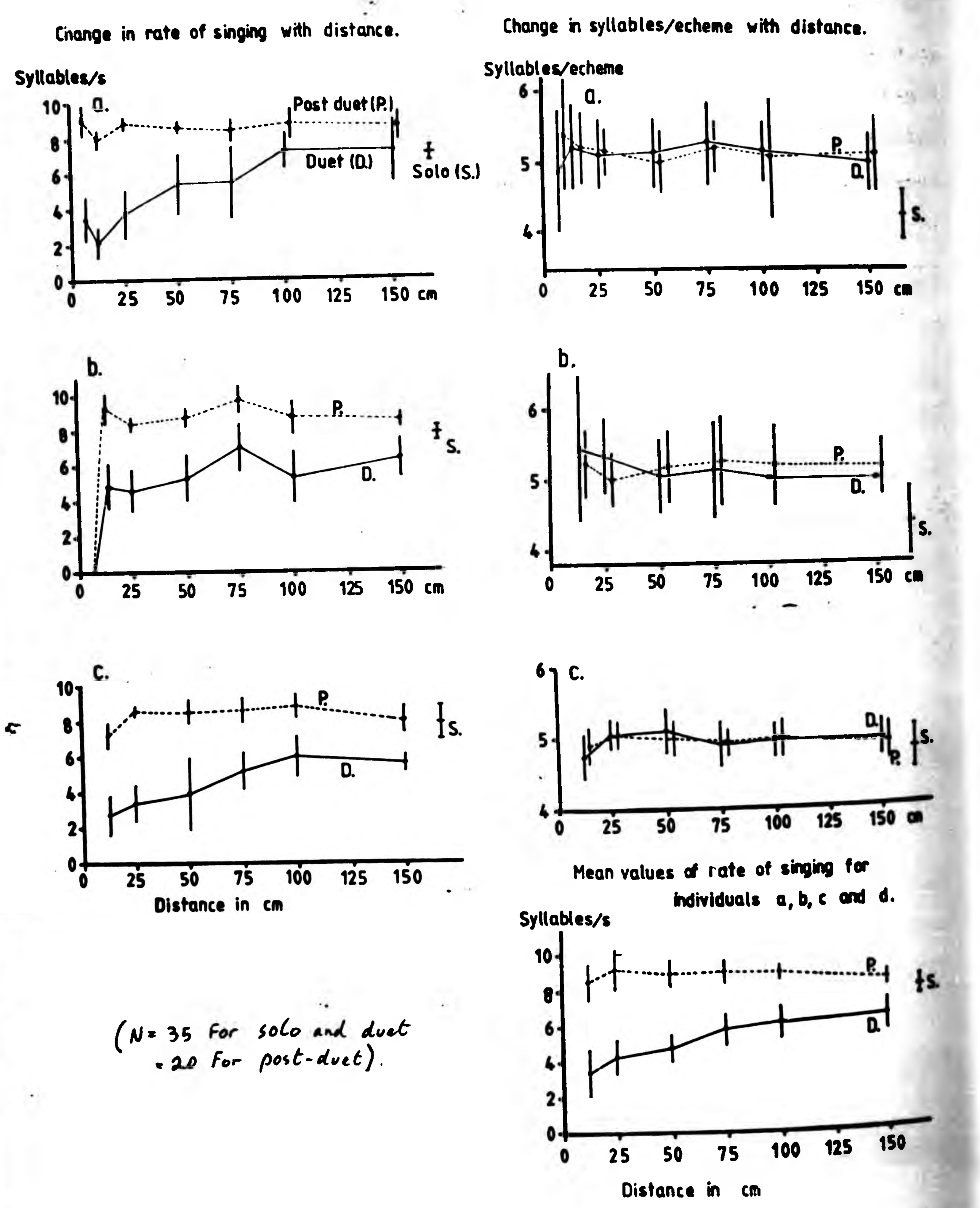
When the temperature around an *albopunctata* duetting with *M. roeselii* is raised, it tends to produce a larger number of amphimorphic echemes, e.g.

Table 24. Individual No. 2. Temperature - 31°C.

Solo.	Duet.		Post-duet.	
	During song sequence.	After pause.	After inhibition.	After duet.
0.00%	11.30%	6.20%	5.90%	4.90%

On three occasions during the duet this individual produced wholly microsyllabic echemes. This topic is pursued in the Discussion (p.180).

Fig. 43. EFFECT OF M. ROESELII WITH A CHANGING SONG INTENSITY.



(N = 35 for solo and duet = 20 for post-duet).

(iii) Changes in the degree of Song Modification with Changing Intensity.

Generally, the most extreme changes in song pattern occur when the influencing insect is singing in close proximity. Fig.43 shows the effect of placing the singing roeselii at various distances so altering the intensity of its song as received by the albopunctata. The points on the graphs represent the mean rate of singing by the albopunctata at measured distances from the singing roeselii (± 1 standard deviation). Three individuals, a to c, are discussed.

The rate of singing of insect a reaches the average solo value at a distance of 100 cm from the roeselii though it is clearly more variable. During the post duet, however, the rate of singing is significantly higher, even at 150 cm ($t = 4.73$, $p < 0.001$). Syllables/echeme are generally more variable and are significantly different from normal singing throughout the range of distances tested ($t = 7.19$, $p < 0.001$ for duet-solo at 150 cm).

The duet rate of singing of insect b even at 150 cm is still significantly lower than the solo rate ($t = 3.13$, $p < 0.01$). The post-duet singing rate at this distance is only slightly higher than solo singing ($t = 1.89$, $p < 0.1$). At close quarters to the roeselii, i.e. under 12 cm, this albopunctata was inhibited from singing. Syllables/echeme are again significantly greater at all distances tested ($t = 4.33$, $p < 0.001$ for post-duet versus solo at 150 cm).

Graph c shows the reaction of an unidentified individual from the Portsmouth population. The rate of singing is substantially depressed at all distances, more than in either of the two previous (French) individuals. Syllables/echeme are, however, less affected.

The last graph shows averaged results for individuals a to c and a fourth (British) individual. Generally the rate of singing gradually increases towards normality as the *roeselii* is moved further away. The post duet scarcely changes, perhaps decreasing very slightly.

Individual variation in *syllables*/*echeme* is too great for any coherent pattern to emerge when results from different individuals are averaged. In most individuals only a very slight reduction in the mean value is observed with increasing distance between the two singers.

As stated previously, many individuals are totally inhibited from singing on hearing the song of *M. roeselii*. Some of these individuals show the same reaction even though the *roeselii* may be singing some distance away. One insect was inhibited at all distances under 3 metres, while another refused to sing when the *roeselii* was singing 6.5 m away. It should be remembered that these experiments were conducted under laboratory conditions, with caged insects. Behaviour under conditions of choice is discussed below

(iv) Behavioural Aspects of the Interactions.

During these interspecific interactions no easily identified behavioural sequences emerged (e.g. aggressive interactions or courtship sequences). On one occasion the *albopunctata* was observed to rapidly approach the singing *roeselii* which quickly jumped out of reach thus ending what appeared to be an aggressive encounter.

Generally during an acoustical interaction between these two species, increased locomotory activity by the *albopunctata* can be observed, particularly when the insect is inhibited from singing. To ascertain if the insects were trying to move away from the singing *roeselii*, an *albopunctata* was put into a rectangular net cage (100x12x12 cm) and encouraged to settle by

Table 25. Results of Negative Phonotaxis Trials.

Insect No.	Trial No.	Time taken for onset of movement in s	Rate of movement in cm/s	Notes.
1.	1.	110.0	2.50	Moved to opposite end of cage (i.e. 3 metres).
	2.	1.0	2.83	
2.	3.	--	0.00	No movement, immature non-singing adult.
	4.	--	0.00	
3.	5.	90.0	0.33	Moved 1.0 m
	6.	50.0	1.00	Moved 1.5 m
4.	7.	5.0	0.20	Moved 0.6 m only.
	8.	20.0	0.95	Moved 0.9 m
5.	9.	7.0	1.33	Moved to opposite end of cage.
	10.	30.0	1.00	
6.	11.	120.0	2.17	Moved 3.0 m
	12.	3.0	0.50	Moved 1.7 m
7.	13.	15.0	0.67	Moved 1.0 m
	14.	5.0	1.67	
8.	15.	--	0.00	No movement.
	16.	--	0.00	
9.	17.	45.0	0.50	Moved 0.9 m
	18.	16.0	2.67	Moved 1.9 m
10.	19.	5.0	3.17	Rapid movement to opposite end of cage.
	20.	5.0	2.80	
11.	21.	30.0	1.50	Moved 2.2 m
	22.	1.5	1.67	Moved 1.6 m
12.	23.	0.5	5.00	Moved 1.5 m very rapidly.
	24.	0.5	1.90	Moved 2.4 m
13.	25.	55.0	1.50	Moved 1.8 m
	26.	10.0	2.00	Moved 3.0 m
14.	27.	7.0	1.17	Moved 2.2 m
	28.	2.0	2.22	Moved 1.0 m

directing an 'Anglepoise' lamp on one end of the cage. When the insect had settled, a separate, small net cage containing *roeselii* males was placed next to the *albopunctata*. The behaviour of the *albopunctata* was observed as the *roeselii* began to sing. Each individual was tested in this way three times. Of 16 animals 12 moved down the cage whenever the *roeselii* started to sing. This movement away from the sound source, and also from the heat of the lamp (to which these insects are normally attracted) occurred in each of the three trials. One other individual showed inconsistent behaviour, exhibiting negative phonotaxis in only one of the trials. The time taken to start moving after the onset of *roeselii* song varied from one or two seconds to one minute. Assuming an equal probability of the *albopunctata* moving or staying still the observed ratio tested by χ^2 is fairly significant ($p < 0.05$).

This basic test was repeated in the field. Here the *albopunctata* was put into a gauze 'tent' (see p.18) in open grassland. Prior to each trial a control cage containing no insects was placed next to the *albopunctata*. On no occasion did this action appear to startle the insect or cause it to move. This cage was then replaced by one containing *roeselii* males. Six minutes was allowed for each trial starting from when the *roeselii* commenced singing. The time taken for the *albopunctata* to react to this singing was recorded, as was the subsequent rate of movement (the walking speed of an undisturbed insect is approximately 3 cm/s). In the absence of any disturbance, acoustic or otherwise, most insects moved very little. The results of 28 trials with 14 insects are shown in table 25. Once again a significant proportion, 12 out of 14, show negative phonotaxis to the song of *M. roeselii* ($p < 0.01$).

(v) Ecological Aspects.

In the field juveniles (i.e. non-singing) of both species can be found living together in the same square metre of grassland or roadside verge. In an area of Bromus/Brachypodium grassland 38 random quadrats, 2.5 m square, were taken and the incidence of juvenile males noted. The data are shown in table below.

Table 26.

Quadrats with		Quadrats with M. roeselii present	absent.
P. albopunctata	present,	31.6%	15.8%
	absent.	36.8%	15.8%

By arranging the data in this form (the 2 x 2 contingency table) a chi-square value is easily computed which indicates the probability of association between the two species, (see Southwood 1966). The value for the above table is 0.017. This is well below the value at the 5% level; one concludes therefore that there is no association. Thus, juveniles of both species occur together independently in the same vegetation.

The same test was performed on the adult singing populations and produced the following results (from 58 random quadrats).

Table 27.

Quadrats with		Quadrats with M. roeselii present	absent
P. albopunctata	present,	6.9%	27.5%
	absent.	39.8%	25.8%

In only 4 quadrats (6.9%) were males of both species found. This suggests that the males are now negatively associated and the large value of chi-square, 7.1, significant at the 1% level indicates that this is unlikely to be due to chance. Using the same data to calculate Cole's coefficient of

Fig.44. BELT TRANSECTS 1 METRE WIDE THROUGH THE CAUSSE VEGETATION SHOWING INCIDENCE OF PLATYCLEIS AND METRIOPTERA.

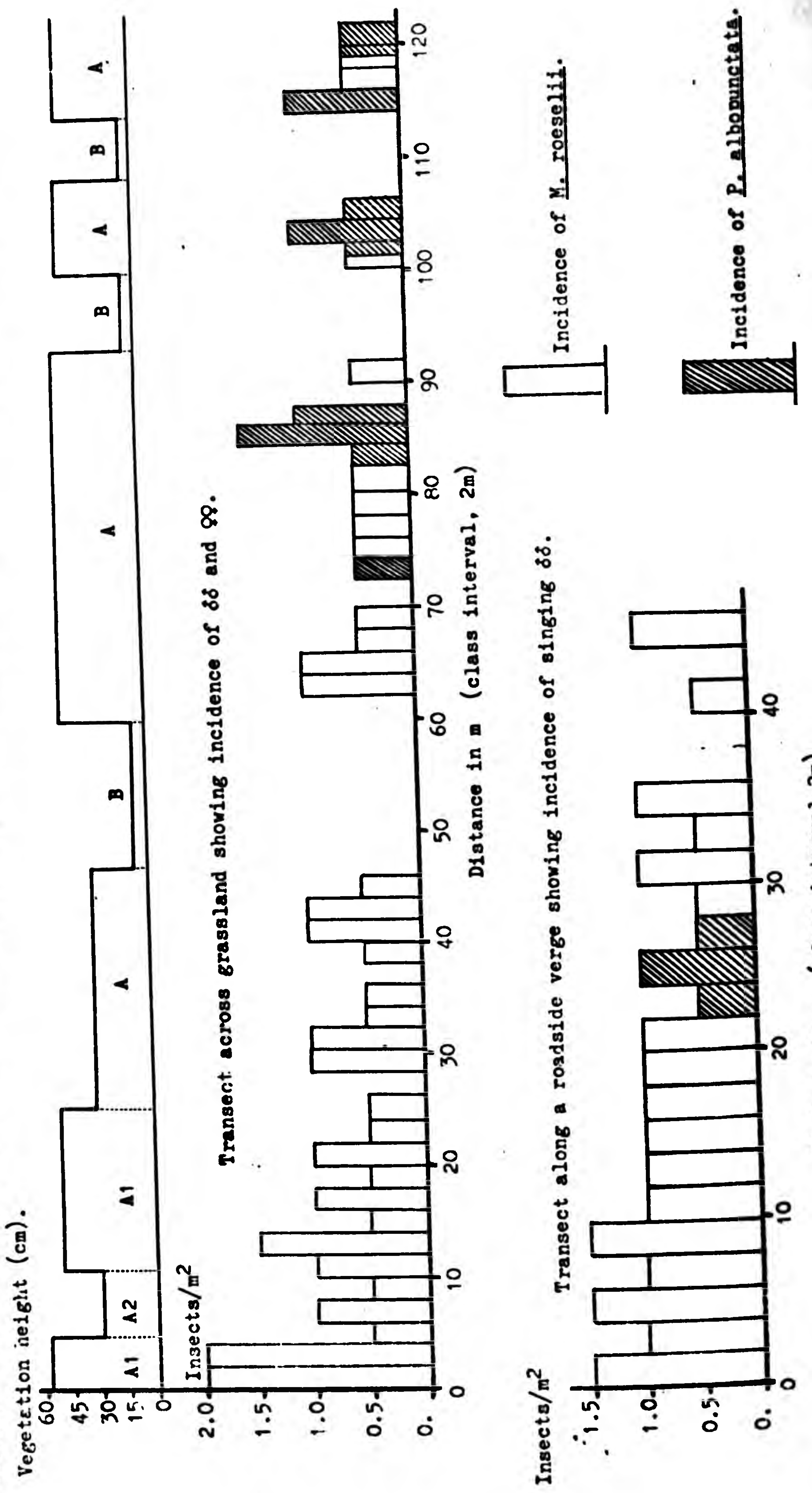


Fig. 44 (facing page) shows data from two belt transects one metre in width. The first, 120 metres long, shows the population density of P. albopunctata and M. roeselii, both males and females, the type of plant community and the average height of the vegetation. The plant associations are as follows:-

A1.

A.
Brachypodium pinnatum.
Bromus erectus.
Carex glauca.

A2.
Arrhenatherum elatius.
Trisetum flavescens.
Galium verticillatum.
Centaurea nigra.

B.
Thymus serpyllum.
Anthyllis hermaniae.
Ononis striata.
Festuca ovina.
Stipa pennata.
Briza maxima.

The second transect shows the distribution of males only along a roadside verge where the principal grass species are Arrhenatherum elatius and Dactylis glomerata. No changes occur in this plant community along the length of the transect.

interspecific association, (Cole 1949) a figure of -0.57 is produced (standard error ± 0.20). The coefficient ranges from +1, (complete positive association) through 0, (no association) to -1 (complete negative association).

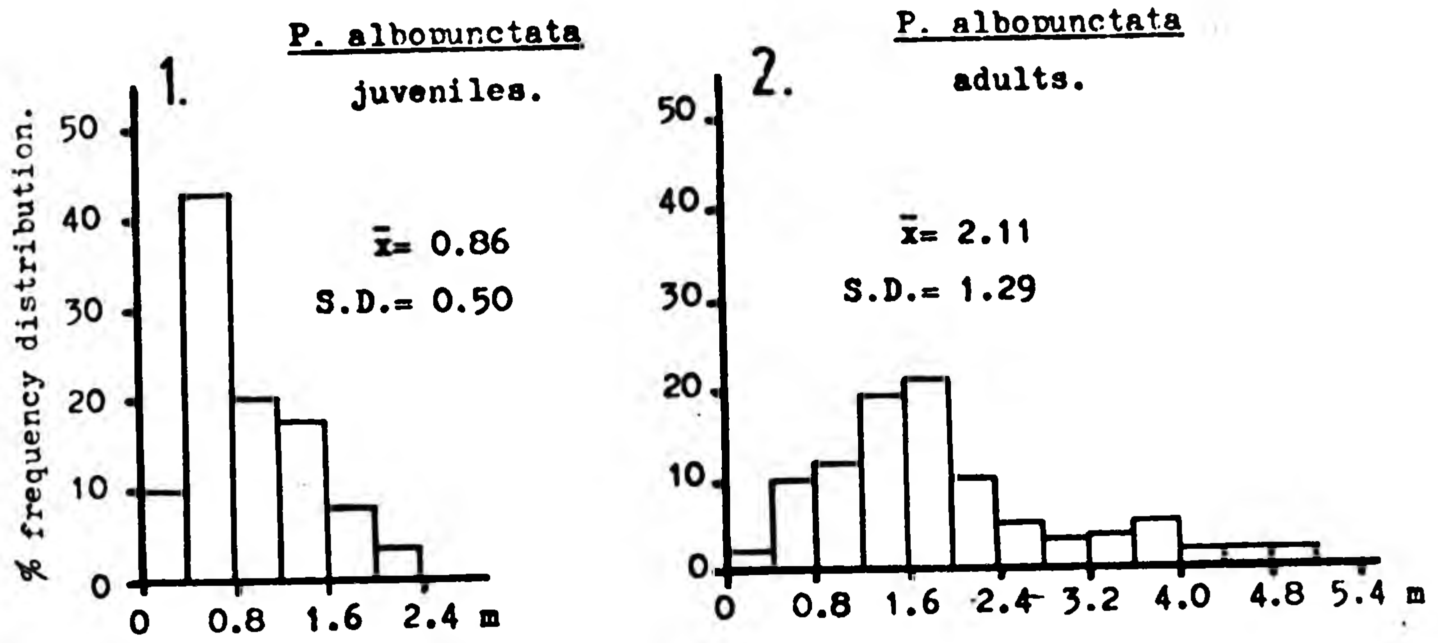
It is noticeable in the field that P. albopunctata is not found in a habitat where the M. roeselii population is very dense even though the habitat may be ideal for the albopunctata (see fig.44). Occasionally a female albopunctata can be found in these dense roeselii colonies. When the roeselii population is less dense, i.e. less than 0.5 insects/m^2, then the albopunctata may be found within a few metres from any given roeselii individual.

Fig. 45 summarizes all the data on nearest-neighbour distances for males of both species in various habitats. In areas where both species occur together, juvenile roeselii males can frequently be found less than one metre from juvenile albopunctata males. Thus the distribution of juvenile interspecific nearest neighbours (graph 3) resembles the distribution of juvenile albopunctata nearest neighbours (graph 1). When adult, P. albopunctata males are generally found farther apart (graph 2), while nearest-neighbour distances between albopunctata and roeselii males are still greater, usually over two metres. On no occasion was a male albopunctata found any closer to a male roeselii than 0.5 metres. Four instances were recorded of an albopunctata attempting to sing at distances between 0.5 and 1.0 metres from a singing roeselii. On each occasion the albopunctata was completely inhibited whenever the roeselii sang. Partial inhibition and slight retardation of echeme rate was observed on two occasions where the roeselii was singing between 1.0 and 2.0 metres away. The presence of low walls or rock outcrops in the habitat that deflected the song of the

Fig. 45. SUMMARY OF DATA ON NEAREST NEIGHBOUR DISTANCES.

Graph 1. Inter-individual distances between juvenile ♂ P. albopunctata.

Graph 2. Inter-individual distances between adult ♂ P. albopunctata. Data from various habitats.



Graph 3. Inter-individual distances between juvenile ♂ P. albopunctata and juvenile ♂ M. roeselii.

Graph 4. Inter-individual distances between adult ♂ P. albopunctata and adult ♂ M. roeselii.

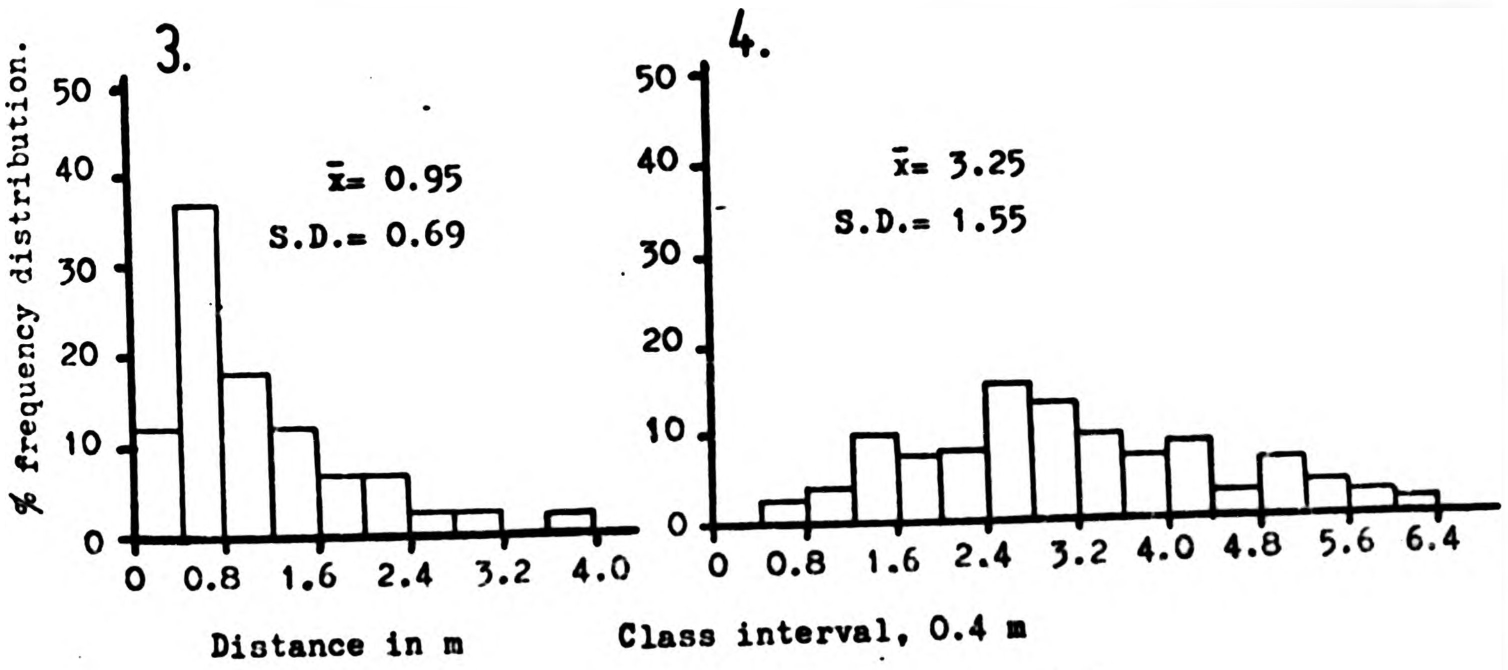
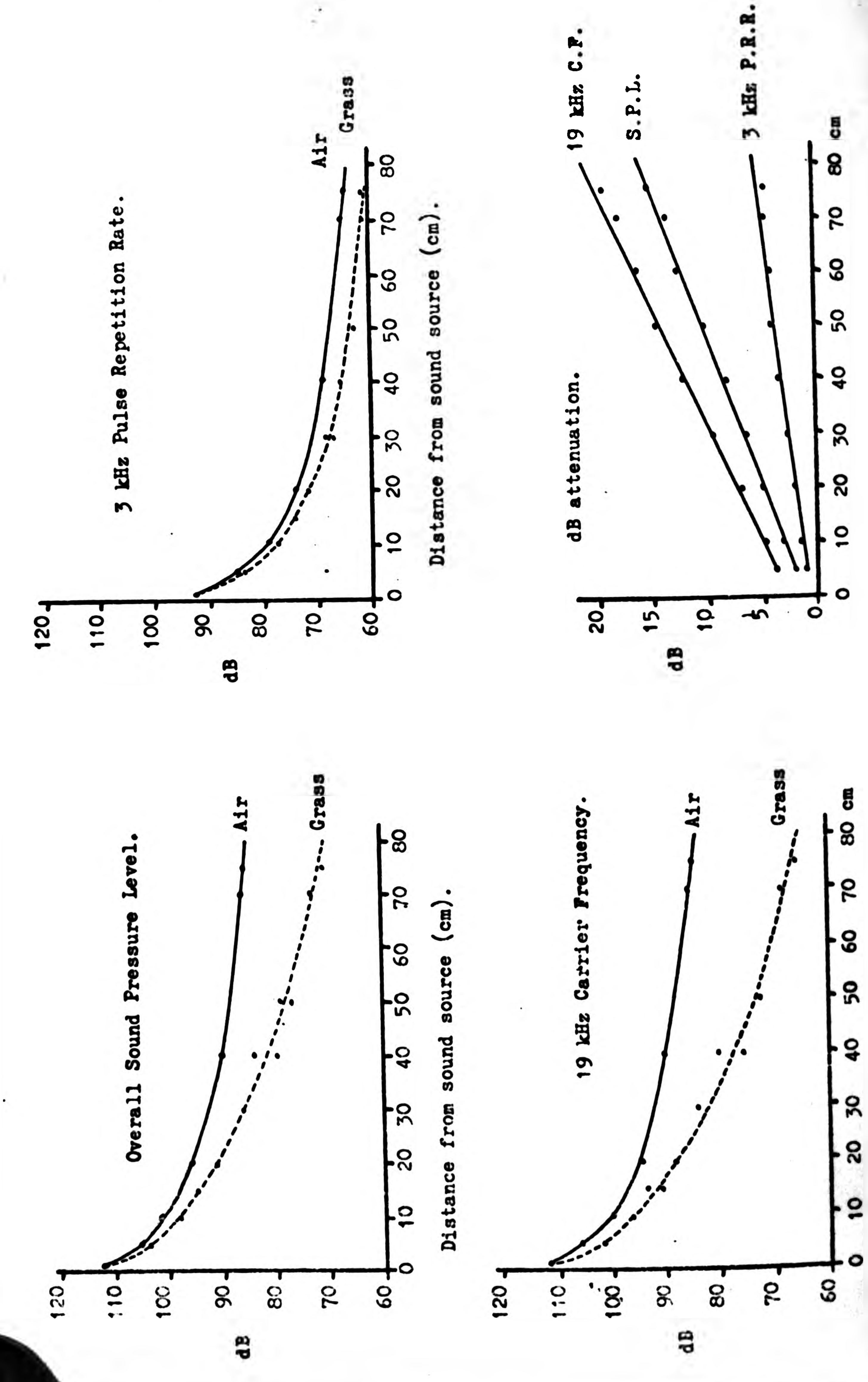


Fig. 46. ATTENUATION OF A COMPLEX SOUND SIGNAL.

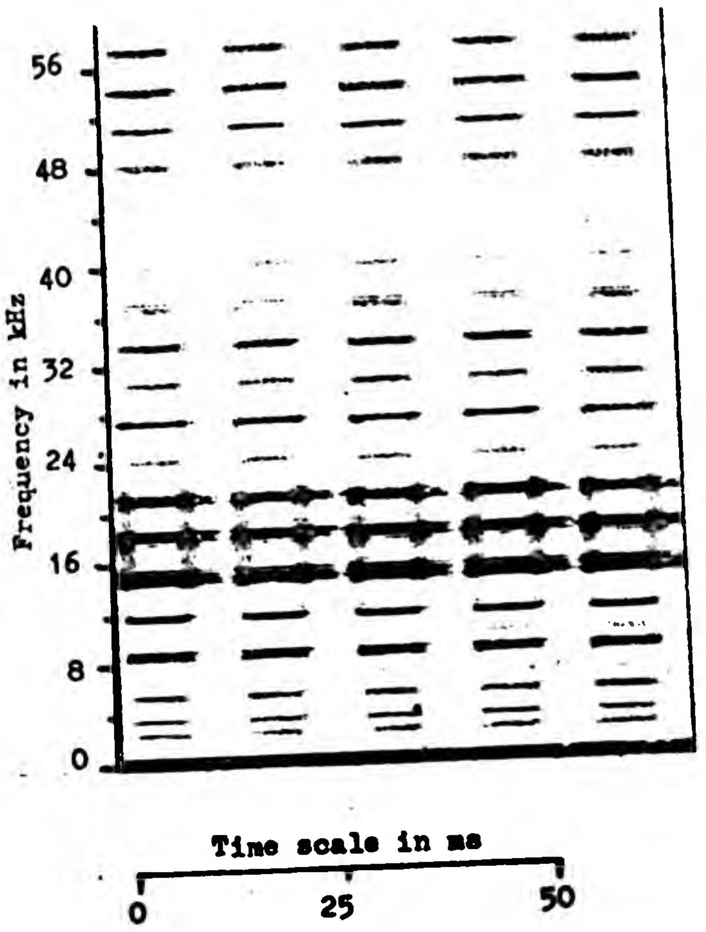


roeselii allowed the albopunctata to sing normally in fairly close proximity to the Metrioptera. Similarly, the denser the vegetation, the closer a male albopunctata could be found to a singing roeselii.

The attenuating properties of graminaceous vegetation were investigated in the laboratory by passing a synthesized M. roeselii song through a 75 cm length of grass sward. The average height of the grass was 35 cm. The graphs in fig.46 show the progressive attenuation of the various components of the song. Intensity was measured at various distances from the sound source both in the grass (dotted line) and in air with the grass removed. The high frequency component (carrier frequency) shows the highest attenuation by the grass. The intensity of this component is reduced by 20 dB at 75 cm, compared with its intensity in air at that distance. The lower frequency pulse-repetition rate is only slightly attenuated by the grass, with a reduction of 5 dB at 75 cm from the sound source. The sound pressure level of the whole song spectrum is reduced in intensity by 15 dB after its passage through the grass, compared with its intensity in air.

Fig.47 shows sonagrams of the transmitted and received signal. The gain controls on the sonagraph were not altered so that the two spectra are comparable. Passing the signal through the grass results in the reduction of the higher frequencies and the comparative enhancement of the lower frequencies. The highest frequencies are lost altogether. Thus the pattern of the spectrum is progressively modified as the signal passes through the grass. The peak frequency changes, shifting in the direction of the lower frequencies, e.g. in the example illustrated, the peak frequency changes from 19 kHz to 16 kHz after passing through the grass. Some loss of clarity in the syllable pattern is also apparent in the signal received through the grass.

Fig. 47. ATTENUATION OF A COMPLEX SOUND SIGNAL

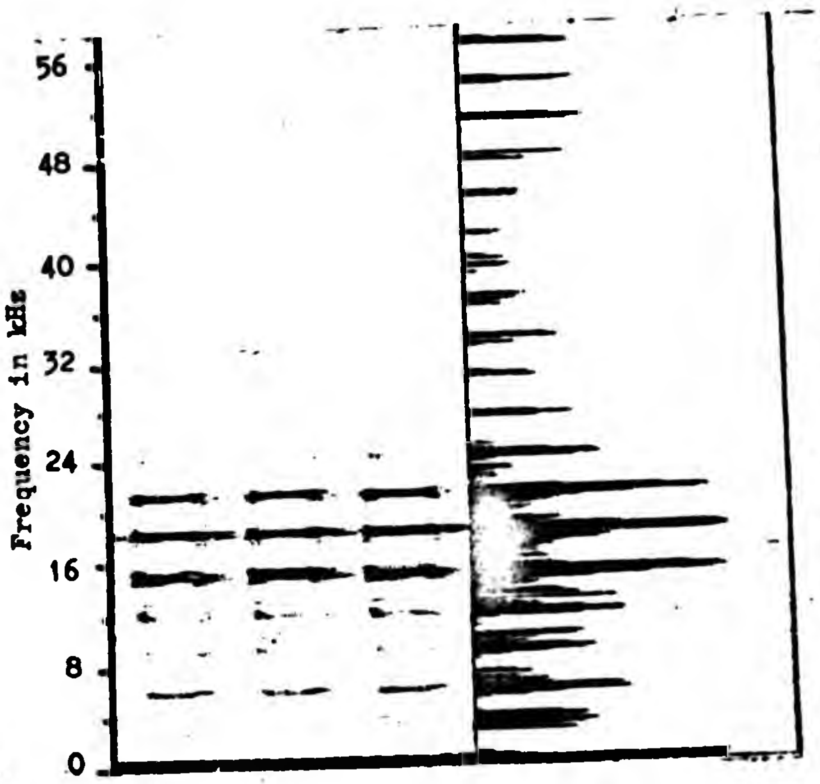


Transmitted signal:-

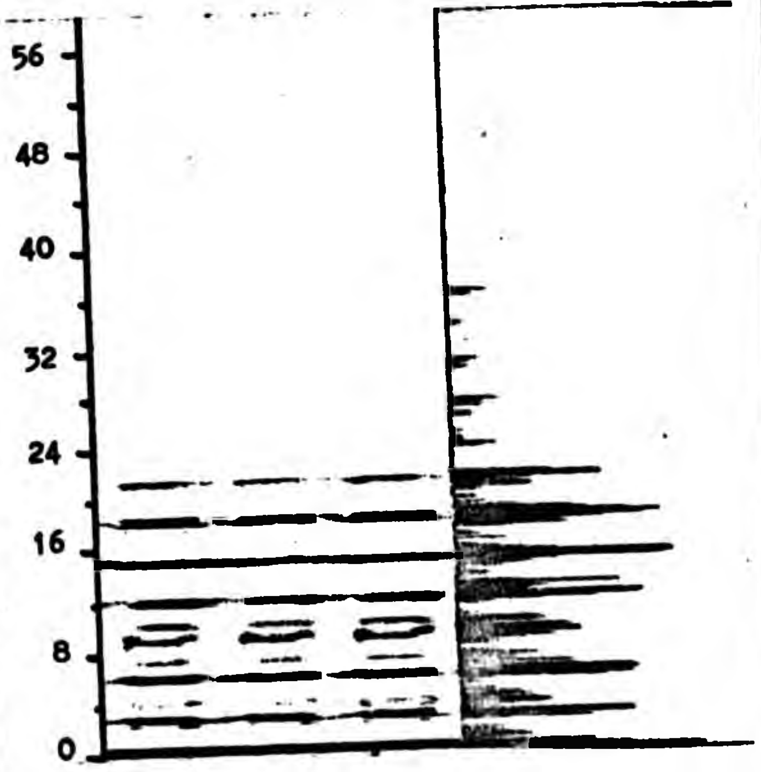
Carrier frequency - 19 kHz

Pulse repetition rate - 3 kHz

"Syllable" repetition rate - 72/s

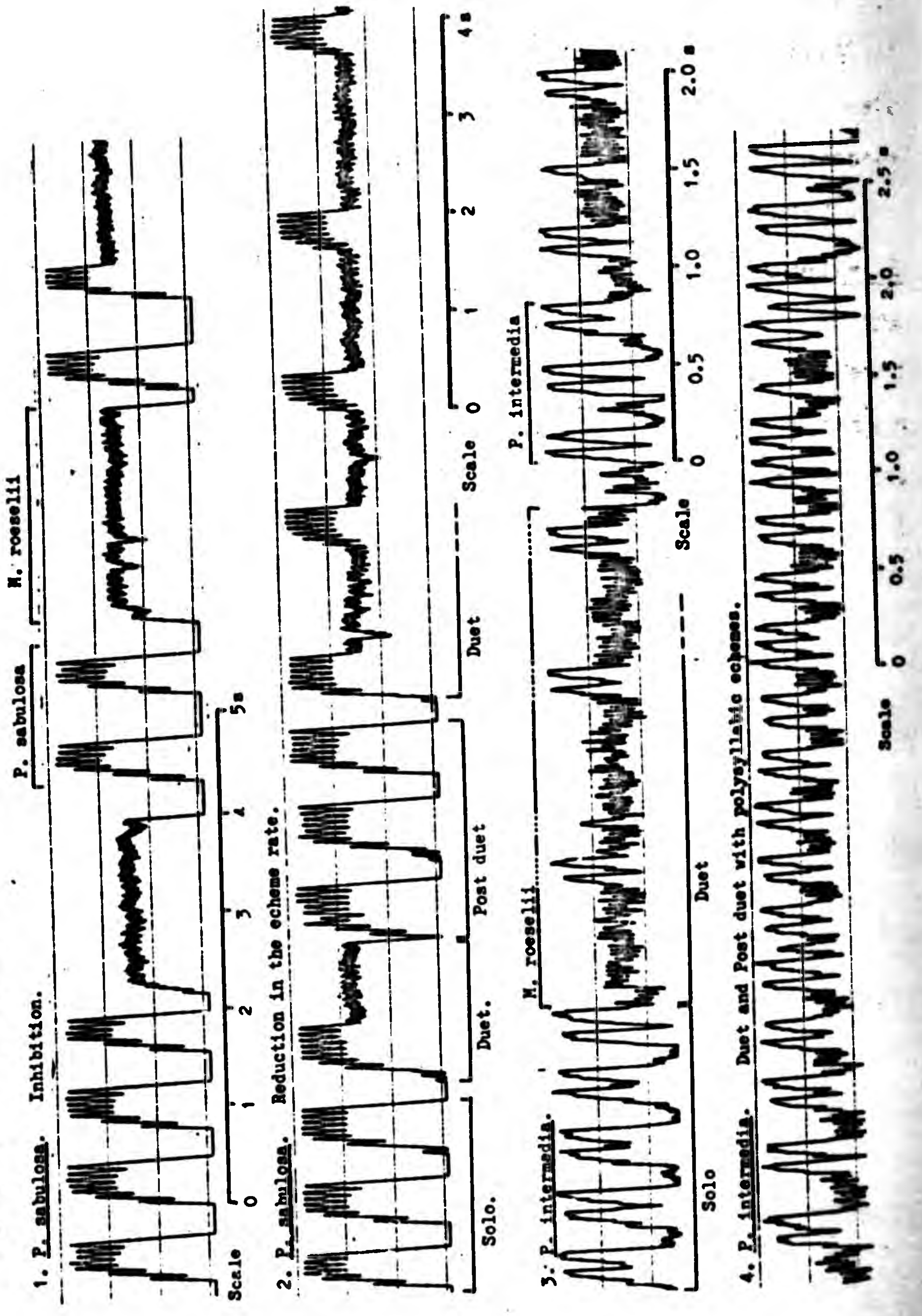


Received signal at 75 cm from sound source: open field.



Received signal at 75 cm from sound source, passing through grass.

Fig.48. **EFFECT OF M. ROESELII ON SONGS OF OTHER PLATYCLEIS SPECIES.**



2. The P. sabulosa/M. roeselii Interaction

It has been shown in the previous sections that the temporal and spectral parameters of the song of P. sabulosa are similar to those of P. albopunctata. Intraspecific acoustic behaviour also seems similar. It is therefore of interest to record the reaction of P. sabulosa to the song of M. roeselii.

Generally this reaction is comparable to that shown by P. albopunctata, though P. sabulosa seems more susceptible to inhibition (see fig.48, trace 1). However, the data on this interaction are comparatively limited, as P. sabulosa is a nocturnal singer while M. roeselii is diurnal. The roeselii can be induced to sing at night by illuminating it with a lamp. The resulting bout of singing is usually brief and the bright illumination may affect the behaviour of the sabulosa, possibly reducing its motivation to sing.

Interactions with five sabulosa individuals have been recorded. Three of these individuals were almost always inhibited during the song of the roeselii. The remaining two interactions where duetting occurred have been analysed in the same way as the albopunctata/roeselii interactions. The results are shown in table 28. The echeme duration of both individuals is increased during the duet and post-duet. Generally the number of syllables increases by one during these phases though occasionally nine- and ten-syllable echemes are produced. The echeme rate of P. sabulosa is usually much reduced during the duet; and during the post-duet phase it rarely exceeds that of normal singing. The rate of singing, however, as in albopunctata, is on average higher than normal during the post-duet as a result of the lengthened echemes sung during this phase. The two rate parameters measured are more variable during the duet

Table 28. Data for the P. sabulosa/M. roeselii interaction

Individual no. 1.		Solo.	Duet.	Post-duet.
Syllables/echeme.	$\bar{x}$	6.38	7.02	7.11
	S.D.	0.61	0.56	0.62
	N.	41	45	38
Echeme rate. (Echemes/s)	$\bar{x}$	1.37	0.72	1.25
	S.D.	0.07	0.09	0.11
	N.	20	22	18
Rate of singing. (Syllables/s)	$\bar{x}$	8.66	4.95	8.71
	S.D.	0.59	1.03	0.88
	N.	19	36	24
Individual no. 2				
Syllables/echeme.	$\bar{x}$	6.26	7.34	6.80
	S.D.	0.72	0.78	0.88
	N.	34	57	48
Echeme rate.	$\bar{x}$	1.27	0.76	1.25
	S.D.	0.07	0.15	0.11
	N.	17	18	14
Rate of singing	$\bar{x}$	8.18	5.42	8.41
	S.D.	0.59	1.21	0.79
	N.	15	39	23

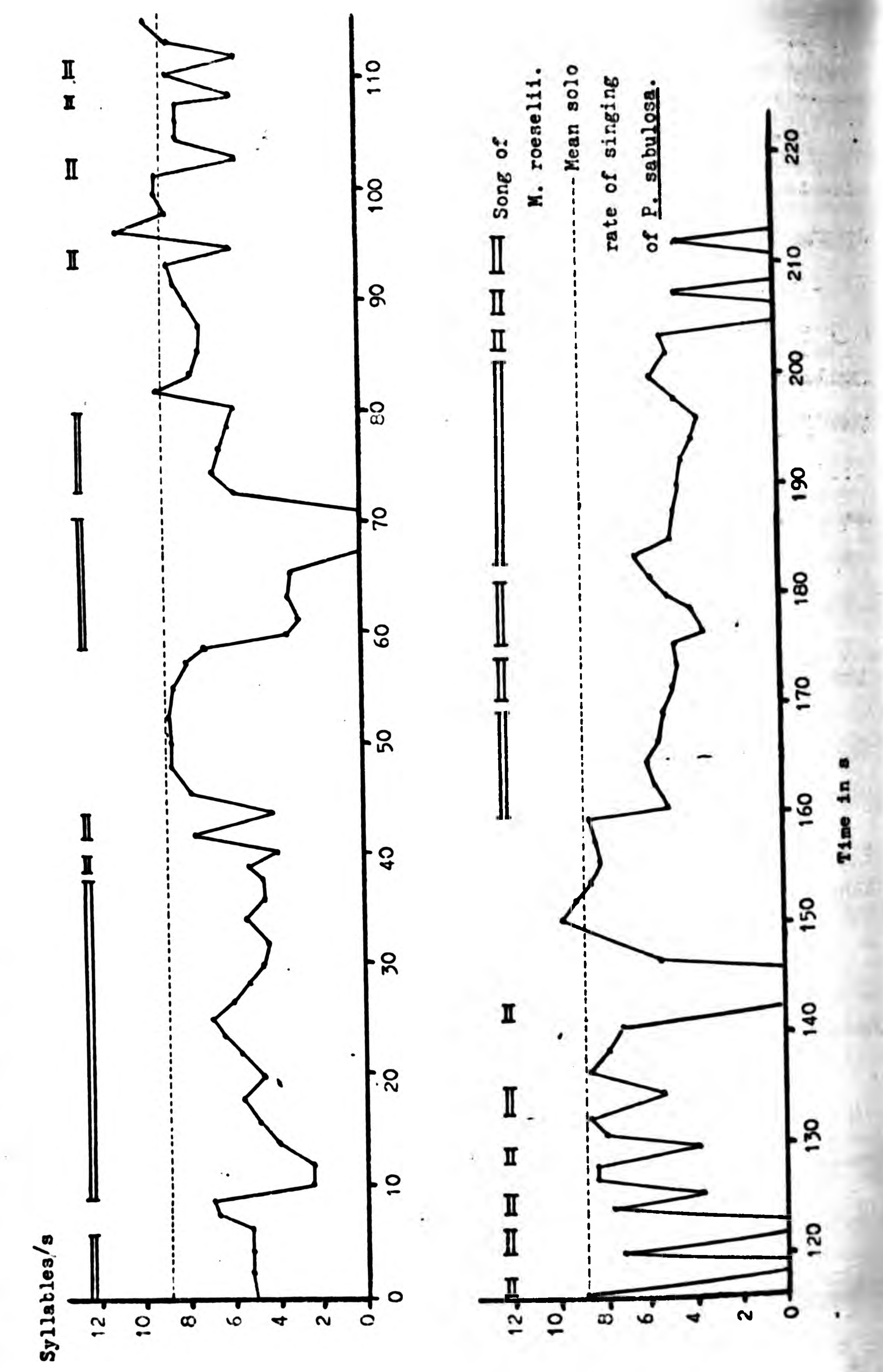


Fig.49. EFFECT OF M. ROESELII ON THE RATE OF SINGING OF P. SABULOSA.

and post-duet, in comparison to solo singing. Variability of syllables/echeme shows little change, however.

The rate of singing of a third individual is plotted against time in fig.49 . The large reduction in the rate of singing during the duet is apparent. Towards the end of this interaction the duetting behaviour of P. sabulosa suggests that the song of M. roeselii is exerting a stimulatory effect as well as an inhibitory one: at around 210 s on the time axis it can be seen that P. sabulosa synchronizes two brief song sequences with the brief emissions of the roeselii. The rate of singing of the sabulosa during these sequences is, however, half that of normal solo singing. This stimulatory effect by the song of M. roeselii has been observed for both P. sabulosa and P. albopunctata where hitherto silent individuals were apparently stimulated to sing upon hearing brief emissions of roeselii song. If duetting with the Metrioptera then ensued, the normal inhibitory effect of this species' song upon the singing of the Platycleis species was observed. For example, in the interaction illustrated in fig.49 the sabulosa is subsequently completely inhibited by a long sequence of roeselii song.

3. The M. brachyptera/M. roeselii Interaction.

The frequency and temporal pattern of the song of M. brachyptera are also similar to parameters in the song of albopunctata. Whereas P. sabulosa has a longer echeme and slower echeme rate than P. albopunctata, M. brachyptera has a shorter echeme and faster echeme rate. Although this interaction has been examined by McHugh (1971), new recordings have been made and analyzed in order that the data may be compared. The results for one individual are shown in table 29.

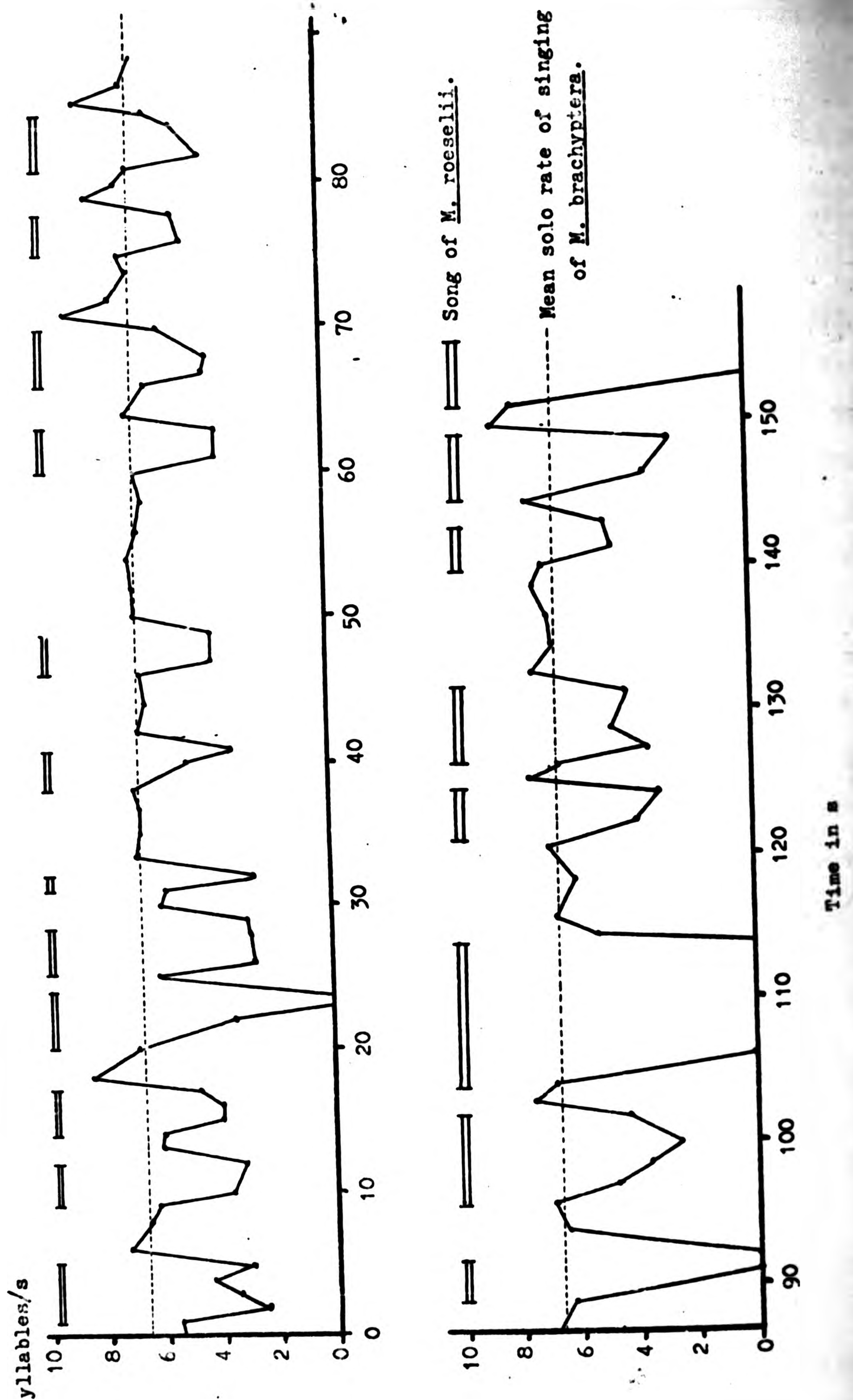


Fig. 50. EFFECT OF *M. ROESELII* ON THE RATE OF SINGING OF *M. BRACHYPTERA*.

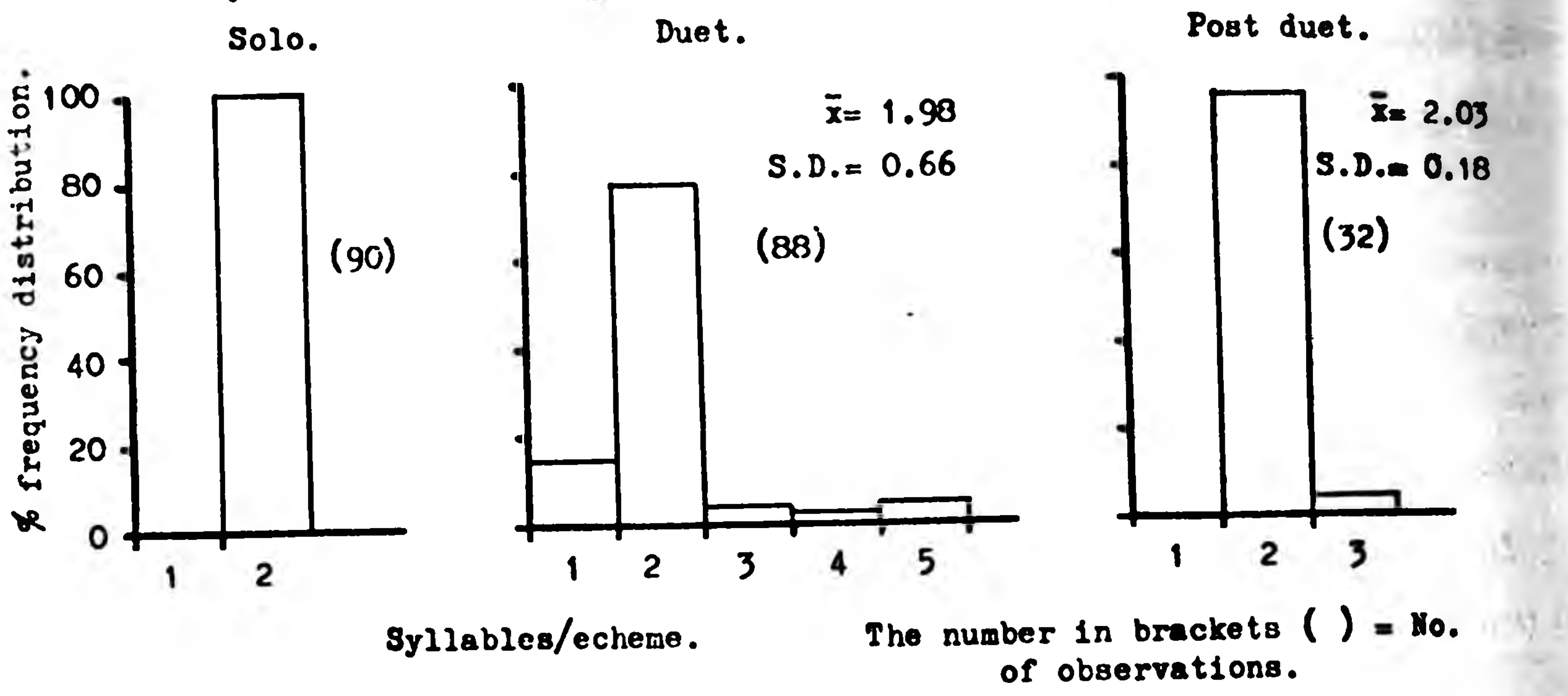
Table 29. The *M. brachyptera*/*M. roeselii* Interaction.

		Solo.	Duet.	Post-duet
Syllables/echeme.	$\bar{x}$	3.00	3.42	3.06
	S.D.	0.00	0.51	0.22
	N.	80	62	71
Echeme rate. (Echemes/s)	$\bar{x}$	2.20	1.15	2.40
	S.D.	0.17	0.32	0.21
	N.	34	40	30
Rate of singing. (Syllables/s)	$\bar{x}$	6.66	3.89	7.10
	S.D.	0.36	0.92	0.79
	N.	27	37	35

The response of this species to the song of *M. roeselii* is very similar to that of the two *Platycleis* species. Syllables/echeme are increased during the duet; only a slight increase occurs during the post-duet (in this individual). This is the more interesting in that syllables/echeme for this species, unlike the two *Platycleis*, show no variation during solo singing. The echeme rate and the rate of singing are depressed during the duet. Both these parameters show a rebound effect during the post-duet. All parameters are more variable during the interaction than during solo singing. The rate of singing of this individual is shown graphically in fig. 50. The depression in the rate of singing during the duet is evident, while during the post-duet there is often a large rebound to values well above that of normal solo singing. After 155 seconds of interaction the *brachyptera* is completely inhibited from singing.

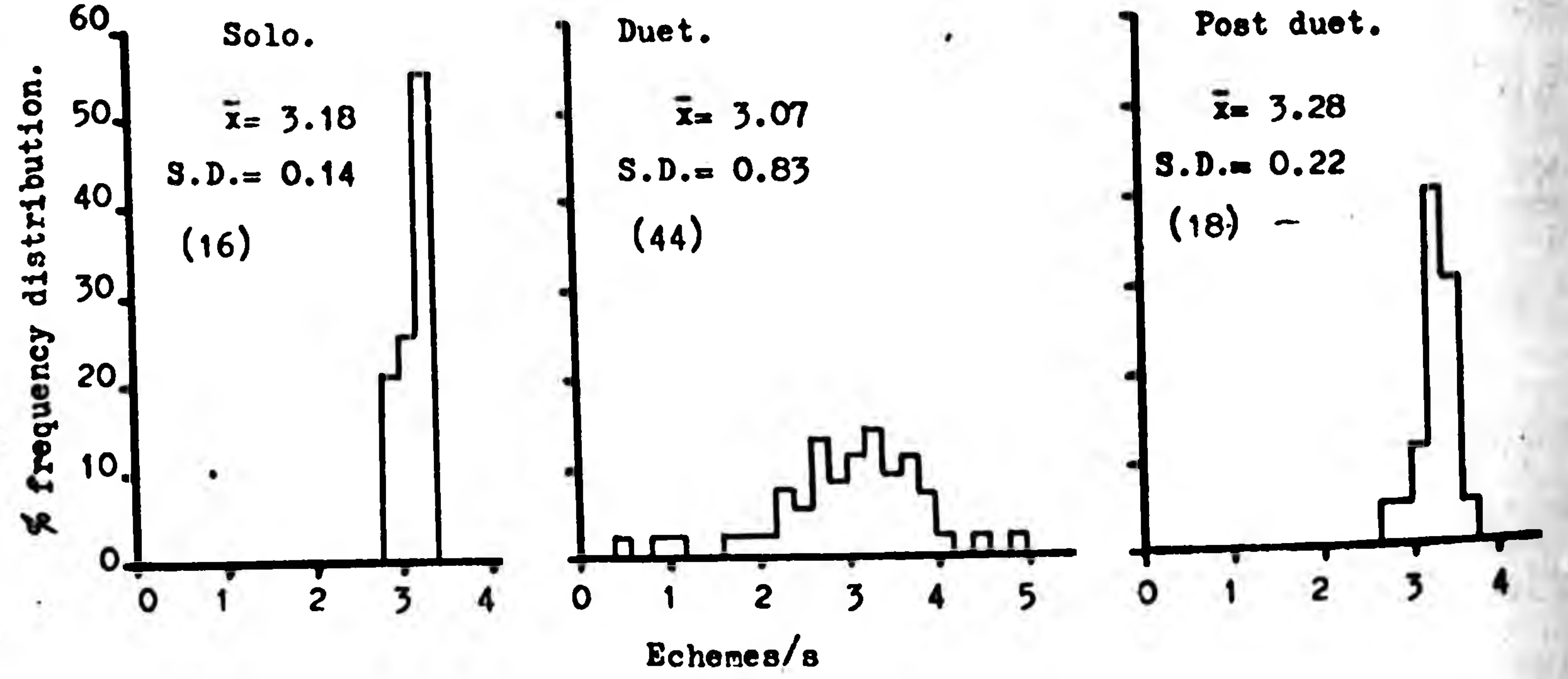
Fig. 51. THE EFFECT OF *M. ROESELII* ON THE SONG OF *P. INTERMEDIA*.

1. Syllables/echeme.

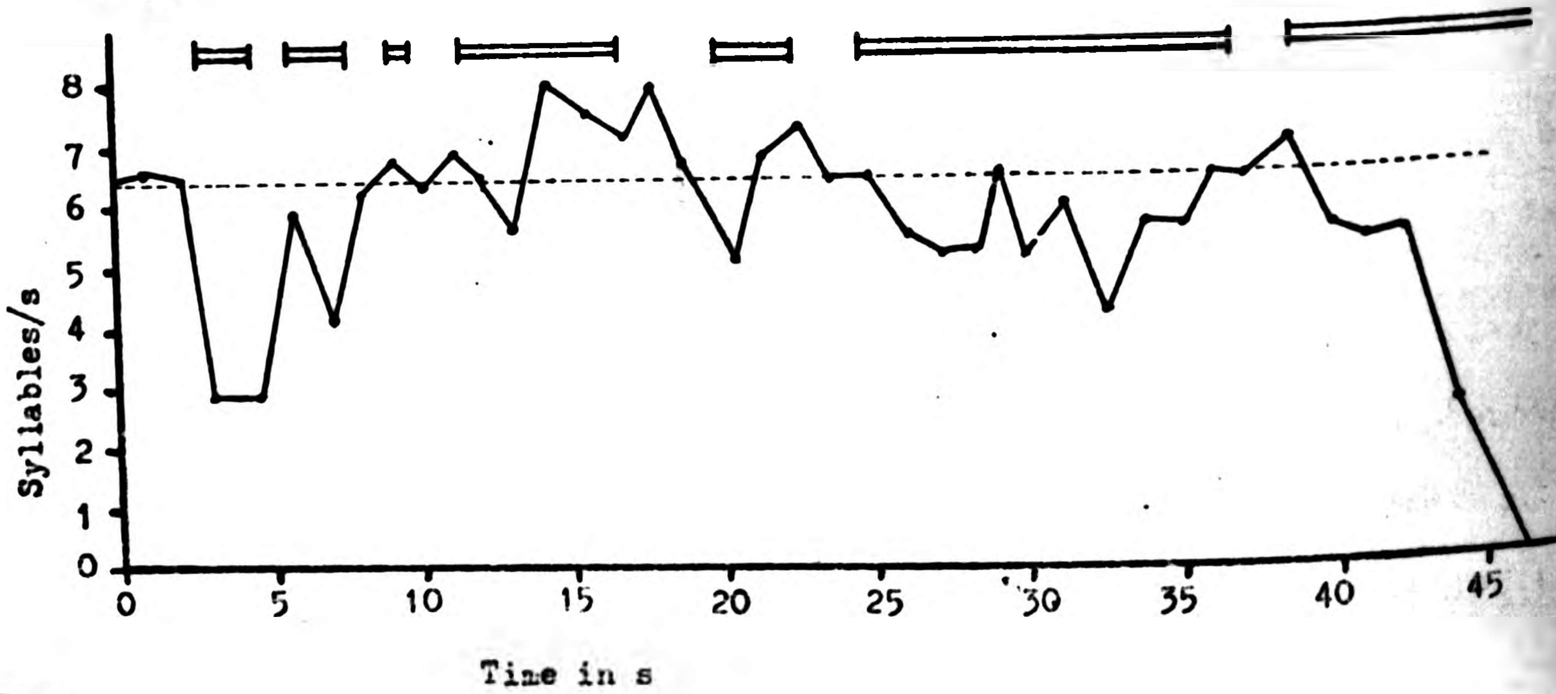


The number in brackets ( ) = No. of observations.

2. Echeme rate.



3. Rate of singing in syllables/s



4. The *P. intermedia*/*M. roeselii* Interaction

A recording of this interaction made by Broughton has been analysed to produce the data shown in fig. 51. Level recordings of sections of this interaction are also shown in fig. 48, where trace 3 indicates a large reduction in the echeme rate during the duet. However, as the interaction progresses the echeme rate during the duet increases to values that equal and exceed the value for normal solo singing. At this stage the normal disyllabic rhythm is modified: either, apparently, by an extra syllable being sounded in the echeme interval so producing a pentasyllabic echeme, or by echemes simply being extended to produce tri- and tetrasyllabic echemes. Where pentasyllabic echemes are produced the third (middle) syllable is often of lower amplitude (see trace 4 in fig. 48) so suggesting the derivation proposed above. When these long echemes are produced large peaks in the rate of singing occur as is shown in graph 3, fig. 51, e.g. at around 15 seconds on the time axis.

Later in the interaction the rate of singing during the duet is once again reduced, both as a result of a reduction in the echeme rate, and by the sporadic production of mono-syllabic echemes. Finally, after 45 seconds of interaction singing, this individual is inhibited.

The reaction by *P. intermedia* to the song of *M. roeselii* differs in two respects from the reactions shown by the other influenced species considered so far. Firstly, echemes can be either reduced or extended in duration during the duet. In this individual in fact, echemes are slightly shorter on average during the duet. Secondly, the echeme rate can increase during the duet to values above that of normal solo singing. This has not been observed in the duet singing of *P. albopunctata*,

P. sabulosa or M. brachyptera. A possible explanation for this is offered in the Discussion (p. 173).

5. The P. affinis/M. roeselii Interaction

The song of Platycleis affinis has already been analysed in detail by Broughton (1955) and Samways (1975, 1976a). A brief description of the song should therefore suffice for the following discussion. Unlike the other Platycleis species P. affinis does not sing with a regular tempo. The echemes themselves are extremely variable in duration, ranging from 0.5 s or less, to over 10 s, comprising two to seventy syllables. Usually echemes are amphimorphic, ending with five to ten microsyllables. An equally variable interval then follows until the next echeme is produced, (e.g. from 1 to 16 s). However, the frequency characteristics of the song are similar to those of the other Platycleis species. A low-frequency component is present at around 1 kHz (the pulse repetition rate) while the main high-frequency energy bands lie between 13 and 30 kHz.

A twelve-minute section of a recording of an interaction between P. affinis and M. roeselii has been analysed. The singing behaviour of P. affinis seems to be unaffected by the roeselii song. Echeme duration and their rate of production remain unaltered throughout the long or short emissions of roeselii song. The production of microsyllables at the end of the echeme seems to remain unchanged as does the syllable rate within the echeme. These considerations apply to both the duet and post-duet phases. Thus, in contrast to the other Platycleis species P. affinis is apparently able to sing quite normally in the presence of a singing roeselii. Affinis, however, normally sings in unison with conspecifics (see also p.173).

Table 30. The *P. albopunctata*/*G. glabra* Interaction

		Solo.	Duet.	Post-duet.
Albopunctata no. 1.				
Syllables/echeme.	$\bar{x}$	4.95	4.95	4.93
	S.D.	0.20	0.21	0.23
	N.	65	97	50
Echeme rate.	$\bar{x}$	1.84	1.80	1.85
(Echemes/s)	S.D.	0.30	0.21	0.19
	N.	62	65	45
Albopunctata no. 2.				
Syllables/echeme.	$\bar{x}$	4.09	4.19	4.10
	S.D.	0.36	0.42	0.47
	N.	68	109	102
Echeme rate.	$\bar{x}$	2.81	2.58	2.76
	S.D.	0.18	0.25	0.18
	N.	48	46	39

Albopunctata no. 2 reacting to the song of *M. roeselii*.

		Solo.	Duet.	Post-duet.
Syllables/echeme.	$\bar{x}$	4.08	5.26	4.97
	S.D.	0.35	1.10	0.66
	N.	40	37	30
Echeme rate.	$\bar{x}$	2.80	1.26	2.88
	S.D.	0.18	0.54	0.11
	N.	48	42	25

6. The *P. albopunctata*/*G. glabra* Interaction.

The song of *Gampsocleis glabra* provides an ideal control as the temporal parameters of its song are similar to those of *M. roeselii* while the spectral parameters are quite different (see fig.16, p.55). The primary, subjective impression is that the song of *G. glabra* has little effect on the singing behaviour of *P. albopunctata*, even when the insects are singing in close proximity. However, detailed analyses suggest that changes sometimes occur in the song of the *albopunctata*, although such changes are of small magnitude.

Table 30 shows data on interactions for two *albopunctata* individuals. The first individual shows virtually no change in syllables/echeme throughout the interaction. Similarly, the slight difference in the figures for the echeme rate reflect no significant difference between solo singing and singing during the duet and post-duet, (e.g. comparing solo and duet, $t = 0.88$, $p > 0.1$).

The singing of individual no. 2 seems slightly more affected by the song of *G. glabra*. The value for syllables/echeme during the duet is, however, not significantly different from that of solo singing ($t = 1.62$, $p > 0.1$), though the echeme rate during the duet is significantly reduced ($t = 5.1$, $p < 0.001$). This reduction, however, is seen to be of small magnitude when compared to the depression in the echeme rate that occurs when the same individual duets with *M. roeselii*, (see table 30). This *albopunctata* was frequently inhibited during its interaction with the *roeselii*. No inhibitions were recorded during its interaction with *G. glabra*.

After a duet with *G. glabra*, the singing of *P. albopunctata* shows no rebound. As the results have shown, a rebound in the echeme rate is usual during the post-duet when albopunctata interacts with M. roeselii. Thus the effects of the song of G. glabra on the singing behaviour of P. albopunctata appear to be negligible in comparison to the highly disruptive effects of the song of M. roeselii. This topic will be further discussed, in relation to other interspecific interactions, in the next section (p. 164).

DISCUSSION.

Before discussing the variation of song resulting from interspecific interactions, other sources of variation must first be recognized and, if possible, the effects on the song understood. Such sources of variation can be classified into the abiotic, e.g. temperature, humidity; or biotic, e.g. the acoustic, tactile, or other contact with another individual. A biotic source of variation that acts on the population as opposed to the individual is that which is genetic in origin, resulting in variation in physiology and morphology and thus to individual variation of song.

Most of the parameters of the song of P. albopunctata vary in a predictable manner with temperature. The rate of singing increases linearly with rising temperature, while syllable period and duration decrease. Walker (1975), analysing large quantities of such data concludes that the linear model provides the best fit for the observed data (as opposed to exponential changes of rate with temperature). The deviations from linearity seen here in the curves for syllable interval (fig. 4, p.32) are a summary of the slight deviations from linearity in either, or both, syllable duration and period.

Another more obvious change in the pattern of the song is the decrease in syllable number with increasing temperature, seen in many individuals (see fig. 3, p.30). The reason for this is obscure. It is possible that the singing of relatively long echemes at low temperatures generates internal heat thereby facilitating singing activity. However, an equally long echeme interval follows each echeme so that no overall increase in singing activity occurs. Such changes in syllable number recall the reverse situation in *Pterophylla camelifolia* where southern populations (presumably singing in warmer temperatures) have more syllables in the echeme than northern populations (Shaw 1966, 1968, Alexander 1968). Such comparisons may be inappropriate if these differences in *Pterophylla* are genetically determined as Alexander (1968) has suggested. However, it seems that the effects of temperature on the the echeme content of *Pterophylla* individuals has not been tested. No geographical variation has been observed in northern and southern *albopunctata* populations.

The effect of humidity on singing behaviour has not been investigated. Although Farnworth (1972) recorded small increases in wingbeat frequency in the cockroach as humidity decreased, Walker (1975) concluded that humidity had no appreciable effect on singing rate in various North American tettigoniids.

Variation in song between *albopunctata* individuals is appreciable, though it does not exceed certain species-specific limits (e.g. an eight-syllable echeme has never been heard from a solo singing individual). Within these limits, syllable number, duration and period are characteristic in each individual (see figs. 6 & 7, pp. 36-38). So too is the manner of song delivery, some individuals singing in discrete sequences while others sing continuously; often, however, showing a regular oscillation in singing activity (see p. 36). In any one individual such song parameters are very stable, particularly the syllable period, where any variation in syllable duration is followed by an equal and opposite variation in the interval, so maintaining a constant syllable rate. The echeme rate, however, is clearly much more variable (see fig. 6) by virtue of the echeme interval being plastic in nature. During intra- and interspecific interactions variability of the echeme rate is also emphasized, while the syllable rate remains unaffected by the acoustic input. Samways (1975, 1977c) demonstrates statistically the difference in variability between syllable rate and echeme rate in P. intermedia. These observations are consistent with the model of independent syllable and echeme oscillators that has evolved from the work of Ewing & Hoyle (1965), Bentley (1969a,b), Otto (1971) and Kutch & Otto (1972). The rhythmical firing of these pacemaker cells in the mesothoracic ganglion is largely independent of cerebral control (see review by Huber 1974). More recently, Bentley (1977) has demonstrated the functional independence of echeme and syllable oscillators in Gryllus by showing that the echeme rate varies linearly with the artificial stimulus frequency, while syllable rate and number remain unchanged. It is possible that syllables are generated by a continuously active pacemaker such as Simmons (1977) has shown to operate in a cicada with a discontinuous song. The rhythmic firing of interneurones inhibits the syllable train, so organising the song into echemes and echeme intervals (Bentley 1969b). It is these pacemaker cells that would be susceptible to acoustic input, so as to produce the extended, or shortened echeme intervals seen in intra- and interspecific duetting (see also Jones 1966a, Shaw 1968 and Walker 1969c for data on artificial acoustic stimulation).

No data are available on rhythms of longer periodicity that might control the length of song sequences. The even longer rhythms of diurnal singing activity are shown to originate from the supraoesophageal ganglion (Rence & Loher 1975).

Despite the constancy of syllable period within the individual this parameter can vary between individuals by as much as 20 ms (or 25% of the average population value; see fig. 7, p. 38). Other song parameters can show even larger individual differences. The high-frequency components of the song vary according to the size of the individual (the mirror frame in particular). This scale of variation raises the question: what are the important parameters of the song for intraspecific communication and how are these parameters perceived?

Cues used by the female in orienting towards the song of the male have been determined in many species. In some the frequency of the song appears to be unimportant as long as the temporal parameters are correct (see review by Dumortier 1963, Zaretsky 1972). However, in most of the species tested, to obtain the best phonotactic response, it was necessary for the carrier frequency to correspond closely to that of the natural song (Hill 1974, 1975; Popov et al 1975, 1977; Ulagaraj & Walker 1975). Superimposed over this requirement is the parallel need for at least one temporal parameter of the song to be correctly reproduced in the test signal. Different species require different parameters; it may be the echeme rate (Walker 1957), number of syllables per echeme (Dumortier 1963), syllable duration, or combinations of these parameters (Shuvalov and Popov 1973, Popov and Shuvalov 1977). In species where the song consists of a continuous trill the continuity of the signal or the syllable repetition rate may be the important factor (Walker 1957, Bailey and Robinson 1971, Popov and Shuvalov 1977). Character displacement of the female phonotactic response has been observed by Popov and Shuvalov (1977); these authors rightly stress the importance of the acoustic environment in determining the principal phonotactic parameters of a species song.

Parameters of the song of *P. albopunctata* that might therefore be important for female phonotaxis are the frequency spectrum, echeme and syllable rate, and quite probably the number of syllables per echeme. In the field the range of *P. albopunctata* meets the ranges of two closely related species that sing with echemes of 2 and 7 - 8 syllables, *P. intermedia* and *P. sabulosa* respectively. *Acoustic* sympatry (species being in acoustic range of each other), however, has not been demonstrated (see Samways 1976*c*) so the importance of syllable number in maintaining species-specific isolation must remain speculative.

Neurophysiological studies, e.g. Kalmring 1975 and Lewis *et al* 1975, show that broadcast syllables result in the firing of two main types of auditory neurones; one phasic, firing at the onset and, in some species, the end of the syllable (Lewis *et al* 1975); the other, tonic, firing throughout the duration of the syllable. Thus, syllable duration and rate are encoded and information is therefore available concerning echeme rate and duration. One possibility for the reactivity shown by *P. albopunctata* to the song of *M. roeselii* is that the *albopunctata* perceives the *roeselii* syllables, which are shorter, as conspecific aggressive syllables (see also McHugh 1971). The syllable repetition rate of the *roeselii* song, however, does not correspond to the syllable rate of the *albopunctata* microsyllabic echeme and in any case, *albopunctata* does not react aggressively to the song of *roeselii*. It is necessary, therefore, to seek other reasons for this interaction.

Less is known about the coding of the various frequency components of the song. In the crickets and bush crickets with resonant songs, as mentioned in the Introduction, the lower peak of auditory sensitivity seems sharply tuned to the frequency of the proclamation song. In these resonant singers little variation is seen in the value of the carrier frequency, e.g. in G. glabra the carrier frequency of 7 individuals tested was found to lie within the range of 11.5 to 14 kHz.

In non-resonant singers such as P. albopunctata, not only does the song consist of many more frequencies (i.e. the low-frequency component and a wide band of high-frequency components) but the peak frequencies of the song are extremely variable. Loher and Broughton (1955) noted similar variation in some acridid songs. Selection for constant size of the sound-producing structures seems to be relaxed in the populations studied so that individuals can be found with carrier frequencies ranging from 19 to 32 kHz. A hearing system sharply tuned to the average carrier frequency of 25 kHz would appear inappropriate as species-specific information would be lost. It is more probable that the whole of the broad-band spectrum is perceived and forms perhaps the first bit of information in the species-specific recognition process.

There is both behavioural and neurophysiological evidence that suggests broad-band reception in these bush crickets. Samways (1975) noticed that the singing behaviour of P. intermedia remained unaffected by the continuous song of a neighbouring Homorocoryphus nitidulus, a resonant singer at 16 kHz. P. intermedia, a broad-band singer with a carrier frequency of around 16 kHz, is however, adversely affected by the continuous song of M. roeselii which has a similarly broad-band high-frequency spectrum.

Recent work on the tettigoniid, Decticus verrucivorus (Rheinlaender 1975, Kalmring, Lewis & Eickendorf, in press) shows that the auditory system consists of many receptor units each with differing frequency and intensity responses. Their auditory threshold curves are generally V shaped; some of them show peaks that correspond to the frequency peaks of the song. The peak responses of other units are distributed fairly evenly along the frequency scale so that not only can the insect respond to a wide range of frequencies but also it is presumably capable of a reasonable degree of frequency discrimination. Thus, in addition to the broad-band songs of conspecifics, the insect may also recognize the calls of predators or detect the broad-band noise of disturbed vegetation (see Samways 1976d).

With these considerations in mind it would seem surprising if Nocke's (1975) theory applied equally to all tettigoniids. He suggests that the ear acts as a narrow-band receptor due to the resonance of the acoustic trachea (see Zeuner 1936), the dimensions of the trachea being such that resonance occurs at the peak frequency of the song (see also Paton et al 1977). Alternately, as would seem more adaptive, particularly in non-resonant singers or in species where body size is variable, this trachea may act as an exponential horn accepting a wide range of frequencies (Lewis 1974, Lewis et al 1975). Recently in crickets, Hill and Boyan (1977) have shown experimentally that tuning in the single ear does not depend on tracheal resonance but on unknown mechanisms at the receptor sites.

Rheinlander's (1975) study on Decticus affords an understanding of how a resonant song is distinguished from a non-resonant song with the same carrier. The broad-band song presumably stimulates peripheral units in addition to those responding to the carrier frequency. There is another possible way of differentiating these two song types. This is the presence in non-resonant songs of a low frequency component -

the tooth-impact rate, though Spooner (1968) considered this to be unimportant in species-specific recognition. The shape of the low-frequency sweep seems too variable in the Platycleis species for this parameter to be significant in intra-generic song discrimination. However, the shape of these sweeps in the two Metrioptera species seems to be fairly constant and species-specific and thus may carry information (see Broughton et al 1975). Bailey (1976) noted that the songs of Ruspolia (Homorocoryphus) species living in dense vegetation (forest-edge grasslands in Uganda) were non-resonant, the syllables consisting of discrete tooth-impact pulses. The presence of low-frequency components may confer distance information in dense vegetation as they are less prone to distortion and attenuation than are the high frequencies (Lewis, Seymour & Broughton 1975). Similarly, Morton (1975) finds that birds living in open grassland environments use songs with low-frequency temporal components, amplitude or frequency modulations; whereas birds of the forests use pure-tone songs. He suggests that use of pure-tone songs is selected against in open environments because of the rapid attenuation and distortion of high-frequency pure tones by air turbulence, wind and temperature gradients that are characteristic of open environments. Clearly the sound environment of a species must be considered in any attempt to ascribe functional significance to particular song parameters.

The low-frequency tooth impact component in the songs of certain bush crickets may therefore be selected to carry information. If so, then with regard to the extent of individual variation of the tooth impact rate, its reception would be facilitated by broad-band receptors. Alternatively, or as well, the function of the discrete tooth impacts may be to produce a species-specific broad band, high-frequency song spectrum. The importance of the high-frequency components in generating the appropriate tympanal response has been shown by the work of Howse et al (1971) and Lewis et al (1971). Subjecting M. brachyptera to an ultrasonic recording of its song, the authors obtained a good response from the tympanal nerve. Use of an 'audio' recording, in which the high frequencies were cut, resulted in a poor response.

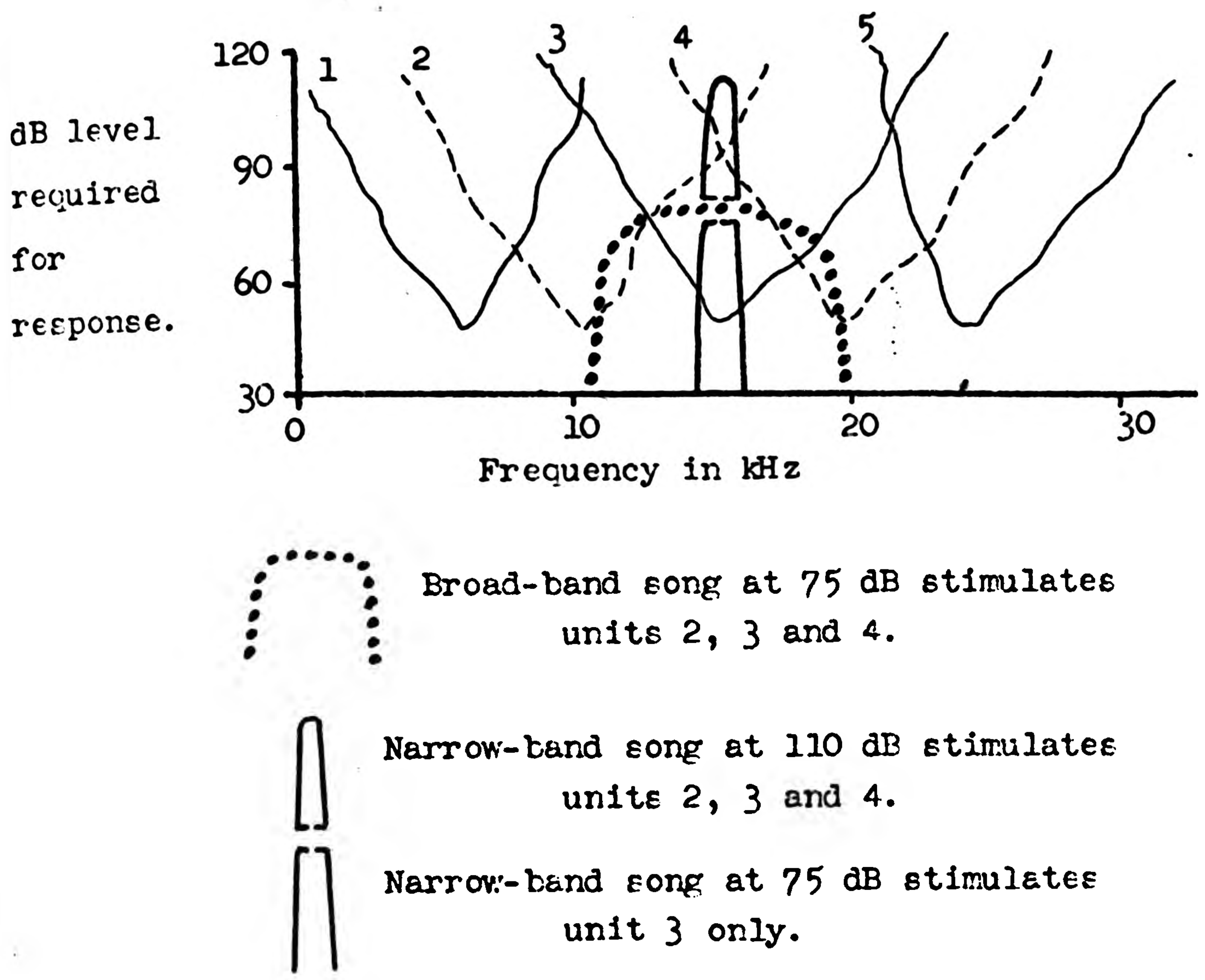
The broad band nature of the songs of the Platycleis and Metrioptera species studied here is further enhanced by the presence of other emphasized frequencies or changes in the carrier. It is not, however, clear how these are produced. The detailed movements of the mirror frame have been studied by Bailey (1970) and Bailey & Broughton (1970) in a resonant singer. It is possible that different modes of vibration occur in non-resonant singers, particularly as the morphology of the mirror frame varies, even between closely related species (see figs. 10, 18, 19). In species such as P. albopunctata and P. sabulosa where two similar emphasized frequencies can be produced (e.g. 23 and 28 kHz) two segments of the mirror frame may vibrate at different rates; e.g. the two heavily sclerotized, anterior and mediolateral mirror veins (corresponding to dimensions p and q in fig. 20). Such secondary emphasized frequences are not seen in the song of M. roeselii which has a circular mirror frame, but significant frequency modulation occurs in the carrier in this species. (See also Bennet Clark 1970, Bailey & Broughton 1970 and Pipher & Morris 1974 for further instances of frequency modulation). Morris (1970) notes that the two stridulation modes of M. sphagnorum, each with a different frequency spectrum, are obviously produced with the same tegminal apparatus. He suggests that the way in which the file and plectrum are engaged might affect the frequency content of the song (see also Morris & Pipher 1972). In this context it is noticeable how the V-shaped sweep of the high-frequency carrier in the song of *M. roeselii* correlates with the structure of the file (and therefore also with the shape of the low frequency sweep). Small, densely packed teeth produce the higher ultrasonic frequencies at the beginning and end of the syllable. The lower ultrasonic frequencies occur centrally where the teeth are larger (see fig. 19). Similarly, when file and plectrum engage on the faster, opening wing stroke, higher frequencies are produced. This suggests that the carrier frequency can be raised or lowered within certain limits by altering the amount of energy received by the emitter. The contact pressure between file and plectrum, the shape of the tooth (e.g. height) or the speed of the wing-stroke might serve to alter the amount of energy received by the system at a given tooth impact. As mentioned above, other structures may selectively enhance certain wavelengths from the wide range of frequencies produced by each toothstrike transient. Bailey & Broughton (1970) have suggested as sources of such resonances unknown structures in either tegmen or the roughly conical air space enclosed by the tegmina and the dorsal surface of the body during stridulation. Clearly, this is a topic for future research.

By whatever method, *P. albopunctata*, *sabulosa*, *M. roeselii* and *brachyptera* all produce broad-band frequency spectra with a virtually identical frequency compass. Assuming these species to have an auditory system similar to that of Decticus (Rheinlaender 1975) then it is likely that exactly the same receptor units are stimulated by each of these songs. In albopunctata, for example, the song of roeselii, in terms of the spectral aspect alone, carries the same information as does the conspecific song. The "attention" of the albopunctata is engaged so that it reacts to the roeselii as it might to the song of a conspecific. Due to the continuous nature of the roeselii song however, this reaction is itself modified as will be discussed later.

Spectral similarity of songs is therefore postulated as a primary reason for song modification. This was surmised by Samways (1975, 1976) for the P. intermedia/affinis interaction and is confirmed here by the use of G. glabra as an experimental animal. The two energy bands in this song lie immediately above and below the single ultrasonic energy band of P.albopunctata apparently allowing albopunctata to sing normally during an interaction. The song of G. glabra may well be perceived by the albopunctata (see Kalmring 1975, Rheinlaender 1975) but without exciting the appropriate neural centres as does the song of the roeselii.

Samways (1977a) noted however, that at very close quarters, i.e. within a few centimetres, the song of H. nitidulus could induce song modification in P. intermedia (see also p.159 this discussion). This is explicable, given that the auditory system consists of a series of frequency receptors with overlapping auditory response curves as shown by Rheinlaender (1975). It is possible therefore for a resonant song at high intensities to stimulate the same units as a non-resonant song, with the same carrier frequency. The following diagram should serve to clarify this argument.

Auditory response curves for five hypothetical units.



Assuming that species such as P. albopunctata and P. sabulosa react to the song of M. roeselii as they would to the song of a conspecific, then a detailed consideration of species-specific behaviour may throw more light on the phenomenon of song modification.

It is clear from the results that the conspecific duetting behaviour of P. albopunctata is not easily defined. When perfect alternation occurs this behaviour is directly comparable to the alternation of Pterophylla camellifolia in which, like albopunctata, the 1:1 ratio of echeme interval to duration of solo song results in the individual echeme rate being halved during alternation (Shaw 1968). From his studies it is clear that Pterophylla is a 'good alternator'; rarely do echemes overlap and the interval between the echemes of the two individuals remains relatively constant. By comparison therefore, *albopunctata* is a very poor alternator. When alternation does take place the model of mutual reciprocal inhibition proposed by Jones (1966a&b) for *Pholidoptera* seems entirely appropriate. Thus, a signal of the correct frequency sounded during the echeme interval acts to prolong that interval by inhibiting the oncoming echeme. The presence or absence of amplitude modulation in this signal does not appear to alter its inhibitory properties (Jones 1966b). As the song of *M. roeselii*, therefore, constitutes a continuous inhibitory signal, total inhibition of song might be expected in *albopunctata*. This is often seen; moreover, in *sabulosa*, a species showing a greater tendency to alternate than *albopunctata*, the song of *roeselii* generally exerts a greater inhibitory effect.

However, in both intra- and interspecific interactions the influenced insect shows adaptation to the song of the more continuous singer. Rowell & McKay (1969) have demonstrated a rapidly habituating auditory interneurone in an acridid, though adaptation is not seen in the tympanic nerve (Michelson 1966). This adaptation may be due to, or concomitant with, a gradual increase in excitation. The work of Jones (1966a&b, 1974) and Heiligenberg (1966, 1969) has shown that inhibitory signals can have a parallel excitatory effect on the insect nervous system. Thus *Pholidoptera griseoaptera*, a customary alternator, eventually interrupts a continuous, inhibitory artificial signal (Jones 1966b). A possible neurophysiological model for such behaviour comes from the work of Willows, Dorset & Hoyle (1973) on the escape response in *Tritonia*. Here, reciprocally inhibitory neurones exert parallel excitatory effects via a commonly connected excitatory neurone (see also Getting 1977).

The intraspecific duetting of P. albopunctata, however, cannot only be considered in terms of the inhibitory and excitatory effects of acoustic signals, for the effects of dominance generally become apparent as the duet proceeds. The net effect of this is that the song of the dominant becomes more continuous, the insect singing close to the normal solo echeme rate, while the song of the subordinate tends to become intermittent in nature. In species which alternate, the best criterion of dominance is overall singing activity; in particular, which insect starts the duet sequences (Busnel 1966, Shaw 1968). This was also observed in the dominant albopunctata individuals (see p. 83).

It is interesting that in albopunctata, the subordinate individual is able to interrupt the echemes of the dominant at any point. Interruptions by the dominant insect, however, become increasingly infrequent after the first 60 ms of the subordinate's echeme. As mentioned on p.82, this corresponds to previously published data on the auditory reaction in singing insects. For example, Jones & Dambach (1973) showed similar reaction times to inhibition in Gryllus. In this context, the 60 ms represents the time taken for transduction of the signal to the inhibitory centres in the insect's brain. Thus, an echeme may still be initiated during this period before inhibition operates. Similarly, an insect takes approximately 60 ms (this reaction time is temperature-dependent) to react to the end of an inhibitory signal and recommence chirping. Such a reaction time is seen in fig. 26 (p.81) between the end of the subordinate's chirp and the next echeme of the dominant albopunctata. The tendency of the subordinate to interrupt, or "break through" (Jones 1966) may be due to the excitatory effects of the relatively incessant song of the dominant. The subordinate may even be stimulated to chirp on hearing individual syllables in the echeme of the dominant, so synchronizing the onset of its echeme with any of the perceived syllables. Thus a multimodal distribution of interruptions by the subordinate is seen (fig. 25 graph 1, p. 80). An additional effect of excitation is seen in the relatively longer echemes of the subordinate. Shaw (1968) observed the same phenomenon during the aggressive duets of P. camellifolia; the individual with the reduced echeme rate sang relatively longer echemes. In Pholidoptera such excitatory effects may result in individually increased echeme rates by alternating males (Jones 1966). An increase above that of solo singing is possible during alternation in this species as the ratio of echeme interval to echeme duration is very high. During the albopunctata duets, however, the excitatory effects seem to operate in one direction, from dominant to subordinate, probably due to the differential in singing activity. Thus, the subordinate receives more excitatory stimuli than it broadcasts, and, as a result of its reduced singing activity, probably suffers a net increase of unreleased motivational energy. An accumulation of motivation to sing is suggested also in solo singing where sometimes, after a sequence interval, the first echeme includes microsyllables, indicative of a high state of excitation. It seems as though motivation increases during the sequence interval and "overflows" during the first echeme of the sequence.

This type of unison singing in albopunctata, where echeme length and often syllable length are obscured, would seem to be disadvantageous if these parameters are important for female phonotaxis (see review by Alexander, 1975). In fact, in the field, intraspecific duetting was rarely encountered in the populations studied, since the males were regularly spaced in the habitat. When singing males were found together the dominance-subordinance relationship was evident. It would seem advantageous, if the subordinate is to compete for females effectively, for it to move away from the acoustic influence of the dominant. Since juvenile males are randomly distributed, the singing activity of the adults is at least one factor governing regular spacing. Moreover, in dense vegetation, where song suffers greater attenuation, males are found closer together than in sparse vegetation. Acoustic repulsion between singing conspecifics is, however, difficult to demonstrate in the laboratory; males in a 100 x 12 x 12 cm cage appeared attracted by singing activity. However, five males released into a 3 x 1.3 m cage overlying natural vegetation distributed themselves regularly within two days. Morris (1967, 1971) has demonstrated positive phonotaxis by male conocephalines to the conspecific song, yet field populations of these males are territorially dispersed. Morris suggests that males perceiving a song above a certain intensity threshold are stimulated to approach. Males beyond this critical distance are either acoustically repelled, or they may simply fail to respond to the low intensity song. Another reason for unresponsiveness may be the progressive lowering with distance, of the frequency spectrum of the song due to attenuation (see fig.47,p.140). In the conocephalines, male encounters are distinctly aggressive in nature and result in the silent withdrawal of the loser, leaving the victor singing in the original territory. Subordinate males must therefore undergo a change of responsiveness to the song, i.e. from attraction to repulsion. Similar behaviour can occur in M. roeselii (Zippelius 1949, Morris 1971, McHugh 1971).

No such fighting behaviour has been observed in P. albopunctata. It may be that the subordinate individual suffering the greatest degree of song modification simply moves away from the continuously singing dominant. If this is so, then the negative phonotaxis shown by this species to the song of M. roeselii is a clear case of preadaptation; a response derived from an existing behavioural pattern. The song of roeselii may, in its continuity, represent an exaggerated version of the song of a dominant albopunctata. Thus, it may constitute a supranormal stimulus (Tinbergen 1951) and so produce the often rapid responses observed (see table 25, p.131). If this reasoning is correct, then it follows that males react primarily to the frequency content of the song. The amplitude modulation pattern may not be necessary for male spacing behaviour. This behaviour can be seen to be adaptive in the case of P. albopunctata, for males remaining in the acoustic field of M. roeselii (as a result of song modification, inhibition, or simply through their songs being masked by the continuous singing of the roeselii) probably attract few females.

Intraspecific duetting in P. sabulosa is very similar to that of P. albopunctata. In the pair studied, however, the subordinate not only sang less than the dominant but was inhibited by its echemes. This contrasts with the behaviour of albopunctata in which the subordinate, though singing less than the dominant, is not inhibited by its echemes. Instead, the subordinate interrupts the echemes of the dominant (see

p. 98). This difference shown by the sabulosa pair may have been due to an individual trait. Alternatively, it is possible to speculate that this slight difference in behaviour has a phylogenetic basis. P. albopunctata may have evolved from a species with a short echeme, sung in synchrony by duetting or chorusing individuals (as in Oecanthus, Walker 1969; and P. intermedia, Samways 1975,1976a). A subordinate albopunctata having possibly a vestigial reactivity to the echemes of the dominant might therefore be stimulated to synchronize. P. sabulosa possibly evolved from a species with a long echeme, sung in alternation by neighbouring individuals. In this case therefore, the subordinate would be inhibited by the echeme of the dominant. Despite the similarity in song between these two species, they are not considered, on morphological grounds, to be especially closely related (S.E.Thomas, Ph.D. thesis in preparation, London University).

It seems not unreasonable to propose that the Platycleis species evolved from an ancestor that occupied a three-dimensional habitat such as bushes and shrubs. Such a habitat requirement would be likely to impose a clumped distribution on the population and, like many present- day species which occupy this habitat, the ancestral bush-cricket might alternate or synchronize echemes. In Europe, man's activities have resulted in an increase in the grassland (a two-dimensional) habitat, and provided an opportunity for some species to extent their range into this. The responses controlling alternation and synchrony would then be relaxed in association with the tendancy of males to space themselves out in this homogeneous habitat. Regular distributions are commonly found in animals living in habitats where resources are spread evenly over a large area (see Emlen 1973). Thus ground dwelling crickets are usually territorial (Alexander 1960,1961), acridids generally restrict their movements to 'home ranges' (E.J.Clark 1948, Chapman 1962, D.P.Clark 1962, Young 1971, Otte & Joern 1975). In such habitats regular spacing of males probably serves to maximize the number of successful matings both by virtue of an increased probability of any female being close to a male and by reducing the chances of interference from other males during the mating sequence, the process of which can be prolonged (see Alexander 1961, Gwynne 1977). For these reasons species where males remain in close acoustical contact and alternate or synchronize chirps nevertheless maintain an area of 'personal space' (see Marler & Hamilton 1966) which is defended by means of aggressive behaviour sometimes including aggressive songs (see Busnel 1966, Jones 1966, Shaw 1968, Bailey 1976, Samways 1976b). The Platycleis species have apparently, in the localities visited, extended this space so that individuals are dispersed beyond the range where songs interact. The results of marking experiments on albopunctata (see p. 84) suggest that, for most individuals, this space is not fixed to a particular location, for males seem quite mobile, particularly earlier in the season. Other workers have similarly found that 'territorial' orthopterans often move their location after a variable period of time (Morris 1967, 1971, Otte & Joern 1975).

The acoustic behaviour of M. trachyptera has not here been studied in as much detail as that of the Platycleis species. Observations of duetting insects in the lab and visits to natural populations in the field leave the impression that the acoustic behaviour of this species is very similar to that of P. albopunctata. Its reaction to the song of M. roeselii is certainly very similar to that shown by albopunctata (see also p.145, and McHugh 1971).

Synchronous singing in P. intermedia has been investigated by Samways (1975, 1976a). The principal mechanism by which synchrony is maintained is by the follower extending its echeme interval in response to its perception of the first syllable of the leader at least 50 ms (reaction time) before its own echeme is sounded. Similarly, Walker (1969) showed that in Oecanthus fultoni, an artificially broadcast echeme perceived late in the echeme interval (i.e. immediately preceding the experimental insect's echeme) resulted in the following echeme interval being reduced. Echemes broadcast early in the echeme interval, however, resulted in that interval being extended. Samways (1976a) notes that intermedia can also shorten the echeme interval, thus increasing the echeme rate and maintaining synchrony with an individual singing at a faster rate. These responses are also seen when intermedia reacts to the song of M. roeselii. Here, unlike the previous species considered, echeme rates can be either reduced or increased during the duet (p. 149). Extended intervals are often produced during the initial phase of the duet, probably in response to the perception of roeselii song during the echeme interval. Reduced echeme intervals often occur in the later phase of the duet and thus may be due to excitatory effects of the spectrally similar roeselii song. Very similar effects are seen in the response of intermedia to the song of P. affinis (Samways 1975, Samways & Broughton 1976)

Thus the responses of those species that modify their songs when duetting with a conspecific are also seen in interspecific duets, if the frequency spectrum of the allospecific's song is similar. Species that do not modify their songs intraspecifically but tend to chorus in unison show no change in singing behaviour in interspecific interactions (e.g. the M. roeselii/P. affinis interaction, p.150) even though the frequency spectra of the songs may be similar.

However, it is clear that the songs of the species studied by Broughton (1965), McHugh (1971), Samways (1975, 1976) and in this thesis also show changes resulting from interactions with allospecifics, that are not found during solo singing or intraspecific duetting. These effects are specifically the long periods of complete inhibition of song and secondly, the occurrence of long polysyllabic echemes.

There is clearly much individual variation in the responses of influenced species to influencing species, a point also stressed by McHugh (1971). He found many M. brachyptera and M. bicolor individuals were easily inhibited by the song of roeselii while others were able to duet with varying degrees of 'success'. The same is true in the case of P. albopunctata. This species also, in a recording by Broughton, showed complete inhibition to the song of P. affinis, a species with a slightly lower, though broadly overlapping song spectrum (see Samways 1976a). The albopunctata resumed singing during the intervals of affinis but showed no rebound in singing activity. Possibly motivation was low in this individual. Furthermore, the larger physical size of the affinis may, in addition to its song, have exerted a dominance effect over the albopunctata.

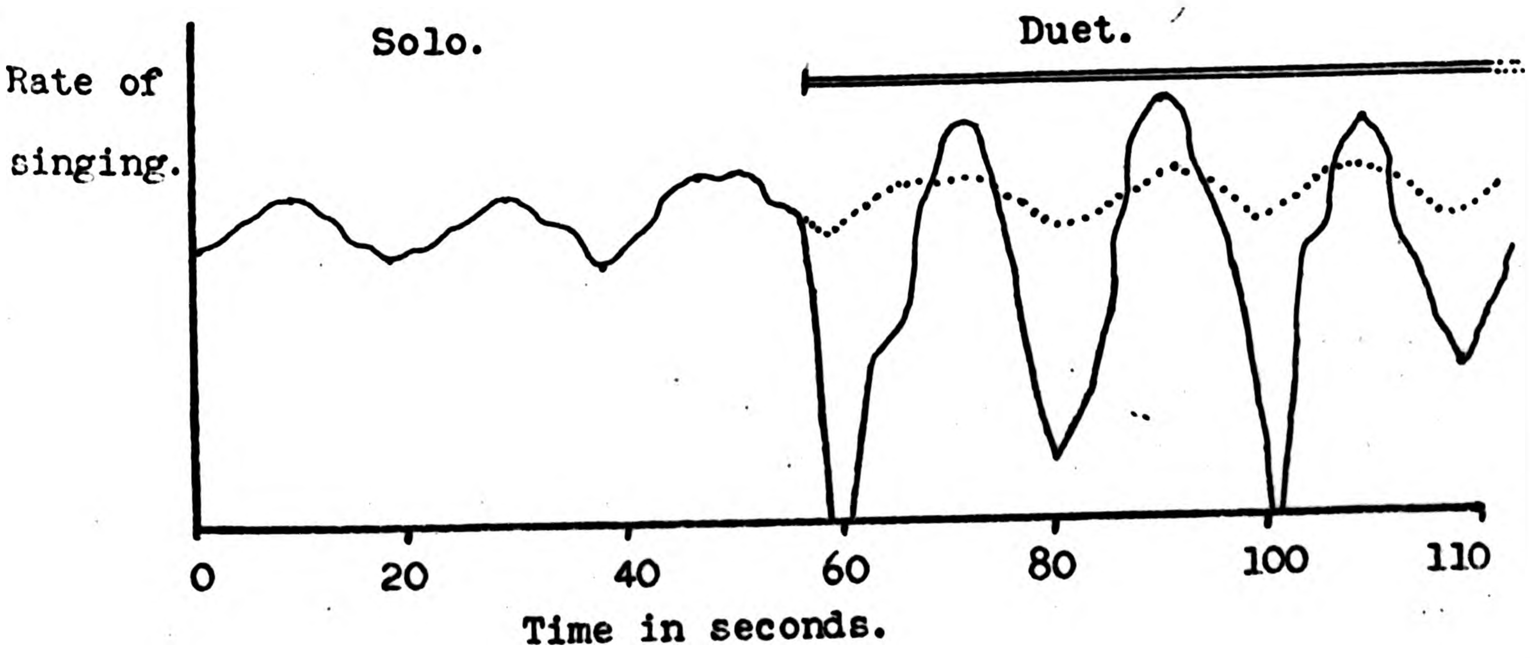
Other individuals, however, may duet with the influencing species in a manner characteristic of that individual. One such characteristic is the increase in echeme length in most individuals. Six-, seven-, and eight-syllable echemes are common; some individuals show a greater increase (Broughton 1965). The similar phenomenon in Pterophylla camellifolia where the insect increases its echeme duration in response to broadcast echemes of increasing duration was interpreted by Pierce (1948) as a form of psittacism. In the case of polysyllables produced by albopunctata, one of Broughton's (1965) suggestions was that the continuous song of the roeselii may interfere with a process of auditory feedback resulting in a form of stuttering (analogous to the Lee effect in humans, Lee 1950). However, it is not known if feedback is necessary for either song development or normal singing behaviour. Alexander (1968) destroyed the typanal organs of a nymphal Oecanthus fultoni which nevertheless, when adult, produced normal echemes except for one small detail; the tegmina engaged also on each opening stroke. Thus the syllables comprised two hemisyllables. This has occasionally been seen in young untreated albopunctata and sabulosa adults which first show singing activity around ten days or longer after the terminal moult. This type of singing, which may in addition be unusually low in intensity, soon gives way to normal singing where the opening strokes produce no sound. Similar results were observed in two albopunctata specimens in which the tympanal membranes were pierced before singing activity commenced. The stridulatory file was removed from two young adults which nevertheless developed and continued to show the appropriate but silent tegminal movements. These brief experiments suggest that auditory feedback is not required for development or maintenance of the basic song pattern though there does appear to exist, in some individuals, a period of consolidation in which coupling of file and plectrum is improved. Proprioceptive feedback, from sensory hairs on the tegmina (Popov 1971, Moss 1971) may therefore be operating during this period.

During this phase, Pterophylla may produce long echemes (e.g. seven syllables or more). After a period of three weeks songs have stabilized at around two to four syllables (Shaw 1975). This phenomenon has not been observed in Platycleis.

Alexander (1960) and Shaw (1968), like Pierce, were able to induce *Pterophylla* to increase its echeme duration in response to artificial signals. Alexander (1968) suggested that this was due to rebound excitation resulting from inhibition. Thus, within limits, the response duration was proportional to the inhibition time. This mechanism may operate in *albopunctata*, perhaps in the initial stages of the duet with *roeselii*, when echeme interval and duration may increase. However, other factors must be involved, for as the interaction progresses the echeme interval decreases while echeme duration increases (see fig.34, p.104). Heiligenberg (1966, 1969) in his studies on duetting in *Acheta* identified two forms of excitation, one phasic with a half-life of two seconds (this form of excitation possibly operates in the song modification shown by *Pterophylla*); the other, tonic, occurring particularly when the stimulus rate is high, has a half life of up to 140 seconds. Jones (1966, sub 1975) indicates that these two modes of excitation also occur in *Pholidoptera griseoaptera*, tonic excitation being evident when one partner stops singing and the other continues at a faster rate than in normal solo singing. This seems directly analogous to the post-duet rebound in singing activity seen in interspecific interactions.

Thus, to sum up so far; the song of *roeselii*, as it affects a singing *albopunctata*, may exert parallel phasic excitatory and inhibitory effects that serve to prolong the echeme interval and possibly also stimulate the production of echemes which may show an increase in duration. The continuous nature of the *roeselii* song would appear to amplify these effects over and above that seen in intra-specific duetting. In addition there appears to be a cumulative, tonic excitatory effect which becomes apparent at the post-duet (particularly after long duets) and often during the duet. This long-term excitation may also have parallel depressant effects leading to repeated inhibitions and finally to complete inhibition. This was often observed by McHugh (1971), and during this study.

A further complication in the *albopunctata*/*roeselii* interaction is that these externally imposed effects appear, in most individuals, to be operating on an endogenous rhythm of motivation. This is suggested where the rate of singing of some *albopunctata* individuals becomes cyclical as the duet progresses, the cycles being of similar periodicity to those seen in solo singing (see p.36). The parallel excitatory and inhibitory effects of the *roeselii* song probably serve to amplify this endogenous singing rhythm in *albopunctata*. The excitatory component acts preferentially when motivation to sing is increasing. Thus, singing activity is elevated to levels above that of normal solo singing. The inhibitory component acts preferentially when motivation is decreasing serving to further depress singing activity. This effect can be illustrated graphically.



The results of the multiple linear regression analysis (p.117) are in keeping with this hypothesis. When motivation in *albopunctata* is high, interruptions by *roeselii* result in a relatively small depression in the rate of singing which is then usually followed by supra-normal singing activity including the production of polysyllabic echemes. Cessation of singing by *roeselii* when motivation in *albopunctata* is high results in a high rate of rebound singing, again, often with polysyllabic echemes. At these times excitation by the *roeselii* song is predominant over inhibition. Conversely, when motivation is low, inhibition is predominant over excitation so that interruptions cause large depressions in the rate of singing, and little rebound singing activity is seen at the end of the duet.

Samways (1975, 1977c) may have been observing a similar phenomenon when, by examining the echeme parameters of *P. intermedia*, he was able to predict the type of ensuing interaction with *P. affinis*. If, immediately prior to interruption by *affinis*, the echeme interval of *intermedia* was relatively long (i.e. low rate of singing) *intermedia* was subsequently inhibited. Duetting between the two species occurred when the echeme interval of *intermedia*, prior to interruption, was short (high rate of singing). However, Samways searched for, but failed to find cycles in the solo rate-of-singing of *intermedia* and therefore suggested that the cycles of duetting and inhibition during the interaction were a result of the periodic emissions of *affinis*. An inhibition would be followed by a post-inhibitory rebound in the rate of singing of *intermedia*. Its motivation would now be sufficient to enable the insect to carry on singing throughout the next emission of *affinis*. Motivation would then decrease resulting in another inhibition, and so on. Clearly similar principles are involved to those in the albopunctata/roeselii interaction.

The singing activity of albopunctata in response to the roeselii song stimulus also seems to be paralleled by the flight activity of the aphid in response to a periodically presented landing-target stimulus (see Kennedy 1974 et ante). This is perhaps not surprising as song production and flight are likely to have a common neuronal basis (Elsner 1974). Presentation of the target inhibits flight by eliciting the landing response. Brief presentations of the target (which could be swung out of view thus preventing actual landing) reduced flight activity during the actual presentation but resulted in a 'post presentation' rebound to higher flight activity. Presentation of the target exerts excitatory and inhibitory effects on flight activity. The response observed depended very much on the antecedent behaviour. After a long flight, target presentation deeply depressed flight activity (this seems comparable to inhibitions produced by roeselii when the rate of singing of albopunctata is decreasing at the end of a song sequence). When the aphids had already been induced to reduce flight activity by prior presentations of the target, the test presentation served to increase flight activity. Motivation to fly had presumably been increased by inhibiting flight prior to the test so that the excitatory components of the test presentation predominated. This seems analogous to the increase in singing activity in albopunctata resulting from an interruption by roeselii when the rate of singing by albopunctata is increasing.

The production of microsyllables by some albopunctata during the interaction is a further indication of the excitatory effects of the *roeselii* song, inasmuch as production of these syllables is normally limited to more or less aggressive intraspecific encounters. During interspecific duetting these microsyllables are particularly associated with the post-inhibitory phase and are presumably an expression of excitation that has accrued during the phase of inhibition. Excitation was more evident at higher temperatures (McHugh 1971 observed that *M. brachyptera* was easily *inhibited* by *roeselii* at *low* temperatures). Though the number of individuals producing such microsyllables were few, the reduction frequently seen in some syllable durations during the duet and post-duet (fig. 41, p. 123) suggests that echemes are often modified *in the direction of* the microsyllabic echeme. Similar echemes are produced by *intermedia* in response to the song of *affinis* (Broughton 1965, Samways 1975, 1976*b*). It is likely that similar processes are operating during this interaction.

Work on the role of the brain in insect communication (see review by Huber 1974) provides some evidence in support of the theories on inhibition and excitation derived from behavioural work (Kennedy 1974 *et ante*, Samways 1975, Moorehouse et al 1978). Otte (1971) was able to elicit proclamation song in *Gryllus* by stimulating the brain. Higher stimulus rates or intensities produced courtship or rivalry song. However, males already singing the proclamation song required less stimulation for the production of rivalry echemes, suggesting that excitation is additive. It was also possible to inhibit song by brain stimulation. When the inhibitory stimulus was lifted, a post-inhibitory rebound in singing activity was observed. At the neuronal level, post-inhibitory rebound-activity has been demonstrated by many workers (Sherrington 1947, Maynard 1961, Bullock & Horridge 1965, Perkel & Mulloney 1974). The resulting excitation may be cumulative (Maynard 1961). Thus the lack of rebound excitation may contribute towards the total inhibition of albopunctata when singing by roeselii becomes more continuous, thereby reducing the number of opportunities for post-duet rebounds (see for example, fig. 39, individual f). As mentioned previously, artificial stimulation does not modify syllable rate (Huber 1974, Bentley 1977).

In all the interspecific interactions where roeselii has been used as the influencing insect, the results of excitation are manifested by the production of polysyllabic echemes during the duet and post-duet. In the P. affinis/intermedia interaction, however, polysyllabic echemes are typical of the post-duet and are not often produced during the duet (Samways 1975). P. intermedia, being a synchronous singer, may therefore not be so subject to phasic excitation resulting from inhibited echemes, as are alternating species. Alternatively, the echemes of affinis may be too short in duration for excitation to predominate over inhibitory effects until after the cessation of affinis song. This idea is supported by the occasional occurrence of polysyllabic echemes in the duet song of intermedia towards the end of a long affinis echeme. Samways (1975, 1976a) has suggested that the similarity between the syllable parameters of affinis and intermedia might result in the syllables of affinis exerting a stabilizing effect on the disyllabic echemes of intermedia during the duet. This seems especially valid in the light of the polysyllabic echemes produced by intermedia during the duet with M.

roeselii (see p. 148).

A brief survey of reported interspecific interactions in bush crickets can now be attempted with the hypotheses suggested in this study borne in mind.

In 1930 Baier noticed that *Pholidoptera griseoaptera* was inhibited from singing during the long song-sequences of *Tettigonia viridissima*, singing in the same cage. Both insects have very broad high-frequency spectra. Though the energy peaks differ, there is nevertheless a large degree of overlap (Dubrovin & Zhantiev 1970). Thus the song of *T. viridissima* might, at high intensities, be expected to inhibit *Pholidoptera*, a rigid alternator (Jones 1966).

The interaction between *Orchelimum bradleyi* and *O. militare* seems similar (Fulton 1934). The former, a species alternating discrete echemes, is inhibited by the latter, a continuous singer. Busnel (1956) noted that members of the *Ephippiger* genus which alternate with conspecifics also show interspecific alternation. Detailed frequency analyses are not available for these species. It is likely, however, that congenerics have similar frequency spectra (Loher & Broughton 1955, Bailey & Robinson 1971, Dubrovin & Zhantiev 1970, Samways 1976*a*).

Alexander (1975) reports very briefly a rather puzzling interaction between *Neoconocephalus exiliscanorus* and *N. nebrascenis* (species with identical frequency spectra, Alexander 1956). Here the latter inhibits the former though both species show an imprecise synchrony between conspecifics (Alexander 1956). This interaction may be similar to the *affinis*/*intermedia* interactions in which *intermedia* is silenced by *affinis*. The echemes of *exiliscanorus* are relatively short and repeated regularly (like *intermedia*), while the echemes of *nebrascenis* consist of long syllable trains in which the syllable repetition rate is double that of *exiliscanorus*. Once again the influencing species is the more continuous singer.

Many of the interactions observed by Broughton (1965) can be at least partially understood given a background knowledge of the species' normal acoustic behaviour. Species that alternate or synchronize show modifications in the echeme rate as a result of 'attempts' to retime echemes to an inappropriate stimulus (see also Samways & Broughton 1976) Echeme extension is uncommon unless both insects are chirping at a high rate (Samways & Broughton 1976), or the song of the influencing species consists of long syllable trains. Continuous song, by its very nature, seems to exert the greatest inhibitory and excitatory effect on discontinuous (i.e. chirping) singers. Motivational states can also determine the type of interaction observed.

During this study no instances were recorded of the songs of influenced species affecting the song of *M. roeselii*. This is consistent with the ability of *roeselii* to chorus in unison with conspecifics with no resulting song change. However, Broughton (pers. comm.) has observed occasions where *roeselii* has been temporarily silenced by the onset of song from *albopunctata*, while McHugh (1971) observed that *roeselii* could be inhibited by the equally continuous song of *M. bicolor*. These inhibitions may be due to 'startle responses' or they may reflect the type of behaviour that can occur in an intense interaction between a caged dominant-and-subordinant *roeselii* pair where the subordinate may be inhibited from singing (McHugh 1971).

The ecological consequences of the disruptive effect of *roeselii* song on the singing behaviour of *P. albopunctata* are most interesting. Both species often occupy the same vegetation: in such areas the nymphs may be found in the same grass tuft. The negative phonotaxis of albopunctata males to the song of roeselii would seem to be the mechanism maintaining interspecific spacing between the adult males. As the distance between interacting insects increases, the severity of song modification in albopunctata decreases, as fig. 43 (p. 128) shows. The rate of singing shows a uniform increase with increasing distance between the two singers, due to the increase in the echeme rate. However, the echeme duration remained greater than normal throughout the distances tested. It is interesting to speculate therefore, that tonic excitation is a function of the frequency of the roeselii song, while inhibition (and therefore probably phasic excitation) is a function of the intensity of that signal. In the laboratory low-intensity roeselii song occasionally stimulated hitherto silent albopunctata or sabulosa individuals to duet.

In the field the disruptive effects of the roeselii song are further reduced by vegetational attenuation. Thus, the interspecific separation of males is generally on a small scale; the mean inter-specific nearest-neighbour distance is only slightly greater than that found between albopunctata males. Nevertheless, this is apparently sufficient to exclude albopunctata from areas of high roeselii density (see fig. 44) where nearest-neighbour distances between roeselii males ranges from a half, to a little over one metre. When this distance exceeds three metres then, depending on the density of the vegetation, it is possible to find an albopunctata male interdigitated between roeselii males.

Thus, albopunctata can be excluded from areas of prime habitat as a result of competition for wavelengths on which to broadcast song. One wonders how strong this type of competition might be between species which broadcast song on similar wavelengths. Samways (1977a) found that the song of P. intermedia was modified in the field by affinis, but detected no tendency for the intermedia to move away from singing affinis individuals. This might be because intermedia males show no tendency to space out so as to reduce intraspecific acoustic interference. Neighbouring males instead synchronize their echemes (Samways 1975, 1976a). If the incidence of song modification is high the reproductive efficiency of the species may be impaired. Adaptations that result in the separation of the two interacting species, or their times of singing, may therefore be selected for. For example, albopunctata and roeselii are sympatric in many localities throughout France. Often, however, the populations are, strictly speaking, contiguously allopatric, e.g. roeselii occupying valley bottom grasslands adjacent to albopunctata populations on the hillsides. A boundary such as a road may serve to separate populations which are otherwise occupying the same vegetation. The behaviour of albopunctata in response to acoustic interference may prevent overlap of populations in these localities. As roeselii is flightless, population dispersal must be very slow. This probably prevents albopunctata from being ousted from favourable habitats in areas of sympatry.

Mechanisms that appear to prevent potentially dysgenic interspecific interactions have also been observed in frogs (Littlejohn & Martin 1969) and birds (Cody & Brown 1969, Ficken, Ficken & Hailman 1974). Here, temporal separation of acoustic emissions prevents interference. Similarly, alternation of song phrases by neighbouring males facilitates maximum information transfer within white-throated sparrow populations (Wasserman 1977).

As a complete antithesis, Counter & Henke (1977) have suggested that a form of acoustic commensalism occurs in two sympatric bush-cricket species. The two species have similar high-frequency spectra but the song of one is of a higher intensity. The authors suggest that the song of the louder singer, *Neoconocephalus robustus* might also attract *N. ensiger* females into the general area of sympatry. The softer song of *N. ensiger* with its species-specific syllable repetition rate might then be perceived by *ensiger* females. This contention, however, remains to be demonstrated experimentally.

Instances of song interactions may continue to be found, particularly in the light of man's increasingly disruptive effects on natural communities. For example, Samways (1977*b*) ascribes the occurrence of song interaction between *affinis* and *intermedia* to farming activities which cause atypical population movements of *affinis*. While the *albopunctata* and *roeselii* populations do not appear to be affected by present-day agriculture it is possible that over the centuries man's farming activities have modified the regional distribution patterns of these species. For example, *M. roeselii* is typically found in moist lowland or valley grasslands. Therefore, this species may have originally been absent from the limestone uplands. The process of forest clearance on the Causse created the open grassland habitat; the building of roads into the region would create potential 'corridors' for population movement along the grassy roadside verges and hedgerows into the upland grasslands. In this way an essentially lowland species can extend its range into the hills so becoming sympatric with upland species such as albopunctata. However, roeselii populations must be adversely affected by grass cutting, for this species lays its eggs in grass stems, in contrast to albopunctata which lays its eggs directly into the ground (Lewis & Broughton, in press). This dependence on uncut grass, in addition to its flightless condition, must reduce the rate of population dispersal of roeselii, especially in areas which are heavily farmed. The Causse grasslands, however, are relatively undisturbed.

When roeselii and albopunctata populations become broadly sympatric, acoustic allopatry must be restored when adults commence singing, in order to maximize the reproductive potential of the albopunctata populations. It is clear that the occurrence and possible ecological consequences of acoustic interactions between species should now be considered in theories of the evolution of animal communities and the communicatory systems of the animals within them.

CONCLUSIONS.

1. Variation in the song of P. albopunctata has been examined. The extent of individual variation in the spectral parameters suggests that the auditory system functions as a broad-band receptor, rather than a finely tuned, narrow-band receptor. Neurophysiological evidence is accruing to support this view. P. albopunctata is therefore responsive to the spectrally identical song of M. roeselii Insects with dissimilar song spectra are unlikely to interact acoustically.

2. Studies of intraspecific duetting in albopunctata reveal a complex set of responses that not only change with time but also differ between the two individuals. Alternation of echemes may occur due to reciprocal mutual inhibition. Generally, however, duets resolve into interactions where the dominant individual sings steadily and the subordinate sings infrequently. Echemes of the dominant are still susceptible to delay due to the acoustic output of the subordinate. At such times the duet takes the form of a unison chorus rather than precise alternation. There is some evidence to suggest that the subordinate extends its echemes slightly as a result of the excitatory effects of the relatively incessant song of the dominant. The lack of precise synchrony or alternation of echemes is consistent with the regularly spaced distribution of singing males seen in the field.

3. These same responses of albopunctata can be recognized in the interspecific interactions with M. roeselii. Echemes are delayed due to the inhibitory acoustic input

from *roeselii*. Echemes are extended due to the excitatory effects of the continuous *roeselii* song. The interplay of parallel inhibitory and excitatory effects, and the endogenous cycle of singing activity of *albopunctata* results in large fluctuations in its rate of singing. Echeme extension by *albopunctata* occurs typically when motivation to sing is high, especially at the post-duet phase but also during the duet. Inhibition, both temporary and total, is often encountered.

4. Song modification rarely occurs in the field despite close sympatry between these two species. Negative phonotaxis by *albopunctata* to the song of *roeselii* produces interspecific spacing so that individuals are generally beyond the acoustic range of their neighbours. This behaviour results in *albopunctata* being excluded from areas of prime habitat by high-density *roeselii* populations.

5. Studies on interactions between different species suggests that insects which normally adjust their song output to match the song of a conspecific will suffer song modification if subjected to an allospecific song with a similar frequency spectrum. Song modification will be enhanced if the allospecific song is relatively continuous.

APPENDIX.

The REGRE programme for Multiple Linear Regression Analysis.

Multiple Linear Regression

In the Scientific Subroutine Package, multiple linear regression is normally performed by calling four subroutines in sequence.

1. CORRE - to find means, standard deviations, and correlation matrix
2. ORDER - to choose a dependent variable and a subset of independent variables from a larger set of variables
3. MINV - to invert the correlation matrix of the subset selected by ORDER
4. MULTR - to compute the regression coefficients b_0, b_1, b_2, ..., b_m, and various confidence measures

The subroutine CORRE works in either of two ways: (1) it expects all observations in core, or (2) it triggers a user-provided input subroutine, DATA, to read one observation at a time into a work area. In either case, the user must provide a subroutine named DATA (see "Subroutines Required" in the comment cards description of subroutine CORRE).

Subroutine MULTR

This subroutine performs a multiple regression analysis for a dependent variable and a set of independent variables.

Beta weights are calculated using the following equation:

$$\beta_j = \sum_{i=1}^{k} r_{iy} \cdot r_{ij}^{-1} \qquad (1)$$

where r_{iy} = intercorrelation of i^{th} independent variable with dependent variable

r_{ij}^{-1} = the inverse of intercorrelation r_{ij}

$i, j = 1, 2, \ldots, k$ imply independent variables

r_{iy} and r_{ij}^{-1} are input to this subroutine.

Then, the regression coefficients are calculated as follows:

$$b_j = \beta_j \cdot \frac{s_y}{s_j} \qquad (2)$$

where s_y = standard deviation of dependent variable

s_j = standard deviation of j^{th} independent variable

$j = 1, 2, \ldots, k$

s_y and s_j are input to this subroutine.

The intercept is found by the following equation:

$$b_0 = \overline{Y} - \sum_{j=1}^{k} b_j \cdot \overline{X}_j \qquad (3)$$

where $\overline{Y}$ = mean of dependent variable

$\overline{X}_j$ = mean of j^{th} independent variable

$\overline{Y}$ and $\overline{X}_j$ are input to this subroutine.

Multiple correlation coefficient, R, is found first by calculating the coefficient of determination by the following equation:

$$R^2 = \sum_{i=1}^{k} \beta_i r_{iy} \qquad (4)$$

and taking the square root of R^2:

$$R = \sqrt{R^2} \tag{5}$$

The sum of squares attributable to the regression is found by:

$$SSAR = R^2 \cdot D_{yy} \tag{6}$$

where D_{yy} = sum of squares of deviations from mean for dependent variable

D_{yy} is input to this subroutine.

The sum of squares of deviations from the regression is obtained by:

$$SSDR = D_{yy} - SSAR \tag{7}$$

Then, the F-value for the analysis of variance is calculated as follows:

$$F = \frac{SSAR/k}{SSDR/(n-k-1)} = \frac{SSAR(n-k-1)}{SSDR(k)} \tag{8}$$

Certain other statistics are calculated as follows:

Variance and standard error of estimate:

$$s^2_{y.12\ldots k} = \frac{SSDR}{n-k-1} \tag{9}$$

where n = number of observations

$$s_{y.12\ldots k} = \sqrt{s^2_{y.12\ldots k}} \tag{10}$$

Standard deviations of regression coefficients:

$$s_{b_j} = \sqrt{\frac{r^{-1}_{jj}}{D_{jj}} \cdot s^2_{y.12\ldots k}} \tag{11}$$

where D_{jj} = sum of squares of deviations from mean for j^{th} independent variable. D_{jj} is input to this subroutine.

$j = 1, 2, \ldots, k$

Computed t:

$$t_j = \frac{b_j}{s_{b_j}} \tag{12}$$

$j = 1, 2, \ldots, k$

These subroutines are available in the IBM manual -

System/360 Scientific Subroutine Package

Version III

Programmer's Manual

Program Number 360A-CM-03X

The Scientific Subroutine Package (SSP) is a collection of over 250 FORTRAN subroutines divided, for the sake of presentation, into two groups: statistics and mathematics. Also, over 200 subroutines are presented in both single and double precision mode. SSP is a collection of input/output-free computational building blocks that can be combined with a user's input, output, or computational routines to meet his needs. The package can be applied to the solution of many problems in industry, science, and engineering.

Version 3 of the Scientific Subroutine Package for System/360 incorporates and extends the capabilities of the original SSP/360. This version provides over 40 new mathematical and statistical subroutines 24 of which are in both single- and double-precision FORTRAN. Examples of the new capabilities are the use of the QR iteration for obtaining eigenvalues of a matrix, and the nonparametric test of Kolmogorov-Smirnov.

This manual contains sufficient information to permit the reader to understand and use all of the subroutines of the Scientific Subroutine Package.

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