

FEEDING HABITS OF THE ACRIDIDAE (ORTHOPT.)

AND

FACTORS WHICH DETERMINE THEM.

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1. INTRODUCTION.

The object of the present work was to answer three questions. These were, what plants are normally eaten by grasshoppers and locusts, how are they eaten, and why are they eaten in preference to others.

During the present century, a considerable amount of work has been done on these insects. Many aspects of their morphology have been thoroughly investigated and much has been done on the biology and control of swarming locusts. Nevertheless, practically all the work on feeding has been concerned with their rate of growth on different plants rather than actual food preferences.

A certain amount has been done, in North America and Russia especially, on the plants eaten by grasshoppers. The Russian papers are all in that language and are rather inaccessible, those on the American species consist almost entirely of incomplete lists of plants consumed. The papers by Criddle (1933) and Isely (1938) are outstanding on this aspect. Langford (1930), in another American paper, dealt briefly with certain aspects of behaviour involved in this problem but made no study of sense organs. Clark's work on some aspects of the ecology of the British species, (1948), covers a wide field. His work consists entirely of field observations and there is a section dealing with food preferences.

No paper dealing with a survey of the factors and behaviour concerned in the choice of food by grasshoppers has yet been published. A few papers are available which deal with individual senses, usually as a small section in a larger paper covering a selection of insect types representing a number of orders. The present investigation is, therefore, breaking new ground on this important topic.

The insects used in this work were as many of the British grasshopper species as could be obtained, either locally in Berkshire or by travelling to known localities. After a time it was found possible to maintain stocks of certain species under laboratory conditions, throughout the year, but at the beginning of the investigation much of the preliminary work had to be done on Locusta migratoria L. and Schistocerca gregaria (Forsk) as they were the only suitable material which was available.

As far as possible, the observations made in the laboratory have been followed up by field work and vice-versa. Only twenty months were spent on experimental work and, as a result, some aspects of the problem have not been as exhaustively studied as one would wish.

2. METHODS OF REARING.

It is surprising when one considers their easy collection and identification, and their large size compared with many insects, that the Acrididae have not been more extensively studied in the past. Locusts can be successfully reared in captivity without much trouble, but grasshoppers are more difficult and require more careful treatment, which is probably one of the reasons why they have been neglected.

Young locust hoppers were kept in cages 13 inches long by 14 inches wide and 16 inches in depth. Except for the front, each was made of wood and had a perforated zinc panel let into one side. The front was of glass to allow easy observation. The floor was a sheet of metal which could be removed when cleaning out the cage. There was a door in the lid of the cage which was used to introduce food. A 40 watt electric light bulb was suspended from the middle of the lid. The floor of the cage was covered with a layer of coarse sand to a depth of about half an inch and a few branched twigs were arranged in the cage so that the insects could get as near as they wished to the source of light.

Fourth and fifth instar hoppers and adult locusts were kept in larger cages 24 inches cube. The only difference in the design was that the door was on one side, and the lid was nailed down. A 100 watt bulb was used in these cages.

All locust cages were kept in a Constant Temperature Room running at 29°C and 68-70 per cent relative humidity. The

temperature inside the small cages was increased by 4°C when the light was on and by 3°C in the larger cages. The humidity obviously was temporarily raised when fresh food was introduced and was less constant than the temperature.

Food was provided twice each day, usually Holcus mollis L. as this was easily obtained and was readily eaten. The grass-tufts were placed in water to keep them fresh for as long as possible.

Young grasshoppers were usually kept in cylindrical celluloid cages with a metal base and a perforated detachable lid. These cages were 15 inches deep and had a diameter of 8 inches. A 25 watt electric light bulb was suspended from the lid. Large nymphs and adults were kept in small locust cages. All grasshoppers were kept in the laboratory, the temperature inside the cages being about 4°C above that of the room which was usually around 20°C . Food was given once a day.

It was found that by switching off the light for 12 hours on alternate nights, the length of life of the insects was increased, although the rate of development remained the same. While the light was on, the grasshoppers tended to move around, whereas they settled down and rested while in darkness.

Normally, it was not found necessary to provide water except when the insects were being starved for experimental purposes. The surface of the grass was often slightly moist with dew when it was collected in the early morning and, Holcus

mollis L., the grass usually given, is rather a succulent species. Very wet grass was never given as it was found that excessive moisture frequently caused an epidemic of an enteric disease which resulted in a high mortality among the stock. Locusts were more susceptible than grasshoppers to this, but rain-soaked grass was always kept until dry before it was placed in the cages.

Nine of the ten British Acrididae have been collected as adults from the fields and kept for a number of weeks in the laboratory. Only Chorthippis vagans (Fieb.) has not been subjected to laboratory conditions in connection with the present work. Adults collected in the field will often survive in the laboratory long after all the individuals out of doors have died. This is particularly true of the late species Chorthippus bicolor (Charp) and Gomphocerippus rufus (L).

The six species, Chorthippus bicolor, C. parallelus (Zett.), C. albomarginatus (De Geer), Gomphocerippus rufus, Myrmeleotettix maculatus (Thunberg) and Omocestus ventralis (Zett.) all laid egg-pods freely in the half an inch layer of dry coarse sand on the floor of the cages. The pods were usually deposited in the corners of the cages or near the base of the twigs, but sometimes they were laid in the loose sand. The following figures give an indication of the readiness with which pods were laid. Fifty-three females of Chorthippus albomarginatus which were collected at Walberswick, Suffolk, on August 4th 1951, deposited a total of 463 pods, an average of 8.7 pods/female. The

last adult died on October 18th, but as several died within a few days of collection, probably because of injuries received in transit, some females may have deposited as many as a dozen pods in captivity. From the date of collection, it is probable that a few pods had already been laid when the insects were collected. In several species, among them Chorthippus albomarginatus and Myrmeleotettix maculatus, the first laid pods are always the largest and may contain the maximum of 10 eggs, those laid towards the end of adult life are often small, contain only 2 or 3 eggs, and are imperfectly formed. In other species, among them Gomphocerippus rufus and Omocestus ventralis, the size of the pods does not diminish with the age of the female.

Mecostethus grossus (L.), Omocestus viridulus (L.) and Stenobothrus lineatus (Panzer) deposit their pods at the base of tufts of grass. To obtain pods from these species it was necessary to provide whole plants of grass. When the plants were subsequently pulled to pieces, the egg pods were found adhering to the leaf sheaths at soil level right in the heart of the tussocks. It is more difficult to induce oviposition in these species and only a few pods were obtained.

Individual females were observed to copulate as many as four times during adult life in the cages. For an experiment, all the males were removed from a cage of Chorthippus parallelus for a period of 8 days. After the experiment they were replaced and it was noticed that of the fourteen, nine were in copulation within ten minutes and

twelve within half an hour. It is very remarkable that pairs in copulation are so rarely observed in the field. Oviposition is still more rarely seen out of doors, it was seen only twice during about 200 hours spent in watching grasshoppers in their natural habitats.

Holes were made in the floor of the locust cages. Under these were placed jars containing damp sand in which the female locusts oviposited freely.

The egg pods were stored in layers in containers of damp sand. When a new stock of hoppers was required, locust pods were removed and placed in the Hatching Room at a temperature of 29°C and about 70% relative humidity. In connection with her work on Acrididae, Dr. N. Waloff found it possible to break the diapause of grass-hopper egg-pods by subjecting them to a low temperature for about five weeks. This technique was used here. The pods were placed in shallow petri-dishes and left in a refrigerator at 0°C for a minimum of five weeks, after which they were transferred to the hatching room. Here they were arranged on a layer of damp sand on a tray and each pod was covered with a 3 X 1 inch specimen tube. The sand was kept moist. Hatching usually began on the tenth day and continued for about five days. Some pods hatched before others, and there was often three days difference between eggs from one pod. This treatment was found to be very successful and resulted in about 95% of the pods hatching. In the first season, a batch of grasshopper pods was successfully

forced at Christmas. By carefully staggering emergence, it was found possible to have grasshoppers in any month of the year from that time onwards.

Although the percentage hatching of the pods was the same for every species, there was considerable difference in the subsequent survival of the young nymphs. The species which thrived the best were Chorthippus albomarginatus (c. 60% survival) C. bicolor (c.40%) and Gomphocerippus rufus (c.50%), whilst Omocestus viridulus and Chorthippus parallelus were less satisfactory (10-20%). Omocestus ventralis nymphs grew very slowly, taking nine weeks to reach the adult stage instead of the usual five and the mortality rate in all instars was very high. (Total survival c.5%). From the behaviour of this species in the cages it is thought that it required more shade than was provided. This may also account for the poor survival rate of O.viridulus and C.parallelus. On the other hand, this would seem to be unlikely in the case of Myrmelotettix maculatus, a species which frequents dry pastures with considerable bare patches of soil where it can sun itself, but every nymph from a batch of more than 200 which was hatched, died in the first two instars. No Stenobothrus lineatus were reared to the adult stage but as only a few egg pods were available this does not necessarily indicate that this species is as difficult to rear under these conditions as M.maculatus.

Only 2 pods of Mecostethus grossus were obtained and they became too dry in storage, despite the precautions taken, so that the eggs which they contained all shrivelled up.

Thus, compared with Locusta migratoria in which the rate of survival is usually about 95%, grasshoppers are more difficult to breed from the egg in the laboratory under similar conditions, but reasonable success can be obtained with some species. As these can be reared under laboratory conditions during the winter months by artificially breaking the diapause, research work need not be hampered by the great disadvantage of the short duration in the summer when adult grasshoppers are available out of doors.

3. THE RANGE OF PLANTS EATEN.

a) Summary of Previous Work.

For a long time it was generally believed that locusts and grasshoppers are omnivorous feeders. Uvarov (1928) pointed out that various species exhibit a different range of food plants, some species being more restricted than others. Isely (1938) showed that the majority of the species which he studied were oligophagous rather than polyphagous. Acrididae, therefore, are selective feeders although some species have much wider tastes than others. Monophagous species are rare. Uvarov cites the Caspian grasshopper, Derycoris tibialis Pall., as feeding throughout its life on Anabasis aphylla, a thick-leaved halophilous plant.

The three big sub-families of Acrididae exhibit different ranges of food selection. From the work of Criddle (1933) and Isely, on the North American grasshopper fauna, it appears that the Acridinae are, with few exceptions, grass feeders. Boottettix argentatus Bruner is always found in close association with Larrea tridentata, and Acrolophitus hirtipes (Say.) is said to subsist almost exclusively on members of the family Boraginaceae, showing a preference for Lithospermum angustifolium although also eating some allied plants. Criddle states that when this species was tested with more than 100 other plants of different families, only Phacelia campanularia proved to be in any way acceptable to it.

The second major sub-family, the Oedipodinae, have more varied tastes. Some feed on grasses, some on broad-leaved plants generally or specifically, and a large number are mixed feeders, feeding perhaps mainly on grasses, but including a number of herbs also, in their normal diet.

The third group, the Catantopinae, contains a high percentage of herbivorous species. The majority are mixed feeders and only a very few select grasses exclusively. The three common North American species of the genus Melanoplus, M. mexicanus (Saus.) M. bivittatus (Say.) and M. femur-rubrum (De.G.) feed on a very wide range of food plants, and have even been recorded as feeding on Poplar trees resulting in defoliation. (In this respect, however, Uvarov draws attention to the need for great caution when examining the records of feeding. Locusta migratoria (Oedipodinae) swarms often settle on trees when seeking water, and nibble the leaf-stalks so that the leaves fall to the ground but are not eaten.) A fourth species of Melanoplus, M. bouditchianus (Hebd.) is said to feed almost entirely on Artemisia cana. Isely has drawn attention to the large number of observations which suggest that the family Compositae is specially favoured by grasshoppers of this group.

The following summaries by Criddle (1933) and Isely (1944) will make clear the differences in tastes between representatives of these three sub-families. Both are compiled from studies on North American species.

A. Criddle.

Sub-family	Grass Feeders	Sedge Feeders	Broad- leaved plant feeders	Mixed Feeders	Total
Acridinae	14	2	1	0	17
Oedipodinae	8	0	6	16	30
Catantopinae	5	0	10	15	30

B. Isely

Sub-family	Grass Feeders	Sedge Feeders	Broad- leaved plant feeders	Mixed Feeders	Total
Acridinae	20	0	3	0	23
Oedipodinae	9	0	7	8	24
Catantopinae	4	0	23	10	37

Some species have been observed to eat vegetation which is poisonous when their normal food-plants are not available. La Baume records feeding by Doclostaurus maroccanus Thub. on Peganum harmala in Turkey with fatal results.

In some species it has been noted that the number of plants used for food increases with development of the nymphs. In Transcausasia first instar hoppers of Doclostaurus maroccanus feed almost exclusively on Poa bulbosa, but with each moult the number of food plants increases. (Sviridenko, 1924).

Dr.N.Waloff, who has had first hand experience with this species, believes that the initial feeding on Poa may be due to the short duration of this ephemeral plant. Pfadt (1949) also believed this to be the reason why Aulocara ellidti (Thos.) changes its food plant from Poa secunda to Agropyron smithii after the second instar. Analogous facts were observed in Locusta migratoria by Kulagin (1922), who accounted for them by the greater development of the nerve endings associated with taste in the first two instars as compared with the later stages (Uvarov 1928).

The only previous work on the food preferences of British Acrididae is that of Clark (1948). He lists a number of plants which he observed being eaten, either in confinement or in the field. Most of his work was on calciferous ground, and, as a result, the majority of the plants included, are those normally associated with chalk and limestone pastures. His observations on feeding in the field include 216 on grasses, 8 on a Sedge (Carex flacca Schreb) and 89 on broad-leaved plants. Seven species of grasshopper were used, but most of his work appears to have been on Chorthippus parallelus, C.bicolor and Gomphocerippus rufus as 240 of the total of 313 records concern these insects. He also made a number of observations on grasshoppers confined under two-pound jam-jars, 5 under each, either in their natural habitats or in his garden. He hoped by this means to be able to decide from the order in which the plants

disappeared, the actual scale of preference for the plants. He found that a few herbs were as acceptable to the insects as the majority of grasses. These plants included Trifolium repens L., Lotus corniculatus L. and Poterium sanguisorba L.. He also found that the grass Bromus erectus Huds. and a number of herbs which were not touched as long as some other plants were present, were eaten, at least in part, as the supply of preferred vegetation became exhausted. There was also a third group of plants which remained untouched or scarcely nibbled throughout the five-day experiments.

b) Present Work.

Of the eleven species of Acrididae recorded as occurring indigenously in Britain, nine definitely belong to the sub-family Acridinae and one, Oedipoda caerulescens (L) which is said to occur on St. Mary's in the Scilly Isles, although this has not been confirmed, to the sub-family Oedipodinae. The position of Mecostethus grossus remains in some doubt, as recently it has been suggested that in some of its features it more closely resembles the Oedipodinae than the Acridinae in which it has been placed. Locusta migratoria is the only species of the Oedipodinae which has been extensively used in the present investigation, and Schistocerca gregaria is the sole representative of the Catantopinae which has been studied. Of the ten British Acridinae, all but Chorthippus vagans have received at least some attention, but Chorthippus bicolor, C.albomarginatus and Gomphocerippus rufus, being the three

species which are most easily kept in captivity, have been used most extensively.

The degree of acceptability of the plants tested was assessed in three categories only - not eaten, only nibbled, and eaten.

Field Observations. During the late summer of 1951, about 200 hours were spent in watching grasshoppers in the field. Most of this work was done on chalk pastures as was that of Clark. In not a single instance was prolonged feeding observed on any species of broad-leaved plants, although a wide variety of plants was seen to be nibbled. These plants included Poterium sanguisorba L., Lotus corniculatus L., Humex acetosella L., Cirsium acaule (L), Galium mollugo L., Asperula cynanchica L., Linum catharticum L., Veronica chamaedrys L. Origanum vulgare L. Calamintha officinalis R. and S. and the moss, Hypnum cupressiforme. In all, 21 records were made of rejection by grasshoppers after they had slightly chewed the edge of a leaf. Of these records 18 refer to Chorthippus parallelus and 3 to C. bicolor. On the other hand, these insects were observed feeding on a grass on 83 occasions. The commonest grass in the habitat was always Festuca ovina agg. on which 52 of the observations were made. The other grasses were, Agrostis vulgaris agg. (12), Holcus lanatus L. (9), Trisetum flavescens (L) 4, Dactylis glomerata L. (3) Poa trivialis L. (2) and Anthoxanthum odoratum L. (1). This order is also an approximation to the order of abundance of the individual species. Arrhenatherum elatius (L).

and Bromus erectus Huds. also occurred not uncommonly in some of the localities visited, but no observations were made of either nibbling or sustained feeding on either of these grasses.

A few experiments were carried out on grasshoppers confined in their natural habitats. The only species used in this work was Omocestus viridulus, three pairs of which were confined in the field under each cage. The cages used were of celluloid, cylindrical in shape, 12 inches high and with a diameter of 8 inches. One end was covered with muslin whilst the open end was placed over a selection of growing plants. Each sample of natural vegetation was chosen with care so as to include at least one or two herbs as well as a choice of grasses. The cages were examined every day, but after three days the vegetation under each was usually beginning to show signs of dessication by shrivelling up, and it became necessary to transfer the cage to a new position. Altogether 23 of these confined field experiments were carried out, but in not a single instance was there any evidence of proper feeding on any plant other than grasses, sedges or rushes and their allies, although signs of nibbling at the edges of the leaves of some other plants indicated attempts at feeding. This was true even when the supply of grass ran out, as was often the case on the second day of the experiment. The plants which were observed to be nibbled were - Rumex acetosella L., Veronica chamaedrys L., Cirsium arvense (L.), Lotus corniculatus L., Achillea millefolium L., (once only), Stellaria media Vill. and Polygonum aviculare L.

The first table is a summary of the results obtained.

TABLE 1.

Results of experiments in which 3 pairs of adult Omocestus viridulus were confined over growing natural vegetation to observe which plants were eaten. The figures given represent a summary of 23 experiments.

Type of Plant	No. of Species	Eaten (including nibbled)	Not eaten
Grasses	11	29	0
Sedges	2	3	0
<i>Luzula campestre</i>	1	5	0
Rushes	1	1	0
Herbs	28	13 (nibbled only)	36
Mosses	2	0	5

It is significant that signs of nibbling of broad-leaved plants did not appear until the supply of grass was almost exhausted. (A complete list of the plants used in this work and an indication of the degree to which each was eaten, is given in Appendix A.)

Laboratory Experiments on Food Selection.

(1) Choice of plants other than grasses.

As a preliminary investigation, a number of plants belonging to a wide variety of families were placed in a cage containing adults of Chorthippus albomarginatus which had

been starved for 24 hours. The insects were closely watched to ascertain their reactions to the different foods. Apart from grasses, very few plants were more than nibbled, although in one or two cases, the leaves were slightly eaten when no grasses were present. Luzula campestre (L). and a number of species of Carex appeared to be almost, if not quite, as acceptable as grass and Juncus effusus L. and J. bufonius L. the only rushes used, were also eaten in part. However, when deprived of water as well as food for 48 hours, the list of acceptable plants considerably lengthened. It was noticed that certain more succulent plants which had previously been left untouched, among them Cerastium vulgatum L., Lotus corniculatus L. and Sonchus arvensis L., or only very slightly eaten, as Rumex acetosella L., Taraxacum officinale Weber, Stellaria media Vill. and Carduus nutans L. were now readily chewed.

Chorthippus bicolor, Gomphocerippus rufus, Myrmeleotettix maculatus and Omocestus viridulus adults were given a similar choice of foods but the number of plants employed in their case was more restricted. They showed the same range of selection, choosing grasses to the exclusion of other plants except in a few instances. Locusta migratoria hoppers and adults also showed a similar selection but hoppers of Schistocerca gregaria appeared to feed as readily on a whole host of broad-leaved plants as they did on grasses. When presented with 42 plants belonging to 18 natural families, they were observed to eat

no fewer than 34 species. A few of the more bitter plants like ivy (Hedera helix L.) were rejected, but the Tomato, (Lycopersicon esculentum Hill.) was eaten freely. No attempt was made to rear this insect on a mixed diet, but these casual choice trials suggest that, under natural conditions, it is a very mixed feeder. This is the species which causes extensive defoliation and stripping bare of the vegetation when outbreaks occur in Africa and South-West Asia, and it is to a large measure responsible for widespread belief that locusts and grasshoppers will feed upon almost anything green.

As a final test of the acceptability of the herb Lotus corniculatus L. to grasshoppers, this was introduced simultaneously with the grass Holcus mollis L. into cages containing 4 species of these insects which had previously been deprived of food for 24 hours. The number of grasshoppers feeding on each plant at five-minute intervals was noted for one hour. This experiment was repeated using Thymus serpyllum agg with Holcus mollis. Similar experiments were carried out giving as the choice the two grasses Holcus mollis and Dactylis glomerata L. and the herbs Lotus corniculatus and Thymus serpyllum agg. It will be seen on inspection of Table 2, where the results are summarised, that although the same number of insects was used in each case, far more were observed feeding when 2 grasses were being tested against each other than in the instance of 2 herbs. The striking choice of Holcus over either of the broad-leaved plants leaves no doubt as to which plant is preferred.

Table 2. Summary of Experiments to test the relative acceptability of 2 grasses and 2 herbs. Each figure represents the sum of the twelve counts made at 5 minute intervals for one hour of the number of grasshoppers feeding on each heap of food.

TABLE 2.

	<i>Omocestus viridulus</i>	<i>Myrmeleotettix maculatus</i>	<i>Chorthippus bicolor</i>	<i>Stenobothrus lineatus</i>
No. of insects.	30	30	70	20
No. of Trials	63	54	132	54
<u>Lotus</u> eaten	5	9	17	1
<u>Holcus</u> eaten	58	45	115	53
Percentage on <u>Holcus</u>	92	83	87	98
No. of Trials	61	61	132	50
<u>Thymus</u> eaten	3	5	17	6
<u>Holcus</u> eaten	58	66	105	44
Percentage on <u>Holcus</u>	95	93	86	88
No. of Trials	121	83	187	74
<u>Holcus</u> eaten	70	49	80	41
<u>Dactylis</u> eaten	51	34	107	33
Percentage on <u>Holcus</u>	58	59	43	55
No. of Trials	40	57	134	37
<u>Lotus</u> eaten	19	31	38	13
<u>Thymus</u> eaten	21	26	96	24

11. Choice of grasses. As a result of introducing a variety of different kinds into the cages, it was found that most grasses are palatable to British grasshoppers and to Locusta migratoria. Forty-eight different species of grass were fed to hoppers of this insect, and of these, only six Anthoxanthum odoratum L., Arrhenatherum elatius (L), Brachypodium sylvaticum (Huds). Melica altissima, Briza minor L. and Bromus erectus Huds., were not readily eaten. All were at least slightly chewed, the Anthoxanthum, Arrhenatherum and Melica the least. Later, these same six grasses were fed to adults of Chorthippus albomarginatus but in this instance only the Arrhenatherum was rejected. Even this species was eaten by grasshoppers in field experiments when no alternative grass was available, in preference to broad-leaved plants. These grasses rejected by Locusta were specific, for, although Brachypodium sylvaticum was not eaten, B. pinnatum (L) was found to be very acceptable. The same was true of the species of Melica used, whilst M. altissima was practically untouched. M. nutans L. and M. uniflora were readily eaten.

Certain kinds of grass are preferred to others. This was shown by presenting hungry Locusta hoppers with a choice of two grasses and counting the number feeding on each at five minute intervals for a total of forty minutes. Each grass was chopped up coarsely and arranged in a heap on a piece of paper. This was to ensure that the heaps were of the same size. The pieces of paper with the grass were then placed on the floor

of the cage containing the Locusts at an equal distance from the light source. In this experiment, eight different species of grass were used and each was tested four times with each of the other seven species. In successive tests, the relative positions of the grasses were exchanged. This was to eliminate any bias to one side of the cage. A different batch of hoppers was used for each experiment. The numbers obtained for each five minute count, eight in all, were summed and a χ^2 test performed on each group of four results obtained for every possible combination of pairs. It will be seen that there were thirty-six of these pairs, each of which was tested four times.

TABLE 3A.

Summary of numerical grass preference experiments with hoppers of *Locusta migratoria*. The figures are the sum of 8 readings taken at five-minute intervals.

	<i>Arrhenatherum elatus</i>	<i>Anthoxanthum odoratum</i>	<i>Deschampsia flexuosa</i>	<i>Agropyron caninum</i>	<i>Alopecurus pratensis</i>	<i>Bromus sterilis</i>	<i>Holcus mollis</i>	<i>Festuca ovina</i>
<i>Arrhenatherum elatus</i>	35-40 76-45 60-53 54-61	16-54 26-90 68-88 95-22	72-103 60-107 63-102 42-71	13-106 25-86 46-101 35-62	44-112 63-63 46-76 17-122	48-107 13-139 64-79 43-86	23-118 36-96 33-174 41-197	43-93 34-126 29-176 16-109
<i>Anthoxanthum odoratum</i>	54-16 90-26 88-68 22-95	52-56 70-40 47-60 42-57	55-35 75-30 103-132 41-74	52-26 75-89 107-67 29-123	49-98 71-63 67-71 40-86	27-122 63-104 71-71 100-69	76-90 82-172 60-141 48-180	94-93 85-101 62-143 54-181
<i>Deschampsia flexuosa</i>	103-72 107-60 102-63 71-42	35-55 30-75 132-103 74-41	30-46 58-60 64-57 70-55	62-90 74-94 36-99 67-70	33-59 100-129 101-84 94-95	89-97 133-66 42-152 60-86	82-74 67-85 80-114 80-121	109-97 82-159 56-135 84-134
<i>Agropyron caninum</i>	103-13 86-25 101-46 62-35	26-52 89-75 67-107 123-29	90-62 94-74 99-36 70-67	58-43 70-59 48-61 52-65	54-88 91-67 44-69 87-45	47-109 64-67 46-79 60-73	56-72 50-106 52-129 80-79	43-100 54-94 50-97 51-94
<i>Alopecurus pratensis</i>	112-44 63-63 76-46 122-17	98-49 63-71 71-67 86-40	59-33 129-100 84-101 95-94	88-54 69-91 69-44 45-87	52-57 60-50 63-52 58-54	41-44 69-59 38-77 80-68	26-54 58-78 63-111 61-94	77-53 68-114 46-114 44-138
<i>Bromus sterilis</i>	107-48 139-13 79-64 86-43	122-27 104-63 71-71 69-100	97-89 66-133 152-42 86-60	109-47 67-64 79-46 73-60	44-41 59-69 77-38 68-80	90-42 63-60 68-51 72-48	58-134 80-83 87-46 65-65	72-54 93-70 72-125 60-73
<i>Holcus mollis</i>	118-23 96-36 174-33 197-41	90-76 172-82 141-80 180-48	74-82 85-67 114-80 121-80	72-56 106-50 129-52 79-80	54-26 78-58 111-63 94-61	134-58 83-80 46-87 65-65	58-79 72-60 82-65 69-67	78-85 102-78 92-83 110-92
<i>Festuca ovina</i>	93-43 126-34 176-29 109-16	93-93 101-85 143-62 181-54	97-109 159-82 135-56 134-84	100-43 94-54 97-50 94-51	53-77 114-68 114-46 138-44	54-72 70-93 125-72 73-60	85-78 78-102 83-92 92-110	64-69 57-65 70-62 75-68

TABLE 3 B.

Analysed results of Table 3A. The name under the degree of significance is that of the species of grass preferred.

	Arrhenatherum elatus	Anthoxanthum odoratum	Deschampsia flexuosa	Agropyron caninum	Alopecuris pratensis	Bromus sterilis	Holcus mollis	Festuca ovina
Arrhenatherum elatus	Not sig	Not sig	sig. <1-20 >1-50	sig. <1-100	sig. <1-50 >1-100	sig. <1-50 >1-100	sig. <1-100	sig. <1-100
			Deschampsia	Agropyron	Alopecuris	Bromus	Holcus	Festuca
Anthoxanthum odoratum	Not sig.	Not sig.	Not sig.	Not sig.	Not sig.	Not sig.	sig. <1-50 >1-100 Holcus	sig. <1-100 Festuca
Deschampsia flexuosa	sig. <1-20 >1-50	Not sig.	Not sig.	sig. <1-20 >1-50	Not sig.	Not sig.	sig. <1-20 >1-50 Holcus	Not sig.
	Deschampsia			Agropyron				
Agropyron caninum	sig. <1-100	Not sig.	sig. <1-20 >1-50	Not sig.	Not sig.	sig. <1-20 >1-50 Bromus	sig. <1-20 >1-50 Holcus	sig. <1-100 Festuca
	Agropyron		Agropyron					
Alopecuris pratensis	sig. <1-50 >1-100	Not sig.	Not sig.	Not sig.	Not sig.	Not sig.	Not sig.	sig. <1-20 >1-50 Festuca
	Alopecuris							
Bromus sterilis	sig. <1-50 >1-100	Not sig.	Not sig.	sig. <1-20 >1-50	Not sig.	Not sig.	Not sig.	Not sig.
	Bromus			Bromus				
Holcus mollis	sig. <1-100	sig. <1-50 >1-100	sig. <1-20 >1-50	sig. <1-20 >1-50	Not sig.	Not sig.	Not sig.	Not sig.
	Holcus	Holcus	Holcus	Holcus				
Festuca ovina	sig. <1-100	sig. <1-100	Not sig.	sig. <1-100	sig. <1-20 >1-50	Not sig.	Not sig.	Not sig.
	Festuca	Festuca		Festuca	Festuca			

Examination of Table 3A shows that Arrhenatherum elatius L. was rejected in favour of all the other seven species whilst Holcus mollis and Festuca ovina agg. were always readily eaten. The degree to which each grass is eaten depends on the choice available. When the choice is between Deschampsia flexuosa (L). and Arrhenatherum elatius, the Deschampsia is selected, when it is Deschampsia and Agropyron caninum Beauv, or Holcus mollis, the number of hoppers feeding on Deschampsia is relatively fewer.

The results of the statistical analysis show very definite preferences and it is possible to arrange the grasses in an approximate order of acceptability although a few appear to be more or less equally palatable. The actual figures obtained are set out in Table 3A whilst the results analysed to show the level of significance, more than 1-20, more than 1-50 or more than 1-100, and the grass preferred in Table 3B. Table 4 is based on Table 3B and arranges the eight grasses in an order of preference by taking into account the relative degree of significance.

TABLE 4.

Grasses arranged in order of preference based on Table 3B. The eight grasses were compared in all possible pairs and the significance of the differences in numbers of Locusts feeding was assessed by a χ^2 test. The values of P for each test were summed and the most preferred grass was that for which the total P was the smallest.

Species of Grass	Degree of Significance when preferred			No. of sets which were not significant in either direction.	Degree of Significance when not preferred.		
	1-100	1-50	1-20		1-20	1-50	1-100
1. Festuca ovina	3	0	1	3	0	0	0
2. Holcus mollis	1	0	2	3	0	0	0
3. Bromus sterilis	0	1	1	5	0	0	0
4. Alopecurus pratensis	0	1	0	5	1	0	0
5. Agropyron caninum	1	0	1	2	2	0	1
6. Deschampsia flexuosa	0	0	1	4	2	0	0
7. Anthoxanthum odoratum	0	0	0	5	0	1	1
8. Arrhenatherum elatius	0	0	0	1	1	2	3

A similar experiment to that overleaf was performed using adults of five British species of grasshopper. Seven grasses were tested in turn against Holcus mollis and the experiments repeated four times except in the case of Omocestus ventralis. Festuca ovina agg., Holcus mollis and Dactylis glomerata were acceptable as food plants. Brachypodium sylvaticum (Huds), a grass which was rejected by Locusta hoppers, was eaten by these grasshoppers at least as much as Holcus. The suggestion that grasshoppers like Sylvatic grasses less than field species appears to be without foundation. Arrhenatherum elatius and Anthoxanthum odoratum appear unfavourably as for Locusta and the coarse grasses of acid moorland, Nardus stricta L. and Molinia caerulea (L.) also were not freely eaten. The results are summarised in Table 5A and after being analysed statistically by a χ^2 test, their significance is given in Table 5B. From this and other experiments as well as from field observations, there appears to be little difference between the food preferences of those British grasshoppers studied in this work.

TABLE 5A.

Summary of numerical grass preference experiments with adults of some British grasshoppers. The figures are the sum of 6 readings taken at five-minute intervals.

		Holcus mollis (A)						
		X (B)						
	Dactylis glomerata	Nardus stricta	Molinia caerulea	Brachypodium sylvaticum	Anthoxanthum odoratum	Festuca ovina	Arrhenatherum elatus	
	A	B						
Myrmeleotettix maculatus	39 - 313	88 - 21	50 - 69	29 - 28	30 - 41	134 - 49	16 - 13	
	93 - 87	91 - 67	78 - 27	47 - 53	146 - 51	35 - 65	61 - 60	
	96 - 90	79 - 34	84 - 36	120 - 79	61 - 24	53 - 47	69 - 9	
	22 - 74	49 - 37	35 - 11	65 - 28	45 - 64	46 - 57	64 - 33	
Chorthippus albomarginatus	129 - 211	241 - 60	168 - 84	100 - 93	141 - 56	144 - 123	136 - 61	
	99 - 60	174 - 76	75 - 50	101 - 83	112 - 93	113 - 139	209 - 29	
	166 - 102	150 - 131	132 - 84	58 - 42	196 - 49	41 - 59	158 - 51	
	115 - 126	115 - 57	113 - 65	78 - 111	124 - 72	150 - 62	181 - 41	
Chorthippus bicolor	82 - 130	174 - 20	40 - 20	107 - 116	95 - 76	85 - 86	168 - 119	
	11 - 97	159 - 142	79 - 40	52 - 48	129 - 69	147 - 155	69 - 46	
	74 - 151	148 - 104	54 - 42	59 - 41	101 - 72	48 - 52	150 - 85	
	132 - 69	83 - 63	198 - 70	112 - 79	132 - 91	68 - 125	91 - 70	
Stenobothrus lineatus	51 - 76	28 - 29	37 - 26	29 - 29	129 - 39	20 - 21	40 - 0	
	83 - 51	73 - 116	74 - 95	60 - 40	38 - 17	94 - 106	77 - 4	
	91 - 59	68 - 37	32 - 54	63 - 52	57 - 32	50 - 50	50 - 3	
	42 - 38	17 - 35	52 - 19	32 - 26	20 - 18	47 - 42	66 - 2	
Omocestus ventralis	41 - 111	51 - 95	108 - 25	17 - 60	159 - 63	128 - 58	97 - 36	
	28 - 67	83 - 17	87 - 16	17 - 83	7 - 53	69 - 31	91 - 14	
	54 - 24	36 - 13	62 - 10	46 - 36	39 - 48	17 - 96	83 - 25	

TABLE 5B.
Analysed results of Table 5A.

	Holcus mollis X						
	Dactylis glomerata	Nardus stricta	Molinia caerulea	Brachypodium sylvaticum	Anthoxanthum odoratum	Festuca ovina	Arrhenatherum elatus
Myrmeleotettix maculatus	sig. < 1 in 100	sig. < 1 in 100	sig. < 1 in 100	Not sig.	sig. < 1 in 20 > 1 in 50 Holcus	Not sig.	sig. < 1 in 100 Holcus
Chorthippus albomarginatus	Not sig.	sig. < 1 in 100 Holcus	sig. < 1 in 100 Holcus	Not sig.	sig. < 1 in 100 Holcus	Not sig.	sig. < 1 in 100 Holcus
Chorthippus bicolor	sig. < 1 in 100 Dactylis	sig. < 1 in 100 Holcus	sig. < 1 in 100 Holcus	Not sig.	sig. < 1 in 100 Holcus	Not sig.	sig. < 1 in 100 Holcus
Stenobothrus lineatus	Not sig.	Not sig.	Not sig.	Not sig.	sig. < 1 in 100 Holcus	Not sig.	sig. < 1 in 100 Holcus
Omocestus ventralis	sig. < 1 in 20 > 1 in 50 Dactylis	Not sig.	sig. < 1 in 100 Holcus	sig. < 1 in 100 Brachypodium	Not sig.	Not sig.	sig. < 1 in 100 Holcus

Although the grass-blade is normally the part of the plant which is eaten, in captivity grasshoppers will feed quite readily on the young inflorescences. When the flower spike is fully opened or setting seed, the glumes are usually too tough to be easily eaten and are generally left alone. Feeding on the flowers was only observed on two occasions in the field (both on Festuca ovina agg.) but this was no doubt because most field observations were made on closely grazed turf where the flower-heads were nibbled off by rabbits before they had properly formed.

Fifth stage hoppers of Locusta were found to feed quite freely on grated or thinly-sliced portions of the storage organs of swedes, carrots and parsnips. The tubers of Ranunculus ficaria L. were partly eaten, but the potato and beetroot were rejected after a few tentative attempts at nibbling. These insects will also chew pieces of paper and muslin when hungry, and it is well-known that moulting hoppers are very liable to be attacked and eaten before they can completely free themselves from their exuviae. The cast skins of locusts are always eaten, even by well-fed insects. This does not always take place in cages of grasshoppers, nor do these insects appear to be so subject to cannibalism.

Observations on nymphs of Acrididae suggest that they show the same preferences as the adults. The tougher kinds of grass are often left strictly alone by the very young hoppers as their jaws can make little impression on them. However, even these

are eaten as soon as the teeth on their mandibles are powerful enough to be able to bite into the more tender and succulent regions of the leaf-blades.

The implications of these results are summarised in the general discussion.

Section 4 describes the attempts to find out the more important factors which determine the selection of grasses.

4. FEEDING HABITS.

1) Method of Feeding.

If food is introduced into a cage containing a starving grasshopper, the insect can often be observed to make the following sequence of actions. It will first orientate itself to face the food, then begin to walk forwards. As in all normal locomotion, the tips of the antennae are periodically brought to bear on the surface on which it is walking. When near the food, the grasshopper may cover the rest of the distance in a single hop, or it may walk the whole way.

On reaching the food, the insect first touches it with its antennae as if to make sure that it really is plant material, then with its mouth parts. Under the microscope the details can be easily watched. The head is lowered until the surface of the labrum touches the leaf. Next the tips of the palpi are brought to bear on the leaf a number of times in quick succession, just lightly touching it each time. The extreme tips of the palpi are the site of some of the taste organs in Acrididae, their position being indicated by a slight darkening of the surrounding area of the cuticle. Finally, the insect closes its mandibles on the edge of the leaf taking first a small bite as a sample, for it can be seen to thoroughly chew up this fragment in the buccal cavity before taking a second bite. A second small bite may sometimes be taken, but usually the grasshopper either moves away when, for some reason, the

food is not to its liking, or settles down to a meal.

The insect bites off pieces of the leaf with a downward action, removing crescentic areas each time. During the actual bites, the palpi are usually kept a short distance above the leaf surface, but in a few cases they were observed to be occasionally lowered so as to touch the leaf periodically. At the end of each downward movement, the grasshopper raises its head, and, after feeling again for the edge of the blade with its palpi, begins to take out another slice. Frequently the forelegs are used to steady the grass, being held just in front of the labrum, that is, at a point near the beginning of the bites.

When the insect has been feeding for about a minute a large piece of the leaf has often been removed. As a result, it becomes necessary to draw up the whole body slightly if the next bite is to begin at the same place as before. Alternatively, it may select a new area for feeding, usually one a short distance below the previous site.

In the case of grasses with rather narrow leaf blades, (Nardus stricta, Festuca ovina, Deschampsia flexuosa, etc.) these biting movements will usually cut the leaf right through in four or five strokes. The part above the biting area is then left hanging down by a narrow strip of the leaf tissue or is allowed to fall right off.

ii) Duration of Meals.

Later it will be shown that leaf shape has little effect

in food selection by grasshoppers and locusts. However, leaf form and toughness undoubtedly have a considerable influence on the time taken over a meal. The fact that the finer grasses like Festuca ovina agg. and Deschampsia flexuosa are more difficult to chew than Holcus mollis and similar species, although they are freely eaten, is important when conducting experiments on food preferences which involve numerical estimations.

Figure 1 shows the number of Locusta hoppers feeding on each of a series of four broad-leaved grasses at each five-minute period of an experiment lasting 45 minutes, expressed as a percentage of the total count on each for the whole duration of the experiment. It will be observed that the highest number recorded was 10 minutes after the start of the experiment. Figure 2 shows the comparable results obtained when using the acicular grasses Festuca ovina agg. and Deschampsia flexuosa. There is no pronounced peak as in Figure 2, indicating that a longer time was spent over the meals in these cases. It is interesting to compare here the graphs for the unpalatable grasses, Arrhenatherum elatius and Anthoxanthum odoratum. (Figure 3). These show a peak at the first reading (i.e. 5 mins.) instead of 10 or 15 minutes after the start of the experiment as in the other 6 grasses.

In the above instances, the variation in time taken over meals on different kinds of grass is due to differences in shape between the leaf-blades. This same difference in the rate of feeding can be observed when a comparison is made between the

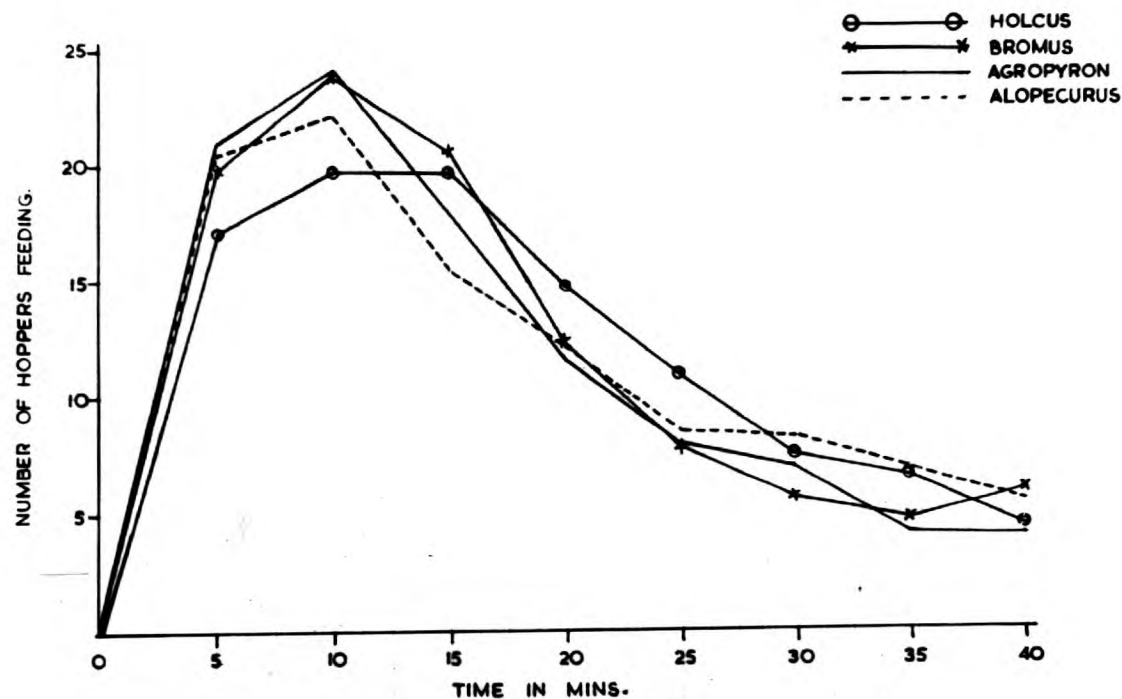


Figure 1. Experiment to show the time spent by *Locusta* hoppers when feeding on broad-leaved grasses. Grasses used - *Holcus mollis*, *Bromus sterilis*, *Agropyron caninum* and *Alopecurus pratensis*.

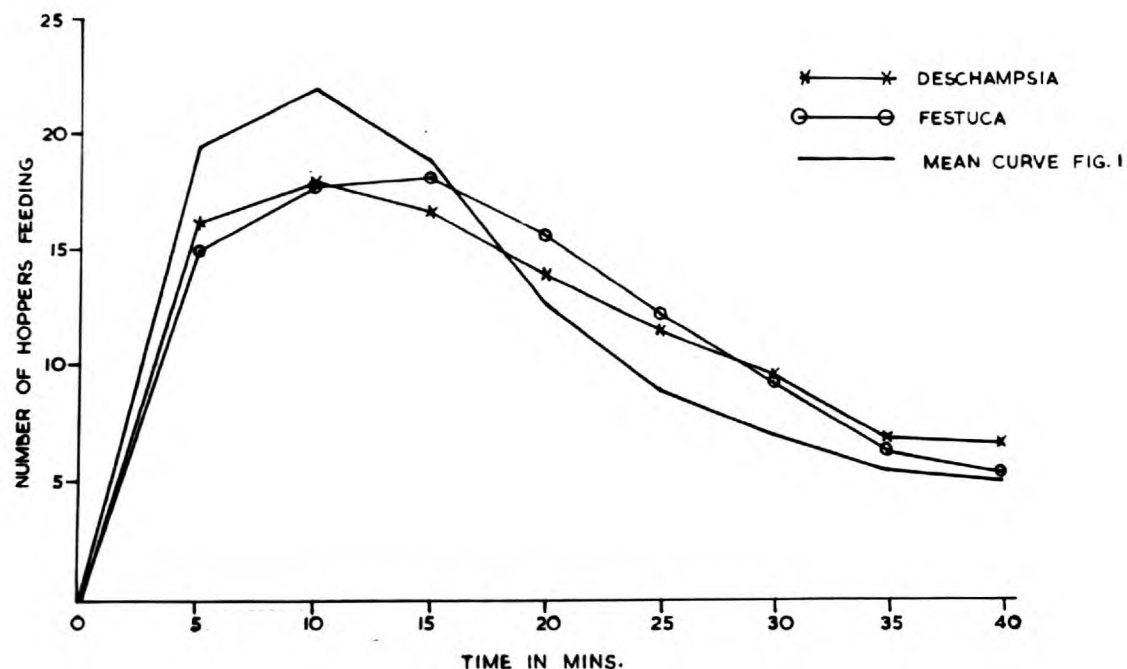


Figure.2. Experiment to show the time spent by *Locusta* hoppers when feeding on narrow-leaved grasses. Grasses used - *Deschampsia flexuosa* and *Festuca ovina*. For comparison, the mean of the four curves in Figure 1 is also shown.

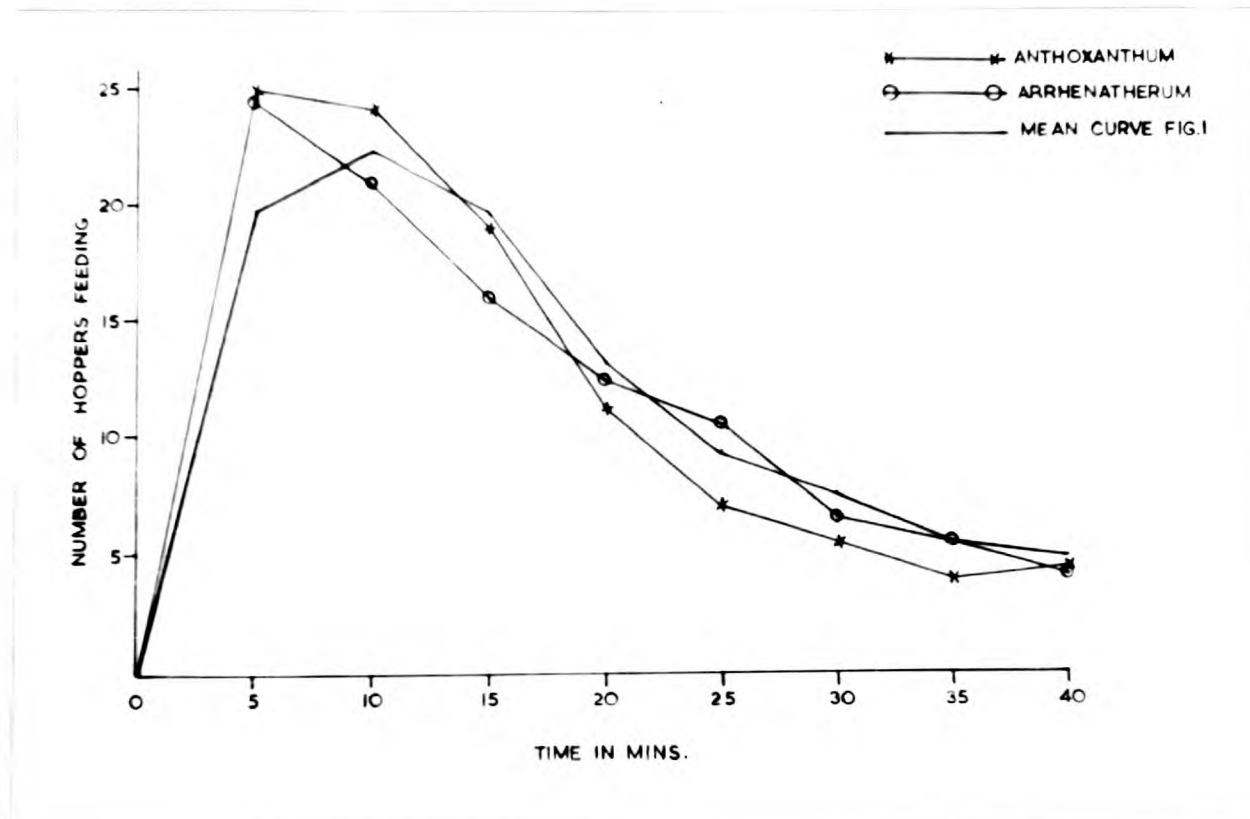


Figure 3. Experiment to show the time spent by Locusta hoppers when feeding on unpalatable grasses. Grasses used - Anthoxanthum odoratum and Arrhenatherum elatius. For comparison, the mean of the four curves in Figure 1 is also shown.

times taken on Holcus mollis and Bamboo. The latter is a very much tougher grass (probably about 6 times as tough). The results of an experiment under comparable conditions with those described above, are shown in Figure 4.

The effect of a longer time being spent on grasses which are tougher and more difficult to chew is to make them appear in a more favourable light than is truly the case. Thus, in the experiment described below, comparing the palatability of Holcus and Bamboo for locust hoppers of different ages, (see Page 75), the apparent preference for Bamboo shown by the fourth and fifth stages is probably due to a longer time being spent on this grass because of its greater toughness. These two grasses are probably really equally acceptable to the hoppers.

Observations were made in the laboratory on the length of time individuals spent on a single meal in the cages. Holcus mollis was the grass used in all this work. The results are summarised in Table 6. Five males and five females of three species of grasshopper were used.

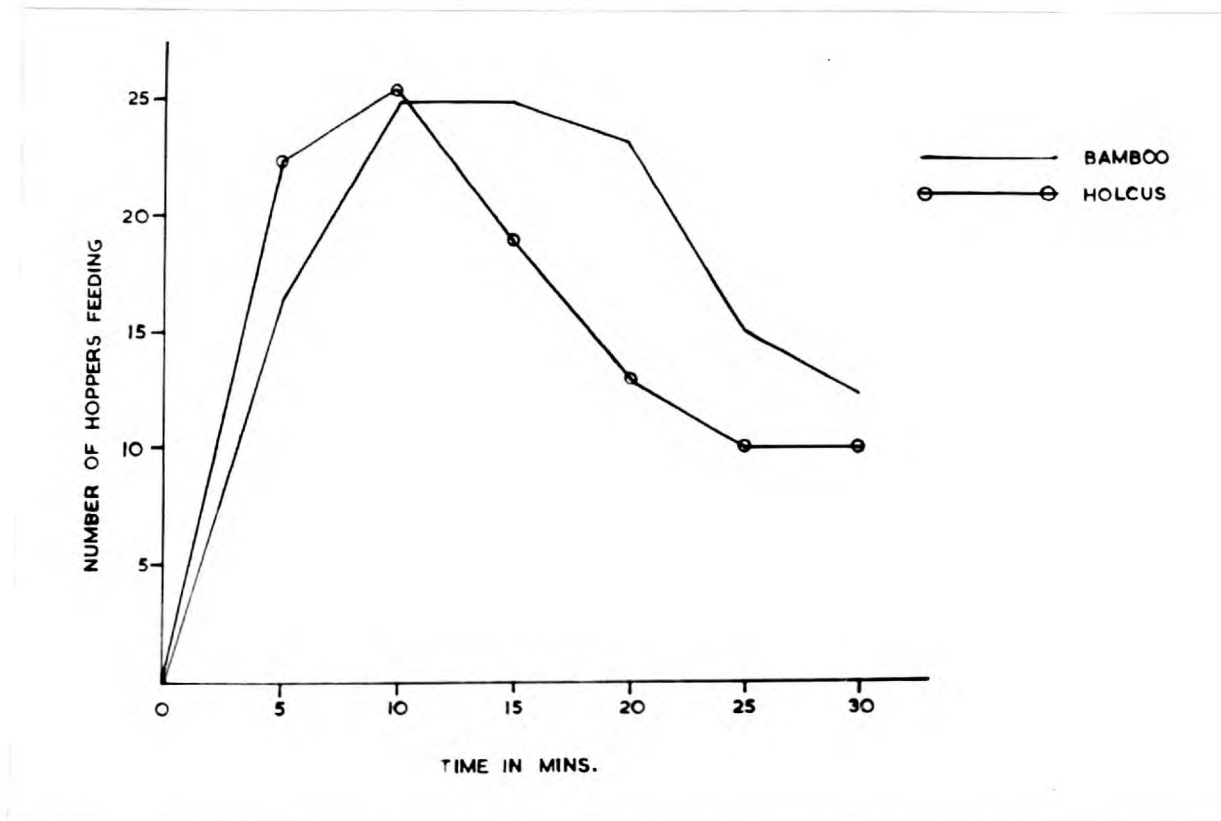


Figure 4. Comparison between the time spent by *Locusta* hoppers feeding on *Holcus mollis* and on Bamboo (*Bambusa* sp.). The curve for Bamboo is very like those for the acicular grasses *Festuca* and *Deschampsia* (see Figure 2.).

TABLE 6.

Summary of the length of time spent by three species of Acrididae on individual meals.

Species	Average Time (Mins.)	Total No. of observa- tions.	0-5 mins.	6-10 mins.	11-15 mins.	16-20 mins.	21-25 mins.	26-30 mins.	31-35 mins.	36-40 mins.
<u>Chorthippus albomarginatus.</u>										
Males	13.5	25	4	5	7	4	4	1	0	0
Females	11.5	29	8	14	7	3	6	1	0	0
<u>Chorthippus bicolor</u>										
Males	18	13	1	3	3	1	3	1	0	1
Females	15	15	1	5	4	2	1	1	0	1
<u>Gomphocerippus rufus</u>										
Males	16.5	5	0	2	0	2	1	0	0	0
Females	15.5	20	0	8	4	3	3	2	0	0

These results suggest that males spend a slightly longer time on their meals but that females feed more frequently. The small number of observations in each case, however, makes it impossible to present this as more than a suggestion. The figures also indicate that the duration of meals is slightly different for different species of grasshopper. Thus, the meals of Gomphocerippus rufus appear to be longer than those of Chorthippus albomarginatus. Meals of more than half an hour's duration seem to be rare in these species.

No records were kept of the length of meals in the field. The impression received was, however, that they seldom lasted longer than 10 minutes and were usually considerably shorter. Frequent short meals seemed to be usual, but it is difficult to watch grasshoppers in the field for any length of time without betraying one's presence by making a slight movement, which disturbs the insects and interrupts their normal behaviour.

The frequency of feeding in the laboratory was very irregular and enormous variation occurred between individuals of the same species. Table 7 summarises some of the few records kept by watching marked insects in laboratory cages. By far the bulk of the time is spent by grasshoppers in "sunning" themselves on the sides of the cage or on the twigs near the electric light bulb. Wild individuals also appear to spend the major part of their lives in sunning themselves on bare patches of soil or at the tops of grass tussocks in fine weather, and at the bases of the plants in dull periods.

TABLE 7.

Observations made on confined marked individuals of 2 species of Acridid to show the frequency with which feeding occurs.

		<u>Number of Meals</u>							
		<u>Males</u>				<u>Females</u>			
		1	2	3	4	1	2	3	4
Chorthippus albomarginatus	10 $\frac{1}{2}$	3	3	6	1	6	5	0	5
	9 $\frac{3}{4}$	1	0	1	0	2	2	1	3
	9 $\frac{1}{2}$	4	1	1	1	2	3	3	4
	4	1	1	0	1	2	0	1	0
Total	33 $\frac{3}{4}$	9	5	8	3	12	10	5	12
Total time spent in feeding (mins).		118	57	110	43	191	121	36	102
Chorthippus bicolor	10	2	2	1	1	1	1	0	1
	9	1	1	1	1	1	4	1	2
	6	1	2	0	0	1	1	1	1
Total	25	4	5	2	2	3	6	2	4
Total time spent in feeding (mins.)		93	88	30	25	56	61	23	86

Langford (1930) found that the number of times per day when feeding takes place is, in part, determined by the food. Adults of Melanoplus bivittatus when feeding on lettuce averaged 5.7 feeding periods whilst there were 3.2 on alfalfa in a 12 hour day. The average length of each feeding period was 16 minutes.

iii). Time of Day when Feeding takes place.

The time of day when feeding occurs under natural conditions is directly dependent on the weather. Observations show that grasshoppers move into patches of taller and denser vegetation in the evening. Here they probably get some small degree of shelter from the sudden fall in temperature at the onset of darkness. During the day, most of the time is spent in the barer patches to obtain the maximum solar radiation. The exposed soil is warmer and grasshoppers love warm conditions.

In the early morning, the grass is cold and wet with dew. At such times no grasshoppers are in evidence, they can only be found by groping down among the basal sheaths of the grass clumps. As the sun rises in the sky, and the grass dries out and the temperature at ground level rises, so the grasshoppers begin to appear in the open. Feeding takes place almost immediately, then they usually go off to sun themselves. On summer days when the sun is obscured by banks of cloud for long periods at a time, soon after the sun is hidden the grasshoppers disappear. When the clouds have rolled by, they reappear and often take a short meal immediately. These are the kind of weather conditions which are most suitable for watching the feeding behaviour

of grasshoppers out of doors, for, it is on such days that they probably take most meals. On cloudless days, feeding is more difficult to observe, the insects are less active, and probably take a few long meals rather than a whole series of short feeds. Acrididae also appear to be sensitive to wind, for, on windy days, they are usually not much in evidence. The effect of exposure of site and position of wind-breaks on the abundance of Acridid population in certain areas is more fully discussed in Appendix B.

In cages in the laboratory, when the light is switched on in the morning, the grasshoppers are usually down among the grass on the floor or squeezed in among the bases of the shoots of food in the pots in the corners. Soon afterwards they become active although the rise in temperature when the bulb is on is only 3-4° C. They then feed. From this it would seem that it is the change in temperature which makes them more active rather than the air reaching a certain minimum. Humidity also is probably an important factor, but this has not been studied in the laboratory.

TABLE 8.

Observations made in the laboratory on the length of time between switching on the light in the cages and the start of feeding by some species of Acrididae.

Within		Total from start of observations.
0 - 15 mins.	30	30
15 - 30 mins	15	45
30 - 45 mins	10	55
45 - 60 mins	8	63
60 - 90 mins	10	73
90 - 120 mins	4	77
More than 120 mins	24	101

In Table 8 are the results of 101 observations made by switching on the light in a cage and observing how soon afterwards the insects commenced to feed. The species used were Chorthippus albomarginatus (26 observations), C. bicolor (38) Omocestus viridulus (8), Stenobothrus lineatus (13) and Gomphocerippus rufus (16).

The temperature in the cages reached its maximum after about 10 minutes, and this was when the highest percentage of grasshoppers began to feed. As a result, it is improbable that feeding was induced by the sudden increase in illumination.

5. THE FACTORS WHICH INFLUENCE THE FINDING AND SELECTION OF FOOD.

A. Habitat.

At the beginning of this work it was thought that some food factors might determine the habitat of the British Acrididae. Subsequent work showed that the composition of the flora in each habitat studied is seldom limiting. This is because there are very few places where some kind of grass will not grow and none of the British grasshoppers confines its feeding to a limited number of grasses only. Laboratory work shows that British grasshoppers will feed readily on many more species of grass than those which normally occur in their natural habitats.

On heathland it is noticeable that grasshoppers are more abundant near paths and in the other open spaces where tufts of grass are to be found, than in heather. Quadrat work has shown that the common grasshopper of heaths, Myrmeleotettix maculatus only occurs in the vicinity of grass, in the pure Callunetum it is absent.

The following types of habitat were examined - fields, water meadows, chalk pastures, woods and glades, heaths, fens, saltmarshes, sandunes and mountains, although most work was done in the habitats occurring within easy access of Reading.

It is the structure of the vegetation and not the composition which acts as a limiting factor.

This part of the work is fully described and its implications are discussed in Appendix B.

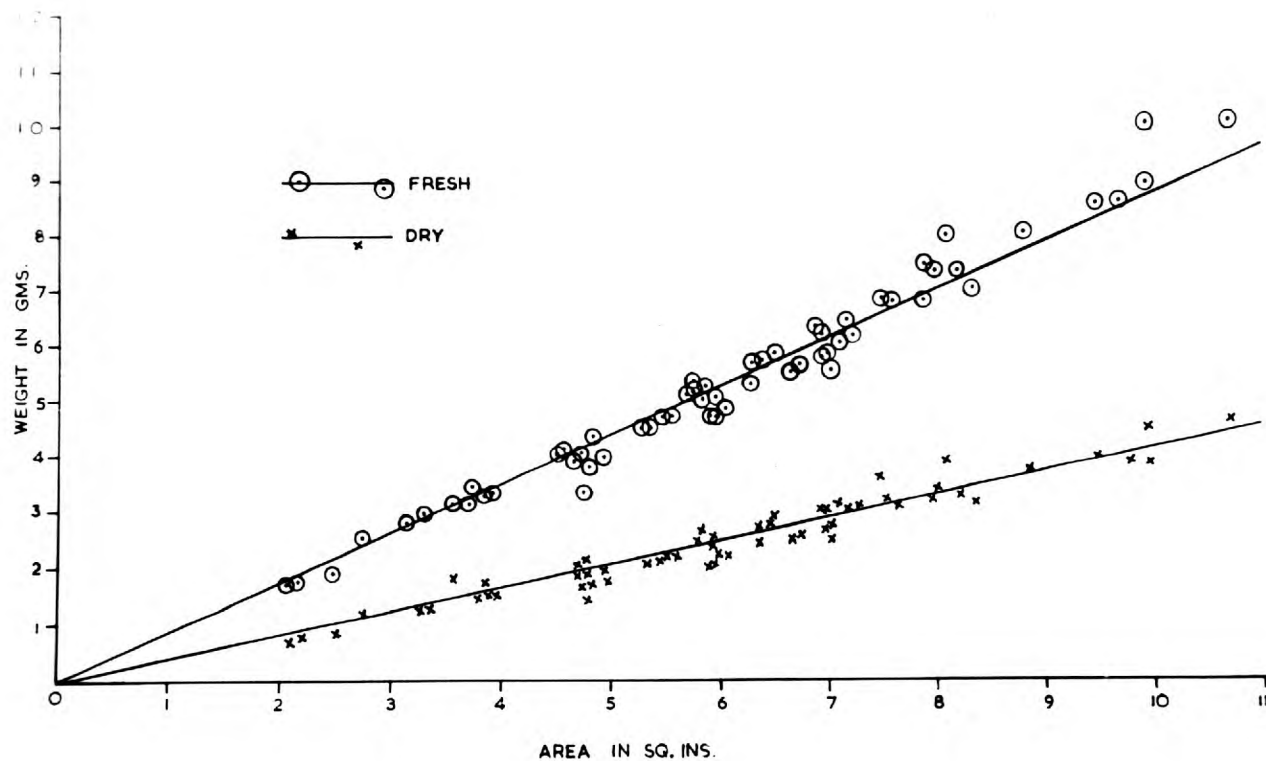


Figure 5. The relationship between surface area and weight (fresh and dry) of bamboo leaves. Area, range 0 - 11 sq. ins. Weight, 0 - 1.2 gms. The lines represent the means of the 60 measurements.

B. Experiments on Senses and Sense Organs.

Bamboo was used as the standard food in the following experiments as the shape of its leaves permits easy measurement with squared paper. The narrow blades of most Gramineae cannot be measured accurately in this way. Another reason for its choice is that it remains fresh longer than any of the common British grasses when kept in jars of water in the Constant Temperature Room.

The relationship between surface area and fresh and dry weight of Bamboo leaves is expressed graphically in Figure 5. The average weight per square inch of the 60 leaves used was: fresh - 0.039 gms., dry - 0.042 gms. The points all lie near to the mean line, so it was justified to use surface area as the measurement of quantity of food eaten. The leaves used in the experiments were all of approximately equal size (6 square inches).

1) The Eyes and Sight.

To determine the importance of sight in the location of food, an experiment was set up using two pairs of adult Locusta migratoria. Two days previously the eyes were blackened over with "Joy" cellulose paint applied thickly with an artist's paint brush. These were fed on Bamboo shoots in a large cage and the surface area of leaf eaten every 24 hours was taken as the measurement of feeding. A similar cage containing two pairs of normal untreated locusts was used as a control. All the insects were of the same age. The results are shown in Table 9A.

Later a similar experiment was carried out using four pairs of adult locusts. In this instance the dry weight of frass produced every 24 hours was taken as the measurement of feeding. These results are set out in Table 9B. In both these experiments, two days elapsed between the blackening out operation and the taking of the first measurement. In a third experiment on similar lines to the second, three days elapsed before the first measurement was made and five pairs of adult locusts were used in each cage. These results are shown in Table 9C.

TABLE 9.

Experiment to test the effect on food consumption of blackening over the eyes of adult locusts.

No. of days from date of blackening over the eyes.	<u>Experiment 1.</u>		<u>Experiments 2 and 3</u>			
	Results expressed as Total Area of Bamboo leaf surface in sq. ins. eaten by 2 pairs of locusts in each cage.		Results expressed as Total Weight of dry frass in gms. produced in each cage.			
	Table A		By 4 pairs of locusts Table B.		By 4 pairs of locusts. Table C.	
	Control Cage	Treated Cage	Control Cage	Treated Cage	Control Cage	Treated Cage
1	X	X	X	X	X	X
2	X	X	X	X	X	X
3	10.46	6.88	0.96	0.30	X	X
4	0.03	2.64	1.48	0.51	3.85	3.55
5	15.73	1.91	0.98	0.51	6.08	5.33
6	18.18	5.82	1.165	0.51	4.43	3.58
7	16.62	4.57	0.965	0.52	4.65	2.98
8	18.44	3.21	1.265	0.74	4.77	3.91
9	X	X	1.01	0.84	X	X
10	X	X	1.125	0.80	X	X
A Area eaten Total	79.46	25.03	8.94	4.73	23.79	19.35
B.C.Weight of frass						
Mean/Day/Locust	3.31	1.04	0.140	0.074	0.476	0.387

In all cases, the Bamboo was kept in a jar of water in one corner of the cage. To reach it, the locusts either had to climb up the side or jump direct from the floor of the cage.

These results indicate either that the insects found some difficulty in finding the food when their eyes were blackened over or that the effect of the treatment was to reduce activity and consequently the quantity of food eaten by the treated insects was less than by normal locusts. Two of the locusts died in the course of the first experiment and were replaced but no other deaths occurred. However, normal locusts will live for several days when deprived of food and it is probable that every insect in all the experiments fed at least once. It is difficult to account for the considerable variation in the figures of Experiment 1 or for the tendency of the figures of Experiment 2 to rise as it proceeded. This may have been due to the layer of paint becoming thin as a result of the insects' frequent attempts to scratch it off with the spines on their forelegs, or although it seems less likely, to the locusts adapting themselves to their condition by making greater use of some other sense organ.

The big difference between the daily mean per locust in Tables B and C can probably be accounted for by the difference in age, and therefore in physiological condition, of the insects. Those used in Experiment C were considerably older, being in the mature state where higher metabolism may be expected to occur.

On the whole, from these results, it appears that a blackening of the eyes does have some effect on the ability of the insects to find their food. Whether this is really due to reduction in the insects' activity due to darkness was tested by carrying out an experiment using normal locusts, one batch being kept permanently illuminated whilst the other was in total darkness.

Two celluloid-type cylindrical cages were used, one was surrounded with black paper, whilst the other was kept illuminated by placing an electric light bulb on each side. A tank of water between them and the cage reduced the effect of the heat of the bulbs. This precaution proved to be quite adequate, as the temperature inside both the cages was the same, 21°C. Four adult locusts were used in each cage and an abundant supply of Bamboo was constantly maintained. The results were expressed as the area of leaf surface eaten per day. (Table 10)

TABLE 10.

Experiment to test the effect of darkness on the food consumption of adult locusts.

Day	Area eaten in darkness (in sq. ins.)	Area eaten in light (in sq.ins.)
1	0.97	9.04
2	1.19	7.61
3	3.68	7.39
4	0.91	1.04
5	0.71	4.10
Total	7.46	29.18
Mean/day/locust	0.373	1.459

These figures show clearly that the quantity of food eaten is considerably less in darkness. Undoubtedly, the insects are far less active than in the light and consequently require less food to maintain normal health. This probably accounts for the smaller amount of food eaten by locusts with their eyes covered with paint.

Langford (1930) has shown that, provided a suitable temperature is maintained, locusts can develop and grow as well in the dark as in the light. It was felt that work on the time taken for these insects to develop to maturity was outside the scope of the present study.

A tendency to follow patterns has been observed in a number of different insects. (Tischler 1936). Coccinella, when placed on a white background with black stripes tends to follow the stripes and turn corners when they are angulated. This response, which is referred to as "skototaxis" appears to be best developed in phytophagous insects and is perhaps associated with their habit of following stalks and branches in their search for leaves. (Wigglesworth 1951).

One side of a square cage was covered with a vertical pattern. This was made by pasting strips of black paper about 5 millimetres wide on a white background so as to produce a regular black and white striped effect. The opposite side of the cage was covered in successive experiments by a sheet of white paper, black paper and a sheet of similar striped paper, but with the stripes running horizonatally. Adults of the

grasshopper Gomphocerippus rufus were introduced into the cage singly and watched to see in which direction they would walk. The usual procedure was for the insect to remain motionless in the middle of the cage for a minute or so, then it slowly moved round in a circle and oriented itself to face one side. After a further brief pause, it walked to the side and climbed up. Each experiment was carried out 60 times. The cage was turned after each set of five readings in order to eliminate any bias due to uneven illumination or any other factors. The results obtained are set out in Table 11.

Table 11.
Experiments to show the attraction of adult Gomphocerippus rufus to vertical stripes.

Expt. No.	Vertical Stripes	White Paper	Total
1	15	5	20
2	17	3	20
3	18	2	20
Total	50	10	60

Expt. No.	Vertical Stripes	Black Paper	Total
1	14	6	20
2	16	4	20
3	15	5	20
Total	45	15	60

Expt. No.	Vertical Stripes	Horizontal Stripes	Total
1	16	4	20
2	13	7	20
3	14	6	20
Total	43	17	60

There is obviously a preference for the vertical stripes in every experiment.

Next, the inside of a large cylindrical cage with a

diameter of 24 inches was lined with paper on which vertical strips of black paper of four different widths had been arranged in sequence. The width chosen were 2 mms., 5 mms., 9 mms., and 15 mms. and they were arranged as shown in Figure 6. In this case, the grasshoppers were introduced into the cage 3 at a time, and 120 observations were made as follows -

No. of grasshoppers.	2 mms.	5 mms.	9 mms.	15 mms.	Off stripes.
	21	18	24	27	30
Totals			90		30

There was no preference for one width of stripes.

It was very noticeable that when walking up the stripes, grasshoppers attempted to follow the edges. This would be in accordance with the supposition that the vertical pattern appeared to them as vertical blades of grass outlined against the light background of the sky. Alternatively, it might mean that the slightly raised edges of the stripes allowed a better foothold for upward movement.

To test this, a design of vertical stripes was prepared using black Indian ink in place of strips of black paper. The same tendency to walk along the edges of the stripes was noted although in this case there was no surface roughening at the stripes.

The final experiment with stripes was carried out in a celluloid cage 18 inches cube, one side of which was covered by a sheet of white paper on which a pattern of sinuate and angular stripes had been drawn. Adults of Chorthippus parallelus

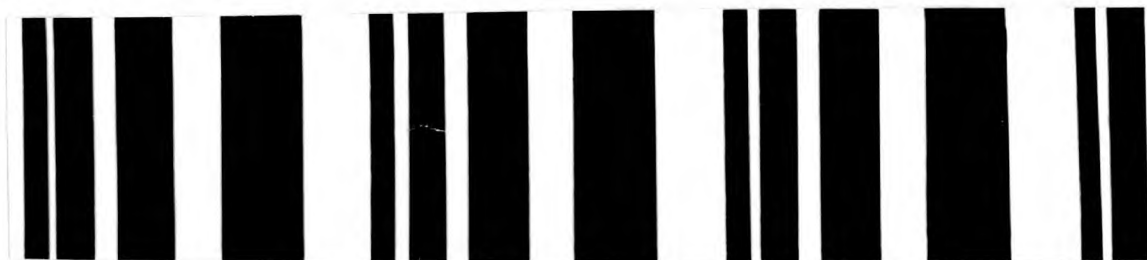


Figure 6. Diagram to show the relative widths of stripes and the distances between them in an experiment to test the preference of grasshoppers for stripes of different widths.

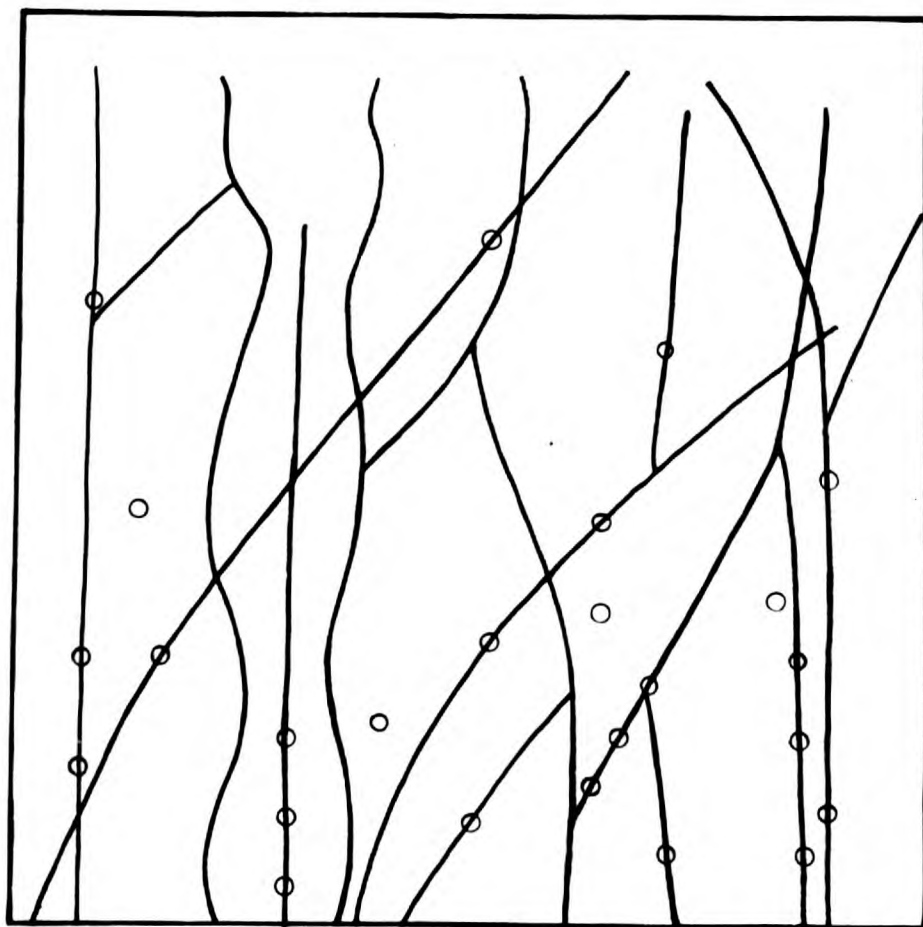


Figure 7. Copy of chart obtained in an experiment to show that grasshoppers are attracted to stripes. The positions where grasshoppers rested are marked by circles. Only 4 individuals out of 25 did not settle down on or at the edge of a stripe.

were introduced 4 at a time into this cage. After about 2 minutes they oriented themselves to face the pattern, then after the usual brief pause they walked towards the pattern and, on reaching it, proceeded to climb up along the edges of the stripes. Periodically they stopped and apparently attempted to feed at the edges of the stripes. Finally, they settled down, in nearly every instance selecting some position touching the black lines. Their positions were then noted on the chart before they were removed and replaced by 4 others. Figure 7 is a copy of the chart.

It will be seen that only 4 of the 25 grasshoppers used finally rested in a position away from the stripes. From these experiments it might be expected that grass in an upright position would be preferred to grass in a horizontal position. This may be because upright grass is easier to manipulate with the jaws, as is very probable from the method of feeding adopted by Acrididae (see Section 4), or because it is more easily seen against the light background of the sky.

To test this, 25 adults of Chorthippus albomarginatus were provided with a choice of upright and horizontal grass on 6 consecutive days. An abundant supply of grass in both positions was distributed over the floor of the cage with internal measurements of 24 inches sube. The sides of the cage were of coarse gauze and the relatively small number of individuals used, together with these features of the apparatus

made the conditions of the experiment as natural as possible. The results are shown in Table 12.

TABLE 12.

Preference of Chorthippus albomarginatus for upright or horizontal grass.

Day	No. of hours of Expt.	No. of Grass-hoppers present	No. feeding on upright grass	No. feeding on horizontal grass	Total No. of observations.
1	8	25	11	4	15
2	8	25	20	8	28
3	8	25	18	17	35
4	8	25	42	16	58
5	7	25	28	10	38
6	6	25	20	7	27
Total	45		139	62	201

A striking preference for upright grass over grass in a horizontal plane is shown by these figures. As both kinds of grass were scattered all over the floor of the cage the explanation for this cannot be that the vertical grass was more easily located. The upright blades are therefore singled out by the grasshoppers as preferable food material. This may be because they appear as a pattern of dark vertical stripes against the light background of the sky, a pattern which is attractive to grasshoppers as has already been demonstrated.

ii) The Sense of Smell.

a. Summary of work on the sense of smell in insects generally.

There is little doubt that the majority of phytophagous insects are attracted to their host plants by a sense of smell. The relation between the insect, the odour of its food plant

and plant chemistry, was first pointed out by Verschaffelt (1910). His work on the attraction of Pieris larvae to the mustard oils and closely related chemicals in many of the Cruciferae was a pioneer work.

Since that time a considerable amount of work has been completed on the attraction by insects to odours. Much of this study has been on Lepidopterous larvae. Dethier has shown (1937) in the case of larvae of the milkweed butterfly, Danaus plexippus, that when separated from their food-plant Asclepias by a wire screen, they describe searching movements when over leaves of this plant but maintain a straight path when over the leaves of other plants. He also showed (1941) that species of Papilio which now feed on plants of Umbelliferae, originally fed on plants of the family Rutaceae. The same attractant chemicals occur in both families. Dethier has also published a comprehensive work on chemical insect attractants and repellents (1947).

Brues (1920) pointed out that among the members of some families of butterflies, there is a tendency to select as food plants, species belonging to only a few genera. Again, this is probably because only these plants contain the chemicals which are attractive to the butterflies.

Smell has also been shown to be important as a sex attractant. (Valentine 1931, and many others).

The seat of the sense of smell has been disputed for many years. Marshall (1935) reviews the early theories and shows that at some time practically every external organ of the insects body

has been credited with the centre of olfactory perception. To-day, the majority of workers in this field regard the antennae as the most important olfactory organs, for instance Von Fritsch in bees, Valentine in Tenebrio molitor (1931), Crombie in Rhizopertha dominica (1941) and Mininch (1921).

Glaser (1927) came to the conclusion that the antennae are used for long-distance perception and that the palpi are the more important organs at short range. He worked on the Cockroach, Periplaneta americana.

McIndoo attempted to demonstrate that other organs of the insect body were as important olfactory organs as the antennae. He regarded certain pits on the head capsule, head appendages, legs, dorsum of prothorax and last abdominal segment and on the anal prolegs of Lepidopterous larvae as olfactory organs. These same pits he found in a variety of insects (1919) including the Orthoptera (1920). In this group he regarded the wing-bases as the major centre of stimulation but as this has not been corroborated by morphological and experimental study, it can be dismissed (Marshall 1935).

The present opinion, therefore, is that the antennae are the main olfactory organs but that structures in other parts of the body may serve a subsidiary function.

b. Present Work. A similar set of experiments to those performed in connection with sight (see P. 43) was carried out on adult locusts to observe the effect of amputating the antennae on the amount of food consumed. The results are shown in Table 13.

TABLE 13.

Results of Experiments with adult locusts to test the effect on food consumption of amputating the antennae.

Experiment 1.Experiment 2.

No. of days from date of amputation of antennae. Results expressed as Total Area of Bamboo leaf surface in sq.ins.eaten by 2 pairs of adult locusts in each cage. Results expressed as Total Weight of Dry Frass in gms produced in each cage. By 4 pairs of Adult Locusts. By 5 pairs of Adult Locusts.

TABLE A.TABLE B.TABLE C.

Control Cage Treated Cage

Control Cage Treated Cage Control Cage Treated Cage

1	X	X	X	X	X	X
2	X	X	X	X	X	X
3	10.46	13.09	0.96	0.33	X	X
4	0.03	9.29	1.48	0.56	3.85	3.84
5	15.73	27.04	0.98	0.595	6.08	4.46
6	18.18	16.98	1.165	0.52	4.43	3.31
7	16.62	8.96	0.965	0.48	4.65	3.44
8	18.44	7.12	1.265	0.84	4.77	0.60
9	X	X	1.01	0.925	X	X
10	X	X	1.125	1.295	X	X

A. Area eaten

TOTAL

79.46

82.48

8.94

5.54

23.79

15.65

B.C.Wt.of Frass

Mean/Day/Locust.

3.31

3.435

0.140

0.087

0.476

0.313

All the insects used in Experiments A and B survived for the duration of the test but four deaths occurred towards the end of Experiment C. Locusts which have had their antennae amputated must suffer considerably from shock. A more satisfactory technique would be to coat the surface of the antennae with a substance which effectively blocks the olfactory organs and prevents them being used. However, the antennal cleansing mechanism on the legs of these insects is so efficient that it is difficult to find a substance which cannot be scraped off.

Making a slight allowance for the effect of the injury, the results show that the antennae are not important organs for the finding of food by Acrididae. Observations on normal grasshoppers under confinement show that at frequent intervals they bring their antennae to bear on the surface on which they walk, but the movement of these organs is not more pronounced when starving individuals are in close proximity with a supply of food. It appears that the antennae of Acrididae are chiefly employed as tactile organs.

Figure 8 is a diagram of the apparatus used to test the sense of smell of Acrididae. This consisted of a cylindrical glass container, 12 inches high and with a diameter of 7 inches, the floor of which was divided in two by an inch deep partition. In each half were placed the substances being tested and then they were covered by a circular sheet of wire gauze which prevented the insects from coming into contact with them.

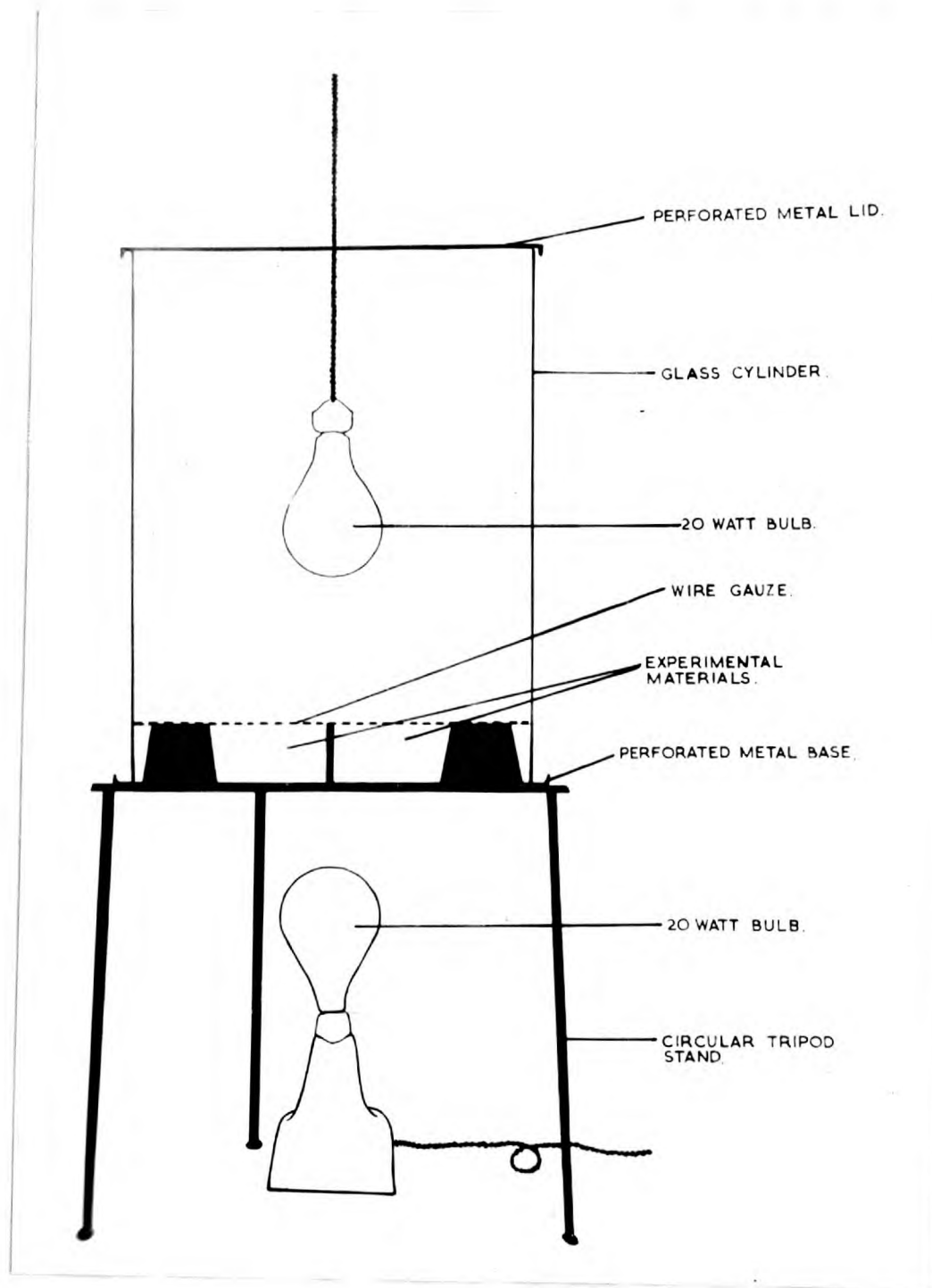


Figure 8. Diagram of apparatus used to test the olfactory sense of Acrididae.

The apparatus was placed on a large circular tripod stand. A 20 watt electric light bulb was suspended from the lid of the cage and another was mounted under the tripod. The position of the bulbs was adjusted until they were an equal distance from the gauze partition. This was to prevent the insects from moving towards the source of heat and light. About 20 first and second stage hoppers of Locusta were used in each experiment but the actual number differed slightly between tests. At 5 minute intervals six counts were made of the number of insects over each section. A record was also kept of the number of individuals on the sides of the cage. Each figure in Table 14 represents the sum of the six counts made in each experiment. Twelve experiments were carried out on a choice of green raffia and Holcus mollis, ten on green raffia and Arrhenatherum elatius, twelve on Holcus and Arrhenatherum and eight on yellow and green raffia. This last test was made in order to see whether the dye used to colour the raffia was having a repellent effect. From the results, it seems that this may have been the case to a slight extent. None of the other sets of results was significant between the two sides.

TABLE 14.

Experiment with first and second stage hoppers of *Lucusta* to demonstrate the presence of a sense of smell used to detect food. Each figure is the sum of six counts made at five-minute intervals.

	Green Raffia	<i>Holcus mollis</i>	Hoppers on sides, etc.
No. of Trials 12	59	38	29
	53	50	23
	49	51	26
	72	31	23
	28	72	14
	11	90	13
	21	80	13
	23	51	40
	106	23	36
	103	35	24
	67	64	31
	53	64	45
Total	645	649	317
Average	54	54	26
<u>Green Raffia <i>Arrhenatherum elatius</i></u>			
No. of Trials 10	64	49	37
	54	61	35
	39	80	31
	20	81	31
	51	43	22
	63	43	22
	71	20	35
	51	59	16
	61	43	22
	63	34	22
Total	537	513	273
Average	54	51	27
<u><i>Holcus mollis</i> <i>Arrhenatherum elatius</i></u>			
No. of Trials 12	55	46	25
	48	54	24
	30	63	33
	66	28	32
	54	46	14
	40	54	20
	53	46	33
	34	70	28
	42	59	25
	49	50	27
	54	36	36
	36	50	40
Total	561	602	337
Average	47	50	28

TABLE 14. (Continued).

	Yellow Raffia	Green Raffia	Hoppers on Sides, etc.
No. of Trials 8	53	43	30
	66	37	23
	74	39	13
	59	48	19
	77	64	27
	83	50	35
	67	69	32
	75	59	34
Total	554	409	213
Average	69	51	27

No preference was shown for the side with the more suitable food in any combination used. There were as many hoppers over the section containing the grass Arrhenatherum elatius as there were over Holcus mollis. It has already been shown (see P.25) that Arrhenatherum is a very unpalatable grass to locust hoppers, whereas Holcus is one of the most preferred.

This apparatus is similar to that used by Chun-Teh-Chin in his work on Leptinotarsa decemlineata (1950) and by Dethier (1937).

From these experiments it appears that the sense of smell is not used to locate food by these insects. Some work was also done with a Y-shaped olfactometer. Figure 9 is a diagram of this apparatus.

This was a glass tube with an internal diameter of about an inch and rather more than 12 inches in total length. One arm of the Y was connected to a tube containing crushed Holcus, reduced to this condition by pounding it with a little water in a pestle and mortar, while the other led to a similar tube containing damp cotton wool. These tubes were connected with a pressure gauge. The stem end of the Y was closed with a rubber bung after an insect had been introduced. Also at this end of the apparatus was a small outlet tube connected by pressure tubing to a suction pump. When this was turned on, a stream of air was drawn through the apparatus, the gauge being used to ensure that an equal flow passed down each arm of the Y. The insects passed more rapidly down the apparatus if the stem of the tube was surrounded with black paper to about an inch of the fork. The diameter of the

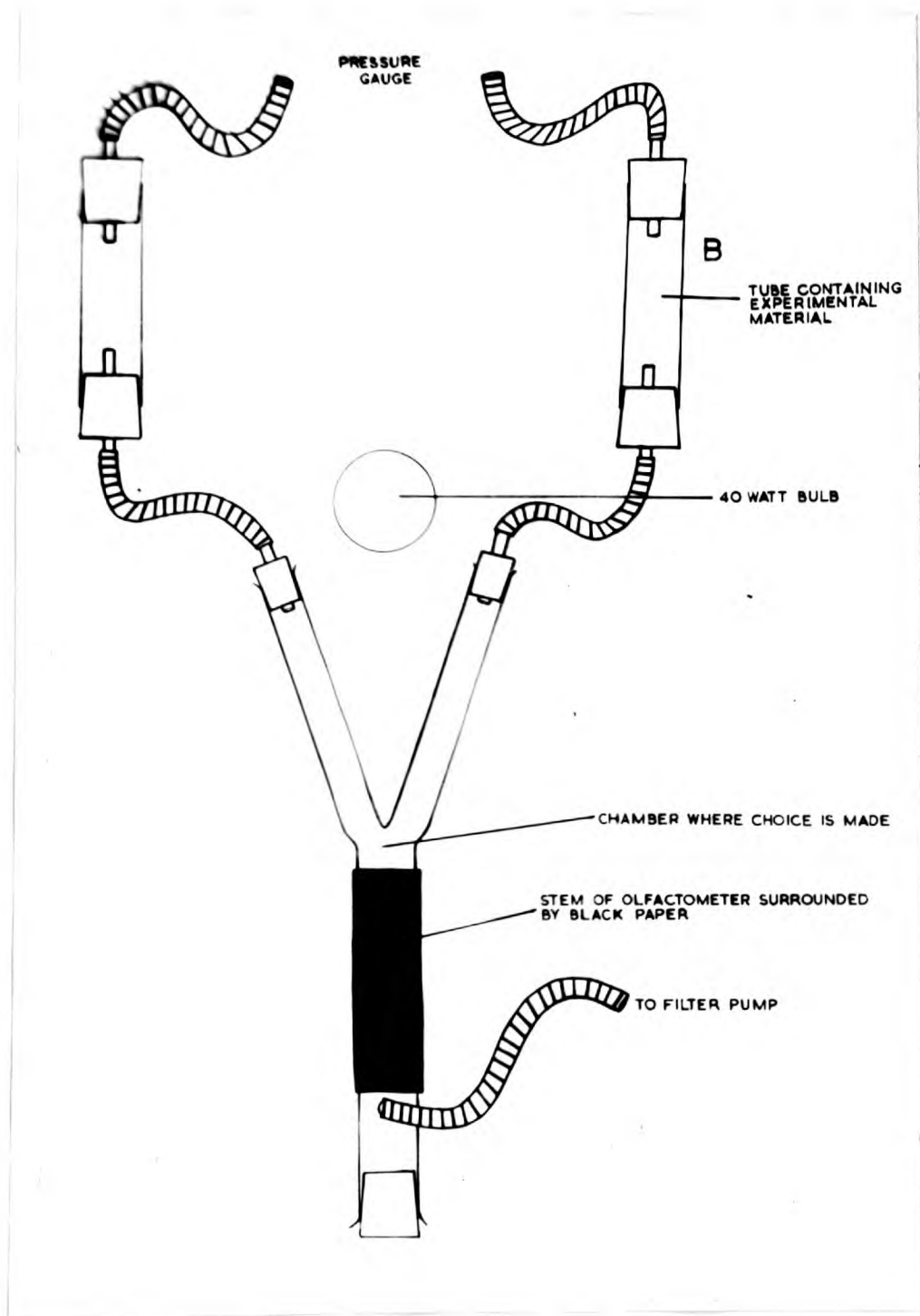


Figure 9. Diagram of olfactometer used in experiments with Acridid nymphs.

tube was wide enough to allow adult grasshoppers to walk through the arms but nymphs of Chorthippus parallelus, Locusta migratoria and Schistocerca gregaria were actually used in the experiments. The insect usually began to move down the tube towards the source of light almost immediately after it was introduced. On reaching the point where the black paper ceased, it would stop for some time. This should have enabled it to detect from which arm the smell of grass was coming. In a few instances, it moved too quickly down the tube for it to have been able to detect a smell from one direction. In these cases, which took place with the same frequency down both arms, a separate record was made.

At the beginning of this work, it was noticed that there was a tendency for each hopper to enter the same arm of the olfactometer that was entered by its predecessor. It is possible that this may be associated in some way with the marching behaviour of these insects. The action of the palpi suggests that they were the organs used in this perception. By rinsing out the tube with absolute alcohol after each test, this tendency was stopped and the selection of the arms became random. It seems possible that some kind of trail is left which enables the hoppers to keep together in little bands.

The figures in Table 15 are insects which should have had time to locate the scented stream of air and choose their path accordingly. Again, there is no evidence that Acrididae possess a well defined olfactory sense.

TABLE 15.

Olfactometer experiments with Acridid nymphs.

	Cotton Wool	Holcus	Total
<u>Chorthippus parallelus</u>	15	25	40
	22	18	40
Total	37	43	80
<u>Locusta migratoria</u>	15	25	40
	21	19	40
Total	36	44	80
<u>Schistocerca gregaria</u>	24	16	40
	18	22	40
Total	42	38	80

iii) The palpi and taste.

Taste is a very important factor in the food selection of grasshoppers and locusts. Already it has been shown that the grass Arrhenatherum elatius is rejected by hoppers of Locusta and several British grasshoppers in captivity, and by watching the behaviour of these insects, it is seen that this plant is only rejected after a preliminary nibble at the edges of a blade. The results of experiments to test the palatability of this grass compared with Holcus mollis are set out in Table 16 and Figure 10. They show the numbers feeding on each grass at five minute intervals. Examination of this will show that whereas the number feeding on Holcus steadily increases for 15 minutes, then gradually falls off, the number on Arrhenatherum decreases from the first count (5 mins.). Although both kinds of grass attract the same number of hoppers in the first place,

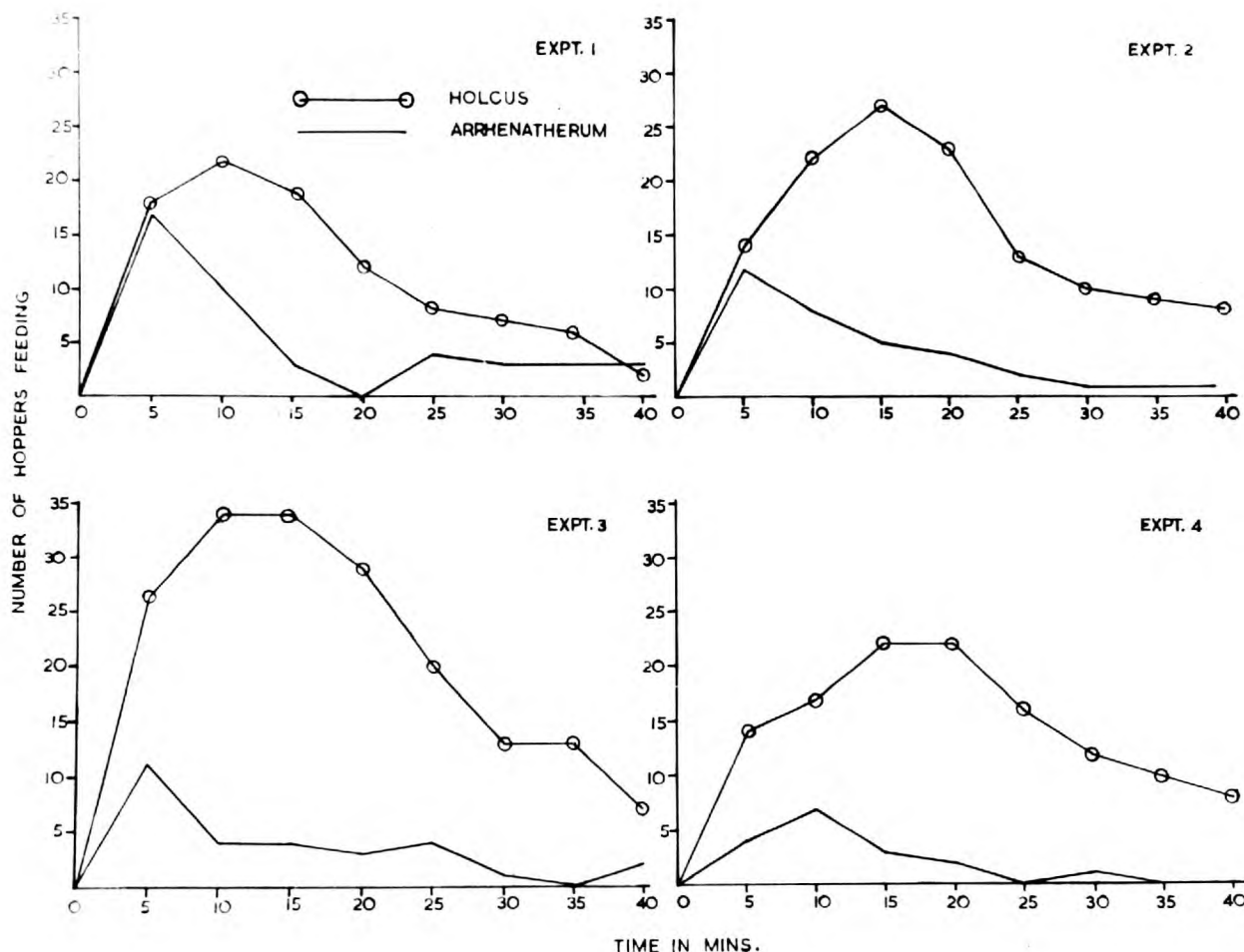


Figure 10. (Part 1). Results of four experiments to show the relative palatability of two grasses, Holcus mollis and Arrhenatherum elatius to Locusta hoppers. The curves for Arrhenatherum show the rejection of this grass only after preliminary attempts at feeding. Thus, the maximum count on this unpalatable grass is usually after 5 minutes but is 10-20 minutes on Holcus.

once the insects have sampled Arrhenatherum, they move across to the Holcus and progressively add to the number there. They continue to nibble at pieces of Arrhenatherum until they come upon a fragment of Holcus, when they settle down to feed systematically.

Table 16 and Figure 10 should be compared with Table 17 and Figure 11 which show the results obtained in a Holcus mollis x Festuca ovina agg. choice experiment. These indicate an initial rise in the number feeding on both grasses, consistent with the view that both species are acceptable to the insects.

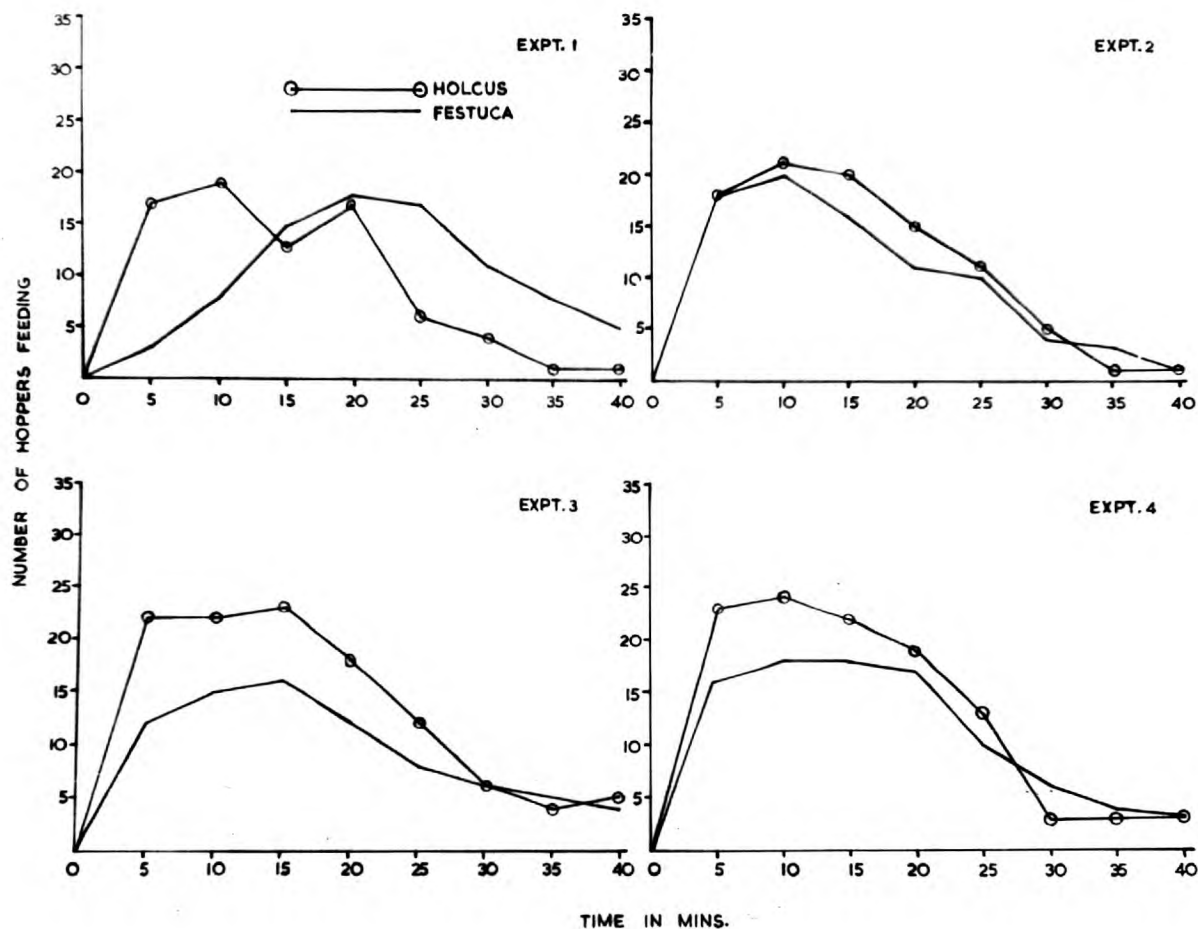


Figure 11. (Part 1). Results of four experiments to show the relative palatability of two grasses, *Holcus mollis* and *Festuca ovina* to *Locusta* hoppers. Both grasses are palatable to these insects.

TABLE 16.

Results obtained in Holcus mollis X Arrhenatherum elatius choice experiments, showing the number of Acrididae feeding on each at five-minute intervals.

Time in Mins.	<u>Chorthippus albomarginatus</u>										Total	
	<u>Holcus mollis</u>					<u>Arrhenatherum elatius</u>				H	A	
5	15	36	21	17		8	10	26	8	89		52
10	18	41	25	21		7	8	7	5	105		27
15	20	39	26	25		7	1	6	8	110		22
20	22	24	22	23		10	2	3	4	91		19
25	19	26	20	24		9	4	0	3	89		16
30	15	18	17	25		10	1	0	4	75		15
35	14	11	9	19		6	2	3	4	53		15
40	8	7	11	12		3	0	4	2	38		9
45	5	7	7	15		1	1	2	3	34		7
Totals	136	209	158	181		61	29	51	41	866		182
<u>Locusta migratoria (nymphs)</u>												
5	18	14	14	26		17	12	4	11	72		44
10	22	22	17	34		10	8	7	4	95		29
15	19	27	22	34		3	5	3	4	102		15
20	12	23	22	29		0	4	2	3	86		9
25	8	13	16	20		4	2	0	4	57		10
30	7	10	12	13		3	1	1	1	42		6
35	6	9	10	13		3	1	0	0	38		4
40	1	8	8	7		3	1	0	2	24		6
Totals	93	126	121	178		43	34	17	39	516		123

TABLE 17.

Results obtained in Holcus mollis X Festuca ovina agg. choice experiments, showing the number of Acrididae feeding on each at five-minute intervals.

Time in Mins.	<u>Chorthippus albomarginatus</u>								<u>Total</u>	
	<u>Holcus mollis</u>				<u>Festuca ovina</u>				<u>Holcus</u>	<u>Festuca.</u>
5	28	18	16	8	17	17	4	14	70	52
10	25	21	16	12	22	20	5	19	74	66
15	25	19	17	16	26	24	8	21	77	79
20	20	20	18	15	24	24	9	22	73	79
25	21	14	17	14	15	23	6	20	66	64
30	10	8	20	9	7	14	7	16	47	44
35	5	7	20	13	6	5	9	14	45	34
40	5	4	14	6	3	9	5	11	29	28
45	5	2	12	5	3	3	9	6	24	21
Totals	144	113	150	98	123	139	62	143	505	467
Time in Mins.	<u>Locusta migratoria</u>								<u>Total</u>	
	<u>Holcus mollis</u>				<u>Festuca ovina</u>				<u>Holcus</u>	<u>Festuca.</u>
5	17	22	18	23	3	12	18	16	80	49
10	19	22	21	24	8	15	20	18	86	61
15	13	23	20	22	15	16	16	18	78	65
20	17	18	15	19	18	12	11	17	69	58
25	6	12	11	13	17	8	10	10	42	45
30	4	6	5	3	11	6	4	6	18	27
35	1	4	1	3	8	5	3	4	9	20
40	1	5	1	3	5	4	1	3	10	13
Totals	78	112	92	110	85	78	83	92	392	338

This rejection of unacceptable plants by grasshoppers was observed both in the field and in the laboratory. In each instance the grasshopper would wander away after first nibbling at the edge of a leaf, often chewing at the next blade on the same shoot of vegetation. Plants on which these attempts to feed were noted included Lycopersicon esculentum Hill, Narcissus pseudo-narcissus L., Helianthemum sp., Chrysanthemum parthenium (L. and species of moss, some of which, to us, have a very pronounced and unpleasant bitter taste and smell.

It might be argued that the above observations could be as easily explained on the grounds of relative hardness. That this is not the factor concerned in this case can easily be demonstrated by offering the grass Dactylis glomerata which is a much tougher species than Arrhenatherum elatius, but one on which they will feed very readily.

The experiments carried out on adult locusts to test the effect on feeding of blackening over the eyes and amputating the antennae were also performed using insects with their palpi removed. The results are set out in Table 18 (for experimental details see P. 43).

Allowing for the shock due to the operation, two of the locusts so treated died on the fourth day of experiment C and were replaced; these figures show that loss of the palpi does not seriously handicap the insects in finding the food.

TABLE 18.

Experiments with adult locusts to test the effect on food consumption of amputating the palpi.

No. of days from the date of amputation of the palpi.	EXPERIMENT 1.		EXPERIMENT 2.			
	Results expressed as Total area of Bamboo Surface in sq. ins. eaten by 2 prs. of Adult Locusts in each cage.		Results expressed as Total Dry Weight of Frass in gms. produced in each cage. By 4 pairs of Locusts		By 5 pairs of Locusts.	
	Table A.		Table B.		Table C.	
	Control Cage	Treated Cage	Control Cage	Treated Cage	Control Cage	Treated Cage
1	X	X	X	X	X	X
2	X	X	X	X	X	X
3	10.46	8.43	0.96	0.74	X	X
4	0.03	11.05	1.48	1.17	3.85	2.34
5	15.73	13.29	0.98	0.77	6.08	4.24
6	18.18	13.49	1.165	0.96	4.43	3.64
7	16.62	17.28	0.965	0.97	4.65	3.64
8	18.44	16.23	1.265	1.25	4.77	3.37
9	X	X	1.01	1.43	X	X
10	X	X	1.125	1.32	X	X
A area eaten Total	79.46	79.77	8.94	8.61	23.79	17.22
B C Wgt. of Frass						

C. POSSIBLE CHEMICAL ATTRACTANTS AND REPELLENTS.

On this aspect of the problem, only preliminary exploratory experiments have been attempted. It is probable that an essential oil present in the cells of the plants plays an important role in deciding whether or not they are eaten. Most grasses are eaten, as are sedges and rushes, and all these plants have foliage of a similar type. However, the leaves of Galanthus nivalis L. and Narcissus pseudo-narcissus L. are of a form similar to these but are not eaten. The leaves of bamboo are different from the blades of most grasses but they are freely eaten. The writer was unable to find any reference to a chemical present in most Grasses. Sedges and Rushes which could account for their almost equal degree of acceptability.

A quantity of Holcus mollis and Arrhenatherum elatius were, in turn, subjected to ether extraction in a large Soxhlet apparatus for 48 hours. It was found that the grass was, as a result of this treatment, left in such a limp condition that the mandibles of the grasshoppers were unable to bite into it. Attempts to restore turgidity were all unsuccessful, doubtless due to unavoidable removal of the wax layer on the epidermis as well as the oils present in the internal tissues of the grasses. The insects also refused to eat tissue paper which had been soaked in the extract, although hungry locusts will often bite tissue paper to pieces if given the opportunity. However, no biting response was obtained within 15 minutes in an experiment testing the reaction of grasshoppers to white paper, (see P.79)

so it seems that grasshoppers are less willing than locusts to try to feed on unfamiliar substances.

Likewise, the addition of cumarin to bran failed to make the bran any more acceptable to locusts. This substance is present in many grasses, but is, unfortunately, soluble only in organic solvents which makes it a difficult chemical to use for experimental work of this kind.

H. and M. Frings (1949) did a considerable amount of work on the loci of contact chemoreceptors in insects. They found that contact receptors (i.e. organs of taste) were present in the grasshopper Melanoplus differentialis, at the tips of the maxillary and labial palpi and on the hypopharynx but nowhere else on the mouth-parts or on any other parts of the body. They also tested the cockroach, Periplaneta americana, for thresholds of sucrose. The insects were starved for 24 hours, then given water to satiety. It was found that normal cockroaches were sensitive to dilutions of sucrose solution between 0.028 - 0.057 M but from earlier work (Frings 1946) it would appear that some individuals of this species can detect a solution still more dilute. Results of amputation of the organs bearing the chemoreceptors suggested that the hypopharynx is the most sensitive of these structures. With all these organs removed, no response was observed to sugar solutions when the insects were sated with water.

The only study of this kind made in the present investigation was on sucrose solutions of strengths varying between M - 0.01 M using normal adults of Chorthippus parallelus. Sugar is a much

more unusual food substance for grasshoppers than it is for cockroaches, and as a result, these results are less valuable than they would be if a more normal food substance had been used. They are set out fully in Table 19.

Delicate needles were made for this work by mounting thin stainless steel pins on lengths of glass tubing by means of sealing wax. The insects were mounted on their backs, being held in position by a lump of black wax on the pronotum. Kicking by the hind legs, which might have freed the insects, was prevented by holding these down, also with a small ball of wax. This wax melts at a moderately low temperature and therefore can be applied without much risk of burning the insect. It quickly sets very hard at room temperature.

Droplets of distilled water were brought to the grasshopper's mouth until no more were swallowed. The ends of the palpi were then touched with droplets of sucrose solution, beginning with the most dilute (0.01 M) until a positive response was stimulated. This was judged as movements of the mandibles, a repeated opening and closure. The procedure was usually repeated for the next two higher concentrations. This was to ensure that the biting movement was not accidental. Finally, a droplet of water was given to see whether the response could be attributed to thirst, that is, reaction to the solvent and not to the solute.

TABLE 19.

Experiment to determine the threshold of taste for sucrose solution using starved adults of Chorthippus parallelus.

<u>Concentrations of Sucrose Solution.</u>									
<u>Trial</u>	<u>M</u>	<u>0.5M</u>	<u>0.2M</u>	<u>0.1M</u>	<u>0.08M</u>	<u>0.06M</u>	<u>0.04M</u>	<u>0.02m</u>	<u>0.01M.</u>
1	.	.	.	.	✓	✓	?	X	X
2	.	.	.	✓	✓	✓	X	X	X
3	.	.	✓	✓	✓	X	X	X	X
4	.	.	.	.	✓	✓	?	?	X
5	.	.	.	✓	✓	✓	X	X	X
6	X	X	X	X	X	X	X	X	X
7	.	.	.	✓	✓	✓	X	X	X
8	.	.	✓	✓	✓	✓	X	X	X
9	.	.	.	.	✓	✓	?	X	X
10	.	.	.	✓	✓	✓	X	X	X
11	.	.	✓	✓	✓	X	X	X	X
12	.	.	.	.	.	.	✓	✓	X

A similar range of salt solutions was tested on the same grasshoppers following this experiment, but no response was elicited at any concentration. Either this solution has a repellent effect or the grasshoppers are unable to distinguish it from distilled water.

The mean of the eleven results in Table 19 which show a positive response to sucrose solution is 0.064 M. The observed range was 0.02 M - 0.1 M. The twelfth insect was either unable to detect an M solution or, as is more probable, was not hungry.

In the experiment to demonstrate the importance of surface texture of leaf in food selection, (see P. 79), only one of the plants used failed to elicit a biting response in the grasshoppers. This was Cupressus lawsoniana. As this plant contains strongly aromatic resins, it is possible that these substances are repellents to some Acrididae. If this is the case, here we have the only positive evidence of an olfactory sense in grasshoppers in this work.

D. PHYSICAL PROPERTIES OF THE FOOD.

1) Toughness.

It was desirable to have an apparatus for measuring the comparative hardness and toughness of different kinds of grass. A diagram of the simple apparatus which was constructed is shown. (Figure 12). It consisted of a little box of stout paper through the bottom of which was stuck a number 10 entomological pin. A length of fine glass tubing slightly shorter than the pin was pushed into the cork bung of a 3 x 1 inch specimen tube. The blade of grass being measured was stretched across the mouth of the tube, then the cork was inserted carefully so that the grass remained taut. Next, the pin was introduced into the glass tubing. Silver sand was then slowly poured into the paper box until the point of the pin just penetrated the blade of grass. The sand was then removed and weighed. The apparatus was more rigid if a small flat piece of cork was stuck with glue to the underside of the paper box.

The results obtained with this rather crude piece of apparatus were surprisingly consistent for each kind of grass tested. Table 20 shows the relative toughness of some common British grasses estimated by this method. Ten measurements were made on each species.

This apparatus cannot be used for grasses with fine leaves like Festuca ovina and Nardus stricta. The form of Deschampsia flexuosa with its narrow but rather thick leathery leaves was difficult to test in this way, as the pin sometimes penetrated

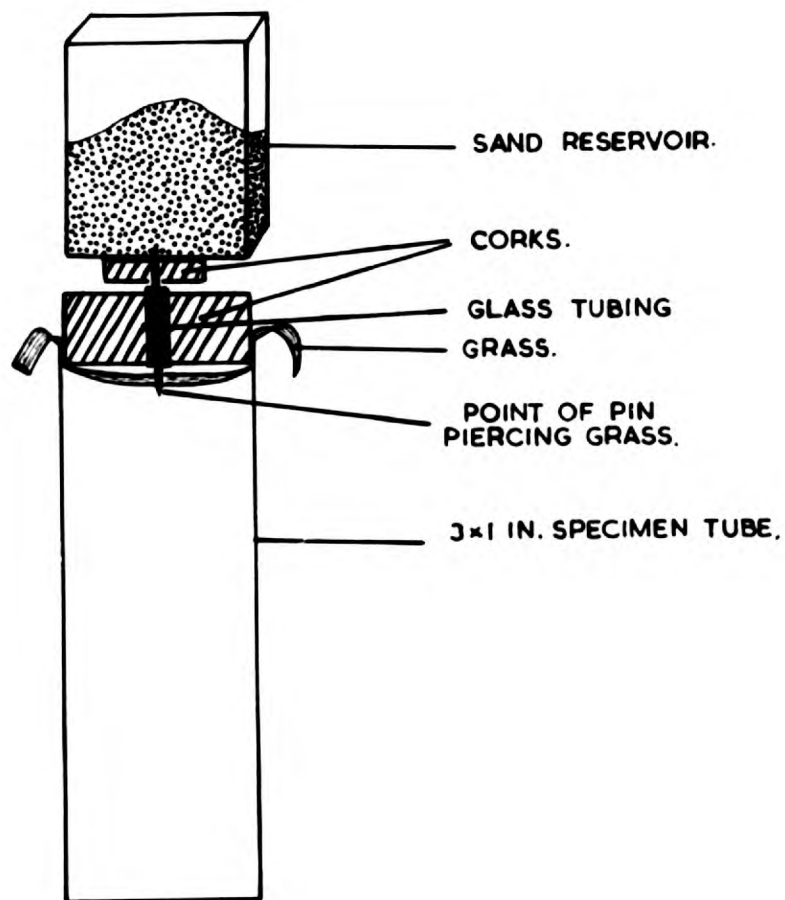


Figure 12. Diagram of apparatus used to measure the relative toughness of different kinds of grass.

the substance of the leaf at an oblique angle instead of vertically. This causes a certain amount of discrepancy in the results.

The paper box sand reservoir, as constructed, held only 25 gms of sand. The weight was insufficient to penetrate the leaf of bamboo.

Measurements were also made on different regions of the leaf of Holcus. These show that the toughest part of the leaf is at the apex as might be expected in leaves of this form. (Table 21). The comparative measurements on the seven grasses listed in Table 20 were made approximately at the middle of the blades, the leaves chosen being, as far as could be determined, of more or less the same age and condition for every species.

TABLE 20.

The relative toughness of some British grasses measured by the "sand reservoir" method. The figures are the weight of sand in grams required to push the point of the pin through the blade.

No.	<i>Holcus mollis</i>	<i>Bromus sterilis</i>	<i>Anthoxanthum odoratum</i>	<i>Alopecurus pratensis</i>	<i>Arrhenatherum elatus</i>	<i>Agropyron caninum</i>	<i>Deschampsia flexuosa.</i>
1	4.35	5.30	5.57	6.42	5.97	6.64	9.62
2	3.71	4.55	5.52	6.08	6.50	6.78	15.79
3	4.38	4.33	6.02	5.73	6.48	6.46	11.61
4	3.64	4.74	5.69	6.75	5.97	6.42	11.32
5	4.23	4.39	5.47	6.42	6.02	6.67	15.37
6	4.27	4.52	5.04	5.72	5.86	5.83	13.71
7	3.97	4.11	5.34	5.66	5.53	6.40	10.91
8	4.47	4.12	5.45	5.72	6.00	5.98	10.56
9	4.64	4.41	5.58	5.38	6.40	6.22	11.46
10	4.31	4.21	5.33	5.52	5.56	6.20	11.89
Mean	4.21	4.47	5.50	5.94	6.03	6.36	12.22

TABLE 21.

Holcus mollis. Measurements taken at different positions along the blade by the "sand reservoir" method. Figures are grams weight of sand.

	a) Base	b) Middle	c) Apex
L.1	3.15	3.46	4.31
L.2	3.11	3.44	3.71
L.3	2.68	3.25	3.66
L.4	3.43	3.55	4.84
Mean	3.09	3.43	4.13

When first instar hoppers of Locusta migratoria were fed with leaves of Bamboo, it was noticed that the insects moved along the edges of the leaves, frequently stopping to nibble, until they reached a place where the leaf was thinner and where they could insert their small jaws. In leaves of the shape of those of Bamboo, the thinnest region is near the apex, and, after a time, all the feeding hoppers were congregated at the apices of the leaves. When this experiment was repeated with older hoppers there was considerably less activity before the insects settled down to feed. This suggests that although Bamboo is, on the whole, a suitable food for Locusts, the leaves are too tough for the early stages which prefer to feed on a softer plant.

A batch of Locusta hoppers were taken straight from the egg and were daily given a choice of Bamboo and Holcus mollis until most of them had reached the fifth (penultimate) instar.

The number of hoppers feeding on each was counted at five-minute intervals for 30 minutes each day. The sum of the 6 readings obtained each day are set out in Table 22A, and, for a repetition of this experiment, in Table 22B.

These figures support the theory expressed above that toughness plays a part in the food selection of young hoppers. Using the "sand reservoir" method for measuring the relative toughness of grasses, Bamboo was 25+ whilst Holcus mollis was 4.2. Bamboo is probably a much tougher plant than any which the British grasshoppers encounter in their natural habitats but, first stage nymphs of all the British Acrididae are very much smaller than newly hatched hoppers of Locusta. Third stage hoppers of Locusta are perhaps comparable in size with the adult females of Chorthippus bicolor and these results show that by the third instar, the hoppers were able to feed almost as readily on Bamboo as on the softer grass.

TABLE 22.

The relative acceptability of *Holcus* and Bamboo to *Locusta* hoppers of different stages.

<u>TABLE 22A.</u>		No. on	No.	Total	Percentage	Average
Day	Instar	<i>Holcus</i> <i>mollis</i>	on Bamboo	Number	of Total on Bamboo	Percentage on Bamboo/Instar.
1	1	75	24	99	24.2	18.4
2	1	97	26	123	21.1	
3	1	167	18	185	9.8	
4	1 and 2	152	73	225	32.4	25.2
5	1 and 2	249	58	307	18.9	
6	2	297	96	393	24.4	
7	2 and 3	151	126	277	45.5	44.8
8	2 and 3	178	227	405	56.0	
9	2 and 3	308	154	462	33.3	
10	3 and 4	238	232	470	49.4	58.4
11	3 and 4	180	299	479	62.5	
12	3 and 4	229	209	438	47.7	
13	3 and 4	164	328	492	66.6	
14	4	154	297	451	65.9	
15	4 and 5	153	132	285	46.3	

TABLE 22B.

1	1	X	X	X	X	
2	1	281	108	389	27.8	(24.0)
3	1	261	66	327	20.2	
4	2	242	25	267	9.4	
5	2	150	37	187	19.8	18.9
6	2	185	70	255	27.5	
7	3	194	188	382	49.2	
8	3	381	69	450	19.3	33.4
9	3	176	82	258	31.8	
10	3 and 4	132	103	235	43.8	
11	4	107	109	216	50.5	
12	4	183	187	370	50.5	50.9
13	4	123	298	421	70.8	
14	4	164	105	269	39.0	
15	4 and 5	110	114	224	50.9	
16	5	80	105	185	56.8	

For the following experiment it was necessary to know the length of time food was retained in the gut after the meal. To test this, 12 adult males of Gomphocerippus rufus were each confined in a 3 x 1 inch specimen tube for a period of 48 hours after being provided with a few leaves of Lolium perenne on which to feed. The food was removed after 30 minutes, and the number of frass pellets produced by each individual was counted every quarter of an hour. The results are set out in Table 23.

Examination of particles in the frass gives additional evidence of the effect of toughness of the food on the insects. Adult males of Gomphocerippus rufus were deprived of food for 48 hours to allow the contents of the gut to be fully expelled. They were then fed on five different kinds of grass and the frass pellets which they subsequently produced were examined microscopically. The size of the particles present was measured in each case. For this a micrometer eye-piece was used. Histograms are given for each grass. (Figures 13 A,B,C,D and E and Figure 14, A,B,C.) These show the number of particles in size groups arbitrarily chosen, in each batch of 100 measurements. Three hundred measurements were made on each species of grass, those selected for this work being Bamboo, Holcus mollis, Poa annua, Lolium perenne and Dactylis glomerata. In the faecal pellets of Bamboo there are considerably more particles in the smaller size groups compared with those of the other grasses used. This suggests that as this grass is exceptionally tough and difficult to chew these grasshoppers find it necessary to bite

TABLE 23.

The accumulated number of frass pellets produced by 12 males of *Gomphocerippus rufus* after a meal. Counts were taken at 15 minute intervals for 10 hours then only after 11.5, 25.5 and 48 hours, but the full number of readings is given only for the first 6 hours in this Table.

	0		1		2		3		4		5		6	7	8	9	10	11	25	48												
	.30	.45	.0	.15	.30	.45	.0	.15	.30	.45	.0	.15	.30	.45	.0	.30	.0	.0	.0	.0	.30	.30	.0									
1	0	1	1	2	2	3	3	4	5	5	6	6	7	7	8	8	9	10	10	10	10	10	10	11	11	12	12	12	13	15	15	
2	0	1	1	1	2	3	4	4	5	6	7	8	9	10	10	10	11	12	12	12	13	13	13	13	14	14	15	15	16	18	18	
3	0	1	1	2	2	3	3	3	4	5	5	6	6	7	7	7	8	8	8	9	9	9	9	10	10	11	11	12	12	15	15	
4	0	1	1	1	1	2	3	3	3	4	4	5	6	6	6	6	6	7	7	7	7	8	8	8	8	9	9	9	9	10	11	11
5	0	1	2	2	3	3	4	5	5	6	6	6	7	7	7	7	8	8	8	8	9	9	9	9	10	11	11	12	12	12	13	13
6	0	0	0	0	0	1	1	2	2	3	3	4	4	5	5	5	6	6	7	7	7	8	8	8	8	9	10	10	11	12	13	13
7	0	1	1	1	2	2	3	3	3	4	4	4	5	5	6	6	7	7	7	8	8	8	8	9	10	11	11	12	12	13	14	14
8	0	0	0	0	0	0	1	1	1	2	2	3	3	3	4	4	4	4	5	5	5	6	6	6	6	7	8	8	9	9	11	11
9	0	1	1	1	1	1	2	2	2	3	3	4	5	5	5	6	6	7	7	7	8	8	8	8	8	9	9	10	10	11	12	12
10	0	0	1	1	1	2	2	3	3	4	5	5	6	6	7	8	8	8	8	8	8	9	9	9	10	10	11	12	12	13	14	14
11	0	1	1	1	2	2	3	3	4	5	5	6	6	7	7	7	8	8	8	8	8	9	9	9	9	9	10	10	10	10	11	11
12	0	0	0	0	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	4	4	4	4	4	4	5	5	5	5	7	8

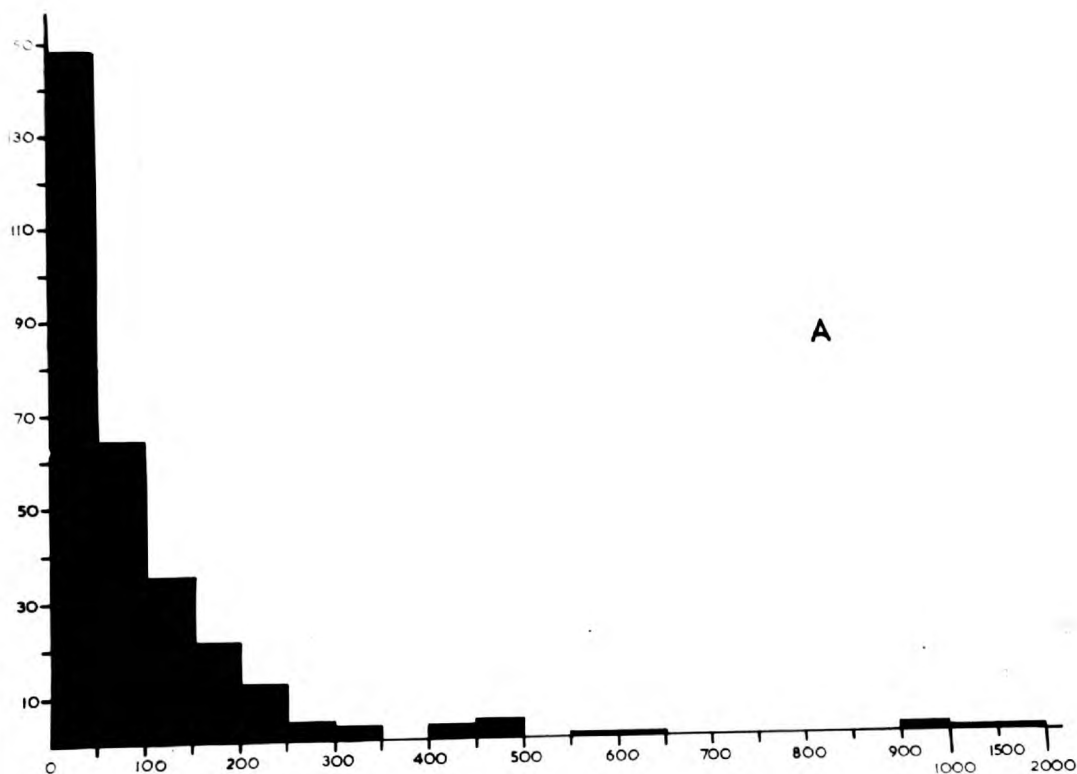
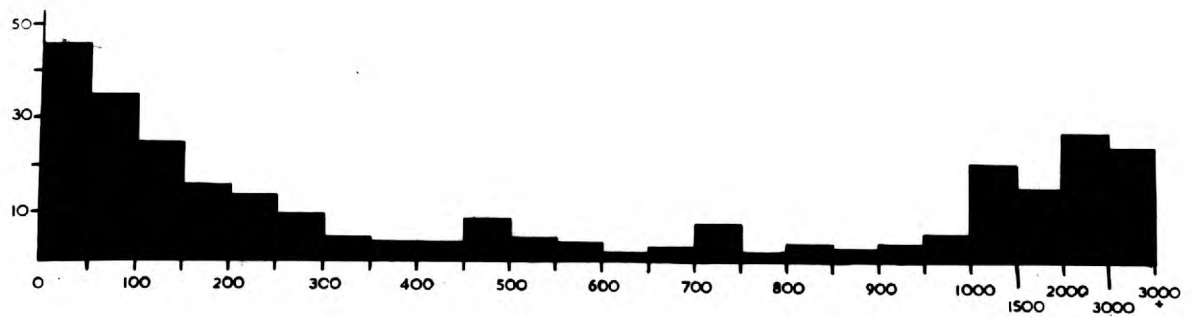


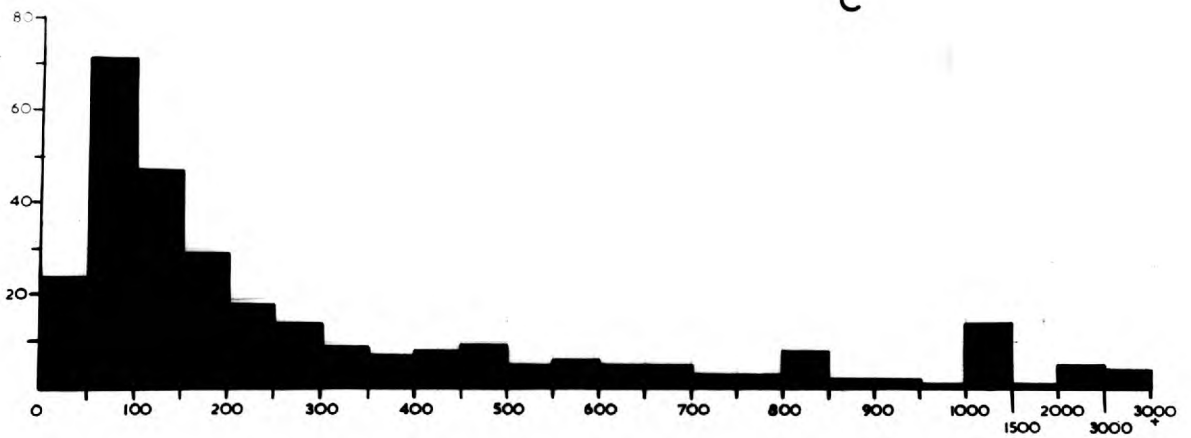
Figure 13. A -E. Histograms showing the number of particles of different size groups in the frass of adults of Gomphocerippus rufus after they had been fed on grasses of different degrees of toughness. Particles measured with a granulated eye-piece. 300 measurements made on each kind of pellet. 3,500 units of particle size = 1 sq mm. Toughness of grasses measured by "sand-reservoir" method and expressed in gms, weight required to push pin through leaf-blade.

A. <u>Bamboo (Bambusa sp.)</u>	Toughness	25
B. <u>Dactylis glomerata</u>	Toughness	7.5
C. <u>Holcus mollis</u>	Toughness	4.2
D. <u>Poa annua</u>	Toughness	4.0
E. <u>Lolium perenne</u>	Toughness	3.5

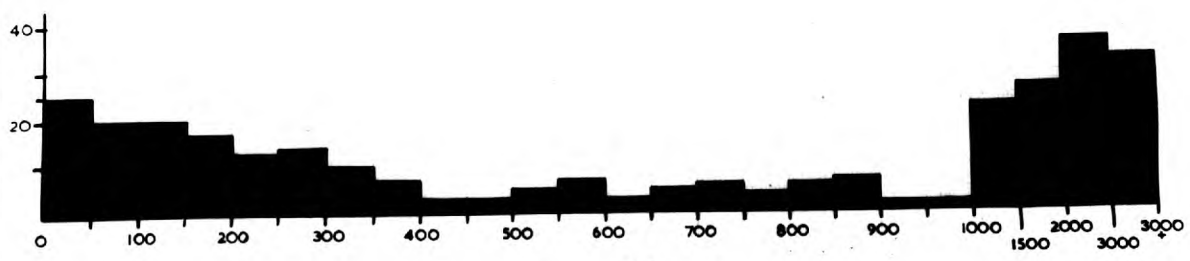
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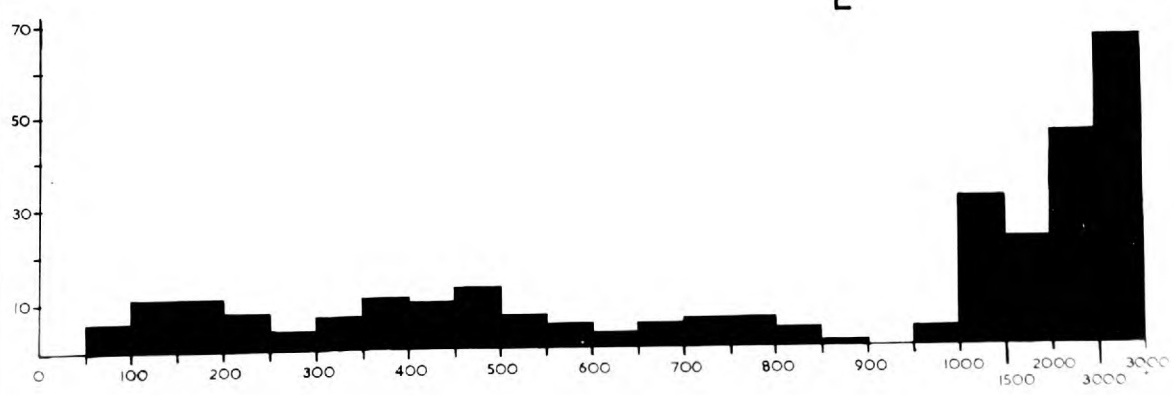
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D



E



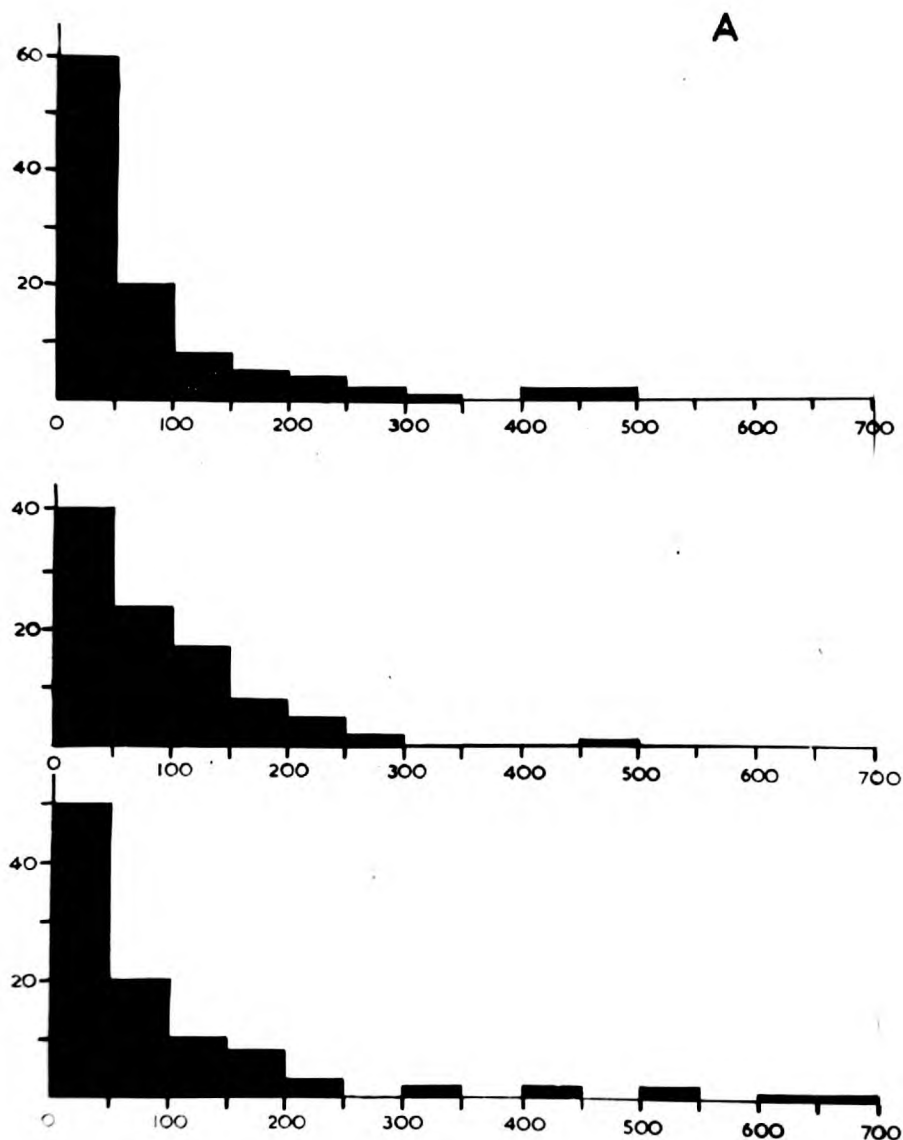
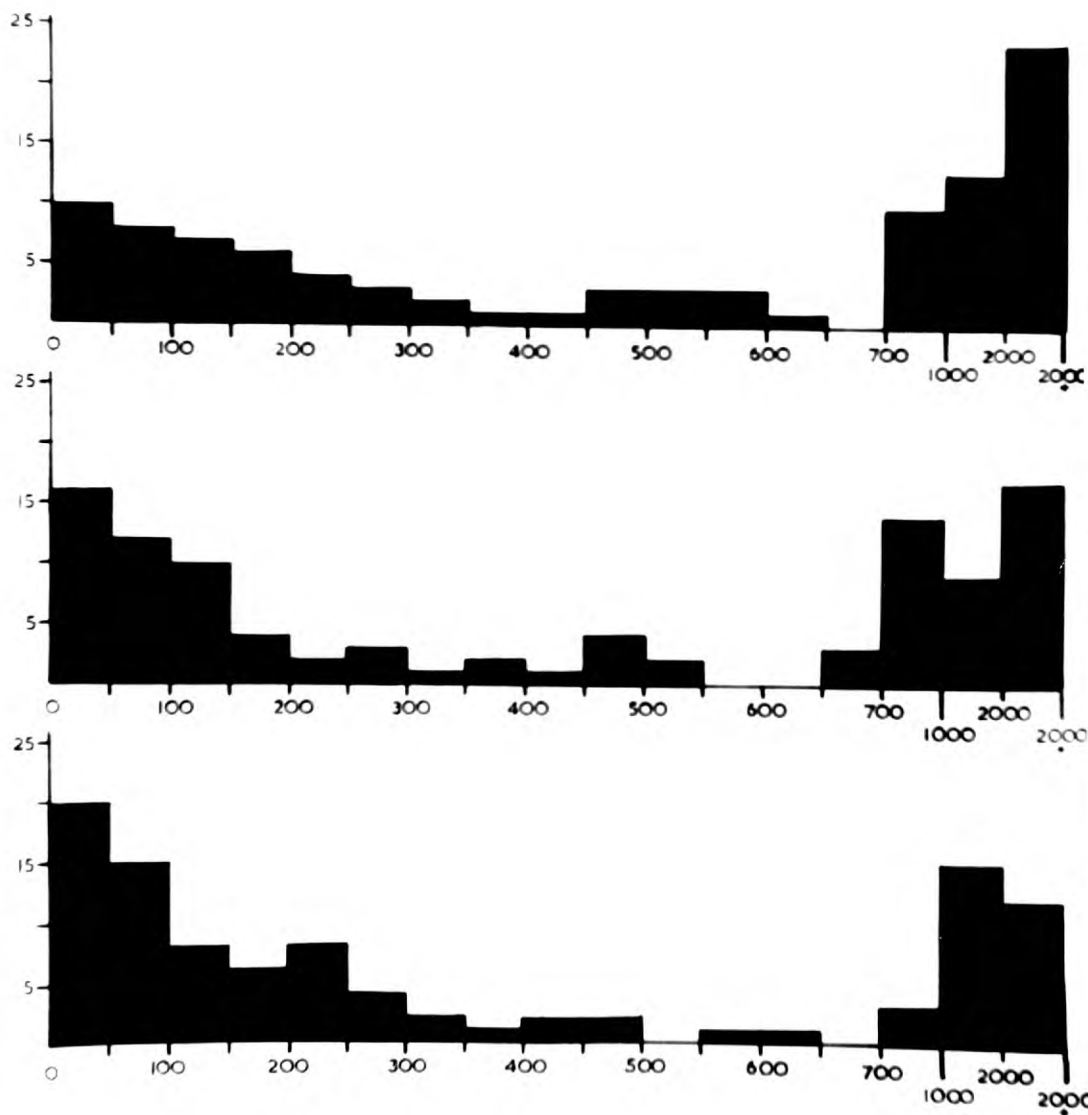


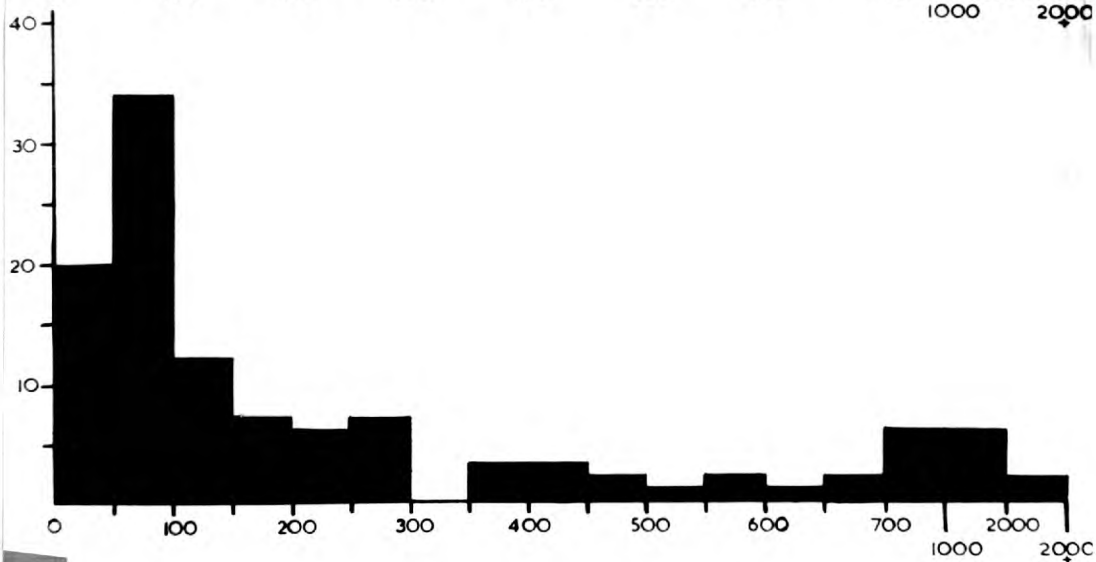
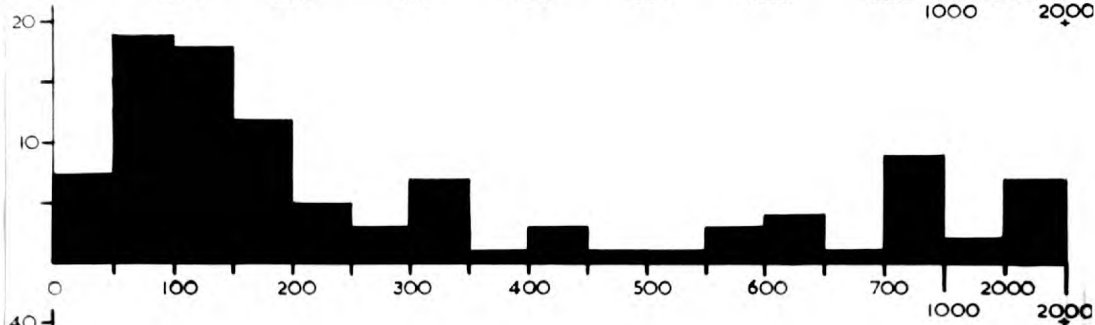
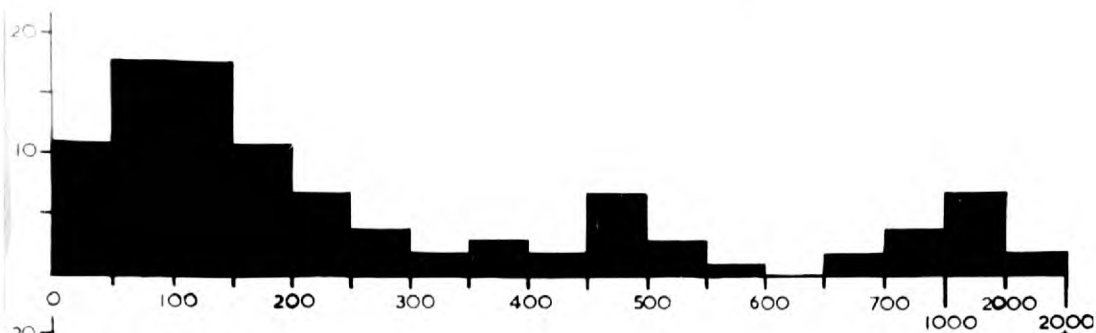
Figure 14, A - C. Measurement of particle size in frass as in figure 15. Three pellets of each type were examined separately to show the amount of variation between them. 3,600 units of particle size = 1 sq. mm.

A. <u>Bamboo (Bambusa sp.)</u>	Toughness	25
B. <u>Dactylis glomerata</u>	Toughness	7.5
C. <u>Holcus mollis</u>	Toughness	4.2

B



C



off smaller fragments than when feeding on softer species.

These figures show that defaecation virtually ceased after one day.

ii) Texture of Leaf Surface.

From the very considerable differences in surface texture between such grasses as Holcus mollis and Bamboo it cannot be expected that this factor plays a very important part in food selection by grasshoppers. Already it has been pointed out that these insects when hungry will not hesitate to nibble at the leaves of a very wide variety of different plants, some densely hairy, others perfectly glabrous.

If texture plays a part in this selection an indication of this should be given from a study of the time taken to elicit a biting response by grasshoppers on different plants. Therefore, a series of 10 tests were carried out on 5 males and 5 females of Gomphocerippus rufus by placing them in contact with a number of different plants in turn, using both grasses and broad-leaved plants as well as raffia and paper, and watching them closely for 15 minutes to observe if and when nibbling first took place. Table 24 gives the results obtained.

As a biting response was obtained in every instance except for Cupressus and Paper, it seems that texture plays no important part in food selection. The failure to chew Cupressus may be because the resins of Gymnosperms are repellent (see P.71) and it is possible that the sense of smell of these insects is able to detect the general smell of vegetation without being able to

distinguish the aroma of grasses from that of other plants. This would explain the absence of nibbling on the paper. Attempts to chew at the edges of leaves with very different textures were observed with apparently equal readiness (compare the smooth shiny leaves of Rhododendron with those of Agrostemma coronaria which have a dense mat of silky hairs clothing both surfaces).

TABLE 24.

Experiment to show the time taken to elicit a biting response by adults of Gomphocerippus rufus when presented with plants, etc. of different surface textures.

Plant, etc. being tested	No. of grass-hoppers i.e. No. of Tests.	No. of times a response was observed within 15 mins.	Av. Time/ response.	Av. Time in mins./ response not taking into account the "no responses".
<u>Plants/Grasses.</u>				
1. <u>Holcus mollis</u>	10	10	1.3	1.3
2. <u>Holcus mollis</u> (Dupl)	10	7	7.3	3.5
3. <u>Bamboo</u>	10	9	6	5
4. <u>Arrhenatherum elatius</u>	10	9	4.8	3.7
5. <u>Deschampsia flexuosa</u>	10	8	6.1	3.9
<u>Plants other than Grasses</u>				
1. <u>Juncus effusus</u>	10	8	4.8	2.3
2. <u>Digitalis purpurea</u>	10	8	4.5	1.8
3. <u>Rhododendron</u>	10	10	4.3	4.3
4. <u>Anchusa sempervirens</u>	10	8	4.1	1.4
5. <u>Agrostemma coronaria</u>	10	8	5	2.5
6. <u>Chrysanthemum</u>	10	8	5.9	3.6
7. <u>Cupressus lawsoniana</u>	10	0	-	-
<u>Other Substances.</u>				
<u>Raffia</u>	10	6	7	1.7
<u>Strips of Paper</u> (White smooth surface)	10	0	-	-

ii) Shape and position of Leaf.

As biting responses can be induced with equal ease on broad, narrow, entire and dissected leaves, the shape of the leaf

appears to be of no importance in food selection, i.e. the shape cannot be a "sign stimulus" in this reaction. (See Discussion Page 96). Results of an experiment comparing the number of grasshoppers feeding on upright and horizontal grass are given and discussed above. (See Page 51).

iv), Age of Leaf.

Within broad limits, this appears to have little effect on food selection. Yellowing leaves are quite readily eaten as long as they remain turgid, when they begin to wither, however, they are difficult to chew. Very old dry leaves may be too tough to eat. If grass in the cages is not kept in water it quickly dried up and became brittle. Even in this state, grasshoppers, if hungry, would make repeated attempts to chew it but without success.

TABLE 25.

Experiments with adult locusts to test the effect on food consumption of amputating the antennae amputating the palpi, blackening over the eyes. One experiment was also carried out on locusts in which all these sense organs had been treated. The figures in Experiment 1 are sq. ins. of grass eaten, those in Experiments 2 and 3 weight of dry frass in gms. The majority of these results have previously been given in Tables 9, 13 and 18.

No. of days from start of Expt.	Experiment 1 (4 locusts)					Experiment 2.							
	Con- trol	Eyes black- ed	Antennae removed	Palpi removed	All sense organs removed or black- ed out.	Con- trol	Eyes black- ed	Antennae removed	Palpi re- moved	Con- trol	Eyes black- ed	Antennae re- moved	Palpi re- moved
1	X	X	X	X	X	X	X	X	X	X	X	X	X
2	X	X	X	X	X	X	X	X	X	X	X	X	X
3	10.46	6.88	13.09	8.43	0.81	0.96	0.30	0.33	0.74	X	X	X	X
4	0.03	2.64	9.29	11.05	0.87	1.48	0.51	0.56	1.17	3.85	3.55	3.84	2.34
5	15.73	1.91	27.04	13.29	3.65	0.98	0.51	0.595	0.77	6.08	5.33	4.46	4.24
6	18.8	5.82	16.98	13.49	5.30	1.165	0.51	0.52	0.96	4.43	3.58	3.31	3.64
7	16.62	4.57	8.96	17.28	4.53	0.965	0.52	0.48	0.97	4.65	2.98	3.44	3.64
8	18.44	3.21	7.12	16.23	6.90	1.265	0.74	0.84	1.25	4.77	3.91	0.60	3.37
9	X	X	X	X	X	1.01	0.84	0.925	1.43	X	X	X	X
10	X	X	X	X	X	1.125	0.80	1.295	1.32	X	X	X	X
A area eaten													
TOTAL	79.46	25.03	82.48	79.77	22.06	8.94	4.73	5.54	8.61	23.79	19.35	15.65	17.22
B.C.Wgt. of Frass.													
Mean/ Day/ Locust	3.31	1.04	3.435	3.32	3.677	0.140	0.074	0.087	0.135	0.476	0.387	0.313	0.344

6. MORPHOLOGY OF MANDIBLES AND CROP.

A. Mandibles.

The morphology of the mouth parts of a few species of Orthoptera and related insect orders has been investigated by a number of workers.

In the present work, permanent slide mounts were made of the maxillae and labia of the eleven British Acrididae and of Locusta migratoria and Schistocerca gregaria. The differences between these thirteen species are slight, apart from size, the chief variation is in the degree of sclerotization of the tooth-like ligulae and of the paraglossae.

A much wider variation is found in the morphology of the mandibles. Uvarov, (1928), first drew attention to the marked differences in the mandibulate "teeth" of some species of Acrididae. Isely, (1944), made an extensive study of the mandibular morphology of a large number of the Acrididae and Tettigonidae of the North American States of Texas and Colorado. He showed that, in many species, the mandibles are specially adapted to the type of vegetation which is the normal food.

In earlier work on the food preferences of forty species of Acrididae, (1938), Isely found that these insects fall into two groups of approximately equal size - the grass feeders and the herb feeders. Some of the species he chose were mixed feeders, but usually these showed a preference for one of these two types of vegetation.

Among the types chosen for his morphological work are representatives of each of the main sub-families of the Acrididae, twenty-four are Acridinae, twenty-four are Oedipodinae, four are now placed in the new group Romaleinae and thirty-seven are Catantopinae.

Of the thirteen species studied in the present work, ten belong to the Acridinae, two to the Oedipodinae and one to the Catantopinae. Of these, laboratory experiments and field observations have shown that ten are almost exclusively grass feeders and one, Schistocera gregaria, the only representative of the Catantopinae, is a mixed feeder. The food preferences of Oedipoda caerulea and Chorthippus vagans have not been studied in the present work. A wide variation in the structure of the mandibles was not expected as most of the species have similar feeding habits. Nevertheless, interesting differences were found and in the following grouping, species with a similar mandibulate pattern have been placed together. Five principal groups are recognised.

- | | | |
|----------|-----------|---|
| Group 1. | 1 species | <u>Schistocera gregaria</u> . |
| 2. | 2 species | <u>Chorthippus vagans</u> , <u>Oedipoda caerulea</u> . |
| 3a. | 4 species | <u>Mecostethus grossus</u> , <u>Stenobothrus lineatus</u> , <u>Chorthippus parallelus</u> , <u>Locusta migratoria</u> . |
| 3b. | 1 species | <u>Myrmeleotettix maculatus</u> . |
| 4. | 3 species | <u>Omocestus viridulus</u> , <u>O. ventralis</u> , <u>Chorthippus bicolor</u> . |
| 5. | 2 species | <u>Gomphocerippus rufus</u> , <u>Chorthippus albomarginatus</u> . |

The considerable differences between the mandibles of the four British species of Chorthippus are perhaps interesting systematically. Similar differences in the members of one genus were noted by Isely.

Isely distinguishes three main types of Acridid mandibles, broad-leaved plant feeding, grass feeding and mixed plant feeding. Intermediates occur between each type. Of the five groupings listed above, 1 is of the mixed feeding type, and groups 3-5 are all graminivorous. Group 2 is intermediate.

The asymmetry of grasshopper mandibles, and the curious feature that the left mandible overlaps the right, have been discussed and figured by Uvarov and by Snodgrass (1928). Each mandible consists of a main body and two lobe-like regions, the biting or incisor lobe and the grinding or molar lobe. (See Fig. MA A-F). The teeth and ridges of the right mandible fit into those of the left. In graminivorous species, the jaws are said to interlock more closely than in the other types. In these species, too, the bevelling of the distal edge of the right incisor lobe is usually more pronounced.

Wherever possible, a number of individuals of each species was examined. In most cases only slight differences were observed between specimens of the same species. These consisted of variation in the area of darkening (where the jaw is fully exposed and not covered by integument or the overlap of the opposite mandible) and in the degree of sharpness of the incisor

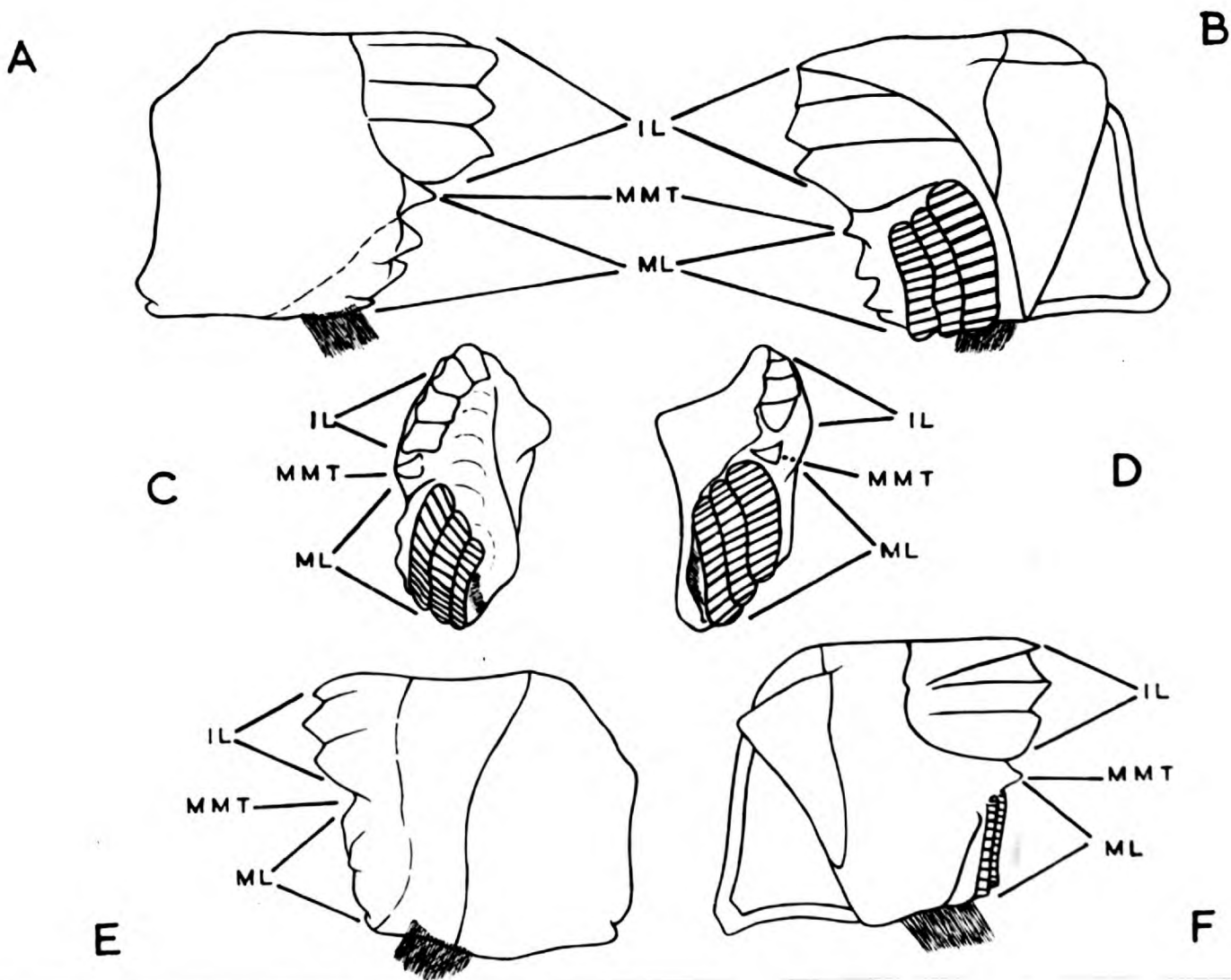


Figure MA. Diagrams to show the principal features of Acridid mandibles. A.B.C. Left mandible. A. Antero-lateral view, B. Postero-lateral view, C. Mesial view, E. Antero-lateral view, F. Postero-lateral view.

I.L. incisor lobe, MMT. median molar tooth, ML. molar lobe.

teeth. In old individuals, the teeth become broken and worn through constant use, so young adults were examined whenever available. Drawings of the two views of each mandible are included for the thirteen species described (Figs. 15-27). Fig. MB is included to show the distribution of light and dark areas and the variation in the degree of sclerotisation between four selected species. The dorsal row of bristles ("Brustia" of some authors) has been omitted from all these drawings for the sake of clarity of outline. For details of structure of these four species, Figs 17, 18, 22 and 26 should be examined.

ii) DESCRIPTIONS OF TYPES.

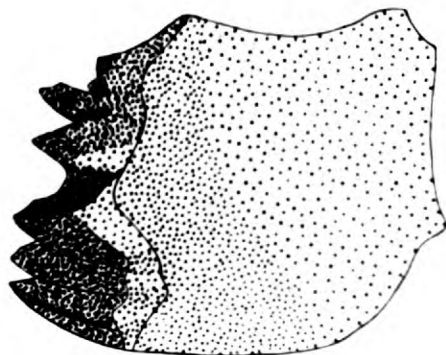
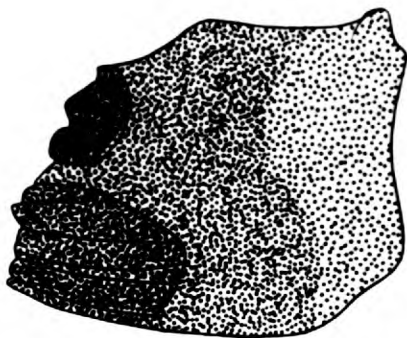
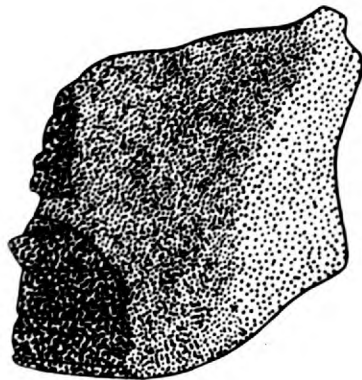
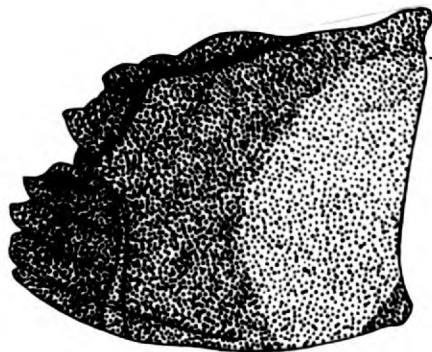
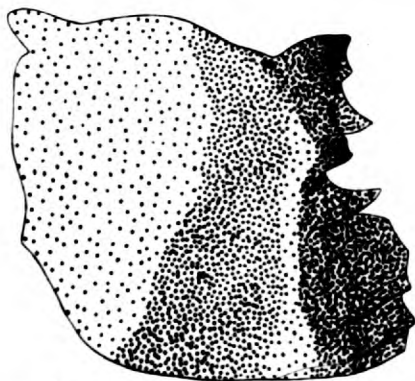
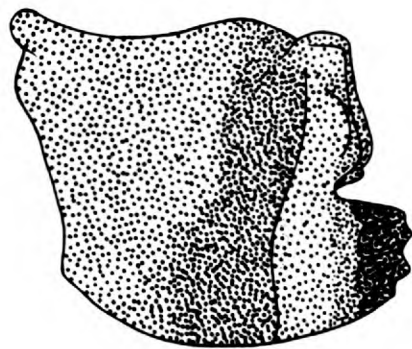
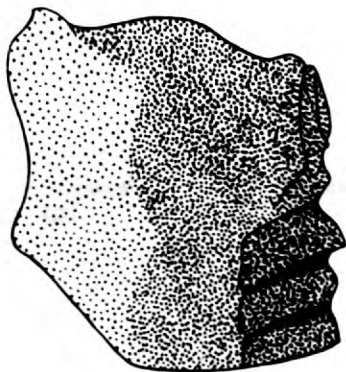
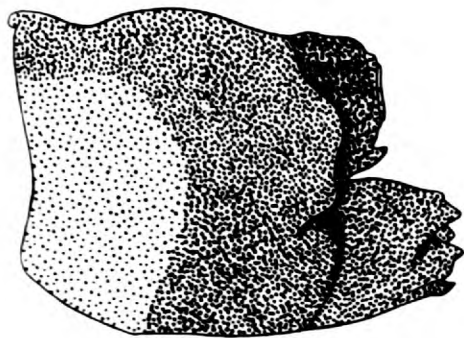
Group 1. Schistocerea gregaria (Fig. 15). In this species, the left incisor lobe is distally marked along the cutting edge by four teeth. The right lobe has three large teeth. All the incisor teeth are sharply pointed, thick and strong. The teeth on the molar lobe of the right jaw are well developed and arranged, more or less in two ridges, each bearing two dentes. The dorsal tooth on each ridge is the more prominent. The molar lobe of the right mandible is a well marked structure consisting of a series of ill-defined ridges, the most anterior being more or less independent of the ridge pattern and tooth-like. The other ridges are raised into prominences to a very much lesser extent. Between the molar and incisor lobes of each jaw there is an extra tooth. This is small on the right jaw but very prominent on the left.

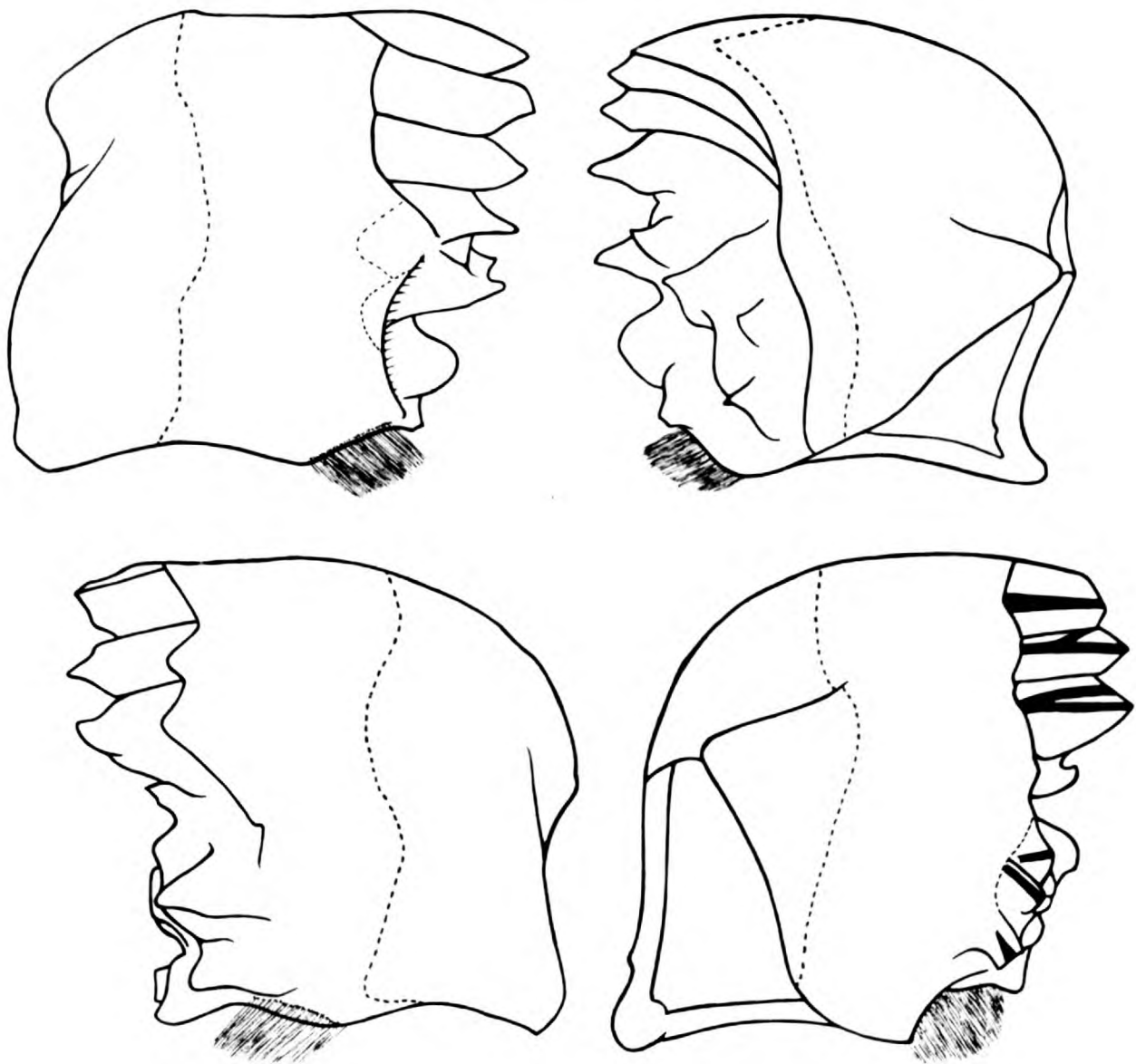
Figure MB. Antero-lateral and Postero-lateral views of the mandibles of four selected species of Acrididae to show the variation in the distribution of the light and dark area. (For clarity of outline, the brustia have been omitted.

Top row. Reading left to right. Oedipoda caerulescens, Myrmeleotettix maculatus, Chorthippus albomarginatus.

Middle Row. L. to R. Mecostethus grossus, O. caerulescens.

Bottom row. L. to R. M. maculatus, C. albomarginatus, M. grossus.





Figures 15-27. Antero-lateral and Poster-lateral views of left and right mandible of 13 species of Acrididae.

Figure 15. *Schistocera gregaria*.

GROUP 2. Chorthippus vagans. (Fig. 16). The left mandible of this species bears four long teeth on the incisor lobe and three ridges of teeth on the molar lobe. Of these molar ridges, the two posterior are more or less flattened and their teeth are blunt. The two anterior teeth are almost separate, being joined only at the base. The marginal tooth is well developed on both jaws. The right mandible is more graminivorous in its structure. It bears three incisor teeth and the molar lobe is made up of a series of raised ridges bearing rather blunt teeth.

Oedipoda caerulescens. (Fig. 17). In this insect the left incisor lobe bears four pointed teeth. The marginal teeth are exceptionally well developed being four in number, two of which are as long as the incisors. The molar lobe of this jaw consists of three rather flat ridges. The right incisor lobe bears three somewhat blunt teeth but the molar region is well-formed and the ridge pattern is very indistinct owing to the independent arrangement of the molar teeth. There is one marginal tooth. The small size of the molar area of the right mandible and the strong development of teeth in the same region in the left jaw are very peculiar.

GROUP 3A. Mecostethus grossus. (Fig. 18). The left jaw bears four strongly pointed teeth on the incisor area and a small marginal tooth. The molar area consists of three flat ridges and two anterior teeth. The molar ridges occupy a considerable area on the posterior-dorsal surface of this jaw. The boundaries of

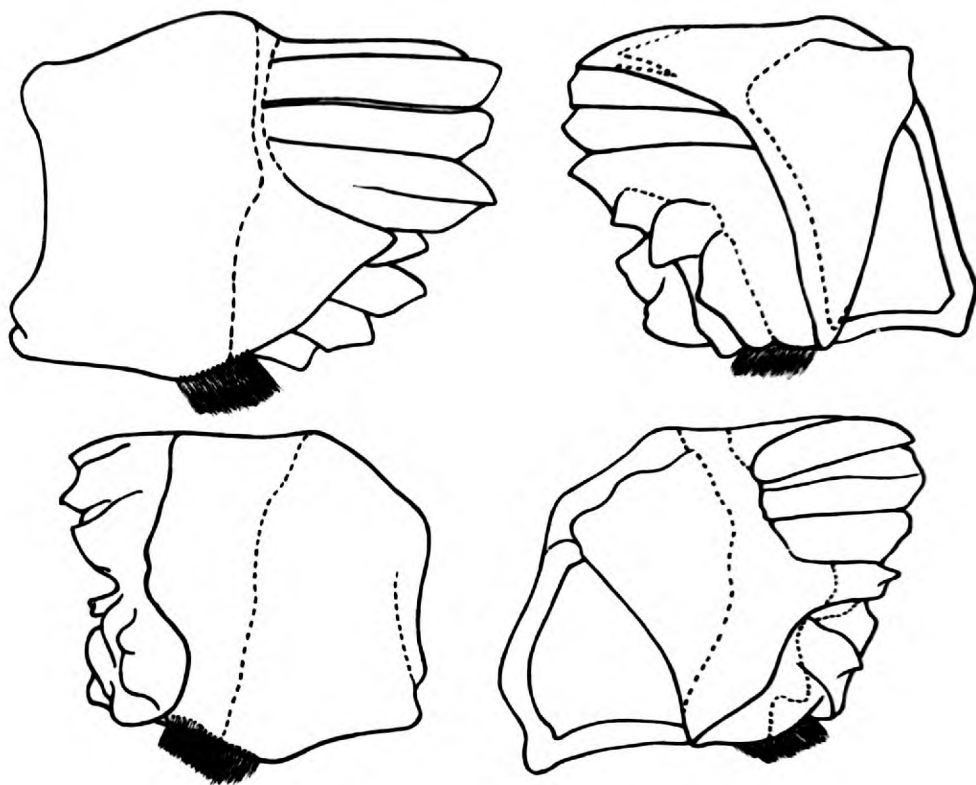


Figure 16. Chorthippus vagans.

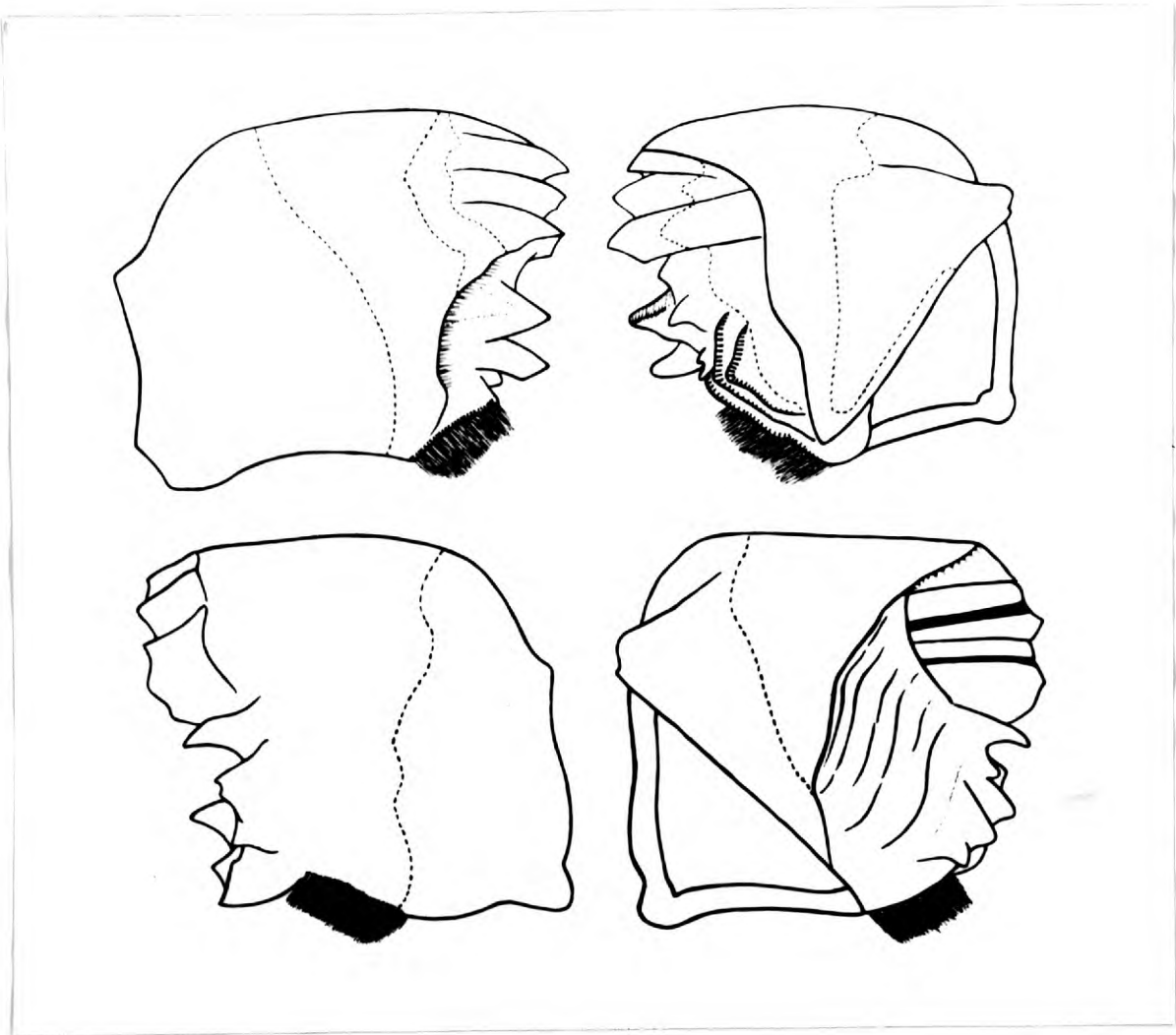


Figure 17. Oedipoda caerulea.

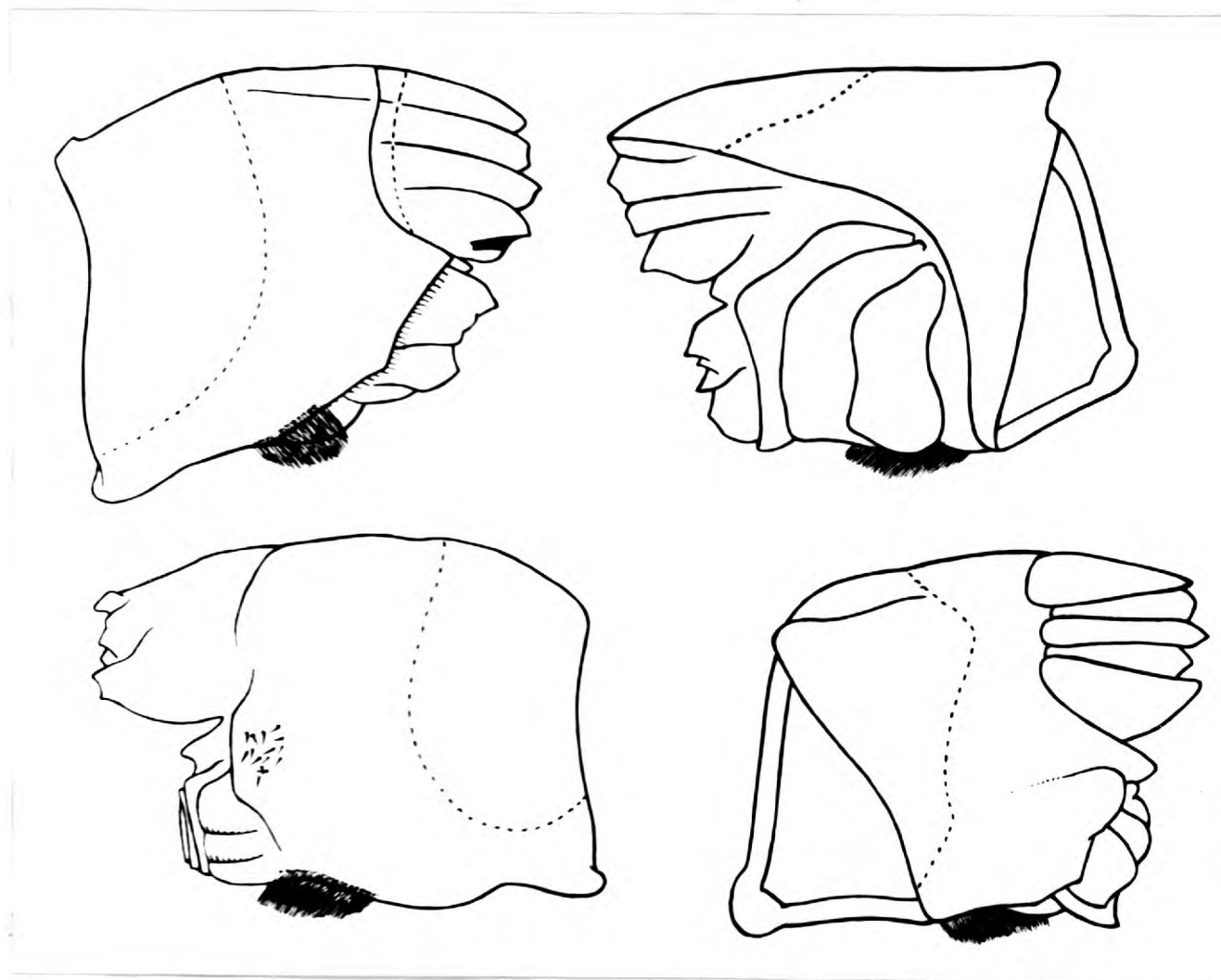


Figure 18. Mecostethus grossus.

the individual incisor teeth of the right mandible are obscure as the middle tooth appears to be considerably sub-divided in this species. The molar area is prominent and bears a series of flat ridges.

Chorthippus parallelus. (Fig. 19). Apart from a few minor details, the mandibles of this insect are very similar to those of the foregoing. The sclerotisation is not as strong, and the molar area of the left jaw bears four flat ridges instead of three. This is because the two anterior teeth present in this position in Mecostethus are here replaced by a ridge.

Stenobothrus lineatus (Fig. 20). The mandibles of this species are like the previous types but the molar area of the left jaw is in a condition intermediate between them.

Locusta migratoria. (Fig. 21). This is like Chorthippus parallelus but the mandibles are more powerful owing to greater sclerotisation and relatively longer incisor teeth.

GROUP 3B. Myrmeleotettix maculatus. (Fig. 22). The jaws of this grasshopper are intermediate in type between those of Group 3A and Group 4. The incisor teeth are blunter than those of the previous species but more pointed than those which follow.

GROUP 4. Chorthippus bicolor (Fig. 23) and Omocestus viridulus (Fig. 24).

The only important difference between the mandibles of these species and those which have already been described lies

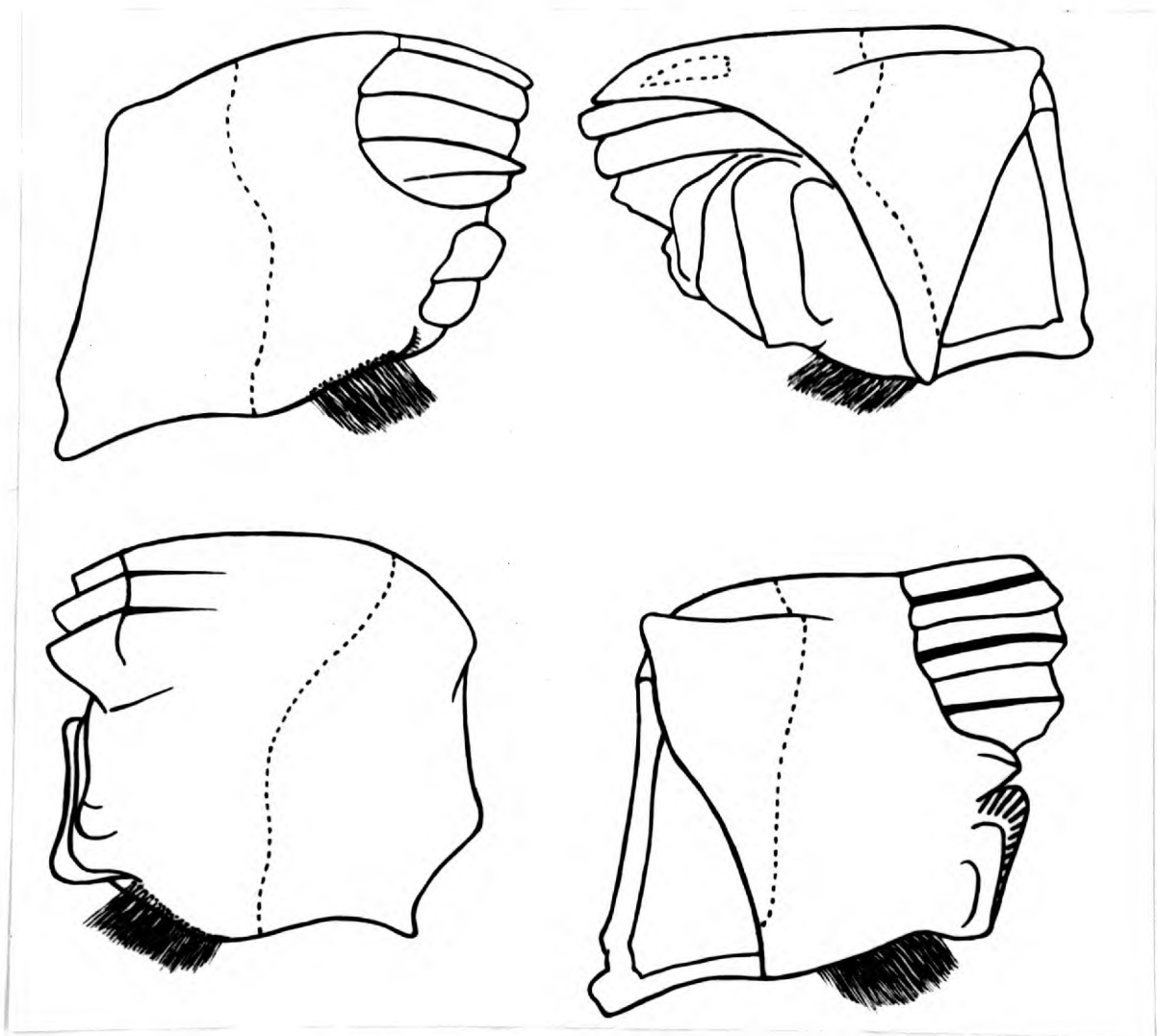


Figure 19. Chorthippus parallelus.

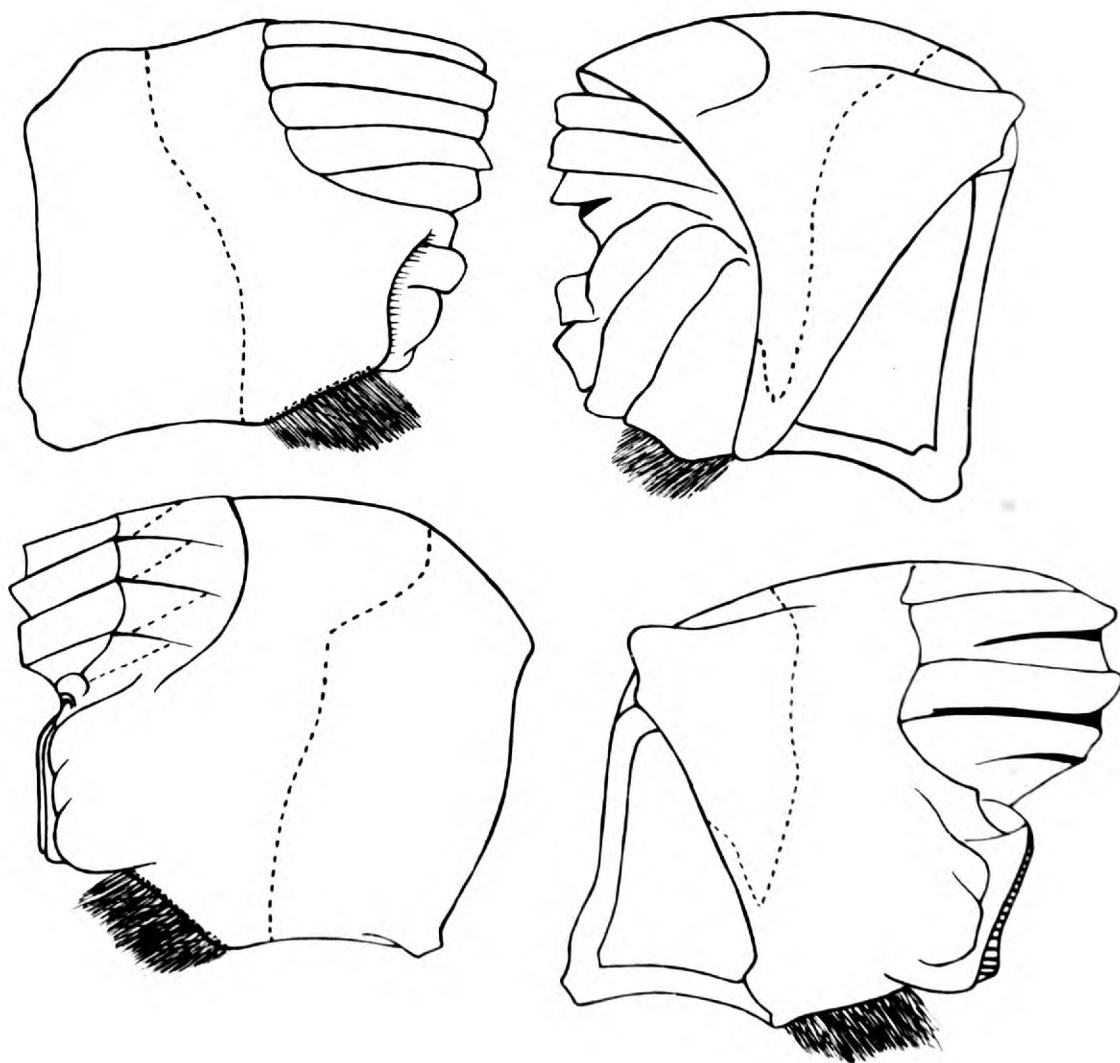


Figure 20. Stenobothrus lineatus.

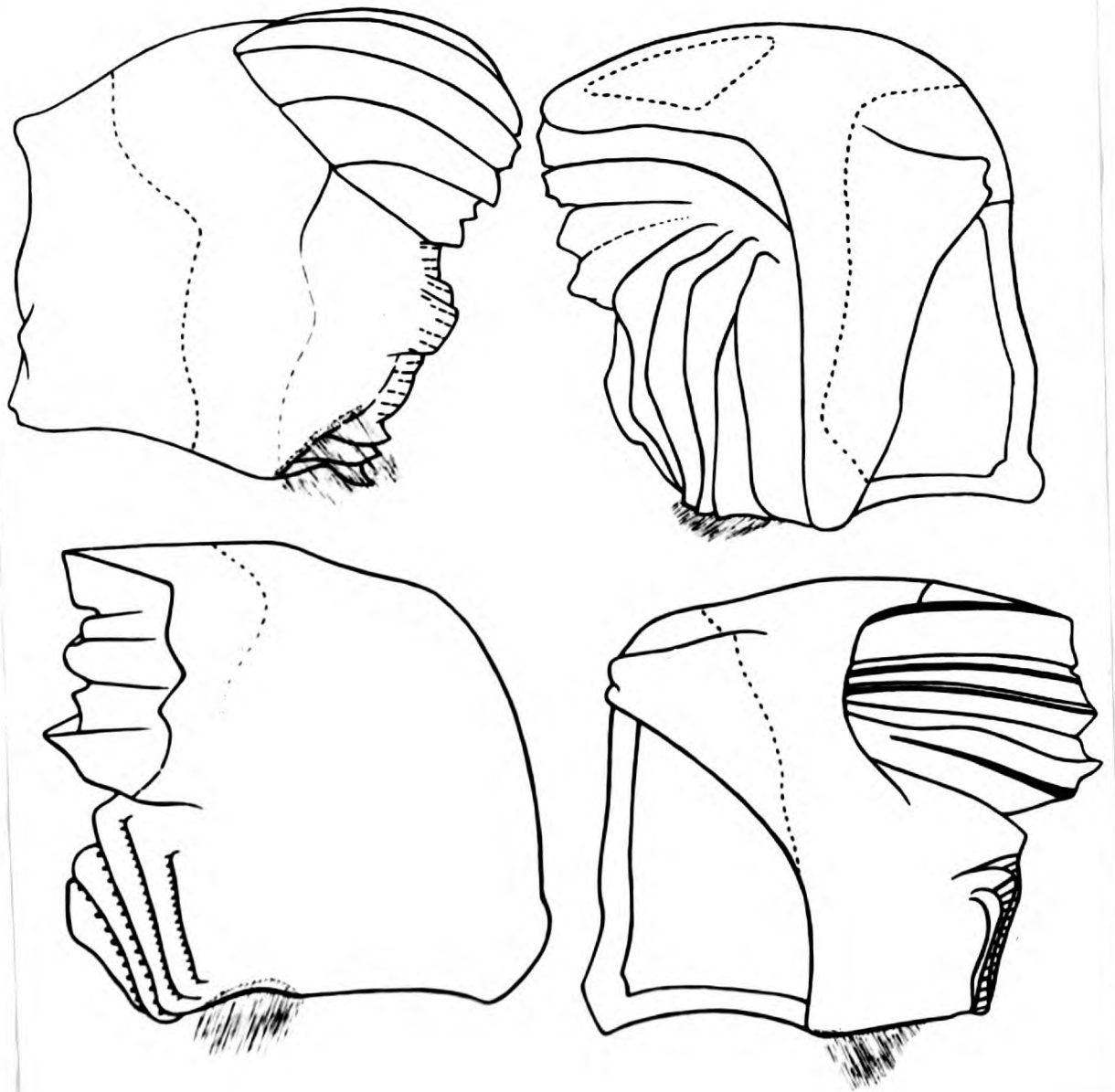


Figure 21. Locusta migratoria.

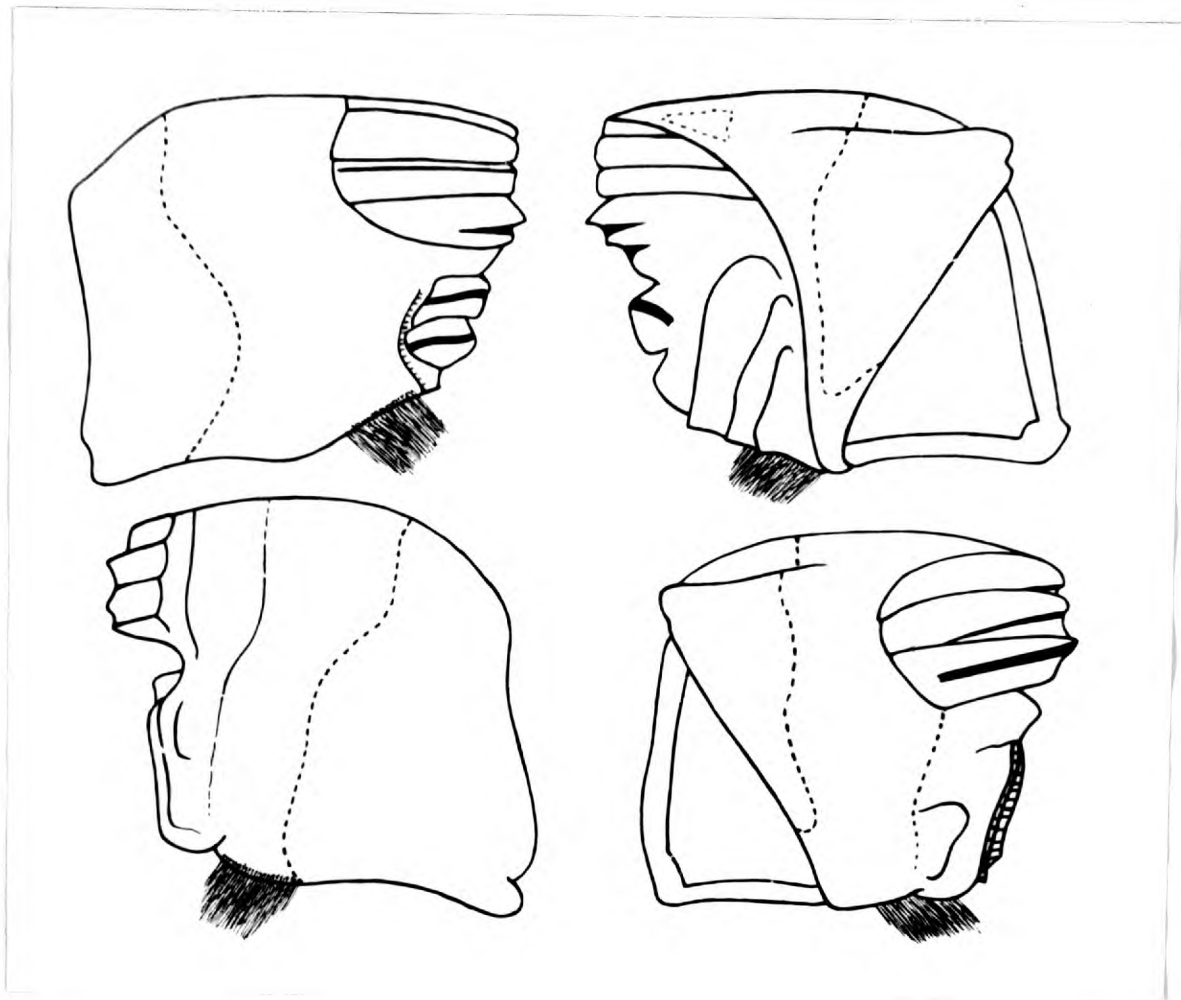


Figure 22. Myrmeleotettix maculatus.

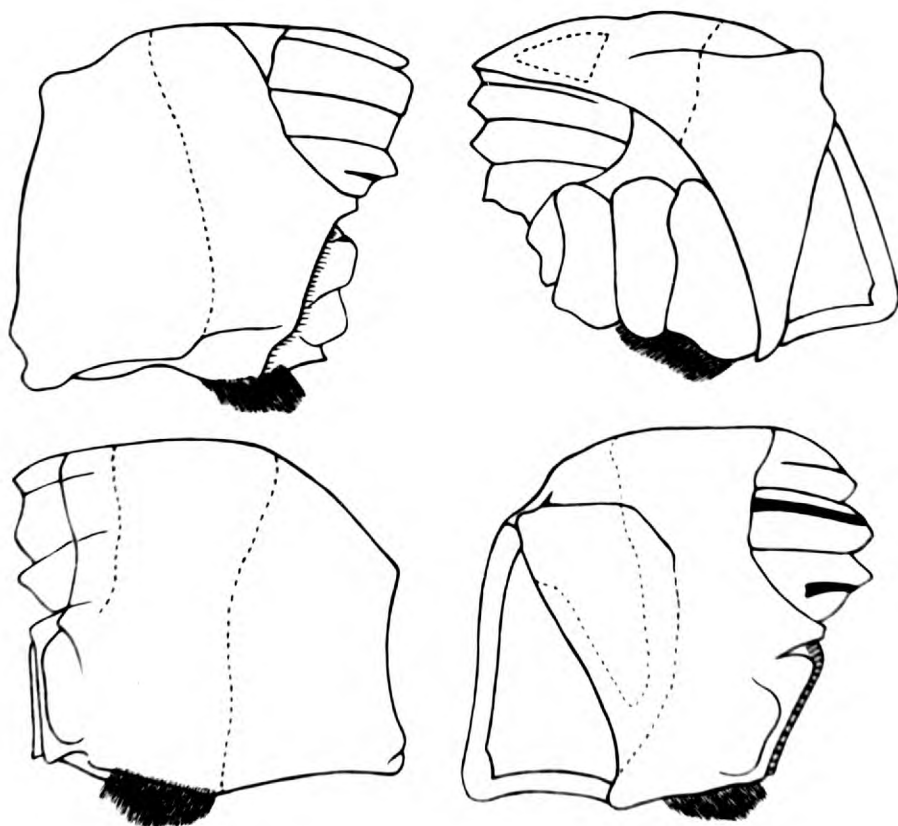


Figure 23. Chorthippus bicolor.

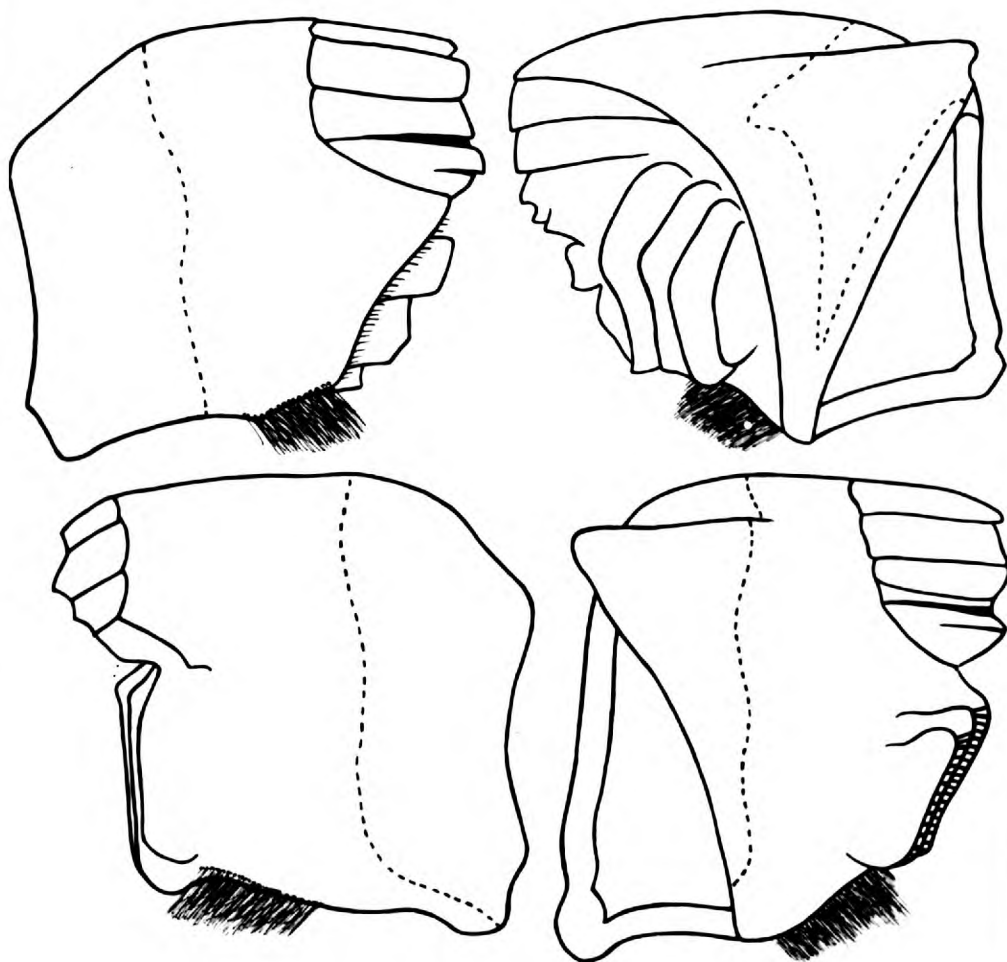


Figure 24. Omocestus viridulus.

in the incisor lobes. These bear very much blunter teeth.

Omocestus ventralis. (Fig. 25). In this insect, the incisor area is relatively small compared with the molar area.

GROUP 5. Chorthippus albomarginatus (Fig. 26) and Gomphocerippus rufus (Fig. 27). In this last group,

the incisor teeth are so blunt that they appear almost rectangular in outline, but in other respects the mandibles resemble those in Group 4.

iii) DISCUSSION.

From the foregoing descriptions and figures, it is seen that, although the majority of the types discussed here have typically graminivorous mandibles with only minor specific differences, nevertheless there are three types which incorporate some of the features of those species which feed on broad-leaved plants. The characters of the two types of mandibles are summarised below.

Broad-leaved plant type	Graminivorous type.
1. The incisor teeth are pointed.	The incisor teeth are blunt.
2. The incisors of the left jaw are short.	The incisors of the left jaw are long.
3. The jaws overlap and interlock considerably and the distal edge of the right incisor lobe is not bevelled.	The left jaw only slightly overlaps the right and the distal edge of the right incisor lobe is bevelled.
4. The molar lobes consist of several teeth surrounding a concavity.	The molar lobes consist of a series of ridges and furrows.
5. Marginal molar teeth are well-developed.	Marginal molar teeth are poorly developed.

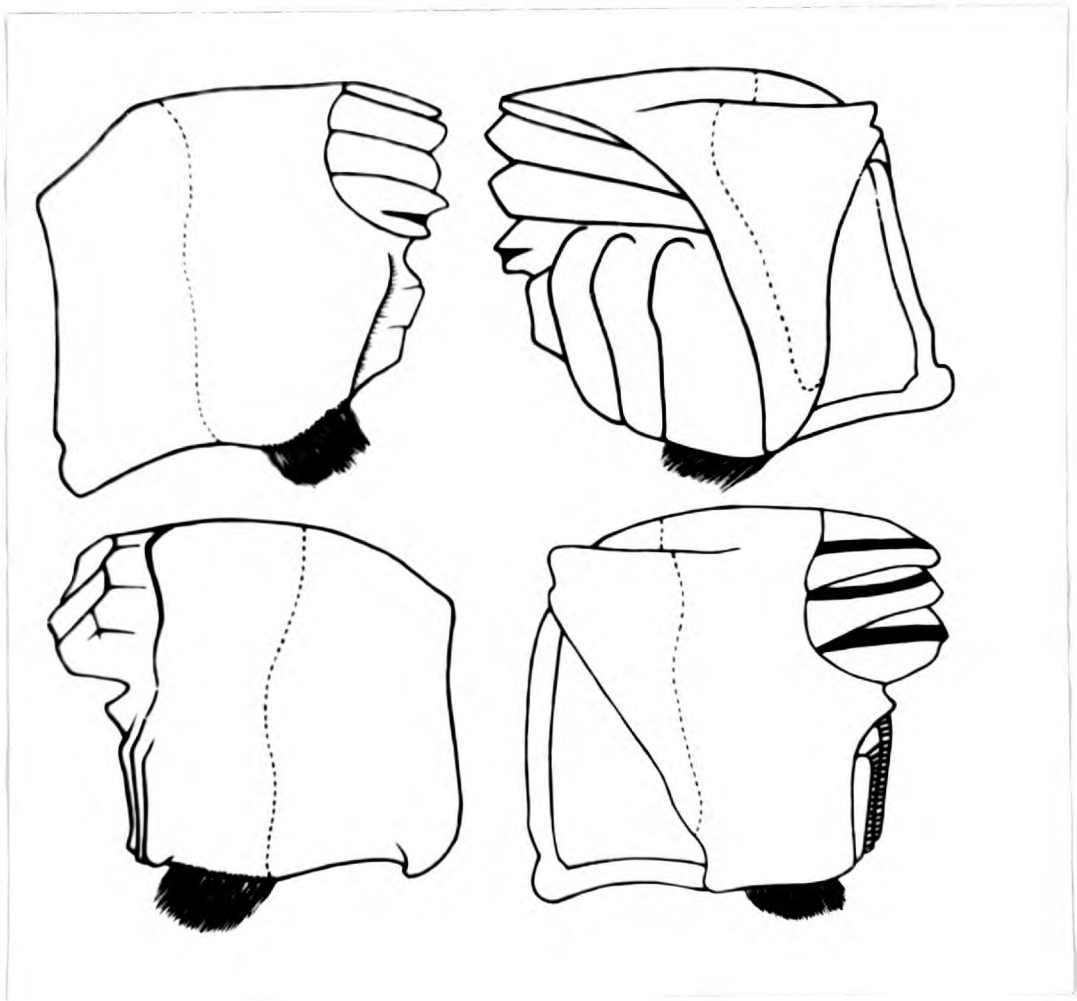


Figure 25. Omocestus ventralis.

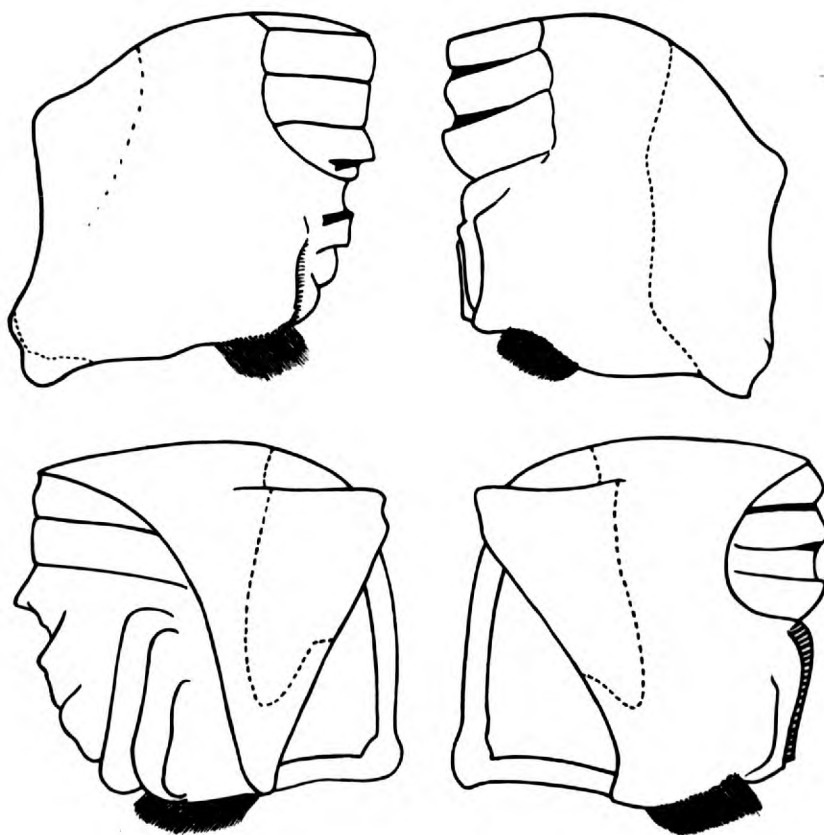


Figure 26. Chorthippus albomarginatus.

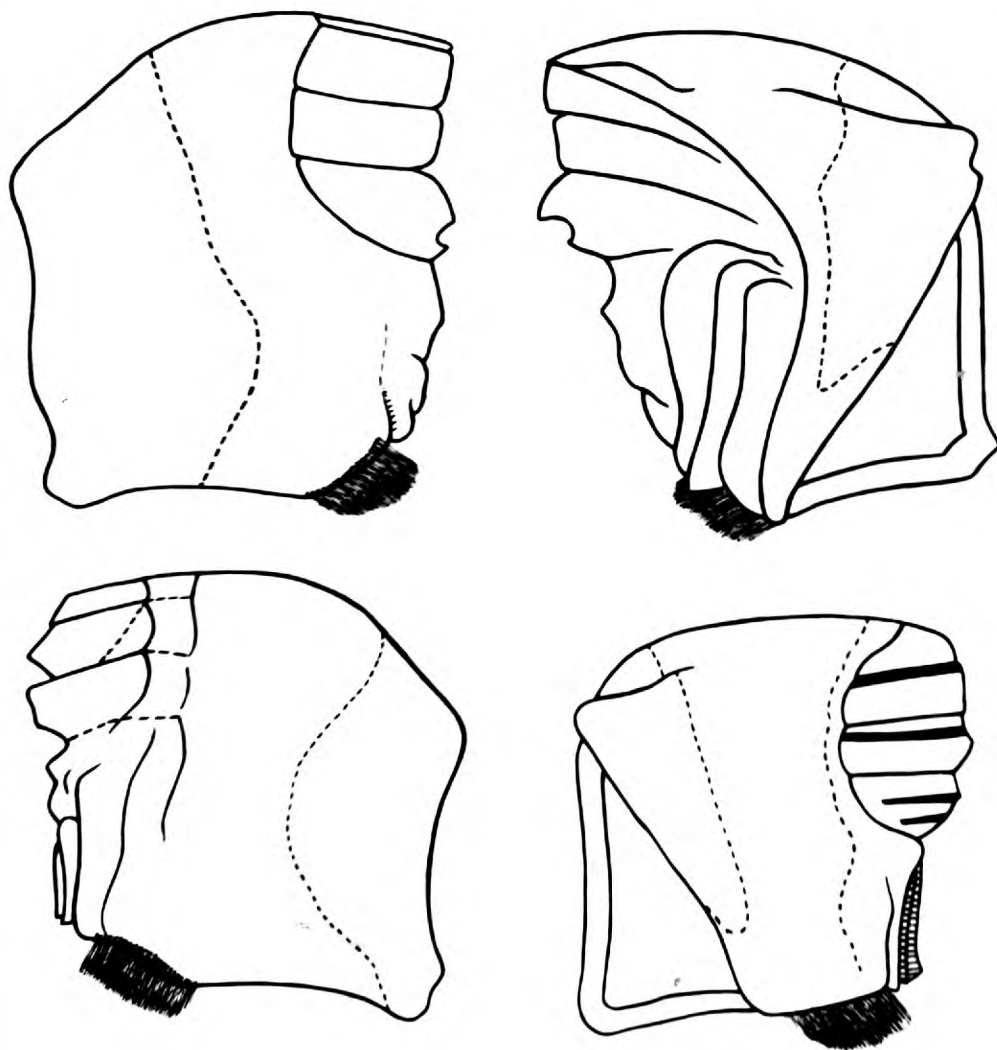


Figure 27. Gomphocerippus rufus.

B. THE CROP.

The structure of the alimentary canal of a few species of Acrididae has been investigated by Uvarov (1928), Hodge (1936, 1939), Chauvin (1938) and Tietz (1923). It is a more or less straight tube from mouth to anus except for the pharynx which leads vertically from the buccal cavity to the crop, and the small intestine which is normally considerably flexed, also in a vertical direction. It is divided histologically into three sections, fore-gut, mid-gut and hind-gut. Of these, the first and last are lined with ectoderm and are shed at each ecdysis. The mesenteron is thin-walled and is the seat of absorption as in all insects.

The crop is a muscular organ of considerable dimensions and, in Acrididae, is the centre of the digestive processes. It also serves as a storage chamber. Internally, the wall of this organ is thrown into a series of longitudinal ridges. Each ridge is armed with numerous minute conical spines throughout the anterior two-thirds of its length. The posterior region of the crop is sometimes called the gizzard. Anteriorly, the crop bears a pair of lateral areas where the spines are specially well-developed on rather broad elevations of the wall. Here, there may be several rows of spines on each ridge. (Fig.28).

Examination of the prominent lateral ridges of the crop, of each of the 11 British species of Acrididae, showed that there are well-marked differences between some of them. On.

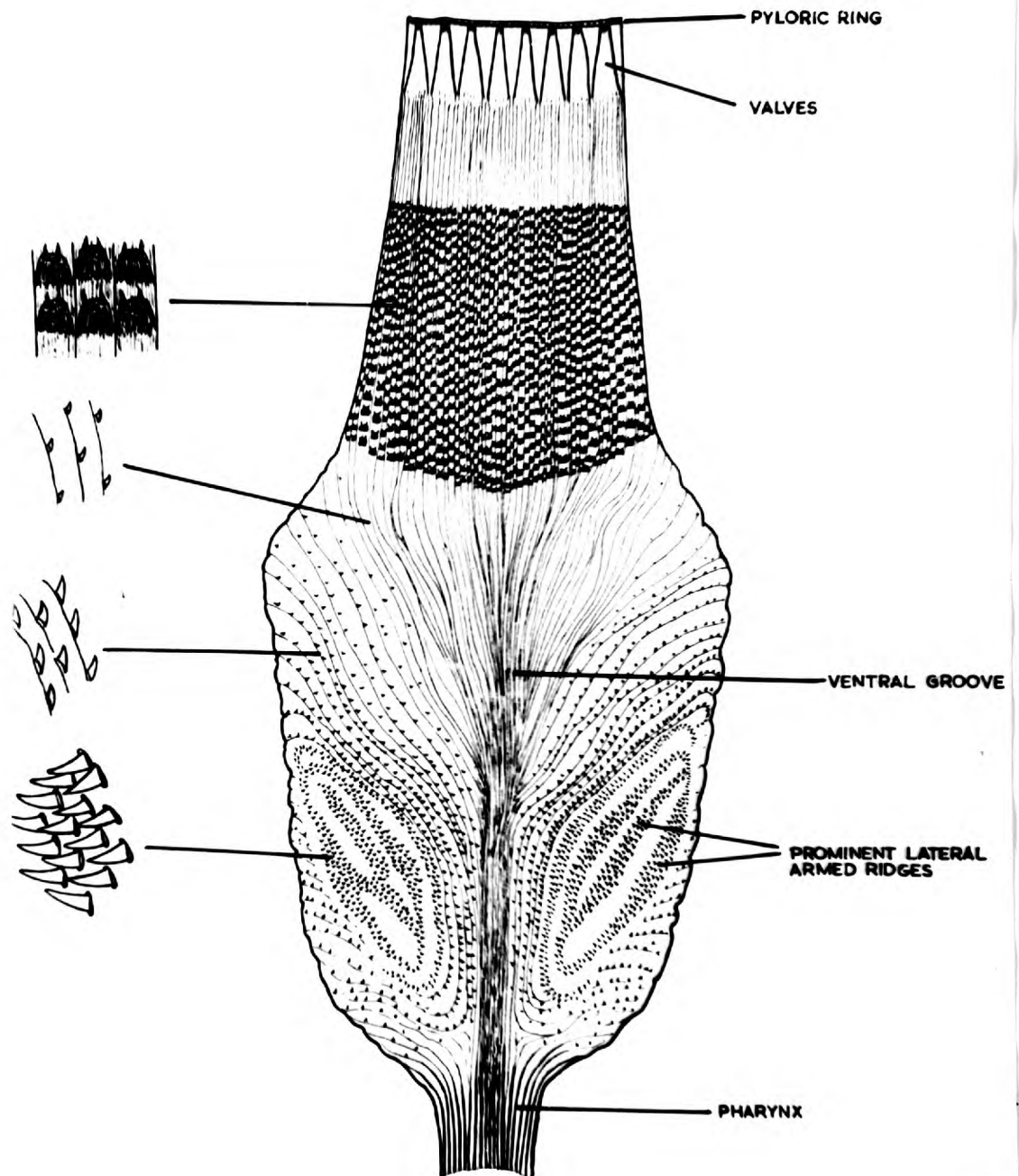


Figure 28. Internal armature of the crop of *locusta migratoria* as exposed by slitting the dorsal wall longitudinally and pinning back the cut edges.

the whole, the armature was better developed in the female sex than in the male. There was considerable variation between individuals of the same species and sometimes even between opposite sides of the crop of the same individual.

The variation is well shown in Figure 29 A-F. In some individuals the rows of teeth are fused to a greater or lesser extent and there is also considerable variation in the number of teeth in each row. These illustrations are selected from 50 slides in order to show extremes of variation. Most specimens of this species (Chorthippus bicolor) had an arrangement of three, more or less, independent rows of teeth.

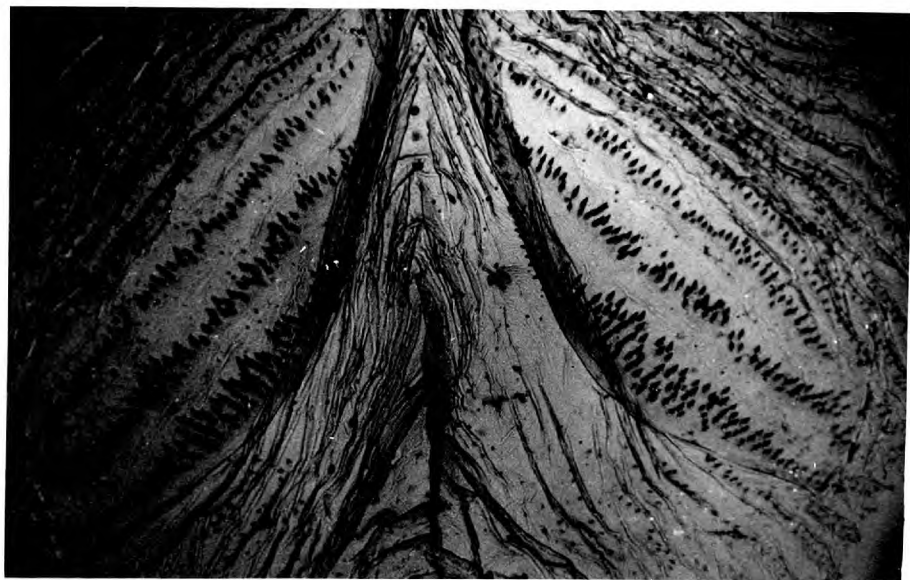
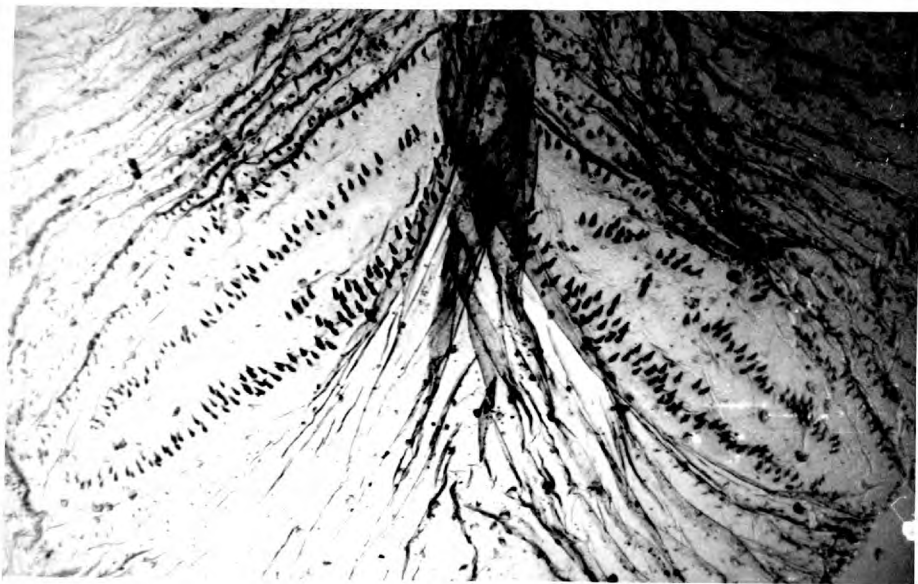
Chorthippus albomarginatus (Figure 30) and C. parallelus (Figure 31) also have an arrangement of this type but in C. vagans (Figure 32) the teeth are small, few in number and the rows are widely spaced.

In this species, fusion between adjacent rows of teeth is less likely to take place.

In Omocestus viridulus, (Figure 33) and O. ventralis, (Figure 34 A,B) the teeth are large and numerous and adjacent rows often show signs of fusion.

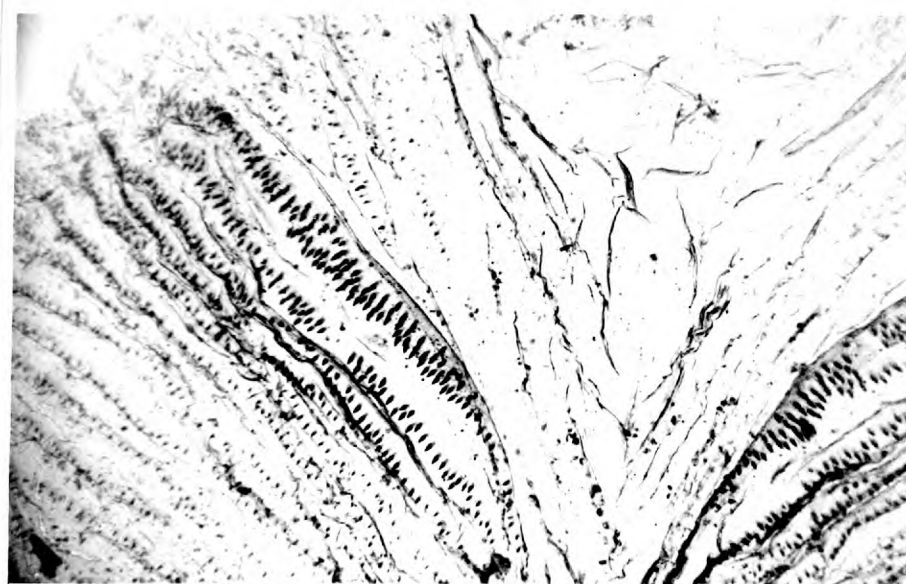
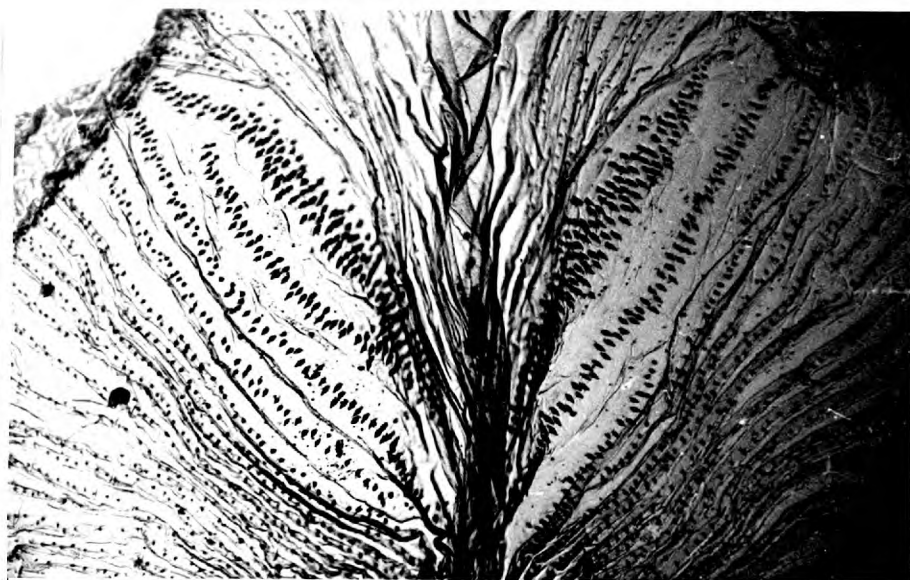
In Stenobothrus lineatus, (Figure 35 A,B.), the rows are fairly widely spaced, the teeth are large and numerous and are usually arranged in two or three discrete rows.

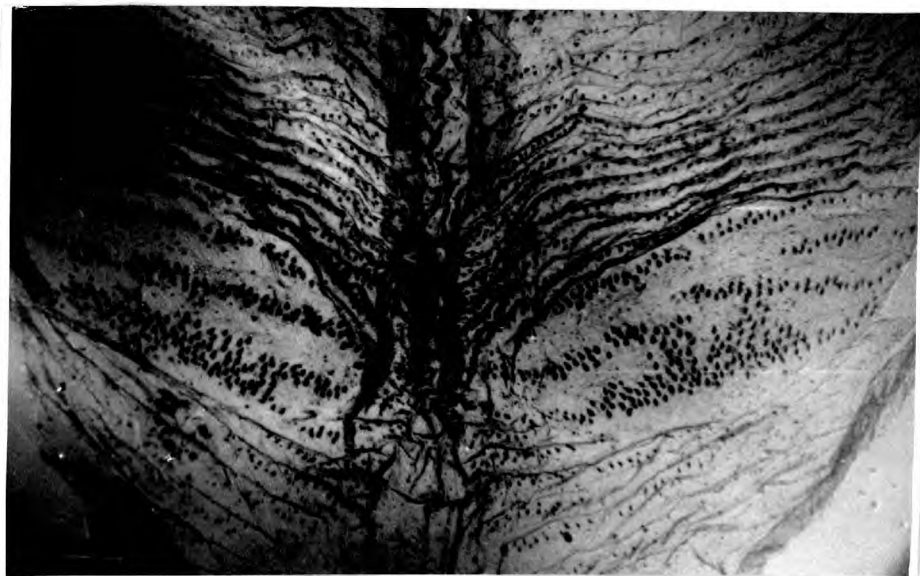
In Myrmeleotettix maculatus, (Figure 36 A,B.), considerable variation occurs both in the number of rows and in the number



Figures 29-39. Photomicrographs of the prominent lateral armed ridges of the crop of the 11 British species of Acrididae from permanent mounts. Specimens prepared by opening the crop and making a dorsal longitudinal cut.

Figure 29. A-F. Chorthippus bicolor.





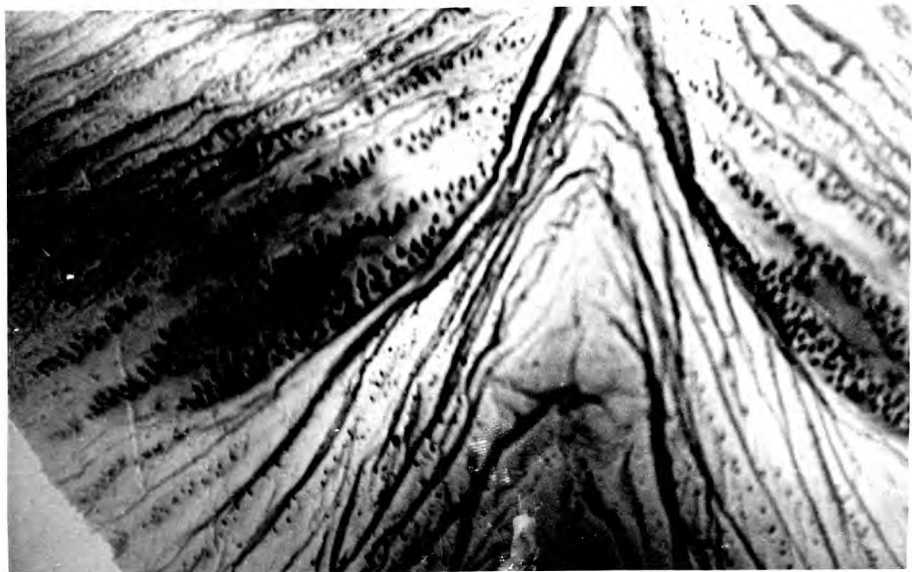


Figure 30. Chorthippus albomarginatus

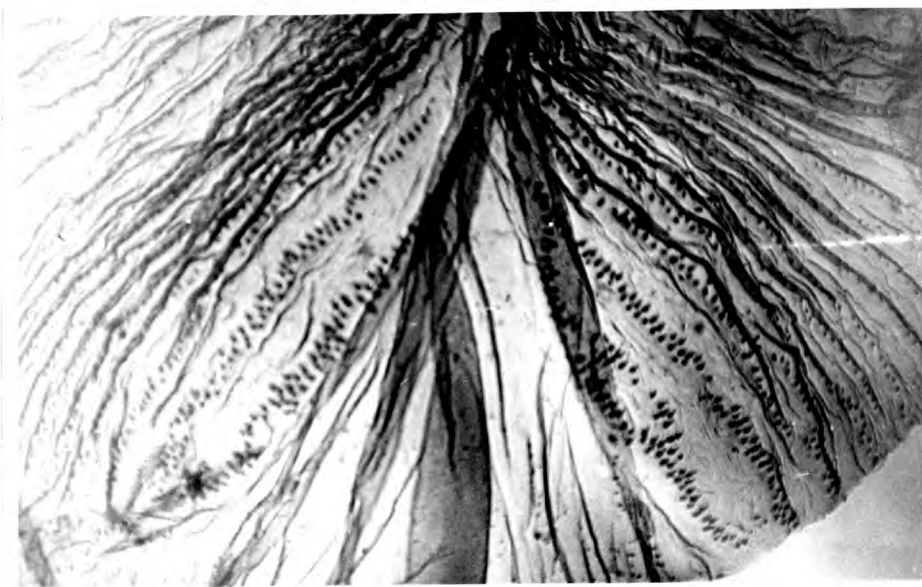


Figure 31. Chorthippus parallelus.

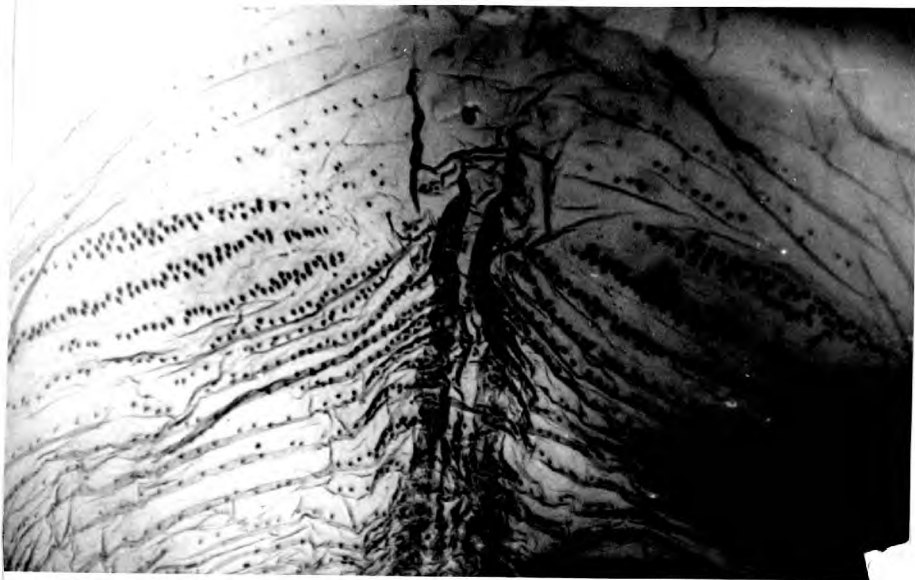


Figure 32. Chorthippus vagans.



Figure 33. Omocestus viridulus.

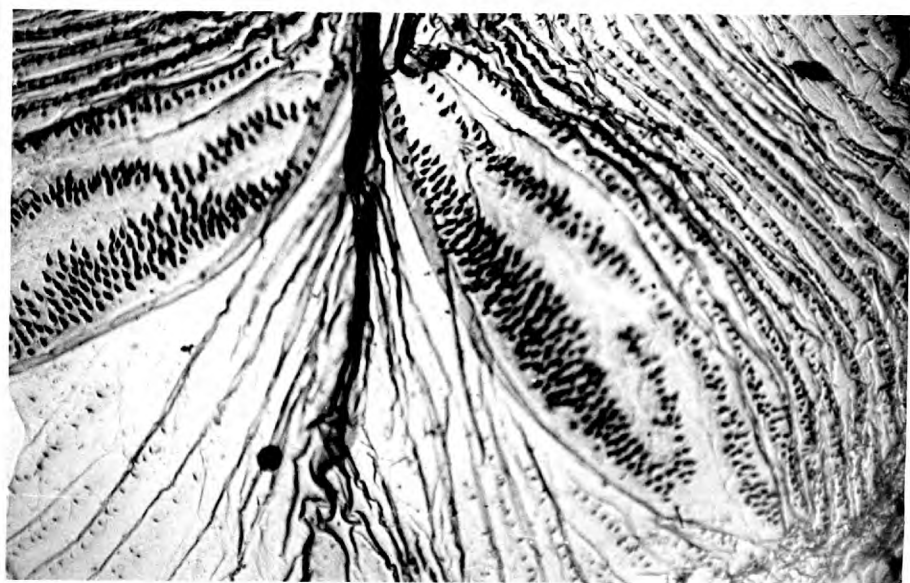
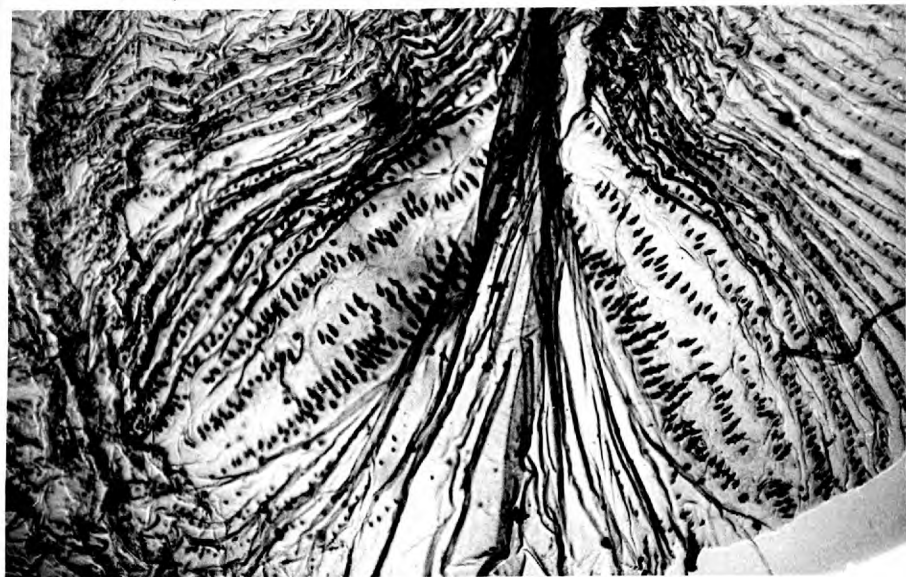


Figure 34. A,B. Omocestus ventralis.

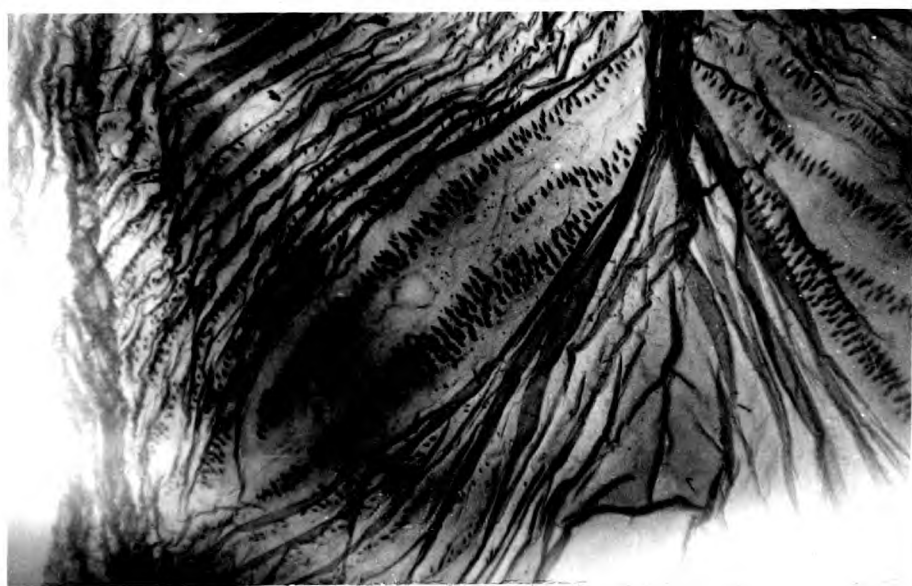
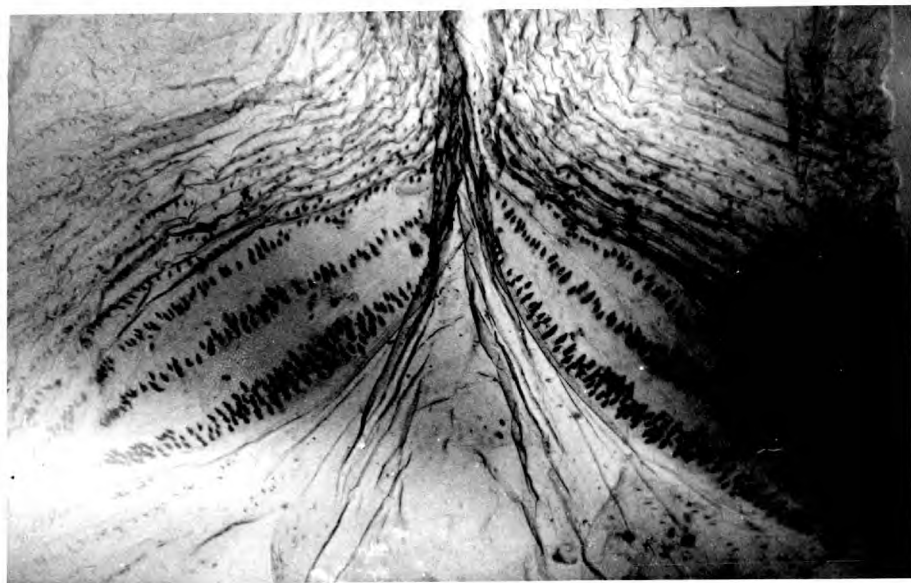


Figure 35. A,B. Stenobothrus lineatus.

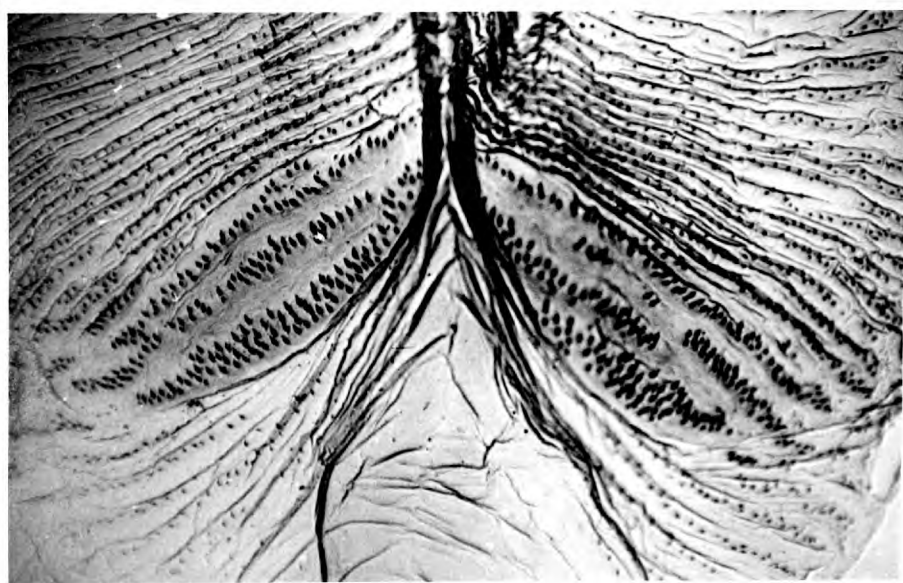


Figure 36. A,B. Myrmeleotettix maculatus.

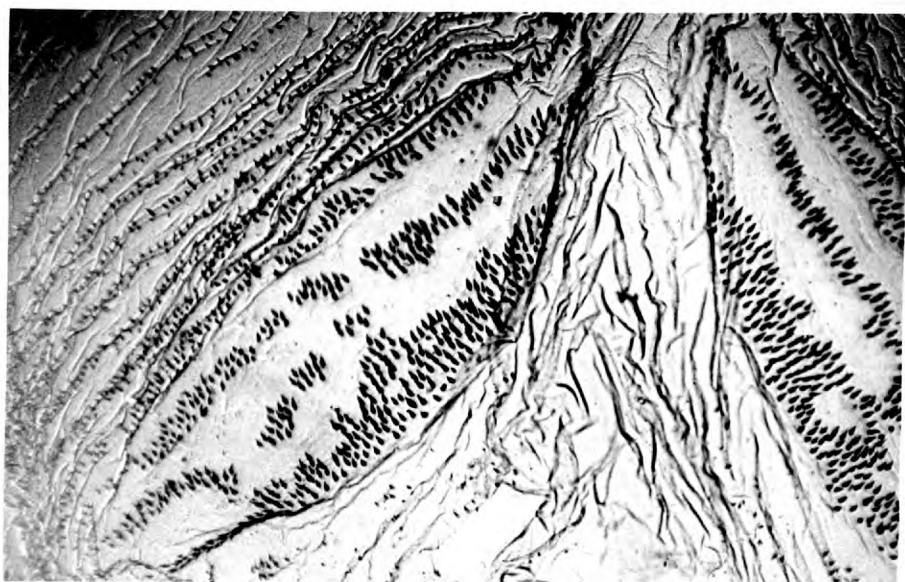
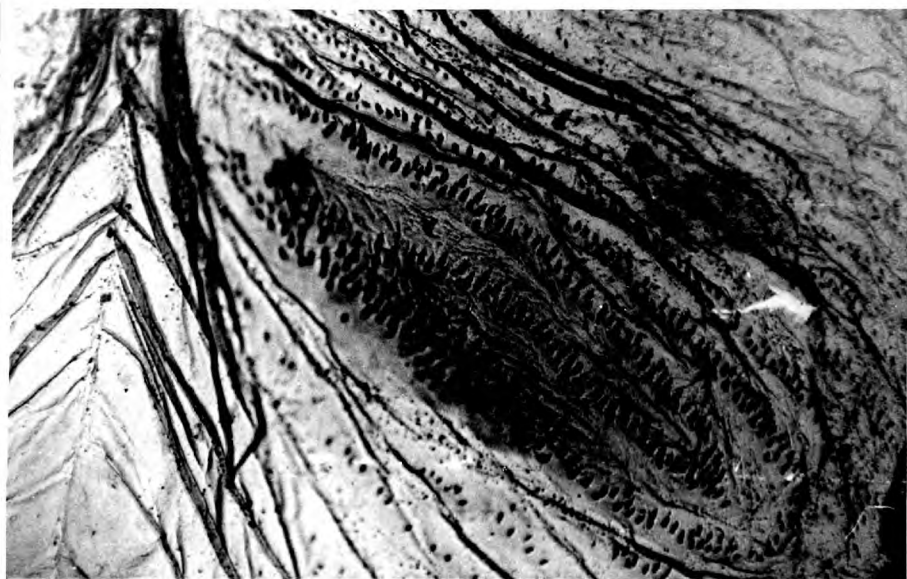


Figure 37. A,B. Gomphocerippus rufus.

of teeth. In the commonest condition, the teeth are sparse and the rows are well spaced.

Gomphocerippus rufus, (Figure 37 A,B.), has large and numerous teeth, often arranged in rather ill-defined rows.

An enormous variation was observed between individuals of Mecostethus grossus (Figure 38 A,B.) but usually the rows are well-defined. Fusion between adjacent rows occurs only rarely in this species.

In Oedipoda caerulescens, (Figure 39), the degree of development of the teeth is the poorest of all the 11 species examined. Usually only two rows with a few teeth are present.

A typical arrangement of the crop armature of Locusta migratoria is shown in Figure 28. This drawing also shows the asymmetry between opposite sides, a common feature in many Acrididae.

The significance of the findings in this section of the work is discussed in Section 7 (see Page 100).

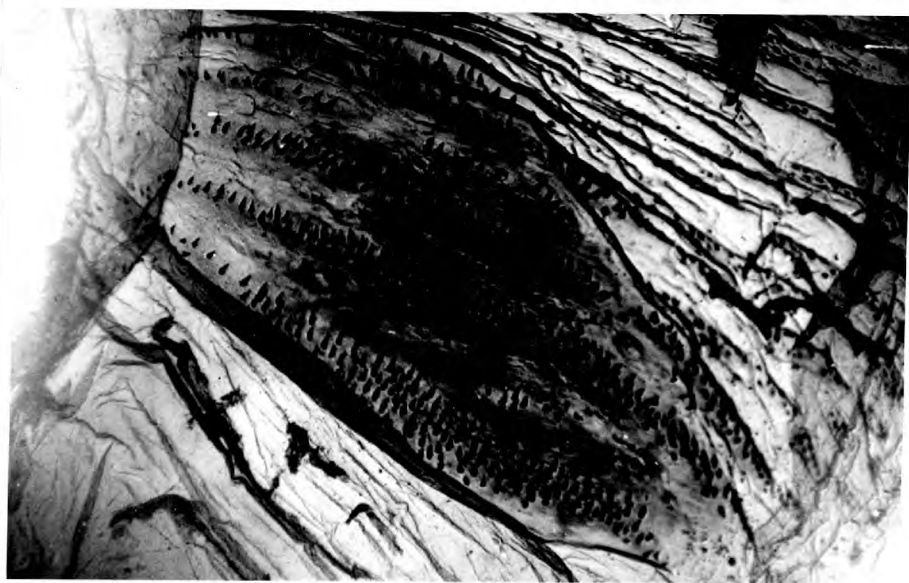
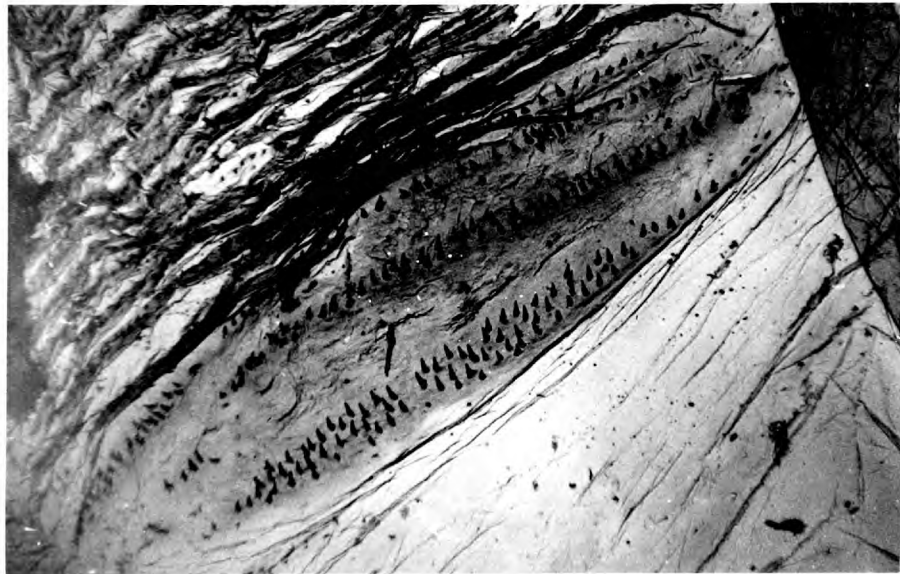


Figure 38. A,B. Mecostethus grossus.

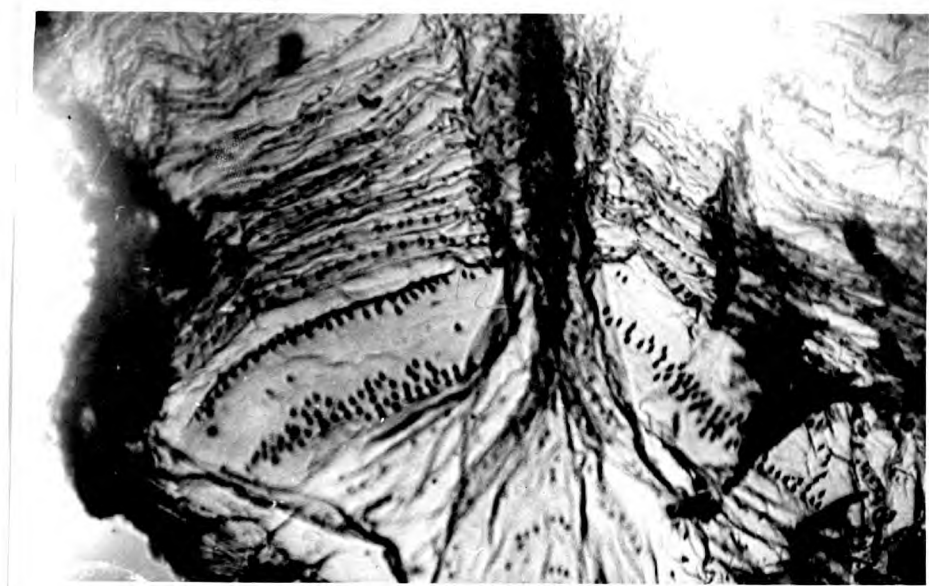


Figure 39. Oedipoda caerulescens.

7. DISCUSSION.

It appears that the nine species of British Acrididae which have been studied in the Food Preference section of this work are, under normal conditions, exclusively grass feeders. Under certain special circumstances, as for instance in times of drought, they may turn to broad-leaved plants. It is interesting to note here that Griddle (1935) drew attention to the fact that certain plants are much more readily consumed during hot weather than at other times of the year. It was observed in America in 1932, that during a very hot spell, the weed Sonchus arvensis L., was so intensely attacked by the grasshopper Melanoplus bivittatus that hundreds of acres were stripped bare. As a result, he suggested that some plants are selected by insects at times because of their moisture content. This appears to be supported by the present observations, for, it was found that when grasshoppers were deprived of water as well as food for 48 hours, they could be induced to feed on a number of plants which previously they would not touch. These plants were rather succulent species.

On the other hand, from the work of Clark (1948), one concludes that there are a number of herbs which are frequently consumed by our native grasshoppers. One of these is Lotus corniculatus L. but the present investigation indicates that there is no justification for believing it to be preferred any more than many other plants. It was, however, one of the

species which was partly eaten when grasshoppers were deprived of water. It is difficult to account for the big difference between my own field observations and those of Clark. He was able to make more observations, but even so, if these species of grasshopper feed as regularly on some broad-leaved plants as his records appear to indicate, some instances of prolonged feeding should have been observed. The three most favoured herbs listed by him, Poterium sanguisorba L. (17), Trifolium spp (18) and Lotus corniculatus L. (19), were all present, often abundantly, on the sites which were visited. On the whole, herbs were more numerous than grasses in the places where this work was carried out but nevertheless there were four times as many instances of attempts to feed on grasses than on broad-leaved plants. This alone suggests that there is some factor which indicates to a grasshopper that grasses are a more suitable food than other plants. The two most likely explanations of this attraction are the shape of the blade of grass and an odour which is associated with it.

A preliminary study of the factors which play some part in determining the selection of food by Acrididae was made.

Most of the British native grasses were found to be acceptable as food. No attempt was made to rear these insects on different grass diets as it was felt that this aspect was outside the scope of the problem. Quantitative experiments showed that certain kinds of grass were preferred to others but

that as far as the grasshoppers used were concerned, their choice of food was extremely similar. It was also found that the choice of grass eaten depended on the variety which was offered. The conclusions arrived at in the laboratory on the food selection of these insects were confirmed, to a large extent, by watching the insects in their natural surroundings and by means of confining them on a selection of growing plants in the field.

Following this, a series of laboratory experiments to determine the senses employed in locating the food was carried out. These consisted of, in turn, blackening over the eyes and amputating either the antennae or the palpi. The results showed that interference with the antennae and the palpi had no effect on the quantity of food eaten. In this instance, results of covering over the eyes were conflicting, but the fact that these organs are well developed in Acrididae suggests that they are important. Subsequent work proved conclusively that this is the case.

From the results of experiments with a glass olfactometer and by covering the food with wire gauze, it was concluded that the olfactory sense of Acrididae is of little importance in the finding of food. An interesting result which suggests the presence of olfactory reactions was obtained in the olfactometer experiments where, initially, the insects were observed to follow each other's trails. However, it is possible that the cause of this is a liquid trail which is detected by the organs

of taste on the palpi rather than an olfactory stimulation. More definite indication of an olfactory sense was the total rejection of shoots of the Gymnosperm, Cupressus lawsoniana. This was the only plant on which starved grasshoppers would not make a biting response within fifteen minutes in 10 tests. From this it seems that although the sense of smell is poor, grasshoppers can detect certain very powerful odours like the resinous oils of Coniferae. From the reactions of the grasshoppers to these substances they appear to be of the nature of repellents. As pieces of paper also failed to induce a biting response by the insects it also seems that at short distances the Acrididae are able to appreciate the general smell of vegetation but not the specific odours of groups of plants.

This does not mean necessarily that grasshoppers have no sense of smell. It is possible that smell is important in some other activities such as mating. In nature, a well developed sense of smell is not required to locate food for there is always an abundance of suitable grass at close hand at least in the case of the British Acrididae studied in the field. (See Appendix B). On the other hand, a study of some of the more selective feeders among the Acrididae might show that in these species smell plays a more important role in the finding of food.

A study of the method of feeding employed by grasshoppers showed that leaves in a vertical plane were more easily manipulated with the jaws than those lying flat. A downwards

biting action is probably easier than one horizontally. Undoubtedly, the rosette habit of many plants of chalk pastures makes their leaves difficult to chew whereas the upright blade of a grass is much more easily eaten. An experiment showed conclusively that upright blades of grass attract more individuals than blades lying flat on the floor of a cage. Grasshoppers resting on grass lying flat often moved to tussocks standing in a natural position, before commencing to feed. Experiments with dark stripes of paper and other patterns showed that these insects are able to appreciate form and are attracted to a pattern of vertical black and white stripes (Skototaxis).

From these experiments it was concluded that the choice of grasses as food is probably primarily due to the attraction of the grasshoppers to dark upright stripes against a light background of sky. Thus, sight is the important sense in food location, but it cannot be the only factor involved, as feeding on a reduced scale also takes place in complete darkness.

It is thought that after the grasshopper is attracted to the plant by a behaviour mechanism involving skototaxis, the biting reflex is elicited. A biting reflex was observed in grasshoppers which had climbed up black stripes of paper. Climbing vertical stripes may be a "sign stimulus" comparable with those described by Tinbergen (1951) which releases the reflex of biting. Tinbergen showed that the feeding response of the water-beetle Dytiscus marginalis is released by chemical

and tactile stimuli exclusively. (1936). A watery meat-extract caused the beetles to hunt and capture every solid object they touched. From this he concluded that such "errors" are caused by the animal responding blindly to only part of the total environment although its sense organs are able to receive the whole of the environmental factors. Thus, even when a sense organ is involved in releasing a reaction, only part of the stimuli that it can receive are actually effective. As a rule, an instinctive reaction responds to only a very few stimuli, and the greater part of the environment has little or no influence, even though the animal may have sensory equipment for receiving numerous details.

The biting of leaves of other shapes can be explained on the basis of abnormal behaviour or a result of enforced starvation which makes the reflex of biting become operative without the necessity for a "sign stimulus" release. However, it appears certain that stripes play an important role in stimulating response of this kind and the reason why attempts to feed on grasses, sedges and rushes are more frequently observed in nature than on herbs is probably due to the stimulation of feeding brought upon by climbing up the leaf-blades of plants of this type.

Once the biting reflex has been initiated, other factors begin to operate. Thus, although grasshoppers may be attracted to certain plants because of their form, it does not automatically follow that they will eat them. Biting and tasting the food,

which may then be immediately rejected as unacceptable, is the normal feeding habit of these insects. A beginning was made on experiments of taste discrimination and it was found that a biting response could be elicited by sucrose solutions of 0.02-0.01 M concentration. Attempts to isolate the essential oils of the food were unsuccessful but it is felt that, as with most phytophagous insects these have an important influence in the selection of plants for food.

Toughness undoubtedly plays a part in food selection although Acrididae have powerful jaws. Toughness was shown to influence the feeding of young hoppers of Locusta but to have little effect on the habits of the older nymphs or the adults. The texture of leaf surface seems to be quite unimportant. The physical factors of the food are most important in the selection of food by young nymphs.

Parts of the plant other than the leaves may be eaten occasionally. The young inflorescences of certain grasses were eaten by grasshoppers both in the laboratory and in the field. Locusts were also induced to feed on the storage organs of certain "root" crops. I cannot explain why Swedes, carrots, parsnips and the tubers of Ranunculus ficaria L. were eaten but not red beet or potatoes. Carrots and beet store sugar whereas the potato and parsnip contain starch.

Some observations were made on the size of particles in the frass of grasshoppers after they had fed in turn on

different grasses. The particles are very much smaller when the insects have fed on a tough grass like Bamboo than when they have eaten soft meadow grasses.

A study of the internal armature of the crop of the British species of Acrididae gave some interesting information, although the big variation between individuals of the same species makes it difficult to draw any definite conclusions from this part of the work. All that can safely be said from consideration of so few types is that in the two species where the armature is most poorly developed, Oedipoda caerulescens and Chorthippus vagans the teeth of the mandibles are most prominent. This may be a coincidence or the degree of development of the teeth of these organs may be a parallel evolution, one increasing while the other is reduced. It is unfortunate that no feeding experiments were carried out on these two species but they are the rarest of the British Acrididae and no material could be obtained. (There is some doubt whether Oedipoda caerulescens really does occur in any of the Scilly Isles. If the old records cannot be corroborated, it has no claim to inclusion in the British fauna list.)

Study of the mandibular morphology of the species used in laboratory and field experiments and those which have been studied in the field, suggests that the species which have the best-developed mandibles are those which occur in the field in

habitats where tough grasses predominate. Mecostethus grossus and Chorthippus parallelus both frequent bogs where the only grass present is Molinia caerulea: (Mecostethus is almost confined to this type of habitat in Britain); and the jaws of both these species are heavily sclerotised and have sharp teeth. Isely studied more than a hundred species of North American Acrididae in his work on mandibular morphology, and he showed that a definite correlation exists between the food plants and the mandibular development of the insects. As only a few species are available in Britain, and as most of these have similar habits, striking differences in jaw structure cannot be expected.

The feeding habits of the two sexes may be a little different. Some results suggest that in some species at least, the length and frequency of meals is not the same in the female as in the male, the former taking more but individually shorter meals than the latter. Some work was carried out on the environmental and climatic conditions necessary for feeding to occur. It is felt that more observations on these lines would provide valuable and interesting information.

A survey of the habitats frequented by grasshoppers in Britain, showed that the specific composition of the vegetation is seldom a factor limiting Acridid distribution. The structure of the plant community, especially height and percentage cover, are important in this respect. The reason why some species prefer one type of habitat whilst others favour a totally

different kind of association is largely on account of this. The structure of the plant community is important in deciding the suitability of oviposition sites, and the oviposition habits of some species are very different from those of others. However, as Clark has already indicated, the Acridid fauna of Britain is not large, for the climatic conditions are not optimal for these insects. A number of species are here at the extreme limit of their range, and they are all relatively vigorous non-exacting types with a wide geographical distribution. As a result they are less abundant in Britain than in the more favourable parts of their range, and their demands on the local structure of the environment may be more exacting than in regions of more suitable climatic conditions.

SUMMARY.

1. The British species of Acrididae which have received attention in this work are normally grassfeeders.
2. Under exceptional conditions of drought they may consume certain other plants which have a high water content.
3. Certain species of grass are more acceptable than others.
4. The choice of grass eaten depends on the range available from which the insect can select.
5. Grasshoppers are able to appreciate form. They are attracted to vertical stripes and as grass may appear to them as a pattern of dark lines against the light background of the sky, this may play an important part in recognising the blades among other vegetation.
6. Upright blades of grass are preferred to those lying flat.
7. Leaves in a vertical plane are easier to chew than those which are horizontal.
8. The climbing of vertical stripes or blades of grass may serve as a "sign stimulus" to initiate a biting action.
9. There is no evidence that a sense of smell is important in the location of food by Acrididae.
10. It is possible that they are able to recognise a general odour of vegetation close at hand and that they can detect certain strongly repellent substances such as the resinous oils of certain Gymnosperms.
11. Taste is very important in the selection of food following

the initiation of the biting response. From observations, it seems that normal feeding habits consist of trial and error. The insects are unable to decide on the suitability of plants prior to a preliminary nibble.

12. Toughness is also an important factor, particularly in the case of the young stages.

13. The toughness of the food eaten determines the size of particles in the frass pellets. The tougher grasses result in smaller particles in the frass.

14. Texture appears to be of little importance in the initiation of a biting response in hungry grasshoppers.

15. The initiation of feeding appears to be connected with a rise in the temperature of the surroundings.

16. The length of time spent in feeding varies according to the toughness and form of the grass.

17. Males probably spend a slightly longer time than females on individual meals but the latter feed at more frequent intervals.

18. Some species feed for longer periods than others.

19. More feeding takes place in the light than in darkness.

20. Only a small proportion of the total hours of daylight are spent in feeding.

21. After a meal of grass, the gut is completely emptied of food after about 24 hours, but more than half of the frass pellets produced are voided within the first 5 hours.

22. The mandibles are adapted to the range of food normally.

consumed. Even among the small Acridid fauna of Britain there are striking differences in the manibular morphology between the species. Those grasshoppers which normally feed on tough kinds of grass, have jaws which are strongly sclerotised and have well developed teeth.

23. There is considerable variation in the internal armature of the crop. Unfortunately, a wide range of variation is found between individuals of the same species, and opposite sides are often asymmetrical. As a result it is difficult to reach definite conclusions on the relation between the food and the internal armature of this organ.

24. Those British grasshoppers which have been studied in their natural habitats are never found in the absence of grass. Apart from this, the specific composition of the vegetation in the habitat is of little importance in limiting the distribution of the species.

25. The structure of the vegetation in the habitat is a limiting factor in the distribution of Acrididae, either on account of its effect on the microclimate or on the availability of suitable oviposition sites.

26. Different species require different optimum conditions to build up their maximum population densities.

27. Usually the highest density occurs in habitats with a percentage cover of 80-100% and with a generally short turf but with a few patches of taller vegetation where the grasshoppers can retire at night and in inclement weather.

APPENDIX A. List of plants used in feeding trials in laboratory and field experiments with notes on their acceptability. Degree of acceptability judged in three categories only - eaten (2), nibbled (1), not eaten (0). Species used - Chorthippus bicolor, C.albomarginatus, Omocestus viridulus, Locusta migratoria, Schistocerca gregaria.

	<u>C.bicolor</u>	<u>C.albomarginatus</u>	<u>O.viridulus</u>	<u>L.migratoria</u>	<u>S.gregaria</u>
<u>Ranunculaceae.</u>					
<u>Clematis vitalba</u> L.	-	0	-	-	-
<u>Ranunculus bulbosus</u> L.	-	-	-	0	1
<u>R. repens</u> L.	-	0	0	-	-
<u>R. ficaria</u> L.	-	-	-	0	-
<u>Aquilegia vulgaris</u> L.	-	0	-	-	-
<u>Helleborus foetidus</u> L.	-	-	-	0	-
<u>Papaveraceae.</u>					
<u>Papaver nudicaule</u> L.	-	1	-	-	-
<u>Fumariaceae</u>					
<u>Fumaria officinalis</u> L.	0	0	-	-	-
<u>Cruciferae</u>					
<u>Cheiranthus cheiri</u> L.	-	-	-	0	-
<u>Arabis caucasica</u> Willd.	-	-	-	1	-
<u>Cardamine hirsuta</u> L.	-	-	-	0	-
<u>Aubretia deltoidea</u> D.C.	-	-	-	1	-
<u>Capsella Bursa-pastoris</u> Weber	-	2	-	2	2
<u>Brassica rapa</u> L.	-	-	-	0	-
<u>B. napus</u> L.	-	-	-	1	-
<u>Coronopus didymus</u> Sm.	-	0	-	0	-
<u>Iberis amara</u> L.	0	-	-	-	-
<u>Berberidaceae</u>					
<u>Berberis</u> Sp.	-	-	-	0	-
<u>Cistaceae</u>					
<u>Helianthemum chamaecistus</u> Mill	-	0	-	1	-
<u>Resedaceae.</u>					
<u>Reseda lutea</u> L.	-	0	-	-	-

C.bicolor C.albomarginatus O. viridulus L.migratoria S.gregaria.

Violaceae

Viola riviniana Reichs - - - - -

V.hirta L. 0 0 - 0 -

V.arvensis agg. - 0 - - -

Caryophyllaceae

Cerastium vulgatum L. 1 1 0 2 2

C.tomentosum L. - - - 2 -

Stellaria media Vill. 1 2 0 2 2

S.graminea L. - - - 0 -

Agrostemma coronaria Desr. - 0 - 0 -

Melandrium alba Mill. - 0 - - -

Hypericaceae

Hypericum perforatum L. - 0 - - -

H. humifusum L. - 0 - - -

Geraniaceae.

Geranium robertianum L. - - - 0 -

G.molle L. - 0 - - -

G.lucidum L. - - - 0 -

Oxalis corniculata L. - 0 - - -

Papilionaceae

Trifolium pratense L. 1 1 - 1 2

T. repens L. 0 0 - 1 2

Lotus siliculosus L. 1 1 - - -

L.corniculatus L. 0 1 0 1 2

Hippocrepis comosa L. - 0 - - -

Omonis repens L. 0 0 - - -

Lathyrus pratensis L. - 0 0 - 1

Rosaceae

Rubus fruticosus agg. - - - 0 -

Spiraea ulmaria L. - - - 1 -

Fragaria vesca L. 0 0 - - 1

Potentilla procumbens Sibth - 0 0 - 2

P. anserina L. - 1 - - -

Agrimonia eupatoria L. - 0 - - -

Poterium sanguisorba L. 0 0 - 0 -

C.bicolor C.albomarginatus O.viridulus L.migratoria S.gregaria.

Umbelliferae

Daucus carota L.	0	1	-	1	2
Pastinaca sativum B and H	-	-	-	0	-
Sanicula europaea L.	-	-	-	0	-

Onagraceae

Epilobium montanum L.	-	0	-	0	-
E. angustifolium L.	-	0	-	-	-
Circaea lutetiana L.	-	-	-	-	1

Araliaceae.

Hedera helix L.	-	0	-	0	0
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Caprifoliaceae.

Lonicera peri-clymenum L.	-	-	-	0	-
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Rubiaceae.

Galium saxatile I.K.	-	0	0	-	-
Galium mollugo L.	-	0	-	-	-
G. aparine L.	-	-	-	1	-
G. verum L.	-	0	0	-	-
Asperula odorata L.	-	-	-	0	-

Compositae.

Bellis perennis L.	0	0	0	0	-
Erigeron canadensis L.	-	0	-	-	2
E. acer L.	-	0	-	-	-
E. borealis Dr.	-	0	-	-	-
Gnaphalium uliginosum L.	-	-	-	0	-
Achillea millefolium L.	1	-	-	-	2
Chrysanthemum parthenium Bernh.	-	0	-	-	1
C. corymbosum L.	-	-	-	0	-
Matricaria suaveolens Buch.	-	0	-	0	-
Tanacetum vulgare L.	-	0	-	0	-
Artemisia vulgaris L.	-	-	-	0	-
Senecio vulgaris L.	-	0	-	0	2
S. jacobaea L.	-	0	-	-	-
Arctium lappa L.	-	0	-	-	-
Cirsium acaule Weber	1	1	-	-	-
C. lanceolatum Scop.	1	1	-	-	2
Carduus nutans L.	2	2	-	-	-

C.bicolor C.albomarginatus O. viridulus L.migratoria S.gregaria.

Hieracium pilosella L.	0	0	0	0	-
Taraxacum officinale agg.	1	2	0	2	2
Sonchus arvensis L.	-	1	-	1	2
Hypochaeris radicata L.	-	1	-	-	2
Tussilago farfara L.	-	0	-	-	-
Inula helenium L.	-	0	-	-	-
Centaurea nigra L.	-	0	-	-	-
<u>Dipsacaceae.</u>					
Scabiosa arvensis L.	-	0	-	-	-
S. columbaria L.	-	0	-	-	-
<u>Campanulaceae.</u>					
Legousia hybrida Del.	-	1	-	-	-
Jasione montana L.	1	1	-	-	-
Campanula pyramidalis L.	2	1	-	2	-
C.glomerata L.	2	2	-	-	-
<u>Ericaceae.</u>					
Calluna vulgaris Hull.	0	0	-	0	-
Erica cinera L.	0	0	-	0	-
Rhododendron ponticum L.	-	0	-	0	-
<u>Primulaceae.</u>					
Lysimachia nummularia L.	-	-	-	1	-
Primula vulgaris Huds.	-	0	-	0	-
<u>Gentianaceae.</u>					
Gentiana amarella L.	0	0	-	-	-
Blackstonia perfoliata Huds.	-	0	-	-	-
Centaureum centaurium Dr.	-	0	-	-	-
<u>Boraginaceae.</u>					
Symphytum tuberosum L.	-	-	-	0	1
Myosotis arvensis Hill.	1	1	-	1	2
Anchusa sempervirens L.	0	1	-	0	1
Cynoglossum officinale L.	0	1	-	-	-
Echium vulgare L.	-	0	-	-	-
<u>Solanaceae.</u>					
Solanum tuberosum L.	0	1	-	1	1
S. nigrum L.	0	0	-	-	0
S. dulcamara L.	-	0	-	0	-
Lycopersicon esculentum Hill.	0	0	-	0	0

C.bicolor C.albomarginatus O.viridulus L.migratoria S.gregaria.

Crassulaceae.

Sedum acre L. 0 - - - -

Convolvulaceae.

Convolvulus arvensis L. 0 0 - - 0

Schophulariaceae.

Veronica serpyllifolia L. - - 0 - -

V. chamaedrys L. 1 1 1 1 2

V.officinalis L. - 1 0 - 2

Linaria repens Mill. 0 0 - - -

L.vulgaris Mill. 0 0 - 0 -

Verbascum thapsus L. 0 0 - 0 0

V.blattaria L. 0 0 - - -

Euphrasia officinalis agg. 0 0 - - -

Digitalis purpurea L. - 0 - 0 -

Verbenaceae.

Verbena officinalis L. - 1 - - -

Santalaceae.

Thesium humifusum D.C. 0 0 - - -

Labiatae.

Clinopodium vulgare L. 0 0 - - -

Thymus serpyllum agg 0 0 0 0 0

Calamintha officinalis I.K. 0 0 - - -

C.acinos Scheele - 1 - - -

Salvia verbenaca L. 0 0 - - -

Lamium purpureum L. - - - 1 1

L. album L. - 0 - 0 -

Prunella vulgaris L. 0 0 0 0 2

Stachys sylvatica L. - - - 0 -

Plantaginaceae.

Plantago lanceolata 0 1 0 0 1

P. media L. 0 0 0 0 1

Chenopodiceae.

Chenopodium album L. - - 0 - -

Beta vulgaris L. - - - 0 -

Polygonum convolvulus L. - 0 - - 0

P.aviculare L. - 0 0 - 0

P. persicaria L. - 0 0 - -

Rumex crispus L. - 0 - 0 -

C.bicolor C.albomarginatus O.viridulus L.migratoria S.gregaria.

R. acetosella L.	0	0	0	1	2
<u>Euphorbiaceae.</u>					
Euphorbia helioscopia L.	0	0	-	-	-
Mercurialis perennis L.	-	-	-	0	-
<u>Liliaceae.</u>					
Muscari racemosum Lam.and D.G.	-	-	-	0	-
<u>Araceae.</u>					
Arum maculatum L.	-	-	-	0	-
<u>Amaryllidaceae.</u>					
Narcissus pseudo-narcissus L.	0	0	0	0	0
Galanthus nivalis L.	-	0	-	0	-
<u>Liliaceae.</u>					
Convallaria majalis L.	-	2	-	-	-
<u>Juncaceae.</u>					
Juncus bufonius L.	-	2	-	-	-
J. effusus L.	2	2	-	2	2
J. conglomeratus L.	-	-	2	-	-
Luzula campestre D.C.	2	2	2	2	2
<u>Cyperaceae.</u>					
Carex flacca Schreb.	2	-	2	-	-
C. caryophyllaea Latour	2	-	2	-	-
C. disticha Huds.	-	-	2	-	-
C. riparia Curtis	-	-	-	2	-
C. vulpina L.	-	-	2	-	-
Scirpus sylvaticus L.	-	-	-	2	-
<u>Gramineae.</u>					
Digraphis arundinacea L.	-	2	-	-	-
Anthoxanthum odoratum L.	1	1	1	0	-
Alopecurus pratensis L.	2	2	-	2	-
A. myosuroides Huds.	-	-	-	2	-
Milium effusum L.	-	-	-	2	-
Phleum pratense L.	2	-	-	2	-
P. nodosum L.	-	-	-	2	-
Agrostis stolonifera (L)	-	-	-	2	-
A. spici-venti	-	-	-	2	-
A. vulgaris With.	2	2	2	1	-
A. alba L.	-	-	-	2	-
A. canina L.	-	-	-	2	2

C.bicolor C.albomarginatus O.viridulus L.migratoria S.gregaria.

Polypogon monspeliensis Desf.	-	-	-	2	-
Lagurus ovatus L.	-	-	-	2	-
Aira praecox L.	-	-	2	-	-
Deschampsia caespitosa Beauv.	-	-	-	2	-
D.flexuosa Trin.	2	2	2	2	-
Holcus lanatus L.	2	2	2	2	-
H.mollis L.	2	2	2	2	2
Trisetum flavescens Beauv.	2	2	2	-	-
A.pubescens Huds. (Avena)	2	-	-	-	-
Arrhenatherum elatius Mert.and Koch.	1	1	1	0	-
Sieglingia decumbens Bernh.	2	2	2	-	-
Phragmites communis Trin.	-	-	-	2	-
Cynosurus cristatus L.	2	2	-	2	-
Koeleria gracilis Pers.	2	2	2	2	-
Molinia caerulea Moench	2	2	2	-	-
Melica nutans L.	-	-	-	1	-
M.uniflora Retz.	-	2	-	2	-
M.altissima	-	-	-	0	-
Dactylis glomerata L.	2	2	2	2	-
Briza media L.	2	2	-	-	-
B.minor L.	-	-	-	0	-
Poa pratensis L.	2	2	-	2	-
P.trivialis L.	2	2	-	-	-
P.nemoralis L.	-	2	-	2	-
P.annua L.	2	2	2	2	-
P.caespitosa	-	-	-	1	-
P.palustris L.	-	-	-	2	-
P. compressa L.	-	-	-	2	-
Glyceria aquatica agg.	-	-	-	2	-
Puccinellia maritima Mert and Koch.	-	2	-	-	-
Festuca elatior L.	2	2	2	-	-
F.ovina L.	2	2	2	2	-
F.rubra L.	2	2	2	2	-
Bromus sterilis L.	2	2	2	2	-
B.erectus Huds.	2	2	2	2	-

C.bicolor C.albomarginatus O.viridulus L.migratoria S.gregaria.

B. mollis L.	-	-	-	2	-
B. asper Murr.	-	-	-	1	-
Brachypodium pinnatum Beauv.	-	-	-	2	-
B. sylvaticum R. and S.	2	2	2	0	-
Lolium perenne L.	2	2	2	2	-
Agropyron pungens R. and S.	2	2	-	1	-
A. repens L.	-	-	-	2	-
A. caninum Beauv.	-	2	-	2	-
Secale cereale L.	-	-	-	2	-
Triticum aestivum L.	-	-	-	2	-
Nardus stricta L.	1	1	1	1	-
Hordeum hysfrix	-	-	-	2	-
H. jubatum L.	-	-	-	2	-
Elymus canadensis L.	-	-	-	1	-
Bambusa sp.	2	2	-	2	-
Lepturus cylindricus Trin.	-	-	-	2	-

APPENDIX B. FIELD OBSERVATIONS ON BRITISH GRASSHOPPERS.

These observations were made as initially it was hoped that some food factors determined the habitat. Through the course of this work, this hypothesis was dismissed, but as the habitat distribution of the species in Britain appears to be still very inadequately known, it was decided to continue this part of the research.

Descriptions and keys to the identification of the British Acrididae can be found in Burr (1936), Lucas (1920) and Hincks (1949).

Accounts of the habitats of the British species are found in Lucas and Burr but are very brief and in some instances quite misleading. In connection with the present work, the writer has made notes on the different kinds of habitat where grasshoppers were observed and, although the area covered is limited, in view of the small amount of information which is available in the literature, it is thought worth while to include these observations here.

An important observation was that in not a single instance were grasshoppers found in the absence of some kind of grass. Habitats where grasses do not constitute at least a small feature of the vegetation are few in number, even on the tops of Britain's highest mountains some grasses are to be found. However, grasshoppers do not occur everywhere that grasses are to be found, but it seems that the presence of some kind of

grass is necessary for the occurrence of the British Acridid fauna. On dry heathland, it is very noticeable that grasshoppers are confined to damper hollows where Molinia caerulea flourishes (Chorthippus parallelus) or to the often localised patches of Nardus stricta, Molinia, Deschampsia flexuosa and Triodia (Sieglingia) decumbens among the Erica-Callunetum sward (Myrmeleotettix maculatus).

The nearest approach to a pure community of herbs inhabited by grasshoppers was seen in a beechwood glade in South Oxfordshire. The glade was on a south-west facing spur of the Chilterns and the area concerned covered about an acre. The ground flora was a very unusual community composed in the main of Sedum acre L. with patches and a few isolated plants of Iberis amara L. At first glance, these two plants appeared to comprise the whole flora and the presence of a very low density of adults of Chorthippus bicolor aroused considerable interest. However, after some careful search at the base of the plants, a thin straggling growth of Agrostis canina L. was found, enough to support the few grasshoppers. Subsequent laboratory work showed that neither Sedum nor Iberis is eaten by this insect.

Many factors are likely to influence the occurrence of grasshoppers. Observations have been made on percentage cover of the ground but the hardness and other physical properties of the soil which must be important in the selection of oviposition sites have not been examined. Likewise, the

importance of microclimatic factors cannot be too strongly stressed. All these are outside the scope of the present study which must be strictly limited to purely vegetative factors. This work can only give some indication of how far the composition of the vegetation acts as a limiting factor to grasshopper occurrence in this country.

Vestal (1913) drew attention to the fact that certain species of Acrididae are more ecologically plastic than others. He cited as an example, Melanoplus atlantis which occurs regularly in North America in meadows, dry open grassland, and in open forest. It is evidently a species which can endure a variety of conditions. Although certain species inhabit sites which appear to have very different physical conditions, there are usually certain features which are common to all. Thus, the common British grasshopper, Myrmeleotettix maculatus, is found abundantly on dry heathland but is also very common on the chalk downs. The flora of these two habitats is very different, but there is at least one very important condition which is common to both, the low percentage cover of the vegetation, and hence, the abundance of bare patches of soil surface. This will receive further treatment in the account of the species which follows.

Sometimes a species is confined in one country to one type of habitat, but it is not so restricted in other countries. This is well exemplified by Chorthippus albomarginatus, an insect confined in Britain to saltmarshes and sand-dunes on the coast, except for a few scattered inland stations, but which occurs

commonly in inland districts on the continent. Likewise, Gomphocerippus rufus occurs in this country in open spaces in the southern counties but on the Continent it is equally frequent in woods.

The probable explanation of this is that both these species, in Britain, are at the limit of their range and, consequently, their degree of plasticity is low.

Clark's observations showed that, on the whole, grasshoppers do not regularly frequent places which have both a high percentage cover and tall plant growth. If, however, the vegetation is less than 60 cms (about 2½ ins) high the concentration of some species may be quite high even when the cover is a hundred per cent. In the same way, a high Acridid density is rarely found where the amount of exposed soil surface is more than fifty per cent. The optimum conditions of height and percentage cover of the vegetation are not the same for every species. Whereas Myrmeleotettix maculatus prefers fairly short turf with a low percentage cover, Gomphocerippus rufus and Chorthippus parallelus are more abundant in taller vegetation with a higher percentage cover.

However, it should be pointed out that when a high density of grasshoppers occurs in a habitat with tall and dense plant growth, the factor which has allowed the population to reach a high level may not be the nature of the vegetation but some other factor which is exerting a more powerful influence and so counter-acting the effect of the unfavourable conditions. This factor may be one of many, the water content of the soil, the exposure

of the site to the sun, abundance of suitable oviposition sites, etc. Mecostethus grossus occurs in the New Forest in acid bogs, with tussocks of Molinia between which is a dense growth of Sphagnum moss, or the Molinia may stand like islands, completely surrounded by surface water. In Norfolk, it is found in reed-beds, in the Fens and Broadlands in localities where coarse marshland plants like Phragmites communis Trin. and Iris pseudacorus L. make up the vegetation. The composition of the flora is very different in the Fen Country and the New Forest bogs but the important factor that Mecostethus needs, very wet conditions, is common to both. Chorthippus parallelus too, although also found in quite dry situations, is often common in Molinia-Sphagnum bogs where the vegetation is thick, luxuriant and completely covers the soil. From these examples it is clear that when investigating the optimum conditions for a species it is important to study as many different types of habitat as possible. Examples of every ecological niche which the species occupies should be examined.

Clark did most of his population studies in chalk grassland as this was the prevailing habitat in the district where he lived. This must be taken into account when examining his findings.

It is probably significant that the three species, Omocestus viridulus, Stenobothrus lineatus and Mecostethus grossus, which are usually associated with rank vegetation, often without any exposed surface soil between the plants, lay their egg pods among the leaf sheaths at the base of shoots and tussocks of grass and not within the soil. Hence, exposed soil is not necessary to

these insects, but species like Chorthippus bicolor and Myrmeleotettix maculatus would be unable to find suitable oviposition sites and would not be able to build up a high density in a locality with dense plant growth.

In determining to what extent the occurrence of the British Acrididae is dependent on the composition and structure of vegetation, it was necessary to make detailed floral lists of each locality visited and make notes on percentage ground cover and height of the plants. The plant species were recorded in the following categories, dominant, co-dominant, sub-dominant, common, frequent and occasional. An estimation of population density of each species of grasshopper present was made. The estimation of ground cover was made by inspection, usually a metre quadrat was employed to aid this, and was the amount of soil surface exposed and not covered by leaf rosettes, etc.

The method of estimating population density needed to be both accurate and quick. In the short amount of time available for this part of the work it was necessary to visit as many places as possible and often two or three different sites were examined in one day. Sweeping has been much used in the past but as a method of estimating absolute numbers rather than relative abundance of several species, it is practically useless. A discussion on the methods of estimating numbers can be found in Clark (1948). The method used in the present investigation was a sight-time count. A count was made of the number of individuals of each species seen in five minutes in the habitat. Each count was repeated

3-12 times according to the nature of the habitat or the degree of variation between the readings. This method gives a reliable figure for the relative abundance of the species and the results can be used as a figure of absolute density if checked occasionally in each type of vegetation against results obtained by a more accurate method. For this type of work the best method of assessing absolute density is the quadrat. The metre quadrat is the best size to use for adult Acridids, and for this work, the squares were made up in the sites where they were used. Each consisted of four wooden stakes, pointed at one end, between which was stretched some strong white string to enclose an area of one metre square. The quadrats were set out in rows at equal distances apart, the positions of the quadrats alternating in adjacent rows. The number of squares in each row and the distance between them varied a little between the stations studied. From twenty to thirty quadrats were used in each estimation.

Quadrats of this type are easily assembled and dismantled and have the advantage over permanent metal squares of being easily transported on a bicycle. The white string is very conspicuous and easily detected when the counts are made but it is not likely to hamper movements of the insects in and out of the confined areas. Thirty squares can be pegged out in an hour. After setting up the quadrats, they were left for a minimum of six hours to allow the insects to recover from the disturbance and return to their former stations if they wished.

The following trial was carried out in order to determine the importance of standardising the hour of the day when counts were made. Twenty-two quadrats were set up and left overnight. On the following day, counts were made in early morning, in the afternoon and at dusk. Four species of grasshopper were present in the area but no individuals of one, Omocestus viridulus, appeared in any quadrat. The results are summarised in Table 26.

TABLE 26.

Field trial to determine the importance of standardising the time of day when counts of grasshopper density are made. Twenty-two quadrats were used in this trial.

Time of day.	Chorthippus bicolor	Chorthippus parallelus	Stenobothrus lineatus	Omocestus viridulus
10.00 hrs	29	18	6	0
15.00 hrs	32	22	7	0
18.00 hrs	30	13	7	0
Total	91	53	20	0
Mean	33.33	17.66	6.66	0
Density/ sq. metre	1.38	0.80	0.33	-

The results were consistent but as the insects are more active in the hotter part of the day, subsequent counts were always made in the evening. For this work, thirty squares were usually employed. Care was taken to avoid disturbance as much as possible when setting up the quadrats. When the census was made, to ensure that every grasshopper present was counted, the vegetation was thoroughly examined as some individuals were

usually resting near the ground, and in this inactive state might easily have been overlooked.

A survey of the grasshopper fauna of different habitats is given below. The tables included are selected from a large number of counts. A full summary of the results is given in Table 34 at the end of this section.

(1) Heaths and Dry Moors.

This type of habitat is considered first because the distribution of grasshoppers among heather illustrates conclusively that a grass component in the plant community is necessary for the occurrence of an Acridid population.

Grasshoppers are absent from pure Callunetum. They occur at a low density in thin heather where a sparse growth of moorland grasses is found and more abundantly in places where the grass is dominant over the heather. On dry grassy heaths where Agrostis tenuis, Deschampsia flexuosa and Nardus stricta are dominant and Erica cinerea, Calluna vulgaris and Sieglingia (Triodia) decumbens are present as less conspicuous components of the community, Myrmeleotettix maculatus sometimes attains a density of more than three per square metre. However, a few small tussocks of Molinia and Deschampsia growing on a path between a dense growth of Calluna and Erica often support a flourishing colony of this insect. It is the characteristic grasshopper of British heaths but Chorthippus parallelus also occurs on

heather moors but usually in damper situations than those inhabited by M. maculatus.

Tables 27 and 28 shew the results of quadrat counts on two heaths in Southern England.

The area of Chobham Common where this count was made included a damp zone of tall dense pure Molinetum. Quadrats A10-13 and B10-13 were in this zone. Over the rest of the area of the trial, as on Mortimer Common, Calluna vulgaris, Erica cinerea, Ulex minor and Molinia were present in varying amounts, the Calluna and Erica usually being dominant while the Molinia occurred as scattered single plants or in small colonies.

TABLE 27.

Quadrat count on Mortimer Common, Berks. September 3rd 1951.

Quadrat Number	Type of Vegetation	% Cover of Vegetation	Ht. of Vegetation in inches.	<i>Myrmeleotettix</i> <i>maculatus</i>	<i>Chorthippus</i> <i>parallelus</i>	<i>Metrioptera</i> <i>brachyptera</i> (<i>Tettigoniidae</i>).
A ₁	M	60	4	-	-	-
B ₁	M	95	2-6	1	-	1
C ₁	EC	70	1-3	-	-	-
A ₂	M	60	4	-	-	-
B ₂	M	30	2-6	1	-	-
C ₂	M	75	2-6	1	-	-
A ₃	EC	70	4	-	-	-
B ₃	M	80	6-9	-	-	1
C ₃	M	85	4-6	1	1	-
A ₄	EC	70	4	-	-	-
B ₄	M	85	4-7	1	-	1
C ₄	M	95	5-8	2	-	-
A ₅	EC	70	2	-	-	-
B ₅	M	80	6-9	-	-	-
C ₅	M	75	3-6	-	-	1
A ₆	M	70	5	2	-	-
B ₆	M	65	4	-	-	-
C ₆	M	95	4-8	1	-	-
A ₇	M	80	6-9	-	-	1
B ₇	M	90	6-9	-	-	-

TABLE 27 (Continued).

Quadrat Number	X Type of Vegetation	% cover of Vegetation	Ht. of Vegetation in inches.	Myrmeleotettix maculatus	Chorthippus parallelus	Metrioptera brachyptera (Tettigoniidae).
C ₇	M	90	6-9	-	-	1
A ₈	M	90	6-10	-	-	1
B ₈	EC	70	3-5	-	-	-
C ₈	EC	50	2-3	-	-	-
A ₉	EC	85	4-6	1	-	1
B ₉	EC	65	4	-	-	-
C ₉	EC	65	4-6	-	-	-
A ₁₀	M	60	3	-	-	-
B ₁₀	EC	70	3-5	-	-	-
C ₁₀	M	50	3-9	-	-	-
Total 30				11		

X Type of Vegetation EC = Erica-Callunetum

M = Molinia present.

TABLE 28.

Quadrat count on Chobham Common, Surrey, August 24th, 1951.

Quadrat Number	Type of Vegetation	% Ground cover of vegetation	Ht. of vegetation in inches	Chorthippus parallelus	C. bicolor	Myrmeleotettix maculatus	Metrioptera brachyptera
A ₁	M	90	15	1	-	-	1
B ₁	M	90	12	1	-	-	-
A ₂	M	80	12	-	-	-	-
B ₂	EC	80	12	-	-	-	-
A ₃	M	40	6	-	-	-	-
B ₃	M	90	6	2	-	1	-
A ₄	EC	90	9	-	-	-	-
B ₄	M	90	6	-	-	1	-
A ₅	M	65	6	-	-	1	-
B ₅	M	95	12	-	-	-	-
A ₆	EC	80	6-9	-	-	-	-
B ₆	EC	65	6	-	-	-	-
A ₇	EC	80	6-9	-	-	-	-
B ₇	EC	80	6-9	-	-	-	-
A ₈	M	80	6-9	-	-	1	-
B ₈	EC	80	6-9	-	-	-	-
A ₉	M	80	6-9	-	-	-	-
B ₉	M	70	6-9	-	-	-	-
A ₁₀	M	95	6-9	1	-	-	-
B ₁₀	M	95	9-12	1	-	-	-

TABLE 28 (Continued)

Quadrat Number	Type of vegetation	% Ground cover of Vegetation	Ht. of vegetation in inches	Chorthippus parallelus	C. bicolor	Myrmeleotettix maculatus	Metrioptera brachyptera
A ₁₁	M	100	9-12	1	-	-	1
B ₁₁	M	100	9-12	3	-	-	2
A ₁₂	M	95	9-12	2	-	-	-
B ₁₂	M	100	12-15	2	-	-	1
A ₁₃	M	100	18-24	1	-	-	-
B ₁₃	M	100	18-24	1	-	-	1
Total 26	-	-	-	16	0	5	6

The following is a summary of the results in Tables 27 and 28.

% Cover	No. of Quadrats		M. maculatus		C. parallelus		M. brachyptera.	
	(27)	(28)	(27)	(28)	(27)	(28)	(27)	(28)
0 -50	3	1	1	1	0	0	0	0
55 -70	13	3	2	1	0	0	0	0
75 -85	8	8	4	1	1	0	5	0
90-100	6	14	4	2	0	16	5	6
Total	30	26	11	5	1	16	10	6
Mean % cover			80	73	-	96	86	98
<u>Ht. in ins.</u>								
0 - 3	4	0	0	0	0	0	0	0
3 - 6	19	5	9	4	1	2	4	0
6 - 9	7	9	2	1	0	1	6	0
9 -24	0	12	0	0	0	13	0	6
Total	30	26	11	5	1	16	10	6
Mean ht. in ins.			5	6	-	12	6.5	12

These results show clearly that on heaths C. parallelus tends to occur in areas of tall dense vegetation whereas M. maculatus prefers regions of shorter growth with a lower percentage cover. No individuals of either of these species were found in a quadrat which did not enclose at least one small tussock of Molinia. The mean density over these areas was at about the level usual in a habitat of this type. On open heaths with numerous damp hollows containing Eriophorum, Narthecium ossifragum and Drosera, the coarse grasses are more abundant and C. parallelus sometimes attains a density of more than 3 per square metre. The M. maculatus in such places are confined to the dry ridges. They are never

present in dense closed vegetation and seldom where the ground cover exceeds 95 per cent.

The following three species are also found on heaths occasionally - Chorthippus bicolor, Omocestus viridulus, Stenobothrus lineatus. The only known British station for Chorthippus vagans is an area of heathland on the Hampshire-Dorset border and the few inland localities where C. albomarginatus has been recorded are mostly on heaths.

ii) Damp Heaths and Bogs.

On damp acid moors, the characteristic British grasshopper is Chorthippus parallelus. The flora consists of Molinia caerulea (dominant), Erica tetralix, Narthecium ossifragum, Eriophorum spp. and Cirsium palustre with occasional patches of Drosera spp., Viola palustris and Comarum palustre. Sphagnum mosses also occur, sometimes commonly. In three places with a habitat of this type, part of Chobham Common, Surrey, Hook Common, Hants and Owlsmoor Bog, Berks, a density of nearly 3 / sq. metre was noted and populations of 2 / sq metre were recorded in several stations.

Mecostethus grossus occurs in Sphagnum bogs in the New Forest, Hampshire, a few other places in Southern England, the Norfolk Broad and Fens, and in many parts of Ireland. It has also been recorded from Scotland. In Denny Bog in the New Forest it occurs in a habitat where surface water covers the ground to a depth of several inches and where Molinia, Sphagnum and Eriophorum comprise the only vegetation. Much of the ground

consists of hummocks of Sphagnum through which grow tussocks of Molinia and occasional Eriophorum. The Sphagnum stands as islands, usually surrounded by water. In Matley Bog the insect occurs in a rather drier situation among Molinia, Erica tetralix, Sphagnum, Lotus uliginosus and Myrica gale L. In Norfolk it is usually associated with Molinia, Sphagnum and Myrica gale. Very wet conditions appear to be essential for the occurrence of this species.

iii) Woods.

The only British grasshopper which is usually associated with woods is Omocestus ventralis. It occurs in wide heathy rides and in heathy glades and has been recorded from many parts of Britain. In Hampshire and South Berks it occurs on the edges of oak woods as well as in open rides and glades, often on the damp ground at the edge of a heather association where the heaths are subdominant to the grasses Molinia, Agrostis tenuis and Sieglingia decumbens. In a locality near Lyndhurst in the New Forest, sixty adults were collected in less than one hour. It appears to be usually abundant where it is found but very local in its occurrence.

Chorthippus bicolor also occurs in wide rides in woods and several other species are sometimes found in glades according to the size of the area and the nature of its vegetation.

iv) Mountains.

Chorthippus parallelus, Myrmeleotettix maculatus and Omocestus viridulus all occur on mountains, the first two-named

usually only on the lower slopes and in the valleys. In the Scottish Highlands I have seen Omocestus viridulus between 2000-2500 ft. Here it is usually confined to the sides of deep gulleys cut out by the mountain streams, where the vegetation is composed, in the main, of such dwarf plants as Festuca ovina, Lotus corniculatus, Prunella vulgaris and Antennaria dioica.

v) Water Meadows.

The two species of grasshopper which are most often associated with damp meadows are Chorthippus parallelus and Omocestus viridulus. In heavily grazed meadows, grasshoppers are usually few in number but in rank herbage at the edge of a field, they may be present at a fairly high density. Often there is a region of coarse and luxuriant plant growth at the foot of a slope where damp conditions prevail and these two species occur plentifully.

vi) Dry Fields and Pastures.

The chalk downs sometimes support a high grasshopper population. The following six species all occur in stations of this type - Chorthippus bicolor, C. parallelus, Omocestus viridulus, Gomphocerippus rufus, Myrmeleotettix maculatus and Stenobothrus lineatus.

A survey made at different positions on the slope of a hill shows that the several species present are differently distributed. The results obtained by a sight-time count on three species of Acrididae in three hill localities are shown in Table 29. Estimations were made at three different positions

on the slope at Watlington and two at Basildon and Whitchurch. On these chalk hills the vegetation becomes sparser and shorter as one ascends the slope. The bottom position at Watlington was a field, cultivated some years previously but now recolonised thinly by natural vegetation. No grasshoppers were present. At Whitchurch and Basildon, natural vegetation covered the whole slope. The figures given are all means of a number of counts.

TABLE 29.

The distribution of three species of Acrididae on chalk hills. Estimations of density made by the sight-time method. Relative abundance only.

Species	Position of Count	Whitchurch Oxon	Basildon Berks	Watlington Oxon	Total	Mean
<i>Myrmeleotettix maculatus</i>	Bottom	0	-	0	0/2	0
		(-	0	0	0/2	0
	Mid	(5.5	2.5	3	11/3	3.7
	Top	-	-	7.5	7.5/1	7.5
<i>Chorthippus bicolor</i>	Bottom	11	-	0	11/2	5.5
		-	7	1	8/2	4
	Mid	25	8.5	0	33.5/3	11.2
	Top	-	-	0	0/1	0
<i>Chorthippus parallelus</i>	Bottom	4.5	-	0	4.5/2	2.25
		-	20.5	18	38.5/2	19.25
	Mid	2	10	12	24/3	8
	Top	-	-	2	2/1	2

These figures show that *Myrmeleotettix maculatus* is absent from the lower slopes, *Chorthippus bicolor* is generally distributed except at the summit and *C. parallelus* is most abundant near the foot of the hills but occurs right up to the top in decreasing numbers.

A more detailed survey of Watlington Hill is shown in Table 30. This area is very suitable for study of this kind as it can

be readily divided into a number of well-marked zones of vegetation. Five species of Acrididae are present.

There is a total absence of all species of grasshoppers from Zones A and C where the vegetation is uniform and short. A few were present in Zone E, two were seen in fifteen minutes surveying. In areas of uniform vegetation there is no shelter from extremes of temperature. The behaviour of grasshoppers in the field has shown that they appear in the open only when the sun is shining, at other times they shelter in tussocks of taller and denser plant growth.

In Zone A, Agrostis stolonifera was dominant. In B, Arrhenatherum elatius was dominant with Festuca ovina abundant. Festuca, Carex flacca and Funaria (moss) were co-dominant in C. Zone D was very heavily rabbit grazed but considerably less so than C or E. Here, Bromus erectus, Holcus lanatus and Carex were co-dominant with Arrhenatherum, Agrostis, Festuca, Hypnum cupressiforme (moss) and Calamintha officinalis abundant. In E, Festuca, Thymus serpyllum agg., Hypnum and the lichen Cladonia sp. were co-dominant while Arrhenatherum, Bromus, Festuca and Hypochaeris radicata were equally abundant in F. Bromus was dominant in Zone G with Festuca, Calamintha and Origanum vulgare abundant. In H and I the dominant was Festuca with Hypnum, Linum catharticum, Thymus, Hieracium pilosella, Carex and Fragaria vesca all abundant. From this can be seen that there was no shortage of edible grass in any of the zones. It is

possible that Agrostis is not suitable for satisfactory growth although it is eaten but this aspect is outside the scope of this work and has not been investigated. Festuca, however, was always present in the Zones B-I and this grass has been much used in breeding stocks as well as in laboratory experiments and is a very suitable food.

It is noteworthy that C.parallelus was most abundant in Zones B,F and G and these areas have the tallest vegetation. In D and H they were quite plentiful, but here it was noticeable that their occurrence coincided with the presence of tussocks of coarser growth. There is no doubt that this species shows a marked preference in this country to communities of ranker and denser vegetation than those frequented by other Acrididae.

Table 31 gives the results of sight-time counts made on Lowbury Hill, Berks.

TABLE 30.

A. survey of the relative abundance of five species of Acrididae on Watlington Hill, Oxon on September 21st, 1951. 10 = 1/sq. metre approx.

- A. Dry field at bottom of hill. Once cultivated, now wild.
 B. Local area where tall *Arrhenatherum* is dominant. 50 yards long, 20 yards wide.
 C. Zone of very uniform vegetation.
 D. Zone on same horizon of hill as C but to the West. Veg. same composition as C. but slightly taller and grasses growing in tussocks.
 E. Short turf halfway down hill.
 F. Zone on same horizon of hill as E but to West. Much taller and denser plant growth.
 G. Zone also about halfway down hill but slightly higher.
 H. Near top of hill. Ground becoming more stony. Herbs mostly prostrate and rosette habit types.
 I. Summit ground, very broken and stony. Vegetation very dwarf.

Zone	Ht. of vegetation in inches.	% cover of vegetation	<i>Chorthippus parallelus</i>	<i>Chorthippus bicolor</i>	<i>Myrmeleotettix maculatus</i>	<i>Omocestus viridulus</i>	<i>Stenobothrus lineatus</i>	<i>Tetrix vittata</i>
A	$\frac{1}{2}$ - 1	95-100	0	0	0	0	0	0
			0	0	0	0	0	0
			0	0	0	0	0	0
B	2 - 24	100	22	5	0	0	0	0
			19	2	0	2	0	0
			21	6	0	2	0	0
	av. 9		17	8	0	1	2	0
C	1 - 3	90-95	0	0	0	0	0	0
			0	0	0	0	0	0
			0	0	0	0	0	0
D	1 - 3	95-100	10	6	0	0	1	10
			5	3	0	0	0	8
			8	5	0	0	0	4
	av. 2		11	3	0	0	0	8
E	$\frac{1}{2}$ - 1	50-90 (av. 75-80)	0	0	0	0	0	0
			0	1	0	0	0	2
			1	0	0	0	0	0

TABLE 30 (Continued).

Zone	Ht. of Vegetation in inches	% cover of vegetation	Chorthippus parallelus	Chorthippus bicolor	Myrmeleotettix maculatus	Omocestus viridulus	Stenobothrus lineatus	Tetrix vittatum
F	1-9 (av.3-4)	95	21	8	0	1	0	2
			18	0	0	1	0	1
			13	1	0	2	0	0
			19	1	0	2	0	0
G	3-10 (av.4-5)	90-100	21	1	0	3	0	0
			14	0	0	0	0	0
			16	0	0	0	0	0
			16	2	0	1	0	0
H	1½-4	90-95	9	0	2	1	0	0
			10	0	5	0	0	0
			12	1	1	1	0	0
			14	0	3	1	1	0
			14	0	3	0	1	0
			13	1	5	1	0	0
I	1½-11½	90-95	4	0	7	0	0	0
			0	0	7	0	0	0
			1	0	9	0	0	0
			4	0	9	0	0	0
			1	0	6	1	0	0
<u>MEANS</u>								
A	1-1	95-100	0	0	0	0	0	0
B	2-24	100	20	5	0	1	0.5	0
C	1-3	90-95	0	0	0	0	0	0
D	1-3	95-100	8.5	4	0	0	0	7.5
E	1-1	50-90	1	1	0	1.5	0	2
F	1-9	95	18	1	0	1	0	1
G	3-10	90-100	17	1	0	1	0	0
H	1½-4	90-95	12	0.5	3	0.5	0.5	0
I	1½-11½	90-95	2	0	7.5	0	0	0

TABLE 31.

Summary of sight-time count made at Lowbury Hill, Berks, September 19th 1951, to show the relative abundance of the Acrididae present in different zones. Figures represent averages 10 = 1" sq. metre approx.

Zone A. Dense downland turf with Festuca ovina agg. (Dominant)

Zone B. Gully with tall dense growth of Bromus erectus, Festuca, Phleum pratense, Brachypodium sylvaticum, all locally dominant.

Zone C. Thin turf with broken chalk rubble, Dactylis glomerata, Poterium sanguisorba, Thymus all co-dominant.

Zone D. Dense downland turf with Dactylis glomerata dominant.

Zone	Ht. of vegetation in inches	% cover	No. of counts	Chorthippus parallelus	Chorthippus bicolor	Myrmeleotettix maculatus	Stenobothrus lineatus	Omocestus viridulus
A	2-9 (av.4-6)	95-100	8	8	2.5	0.5	2.	0
B	6-15 (av.9)	100	4	16	9	0	1	3
C	1-6 (av.3)	50	7	6	7	0.5	0	0
D	1-6 (av. 3)	90-95	5	27.5	16.5	0	2	0.5

All the above tables show that Myrmeleotettix maculatus shows a decided preference for broken ground with a short plant growth and a low percentage cover. Areas of this type are frequently found on or near the tops of chalk hills and this grasshopper is often common in such situations.

Stenobothrus lineatus is present in a low density on some chalk hills. As in other types of habitat, Omocestus viridulus is most abundant in zones of taller and denser plant growth than those where the vegetation is short and sparse.

Chorthippus bicolor is not as exacting in its choice of habitat as many British Acrididae. It shows a slight preference for fairly short vegetation but clumps and tussocks of taller growth to afford shelter must be present if it is to reach a fairly high density. A density of about 2/sq. metre was observed on a dry roadside bank where vegetation was tall (9 ins.) and fairly dense (90-95%). The dominant plant was Bromus erectus, which was the only grass present, broad-leaved plants were only occasional. C. parallelus and Stenobothrus lineatus were also present in densities of 1/2 sq. metres and 1/9 sq. metres respectively. On a similar dry bank where Bromus was 18-24 ins. high, C. bicolor occurred at a concentration of 1/20 sq. metres and Gomphocerippus rufus at 1/10 sq. metres.

In my experience of Gomphocerippus rufus on the chalk hills of Surrey, Berks and S. Oxon., this species is usually found on rather rough ground off the grassy slopes of the hills where

coarse plant growth predominates. It is often associated with rabbit warrens at the foot of the downs. A summary of the counts made on the Acridid fauna of a chalk hill at Whitchurch, Oxon, is given in Table 32.

These figures show clearly that Gomphocerippus rufus prefers rough ground with coarse vegetation. Similar observations were made with this species elsewhere on the Downs.

TABLE 32.

Summary of sight-time counts made on Whitchurch Hill, Oxon, September 5th 1951. Figures represent averages 10 = 1/sq.metre approx.

- Zone 1. Broken ground around a rabbit warren. South facing slope. Vegetation from 3-24 ins. high. Percentage cover 50-100% locally. Vegetation composed of a variety of coarse weeds and grasses.
- Zone 2. Similar ground to Zone 1 but on the East facing slope. Small area of shrubs present. Other vegetation 6-36 ins high and 50-100% cover. Coarse weeds and grasses.
- Zone 3. Area adjoining Zone 2. Turf pasture slightly broken up by a series of horizontal ridges. Height of vegetation 1-6 ins., percentage cover 70-90%. Co-dominant - Carex flacca, Poterium sanguisorba, Cirsium acaule, Avena pratensis. Other chalk downland plants present in varying amounts.
- Zone 4. Mid-way up South slope. Vegetation thin, only 50% cover except in a few pockets, composed of stunted heavily grazed grasses and prostrate herbs.
- Zone 5. Bottom of South slope. Vegetation as in Zone 4 but less heavily grazed. Ground cover 90-100%. Height 1-9 ins.

Zone	No. of Estimations	Chorthippus bicolor	Chorthippus parallelus	Gomphocerippus rufus	Myrmeleotettix maculatus	Stenobothrus lineatus	Tetrix vittatum.
1	5	8	9	8	0	0	0
2	5	6	9.5	9	0	0	0
3	5	5.5	9	3	0	1	5.5
4	8	3.5	2	0	5.5	0.5	0
5	4	11	4.5	0	0	0	0

vii) Saltmarshes and Sand-dunes.

The characteristic grasshopper of British saltmarshes is Chorthippus albomarginatus. In such places it sometimes reaches a very high density. The highest concentration which was seen in the course of this work was 8/sq. metre which is considerably higher than that observed for any other species in any habitat.

Other grasshoppers, notably C.bicolor and Myrmeleotettix maculatus also occur on sand-dunes but appear to be generally absent from the wetter maritime communities.

In early August 1951, a survey was made of the C. albomarginatus population at Blythburgh salterns on the Suffolk coast. No grasshoppers were present in the Spartina Townsendii zones, probably because these areas are covered at high tides. The insects first appeared in the zone of drier mud where Aster tripolium L., Spergularia salina Presl., Obione portulacoides (L), Lepturus filiformis Trin. and Glyceria maritima (L) are co-dominant. Here, the density varied from 1-3/sq. metre.

As one approached the sea bank, a protective artificial earth wall, Agropyron pungens put in an appearance, first as a few scattered plants then increasing in abundance until it became the dominant plant. In this zone, where Spergularia, Lepturus and Juncus maritimus Lam. were sub-dominant, the density of Chorthippus albomarginatus was locally as high as 8/sq. metre with an average of 6/sq. metre. On the bank, Agropyron was the only plant present over a considerable area, the only other vegetation being a few plants of Arrhenatherum

elatus, Bromus sterilis and Ballota nigra L. The grasshoppers were very abundant, 3-7/sq. metre, with an average of about 5/sq. metre. On the bank the vegetation was 1-2 feet high and fairly dense, elsewhere it varied from 70-90% cover and from 1-12 inches high depending on the plant present.

Behind the dunes and sea wall at Walberswick, there is a somewhat damp area where salt-marsh and sand-dune plants are intermixed. This is backed by a considerable area where Phragmites communis extends in a wide belt for about a mile inland. This area is divided by a few banks where Agropyron flourishes. Here, Chorthippus albomarginatus reached a density of about 1/sq. metre in rather dense growth nearly two feet high. A few sight-time counts were made on the mixed sand and gravel area behind the dunes. Here, the ground cover ranged from 10-50% and the vegetation varied considerably in height. Locally dominant were Sedum acre, Festuca rubra and Agropyron pungens whilst Trifolium arvense, Silene maritima, Lotus corniculatus and Beta maritima were all locally plentiful. In places, especially in the Sedum-Festuca areas, colonies of Myrmeleotettix maculatus were present. Chorthippus albomarginatus and C. bicolor were scattered over the area, the former at a density ranging from 1-3/sq. metre, the latter much less. (See Table 33).

TABLE 33.

Summary of sight-time counts made on the Acridid population at Walberswick, Suffolk, on August 3rd 1951. These figures give relative abundance only. For absolute density 10 = 1/sq. metre approx.

Estimation	Chorthippus albomarginatus	Chorthippus bicolor	Myrmeleotettix maculatus.
1	10	1	1
2	10	2	4
3	11	3	4
4	15	4	3
5	18	4	2
Total	64	14	14
Mean	13	3	3

This habitat was separated from the Phragmites swamp by a dyke. Near this, the Agropyron increased in abundance until it was the only plant present. The only grasshopper in this community was C.albomarginatus.

Among other stations where C.albomarginatus has been studied are saltmarshes at Lyminster, Hants and dunes at Poole and Studland in Dorset. In the latter places it occurred most abundantly in the damper hollows between dune ridges where the vegetation was less coarse, denser and composed of more species.

SUMMARY OF THE HABITATS OF BRITISH ACRIDIDAE.

Chorthippus parallelus. One of the commonest and most widespread species. It is the only species which occurs regularly in damp meadows and is often abundant in damp places on heaths and moors. It is also common on the chalk downs but, in such places, it is noticeable that it usually congregates at the bottom of the slopes where the vegetation is more luxuriant.

C.bicolor. Also a common British species but it tends to frequent drier habitats than the foregoing. It occurs, often abundantly, in dry pastures, on the edges of heaths and occasionally in scrubby woodland and on sand-hills.

C.albomarginatus. Although on the Continent this insect occurs both on heaths inland and on sand-dunes and salterns near the coast, in Britain it is very rarely found far from the sea. In these situations it often occurs at a high density.

Myrmeleotettix maculatus. This insect is usually found on rather dry ground among thin vegetation. It is common on heaths in patches of grass among heather and bilberry and also frequents sand-hills near the coast and barer ground on chalk downs. In the latter habitat it is sometimes abundant on the tops of the hills where the vegetation is sparse and there is an abundance of loose broken chalk rubble. This rubble probably gives it the same protection as outstanding tussocks of rank vegetation and, for this reason, patches of tall growth are not as essential for the occurrence of this insect as in the case of other species.

Gomphocerippus rufus. In Britain, this species is very local in its occurrence. It is found on grassy hillsides especially where the ground is broken. For this reason it is often associated with rabbit warrens near the foot of the downs. It is a much more common insect on the Continent and there, it is sometimes plentiful in woodland rides and clearings. (There are old records of its occurrence in the New Forest and on sandhills).

Omocestus viridulus. One of the most widespread British Acrididae. Although common, it is rarely found at a high population density. (More than 1/2 sq. metres appears to be exceptional). It shows a preference for rather tall vegetation but it also occurs on short downland turf. It is frequently associated with C. parallelus on the damp edges of woods and in fens but rarely on open moors.

O. ventralis. A local insect of heathy woods where it occurs in glades and wide open rides. It is sometimes plentiful in its stations.

Stenobothrus lineatus. This is an insect of dry places but it is seldom common. I have seen it on the edges of heaths and on sandy and chalk pastures in Norfolk, Suffolk, Oxon, Berks, Hants and Surrey but always at a very low density.

Mecostethus grossus. This insect occurs only in damp places. In the New Forest it inhabits acid Molinia bogs and is also found in the Norfolk Fens and Broad.

A summary of the abundance of the British Acrididae studied in this work, in habitats of different types of vegetation, is included (Table 34).

C. DISCUSSION.

Although the differences in the general composition of the vegetation between the different kinds of habitat occupied by British grasshoppers might at first sight suggest that the limitation of the species to these habitats is directly connected with the distribution of essential food plants, this is not so. Uvarov (1928) has already pointed out that vegetation does not influence the selection of habitat by many Acrididae because of its food value. It is said that the favourite food of Locusta migratoria is the reed, Phragmites communis and that this is the reason why the typical habitat of the insect is reed-beds, but this is an exceptional case. From a consideration of the different habitats occupied by Myrmeleotettix maculatus, it follows that this grasshopper must feed regularly on a number of different kinds of grass. On heaths it is found in association with Festuca ovina, Deschampsia flexuosa, Triodia (Sieglingia) decumbens and Nardus stricta although it may not feed on all these. On the downs, Festuca ovina is often dominant where it occurs and by the sea it occurs in a community composed of Festuca rubra, F. juncifolia, Agropyron junceum and A. pungens.

It is possible that the favourite food-plant of Mecostethus

grossus is Molinia although it feeds regularly on other grasses in the laboratory. It is more likely that the peculiar tussock-forming habit of the plant is desirable for successful oviposition. Many of the British Acrididae, however, are like M. maculatus in that they commonly occur in a variety of plant associations, and must, therefore, have several food plants. It seems, therefore, that it is the structure of the vegetation rather than its composition, which is important in limiting the distribution of a grasshopper species. Most grasses appear to be suitable food-plants for these insects, and they never occur where grass is absent. Most species require at least a few tussocks of tall vegetation wherein to shelter in unfavourable weather conditions. For this reason uniform close turf does not support a high grasshopper population. At the same time, uniform tall plant growth does not appear to be suitable for many species. A habitat which has both types often has a considerable grasshopper population.

The majority of the British species occur in open places. Only one species, Omocestus ventralis, can be regarded as a woodland insect. Few species occur on mountains. Omocestus viridulus is sometimes plentiful on the lower slopes and Chorthippus parallelus and Myrmeleotettix maculatus also occur in mountainous districts of Scotland. One reason for this may be that in Britain, most species are approaching the northern limit of their range, and our mountains are mainly in the north-west of the country.

Windbreaks in the form of hedges may be important in building up high densities of grasshoppers. It is noticeable that south facing slopes usually support more grasshoppers than those facing north. The amount of insolation is important as grasshoppers are sun-lovers.

Gause (1932) pointed out that a study of the correlation between the density of a population and its environment represents the leading problem of ecology. Field investigation requires a detailed examination of the environment and of the density of the population under different conditions. With Acrididae, the density of the plant cover is of very great importance, for on this depends the microclimate to a great extent. In dense cover, the relative humidity of the atmosphere is greater and the temperature is lower than in areas with scanty cover where the soil is more heated and the vegetation is better aerated. The factors which are most likely to restrict grasshoppers to certain types of habitat are those connected with the microclimate, (temperature, relative humidity and evaporating power of the air), and the availability of suitable oviposition sites. It is, therefore, the structure of the vegetation and not its composition which it is important to examine. From the present investigation, there is no evidence which suggests that any of the British Acrididae are limited in their distribution by the occurrence of particular plant species.

TABLE 34.

The relationship between density of adult Acrididae and vegetation structure.

Chorthippus parallelus	% cover	Ht. in ins.	Adult density per sq. metre.						
			0.1	0.1-.3	0.3-.6	0.6-1	1-2	2-3	3
(188)	50-80	3	2	0	0	0	0	0	0
	"	3-6	1	1	0	0	0	0	0
	"	6-12	4	3	4	2	0	0	0
	80-95	3	2	1	0	0	0	0	0
	"	3-6	2	1	1	0	0	0	0
	"	6-12	3	2	2	0	1	0	0
	"	12	4	4	3	5	2	1	0
	95-100	3	3	1	0	0	0	0	0
	"	3-6	4	4	4	2	0	0	0
	"	6-12	4	2	5	5	4	2	0
	"	12	4	3	3	2	2	1	0
	100	3	8	3	3	1	0	0	0
	"	3-6	4	1	3	4	5	3	0
	"	6-12	4	2	6	8	7	2	0
	"	12	5	3	3	4	6	1	0
<u>C. bicolor</u>									
(183)	50	3	0	0	0	2	3	1	0
	"	3-6	0	0	0	2	4	2	0
	"	6-12	0	0	0	0	2	0	0
	50-80	3	1	2	3	4	3	1	0
	"	3-6	3	6	6	5	2	0	0
	"	6-12	2	2	1	2	1	0	0
	80-95	3	2	2	1	0	0	0	0
	"	3-6	4	7	6	6	4	3	1
	"	6-12	3	3	1	2	2	1	0
	"	12	3	1	1	0	2	0	0
	95-100	3	1	1	0	0	0	0	0
	"	3-6	5	5	6	4	3	2	1
	"	6-12	3	2	2	1	1	0	0
	"	12	2	1	2	0	0	0	0
	100	3	1	2	0	0	0	0	0
	"	3-6	3	3	1	2	0	0	0
	"	6-12	2	3	3	1	1	0	0
	"	12	1	0	1	2	0	0	0

TABLE A34 (Continued)

<u>C. albomarginatus</u>	% cover	Ht. in ins.	0.1	0.1-.3	0.3-.6	0.6-1	1-2	2-3	3
(48)	50	3-6	0	1	0	0	0	0	0
	"	6-12	0	1	0	1	2	0	0
	50-80	3	0	0	0	0	0	0	0
	"	3-6	0	2	0	2	1	0	0
	"	6-12	1	0	1	0	2	2	3
	"	12	0	0	0	2	1	0	0
	80-95	3	1	0	0	0	0	0	0
	"	3-6	0	0	1	0	0	0	0
	"	6-12	0	0	1	0	2	1	2
	"	12	0	0	1	1	0	1	0
	100	3	0	1	0	0	0	0	0
	"	3-6	0	1	0	1	0	0	0
	"	6-12	0	0	0	1	1	1	0
	"	12	0	0	1	1	3	2	3
<u>Omocestus viridulus</u>	50-80	6-12	1	0	0	0	0	0	0
	"	12	3	1	2	0	0	0	0
(70)	80-95	3	0	1	0	0	0	0	0
	"	3-6	1	1	0	0	0	0	0
	"	6-12	2	0	1	0	0	0	0
	"	12	3	1	2	1	0	0	0
	95-100	3	0	1	0	0	0	0	0
	"	3-6	5	3	2	0	0	0	0
	"	6-12	4	1	0	0	0	0	0
	"	12	2	3	1	2	0	0	0
	100	3	2	1	0	0	0	0	0
	"	3-6	4	0	1	0	0	0	0
	"	6-12	7	2	0	0	0	0	0
	"	12	2	3	2	0	0	0	0
<u>Stenobothrus lineatus</u>	50	3	2	0	0	0	0	0	0
	"	3-6	1	0	0	0	0	0	0
(39)	"	6-12	1	0	0	0	0	0	0
	50-80	3	1	2	0	0	0	0	0
	"	3-6	1	1	0	0	0	0	0
	"	6-12	0	1	0	0	0	0	0
	"	12	1	0	0	0	0	0	0
	80-95	3	0	1	0	0	0	0	0

TABLE 34 (Continued)

% cover Ht. in ins.			0.1	0.1-.3	0.3-.6	0.6-1	1-2	2-3	3
<u>Stenobothrus lineatus</u> (Continued)	80-95	3-6	1	0	1	0	0	0	0
	"	6-12	0	2	0	0	0	0	0
	"	12	1	0	0	0	0	0	0
	95-100	3	2	0	0	0	0	0	0
	"	3-6	1	3	1	0	0	0	0
	"	6-12	0	4	2	1	0	0	0
	"	12	1	0	0	0	0	0	0
	100	3	1	0	0	0	0	0	0
	"	3-6	1	2	0	0	0	0	0
	"	6-12	3	0	0	0	0	0	0
<u>Myrmeleotettix maculatus</u> (62)	50	3	1	0	0	0	0	0	0
	"	3-6	2	0	0	0	0	0	0
	"	6-12	1	0	0	0	0	0	0
	50-80	3	2	3	2	1	0	0	0
	"	3-6	2	4	5	2	1	3	0
	"	6-12	1	1	0	0	0	0	0
	80-95	3	2	2	1	0	0	0	0
	"	3-6	1	2	4	4	3	3	2
	"	6-12	2	2	0	0	0	0	0
	95-100	3	1	0	0	0	0	0	0
	"	3-6	1	1	0	0	0	0	0
<u>Gomphocerippus rufus</u> (42)	50-80	3	0	0	1	0	0	0	0
	"	3-6	0	3	3	4	1	0	0
	"	6-12	0	1	2	1	0	0	0
	"	12	0	1	0	0	0	0	0
	80-95	3	0	2	0	0	0	0	0
	"	3-6	0	1	2	1	0	0	0
	"	6-12	1	0	0	0	0	0	0
	"	12	0	2	4	3	0	0	0
	95-100	3	1	0	0	0	0	0	0
	"	3-6	0	1	0	0	0	0	0
	"	6-12	0	2	0	0	0	0	0
	"	12	0	1	1	0	0	0	0
	100	3-6	0	1	0	0	0	0	0
	"	6-12	1	0	0	0	0	0	0
	"	12	1	0	0	0	0	0	0

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