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TITLE ASPECTS OF ACOUSTIC INTERACTION IN THE BUSHCRICKET GENUS METRIOPTERA (ORTH., TETTIGONIOIDEA)

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ASPECTS OF ACOUSTIC INTERACTION
IN THE BUSHCRICKET GENUS METRIOPTERA
(ORTH., TETTIGONIOIDEA)

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ABSTRACT

This study is an investigation of the behaviour of male bushcrickets of the genus *Metrioptera*. The situation investigated was that arising when two males of different species are placed in the same enclosure. A large number of such experiments was made and in each case observations were made on the movements of the insects, particularly with respect to one another. Their stridulations were recorded and subsequently analyzed with a view to detecting influences by the song of one insect upon song production by the other.

Attempts were made to relate the behaviour to that observed in similar circumstances when the two males belonged to the same species. In the latter cases, clearly recognizable aggression and homosexual courtship were much commoner, and there was a much stronger tendency for the defeated insect to return to the victor. In one species, the influence of pre-conflict caging conditions was studied.

Four species of *Metrioptera* were utilised: *M. roeselii* (HAGENBACH), *M. brachyptera* (L.), *M. bicolor* (PHILIPPI), and *M. sepium* (YERSIN). Nearly all of the experiments were confined to the first three species. It was found that the stridulations of *roeselii* and *bicolor* tended to inhibit song output in *brachyptera*. In interactions between *roeselii* and *bicolor*, either insect could be inhibited, but it was more often *bicolor*. A visit was made to a German locality where *roeselii* and *bicolor* occurred naturally in the same place, and inhibition effects were observed

to take place between them in the field.

One brachyptera out of thirteen tested produced chirps with more syllables than usual, when exposed to roeselii song. It did not modify its chirps in response to bicolor song, perhaps because of the more discrete nature of the latter. The phenomenon is discussed in relation to Broughton's (1965) discovery of song modification in Platycleis denticulata (PANZER).

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MATERIALS AND METHODS

DISCUSSION

The nomenclature of Broughton (1964) has been adopted whenever possible.

INTRODUCTION

'A quoi bon l'appareil sonore du locustien? Je n'irai pas jusqu'à lui refuser un rôle dans la formation des couples, jusqu'à lui nier un murmure persuasif, doux pour celle qui l'écoute; ce serait m'insurger contre l'évidence. Mais sa fonction fondamentale n'est pas là. Avant tout, l'insecte l'utilise pour dire sa joie de vivre, pour chanter les délices de l'existence, le ventre plein et l'échine au soleil."

-FABRE

Many species of Orthoptera produce sounds and the real reasons for this production have been only partially descried. The pronouncement of Fabre (1897) is of course easily attacked. Chopard (1945) points out that one can remove the bushcricket from its sunny environment and put it into a jar in the dark: it nevertheless soon resumes its song. He cannot however tell us why it does this. In his earlier (1938) classification of orthopteran singing he employs the term <u>stridulation indifférente</u> for this kind of emission, where no special reason is apparent. There are three other types. <u>Stridulation réflexe</u> is produced in response to a simple external stimulus. An example is the distress sound made by the bushcricket <u>Ephippiger</u> when roughly handled. <u>Stridulation psychique</u> is produced in response to complex stimuli, for instance the presence of another male insect, which in some Orthoptera elicits the production of an 'aggressive' song. Finally there is stridulation sexuelle, produced only in the presence of females and functioning as a preliminary to copulation.

Faber (1929, 1932, 1953) has proposed more ambitious schemes: initially he considered that there were twelve kinds of song, but in the most recent study this is increased to twentyeight. Pumphrey (1951) selected from this classification four main types: (i) ordinary song, 'which seems to signify that the singer is disengaged and ready for anything'; (ii) the serenade, or courtship song; (iii) the rivals" duet, singing exchanged between males; (iv) the Paarungslaut or shout of triumph, made immediately before copulation. He adds that a fifth sort of song may occur during copulation. Haskell (1957, 1961) gives practically the same list, but adds as his fifth type 'copulation song', which he says is produced if the copulation is disturbed.

The subject of song classification is reviewed by Frings and Frings (1958) and by Dumortier (1964). Dumortier suggests a primary separation into two categories. Firstly there are emissions leading to the creation of a situation which satisfies a need or tendency, and secondly there are emissions associated with a 'hostile' or defensive attitude. The first group contains 'calling, congregational and premating songs' and must therefore include stridulation indifférente. The second group contains " rivalry song, disturbance sounds and protective sounds.".

It is clear that whatever the reason for the male's production of stridulation indifférente, it does in some cases have the effect of attracting distant females towards him. This is the typical situation in tettigoniids and gryllids, as opposed to that often found in acridids. Regen (1913) found that a female field cricket (Gryllus campestris) was attracted to the song of a male transmitted through a telephone receiver. Dumortier (1964) was able to make a female Ephippiger walk away from a silent male towards a loudspeaker from which male song was being broadcast. Khalifa (1950) found however that in the house cricket (Acheta domesticus), vision became important when the partners came close together.

Alexander (1961, 1962) suggested that the first Tettigonioidea to evolve soundproducing mechanisms used them solely in close proximity, as a precopulatory manoeuvre, the sounds being very soft. Selection then operated to improve the efficacy of both production and reception, and consequently the distances between insects for which stridulation could still retain significance could increase. 'As distance and directionality increased the calling function as it now exists emerged; the presence of the female is no longer required to elicit the signal.'

It is now necessary to account for Dumortier's second group. Alexander (1961) says that it seems inevitable that the song 'should have frequently developed significance for other males'. He is discussing the behaviour observed between males of Gryllus campestris. The aggressivity of this animal has been recognized for a long time. Darwin (1871) noted 'when two male field-crickets (Gryllus campestris) are confined together, they fight till one kills the other.'. Alexander found that in his colonies fights would occur at times but that little real physical damage was done. He concluded that these fights, during which stridulatory exchanges occurred, were connected with the maintenance of linear dominance hierarchies such as those reported by Kato and Hayasaka (1958) in two other cricket species. A high position in the hierarchy and the ability to win fights were not usually consequences of greater strength, but they might be augmented by isolation of the individual prior to the conflict, by allowing it to copulate a short time before, by its having won other fights recently, or by its being on its 'home territory'. In some cases however, especially in all-male groups, encounters between males would result not in fighting but in a kind of homosexual courtship, which might even lead to attempted copulation, but would stop short before spermatophore transfer.

This study of crickets by Alexander is extremely thorough and we have less information about the phenomena of male rivalry in the other groups of Orthoptera. Otte (1970) has examined the behaviour of a large number of American Oedipodinae and Acridinae, and gives a section on 'aggression' for each species. M.-C. Busnel (1967) gives an account of the situation in the tettigoniid Ephippiger. Two adjacent males will sing 'duets', alternating their short chirps. Almost always one (the 'leader') sings more, but the best criterion of hierarchical dominance is the percentage of triggering. The leader initiates singing in 60-98 % of cases. It explores the territory more quickly, attracts more females than the other male, and will attack the other male, causing it to retreat. A number of parallels with vertebrate hierarchy phenomena are suggested. Jones (1966a) has studied alternation behaviour in the bushcricket Pholidoptera griseoaptera. Again, two males alternate their chirps, or occasionally synchronize them. Jones states that the pattern of this interaction appears to be determined chiefly by mutual inhibition: while one insect sings, singing by the other is inhibited. There is also a mutual excitatory effect leading to an overall increase in the chirp rate. A similar effect appears to occur in the house cricket Acheta domesticus: Heiligenberg (1966) found that he could increase its chirp rate by playing taped chirps to it. He also found (1969) that a stimulus chirp not coinciding with a chirp of the cricket would inhibit chirping from the 40th to the 180th millisecond following stimulus onset. It would also increase the chirp rate by approximately 0.3 chirps per second.

The real function of the behaviour is uncertain. Jones (1966a) says that it may have territorial significance in Pholidoptera, but territoriality is a less prominent phenomenon in tettigoniids than in Alexander's crickets, which live in burrows. Alexander (1957a) says that the function of male conflict may be to produce a spacing effect. In fact we have very little information on the movements of orthopteran populations, with the exception of Acrididae. In addition to the extensive studies of locust swarms, which are not really relevant to the present work, there are papers by Clark (1948), Chapman (1952) and Richards and Waloff (1954), dealing with the ecology and movements of acridids in the field. These authors stress the very small amount of movement which actually occurs when the insects are undisturbed, but they have little to tell us about territoriality. A more fruitful approach would appear to be direct investigation of behaviour in the laboratory, and a subsequent return to the situation in the field. This is the approach I have adopted in the present study.

The obvious first step in investigating acoustic exchanges between males was to replace one insect with another source of sound, preferably similar, and to see if attention continued to be elicited. Regen (1926) found that he could induce alternation between *Pholidoptera aptera* males and a variety of artificial signals, such as sounds produced by a Galton whistle. Busnel and Loher (1955) used artificial signals of 1 minute duration, separated by 1 minute intervals, with the acridid *Chorthippus jucundus*, and found that it sang during the silences but not during the signals. Jones (1963, 1964, 1966b) worked with pure tones produced by a signal generator and found that the chirp rate of *Pholidoptera griseoaptera* would decrease while the signal was being emitted, and then 'rebound' when it stopped, exceeding the normal rate. The resemblance of this to the inhib ition and excitation occurring in normal alternation is clear. The criteria which a signal must satisfy in order to influence the song of an insect are uncertain. Busnel and Dumortier (1954) and Busnel, Dumortier and Busnel (1956) worked on female *Ephippigers* using Galton whistles, artificial birdcalls &c., and concluded that the significant part of the sound was the *transient*: the more abruptly the sound began or stopped, the greater its effect. Jones (1963) found that transients had little place in his work with *Pholidoptera* inhibition. I do not intend to deal at length with the controversies over orthopteran song recognition: the classical view that the only significant part of the signal is its amplitude modulation is stated by Haskell (1956). More recently, Michelsen (1971) has shown that some frequency discrimination occurs in the locust ear: the behavioural significance of this is as yet unknown.

Whatever the elements required to influence the song of an orthopteran may be, the fact that something as far removed from Nature as the *sound* of a signal generator can produce an effect similar to that of the song of a conspecific suggests that there may well be other incidental sounds in the field which are liable to influence stridulating bushcrickets. The more similar they are to the song of the species in question, it would seem, the greater the likelihood of an effect. It might, then, be conjectured that the songs of related species would produce effects similar to those of the artificial signals, and this has in fact been observed. Baier (1930) noticed that a *Pholidoptera griseo-*

aptera male which was caged with a *Tettigonia viridissima* male stopped singing when the latter sang, but resumed at once when it finished. Personal observation of these species in Britain has shown me that they rarely occur in exactly the same place: the only true overlaps I have seen were near Jevington, E. Sussex (1963) and Torcross, Devon (1971). Fulton (1934) worked with *Orchelimum militare*, which has 'long fluttering notes delivered with great irregularity'. He placed it near *O. bradleyi*, which sings with 'buzzing notes at a rather regular rate, about one per second'. Following Broughton's (1964) terminology, the 'notes' of *militare* would appear to be 'trills' and those of *bradleyi* 'chirps'. The song of *militare* inhibited that of *bradleyi*. Sometimes the latter could work in two or three chirps between the *militare* utterances, but when these were more rapid there was a simple 1/1 alternation. He found that *militare* would start while *bradleyi* was singing, but *bradleyi* would not start while *militare* was singing.

Busnel, Busnel and Dumortier (1956[illegible]) studied five species of *Ephippiger*, all occurring in geographically separate environments. Alternation between males of different species was consistently found. Weih (1951) worked on various acridid species and found that in some cases the males of one species alternated with those of another; in other cases alternation was rare.

Several workers have investigated interspecific relations between males and females. Lutz (1926) watched a male *Orchelimum* singing and antennating a female *Melanoplus*, an acridid. By contrast Jacobs (1953), Perdeck (1957) and Walker (1957) studied sympatric Orthoptera and found no response by the female of one species to the song of the male of the other. Perdeck, working with *Chorthippus brunneus* and *C. biguttulus* was in fact able to hybridise them in the laboratory, but only three or four hybrids were reported from the field. Perdeck gives a survey of interspecific effects in various groups of animals. Spooner (1968) found that the songs of nine species of Phaneropterinae were species-specific. Walker (1956) says that occasionally interspecific attraction has been observed between male and female Oecanthinae under laboratory conditions. Busnel, Busnel and Dumortier (1956) found that female *Ephippigers* were often attracted to allopatric males and that in some cases the entire courtship sequence would occur, followed by copulation and spermatophore transfer. Dumortier (1963) gave females a choice between males of their own and another species, and found that there were always some females which were attracted towards the song produced by the other species.

Returning to the question of interspecific interactions between male bushcrickets, Broughton (1965) gives an account of a variety of combinations. In many cases alternation was observed and in others the song of one species inhibited song production by the other, as in Baier's experiment. One of the most effective inhibitors was *Metrioptera roeselii*, which produces a sustained trill. Broughton intended to study the effect of this on the stridulation of the other British *Metrioptera*, *M. brachyptera*, but did not have any *brachypteras* at the appropriate time and therefore substituted a male *Platycleis denticulata*, which produces similar short chirps. The effect of *roeselii* song was to partially inhibit chirping, but when *denticulata* chirps did break through the *roeselii* trill, they were modified, being longer and having more syllables than before. Broughton also observed song modification in *Platycleis intermedia* (then thought to be *P. sabulosa*), subjected to the singing of *P. affinis*, and several other species.

The effects observed by Broughton were quite distinct from the simple cases of chirp rate alteration reported by other workers. There was a further complexity in that the new, modified song bore a closer resemblance to the song of the influencing species than it had done before, so that one had the impression that some vague kind of learning process might be taking place. This recalls the work of Pierce(1948), Alexander(1960) and Shaw (1966) on the bushcricket *Pterophylla camellifolia*. They found that the insect could be made to emit chirps containing a certain number of syllables, in response to the production, by the experimenter, of mock 'chirps' containing the same number.

Broughton considered it unlikely that his *denticulata* was attempting to imitate the *roeselii* trill by extending its own short chirps, and suggested that the *roeselii* song might be interfering in a feedback mechanism by which the denticulata regulates its song output, and thus producing a 'stutter'. Nonetheless, this is a strange phenomenon. Walker(1962) emphasized the insubordination of cricket song structure to external conditions, and Kutch and Huber (1970) gave evidence that song patterns in crickets depend mainly upon centrally programmed phasing mechanisms with very limited modulation by peripheral control. It was in the hope of clarifying the problems arising from Broughton's work that the present study was undertaken.

PRESENT STUDY

The first aim of the present study was to investigate the interaction which Broughton had intended to observe, that of males of *Metrioptera roeselii* and *M. brachyptera*. My intention was to provide information on the behaviour, if any, accompanying the acoustic interaction, and to attempt to correlate this with the intraspecific behaviour of males. A second aim derived from Broughton's observation, made in 1965, that in certain German localities *M. roeselii* and a third species, *M. bicolor*, could be found living in close proximity. If an interspecific interaction between *Metriopteras* in the laboratory could be of interest, one occurring naturally in the field would be of much greater interest, and a visit was therefore made to the German sites to investigate the situation. With *bicolors* brought back from Germany the third combination, *bicolor/ brachyptera* was also studied, and a few observations were also made on a fourth species, *M. sepium*, encountered casually in the South of France in 1969.

MATERIALS AND METHODS

The Insects

Very little has been published on the genus *Metrioptera* beyond taxonomy and geographical records. Zippelius (1948) gives an account of courtship in *M. roeselii*, *brachyptera* and *bicolor*, and also deals with the variation of the song of *bicolor* with temperature. Morris (1970) considers acoustic behaviour in the Canadian *M. sphagnorum*. Howse, Lewis and Pye (1971) describe responses to song in the tympanic nerve of *brachyptera*. Accounts of the two British species are given by Lucas (1920), Burr (1936) and Ragge (1965). Harz (1957, 1960) also describes *bicolor*, and Chopard (1951) describes all four species under consideration here. My summary is very superficial:

Metrioptera (Roeseliana) roeselii (HAGENB.).

The general colouration is glossy brown and although Lucas mentions occasional bright green specimens, I have seen little variation in the appearance. The male is about 16 mm. long; the female slightly larger. The tegmina are pale greenish brown and, characteristically for the genus, shorter than the abdomen.

This is a grassland species. On the Continent it is very widespread, on roadside verges and on rough pastureland, but in Britain it is restricted, although often locally abundant. According to Payne (1957) its normal Essex locality is 'long grass between a road and a cultivated field'. I associate it with damp marshy ground in Britain, but on the Continent it seems tolerant of quite dry situations.

The variety *diluta* (CHARP.), of which two specimens were used in the present research, has long tegmina, passing the tip of the abdomen. It is much rarer than the normal variety but it has been reported in England, by Chapman (1948), Payne (1957, referring to Ragge, Menzies and Airy Shaw) and by Burr (1936), who states that Blair found a *roeselii* colony near Benfleet in Essex, of which 30% were *diluta*. Ramme, he adds, found a colony in the Bialowicz forest in Poland, of which 50% were *diluta*. Ramme believed this to be the focus of distribution. One of my specimens was found on the hills above Tübingen and it is of interest to note that it had been found near Tübingen previously, by Krauss in 1871, according to Zacher(1917). Burr (1910) also states that it occurs near Tübingen. There is little information as to why longwinged (macropterous) individuals should appear amongst shortwinged Orthoptera. Ramme (1931) examined gonadial sections of *diluta* and of normal *roeselii* and found damage in the former which he said accounted for its assumed lack of fecundity. Alexander (1957b) reports that the crickets *Acheta pennsylvanica* and *A. rubens* will produce longwinged individuals in the laboratory if reared in crowded conditions on high-protein dog food.

The song of *roeselii* (and of *diluta*) is a high penetrating trill. (see fig 1) If the recorded song is slowed down it is found to consist of an undivided sequence of syllables, whose rate is correlated with the temperature. Jones (Ph. D. thesis, 1966) gives a temperature/ syllable rate graph for a single individual. I have compared this with results obtained from several other *roeseliis* and was surprised to find a very uniform response with very little deviation from Jones's graph.

Metrioptera brachyptera (L.).

The appearance is similar to that of roeselii but there tends to be more green in the body markings. Colour can never be trusted as a criterion of species amongst Metriopteras, but keys at least as far back as Stephens (1835) refer to the pale streak on the perimeter of the pronotal sideflaps, which in roeselii extends right round but in brachyptera occupies only the hind border. This is at least a useful field character and I have personally never found an exception.

In Britain brachyptera is a typical inhabitant of acid bogs and is consequently unlikely to be found in conjunction with roeselii (but c.f. page 63). Lucas associates it specifically with the cross-leaved heath Erica tetralix but Burr (1936) says that he has found it in shrubs and amongst bog myrtle, and adds that Ramme found it on the banks of Lake Freiberg chirping amongst bulrushes almost in the water, and also in Thuringia amongst bilberry (Vaccinium myrtillus).

A macropterous variety (var. marginata THUNB.) occurs both on the Continent and in Britain, but I have never found it.

The song consists of discrete chirps, about 2-3 per second(see fig. 2) The mechanism of chirp production has been studied by Lewis (personal communication, 1970). A typical chirp contains three loud hemisyllables produced by closing the tegmina. The sounds made by opening the tegmina are too quiet to be detected with the apparatus I used. For the purposes of this study I shall ignore these and refer to the normal trisyllabic brachyptera chirp. The insect quite often produces tetrasyllabic chirps also, and occasionally other irregularities. There is a correlation of chirp rate with temperature (Jones: Ph.D. thesis, 1966).

Metrioptera (Bicolorama) bicolor (PHIL.).

About the same size as roeselii and brachyptera but usually bright applegreen, although Broughton (personal communication, 1970) informs me that he has encountered individuals whose colour was practically the same as that of roeselii. This is again a pastureland species, but less common than roeselii and not found in Britain. A macropterous variety (var. sieboldi) occurs, but I have never found it.

The song (see fig. 3) is composed of compound sequences of three-part (trisyllabic?) chirps, which at high temperatures become fused into a trill almost as fast as that of roeselii. The mechanism of tegminal movement associated with its production has not been studied.

Metrioptera (Sepiana) sepium (YERSIN).

This is a large (20-25 mm.) reddish brown insect found in Mediterranean localities, living on low plants. No macropterous variety has been reported. The song (see fig. 4) is a harsh noise, a sequence of two-part chirps which sound fairly discrete whatever the temperature. No observations have been made on the tegminal manoeuvres.

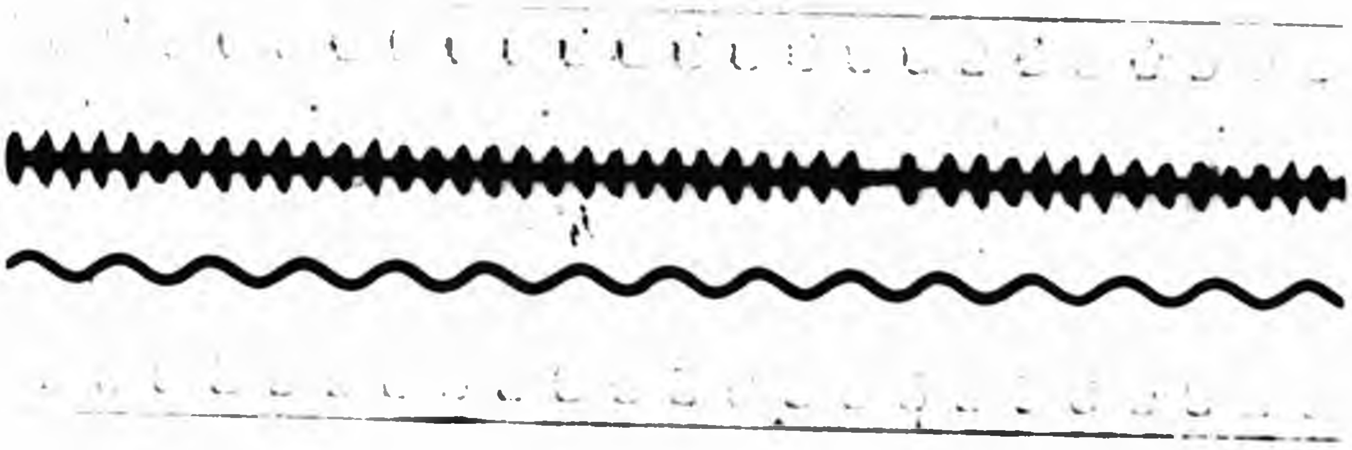


Fig. 1. Oscillogram of song of <u>roeselii</u> (11). Recorded 18 September 1970 at 32 degrees. Marker: 1 cycle = 0.125 seconds.

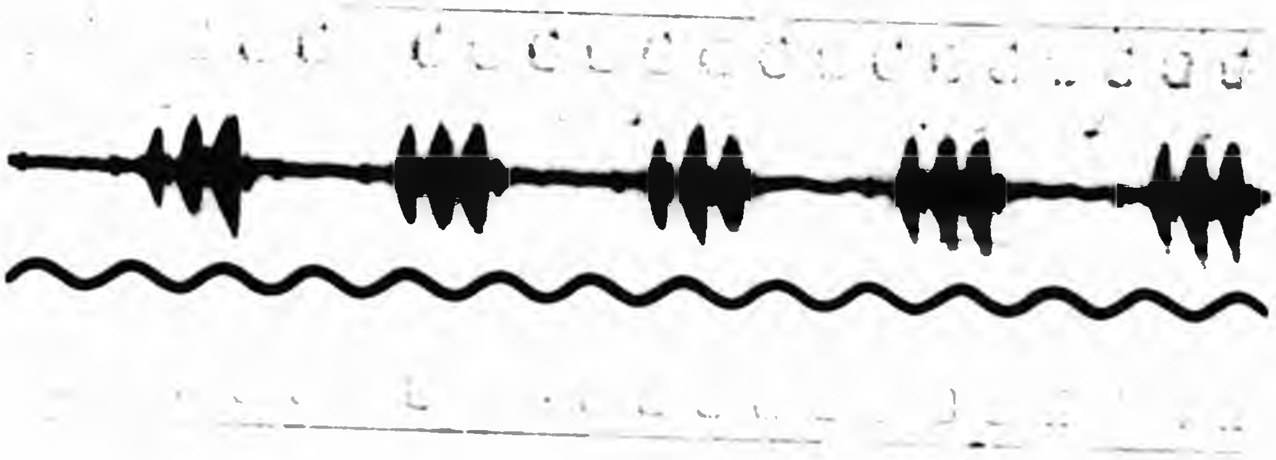


Fig. 2. Oscillogram of song of <u>brachyptera</u> (11). Recorded 16 September 1970 at 26½ degrees. Marker: 1 cycle = 0.125 seconds.

Fig. 3. Oscillogram of song of *bicolor* (9). Recorded 29 August 1970 at 29 degrees. Marker: 1 cycle = 0.125 seconds.

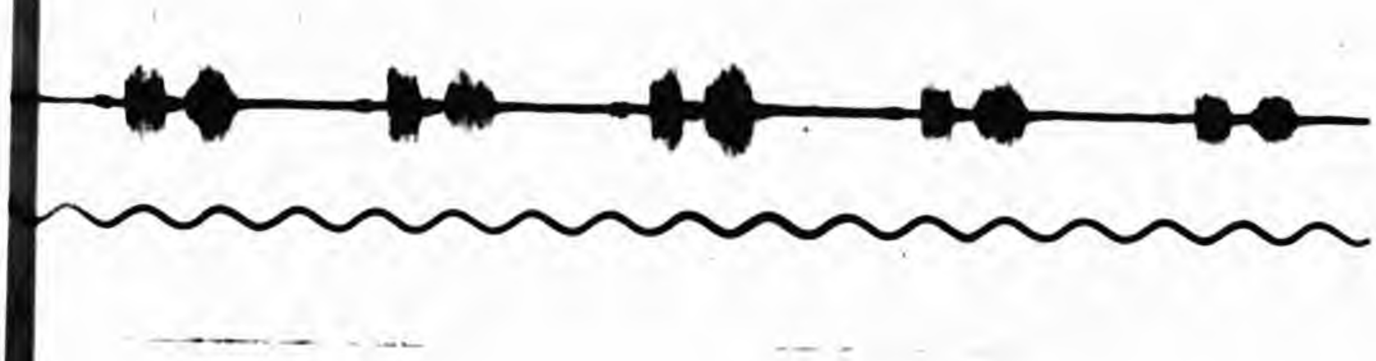
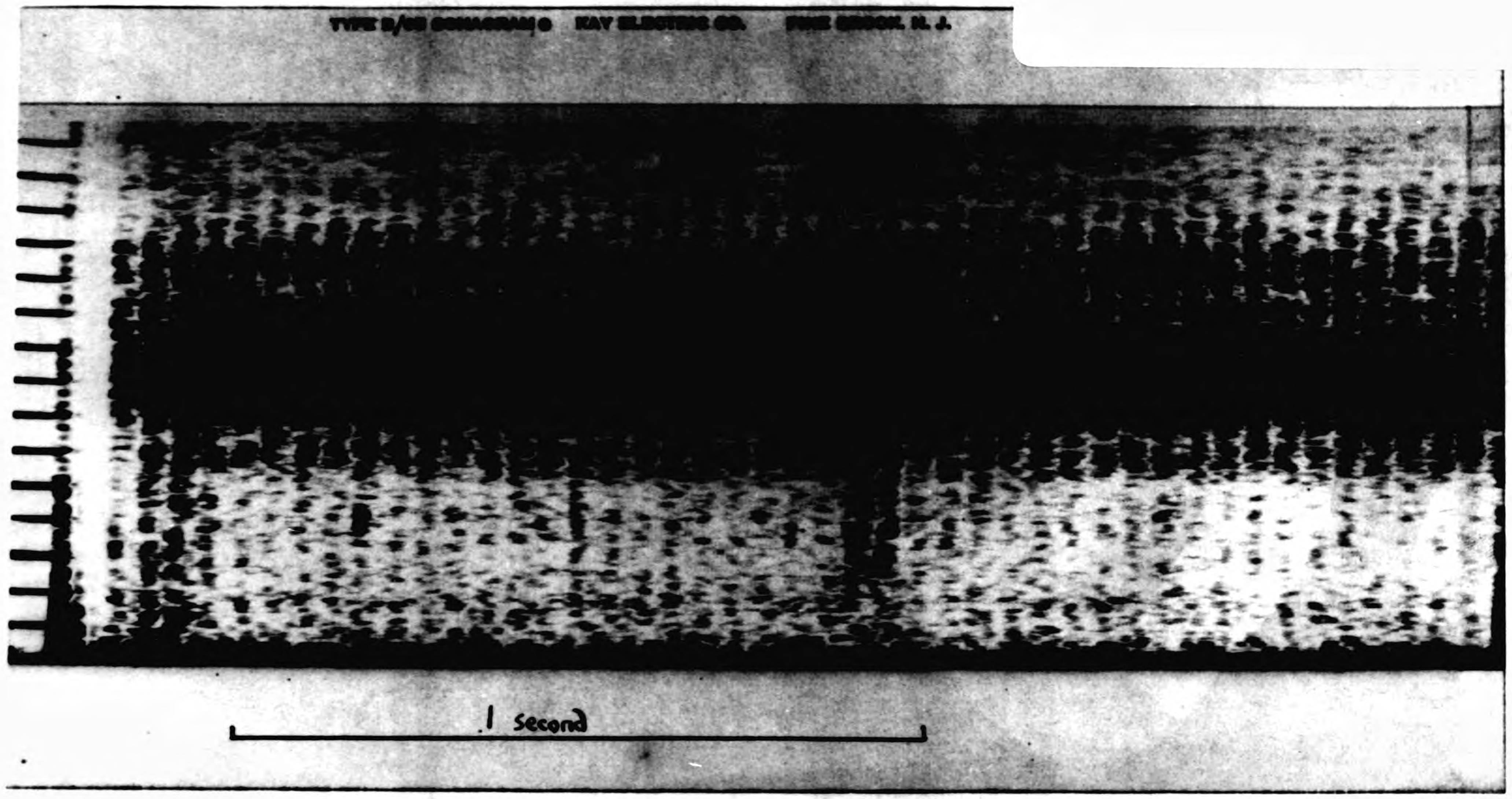


Fig. 4. Oscillogram of song of *sepium* (2). Recorded 18 August 1969 at 24 degrees. Marker: 1 cycle = 0.125 seconds.

Fig. 5. Sonagram of song of *roeselii* (11). Recorded 18.9.1970; temperature 32 degrees. Range: 85 - 8,000 Hz. Marker interval: 500 Hz.



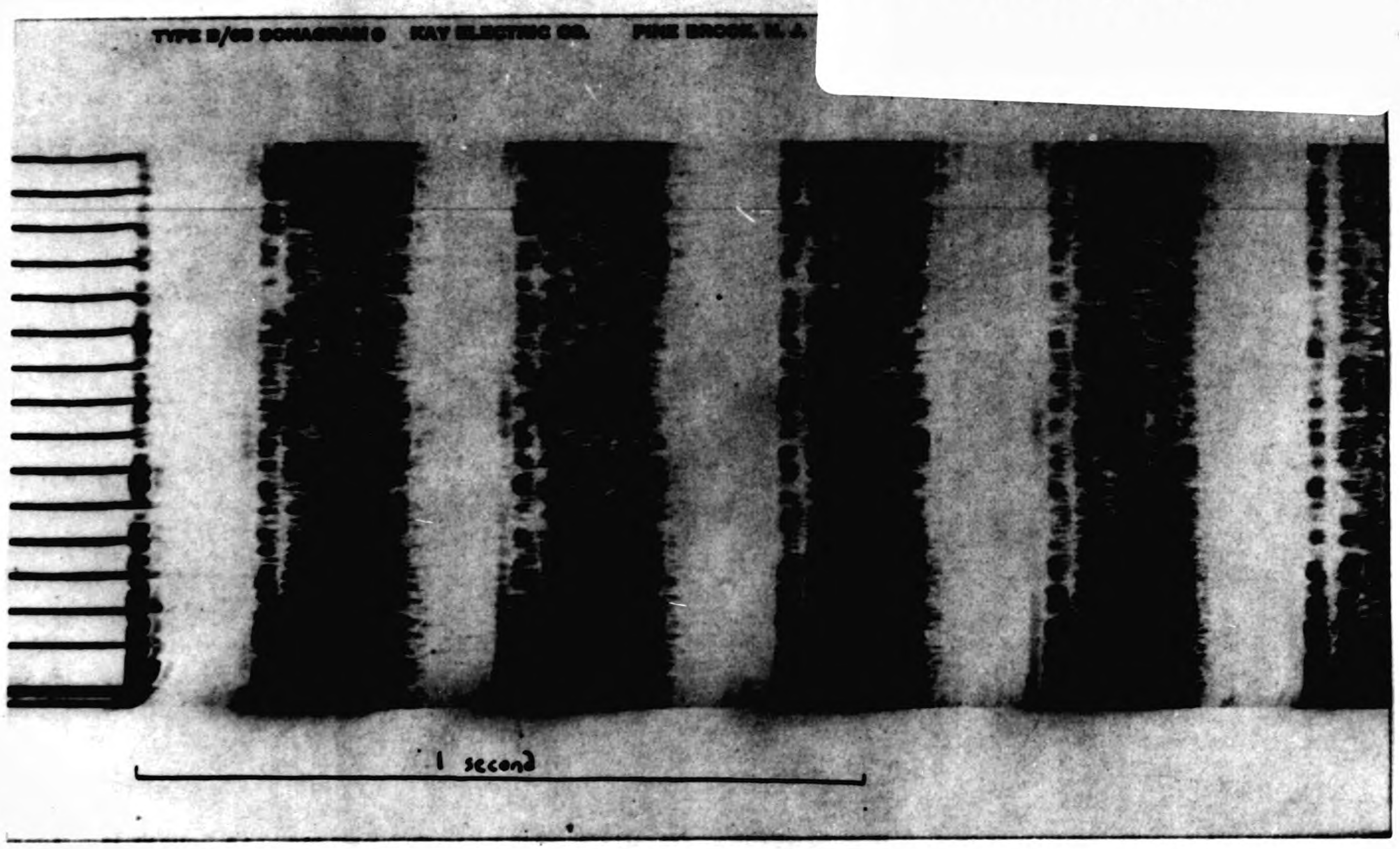


Fig. 6. Sonagram of song of <u>brachyptera</u> (11). Recorded 16.9.1970; temperature 26½ degrees. Range: 85 - 8,000 Hz. Marker interval: 500 Hz.

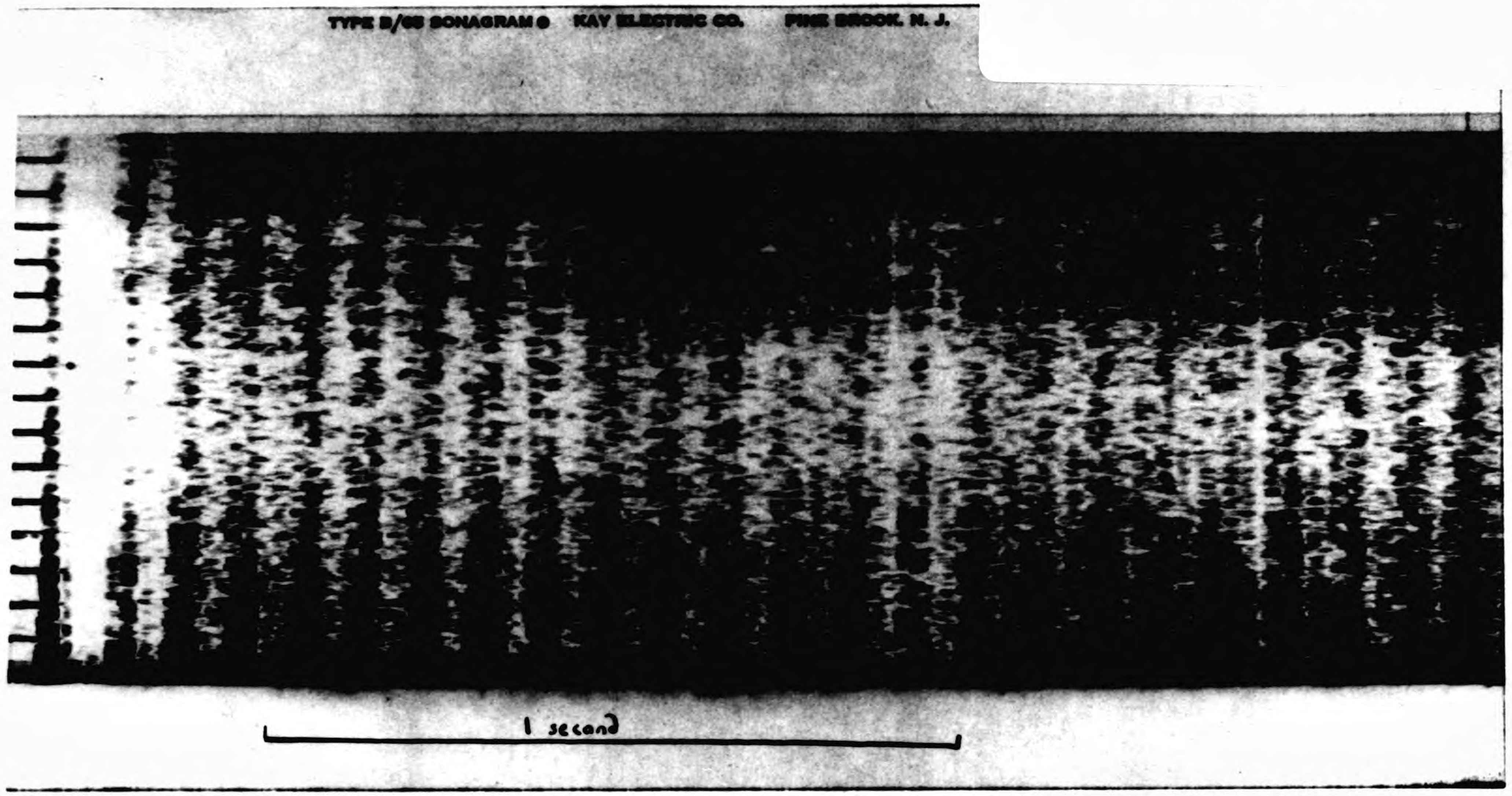


Fig. 7. Sonagram of song of
bicolor (9). Recorded 29.8.1970;
temperature 29 degrees.
Range: 85 - 8,000 Hz.
Marker interval: 500 Hz.

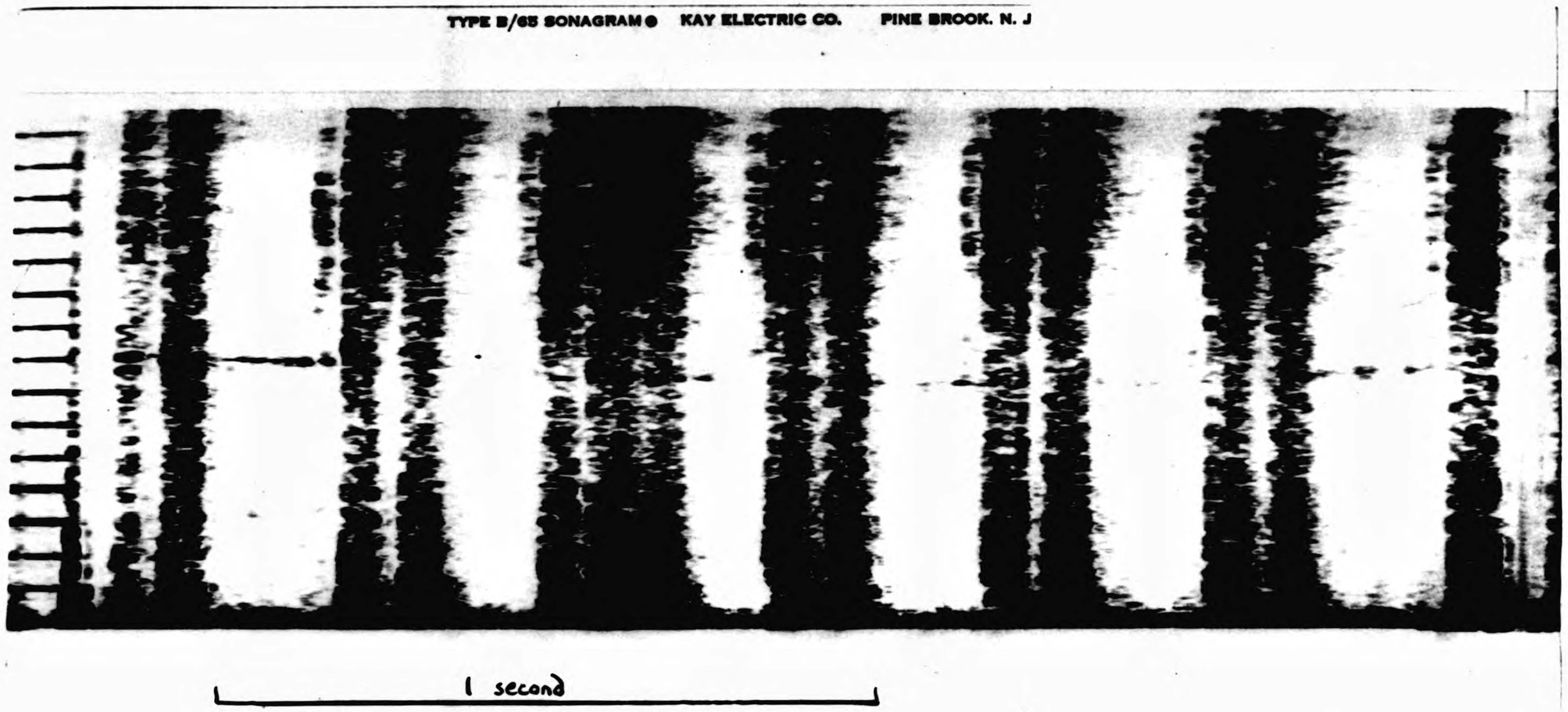


Fig. 8. Sonagram of song of
sepium (2). Recorded 18.8.1969;
temperature 24 degrees.
Range: 85 - 8,000 Hz.
Marker interval: 500 Hz.

Collection of Insects

The techniques applied in the capture of bushcrickets have been fundamentally identical for all the species of Metrioptera here considered. Although before commencing the present project I had occasionally obtained individuals by sweeping densely populated stretches of grassland, I had often found that legs and antennae were lost or broken in the process. I therefore decided to adopt the method of tracking down single males by their song. As the work was chiefly concerned with the behaviour of pairs of males, few females were required and usually sufficient were discovered fortuitously in the search for males.

Conditions of Collection

In my experience it has rarely been profitable to attempt collection on cold or rainy days. In these circumstances Metrioptera is unlikely to stridulate: it will descend to the bases of grassclumps and if disturbed will crawl further in rather than spring out like an acridid. Moisture on the vegetation does not appear to influence the insect's readiness to sing but absence of direct sunlight causes a striking diminution in output. Excessive wind makes it impossible to identify the sound's point of origin. The best results were always obtained on hot calm days.

Detection of Insects

For some years prior to the commencement of this project I had had experience of the collection of tettigoniids. I had consistently found it necessary to sensitize myself to the particular utterance of the species for which I was searching. I was able to do this only in the field, where the stridulation appears against a background of birdsong, songs of other insects &c. The recorded song, played through an ordinary loudspeaker, did not generally suffice to enable me to recognise the live animal. After some time I found that acridid and tettigoniid stridulations were involuntarily distinguished, only the latter being noticed. At this stage I might for example be walking along a country path and suddenly arrest myself in response to the sound of a tettigoniid perhaps fifteen or more feet away to one side. I would then advance on the insect, placing my feet circumspectly and stopping at once if the sound was cut off. I would remain for some minutes motionless and vigilant: when the sound resumed I would continue my approach. I usually had to walk further than initially anticipated: the ventriloquism of Orthoptera is wellknown. Fabre (1899) describes ventriloquism in the European treecricket <u>Oecanthus pellucens</u>. This insect, which I have personally traced and captured by its song, produces a very deceptive effect. Scudder (1892), dealing with Orthoptera in general, suggests that the observer circle round the animal as a means of overcoming its ventriloquism. In some cases I have found this technique useful. He also advocates the making of artificial 'stridulation' noises to encourage the insect to sing, but this has never worked for me. When very close to the insect I would stare at the vegetation and if I failed to see my quarry I would trample the area immediately in

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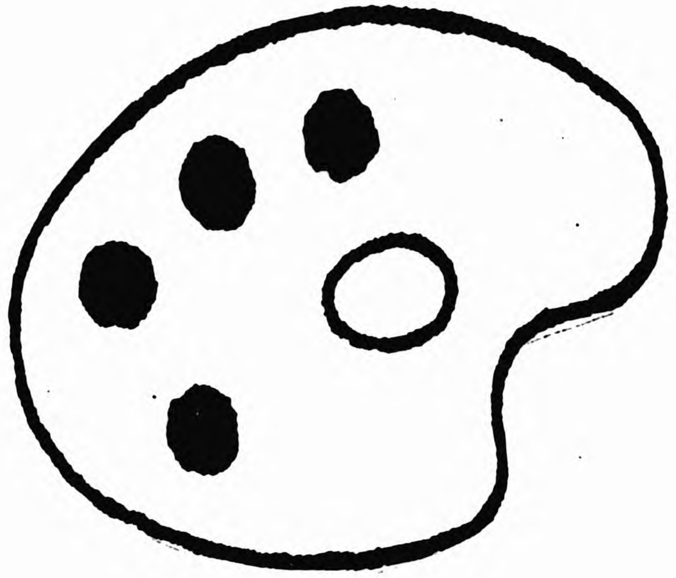


Fig. 9 Collecting Metrioptera brachyptera near Wych Cross, Sussex.

front of me, whereupon it would usually jump out. Once seen it would remain conspicuous although a series of jumps might be accomplished. If I failed to uncover the insect I would depart, and returning ½ hour or more later I would often find that singing had recommenced.

Capture of Insects

Metrioptera normally sings much closer to the ground than genera such as *Tettigonia*, *Ephippiger* and the Phaneropterines, and if it is seen resting on vegetation near ground level, the most convenient method of capture is to slowly manipulate an inverted glass jar of about four inches diameter so that its mouth is above the insect, and then to thrust it suddenly down as far as possible. I usually found that the insect would leap upwards into the jar, and that if it instead descended into the vegetation I could disturb this either by sideways movements of the jar or by raising the jar slightly and pulling aside the s stems from beneath. When the insect was in the jar I would slide my hand under the mouth and then bring up the jar, right it, and close it with a lid.

Other Types of Capture

If the insect was sitting on a grass stem some way above ground level I might gently surround it with cupped hands which I would then bring suddenly together so as to imprison it. I would then slide them up the stem, leaving the bushcricket trapped in their cavity. If the vegetation was too prickly for this I would surround the animal by a jar and its lid, and bring them together in the same way. An insect which was escaping could be caught in one hand. This was easiest done on short turf, the hand being brought down on top of it, but I was also sometimes able to snatch an insect from a plantstem with one hand. With practice it became easy to employ such techniques without damaging the captive.

Differences between Species Considered

As a rule M. brachyptera is somewhat harder to catch than M.roeselii or M. bicolor but this is in part a consequence of its softer song and the more prickly environment favoured. M. sepium was found an extremely difficult subject, capable of jumping several feet and immediately dropping into a labyrinth of roots from which it could not be retrieved.

Transport from the Field

It was usual in the present research to convey insects from the field to the laboratory in cardboard boxes measuring 10"x7"x3", their lids being chiefly occupied by a gauze panel. A round hole in the floor of each was fitted with a gauze sleeve through which insects and food were introduced, and which was subsequently knotted to prevent escape. This type of box was designed in the Zoology Department of Nottingham University. In some cases insects were transported in the large glass jars which had been used to catch them. Metrioptera is a good traveller unlike some genera (e.g. Meconema) which may lose legs &c. in transit. This can be a real problem, despite Uvarov's (1928) comment that voluntary autotomy is a doubtful phenomenon.

Even in the case of the bicolor males which were collected in Southern Germany in August 1970 and brought home by car two weeks later, still in the same boxes, there were few casualties.

Diet

No more than eight individuals would be put together into a box of the type described, although cannibalism is less of a problem in this genus than in some others (e.g. Pholidoptera, Meconema). A handful of leaves, grasses and flowers, not necessarily from the locality where the insects occurred, plus some dry cereal and seed mixture, provided nourishment for several days. Metrioptera has a wide food range. Although brachyptera is generally confined to heathland it does not require plants from this type of environment for sustenance. A pure vegetable diet appears to be perfectly adequate although both roeselii and brachyptera (especially the latter) have been observed in captivity to consume the bodies of dead flies offered to them.

Housing of Insects

Most of the time it was necessary to maintain simultaneously a large number of small groups, or single insects, in such a way as to eliminate physical contact and minimize acoustic contact between them. A large number of cages were thus required, and the simplest solution was to continue to use the boxes or jars in which the insects had been transported. The cereal mixture tended to rot in the jars, which accordingly were employed as little as possible, but the boxes were quite satisfactory. The food was kept fresh by sprinkling water over the gauze lids of the boxes and it was noted that the occupants normally climbed up to drink this. Whenever possible, the boxes were placed in sunlight, as bushcrickets require radiant heat.

Conditions of Study

A distinction must be noted between the work undertaken in 1969 and that in 1970. The former was principally concerned with roeselii and brachyptera- intraspecific and interspecific behaviour- and was carried out in two flats in different parts of London. The conditions available at the laboratory of the City of London Polytechnic were obviously totally inappropriate to this type of work since the insects would have to be carried some distance from the room where they were housed to a quieter place where they might be individually recorded, and because of the continuous risk of disturbance by other persons working in the building. Further, some recordings were made at night or in the early morning and it was clearly going to be much more profitable to live in the same place where the insects were kept so that any unexpected events at odd hours would not be missed. Nonetheless, the flats in London suffered from two deficiencies- admittedly to a lesser degree than the College but still enough to make the total output of workable recordings small. There was a high level of incidental noise due to traffic, and a low temperature as the rooms did not face South and direct sunlight was rarely encountered for long. Artificial heating, either by electric fire or by placing an anglepoise lamp near the recording cage, was generally unsuccessful (c.f.

page 39). The research conducted in 1970 was at my home in Newhaven (Sussex). Here it was possible to keep the bushcrickets permanently on tables in front of Southfacing windows, and also to maintain the recording cage in direct sunlight. The quantity of successful recording obtained in 1970 was in consequence much greater, and the quality better due to the quieter surroundings. Better acoustic isolation could be obtained also, different species being kept in separate rooms to reduce any effects of adaptation to one anothers" songs.

Identification of Individuals

All insects used were marked with one or more spots of 'Humbrol' quickdrying paint applied to the pronotum. In work on Acheta domesticus in 1968 it was found that such patches were easily removed unless the integument beneath the patch had been previously degreased with toluene, but in the case of Metrioptera paint was almost never lost. Spots were not normally applied to legs or antennae as these might subsequently break off and render the insect unrecognizable.

Temporal Distribution of Experiments

The temporal distribution of experiments was determined by the times of maximal singing of each species. It was found that as length of time in captivity increased, especially when little sunlight was provided, the portion of the day during which the bushcrickets maintained continuous song gradually diminished. Research on the activity cycle in Orthoptera has been limited (Lutz 1932; Dumortier, Brieu and Pasquinelly 1957; Nielsen- in press).

The *Metrioptera* cycle is certainly much more irregular than that of *Ephippiger*, the chief subject of existing information. *M. sepium* tended to commence singing in the late afternoon and continue until about dawn, but with time it began later and later so that there was progressively less chance of obtaining good interactions between it and *roeselii* or *brachyptera*, which tended to dominate the hot part of the day. In Newhaven *brachyptera* was in fact found to sing all round the clock and *bicolor* only stopped for a few hours in the early morning, resuming about 8.30 a.m., but *roeselii* could usually be relied upon between 8 a.m. and 2 p.m. only. In the field I have also noticed a diminution of *roeselii* song in the afternoon, in England and Germany, but there are always occasional outbursts. Alexander (1956) noted the times at which Orthoptera and cicadas began to sing outdoors in the evening, and found that the only consistent influence on different days was the level of light intensity.

It was normal in the 1970 experiments to devote the mornings to *roeselii* interactions and the afternoons to *brachyptera/bicolor* ones.

Arrangement of Experiments

The cage in which experiments were conducted was a wooden frame measuring ~~1'x18½"x8½"~~ 30·5cm X 47cm X 21·5cm, supporting muslin gauze walls and a sheet of muslin which could be draped over the top. The bottom was open and the cage rested on rough cloth to reduce echoes. Microphones were supported by retort stands around the cage. There was not normally anything inside the cage except the insects being studied. Nearly all the experiments involved the use of two insects. In the interspecific interactions it was soon realised that roeselii was generally the species most ready to resume singing after the disturbance of having been put into the cage, and brachyptera the least ready. Therefore in an interspecific experiment the normal procedure was to initially introduce the less vociferous singer, and when it was singing, to cautiously put in the other. It was found that with simultaneous insertion the weaker singer might never begin at all, being apparently inhibited by the song of the other. It was usual to place two boxes containing singing males of the 'weaker' species at either end of the recording cage, as the experimental insect would begin sooner if it could hear the song of a conspecific. These boxes were removed as soon as the experimental insect was singing adequately.

Conduct of Experiments

Two Akai high sensitivity microphones were mounted at opposite ends of the recording cage, and then moved to suitable positions when the insects settled down. This had to be done delicately as a sudden movement of the hand would startle a bushcricket and silence it. The case of brachyptera was especially trying, the sounds made being so quiet that that to obtain a good recording the microphone needed to be within one inch of the insect. It was found that when a microphone was held in the hand too much noise was produced on the corresponding track, so retort stands were always employed. The recording was monitored on stereophonic headphones. Naturally, the further apart the two singers were, the less crosstalk occurred on the tapes. Unfortunately, the most interesting effects took place when the insects were close together. If the distance separating them was over 45 cm ~~eighteen inches~~ it would be quite usual for each to remain apparently oblivious of the other's presence and sing as if alone. However, in many cases one insect would be attracted towards the other and eventually physical contact between the two would occur. It was important that no external factors should interfere with this and this is the primary reason for the failure of the anglepoise lamp experiments mentioned on page 35. With a lamp, only one small region of the cage was heated, and both insects naturally moved into this region. No conclusions could then be drawn concerning mutual attraction. In spite of the high temperatures achieved the insects did not usually sing as much as they would have done in sunlight. Further, it was not possible to discover the temperature of the insect as there was a strong gradient near the bulb, and bringing a thermometer near the insect would arrest stridulation. Even with sunlight there were occasional problems when one part of the cage became more strongly illuminated than another.

Documentation of Experiments

The objects of the experiments were to obtain taperecordings of the songs produced by the bushcrickets and to obtain an account of their behaviour with respect to one another whilst in the cage. As this behaviour was often a complex and rapid series of movements following a long stationary period it was necessary to watch the insects continually. I could not therefore write an account of what I saw, concurrently, and in any case the events often occurred too swiftly to be accurately transcribed. Accordingly, a statement of what took place was spoken so as to be recorded with the singing on the tape. It was normal to begin each recording by giving the time, temperature, which insects were being used, and how far apart they were. In subsequent analysis it was found that the spoken statements about the insects' activities which punctuated the recordings were useful as markers to locate particular passages, although they did sometimes coincide with interesting pieces of stridulation, rendering them impossible to analyze.

Recording Equipment

The 1969 recordings were made on an Akai X-IV fourtrack taperecorder, which had four speeds. The frequency response at 1⅞ i.p.s. (inches/s = 4.76 cm/s) was ± 3dB 30 to 11,000 Hz., and that at 7½ i.p.s. (19 cm/s) was ± 3dB 40 to 20,000 Hz. On the basis of other workers' experience with the equipment it was decided to record most of the routine behavioural material at 1⅞ i.p.s., giving occasional specimens at 7½ i.p.s. for physical analysis. It was however found that the quality of the matter recorded at 1⅞ i.p.s. was often so poor that no reasonable results could be obtained with the analyzing equipment, while the higher-speed specimens within these recordings gave excellent results.

Accordingly, nearly all of the 1970 recordings were made at 7½ i.p.s., first on the same machine, later on an Akai X-300 (also fourtrack, with speeds of 3¾ and 7½ i.p.s.). The frequency response using the Akai microphones in connection with this machine, as was done, is unknown; with a Brüel and Kjaer microphone and a speed of 7½ i.p.s. it would be 3dB 30 to 24,000 Hz. In any event, the quality is superior to that obtained with the X-IV. The tape used was BASF triple play. Except for one tape recorded in 1969, all recording was stereophonic, my objective being to obtain the songs of the two insects separately on separate tracks.

Analyzing Equipment

Recordings were played into a Sefram 'Rapidgraph' multichannel pen recorder, each track supplying a separate pen, the intention being to obtain separate traces alongside one another. It was found that this rarely succeeded, as a result of inadequate pen and paper speeds and of crosstalk between the tracks, which could never be entirely eliminated. It was therefore decided to play a single track into a Brüel and Kjaer level recorder 2305, with a frequency range of 10-200,000 Hz (stylus movements limited, however, to a range below 100 Hz). This produced a trace on waxed paper.
A speed of 1 cm./sec. was found workable, the recordings being played at half speed, to give a virtual 2 cm./sec. time scale.
In the *roeselii*/*brachyptera* and *roeselii*/*bicolor* interactions, it was usually found that a recording in which the *brachyptera* or *bicolor* had been closer to the microphone than the *roeselii*

would give a good result. The level of the baseline would rise whenever the roeselii sang and the chirps of the other insects would stand out above it. Unfortunately, the waxed paper records do not show up sufficiently clearly for examples to be presented here so an ink trace on paper has been obtained using the same machine set for 3 cm./sec., the tape again being played at half speed. (See figs 10,11,12,20). Sometimes a very clear result was obtained also with bicolor/ brachyptera interactions but generally the similarity of their chirps led to confusion when both sang simultaneously.

The waxed-paper technique was more suitable than the pen and ink for analysis because a thinner line was obtained and measurement was more accurate. In spite of the decision to analyze material from one track only, all the recordings made in 1970 were stereophonic. The reasons for this were that it was often impossible to predict which of the tracks would analyze the more clearly and that because the insects sometimes walked about in the course of the experiment the best results might be obtained by using one track for one part of the analysis and the other for a later one. Stereophonic recordings were of course suitable for use with an oscilloscope, but in practice it was found that oscillograms were not very helpful. Due to the capacity of the camera, only a very short section of a recording could be analyzed at a time and there was no means of giving a time scale when both traces were used for signals (filmspeed is a very unreliable indicat-

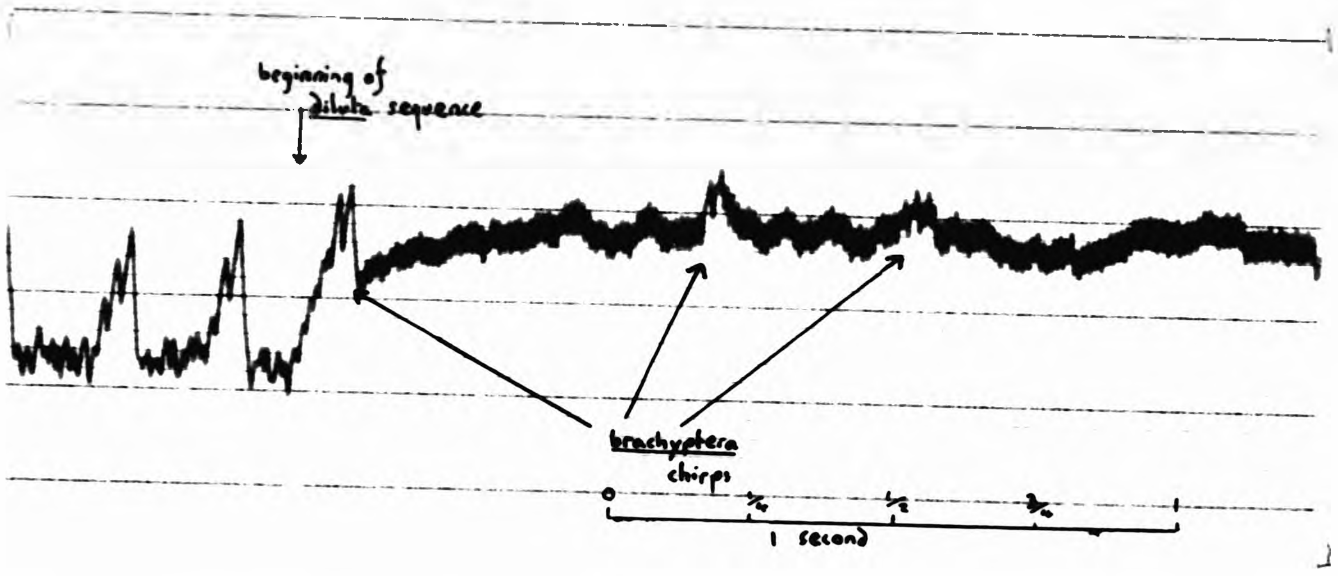


Fig. 10 Interaction of *brachyptera* (14), with *diluta* (2), see page 80. Note decrease in *brachyptera* chirp rate when *diluta* sings.

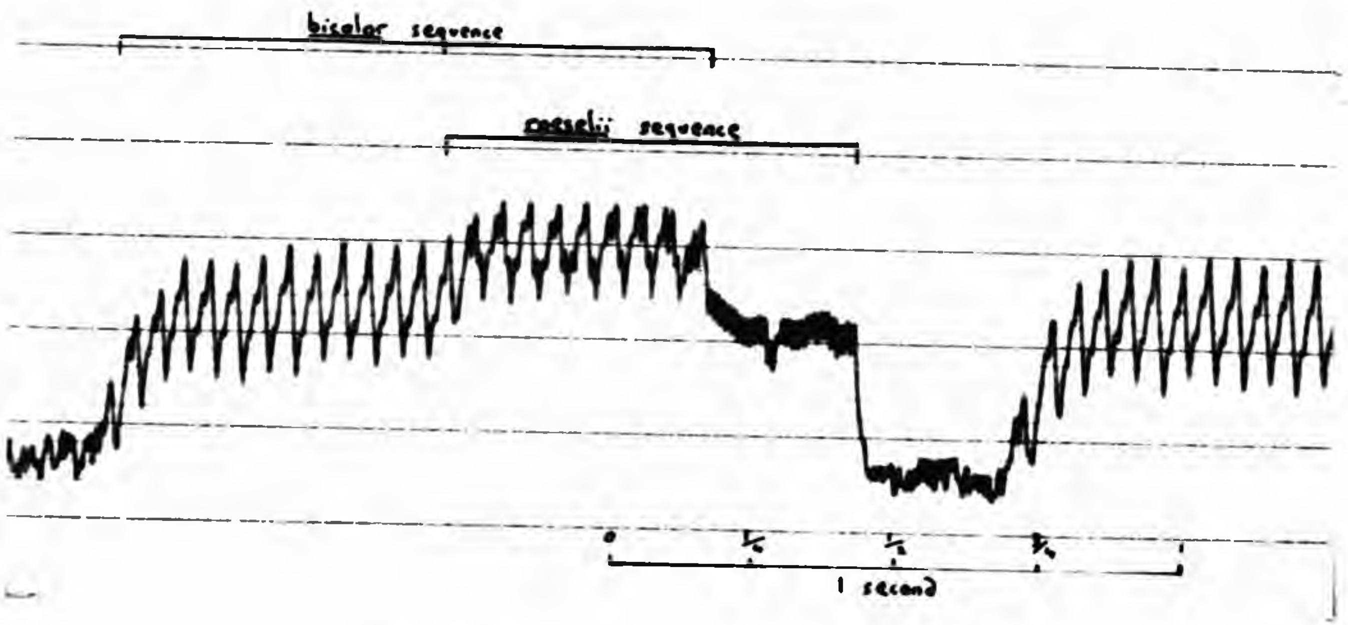


Fig. 11 Interaction 6. of *bicolor* (3), with *roeselii* (10), see page ~~130~~. 121.

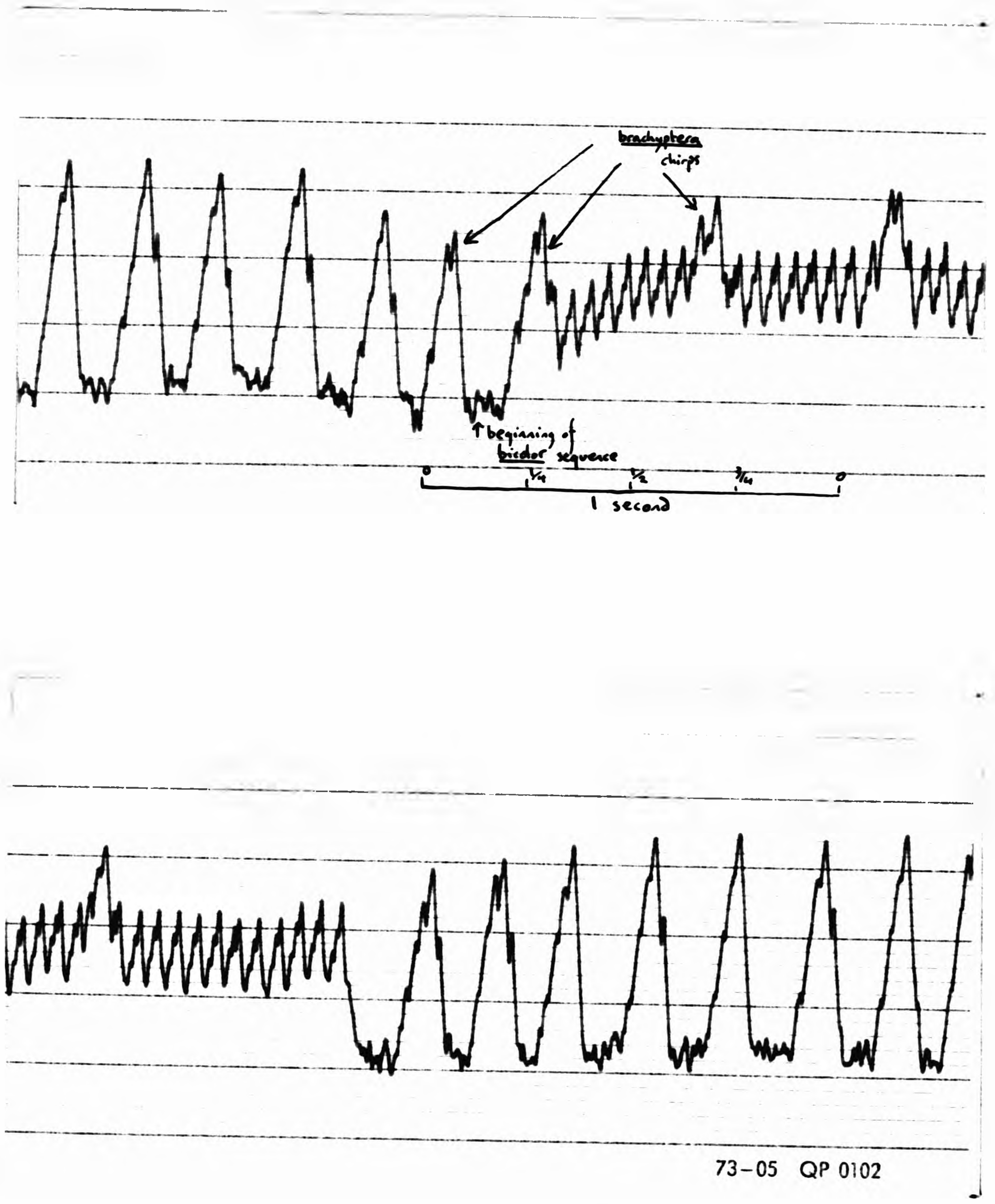


Fig. 12 Interaction 3. of *brachyptera* (15), with *bicolor* (6), see page 156. The two sections are continuous.

ion). Further, crosstalk occurred on the oscillograms just as much as with the Sefram traces.

Rearing

Females laid their eggs in vegetable matter inside the boxes, and these were removed with a view to rearing, but the project was not carried through. Information was received from Dr J. C. Hartley of Nottingham University to the effect that *Metrioptera* eggs were much more difficult to incubate than those of most bushcricket genera. This is because they are very dark and it is impossible to ascertain microscopically the condition of the developing embryo and hence the time at which an egg should be cooled for diapause. In addition, as the eggs of *roeselii* and *brachyptera* are laid in narrow plant-stems, it is difficult to extract them from a large tangle of herbage. In comparison with this, it is relatively simple to obtain these species in the field, only a few weeks later than the time at which laboratory-reared individuals would reach adulthood.

Details of Numbered Male Insects used in the Experiments

Metrioptera roeselii

r(0) S. Cyprien Plage (Hérault), France. 4 July, 1969. Swept in long damp grasses.

r(1-6) Domme (Dordogne), France. 11 July 1969. Caught by hand in long grass on a hillside.

r(7-9) Creeksea, Essex. 12 September 1969. Caught in glass jar amongst clumps of short grass and nettles in public car park.

r(10-12) Erlangen, W. Germany. 17 August 1970. Caught by hand in low herbage on marshy ground.

Metrioptera roeselii var. diluta

d(1) Domme (Dordogne), France. 11 July 1969. Caught by hand in long grass on a hillside.

d(2) Tübingen, W. Germany. 29 July 1970. Caught by hand in long grass on hillside above Panoramaweg.

Metrioptera brachyptera

br(1-4) Wych Cross, Sussex. 24 August 1969. Caught in glass jar on heather and long grass.

br(5-9) Wych Cross, Sussex. 24 September 1969. Caught in glass jar on heather and long grass.

br(10-19) Wych Cross, Sussex. 24 August 1970. Caught in glass jar on heather and long grass.

Metrioptera bicolor
(see fig. 21, p. 101)

bi(1-11) Weiler, W. Germany. 7 August 1970. Caught by hand amongst wild flowers and low herbage on sloping pastureland.

Metrioptera sepium

s(1-2) La Môle (Var), France. 21 July 1969. Caught by hand in dense low herbage.

OBSERVATIONS

1. Intraspecific Behaviour of Males

(a) *M. roeselii*

Introduction

Most of my observations on male rivalry were with this species. I found that if two males which had just been captured in the field, or which had been caged alone for several days, were placed together in an observation chamber, one would begin to sing and the other to move towards it. They would meet and antennate one another, and might then move apart but would more frequently engage in a 'bloodless battle', the loser of which would either move rapidly away, or else fall from its position to the floor of the chamber, while the other bushcricket would continue to sing. This is quite similar to the fighting recorded by Nielsen et al (1970) in *Tettigonia viridissima* in the field. One participant, usually the one sitting highest, jumps after the other, which then drops to the bottom of the vegetation. They say that they did not observe bodily contact in this species. A general discussion of rivalry behaviour in insects is given by Richards (1927).

I have the impression that fighting in Tettigoniidae is never as violent as that described by Alexander (1961; see page 11) in crickets. Like Alexander's crickets, my *Metrioptera* seemed sometimes to modify their fighting behaviour into homosexual courtship. I have seen similar behaviour in *Ephippiger ephippiger* males, and Broughton (1955) reports seeing it in Platycleis affinis. (For an example of homosexual courtship in roeselii see pages 51-53). My observations on Ephippiger (made at the Laboratoire de Physiologie Acoustique de l'Institut National de la Recherche Agronomique, Jouy-en-Josas, in 1968) indicated to me that the leader tended to spend relatively more time in the more 'agreeable' parts of the chamber, i.e. those parts in which any Ephippiger would rest if alone. The only occasions in which I have seen comparable behaviour in roeselii have been when an anglepoise lamp was used to heat the cage. The leader would usually hang beneath the hot bulb and attack any insect approaching the area. In both Ephippiger and Metrioptera the losing insect will return many times to the leader but eventually remain in the 'disagreeable' region.

Experiments

A series of tests were made with the M. roeselii var. diluta captured on 11 July 1969 at Domme. A number of other roeseliis captured in the same field on the same day were caged together. The diluta was caged alone and tended to sing a great deal and to dominate any other roeselii briefly placed with it. In mid-August I conducted a series of experiments in which the diluta was placed in an observation cage and one of the other roeseliis added when the diluta was singing. Most of the action would occur on the roof of the cage, from which the diluta usually hung. After a number of encounters the roeselii was removed and another added. This was done with eight numbered roeseliis: successive encounters are lettered.

16 August 1969 Temp. 28–34 deg.

1st roeselii

(a) roeselii climbs towards diluta and brushes it with its antennae: roeselii falls to ground, climbs up again.

(b) the same, but diluta strikes roeselii with a foreleg and makes a burst of sound as roeselii falls.

(c) the same, but diluta also antennates roeselii, singing.

(d) roeselii stops close to diluta and waits. Then both rush together and fall together to ground; diluta springs immediately to roof again; roeselii climbs up again.

(e) roeselii starts singing: some mutual inhibition but sound of diluta eventually becomes continuous and roeselii stops. Then diluta approaches roeselii and touches it with its antennae: it falls, and diluta starts walking around.

(f) roeselii falls apparently of its own accord; climbs up again.

(g) diluta approaches roeselii and sings at it: roeselii falls. No physical contact.

2nd roeselii

(a) roeselii climbs towards diluta, stops and waits, then alternates short bursts of sound with it. Then they rush together: roeselii falls to ground and then climbs up again.

(b) diluta approaches roeselii from behind, antennates its antennae, turns and walks away.

(c) both walking meet face to face. They rush together, biting: roeselii falls, climbs up.

16 August 1969 Temp. 28–34 deg.

1st roeselii

(a) roeselii climbs towards diluta and brushes it with its antennae: roeselii falls to ground, climbs up again.

(b) the same, but diluta strikes roeselii with a foreleg and makes a burst of sound as roeselii falls.

(c) the same, but diluta also antennates roeselii, singing.

(d) roeselii stops close to diluta and waits. Then both rush together and fall together to ground: diluta springs immediately to roof again; roeselii climbs up again.

(e) roeselii starts singing: some mutual inhibition but sound of diluta eventually becomes continuous and roeselii stops. Then diluta approaches roeselii and touches it with its antennae: it falls, and diluta starts walking around.

(f) roeselii falls apparently of its own accord; climbs up again.

(g) diluta approaches roeselii and sings at it: roeselii falls. No physical contact.

2nd roeselii

(a) roeselii climbs towards diluta, stops and waits, then alternates short bursts of sound with it. Then they rush together: roeselii falls to ground and then climbs up again.

(b) diluta approaches roeselii from behind, antennates its antennae, turns and walks away.

(c) both walking meet face to face. They rush together, biting: roeselii falls, climbs up.

(d) *diluta* approaches *roeselii* behind, antennates, bites *roeselii*'s hind tibiae, turns and moves off. As it does so, *roeselii* turns and antennates it.

(e) they meet face to face and then separate, *diluta* moving away.

(f) *diluta* comes towards *roeselii* from behind, trying to bite its hind legs. Short bursts of sound by both, then *roeselii* turns. A struggle: *roeselii* falls to ground, climbs up again.

(g) several encounters in which both keep coming together and then turning and walking away without ever getting close enough for physical contact. Only *diluta* is singing.

(h) *roeselii* approaches *diluta* from behind: *diluta* curves its abdomen down: *roeselii* walks over the back of *diluta*, tasting the dorsal surface of *diluta*'s abdomen, and walks on. During this, *diluta* sings several times.

(i) they meet face to face: *diluta* bends its abdomen down and *roeselii* walks over the top of it and away: *diluta* turns and pursues it, singing.

(j) they meet face to face, both giving out short bursts, and antennate. Then *roeselii* stops singing, and both turn away and move off, downwards. Then *diluta* follows *roeselii* some way, then stops and turns back. Then *roeselii* climbs again.

(k) succession of single short bursts of song: *d*, *r*, *r*, *d*, *d*, *r*, *d*, *r*, *d*, *d*, *r*, *d*, *r* plus *d* (simultaneous), *r*, *d*, *d*, *d*, *r*, *d*, *d*, *d*, then all *d*. Insects ½inch apart: *roeselii* still, *diluta* walking back and forth. Then *diluta* approaches *roeselii* and climbs on to it: roeselii sings, then diluta. Then roeselii starts to walk away: sudden fight and roeselii drops to ground: diluta sings and goes on singing; roeselii climbs up.

3rd roeselii

(a) continual diluta song; roeselii approaches to 3 inches of diluta but does not sing. After ½ hour no further progress.

4th roeselii

(a) roeselii approaches to within 4 inches of diluta. Alternation of bursts. Later diluta advances and bending its abdomen downwards climbs on to roeselii facing in the opposite direction. Tries to touch tip of roeselii's abdomen with mouthparts. Then roeselii moves off and diluta follows it. (See page 48).

(b) diluta rushes at roeselii from behind and roeselii jumps forwards landing on the ground. Then, only diluta sings; roeselii climbs up.

(c) diluta approaches roeselii from behind and brushes it with its antennae: roeselii falls, then climbs up.

(d) both give out alternating bursts, moving together, and then diluta starts to move away. Then they come together again and antennate: roeselii turns away and diluta climbs on to it. Then both fall; diluta has fallen to a lower point: it sings and then climbs towards roeselii.

(e) diluta pursues roeselii and there is a struggle: roeselii falls, diluta sings.

5th roeselii

(a) roeselii climbs to within 6 inches of diluta but does not sing; diluta sings throughout.

19 August 1969   Temp. 24 deg.

6th *roeselii*

(a) *roeselii* remains silent at bottom of cage whilst *diluta* sings above.

7th *roeselii*

(a) *roeselii* starts singing, then stops. A long interval and then they meet head on and *diluta* sings: *roeselii* jumps away across cage.

(b) *diluta* approaches silent *roeselii*, antennates and then jumps at it: *roeselii* jumps to the ground, and then sings and starts to climb.

(c) *diluta* comes down to meet *roeselii*: they meet head on and both fall to ground: *diluta* at once leaps away from *roeselii* and sings, on ground.

(d) *diluta* approaches *roeselii* from behind and bites its hind tibiae, and sings; *roeselii* jumps to the roof of the cage and then circles back towards *diluta*. Experiment terminated.

8th *roeselii*

(a) *roeselii* approaches *diluta* and antennates it: *diluta* curves abdomen down. From above and behind, *roeselii* tries to get its front legs on to *diluta*'s tegmina: *diluta* straightens abdomen, turns to face *roeselii*, which moves away. Only *diluta* is singing during this.

(b) the same thing happens again.

(c) *roeselii* advances to meet *diluta* head on: they antennate, and *diluta* sings and turns away from *roeselii*, bending its abdomen down and exposing the dorsal surface, which roeselii tastes. Then diluta turns to face roeselii, straightening its abdomen, and then turns away, curving it again. While roeselii again tastes the abdomen, diluta sings: then roeselii walks away. (See page 48).

(d) they meet and diluta turns, exposing its abdomen, and then turns back. There is a struggle and both fall to the ground. Still only diluta is singing.

Other roeseliis

The male r(O), which had been housed since 4 July with a female captured at the same time and place, was much more lively than the Domme males. When put with the diluta, both it and the diluta sang continually. The roeselii approached the diluta and then moved away and remained stationary for a long time. Suddenly diluta rushed forwards, meeting it head on: roeselii jumped away and remained silent, while diluta sang.

On 20 August a male Domme roeselii that had just copulated was put into the chamber with the diluta, which was singing. It made no sound nor any movements towards the diluta.

When males that have already been kept in a box together are put into the observation chamber they will usually sing, apparently ignoring one another, and if they do meet will not usually fight, although in one case I observed a male tasting another's back. The exception to this was the diluta, which after being confined for three days with the other Domme roeseliis, continued to have fights with them.

(b) Other species

The other *Metriopteras* have been less thoroughly studied in this respect but my general impression is that the intra-specific behaviour of male *brachypteras* is less violent than that of *roeseliis*. When male *brachypteras* are placed together in a box they will as a rule take up a certain position, often very close together, and remain stationary for a long time, both singing. The songs usually have a period of alternation followed by a period of synchrony, then more alternation &c.

M. bicolor appears to resemble *roeselii* in its 'bloodless battles' and in these it is common for a kind of *squeaking* noise to be uttered during the actual struggle. I have witnessed this in the field in Germany. The sound has also been heard from *roeselii*, in interspecific encounters, and bears some resemblance to the distress sounds of *Ephippiger*. Miss S.E. Faggetter in her work on the genus *Platycleis* has frequently noticed sounds of this kind produced during physical encounters (personal communication, 1969).

Only two males of *M. sepium* were studied, and since these were caged together, any aggressive tendencies they may have initially possessed were lost. If they were placed in a cage together they would sing in alternation all night without making any attempt to approach or touch one another.

2. Sexual Behaviour

Introduction

The bending of the abdomen observed in the *diluta* when it encountered other males in some cases is very reminiscent of the bending movements made by a male bushcricket about to copulate. Moreover, the tasting of its back resembles the tasting of the male's back by the female which is a frequent event in precopulatory behaviour. It will be valuable when considering interspecific behaviour to bear in mind the kind of sexual behaviour normally observed in Orthoptera. Tettigoniid copulation is described by Fabre (1897) for *Decticus albifrons*, and by Harz (1957) for a number of species. Some details concerning the species here considered are given by Zippelius (1948). The tasting of the male's back implies that there are glands in the area whose secretion attracts the female. Such glands are known in Gryllacrididae (Gurney, 1947) and in the tettigoniid *Bradyporus multituberculatus* (Boldyrev, 1928, quoted by Gurney). Chopard (1938) says they must also exist in many bushcrickets.

Copulation of *M. roeselii*

I observed this several times. In one case a male was placed in a box containing a female. The first sign of recognition was the pointing of one antenna of the male towards the female. The female approached the silent male and climbed from behind on to its back, tasting it. The male, whose abdomen had been bent downwards in a loop, bent the tip upwards, evidently in an

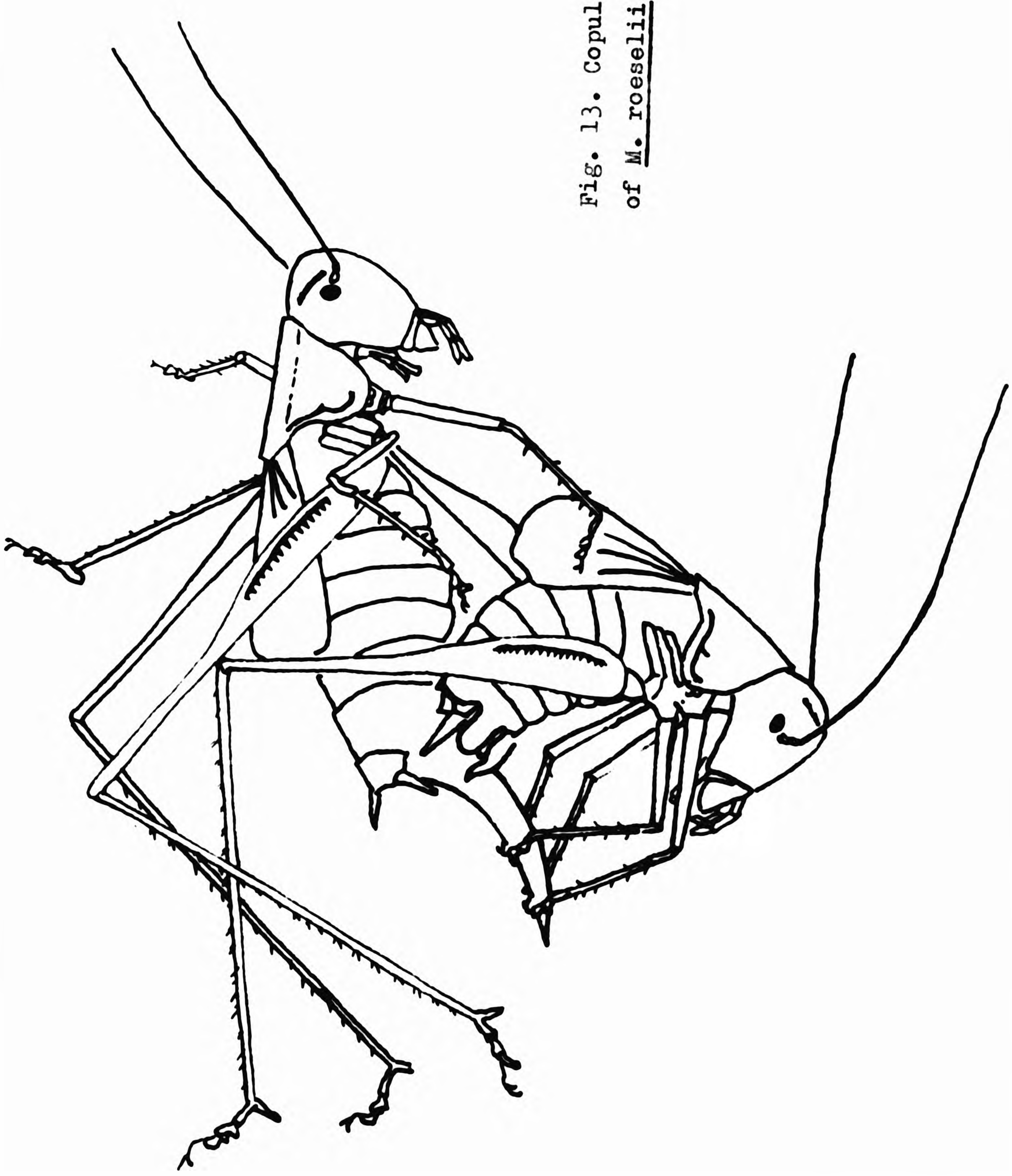


Fig. 13. Copulation of M. roeselii.

attempt to meet the tip of the female's abdomen, but the female continued walking over the male. The male stridulated - four one-second bursts approximately two seconds apart - and during this the female circled round and climbed again on to the male's back. This time the male succeeded in gripping the female's ovipositor base with its cerci, and the ovipositor with its 1st and 2nd legs (see fig. 13). Copulation took 38 minutes and about halfway through the insects toppled on to their sides and lay there. Six minutes after the completion of spermatophore transfer the male resumed stridulation.

Copulation in Other Species

Three other roeselii copulations were observed, all basically the same as this, and in each case the male resumed singing very soon after its separation from the female - in the case of diluta (1) in less than two minutes. A sepium copulation was also observed: it was similar in the relative position of the participants, but less movement occurred. The precopulatory behaviour of the female - tasting the male's back - was also similar to that seen in roeselii. These copulations differ slightly from those I have observed in Tettigonia viridissima, Conocephalus dorsalis and C. discolor, where the male lies on his back beneath the female, supported by her ovipositor, facing in the opposite direction from her.

Situations with Two Males

When a female is put into a box containing two singing males, it will usually pass from one to the other, and may mate with either, not necessarily the one which sings most. In the case of sepium, a female was placed in a box containing males (1) and (2) at 9.15 p.m. on 18 August 1969. The temperature was 24 degrees and a red bulb was used for illumination, as ordinary electric light had been observed to curtail stridulation. The males were sitting three inches apart on the end wall of the box, alternating bursts of song. The female approached and reached male (1) and tasted the back of its abdomen, whereupon the male sang and the female drew back, moved towards male (2), and then returned and again tasted (1)'s abdomen. It next moved towards (2) and antennated it, pursued by (1), which was doing the greater part of the singing. The female turned to (1) and antennated it, and (1) climbed over the female and tasted its abdomen. This reversal of the normal procedure was seldom seen. After this (2) came to do most of the singing. An attempt by (1) to copulate with the female failed: it was shaken off, making squeaking noises. Now (1) and (2) moved very close together and the female retreated six inches away. It then approached (2), moved away again, moved towards (1) and remained very close, motionless, facing it, for about 10 minutes. Then it circled around (1), tasted its abdomen, walked away, approached (2), moved off again and then back, climbing on to the back of (2), which was hanging from the roof. It, (2), bent its abdomen into a loop and appeared to be copulating with the female, but she suddenly pulled away, then returned. The principal singer was still (2). The time was now 11 p.m., and little movement was taking place. The female walked over to (1) and tasted its abdomen several times. I stopped the experiment at midnight.

The following two nights, another female was placed with (1) and (2), and similarly moved from one to the other, finally copulating with (2) on 20 August. In this case (2) was singing more than (1), but in a similar experiment with two roeselii males and a roeselii female on the same day, the female mated with the male which was singing the less. Again, a movement from one male to the other prior to copulation was observed. Two experiments with diluta (1) and another male roeselii both terminated in copulation between the female and the diluta, which was the leader in this case. As stated above (page 11), M.-C. Busnel points out that leaders tend to attract more females. An experiment with brachypteras (1) and (4) and a female brachyptera, undertaken on 15 September 1969, gave a similar result to the others but it was clear in this case that the presence of the female stimulated singing. In an interspecific experiment on 14 September 1969 brachyptera (4) was caged with three roeseliis at 9.48 a.m. (temperature 19 degrees): by 10.42 a.m. it was silenced by their song. A female brachyptera was placed in the cage at 11 a.m. The male resumed singing and by 11.23 a.m. was singing so continuously that when a further eight roeseliis were added, it still managed to hold out for ten minutes before being quelled.

3. Interspecific Behaviour of Males

(a) *M. sepium*

The study of this species was rather peripheral and only four interspecific experiments were made: three with *roeselii* and one with *brachyptera*. In the *roeselii* experiments the insects were placed in adjacent boxes and a microphone supported over each box. In the first one, on the morning of 12 August 1969 at about 3 a.m. (temperature 25 degrees), a box containing 11 *roeseliis* (from Domme, 11 July 1969) was placed next to the box containing *sepium* (2), which was singing. At first the *sepium* appeared to be inhibiting the *roeseliis*, but it was itself eventually silenced by a massive *roeselii* chorus. Examination of the Brüel and Kjaer level recorder's analysis of the sequence shows no visible difference between *sepium* stridulation produced concurrently with *roeselii* stridulation and that produced between *roeselii* bursts. Part of the recording is represented in fig. 14. It can be seen that initially a *roeselii* burst silences *sepium* but subsequently concurrent song becomes general, with *roeselii* gradually singing more and more, and *sepium* less and less. Finally *sepium* is completely silent.

In the two other experiments with *sepium* and *roeselii*, both *sepiums* (1) and (2), caged together, were used. On 12 August 1969 at 7 p.m. (temperature 28 degrees) their box was placed next to that containing *diluta* (1). First the *sepiums* uttered a few chirps, then *diluta* began to sing continuously, and then, inexplicably, it stopped and the *sepiums* recommenced. On 13 August 1969

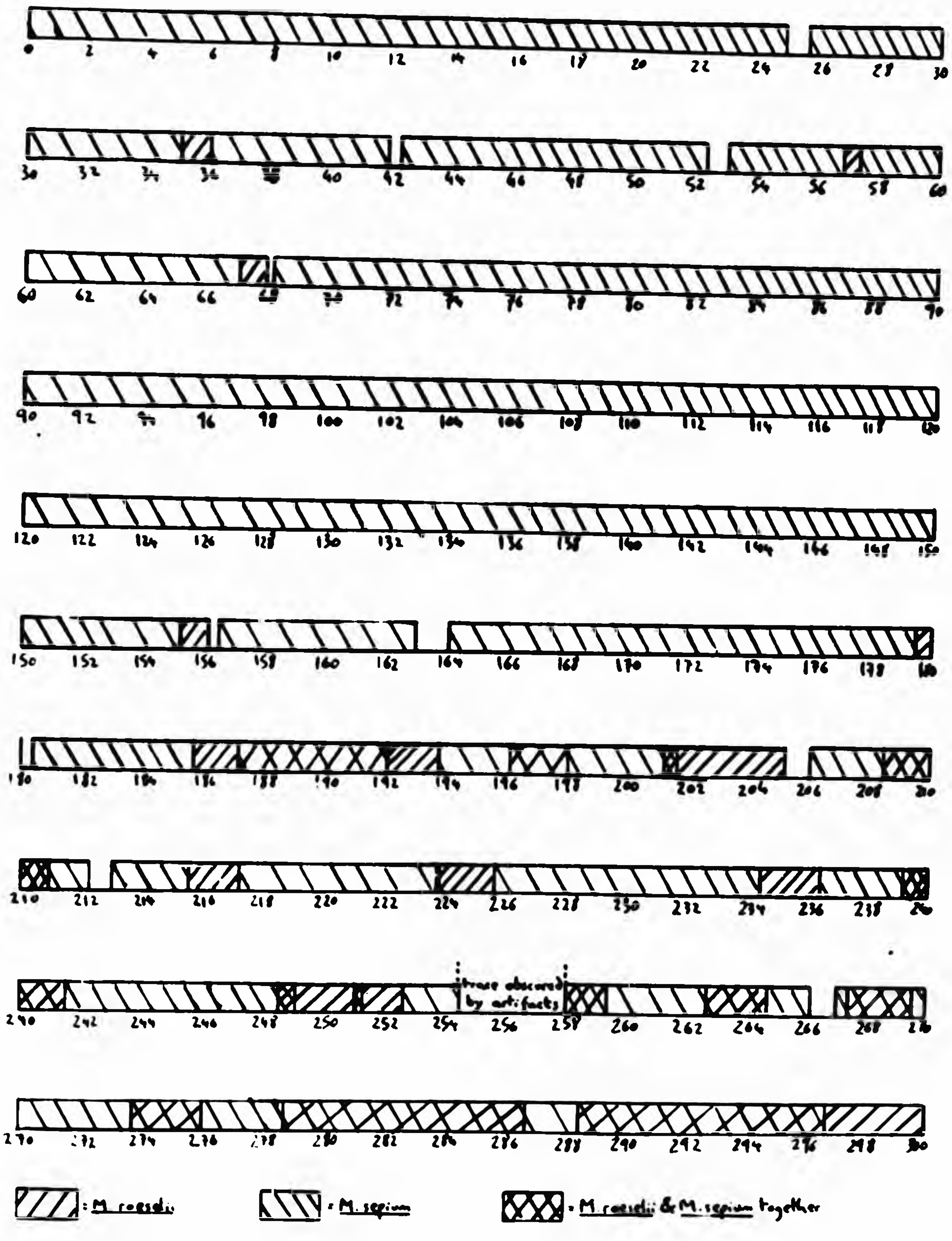


Fig. 14. Song output in sepium/roeselii interaction. Time in seconds.

at 8.30 p.m. the same sepiums were placed next to the box containing the 11 roeseliis used above. The temperature was 19 degrees. Continuous song was emitted by both species, indistinguishable in arrangement and syllable rate from that produced normally. At 9 p.m. the experiment was stopped: it was considered that a condition of toleration had come about.

A single experiment with sepium and brachyptera was attempted on 26 August 1969 at 00.58 a.m., the temperature being 18 degrees. The insects, sepium (1) and brachyptera (1), were placed together in the recording cage and two microphones were positioned for a stereophonic recording. Unfortunately, both insects walked about continually and it was not possible to obtain recordings free of crosstalk. Because of similarities in the song structure it was very hard to pick out on the resultant Brüel and Kjaer trace which syllables were due to which insect when both were singing simoultaneously. The general impression is of absence of any effect by one insect on the other. At 1.35 a.m. both insects were still singing and the experiment was stopped.

(b) Interaction of *M. roeselii* and *M. brachyptera*

Introduction

I suggested earlier (page 21) that these two species were always allopatric in Britain. On the continent this does not appear to be the case. Ramme (1936) found them together in the Grunewald (between the Grunewald station and the Schildhorn) in 1935. His earlier observations on the differences in their habitats are repeated by Burr (1936) and Freeman (1937). He found that in the Tirol *roeselii* was an inhabitant of cultivated ground, and was replaced on higher, stony ground by *brachyptera*. He quotes La Baume who says that in W. Prussia *roeselii* is found only in wet places and *brachyptera* only in dry, but he adds that personally, in the Alps, he has found that this law does not hold. Obviously the significance of my observations would be greatly enhanced could it be shown that interactions such as the following really occur in natural bushcricket populations. M.D.R. Jones (personal communication, 1970) informs me that he encountered the species together in 1970 in a German locality, but we have no information on their behaviour there.

Experiments

The fundamental effect of the song of *roeselii* upon a singing *brachyptera* is to slow down the rate of chirping and eventually to silence the insect completely. The behaviour accompanying this varies: sometimes the insects appear to ignore one another completely and sometimes they are attracted together. As there was usually a stage in the inhibition process at which the *brachyptera* would sing only during the pauses in the *roeselii* song, it was normal to silence the *roeselii* when no *brachyptera* song at all had been produced for the past few minutes. If the *brachyptera* did not resume singing within 30 seconds of this (the *roeselii* was not permitted to sing again in this period), it was considered to be *totally inhibited*. The effect of this inhibition would sometimes last for several hours if the *brachyptera* was now placed in a silent room, before stridulation was resumed.

Successful experiments were conducted with thirteen *brachypteras*: those numbered (1), (2), (4), and (7) were studied in 1969, and those numbered (11), (12), (13), (14), (15), (16), (17), (18) and (19) in 1970. By 'successful' I mean that both insects sang during the experiment: it was however only in some cases that effects of inhibition occurred. When the two insects continued singing for so long that I became convinced that the *brachyptera* was capable of continuing indefinitely in spite of the *roeselii* interference, I would say that a state of toleration had come about, and stop the experiment.

All the *brachypteras* used here were caged in male groups, never isolated, nor caged with females.

brachyptera (1)

1. 30 August 1969. 9.20 a.m. Temperature 17 degrees. Tape reference 3.1.0. Interacting insect *roeselii* (1), caged previously with other male *roeseliis*.

   Behaviour: Both insects attract one another, reaching 1½", but *roeselii* moves far more than *brachyptera* and later retreats 10" away. Eventually *brachyptera* stops, and then suddenly begins to move off.

Final result: Inhibition of brachyptera.

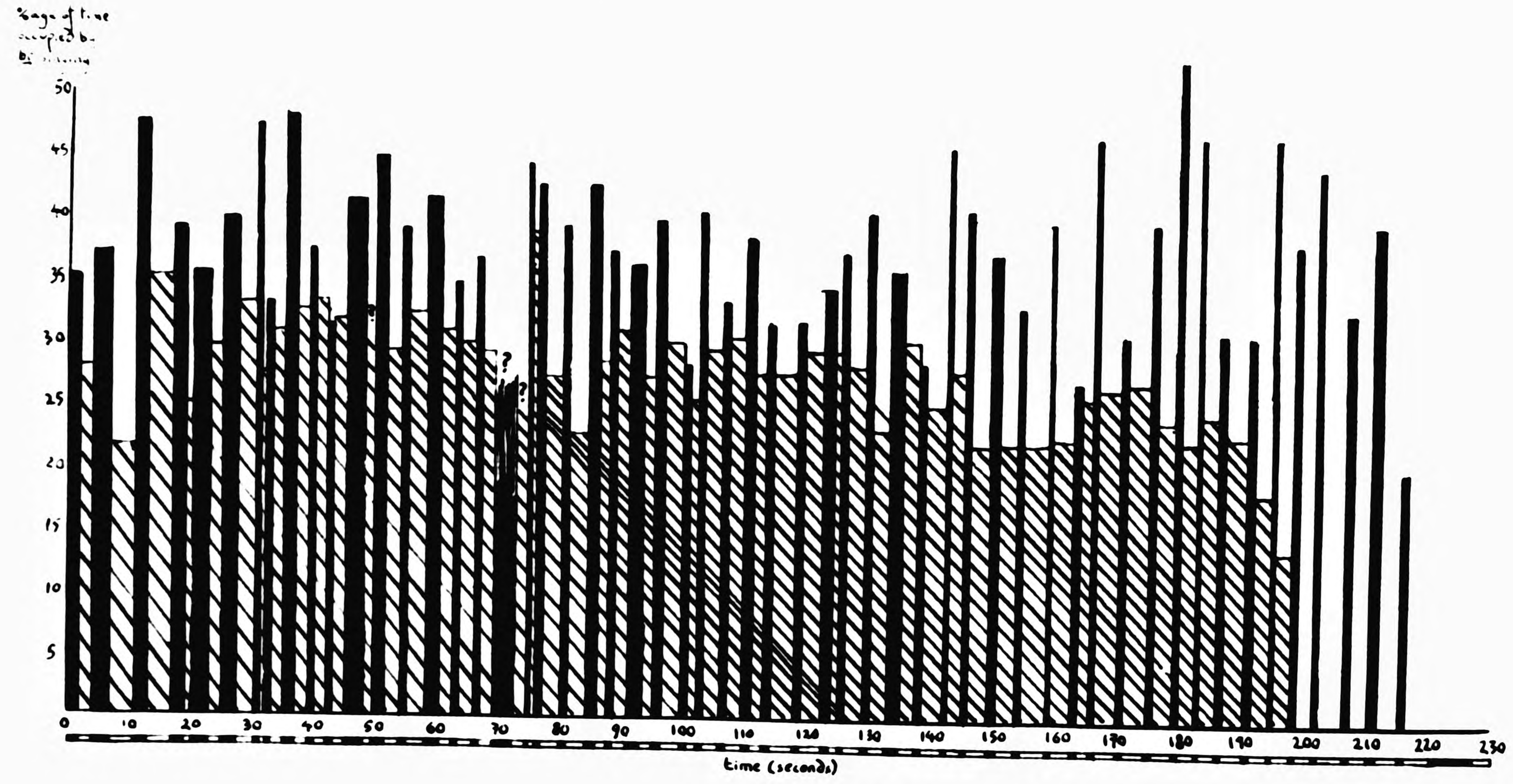
Additional Notes: Histograms 1 and 2 show the last 7 2/3 minutes of the inhibition. Quantity of brachyptera song is plotted against time. As the roeselii sequences or their intervals are usually so short as to contain very few brachyptera chirps, the estimation of quantity of song as a rate of so many chirps per second would be highly inaccurate. Accordingly, the separate chirps represented on the recording paper have been measured with dividers and the sum of the chirplengths within each roeselii sequence or interval has been divided into the total length of the sequence or interval, so as to give the "percentage of time occupied by brachyptera singing.'.

Several features of the histograms should be noted. Firstly, the brachyptera occupies a greater percentage of the available time during the silences between roeselii sequences than during those sequences. Secondly, this disparity increases until brachyptera song during that of roeselii has fallen to 15%, after which it occurs only in the intervening silences, falling there later to 21% and then cutting off. After a period of about 36 seconds (histogram 2) the brachyptera song resumes, firstly in the silences and then also in the roeselii sequences (again at a lower level in the latter). The levels rise almost to their former height before subsiding as before. Finally there is a third small resurgence of brachyptera song, this time only during the silences, and the insect is thereafter totally inhibited.

Histogram 1

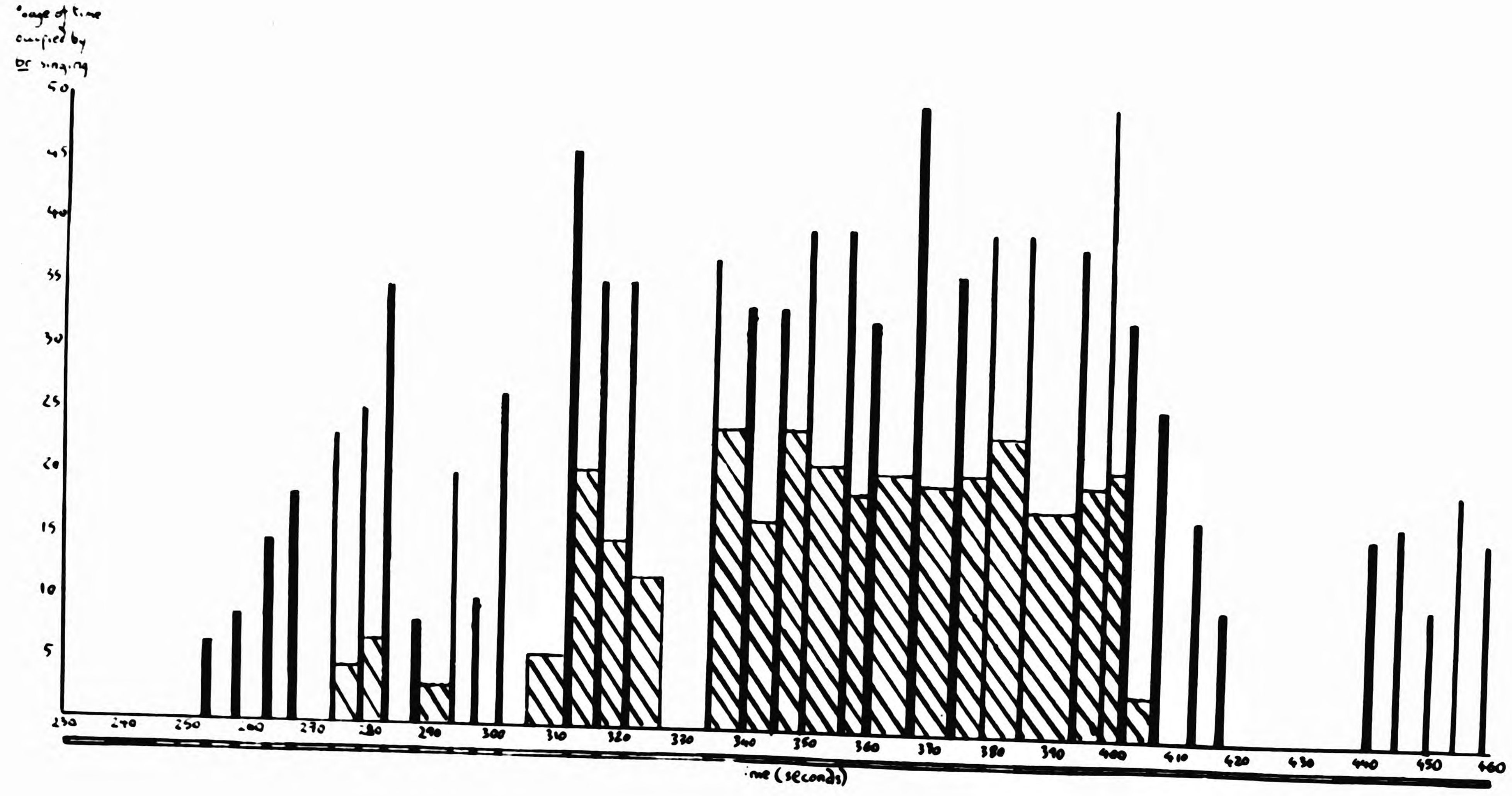
<u>brachyptera</u>/<u>roeselii</u> interaction: <u>br.</u>/<u>r.</u>, part 1

base strip shows periods of silence (black) & <u>roeselii</u> activity (white)
histogram shows <u>brachyptera</u> activity in periods of silence (black)
& <u>roeselii</u> activity (shaded)



Histogram 2

brachyptera roeselii interaction: br_1/r_1, part 2



It should also be noted that the nature of the roeselii song during these histograms changes, the gaps in it becoming shorter and further between. This has nothing to do with the brachyptera: exactly the same phenomenon occurs when a solitary roeselii sings: see fig. 15. It does however tend to promote the inhibitory effect (see page 162) and dictate the form of the histogram. Comparison should be made with the histograms shown later in this section.

In several interactions, particularly the present one, counts were made of the number of 2-, 3- and 4- syllabic brachyptera chirps occurring during and between roeselii sequences. It was eventually decided that no real correlation could be established. The distribution of 2- and 4-syllabic chirps is highly sporadic. In the central portion of the present recording the brachyptera song consists almost entirely of tetrasyllabic chirps, and then for no apparent reason it again becomes trisyllabic. On the other hand many recordings appear to be devoid of any but trisyllabic chirps.

No effect whatsoever has been observed in any recording of roeselii song which can be attributed to the proximity of a singing brachyptera. A close correlation of syllable rate with temperature has been observed in the several individuals studied from this viewpoint and the levels have constantly been very close to those shown by Jones for one individual roeselii as stated above (page 20).

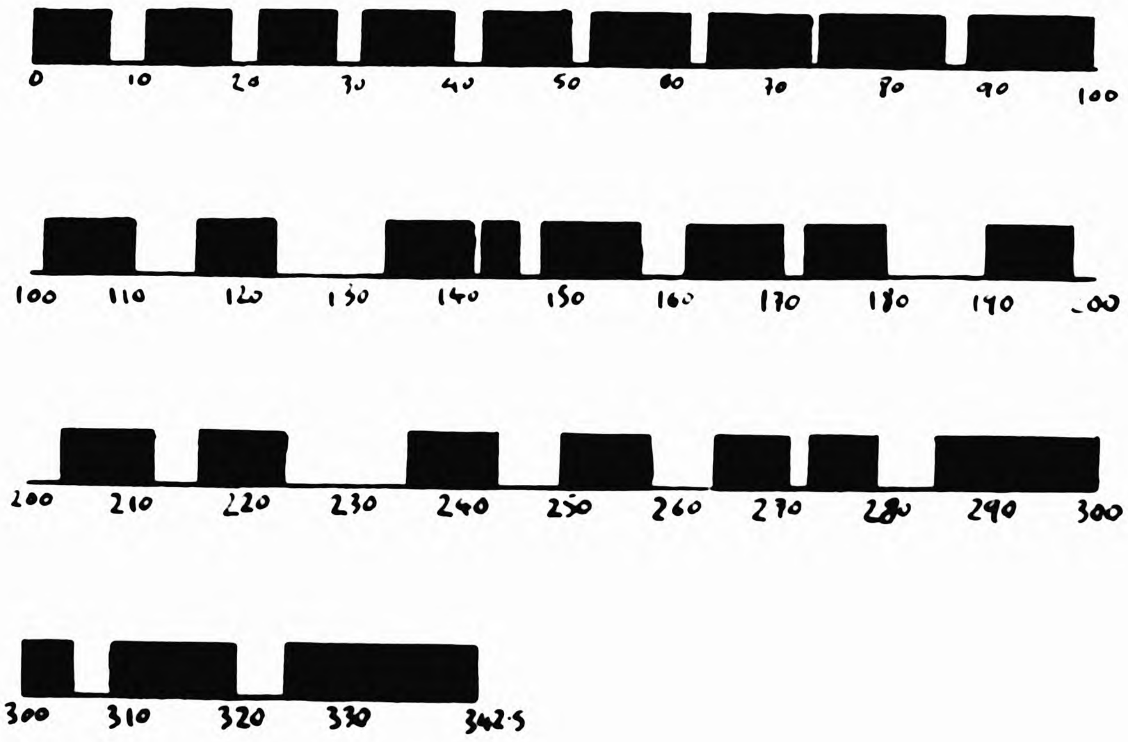


Fig. 15. Sequences (black) and intervals of roeselii (11). Time in seconds.

Recorded 16.9.1970

Temp. 32 degrees.

2. 4 September 1969. 10.45 a.m. Temperature 19 degrees. Tape reference 3.2.342. Interacting insect *roeselii* (1), caged previously with other male *roeseliis*.

Behaviour: Both insects sit still and sing.

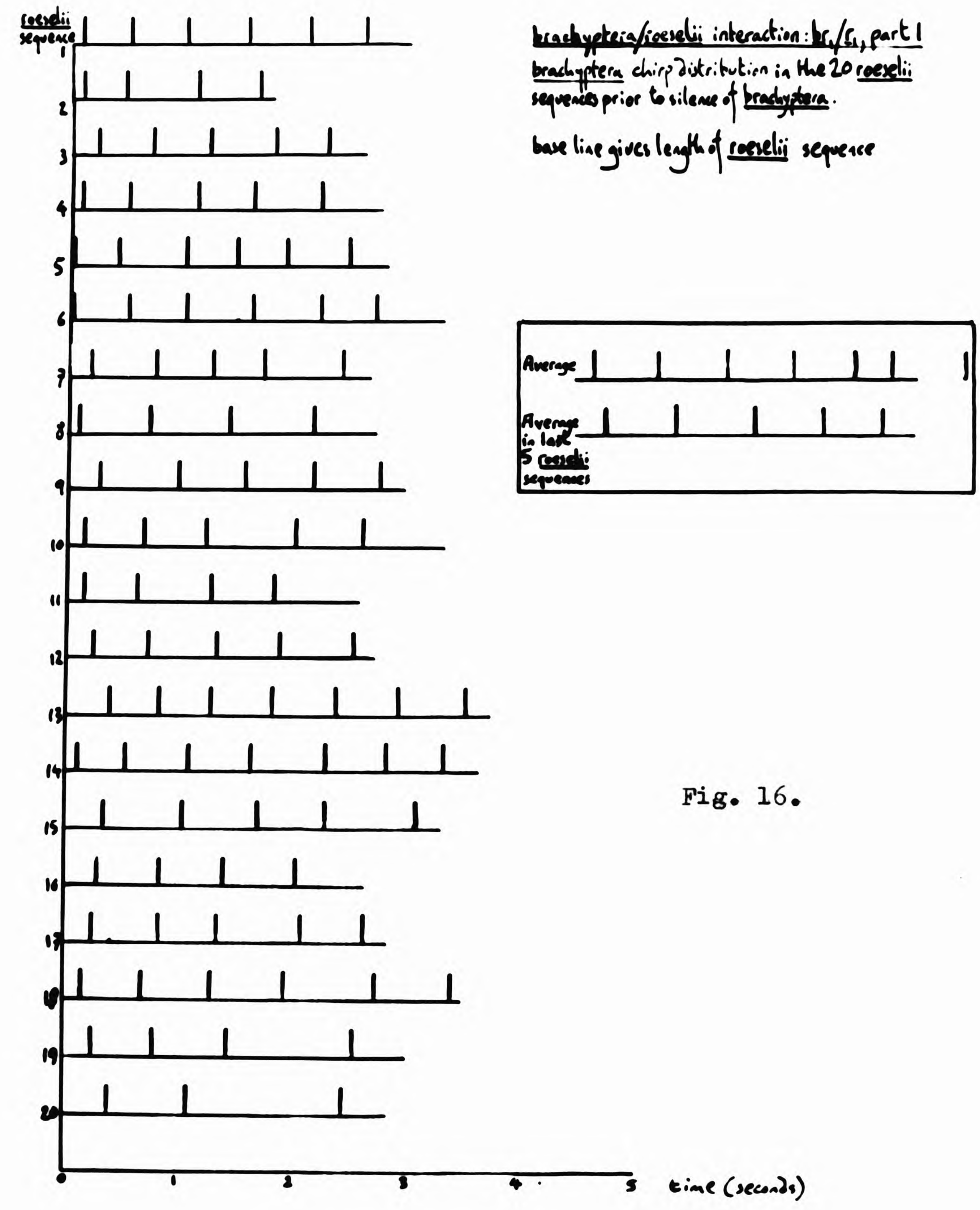
Final result: Inhibition of *brachyptera*.

Additional Notes: Here also a 'resurgence' by the *brachyptera* took place before it was finally silenced. Figs 16 and 17 show the arrangement of *brachyptera* chirps within the 20 *roeselii* sequences immediately prior to the first silencing of *brachyptera* and within the 13 *roeselii* sequences immediately prior to the second. It should be noted in the first that only at the very end does there appear to be a diminution in chirp rate during the *roeselii* sequence. In the second there is almost no diminution at all, just a sudden halt. The silences between these *roeselii* sequences are too short to contain *brachyptera* chirps but in the earlier parts of the recording, where they are longer, a considerably higher chirp rate during the silences than during the *roeselii* sequences is ~~of course~~ observed.

3. 30 August 1969. 1.06 p.m. Temperature 18 degrees. Tape reference 3.1.719. Interacting insect *roeselii* (4), caged previously with other male *roeseliis*.

Behaviour: Both insects walk about without apparent awareness of one another.

Final result: Toleration.



brachyptera/roeselii interaction: br_1/r_1, part 1

brachyptera chirp distribution in the 20 roeselii sequences prior to silence of brachyptera.

base line gives length of roeselii sequence

Fig. 16.

<u>brachyptera/roeselii</u> interaction: <u>br./r.</u>, part 2
<u>brachyptera</u> chirp distribution in the 13 <u>roeselii</u>
sequences prior to silence of <u>brachyptera</u>
base line gives length of <u>roeselii</u> sequence

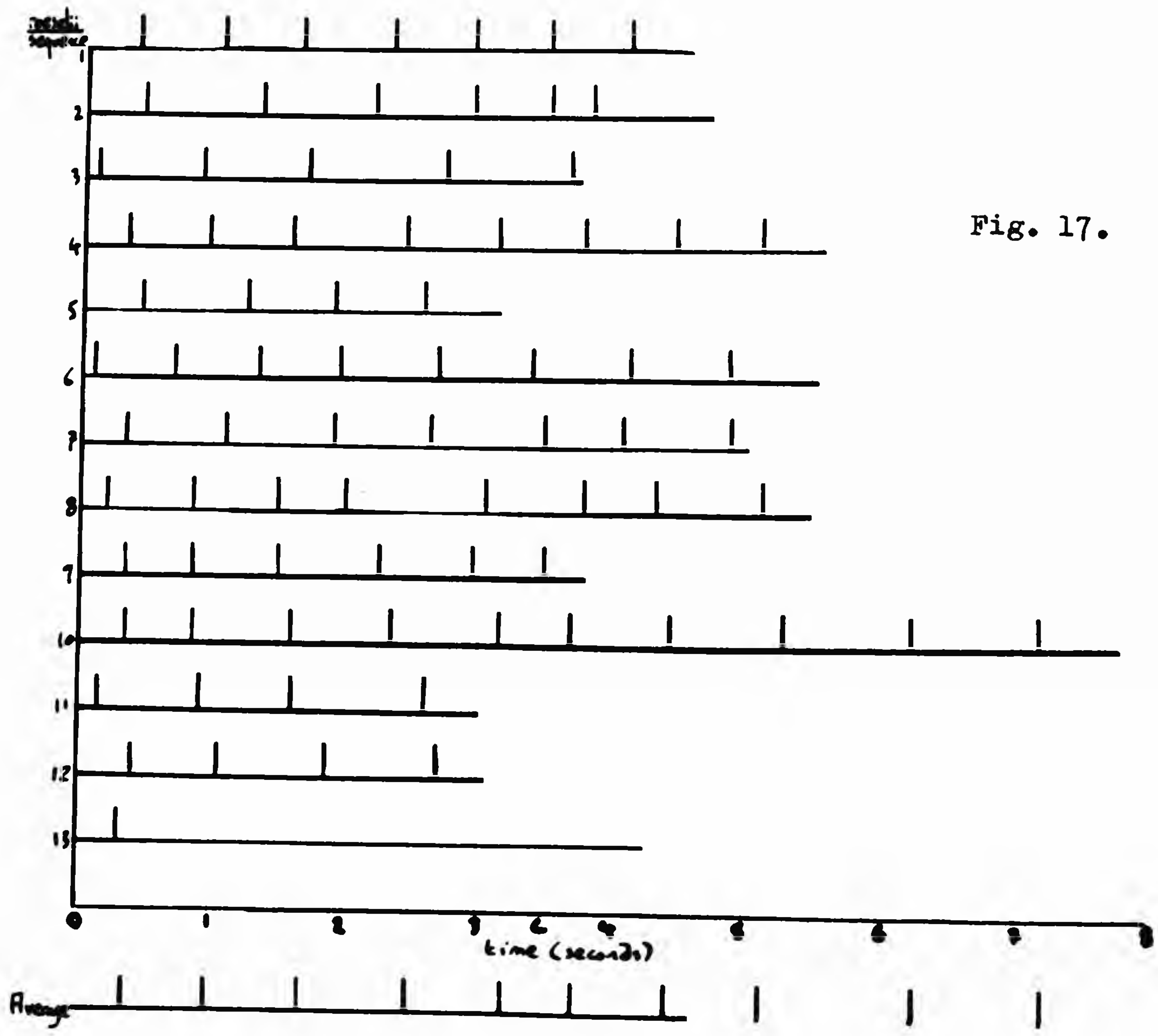


Fig. 17.

4. 6 September 1969. 3 p.m. Temperature 20 degrees. Tape reference 3.2.636. Interacting insect roeselii var. diluta (1), caged alone previously.

Behaviour: brachyptera attracted to vigorously singing diluta: gets very close and remains there, silenced. A box of brachypteras brought into the vicinity to try and stimulate the brachyptera to resume is also silenced after a few minutes' song.

Final result: Inhibition of brachyptera.

5. 7 September 1969. 11 a.m. Temperature 19 degrees. Tape reference 3.2.737. Interacting insect diluta (1), caged alone previously.

Behaviour: brachyptera moves away from diluta; later stops singing.

Final result: Inhibition of brachyptera.

brachyptera (2)

1. 31 August 1969. 12.35 p.m. Temperature 18 degrees. Tape reference 3.1.1128. Interacting insect roeselii (4), caged previously with other male roeseliis.

Behaviour: Both walk about, apparently ignoring one another.

Final result: Inhibition of brachyptera

2. 2 September 1969. 12.48 p.m. Temperature 18 degrees. Tape reference 3.1.1431. Interacting insect roeselii (4), caged previously with other male roeseliis.

Behaviour: Both sit still, singing.

Final result: Inhibition of brachyptera.

brachyptera (4)

1. 3 September 1969. 10.30 a.m. Temperature 18 degrees. Tape reference 3.1.1450. Interacting insect diluta (1), caged alone previously.

   Behaviour: Both sit still and sing.

   Final result: Inhibition of brachyptera.

2. 3 September 1969. 11.10 a.m. Temperature 18 degrees. Tape reference 3.2.33. Interacting insect roeselii (1), caged previously with other male roeseliis. A box of stridulating brachypteras is in vicinity of experiment to sustain song of experimental brachyptera.

   Behaviour: Both sit still and sing.

   Final result: Inhibition of brachyptera, but experiment interrupted ~~before~~ while it is ~~total.~~ still partial.

3. 4 September 1969. 11.20 a.m. Temperature 19 degrees. Tape reference 3.2.401. Interacting insect diluta (1), caged alone previously. A box of stridulating brachypteras is in vicinity of experiment to sustain song of experimental brachyptera.

   Behaviour: brachyptera approaches diluta, getting very close, and they circle round one another, singing. Then brachyptera walks off but is arrested when diluta sings. Then it goes on towards the box containing the other brachypteras. Then it returns to diluta and tries to get on to the back of its tegmina but falls away and walks off again.

   Final result: Inhibition of brachyptera.

brachyptera (7)

1. 27 September 1969. 8 a.m. Temperature 16 degrees. Tape reference 3.2.1023. Interacting insect roeselii (9), caged previously with other male roeseliis.

Behaviour: Both walk about apparently ignoring one another. Eventually brachyptera gets 3" from roeselii, and then stops singing.

Final result: Inhibition of brachyptera.

2. 27 September 1969. 9.58 a.m. Temperature 16 degrees. Tape reference 3.2.1095. Interacting insect roeselii (7), caged previously with other male roeseliis.

Behaviour: roeselii moves towards the singing brachyptera, then away, and stops singing for a time. Resumes, then both insects move together, then apart. Eventually brachyptera stops singing and begins moving rapidly away from roeselii.

Final result: Inhibition of brachyptera.

Additional Notes: Fig. 18 shows the arrangement of brachyptera chirps in the last nine roeselii sequences immediately prior to the inhibition of brachyptera, but unlike figs 16 and 17, also shows the arrangement within the intervening silences, these being longer here. The higher chirp rate during the silences is immediately evident and it is seen that after a time chirp production ceases altogether during roeselii sequences, persisting only between them. As before, however, no clear gradient is observed in the distribution within the roeselii sequences or silences: the insect just

<u>brachyptera/roeselii interaction: br3/r3</u>

brachyptera chirp distribution in 9 successive **roeselii** sequences & intervening silences (labelled respectively r & s)
base line gives length of **roeselii** sequence or silence

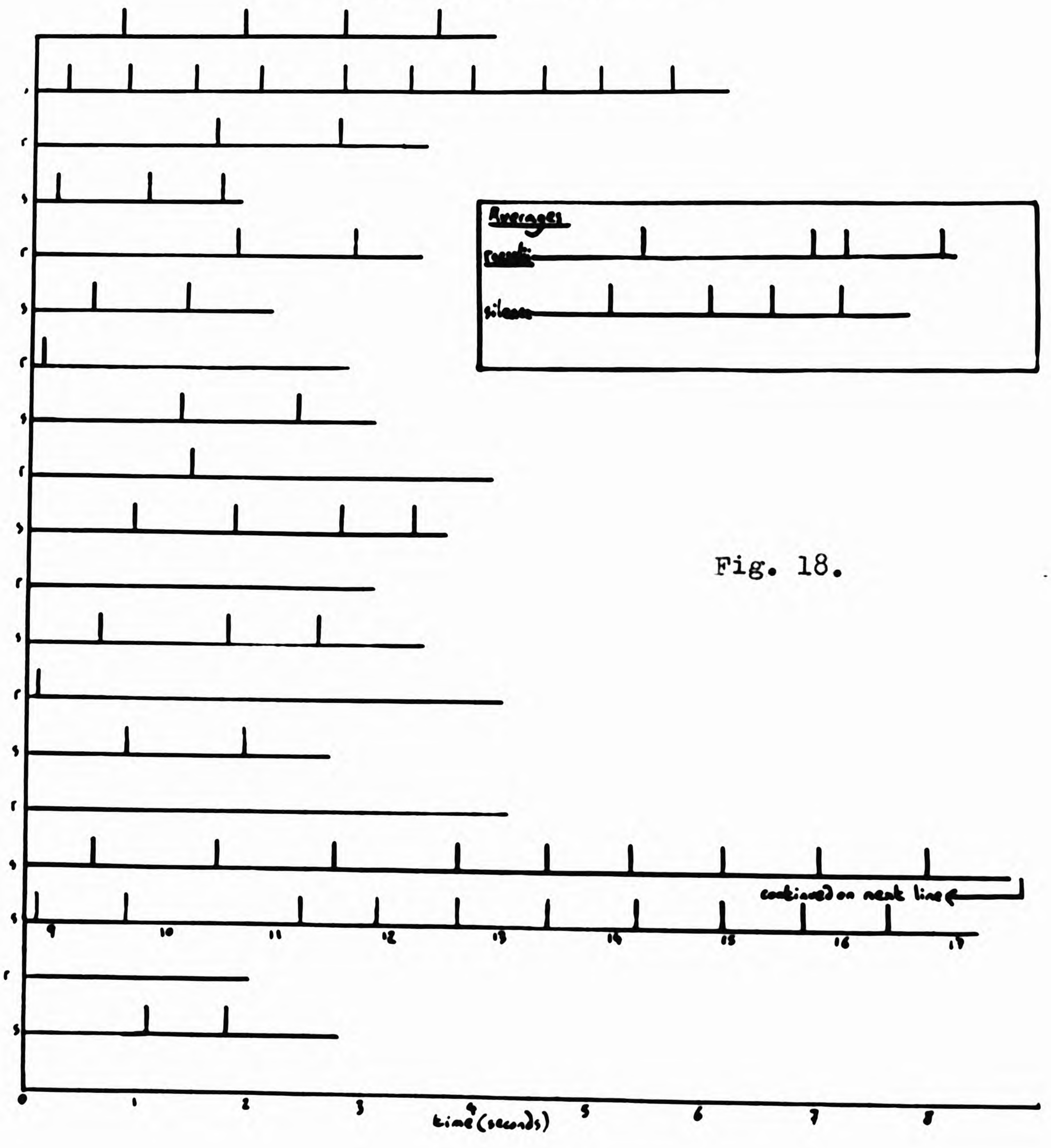


Fig. 18.

stops beyond a certain point.

3. 27 September 1969. 10.40 a.m. Temperature 16½ degrees. Tape reference 3.2.1259. Interacting insect roeselii (8), caged previously with other male roeseliis.

Behaviour: roeselii moves towards singing brachyptera. A phenomenon was noticed here which recurred frequently in experiments where a roeselii was moving towards another singing insect, that is, while it was actually in motion it did not sing, but paused frequently on the way emitting bursts of sound. I have also seen this kind of progress in the behaviour of isolated males, but much less frequently.

Final result: Inconclusive

brachyptera (11)

1. 17 September 1970. 9.50 a.m. Temperature 19 degrees. Tape reference 13.2.448. Interacting insect diluta (2), caged alone previously.

Behaviour: diluta moves towards singing brachyptera, antennates it and touches it with its legs; brachyptera moves off rapidly but continues singing for some time.

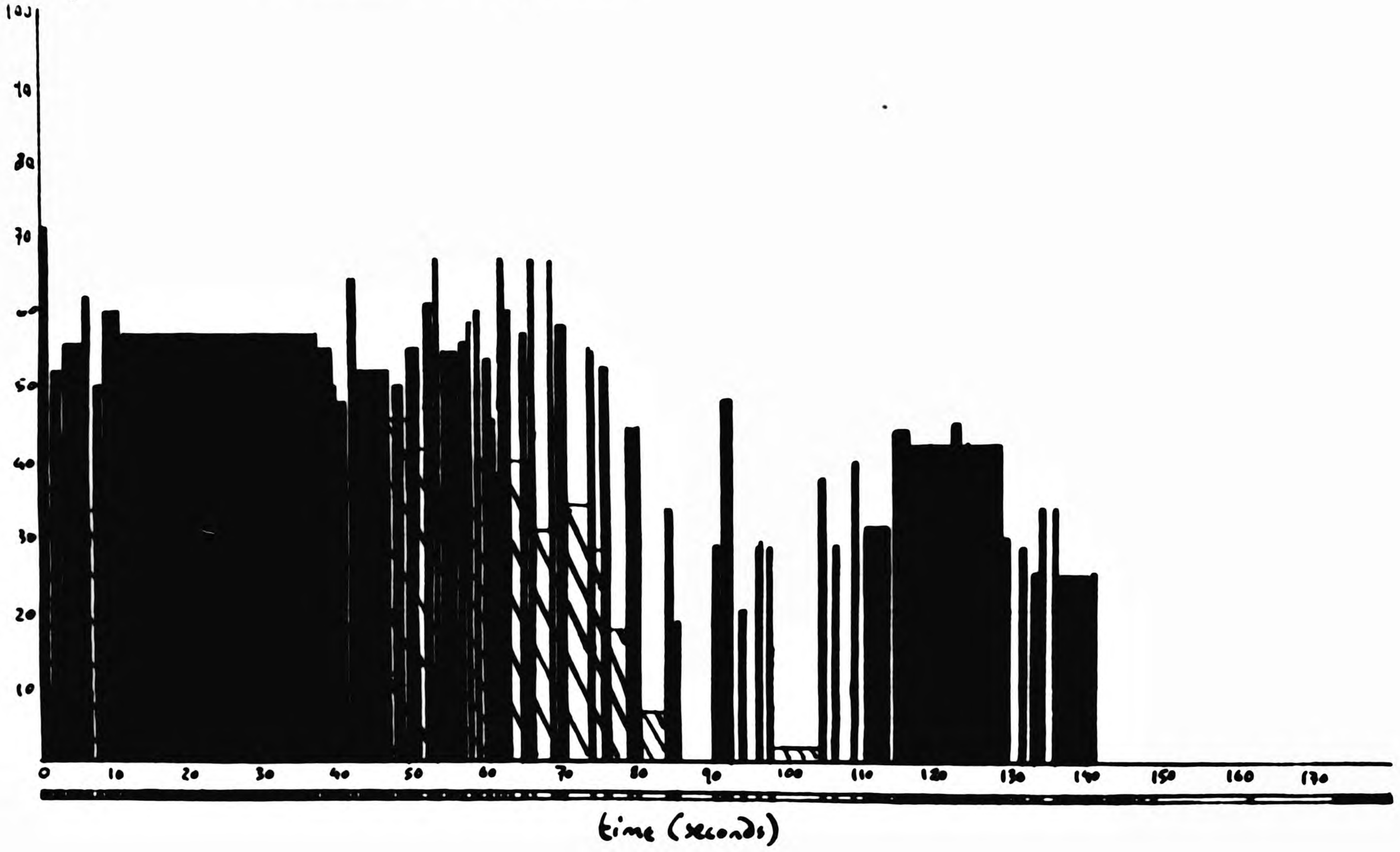
Final result: Inhibition of brachyptera.

Additional Notes: Histogram 3 shows a different arrangement to histograms 1 and 2 as there are much longer intervals in the roeselii song, but there is no justification for attributing this to inhibition of the roeselii by the brachyptera, either on behavioural grounds, or from a study of the roeselii chirprate made by slowing the recording. It would be quite normal for an isolated roeselii to produce

Histogram 3

<u>brachyptera</u>/<u>roeselii</u> interaction: br_4/d_2

base strip shows periods of silence (black) & <u>roeselii</u> activity (white)
histogram shows <u>brachyptera</u> activity during periods of silence (black)
& <u>roeselii</u> activity (shaded)



this kind of song arrangement. The long intervals near the end of the histogram appear responsible for the resurgence of brachyptera song which occurs after the gentle slope at 70-90 seconds. The relation of song levels during roeselii emissions and silences is as before and the earlier disappearance of the former is again seen.

2. 18 September 1970. 10.47 a.m. Temperature 32 degrees. Tape reference 13.2.1831. Interacting insect roeselii (11), caged previously with other male roeseliis.
   Behaviour: No movement: they rest 1½" apart.
   Final result: Toleration.

brachyptera 12

1. 16 September 1970. 11.52 a.m. Temperature 26 degrees. Tape reference 13.1.887. Interacting insect roeselii (11), caged previously with other male roeseliis.
   Behaviour: No movement: they rest 11" apart.
   Final result: Toleration.

brachyptera 13

1. 4 September 1970. 10.15 a.m. Temperature 21 degrees. Tape reference 9.2.1360. Interacting insect roeselii (10), caged alone previously.
   Behaviour: No movement: they rest 15" apart.
   Final result: Toleration.
2. 4 September 1970. 12.30 p.m. Temperature 26 degrees. Tape

reference 9.2.1718. Interacting insect diluta (2), caged alone previously.

Behaviour: diluta sits quiet a long time, then walks to a point ½" from brachyptera and makes three short noises, silencing the brachyptera.

Final result: Inhibition of brachyptera.

brachyptera (14)

1. 19 September 1970. 11.10 a.m. Temperature 30 degrees. Tape reference 14.2.962. Interacting insect roeselii (11), caged previously with other male roeseliis.

   Behaviour: No movement: they rest 1½" apart.

   Final result: Toleration.

2. 19 September 1970. 11.45 a.m. Temperature 30 degrees. Tape reference 14.2.1230. Interacting insect diluta (2), caged alone previously. (c.f. fig 10, page 43).

   Behaviour: brachyptera falls twice to the ground from a point about 8" from diluta - no apparent reason. The second time it climbs up, it reaches a point about 2½" from diluta and there later stops singing.

   Final result: Inhibition of brachyptera.

brachyptera (15)

1. 18 September 1970. 9.52 a.m. Temperature 32 degrees. Tape reference 13.2.1349. Interacting insect diluta (2), caged alone previously.

   Behaviour: They rest motionless 1½' apart. Suddenly brachyptera stops singing and begins walking to and fro at right angles to a line drawn from it to the diluta.

Final result: Inhibition of brachyptera.

Additional Notes: Examination of the recording made of this interaction shows the presence of numerous brachyptera chirps in which the syllable number and chirp length are greater than normal. This phenomenon appears to be identical with that observed by Broughton in the Platycleis denticulata/ Metrioptera roeselii interaction (c.f. page 17). In table 2 (page 84) the recording is divided into successive 5-second periods and a breakdown of the brachyptera chirps in each period is given. The results are summarised in table 4 (page 95). It will be observed that the chirps with large numbers of syllables are practically all found while diluta is singing, that the highest number of syllables occurring in one chirp is 17, and that there is a section of the recording when the production of such chirps reaches its highest level, after which they become scarcer.

Histograms 4-6 show thechanges in brachyptera song output for this recording. Very long chirps (over 0.15 seconds) are indicated and it can be seen that these occur in the region 30-200 seconds. It will also be seen that there are a number of very long uninterrupted roeselii sequences, separated by groups of very short ones in which brachyptera levels rise higher. The general rule previously observed, that the levels are higher during intervals than during roeselii sequences,

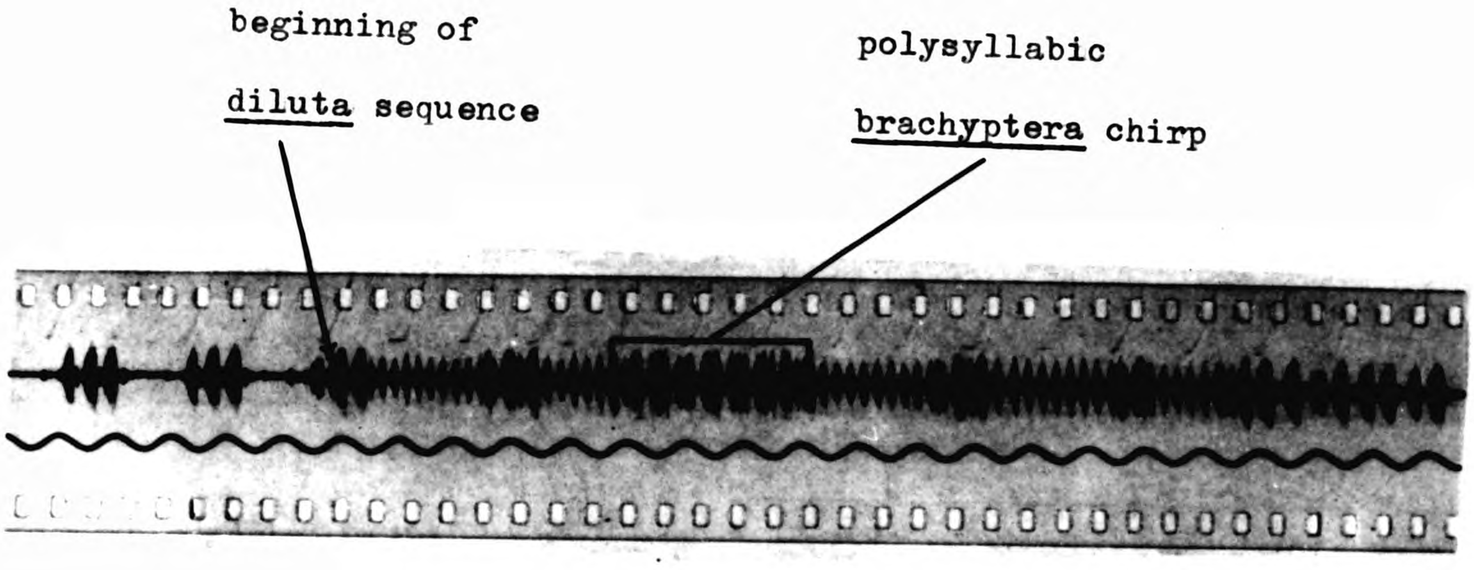


Fig. 19. Production of polysyllabic chirps by brachyptera (15): Interaction 1. Marker: 1 cycle =0.125 seconds.

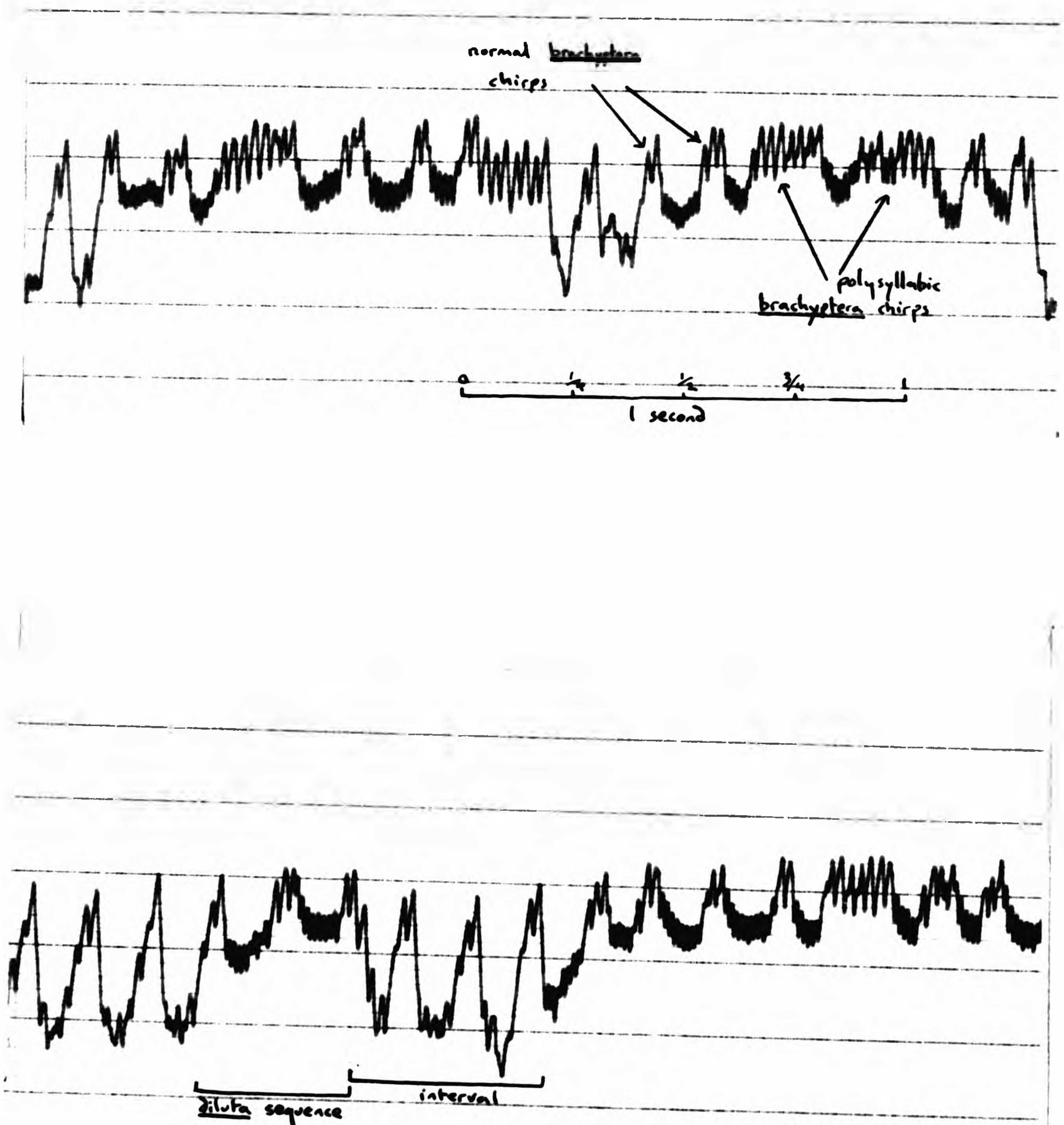


Fig. 20 Interaction 1. of **brachyptera** (15), with **diluta** (2), see page 81. The second section commences two seconds after the end of the first. Compare fig. 10.

Table 2

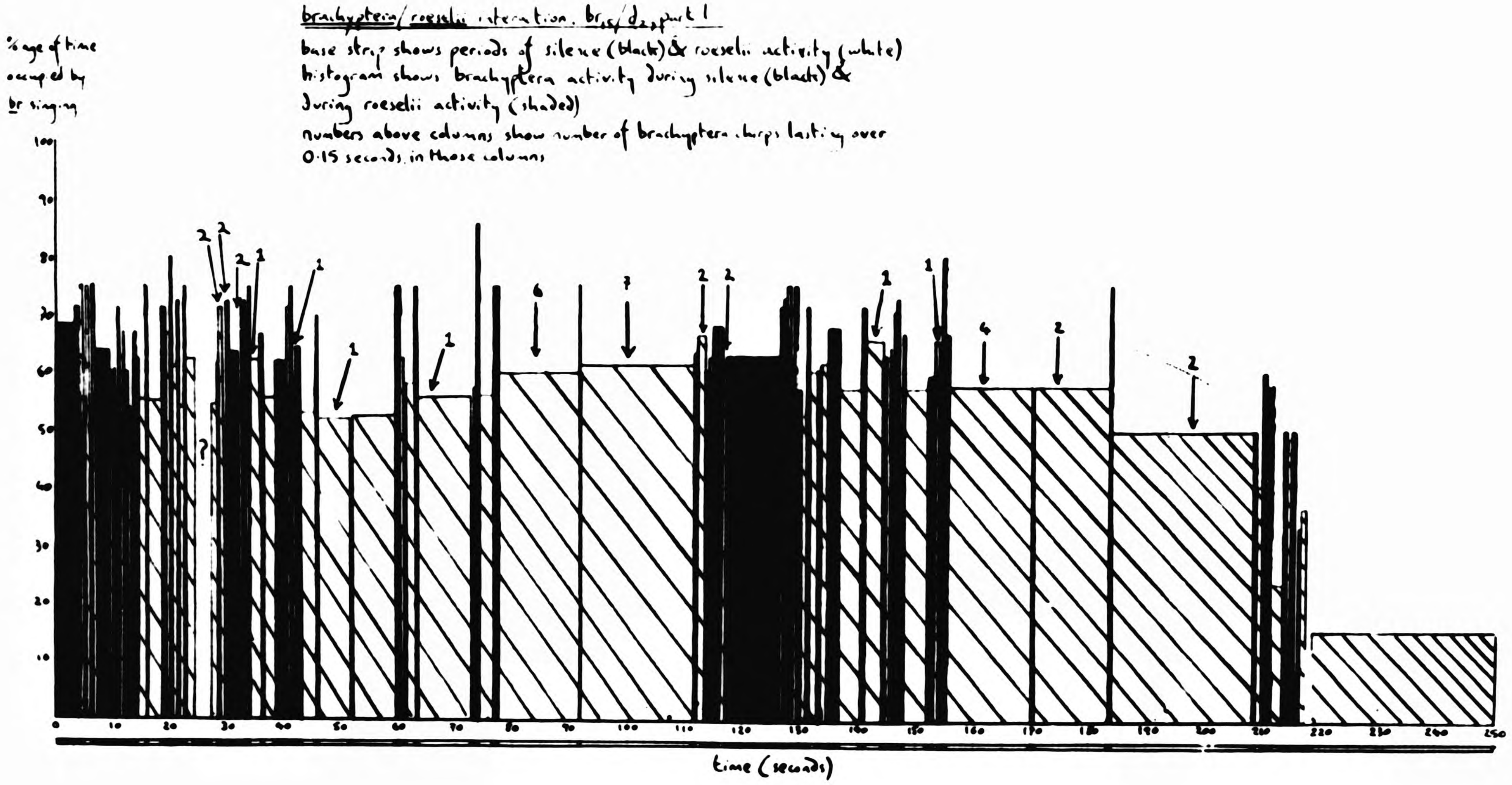
This table analyzes successive 5-second periods in the brachyptera (15)/diluta(2) interaction and gives for each period the number of chirps produced by the brachyptera during roeselii sequences and during the intervals between them. For each group the number of trisyllabic chirps is stated, and also the number of other chirps with an indication of how many syllables they contain. For example, '2x4s' means 'two tetrasyllabic chirps', &c.

ROESELII SEQUENCE		INTERVAL	
trisyllabic	other	trisyllabic	other
14		25	
27	2x4s	7	
31	1x4s	7	
15		17	
16	3x8s 1x9s	12	
18	4x4s 1x7s	14	
19	1x4s	20	
23	1x4s 1x8s	10	
35	1x4s 1x9s		
31		2	
26	1x4s	7	
32	2x4s	2	
34	1x11s		
33	1x4s	5	
25	2x4s 1x8s	7	
30	1x4s 1x8s 1x11s	1	

ROESELII SEQUENCE		INTERVAL	
trisyllabic	other	trisyllabic	other
25	1x7s	3	
29		5	
34	2x4s 1x12s		
34	1x12s 1x13s		
30	1x4s 1x8s 1x9s 1x11s 1x16s		
15	3x4s 1x6s 1x8s	18	
4	1x17s	30	
3		33	1x4s
23	2x4s	12	
25	1x4s	9	2x4s 1x10s
29	2x4s 1x8s	5	
19	1x4s 1x10s	14	
26	1x5s 1x8s	11	
20	1x1s 3x4s 1x9s	7	
39	1x4s		
32	1x4s 2x8s 1x9s		
31	4x4s 1x8s	3	
35	1x4s 1x11s		
35	3x4s		
34	1x4s	3	
38	1x4s		
33	2x4s 1x5s 1x8s		
30			
26	1x4s		
19		4	

ROESELII SEQUENCE		INTERVAL	
trisyllabic	other	trisyllabic	other
12	1x4s	7	
8		14	
18	1x1s		
17	2x4s		
21	1x4s		
21	1x4s		
15			
4			
4			
no brachyptera for 20 secs		no intervals for 20 secs	
3		7	
		no intervals	
3			
21			
21	1x4s		
5			
		no intervals	
2			
4			
2			
		no intervals	
		no intervals	

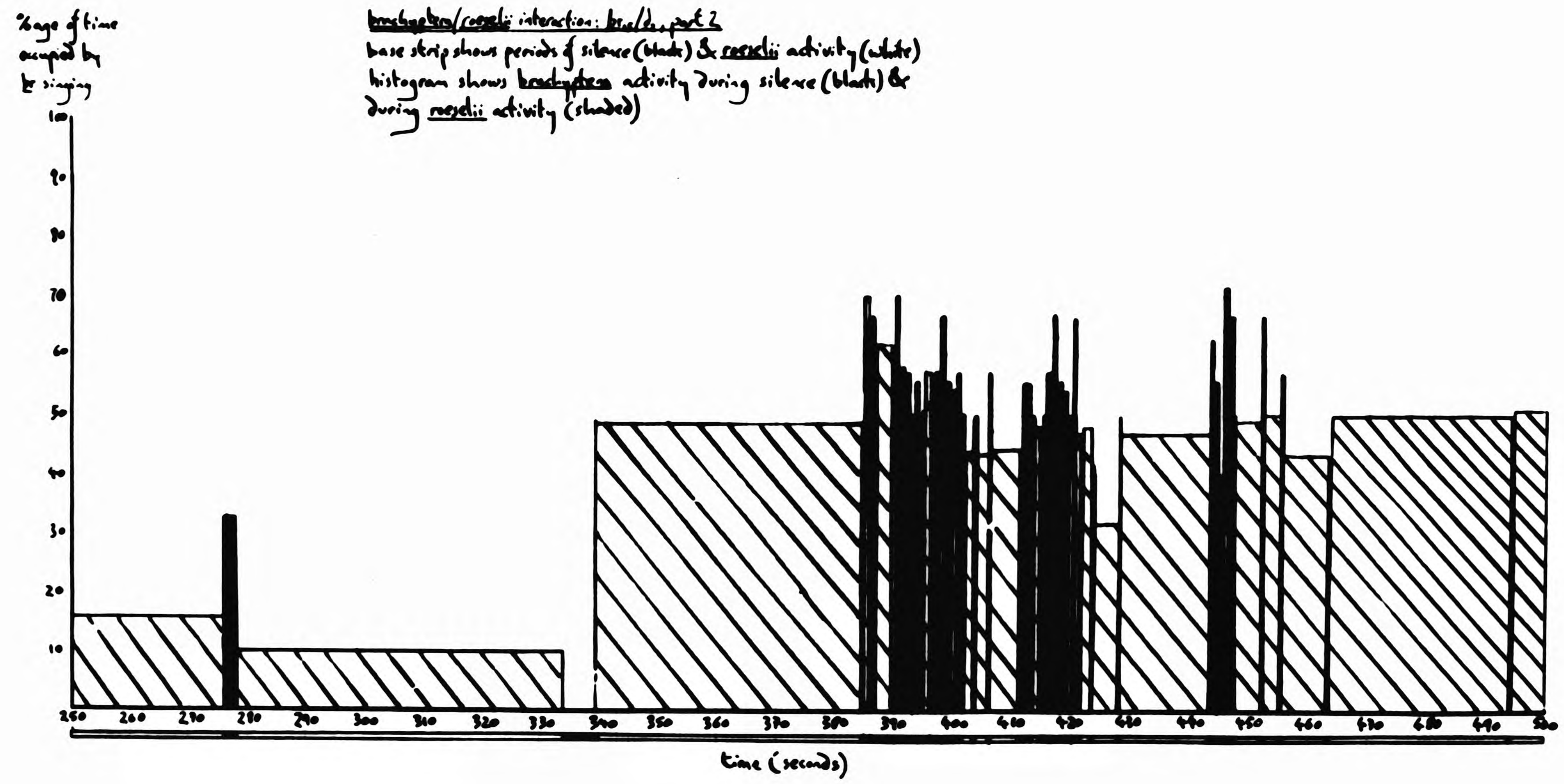
Histogram 4



brachyptera/roeselii interaction. br15/d2 part 1

base strip shows periods of silence (black) & roeselii activity (white)
histogram shows brachyptera activity during silence (black) &
during roeselii activity (shaded)
numbers above columns show number of brachyptera chirps lasting over
0·15 seconds in those columns

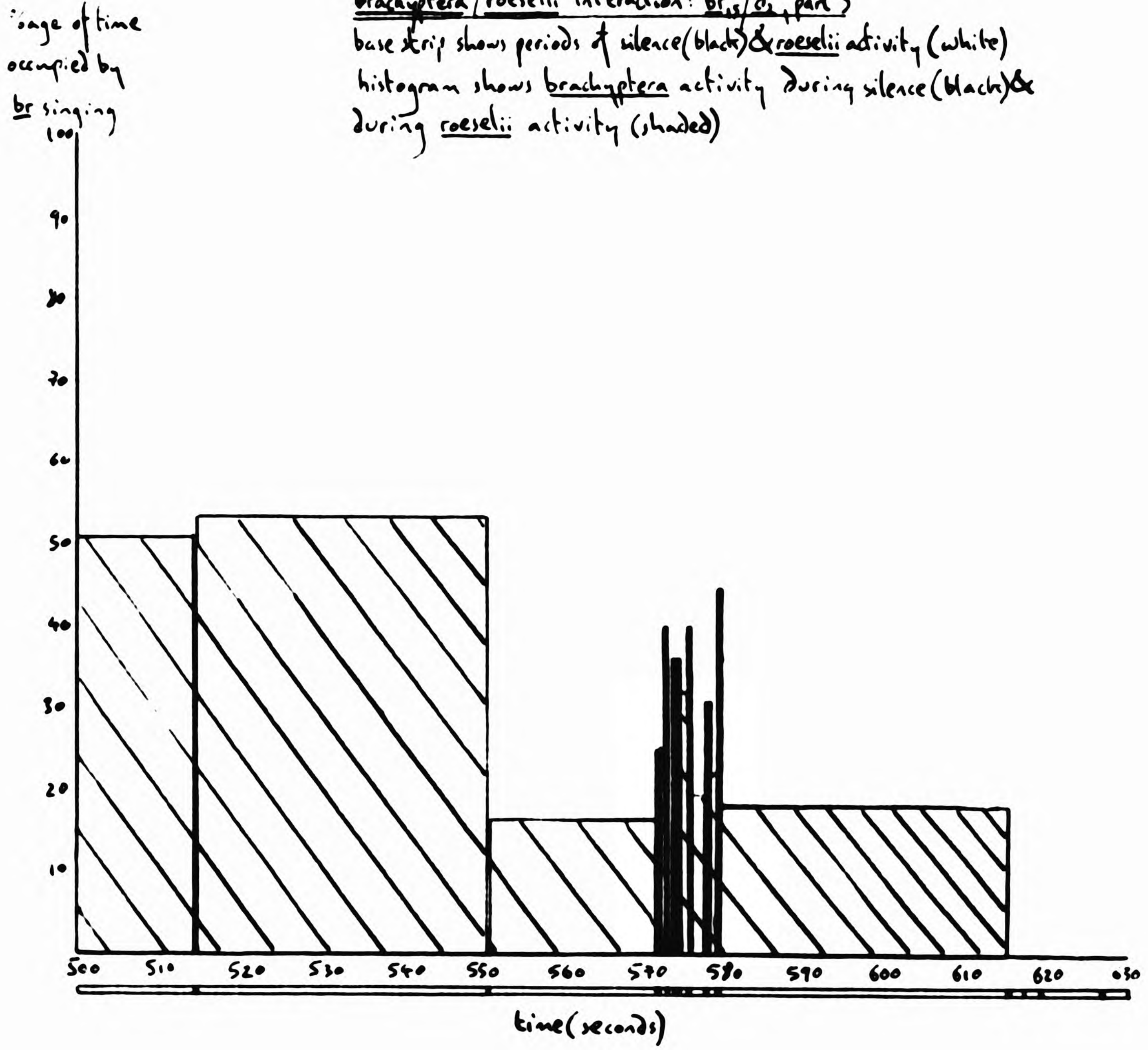
Histogram 5



brachyptera/roeselii interaction: br/ro, part 2
base strip shows periods of silence (black) & roeselii activity (white)
histogram shows brachyptera activity during silence (black) & during roeselii activity (shaded)

Histogram 6

<u>brachyptera</u>/<u>roeselii</u> interaction: br_{15}/d_2, part 3
base strip shows periods of silence (black) & <u>roeselii</u> activity (white)
histogram shows <u>brachyptera</u> activity during silence (black) &
during <u>roeselii</u> activity (shaded)



does not appear to apply here except near the end, and unlike the earlier analyses, this one shows the final brachyptera chirps being uttered during a long roeselii sequence. At the silence which eventually followed this, the brachyptera was totally inhibited, according to my definition.

Fig. 19 shows an oscillogram of a polysyllabic brachyptera chirp, and fig. 20 a Brüel and Kjaer trace of part of the recording.

2. 19 September 1970. 10.20 a.m. Temperature 26 degrees. Tape reference 14.2.0. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: brachyptera walks about, varying from 1" to 1½" from roeselii.

Final result: Toleration.

Additional Notes: Polysyllabic brachyptera chirps also occur in a section of this recording: see table 3, on page 91. They become rare after a time and the roeselii song breaks into short bursts separated by short intervals. It is not considered that this is due to influence by the brachyptera, because solitary roeseliis have sometimes been heard to sing similarly, but it is suspected that this 'dilution' of the song may have enabled the brachyptera to hold out against it. Because of the particular interest of the recording, the experiment was maintained for well over an hour, but eventually the recorder was stopped when it became apparent that no new developments were likely to occur.

Table 3

This is arranged like table 2, and refers to the *brachyptera* (15)/*roeselii* (11) interaction.

ROESELII SEQUENCE		INTERVAL	
trisyllabic	other	trisyllabic	other
16		18	
28	1x4s	4	
23	1x4s	5	
17	1x4s 1x6s 1x10s	18	
17	2x4s 2x8s	11	
25	2x4s	7	
31	1x4s	7	
28	2x4s	9	
26	1x4s	10	
31	1x4s	5	
30	2x4s 1x7s	1	
30	4x4s		
32	2x4s		
32	1x4s	2	
17	3x4s 1x5s 1x7s		
21	5x4s		
18	2x4s		
13	3x4s		
24	2x4s	3	
23		3	
21	3x4s	3	
24	2x4s	4	

ROESELII SEQUENCE		INTERVAL	
trisyllabic	other	trisyllabic	other
25	4x4s	2	
16	2x4s	2	
23	1x4s	3	
15	1x4s		
12		3	
8	1x4s	1	
21	3x4s	1	
18	2x4s	1	
17	1x4s	3	
10		1	
12		1	
20		3	
17		3	
6		3	
		3	
		2	
6		3	
17	2x4s	3	
4		5	
10		6	
12		3	

Period of 80 seconds during which brachyptera is almost silent: it produces only 14 chirps, all trisyllabic. 20 seconds before the end of the period, the observer touches roeselii, silencing it. All the 14 chirps occur during roeselii sequences.

ROESELII SEQUENCE		INTERVAL	
trisyllabic	other	trisyllabic	other
		2	
		21	1x4s
5	2x5s	18	2x5s
22		5	
26		4	
31			
27		4	
26	1x4s	4	
26		3	
31			
30			
28	1x4s	3	
29		4	
28		5	
31	2x4s		
27	1x4s 1x12s	3	
28		6	
25	1x4s	6	
27	1x4s	6	
25	2x4s	6	
26		9	
23	3x4s	8	
26	2x4s	5	
19		13	
25	1x4s	6	

<u>ROESELII</u> SEQUENCE		INTERVAL	
trisyllabic	other	trisyllabic	other
19	1x4s	14	
24	2x4s	11	
29		8	
25	1x4s	6	
26		5	
29		5	
26	1x5s	12	
26	2x4s	7	
28		6	
25	1x4s	8	
27		8	
25	2x4s	8	
26	2x4s 1x9s	7	
23		12	
23		13	
24	1x4s	11	
20	2x4s	12	
26		9	
27		8	

Table 4

Summary of tables 2 and 3.

No. of syllables in *brachyptera* chirp.	TABLE 2 (duration 330 secs)		TABLE 3 (duration 515 secs)	
	roeselii seq.	interval	*roeselii* seq.	interval
1	2			
3	1258	321	1779	473
4	47	3	87	1
5	2		4	2
6	1		1	
7	2		2	
8	14		2	
9	5		1	
10	1	1	1	
11	4			
12	2		1	
13	1			
16	1			
17	1			

brachyptera 16

1. 19 September 1970. 9.08 a.m. Temperature 24 degrees. Tape reference 14.1.1432. Interacting insect diluta (2), caged alone previously.

   Behaviour: No movement: they rest 9" apart.

   Final result: Toleration.

2. 19 September 1970. 9.40 a.m. Temperature 24 degrees. Tape reference 14.1.1736. Interacting insect roeselii (11), caged previously with other male roeseliis.

   Behaviour: No movement: they rest 1" apart.

   Final result: Toleration.

brachyptera 17

1. 20 September 1970. 9.10 a.m. Temperature 27 degrees. Tape reference 14.2.1725. Interacting insect diluta (2), caged alone previously.

   Behaviour: No movement: they rest 10" apart.

   Final result: Toleration.

2. 20 September 1970. 9.30 a.m. Temperature 30 degrees. Tape reference 14.2.1917. Interacting insect roeselii (11), caged previously with other male roeseliis.

   Behaviour: No movement: they rest 1" apart.

   Final result: Toleration.

brachyptera 18

1. 20 September 1970. 9.45 a.m. Temperature 30 degrees. Tape reference 15.1.0. Interacting insect roeselii (11), caged

previously with other male roeseliis.

Behaviour: brachyptera continually moves about, between 1" and 1½' from roeselii.

Final result: Inhibition of brachyptera.

Additional Notes: Histogram 7 is an illustration of the 'wearing down' effect produced by a long roeselii sequence upon the brachyptera level in the succeeding interval: this has fallen to about 33%. There is no further singing during roeselii sequences, although a resurgence phenomenon is again observed.

brachyptera 19

1. 20 September 1970. 11.05 a.m. Temperature 32 degrees. Tape reference 15.1.511. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: brachyptera rests 1¼" from roeselii, then begins moving further away and ceases singing.

Final result: Inhibition of brachyptera.

Additional Notes: Histogram 8 shows the usual features, including a resurgence phenomenon, but as with brachyptera (15) the last chirps are produced during roeselii song.

previously with other male roeseliis.

Behaviour: brachyptera continually moves about, between 1" and 1½' from roeselii.

Final result: Inhibition of brachyptera.

Additional Notes: Histogram 7 is an illustration of the 'wearing down' effect produced by a long roeselii sequence upon the brachyptera level in the succeeding interval: this has fallen to about 33%. There is no further singing during roeselii sequences, although a resurgence phenomenon is again observed.

brachyptera 19

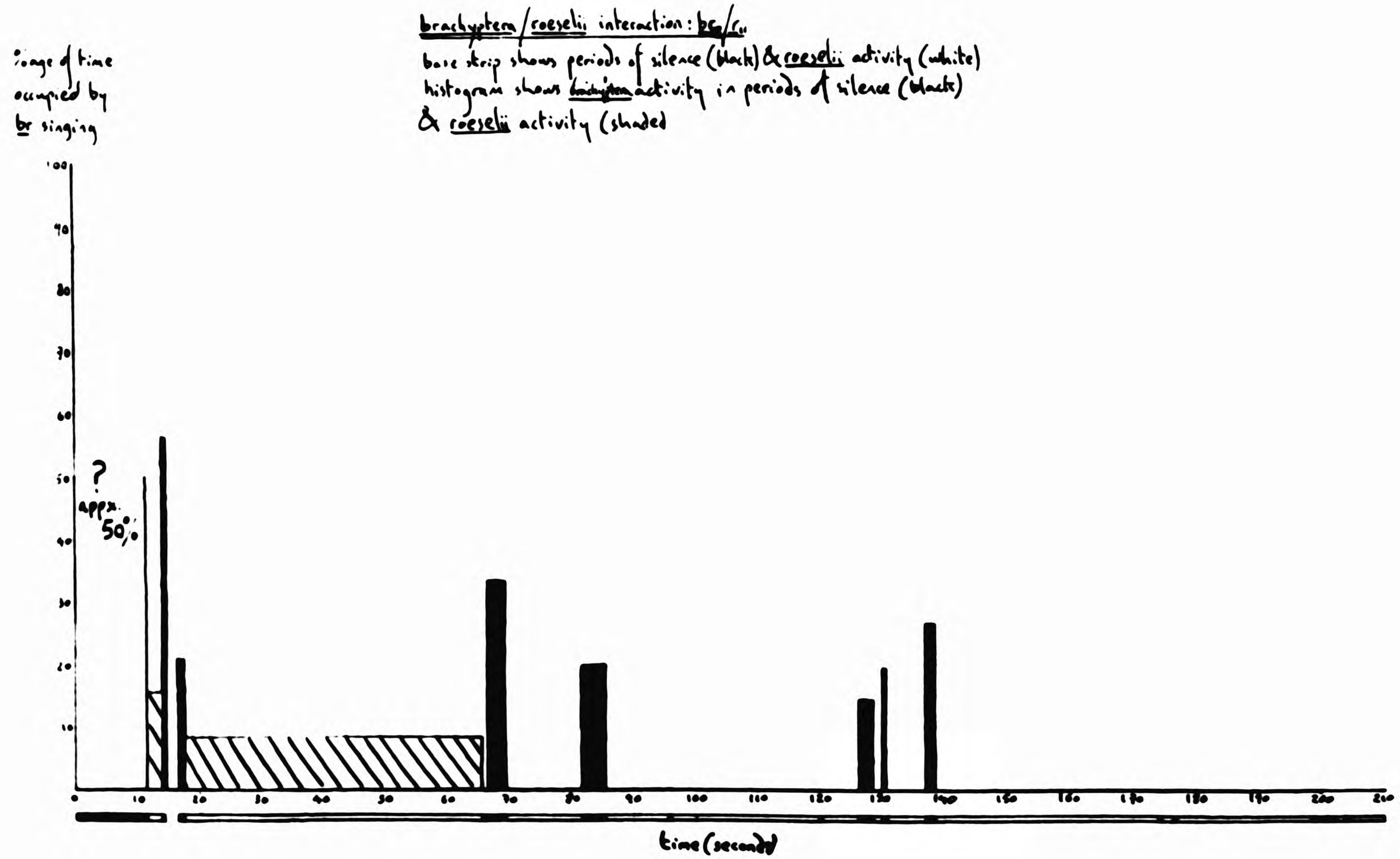
1. 20 September 1970. 11.05 a.m. Temperature 32 degrees. Tape reference 15.1.511. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: brachyptera rests 1¼" from roeselii, then begins moving further away and ceases singing.

Final result: Inhibition of brachyptera.

Additional Notes: Histogram 8 shows the usual features, including a resurgence phenomenon, but as with brachyptera (15) the last chirps are produced during roeselii song.

Histogram 7



brachyptera/roeselii interaction: bc/ru

base strip shows periods of silence (black) & roeselii activity (white)

histogram shows brachyptera activity in periods of silence (black)

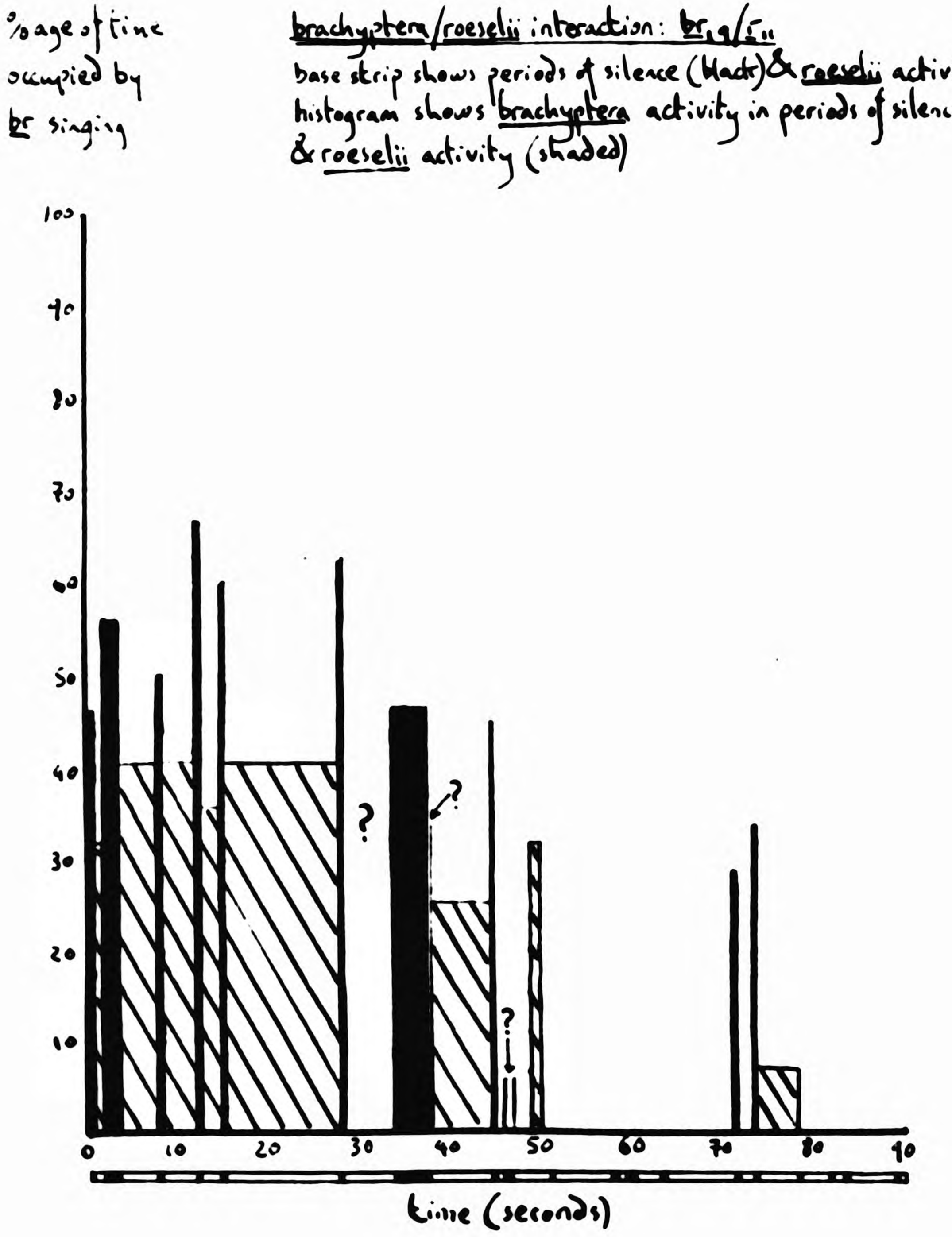
& roeselii activity (shaded

Histogram 8

brachyptera/roeselii interaction: br$_{19/5\,11}$

base strip shows periods of silence (black) & roeselii activity (white)

histogram shows brachyptera activity in periods of silence (black) & roeselii activity (shaded)



(c) Interaction of *M. roeselii* and *M. bicolor*

Field Observations

As stated on page 18, an expedition was made in July–August 1970 to the German sites where in 1965 Broughton had found these two species living in close proximity. *M. roeselii* was found to be very abundant in the Tübingen region but *bicolor* was not in evidence in Broughton's original locality and a general search of the area was therefore undertaken. It is possible to become sufficiently sensitized to the stridulations of bushcrickets to recognise species in neighbouring fields as one passes along the road in a vehicle. Freeman (1938) says that cycling around in Essex is an effective way of finding *roeselii*, and I myself found in Germany that I could distinguish this species very clearly from my car as I drove about in search of *bicolor*. I eventually discovered a *bicolor* community of the type I required on semi-agricultural land about 1 km. from the village of Weiler (see fig. 21), on the Rottenburg– Hechingen road. Fig. 22 gives an approximate idea of the distribution of *Metriopteras* in the area. At the top of the hill it was bounded by woodland (in which the only tettigoniids heard were some *Pholidoptera* sp.), and on the other three sides by a pure *roeselii* population which had to some extent infiltrated into it. Most of my work was done in the strip of vegetation alongside the track (areas A, B, C, G and H). This was mixed grassland, chiefly *Brachypodium* sp., with frequent clusters of Horseshoe Vetch (*Hippocrepis comosa*).

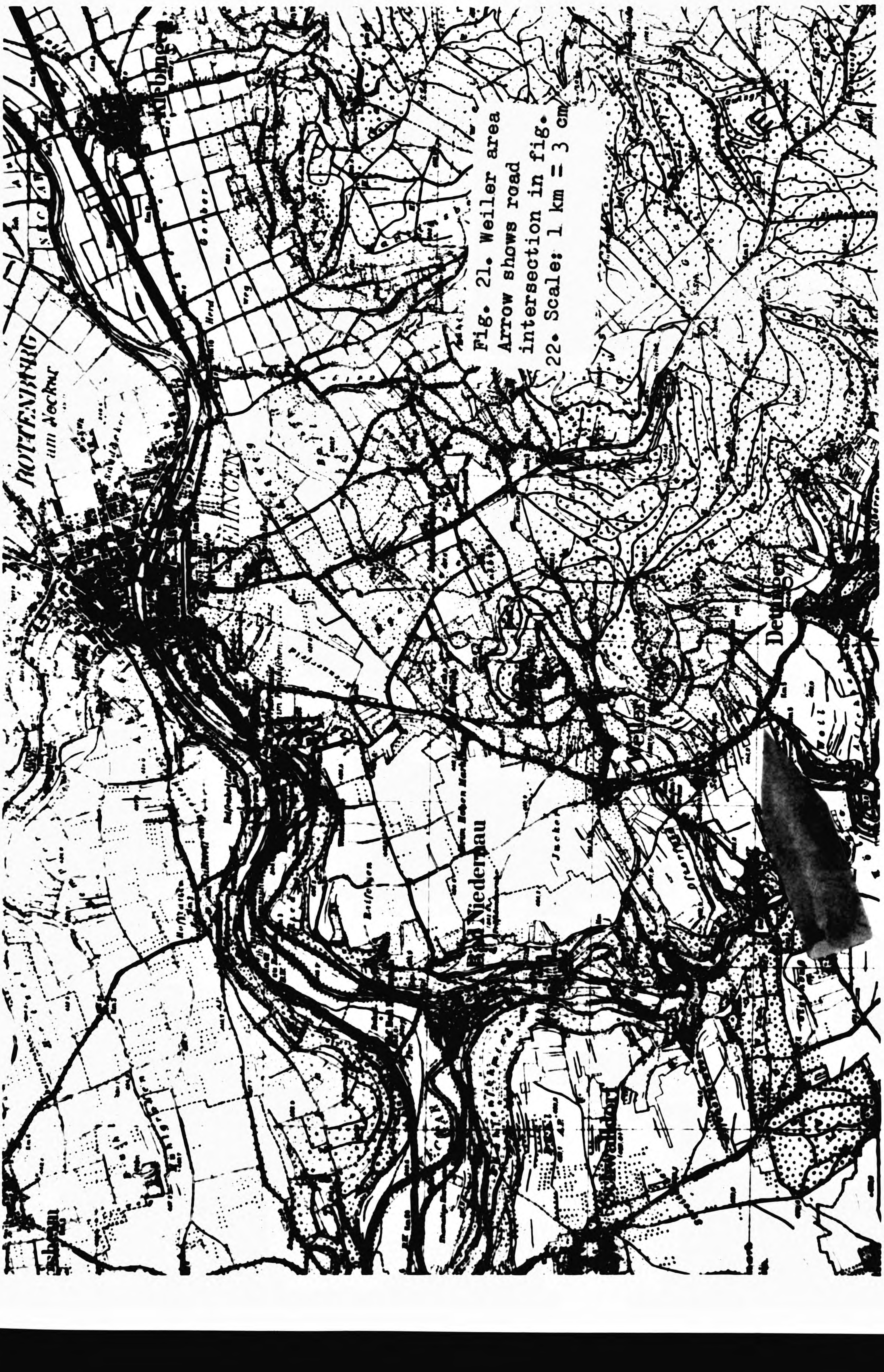


Fig. 21. Weiler area
Arrow shows road
intersection in fig.
22. Scale: 1 km = 3 cm

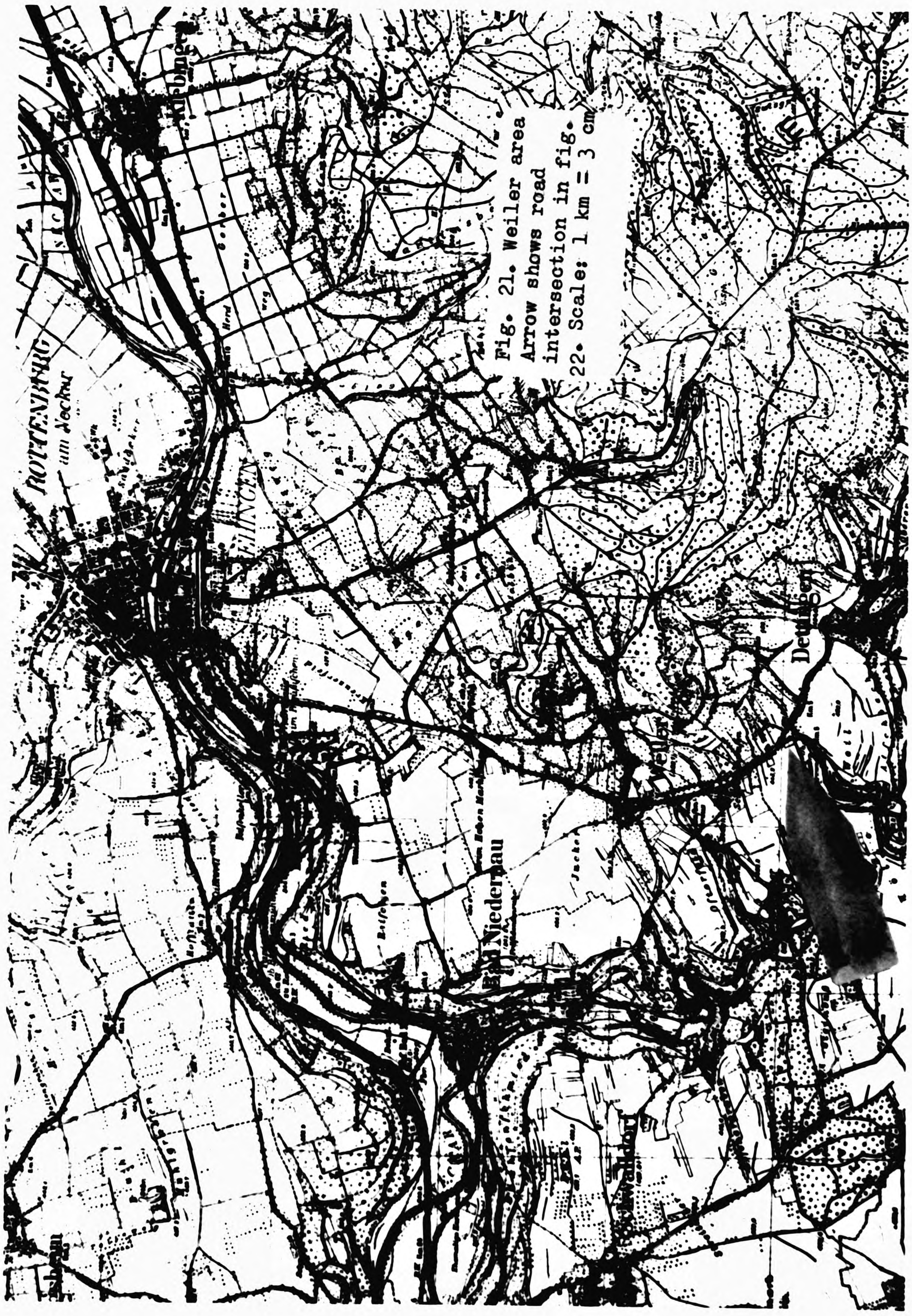


Fig. 21. Weiler area
Arrow shows road
intersection in fig.
22. Scale: 1 km = 3 cm

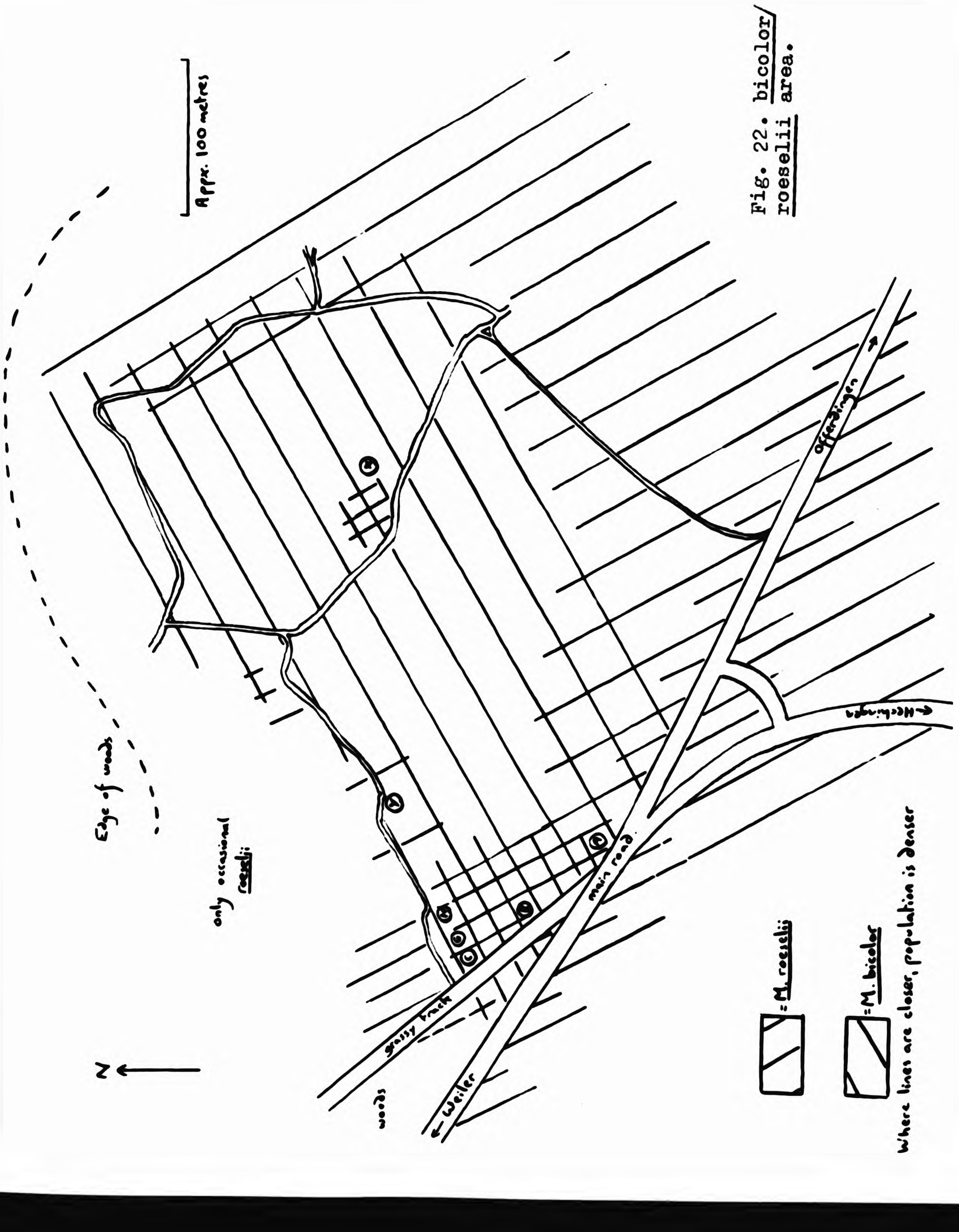


Fig. 22. *bicolor/roeselii* area.

Fig. 23 . Edge of the Weiler road at the junction with the track shown on fig. 22 . The view faces Northeast. The herbage in the foreground contains a dense roeselii/bicolor mixture; the short grass further back contains mostly bicolor, in less abundance.

Fig. 24 . Area B, facing North. Field method for recording two interacting insects stereophonically.

Fig. 25 . Facing North along the narrow path shown on the left in fig. 22 : areas G and H are seen on the right here.

Fig. 26 . Facing South just below point Y on the same path.

Hardheads, Black Knapweed, Plantain and Bird's-foot Trefoil were all very abundant, and to a lesser extent Lady's Bedstraw, Hogweed, Rest-Harrow and Tufted Vetch occurred. There were many acridids, and also Gryllus campestris and Nemobius sylvaticus. On the opposite side of the main road Tettigonia viridissima was heard, but not in the area itself. Decticus verrucivorus was found in areas C and G, and two males ten feet apart often appeared to be duetting across an expanse of stridulating Metriopteras.

I attempted to make stereophonic tape recordings of bicolor/roeselii couples but various factors complicated this. Near the road the greatest mixing of species occurred, but here traffic noise tended to spoil recordings. When a suitable occasion was available, it was not usually found that merely a couple of insects would be interacting. There were always several individuals, and the principle of the mutual sustaining of song mentioned above in connection with brachyptera (page 74) appeared to operate. Nearly all the bicolor/roeselii couples heard were four feet or more apart. In a week's observing, five couples were found three feet apart, one couple two feet apart, one eighteen inches apart and one six inches apart. The latter was in a small dense mass of vegetation at point X (fig. 22). Here the population was almost pure bicolor except where such clumps of vegetation or bushes did arise. Although roeselii lived on quite short grass outside the experimental area, it seemed to me that here a number of individuals might be islanded in a bank of Horseshoe Vetch, and that a state of toleration not elsewhere developed might come about. The pair two feet apart were here also, and it was clear that their songs were affecting one another, because one would begin when the other stopped. With a couple three feet apart in area A, it seemed that roeselii was inhibiting the stridulation of bicolor. With the couple eighteen inches apart, which were on an isolated bush at point Y, roeselii seemed to be inhibited by bicolor. When bicolor ceased, roeselii began to sing. Twice I touched bicolor with my finger, stopping it, and roeselii at once stridulated. Then bicolor jumped to a point one foot from roeselii, and then again a further six inches away. Then roeselii jumped about one foot further off.

Silent male bicolors were several times observed very close to singing roeseliis and I assumed they had been attracted and then inhibited. I tried to set up interactions by placing one insect close to another and found that bicolor would usually remain where it was placed, but roeselii, generally much more active, would always move further off. Placing bicolor amongst singing roeseliis, I heard it begin to sing twice out of eight attempts, but the recordings obtained were unimpressive.

Two insects seen in area G, three feet apart, showed a curious form of behaviour. They were alternating short (2 secs) bursts of song, the temperature being 33 degrees, and the roeselii began moving towards the bicolor until 1½ feet away, stopping to sing (and inhibit the bicolor) on the way four or five times. During this process the bicolor moved round the grass stem on which it was sitting, so that the stem was between it and the roeselii. It then resumed singing and both continued for some time in this position. It seemed that the stem's acoustic shielding was allowing the bicolor to tolerate the song of the nearby roeselii.

Whilst staying in this part of Germany I was informed by Professor A. Faber of Tübingen that a mixed bicolor/roeselii population could be found on a hill above Pfullingen, which I therefore visited. I found that this was a higher and more exposed locality than the Weiler one, with very short turf amongst which occasional Metriopteras were found. The density of individuals was very low, however, and although I heard some intraspecific stridulatory exchanges, I never heard any interspecific ones. This strengthens my suspicion that interspecific behaviour in the field occurs only when population pressure forces individuals to remain 'uncomfortably' close to one another.

Laboratory Observations

None of the field recordings obtained was of a very high quality. I had not attempted to mark insects in the field: in the first place there were so many that the chances of re-encountering an individual in another interspecific interaction were small, and secondly, it was often impossible to get a proper look at the bushcrickets from which I was recording, let alone to capture both for marking. Consequently I was never sure whether or not the same insect had been recorded more than once. It was decided therefore to collect a number of bicolors and to work on them at home under more rigorous conditions. I considered obtaining specimens of roeselii from the same locality. This would have increased the validity of my experiments as approximations to field interactions but it would have meant keeping the two species close together for about two weeks, and I was reluctant to do this, fearing a possibly enduring effect on the behaviour of bicolor with respect to roeselii. I did in fact collect roeseliis in Germany, from Erlangen, but this was almost immediately before my departure, and they were not long with the Weiler bicolors.

Eleven of the bicolor males - numbered (1)-(11) - were tested against roeseliis. They were first kept in two groups in the cardboard boxes wherein they had been transported. After testing they were caged singly and about a week later some were retested. They were then caged with females, each box holding one male and one female, for about a week, and tested again.

Finally, the females were removed and the males all caged together for about a week and then retested once more. Unless otherwise stated, the bicolor always starts singing before the roeselii.

bicolor (1)

Previously caged with other males.

1. 24 August 1970. 11.55 a.m. Temperature 21½ degrees. Tape reference 7.1.453. Interacting insect diluta (2), caged alone previously.

   Behaviour: They sit still about 1" apart. When bicolor stops it is revived by bringing a box of stridulating bicolors near the cage, but when this is removed diluta silences it again, and it moves off.

   Final result: Inhibition of bicolor.

   Additional Notes: Histogram 9 is, apart from one unusually high level during roeselii song, not unlike a brachyptera/roeselii histogram. The percentages are similar, there is a regular descent and a resurgence, and the last sounds of the bicolor are arrested by the re-entry of roeselii. It will however be found that in most of the succeeding histograms levels are considerably higher, the song of bicolor being far more continuous than that of brachyptera.

Previously caged with a female.

2. 30 August 1970. 11.40 a.m. Temperature 24 degrees. Tape reference 9.1.1185. Interacting insect roeselii (10), caged alone previously.

   Behaviour: No movements: they sit about 1" apart.

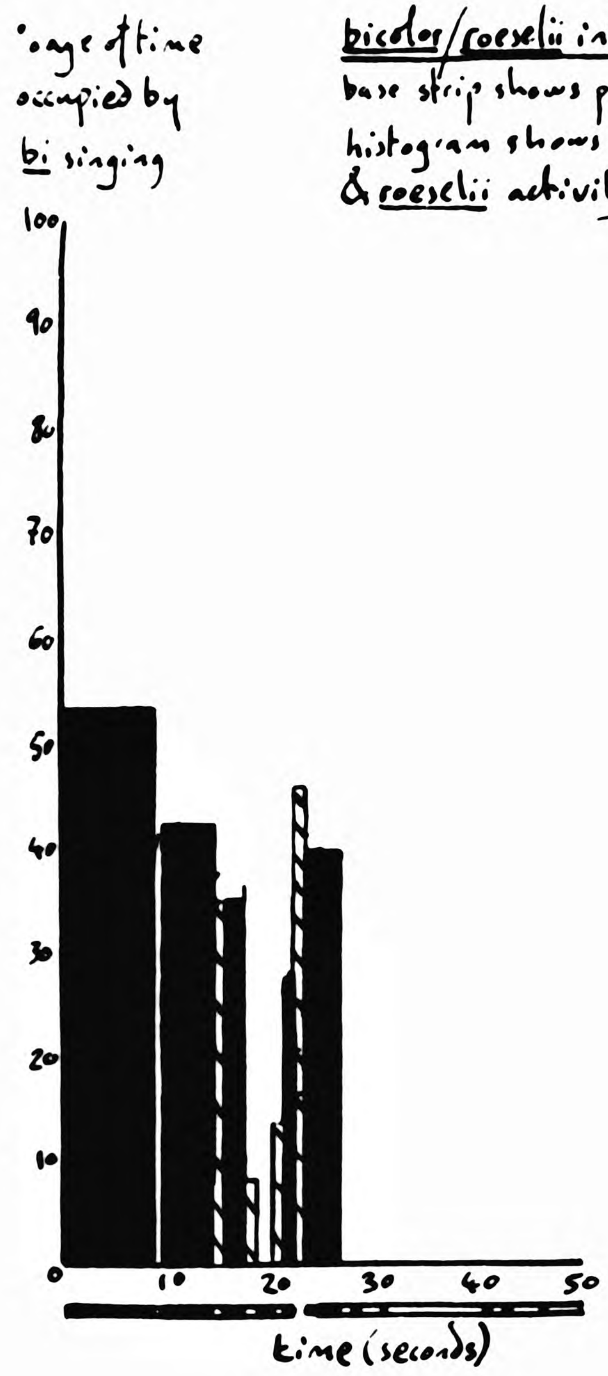
   Final result: Toleration.

3. 30 August 1970. 12.15 p.m. Temperature 24 degrees. Tape

Histogram 9

<u>bicolor</u>/<u>roeselii</u> interaction: bi$_1$/♂$_2$

base strip shows periods of silence (black) & <u>roeselii</u> activity (white)
histogram shows <u>bicolor</u> activity in periods of silence (black)
& <u>roeselii</u> activity (shaded)



reference 9.1.1369. Interacting insect diluta (2), caged alone previously.

Behaviour: bicolor moves about, approximately 9" from diluta. They alternate short bursts: eventually diluta is silenced.

Final result: Inhibition of diluta.

Additional Notes: The same insects were used here as in interaction 1., but there it was bicolor that was inhibited. The two species seem more evenly matched than roeselii and brachyptera and it is therefore commoner to find situations where each is able to tolerate the other's presence. However, the inhibition of roeselii here and elsewhere does not appear to involve any song modification. The syllable rate, which, in the absence of any grouping into chirps, might perhaps have been expected to slow down like the chirps of brachyptera, in fact remains constant. Interruptions by roeselii just become less and less frequent, and finally stop altogether. It should be added that when a bicolor was really singing vigorously, it was usually necessary to have a box of singing roeseliis in the room when introducing the interacting roeselii, so as to facilitate its starting to sing.

4. 7 September 1970. 11.22 a.m. Temperature 34 degrees. Tape reference 11.1.295. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: roeselii moves towards bicolor, and they begin to antennate. Then bicolor moves off and roeselii moves to a point where it is shielded by a piece of cardboard from bicolor. Then bicolor moves further away but continues singing.

Final result: Toleration.

5. 7 September 1970. 11.38 a.m. Temperature 33 degrees. Tape reference 11.1.872. Interacting insect roeselii (10), caged alone previously.

Behaviour: roeselii moves towards bicolor: bicolor sings and roeselii falls off roof, then returns silent to bicolor, which stops singing and brushes roeselii with its antennae, making short squirting noises and kicking at roeselii, which jumps away. I then remove roeselii from the box and replace it at 11.53 a.m. The insects now sit 1" apart and sing continuously, apparently ignoring one another.

Final result: Toleration.

6. 7 September 1970. 1.40 p.m. Temperature 35 degrees. Tape reference 11.1.1423. Interacting insect diluta (2), caged alone previously.

Behaviour: diluta is the first insect to sing. They rest 8" apart and eventually diluta is silenced.

Final result: Inhibition of diluta.

Caged again with other males.

7. 13 September 1970. 11.15 a.m. Temperature 27 degrees. Tape reference 12.1.1246. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: The insects are about 9" apart but bicolor seems to be trying to escape from roeselii although it keeps singing.

Final result: Toleration.

8. 13 September 1970. 11.58 a.m. Temperature 24 degrees. Tape reference 12.1.1456. Interacting insect diluta (2), caged alone previously.

Behaviour: bicolor, originally 1' away, moves to a point 8" away, then goes back and rests.

Final result: Toleration.

9. 15 September 1970. 10.10 a.m. Temperature 18 degrees. Tape reference 12.2.0. Interacting insect diluta (2), caged alone previously.

Behaviour: No movement: they rest 6" apart.

Final result: Toleration.

bicolor (2)

Previously caged with other males.

1. 22 August 1970. 11.00 a.m. Temperature 20-28 degrees. Tape reference 6.1.44. Interacting insect roeselii (10), caged alone previously.

Behaviour: bicolor begins singing after roeselii and partially inhibits it, then pursues it. They antennate and walk apart, then come together and remain so, antennating. Eventually bicolor stops singing, but it resumes when a box of singing bicolors is brought near. This is then removed. Suddenly bicolor moves away to 6", and soon after this stops singing.

Final result: Inhibition of bicolor.

Previously caged alone

2. 26 August 1970. 11.55 a.m. Temperature 25 degrees. Tape reference 7.2.4. Interacting insect roeselii(10), caged alone previously.

Behaviour: The insects move very close together and rest. Eventually bicolor just stops singing.

Final result: Inhibition of bicolor.

Previously caged with a female.

3. 5 September 1970. 10.10 a.m. Temperature 27½-36 degrees. Tape reference 9.2.1798. Interacting insect roeselii(10), caged alone previously.

Behaviour: roeselii appears very agitated, and keeps walking and jumping around but hardly sings at all, perhaps because bicolor is singing so much, despite the use of a box of singing roeseliis in the vicinity.

Final result: Inhibition of roeselii.

4. 5 September 1970. 11.40 a.m. Temperature 34 degrees. Tape reference 9.2.1888. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: Both move together and apart several times. The first insect to sing was roeselii.

Final result: Inhibition of roeselii.

5. 7 September 1970. 10.10 a.m. Temperature 33 degrees. Tape reference 10.2.1520. Interacting insect diluta (2), caged alone previously.

Behaviour: diluta is still; bicolor walks about a little. Distance averages 1".

Final result: Toleration.

Caged again with other males.

6. 13 September 1970. 9.10 a.m. Temperature 18-25 degrees. Tape reference 11.2.1915. Interacting insect diluta (2), caged alone previously.

Behaviour: diluta moves to a point 2" from bicolor, but this could be interpreted as attraction to a warmer part of the cage. Then bicolor moves down to it and they meet face to face. They keep meeting, antennating and moving apart; diluta takes time to begin singing well.

Final result: Toleration.

7. 13 September 1970. 10.40 a.m. Temperature 29 degrees. Tape reference 12.1.898. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: I tried this twice with roeselii singing first, 8" away, and on both occasions roeselii inhibited bicolor, which began to move away when it stopped singing. I then tried it with bicolor singing first, 4" away.

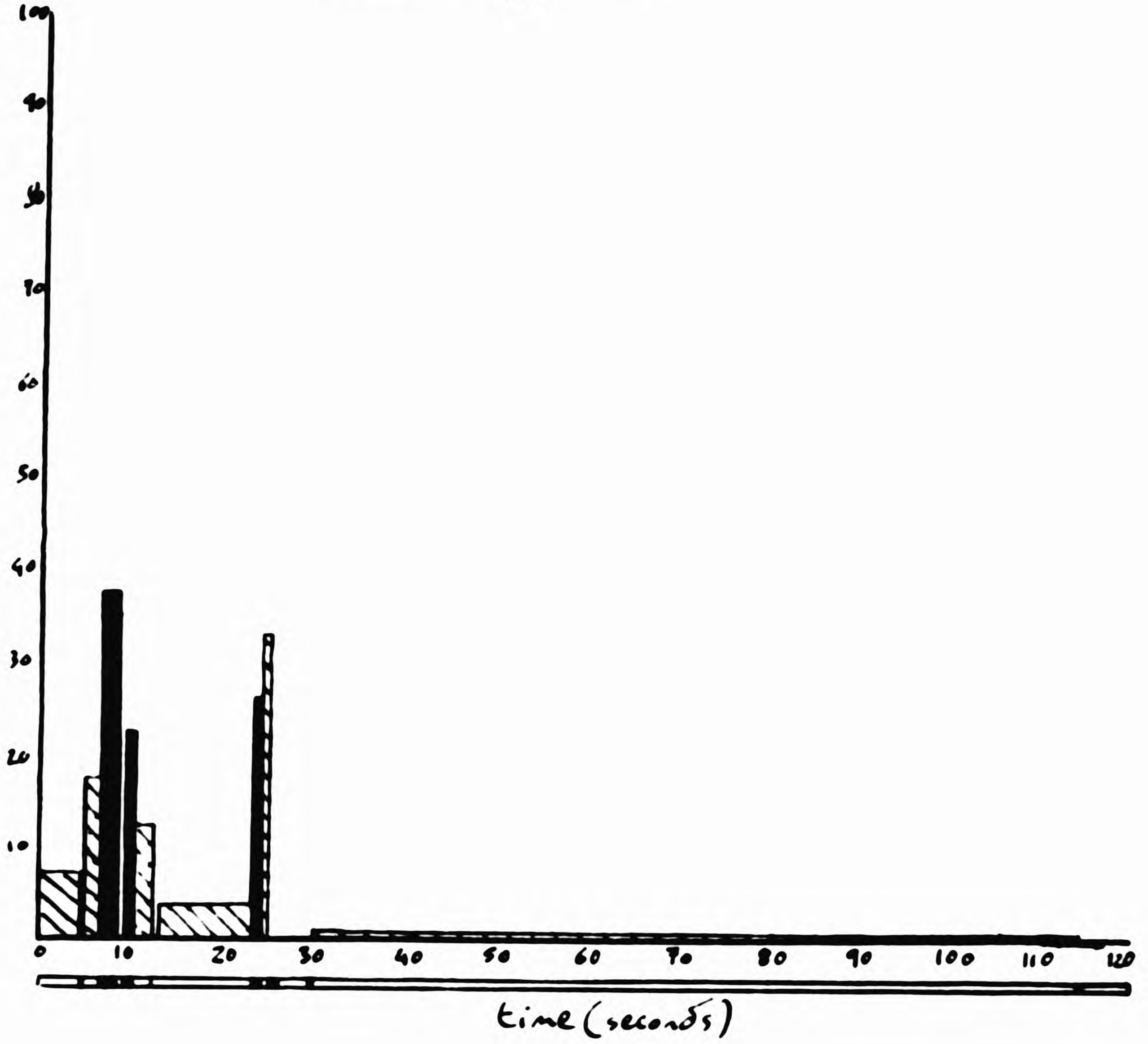
Final result: Toleration.

Additional Notes: See histogram 10. The inhibition of bicolor takes place during a very long uninterrupted roeselii sequence, which would not have been produced had roeselii not had a good start. Levels are again rather low.

8. 22 September 1970. 9.55 a.m. Temperature 21 degrees. Tape reference 15.1.1026. Interacting insect diluta (2), caged alone previously.

Histogram 10

<u>bicolor</u> /<u>roeselii</u> interaction: <u>bic/ro</u>
base strip shows periods of silence (black) & <u>roeselii</u> activity (white
histogram shows <u>bicolor</u> activity in periods of silence (black)
& <u>roeselii</u> activity (shaded)



Behaviour: The silent *diluta* moves to a point 1" from the singing *bicolor*, follows it when it moves off, and antennates it. The *bicolor* circles round and antennates the *diluta* from behind: *diluta* turns and antennates *bicolor*, which drops back making clicking sounds. Then *diluta* moves off.

Final result: Inconclusive.

9. 22 September 1970. 11.25 a.m. Temperature 22 degrees. Tape reference 15.1.1230. Interacting insect *roeselii* (11), caged previously with other male *roeseliis*.

Behaviour: The silent *roeselii* approaches the singing *bicolor* and antennates it; then sits still, silent, 2" away.

Final result: Inconclusive.

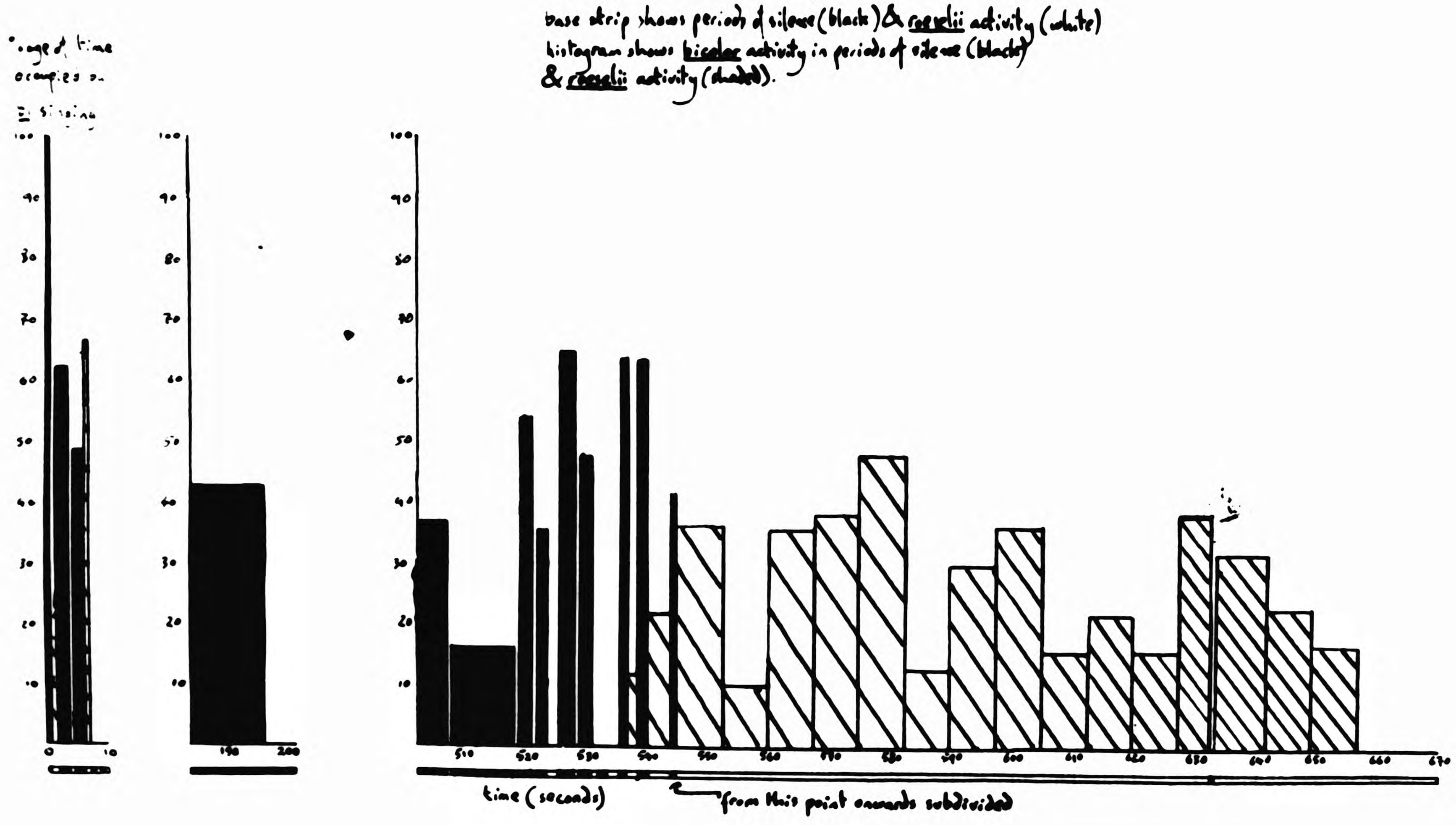
10. 25 September 1970. 10.30 a.m. Temperature 29 degrees. Tape reference 15.2.1715. Interacting insect *roeselii* (11), caged previously with other male *roeseliis*.

Behaviour: They sit still 5" apart.

Final result: Inhibition of *bicolor*.

Additional Notes: This is an inhibition with two resurgences which were brought about artificially when the *roeselii* was silenced to see whether the *bicolor* would resume, as a test for total inhibition (see page 64). The effects are shown in histogram 11. In the first resurgence the *bicolor* seems to have been almost totally inhibited: as soon as the *roeselii* resumes it is completely silenced. In the second, however, it appears to have recovered, and as with histogram

Histogram 11



<u>bicolor/roeselii</u> interaction : <u>bic/r.</u>

base strip shows periods of silence (black) & <u>roeselii</u> activity (white)
histogram shows <u>bicolor</u> activity in periods of silence (black)
& <u>roeselii</u> activity (shaded).

10 a long uninterrupted roeselii sequence finally quells it. I have divided this into sections to show the variations in bicolor level in different parts. The descent in the latter part is typical of much that we have seen but the really interesting feature of the second resurgence is that at first bicolor is only prepared to sing in the intervals between roeselii sequences, and then it develops a rising level of tolerance, singing for approximately 12%, 22% and 37% of the time during roeselii song.

bicolor (3)

Previously caged with other males.

1. 22 August 1970. 1.20 p.m. Temperature 30-31 degrees. Tape reference 6.1.771. Interacting insect roeselii (10), caged alone previously.

   Behaviour: At first a box of singing bicolors is near the cage but the bicolor moves away from them, towards the roeselii, and antennates and pushes past it. Eventually it rests 1" away, antennating. The roeselii is silenced. With a box of stridulating roeseliis it is twice made to resume, but is then silenced again.

   Final result: Inhibition of roeselii.

Previously caged alone.

2. 27 August 1970. 9.40 a.m. Temperature 22-24 degrees. Tape reference 7.2.685. Interacting insect roeselii (10), caged alone previously.

Behaviour: roeselii walks about, not singing much; bicolor advances from 1' to 6" away and then rests.

Final result: First roeselii inhibited, then bicolor.

3. 28 August 1970. 9.30 a.m. Temperature 25 degrees. Tape reference 8.1.810. Interacting insect diluta (2), caged alone previously.

Behaviour: bicolor moves towards diluta but suddenly stops moving when diluta sings, then goes on. Reaching diluta it sings, moves off, and is itself silenced. It resumes its song when a box of singing bicolors is brought near. Then diluta moves to a point 2" away, then returns to a point 1" away. They meet head on: then bicolor moves away and stops singing. It is restarted as before. Then diluta gets so close that its tegmina touch bicolor. The insects stay together antennating. Suddenly diluta makes a sound and starts moving off rapidly, then jumps away: bicolor goes on singing. This looks very like courtship behaviour.

Final result: Inconclusive.

4. 28 August 1970. 11.10 a.m. Temperature 32 degrees. Tape reference 8.1.1078. Interacting insect diluta (2), caged alone previously.

Behaviour: In contrast to the preceding experiment, diluta is put first into the cage, and allowed to sing before bicolor is introduced. The latter appears very agitated and jumps about emitting short bursts of sound.

Final result: Inhibition of bicolor.

5. 28 August 1970. 11.30 a.m. Temperature 30 degrees. Tape reference 8.1.1120. Interacting insect <u>diluta</u> (2), caged alone previously.

<u>Behaviour</u>: This time the <u>bicolor</u> is put in first, as usual. Initially it moves to a point 4" from <u>diluta</u>, then to one 15" away. The songs of both then become continuous.

<u>Final result</u>: Toleration.

<u>Previously caged with a female.</u>

6. 6 September 1970. 10.10 a.m. Temperature 29 degrees. Tape reference 10.1.435. Interacting insect <u>roeselii</u> (10), caged alone previously. (c.f. fig.11, page 43).

<u>Behaviour</u>: <u>roeselii</u> walks towards <u>bicolor</u>, antennates it, walks off; <u>bicolor</u> moves towards <u>roeselii</u>, stops singing, then moves away again.

<u>Final result</u>: Inhibition of <u>bicolor</u>.

7. 7 September 1970. 10.50 a.m. Temperature 34 degrees. Tape reference 11.1.0. Interacting insect <u>diluta</u> (2), caged alone previously.

<u>Behaviour</u>: <u>bicolor</u> walks about; <u>diluta</u> remains still and then abruptly stops singing. This doesn't seem like inhibition.

<u>Final result</u>: Inconclusive.

<u>Caged again with other males.</u>

8. 15 September 1970. 11.42 a.m. Temperature 27 degrees. Tape reference 12.2.783. Interacting insect <u>diluta</u> (2), caged alone previously.

<u>Behaviour</u>: No movement: they sit still 6" apart.

Final result: Inhibition of diluta.

9. 24 September 1970. 11.00 a.m. Temperature 31 degrees. Tape reference 15.2.893. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: bicolor, initially 15" from roeselii, moves 3" closer and thereafter does not move.

Final result: Toleration.

bicolor (4)

Previously caged with other males.

1. 23 August 1970. 9.05 a.m. Temperature 19 degrees. Tape reference 6.1.1155. Interacting insect diluta (2), caged alone previously.

Behaviour: They rest stationary 1" apart. A sudden diluta burst coincides with a jump by bicolor to a point further away. Later diluta sings less, then moves off, silent.

Final result: Inhibition of diluta.

Previously caged alone.

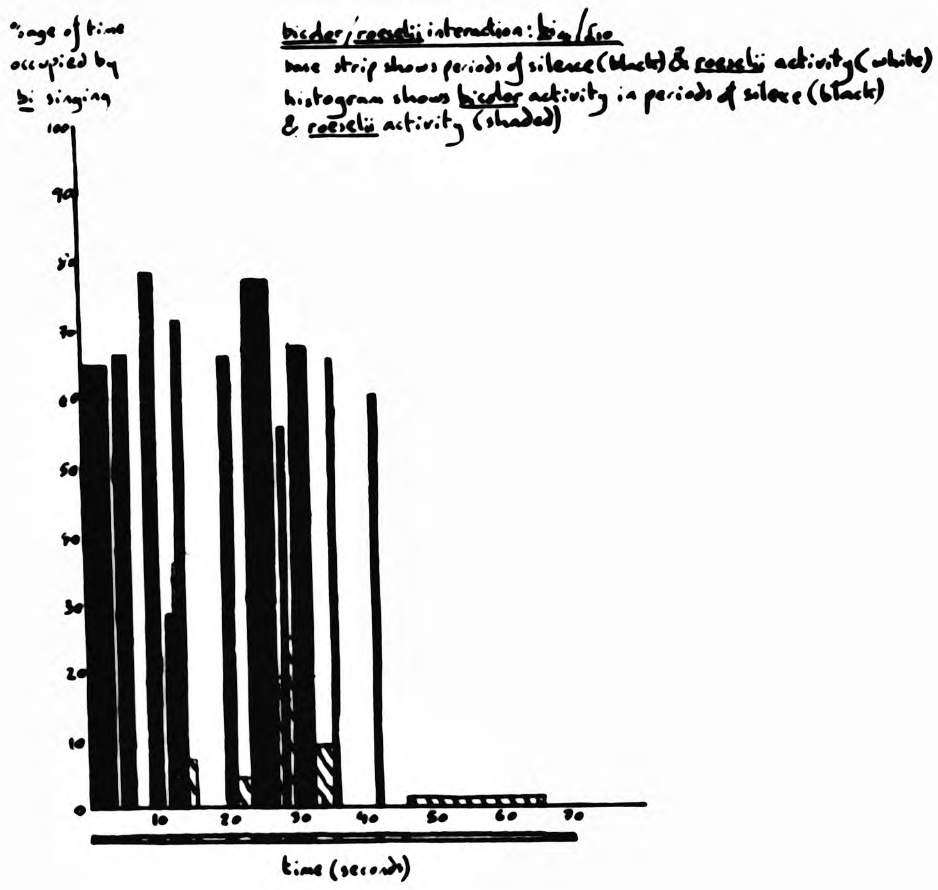
2. 26 August 1970. 12.50 p.m. Temperature 32 degrees. Tape reference 7.2.493. Interacting insect roeselii (10), caged alone previously.

Behaviour: No movement: they rest 1' apart.

Final result: Inhibition of bicolor.

Additional Notes: Histogram 12 shows a typical inhibition of bicolor by roeselii, with more bicolor song in intervals than in roeselii sequences, a decline towards the end, and

Histogram 12



a final long roeselii sequence during which the bicolor song finally ceases.

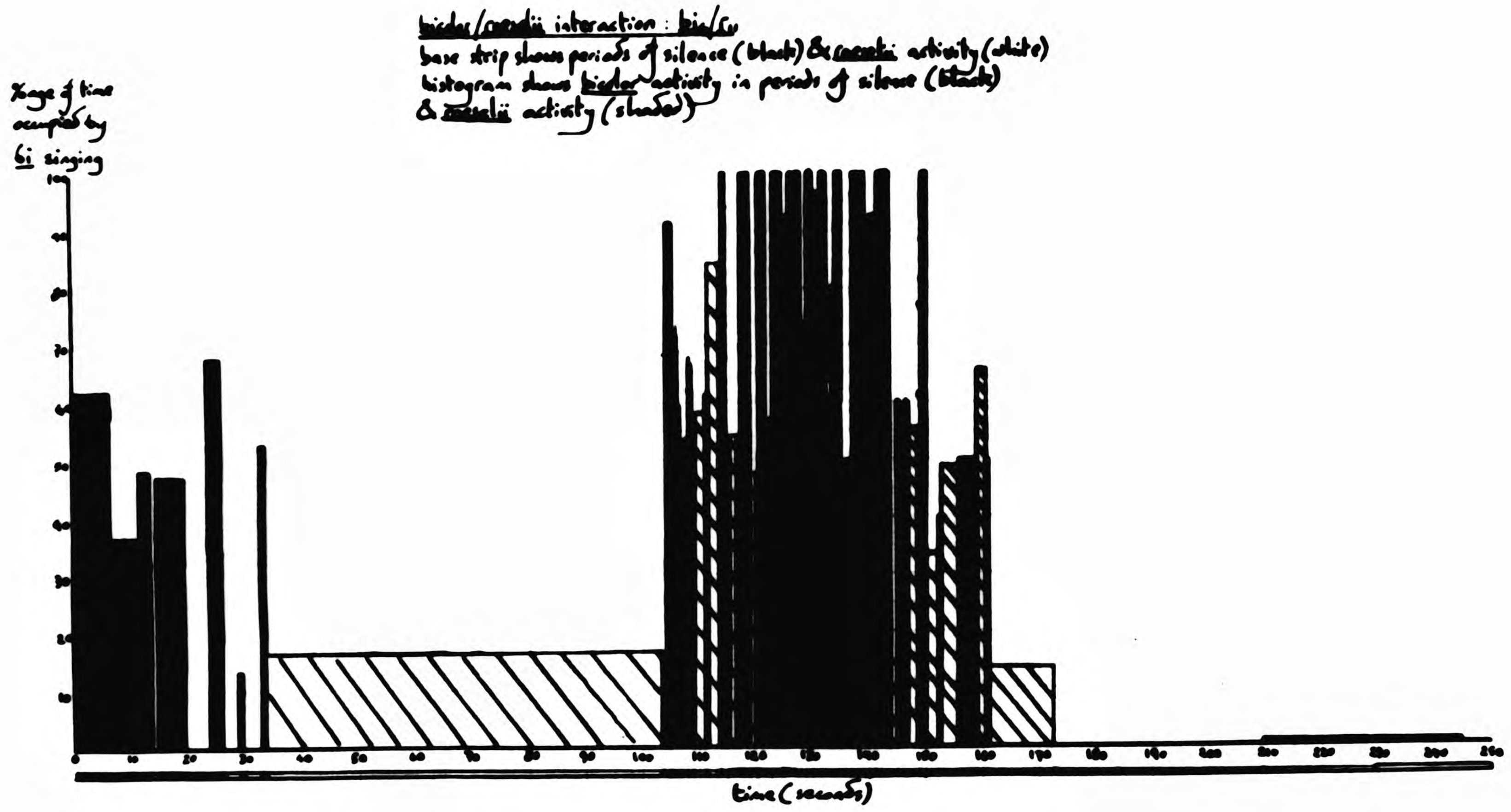
3. 27 August 1970. 11.00 a.m. Temperature 30 degrees. Tape reference 8.1.970. Interacting insect diluta (2), caged alone previously.
Behaviour: In a pause in the bicolor song, diluta begins singing. Then bicolor moves rapidly towards diluta and suddenly jumps to a point 2" away from it, and is silent.
Final result: Inhibition of bicolor.

Previously caged with a female.

4. 6 September 1970. 10.35 a.m. Temperature 30 degrees. Tape reference 10.1.1024. Interacting insect roeselii (10), caged alone previously.
Behaviour: They sit still 1' 8" apart.
Final result: Toleration.

5. 6 September 1970. 11.50 a.m. Temperature 26-28 degrees. Tape reference 10.1.1600. Interacting insect roeselii (11), caged previously with other male roeseliis.
Behaviour: The bicolor moves towards the roeselii: both are singing. Later bicolor walks away, then jumps further, silent.
Final result: Inhibition of bicolor.
Additional Notes: The beginning of histogram 13 resembles histogram 11, but the bicolor manages to hold out through the long roeselii sequence, after which the roeselii song becomes very intermittent and the bicolor output rises, often to 100% for both roeselii sequences and intervals. In this part

Histogram 13



of the trace each roeselii sequence, and each interval, are usually only long enough to contain one bicolor chirp. Because of the short distances, calculation of the percentages is much less accurate than elsewhere and the value '100 %' is highly approximate. The last bicolor emission is a resurgence during a long roeselii sequence.

6. 7 September 1970. 12.30 p.m. Temperature 35 degrees. Tape reference 11.1.1150. Interacting insect diluta (2), caged alone previously.

Behaviour: No movement: they sit 1' apart.

Final result: Inhibition of bicolor.

Caged again with other males.

7. 16 September 1970. 9.35 a.m. Temperature 21½ degrees. Tape reference 12.2.968. Interacting insect diluta (2), caged alone previously.

Behaviour: Obviously some inhibition occurs, but not enough to completely stop bicolor or diluta. Eventually bicolor approaches to 6" of diluta, and then retreats to 1' away.

Final result: Toleration.

8. 16 September 1970. 10 a.m. Temperature 30 degrees. Tape reference 12.2.1498. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: roeselii approaches bicolor and antennates it: bicolor jumps to a point 8" away and rests there.

Final result: Toleration.

9. 23 September 1970. 11.15 a.m. Temperature 29 degrees. Tape reference 15.1.1700. Interacting insect dilata (2), caged alone previously.

Behaviour: Initially they rest 10" apart, then dilata moves 8" further away and rests again.

Final result: Toleration.

10. 24 September 1970. 11.30 a.m. Temperature 31 degrees. Tape reference 15.2.1485. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: They sit still 1½" apart.

Final result: Toleration.

bicolor (5)

Previously caged with other males.

1. 23 August 1970. 11.15 a.m. Temperature 26 degrees. Tape reference 6.1.1367. Interacting insect roeselii (10), caged alone previously.

Behaviour: At first roeselii appears to be inhibited but it recovers. The insects rest about 1' apart. An attempt to test 'acoustic shielding' (see page 107) by placing bicolor on an upright stem does not succeed: bicolor remains on the side of the stem towards roeselii.

Final result: Toleration.

Previously caged alone.

2. 27 August 1970. 10.15 a.m. Temperature 24 degrees. Tape reference 7.2.948. Interacting insect roeselii (10), caged

alone previously.

<u>Behaviour</u>: They remain stationary 8" apart.

<u>Final result</u>: Toleration. Perhaps <u>bicolor</u> was not inhibited because it got a very good start.

3. 27 August 1970. 10.50 a.m. Temperature 25 degrees. Tape reference 7.2.1188. Interacting insect <u>diluta</u> (2), caged alone previously.

<u>Behaviour</u>: They remain stationary 1" apart.

<u>Final result</u>: Toleration, then <u>diluta</u> inhibited.

<u>Previously caged with a female.</u>

4. 7 September 1970. 9.05 a.m. Temperature 21 degrees. Tape reference 10.2.724. Interacting insect <u>diluta</u> (2), caged alone previously.

<u>Behaviour</u>: They remain for some time 3" apart, then <u>diluta</u> begins moving as if trying to get away from <u>bicolor</u>.

<u>Final result</u>: Toleration.

5. 7 September 1970. 9.25 a.m. Temperature 23 degrees. Tape reference 10.2.1165. Interacting insect <u>roeselii</u> (10), caged alone previously.

<u>Behaviour</u>: One corner of the cage is illuminated by the Sun. Both insects move into this and rest 3" apart. Later <u>roeselii</u> moves away from <u>bicolor</u>.

<u>Final result</u>: Toleration.

6. 7 September 1970. 9.40 a.m. Temperature 25 degrees. Tape reference 10.2.1312. Interacting insect <u>roeselii</u> (11), caged previously with other male <u>roeseliis</u>.

Behaviour: No movement: they sit 8" apart.

Final result: Toleration.

bicolor (6)

Previously caged with other males.

1. 24 August 1970. 9.15 a.m. Temperature 20 degrees. Tape reference 6.2.871. Interacting insect roeselii (10), caged alone previously.

Behaviour: roeselii, which was put in first, manages to hold out against bicolor, but both insects run away from each other. Final result: Toleration.

Previously caged alone.

2. 27 August 1970. 11.40 a.m. Temperature 31 degrees. Tape reference 7.2.1397. Interacting insect roeselii (10), caged alone previously.

Behaviour: The roeselii approaches the singing bicolor and makes short squirting noises about 1" away. It walks away and makes more of these noises, and then returns. They face one another and antennate. Then bicolor moves away and roeselii follows a short way. When bicolor is 1' away, roeselii suddenly starts to sing normally, and goes on. Final result: Toleration.

3. 27 August 1970. 12.50 p.m. Temperature 29 degrees. Tape reference 8.1.358. Interacting insect diluta (2), caged alone previously.

Behaviour: No movement: they sit 6" apart.

Final result: Inconclusive. (Sudden arrest of diluta.)

4. 28 August 1970. 11.50 a.m. Temperature 33 degrees. Tape reference 8.1.1363. Interacting insect roeselii (10), caged alone previously.

Behaviour: No movement: they sit 1½" apart.

Final result: Toleration.

5. 28 August 1970. 12.08 p.m. Temperature 29-32 degrees. Tape reference 8.2.0. Interacting insect diluta (2), caged alone previously.

Behaviour: Separating distance 8"; diluta has moved so that a piece of cardboard lies between it and bicolor. (Shielding?)

Final result: Inhibition of diluta.

Previously caged with a female.

6. 6 September 1970. 12.15 p.m. Temperature 30 degrees. Tape reference 10.2.0. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: No movement: they sit 6" apart.

Final result: Toleration.

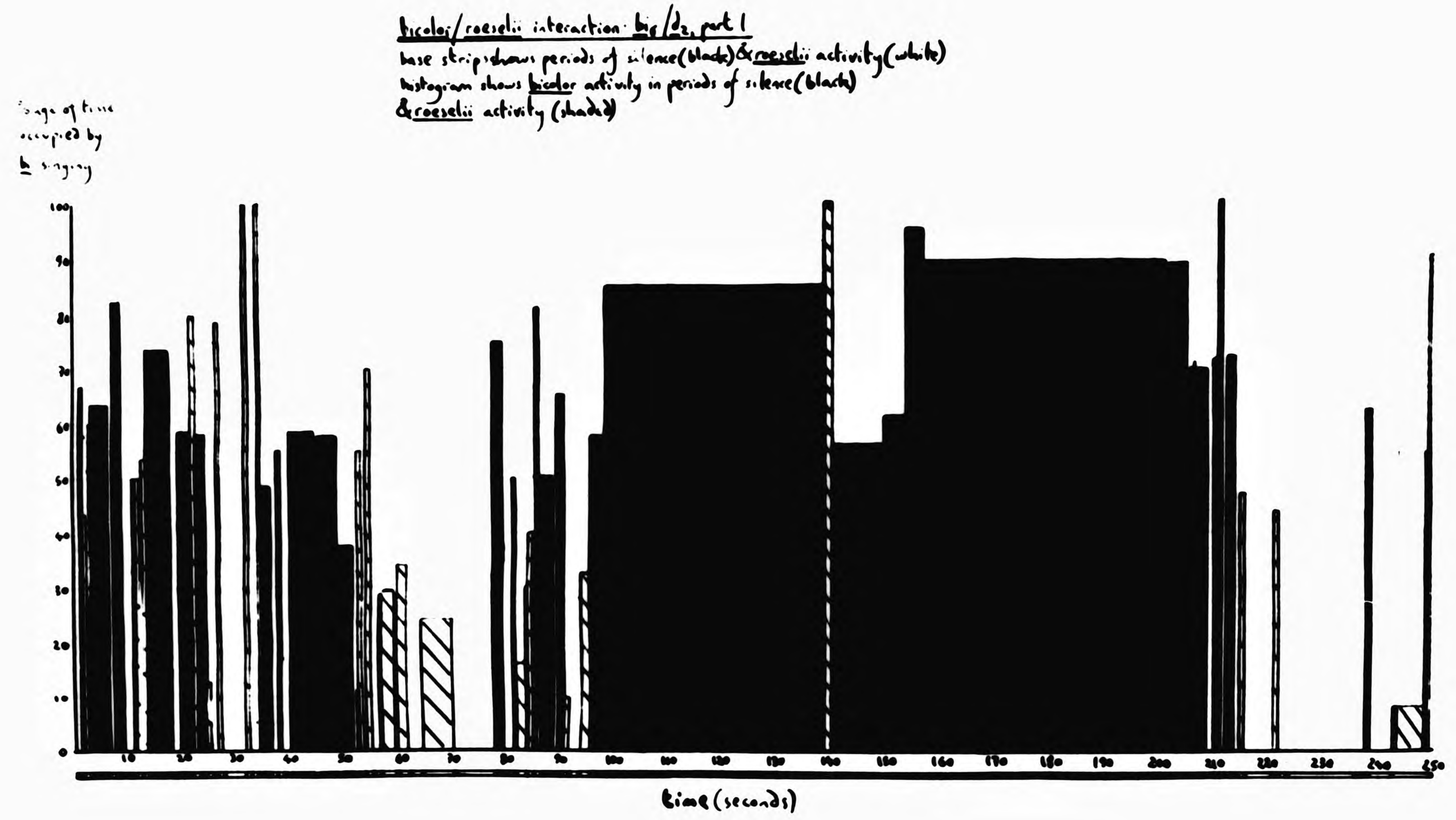
7. 6 September 1970. 12.45 p.m. Temperature 30 degrees. Tape reference 10.2.596. Interacting insect roeselii (10), caged alone previously.

Behaviour: roeselii, singing, moves to within 3" of bicolor.

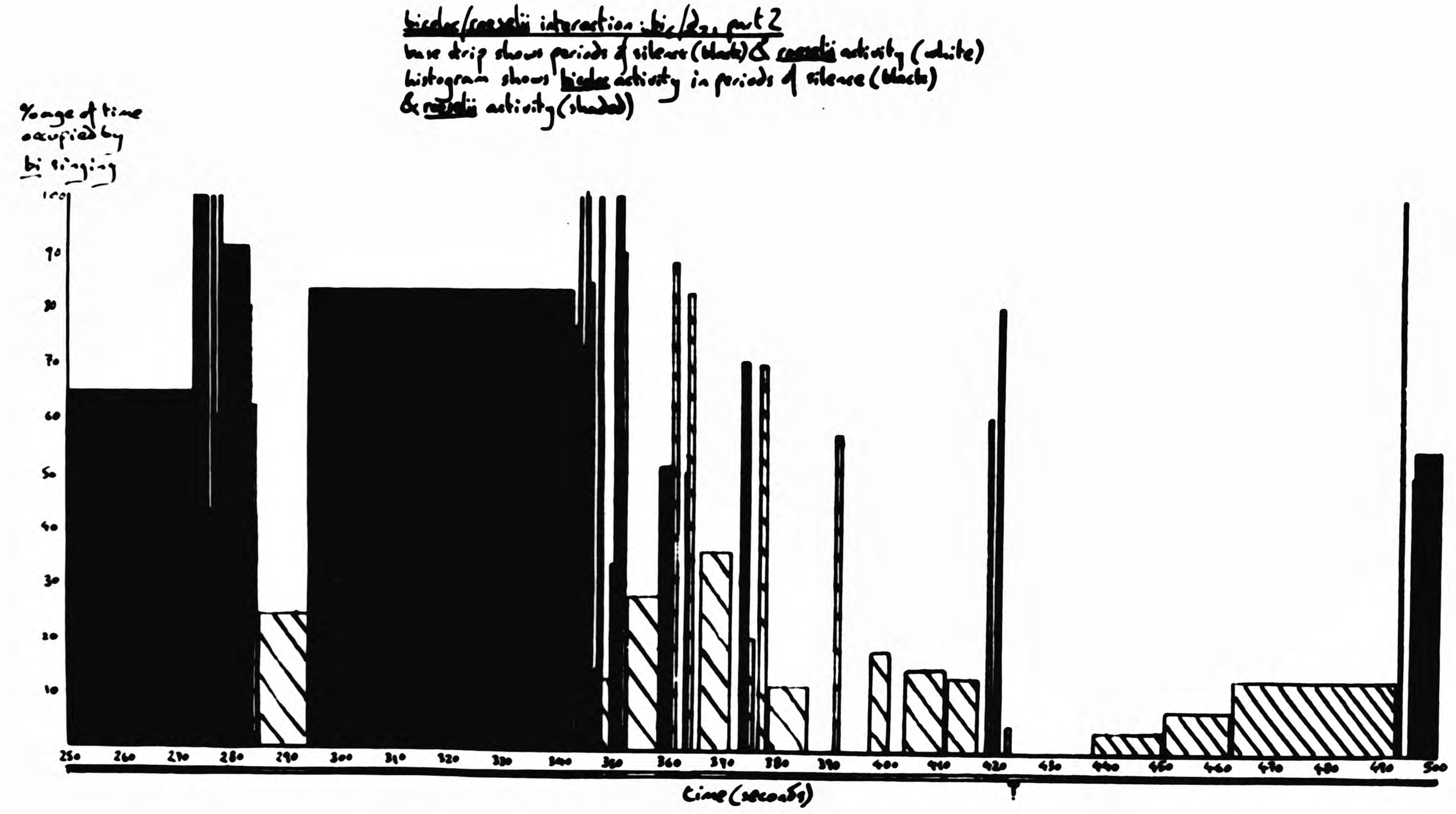
Final result: Inconclusive: bicolor refuses to sing.

8. 10 September 1970. 11.05 a.m. Temperature 23 degrees. Tape reference 11.1.1605. Interacting insect diluta (2), caged alone previously.

Histogram 14

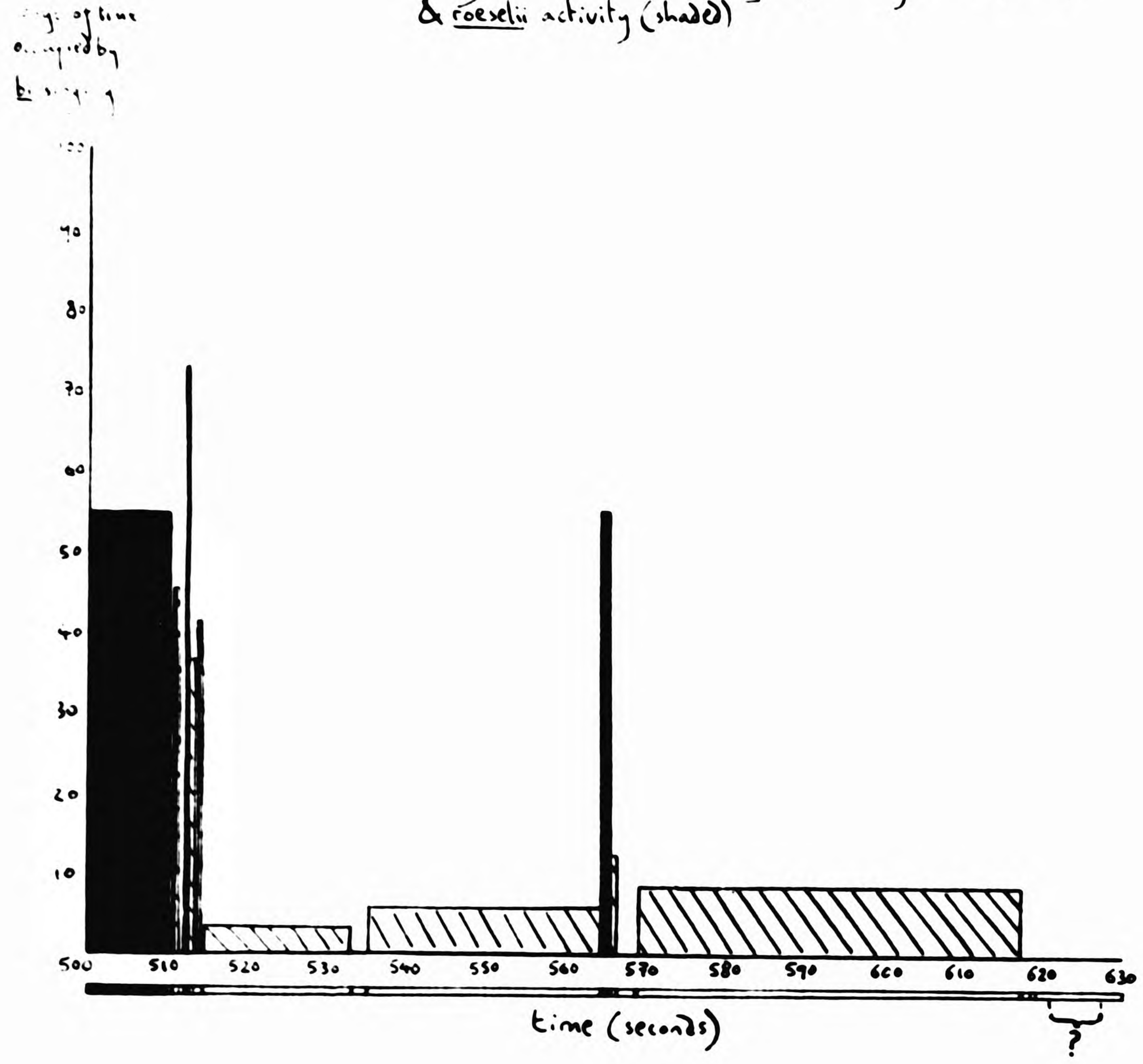


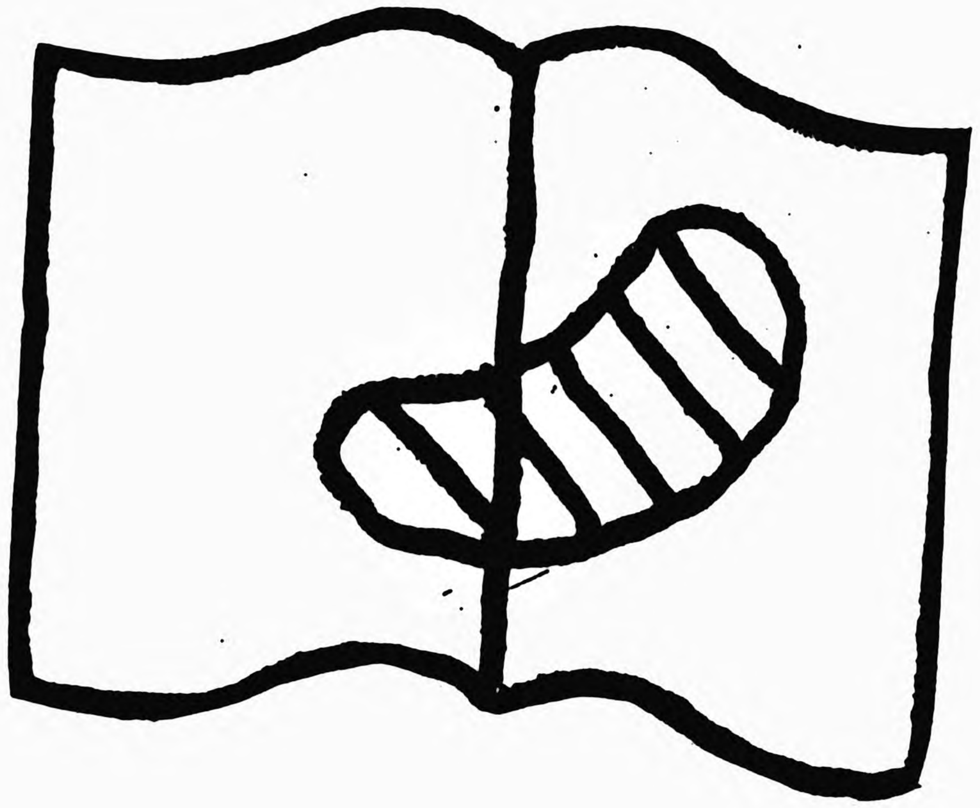
Histogram 15



Histogram 16

bicolor / roeselii interaction · bi$_{0}$/♂$_{2}$, part 3
base strip shows periods of silence (black) & roeselii activity (white)
histogram shows bicolor activity in periods of silence (black)
& roeselii activity (shaded)





Behaviour: They rest 4" apart, then *diluta* moves a further 2" away.

Final result: Inhibition of *bicolor*.

Additional Notes: This interaction has been analyzed at length: see histograms 14, 15 and 16. In the earlier parts are several long periods in which *roeselii* does not sing and in which high levels of *bicolor* song build up, but after this a strange phenomenon occurs: *bicolor* sings in the *roeselii* sequences in preference to the intervals between them. This is a reversal of the usual state of affairs. The levels descend, and then at 440 seconds begins a resurgence of *bicolor*, specifically during the singing of *roeselii*. Only at 495 seconds does it begin to sing in a silent period. The final stages are low *bicolor* levels during extended *roeselii* sequences.

9. 10 September 1970. 11.40 a.m. Temperature 23 degrees. Tape reference 11.2.363. Interacting insect *roeselii* (10), caged alone previously.

Behaviour: No movement: they rest 9" apart.

Final result: Inhibition of *bicolor*.

Caged again with other males.

10. 13 September 1970. 12.20 p.m. Temperature 22 degrees. Tape reference 12.1.1756. Interacting insect *roeselii* (11), caged previously with other male *roeseliis*.

Behaviour: The silent *roeselii* moves towards the singing *bicolor*, climbs on to it and off again; *bicolor* starts walking, and passes *roeselii*, which stridulates. At this, *bicolor* stops momentarily. Eventually they sit motionless 1" apart; *roeselii* stops singing, then resumes.

Final result: Toleration, the closest instance seen.

11\. 24 September 1970. 10.10 a.m. Temperature 28 degrees. Tape reference 15.1.1981. Interacting insect *roeselii* (11), caged previously with other male *roeseliis*.

Behaviour: They rest 3" apart (later 5" through my interference). Whenever I stop *roeselii*, *bicolor* sings, but only then, and unless disturbed *roeselii* sings continuously.

Final result: Inhibition of *bicolor*.

bicolor (7)

Previously caged with other males.

1\. 24 August 1970. 10.15 a.m. Temperature 23 degrees. Tape reference 7.1.0. Interacting insect *diluta* (2), caged alone previously.

Behaviour: *diluta*, silent, moves towards the singing *bicolor* and makes squirting sounds at it (my impression): then moves back. Approaches and retreats again. A box of singing *roeseliis* is brought near: *diluta* begins to sing normally.

Final result: Inhibition of *diluta*.

Previously caged alone.

2\. 28 August 1970. 1.02 p.m. Temperature 27-29 degrees. Tape reference 8.2.380. Interacting insect *roeselii* (10), caged alone previously.

Behaviour: The insects emit alternate short bursts. They move together until they are 1" apart; bicolor makes brief squirting noises; roeselii moves 2" further away; bicolor follows; roeselii curves its abdomen downwards; bicolor antennates it and tastes the back of its abdomen and a hind tibia. When its hind tibia is tasted roeselii jumps forwards, then turns and comes back until they are ½" apart; bicolor stops singing but makes no attempt to move away. They antennate: roeselii draws back ½". Then they start to circle round one another, and roeselii antennates bicolor, which makes a sound. After some time bicolor suddenly jumps to a point 1" away and resumes singing.

Final result: Toleration.

3. 29 August 1970. 9.30 a.m. Temperature 20-21 degrees. Tape reference 8.2.1210. Interacting insect diluta (2), caged alone previously.

Behaviour: bicolor moves to 3" from diluta, then rests.

Final result: Inhibition of bicolor.

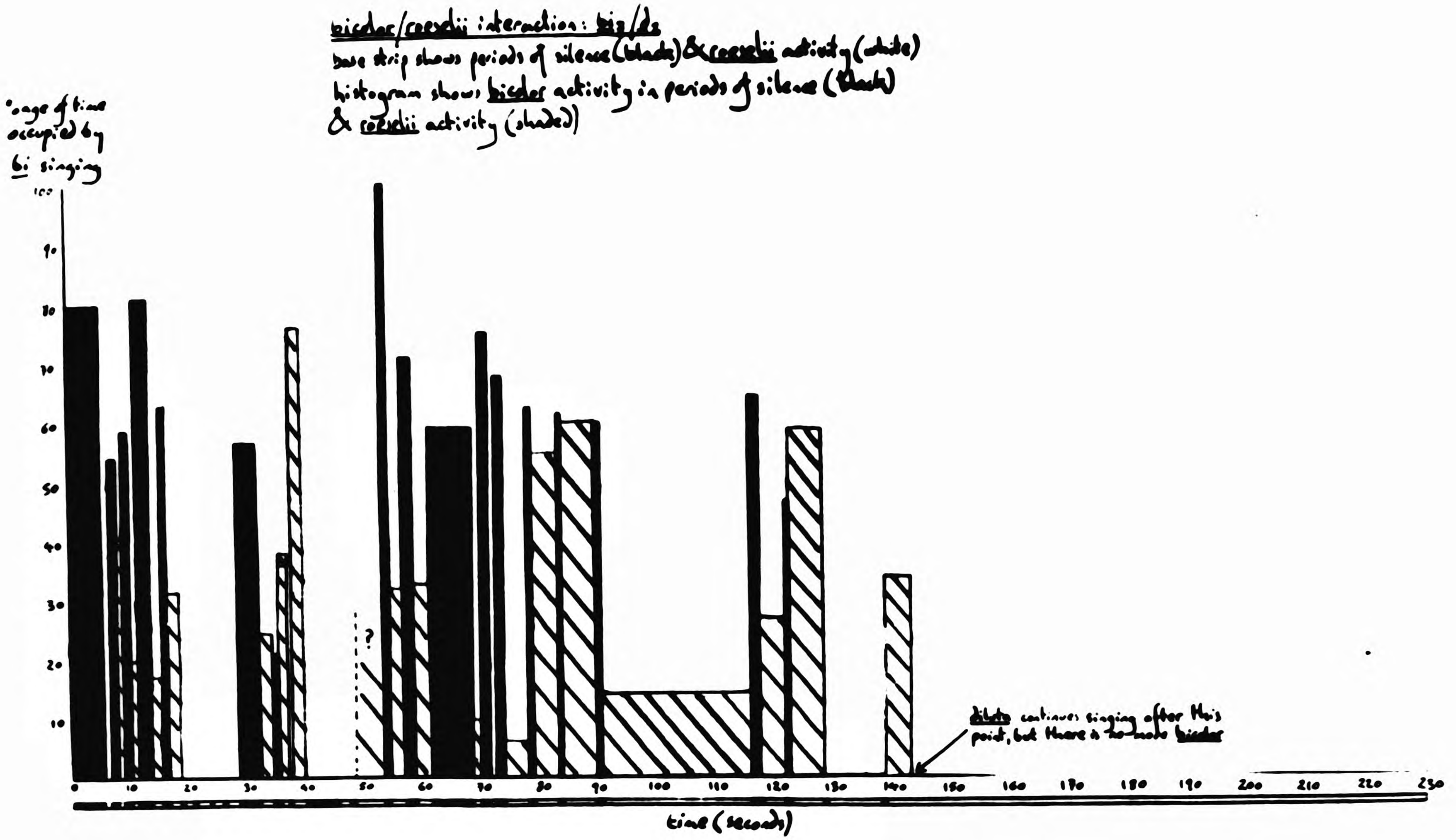
Additional Notes: Histogram 17 is a further demonstration of increased toleration by bicolor of roeselii song, reduced levels of singing, a slight resurgence effect, and termination of bicolor song during a long roeselii sequence.

Previously caged with a female.

4. 9 September 1970. 12.05 p.m. Temperature 26-26½ degrees. Tape reference 11.2.537. Interacting insect diluta (2), caged alone previously.

Behaviour: No movement: they rest 10" apart.

Histogram 17



Final result: Toleration.

5. 9 September 1970. 1.20 p.m. Temperature 26 degrees. Tape reference 11.2.814. Interacting insect roeselii (10), caged alone previously.

Behaviour: No movement: insects rest 15" apart.

Final result: At first bicolor inhibited, then roeselii.

6. 9 September 1970. 1.50 p.m. Temperature 25 degrees. Tape reference 11.2.1086. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: They rest 15" apart; later bicolor moves to a point 6" from roeselii. Final result: Inconclusive: sounds like inhibition of bicolor, but roeselii stops abruptly.

bicolor (8)

Previously caged with other males.

1. 26 August 1970. 9.30 a.m. Temperature 20 degrees. Tape reference 7.1.680. Interacting insect diluta (2), caged alone previously.

Behaviour: No movement: they sit 1" apart.

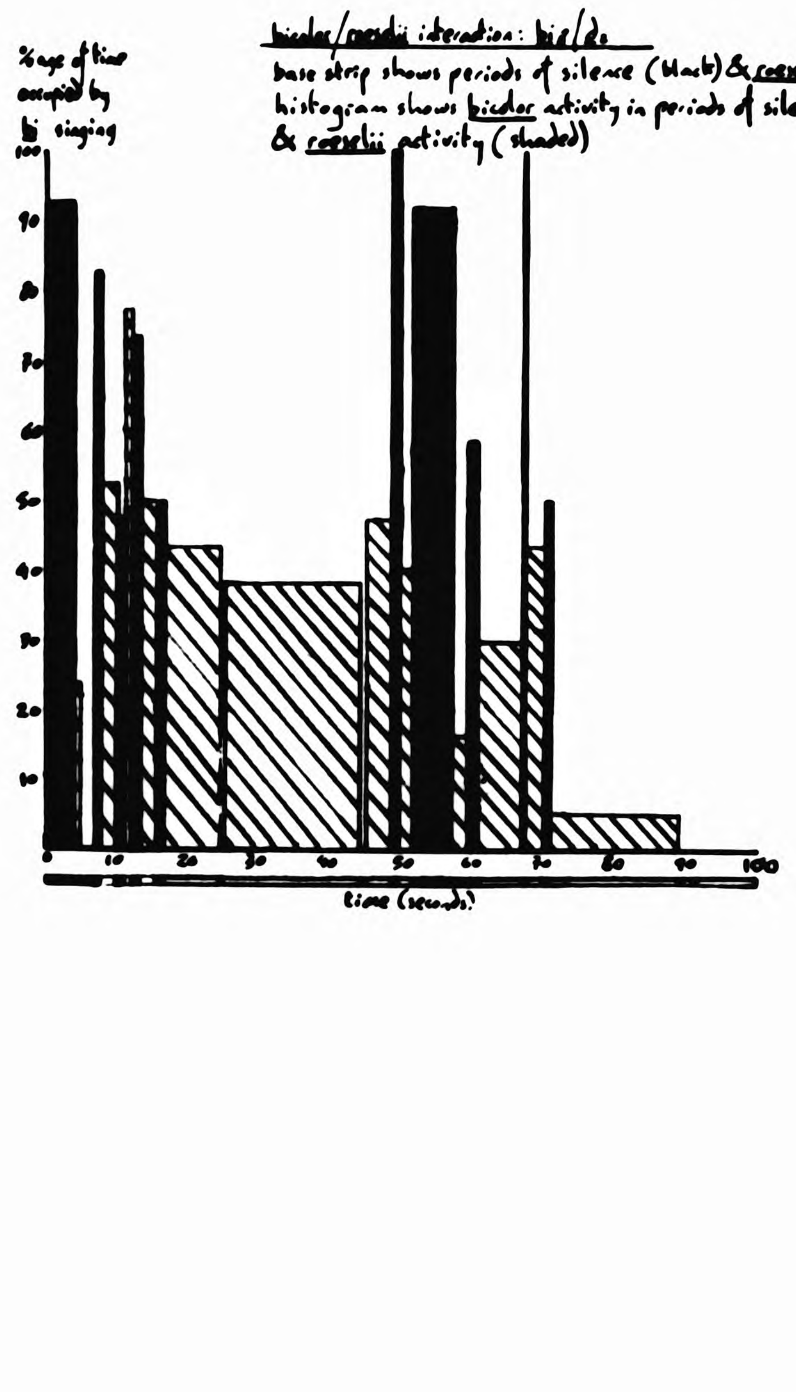
Final result: Inhibition of bicolor.

Additional Notes: Histogram 18 shows no special peculiarities, no resurgence, and an overall level difference not unlike those encountered with brachyptera.

Previously caged alone.

2. 29 August 1970. 10.40 a.m. Temperature 23 degrees. Tape reference: 8.2.1437. Interacting insect roeselii (10),

Histogram 18



caged alone previously.

Behaviour: No movement: they sit 8" apart.

Final result: Inhibition of bicolor.

3. 29 August 1970. 12.00 noon. Temperature 25 degrees. Tape reference 5.2.1084. Interacting insect diluta (2), caged alone previously.

Behaviour: Separating distance 1". At first diluta appears to inhibit bicolor; later it recovers and diluta moves 3" further away.

Final result: Toleration.

Caged again with other males.

4. 11 September 1970. 1.45 p.m. Temperature 26 degrees. Tape reference 11.2.1642. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: roeselii makes one sound and moves towards the singing bicolor, which moves off before roeselii reaches it. There is no more sound from roeselii.

Final result: Inconclusive.

bicolor (9)

Previously caged with other males.

1. 26 August 1970. 10.10 a.m. Temperature 24 degrees. Tape reference 7.1.980. Interacting insect diluta (2), caged alone previously.

Behaviour: No movement: they sit 1" apart.

Final result: Inhibition of bicolor.

Additional Notes: Histogram 19 is noteworthy for the regularity of the decline in bicolor levels, and shows this first taking effect in the intervals and then in the roeselii sequences. The end is typical and there are no resurgences.

Previously caged alone.

2. 29 August 1970. 12.35 a.m. Temperature 29 degrees. Tape reference 9.1.0. Interacting insect roeselii (10), caged alone previously.

Behaviour: Bicolor, initially 8" away, moves to a point 1" away and then rests.

Final result: Toleration.

3. 29 August 1970. 1.10 p.m. Temperature 25 degrees. Tape reference 9.1.400. Interacting insect diluta (2), caged alone previously.

Behaviour: When put in, diluta walks up to bicolor, which is singing furiously; bicolor makes squirting sounds and diluta retreats to 2" away. It looks as though diluta can get no chance to begin singing. Final result: Inconclusive.

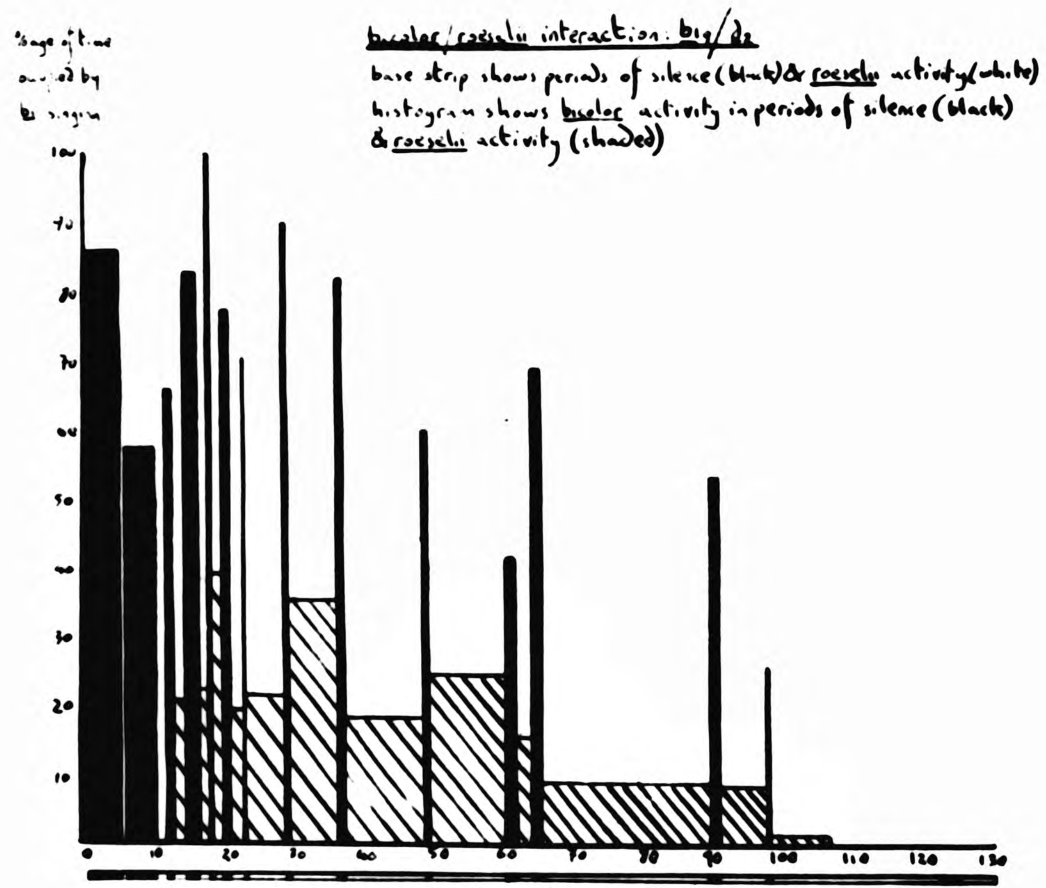
Caged again with other males.

4. 16 September 1970. 11.25 a.m. Temperature 31 degrees. Tape reference 13.1.580. Interacting insect roeselii (11), caged previously with other male roeseliis.

Behaviour: roeselii is stationary; bicolor moves about a good deal, generally about 10" away.

Final result: Toleration

Histogram 19



bicolor (10)

Caged previously with other males.

1. 26 August 1970. 11.00 a.m. Temperature 26 degrees. Tape r reference 7.1.1107. Interacting insect diluta (2), caged alone previously.

   Behaviour: diluta moves towards bicolor, turns away and begins to sing: bicolor then moves towards it until 9" away, and rests.

   Final result: Toleration.

Caged alone previously.

2. 30 August 1970. 9.30 a.m. Temperature 21-24 degrees. Tape reference 9.1.512. Interacting insect roeselii (10), caged alone previously.

   Behaviour: No movement: they sit 2" apart.

   Final result: Inhibition of bicolor.

3. 30 August 1970. 10.10 a.m. Temperature 27 degrees. Tape reference 9.1.636. Interacting insect diluta (2), caged alone previously.

   Behaviour: The diluta, silent, moves towards the bicolor, which is singing, and remains stationary 1" away for some minutes. Suddenly bicolor moves forward and antennates it. Shortly after, diluta moves off and begins to sing.

   Final result: Toleration.

Caged again with other males.

4. 11 September 1970. 1.10 p.m. Temperature 22½ degrees. Tape reference 11.2.1542. Interacting insect roeselii (11), caged

previously with other male roeseliis.

Behaviour: They rest 10" apart; bicolor has little chance to start.

Final result: Inhibition of bicolor.

bicolor (11)

Previously caged with other males.

1. 16 September 1970. 10.30 a.m. Temperature 30 degrees. Tape reference 12.2.1731. Interacting insect diluta (2), caged alone previously.

   Behaviour: bicolor approaches from 10" to 4" of roeselii, then for no apparent reason drops to the floor and goes on singing 6" away.

   Final result: Toleration.

2. 16 September 1970. 11.00 a.m. Temperature 32 degrees. Tape reference 13.1.0. Interacting insect roeselii (11), caged previously with other male roeseliis.

   Behaviour: The initial impression is that bicolor is being inhibited. It is 1' from roeselii, approaches to within 8", then retreats again to 1' away.

   Final result: Toleration.

(d) Interaction of *M. bicolor* and *M. brachyptera*

The principal reason for studying *bicolor/ brachyptera* interactions was the availability of material during the summer of 1970. It was initially thought that the juxtaposition of these species was of purely academic significance. It was subsequently learnt from Mr K. Harz of Gröbenzell-bei-München that in a German locality of his aquaintance, *bicolor* had in 1969 invaded a *brachyptera* habitat, and that the two species were to be found living together there.

Generally, these interactions were much less easily arranged than the ones hitherto considered. Usually, *brachyptera* is a sensitive insect, ceasing to sing at a slighter disturbance than would *roeselii* or *bicolor*, and although some specimens would stridulate sitting on my finger, it was more frequent to find that a solitary individual would remain silent for a whole afternoon. As these difficulties were less evident with the *roeselii/ brachyptera* interactions, which were conducted chiefly during the morning, it is suspected that although in the field and when caged collectively *brachyptera* sings throughout the day, it may, like *roeselii*, be readier to sing in the morning than in the afternoon.

All the *brachypteras* used were caged between experiments with other male *brachypteras*.

brachyptera (10)

1. 26 August 1970. 4.00 p.m. Temperature 29 degrees. Tape reference 7.2.677. Interacting insect bicolor (1), caged alone previously.

   Behaviour: The first, short sound made by bicolor, silences brachyptera for one hour.

   Final result: Inhibition of brachyptera.

brachyptera (11)

1. 27 August 1970. 3.00 p.m. Temperature 33 degrees. Tape reference 8.1.794. Interacting insect bicolor (6), caged alone previously.

   Behaviour: bicolor, silent, walks up to brachyptera, which is singing, comes face to face, and antennates it. At once brachyptera stops singing, and bicolor then begins singing.

   Final result: Inhibition of brachyptera, not acoustic.

2. 28 August 1970. 3.00 p.m. Temperature 28 degrees. Tape reference 8.2.1063. Interacting insect bicolor (8), caged alone previously.

   Behaviour: bicolor, silent, moves to a point 1" from the singing brachyptera, makes a single squirting sound and turns away: brachyptera pursues it fast, antennates it and then turns back. Then bicolor sings, silencing brachyptera immediately. Now bicolor pursues brachyptera and antennates it: brachyptera appears to be trying to get away, then turns back towards bicolor and antennates it whereupon it sings:

brachyptera then turns and walks away. (Later the interaction is again attempted but the noise of putting bicolor into the cage silences brachyptera: bicolor then walks to it and antennates it, and it crosses to the other side of the cage.)

Final result: Inhibition of brachyptera.

3. 10 September 1970. 3.50 p.m. Temperature 24 degrees. Tape reference 11.2.1212. Interacting insect bicolor (10), caged alone previously.

Behaviour: bicolor walks, then jumps, singing, to a point 1" from brachyptera, which moves off, then returns and then moves off to a point 1½" away, silenced.

Final result: Inhibition of brachyptera.

4. 16 September 1970. 1.50 p.m. Temperature 29½ degrees. Tape reference 13.1.1208. Interacting insect bicolor (9), caged previously with other male bicolors.

Behaviour: bicolor approaches to a point 10" from brachyptera, then both sit still.

Final result: Toleration.

5. 16 September 1970. 2.05 p.m. Temperature 27½ degrees. Tape reference 13.1.1508. Interacting insect bicolor (2), caged previously with other male bicolors.

Behaviour: They rest 15" apart. Suddenly brachyptera stops singing and begins walking back and forth at right angles to a line drawn from it to bicolor.

Final result: Inhibition of brachyptera.

Additional Notes: In every respect histogram 20 presents the aspect of a *roeselii/ brachyptera* interaction without a resurgence effect. It does not appear to matter, to judge by this, which species is responsible for the inhibition, from *brachyptera*'s point of view.

6. 16 September 1970. 2.50 p.m. Temperature 24 degrees. Tape reference 13.1.1732. Interacting insect *bicolor* (1), caged previously with other male *bicolors*.

Behaviour: *bicolor*, singing, approaches to a point 1" from the singing *brachyptera*, which then stops singing and moves off.

Final result: Inhibition of *brachyptera*.

Additional Notes: The differences between histograms 21 and 19 are interesting. The first part of histogram 21 shows a very intermittent *bicolor* song like that in histogram 12, but here the difference between *brachyptera* stridulation during *bicolor* sequences and during intervals is maintained in spite of the very short times involved. The collective inhibitory effect of this *bicolor* singing tells in the decline during the succeeding three intervals in the last of which the *brachyptera* makes its last chirps.

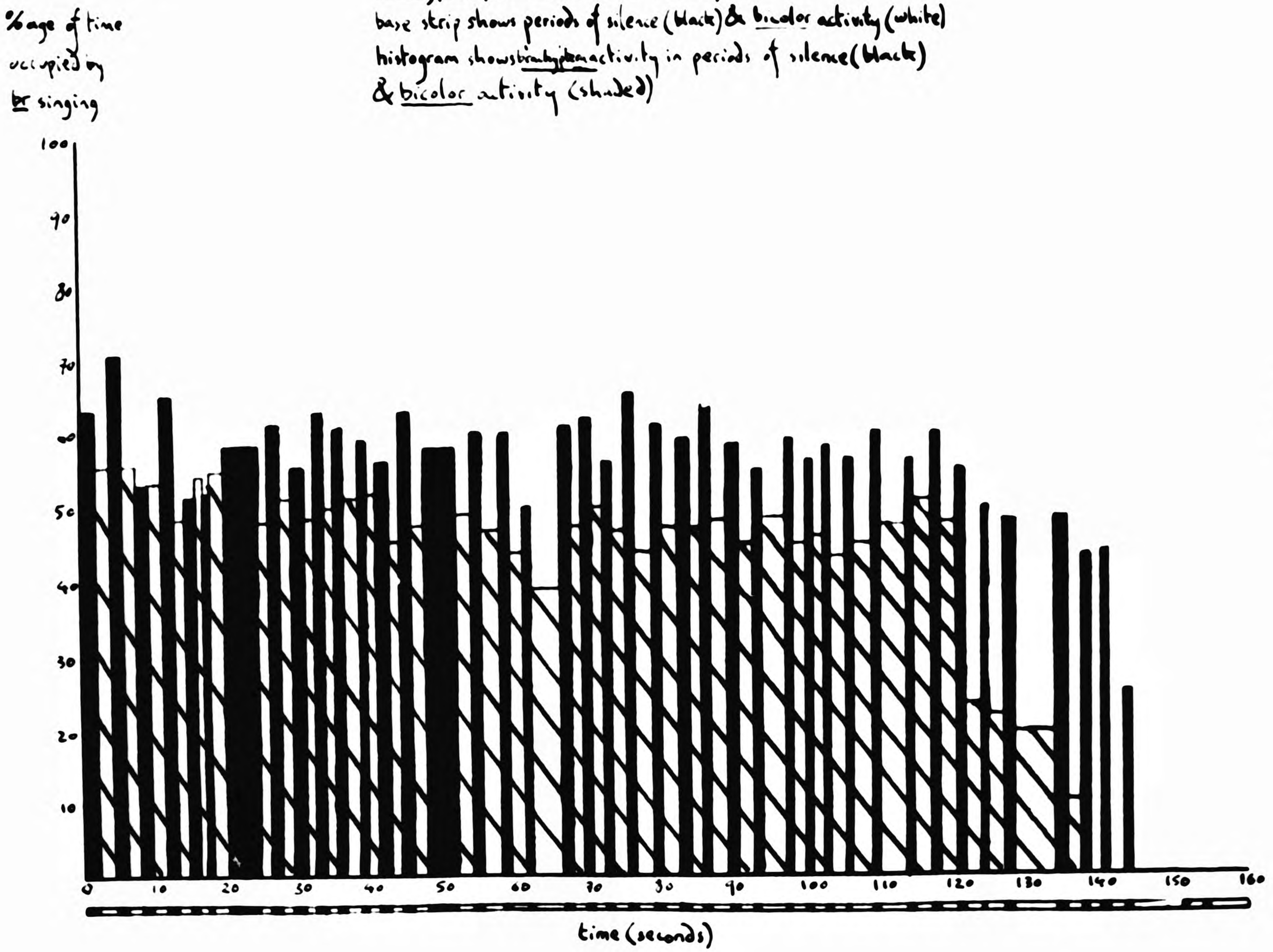
7. 16 September 1970. 3.20 p.m. Temperature 26½ degrees. Tape reference 13.2.0. Interacting insect *bicolor* (3), caged previously with other male *bicolors*.

Behaviour: They sit still 14" apart. Eventually *brachyptera* stops singing and begins walking back and forth at right

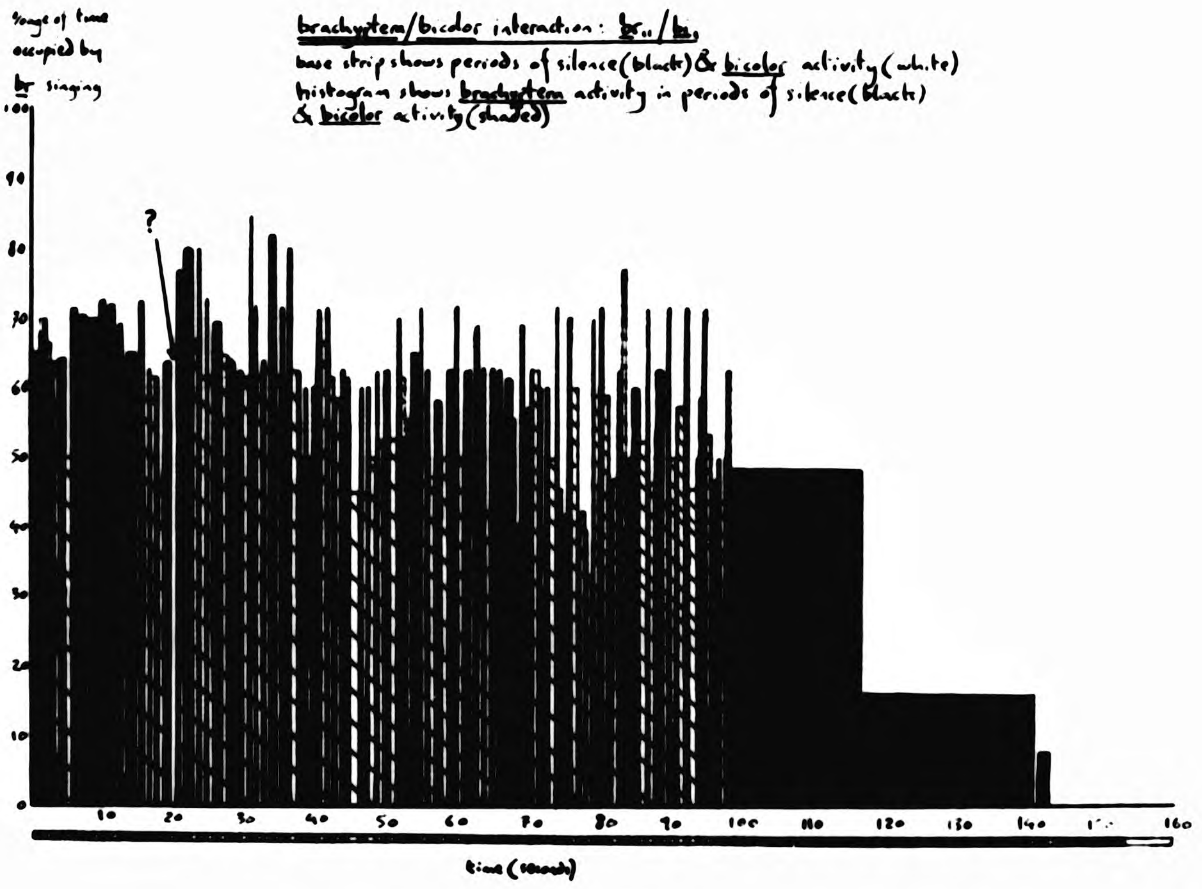
Histogram 20

brachyptera/bicolor interaction: br$_{11}$/bi$_{3}$

base strip shows periods of silence (black) & bicolor activity (white)
histogram shows ~~brachyptera~~ activity in periods of silence (black)
& bicolor activity (shaded)



Histogram 21



angles to a line drawn from it to the bicolor.

Final result: Inhibition of brachyptera.

8. 16 September 1970. 4.10 p.m. Temperature 24-27 degrees. Tape reference 13.2.241. Interacting insect bicolor (4), caged previously with other male bicolors.

Behaviour: brachyptera starts to move towards bicolor, stops when it reaches the limit of the sunlit part of the cage, turns back into the sunshine, and is silenced.

Final result: Inhibition of brachyptera.

9. 17 September 1970. 2.00 p.m. Temperature 26½ degrees. Tape reference 13.2.857. Interacting insect bicolor (4), caged previously with other male bicolors.

Behaviour: This time there are no complications due to shadow. At first bicolor is 1½' from brachyptera: it moves 3" closer and sits still. Eventually brachyptera is silenced and moves off.

Final result: Inhibition of brachyptera.

brachyptera(12)

1. 28 August 1970. 4.40 p.m. Temperature 25 degrees. Tape reference 8.2.1177. Interacting insect bicolor (8), caged alone previously.

Behaviour: bicolor, silent, moves to a point 1" from the singing brachyptera. Suddenly brachyptera stops, but it is possible that sounds in the room disturbed it.

Final result: Inconclusive.

brachyptera (13)

1. 30 August 1970. 2.20 p.m. Temperature 32 degrees. Tape reference 9.2.0. Interacting insect bicolor (8), caged alone previously.

Behaviour: Both insects are singing. Firstly bicolor moves towards brachyptera and antennates it. There is a slowing in brachyptera's chirp rate. Then brachyptera bends its abdomen down and touches the tip of bicolor's abdomen with it: bicolor makes one abrupt sound and moves to a point 1' away. It returns and brachyptera abvances with a bent abdomen to meet it: bicolor retreats, then returns and antennates brachyptera. They assume a copulatory position with brachyptera beneath taking the position of the male. There are kicking movements by both, and bicolor moves off to a point 8" away, then returns, meets brachyptera head on, antennating it, circles round it, moves to a point 8" away, makes a sound and then jumps towards brachyptera, landing 1½" away. It antennates brachyptera, which pushes it away with a hind leg: bicolor moves off, returns, moves off, returns, climbs over brachyptera and then suddenly jumps off. It then jumps back, climbs over brachyptera and assumes a copulatory position again. Only at the beginning of this recording and when indicated does bicolor sing.

Final result: Toleration.

2. 30 August 1970. 2.40 p.m. Temperature 34 degrees. Tape reference 9.2.557. Interacting insect bicolor (10), caged alone previously.

Behaviour: No movement: they rest 1½" apart.

Final result: Toleration, then bicolor suddenly silenced.

3. 30 August 1970. 3.05 p.m. Temperature 34 degrees. Tape reference 9.2.707. Interacting insect bicolor (2), caged previously with a female bicolor.

Behaviour: They move together and apart several times.

Final result: Inconclusive: bicolor does not sing enough.

4. 4 September 1970. 3.20 p.m. Temperature 25 degrees. Tape reference 9.2.1731. Interacting insect bicolor (1), caged previously with a female bicolor.

Behaviour: The silent bicolor moves to a point 1½" from the singing brachyptera, waits several minutes and then sings, silencing the brachyptera, which turns towards it and antennates it from behind, and then moves off.

Final result: Inhibition of brachyptera.

brachyptera (14)

1. 10 September 1970. 2.12 p.m. Temperature 22½ degrees. Tape reference 11.2.1733. Interacting insect bicolor (10), caged alone previously.

Behaviour: bicolor, initially 8" from brachyptera, jumps towards it and follows it about; brachyptera approaches to a point 1" away but when bicolor turns towards it it backs away, and later stops singing.

Final result: Inhibition of brachyptera.

2. 19 September 1970. 3.15 p.m. Temperature 33 degrees. Tape reference 14.2.1605. Interacting insect bicolor (9), caged previously with other male bicolors.

Behaviour: Both insects are singing: brachyptera approaches to within 3" of bicolor, turns away, approaches again to 4" away, turns away and is silenced.

Final result: Inhibition of brachyptera.

Additional Notes: This is a rapid inhibition as can be seen from histogram 22. No real comparison with the other histograms can be made from so little material.

brachyptera (15)

1. 20 September 1970. 2.10 p.m. Temperature 26½ degrees. Tape reference 15.1.1276. Interacting insect bicolor (9), caged alone previously.

Behaviour: bicolor moves to a point 3" from brachyptera, then back to a point 6" away and sits still.

Final result: Toleration.

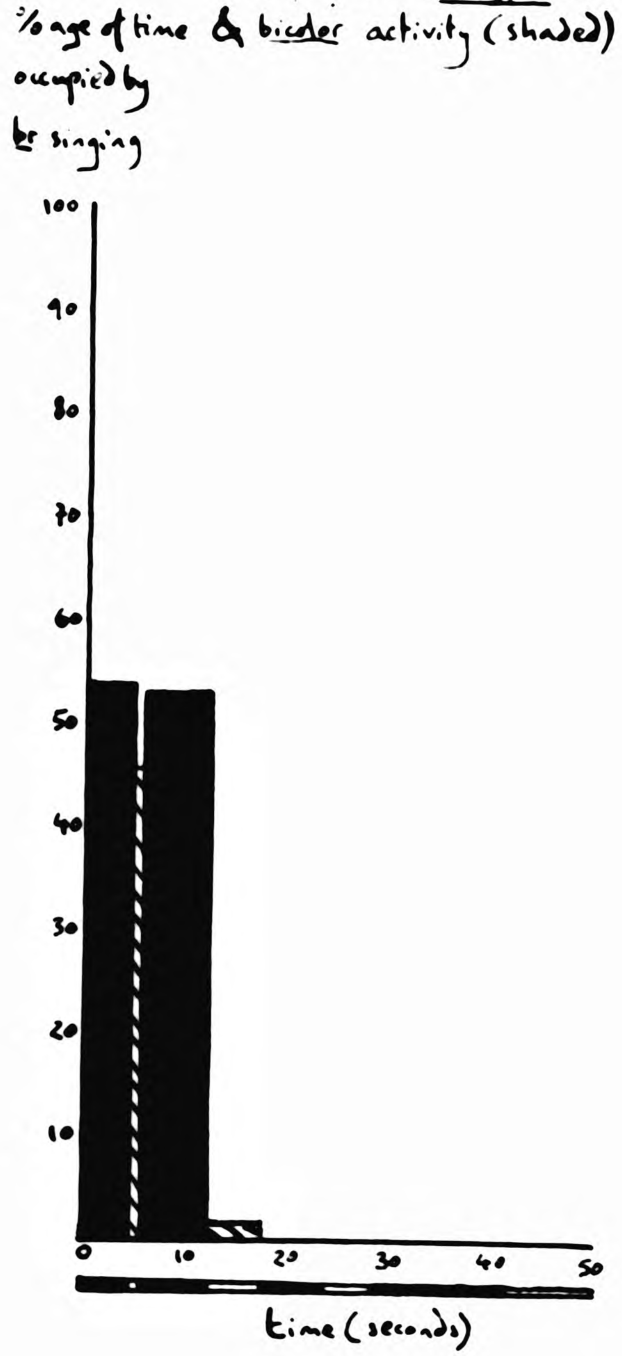
Additional Notes: This is the brachyptera which produced polysyllabic chirps under the influence of roeselii (see pages 81-95). Absolutely none were found in any of its three bicolor interactions, nor was there any special difference from other bicolor/ brachyptera interactions.

Histogram 22

brachyptera / bicolor interaction: br19 / bg

base strip shows periods of silence (black) & bicolor activity [illegible]

histogram shows brachyptera activity in periods of silence (black) & bicolor activity (shaded)



2. 20 September 1970. 2.30 p.m. Temperature 35 degrees. Tape reference 15.1.1500. Interacting insect bicolor (2), caged previously with other male bicolors.

Behaviour: They rest motionless 9" apart.

Final result: Toleration.

3. 25 September 1970. 12 noon. Temperature 32 degrees. Tape reference 15.2.1810. Interacting insect bicolor (6), caged previously with other male bicolors.

Behaviour: They rest motionless 16" apart.

Final result: Inhibition of brachyptera.

Additional Notes: Because of the special interest of this brachyptera the inhibitory interaction has been analysed in histogram 23. A growth of bicolor song is seen, and a faint resurgence effect where it temporarily lapses. But there are really no special features.

brachyptera (16)

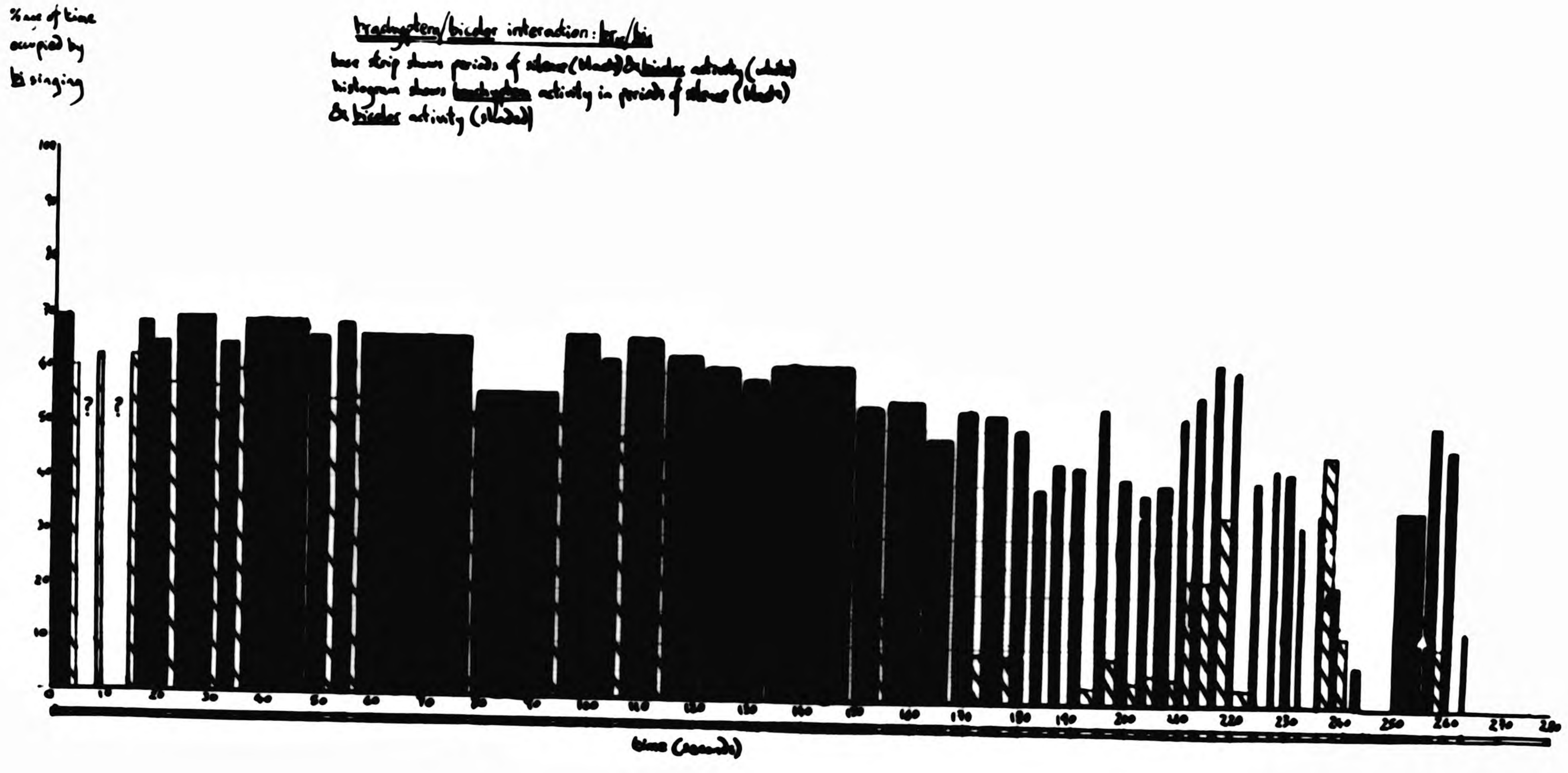
1. 18 September 1970. 1.10 p.m. Temperature 36½ degrees. Tape reference 14.1.501. Interacting insect bicolor (9), caged alone previously.

Behaviour: bicolor moves towards brachyptera but passes it 4" away and eventually rests 1' away.

Final result: Toleration.

2. 18 September 1970. 1.45 p.m. Temperature 33 degrees. Tape reference 14.1.1056. Interacting insect bicolor (10), caged alone previously.

Histogram 23



Behaviour: They rest 1½" apart and brachyptera suddenly stops, but I think this is due to disturbance by me.

Final result: Inconclusive.

brachyptera (17)

1. 23 September 1970. 1.30 p.m. Temperature 33 degrees. Tape reference 15.1.1899. Interacting insect bicolor (9), caged alone previously.

   Behaviour: No movement: they rest 10" apart.

   Final result: Inhibition of brachyptera.

2. 23 September 1970. 1.52 p.m. Temperature 33 degrees. Tape reference 15.1.1953. Interacting insect bicolor (10), caged alone previously.

   Behaviour: They rest motionless 1½" apart. There is not enough bicolor song, but when it does sing the brachyptera chirp rate slows, so presumably inhibition could occur.

   Final result: Inconclusive.

brachyptera (19)

1. 21 September 1970. 11.56 a.m. Temperature 29 degrees. Tape reference 15.1.694. Interacting insect bicolor (2), caged previously with other male bicolors.

   Behaviour: No movement: they rest 1½" apart.

   Final result: Toleration.

2. 21 September 1970. 12.30 p.m. Temperature 32 degrees. Tape reference 15.1.963. Interacting insect bicolor (3), caged

previously with other male bicolors.

Behaviour: No movement: they rest 10" apart.

Final result: Inhibition of brachyptera.

DISCUSSION

1. Aims and Limitations of Project

Rationale of Experimentation

The objective of this work has been to investigate the acoustic and other behaviour involved in interspecific interactions in the genus *Metrioptera*. I have tried to gather as much information as possible within the short time during which adult bushcrickets are available in the year. I have attempted to sound out diverse aspects of the interaction phenomenon rather than to obtain a uniform block of data exhausting a particular small field. If the interaction summary tables (pages 166-168) are examined they will be seen to lack symmetry: some combinations of two individuals have been tried several times, others not at all. The explanation for this is that on particular days certain insects happened to be particularly vociferous whilst others were not. On other days it might be the other way about. I would arrange an experiment because I expected it to produce a recording on which both insects were singing, rather than because it appeared next on the programme of combinations.

Threshold of Inhibition

In this research no attempt was made to discover what dosage of the song of the inhibiting insect was needed to produce total inhibition in the other insect. There are several reasons for this. Consider a *roeselii/brachyptera* interaction. The *brachyptera* is singing in the recording cage and the *roeselii* is put in. It would be entirely impractical to start the taperecorder now: by the time the *roeselii* has commenced I might be almost at the end of the reel and have to lose valuable song whilst putting on a new one. The only reasonable technique is to wait until *roeselii* makes its first sound and then switch on the taperecorder, hoping that the click produced in so doing will not silence the insect. This means however that I do not have a complete record of the circumstances leading to inhibition: the first sound has been forfeited.

Not only is the beginning of inhibition undefined, the endpoint is also. If the *brachyptera* has stopped singing it may or may not be totally inhibited. The only way I can test this is to stop the *roeselii*'s singing by mechanically disturbing it. If the *brachyptera* does not resume singing within thirty seconds (during which the *roeselii* is silent) I consider that it is totally inhibited. However, had I silenced the *roeselii* thirty seconds earlier the *brachyptera* might still have failed to resume. I have thus perhaps exposed it to thirty seconds of superfluous inhibiting influence. On the other hand if it does resume its song I have broken the continuity of the interaction and when the *roeselii* again begins to stridulate it will probably have to continue for longer than it otherwise would in order to inhibit the *brachyptera*, which has as it were built up its chirping potential during the silence. A further factor is that in mechanically disturbing the *roeselii* to silence it I may inadvertently have disturbed the *brachyptera*.

Histogram 11 (page 118) is of interest in this context. The *roeselii* was silenced three times because the *bicolor* was thought to be totally inhibited: in the first and second cases the *bicolor* resumed its song; in the third it really was totally inhibited.

Inconstancy of Inhibiting Influence

Even if it were possible to pinpoint the beginnings and endings of inhibiting songs the quantity of song involved would still be indeterminate. Both roeselii and bicolor produce long trills with intervals of various lengths in various places. Usually as the song continues the intervals get fewer and shorter, but no two inhibiting passages are identical and therefore no absolute comparisons can ever be made. It seems clear anyway that the insect which will be inhibited gains, during the intervals in the other's song, capacity to continue, and can hold out for a long time if this song is sufficiently intermittent, as in the case of the interaction of roeselii (11) and brachyptera (15) (page 90).

The solution to most of these problems would be to replace the inhibiting insect with an ionophone through which would be played a recording of its song, without intervals, from a tape loop. Exposure time and amplitude could then be varied at will. The problem of when to stop would remain, but at least there would be no need to mechanically disturb the experiment. This is speculation on my part, but I suspect that so many factors such as age, metabolic level, degree of inhibition already present as a result of current ambient sound and the cumulative effect of sounds previously heard might be involved in determining the exposure required to achieve total inhibition, that the same individual would never require the same exposure on any two distinct occasions. Nor am I certain that the concept of 'total inhibition' is as simple as I have implied. Evidently there is a point in exposure time on one side of which the insect will resume stridulation after a relatively short interval, and on the other side of which it will resume after a much longer interval, but I have made no attempts to time the latter beyond noting that in some cases it was several hours. ~~Having completed~~ Completing one experiment I would remove the insects from the cage so as to set up another experiment, and this mechanical derangement would naturally augment the inhibited insect's reluctence to sing. Had I left it alone in the cage in silence and recorded the time passed before it recommenced singing (which would probably be so long as to involve significant changes in temperature) I would have accomplished far fewer experiments.

Technical Drawbacks

The irregularity of results is due not only to the irregular arrangement of experiments but also to the variation in the quality of recordings. Some recordings sounded simple and distinct, yet the analyzing equipment failed to provide from them a reasonable trace. Others gave results easily susceptible of interpretation although they themselves sounded unclear. As stated before (page 42), crosstalk was a particularly difficult effect in the bicolor/brachyptera interactions. The solution would have been to separate the insects with a partition having a microphone on each side, but like the ionophone experiments just proposed, this would have sacrificed the behavioural aspect of the study, which was of great importance. I had to make it possible for the animals to reach one another and I had to correlate their behaviour with respect to one another with their acoustic behaviour. The major instrument of analysis employed (Brüel and Kjaer level recorder) used only one of the two tracks produced in each recording, so a certain amount of crosstalk was in fact required, but it was still a great advantage to have two microphones set up at opposite ends of the cage as the insects were often liable to walk about. The ideal recording would have the insect with the more discrete song (brachyptera in preference to roeselii or bicolor; bicolor in preference to roeselii) the louder.

Real Interpretation

A final objection which might be raised is to ask how I really knew that an insect was being inhibited, and not making a halt in its singing as it might do if alone. There is of course no absolute proof, and the simplest answer is to say that a number of impressions combined to produce the conviction. This could be communicated to another person by playing many recordings to him. A further demonstration, which I was able to carry out several times with natural roeselii/bicolor interactions in the field at Weiler, was to produce song at will from a bicolor by mechanically stopping the stridulation of a nearby roeselii.

2. Comparison of Types of Interaction

(a) Results of Interactions

Hierarchy

The three tables on pages 166-168 summarize the outcomes of 114 interactions between three species of Metrioptera. The 13 inconclusive experiments which were considered worth listing in the Results section have been omitted; so has the bicolor/brachyptera interaction (brachyptera (11), experiment 1, page 146) in which the bicolor silenced the brachyptera by touch instead of by singing at it. The total figures for each type of interaction give the following impression (which I had also formed in the course of performing the experiments). The commonest result of a roeselii/brachyptera interaction is the inhibition of the brachyptera: this happened 17 times, there were 10 tolerations, and roeselii was never inhibited. The same is true of bicolor/brachyptera interactions: brachyptera was inhibited 14 times, there were 7 tolerations, and bicolor was never inhibited. The matching of roeselii and bicolor is more equal, the usual outcome being toleration, which occurred in 35 experiments. When one partner is inhibited it is more likely to be the bicolor than the roeselii (21 bicolor inhibitions against 10 roeselii ones). The impression produced is of a hierarchy of 'dominance':

roeselii
bicolor
brachyptera

The very sparse information that I have on sepium suggests

Table 5

Summary Table for roeselii/brachyptera Interactions

All brachypteras involved were caged in male groups between experiments.

brachyptera	brachyptera inhibitions	tolerations
(1)	4	1
(2)	2	
(4)	3	
(7)	2	
(11)	1	1
(12)		1
(13)	1	1
(14)	1	1
(15)	1	1
(16)		2
(17)		2
(18)	1	
(19)	1	
Total	17	10

Table 6

Summary Table for roeselii/bicolor Interactions

Key:

A: bicolor caged before experiment with other male bicolors

B: bicolor caged alone before experiment

C: bicolor caged before experiment with a female bicolor

D: bicolor again caged before experiment with other male bicolors

bicolor	bicolor inhibitions				tolerations				roeselii inhibitions				Totals		
													bicolor inhibitions	tol.	roeselii inhibitions
	A	B	C	D	A	B	C	D	A	B	C	D			
(1)	1						3	3			2		1	6	2
(2)	1	1		1			1	2				2	3	3	2
(3)		2	1			1		1	1			1	3	2	2
(4)		2	2				1	4	1				4	5	1
(5)					1	1	3			1				5	1
(6)			2	1	1	2	1	1		1			3	5	1
(7)	1	1				1	1				1		2	2	1
(8)	1	1				1							2	1	
(9)	1					1		1					1	2	
(10)		2			1	1							2	2	
(11)					2									2	
Total	5	9	5	2	5	8	10	12	2	2	3	3	21	35	10

Table 7

Summary Table for *bicolor*/*brachyptera* Interactions

All brachypteras involved were caged in male groups between experiments

brachyptera	*brachyptera* inhibitions	tolerations
(10)	1	
(11)	7	1
(13)	1	2
(14)	2	
(15)	1	2
(16)		1
(17)	1	
(19)	1	1
Total	14	7

that its position is at the same level as *bicolor* or perhaps very slightly lower (2 tolerations – one of *roeselii* and one of *brachyptera* –; one case of inhibition by *roeselii*; one experiment with *roeselii* inconclusive). Unfortunately, since I only had *sepiums* in 1969 and *bicolors* in 1970 no interactions between these species could be attempted.

It must be remembered that this interspecific 'dominance' is not the same thing as the intraspecific dominance which was discussed in the Introduction (page12). It would be interesting to investigate the relation between the two – for example to discover whether the *bicolors* which inhibited *roeseliis*, and the *brachypteras* which were not inhibited, contained a greater proportion of 'leaders' than the others.

Effects of Previous Caging

As stated in the Introduction (page11), Alexander (1961) found that a male cricket was more likely to win a fight with a male of the same species if it had been caged alone for some time previously. Leroy (1966) also found that crowding tended to reduce the aggressivity of crickets. It would follow that, if the same rule holds for *Metrioptera*, and if these factors can be shown to affect an individual's success in an interspecific interaction, some evidence will have been produced suggesting that intraspecific and interspecific dominance are related attributes. In studying *bicolor* I first caged individuals in male groups prior to experimentation, and later alone prior to experimentation. The ratio number of *bicolors* inhibited: number of tolerations: number of roeseliis inhibited was however rather similar for the two categories (5:5:2 and 9:8:2 respectively).

Alexander also found that an individual's success was increased if it had copulated shortly before the conflict. The bicolors were caged with females for some time before testing, and copulations occurred, although no attempt was made to measure the time passed between copulation and conflict. The ratio for this category was 5:10:3. The figures are small, but there is obviously a greater proportion of more successful insects. It would be unwise to draw conclusions before confirming with bicolor Alexander's observations on the influence of copulation on cricket behaviour. Jacobs (1955) found that male Plathemis dragonflies became less active and were easily driven away by other males, after having mated 20 or more times. If this tendency also appears in Metrioptera, there will probably be an optimal frequency of copulation to produce the greatest leadership ability in each individual.

When returned to male groups the increased 'singing potential' of the bicolors remained high (ratio 2:12:3). Thus the total result for males initially caged with other males or alone is 14:13:4, whilst that for males caged with females or subsequently with other males is 7:22:6.

No investigations of this kind were made with brachyptera, but some of the roeseliis used were caged in male groups and others alone. This did not appear to produce any change in their interaction behaviour.

Effects of Temperature

If the experiments with *brachyptera* given in the interaction summary tables are regrouped according to the temperatures at which they took place, the following distinction may be seen:

roeselii/brachyptera	Inhibition of *brachyptera*	Toleration
21 degrees and above	5	9
below 21 degrees	12	1
bicolor/brachyptera		
29 degrees and above	5	6
below 29 degrees	9	1

In both cases it is seen that toleration is rare in the lower temperature bracket, and inhibition usual. This suggests that above a certain temperature the song of *brachyptera* is produced at a rate too high for it to be easily inhibited, and toleration is therefore more likely to occur. This temperature however is higher when the inhibitor is *bicolor* than when it is *roeselii*, in spite of the fact that *roeselii* appears to be the more effective inhibitor. I can find no way to reconcile this observation with the conclusions previously drawn regarding the three species, and I think it best to suspend judgement until more results are available.

With regard to the *roeselii/bicolor* interaction, there does not appear to be any significant change in the kind of result according to the temperature of the experiment.

Distinction of M. *roeselii* var. *diluta*

A comparison of the number of inhibitions achieved by normal roeseliis with that achieved by the two diluta individuals shows a more formidable inhibiting power possessed by the latter:

	normal roeseliis		diluta roeseliis	
	brachyptera or bicolor inhibitions	tolerations	brachyptera or bicolor inhibitions	tolerations
against brachyptera	8	2	9	8
against bicolor	9	13	12	22
Total	17	15	21	30

	roeselii inhibitions	diluta inhibitions
against bicolor	6	4

If the temperature analysis of the roeselii/brachyptera interactions is further divided, according to whether normal roeseliis or dilutas were used, it is found that three of the five inhibitions occurring above 21 degrees are due to diluta, whilst only five of the twelve occurring below 21 degrees are. There were no tolerations of diluta below 21 degrees: the two which did occur were at 24 and 27 degrees. It might seem likely that the greater tegminal area in diluta leads to a louder song and that this is more efficacious in producing inhibition, but in the one case where intensity was able to be measured, the roeselii's song was found to be louder than the dilutas. This may however not be the general rule.

Table 8 - Behavioural Tendencies

Effect	roeselii/ brachyptera		roeselii/bicolor			bicolor/ brachyptera	
	inhib.	tol.	bicolor inhib.	tol.	roeselii inhib.	inhib.	tol.
Influencing insect							
attracted	2			5		4	2
attracted, then repelled			1	1			2
repelled			1	4	1		
Influenced insect							
attracted	3		3	1	1		
attracted, then repelled			2	5		3	
repelled	1			2	1		
Both insects							
attracted	2		1	1		1	
attracted and repelled			1	3	1		
repelled				1			
Neither insect shows marked behaviour	9	10	12	12	6	6	3
Total	17	10	21	35	10	14	7

(b) Behaviour accompanying Interactions

Behavioural Tendencies Table

Table 8 (page 173) summarizes locomotor tendencies – movement by one insect towards or away from the other. Only the interactions included in tables 5–7 have been considered. The terms 'influencing insect' and 'influenced insect' refer to the interspecific hierarchy shown on page 165. Whatever the outcome of an interaction, the insect belonging to the species which is higher in the hierarchy is termed the 'influencing insect' and that belonging to the lower species the 'influenced insect'.

There is no simple criterion of 'attraction'. If the second insect which was put into the cage walked in a straight line towards the other for several inches and stopped when close, it was considered to be 'attracted". It was usual for it to be put in at a point as far as possible from the other, so as to avoid mechanical disturbance of the other. Therefore almost any movements it made would bring it closer. In practice, however, I had little difficulty in deciding that in some cases "attraction" or 'repulsion' were taking place, as opposed to what I regarded as 'apparently random movements".

Comments on Table 8

The figures in the table are obviously too small to be proportionally meaningful but two things may be noted. Firstly, in roeselii/brachyptera and bicolor/brachyptera interactions the influencing insect was hardly ever repelled, whereas in bicolor/roeselii ones it often was. I think this supports the conclusion that the former interactions are less 'equal' than the latter. Secondly, the more involved types of behaviour ('Both insects attracted and repelled') occurred only with roeselii/bicolor combinations, particularly those leading to toleration, and I conclude that in these more equal contests the attracting and repelling tendencies present in both partners were able to emerge at different times.

Significance of Interaction Behaviour

To try to understand the significance of this interspecific behaviour I shall compare it with the intraspecific behaviour of roeselii treated earlier (pages 47-53). It was suggested (page 55) that this itself is related to courtship behaviour in the Tettigonioidea. However, courtship behaviour is much more uniform than interspecific interaction behaviour. In courtship, the female is attracted towards the singing male; in interspecific interaction either male may be attracted towards the other. In this respect, therefore, it cannot be said that one insect corresponds to the male and the other to the female. In courtship, bending movements of the abdomen may be made by either male or female, but they are much commoner in the male. Either insect may taste the dorsal abdominal surface of the other (see page 58), but it is far commoner for the female to taste the male's back than the other way about. In the intraspecific behaviour of males, it was the dominant insect that made abdominal bending movements and exposed his abdomen for the other to taste. It may be concluded that the dominant insect takes the part of the male and that the other insect is attracted towards him in the same way as a female would be. In comparing this with the three main types of interspecific interaction, I shall take them separately:

i) roeselii/brachyptera

The behaviour in these interactions is far less uniform than that seen between roeselii males. Only in one case, the third brachyptera (4) interaction, is to be seen anything resembling courtship: the diluta tries to climb on to the back of the brachyptera (page 74). This would make the diluta correspond to the female and the brachyptera to the male. The diluta is here the influencing insect: it eventually inhibited the brachyptera. As we have said that the dominant insect in intraspecific interactions corresponds to the male in courtship there is clearly an inconsistency: either the 'male' and 'female' roles do not correspond in the two kinds of interaction, or else the roles of influencing and dominant insect do not correspond.

Generally speaking, roeselii/brachyptera interactions involve very little physical contact and no 'bloodless battles' of the type usually observed in roeselii intraspecific male interactions. It has of course been noted that brachyptera was not seen to exhibit much antagonism in its own intraspecific behaviour (see page 54).

ii) roeselii/bicolor

Here an even greater range of behaviour is manifest. In the majority of cases very little takes place: for example antennation of one insect by the other. Short 'squirting' noises such as those emitted by the diluta in the second brachyptera (13) interaction (page 80) or by sepium and bicolor in their intraspecific behaviour were produced in two cases by roeseliis and in two cases by bicolors. In two cases a bicolor repelled a roeselii which had been attracted to it, by kicking with the hind leg (this is a standard defensive movement in tettigoniids). In one case a roeselii got so close to a bicolor that its wings touched it: this gave the appearance of courtship. In another case the roeselii climbed on to the back of the bicolor. The first of these interactions was inconclusive and the second (the tenth bicolor (6) interaction, page 134) led to toleration.

Only in a single instance out of the roeselii/bicolor interactions, the second bicolor (7) interaction (pages 135-6), did tasting of the curved abdomen occur: the roeselii curved its abdomen and the bicolor tasted the back of it. The result of the experiment was a state of toleration after bicolor had leapt one foot away. The 'male/female' correspondence accords with that found in the intraspecific interactions, but not with that found in the roeselii/brachyptera interaction.

iii) bicolor/brachyptera

Here again mutual antennation is common and bicolors have been heard to produce 'squirts', in one case silencing the brachyptera with them. The most interesting behaviour accompanied the interaction of bicolor (8) and brachyptera (13) (page 152). In this case it was extremely evident that a copulatory position was being attempted, with brachyptera taking the male position and bicolor the female one. Both insects appeared to be striving to achieve the position and there was very little singing by the bicolor. Metrioptera females of course do not sing, but any conclusion that this is why the bicolor was so quiet would be highly speculative. It is true that the dominant males in intraspecific interactions, which appear to correspond to courting males, do most or all of the singing, but in some of the interspecific experiments considered above, the insect playing the 'female' role has been quite as vociferous as the other. The appropriation of male and female roles corresponds to that in the roeselii/brachyptera interaction but not to that in the other interactions.

It is clear that both interspecific and intraspecific interactions are to an extent related to courtship behaviour, but the rarity of convincing courtship-like behaviour (only four cases out of over 128 experiments) makes one wary of formulating rules. There is clearly much scope for research, e.g. with castrated males, in this field.

(c) Acoustic Phenomena

Cessation of Song

One of the clearest tendencies seen in the histograms is that of brachyptera to arrest its song when that of roeselii or bicolor begins, and to resume when they end. It is therefore usual for the last chirps produced by the brachyptera, before it is totally inhibited, to appear during an interval between sequences from the influencing insect. The re-entry of the latter's song silences it at once. By contrast, bicolor usually appears to continue singing through a roeselii sequence until it can 'hold out no longer', whereupon it stops. It may in fact temporarily increase its song output during roeselii periods as in histograms 14-17. It seems that in these cases an excitatory as well as an inhibitory influence is exerted, but that the latter finally triumphs. As there was no movement in these cases, this cannot be correlated with attraction to and repulsion from roeselii. Jones (1966b, Ph. D thesis 1966) refers to antagonistic excitatory and inhibitory influences resulting in an overall increase in Pholidoptera's chirprate during a period in which the insect is subjected to intermittent artificial signals. When the signals are actually being emitted the chirprate slows. He suggests a parallel with the antagonistic influences controlling flight activity in Aphis fabae, studied by Kennedy (1966). However, the phenomena observed here - singing in the roeselii sequences in preference to the intervals

– are quite unlike those considered by Jones. (I have been informed by Jones (personal communication, 1971) that he has encountered in *Pholidoptera* effects of total inhibition as defined above (page 64), but his published work deals with short-term inhibition only.)

The last sounds made by *roeselii* in an interaction where it is inhibited by *bicolor* tend to be during rather than between *bicolor* sequences. The same thing appears to hold true for the single *roeselii/sepium* interaction analyzed (pages 60-61). At the beginning, *sepium* behaves like *brachyptera*, cutting off its song when *roeselii* enters, but as the gaps in the *roeselii* song become fewer it appears to acquire a tolerance for *roeselii* song and there is more concurrent singing by both. Later the *sepium* sings less and less, and then stops during a *roeselii* sequence.

Resurgence

The phenomenon previously referred to as resurgence, whereby the insect that appears to have been inhibited produces a renewed bout of singing, increasing and then declining but never attaining the earlier levels, would appear to be considerably commoner in the *roeselii/ brachyptera* interactions than in the other types, but no special comments on its significance can be made.

Overall Effects on Song Structure

In the case of the inhibition of *roeselii* by *bicolor* no histograms have been constructed as there is very little variety in the data. Both insects sing almost without any halt for several minutes and then roeselii gradually sings less and less, finally stopping.

With the inhibition of bicolor by roeselii I have of course given a large number of histograms. The song of bicolor, as stated (page 22) consists of sequences of chirps. As the singer continues, the intervals between sequences become shorter and fewer. When bicolor is inhibited by roeselii, the reduction in the time its singing occupies, as shown on the histograms, results from the combination of (i) the reduced chirp rate, and (ii) the greater number and length of intervals between sequences, at any particular time, than would have been obtained had the roeselii not been present. It was not felt that any great advantage was to be gained by the separation in analysis of (i) and (ii). Doubtless it would have been possible to obtain a record of the average number, length and distribution of intervals in a collection of bicolor recordings, and to compare a similar average at the same temperature for the same insect subjected to roeselii singing, but firstly there would be an indeterminate variation due to the amount of bicolor stridulation which had occurred prior to the experiment, and secondly, as explained on page 162, the inconsistent nature of the roeselii song prevents all absolute comparisons. This type of experiment might however give good results if the roeselii were replaced with a continuous roeselii recording or an artificial signal.

With brachyptera, chirping is much more uniformly maintained:

the chirps are further apart but liable to continue for longer without a halt. When there is a halt, it often indicates that some external agency has disturbed the animal. Thus nearly all of the reduced song output in the histograms is accounted for by simple chirp rate diminution.

Effects on the Syllabic Structure of the Song

In the present work, modification of the chirp in response to the song of another species has been observed only in brachyptera, and then in only one of the 13 individuals studied. Analysis of the distribution of 2-, 3- and 4-syllable chirps in other individuals showed absolutely no correlation with the presence or absence of roeselii, or with the stage of inhibition attained. In brachyptera (15), however, a large number of polysyllabic chirps were produced in each of two interaction experiments with roeselii (see pages 80-95). These chirps were mostly produced during singing by the roeselii. One interaction led to inhibition of the brachyptera, the other to toleration. I also conducted three experiments with brachyptera (15) and bicolors (pages 154-157), one of which led to the inhibition of the brachyptera and two to toleration. It is remarkable that in these experiments every brachyptera chirp produced was trisyllabic. Previous results have suggested that from the point of view of brachyptera, inhibition by roeselii is the same as inhibition by bicolor: histograms and columns in the summary tables are fairly similar, whichever species is responsible for the inhibition. Here however there is a striking difference: only *roeselii* song produced syllable number increase. It is noteworthy that in the syllable number increase phenomenon reported in *Platycleis denticulata* by Broughton (1965), the insect producing the effect was again *roeselii*. The significance of the phenomenon is obscure and the data are scanty but as I found it in only one individual out of 13 it is possible that with *denticulata* also it may be peculiar to certain individuals only. My *brachyptera* (15) showed no structural peculiarities and its behaviour during the interactions, and the histograms obtained therefrom, appear to be altogether typical of *brachyptera*.

Broughton's work is the only available source of information on syllable number increase phenomena in interspecific interactions, with which the present study can be compared, but there do exist a number of accounts of similar effects resulting from the use of artificial signals, or from intraspecific interactions. The artificial signal work concerns the American tettigoniid *Pterophylla camellifolia* (Fabricius). Pierce (1948) studied a single male of this species and found that it would alternate with sounds made by his assistant in imitation of its own song. 'By treating him kindly (by administrations of food) and unpleasantly (by a series of yells), we succeeded in causing him to make 3, 4 or 5 of his pulses, corresponding more or less accurately to 3, 4 or 5 squawks made by my assistant. This operation proved conclusively...that he could to some degree count and follow, at his own pitch, a series of discrete shouts made by a human, with widely different pitches and quality.' A second male of the same species was studied by Alexander (1960), who found that it could be stimulated to sing by tapping a typewriter. It normally emitted 'two-pulse phrases' but could be made to produce 'three-pulse phrases' and on one occasion 'four-pulse phrases' by using the typewriter to make 'phrases' of three or four taps. When the typewriter was tapped fast for a time, song production was inhibited. Alexander states that if it had been tapped continuously for sufficiently long, the insect would presumably not have sung at all afterwards. This state of affairs would appear to resemble my 'total inhibition'.

Shaw (1966) continued the study of this species and found that a male producing 'two-pulse phrases' changed to producing threes after being caged for a time near another male which was producing threes. This result resembles an intraspecific interaction observed by Faggetter (personal communication, 1971) in Platycleis sabulosa. A male producing 8-syllable chirps was resting close to a second male producing 6-syllable chirps. (Most of the singing of this species consists of chirps of from 5 to 8 syllables). The first male suddenly emitted a 9-syllable chirp, and then a series with gradually increasing numbers of syllables, culminating in a 21-syllable chirp. As the second individual was actually producing chirps of a lower syllable count than those of the first, the concept of 'imitation' (Pierce's term) would appear to be ruled out here. A closer parallel might be drawn with the production of long chirps studied by Jones (1966a) in Pholidoptera griseoaptera. Members of this species frequently increase the length and syllable content of their chirps when alternating in close proximity, and it has been thought of as a sort of aggression. The associated behaviour is also aggressive. Jones found that when a griseoaptera was moved closer to another with which it was alternating, long chirp production was sometimes initiated. However, this type of song has never in my experience been encountered with alternating brachypteras.

Morris (1970) studied the Canadian Metrioptera sphagnorum, which has two 'stridulation modes'. Mode I is intense and has an ultrasonic-dominated spectrum; mode II is less intense and has an audio-dominated spectrum. Morris states that 'On several occasions in the laboratory when a singer was approached within a few inches by a silent conspecific male, stridulation mode II was prolonged apparently in response to the approaching individual. The silent male then withdrew and the singer reverted to the normal cycle without ever having ceased to stridulate'. Each mode involves the alternation of two types of 'pulse train', long- and short-duration. The structure of the short-duration train is unresolved, but the long-duration one consists of 4 or 5 'pulses' in stridulation mode I, and over 40 in stridulation mode II. If these 'pulses' correspond to our 'syllables', then there is a clear parallel with the phenomena observed by Faggetter and Jones. It is of particular interest to note that the amplitude is decreased, rather than increased, as one might expect, in the aggressive song. The significant attribute of aggression would appear to be syllable (or 'pulse') number increase.

There is therefore a similarity between the behaviour of my *brachyptera*, or Broughton's *denticulata*, in interspecific interactions, and that of certain other species in intraspecific interactions. I have never observed the production of polysyllabic *brachyptera* chirps in intraspecific interactions. My experience of *denticulata* is limited, but I understand that it exhibits no unusual acoustic behaviour in intraspecific interactions either (Broughton: personal communication 1971). It is possible to make speculations, to suggest that perhaps the ancestors of *brachyptera* and *denticulata* produced aggressive songs in response to the songs of conspecifics and that this faculty has now been largely lost and only appears in some individuals when they are exposed to especially 'penetrating' influences, such as *roeselii* song. But there is no real evidence.It is certainly easier to credit the animals with 'aggression' than with 'learning'. A third hypothesis was made by Broughton, who suggested that the *roeselii* song was interfering with the stridulation feedback mechanism in the inhibited insect. However, work by Huber and his associates (personal communication, 1970) throws doubt on the existence of feedback mechanisms: a strain of crickets whose tegmina were too small to meet, and which were therefore incapable of sound production, continued to make movements of the tegmina which would have given rise to normal regular chirping were the tegmina sufficiently large.

If Broughton's hypothesis is correct there is an immediate conclusion as concerns brachyptera (15), viz. that there is a certain threshold beyond which a signal will interfere with the feedback mechanism. It would seem that the song of roeselii passes this threshold whilst that of bicolor does not. What are the significant differences between the songs in this context? Amplitude is unlikely to be important. Possibly roeselii tends to be louder than bicolor, but brachyptera (15) was affected by roeseliis at a distance of 1-1½ feet and not by bicolor(9) at 3-6 inches or bicolor (2) at 9 inches. My suspicion is that the important difference is the more discrete nature of the bicolor song. I mentioned earlier (page 161) that if given occasional brief silences at the right time a brachyptera can maintain its singing for far longer than it otherwise would. It may follow from this that because a second of bicolor stridulation contains more milliseconds of silence than a second of roeselii song, the former is a less effective inhibitor than the latter, and at the same time a less potent source of interference in feedback mechanisms.

I am more inclined to favour Broughton's feedback hypothesis than the aggression hypothesis, although it is conceivable that both could share responsibility for the effect. This is because no aggressive behaviour was seen to accompany the syllable number increase phenomena. Neither insect made any special movements towards or away from the other, and brachyptera's increased syllable production did not appear to affect roeselii's singing. Admittedly in the second roeselii/brachyptera interaction, the roeselii song became very particulate after a time, and the brachyptera was never inhibited, but the roeselii continued to sing like this long after the brachyptera had stopped producing polysyllabic chirps. It is not impossible that the brachyptera could have produced a persisting effect on the roeselii, but I consider that it is extremely unlikely.

3. Biological Significance of Interaction

Individual Significance

The real significance of interspecific interaction, such as occurs between roeselii and bicolor in the field at Weiler, is not understood, but it is probably related functionally to intraspecific interaction. Both types of situation lead to the same result: one insect retains its position and continues to sing whilst the other becomes silent for a time and may leave the area. This is obviously a greater advantage for the former when the defeated insect belongs to the same species and might be a competitor for a nearby female, but it is also an advantage when the defeated insect was merely making it harder for the other's song to be heard. I never observed interspecific heterosexual attraction in Metrioptera.

Interaction phenomena appear to maintain hierarchies and territories. These phenomena have been extensively studied amongst vertebrates, but they remain generally obscure as regards invertebrates and it is not advisable to make assumptions about invertebrate hierarchy and territoriality on the basis of vertebrate behaviour. There are only a few examples which can be quoted from the invertebrates for comparison. Alexander (1961), discussing cricket hierarchies, paralleled the behaviour of Polistes wasps, crayfish, and the fiddler crab Uca. The latter was instanced also by Moore (1952) as a case of territoriality: he further mentioned the carrion beetle Necrophorus as exhibiting clear territories. Lin (1963) studied the cicada killer wasp Sphecius and found that the males set up territories around their holes and will even defend them against thrown pebbles. Territoriality is also a marked feature of the life of social insects. None of these examples, however, seem to resemble the bushcricket situation very closely. The most useful comparison would probably be with the territoriality of dragonflies.

The territories of both bushcrickets and dragonflies seem to be very ephemeral and in continuous flux, partly because the insects do not have any kind of nest or burrow around which a territory can centre. St Quentin (1934) decided that dragonfly territories had no reproductive significance and functioned solely as hunting grounds. Jacobs (1955) believed that they prevented disturbance of courtship and egglaying. Moore (1952) stated that, because they do not remain in an area for long enough, 'dragonflies do not possess territories in any accepted sense of the word'. He drew attention to the clashes between males and said that there was no evidence that they were due primarily to aggressive behaviour, but that they might result from a failure to distinguish the sexes. There is obviously some similarity, but not a direct correspondence, between intraspecific male conflicts in dragonflies and bushcrickets. Moore, in Corbet, Longfield and Moore (1960), described experiments in which pairs of conspecific male dragonflies were brought together. With Aeshnines there was usually an immediate attempt to mate, whereas with Libellulines clashes occurred about twice as often as attempts to mate. He also brought together males of different species and found that they usually ignored one another, but that Aeshnines sometimes attempted to mate and Libellulines to clash. Here again we see a parallel with bushcricket behaviour.

Group Significance

In considering the disposition of bushcricket populations a further comparison with dragonflies may be valid. Kormondy (1961) said of dragonflies that 'territoriality deters some individuals from moving and necessitates the movements of others'. Corbet (1962) stated 'Overpopulation of the breeding site is mitigated by male interaction and by females being driven away when male competition is intense'. Corbet further cites Moore (1957) as saying that some individuals expelled in this way disperse to colonise new breeding sites. I am not trying to suggest that a bushcricket defeated in an encounter would depart to colonise a new site in the same way as the highly mobile dragonflies. A series of conflicts might however tend to drive some individuals across stretches of unattractive ground away from the population centre. Colonisation of an area by bushcrickets is slow, as Harvey (1938) showed in his successive counts of the numbers of brachyptera found on heathland which had been burnt and was being reinvaded. The invasion of all suitable areas is obviously impossible, but quite small habitats surrounded by wide bands of unsuitable terrain do get discovered. Diver and Diver (1933) studied the occurrence of brachyptera, and of Conocephalus dorsalis, in a region of marshy heathland and noted that only two small areas of rushland suitable for dorsalis were uncolonised. These were separated from the nearest populations by 400 and 500 yards respectively of plateau heath. Diver and Diver conclude that this constitutes an effective barrier. They state also that brachyptera's colonisation of a 'little grassy dip indicates that it can wander over pure heather for distances as great as 200 yards'. Payne (1957), considering Pholidoptera griseoaptera, says that it 'may occur in abundance in a bramble thicket twenty yards square, but nowhere else for a mile or so.'. The 'islands' of roeselii which I discovered amongst pure bicolor at Weiler, in occasional high tufts (see page 105) were also a long way from any large roeselii populations. However, in considering these cases, it must be remembered that there is no information as to whether the species has colonised a small isolated habitat or whether the population is a relic of an originally much larger one, existing at a time when the habitat was more extensive.

Generally speaking, it seems to be unusual, in Europe at any rate, for many tettigoniid species which sing at the same time to be sympatric. Vestal (1913) stated 'No two grasshopper species have identical habit-preferences'. Gause (1930) made a mathematical study of eleven acridid and four tettigoniid species and found that the ecological plasticity was greater among the acridids ($\sigma = 1.31$) than among the tettigoniids ($\sigma = 1.15$). We are really very ignorant of the habitat requirements of bushcrickets. Strohecker (1937) measured six factors in trying to assess orthopteran habitats: i) evaporation, ii) soil moisture, iii) soil pH, iv) soil temperatures, v) sunlight intensities, vi) ultraviolet radiation. It is likely that all these are important.

In Sussex I find an almost universal exclusion of species from one anothers' habitats. Tettigonia viridissima occurs chiefly along a narrow coastal strip, behind which is another, less continuous, occupied by Conocephalus discolor. At one point on the coast Tettigonia is replaced by Platycleis denticulata. In marshy places C. dorsalis is common, and the others absent. (Further North it can overlap with brachyptera, which occurs on the heathland of Ashdown Forest). I know of a small area of downland where the only bushcricket to be found is Decticus verrucivorus. In oaktrees inland one finds Meconema thalassinum.

On the continent also, mutual exclusion of tettigoniid species has been noted. M.-C. Busnel (1963) has pointed out the geographical separation of Ephippiger species in the South of France, and Dr J.C. Hartley (personal communication to S.E. Faggetter, 1971) suggests that the situation is even more precise than Busnel says, practically every hillside having its own distinct form of Ephippiger. Miss Faggetter (Ph.D thesis, 1971) has studied geographical variation in the genus Platycleis in Europe, and finds again a tendency to mutual exclusion and considerable local variation.

It is possible that acoustic factors may be important in determining this kind of separation. The effect of group singing would be, as it were, to unify the population and define its boundaries. Haskell (1958) discusses group singing and suggests that it may attract newly emerged males to the population centre, but adds that it makes it easier for birds to find their prey. Jones (1966a), however, suggests that group singing may make it harder for a predator to select an individual to attack. If this be so, a bushcricket having a great capacity to inhibit competitors would eventually become conspicuous by its acoustic isolation and therefore more liable to predation. It seems feasible that there might be a certain optimal distance between individuals which would lead to the greatest success for the population. This would be determined by what Haskell (1955) termed the champ acoustique – the area surrounding a given stridulating insect in which its stridulation is sufficiently loud to at least stimulate the receptors of another individual. Jones argues that the function of intraspecific rivalry might be to 'space out' the males, and says that this would lead to a greater probability that all the available females would be inseminated. Perhaps the conflicting forces of attraction and repulsion which have been posited (see page 179) to explain some of the observations might serve to maintain an optimal distance between individuals. Generally speaking, there appears to be more repulsion, or repulsion over a greater distance, in the interspecific interactions than in the intraspecific ones. In the latter, the defeated insect will retreat some way, then turn and come back for another attempt (see pages 49-53). In the former, the defeated insect, when it has remained for as long as it seems able to remain in the presence of the other, will usually just stop singing, and if it moves away will not usually show any tendency to return (see for example table 8, page 173). The effect of these phenomena upon a uniform mixture of two species occupying a limited area would be a tendency to split into two separate groups, one of each species. Slight differences in habitat preference would become accentuated. It seems to me probable that this is what has taken place at Weiler.

CONCLUSIONS

1. When males of different species of Metrioptera are caged together, the singing of one will tend to inhibit that of the other. Inhibition may initially take the form of slowing of the inhibited insect's song while the inhibitor sings, then of suppression of its song in those periods, and finally of complete silence extending also through gaps in the inhibitor's song. If the inhibitor's song continues for long enough, and if the inhibitor is then removed, it may be minutes or even hours before the other insect resumes singing.

2. Metrioptera roeselii and M. bicolor tend to inhibit M. brachyptera. When roeselii and bicolor are caged together either can be inhibited, but it is more frequently bicolor. A state of mutual toleration arises more commonly here than in the brachyptera interactions. At a locality in Germany, roeselii and bicolor have been observed to inhibit one another's singing under natural conditions in the field.

3. M. sepium appears to stand at the same level as bicolor in this 'interspecific hierarchy' of roeselii – bicolor – brachyptera.

4. In roeselii and sepium there is no slowing of the song while the inhibitor sings: the roeselii or sepium merely sings less and less often, and then stops.

5. In some interactions, especially roeselii/brachyptera ones, the inhibited insect often produces a 'resurgence' of song before being finally quelled.

6. M. roeselii var. diluta is usually a more effective inhibitor

than normal *roeseliis*.

7. At lower temperatures, toleration by *brachyptera* of the inhibitor's song is rare.

8. The behaviour accompanying interspecific interactions can resemble that occurring in intraspecific interactions, but aggression and homosexual courtship are rarer. In intraspecific interactions the dominated insect tends to return to the leader after being defeated; in interspecific interactions it is rare for the inhibited insect to attempt to return to the inhibitor. It is suggested that this difference may contribute to the separation of *roeselii* and *bicolor* in the German locality studied.

9. In one *brachyptera* out of 13 tested there was a tendency to produce chirps with more syllables than usual when exposed to *roeselii* song. The song of *bicolor* did not affect the *brachyptera* chirping in this way. It is considered that the difference is due to the more discrete nature of the *bicolor* song.

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BIBLIOGRAPHY

ALEXANDER, R.D. (1956) A Comparative Study of Sound Production in Insects with Special Reference to the Singing Orthoptera and Cicadidae of the Eastern United States. Ph.D. dissertation: Ohio State University.

ALEXANDER, R.D. (1957a) The Song Relationships of Four Species of Ground Crickets (Orthoptera: Gryllidae: Nemobius). Ohio Jour. Sci., 57: 153-167.

ALEXANDER, R.D. (1957b) The Taxonomy of the Field Crickets of the Eastern United States (Orthoptera: Gryllidae: Acheta). Ann. Ent. Soc. Amer., 50: 586-602.

ALEXANDER, R.D. (1960) Sound Communication in Orthoptera and Cicadidae. In Animal Sounds and Communications, ed. W.E. Lanyon and W.N. Tavolga. Symp. Amer. Inst. biol. Sci., 7: 38-92.

ALEXANDER, R.D. (1961) Aggressiveness, Territoriality and Sexual Behaviour in Field Crickets. Behaviour, 17: 130-223.

ALEXANDER, R.D. (1962) Evolutionary Change in Cricket Acoustical Communication. Evolution, 16:(4): 443-467.

ALEXANDER, R.D. (1967) Acoustical Communication in Arthropods. Ann. Rev. Ent., 12: 495-526.

BAIER, L.F. (1930) Contribution to the Physiology of the Stridulation and Hearing of Insects. Zool. Jahrb. Abt. Allg. Zool. u. Physiol., 47: 151-248.

BOLDYREV, B.T. (1928) Biological Studies on Bradyporus multituberculatus F.W. (Orth., Tettig.) Eos., 4: 13-56.

BROUGHTON, W.B. (1955) Notes sur quelques Caractères Acoustiques de Platycleis affinis Fieber (Tettigoniidae). Ann. Inst. Natl. Recherche Agron., (C), Ann. Épiphyt., Fascicule Spécial: L'Acoustique des Orthoptères: 203-247.

BROUGHTON, W.B. (1964) Method in Bioacoustic Terminology, and Glossorial Index. In Acoustic Behaviour of Animals, ed. R.-G. Busnel. Elsevier, Amsterdam. 3-24 and 824-910.

BROUGHTON, W.B. (1965) Song Learning among Grasshoppers? New Scient., 27: 338-341.

BURR, M. (1910) A Synopsis of the Orthoptera of Western Europe. Janson, London.

BURR, M. (1936) British Grasshoppers and their Allies. Janson, London.

* BUSNEL, M.-C. (1967) Rivalité Acoustique et Hiérarchie chez l'Éphippiger. Z. Vergl. Physiol., 54: 232-245.

BUSNEL, R-G. and DUMORTIER, B. (1954) Étude des Caractères du Sifflet de Galton provoquant la Phonotaxie de la Femelle d'Ephippiger bitterensis. C.R.Soc.Biol., 148: 1751.

BUSNEL, R.-G., DUMORTIER, B. and BUSNEL, M.-C. (1956[illegible]) Recherches sur le Comportement Acoustique des Éphippigères (Orthoptères, Tettigoniidae). Bull. Biol. France et Belgique, 90: 219-286.

BUSNEL, R.-G., DUMORTIER, B. and BUSNEL, M.-C! (1956[illegible]) Relations Acoustiques Interspecifiques chez les Éphippigères. Annls Epiphyt., 3: 451-469.

BUSNEL, R.-G. and LOHER, W. (1955) Recherches sur les Actions des Signaux Acoustiques Artificiels sur le Comportement de divers Acrididae males. Ann. Inst. Natl. Recherche Agron., (C), Ann. Épiphyt., Fascicule Special: L'Acoustique des Orthoptères: 365-394.

* BUSNEL, M-C. (1963) Caracterisation Acoustique de Populations d'Ephippiger Écologiquement Voisines (Orthoptères, Ephippigeridae) Ann. Epiphyties, 14: 25-34

CHAPMAN, K. (1952) Ecological Studies on Solitary Acrididae in England and South Africa. Jour. Ent. Soc. Southern Africa, Pretoria, 15: 165-203.

CHAPMAN, K.H. (1948) Roeseliana roeselii (Hagenb.) var diluta (Charp.) (Orthoptera, Tettigoniidae) at Flatford, Suffolk. Ent. month Mag., May 1948: 101.

CHOPARD, L. (1938) La Biologie des Orthopteres. Encycl. Ent. (A) Paul Lechevalier, Paris.

CHOPARD, L. (1945) La Vie des Sauterelles. Histoires Naturelles (6). Gallimard, Paris.

CHOPARD, L. (1951) Orthopteroïdes. Faune de France, 56. Paul Lechevalier, Paris.

CLARK, E.J. (1948) Studies in the Ecology of British Grasshoppers. Trans. Roy. Ent. Soc. London, 99: 173-222.

CORBET, P. (1962) A Biology of Dragonflies. Witherby, London.

CORBET, P., LONGFIELD, C. and MOORE, N.W. (1960) Dragonflies. Collins, London.

DARWIN, C. (1871) The Descent of Man and Selection in Relation to Sex. John Murray, London.

DIVER, C. and DIVER, D. (1933) Contributions towards a Survey of the Plants and Animals of South Haven Peninsula, Dorset. II, Orthoptera. J. animal Ecol., 2: 36-69.

DUMORTIER, B. (1963) Étude Expérimentale de la Valeur Interspécifique du Signal Acoustique chez les Éphippigères et Rapport avec les Problèmes d'Isolement et de Maintien de l'Espèce. Ann. Épiphyt., *14* (I): 5-23.

DUMORTIER, B. (1964) Ethological and Physiological Study of Sound Emissions in Arthropoda. In *Acoustic Behaviour of Animals*, ed. R.-G. Busnel. Elsevier, Amsterdam.583-654.

DUMORTIER, B., BRIEU, S. and PASQUINELLY, F. (1957) Facteurs Externes contrôlant le Rhythme des Périodes de Chant chez *Ephippiger ephippiger* Fiebig mâle (Orthoptère - Tettigonioidea). *C. R. Acad. Sci., Paris*, *244*: 2315-2318.

FABER, A. (1929) Die Lautäusserungen der Orthopteren (Lauterzeugung, Lautabwandlung und deren biologische Bedeutung sowie Tonapparat der Geradflügler). Vergleichende Untersuchungen I - *Zeits. Morph. Oekol. Tiere*, *13*: 745-803.

FABER, A. (1932) Die Lautäusserungen der Orthopteren II. *Ibid*, *26*: 1-93.

FABER, A. (1953) Laut- und Gebärdensprache bei Insekten Orthoptera (Geradflügler). Teil I. Vergleichende Darstellung von Ausdruckformen als Zeitgestalten und ihren Funktionen. Stuttgart.

FABRE, J.H. (1897) Souvenirs Entomologiques. Études sur l'Instinct et les Moeurs des Insectes. Sixième Série. Librairie Delagrave, Paris.

FAGGETTER, S.E. (~~1971~~) Aspects of Structural and Acoustic Taxonomy in the genus *Platycleis* (Orth., Tettigonioidea). Ph. D. thesis, University of London. (in prep.)

FREEMAN, P. (1937) New British Localities for *Metrioptera roeselii*, Hagenbach, and *Metrioptera brachyptera*, L. (Orthoptera, Tettigoniidae). *Ent. Rec.*, *49*: 34-35.

FREEMAN, P. (1938) The Distribution of *Metrioptera roeselii* Hagenb. in Essex in 1937. *Ent. Rec.*, *50*: 7-8.

FRINGS, H. and FRINGS, M. (1958) Uses of Sounds by Insects. *Ann. Rev. Ent.*, *3*: 87-106.

FULTON, B.B. (1934) Rhythm, Synchronism and Alternation in the Stridulation of Orthoptera. *Jour. Elisha Mitchell Sci. Soc.*, *50*: 263-267.

GAUSE, G.F. (1930) Studies on the Ecology of the Orthoptera. *Ecology*, *11*: 307-325.

GURNEY, A.B. (1947) A New Species of *Pristoceuthophilus* from Oregon, and Remarks on certain Special Glands of Orthoptera (Gryllacrididae, Rhaphidophorinae). *Jour. Wash. Acad. Sci.*, *37*: 430-435.

HARVEY, J.L. (1938) Preliminary Note on the Relations between Grasshoppers and the Recolonisation of denuded Heath- and Moorland Vegetation. Trans. Soc. Brit. Ent., *5*: 291-297.

HARZ, K. (1957) Die Geradflügler Mitteleuropas. Gustav Fischer, Jena.

HARZ, K. (1960) Geradflügler oder Orthopteren. Tierwelt Deutschlands, *46*. Teil. Gustav Fischer, Jena.

HASKELL, P.T. (1955) Intensité Sonore des Stridulations de quelques Orthoptères Britanniques. *Ann. Inst. Natl. Recherche Agron., (C). Ann. Épiphyt., Fascicule Spécial: L'Acoustique des Orthoptères*: 154-167.

HASKELL, P.T. (1956) Hearing in Certain Orthoptera: 2. The Nature of the Response of certain Receptors to Natural and

Imitation Stridulation. J. exp. Biol., 33: 767-776.

HASKELL, P.T. (1957) Stridulation and Associated Behaviour in Certain Orthoptera. I: Analysis of the Stridulation of, and Behaviour between, Males. Br. J. Anim. Behav., 5: 139-148.

HASKELL, P.T. (1958) The Relation of Stridulation Behaviour to Ecology in Certain Grasshoppers. Insectes Sociaux, 5: 287-298.

HASKELL, P.T. (1961) Insect Sounds. Witherby, London.

HEILIGENBERG, W. (1966) The Stimulation of Territorial Singing in House Crickets (Acheta domesticus). Z. vergl. Physiol., 53: 114-129.

HEILIGENBERG, W. (1969) The Effect of Stimulus Chirps on a Cricket's Chirping (Acheta domesticus). Z. vergl. Physiol., 65: 70-97.

HOWSE, P.E., LEWIS, D.B. and PYE, J.D. (1971a) Adequate Stimulus of the Insect Tympanic Organ. Experientia, 27: 598-600.

HOWSE, P.E., LEWIS, D.B. and PYE, J.D. (1971b) Sound Reception in the Bush Cricket Metrioptera brachyptera (L.) (Orthoptera, Tettigonioidea). J. exp. Biol., 55: 241-251.

JACOBS, M.E. (1955) Studies on Territorialism and Sexual Selection in Dragonflies. Ecology, 36: 566-586.

JACOBS, W. (1953) Verhaltensbiologische Studien an Feldheuschrecken. Z. f. Tierpsychol., Beiheft I.

JONES, M.D.R. (1963) Sound Signals and Alternation Behaviour in Pholidoptera. Nature, 199: 928-929.

JONES, M.D.R. (1964) Inhibition and Excitation in the Acoustic Behaviour of Pholidoptera. Nature, 203: 322-323.

JONES, M.D.R. (1966a) The Acoustic Behaviour of the Bush Cricket *Pholidoptera griseoaptera*. 1: Alternation, Synchronism and Rivalry between Males. *J. exp. Biol.*, *45*: 15-30.

JONES, M.D.R. (1966b): The Acoustic Behaviour of the Bush Cricket *Pholidoptera griseoaptera*. 2: Interaction with Artificial Sound Signals. *J. exp. Biol.*, *45*: 31-44.

JONES, M.D.R., (1966c) Studies on the Acoustic Behaviour of *Pholidoptera griseoaptera* (Degeer), with some account of other Species of Tettigonioidea. Ph.D. thesis, University of London.

KATO, M. and HAYASAKA, K. (1958) Notes on the Dominance Order in Experimental Populations of Crickets. *Ecol. Rev.*, *14*: 311-315.

KENNEDY, J.S.(1966) The Balance between Antagonistic Induction and Depression of Flight Activity in *Aphis fabae* Scolopoli. *J. exp. Biol.*, *45*: 215-228.

KHALIFA, A. (1950) Sexual Behaviour in *Gryllus domesticus* L. *Behaviour*, *2*: 264-274.

KORMONDY, E.J. (1961) Territoriality and Dispersal in Dragonflies (Odonata). *J. N. York ent. Soc.*, *69*: 42-52.

KUTCH, W. and HUBER, F. (1970) Zentrale versus periphere Kontrolle des Gesanges von Grillen (*Gryllus campestris*). *Z. vergl. Physiol.*, *67*: 140-159.

LEROY, Y. (1966) Signaux Acoustiques, Comportement et Systématique de quelques Espèces de Gryllides (Orthoptères, Ensifères). Thèses présentees à la Faculté des Sciences de l'Université de Paris. P. Fanlac, Périgueux.

LEWIS, D.B., HOWSE, P.E. and PYE, J.D. (1971) – see under HOWSE.

LIN, N. (1963) Territorial Behaviour in the Cicada Killer Wasp

Sphecius speciosus (Drury) (Hymenoptera: Sphecidae). Behaviour, 20: 115-133.

LUCAS, W.J. (1920) A Monograph of the British Orthoptera. Ray Society, London.

LUTZ, F.E. (1926) Insect Sounds. Bull. Am. Mus. Nat. Hist., 50: 333-372.

LUTZ, F.E. (1932) Experiments with Orthoptera concerning Diurnal Rhythm. Amer. Mus. Novitates, 550: 1-24.

MICHELSEN, A. (1971) The Physiology of the Locust Ear. Z. vergl. Physiol., 71: 49-128.

MOORE, N.W. (1952) On the So-called 'Territories' of Dragonflies (Odonata - Anisoptera). Behaviour, 4: 85-100.

MOORE, N.W. (1957) Territory in Dragonflies and Birds. Bird Study, 4: 125-130.

MORRIS, G.K. (1970) Sound Analyses of Metrioptera sphagnorum (Orthoptera: Tettigoniidae). Can. Ent., 102: 363-368.

NIELSEN, E.T. (1971) Stridulatory Activity of Eugaster (Orthoptera Ensifera). Ent. exp. et appl.(in press).

NIELSEN, E.T. ~~et al.~~ and DREISIG, H. (1970) The Behaviour of Stridulation in Orthoptera Ensifera. Behaviour, 37: 205-252.

OTTE, D. (1970) A Comparative Study of Communicative Behaviour in Grasshoppers. Miscellaneous Publications, Museum of Zoology, University of Michigan, 141.

PAYNE, R.M. (1957) The Distribution of Grasshoppers and Allied Insects in the London Area. Lond. Nat., 37: 102-115.

PERDECK, A.C. (1957) The Isolating Value of Specific Song

Patterns in Two Sibling Species of Grasshoppers. Behaviour, 12: I.

PIERCE, G.W. (1948) The Songs of Insects. Harvard University Press.

PUMPHREY, R.J. (1951) The Origin of Language: an Inaugural Lecture. Liverpool University Press.

RAGGE, D.R. (1965) Grasshoppers, Crickets and Cockroaches of the British Isles. Warne, London.

RAMME, W. (1931) Verlust oder Herabsetzung der Fruchtbarkeit bei macropteren Individuen sonst brachypterer Orthopterenarten. Biol. Zentralbl., 51: 533-540.

RAMME, W. (1936) Sonderdruck aus 'Märkische Tierwelt' Bd I, Heft 3, Berlin. 224-233.

REGEN, J. (1926) Über die Beeinflussung der Stridulation von Thamnotrizon apterus Fab. (Männchen) durch kunstlich erzeugte Tone und verschiedenartige Gerausche. Sber. Akad. Wiss. Wien, 135: 329-368.

RICHARDS, O.W. (1927) Sexual Selection and Allied Problems in the Insects. Biological Reviews, vol. II, 4.

RICHARDS, O.W. and WALOFF, N. (1954) Studies on the Biology and Population Dynamics of British Grasshoppers. Anti-Locust Bulletin, 17.

ST QUENTIN, D. (1934) Beobachtungen und Versuche an Libellen in ihren Jagdrevieren. Konowia, 13: 275-282.

SCUDDER, S.H. (1892) The Songs of our Grasshoppers and Crickets. Rep. ent. Soc. Ont., 23: 62-78.

SHAW, K.C. (1966) An Analysis of the Phonoresponse of Males of the True Katydid, Pterophylla camellifolia (Fabricius) (Orthoptera: Tettigoniidae). Ph. D. dissertation, University of Michigan.

Quoted in 'Arthropods' by ALEXANDER, R.D., in Animal Communication, ed. SEBEOK, T.A., Indiana University Press, 1968, pp. 167-216.

SPOONER, J.D. (1968) Pair Forming Acoustic Systems of Phaneropterinae Katydids (Orthoptera: Tettigoniidae). Animal Behaviour, 16: 197-212.

STROHECKER, H.F. (1937) An Ecological Survey of some Orthoptera of the Chicago Area. Ecology, 18: 231-250.

UVAROV, B.P. (1928) Locusts and Grasshoppers. Imperial Bureau of Entomology, London.

VESTAL, A.G. (1913) Local Distribution of Grasshoppers in Relation to Plant Associations. Biol. Bull. Woods Hole, Mass., 25: 141-180.

WALKER, T.J. (1956) The Taxonomy and Calling Songs of United States Tree Crickets (Oecanthinae). Ann. ent. Soc. Amer., 49: 772-789.

WALKER, T.J. (1957) Specificity in the Response of Female Tree Crickets (Orthoptera, Gryllidae, Oecanthinae) to Calling Songs of the Males. Ann. ent. Soc. Amer., 50: 626-636.

WALKER, T.J. (1962) Factors Responsible for Intraspecific Variation in the Calling Songs of Crickets. Evolution, 16 (4): 407-428.

WEIH, A.S. (1951) Untersuchungen über das Wechselsingen (Anaphonie) und über das angeborene Lautschema einiger Feldheuschrecken. Z. f. Tierpsychol., 8: 1-41.

ZACHER, F. (1917) Die Geradflügler Deutschlands und ihre Verbreitung. Gustav Fischer, Jena.

ZIPPELIUS, H.-M. (1948) Die Paarungsbiologie einiger Orthopterenarten. Z. f. Tierpsychol., 6: 372-390.

TITLE ASPECTS OF ACOUSTIC INTERACTION IN THE BUSHCRICKET GENUS METRIOPTERA (ORTH., TETTIGONIOIDEA)

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