ON THE BIOLOGY OF SOME COLLEMBOLA OF THE FAMILY ISOTOMIDAE WITH SPECIAL EMPHASIS ON ASPECTS RELATED TO THEIR MICRODISTRIBUTION.

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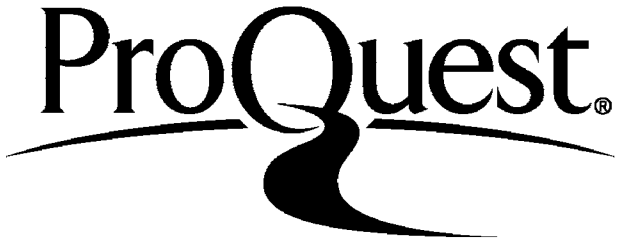

A B S T R A C T

The stadia of the life cycle, age at oviposition, frequency of oviposition and fecundity of parthenogenetic individuals of Folsomia distincta are recorded.

Notes on the behaviour of this species are given particularly in relation to the formation of groups. Semi-permanent social aggregations are formed and maintained by an olfactory stimulation from the animal or a secretion from them, especially by the fourth and fifth instars.

The relationship between the mean individual fecundity of cultures of F. distincta and the mean area available per individual is given. Both the individual fecundity and the number of individuals ovipositing is reduced by disturbances whilst ovipositing or feeding.

The population levels of F. distincta, Isotomina thermophila F. nana and Isotoma notabilis in a meadow are recorded for two years. The greater ability of F. nana and I. notabilis to withstand drought is noted.

The differences in population at the different stations were most easily explained by the exposure of the station to the climate.

The concept of aggregation under natural conditions is discussed. The aggregation of the four species is compared and it is shown that young and old individuals of the same species are equally aggregated.

The relationship between the environment and microdistribution

of each species is investigated. It is noted that the position of young individuals may be due to physical conditions and that the older individuals tend to form social aggregations.

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INTRODUCTION.

Aggregation has long been regarded as the usual state for natural populations of most species of animals. In the past the theory and classification of the phenomenon has engrossed many zoologists. Allee (1931) gives a useful evaluation of previous work. In more recent years statistical methods for the identification and definition of aggregation have been developed particularly as a means to offset the bias which aggregation causes in the distribution of numbers of individuals in samples. However little has been added to the knowledge of how aggregations of soil animals develop. A notable contribution is probably the paper by Salt and Hollick (1946) in which they show that small wireworms showed aggregation more markedly than larger larvae and that the largest larvae were randomly distributed. On this evidence it seems clear that "a group of eggs is laid and the larvae gradually disperse, like the ripples from a stone dropped into water". Nielson (1954) suggested that the density patterning of enchytraeid worms resembled that of wireworms and possibly developed in a similar way. In 1958 the discussion following Hughe's paper on "The study of aggregated populations" at the colloquium on "Research methods in soil zoology" emphasised the need for further information about aggregations particularly with regard to the biology and behaviour of the species studied.

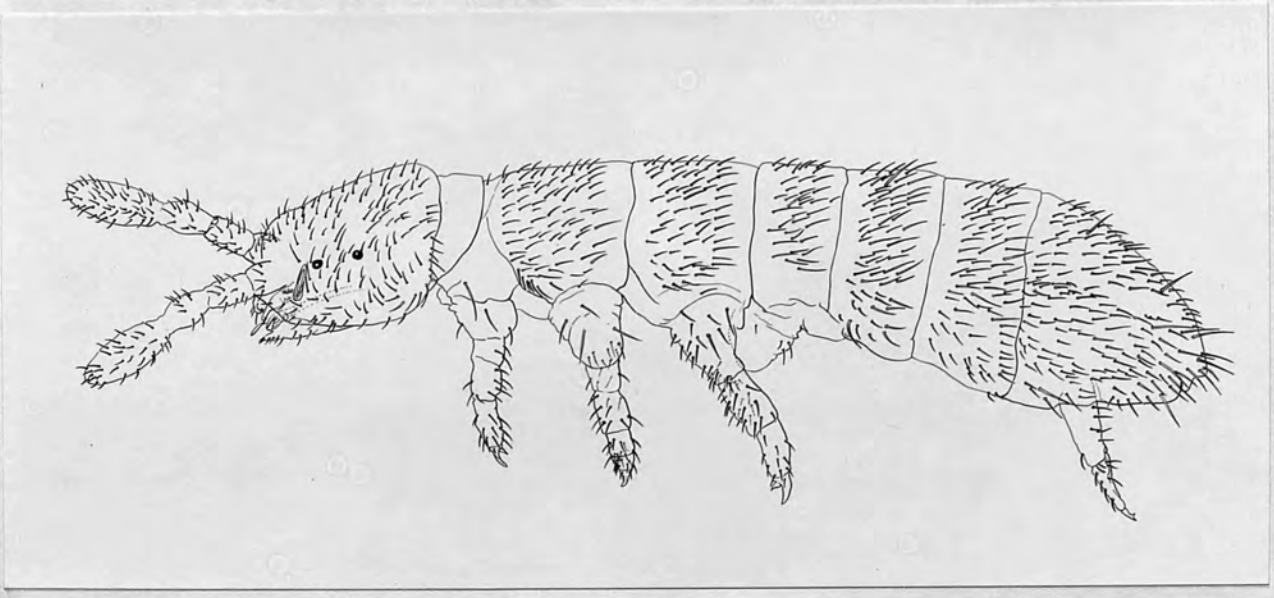
The papers of Ellis (1953, 1956, 1959) and Long (1955) are the only published work known to me in which aggregation of insects, other than accidental gathering due to a reaction to an environmental stimulus, was demonstrated under controlled laboratory conditions. Although the behaviour of locusts or lepidopterous larvae is unlikely to be the same as that of Collembola the methods in looking for social aggregation used are in principle the same. Many experiments to determine the effect of crowding on population growth have been made with insects of various types. In general it has been found that overcrowding adversely affects the rate of population growth. However it is not known in what way the development or permanence of aggregations will be affected by these adverse effects of crowding nor is it known to what extent aggregation can cause conditions of overcrowding.

The work in this thesis was planned using the papers commented on above as a basis and was designed to provide tentative suggestions of the presence, causes and effects of aggregation of arthropods in the soil. The intention was to study a few species of Collembola in the laboratory and in the fields mainly for indications of social behaviour and changes in biology occasioned by the presence of other individuals of the same species. However, although four species were examined in the field, only two of them were sufficiently common for

detailed analysis and it proved possible to raise only one species in sufficient numbers for laboratory experiments. Although the field work was started first and laboratory cultures were bred from individuals from the field, the laboratory experiments are reported in Part I and the field work in Part II, followed by a discussion linking all the work afterwards.

The classification of the species is based upon the key by Gisin (1944) and the more recent key by the same author (1960). All four species examined in the field are members of the family Isotomidae. Two are of the genus Folsomia; F.nana Gisin confirmed by examination of specimens of this species which had been identified by Gisin for Macfadyen; F.distincta Bagnall was examined by Goto who suggested this species was probably a variety of F.candida (Willem). The more recent key by Gisin (1960) lists F. distincta as a variety of F. candida but in this work the name 'distincta' has been kept on account of the easily distinguished and constant character, the lack of inner teeth on the unguis. Specimens with inner teeth were found in other parts of the grounds but never at the experimental stations. One of the other species was identified as Isotomina thermophila (Axelson) and one as Isotoma notabilis (Schafer). These were identified by Lawrence and myself independently.

Fig.0.1. Folsomia nana Gisin



Lateral view of a specimen approximately 1.25 mms. long.

These species all occupy a similar position in the soil, namely on, or just below, the soil surface and amongst the matted roots of the surface vegetation. Haalóv (1958, 1960) gives figures showing that Isotoma notabilis and Folsomia quadrioculata (Tullberg) (a species very similar to F.nana) do not penetrate more than 4 centimetres, and are mostly found in the top 2 centimetres. An annual and daily vertical migration has been reported by Leuthold (1961) for Folsomia quadrioculata and Isotoma notabilis. She also records these animals at far greater depths than found by previous workers or myself in grassland. However the 4 inch samples taken were amply long enough to sample the entire population of Isotomid Collembola. None of these were ever found in the fourth inch and only rarely in the third. The occasions when one or two were found in the second inch were too infrequent to allow anything to be said about vertical distribution. However it did seem that F. distincta was the more frequent species in the 2nd and 3rd inch depths. Onychiurus sp. and Tullbergia sp. were frequently obtained in the4th inch and as it seemed that they occur still deeper (Haalóv 1958, 1960)(Leuthold 1961) they were not included in the investigation.

The four species of Isotomidae were similar in form to F.nana (Fig.0.1). In size they are close to one millimetre

when adult with the exception of F. distincta which in culture rea ches three milimetres but in the field rarely exceeded one and a half millimetres. The four species are all active and capable of quick movement, I.notabilis being the most active in culture and having the longest furca relative to its size. There are two notable differences between the species. F.distincta is pigmentless whereas the others are flecked with grey pigment tending to blue in I.notabilis and green in I.thermophila. The number of ocelli differs in each species; F. distincta has none, F.nana has 2 + 2, I.notabilis4 + 4, and I.thermophila 8 + 8. The presence of eyes could make a difference to behaviour but little is known of the ability of these ocelli to distinguish form or of their efficiency in poor light conditions. Amongst the soil particles and grass roots the lighting would be very poor and sight would be very limited with so many obstructions.

PART I: EXAMINATION OF THE LIFE HISTORY AND BEHAVIOUR OF OF LABORATORY CULTURES OF FOLSOMIA DISTINCTA.

1. Apparatus, Methods and Techniques.

This section describes in detail the apparatus and techniques used generally in laboratory experiments. Any variations made to induce differences in experimental conditions will be mentioned at the appropriate stage.

a, Culture Chambers.

Four forms of chamber were used for the culture of the species in the laboratory. The largest of these consisted of a Perspex 'sandwich box' with a close fitting Perspex lid. These boxes were 4½" by 9¼" and 2½" deep. Sterilised and washed coarse sand was spread in each box to the depth of ½" and moistened. The collembola were released on the sand and no difficulty was encountered in maintaining a humid environment in which the collembola flourished. The design of the other three chambers was the same as that used by Ogel (1957) and Goto (private communication) and is based on the instructions of Searle (1928), Wharton (1946), Liporsky (1953) and Edwards (1955). The containers used were glass specimen tubes 2" high and 1" diameter, and glass crystallising dishes 3 cm.high and either 3 or 5 cm. in diameter. In all these a mixture of 9 parts of pure plaster of paris to 1 part of powdered charcoal was cast to provide a surface 2 cm. below the rim. After drying, the plaster was washed with distilled water and scraped to give a smooth flat surface. The 1" diameter chambers were used for solitary individuals. In order to prevent reflection from the internal surface of the glass

this surface was rubbed with emery powder before the plaster was put into the tube.

These glass containers were used to start the stock cultures from a few individuals caught in the field and were used for all experimental cultures. The 5 cm. diameter chamber was found to be the most convenient for this and was used as the standard chamber.

Originally corks lined with thin polythene sheeting were used to close the glass culture chambers but these stoppers were later replaced by 'Parafilm' covers. This thermoplastic sheeting was found to provide a better seal over the chamber, was cleaner and more convenient in use.

b, Feeding.

All the species in culture were fed with spherical pellets of dried bakers' yeast as made by Allinsons. These pellets were found convenient to store and sterilise and when graded they could be used to provide standard quantities of food. The pellets were graded by sieving. Only those which passed 12, but were retained on 16 mesh sieves were used when critical feeding was desired. The mean weight of these pellets was 0.00137 grams and the minimum mean weight of a selected sample of the 10 smallest pellets was .00092 grams. The stock cultures in the Perspex boxes were fed with this yeast and, in addition, thin slices of raw potato. This may not have been necessary but the potato was always eaten and provided a shelter under which specimens could always be found.

c. Moisture.

A humid atmosphere without free water was maintained within the chamber by keeping the plaster of paris or sand damp. The plaster maintained a relative humidity always in excess of 95%. The addition of charcoal as well as helping to keep the chamber sweet, gave by the intensity of its colour an indication of the moisture content of the plaster.

d, Fungus and Disease.

The growth of fungus in the chamber, a common problem in cultures of soil invertebrates, was not found at all troublesome in the stock cultures on sand and was satisfactorily controlled in the small chambers by regular cleaning. The chambers were examined frequently, daily or on alternate days, and all waste matter, exuviae, fungi and old food, was removed. Food and water were added as necessary. Although a little care prevented fungus growth the crowded cultures especially were liable to a withering disease. At first an infected individual showed signs of partial paralysis and a browning of the extremities of the appendages. Co-ordination between appendage movement seemed to be lost and the antennae would drag on the floor. Usually two days later death would occur and after death the body rapidly decomposed becoming brown and watery. The disease appeared to be contagious and consequently any culture with individuals showing these symptons was destroyed. In order to try to find the cause of this disease infected specimens were stained for fungi and for bacteria and sectioned for optical

examination but on no occasion was any sign of a pathogen observed.

e, Stock Cultures.

The stock cultures were started from a few individuals taken from the meadow used as the site for field work. These cultures in the standard chamber were then raised through several generations to stabilise the genetic make up of the culture. This follows the example of Crombie (1942) in his work on grain infesting insects. At first the cultures were subject to a range of temperature of 8° to 20°C. During this time condensation on the top and walls of the dish tended to trap the younger animals and sometimes the older ones. When possible the cultures were kept at a constant temperature of 25° ± 0.5°C but this proved too high for all but Folsomia distincta. Consequently the other species were kept at a lower fluctuating temperature until an oven was arranged to run at 20°C but even at this temperature the populations could not be increased rapidly enough for experimental purposes. A low optimum temperature for many species of Collembola was reported by Milne (1960) and may be the explanation for the Autumn to Spring peak population levels so common to Collembola in the field.

f. Experimental Cultures.

When the stock culture was of sufficient size, i.e. between 200 and 500 animals, it was transferred to a Perspex box. To start experimental cultures about thirty 4th instar individuals were taken from the stock culture and allowed to oviposit on the plaster in a standard chamber. The eggs were transferred to a small chamber in

which they hatched. The hatchlings were removed from the hatching chamber every 24 hours and usually each experimental culture was formed from a single batch of these hatchlings. The maximum possible age difference between animals in these cultures was 24 hours. Occasionally it was necessary to pool the hatchlings for 48 hours in order to obtain sufficient animals for the larger cultures.

g. Manipulation.

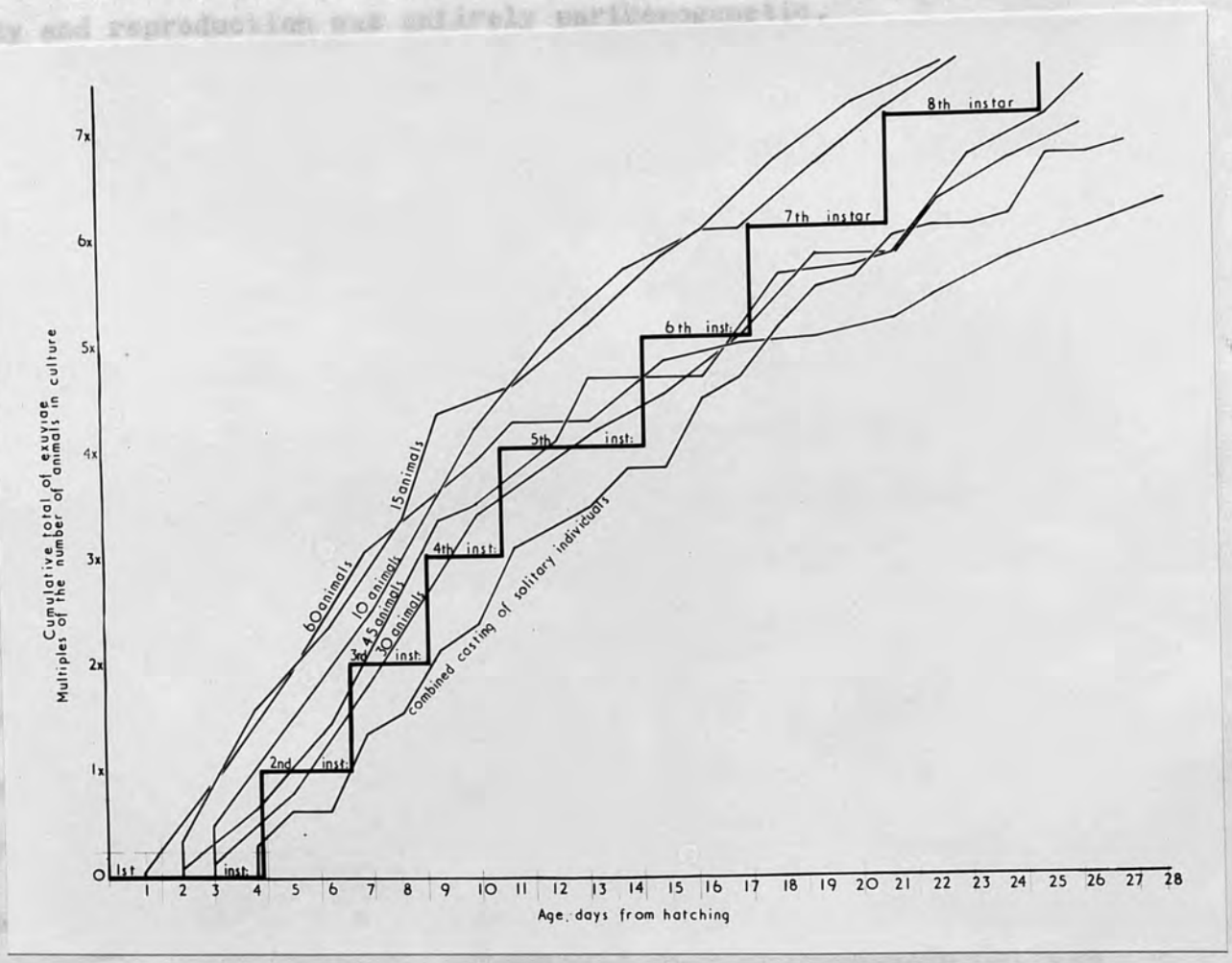
Transfer of the animals was usually made by means of a small aspirator. This consisted of a 3" length of 3/8" glass tube with rubber stoppers at each end. Through each stopper passed a 1½" length of 1/8" glass tube. A rubber tube and mouthpiece were attached to one piece of thin glass tube. The internal opening of this tube was filled by a cotton-wool filter covered by a piece of fine nylon gauze. The other piece of thin tubing extended ½" into the larger tube and was open-ended to allow the animals to be drawn through. The animals apparently suffered no harm when sucked into the aspirator and released into a chamber but if the number of animals in a culture wa s critical an excess of 10% were put in and the number reduced after 2 days. Thus deaths due to injury did not affect the final number in the culture. If other mortality exceeded 20% of the total number in the culture the whole culture was replaced. This was done immediately if the culture became infected by disease.

2. LIFE HISTORY OF FOLSOMIA DISTINCTA.

a. Introduction.

Until recently there was a lack of detailed information about the life history of most species of Collembola. A few had been investigated, notably Sminthurus viridis (Linné) by Maclagan (1932). Milne in his paper recently published (1960) gives information about several more species, including two of the family Isotomidae. One of these, Folsomia candida (Willem) is a very close relative of F. distincta, the life history of which is reported here. It is probable that F. distincta is only a variety of F. candida as placed by Gisin (1960) and Goto (private communication). If this is assumed, a comparison between the life history of these varieties becomes of interest. In general the life histories are very similar, differing mainly on points connected with the fecundity of the animals. The conclusions drawn by Milne on the fecundity of his animals are probably incorrect in view of the effect which the culture density has on oviposition, (pp 71 of this thesis). Also, Milne assumed there was a 1:1 sex ratio in his cultures but in view of the experienee gained in working with F. distincta this seems unlikely and will have led to an over estimation of the mean number of eggs per female. All populations of F. distincta examined during the present work had a very considerable excess of females. It can be assumed therefore, that reproduction would often be parthenogenetic. In view of this all cultures of F. distincta used in experiments consisted of females

Fig.2.1. The rate of development of F. distincta.



The total number of exuviae taken from the culture, divided by the number of animals in the culture, is plotted against the age of the culture, measured in days from the day when the eggs hatched.

The step graph is the development of a typical solitary individual: it is based on the mean dates of ecdysis of eleven solitary individuals. The combined total number of exuviae for these individuals are plotted as a polygon graph.

The data for the other graphs was obtained during experiments showing the relationship between fecundity and crowding, representative cultures being selected.

only and reproduction was entirely parthenogenetic.

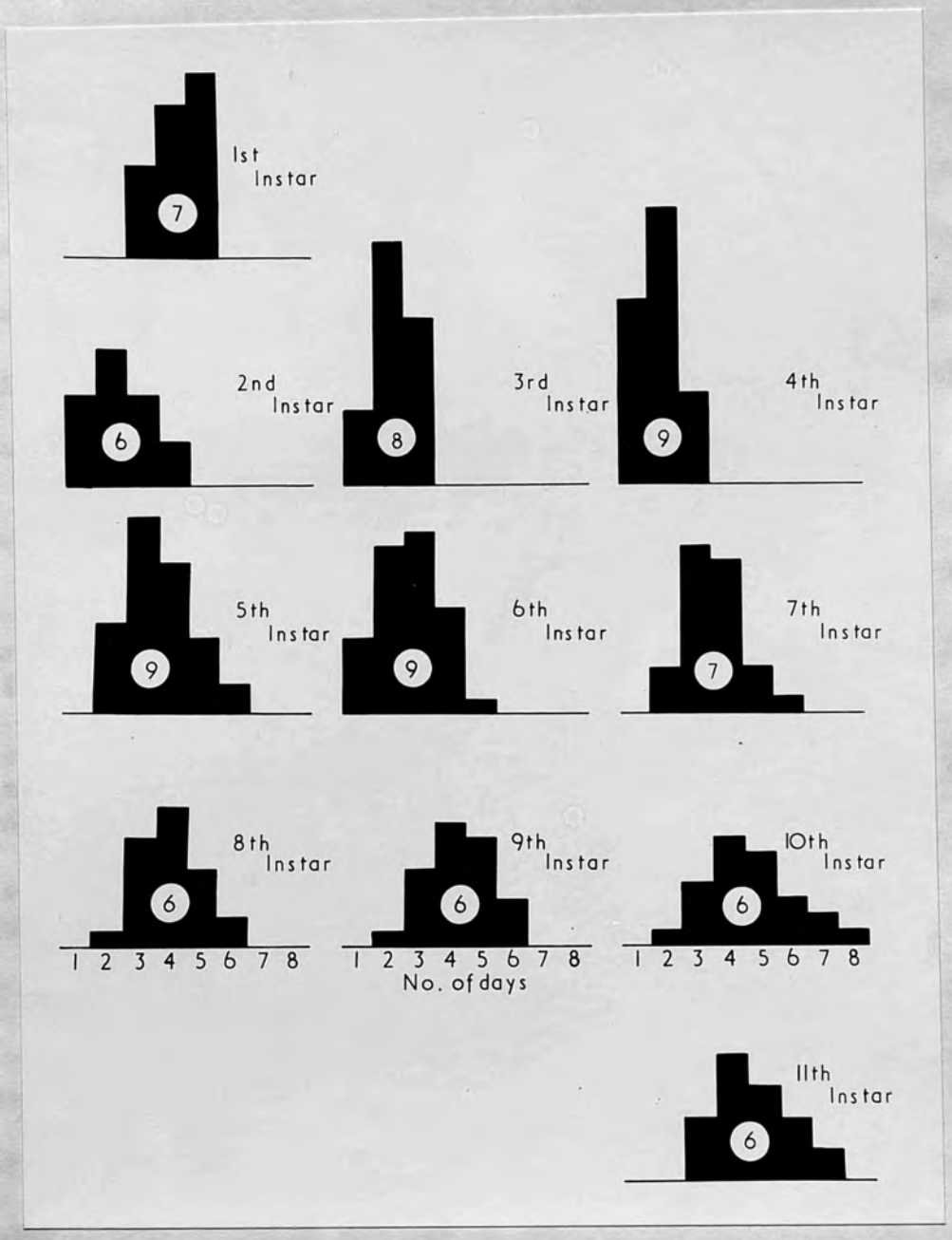
The duration of the embryonic period of F. distincta at 25°C is almost the same as that reported for F.candida at 24°C but the post embryonic, preoviposition period, is rather greater than would be expected if the only cause of the difference was the one degree difference in temperature. It is possible that the use of yeast instead of bracken spores as food caused a more rapid maturation.

It has been possible to add some further details about the duration and number of instars in the life history of F. distincta. In mass cultures the plotted curve of the cumulative total of exuviae found in the chamber tends to be smooth (Fig.2.1) even when all the individuals are of the same age. This is due in part to the difficulty of assessing the number of exuviae after they have been broken and partly eaten but it has also been shown that the variation in age at ecdysis may be as great as the period between two ecdyses, thus giving a smooth curve when the results of several individuals are plotted (Fig.2.1)solitary animals). Because of this the life history given here is based on eleven individuals cultured and recorded individually. The details of the method of culture will be found in the previous section.

b.Stadia of the Life Cycle.

At 25°C the eggs take approximately seven days to develop before hatching. A few hatch on the 5th day but others do not hatch until the 15th day. The eggs remaining after this are so covered in fungal mycelium that, even if they hatch the young are trapped.

Fig.2.2. Frequency histograms for the duration, in days, of each instar, until the 11th, of solitary individuals of F.distincta.



Each individual is given a score; whenever the duration of an instar is not known exactly the score is proportionately divided between the alternate days. The histograms are constructed from the total of these scores; the number of individuals contributing is shown in the white circles.

The first instar is of longer duration, usually 4 or 5 days than the other immature instars, which are of approximately the same duration, usually 2 days. After maturity in the 5th instar the number of days between moults tends to increase as the animal becomes older, rising to about 8 days by the 25th moult. The mature insects continue to moult during their entire life although after about the 10th instar their size and form change very little. The data of the duration of the first eleven instars is summarised in Table 1 and Fig.2.2.

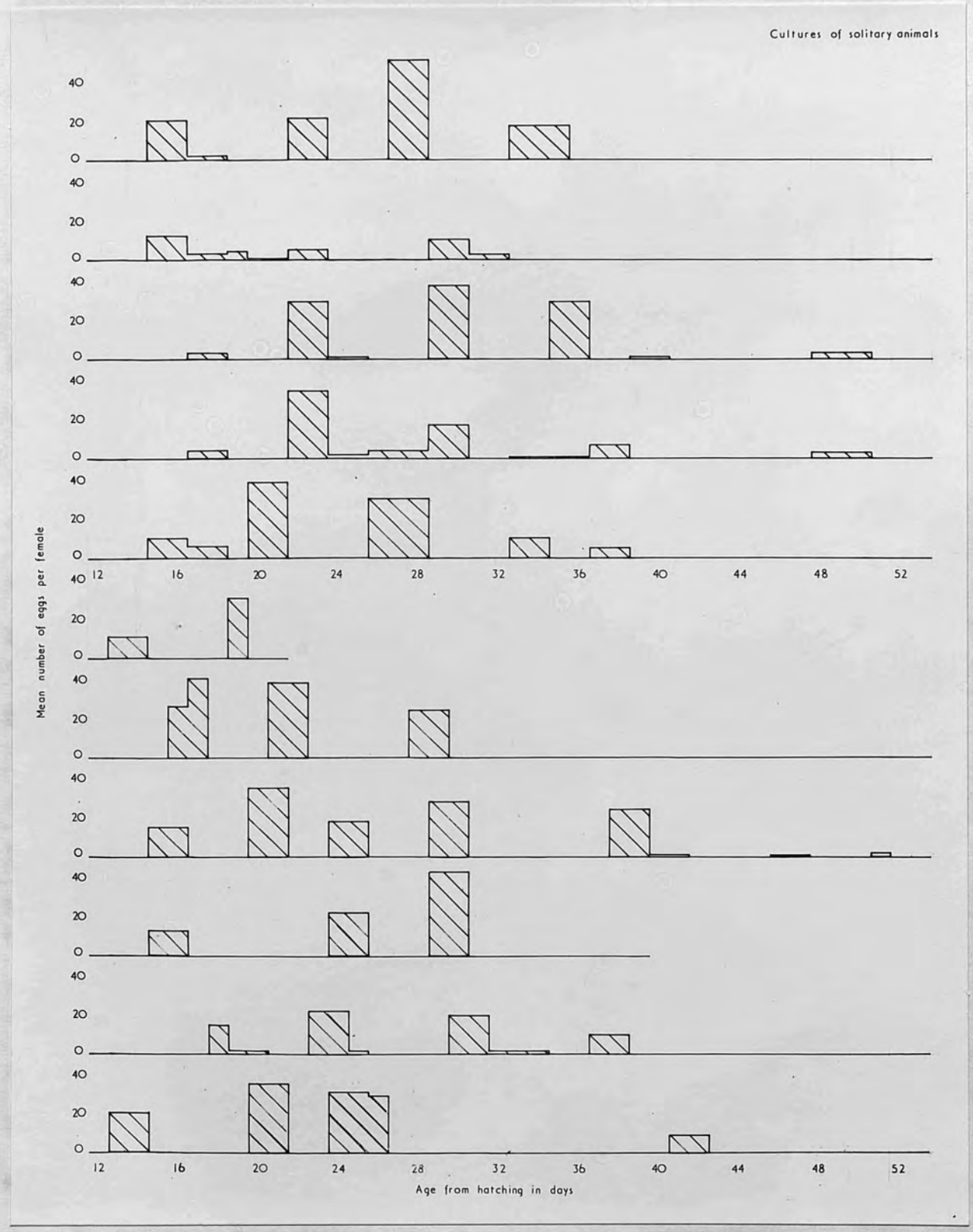
TABLE 1.

Instar	1	2	3	4	5	6	7	8	9	10	11
Mean duration of instar in days($\bar{d}$)	4.2	2.3	2.2	1.8	3.6	2.7	3.6	4.0	4.3	4.7	4.7
Mean age of animal at the end of the instar(days)	4.2	6.5	8.7	10.5	14.1	16.8	20.4	24.4	28.7	33.4	38.1
Number of animals contributing to mean	7	6	8	9	9	9	7	6	6	6	6
$s(\bar{d})$	0.28	0.33	0.09	0.17	0.29	0.30	0.26	0.34	0.38	0.56	0.42

c. Oviposition.

Reproductive maturity, as judged by the appearance of eggs in the chamber, is reached by the end of the 5th instar. The eggs are laid in batches (Fig.2.3) usually just before or just after ecdysis. Sometimes all the eggs of a batch are laid in one day but up to three or four days are sometimes required. Often all the eggs of one batch are found in a single clump. Up to five large batches of eggs have been recorded for a single individual during its life (Fig.2.3).

Fig.2.3. The oviposition cycle of eleven solitary individuals of F. distincta.



Four main batches were laid by each of seven individuals but two animals oviposited only thrde times. Two others, which died early, produced two or three batches of eggs before death, dying on the 21st day and 39th day respectively. By the 42nd day (12th or 13th instar) all major oviposition had ceased; only a very few eggs were laid after this time and no oviposition occurred after the 51st day. During the life of the eleven individuals a mean of 167.5 eggs ($s_{\bar{x}}$ = 19.5) per individual was laid. The mean number of eggs in the batch and the mean age at which oviposition of the batches commenced are shown in Table 2 and Fig.2.4.

TABLE 2.

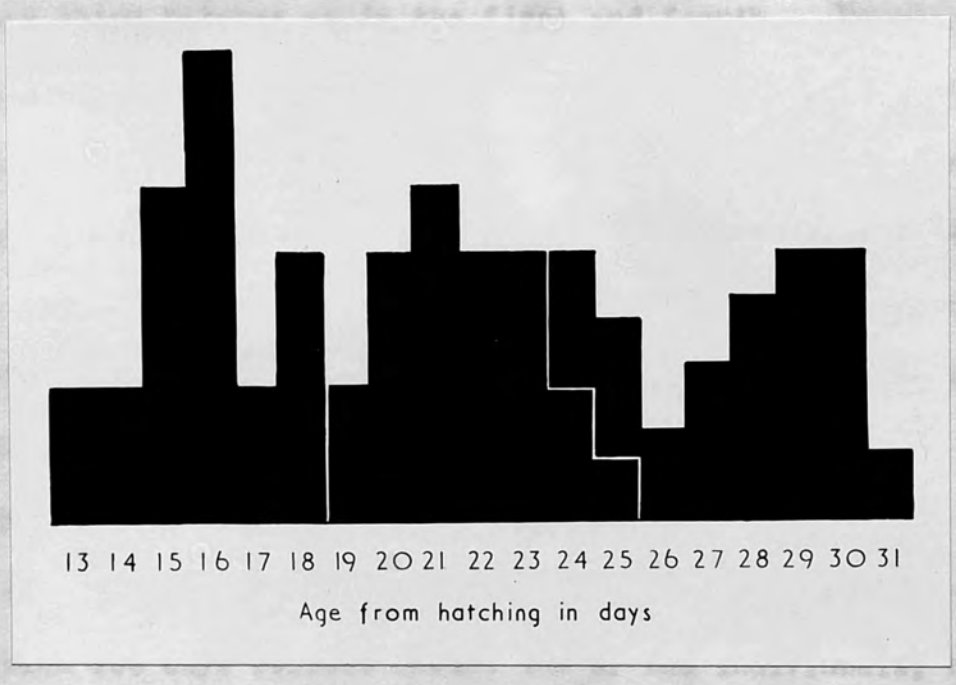
The age (post embryonic period in days) at which oviposition commenced.

Batch	1	11	111	1V
Mean age($\bar{a}$) at which laying of the batch started	15.8	21.8	27.8	35.6
Number of individuals contributing to mean	11	11	10	7
$s(\bar{a})$	0.4	0.5	0.6	1.3
The number of eggs in each batch.				
Mean number of eggs per batch ($\bar{n}$)	29.4	54.2	61.7	26.3
Number of individuals contributing to mean	11	11	10	9
$s(\bar{n})$	5.1	6.4	8.2	7.6

The histograms in Fig 2.3 show the range of age at which laying of each batch commenced.

It is clear from these tables and the figures that the batches

Fig.2.4. The ages at which laying of the first three batches of eggs commenced, by the solitary individuals of F. distincta.



Each individual is given a score; whenever the date of oviposition is not known exactly the score is proportionately divided between the alternate days. The histogram is constructed from the total of these scores.

are well defined and are fixed points in the life history. Normally four batches are laid with over twice as many eggs laid in the second and third batches as in the first and fourth. Usually the first batch is laid during the 5th instar or the early part of the 6th instar; the second in the 7th instar, the third during the 8th instar and the fourth during the 10th or 11th instars. This periodic oviposition agrees with the observations by Strebel (1929) that certain species of Collembola were able to oviposit three times during the life span.

d. Length of Life.

It is somewhat surprising that oviposition is so limited when no less than 160 days elapsed before 50% of the individuals, reared individually, had died. This is over three times the length of the period from hatching to the end of major oviposition. Although the first individual died on the 21st day, during the 7th instar, some were still alive on the 230th day and had moulted more than twenty five times. It is clear that the average life expectation under these cultural conditions far exceeds the reproductive life and it would be very interesting to know if this is so in nature or whether either the reproductive life is extended or the animal's life is curtailed.

3. Behaviour.

a. Introduction.

In this section emphasis is placed on social aspects of the behaviour of F. distincta. Other aspects are only described where the observations help to complete the background. There are several accounts of the behaviour of Collembola in the literature but none is concerned with social behaviour as distinct from sexual behaviour. In view of the parthenogenetic nature of the cultures sexual behaviour could not be included in the present account.

b. General Behaviour.

The following experiments and observations were all made on animals living on smooth plaster surfaces. On these surfaces the animal had a pronounced tendency to keep near the side of the chamber where the plaster met the glass wall. In the cultures they would frequently be found resting with as much of the body as possible in contact with the glass or plaster surface. Contact stimulus was often obtained by the animal resting in a crevice, next to a granule of plaster or underneath the food and this was most obvious with the younger animals. The tendency to go to the side of the chamber was obvious with animals cultured on fine smooth sand, but not when coarse sand with a crumb structure or very coarse glass beads (diam.3-4mm) were used. On slightly finer glass beads (diam. about 1.5mm) or on fine nylon bolting gauze the animals seemed to find difficulty in moving. It appears that the animals prefer to obtain as much contact between their bodies and the solid

environment as possible and therefore prefer a medium of coarse particles or crumbs. On a medium of particles a little smaller than their body size they may find it difficult to move either between or over the particles.

In the culture chambers the animals, when undisturbed, move slowly and rarely for long periods. Upon excitation they run wildly, rapidly and occasionally jump. Such excitement may be caused by contact with solid bodies, air currents or by sudden changes in air pressure: this latter movement was seen when the sealing caps of the culture chambers were pressed in. Unless the stimulation is continued the animals soon settle, preferably in contact with some object. Therefore the chambers were marked into sections with great care to ensure the lines were only very fine scratches, which were usually ignored by the animals.

To determine the time required for an individual to settle after disturbance, it was placed in a clean large culture chamber marked into squares. A complete record of the behaviour and movement of the animal for the first fifteen minutes, after introduction to the chamber, was made by speaking into a tape recorder. At the same time the movement of the animal was plotted on a chart. In some experiments other individuals were present in the chamber.

It is assumed that the dropping of an animal from a small tube into the chamber caused maximum disturbance and that the readings in Table 3 are of the time required to settle.

To allow comparisons between the sets of readings the activity

is analysed into three components: the angle turned is assessed by summing the angles turned through without regard to the direction; the distance walked(when appreciable) was measured on the chart; and the time in movement is expressed as a percentage of the total time.

TABLE 3.

The activity of individuals of F. distincta after being disturbed.

	Time after excitation	Solitary Animals (4 experiments)		One animal in the presence of others (4 experiments)	
	Minutes	Means($\bar{x}$)	$s_{\bar{x}}$	Mean($\bar{y}$)	$s_{\bar{y}}$
Angle turned (Complete turns)(360°)	1-5	9.5	2.0	7.1	1.2
	5-10	0.6	0.1	1.9	0.5
	10-15	0.5	0.2	1.5	0.4
Distance Moved (cms)	1-5	10.1	1.7	8.1	1.6
	5-10	0.8	0.3	0.5	0.5
	10-15	0	-	0	-
% Time spent moving	1-5	65	4.8	21	5.2
	5-10	2	0.9	3	1.7
	10-15	0	-	2	0.9

From Table 3 it can be seen that after the initial period, which might be termed the settling period, more time is invariably spent resting rather than in movement. During these resting periods the animals becomes alert; that is the body is raised on to the claws from its prone resting position in which the legs, ventral tube and furca are in contact with the ground. If other individuals are present the animal often moves and turns, whereas solitary animals may reassume the resting position after about half a second. When relaxed, the head is usually held off the floor and nodded or wagged at frequent intervals. The antennae may rest on the floor

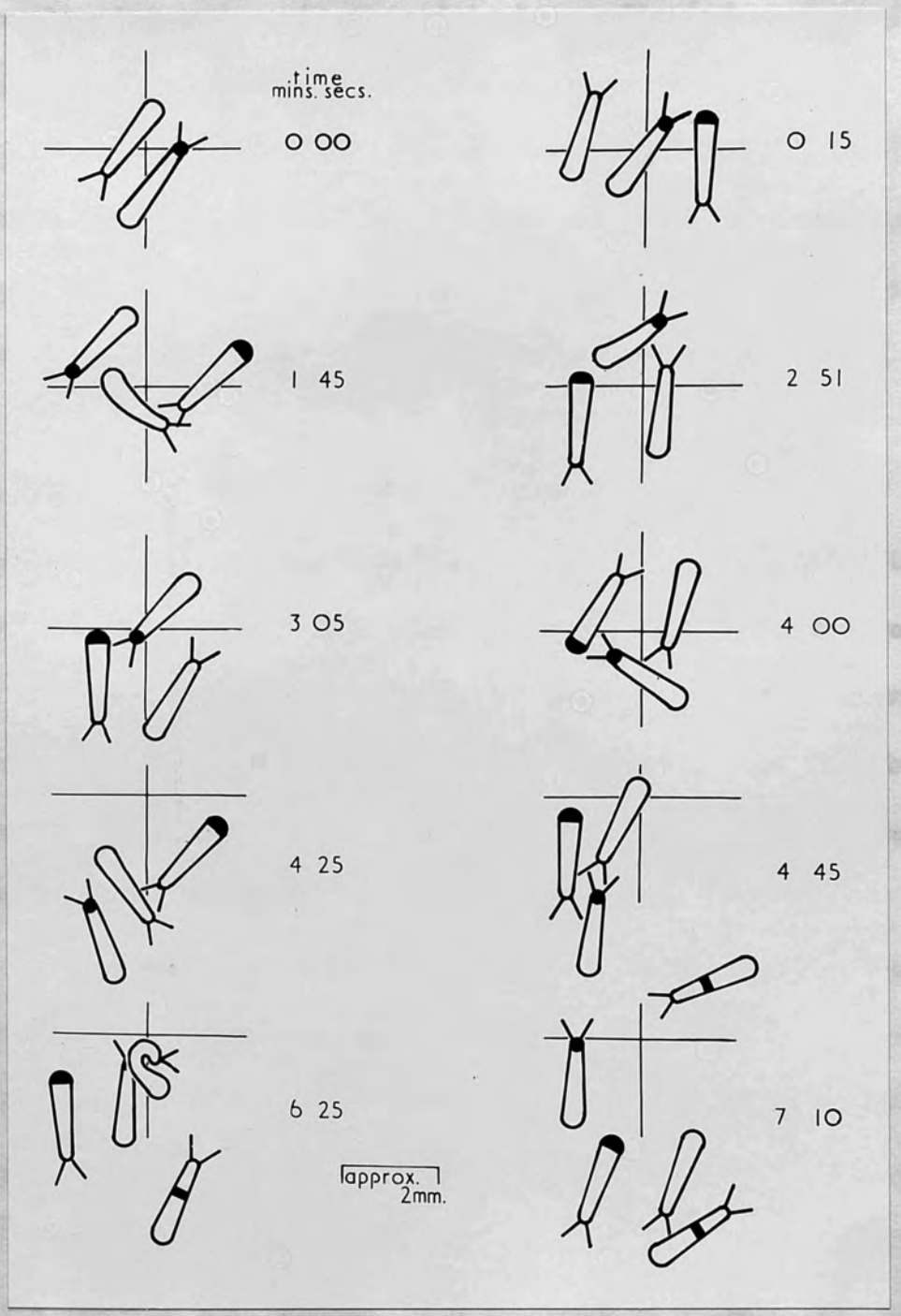
but are usually held high and tense and in very rapid vibration. The impression given is that if an animal can become aware of the presence of another individual by merely turning, it will not move, but otherwise it may change its location. In this way small groups tend to form and, when this happens, subsequent movement is round other animals, thus maintaining the group.

These observations are borne out by the figures in Table 3, from which it will be seen that although non-solitary individuals move approximately as far as solitary ones during the first five minutes after disturbance they move at a greater rate. After the settling period there is an indication of a greater tendency for non-solitary animals to turn. The formation of a group of five animals in about seven minutes, with the rotation of animals about each other is shown diagramatically in Fig.3.1.

The observations on group formation are worth a little further consideration. The majority of the individuals watched in the 'non-solitary' state never touched the other animals, so that it is clear that the group-forming stimulus is not tactile. Nevertheless the observations clearly suggest some form of 'awareness' which may well be directional. This is suggested by the turning without other movement in order to refresh the stimulus.

During the experiments just described, and others when the marking of individuals was attempted, records of various forms of activity were made. These records were examined for any alteration in behaviour other than recorded in Table 3 when other animals were

Fig 3.1. The development and rearrangement of a group of F. distincta.

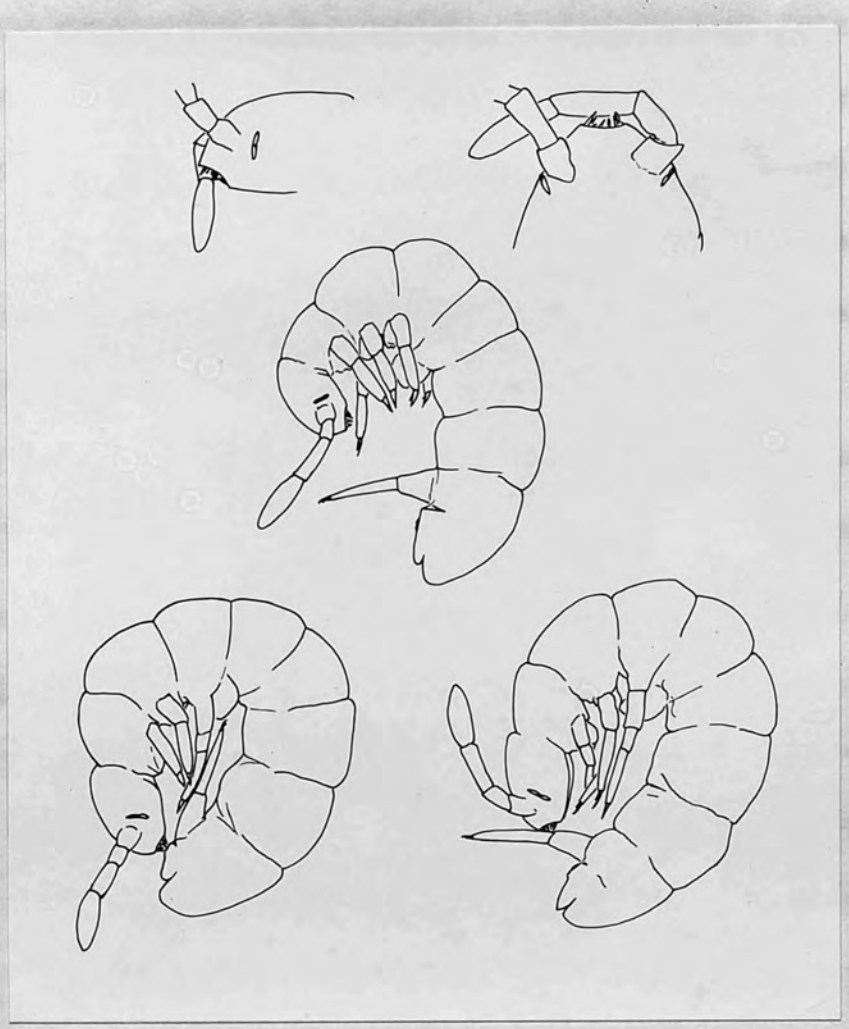


The crossed reference lines are the same ones in each diagram.

present. No changes in the frequency with which the body was tensed while resting nor in antennal or head movement could be noted. Likewise cleaning movements seemed to be unaffected. Cleaning routines which have been described previously (Handschin(1926), Muckerjii(1932), Denis (1949)) are summarised by Paclt (1956) who states that droplets of oral secretion passed from leg to leg during cleaning. This action was not seen during cleaning routines such as are described below which were observed many times during the present work.

The sequence of actions did not seem to be in a regular order or occur at regular intervals. Cleaning in general seemed to be thorough; the only parts never seen to be cleaned were the dorsal surface of head, thorax and abdomen. Only the mouthparts are used for cleaning. The lamellate and fringed maxillae and mandibles are protruded to scrape or comb the cuticle and its setae. The antennae are cleaned most frequently and independently of each other. The antenna to be cleaned is bent across and below the head and is then drawn slowly between the mouthparts which seem to comb the surface. (Fig 3.2). Periods of about seven minutes elapse between successive cleanings of the antennae. Less frequently an animal lies on its side and bends so that the head can reach the ventral surface,(Fig.3.2) The entire ventral surface may then be cleaned or only the legs. If the entire surface is cleaned the following account gives a typical order of events. For fifty seconds the legs and ventral surface of the thorax were cleaned: each leg was cleaned in the same

Fig.3.2. Cleaning position of F. distincta.



Top row; Cleaning the antenna.
Middle; Cleaning the legs.
Bottom; Cleaning the genital aperture and furca.

manner as the antennae. This was followed by cleaning the ventral surface behind the furca especially the genital aperture and the fold in the cuticle behind the furca. The furca was then drawn across the mouthparts and cleaned. Forty seconds later attention was turned to the coxae and especially the ventral tube. The entire sequence took about one and threequarter minutes and is performed quite readily even while the individual is in a group as it is rarely interrupted by the activity of other individuals. The other animals will often tend to avoid close contact with an individual cleaning itself. On only one occasion was an animal seen to interfere with another either young or old. On this occasion an animal was seen scraping, with its mouthparts, the rear leg of an animal lying prone. This animal stood up after half a minute but did not use the rear leg for walking and the body was twisted slightly to that side. The interfering animal approached two others during the following two minutes but did not touch either of them. After about three minutes the injured animal seemed completely recovered.

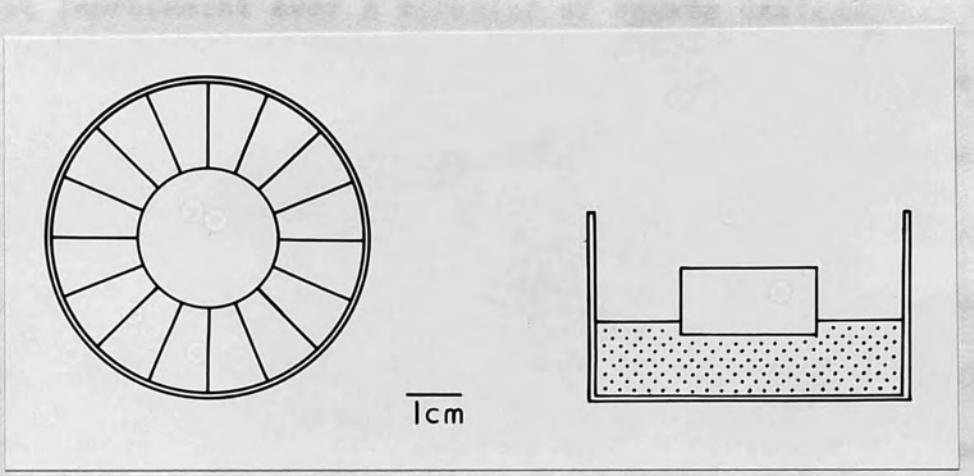
c. Social Behaviour.

Congregation of individuals is seen in cultures of many species of Collembola; it would seem that social aggregation may be natural to these animals and affect their distribution in wild populations. Judd (1949) and Park (1949) have both recorded aggregations in the field and it is well-known that the distribution of many species is not random. Allee in 1931 considered in theory

the grouping of individuals as a result of interaction between them. Ellis (1955) designated this as social aggregation and demonstrated it experimentally with the locusts Shistocerea gregaria (Forsk), and Locusta migratoria (R & F)(1953, 1956 and 1959). It has also been experimentally demonstrated with cultures of the cotton stainer Dyslercus sp. (Kruggel, private communication). Both workers demonstrated by laboratory experiments that aggregation occurred in a uniform environment. Ellis concluded that locusts were brought together over short distances by visual stimuli and possibly kept together by contact, using especially the antennae. Cotton stainers were probably attracted by olfactory stimuli and the groups maintained by contact or chemoreception. Social aggregation was 'learnt' by locusts: Ellis found that until the individuals had become habituated to contact with another individual, groups could not form.

The apparatus used for the experiments with F. distincta (Fig 3.3) was based upon the description by Ellis (1953) of the apparatus used to test locusts. The chamber was a modified culture chamber with an inner glass core made by setting an inverted flat-bottomed tube into the plaster. Lines were drawn on the plaster with a fine scalpel and care was taken to ensure the lines were fine enough not to interfere with the distribution of the animals. Several other forms of aggregation chamber were tried but none proved as satisfactory as the one above. The others included circular chambers as used for cultures and trial

Fig.3.3. The Ring Chamber used to examine aggregation.



Left - plan. Right - cross section.
Stippled areas - Plaster of Paris and charcoal.
Clear areas - Glass.

experiments, solid plaster blocks with the chamber carved out and chambers with substrates of sand and glass beads simulating a more natural environment. The latter media were tried for examination of the three dimensional distribution but no method of observing the position of the Collembola could be found. An annular chamber is a great improvement over a circular or square design. Although effectively linear, an annular chamber is continuous, allowing the animals free movement, whereas circular or square chambers confine the animals with boundaries. Undoubtedly a spherical chamber utilising either the internal or external surface as an experimental area would be ideal. With this form of arena the surface is continuous in all directions and the animals would have complete freedom. This would therefore permit more refined analysis of the results. However a spherical chamber proved to be too difficult to make and use for experiments with Collembola.

It was necessary to ensure even illumination of the chamber during experiments when testing the aggregation responses. This was accomplished by means of the following apparatus. The test chamber was surrounded by six hardboard screens, each 1½ ft. square, to prevent access of stray light. A circular hole was cut in the upper horizontal screen and was filled with a sheet of glass and a light diffusing screen. A pearl electric light bulb (40 watt) with a deep parabolic white reflector was suspended 6" above the window and a bath of acid alum solution between the lamp and the wondow absorbed any heat from the lamp.

The tests were carried out in a constant temperature room at 25°C ± 0.5°C. The plaster and glass were washed with distilled water and the plaster thoroughly moistened. The chamber was then placed between the hardboard screens and left for at least half an hour to equilibrate. Eight animals were then introduced and given half an hour to settle before the position of the animals was recorded. The animals were thoroughly disturbed by a gentle jet of air from a blow pipe and thereby redistributed. Twenty minutes were allowed for them to settle before taking the next reading. In this way four readings were obtained for each trial after which the animals were removed. The chamber was well washed before a further eight animals were put into it. In this way two or four trials were made for each batch (p 41) of insects. Table 4 is a typical example of the form of the readings.

In Table 4 the number of animals in each sector has been recorded. This is more easily and accurately done than recording the numbers of groups and animals in them. Especially as the individuals are aware of the presence of others even when not in contact. During trial experiments both types of readings were made, animals within two animal lengths of each other being counted as associated. A close approximation between the results of the two ways of recording was found but the data was not suitable to test the significance of the difference. Ellis (1953) estimated the distribution in both ways for similar experiments and calculated the significance of the difference between the results of the two

recording methods. It was clearly shown that the two ways of recording led to similar results.

TABLE 4.

Example of the experimental data from tests on social aggregation.

Batch 3rd Instar, cultured in crowded conditions,
(Number of animals in each sector recorded).

						Number of animals in clusters	Number of clusters.
	Sectors	1--4	5--8	9-12	13-16		
Trial	Reading						
1	1	0040	0001	1000	0200	6	2
	2	2411	0000	0000	0000	6	2
	3	2300	0100	0000	1010	5	2
	4	2000	1001	1101	0100	2	1
11	1	0220	2001	0000	0100	6	3
	2	0310	1010	0000	0020	5	2
	3	1100	0000	0001	2012	4	2
	4	0000	1010	3100	2000	5	2
111	1	0000	0101	0041	0001	4	1
	2	0011	0000	0211	2000	4	2
	3	1010	0010	0021	2000	4	2
	4	0220	2001	0000	0010	6	3
1V	1	0010	0000	1002	3001	5	2
	2	0001	0000	0022	1020	6	3
	3	0000	0040	0010	2100	6	2

Here as elsewhere in this work a "cluster" is defined as the occurrence of two or more animals in a sector of the chamber.

In order to check the constancy of the experimental conditions, a few 'blank runs' were made with no animals present. In one set eight thermometers (of the type used for whirling hygrometers) were placed around the chamber. During four series of four readings the temperature, as shown by all thermometers, remained at 25°C ± 0.5°C. During the tests with animals, thermometers were

placed alongside the chamber to verify that the presence of the observer did not raise the temperature above 25.5°C.

The chamber was maintained between 95% and 100% relative humidities by the moist plaster floor. Four blank runs were made with pieces of cobalt thiocyanate paper in the chamber to check the uniformity of the humidity. The paper colour was calibrated by means of a Lovibond comparator and humidity disc (Solomon 1957). No difference was observed between the quadrants of the chamber during the four runs. The uniformity of the intensity of light was checked by briefly exposing a sheet of photographic paper in place of the chamber. When developed this showed no variation in the intensity of colour due to exposure.

Eight batches of F. distincta were tested for social aggregation. These batches differed with respect to age, conditions of the experiment or conditions in the culture (Table 5).

Table 5.

The experimental batches used to determine the conditions in which aggregation occurred.

Batch	Condition in culture	Instar	Light	Number of trials
A	Crowded	2nd	Standard	4
B	"	3rd	"	4
C	"	4th	"	4
D	"	5th	"	4
E	"	Post 5th	"	2
F	"	Post 5th	Dim, Red	2
G	Solitary	5th	Standard	4
H	"	Post 5th	"	2

Before examining the data given in Table 4 and Appendix Table 1

for indications of social aggregation they will be analysed so as to show any irregularities in the experimental conditions.

The uniformity of the conditions during a trial is tested for each batch of animals by assessing the accuracy of the null hypothesis that the number of animals in clusters recorded at the first two readings does not differ from the number of animals in clusters at the last two readings of a trial.

Table 6.

An examination of the data to test the constancy of the condition during a trial.

Batch	Trials	Number of animals in clusters.	Number of animals isolated	$\chi^2_{[1]}$	Probability that the null hypothesis is correct
A	1+2	30	34		
	3+4	36	28	0.78	>0.3
B	1+2	42	22		
	3+4	39	25	0.13	>0.7
C	1+2	44	20		
	3+4	47	17	0.26	>0.5
D	1+2	43	21		
	3+4	49	15	0.97	>0.3
E	1+2	22	10		
	3+4	19	13	0.27	>0.5
F	1+2	19	13		
	3+4	22	10	0.27	>0.5
G	1+2	48	16		
	3+4	41	23	1.33	>0.25
H	1+2	22	10		
	3+4	21	11	0.07	>0.7

It is clearly shown (Table 6) that the null hypothesis is substantially correct. It can, therefore be assumed that any change

in the conditions during a trial had no effect on the number of animals in clusters. There also seems to be no tendency to 'learn' to aggregate during a short time even when the animals have been in complete isolation up till the time of testing (e.g.batches G and H).

The effect of any external factor influencing the position of the clusters can be separated from directional influences within the chamber because the chamber was rotated through 90° after each reading. Different sectors therefore occupied the same position, in relation to an external point for each reading. If the sixteen sectors are numbered clockwise then Table 7 shows the rearrangement of the sectors for each reading, sectors in the same column being in the same position relative to external objects.

Table 7.

The rearrangement of sectors for examining the influence of external stimuli.

Reading	Sectors
1	1 2 3 4 - 5 6 7 8 - 9 10 11 12 - 13 14 15 16
2	5 6 7 8 - 9 10 11 12 - 13 14 15 16 - 1 2 3 4
3	9 10 11 12 - 13 14 15 16 - 1 2 3 4 - 5 6 7 8
4	13 14 15 16 - 1 2 3 4 - 5 6 7 8 - 9 10 11 12

Any irregularity in the distribution due to external stimuli may be examined by testing the accuracy of the following null hypothesis. The frequency with which clusters occurred in the same position relative to an external reference point does not differ from that expected if there was an equal chance of clusters forming in any position.

The data for this examination is shown in Table 8 with the results of the analysis of the contingency tables.

Table 8.

Examination of the data to test the uniformity of external stimuli.

Batch	Frequency of Clusters in each position	Frequency of no clusters in each position	χ^2	Degrees of Freedom	Probability that the null hypothesis is correct.
A	5(3.75) 5 3 2	27(28.25) 27 29 30	2,03	3	> 0.5
B	3(4.25) 3 8 5 4 4 6 1	29(27.75) 29 24 27 28 28 26 31	8.38	7	> 0.3
C	6(4.38) 3 4 3 8 2 4 5	26(27.62) 29 28 29 24 30 28 27	6.55	7	> 0.4
D	3(4.25) 2 5 3 7 3 6 5	29(27.75) 30 27 29 25 29 26 27	5.83	7	> 0.6

Table continued overleaf.

Table 8 contd:

Batch	Frequency of clusters in each position	Frequency of no clusters in each position	χ^2	Degrees of Freedom	Probability that the null hypothesis is correct
E	4(4.00) 2 7 3	28(28.00) 30 25 29	4.00	3	>0.2
F	3(4.50) 7 2 6	29(27.50) 25 30 26	3.69	3	$\doteq 0.3$
G	6(4.25) 5 3 5 4 7 2 2	26(27.75) 27 29 27 28 25 30 30	6.37	7	$\doteq 0.5$
H	4(4.50) 7 5 2	28(27.50) 25 27 30	3.36	3	>0.3

The calculated frequencies had there been an equal chance of clusters forming in any position are shown in parentheses.

It is probable that the null hypothesis is correct and therefore that the external conditions did not cause any irregularities in the distribution of the Collembola during experiments.

A further examination of the data demonstrated the uniformity of the internal environment of the chamber. It is necessary at this point to comment upon the tendency of the animals so to condition the plaster floor where they gather that the area is more likely to have a cluster in succeeding tests. The proof of this is

shown in another analysis of the data (pp52). Because the sectors become conditioned and the internal environment so altered the present examination is based upon whether or not a sector has a cluster at any reading during a trial; in other words whether it becomes conditioned or not during a trial. In Table 9 the sectors have been grouped into quadrants of the ring so that the calculated frequency of conditioning is large enough for the use of χ^2 values in the comparison.

The null hypothesis tested in this table is that no sector has a greater likelihood than another of being conditioned. With the exception of batch 'F' this hypothesis is not disputed. As no explanation for the one high chi squared value could be found it is possible that this value has resulted from the 1 in 20 chance of the data not fitting the expected values. This seems likely because batches 'E' and 'F', which differed only in their external illumination, give the same results in all the following tests. For this reason the analysis of the data of batch 'F' has been included although no conclusions are based on the result of 'F' alone. As it has been shown that there were no irregularities in the experimental conditions the data may be examined for aggregation tendencies shown by the animals.

If the dispersal of the animals is random the numbers of sectors to be expected in each successive frequency class of individuals, 0,1,2..... animals per sector or other unit, may be calculated from the binomial distribution. The binomial distribution is a

Table 9.

An examination of the data to test the uniformity of the internal environment.

Batch	Sectors	Frequency with which sectors are conditioned	Frequency with which sectors are unconditioned	$\chi^2_{[3]}$	Probability that the null hypothesis is correct
A	1-4	3(5.50)	13(10.50)		
	5-8	6	10		
	9-12	8	8		
	13-16	5	11	3.62	> 0.3
B	1-4	9(6.00)	7(10.00)		
	5-8	3	13		
	9-12	5	11		
	13-16	7	9	5.34	>0.1
C	1-4	7(5.75)	9(10.25)		
	5-8	4	12		
	9-12	7	9		
	13-16	5	11	2.38	$\doteq 0.5$
D	1-4	5(5.25)	11(10.75)		
	5-8	4	12		
	9-12	6	10		
	13-16	6	10	1.23	$\doteq 0.75$
E	1-4	3(2.75)	5(5.25)		
	5-8	4	4		
	9-12	2	6		
	13-16	2	6	2.39	$\doteq 0.5$
F	1-4	7(3.50)	1(4.50)		
	5-8	2	6		
	9-12	3	5		
	13-16	2	6	8.63	<0.05
G	1-4	6(6.25)	10(9.75)		
	5-8	8	8		
	9-12	8	8		
	13-16	3	13	4.53	>0.2
H	1-4	3(2.75)	5(5.25)		
	5-8	1	7		
	9-12	3	5		
	13-16	4	4	3.81	>0.3

The calculated frequencies are shown in parentheses.

closer approximation to data from a random distribution, recorded as number of animals per sector than the Poisson distribution (Ellis 1956). Thus a comparison between the observed and calculated numbers of sectors in each frequency class provides a test of the departure from randomness of the distribution. This has been done by testing the following null hypothesis:- "the distribution of sectors between the frequency classes observed in the experiment does not differ from that calculated for the binomial distribution".

In Table 10 it is shown that the null hypothesis is disputed for every batch of animals. It may therefore be assumed that the distribution of the animals at every age is significantly different from that expected of random dispersal. Examination of the data shows that there is an excess of sectors in the high and very low frequency classes and too few in the medium classes. This indicates an aggregated population in contrast to an evenly distributed one from which an excess of the sectors would be found in medium classes. It is interesting to note that the significance of the departure from the random distribution is, for most batches, equally high in the analysis of the distribution in quadrants and octants, Table 10. This can be attributed to either or both of two features: the animals are so aggregated that the effect of the one sector with large numbers biases the calculation even of groups of four sectors or that the sectors with animals are adjacent more frequently than one would expect of a random dispersal. It is probable that the first possibility is partly applicable to every

Table 10.

A comparison of the observed distribution of the animals with that which would be expected if they are randomly dispersed.

Number of sectors in the ring		16				
	Number of trials	Frequency classes 0	1	>1	$\chi^2_{[1]}$	Probability that the null hypothesis is correct
Expected values	4	153	82	21		
	2	76	41	11		
Batch A	4	165	62	29	6.64	0.01
" B	4	174	48	34	25.02	< 0.001
" C	4	184	37	35	40.32	< 0.001
" D	4	186	36	34	40.97	< 0.001
" E	2	89	23	16	12.39	< 0.001
" F	2	87	23	18	13.94	< 0.001
" G	4	183	39	34	36.48	< 0.001
" H	2	89	21	18	16.43	< 0.001

Number of sectors in the ring		8 (octants)					
	Number of trials	Frequency classes 0	1	2	> 2	$\chi^2_{[2]}$	Probability that the null hypothesis is correct
Expected values	4	44	50	25	9		
	2	22	23	13	4		
Batch A	4	56	39	16	17	26.94	< 0.001
" B	4	59	33	24	12	12.44	< 0.01
" C	4	63	32	16	17	26.28	< 0.001
" D	4	70	23	17	18	43.08	< 0.001
" E	2	28	18	12	6	4.21	< 0.2
" F	2	31	15	8	10	16.98	< 0.001
" G	4	65	28	18	17	29.90	< 0.001
" H	2	33	12	8	11	24.46	< 0.001

Number of sectors in the ring		4 (quadrants)						
	Number of trials	Frequency classes 0	1	2	3	>3	$\chi_{[2]}$	Probability that the null hypothesis is correct
Expected values	4	6	17	20	13	7		
	2	3	9	10	7	4		
Batch A	4	13	16	11	12	11	19.3	< 0.001
" B	4	15	12	16	7	14	23.0	< 0.001
" C	4	15	16	10	10	13	22.5	< 0.001
" D	4	17	14	11	6	16	36.3	< 0.001
" E	2	7	8	7	2	8	14.0	< 0.01
" F	2	7	7	8	4	6	8.2	< 0.05
" G	4	17	13	12	7	15	32.70	< 0.001
" H	2	10	4	6	4	8	25.00	< 0.001

batch but it cannot be the complete answer in at least one batch, 'E', because the probability of the null hypothesis being correct is much less for the analysis of quadrants than for that of octants. Examination of the data also suggests that the second possibility is at least the partial explanation. Frequently all the animals are found to be present in one or perhaps two of the quadrants.

A social aggregation would therefore seem to occupy a particularly large area in relation to the animal size. With as few individuals as were used in the experiment physical contact between individuals in an aggregation was unlikely to occur by chance and in practice was infrequent. In these circumstances the formation and maintenance of groups must be by means of an awareness of the presence of other individuals by some sense not requiring tactile stimulation. The use of such a sense has already been indicated by the observation of the behaviour of individuals (p.31). Only three known senses can be used in the formation of social aggregations from distant individuals, visual, olfactory and auditory perception.

Folsomia distincta is completely without eyes or ocelli and therefore a visual image cannot be formed. A sensitivity to light intensity might be sufficient to indicate the presence of other animals but it is unlikely. However since many insects are insensitive to very dim red light a test was made under these conditions, batch 'F'. As is seen in Appendix Table 11 no difference between the number of animals in clusters under a red light and a standard light could be detected. Both batches,'F' and

'E', compared by the analysis of variance, were old animals in their 7th or 8th instar. These large animals were the only ones which could be seen in the dim light. However although it can be assumed that the poorer illumination made no difference to the formation of groups it was not possible to carry out an experiment in complete darkness nor was it possible to prove that red light was equivalent to darkness.

Auditory sense organs and organs perceiving vibrations in the environment may be present in F. distincta but none have been described. As setae can act as displacement receivers (Pumphrey 1940, Haskell 1956) it is likely that some of the many forms of setae found on Collembola may act as vibro-receptors. However no sounds or scratching and tapping of the plaster had any perceptible effect on the behaviour and it seems unlikely that either aerial or terrestial vibrations will play any part in the formation of groups.

Olfactory stimuli have been found to be effective in the formation of groups of Dysdercus sp. (Kruggel, private communication) and would seem to be the most likely agents in the formation of groups of F. distincta. Whether the perception is of an individual or only of a substance secreted by an individual on to its surroundings could not be demonstrated. However it is possible to show that the animals do condition their surroundings so that other individuals are attracted to settle there even if the original individuals are not present.

Table 11.

An examination of the data to determine the probability of conditioning of the sectors.

Batch	Frequency of sectors in each state	Number of sectors with clusters	Number of sectors without clusters	$\chi^2_{[1]}$	Probability that the null hypothesis is correct
A	Conditioned	7	26		
	unconditioned	17	142	0.61	> 0.3
B	conditioned	10	31		
	unconditioned	16	135	4.13	> 0.02
C	conditioned	11	28		< 0.01
	unconditioned	15	138	9.5	> 0.001
D	conditioned	13	28		
	unconditioned	12	139	14.05	< 0.001
E	conditioned	4	17		
	unconditioned	8	67	0.43	> 0.5
F	conditioned	4	16		
	unconditioned	11	65	0.09	> 0.7
G	conditioned	9	35		< 0.5
	unconditioned	15	133	2.43	> 0.1
H	conditioned	7	16		< 0.05
	unconditioned	8	67	5.60	> 0.01

If it is assumed that this conditioning does occur a cluster will so condition that sector that further clusters will be more likely to form there in subsequent readings than in any other sectors. The data is tested for this effect in Table 11, where a sector with two or more animals is regarded as conditioned in the subsequent readings of that trial. Obviously the first readings of each trial cannot be included because no sectors are conditioned, by definition,

at the time of that reading. The null hypothesis tested in Table 11 is that the presence of a cluster of animals on a sector at one reading does not increase the likelihood of a cluster forming there in the subsequent readings for that trial.

It can be seen in Table 11 that animals from crowded cultures condition their surroundings while they are in their 4th and 5th (mature) instars, (batches 'C' and 'D'). The other instars from similar cultures (batches 'A,B,E,F'), although showing a great tendency to aggregate, Table 10, do not condition their surroundings. The animals from solitary cultures in the 5th instar,(batch 'G'), may tend to condition the plaster but the null hypothesis is very likely to be correct, while in the 7th or 8th instar (batch'H') it is almost certain that conditioning of the plaster does occur. It would seem that breeding the animals isolated may cause a delayed development in their ability to condition their surroundings. Experiments with other instars are necessary to determine if the ability to condition surroundings is only developed in the later instars of the solitary individuals.

It has been shown that the degree of conditioning depends upon the age of the animals. If the aggregations are developed or maintained by conditioning of the floor it is likely that the degree of aggregation will be less in those ages in which conditioning is less. The significance of the difference of aggregation has been calculated by an analysis of the variance of the results of the different ages bred in crowded conditions (Appendix Table III).

The results of the older animals were included by treating the two batches of post 5th instars bred in crowded conditions, (batches 'E','F') as one experiment. This is justified by the lack of any difference in variance due to light conditions (Appendix Table II).

The analysis of the variance of the number of animals in the clusters during the trials with each age shows there is a significant difference ($p < 0.01$) between the ages (Appendix Table III). It can be seen from Table 12 that aggregation increases until the animals are mature.

Table 12.

The number of animals in clusters during the trials with each age group.

Instar	2nd	3rd	4th	5th	Post 5th
Mean number of animals in clusters at each reading	4.1	5.0	5.7	5.6	5.1

It seems likely that the greater number of animals in clusters during the trials with the 4th and 5th instars is caused by the tendency of these ages to condition the environment and so increase the tendency of the others to group there. However Ellis (1959) showed that the behaviour in locusts changed slowly as they became habituated to one another. To examine this possibility, the aggregation of the animals which were kept solitary was compared with that of equivalent batches which had been kept in crowded conditions. This comparison is made by an analysis of variance

using the number of animals in clusters as the criterion. Neither the analysis of the aggregation of the 8th instar nor the older animals (Appendix Table IV), disputes the null hypothesis. No difference with regard to aggregation has been shown to exist between the animals from either of the culture conditions. It is therefore probable that fully mature animals do not need to become accustomed to each other before social behaviour is shown. It is difficult to explain why the older animals should show the same amount of aggregation notwithstanding the conditions of the culture from which they have been taken. It is surprising because animals from crowded cultures have been shown to leave the plaster unconditioned while those from solitary cultures seem to condition the plaster (Table 11). This means that conditioning of the surroundings is not essential for group formation; indeed this is demonstrated by the younger instars,(batches 'A' and 'B' in Tables 10 and 11). It is possible that olfactory stimulation by odour from the animals is the most important agent in the formation of groups but when the surroundings are conditioned this increases the ability of the animals to form groups.

The groups formed in culture chambers tend to be semi-permanent especially in the case of the mature animals. This would be expected because once the plaster is conditioned the source of attraction is fixed in position and not dependent upon the individuals. It is interesting to examine the results of recording the position of exuviae in the culture chambers. Before this is reported an account

of the moulting process will be given.

d. Social Behaviour whilst Moulting.

Ripper (1930) and Strebel (1932) reported the formation of moulting societies in Collembola. In view of this a careful watch was kept for any signs of mass moulting but none were seen. It appeared rather that moulting could occur either in or out of groups.

The first obvious sign of a forthcoming ecdysis is when the thorax of an animal begins to pulsate rhythmically while the animal rests. Sometimes the animal lies on its side at this time. Sooner or later a split is seen on the mid-dorsal line of the 1st and 2nd thoracic segments. The split extends to the head capsule and the head is drawn out and the antennae are jerked free. The split extends backwards along the mid-dorsal line to the abdomen and the thorax is heaved out of the old cuticle. The legs are drawn out and usually jerked clear of the exuvium. The exuvium splits part way along thedorsal side of the abdomen which swells as it is freed and so pushes and rolls the old cuticle backwards. Several jerks usually free the furca which is extended straight back. As soon as the animal is free of the old cuticle it is able to run off. Moulting may take as little as five seconds or as long as two or three minutes. The older instars seem to take longer and have more trouble in removing the exuvium than the young. The old exuvium was usually left close to the position where the animal began to moult but in a few instances the skin was dragged along while caught on the furca. This most frequently occurred when the cultures were

more crowded and with the older instars. It may be that the animals are more likely to become disturbed before the exuvium is cast off under these conditions.

Eight cultures were used for the examination of the position of exuviae; four of the cultures had 15 animals and four had 45 animals. Each chamber was divided into eight segments and the number of exuviae in each segment was recorded every time the chamber was cleaned. These records may then be arranged in a table showing the frequency of octants with successive numbers of exuviae. The distribution of the octants amongst the classes will conform to the binomial distribution if the exuviae are cast at random within the chamber. It is therefore only necessary to calculate the binomial distribution and compare it with that observed to determine if the exuviae are cast at random. For convenience in Table 13 the observed distributions have been summed for each of the three periods, 0-10 days, 11-17 days and 18-24 days from the hatching of the eggs. Likewise the calculated binomial distributions for each of the observed distributions, have been summed over the same periods. The comparison may then be made by means of the standard chi squared analysis with the number of frequency classes less two giving the degrees of freedom. This is set out in Table 13 for each of the four cultures of 15 animals. The cultures of 45 animals have not been included in the table because the position of the exuviae is not always that of the moult because of the reasons stated above. In view of this a false conclusion might have been reached had the

calculations been included. The null hypothesis used is that the distribution of the exuviae does not differ from that calculated for the binomial distribution.

Table 13.

A comparison between the observed distribution of exuviae in culture chambers and that calculated for a random dispersion.

Culture of 15 animals	Age	Frequency classes			$\chi^2_{[J]}$	Probability that null hypothesis is correct
		0	1	>1		
1	0-10 days	13(8.7)	6(11.5)	13(11.8)	4.88	<0.05 >0.01
	11-17 "	8(4.2)	7(7.5)	9(12.3)	4.36	<0.05 >0.01
	18-24 "	12(8.4)	12(8.4)	13(11.8)	3.61	<0.1 >0.05
2	0-10 "	7(4.2)	0(4.8)	9(7.0)	7.24	<0.01 >0.001
	11-17 "	18(9.5)	2(11.3)	12(11.2)	15.34	<0.001
	18-24 "	12(6.8)	5(9.0)	7(8.2)	7.36	<0.01 >0.001
3	0.10 "	15(7.5)	4(9.9)	13(14.6)	11.20	<0.001
	11-17 "	17(14.3)	6(11.4)	9(6.3)	4.23	<0.05 >0.01
	18-24 "	15(14.5)	9(11.7)	8(5.8)	1.57	>0.1
4	0-10 "	6(3.1)	4(5.0)	6(7.9)	3.37	<0.1 >0.05
	11-17 "	11(6.7)	5(8.3)	8(9.0)	4.20	<0.05 >0.01
	18-24 "	10(4.8)	2(5.9)	4(5.3)	8.53	<0.01 >0.001

The figures in parentheses are the calculated values.

The null hypothesis is not disputed at the o.05 probability level for three of the distribution. Two of these are of the exuviae from older animals and in view of the comments made above these results must be regarded with caution. No explanation of the exceptional distribution for the exuviae from young animals in culture '4' can be given but it is clear that with a few exceptions the exuviae are distributed at random.

Examination of the data in Table 13 reveals that the departure

from randomness is in all cases due to an excess of sectors without exuviae and this indicates an aggregated distribution. As moulting communities were never observed the grouping of exuviae can only be caused by the animals moulting while in groups or moving to a particular site when about to moult. The latter is a possibility especially as conditioning of areas of the chamber can occur but it was never observed, whereas the animals are known to form groups and moulting of individuals in these groups have been seen.

As the moulting of all the animals in a culture of the same age took a few days to occur,(pp 21), the groups in which moulting occurred must be semi-permanent for the exuviae to accumulate sufficiently to bias the distribution. The semi-permanent nature of the social aggregation is also suggested by observation of undisturbed cultures. These have been watched continuously for over an hour during which time groups have remained in the same position without any signs of total disintegration. Observations of this sort also suggest that the greater likelihood of exuviae being randomly distributed in the larger cultures is in part due to the tendency of the animals in such cultures to be less closely aggregated. This is indicated by the smaller number of sectors of the chamber without individuals and may be due to the fact that 45 animals in 19.6 sq.cm. is a density which may be equal to or greater than that of the animals in groups. Consequently groups would not be likely to form.

e. Social Behaviour while Ovipositing.

It is likely that oviposition also occurs while the animals are in groups. No means of checking this was found. Oviposition was never observed, maybe it is inhibited by the bright light needed for observation. However no daily rhythm in oviposition was caused by the dim light falling on the cultures for twelve hours each day. The eggs may be roughly aged by their colour which at first is a translucent white but after a few hours becomes amber. By using this criterion fresh eggs have been distinguished in the cultures at all times of the day and night. It is also clear that the clumps of eggs, up to eighty or more, are not laid at one time, nor probably by one female. Quite fresh eggs are often deposited on clumps several hours, and sometimes days, old. These clumps are usually found in cavities or crevices in the plaster but may be spread over a flat area.

4. Factors affecting Life History.

a. Introduction.

In previous passages reference has been made to the effect which differing densities of culture population have on the Life History. The effect of changes in the population size and density on the control of fecundity and the rate of increase of population will now be considered.

Two preliminary experiments demonstrated the size of culture from which useful results might be expected. In the first of these four cultures were made at each of the three population sizes, 10, 30 and 90 animals in a chamber of approximately 7 sq. cms. cross section. The temperature varied between 15 and 25°C; the cultures were well fed and were kept in complete darkness. No further environmental control was maintained. The results of this experiment are shown in Table 14 where it is clear that there is an inverse relationship between the number of animals and mean fecundity per individual. It is also noticeable that three of the cultures of 90

Table 14.

The mean fecundity of animals in populations of three sizes.

Area of chamber 7 sq. cms.			
Number of animals	Mean fecundity per female ($\bar{f}$)	Number of cultures	$s(\bar{f})$
10	12.6	4	4.0
30	2.2	3	1.2
90	0.3	1	

could not be kept until mature. The remaining culture was not

healthy but less than 10% of the population died before oviposition began.

The second preliminary experiment indicated when the effect of crowding operated in control of the fecundity.

A culture of 90 animals was kept until oviposition would, under less crowded conditions, have been completed (25th day after the eggs hatched) but no eggs had been laid. This culture was then divided into two parts, one of 60 animals and one of 30 animals. During the next ten days the culture of 30 began to oviposit, 60 eggs in all being laid (a mean of two per female). The culture of 60 still had not oviposited and so was divided equally into two. Soon after this division a few eggs (15 and 25) were laid by each subculture. It is suggested therefore that the reduction in fecundity is due to the inhibition of oviposition.

In view of these preliminary experiments a series of more carefully controlled tests were made to examine the control of fecundity by the population. The experimental designs were such that the significance of any effects could be tested by analysis of variance. This permitted a factorial arrangement of treatments in several experiments and a consequent reduction in the number of cultures needed. The examination of the results by analysis of variance proved to be insensitive in some of the experiments because the residual variance had too few degrees of freedom.

As some treatments are replicated in several of the factorial

experiments, the experiments will be described first, and the fecundity results recorded. The results of all the experiments will then be discussed by considering each treatment separately. In this way the conclusions are more clearly argued.

b. Conditions of Experimental Cultures.

Except when otherwise stated the environmental conditions in all the experiments were as follows:-

Temperature, 25°C ± 0.5°C;

Illumination, very dim for 12 hours each day;

Relative humidity, between 95 and 100% maintained by the permanently damp plaster floor;

Area of chamber, 19.6 sq.cms.

Food, three Allisons yeast pellets for every ten animals;

Sanitation, all fungi, frass, exuviae, eggs and excess food removed every two days at which time the chambers were ventilated.

As the experimental cultures were made from animals hatched during the previous 24 hours, all experimental conditions were imposed on the animals within their first day of post-embryonic life and the temperature and illumination conditions immediately on hatching.

In experiment 1, the population size, area of chamber and amount of food were varied. In the factorial design the following treatments were used:-

Quantities of food:-2:-1 and 3 pellets for every ten animals;

Cross sectional areas of the chamber:-2:-7 and 20 sq. cms;

Sizes of population:-3:-10, 30 and 60 animals.

All other conditions for the culture were as stated above and the order in which the cultures were made was randomnised.

The total apparent oviposition occurring in each culture is shown in Table 15. These figures, as in Tables 16 and 20, necessarily exclude the eggs lost through cannibalism. This loss of eggs has been shown (pp 90) to be unaffected by the density of the population and is probably inconsequential when the eggs are regularly removed.

Table 15.

The number of eggs laid in each culture in experiment 1.

Conditions other than treatments - all standard.					
Area of chamber		7 sq. cms.		19.6 sq. cms.	
Food/10 animals		3 pellets	1 pellet	3 pellets	1 pellet
Number of Animals	10	194(19.4)	92(9.2)	101(10.1)	184(18.4)
	30	38(1.3)	4(0.1)	831(27.7)	568(18.9)
	60	0(0)	0(0)	5(0.1)	0(0)

The figures in parentheses are the mean numbers of eggs per animal.

It was necessary to make the amount of food present dependent on the number of animals in order that sufficient food was present in the large cultures and excessive quantities were not present in the small cultures. The different treatments with regard to food were not included to examine the effect of starvation through shortage of food, a condition which is hardly likely to exist in natural soil, but were designed to simulate starvation through an inability to find food or to feed. For this reason standarised pellets were considered most suitable because they provide discrete sources of

food which were easily placed at random in the chamber. The interdependence between feeding and population size means that the interaction of these treatments in the analysis of variance, (Appendix Table V), is a measure of residual error or of very complex effects.

Experiment 2 was designed to demonstrate any alteration in the effect which changing the population size had on the fecundity when the temperature was lower. The area of the chamber was varied as in experiment 1. Populations of 10 animals were again used but the populations of 30 and 60 were replaced by ones of 45 animals because 60 animals had been found to be too crowded to be healthy and cultures of 30(in the larger chambers) gave fecundities similar to those of cultures of 10 animals. Two levels of temperatures were used, 20°C and 25°C and one set of cultures was alternated every 24 hours between the two temperatures. The entire experiment was made without illumination except when examining the cultures because no light could be provided in the low temperature oven. The fecundities recorded for each culture are shown in Table 16, and the analysis of the result in Appendix Table VI.

An examination of the effect of keeping the animals in complete darkness as compared to those given a 12 hour day can be made by extracting the appropriate results from Tables 15 and 16.

Table 16.

The number of eggs laid in each culture in experiment 2.

Conditions other than treatments - illumination absent, others standard.							
Area of chamber		7 sq. cms.			19.6 sq. cms.		
Temperature		20°C	25°C	20°C/25°C	20°C	25°C	20°C/25°C
Number of animals	10	210 (21.0)	175 (17.5)	30 (3.0)	343 (34.3)	165 (16.5)	0 (0)
	45	217 (4.8)	153 (3.4)	2 (0)	458 (10.1)	190 (4.2)	13 (0.3)

The figures in parentheses are the mean numbers of eggs per animal.

The resulting Table 17, does not comply with the conditions required for an analysis of variance in that the cultures were not made in random order and too few degrees of freedom are available for a test to be sensitive. However for the present purpose observation of the table is all that is necessary.

Table 17.

The number of eggs laid in cultures under different lighting conditions.

Conditions other than treatments - populations of 10 animals, others standard.			
Area of chamber		7.0 sq. cms.	19.6 sq. cms.
Illumination	12 hr.day	194 (19.4)	101 (10.1)
	none	175 (17.5)	165 (16.5)

The figures in parentheses are the mean numbers of eggs per female.

As the accumulation of waste products in the chamber is a function of the number of animals present, this accumulation could be linked with the reduction in fecundity. In order to examine the likelihood of this effect two experiments were made; one to test the

accumulation of gaseous waste (experiment 4). Tables 18 and 19 show the design and results of these experiments.

Table 18.

The number of eggs laid by each culture in experiment 3.

Conditions other than treatment - all standard.					
Chamber condition		Cleaned		Not cleaned	
Removal of eggs		Not Removed	Removed	Not Removed	Removed
Number of animals	15	No results	1335 (89.0)	No results	1171 (78.1)
	45		11 (0.25)		2 (0)

The figures in parentheses are the mean number of eggs per female.

The alternative conditions of the chamber were caused by thoroughly cleaning one set every day and only doing the essential cleaning such as removal of excess food and fungi in the other set. When eggs were laid they were either left *in situ* or removed altogether and once oviposition began more eggs were added to the cultures of 45, if the presence of eggs was desired, because very few were laid. The total was made up to approximately 5 eggs per female. Unfortunately the effect of leaving eggs in the chamber could not be assessed because of a considerable loss of eggs which could only be explained by cannibalism by the adult animals. Cannibalism was not expected and was never observed in the stock or experimental cultures. A hypothetical correction was considered but none seemed satisfactory and so the data from the cultures in which eggs were left is omitted from Table 18.

Table 19.

The number of eggs laid by the culture in experiment 4.

Conditions other than treatments - all standard.			
Volume of air in chamber		19.6 mls.	39.2 mls.
Number of Animals	15	1116 (74.4)	727 (48.5)
	45	639 (14.2)	666 (14.8)

The figures in parentheses are the mean numbers of eggs per female.

As the chambers were open at the same time and as little as possible, the different volumes of air in the chambers meant that different concentration of nitrogenous waste products, carbon dioxide and oxygen developed. If any of these caused a change in the fecundity of the animals it should be indicated. The different volumes were made in the standard large culture dishes by casting the plaster 2 cms. deep in one set but only 1 cm. deep in the other set.

c. Factors controlling Fecundity.

These four experiments provide some useful clues to the factors controlling fecundity of F. distincta. However conclusions must be made carefully because in all experiments the minimum number of cultures were used. It is clearly shown in tables 18 and 19 that no great reduction in fecundity is caused by the accumulation of either gaseous nor solid waste products. An analysis of either table would be too insensitive to small differences to be justified and is unnecessary. It can be assumed that any changes in fecundity in the other experiment, where neither extreme of sanitation existed, are due to changes in the treatment and are not side effects due to accumulation of waste products.

The effect of different population levels is striking in all the experiments and there can be no doubt that in general an increased population has a reduced fecundity. This is clearly shown in experiments 2, (Table 16), 3, (Table 18) and 4 (Table 19), in which the probability that all the observed results are from the same range is very low. In experiment 2 comparing the mean fecundity per female in populations of 10 and 45 animals, the probability is less than 0.01 and in experiment 3 and 4, comparing populations of 15 and 45 animals, the differences are equally pronounced. However in experiment 1 the results are not so clear and so are more interesting. The cultures of 10, 30 and 60 animals in chambers of small area reveal a reduction in fecundity between the smallest and largest populations but this is barely significant ($p < 0.1 > 0.05$ Appendix Table Vc). However cultures of these populations in the large area show differences in fecundity which are significant ($p < 0.05 > 0.01$ Appendix Table Vc). The results show that this is not a simple reduction in fecundity with increasing numbers. This is emphasised by Table 20 in which the mean fecundity per female of the two cultures of each population is compared.

Only the mean of the culture of 60 animals is significantly different from the others at the 95% level but the cultures of 30 animals, seem to lay rather more eggs than the culture of 10 animals.

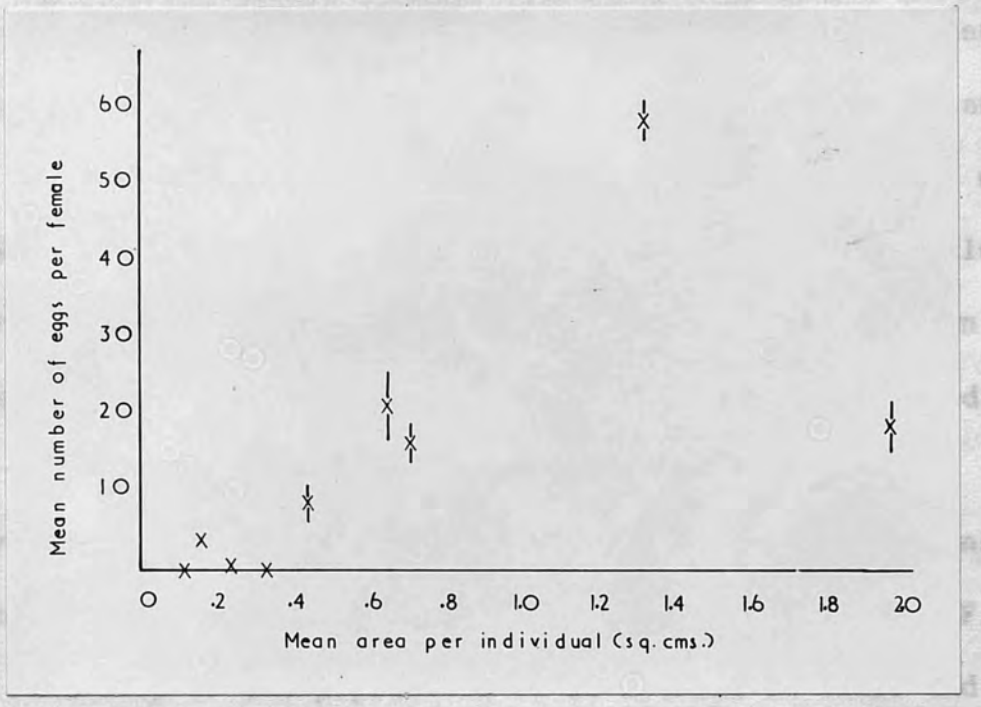
Table 20.

The mean number of eggs per female laid by the cultures in chambers of large area in experiment 1.

Population	10	30	60	animals
Mean fecundity per female	14.25	23.3	0.05	eggs

95% confidence limits for the difference between means ± 15.7

Fig. 4.1. The relationship between crowding and fecundity of F. distincta in cultures.



The points show the mean value for all relevant cultures and the lines indicate the standard error of the mean. All experimental cultures at constant temperature, 20°C or 25°C included; the degree of crowding at oviposition is taken as the criterion for cultures from experiment 5. It is possible that the mean number of eggs from cultures with a mean area of 1.96 sq.cms. is slightly overestimated due to the inclusion of the culture at 20°C.

In cultures of 10 animals reduction in area of the chamber and consequent increase in density has no appreciable effect on the fecundity, means of 14.3 and 14.25 eggs per female being recorded for each area (Table 15). It is equally apparent that a change in area causes no change in the fecundity of cultures of 60 animals (Table 15) but cultures of 30 animals are strongly affected, mean fecundities of 0.7 and 23.3 eggs being recorded for the smaller and larger areas respectively ($p < 0.05 > 0.01$). It is shown in experiment 2 that cultures of 45 animals also are too crowded to permit an increase in fecundity when the area is larger.

By plotting the mean area available to each animal against the mean fecundity per animal a symmetrical figure is obtained (Fig 4.1.). As the fecundity of the population of 10 animals in small and large chambers is almost the same, one expects the optimum mean area for maximum fecundity to lie midway between these two: that is at a mean area per individual of 1.35 sq. cms. This is close to the mean area available to cultures of 15 animals in large chambers and as can be seen the fecundity of these is the apogee of Fig.4.1.

It is also clear that the lack of an increase in fecundity when the larger populations are in the large rather than small chambers is because a limiting mean area per individual must be exceeded before oviposition normally occurs. This limit is apparently nearly 0.44 sq. cms. per animal, corresponding to a culture of 45 animals in the larger chamber. This density of

population also seemed to be about the limit above which groups do not form (pp 59).

The inclusion of the different amounts of food and the different temperatures as treatments permits an examination of the method by which the number of animals controls the fecundity of the population. In experiment 1 it is clear that extra difficulty in finding food did not greatly reduce the fecundity. Had this been so an interaction between the treatments of area and feeding or significant difference between the fecundities at the different levels of feeding might have been found, the difficulty in finding food increasing as the area increased and as the amount of food decreased. Starvation due to insufficient food did not occur in any treatment because care was taken that food was always present. However starvation because insufficient time is spent eating usually due to competition with other animals could occur. This is a factor which Pearl (1932) and Smirnov and Polejaeff (1934) suggested as possibly controlling fecundity. In experiment 1 any effect due to this would increase the variance due to the single treatment, level of feeding, but not the variance of the interaction of population and feeding. The reason for this is explained on page 65 . In Appendix Table Vc it can be seen that this effect is not significant.

In experiment 2 the temperature treatments were included to examine the effect of changing the metabolic rate and physical activity. The interaction between the temperature and other

treatments could be interesting but the difference between the temperatures was not sufficiently great to cause any marked effect on most cultures. This is somewhat surprising because 25°C is probably higher than the optimum and the fecundity might have been expected to increase at a lower temperature. The findings in this work are in accordance with Milne's observations in that of the species in culture only F. candida distincta seems able to reproduce at 25°C. The mean of 10.1 eggs per female from the cultures of 45 animals is well within the expected variation found for cultures of this concentration in other experiments. However the mean of 34.3 eggs per female from the cultures of 10 animals is exceptionally high and may be a real effect of a lowered temperature. It is difficult to explain this increase unless it is assumed that the decrease in fecundity of cultures with a mean area of more than 1.4 is due to extra activity occasioned in the search for the company of other individuals. A reduction in temperature would probably reduce activity and so increase fecundity but it is then inexplicable why the fecundity of crowded cultures is not increased at lower temperatures. The exceptional drop in the fecundity of the cultures kept at the alternate day rhythm suggest that this sort of rhythm disturbs the animals so much that fundamental activities are effected.

As no light can be thrown at this point on the method of control attention is turned to the age at which control (of the fecundity) is functional. From the second preliminary experiment it was

assumed that the high number had to be present during oviposition for the fecundity to be reduced. This assumption was examined more carefully by two experiments, The first of these consisted of a large series of cultures. Half of these were started with populations of 45 animals and two subcultures of 15 animals were taken from one of these cultures at each age. The other half of the series consisted of cultures of 15 animals of which two sets of three were combined at each age to give cultures of 45.
Unfortunately the results were extremely erratic and this was probably due to injury whilst the animals were being transferred between chambers. In view of this a further experiment was planned involving less handling of the animals. In this experiment, experiment 5, each culture was started with a population of 45 animals. At each instar the population of two cultures was reduced to 15 by removing the excess animals (experiment 5a).
The animals were moved very carefully and used to form two supplementary cultures of 15 animals, one from each of the original culture (experiment 5b). One pair of cultures was started with populations of 15 and another pair was never reduced from a population of 45. These provided controls against which to compare the other cultures. The supplementary subcultures were included because it was possible that some form of conditioning of the chamber by large populations might inhibit oviposition even when the populations were reduced. Even though the effect of excreta has already been excluded it is known that this animal conditions an

area so that it is more attractive to other individuals,(p 53 .) As these subcultures were placed into new chambers when the main culture was reduced no form of conditioning could exist.

The mean fecundity of each subculture is shown in Table 21.

Table 21.

The mean number of eggs per female laid by cultures in experiment 5.

Conditions other than population level - standard.

a) Subcultures left in original chamber.

Instar at which culture is reduced to 15 animals.	1st (control)	2nd	3rd	4th	5th	6th	Never (control)
Replication	52.8* 55.3*	48.2 53.7	29.4 54.9	48.0 58.5	43.3 74.1	63.5 72.5	12.1 17.1
Mean	54.1	51.0	42.2	53.3	58.7	68.0	14.9

95% confidence limits for the difference between means = ± 27.3

b) Subcultures placed in clean chambers.

Instar at which culture is reduced to 15 animals	1st (control)	2nd	3rd	4th	5th	6th	
Replication	52.8* 53.3*	55.8**	59.9 71.4	50.9 85.5	56.0 44.8	50.1 59.1	
Mean	54.1		65.7	68.2	50.4	54.6	

* Results duplicated in a and b.
** There was no replication of this class and consequently this result is excluded from the analysis of variance (Appendix Table VII).

The age at which the cultures were reduced appears to have no consistent effect in either part of the experiment. In the analysis of Table 21a both pairs of controls are included. This is done to check that the non-reduced controls have a significantly lower fecundity although it seems higher than might be expected.

As seen in Table 21 it is only the mean of the two non-reduced cultures which differs from the others by a quantity greater than 95% confidence limits. The non-reduced controls were not included in the analysis of Table 21b, Appendix Table VIIb, and, as would therefore be expected, no significant difference due to the treatments were found. It is clear that the age at which the cubtures are reduced does not reduce oviposition as long as the culture is reduced while it can still oviposit. This is particularly shown by those cultures reduced in the 6th instar. In these oviposition has started before reduction during their 5th instar, but the majority of eggs were only laid after reduction of the culture population.

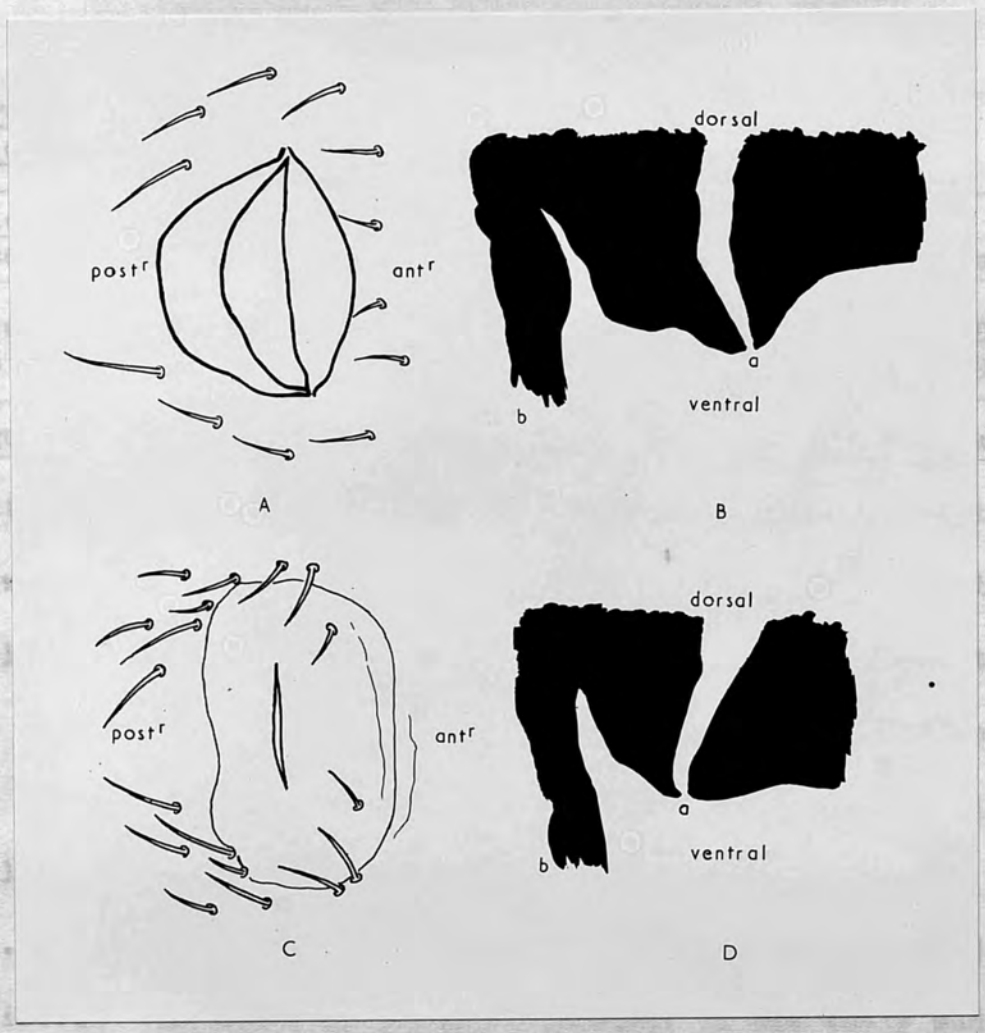
It is also clear that the possible conditioning of the chamber by a previous population does not greatly affect the fecundity. In Table 21 only the sets of culture reduced in the 3rd, 4th, 5th and 6th instars may be compared to assess the effect of leaving the reduced population in the old, possibly conditioned,chamber, because these sets are complete with two cultures in each part of the experiment. The comparison of these cultures is made in Appendix Table VIII and shows that the condition of the chamber does not alter the fecundity and again that the age at which the cultures are reduced in numbers has no effect in altering the fecundity. It would seem therefore that the main control of the fecundity is the immediate presence of a large number of other individuals.

d. Means by which Fecundity is controlled.

There are several methods by which this control could operate. They include the inhibition of maturation of the reproductive organs, or of the eggs, or of the act of oviposition and these may apply either partially to the whole population or wholly to part of the population. Some of these suggestions can be examined further by considering the development of the reproductive organs.

The development of the ovaries was determined by examining the experimental animals after 'clearing' in benzyl alcohol. Occasionally an animal of mature age was found to have undeveloped ovaries but the occurrence of these was not connected with the population size or density. However two conditions of the ovary could be defined easily on the basis of the formation of the egg shells. In some animals the eggs in the ovaries are very poorly defined and difficult to distinguish from surrounding tissue whereas in other ovaries the eggs are easily distinguished by a highly refractive shell. There again seemed to be little correlation between egg shell formation and size or density of the culture. As the experimental populations in experiment 3 are likely to show most difference, being near to optimum and to over-crowding, an analysis of the results has been made in Table 22 and Appendix Table IX. The analysis shows that there is no significant difference between the percentage of animals with eggs shells formed in any of the cultures. Therefore it seems unlikely that the fecundity of the cultures is limited by the final

Fig.4.2. The female genital aperture of adult F. distincta.



A and B The 'open' condition.

C and D The 'closed' condition.

A and C are ventral surface views; B and D are vertical section silhouettes.

a; Genital aperture

b; Furca.

maturation of the eggs.

Table 22.

The percentage of animals with egg shells formed in the ovary in the cultures of experiment 3.

Condition of Chamber		Cleaned		Not Cleaned	
Presence of eggs		Present	Removed	Present	Removed
Number of animals	15	72.7(58.5)	71.4(57.7)	81.8(64.8)	60.0(50.8)
	45	85.7(67.8)	70.3(57.0)	59.7(50.6)	62.9(52.5)

The figures in parentheses are the Angular Transformation(Brownlee 1949)

Attention was therefore turned to any accessory reproductive organs which show differential development. The only organ that seemed likely to fulfil these conditions was the genital aperture and its surrounding plates. This aperture could be classified as open or closed (Fig. 4.2.). In the open condition the plates are swollen and the aperture conspicuous as a slit across the papilla. In the closed condition the lips and aperture are just discernible. The cause of these differences is not fully understood but once open the genital aperture does not seem to revert to a closed condition when the animals cease to lay. No animal which has laid eggs has ever been seen with a closed aperture and no immature animal has ever been seen with an open aperture. However a few individuals have been seen with enlarged apertures but unswollen lips. This suggests that the aperture may enlarge at maturity but the lips only swell when oviposition occurs. If this is the case the extremely few animals seen with genital apertures in doubtful condition can only be explained if oviposition

and maturation occur almost simultaneously.

The relationship between the population size or density and the percentage of animals with open genital apertures is shown using the results of the experiments 1 and 3 in Table 23, a and b.

Table 23.

a) The percentage of animals with the genital aperture open in the culture of experiment 1.

Area of chamber		7.0 sq. cms.		19,6 sq. cms.	
Food		3 pellets	1 pellet	3 pellets	1 pellet
Number of animals	10	90(71.6)	85.7(67.8)	90(71.6)	83.3(65.9)
	30	61.9(51.9)	50.0(45.0)	76.2(60.8)	60.0(50.8)
	60	26.3(30.9)	18.2(25.3)	43.3(41.2)	25.0(30.0)

The figures in parentheses are Angular Transformations (Brownlee 1949)

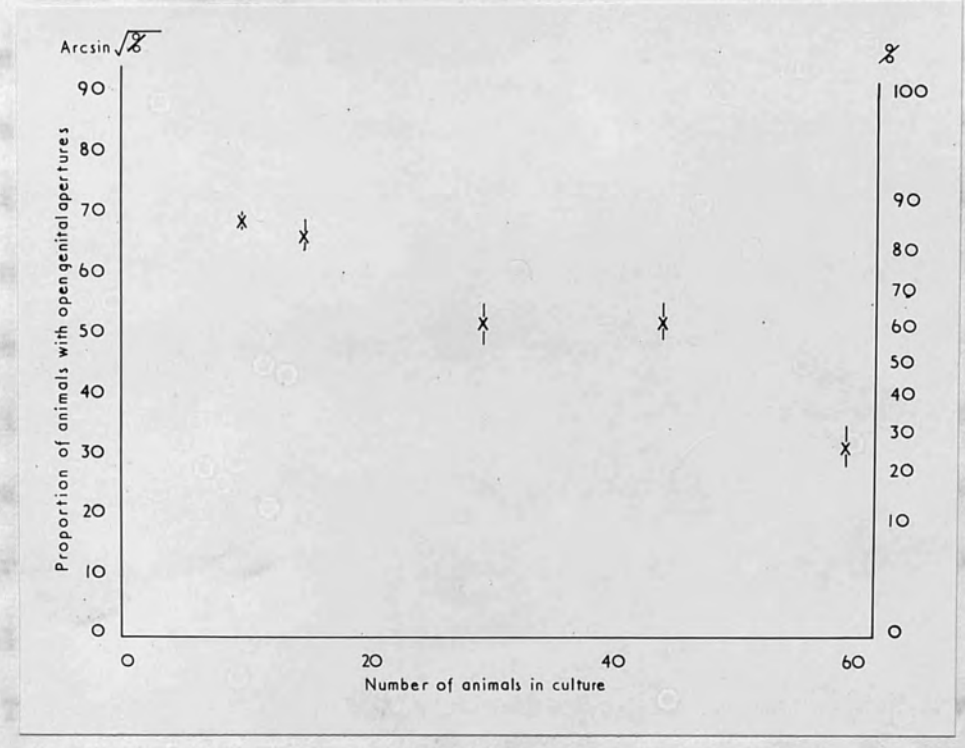
b) The percentage of animals with the genital aperture open in the culture of experiment 3.

Condition of chamber		Cleaned		Not Cleaned	
Presence of eggs		Present	Removed	Present	Removed
Number of animals	15	81.8(64.8)	80.0(63.4)	81.6(64.8)	92.9(74.6)
	45	62.7(52.4)	68.6(55.9)	71.4(57.7)	48.7(44.3)

The figures in parentheses are the Angular Transformation(Brownlee 1949)

In tabulating the results of these experiments the nature of the lips of the genital aperture was taken as the decisive factor in the three animals about which there was doubt. In the analysis of both sets of data it is clear that increasing the population size reduces the percentage of animals with open genital apertures (Appendix Table X. Fig.4.3), but not as much as might have been expected from the data on the reduction of oviposition. It would seem that what little oviposition does occur in large cultures

Fig. 4.3. The relationship between the population size and the development of the genital aperture of F. distincta.



The points show the mean value of all relevant cultures and the lines indicate the standard error of the mean.

could involve many individuals all of which lay one or a few eggs. The different levels of area in experiment 1 did not cause significant changes in the development of the genital aperture and as there is no interaction between the treatments of area and population there is no reason to suppose that changes in area are effective at any population level. It is clear that neither the presence of eggs nor the cleanliness of the chamber causes any change in the proportion of animals with open genital apertures. Surprisingly the different feeding levels did cause significant changes in the development of the genital aperture: a greater number of sources of food appeared to cause an increased number of animals with open genital apertures.

The action of both the population size and feeding level in regulating the development of the genital aperture can be explained by one suggestion: this is that the activity of the animal exercises most control over the development of the genital aperture. It has been shown that when other individuals are present the amount of turning is considerably increased although less distance is walked. Although the animals may disturb each other more frequently when more crowded in a smaller area, it seems that this is less important in the control over the development of the genital aperture than the increased turning due to the awareness of the presence of other individuals. This conclusion is drawn from the fact that the decrease in area seems to have less effect on the development of the genital aperture than an

increase in population. When less food is present, especially a small number of discrete sources as was the case, jostling probably occurs and more activity is thereby caused thus inhibiting the opening of the genital aperture.

e. Growth of a population.

As the growth of a population does not depend only on the fecundity of the population, further observations were made on the cultures used in the experiment. The experiments were primarily designed to obtain information about the fecundity of the species; however the importance of the population size or density on the rate of development and the mortality of the animals can be shown.

It has already been shown (Fig.2.1) that there is little or no difference in the rate of development, based upon frequency of moults, between cultures with 10,15,30,45 or 60 animals.

A further aspect of development is the rate of maturing of the reproductive organs. This is conveniently measured by the length of the preoviposition period, that is the number of days after hatching until the eggs are laid and greatly influences the rate at which a population grows. This period was measured for all the cultures in the first three fecundity experiments and the results are shown in Table 24.

Table 24.

The preoviposition period, in days, for the cultures of experiments 1,2,3.

a) Experime nt 1.

Area of chamber		7 sq. cms.		19.6 sq. cms.	
Food		3 pellets	1 pellet	3 pellets	1 pellet
Number of Animals	10	14.5	11	13.5	11.5
	30	11.5	13	12	11
	60	∞	∞	14.5	∞

b) Experiment 2.

Area of chamber		7 sq.cms.		19.6 sq.cms.	
Temperature		20°C	25°C	20°C	25°C
Number of animals	10	12	14	14.5	13
	45	16.5	14	16	13

c) Experiment 3.

Condition of chamber		Clean	Dirty
Number of animals	15	13	11.5
	15	11.5	10.5
	45	18.5	10
	45	11.5	∞

From inspection of Tables 24, a,b,c, it seems that the preoviposition period is not markedly altered by any of the treatments in experiments 1,2,3, but oviposition may be permanently postponed when the cultures are too crowded. The results do not warrant an analysis and the permanent postponement of oviposition would bias calculations.

Unfortunately it is not easy to assess the relationship between population size or density and mortality because the experimental design was such that cultures with more than 20% mortality

before oviposition was complete were replaced. A record of the cultures replaced during experiments is given in Table 25 and some information is provided about the relation between the population and its mortality.

Table 25.

The number of cultures replaced because more than 20% of the animals died before completeing oviposition.

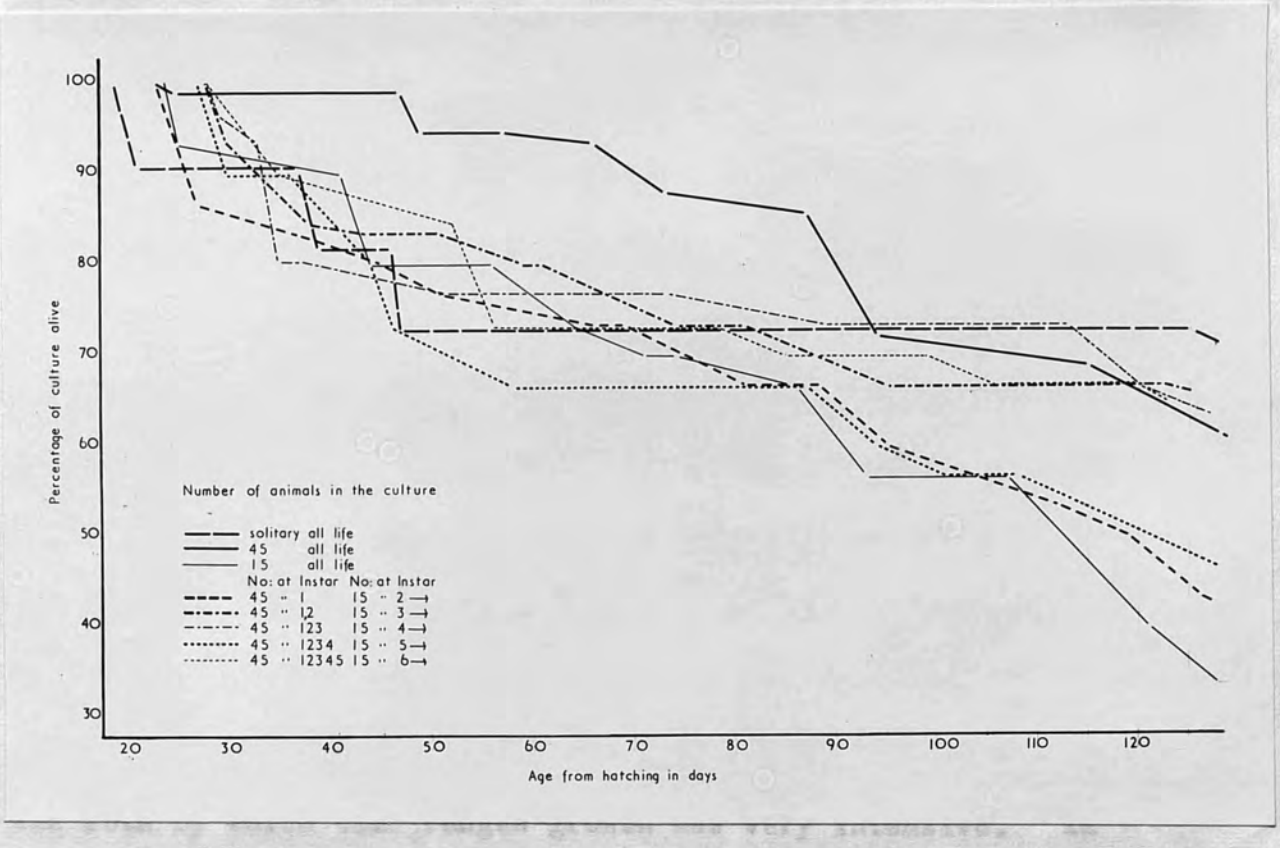
Mean area/ animal.cm^2	1.96	1.31	0.71	0.65	0.44	0.33	0.24	0.16	0.12	0.08
Number of cultures replaced	-	-	-	1	-	1	2	-	2	3
Total number of cultures	5	25	9	2	9	2	6	3	2	4

It is clear that at the higher densities mortality is greater; a population density of 3.0 animals per sq.cm. (0.33 sq.cms. per animal) corresponds to 60 animals in a chamber five cms. in diameter. Examination of the dead animals showed that the mortality was usually due to damage preventing the completion of ecdysis of the older instars, or to the withering disease which has been described on p 16 . This disease seems to be contagious and consequently spread more rapidly in the denser cultures.

A complete record of mortality is available for the cultures which were reduced from 45 to 15 animals during their life and for the solitary individuals discussed on p.21 . In Fig.4.4 these results are plotted as a graph and it is clear that although the

larva

Fig. 4.4. The mortality of F. distincta in culture.



The lines are based on the total values of relevant cultures.

The number of animals contributing to each line is as follows:-

Solitary animals	-	11
45 all life	-	90
15 all life	-	30
15 from 2nd instar	-	45
15 from 3rd instar	-	60
15 from 4th instar	-	60
15 from 6th instar	-	60

large cultures have less mortality at first there is little difference between the various cultures later in life, the three cultures showing greatest mortality having very different conditions with regard to population.

A further aspect of mortality is the fertility of the eggs. This was measured in some batches of eggs laid by the experimental cultures but very few results can be considered. It was not found possible to produce aseptic conditions during the embryonic period and the majority of the batches tested were overgrown by fungi before hatching and consequently few were able to hatch. During the embryonic period the eggs were kept at 20°C under humid conditions, 95-100% R.H. in sterilised culture dishes. They were examined and hatchings removed every day after the 5th and until the 20th by which time fungus growth was very intensive. In Table 26 the results of the six batches with least fungal growth are presented.

Table 26.

The fertility of eggs of F. distincta at 20°C and high R.H.

Ovipositing culture.			
Number of animals	Area(cm^2) per animal	Number of eggs tested	% of eggs hatched
45	0.44	55	54.5
45	0.44	76	11.6
30	0.65	30	36.7
15	1.31	596	32.6
15	1.31	591	50.8
10	1.96	93	41.9

It can be seen that there is no clear relationship between the ovipositing population and the fertility of its eggs which seems

to be between one third and one half of the eggs laid. As these are laid by parthenogenetic females it would be interesting to know if the low fertility is due to the sterility of eggs with male offspring, thus causing the parthenogenetic culture.

Cannibalism is again a form of mortality. It has never been seen in any culture between animals of equal or different ages and no evidence, the disappearance of animals, was recorded. However cannibalism of eggs, although not at first suspected, must have occurred because eggs completely disappeared and this could only happen if they were devoured. The animals were often seen around batches of eggs and sometimes feeding near eggs but were not seen to eat eggs. During the third experiment the eggs were counted and left in the chamber of certain cultures. So many completely disappeared that, even while the animals were probably still laying, decreasing numbers of eggs would be found in the chambers. As cultures of 45 animals laid few eggs more eggs were added to these cultures once oviposition had started. Table 27 gives the rates of loss during periods when the loss of eggs was greatest. In all likelihood no eggs were being laid during these periods, but this cannot be proved.

As far as it is possible to see from these results the rate of cannibalism is equally high in dense and less dense populations. The maximum rates are higher in the small populations but this is

Table 27.

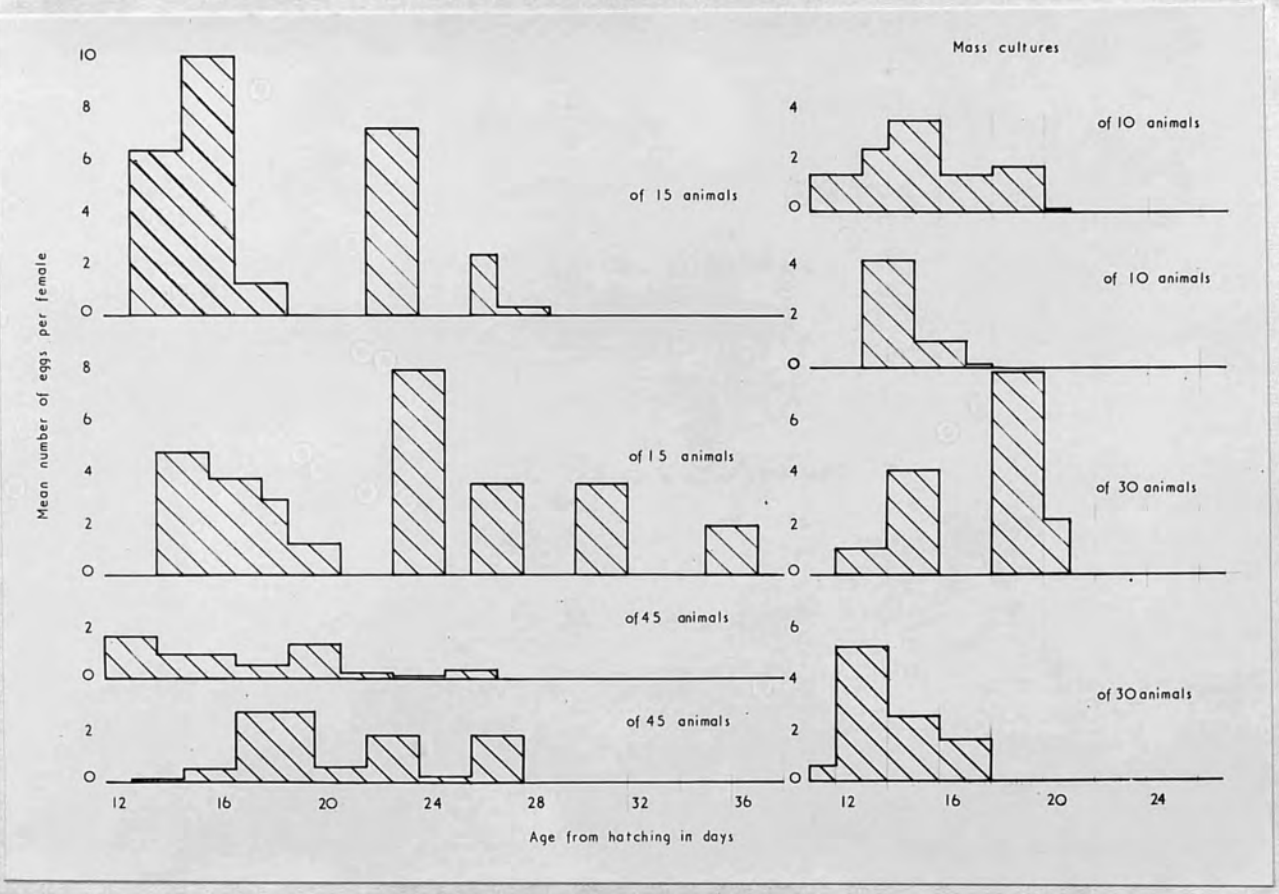
Population (animals)	Period of record (days)	Estimated midperiod total eggs/animals (assuming continual even loss during period)	Average loss eggs/animals/ day(%of mid-period total)	Mean loss eggs/animal/ day(% of mean midperiod total)
15	2	18.0	10.6	
	2	14.0	15.1	
	2	10.1	18.1	
15	2	11.9	14.6	
	3	8.4	16.8	14.27
	2	3.9	60.3*	
45	3	5.9	11.3	
	2	5.3	17.6	
45	2	9.3	11.8	
	3	6.7	13.4	13.24

* This period is exceptional as explained in the text and has not been included in calculating the mean loss.

probably due to the natural dispersion of eggs in clumps. In the dense populations the eggs were mostly artifically introduced and distributed rather more evenly than in the small populations. The complete loss of a single large clump of eggs accounts for the exceptional reading of 60% loss.

Throughout the experiments a count of the number of eggs laid during the life of the Collembola has been used to estimate the fecundity and this has been possible because the majority of eggs are laid by small cultures soon after maturation (Fig.4.5). Any prolonged laying gave rise to such comparatively small numbers of eggs that no serious error was introduced if these eggs were not counted. This situation is very different from that of the

Fig.4.5. The oviposition ages for eight selected typical cultures of F. distincta in chambers with an area of approximately 20 sq.cms.



solitary individuals with which oviposition is periodic for a relatively longer time (Fig 2.3).

Although it seems likely in mass cultures only the first oviposition period occurs and further periods are partly suppressed except in the cultures of 15 animals, a useful comparison of the fecundity of solitary and mass cultures cannot be made without information about the differences in physiology especially as the mean area available per animal has little meaning if only one animal is present. As eggs may be found postmortem, in animals from both solitary and mass cultures which died long after oviposition had ceased, it appears that the potential fecundity of neither group is fully realised and it has not proved possible to estimate the potential fecundity of any cultures.

A sensitivity to population size or density is present in many animals. Norris (1950, 1952, 1959) in work with many species of locusts, found that crowded conditions during life reduced the fecundity of Locusta migratoria (R & F) and Nomadacris septem-fasciata (Serv.). This was also demonstrated for Locusta migratoria by Albrecht et al (1958) and for Pieris brassicae L. by Zaher and Long (1959). The majority of other workers have measured the oviposition rate of the experimental species but, provided that the length of the oviposition period is not altered by crowding, the fecundity and oviposition rates are proportional. Pearl (1932) found that by increasing the density of population he

reduced the oviposition rate of Drosophila melanogaster Meig and Utida (1941) showed the bean weevil Callosobruchus chinensis (L) reacted similarly. Park (1932) working with Tribolium confusum J du V. showed that there was an optimum density above and below which the oviposition rate was reduced. This pattern is apparently followed by F. distincta which is shown to have an optimum density at approximately 0.77 animals per square centimetre, Fig.4.5. This optimum suggests that co-operation between the animals exists until a certain density is reached above which disoperation overrides all co-operation. A number of suggestions have been made by various workers to explain the disoperation. It cannot be doubted that when a population becomes overcrowded disease is more prevalent and the animals are less resistant to adverse regimes. This was demonstrated by Norris (1950) who showed that uncrowded cultures of Locusta migratoria were not adversely affected if fed poor grass but that when the same species under crowded conditions were fed with poor grass, the fecundity was lowered.

Many workers have suggested that the changing environment of the animals due to the accumulation of excreta may cause a sensitivity to density, Crombie (1942). Regular cleaning and ventilation during most experiments with F. distincta reduced the possibility of the environment changing and the experiments designed to examine the effect of accumulating excreta all showed

that the fecundity was little altered by this treatment.

During this work care was taken to ensure that food and oviposition sites were always present. Oviposition sites in the form of small crevices were abundant and competition for these could not exist. Although competition for food, suggested as an important factor by Pearl (1932) and Smirnov and Polejaeff (1934) did not significantly reduce the fecundity of F. distincta, it did reduce the number of individuals able to oviposit, those with open genital apertures. This competition causes a reduction in the rate of feeding due to jostling by other individuals. The effect therefore may be caused through actual starvation or through extra activity and stress.

The only other cause of disoperation is the competition for total space, 'lebensraum'. This is shown to have reduced the fecundity of F. distincta in all but the most overcrowded cultures. Competition of this sort results in increased stress, jostling and possible activity. Retzlaff (1938) suggested that dominant female mice had the best reproductive records because they fought less and Crowcroft and Rowe (1958) considered the anoestrous condition of females in crowded mice population might be due to stress applied by fighting males.

It is rather difficult to explain a competition for 'lebensraum' in a species with a pronounced tendency for social aggregation. Circumstantial evidence supports the suggestion that, although the animals form groups, space between the animals is necessary.

Groups forming in a ring chamber occupied a very large area relative to the size of the animals and it was suggested earlier that 45 animals in an area of 19.6 sq.cms. is too large a population for the formation of groups.

It has been shown that only crowding in the adult instars reduces fecundity. Crowding during the immature instars had no effect on reproduction nor on the pre-oviposition period. It must be assumed therefore that the development of the reproductive organs is not altered by the density of the population as it is in many insects. The period of development between hatching and oviposition is shortened by crowding the larval instars of Pieris brassicae, Plusia gamma L. (Zaher and Long, 1959), Schistocerca gregaria (Forsk) (Chauvin 1941 and Norris 1952) and Callosebruchus chinensis (Utida 1941). Norris (1950) concluded that crowding during the larval instars of Locusta migratoria caused the adults to be more sensitive to crowded conditions and Albrecht et al (1958) in confirming this showed that the sensitivity to isolation was also increased.

Reduction of the fecundity of a population can result either from a general lowering of fecundity of all ovipositing individuals or from a reduction in the number of individuals laying. Zaher and Long (1959) showed that 20% of the females of Plusia gamma laid over 50% of the eggs whether the individuals were isolated or crowded; in this case a reduction of the population fecundity can only be due to a general lowering of fecundity. Crowcroft and

Rowe (1958) noted that female mice, which in a crowded culture were non fecund, became fecund when the culture was transferred to a larger cage. The reverse situation also proved true in that fecund mice became anoestrous as crowding was intensified. From the data here presented it seems that the reduction in the population fecundity of F. distincta is caused by both reduction in individual fecundity (pp 83) and in the number of individuals ovipositing (pp 82). It was possible to demonstrate a reduction in the number of ovipositing individuals in the larger populations and it is interesting to note that no optimum density of culture was found.

It seems probable therefore that the disoperation, shown by the reduction in fecundity, between the animals in populations of densities greater than the optimum is due to excess stress, or perhaps activity, caused by jostling between individuals either in competition for food or for 'lebensraum'.

Little evidence which would explain co-operation could be obtained but as social aggregation is well developed it is possible that the presence of groups encourages the laying of more eggs than usual. It is suggested that more eggs are laid by the ovipositing individuals because the proportions of animals with open genital apertures in cultures of 10 and 15 animals are almost the same but cultures of 15 lay considerably more eggs. It has been assumed that animals with open genital apertures do oviposit even in the

culture of 60 animals but only one or two eggs may be laid. The increased fecundity of cultures of 10 animals at 20°C suggests that reduced activity increases the fecundity.

It is clear that the changes in fecundity of F. distincta will cause major changes in the growth of the population. In order to examine the importance of the fecundity in the control of population growth the mortality of all forms was examined. Natural mortality of adult and larval animals does not usually seem to be dependent on population density but overcrowding leads to the prevalence of disease and this seemed to be shown by F. distincta .

Infertility of the eggs was not shown to be dependent on the parental culture density in F. distincta although Maclagan and Dunn (1936) suggested that reduction of fertility of the eggs of Sitophilus oryzae (L) partially accounted for the reduction in a population's growth as it became large. On the other hand Albrecht et al (1958) showed the fertility of eggs from isolated Locusta migratoria to be only one third that of eggs from crowded cultures. However Crombie (1942) working with Rhizopertha dominica (F), Oryzaephilus surinamensis (L), Acanthascelides obtectus (Say) and Sititroga cerealella (Oliv.) and Norris (1952) with Schistocerea gregaria showed that the fertility of the eggs was independent of the parental population density.

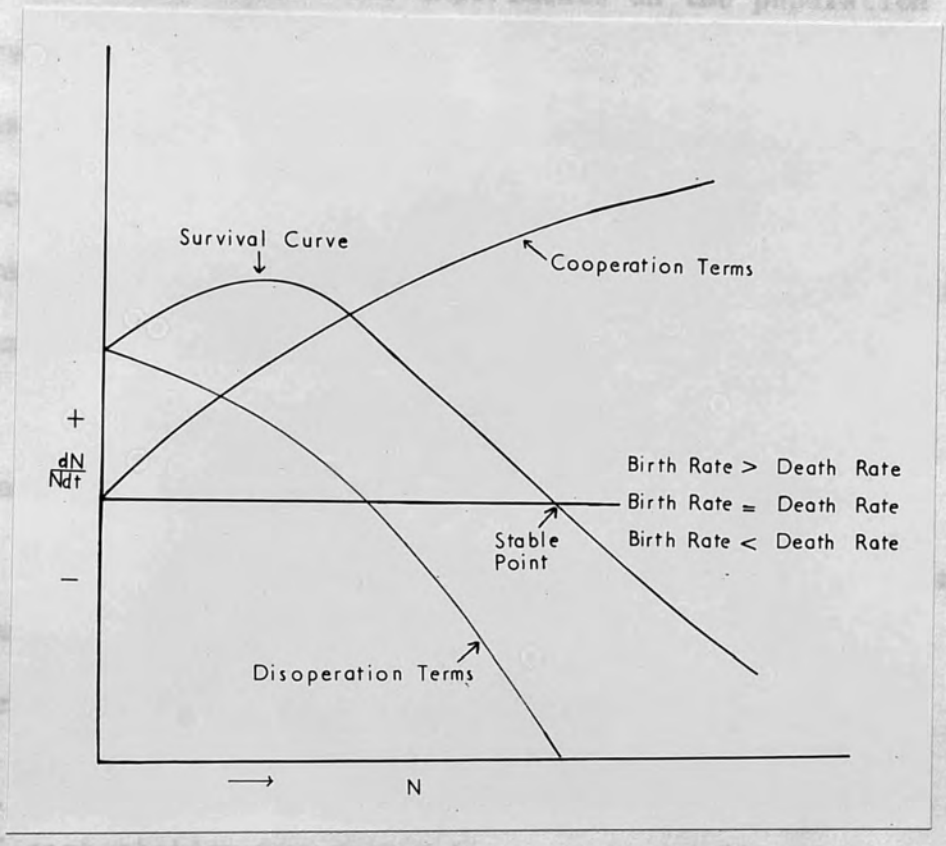
Artificial mortality due to cannibalism is known to occur in many insects. Maclagan and Dunn (1936) considered that cannibalism of eggs and young larvae accounted for the increase of mortality of

these stages as the population of Sitophilus oryzae became larger. Lefkovitch (1961) in a paper to the Royal Entomological Society of London suggested that cannibalism of pupae and prepupae of Cryptolestes turcicus (Grouv.) partially accounted for the reduced population growth in crowded cultures. However although cannibalism of eggs occurred in cultures of F. distincta it did not appear to be related to density and consequently would be strictly in proportion to the population size and number of eggs present.

Of the various aspects of life which control population growth it seems that only the fecundity of F. distincta is dependent on the population density.

As there is an optimum at which maximum fecundity is achieved it is postulated that the growth of parthenogenetic cultures will follow the generalised pattern given by Odum and Allee (1954) Fig. 4.6 which has been shown to apply wholly or in part to many animals.

Fig. 4.6. Survival curve showing components-co-operation and disoperation terms, for a species which increases in numbers at minimum densities. (After Odum and Allee (1954).



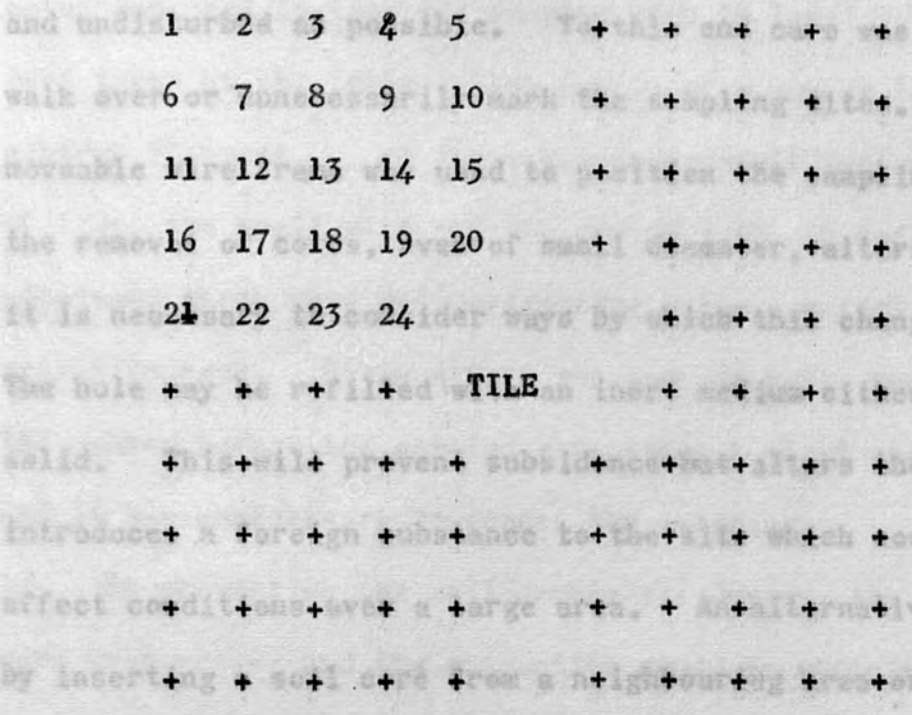
PART II. EXAMINATION OF FIELD POPULATIONS OF FOLSOMIA DISTINCTA AND THREE OTHER SPECIES OF COLLEMBOLA.

a) Introduction.

In order to try to relate the experiments on the population in the laboratory to field populations, a routine sampling programme was started in April, 1959 to last until March, 1961. Thirty six soil samples were taken from part of the grounds of Royal Holloway College on the fourth Tuesday of each calendar month. This programme was completed with the exception of December, 1959 and January, 1960, when one set of samples was taken on the first Tuesday in January. After March, 1960 the number of sampling stations was reduced from nine to three to permit the completion of other experiments.

The nine stations were distributed 55 feet apart in a 3x3 lattice in a patch of uniform grazed meadow described on pp. 115 . The centre of each station was marked by an anchored 6" sq. quarry tile. Around this, samples were taken on the intersection points of a 10 x 10 lattice. This lattice was divided into four areas each containing 24 sampling positions (Fig.5.1.). One position in each area was sampled each month giving a total of four samples from each station. The order in which the positions in each area were sampled was randomised using the table of random numbers given by Fisher and Yates (1949). Each sample consisted of a core of soil 4" long and the vegetation covering it. For extraction the core was divided into 1" lengths which fitted the small cylinder

Fig. 5.1. The layout of a sampling station.



The sampling positions in one area have been numbered.

The lattice lines of the other areas are marked.

All positions are 6 inches from their nearest neighbours.

extractor (p 107). Sampling to a depth of four inches ensured that the entire population of Isotomid Collembola was sampled.

While sampling, the intention was to leave the area as natural and undisturbed as possible. To this end care was taken not to walk over or unnecessarily mark the sampling sites. A moveable wire frame was used to position the sampling tool. As the removal of cores, even of small diameter, alters the environment, it is necessary to consider ways by which this change may be reduced. The hole may be refilled with an inert medium either particulate or solid. This will prevent subsidence but alters the drainage and introduces a foreign substance to the site which could materially affect conditions over a large area. An alternative is to refill by inserting a soil core from a neighbouring area or to replace the original core after the animals have been extracted. The former alternative introduces a population different to the one removed and may therefore make considerable changes. The latter introduces a vacuum into which the population remaining at the site will expand. However, this method was adopted during 1959 as the one least likely to cause undue change. During the summer and autumn of 1959 this was satisfactorily accomplished but when the soil became soft and moist during the winter and during 1960, the holes were found to be naturally eliminated after 2 days, before the cores could be replaced. No refilling seemed to be necessary in these conditions.

Apart from the routine programme, samples were taken for the

examination of the distribution over a small area. These samples were taken in a small square plot situated close to station 'E' during the second week of June, 1960. The 1" diameter corer was used to take 144 samples each 2" long. The samples were taken at the intersection points of a square lattice with centres 3" apart. As there was no rainfall during the first week of June, the small plot and the ground 3 ft. in each direction was moistened three days before sampling using a watering can with a very fine rose. Every effort was made to cover the area uniformly. The evening before the samples were taken a short shower occurred and it was unnecessary to repeat the watering.

By preventing the soil completely drying, the Collembola were kept active and the extraction would be efficient for all samples. Although 2" cores may be too long for extraction in the usual way, the results are quantitavely comparable and the number of animals extracted suggests that the method was satisfactory. Many protura were in fact extracted and the survival of the delicate animals is a good guide to the efficiency of the apparatus. Before extraction the percentage of the samplesarea covered by the main constituents of the vegetation was roughly estimated and the presence of other plants was noted. This proved easy to do because the vegetation was closely grazed and all constituents were in the same range of height. The measurements of physical factors by methods explained on p.112 were made on samples of the soil taken from the walls of the cavity left after the removal of each

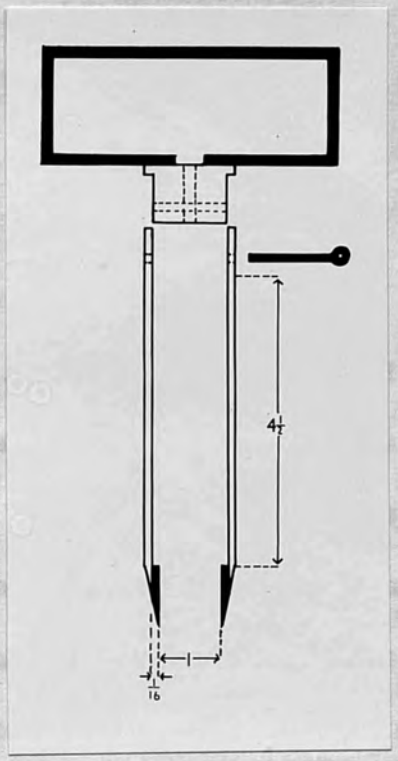
of the cores. These samples were taken to a depth of 2" with the sampling tool, half a core being obtained from each side of the hole.

Two other techniques, to examine the animals in situ, were attempted unsuccessfully. These were the sectioning of embedded soil as described by Haaløv (1953) and Minderman (1956) and the disection of frozen blocks of soil. Either of these techniques had they been successful would have permitted the measurement of the distance between neighbouring individuals. This measurement is considered to be most useful and important in the study of aggregation.

b) Soil Sampling Tool

The soil samples were taken from the meadow turf by means of a metal coring tool similar to that used by Macfadyen (1961) and previous private communication, Alexander and Jackson (1955). The body of the tool was of brass with a removable handle (Fig.5.2). The cutting edge was of hardened steel brazed to the brass and giving a ledge inside on which bakelite rings fitted. Soil samples up to 4" long could be obtained. In practice it was found that the rings became jammed in the tool and often the soil became compressed. For this reason the undisturbed cores were transferred into a rolled sheet of thin card instead of into bakelite rings. Bakelite half rings were placed around the soil after it was removed from the tool, and held together in pairs by elastic bands.

Fig.5.2 Soil Sampling Tool.



Black areas - steel.
Clear areas - brass.

The handle and body of the tool were held together by a steel pin passing through holes in each part.

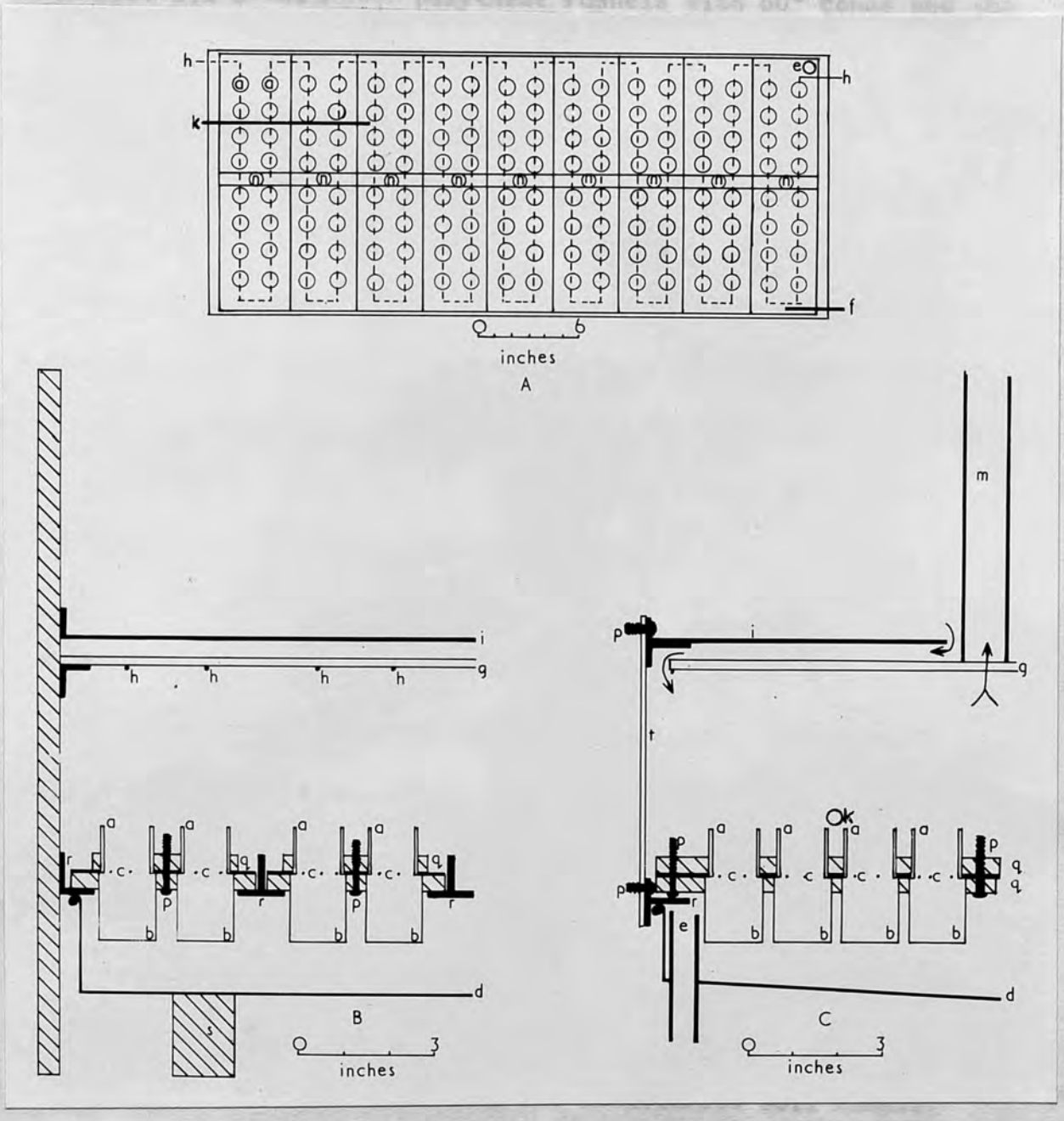
A sharp knife was used to separate the sections of the core. The sections were then inverted and placed in the trays of the extraction apparatus in that position. Thus the essential conditions for soil extraction were met, undisturbed and uncompressed core, inverted position and clean cut surfaces with the soil structure unaltered.

c) Extraction Apparatus for Field Work.

The essential apparatus for field studies was one with which to extract the animals from the soil. This type of apparatus is generally based on one of three principles;- hand sorting, flotation of the animals and sedimentation of the soil, or the emigration of the animals when conditions become unfavourable. The first two methods extract the entire population but are laborious when there are large numbers of samples to be examined. The flotation techniques generally do not distinguish living and recently dead animals and are difficult to use on soil containing much fine organic debris. The third principle, which is used for the Berlese funnel technique (Berlese, 1905) and Tullgren's modification (Tullgren, 1918), extracts only active individuals and for accurate quantitative work must be carefully controlled. This form of extraction apparatus requires little attention and is therefore suitable for use with large numbers of samples.. It was decided to adopt it for the present work.

Two versions of the Tullgren apparatus were made. The simpler

Fig. 5.3. The Tullgren apparatus for quantitative extraction of the soil.



A. Diagramatic Plan. B. Longitudinal Section. C. Transverse section.
Key:-
(a)Bakelite rings for soil samples,(b)aluminium canister for trapping animals,(c)wire mesh supporting the soil, (d)water bath, (e)outlet from water bath,(f)inlet to water bath, (g)asbestos inner roof,(h)750w. electric resistance element, (i)outer roof, (k) thermostat, (m)chimney, (n)chimney vents in asbestos roof, (p)screw bolts which carry wing nuts, (q)wooden shelves, (r)shelf supports, (s)water bath support, (t) removable front or back.

Hatched areas - wood.
Black areas - metal.

comprised six 6" diameter polythene funnels with 60° cones and the stems cut off to give an opening 1¼ inches diameter at the bottom. Each funnel was supported in a plywood framework 4" below a 15 watt electric light bulb. Below each funnel an aluminium staging suspended by elastic bands from the framework, supported a 2 inch diameter crystallising dish. The soil or litter samples were placed in a perforated zinc tray 6" diameter with 2" high walls. This tray stood in the funnel. The animals were trapped in the crystallising dishes in a 30% solution of alcohol, water containing a little Nipagin (methyl p - hydroxybenzoate) as anti-fungal agent, or in damp culture chambers.

This simple apparatus was used for qualitative preliminary investigations and occasionally for rough quantitative work. More precise estimations of the populations were made by using a small cylinder extractor with controlled air conditions, (Macfadyen (1961) and previous private communication.) This apparatus (Fig. 5.3) extracted 144 one inch diameter samples, each 1" long, at the same time and under uniform conditions. The bakelite tubes of 1" internal diameter contained the undisturbed soil sample. Each of these was supported by a ½" galvanised wire mesh immediately above an aluminium canister in which the animals were trapped. These canisters stood in a cold water bath through which tap water flowed continuously giving a temperature varying between 8° and 12°C. A solution in the canisters maintained a water saturated atmosphere below the soil and the water bath kept this cool. A current of

warm air flowed continuously over the samples. This air was warmed by a 750 watt electric resistance element spread over the asbestos roof. The temperature was controlled to approximately 35°C by a bimetallic thermostat set amongst the samples. Extraction was completed in about 5 days but usually the samples were left for 7 days.

To prevent predation and fungal growth in the extracted animal samples a 2% solution of potassium dichromate was used as the extraction fluid in the canisters. The use of dichromate permitted a saturated atmosphere to develop below the soil samples without any likelihood of toxic vapour effecting the emigration of the animals. This solution also had the advantage that the animals were killed in the canisters and were obtained in good condition even after 7 days. Macfadyen (1961) reports deleterious results due to the use of potassium dichromate in confined spaces but this did not occur in the preliminary testing with meadow soil samples and was never observed later. Solutions of Nipagin and Aretan (Methoxyl mercuric chloride) were tried as alternative extraction fluids but were not found entirely satisfactory in preventing fungal growth and did not preserve the animals.

d) Sorting.

After extraction of the animals from the soil the fluid in the canisters was filtered through a fine sintered glass plate. The material retained on the plate was washed with distilled water

then 50% alcohol and rinsed into specimen tubes with70% alcohol. Colloidal suspensions from the soil proved troublesome and increased the already long filtering time. This trouble was partly overcome by heating the fluid to 60°C for a few minutes prior to filtering. Although filter paper on a Buchner funnel gave quick filtration times some smaller individuals were trapped by the fibres and were not easily removed to the storage tubes and so this method was not adopted.

The contents of the specimen tubes were examined in small dishes under a low power stereoscopic binocular microscope. Two examinations were made, one over a white background and the second over a black ground. Thus it is almost certain that all animals were seen and the requisite ones removed with a fine pipette for identification and counting. When it was necessary to check the identification, sex or other features, specimens were mounted on slides with a methyl cellulose mounting medium. The formula for this, given by Baker and Wharton (1952), does not define the grade of methyl cellulose. By trial and error a medium of the best consistency was found using the recipe in Appendix XI. This medium proved satisfactory in use for three years. This has been confirmed by Goto and Lawrence* (private communication). Goto suggested that the optical qualities of the medium for low power observation might be improved by the addition of phenol.

* More recently Lawrence in a private communication has reported a tendency for the carbowax to separate after a number of years.

During 1960/1961 a record was made of the approximate size of the individuals when the routine samples were examined. As accurate measurements of a large number of individuals from the field showed that neither the overall length nor the length of various organs could be used as a criterion to distinguish the instars, the records were kept of the number of individuals occurring in three empirical size ranges. These ranges do not correspond to particular instars but roughly separate the juvenile individuals, under 40% of the full grown length (Agrell, 1941) and the very old individuals from the rest of the population. During routine examination separation of the ranges was effected by a comparison with sets of 10 individuals which provided a standard for each range. More accurate measurements and occasional checks were made with a micrometer eyepiece at a magnification of approximately 40x.

e) Environment Measurements.

Rainfall in the field was measured by means of a standard 4" diameter funnel with a collecting bottle set below ground level. Occasional 24 hour soil surface temperature readings were made with the small thermometer of a type used for whirling hygrometers and infrequently by a mercury in steel recording thermometer. The latter instrument was rarely available for use and only recorded temperature at one station. Daily maximum and minimum soil temperature readings were taken 2" below the surface by a constricted bore mercury maximum thermometer and an alcohol thermometer.

with a dumbbell minimum temperature marker. Both these thermometers operated horizontally on a wooden slide which fitted closely inside a 1" diameter bakelite tube. These tubes were 30" long and permanently set horizontally in the turf. One end opened into a cavity in the soil into which the projecting thermometer bulbs fitted. The bulbs were then 2" below the surface of the soil while the other end of the tube was exposed for the insertion of a wire probe with which the slide was withdrawn for reading. This method of inserting the maximum and minimum thermometers seems to be satisfactory for obtaining accurate temperature readings in undisturbed soil without recourse to exposed apparatus. The field in which these thermometers were placed was frequently occupied by a herd of heifers and by children and consequently it was not possible to leave exposed instruments there for long periods.

The moisture content of the soil was estimated by drying weighed 1" diameter cores of soil at 105°C to constant weight. The loss in weight has been expressed as a percentage of the dry weight and indirectly measures a variety of conditions including the soil structure.

Two methods have been used to estimate the organic content of the soil. The percentage of organic carbon was estimated by digesting the soil with Sodium dichromate and subsequent titration as suggested by Tinsley (1952). These measurements were made on the soil and the underground parts of plants passing through a 2 mm.

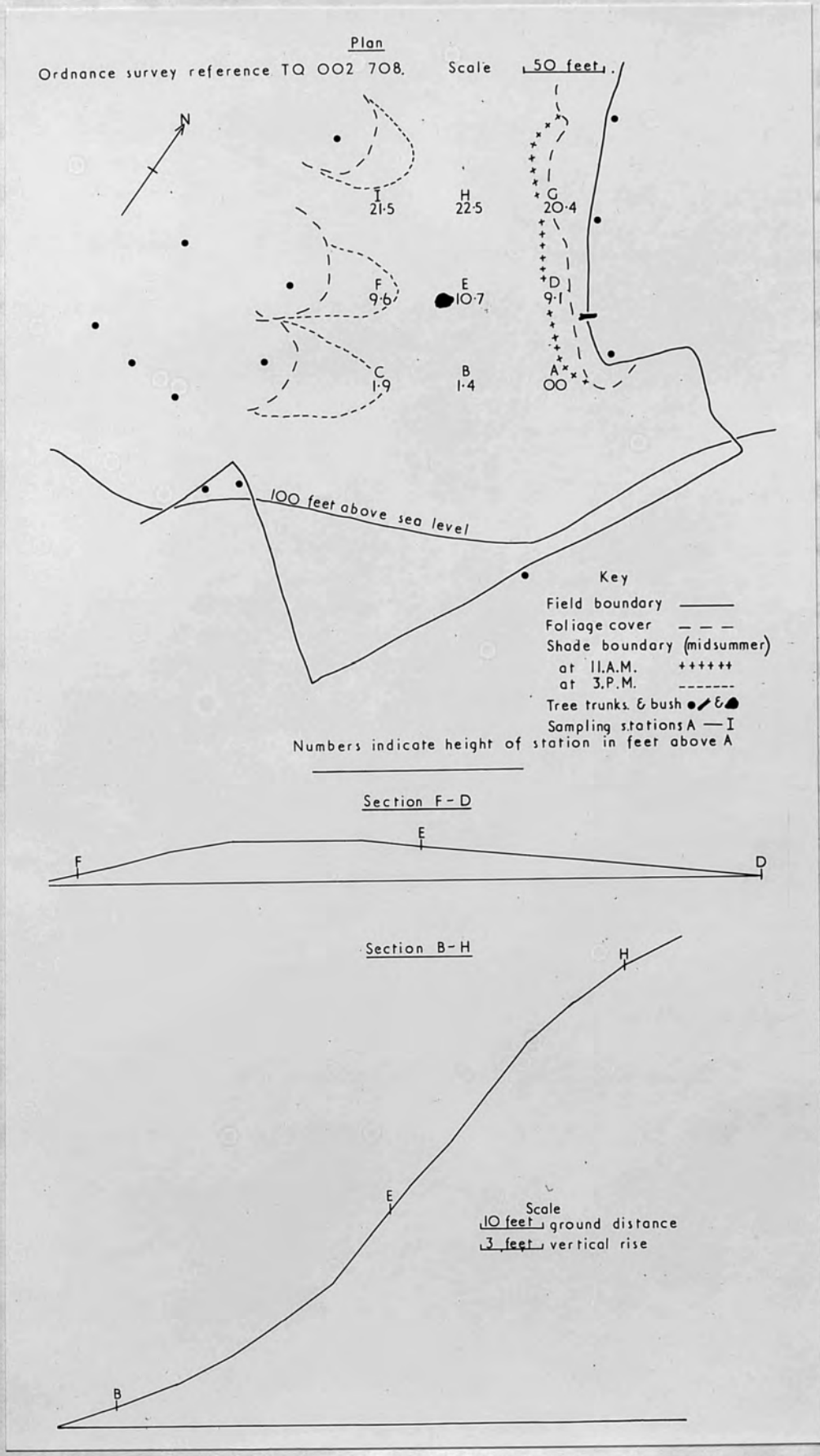
sieve. At other times a comparative estimate of root and organic carbon content was obtained as the loss of soil weight after ignition of air-dry soil together with subsurface vegetation in a furnace at 700°C. The loss in weight is again expressed as a percentage of the dry weight. As the meadow was unlimed and acid no allowance for carbonate was necessary.

The pH of soil samples was determined electrometrically on suspensions of 10 grms. of air-dry soil in 25 ml. of carbon dioxide free distilled water. The soil was thoroughly mixed with the water and allowed to settle for 10 minutes before measurements were taken.

Mechanical separation of stones and gravel was effected by dry and wet sieving through a sieve with round holes 2 mm. in diameter. No further mechanical analysis was made because the soil had a good crumb structure and the crumb size would be the mechanical factor affecting the animals and was judged to be the same in all samples.

Measurements of the vegetation of the areas from which samples were taken was by subjective estimation of the proportions of the various constituents on the soil cover taken with the sampling tool. Other measurements reported in the description of the meadow were made by personal observation on one or more days.

Fig.6.1. Plan and sections of the meadow from which samples were taken.



6. Description of the Meadow.

a) Topography, history and drainage.

The field work was carried out in a meadow on the South East corner of the grounds of Royal Holloway College. This part of the grounds is on the upper part of the London Clay. Neighbouring parts of the grounds are on the Claygate Pebble Beds. A plan of the relevant area of the meadow and its topography is shown in Fig.6.1. In general the area wass a smooth slope facing South East.

This meadow has been under grass since the beginning of the century and probably since 1869. Prior to this it was probably part of a small brickyard. The quantities of broken brick which were found 3 inches or deeper in the soil at the bottom of the slope, probably date from this period and it is possible that the topography is artificial in origin. More recently the meadow has been frequently grazed all year by a herd of about a dozen heifers. Apart from a selective herbicide spray applied annually in late April or early May and a light harrowing with a zigzag harrow at about the same time, there was no cultivation or chemical treatment of the meadow. The herbicide applied was a formulation of M.C.P.A. (4-chloro- 2 methylphenoxyacetic acid) Vigsol Blitzweed Super. This is a growth regulating compound with a more pronounced effect on broad leaf plants, causing their death. The harrowing might be expected to have its greater effect on animal distribution through the spreading of dung and removal of matted and dead grass.

The North Western stations were situated near the top of the slope whereas the South Eastern stations were sited at the bottom of the slope where the ground became level (Fig.6.1). The differences in height between these rows of stations is shown on Fig.6.1 . The stations in each row are at the most a couple of feet different in height. It was clear, especially after heavy rainfall, that the upper stations drained more rapidly than the lower ones. However this difference lasted only a few hours after which the entire area had drained. For this reason sampling was never undertaken in the rain nor until two hours had elapsed after rainfall. Rough estimation of moisture content of samples taken for the estimation of the animal populations never showed the lowest sites to be wetter than the others. On two occasions when more accurate estimations were made no important difference was apparent (Table 28).

Table 28.

The moisture content expressed as % of dry weight, of soil from the upper and lower sampling stations.

Date	Position	Depth	Number of Samples	Mean Moisture Content (Angular transformation)		Standard deviation of the mean
26/5/59	A	0-1"	5	30.22	(25.3)	0.88
	C	0-1"	5	30.82	(26.3)	1.11
	G	0-1"	5	31.06	(26.6)	1.15
	I	0-1"	5	30.76	(26.2)	0.68
9/7/59	B	0-1"	3	17.64	(9.2)	0.60
	B	1-2"	3	19.22	(10.8)	0.79
	H	0-1"	3	18.61	(10.2)	0.48
	H	1-2"	3	18.37	(9.9)	0.25

The corresponding percentage is given in parentheses.

b) Vegetation.

Only one bush occurred within the sampling area; this was a hawthorn, Crataegus oxycantha L., near station F. The nearest branches were about six feet from the station and it is unlikely that the bush affected the conditions there in any way. The bush's shadow did not cross the station at any time and being down hill of the station, little or no change in drainage would be caused. The nearest trees to the area were a row of oaks, Quercus sp along the field boundary about 33 ft. from stations A,D and G. The trees sheltered these stations from wind and sun but with the exception of station G probably did not otherwise affect the conditions. The longest branches of one of the trees over-hung station G and consequently some change in the precipitation would occur there. It is also likely that the roots would extend this far and may have altered the drainage. The fallen leaves from these and other trees were well scattered over the area by wind and, apart from a few small sheltered spots, were not found massed anywhere.

The main grasses at the stations were Agrostis stolifera.L and Festuca pratensis.Huds. Holcus lanatus L and Lolium perenne L, were also identified in the meadow. As few flowers developed on the grasses and the shoots were short through grazing identification of the grasses was difficult and two groups, broad leaved, which was usually Agrostis, and fine leaved usually Festuca were usually distinguished. Agrostis grass occurred over

the entire area but Festuca grass was sparse at sites A,B and C and seemed to be limited to the upper part of the slope where it occurred patchily, Moss, from which Rhytidiadelphus squarrosus (Hedw.), Pseudoscleropodium purum (Hedw.) and Brachythecium velutimum (Hedw.) were identified, was at sites D,E,G and H and was found in much smaller quantities at the other stations. The broad leaved plants were limited in variety and in frequency, presumably due to the use of M.C.P.A. as an herbicide. Towards Autumn growth of these plants was improved and the following were identified: Ajuga reptans.L. Trifolium medium, Huds, Crepis capillaris (L), Lotus corniculatus,L, Achillea millefolium, L. and Plantago sp. These were found with equal frequency in all parts of the area.

c) Soil.

All over the meadow the top 3 or 4 inches of soil were a grey loam, loose with a good crumb structure in the top inch but more compact below this. Under the grey loam at the top of the slope the soil is compact and lighter in colour with a few pebbles; at the bottom of the slope a slight reddish marbling is seen and broken brick is found in place of the pebbles. The surface soil is very fine with virtually no gravel particles not passing a 2 mm. sieve.

Organic carbon and pH measurements were made on soil from six sites in the field. At each site five equal samples were taken and thoroughly mixed. Soil was taken from the pooled sample for

analysis. The organic carbon percentages were determined by digesting the soil with Sodium dichromate. The results of this and of the pH measurements are given in Table 29.

Table 29.

The bulk density, organic carbon content and hydrogen ion concentration of soil taken from the sampling sites in April, 1961.

Site	Depth	Bulk density 2 samples	Organic Carbon content, % dry weight	pH
A	0-2"	1.07, 1.24 gm/cc	4.2	5.20
C	0-2"	.83, .87 gm/cc	4.4	5.20
E	0-2"	.95, .84 gm/cc	3.4	5.05
G	0-2"	1.05, .71 gm/cc	4.5	4.80
H	0-2"	1.14, .93 gm/cc	4.6	5.00
I	0-2"	1.18, 1.06 gm/cc	5.7	5.10

It is clear that the soil is acid over the whole area without marked differences between sites. It is interesting to note here that the pH of this meadow at about 5 is comparable to the unlimed grass plots at Rothamstead. The organic contents of the soil at 'E' and at 'I' seem slightly different from the others but the difference is npt marked and as no trends across the area are apparent it would seem that in general the organic content of the soil is even over the meadow. A notable feature is the trend for the soil to be more compressed towards the end of the shoulder, from stations 'G' to 'I'. This was observed while sampling and is demonstrated by the bulk density measurements. These measurements were made in two undisturbed, oven dried, samples from each site. There would also appear to be a tendency for firmer soil along the Northeastern edge, stations 'A' and 'G'. It is not possible to

state the cause of these trends. It may have been due to cultivation or animals tending to follow the field boundary and higher land. The trend from station G to I may be caused by the increased exposure of H and I to the wind and rain.

d) Other Conditions,

Differences in insolation at each station are difficult to measure but broadly three conditions of shade can be distinguished. The North Eastern stations A,D and G were shaded for part of the morning; 'G' was shaded longest but not after 11.a.m. The South Western stations C,F and I were shaded during the afternoon and the Central stations B,E and H were never shaded. At midday and each side of midday when the sun is warmest no stations were shaded. The shade patterns on Midsummer day are shown in Fig.6.1.

The effect of shelter from winds is again difficult to assess but some conclusions can be made. The scrub and trees on the North Eastern boundary provided protection to most of the area from east winds. The slope of the ground protected the area from the north winds but little protection from the south and west winds was provided although the former were partly deflected by the hedge on the South East boundary. It is concluded that station 'A' would be most protected with stations B,C,D and G partly protected.

The main effect of the wind on the soil would be a cooling and drying due to increased evaporation from the plants and soil. Thus any effect would tend to be shown by different maximum soil temperatures at stations B and H. It is interesting that in 1959

although little differences between these two positions was recorded, the maximum at 'B' was more frequently higher than at 'H', (Fig 6.2). During that summer the soil was dry nearly all the time and little evaporation would occur. The same feature was recorded during the summer of 1960 but the differences were much greater. During 1960 the soil was nearly always moist.

The minimum temperatures during 1959 show very little difference between the two positions, but in 1960 a lower temperature more often occurs near site 'B'. It seems likely that this is due to the topography of the field. A steep slope with a hedge at the bottom is conducive to the formation of a frost pocket and it seems that this occurred to a limited extent. When 24 hour readings were made the differences in tenperature between stations was not more than 1.5°C. A typical set of readings for a clear and an overcast day and night are shown in Fig.6.3.

e) Fauna.

Animals likely to affect the distribution of Collembola were considered in relation to the stations. The effect of mole hills on the site was very obvious. These were more frequent on the level ground at the bottom of the slope but did not encroach on any sampling stations. The presence of ants, mostly Lasius flavus (F), was obvious in the soil samples but seemed equally prevalent at all stations. Usually one in four samples contained one or a few ants. More rarely, in about one out of every

15 samples, ants and their larvae would be found. The movements of the cattle were watched and it became obvious that although grazing occurred over the entire area, the cattle rested more frequently in the sheltered areas by the Eastern boundary or at the bottom of the slope. The effect of this and the probable excess of urine could not be assessed. However observations on the patches of dung suggested that though there might be more of these on the level at the bottom of the slope, there was little variation over the area with the sampling stations.

Larger soil invertebrates, beetle larvae, centipedes, millipedes and earthworms were not usually obtained from the routine extraction of soil samples, although the smaller forms of the arthropods and enchytraeid worms were occasionally found in samples from every station. None of these animals seemed to show preference for any particular station. Mites, especially oribatids and gamasids, were by far the most common group of soil fauna extracted and the distribution of these was noticeably uneven over the area. Protura and wingless thrips also showed a marked unevenness in distribution and although frequently extracted were not common. The extraction of protura is taken as an indication that the extraction apparatus was efficient and that delicate animals were not killed prior to leaving the soil.

As well as the four species of Isotomid Collembola the more active Sminthurid and Entomobryid forms were commonly collected from the upper subsample of each core, and the subterranean forms

Onychiurus sp and Tulbergia sp were found mainly in the deeper cores. The subterranean species showed a preference for the lower stations being most common at station 'B'. However as they apparently occurred at depths greater than four inches the entire population was not sampled.

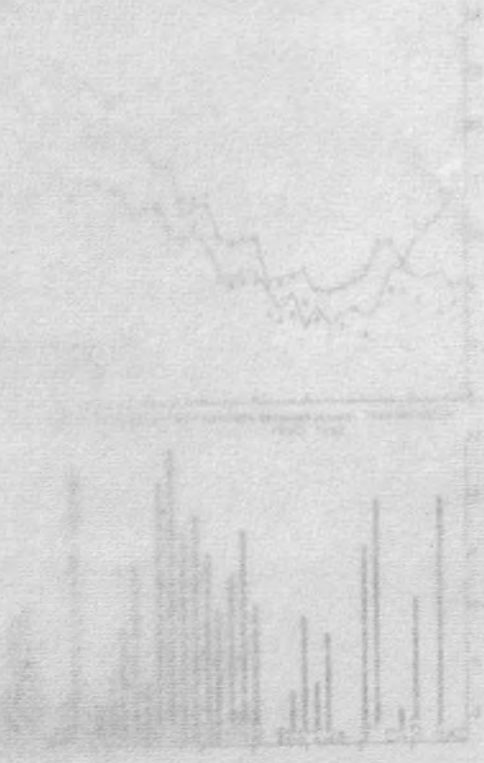
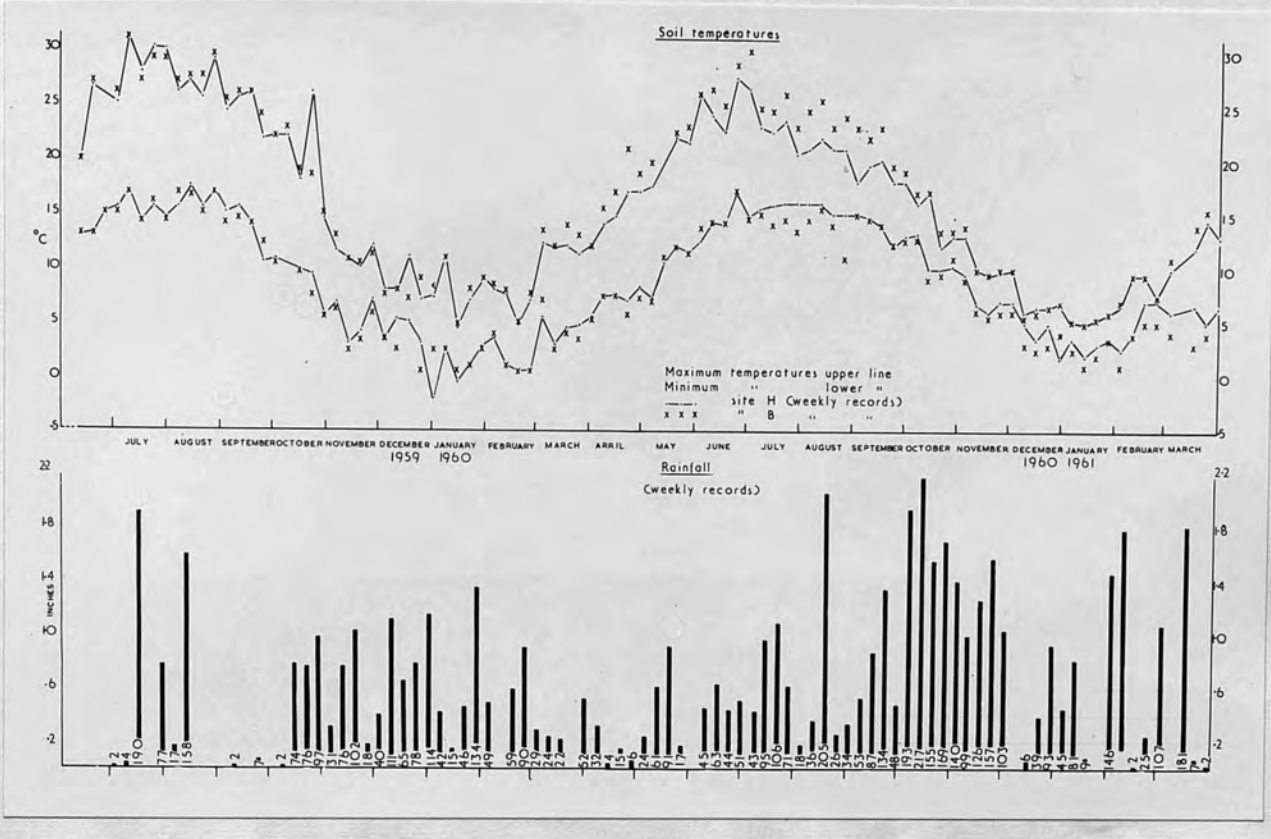
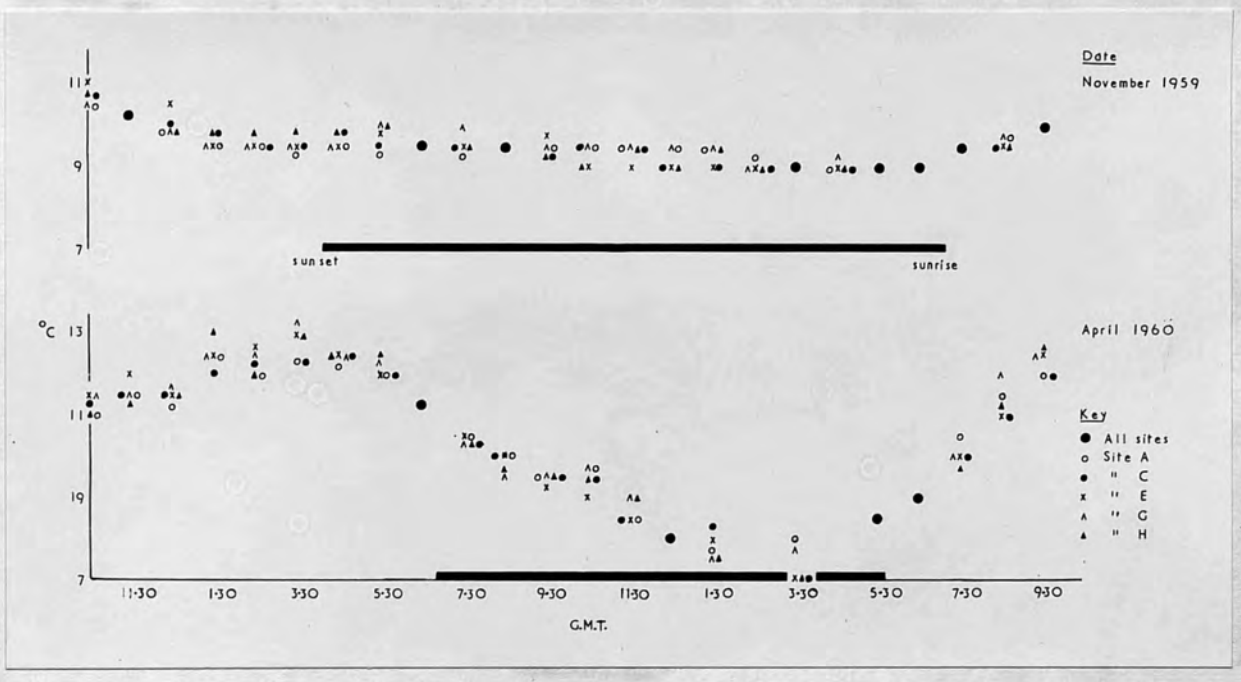


Fig.6.2. Soil Temperatures (graph) and Rainfall (histogram) records for the experimental meadow.



Weekly minimum and maximum temperatures at two sites from the 2nd week in June, 1959 until the last week in March, 1961 are shown. Rainfall is shown as weekly totals with the amount in hundredths of inches noted at the base of each histogram. The record is complete from the beginning of June, 1959 until the end of March, 1961.

Fig.6.3. The temperature of the soil surface at five stations in the meadow.



Readings were taken for 24 hours. The upper set were made during an overcast period and the lower set when the days were sunny and the nights clear. No wind was present during either period. The dark band indicates the period between sunset and sunrise.

7. Variations in Population.

a) Monthly changes in total population.

The samples taken during the period between April, 1959 and March, 1960 cannot be regarded as providing a usual picture of the monthly changes in the populations of the four species of Collembola. The extreme dryness of the early and late summer in 1959 provided conditions not normally encountered in this area and obviously detrimental to the species under study. Neither can the following year until March 1961 be regarded as average as at no time was the surface of the ground completely dry for more than a few days and no droughts occurred (Table 30).

Table 30.

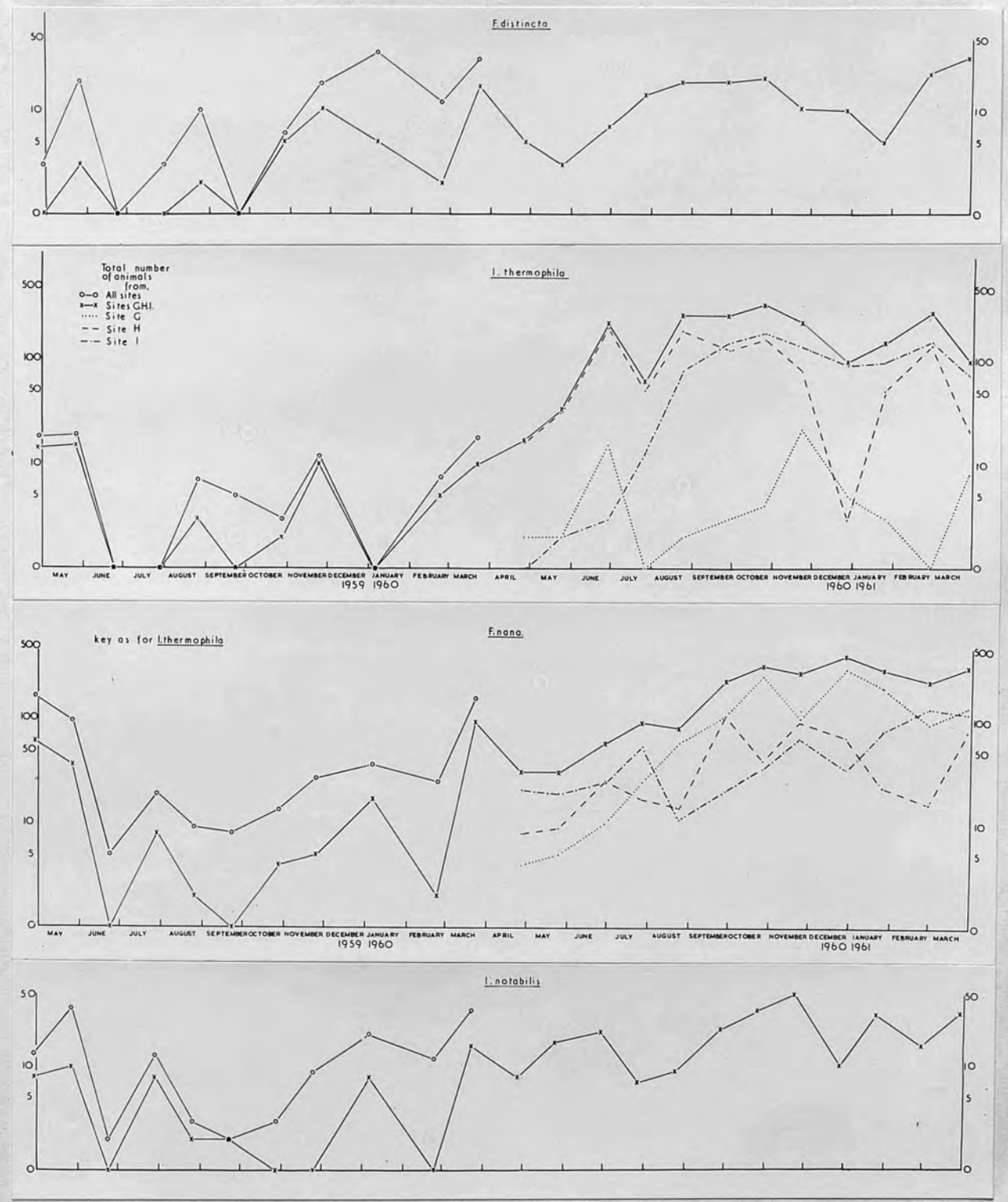
The Summer rainfall in 1959 and 1960.

	1959	1960
June	0.00 inches	1.67 inches
July	2.73 "	3.15 "
August	1.75 "	2.85 "
September	0.09 "	3.08 "

The maximum and minimum soil temperatures near station 'B' during the two years were much the same (Fig 6.2.). An important difference was the tendency for the maximum soil temperature to be lower and the minimum to be higher near station 'H' than near station 'B' during July, August and September of the second year. The reasons for this have been discuesed on pp 120 .

In general during the year April, 1959 - March, 1960 all the species showed high populations in Spring and early Winter with low

Fig.7.1. The numbers of the four species of Collembola extracted from the monthly soil samples.



Thirty six 1" diameter samples, from nine stations, were taken each month except December for the first year: twelve samples from three stations were taken for the second year. The vertical scale is logarithmic.

populations during the summer and late winter (Fig. 7.1.). The populations were all much lower than was expected from the results of a preliminary survey of the grounds made during the Autumn of 1958. The lack of rain during June and early July considerably reduced the active populations of all the species but it is notable that some Folsomia nana and Isotoma notabilis were active enough in June to be extracted. Similarly these two species recovered rapidly enough for some animals to be obtained, especially at stations G,H and I, in July while the other two species did not reach this state until August. A repetition of this situation had been expected in September but was not shown, possibly due to the lower temperatures at the end of September and beginning of October.

The same pattern of survival was found in a laboratory experiment with the naturally dry turf taken from the field in June after two weeks of complete drought. A patch of turf two feet by two feet and two inches thick was lifted from an area between stations D and E. This was cut into nine sods, six of which were trimmed to fit the zinc holders of the simple Tulgren funnel. Three of these sods were inverted and immediately placed over the funnels: The other three were sprayed with a mist of water, inverted and placed over funnels. The set of funnels was then enclosed with polythene sheeting under which damp pads of cotten wool were placed to keep the atmosphere saturated for 12 hours before the

heat was turned on. The final three sods were sprayed and stood in a moist atmosphere for one week at 20°C before being trimmed, placed over the funnels and extracted. Table 31 shows the numbers of Folsomia nana and Isotoma notabilis extracted from each sod.

Table 31.

The numbers of Folsomia nana and Isotoma notabilis extracted from treated sods of dry turf.

	Isotoma notabilis			Folsomia nana		
Treatment	Replication			Replication		
Kept 12 hours in moist air	0	0	0	0	0	0
Sprayed, kept 12 hours in moist air	23	9	2	14	15	2
Sprayed, kept 7 days in moist air	3	2	7	16	11	24

No specimen of either I. thermophila or F. distincta were found in any sample.

The form of extracting apparatus used depends on the assumption that the animals move to maintain a position in moist and cool conditions. The soil is dried slowly from the top, ideally causing an even gradient through the sample to the sieve through which the animals fall. Therefore animals which remain inactive in order to withstand dry conditions or for any other reason will not be collected because they are unlikely to follow the gradient. However if conditions are so improved that any living animals are activated they will be extracted from the soil. This is considered to be the explanation for the difference between the first

and second treatments of Table 31. The third treatment was included to attempt to hatch any eggs present in the soil. It is particularly notable that adult or near adult individuals of two species were present in the soil and viable after prolonged desiccation. This suggests that in their natural environment Collembola are able to withstand extremely dry conditions.

The experiment was repeated with dry turf at the end of September but on this occasion there was no difference between the numbers of each species collected from the different treatments.

From these experiments and the field sampling data it seems that F. nana and I. notabilis are more able to withstand dry conditions than F. distincta or I. thermophila. This may be accomplished by remaining quiescent in small pores between particles of the soil but could not be confirmed by observation. It would also seem that the drought in September was not so severe as that in June probably because heavy dews and a very small shower prevented the soil becoming very dry.

During the second year of sampling extremely moist conditions were prevalent and at no time was the soil dry when sampled. This means that all animals would probably be active and consequently the sample extractions are representative of the total populations present. Sampling was at only three stations G,H and I so to enable comparison between the two years, the monthly totals from these stations have been plotted for both years in Fig.7.1. It was soon clear that the variability of the numbers in the samples

was such that only two species F. nana and I. thermophila were present in sufficient numbers to permit detailed examination of the sample data.

The general trend during 1960 for both species was one of increasing numbers. It is clear that summer temperatures did not retard this increase in numbers. It is therefore likely that the dryness which usually accompanies the higher temperatures causes the drop in Collembola populations frequently observed in summer.

The monthly populations of F. nana are shown by an analysis of variance on the logarithmically transformed data to differ significantly during the year (Appendix Table XIII) and this is probably entirely due to the upward trend. The population of I. thermophila also changed during the year but as the population at each station behaves differently the pattern is somewhat obscured (Fig 7.1 and Appendix Table XIII). Although slower in starting to recover from the previous adverse conditions than F. nana the population of I. thermophila increases more rapidly once conditions become favourable reaching a level which is perhaps normal for this area by the end of June. The population of F. nana increases rapidly until September or October although a peak is shown in June. A sign indicative that the populations have reached maximum level is the reduction in numbers during the winter and increase in the spring to a peak below that of the previous year. This is particularly shown by the populations of I. thermophila. Examination of the graphs for the other two species (Fig.7.1.) does

not show a trend of the same order during the year. A slight tendency to increase may be shown by I. notabilis but this is uncertain due to the great variability of the data.

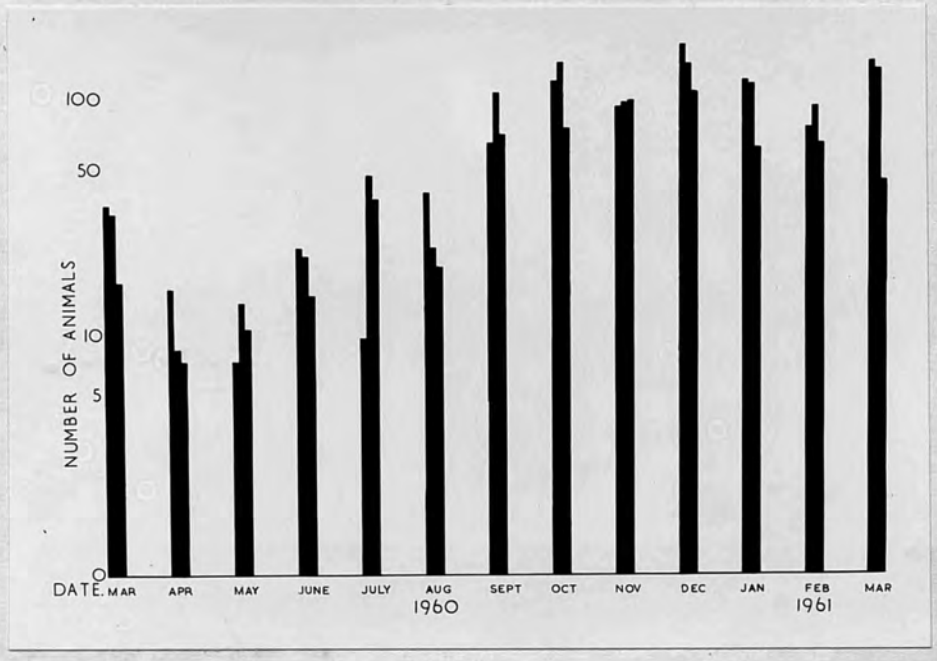
During 1960 - 1961 the numbers of each species in the samples were recorded in the three empirical size ranges, previously mentioned on p. 111 . It is apparent that the relative proportions of each group (Figs. 7.2. 7.3) do not change systematically during the year. As sampling was at monthly intervals and this period is approximately that of the life cycle, detailed variation in the constitution of the population will not be shown. However it is clear that reproduction occurs throughout the year and it seems that the reduction in numbers is probably due to loss or mortality of animals of all ages and not to a reduction of fertility. If the latter had been the case a relatively larger decrease in the number of young animals would have been expected.

b) Macrodistribution.

The differences between the conditions at the stations have been discussed. (pp 116).

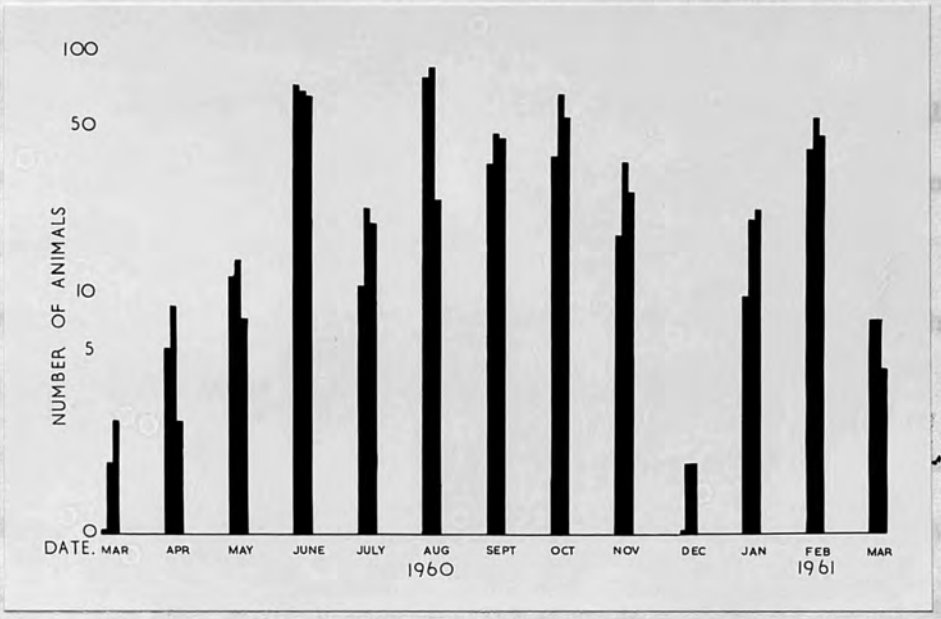
The total number of each species collected from each station by the routine sampling during the two years is shown in Fig.7.4. The pattern generally shown during the first year is one of low populations on the southern stations of the area, Station 'A' being particularly poor for all species. The only condition to which these low populations can be linked would seem to be the extra shelter afforded to this part of the area. This it would seem

Fig. 7.2. The relative proportion found each month of small, medium and large individuals of F. nana from stations G, H, and I.

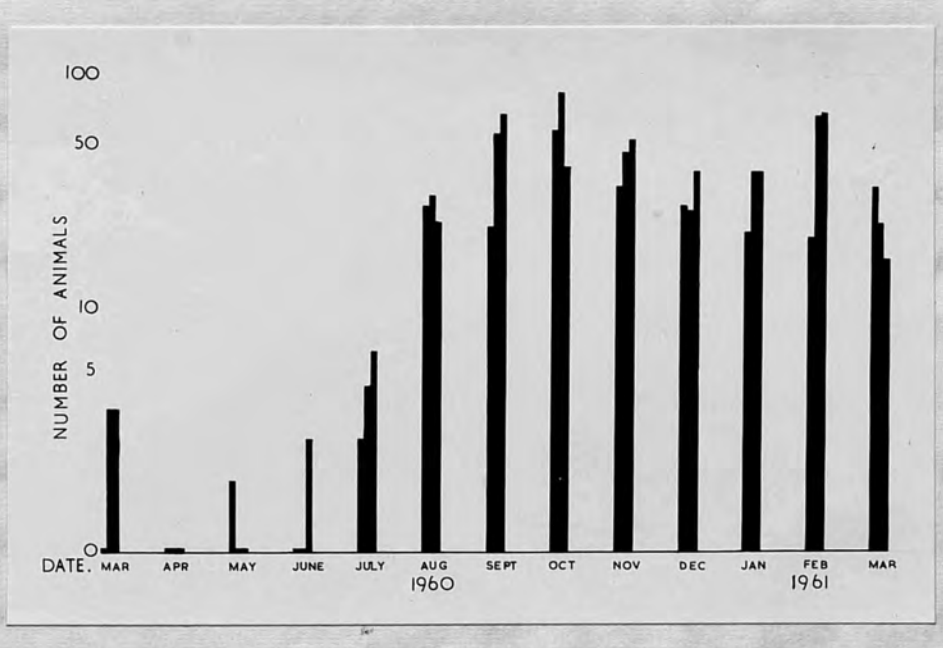


The vertical scale is logarithmic. The first, second and third columns from the left in each set represent the number of small, medium and large individuals respectively.

Fig.7.3. The relative proportions found each month of small, medium and large individuals of I. thermophila



a) From station H.



b) From station I.

The vertical scale is logarithmic. The first, second and third columns from the left in each set represent the number of small, medium and large individuals respectively.

causes less evaporation of moisture and therefore a rather higher daytime soil temperatures (p.) due to insolation. Some curious anomalies between the distribution of the species are shown: Stations D,F, and G at which three of the species are moderately successful is unsuitable for I.thermophila, station 'E' seems to be less suitable for F. distincta whilst it gives the greatest populations of I,notabilis and F. nana. No explanation for these anomalies can be offered from the facts available.

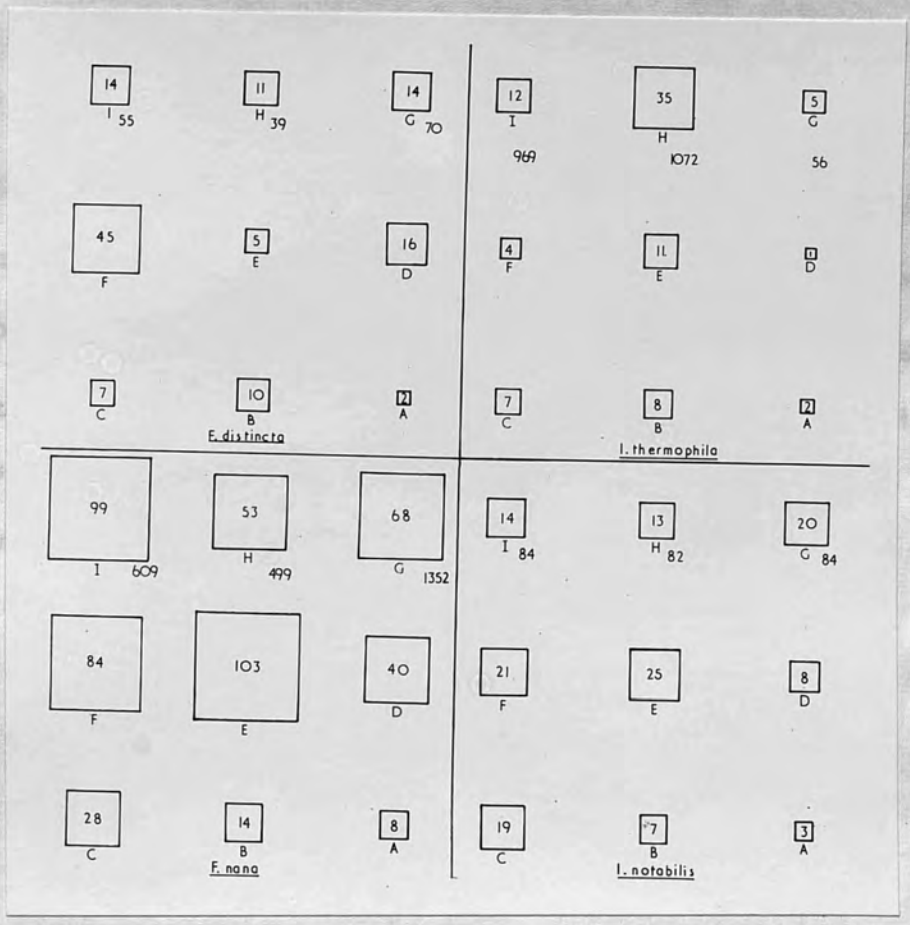
The number of I. notabilis and F. distincta collected from stations G, H and I during the second year confirm the opinion gained from the first year's data, that there is little difference between these stations with regard to their suitability for each of these species.

I. thermophila and F. nana were the most abundant species in the second year. An analysis of variance on the logarithmically transformed data (Appendix Table XIII) shows there to be, as expected, a significant difference between the numbers at each station for both species. Whereas station 'I' seemed most satisfactory for F. nana in the dry year, station 'G' had very much higher populations in the wet second year. This might be explained by the greater exposure of station I maintaining better conditions during the dry year, whereas this was not necessary in the wet year. The time of the growth of the population of F. nana at each station was not significantly different (Fig. 7.1.). From this figure it is also clear that the greatest population increase at

station 'G' was during the autumn and winter, the population being equal again to that at the other stations in the spring of 1961. This might also be explained by the greater exposure of the stations H and I being less beneficial during the winter months.

The picture of I. thermophila is altogether different. By the analysis it has been demonstrated that the total number of animals for the year from each station differs significantly and also that the time and rate of change of the population at each station differs significantly. Examination of the graphs (Figs 7.1. 7.4) makes these points clear for it is obvious that station 'G' is poor during the whole year whereas stations H and I are equally good overall. However the population at station 'I' does not build up to a peak until later in the summer whereas that at 'H' reaches a peak by June. The population at station 'H' also shows a greater drop in the winter than that at 'I'. It is possible that the increased exposure of stations H and I accounts for the greater numbers of I. thermophila at these stations. The difference between the population growth at these stations may be due to greater numbers surviving the dry summer at station 'H' and providing a nucleus for rapid population growth during 1960. This large survival population and the larger drop in numbers in the winter of 1960/1961 might be due to more exposure at station 'H' which is higher than station 'I', but it seems unlikely that there

Fig. 7.4. The number of each species collected at each station from 12 months routine samples.



The letters designate the site. The figures in the square represent the numbers during the period from April, 1959 until March, 1960, and the area of the square is proportionate to that number. The figures outside the square, at G, H and I, represent the number taken from April, 1960 until March, 1961.

could be a great difference between these two stations.

It is interesting to note these two species, F. nana and I. thermophila are so different in their requirements for high populations that their numbers are complementary (Fig 7.4). The totals of the two species collected at stations G,H and I from April, 1960 until March, 1961 are 1408, 1571 and 1578 respectively. At station 'G' F. nana and at station 'H', I thermophila are most abundant but at station 'I' the relative numbers change during the year. F. nana was highest initially but the great increase in in numbers of I. thermophila on recovery from the dry summer gave it superiority in numbers by the end of the year.

8. Microdistribution.

a) Introduction.

It has been shown that the populations at the different stations were different and, that I. thermophila behaved differently in regard to population growth at each station. Under these circumstances all the samples each month from the different stations cannot be pooled for the examination of aggregation. In view of the resulting limited number of samples in each unit a review of the published methods for the study of aggregation was made in order to find a method applicable to these results.

During the years many indices have been suggested for measuring the degree or the significance of aggregation mostly derived from the relationship of the frequency, mean and variance of the data conforming to a Poisson distribution. The most used of these indices are shown in Table 32, (p140).

Curtis and McIntosh (1950) have discussed and tested the indices prior to 1950 with the exception of Fisher's and Cole's. It was clearly established that all are dependent upon the area of the sample when the species is aggregated although most are independent when the data shows a random dispersal. Skellam (1952) suggests that $\frac{s^2}{\bar{x}}$ is independent of the size of the population when the data shows a random distribution; however it is not independent of the size of the population if the species is aggregated. Similarly 'K' is not always dependent on the number of animals, (Bliss and Owen 1958) and its efficiency relies on the assumption

Table 32.

Author	Date	Index	Value for species which is dispersed	
			At random	In aggregation
Gleason	1920	$\frac{f}{n}$	$1-\left(\frac{n-1}{n}\right)^{\Sigma x}$	$>\left(1-\left(\frac{n-1}{n}\right)^{\Sigma x}\right)$
McGinnies	1934	$\frac{\bar{x}}{n}$	1	>1
Fisher	1930	$\frac{\Sigma\left(x-\bar{x}\right)^2}{\bar{x}}$	Varies as χ^2 with N-1 degrees of freedom.	
Clapham	1936	$\frac{s^2}{\bar{x}}$	1	>1
Fracker & Brischle	1944	$\frac{\bar{x}-n}{n^2}$	0.02	>0.02
Cole	1946	$\frac{x-G}{G-(\Sigma x-1)}$	0	>0 → 1.0
Whitford	1949	$\frac{x\,N}{100f^2}$	0.024	
Waters	1959	$*k = \frac{s^2-\bar{x}}{\bar{x}^2}$	Varies from 0 - ∞ higher values indicate aggregation	
Taylor	1961	$b = \frac{\log s^2 - \log a}{\log \bar{x}}$	1	>1

Where x is the number of animals per sample.
n is the expected mean number of animals if the distribution is Poissonian.
f is the number of samples in which the species is represented.
N is the number of samples.
a is a variable dependent on the population and sampling.
*k is the positive exponent parameter of the negative binomial distribution.
s^2 is, as usual, an estimate of the variance.
G is the number of groups.

that the data fits either a Poisson, when K = 0, or a negative binomial distribution.

Of the indices listed, the statistical significance of deviations from a random distribution can be estimated for that of Fisher, from a table of a χ^2 values, and for that of Clapham, Blackman (1942) suggested that a deviation of $2\sqrt{\frac{2N}{(N-1)^2}}$ of Clapham's index from unity is significant of a non random distribution but Greig Smith (1952) suggests a more correct form for the standard deviation is $\sqrt{\frac{2}{N-1}}$ This he attributes to M.S.Bartlett. The 'variance'upon mean' and'chi squared' indices are in principle the same beca use the variance is estimated by $\frac{\Sigma(x-\bar{x})^2}{N-1}$. It is of interest that the 'variance upon mean' values must therefore follow the Q distribution attributed to Lexis by Fisher (1930).

The basic law for the'variance upon mean'ratio is:- $s^2 = a\bar{x}$ in which 'a' is the index for aggregation. This index is dependent upon the population size and a simple step to eliminate this dependence is to change the basic law to $s^2 = a\bar{x}^2$. For theoretical distribution it is now found that the index, still'a', is stabilized and seems independent of the population size. This is only so if it is assumed that the same proportionate division of the animals between the samples indicates an equal degree of aggregation. Taylor (1961) developed the law further:-$s^2 = a\bar{x}^b$ 'b' is apparently a true measure of aggregation but the meaning of variations in 'a' is uncertain and may be caused by population and sampling factors. As an index, 'b' cannot be used to estimate the

aggregation in a single set of samples for it cannot be calculated but it does permit a number of sets to be compared as in the following pages. This is a major advance over all the other indices with the possible exception of 'k' for which a common 'K' can be calculated (Bliss and Owen, 1958).

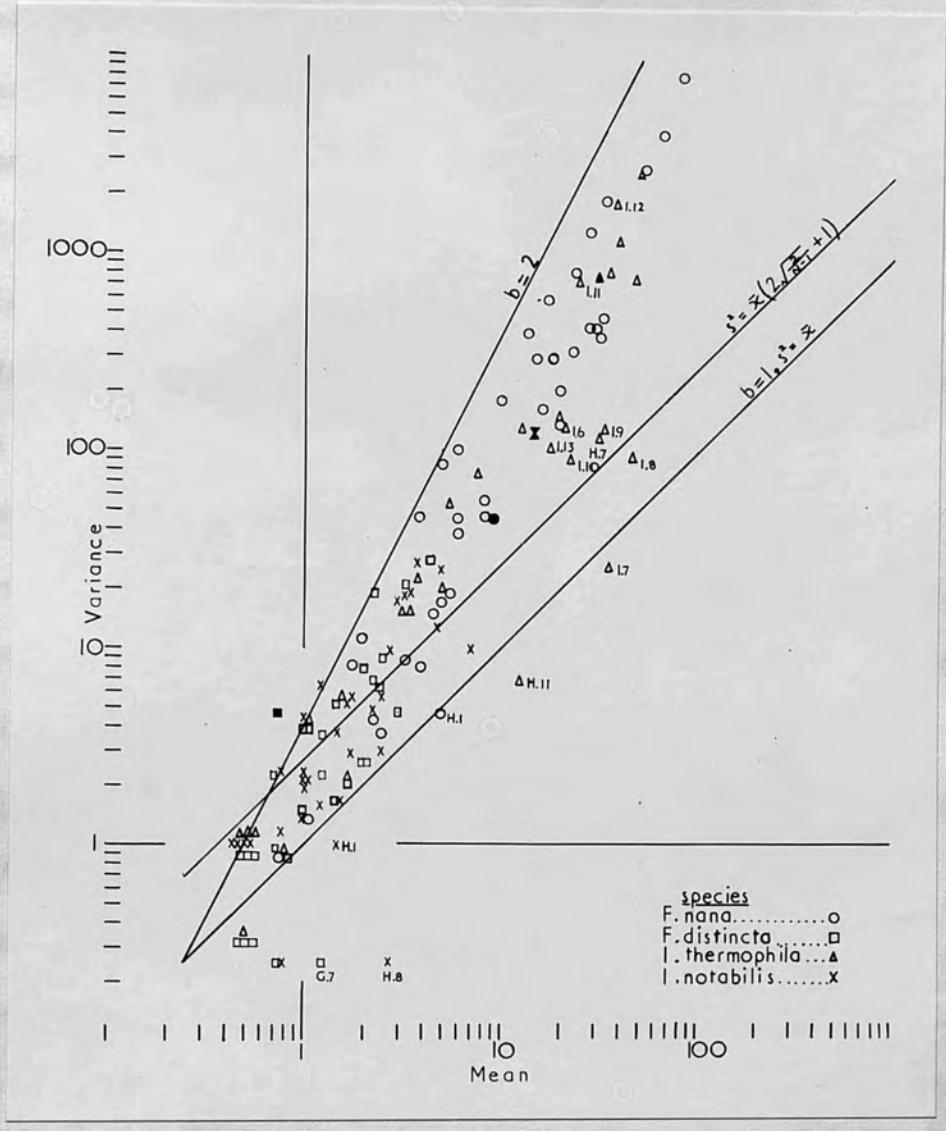
At this point it seems appropriate to examine the concept of aggregation from the natural rather than the statistical aspect. The relationship between the indices of aggregation and sample size is clearly caused by the scale of distribution being measured. The largest scale of distribution is the geographical with which I am not concerned here. Near the lower end of the scale, the changes in population over an essentially uniform habitat are measured as shown in this work by the differences between sites. In still smaller units the distribution of individuals within the area and then the distribution of individuals within groups is measured. Therefore should the distribution be different at the different scales its form as estimated from samples will naturally change with the sample size. Romel (1926, 1930) introduced this idea when he assumed that individuals were concentrated into patches which were regularly distributed. Small samples then demonstrate an aggregated distribution, whereas large ones a regular distribution. An intermediate sample the "Homogenitäts-grenze" would give a random distribution. This type of measurement for the scale of pattern has been more used for

botanical distributions and has been developed by Greig Smith (1961) and Kershaw (1961).

The relationship between density of population and aggregation is more complex and depends much on the behaviour of the species. If the species is of low motility the density in the centres at which reproduction is occurring will be dependent mainly upon the rate of increasein the population. In these circumstances an index of aggregation measuring in effect the difference in density between high and low density areas will increase with the population until a density is reached above which the species cannot survive.

If a factor causing reduction in population is operating particularly in the areas of high density a less aggregated distribution would result as the population decreases. However, if a general mortality, proportioned to the population, occurs over the entire area the level of aggregation surely remains the same although most indices will decrease as the overall population level does. This is clearly shown in Taylor's (1961) examples in which the $\frac{s^2}{\bar{x}}$ ratio decreases with the population but 'b' remains constant. If the species is of high motility aggregation will be mainly obtained or maintained by attraction between the individuals. In these circumstances the density of population is likely to remain close to that preferred by the species regardless of the population size, except at very low populations.

Fig.8.1. The microdistribution index 'b' for each species each month from March,1960 until March,1961.



Identification of erratic points is by station letter and month number. (March 1960 is 1, March 1961 is 13). The solid black points are those based on the 144 samples taken from the small plot in June. Both scales are logarithmic.

It would be natural in these circumstances for a measure of aggregation to tend to decrease as the population increases especially at higher populations when the distribution could become almost even over the entire area.

b). Comparison of aggregation in the four species.

In Fig.8.1. the points plotted correspond to the distribution of the total number of each species at each site each month. The points differing from the general trend have been identified as to month and site.

In general it is clear that all four species behave in the same way at low populations, up to a mean of 10 animals per sample, with the points lying in a broad band around a trend with 'b' a little less than 2. Above this population level only F. nana and I. thermophila can be considered. It is immediately clear that F. nana follows the same trend up to very high populations and that under certain circumstances I. thermophila behaves in the same way. However the latter species shows a peculiar set of points with variance in the region of 100 and means of around 30. These points have been identified as regards station and month as also have the two exceptional points immediately below. It is interesting to note that three of the most extreme points are from data from station I in three consequtive months, September, October and November. Further the points for August and December lie nearer to the general trend but still below it. The significance of this

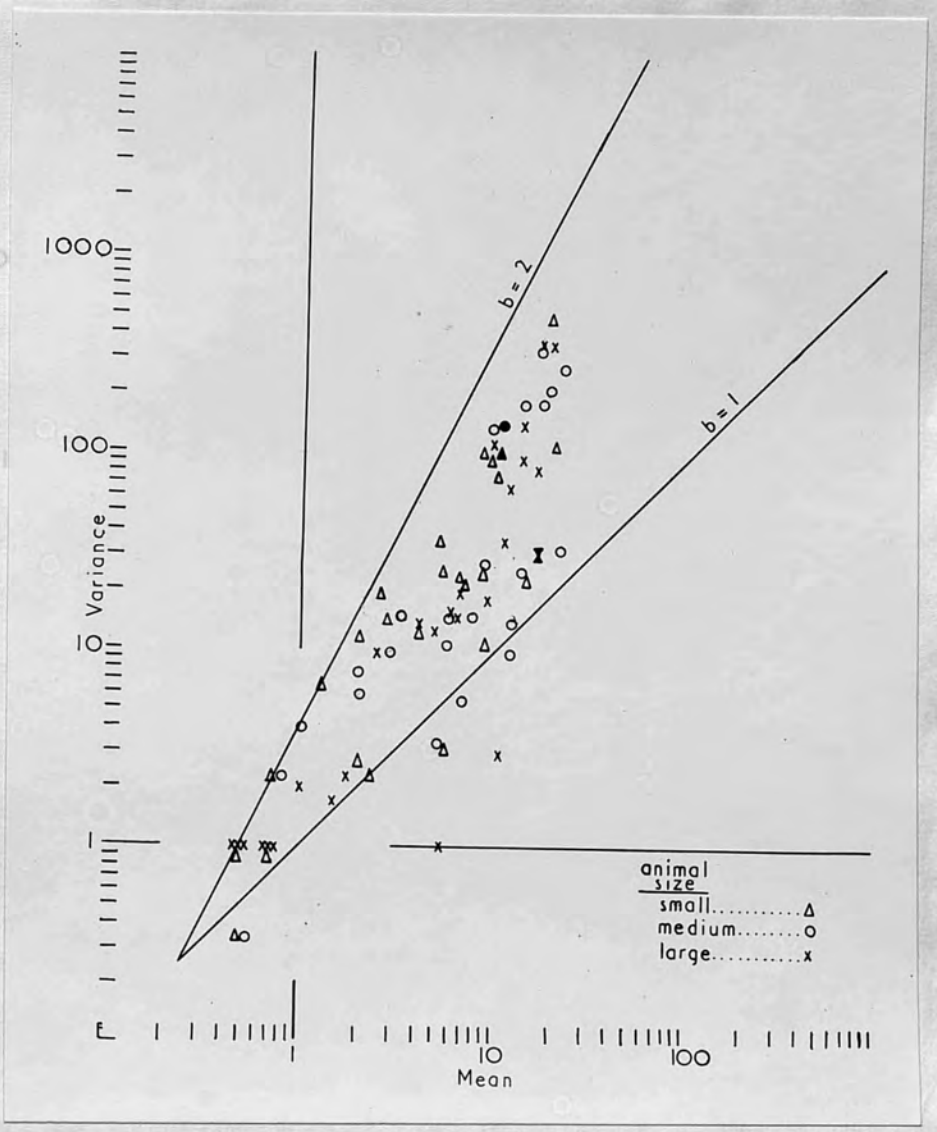
departure from the normal behaviour is difficult to explain. During July and August the population was rising rapidly and was at high levels during September, October and November. The levels, however, are comparable to those found in the following February, at which time the data conforms well to the general trend. It is possible that perhaps the warmer soil temperatures combined with the higher rainfall increased the motility of the species to such an extent that the distribution became nearer to a random one. It is also possible that a control of fecundity exercised by the population density as has been shown to occur with F. distincta, reduces the regeneration in the centres of aggregation, and so reduced the pattern of distribution. The possibility of immigration causing the high numbers cannot be eliminated but does not appear likely from the general information about the field populations. The other extreme points cannot be explained by higher motility on the information available and it is possible that these are the extremes to be expected from data with such a wide variation.

The points for March, April and May, 1960 and March. 1961 which might have been influenced by harrowing or spraying are not different from the general trend. It is clear/therefore that neither factor caused a more even distribution than might have been expected under normal circumstances.

c) Comparison of aggregation in young and old individuals.

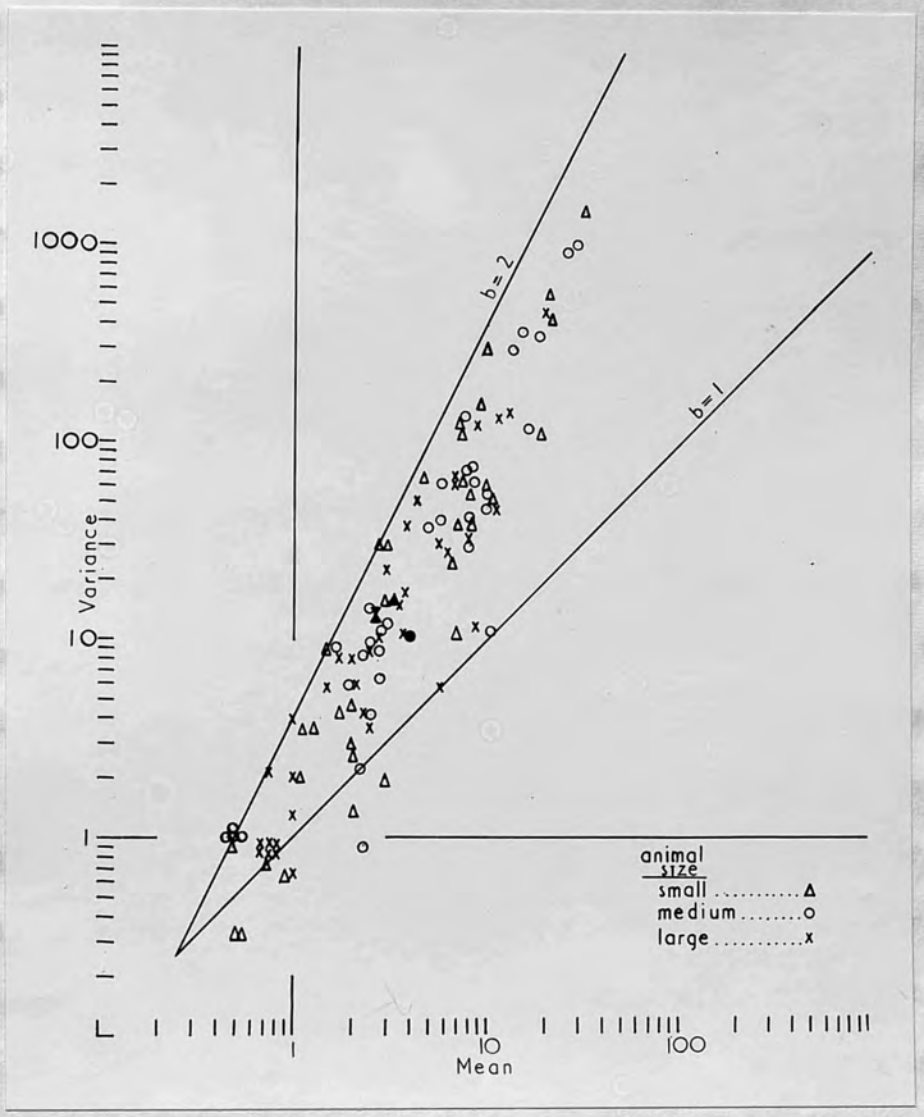
The data for F. nana and I. thermophila is sufficiently large

Fig.8.2. The microdistribution index 'b' for each size range of I.thermophila each month from March,1960 until March,1961.



Solid black points are those based on the 34 samples from the small plot.
Both scales are logarithmic.

Fig.8.3. The microdistribution index 'b' for each size range of F.nana each month from March,1960 until March,1961.



Solid black points are those based upon the 34 samples from the small plot.
Both scales are logarithmic.

to permit separation into the different size ranges. The data may then be plotted as in Figs. 8.2.,8.3., in which the points represent the distribution of one size range at each station in each month. Again an extremely wide variation around the general trend is obvious and is somewhat more pronounced for I.thermophila than for F. nana. For neither species is there any obvious difference between the distributions at each station or for each age group.

The tendency of each species to aggregate was further demonstrated by the samples taken from the small patch. A comparison of the frequency of samples in classes according to the number of individuals present, is made with that expected of a random distribution in the Appendix Table XIV. The comparison is made with 144 samples when the total of each species per sample is utilised and with 34 samples when the size ranges are separated. The small, probably juvenile, individuals are distinguished from the medium and large ranges which,for the comparisons, are not recorded separately. There is less than a 5% chance that the distribution of either I. thermophila or F. nana is random, regardless of whether the size ranges are examined separately or together. The distribution of I. notabilis agrees in general with the previous ones but the large size are most probably randomly dispersed. The size ranges of F. distincta have not been tested separately as the numbers of samples in the higher class of population frequency are too small but examination of the total figures shows that the species

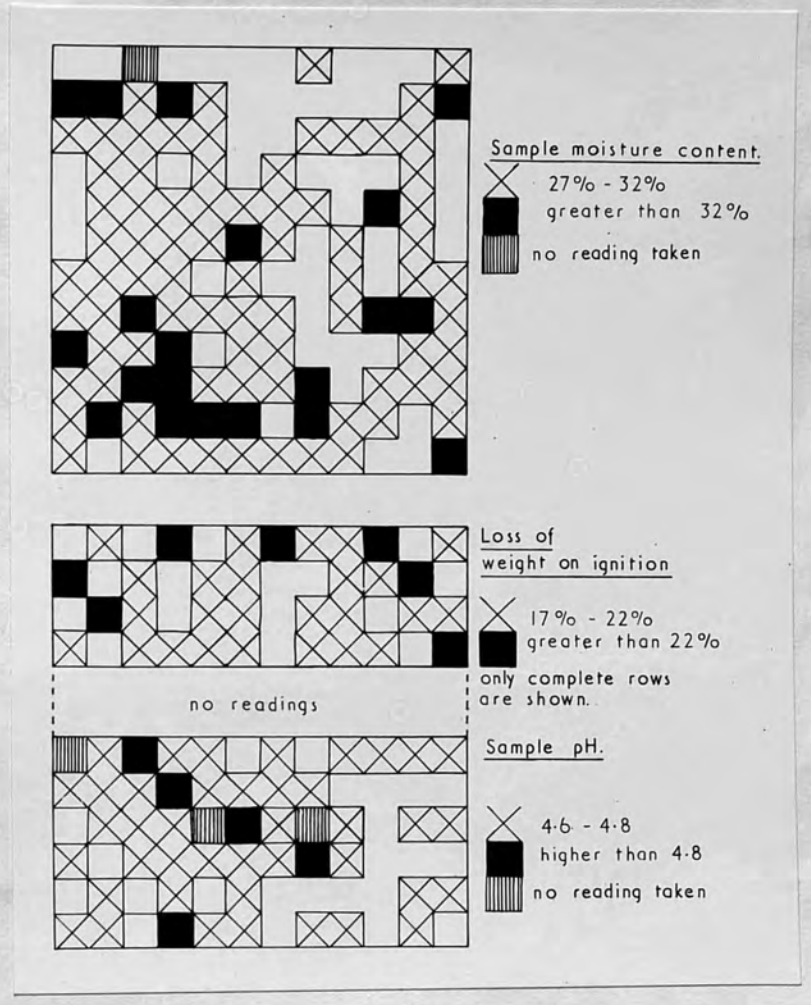
as a whole is aggregated. The mean and variance values have been plotted in Figs.8.1.,8.2.,8.3., and a close agreement to the trend, shown by the other points, is found although the maximum variance possible is very much higher when 34 or 144 samples are included for the estimation of variance.

d) Association between the environment and Collembola.

It is well known that the soil surface is not a uniform environment and that aggregation may be due to attraction or repulsion of the individuals by biological or physical conditions of the soil. Consequently the number of each of the four species of Collembola in the samples from the small plot have been examined for association with these conditions. Clearly all possible conditions could not be incorporated in the examination nor could they all be measured. Therefore three generalised physical or chemical criteria have been measured. Each is dependent on a wide range of conditions. Examination of the association with any biological condition has been confined to the effect of each species upon the others and the effect of the major constituents of the surface vegetation. Plans of the distribution of all these measurements over the small plot are given in Fig. 8.4.,8.5.,8.6.,

The measurements of the soil condition were made on samples taken adjacent to each of the samples extracted to obtain the animals. The moisture content was measured and then half the samples were used for measuring the loss of weight on ignition and

Fig.8.4. The distribution of the soil moisture, and loss of weight on ignition and pH over the area of the small plot.



Each square represents an area, 3 inches square. The level of the factor is given by a 1" diameter sample from the centre of the square.

Fig. 8.5. The distribution of the minor constituents of the vegetation over the area of the small plot.

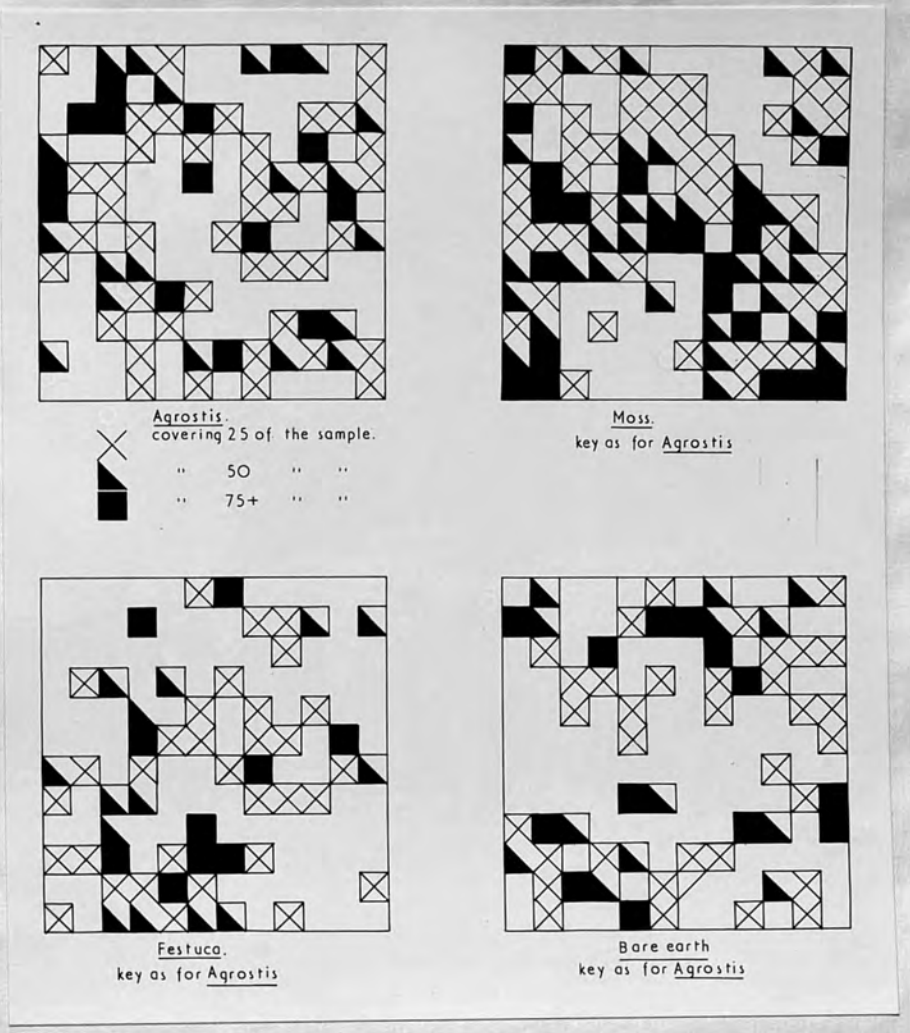
			P						B		
B			P			B	B	B		B	
				B		B	B	B	H	B	P
	B	B				B					
			B	B		B					
						B		B		B	
B		B_L	H	H	B			B		B_H	H
				B	B_H	H		B	B	H	
			H		L		B			B	
B			H		B				B		B_L
		H		B	H		B	H			
	H	H	B			L	B	B			

Species present.

B....Bellis perenne. H....Holcus lanatus.
L....Lotus corniculatus. P....Plantago sp.

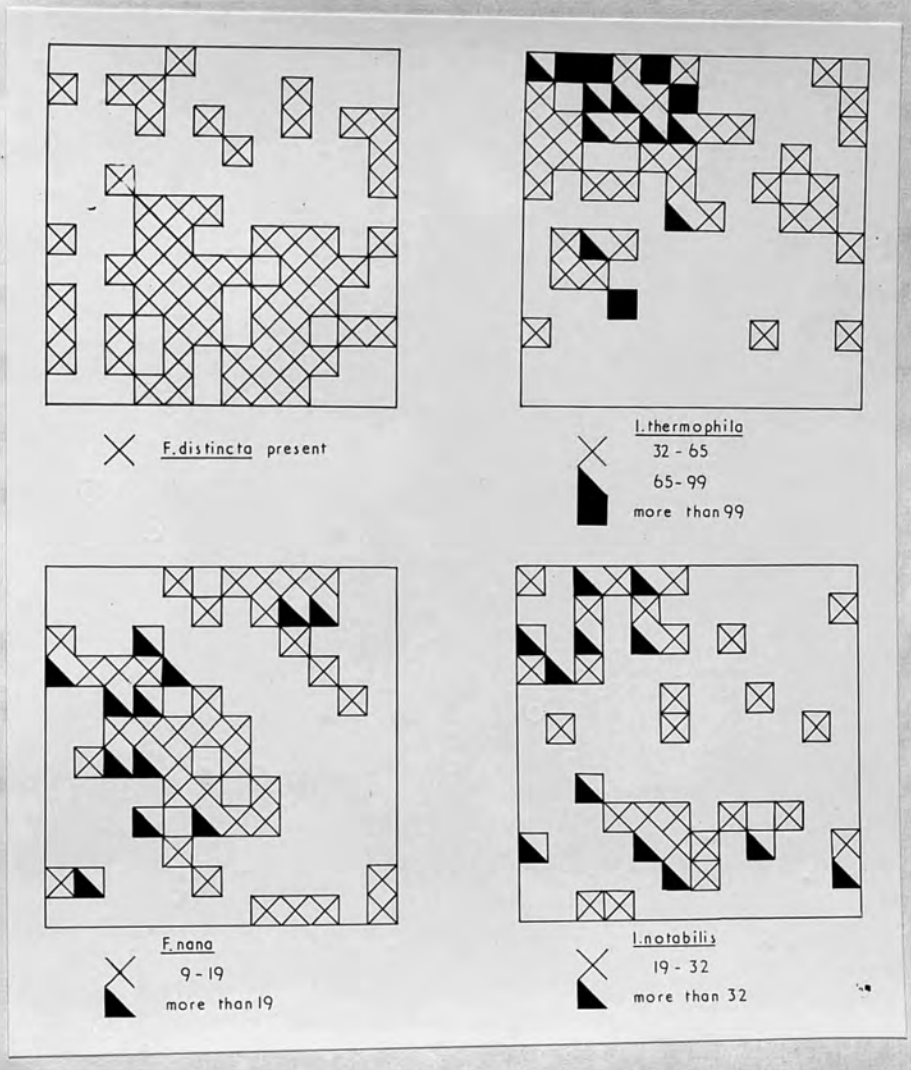
Each square represents an area, 3 inches square. The level of the factor is given by a 1" diameter sample from the centre of the square.

Fig. 8.6. The distribution of the four major constituents of of the vegetation over the area of the small plot.



Each square represents an area 3" square. The level of the factor is given by a 1" diameter sample from the centre of the square.

Fig. 8.7. The distribution of the four species of Collembola over the area of the small plot.



Each square represents an area 3 inches square. The level of the factor is given by a 1" diameter sample from the centre of the square.

the other half for measuring the hydrogen ion concentration of the soil. Linear correlation between the measurements and the numbers of Collembola has been sought by calculating either 'r', the correlation coefficient, or 'd' a non parametric measure of the difference between two groups, whichever is appropriate for the data. The correlation coefficient is calculated either from the standard formulae (Brownlee, 1949) in which case the Collembola counts were transformed to $\log_{10}$ (count + 1) or in the case of the moisture content by a non parametric ranking method.(Quenouille 1959, §§ 24). The latter was used as a rapid test to try the data prior to the application of a more exact test if necessary. However, the coefficient which over estimates 'r' showed conclusively that there was no association. The value 'd' was used as a means of comparing the mean of the values of one measure falling in each class of the other measure when the latter measurement was conveniently divided into two classes. The counts of F. distincta are so low that it is sensible to divide the samples into two classes, those with and those without F. distincta. The environmental measure is then ranked and the mean rank for each class compared by the method given by Quenouille (1959) §§ 14. The difference between the rank means 'd' is tested as a normal deviate with a standard deviation of $\sqrt{\frac{T}{6}\left(\frac{1}{M_1} + \frac{1}{M_2}\right)}$ when T is the total rank score and M_1 and M_2 are the numbers of observations in each class. The results are shown in Appendix Table XV and are

summarised in Table 33.

Table 33.

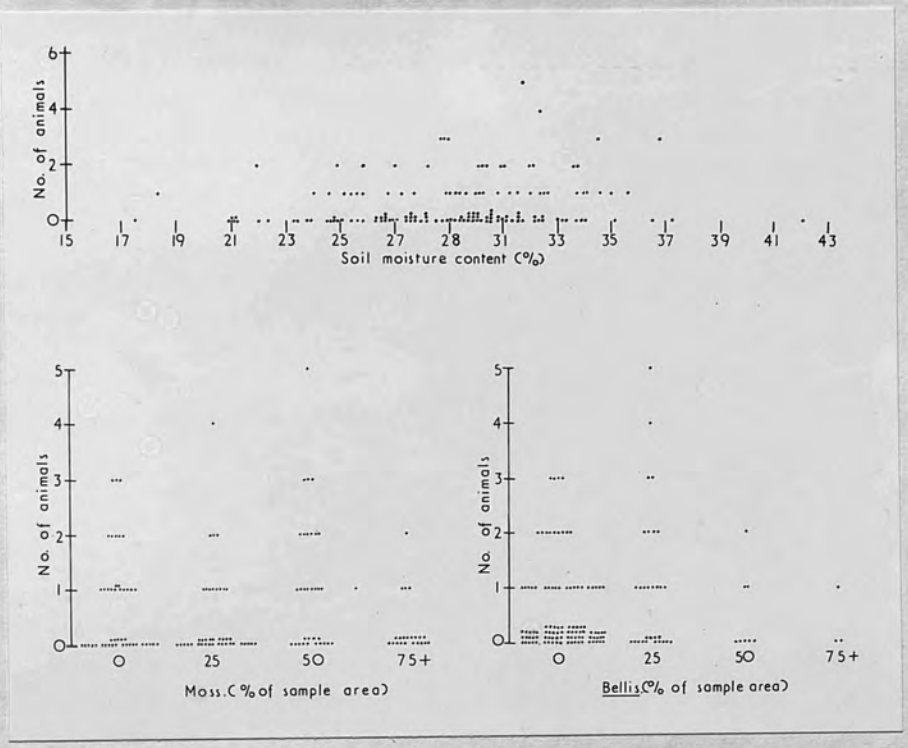
Association between the Collembola and physical factors.

	'd' values		Correlation coefficient (r) †						
	F.distincta		I.thermophila		F.nana		I.notabilis		
Loss on ignition	small 3.1	large 2.4	small 0.33*	large 0.24	small 0.14	large 0.22	small 0.24	large 0.10	N 52
standard error of 'd'	5.0	5.6							
Moisture content	15.8*	2.7	0.05	0.07	0.10	0.04	0.09	0.05	143
standard error of 'd'	7.2	10.5							
pH	4.7	10.3	-0.46***	0.04	0.09	-0.01	0.24*	-0.13	69
standard error of 'd'	4.8	7.5							

† r is estimated by the ranking test of Monotonic Association Quenouille 1959 §§ 24.
Significant values are marked thus:- * $p \leqslant 0.05$
** $p \leqslant 0.01$
*** $p \leqslant 0.001$

It is only the small animals which are in any way associated with any soil condition. Of these the small F. distincta are more frequently present in samples of greater moisture content but the trend when plotted (Fig. 8.8) is not great. The small I.thermophila are probably positively associated with loss on ignition, most likely with the organic content of the soil, and are certainly present in greater numbers in soils of lower pH values. This is rather surprising considering the general acidity of the soil. However these two correlations may be reflections of the same association, possibly with the presence of organic material. The

Fig.8.8. The relationship between the numbers of small F. distincta and the three environmental factors with which significant associations were found.



small I.notabilis are probably present in larger numbers in samples with higher pH values but the correlation is not marked.

In general the number of the four species of Collembola in the sample was not associated with the vegetation. This is shown in Appendix Table XVI and summarised in Table 34, 'd' values have been calculated where appropriate, otherwise the data has been divided into groups suitable for contingency tests. This form of examination is likely to show any kind of association. It is therefore particularly valuable for examining association between animals and vegetation because maximum numbers of the animal species may be expected to occur at an intermediate level of vegetation cover. More or less of the vegetation providing sub-optimal conditions.

The only associations indicated in Table 34 are between small F. distincta and moss and between the same individuals and Bellis both these associations are plotted in Fig.8.8. The association with moss is not at all clear as there tends to be more samples with the species present at both 0% and 50% of moss than one would expect. It would therefore seem that this maybe only a chance relationship and not a trend. The same may be explained for the association with Bellis, but in this case the limitations of the data may disguise any trend as there do appear to be more samples with daisies and small F. distincta than one would expect.

Table 34.

Association between the Collembola and vegetation.

χ^2 values (number of degrees of freedom given in parenthesis).

	F.distincta		I.thermophila		F.nana		I.notabilis	
	small	large	small	large	small	large	small	large
	(2)	(2)	(4)	(6)	(4)	(6)	(4)	(6)
Festuca	2.10	1.52	5.02	12.10	0.91	4.26	6.95	2.54
	(2)	(2)	(4)	(6)	(6)	(8)	(4)	(6)
Agrostis	1.76	1.78	7.77	6.53	1.79	5.53	3.99	9.66
	(2)	(2)	(10)	(8)	(6)	(8)	(6)	(8)
Moss	**11.52	1.03	5.22	3.49	7.76	14.31	7.93	5.15
	(2)	(2)	(6)	(6)	(6)	(8)	(4)	(6)
Bare earth	0.28	2.17	9.50	3.15	2.24	7.26	7.58	6.19

	χ^2_1		'd' values						Standard error of 'd'
Bellis	*3.82	0.04	4.0	8.3	4.0	9.0	3.8	11.7	7.7
Holcus	0.07	0.86	8.5	16.8	2.2	16.7	11.5	6.9	11.4
Dead grass	0.72	0.07	10.6	3.2	7.6	10.0	3.4	6.1	10.0

Significant values are marked thus:-

** $p \leqslant 0.01$

* $p \leqslant 0.05$

None of the correlations demonstrated, between a soil condition and a group of Collembola, suggest that these groups might be positively correlated. A negative association between small I.thermophila and small I.notabilis might be expected on account of their correlations with the hydrogen ion content of the soil; in fact, none was found. The only other correlations to be expected are between the small and large animals of the same species. This would arise from 'family' grouping and failure of the animals to disperse from the oviposition sites. Correlation between the counts of all groups are given in Appendix Table XVII and are summarised in Table 35. Correlation is assessed either by the correlation coefficient, 'd' values or, in the case of the two groups of F. distincta, by a contingency test.

The probability of correlation between small and large individuals of all species is very high as would be expected. However it is surprising that association apparently occurs between the species I. thermophila, F. nana and I. notabilis whatever their size. There are only three combinations of these which are not significant, small I. thermophila with large I. notabilis and with large F. nana and small F. nana with large I. notabilis. It must be noted that the small individuals of I. thermophila showed a high degree of association with the soil pH which was not shown by the other groups.

Table 35.

Association between species of Collembola.

Species	'd' values		Correlation Coefficient (r) (142 degrees of freedom)				
	F.distincta		I.thermophila		F.nana		I.notabilis
	small	large	small	large	small	large	small
I.notabilis large	1.9	28.2**	0.04	0.24**	0.09	0.27**	0.29***
I.notabilis small	0.7	15.0	0.36***	0.23**	0.33***	0.26**	
F.nana large	1.0	24.2*	0.12	0.26**	0.42***		
F.nana small	8.4	11.9	0.19*	0.28***			
I.thermophila large	9.7	22.8*	0.63***				
I.thermophila small	12.4	11.6					
F.distincta large	** +						
Standard error of 'd'	7.22	10.56					

All values are positive coefficients.
+ is based on a 2x2 contingency table $\chi^2_{[1]} = 7.88$ $p = 0.005$.
Significant associations are marked thus:-

*** $p \leq 0.001$
** $p \leq 0.01$
* $p \leq 0.05$

F. distincta presents a rather different picture. The small individuals are not significantly associated with any of the other species; here again it is noted that they showed significant association with other factors. The large F. distincta are however associated with the large individuals of the other species but not with small individuals. It can be concluded from this that this species shows a definite tendency to associate with older individuals

of other species as it becomes older although it may not oviposit with them. It would seem that the other species associate with each other and probably oviposit together otherwise it is unlikely that the young would be as closely associated as they appear to be.

DISCUSSION

There has been little research into the causes of aggregation of animals and none so far as is known, with respect to micro-arthropods of the soil. Glasgow (1938), Macfadyen (1957), Hughes (1958) and Haarløv (1960) are probably the only ones to have considered the aggregation of Collembola. Glasgow examined the distribution of species of Onychiurus and Tullbergia and found them aggregated. Macfadyen noted that the distribution of F. quadrioculata a species very similar to F. nana, was random; so also did Haarløv. The latter author also found that I. notabilis was randomly distributed. Hughes however reported that a species of Folsomia was aggregated. All four species examined in the field, F. distincta, F. nana, I. notabilis, and I. thermophila were found to be aggregated. The distribution of the animals may depend upon the habitat and upon the size of the population but this cannot be detected unless the populations are high.

The work of Allee (1931) may be used as the basis in describing the aggregations. Clearly, with soil arthropods the aggregation cannot be colonial, i.e. with organic connections. The aggregation may be heterotypical, i.e. composed of several species; indeed the significant correlations between the numbers of each species in the samples from the small plot suggest this. However, for simplicity, only associations of the same species, homotypical, have been considered. Two types of aggregation are

then possible; related, in which the individuals composing the aggregations are of the same parentage, and unrelated, in which the individuals are from different parents. Both types may arise through active or passive means and because of social or environmental forces. The value of these terms is only as a means of breaking the theories about the cause of aggregation into units which provide working hypotheses. Thus for an aggregation to be caused by active participation, the gathering of the animals into one spot must be due to a change of activity or direction following stimulation. A passive aggregation is opposite, in that the individuals concerned have taken no part in forming the aggregation. If an aggregation is due to a social force the position of individuals is only accounted for by the present or previous position of others. On the other hand aggregation due to an environmental force depends upon the movement or imprisonment of the individuals by environmental elements, or stimuli, other than that of the animals themselves.

Although regular sampling of the field populations revealed a tendency to aggregate naturally, and showed that the level of aggregation remained constant for most of the year, nothing can be deduced from this as to the cause of the aggregations. However in the laboratory it was shown that there is a strong tendency for F. distincta particularly in the 4th and 5th instars to form aggregations under uniform environmental conditions. The principal factor causing the aggregation seemed to be some

form of chemo-reception of the individuals or of a substance left by them on the floor of the chamber. This accords with the observations of Klingler (1959) as to the attractiveness to F. candida of a source of carbon dioxide and it is possible that the respiration of an individual provides such a source of carbon dioxide. The conditioning of the floor however requires the presence of a different chemical stimulus. Observations of the movement and turning behaviour of an individual suggest that the collection of the animals is due either to a directional perception of another individual causing the animal to remain in one place as long as the stimulus is refreshed by realignment or to frequent turning in the presence of the stimulus restraining the individual from moving away:- klinokinesis.

These results provide a case for the active formation of groups but observations on the oviposition of F. distincta suggest that passive aggregation is also likely. The eggs are naturally laid in clumps and several parents will add eggs to the same clump. If there is no reason for the hatchlings to leave the vicinity of the clump an aggregation will be formed. If one assumes that juvenile individuals are those less than 40 per cent of the full grown length (Agrell 1941) then individuals of the small size range in the field samples represent the juvenile portion of the population. The samples from the small plot show clearly, both by correlation of the numbers of small and large individuals, and

by the indices of aggregation, that juvenile and adult forms of the same species are associated with each other. One may therefore suppose that the parents frequently remain in the vicinity of the eggs after laying and the young do so after hatching.

No data has been collected from laboratory experiments with regard to the effect of environmental stimuli on the species. Passive movement caused by environmental elements can almost certainly be eliminated although Rapoport (1959) comments on the collection of soil micro-arthropods into low areas during heavy rainfall. Normally it seems unlikely that the soil would do more than restrict the rate of travel through it. This restriction would slow the active formation of aggregations but would tend to retain those already formed. Active formation of aggregations due to environmental stimuli are likely. As has already been mentioned F. candida is attracted to a source of carbon dioxide (Klingler 1959), Hypogastrura sp. has been found to collect under squares of coloured material laid on the soil (Matsuda 1953) and Onychiurus sp. is attracted to pads soaked in saccharose and glucose solutions (Mochizuki 1952). Information as to which environmental stimuli were likely to be important in the field was obtained by calculating the association between various possible factors and the number of Collembola in the samples. In fact the three possible attractants mentioned above,

carbon dioxide, colour and sugar, were not measured, partly because of the impracticability of making these measurements and partly because under uniform or near uniform vegetation cover they would vary very little. Only the small individuals were found to be correlated with the physical environment or vegetation. Young F. distincta were more frequently present in soil retaining a higher moisture content and in samples with more moss on the surface. These are likely to be reflections of the same stimulus, for the soil moisture content, which is dependent upon the consolidation, particle and crumb structure of the soil, is also likely to be higher under a good cover of moss. Moss might also tend to grow on soil with better moisture retaining capabilities. Young I. thermophila were present in greater numbers in samples from soil which lost more weight on ignition and in more acid soil. These two measurements may again be reflections of the same stimulus for the pH of the soil is lower in the presence of organic and nitrogenous material. In acid soil the loss of weight on ignition is a reflection of the amount of organic and nitrogenous compounds present. Finally I. notabilis seemed to be present in slightly larger numbers in more alkaline soil.

It is therefore suggested, and it can be no more than a suggestion, that the position of the juvenile instars is, in part, governed by the environment either due to the restriction of oviposition to suitable areas or to the greater mortality of eggs

or hatchlings in unsuitable areas. Although the adults and juveniles are strongly correlated in position with each other the adults showed no association with environmental factors. The lack of alternative information suggests that the older individuals tend to form active aggregations due to a social urge. Supporting evidence for this is found in the association between the position of individuals of each species in the small plot. The combinations, pairs of the species or the size ranges, which lack significant correlation all involve the small, juvenile, size range. Combinations of large individuals all showed significant correlation. This is particularly noticeable in the results for F. distincta. It seems therefore that the older instars of F. distincta actively form aggregations of a social nature whereas the young instars are more often in aggregations formed passively. This is in agreement with the results of the experiments to determine the degree of aggregation of each instar. The aggregations of young individuals may be social in origin due to their parents laying eggs in clumps, or they may be environmental, in which case only those eggs in suitable areas hatch or only hatchlings in suitable areas survive. By inference from the calculated associations it is likely that the origin of the juvenile aggregations is both social and environmental, i.e. the parents lay the eggs in clumps and only those clumps in suitable areas hatch or survive after hatching. There are two other possible explanations, that the adults only

lay eggs in certain conditions or that the young, on hatching, are attracted by certain conditions. The first of these explanations is considered unlikely because the adults were not found associated with environmental conditions. The second is discounted because it seems unlikely that the tiny hatchlings, which move little unless thoroughly disturbed, will follow such slight gradients as exist, along paths as tortuous as those between soil particles.

Allee (1931) and Watt (1960) both considered that crowding could alter any or all aspects of the life history. Examination of field populations to find which aspects are most altered by excessive crowding would be an exceptionally long process, if indeed it is possible, but information can be obtained under simplified conditions in the laboratory. Many experiments of this nature have been made with insect and other pests and these have already been discussed (pp. 92). In general there appears to be an optimum level of crowding, greater and lesser densities proving less beneficial. It is not surprising therefore that maximum mean individual fecundity of F. distincta was obtained when there was a mean area of 1.3 sq. cm. available for each animal in massed cultures. It was surprising to find that solitary individuals in an area of 4.9 sq. cm. had a greater fecundity and a more rhythmical sequence of laying than any massed culture. This can perhaps be explained by the changes in behaviour when an individual

senses the presence of others (pp. 30). Changes, due to crowding, in the length of life, the rate of development or the fertility of the eggs were not observed in any experiments.

It is not always easy to distinguish by what means the physiological processes have been altered for, as many workers have remarked (in particular Allee 1931, Lack 1954) crowding alters the accumulation of excreta and secretions and may alter the food intake. The behaviour of the animals may be changed so that individuals take more or less physical exercise. This change in behaviour, which itself may alter the physiological processes, is an external sign of a change in nervous tension. However a nervous strain may be imposed with no outward sign except the resultant change in life history. In the laboratory it was possible to ensure that food was always present, although disturbance while eating could not be controlled; that the chambers were regularly cleaned and new chambers used in some experiments; that the eggs laid were regularly and frequently removed to reduce cannibalism; and that the oviposition sites were not limited. These controls helped to eliminate the means by which crowding can alter fecundity. Of them all, perhaps cannibalism is the most difficult to estimate and control but the author is fully satisfied that cannibalism was reduced to insignificant levels by frequent removal of the eggs and, when this was done, it was proportional to the number of animals in the culture. As the fecundity is also expressed

in relation to the number of animals the effect of cannibalism of eggs can be ignored. After eliminating these effects, crowding still affected the fecundity. Presumably this is caused by a change in nervous tension due to disturbance or stimulation by other individuals. As there was little likelihood of the development of the ovaries or maturation of the eggs being altered it is likely that the disturbance had most effect while the individuals were ovipositing or about to do so. It is certain that the actual fecundity of the laying individuals changed because although the proportion of the culture with open genital apertures varied inversely with the number of animals in the culture the reduction in larger cultures was too little to account for the greatly reduced mean fecundity. It was interesting to find that the proportion of the culture with open genital apertures also varied directly with the availability of food. This suggests that the effect of crowding was perhaps due to disturbance while feeding, causing partial starvation.

It would seem that if these changes occur under field conditions the centres of crowding will slowly change position, regardless of environmental effects. Lack (1954) suggests that in nature, conditions of crowding rarely become such that adverse effects occur, for in these circumstances the adults tend to move elsewhere. There is slight evidence that this may have occurred when the distribution of I. thermophila at station I

unexpectedly became more random during September, October, and November in 1960. Generally, however, the degree of aggregation remained the same, even at high population levels and the density of population at the centres of aggregation might become such that reproduction is reduced. The only measurements of the mean area per individual available to arthropods of this size range in the soil or similar substance are those made by Ford (1937) and Haarløv (1960). The former estimated that in grass clumps there was about 6.50 sq. cm. of leaf surface per individual when the population was densest. Haarløv calculated that in level pasture, probably the habitat most similar to the field in which the studies were made, the animals in the upper centimetre had a mean area of 0.88 sq. cm. available to them and an area of 1.35 sq. cm. in the second centimetre of soil. These figures are based on the estimated surface available around the pores and cavities in the soil. Haarløv's results suggest that a population density greater than the probable optimum can develop in aggregations. Presumably control of the fecundity will then reduce regeneration at the centres of aggregation and cause a shift in position of the sites of greatest density. Thus more use will be made of the available environment and permanent social or subsocial communities will not develop.

Appendix Table I.

The data recorded during the experiments on the social aggregation of F. distincta.

(The number of animals in each of the 16 sectors of the annular chamber is recorded. Eight animals were used in each experiment and the chamber was rotated 45° between readings).

Batch	Condition of the experiment	Trial & Reading	Data	Number of Clusters	Number of animals in Clusters
A	2nd instar	I 1	0000 0100 3101 1100	1	3
		2	0000 0010 1230 0010	2	5
	Culture-	3	0000 0000 2310 2000	3	7
	crowded	4	0100 0001 2000 1012	2	4
	Lighting-	II 1	0100 1020 1012 0000	2	4
	standard	2	0000 1200 1103 0000	2	5
		3	0000 2100 1003 0100	2	5
		4	0000 0300 0110 1011	1	3
		III 1	2101 0000 0101 0011	1	2
		2	0012 0100 2100 0010	2	4
		3	0001 0102 1020 0001	2	4
		4	1000 0200 1010 0201	2	4
		IV 1	0210 1100 0100 1010	1	2
		2	0200 0000 1010 3100	2	5
		3	0000 0001 2310 0100	2	5
		4	1000 0211 0000 0120	2	4
B	3rd instar Culture crowded. Lighting standard. See Table 4 in text.				
C	4th instar	I 1	0000 0001 2000 1400	2	6
		2	0101 0000 0101 0301	1	3
	Culture -	3	0001 0000 0201 0031	2	5
	crowded	4	0000 0001 0104 0200	2	6
	Lighting -	II 1	0032 0000 0001 1001	2	5
	standard	2	1006 0000 0010 0000	1	6
		3	2101 0020 0020 0000	3	6
		4	0000 0010 2202 0001	3	6
		III 1	2000 0200 1200 0010	3	6
		2	0000 0000 0201 2003	3	7
		3	0000 1000 0200 1040	2	6
		4	1020 2100 1000 0100	2	4
		IV 1	2010 4000 0001 0000	2	6
		2	1002 3000 0100 1000	2	5
		3	2002 3000 0000 0100	3	7
		4	4000 3000 0001 0000	2	7

Table continued overleaf.

Table I contd:

Batch	Condition of the experiment	Trial & Reading		Data	Number of Clusters	Number of animals in Clusters
D	5th instar	I	1	0000 0000 0400 2020	3	8
			2	0000 0001 0221 1001	2	4
	Culture -		3	3000 2000 0100 0020	3	7
	crowded		4	0004 1100 0001 0100	1	4
	Lighting -	II	1	0004 1100 0001 0100	1	4
	standard		2	0000 4000 0121 0000	2	6
			3	0000 6010 0000 0001	1	6
			4	0002 0400 0100 0100	2	6
		III	1	0010 3000 0001 2010	2	5
			2	0020 3100 0010 0001	2	5
			3	0050 0000 1200 0000	2	7
			4	0004 1000 0010 1100	1	4
		IV	1	2100 0000 0120 2000	3	6
			2	2000 0000 0000 1131	2	5
			3	2000 0000 0001 2300	3	7
			4	0000 0000 0101 3300	2	6
E	Post 5th instar	I	1	0400 0002 1000 1000	2	6
			2	3000 0000 1000 2020	3	7
	Culture -		3	0202 1100 0100 0100	2	4
	crowded		4	0200 1000 4010 0000	2	6
	Lighting -	II	1	1031 0000 2001 0000	2	5
	standard		2	0000 1140 0000 1010	1	4
			3	0101 1030 2000 0000	2	5
			4	0100 2002 0100 1001	2	4
F	Post 5th instar	I	1	0030 1010 0010 0200	2	5
			2	1221 0010 0000 0100	2	4
	Culture -		3	0000 2000 0310 0200	3	7
	crowded		4	0002 0000 1002 2100	3	6
	Lighting -	II	1	0010 0041 0100 0001	1	4
	dim red		2	0202 0010 0012 0000	3	6
			3	2200 0000 1001 1010	2	4
			4	1230 0000 1100 0000	2	5

Table continued overleaf.

Table I continued.

Batch	Condition of the experiment	Trial & Reading	Data	Number of Clusters	Number of animals in Cluster
G	5th instar	I 1	0000 0031 1300 0000	2	6
		2	0000 0500 0111 0000	1	5
	Culture - solitary	3	1000 0013 1001 1000	1	3
		4	0012 0002 2000 1000	3	6
	Lighting - standard	II 1	0002 4002 0000 0000	3	8
		2	0100 3002 1000 0100	2	5
		3	0100 1000 1030 0101	1	3
		4	0000 2001 0010 0301	2	5
		III 1	0000 0043 1000 0000	2	7
		2	0101 0000 0030 1110	1	3
		3	1201 0000 0301 0000	2	5
		4	1002 0000 0030 0200	3	7
		IV 1	0000 0000 0223 0010	3	7
		2	0200 2000 0103 0000	3	7
		3	0020 0000 0020 0040	3	8
		4	0211 2000 0001 1000	2	4
H	Post 5th instar	I 1	1230 0000 0000 0020	3	7
		2	1011 0000 0002 0003	2	5
	Culture - solitary	3	4001 0000 0000 0012	2	6
		4	2020 0200 1000 0001	3	6
	Lighting - standard	II 1	0000 0000 1310 0021	2	6
		2	0001 0001 3100 0020	2	5
		3	0101 0000 2000 0112	2	4
		4	0000 0000 0301 0121	2	5

Appendix Table II.

Factorial analysis of variance of the data of batches E and F of the social aggregation experiment (Text p. 50) with respect to conditions of illumination.

Source of variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
Light conditions	1	0	None
Trials	2	2.13	
Readings in trials (residual error)	12	1.13	

Appendix Table III.

Factorial analysis of variance of the data of batches A-F inclusive of the social aggregation experiment (Text p.54) with respect to age.

Source of variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
Ages	4	6.27	$<0.01 > 0.001$
Trials	15	1.03	
Readings in trials	60	1.45	
Residual error)	75	1.37	
(The residual error is obtained by pooling the sums of squares of the Trials and Readings, these being significantly different).			

Appendix Table IV.

Factorial analysis of variance of the data of batches D,E,G,and H of the social aggregation experiment (Text p. 55 =)with respect to conditions of crowding.

Source of variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
	a - 5th instar		
Culture conditions	1	0.06	None
Trials	6	1.07	
Readings in Trials (residual error)	24	2.55	
	b - post 5th instar		
Culture conditions	1	0.25	None
Trials	2	3.08	
Readings in trials (residual error)	12	0.71	

Appendix Table V.

Factorial analysis of variance of the data of experiment 1, Table 15, Text p. 64 .

a) Complete analysis.

Source of Variance		Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
	Area	1	17026	
	Population	2	23442	
	Feeding	1	1200	
1st order interactions	Area/Population	2	17025	$< 0.05 > 0.01$
	Area/Feeding	1	972	
	Feeding/Population	2	695	
2nd order interactions		2	4514	
Residual*		5	2278	

*The residual mean square and corresponding degrees of freedom are obtained by pooling those treatment interactions insignificant compared with the 2nd order interaction.

b) Breakdown analysis for the treatment, area.

i Population = 10 animals.

Source of Variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
Area	1	0.3	
Feeding	1	90.3	None
1st order interaction	1	8556.4	

ii Population = 30 animals.

Source of Variance	Degrees of Freedom	Mean Square	Significant Results. ($p < 0.05$)
Area	1	51076	$< 0.05 > 0.01$
Feeding	1	2500	
1st order interaction	1	1444	
Residual*	2	1972	

iii Population = 60 animals.

No test is possible because too few eggs are recorded.
* See note Appendix Table Va.

Table V continued overleaf.

Table V continued.

c) Breakdown analysis for the treatment, population.

i Area of chamber = 7 sq. cms.

Source of Variance	Degrees of Freedom	Mean Square	Significant Results. ($p < 0.05$)
Population	2	12988	>0.05
Feeding	1	2166	
1st order interaction	2	1604	
Residual*	3	1795	

ii Area of chamber = 19.6 sq.cms.

Source of Variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
Population	2	27470	$<0.05 > 0.01$
Feeding	1	2	
1st order interaction	2	3658	
Residual*	3	2439	

* See note Appendix Va.

Appendix Table VI.

Factorial analysis of the variance of the data of experiment 2, Table 16, Text p. 66 .

Source of variance		Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
	Area	1	4240	
	Population	1	55517	$<0.01 > 0.001$
	Temperature	1	10250	
1st order inter-action	Area/population	1	509	
	Population/ Temperature	1	2461	
	Area/Temperature	1	4445	
2nd order interaction		1	1325	
Residual*		4	2185	

* See note Appendix Table Va.

Appendix Table VII.

Incomplete factorial analysis of the data of experiment 5, Table 21, Text p. 70 .

a) Subcultures left in original chamber.

Source of Variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
Age of Reduction	6	570.7	>0.01
Replication	7	132.7	

95% Confidence limits for the difference between means are ± 27.3

b) Subcultures placed in clean chambers.

Source of Variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
Age of Reduction	4	125	
Replication	5	153.9	None

Appendix Table VIII.

Incomplete factorial analysis of the data of experiment 5, Table 21, Text p. 76 .

Source of Variance	Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
Age of Reduction	3	61.88	
Condition of chamber	1	70.15	
1st order interaction	3	318.07	None
Replication	8	209.11	

Appendix Table IX.

Factorial analysis of the data in Text Table 22, p. 80 .
(analysis of Angular transformation of percentages)

Source of Variance		Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
	Population	1	189	
	Sanitation	1	6216	
	Presence of eggs	1	7022	
1st order inter-action	Population/eggs	1	436	
	Eggs/sanitation	1	3	
	Population/ sanitation	1	5565	None
2nd order interaction		1	13232	
Residual*		4	4809	

* See note Appendix Table Va.

Appendix Table X.

Factorial analysis of the data in Text Table 23, p. 81.
(analysis of Angular transformation of percentages).

a) Data from experiment 1.

Source of Variance		Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
	Population	2	140,033	< 0.001
	Area	1	6,438	
	Feeding	1	15,550	$< 0.05 > 0.001$
1st order interaction	Population/area	2	2,555	
	Area/feeding	1	3,825	
	Population/feeding	2	442	
2nd order interaction		2	3,430	
Residual*		7	2,240	

b) Data from experiment 3.

Source of Variance		Degrees of Freedom	Mean Square	Significant Results ($p < 0.05$)
	Population	1	41,042	$< 0.05 > 0.001$
	Sanitation	1	28	
	Presence of eggs	1	300	
1st order interaction	Population/eggs	1	4,183	
	Eggs/sanitation	1	406	
	Population/sanitation	1	3,829	
2nd order interaction		1	9,876	
Residual*		4	4,573	

* See note Appendix Table Va.

Appendix Table XI.

Recipe for Methyl Cellulose mounting medium.

1. 5 g. Methyl cellulose (Celacol 450)
2. 25 ml. Distilled water
3. 100 ml. Lactic acid
4. 25 ml. Industrial methylated spirit
5. 2 g. Carbowax 4000
6. 1 ml. Diethylene glycol

(Celacol may be obtained from Courtaulds or J.M.Steel, Ltd.)

Mix 1 and 2 tepid and cool in a refrigerator for 2-4 hours.

Mix in 6 and stir in 3.

Dissolve 5 in 4 and add carefully to the rest.

Appendix Table XII.

The total number of animals collected each month at each station.

a) April 1959 until March 1960.

Station	April	May	June	July	Aug:	Sept:	Oct:	Nov:	Jan:	Feb:	March
Species F. distincta.											
A	0	0	0	0	0	0	0	0	0	0	2
B	1	3	0	0	0	0	0	0	4	2	0
C	0	0	0	1	5	0	0	0	1	0	0
D	0	3	0	0	0	0	0	1	0	0	4
E	0	0	0	0	0	0	0	2	3	0	0
F	1	10	0	1	3	0	0	3	11	8	8
G	0	0	0	0	1	0	2	5	0	0	6
H	0	2	0	0	0	0	0	0	3	0	8
I	0	0	0	0	0	0	3	6	2	1	2
Species I. thermophila.											
A	0	0	2	0	0	0	0	0	0	0	0
B	0	0	0	0	0	0	0	0	0	1	7
C	0	1	0	0	1	3	0	0	0	0	2
D	1	0	0	0	0	0	0	0	0	0	0
E	2	0	0	3	3	1	1	1	0	0	0
F	1	1	0	1	0	0	0	1	0	0	0
G	0	1	2	0	0	1	0	0	0	0	1
H	3	2	0	0	1	0	0	0	0	0	6
I	9	10	0	0	0	0	1	9	0	4	2
Species F. nana.											
A	1	2	0	0	1	0	1	0	1	1	1
B	0	2	0	0	1	2	0	0	0	1	8
C	1	1	1	1	1	0	0	0	14	9	0
D	12	17	6								
E	13	9	0	3	4	2	13	11	13	2	33
F	12	26	3	2	1	3	2	10	0	10	15
G	27	21	0	4	1	0	0	0	14	0	1
H	24	4	0	1	0	0	0	3	1	0	20
I	8	10	0	2	0	0	3	2	1	1	72
Species I.notabilis.											
A	0	3	0	0	0	0	0	0	0	0	0
B	1	1	0	0	0	0	0	2	1	2	0
C	0	2	0	0	0	0	0	2	6	6	3
D	1	11	0	1	0	0	0	1	2	0	0
E	2	4	0	0	2	0	2	1	4	0	10
F	1	8	1	0	0	0	0	2	0	3	6
G	6	3	0	0	0	0	0	0	7	0	4
H	0	0	0	5	1	1	0	0	0	0	6
I	1	6	0	2	0	0	0	0	0	0	5

Table continued overleaf.

Table XII continued.

b) April, 1960 until March, 1961.

Station	April	May	June	July	Aug:	Sept:	Oct:	Nov:	Dec:	Jan:	Feb:	March.
Species F. distincta.												
G	2	1	3	7	4	5	9	6	3	0	17	13
H	0	1	2	0	2	8	1	3	8	3	1	10
I	2	0	1	6	12	5	10	5	0	1	4	9
Species I. thermophila.												
G	1	1	14	0	1	2	3	21	4	2	0	7
H	15	31	207	51	191	125	159	78	2	51	142	20
I	0	1	2	12	80	144	182	134	91	97	154	72
Species F. nana.												
G	3	4	9	24	60	109	262	126	321	206	93	135
H	7	8	25	16	13	111	40	95	68	22	15	79
I	20	18	24	54	10	20	33	67	33	79	133	118
Species I. notabilis.												
G	2	6	2	0	4	6	13	11	3	15	1	21
H	4	1	19	4	3	14	11	10	1	4	7	4
I	1	9	0	2	1	2	10	28	5	12	7	7

Appendix Table XIII.

The transformed sample counts of F. nana and I. thermophila, April 1960 until March 1961 and the analysis of variance of the data.

Station		G						H.						I.							
Month	Species	Replication 1	2	3	4	TOTALS	COMBINED TOTALS	Replication 1	2	3	4	TOTALS	COMBINED TOTALS	Relication 1	2	3	4	TOTALS	COMBINED TOTALS	MONTH TOTALS	MONTH TOTALS F+I
Apr.	F. nana	0.30	0	0	0.48	0.78		0.85	0.	0.30	0	1.15		1.30	0.30	0	0	1.60		3.53	
	I.thermophila	0.30	0	0	0	0.30	1.08	1.04	0.78	0	0	1.82	2.97	0	0	0	0	0	1.60	2.12	5.65
May	F. nana	0	0.48	0.48	0	0.96		0	0.30	0	0.90	1.20		0.70	0.30	1.04	0.60	2.64		4.80	
	I.thermophila	0	0.30	0	0	0.30	1.26	1.23	1.15	0.30	0	2.68	3.88	0.30	0	0	0	0.30	2.94	3.28	8.08
Jun.	F. nana	0.48	0	0.48	0.78	1.74		0	0.48	1.15	1.04	2.67		1.34	0	0.60	0	1.94		6.35	
	I.thermophila	0.48	0	0.60	1.00	2.08	3.82	0.70	1.87	2.07	1.15	5.79	8.46	0	0.48	0	0	0.48	2.42	8.35	14.70
Jul.	F. nana	1.11	0	0.30	1.08	2.49		0.70	0.95	0.48	0.48	2.61		1.64	0	1.00	0.48	3.12		8.22	
	I.thermophila	0	0	0	0	0	2.49	0.90	1.49	1.00	0.78	4.17	6.78	0	0.48	0.30	1.00	1.78	4.90	5.95	14.17
Aug.	F. nana	1.46	0	0	1.51	2.97		0.70	0.90	0.48	0	2.08		0.60	0.78	0.30	0.30	1.98		7.03	
	I.thermophila	0.30	0	0	0	0.30	3.29	1.93	1.59	1.38	1.66	6.56	8.64	1.32	1.51	1.42	0.70	4.95	6.93	11.81	18.84
Sep.	F. nana	1.30	1.48	1.46	1.53	5.77		1.28	1.92	0.60	0.95	4.75		0.85	0.70	0	1.04	2.59		13.11	
	I.thermophila	0	0.30	0	0.30	0.60	6.37	1.40	1.68	1.51	1.38	5.97	10.72	1.63	1.59	1.54	1.49	5.25	8.84	12.82	25.93
Oct.	F. nana	2.16	1.04	1.18	1.98	6.36		1.49	0.85	0.48	0.48	3.30		0.70	1.26	0	1.11	3.07		12.73	
	I.thermophila	0	0.30	0.48	0	0.78	7.14	1.93	1.26	1.69	1.00	5.88	9.18	1.67	1.59	1.77	1.60	6.63	9.70	13.29	26.02
Nov	F. nana	1.73	1.49	1.58	0.85	5.65		0.90	1.08	1.04	1.83	4.85		1.15	1.00	1.00	1.57	4.72		15.22	
	I.thermophila	0.70	0	0.30	1.20	2.20	7.85	1.46	1.41	1.40	0.30	4.57	9.42	1.30	1.61	1.49	1.66	6.06	10.78	12.83	28.05
Dec.	F. nana	2.32	0.30	1.83	1.66	6.11		1.72	1.23	0	0	2.95		1.18	0.78	0	1.18	3.14		12.20	
	I.thermophila	0	0.70	0	0	0.70	6.81	0.48	0	0	0	0.48	3.43	1.51	1.43	1.00	1.42	5.36	8.50	6.54	18.74
Jan.	F. nana	1.15	0	2.04	1.93	5.12		1.08	0.48	0.48	0.90	2.94		0	1.36	1.56	1.36	4.28		12.34	
	I.thermophila	0	0	0.48	0	0.48	5.60	1.15	1.76	1.00	1.20	5.11	8.05	0	1.46	1.79	1.00	4.25	8.53	9.84	22.18
Feb.	F. nana	0.90	1.23	1.70	1.34	5.17		1.18	0	0	0.30	1.48		1.99	1.49	0.78	0.48	4.74		11.39	
	I.thermophila	0	0	0	0	0	5.17	1.00	1.89	0.34	1.54	4.77	6.25	1.76	1.95	0.85	0	4.56	9.30	9.33	20.72
Mar	F. nana	1.76	1.04	1.68	1.32	5.80		1.58	1.18	1.26	1.08	5.10		1.79	1.28	1.18	1.43	5.68		16.58	
	I.thermophila	0.30	0.60	0.60	0	1.50	7.30	1.08	0.78	0	0.70	2.56	7.66	0.95	1.28	1.15	1.52	4.90	10.58	8.96	25.54
TOTAL	F.nana	14.67	7.06	12.73	14.46	48.92		11.48	9.37	6.27	7.96	35.08		5.24	9.25	7.46	9.55	39.50		125.50	
"	I.thermophila	2.08	2.20	2.46	2.50	9.24		14.30	15.66	10.69	9.71	50.36		0.44	13.38	11.31	10.39	45.52		105.12	
COMBINED TOTALS		16.75	9.26	15.19	16.96		58.16	25.78	25.03	16.96	17.67		85.44	3.68	22.63	18.77	19.94		85.02		228.62

Appendix Table XIIIa.

Analysis of variance of the counts of two species, F. nana and I. thermophila for the year April, 1960 to March, 1961.
(Transformation Log_{10} N+1)

Source of variance	Degrees of Freedom	Mean Square	Variance Ratio	Tested Against	Significant Results
2 Species, 3 Stations, 12 Months, 4 Replicates.					
Replication	3	0.59			
Species	1	1.17			
Stations	2	2.55			
Months	11	2.18			
Sp x St	2	9.02			
Sp x M	11	0.44			
St x M	22	0.34			
Sp x St x M	22	0.64	3.2	Residual	< .001
Residual	213	0.20			
Total	287				
Species F, 3 Stations, 12 Months, 4 Replicates.					
Replication	3	1.11			
Stations	2	1.04	3.72	St x M	< .05
Months	11	1.46	5.23	St x M	< .001
R x St	6	0.42			
R x M	35	0.22			
St x M	22	0.28	1.30		
Residual	66	0.21			
Total	143				
Species I, 3 Stations, 12 Months, 4 Replicates					
Replication	3	2.96			
Stations	2	10.52	14.88	St x M	< .001
Months	11	1.15	1.62	St x M	
R x St	6	0.27			
R x M	33	0.13			
St x M	22	0.71	5.05		< .001
Residual	66	0.14			
Total	143				
Station G, 2 Species, 12 Months, 4 Replicates					
Replication	3	0.54			
Species	1	16.13	13.81	*	< .01
Months	11	0.72			
R x Sp	3	0.60			
R x M	33	0,14			
Sp x M	11	0.58	3.52	Residual	< .01
Residual	33	0.16			
Total	95				

Table continued overleaf.

Table XIIIa continued.

Source of Variance	Degrees of Freedom	Mean Square	Variance Ratio	Tested Against	Significant Results
Station H, 2 Species, 12 Months, 4 Replicates.					
Replication	3	0.92			
Species	1	2.43	3.51	**	
Months	11	0.80	N.S		
R x Sp	3	0.16			
R x M	33	0.19			
Sp x M	11	0.59	2.9	Residual	.01
Residual	33	0.20			
Total	95				
Station I, 2 Species, 12 Months, 4 Replicates.					
Replication	3	0.22			
Species	1	0.38	N.S	***	
Months	11	0.35	1.65		
R x Sp	3	0.42			
R x M	33	0.31			
Sp x M	11	0.58	4.83	Residual	.01
Residual	33	0.12			
Total	95				

* Tested as the example given by Snedecor (1956) 12.10
$D.F._1 = 1$ $D.F._2 = 95$

** As above $D.F._1 = 1$ $D.F._2 = 13$

*** As above $D.F._1 = 13$ $D.F._2 = 24$

Appendix Table XIV.

The Data for the sample counts of the four species of Collembola from the small plot and comparison of a calculated Poisson distribution.

Folsomia distincta All individuals.

Number of samples (N) 144
Number of individuals (Σx) 108
Mean number of individuals per sample ($\bar{x}$) 0.75

Estimate Variance in the number of individuals per sample (s^2) 4.85

x	Observed distribution	Poisson distribution	Sign of difference
0	85	68.03	+
1	28	51.02	-
2	19	19.13	-
3+	12	5.82	+

degrees of freedom 2 χ^2 21.18 $p < .001$

Isotomina thermophila All individuals.

N 144 Σx 4563 $\bar{x}$ 31.69 s^2 798.20

x	Observed distribution	Poisson distribution	Sign of difference
0-24	75	13.96	+
25-29	16	37.69	-
30-34	8	49.07	-
35-39	7	30.91	-
40+	38	12.37	+

degrees of freedom 3 χ^2 352.00 $p < .001$

I. thermophila Large individuals.

N 34 Σx 368 $\bar{x}$ 10.82 s^2 147.36

x	Observed distribution	Poisson distribution	Sign of difference
0-9	21	12.24	+
10-14	7	17.22	-
14+	6	4.54	+

degrees of freedom 1 χ^2 14.31 $p < .001$

Table continued overleaf.

Table XIV continued.

I. thermophila	Medium size individuals.		
N 34	Σx 555	$\bar{x}$ 16.32	s^2 32.29
x	Observed distribution	Poisson distribution	Sign of difference
0-14	22	11.49	+
15-19	3	15.33	-
20+	9	7.18	+
degrees of freedom 1	χ^2 20.02	$p < .001$	
I. thermophila	Small individuals		
N 34	Σx 354	$\bar{x}$ 10,41	s^2 101.07
x	Observed distribution	Poisson distribution	Sign of difference
0-9	19	13.73	+
10-14	5	15.82	-
15+	10	4.45	+
degrees of freedom 1	χ^2 16.34	$p < .001$	
Folsomia nana	All individuals.		
N 144	Σx 1232	$\bar{x}$ 8.56	s^2 47.08
x	Observed distribution	Poisson distribution	Sign of difference
0-5	58	20.95	+
6-8	25	53.05	-
9-11	20	47.29	-
12-14	14	18.34	-
15+	27	4.37	+
degrees of freedom 3	χ^2 214.32	$p < .001$	

Table continued overleaf.

Table XIV continued.

F. nana Large individuals.			
N 35	Σx 95	$\bar{x}$ 2.71	s^2 13.52
x	Observed distribution	Poisson distribution	Sign of difference
0-1	14	8.61	+
2	8	8.54	-
3	3	7.72	-
4	2	5.24	-
5+	8	4.88	+
degrees of freedom 3		χ^2 10.30	$p < .02$

F. nana Medium size individuals.			
N 35	Σx 139	$\bar{x}$ 3.97	s^2 10.50
x	Observed distribution	Poisson distribution	Sign of difference
0-1	9	3.28	+
2-3	9	12.09	-
4-5	5	12.27	-
6+	12	7.36	+
degrees of freedom 2		χ^2 18.00	$p < .001$

F. nana Small individuals.			
N 35	Σx 122	$\bar{x}$ 3.49	s^2 15.32
x	Observed distribution	Poisson distribution	Sign of difference
0-1	14	4.81	+
2-3	8	14.08	-
4-5	5	11.18	-
6+	8	4.93	+
degrees of freedom 2		χ^2 25.52	$p < .001$

Table continued overleaf.

Ta ble XIV continued.

Isotoma notabilis	All individuals.		
N 144	Σx 2152	$\bar{x}$ 14.94	s^2 120.77

x	Observed distribution	Poisson distribution	Sign of difference
0-8	46	3.45	+
9-11	15	21.59	-
12-14	21	40.74	-
15-17	15	40.64	-
18-20	13	23.87	-
21-23	10	8.92	+
24+	24	4.79	+

degrees of freedom 5 χ^2 559.36 $p < .001$

I. notabilis	Large individuals.		
N 34	Σx 41	$\bar{x}$ 1.21	s^2 0.41

x	Observed distribution	Poisson distribution	Sign of difference
0	10	10.18	-
1	16	12.28	+
2	5	7.40	-
3+	3	4.14	-

degrees of freedom 2 χ^2 2.22 $p > .3$

I. notabilis	Medium size individuals.		
N 34	Σx 275	$\bar{x}$ 8.09	s^2 36.02

x	Observed distribution	Poisson distribution	Sign of difference
0-5	16	6.23	+
6-8	4	13.49	-
9-11	6	10.24	-
12+	8	4.04	+

degrees of freedom 2 χ^2 30.94 $p < .001$

Table continued overleaf

Table XIV continued.

I. notabilis	Small individuals.		
N 34	Σx 258	$\bar{x}$ 7.59	s^2 24.64

x	Observed distribution	Poisson distribution	Sign of difference
0-5	16	7.88	+
6-8	8	14.20	-
9-11	5	9.03	-
12+	5	2.89	+

degrees of freedom 2 χ^2 14.42 $p < .001$

Appendix Table XV.

Association between the Collembola and physical factors.

F. distincta (small)	Present	Absent	Totals	d	Standard error of d
Loss on Ignition					
Number of observation	12	40	52		
Rank scores Total	289	1089	1378		
Mean scores	24.1	27.2		3.1	5.0
Moisture Content					
Number of Observation	53	90	143		
Rank Scores Total	4330.5	5965.5	10296		7.2
Mean Scores	81.7	66.3		15.8*	
pH					
Number of Observation	36	33	69		
Rank Scores Total	1341.5	1073.5	2415		4.8
Mean Scores	37.3	32.5		4.7	
F. distincta (large)					
Loss on Ignition					
Number of Observation	9	43	52		
Rank Scores Total	239	1039	1378		5.6
Mean Scores	26.5	24.2		2.4	
Moisture Content					
Number of Observation	18	125	143		
Rank Scores Total	1338	8958	10296		10.5
Mean Scores	74.3	71.7		2.7	
pH					
Number of Observation	8	61	69		
Rank Scores Total	353	2062	2415		7.5
Mean Scores	44.1	33.8		10.3	

Factor - Loss of weight on Ignition.

Corrected sum of square of Factor 1127.34

Species	Corrected sum of Square of Species	Corrected sum of Products	'r' 50 degrees of freedom
I. thermophila (small)	4.28	22.87	.33*
" " (large)	6.68	20.86	.24
F. nana (small)	6.79	12.02	,14
" " (large)	5.20	17.01	.22
I. notabilis (small)	5.51	19.20	.24
" " (large)	4.94	7.27	.10

Table continued overleaf.

Table XV continued.

Factor - Moisture Content.

Standard error of difference between Rank Totals 405.82
Divisor for difference of Rank Totals to overestimate 'r' 4560

Species	Rank Score Totals for 48 samples. Lowest Moisture Content	Highest Moisture Content	Difference between Totals	'r' ※ 141 degrees of freedom
I. thermophila (small)	3628.5	3401.5	227.0	.05
" " (large)	3546.5	3848.0	301.5	.07
F. nana (small)	3784.0	3336.5	447.5	.10
" " (large)	3789.5	3582.5	207.0	.04
I.notabilis (small)	3796.5	3387.0	409.5	.09
" " (large)	3502.0	3807.0	305.0	.05

Factor - pH

Corrected Sum of Squares of Factor 2.56.

Species	Corrected Sum of Squares of Species	Corrected Sum of ~~Squares of~~ Products	'r' 67 degrees of freedom
I.thermophila (small)	11.04	- 2.45	- .46 ***
" " (large)	8.16	0.18	.04
F. nana (small)	8.90	0.44	.09
" " (large)	6.58	- .03	- .01
I.notabilis (small)	9.06	1.14	.24*
" " (large)	6.65	-.55	- .13

※ estimated by method given by Quenouille (1959) § § 24

Significance.
*** $p \ll .001$
** $p \ll .01$
* $p \ll .05$

Appendix Table XVI.

Association between the Collembola and Vegetation.

Vegetation Festuca.

% of sample covered		0	25	50	χ^2
Species	Number in sample				
F. distincta(small)	Present	31	12	10	
	Absent	64	15	12	2.10
F. distincta(large)	Present	13	4	1	
	Absent	82	23	21	1.52
I. thermophila (small)	0-9	30	11	8	
	10-19	34	6	10	
	20+	31	10	4	5.02
I. thermophila (large)	0-4	19	8	3	
	5-9	30	7	11	
	10-14	16	9	4	
	15+	31	3	3	12.10
E. nana (small)	0-3	38	10	9	
	4-7	29	7	5	
	8+	28	10	8	0.91
F. nana (large)	0	24	6	3	
	1	24	4	6	
	2	18	5	3	
	3+	29	12	10	4.26
I.nota bilis(small)	0-9	46	10	6	
	10-14	17	10	7	
	15+	32	7	9	6.95
I.notabilis(large)	0	31	7	7	
	1	16	5	5	
	2	17	8	4	
	3+	31	7	6	2.54

Table continued overleaf

Table XVI continued.

Vegetation Agrostis.					
% of samples covered		0	25	50	χ^2
Species	Number in sample				
F. distincta(small)	Present	28	16	9	
	Absent	41	26	24	1.76
F. distincta(large)	Present	6	7	5	
	Absent	63	35	28	1.78
I.thermophila(small)	0 - 9	25	18	6	
	10-19	25	14	11	
	20+	19	10	16	7.77
I.thermophila(large)	0 - 6	25	15	6	
	7 -10	20	8	10	
	11-19	15	14	10	
	20+	9	5	7	6.53
F. nana (small)	0 - 3	29	17	11	
	4 - 7	18	13	10	
	8 -11	12	5	7	
	12+	10	7	5	1.79
F. nana (large)	0	18	9	6	
	1	19	6	9	
	2	12	8	6	
	3 or 4	8	10	6	
	4+	12	9	6	5.53
I.notabilis(small)	0 - 9	32	20	10	
	10-14	15	11	8	
	15+	22	11	15	3.99
I. notabilis(large)	0	20	14	11	
	1	19	5	2	
	2	14	8	7	
	3+	16	15	13	9.66

Table continued overleaf.

Table XVI continued.

Vegetation Moss.

% of samples covered		0	25	50	75	χ^2
Species	Number in sample					
F, distincta(small)	Present	19(16.2)	12(16.9)	18(11.8)	4(8.1)	**
	Absent	25(27.8)	34(29.1)	14(20.2)	18(13.9)	11.52
F. distincta(large)	Present	6	4	6	2	
	Absent	38	42	26	20	1.03
I.thermophila(small)	0 - 4	8	3	9		
	5 - 9	7	10	12		
	10-14	9	7	8		
	15-19	8	11	7		
	20-29	5	5	6		
	30+	7	10	12		5.22
I. thermophila(large)	0 - 4	6	10	14		
	5 - 9	16	15	17		
	10-14	9	8	12		
	15-19	6	6	4		
	20+	7	7	7		3.49
F. nana (small)	0 - 3	14	23	20		
	4 - 7	12	14	15		
	8 -11	8	7	9		
	12+	10	2	10		7.76
F. nana (large)	0	5	11	17		
	1	11	13	10		
	2	6	11	9		
	3 or 4	8	7	9		
	4+	14	4	9		14.31
I. notabilis(small)	0 - 9	14	24	24		
	10-14	16	8	10		
	15-19	5	5	10		
	20+	9	9	10		7.93
I. notabilis(large)	0	10	16	19		
	1	8	9	9		
	2	8	11	10		
	3	7	5	6		
	4+	11	5	10		5.15

The figures in parenthesis are the calculated expected values.

Significance ** $p \ll .01$

Table continued overleaf.

Table XVI continued.

Vegetation None.					
Species % of samples covered		0	25	50	χ^2
Species	Number in sample				
F. distincta(small)	Present	31	11	10	
	Absent	53	23	16	0.28
F. distincta(large)	Present	12	5	1	
	Absent	72	29	25	2.17
I.thermophila(small)	0 - 9	24	16	9	
	10-14	14	6	4	
	15-19	13	5	8	
	20+	33	7	5	9.50
I.thermophila(large)	0 - 4	16	9	5	
	5 - 9	26	11	11	
	10-14	19	7	3	
	15+	23	7	7	3.15
F. nana (small)	0 - 3	30	15	12	
	4 - 7	24	9	8	
	8 -11	15	6	3	
	12+	15	4	3	2.24
F. nana (large)	0	15	10	8	
	1	20	8	6	
	2	17	6	3	
	3 or 4	18	2	4	
	4+	14	8	5	7.26
I. notabilis(small)	0 - 9	30	16	16	
	10-14	20	10	4	
	15+	34	8	6	7.58
I. notabilis(large)	0	24	15	6	
	1	14	6	6	
	2	21	4	4	
	3+	25	9	10	6.19

Table continued overleaf.

Table XVI continued.

Vegetation Bellis.

Bellis	Present	Absent	χ^2
F.distincta(small)			
Present	20	33	
Absent	21	70	3.82*
F. distincta(large)			
Present	4	14	
Absent	37	89	0.39

Bellis	Present	Absent	Total	d	Standard error of d
Number of Observation	41	103	144		7.7
I.thermophila(small)					
Rank Scores total	2856.0	7584.0	10440	4.0	
Mean Score	69.6	73.6		4.0	
I.thermophila(large)					
Rank Scores total	2729	7711	10440		
Mean Score	66.6	74.9		8.3	
F. nana (small)					
Rank Scores total	2856.0	7584.0	10440		
Mean Score	69.7	73.6		4.0	
F. nana (large)					
Rank Scores total	2708.0	7732.0	10440		
Mean Score	66.1	75.1		9.0	
I.nota bilis(small)					
Rank Scores total	2860.5	7579.5	10440		
Mean Score	69.8	73.6		3.8	
I.notabilis(large)					
Rank Scores total	3088.5	6551.5	10440		
Mean Score	75.3	63.6		11.7	

Significance * $p \leq 0.5$

Table continued overleaf.

Table XVI continued.

Vegetation Holcus

Holcus	Present	Absent	χ^2
F,distincta(small)			
Present	6	47	
Absent	9	82	0.07
F.distincta(large)			
Present	3	15	
Absent	12	114	0.86

Holcus	Present	Absent	Totals	d	Standard error of d
Number of Observation	15	129	144		11.4
I.thermophila(small)					
Rank Scores total	974	9466	10440		
Mean Scores	64.9	73.4		8.5	
I.thermophila(large)					
Rank Scores total	1313	9127	10440		
Mean Scores	87.5	70.7		16.8	
F.nana (small)					
Rank Scores total	1117	9323	10440		
Mean Scores	74.5	72.3		2.2	
F. nana (large)					
Rank Scores total	1312	9128	10440		
Mean Scores	87.5	70.8		16.7	
I.notabilis(small)					
Rank Scores total	920	9520	10440		
Mean Scores	61.3	73.8		11.5	
I. notabilis(large)					
Rank Scores total	995	9445	10440		
Mean Scores	66.3	73.2		6.9	

Table continued overleaf.

Table XVI continued.

Vegetation Dead Grass					
% of sample covered	>25%	<25%	χ^2		
F. distincta(small)					
Present	6	47			
Absent	15	76	0.72		
F. distincta(large)					
Present	3	15			
Absent	18	108	0.077		
% of sample covered	>25%	<25%	Totals	d	Standard error of d
Number of Observation	21	123	144		10.0
I.thermophila(small)					
Rank Score totals	1713.0	8727.0	10440		
Mean Score	81.6	71.0		10.6	
I.thermophila(large)					
Rank Score totals	1579.0	8861.0	10440		
Mean Score	75.2	72.0		3.2	
F. nana (small)					
Rank Score totals	1385.5	9054.5	10440		
Mean score	65.0	73.6		7.6	
F. nana (large)					
Rank Score totals	1344.0	9096.0	10440		
Mean Score	64.0	74.0		10.0	
I.notabilis(small)					
Rank Score totals	1460.5	8979.5	10440		
Mean Score	69.6	73.0		3.4	
I.notabilis(large)					
Rank Score total	1412.5	9027.5	10440		
Mean Score	67.3	73.4		6.1	

Appendix Table XVII.

Association between the species of Collembola.

F.distincta (small)	Present	Absent	Totals	'd'	Standard error of 'd'
Number of Observations	53	91	144		7.22
I.thermophila(small)					
Rank Score total	3428	7012	10440		
Mean Rank Score	64.7	77.1		12.4	
I.thermophila(large)					
Rank Score tota l	3517	6923	10440		
Mean Rank Score	66.4	76.1		9.7	
F.nana(small)					
Rank Score total	3561.5	6878.5	10440		
Mean Rank Score	67.2	75.6		8.4	
F.nana(large)					
Rank Score total	3876.5	6563.5	10440		
Mean Rank Score	73.1	72.1		1.0	
I.notabilis(small)					
Rank Score total	3865.5	6574.5	10440		
Mean Rank Score	72.9	72.2		0.7	
I.notabilis(large)					
Rank Score total	3905.5	6534.5	10440		
Mean Rank Score	73.7	71.8		1.9	
F. distincta(large)			$\chi^2_{[1]}$		
F.distincta Present	12	6			
" " Absent	41	85	7.88**	With Yates' correction 6.47**	

** Significance $p \leq .01$.

Table continued overleaf.

Table XVII continued

Data for the calculation of the correlation coefficients.
Counts transformed as log (n+1).

Species	I.thermophila		F. nana		I. notabilis	
Size Range	small	large	small	large	small	large
Corrected sum of squares	21.12	19.47	19.48	14.34	17.93	13.96

Species with Species	Corrected sum of Products	Correlation Coefficient 'r' with 142 degrees of freedom
I.thermophila(small) I.notabilis(large)	0.70	0.04
" " " " (small)	7.06	0.36***
" " " F. nana (large)	2.04	0.12
" " " " (small)	3.86	0.19*
" " " I.thermophila(large)	12.84	0.63***
" " (large) I.notabilis(large)	3.90	0.24**
" " " " (small)	4.24	0.23**
" " " F. nana (large)	4.40	0.26**
" " " " (small)	5.47	0.28***
F. nana (small) I.notabilis(large)	1.49	0.09
" " " " (small)	6.18	0.33***
" " " F. nana (large)	6.99	0.42***
" " (large) I.notabilis(large)	3.78	0.27**
" " " " (small)	4.23	0.26**
I.notabilis(small) I.notabilis (large)	4.56	0.29***

Significance * $p \leq .05$

** $p \leq .01$

*** $p \leq .001$

The correlation coefficient is estimated from

$$\frac{\text{Sum of Products}}{\sqrt{\text{Product of the Sum of Squares of both species.}}}$$

Table continued overleaf.

Table XVII continued

F. distincta (large)

	Present	Absent	Total	'd'	Standard error of 'd'
Number of observation	18	126	144		10.56
I.thermophila(small)					
Total Rank Score	1496.5	8943.5	10440		
Mean " "	83.1	71.5		11.6	
I.thermophila(large)					
Total Rank Score	1673	8767	10440		
Mean " "	92.9	70.1		22.8*	
F. nana(small)					
Total Rank Score	1501	8939	10440		
Mean " "	83.4	71.5		11.9	
F. nana (large)					
Total Rank Score	1695	8745	10440		
Mean " "	94.2	70.0		24.2*	
I. notabilis(small)	1550	8890	10440		
Total Rank Score	1550	8890	10440		
Mean " "	86.1	71.1		15.0	
I. notabilis(large)					
Total Rank Score	1758	8682	10440		
Mean " "	97.7	69.5		28.2**	

Significance * p .05

** p .01

REFERENCES

AGRELL, I. 1941. Zur Ökologie der Collembolen. Opusc. ent. 3 (Suppl) pp 1-236

ALBRECHT, F.O., VERDIER, M., BLACKITH, R.E. 1958. Détermination de la fertilité par l'effet de groupe chez le criquet migrateur. Bull. biol. 92 pp 349-427.

ALEXANDER, F.E.S. & JACKSON, R.M. 1955. Preparation of sections for study of soil micro-organisms. Soil Zoology (ed. D.K. McE. Kevan) pp 433-441 Butterworths Scientific Publ., London.

ALLEE, W.C. 1931. Animal aggregations. University of Chicago Press, Chicago. 431p.

BAKER, E.W. & WHARTON, G.W. 1952. An introduction to acarology. The Macmillan Co., New York. 465p.

BERLESE, A. 1905. Apparechio per raccogliere presto ed in gran numero piccoli artropodi. Redia 2 pp 85-89.

BLACKMAN, G.E. 1942. Statistical and ecological studies in the distribution of species in plant communities. I. Dispersion as a factor in the study of changes in plant populations. Ann. Bot., Lond. N.S. 6 pp 351-370.

BLISS, C.I. & OWEN, A.R.G. 1958. Negative binomial distributions with a common k. Biometrika 45 pp 37-58.

BROWNLEE, K.A. 1949. Industrial experimentation. (4th edition). H.M.S.O. London. 194p.

CHAUVIN, P. 1941. Contribution à l'étude physiologique du criquet pèlerin et du déterminisme des phénomènes gregaires. Ann. Soc. ent. Fr. 110 pp 133-272.

CLAPHAM, A.R. 1936. Overdispersion in grassland communities and use of statistical methods in plant ecology. J. Ecol. 24 pp 232-251.

COLE, L.C. 1946. A theory for analysing contagiously distributed populations. Ecology 27 pp 329-341.

CROMBIE, A.C. 1942. The effect of crowding upon the oviposition of grain-infesting insects. J. exp. Biol. 19 pp 311-340.

CROWCROFT, P. & ROWE, F.P. 1958. The growth of confined colonies of the wild house-mouse (Mus. musculus L.): The effect of dispersal on female fecundity. Proc. zool. Soc. Lond. 131 pp 357-365.

CURTIS, J.T. & McINTOSH, R.P. 1950. The interrelations of certain analytic and synthetic phyto-sociological characters. Ecology 31 pp 434-455.

DENIS, J.R. 1949. Ordre des Collemboles. Traité de Zoologie (ed. P.P. Grassé) 9 pp 113-159.

EDWARDS, C.A.T. 1955. Simple techniques for rearing collembola, symphyla and other small soil-inhabiting arthropods. Soil Zoology (ed. D.K. McE. Kevan) pp 412-416. Butterworths Scientific Publ. London.

ELLIS, P.E. 1953. Social aggregation and gregarious behaviour in hoppers of Locusta migratoria migratoriodes (R & F). Behaviour 5 pp 225-260.

—— 1956. Differences in social aggregation in two species of locust. Nature, Lond. 178 pp 1007.

—— 1959. Learning and social aggregation in locust hoppers. Anim. Behav. 7 pp 91-106.

FISHER, R.A. 1930. Statistical methods for research workers (3rd edition). Oliver and Boyd, Edinburgh. 283p.

FISHER, R.A. & YATES, F. 1949. Statistical tables for biological agricultural and medical research. Oliver and Boyd, Edinburgh. 112p.

FORD, J. 1937. Fluctuations in natural populations of Collembola and Acarina (Part 2). J. Anim. Ecol. 7 pp 350-369.

FRACKER, S.B. & BRISCHLE, H.A. 1944. Measuring the local distribution of Ribes. Ecology 25 pp 283-303.

GISIN, H. 1944. Hilfstabellen zum Bestimmen der holarktischen Collembolen. George & Cie, Basel. 130p.

—— 1960. Collembolenfauna Europas. Museum d'histoire naturelle, Geneva. 312p.

GLASGOW, J.P. 1938. A population study of subterranean soil collembola. J. Anim. Ecol. 8 pp 323-353.

GLEASON, H.A. 1920. Some applications of the quadrat method. Bull. Torrey. bot. Cl. 47 pp 21-33.

GOTO, H.E. 1960. Facultative parthenogenesis in collembola (Insects). Nature, Lond. 188 pp 958-959.

GREIG-SMITH, P. 1952. The use of random and contiguous quadrats in the study of the structures of plant communities. Ann. Bot., Lond. N.S. 16 pp 293-316.

—— 1961. Data on pattern within plant communities. I. The analysis of pattern. J. Ecol. 49 pp 695-702.

HAARLØV, N. 1953. A microscopical technique for studying the undisturbed texture of soils. Oikos 4 pp 44-57.

—— 1958. Vertical distribution of mites and collembola in relation to soil structure. Soil Zoology (ed. D.K. McE. Kevan) pp 167-178. Butterworths Scientific Publ. London.

—— 1960. Microarthropods from Danish soils. Oikos Suppl. 3 pp 7-176.

HANDSCHIN, E. 1926. Collembola - Springschwänze. (ed. P. Schulze) Biologie der Tiere Deutschlands 25 (20) pp 7-56.

HASKELL, P.T. 1956. Hearing in certain orthoptera. 1. Physiology of sound receptors. J. exp. Biol. 33 pp 756-766.

HUGHES, R.D. 1958. The study of aggregated populations. (Research methods in soil zoology) Proc. Colloquium of International Society of Soil Science.

JUDD, W.W. 1949. Aggregations of the Snow Flea, Achorutes socialis Uzel, recurring over three years. Canad. ent. 82 pp 84-85.

KERSHAW, K.A. 1961. Association and co-variance analysis of plant communities. J. Ecol. 49 pp 643-654.

KLINGLER, J. 1959. Anziehung von Collembolen und Nematoden durch Kohlendioxyd-Quellen. Mitt. schweiz. ent. Ges. 32 pp 311-316.

LACK, D. 1954. The natural regulation of animal numbers. The Clarendon Press. Oxford. 340p.

LEFKOVITCH, L.P. 1961. Food quantity and density effects in pre-adult Cryptolestes turcicus (Grouv.). Proc. R. ent. Soc. Lond. (C) 26 pp 9,10.

LEUTHOLD, R. 1961. Vergleichende Untersuchungen der Tierwelt verschiedener Wiesenböden in ober bayerischen Raum, unter besonderer Berücksichtigung der Collembolen. Z. angew. Ent. 49 pp 1-49.

LIPORSKY, L.J. 1953. Improved techniques for rearing chigger mites. Ent. News 64 pp 4-7.

LONG, D.B. 1955. Observations on sub-social behaviour in two species of lepidopterous larvae, Pieris brassicae L. and Plusia gamma L. Trans. R. ent. Soc. Lond. 106 pp 421-437.

MACFADYEN, A. 1957. Animal ecology. Pitmans and Sons Ltd., London. 264p.

—— 1961. Improved funnel-type extractors for soil arthropods. J. Anim. Ecol. 30 pp 171-184.

MACLAGAN, D.S. 1932. An ecological study of the Lucerne Flea (Sminthurus viridis Linn.) I and II. Bull. ent. Res. 23 pp 101-145, 151-190.

MACLAGAN, D.S. & DUNN, E. 1936. The experimental analysis of the growth of an insect population. Proc. roy. Soc. Edinb. 55 pp 126-139.

MATSUDA, T. 1953. Some notes on the reaction of Hypogastrura sp. to coloured papers arranged in a farm area. Ecol. Rev., Sendai 13 pp 179-181.

MCGINNIES, W.G. 1934. The relation between frequency index and abundance as applied to plant populations in a semi arid region. Ecology 15 pp 263-282.

MILNE, S. 1960. Studies on the life history of various species of Arthropleone Collembola. Proc. R. ent. Soc. Lond. (A) 35 pp 133-140.

MINDERMAN, G. 1956. The preparation of microtome sections of unaltered soil for the study of soil organisms in situ. Plant and Soil 8 pp 42-48.

MOCHIZUKI, M. 1952. On the chemotropism of Onychiurus yagii Kinoshita to carbohydrates and other substances. Oyo-Konyu 7 pp 165-168.

MUKERJII, D. 1932. Description of a new species of Collembola and its anatomy. Rec. Indian Mus. 34 pp 47-79.

NIELSON, C.O. 1954. Studies on Enchytraeidae. 3. The microdistribution of Enchytraeidae. Oikos 5 pp 167-178.

NORRIS, M.J. 1950. Reproduction in the African Migratory Locust (Locusta migratoria migratoriodes R & F) in relation to density and phase. Anti-Locust Bull. 6 47p.

—— 1952. Reproduction in the Desert Locust (Schistocerca gregaria Forsk) in relation to density and phase. Anti-Locust Bull. 13 49p.

—— 1959. Reproduction in the Red Locust (Nomadacris septemfasciata Serville) in the laboratory. Anti-Locust Bull. 36 46p.

ODUM, H.T. & ALLEE, W.C. 1954. A note on the stable point of populations showing both intraspecific cooperation and disoperation. Ecology 35 pp 95-97.

OGEL, S. 1957. The integument of Folsomia candida. Thesis for D.I.C. (No. 260) Imperial College, London.

PACLT, J. 1956. Biologie der primär flugellosen Insekten. Gustav Fischer Verlag, Jena. 258p.

PARK, O. 1949. A notable aggregation of collembola. Ann. ent. Soc. Amer. 42 pp 7-9.

PARK, T. 1932. Studies in population physiology: the relation of numbers to initial population growth in the flour beetle Tribolium confusum Duval. Ecology 13 pp 172-181.

PEARL, R. 1932. The influence of density of population upon egg production in Drosophila melanogaster. J. exp. Zool. 63 pp 57-84.

PUMPHREY, R.J. 1940. Hearing in insects. Biol. Rev. 15 pp 107-132.

QUENOUILLE, M.H. 1959. Rapid statistical calculations. Hafner Publication Co. Ltd., London. 35p.

RAPOPORT, E.H. 1959. Algunos aspectos de la biologia de suelos. Universidad National del Sur, Bahia Blanca. 23p.

RETZLAFF, E.G. 1938. Studies in population physiology with the albino mouse. Biol. gen. Wien 14 pp 238-265.

RIPPER, W. 1930. Champignon-Springschwänze. Biologie und Bekämpfung von Hypogastrura manubrialis Tullbg. Z. angew. Ent. 16 pp 546-584.

ROMEL, L-G. 1926. Bemerkungen zum Homogenitätsproblem. Svensk bot. Tidskr. 20 pp 441-455.

—— 1930. Comments on Raunkiaer's and similar methods of vegetation analysis and the law of frequency. Ecology 11 pp 589-596.

SALT, G. & HOLLICK, F.S.J. 1946. Studies of wireworm populations. II. Spatial distribution. J. exp. Biol. 23 pp 1-46.

SEARLS, E.M. 1928. A simple method for life history studies of root feeding arthropods. J. agric. Res. 36 pp 639-645.

SKELLAM, J.G. 1952. Studies in statistical ecology. I. Spatial pattern. Biometrika 39 pp 346-362.

SNEDECOR, G.W. 1956. Statistical methods. (5th edition). Iowa State College Press, Ames, Iowa. 534p.

SMIRNOV, E. & POLEJAEFF, W. 1934. Density of population and sterility of the females in the coccid Lepidosaphes ulmi L. J. Anim. Ecol. 3 pp 29-40.

SOLOMON, M.E. 1957. Estimation of humidity with cobalt thiocyanate papers and permanent colour standards. Bull. ent. Res. 48 pp 489-506.

STREBEL, O. 1929. Biologische und Physiologische Untersuchungen un Hypogastrura purpurascens und Sminthurimus niger (Apt., Coll.). Zool. Anz. 84 pp 97-107.

—— 1932. Beiträge zur Biologie, Ökologie und Physiologie einheimischer Collembolen. Z. Morph. Ökol. Tiere 25 pp 31-53.

TAYLOR, L.R. 1961. Aggregation, variance and the mean. Nature, Lond. 189 pp 732-735.

TINSLEY, J. 1952. Methods for assessing the organic matter status of soils. Trans. int. Soc. Soil Science (Commissions II & IV) 1 pp 22-30.

TULLGREN, A. 1918. Ein sehreifacher Auslesapparat für terricole Tierformen. Z. angew. Ent. 4 pp 149-150.

UTIDA, S. 1941. Studies on experimental population of the Azuki Bean Weevil (Callosobruchus chinensis L.) I. The effect of population density on the projeny populations. III. The effect of population density upon the mortalities of different stages of life cycle. Mem. Coll. Agric. Kyoto 48 pp 1-30, 49 pp 21-42.

WATERS, W.E. 1959. A quantitative measure of aggregation in insects. J. econ. Ent. 52 pp 1180-1184.

WATT, K.E.F. 1960. The effect of population density on fecundity of insects. Canad. Ent. 92 pp 674-695.

WHARTON, G.W. & CARVER, R.K. 1946. Food of nymphs and adults of Neoschöngastia indica (Hirst). Science 104 pp 76,77.

WHITFORD, P.B. 1949. Distribution of woodland plants in relation to successive and clonal growth. Ecology 30 pp 199-208.

ZAHER, M.A. & LONG, D.B. 1959. Some effects of larval population density on the biology of Pieris brassicae L. and Plusia gamma L. Proc. R. ent. Soc. Lond. (A) 34 pp 97-109.