BIOLOGY OF SOME DIPLOPODA, WITH SPECIAL REFERENCE TO CYLINDROIULUS PUNCTATUS ~~(LEACH)~~.

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by

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ABSTRACT.

Cylindroiulus punctatus, *Polydesmus angustus* and *Tachypodoiulus niger* are the common millipedes of deciduous woodland floor. Of the three species, *C. punctatus* is specially interesting, since it spends part of its life cycle in leaf litter and part inside the bark of rotten logs. Eggs are laid below the bark and the following three instars also live here. The fourth instars leave the bark and go into litter: here they moult three times to give fifth, sixth and seventh instars. The seventh instars undergo development either in litter or beneath the bark of logs. They moult to give the eighth instars, which in females all become sexually mature, although they continue to moult afterwards. The males cease to moult at eighth instar after attaining sexual maturity.

Two peaks occur in the activity of *C. punctatus* in litter, one in spring and the other in autumn. The first peak occurs at the time of the migration of the adults from the litter into the bark for oviposition, and the second peak when the adults migrate back from the logs into the litter.

In the field, the whole life cycle is completed in about three years, but in the laboratory at a constant temperature of 23°C., and under constant darkness, the life cycle is completed in about two years. Laboratory and field observations show that this species does not show any special preference for leaf or bark of any deciduous tree, as long as they are sufficiently rotten. Distribution of the species is regulated by the availability of the oviposition sites, food and humid surroundings.

Polydesmus angustus is also found in wooded areas rich in decomposing litter. It shows only one peak of activity during its breeding period. The life cycle of P. angustus is more simple than C. punctatus, and is completed in the nature in about 12-14 months. In the laboratory at a constant temperature of 23°C., the life cycle is completed much earlier. It does not migrate into the logs for oviposition, instead it constructs nests on the ground in which eggs are deposited. P. angustus also feeds on the rotten leaves of any deciduous tree, and diet has considerable effects on the duration of its life cycle and the size of the adults.

<u>Tachypodoiulus niger</u> has a wider range of distribution and food preference than either of the two species. It is found both in grassland and in areas rich in decomposing vegetation. It also shows a single peak of activity.

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INTRODUCTION.

Ovington (1962) describes the woodland as most complex of all terrestrial communities. Each organic layer in the woodland supports a variety of animal life, and has its own characteristic microclimate which regulates the ecology of the animals. The role of millipedes in the woodland ecosystem has been discussed by Drift (1951), Schmidt (1952), Kuhnelt (1950), Kubiena (1953, 1955), Gere (1956), and Nielsen (1962). Blower (1955, 1956) has reviewed the biology of the British millipedes and their importance as soil animals. Blower (1955) has distinguished three main habitats in the woodland, which support millipede populations. These are: (1) living aerial parts of the vegetation on the floor, (2) litter and soil layers in the floor, and (3) under the bark and in the rotten wood of tree stumps and logs. In the woodland around the Royal Holloway College compound these three habitats are distinctly represented and preliminary samplings of these habitats indicated the presence of at least eight species of millipedes. These are, Cylindroiulus punctatus (Leach), Polydesmus angustus Latzel, Tachypodoiulus niger (Leach), Polymicrodon polydesmoides (Leach), Glomeris marginata Villers, Schizophyllum sabulosum (Linne), Blaniulus guttulatus (Bosc), and Iulus scandinavius Latzel. Of these, the first three were very common, while others appeared in the samples periodically. The fallen oak logs also supported a rich millipede population, of which C.punctatus and Proteroiulus fuscus (Am Stein) were very common.

Abundance of C.punctatus both in the litter and beneath the bark of oak logs, and the possibilities of its migration into the subcortical spaces of the bark - (Blower, private communication) - prompted the present investigation into the seasonal variation of its population in these two habitats and their importance in the life cycle of the species. Sheer numbers of C.punctatus, inside logs and in litter, suggest the importance of the species in the dynamics of woodland ecosystem, but very little quantitative information on its abundance and distribution in woodland is available. In the present work, attempts have been made to study the seasonal variation in the population of C.punctatus in the woodland floor and to note its significance in the biology of the species. An experimental approach has also been used to study the life cycle and behaviour of C.punctatus under different conditions and to correlate them, as far as possible, with the observed facts in nature.

The seasonal activity and life cycle of Polydesmus angustus have been investigated for comparison with C.punctatus. Finally, the biology of these two species have been supplemented by a study of the seasonal activity of Tachypodoiulus niger.

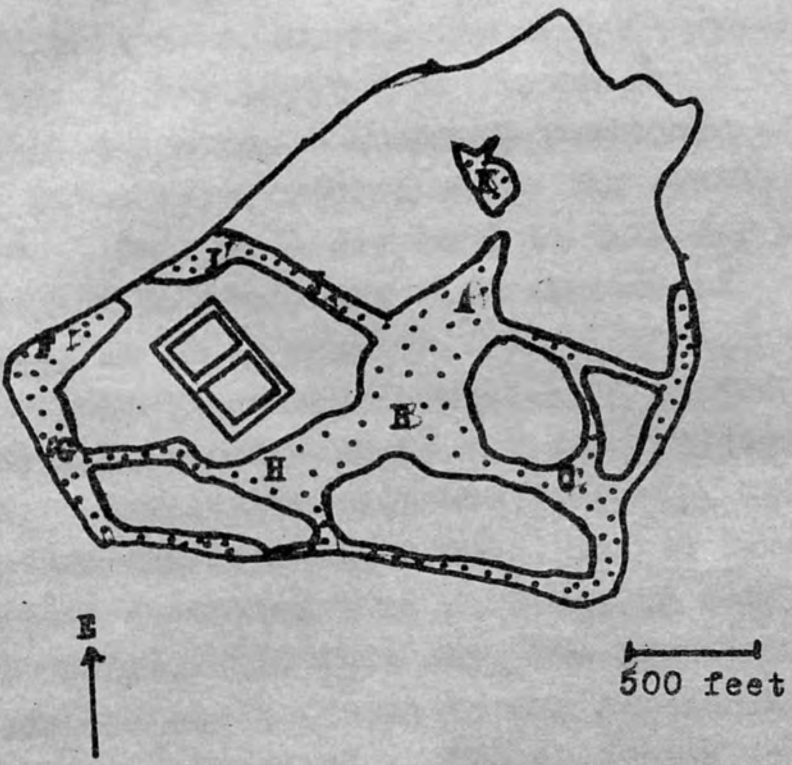
The first four sections of the present thesis deal with various aspects of the field and experimental studies on C.punctatus, section five deals with the life cycle of P.angustus, and in the last section, seasonal activity of these two species and T.niger has been discussed.

DESCRIPTIONS OF STUDY AREAS AND FIELD SAMPLING.

The areas selected for the present study and the type of field work carried out in different areas are described below. Details of the methods employed for different investigations will be given in appropriate parts.

Area A. Located on the South-East side of the Royal Holloway College grounds. The area was rich in oak litter mixed with some beech leaf litter. The whole area was divided into hundred quadrates, each of two feet square. The quadrates were numbered one through hundred, the number of each quadrate being determined by a table of random numbers. The whole area was mapped showing the position and number of each quadrate, and in the field wooden stakes were planted at appropriate intervals to determine the location of different quadrates. The positions of these stakes were also recorded in the map. The quadrate numbers were written down on small cards and they were thoroughly "mixed" in a box. At the time of taking a smaple, one of these cards was drawn and the quadrat~~e~~ bearing that number was sampled. Macfadyen (1957) has pointed out the advantages of this method in long term samplings. This area was sampled for the survey of the population of the adults and immature instars of C.punctatus in the litter at different times of the year.

Area B. This area was also located in the college compound close to the area A and had the same feature as the former. It measured two hundred



Map showing the locations of sampling areas in the Royal Holloway College grounds.
Dotted areas indicate woodland.

feet square and the quadrates were laid down in the similar manner as before. This area was sampled to study the vertical distribution of the adults and immature instars of C.punctatus along the profile of the woodland floor: i.e. in the litter, humus and underlying soil. Sampling sites were selected in the same way as before.

Area C. This area, having the same features as areas A and B, was located on the southern side of the college compound. Quadrate positions and sampling sites were determined in the similar way as before. This area was used to take day and night samples to study the distribution of C.punctatus in these samples.

Area D. This place was located in a wooded area about one mile south-west of the main college compound. Since this area was very big, with large rotten oak logs all around, it was divided into hundred quadrates each covering an area of six feet square. In this way, the positions of both large and small logs in any particular quadrate were determined. The quadrates were numbered by suing a table of random numbers and in mapping the area the position of each oak log in the quadrates was recorded. This area was used for regular sampling of the C.punctatus population in the oak logs and in the surrounding litter. Sampling sites were determined by the method described earlier. Litter was also collected from an area of one foot square within each quadrate, the sampling position being the centre of each quadrate, or the corners (Macfadyen, (1957), depending on the position of the logs in the quadrate.

Area E. This area was located in Burhnam Beeches, about five miles north of the college. The whole area had a rich canopy of oak (Quercus robur L) beech (Fagus sylvaticus L) and birch (Betula alba L). Sampling of the oak logs was done mostly in places with a homogenous canopy of oak trees. As usual, these areas were mapped, divided into quadrates of six feet square and the position of logs were noted in these quadrates. The number of quadrates varied from place to place, depending on the size of the areas investigated.

Areas F-K. These six small areas were located around the college compound, where pit fall traps were sunk to study the activity of different species in litter. All these areas were rich in oak litter, mixed with some beech litter.

Areas L-O. In the text these four areas have been described as biotope A, B, C and D respectively. They were located two miles south of the main college compound. Area L was a wooded terrain with thick oak and beech litter and many logs around. The whole area appeared very shady owing to the presence of large oak and beech trees all around. Area M had the same feature as in L, but undergrowth of green ferns were very common. The area was not very shady. Area N was an open area with thin litter of oak, birch and beech. Patches of shrubs were very common all over the area. Area O was an open area in grassland close to Area L.

All these areas measured fifty feet square from side to side and twenty five pit fall traps were sunk in each of them. Selection of the quadrates for setting up the pit fall traps was done by using the table of random numbers.

In addition to the above areas of study, various experiments were carried out in small selected areas around or outside the college compound. Since no long term field work was carried out in them they will be mentioned in connection with the experiments with which they were associated.

SECTION I

Population characteristics of Cylindroiulus punctatus (Leach) in the woodland floor.

Introduction.

Populations of soil and litter inhabiting arthropods have been studied by various authors and Kuhnelt (1963) has reviewed all the available information on this subject. It appears from the literature that the population of microarthropods have received the attention of most of the authors, and the works of Beier (1950),Volz (1950, 1951), Macfadyen (1952, 1954), Murphy (1955), Knülle (1957) Edwards (1958), Karpinnen (1958), Jensen (1959), Dalenius (1960), Haarløv (1960), Hüther (1961), and Tarras-Wahlberg (1961) may be mentioned. Larger arthropods, including millipedes, have been studied by Drift (1951) in his long term samplings of the beech forest, and Paris and Pitelka (1962) have studied the population of the woodlouse *Armadillidium* in Californian grassland. However, literature has very little to say about the population of *Cylindroiulus punctatus* (Leach), though its biology has been described by Blower (1956). In the present investigation, the seasonal and diurnal variation in the population of *C.punctatus* in litter and its vertical movements along the woodland profile have been studied.

Methods.

I. Litter sampling.

Every month ten "one foot square" samples of litter were taken from the quadrates in Area A. Samples were collected before 10 a.m. Some difficulties were faced in the location of the sample sites and collection of the samples in winter. The sample size was always one foot square. In the laboratory each of these samples was processed by six small Tullgren funnels. Each of these funnels had a top diameter of 15 cm. and a depth of 20 cm. A sieve floor made of $\frac{1}{8}$th mesh hardware was installed in each to support the samples. Heat and light were provided by 25 wat bulbs fixed on the underside side of a covering roof of each funnel. Relatively high humidity in the funnel space below the sample was maintained, because the Haarløv passage (Haarløv, 1947) was narrow and the litter samples were usually moist. The humidity at this region was monitored by cobalt thiocyanate paper, a tehcnique developed by Solomon (1945, 1957), and was found to vary between seventy to eighty percent. The significance of maintaining a relatively high relative humidity in this region has been discussed by Macfadyen (1961). A period of three days was found sufficient to extract the adults and different instars of <u>C.punctatus</u> from the litter.

The efficiency of these funnels was tested by introducing known number of adults and different (IV - VII) instars of <u>C.punctatus</u> into litter, previously cleared of all millipedes by hand sorting. All of them were recovered from the collecting vessel at the end of sixty five hours, after desiccation of the litter began. Also the samples were hand sorted at the end of a three day treatment in the funnels. Only in a few cases were one or two adults obtained. It was, however, difficult to decide whether these animals died out of des~~s~~iccation in the funnels, or if they were already dead at the time of collecting the samples.

II. Litter, humus and soil sampling.

Simultaneous samplings of these three "zones" of the woodland floor were done four times every month to get some ideas about the seasonal variation in the vertical distribution of the adults and the range of distribution of different instars along this profile of the floor. The sample size was one foot square, and samples were taken from area B. After removing the litter, eight "Probes" each of 15 cm. in length, were introduced into the black humus layer. The humus was collected until the ends of these probes were reached and then further pushed into the soil layer. The humus was not always 15 cm., but most of it was sampled this way. Next the soil was spaded out until the end of the probes were reached. Samples from different layers were kept separately. Since sampling by this method left a large hole in the ground, the cards for area~~s~~ sampled were removed before subsequent drawings.

In the laboratory, the samples from different layers were desiccated separately in large Tullgren funnels. Each of these funnels was 30 cm. deep, with a top diameter of 30 cm. and a bottom diameter of 5 cm. The sample was supported on a sieve of hardware cloth of $\frac{1}{8}$th inch mesh. Heat and light were supplied by a 60 wat. bulb housed in the metal cowl above the funnel. When the samples were very wet, air circulation through the Haarlov passage (Haarlov, 1947) was increased by placing rubber tubing ($\frac{1}{2}$ inch in diameter) upright along one side of the funnel between the sample and the wall. This also prevented the condensation of water on the lower surface of the funnels. Relatively high humidity was always maintained on the lower side of the funnels below the samples and this was checked as in other funnels. Efficiency of these funnels was also confirmed by introducing known number of adults and different instars. Three days were sufficient for drying the litter, but five days were necessary for drying the humus and soil if they were wet. Millipedes and other arthropods were collected in small collecting tubes on the lower end of the funnels, containing seventy percent alcohol. Samples from different layers were hand sorted after they had been in the funnels.

These samples were collected before 10 a.m. Before collecting the samples, and also at other times, temperature in the three layers was determined by means of three quick registering mercury thermometers. pH of several samples from these zones was determined colorimetrically.

III. Day and night sampling.

Samples of litter were collected both by day and at night from area C. Four samples were taken every month from the one foot square quadrates in area C. Day samples were taken at 9 a.m. and the night samples were taken at about 12.00 midnight. Selections of the sampling sites were made at random as before. Quadrates for night samples were selected in the day and large wooden stakes were planted in them to identify the locations at night. These samples were extracted by large Tullgren funnels described before.

Results.

I. Litter Sampling.

I. Population density in litter. (Figs. 1.1 and 1.2).

An estimation of the seasonal variation in the population densities of the adults and immature instars of *C.punctatus* may be obtained from Table I.1. The figures, based on ten samples each month, would indicate that the density of the population tends to increase in certain months of the year. Absolute density of *C.punctatus* in the litter is admittedly difficult to determine from these samples, because of the vertical movements that the population undergoes in certain seasons of the year. Nevertheless, these figures would give an indication of the population fluctuations in the litter, though they represent the minimal density estimates. Friedman two way analysis of variance by ranks indicates a significant difference in the figures admitted in various columns.

Table 1.1. Litter population of the adults and immature instars of <u>Cylindroiulus punctatus</u> Leach.

Month	No.of samples	Mean (±S.E) no. of adults per one square foot sample.	Mean (±S.E.) no. of immature instars per one sq.foot sample.
Nov'61	10	9.0 ± 1.2	6.3 ± 0.45
Dec.	10	6.0 ± 0.75	4.5 ± 0.74
Jan'62	10	10.0 ± 1.23	7.8 ± 1.23
Feb.	10	10.8 ± 1.54	7.7 ± 0.95
Mar.	10	16.0 ± 1.57	8.5 ± 1.23
Apr.	10	17.0 ± 1.67	9.5 ± 0.80
May	10	14.4 ± 2.05	8.8 ± 0.84
June	10	12.0 ± 1.23	9.4 ± 1.45
July	10	7.0 ± 0.45	6.2 ± 0.65
Aug.	10	7.6 ± 0.58	5.0 ± 0.45
Sept.	10	13.0 ± 1.48	10.2 ± 1.85
Oct.	10	14.5 ± 1.34	9.3 ± 0.95
Nov.	10	11.4 ± 0.89	6.5 ± 0.85
Dec.	10	4.4 ± 0.45	1.8 ± 0.45
Jan'63	10	3.6 ± 0.87	1.1 ± 0.35
Feb.	10	6.4 ± 0.45	2.5 ± 0.75
Mar.	10	11.0 ± 1.75	8.5 ± 1.35
Apr.	10	9.2 ± 0.86	2.6 ± 0.36
May	10	8.6 ± 0.95	3.3 ± 0.74
June	10	5.0 ± 1.02	4.4 ± 0.74
July	10	4.4 ± 0.74	3.4 ± 0.38

It can be seen from this table that two peaks occur in the density of adult population round the

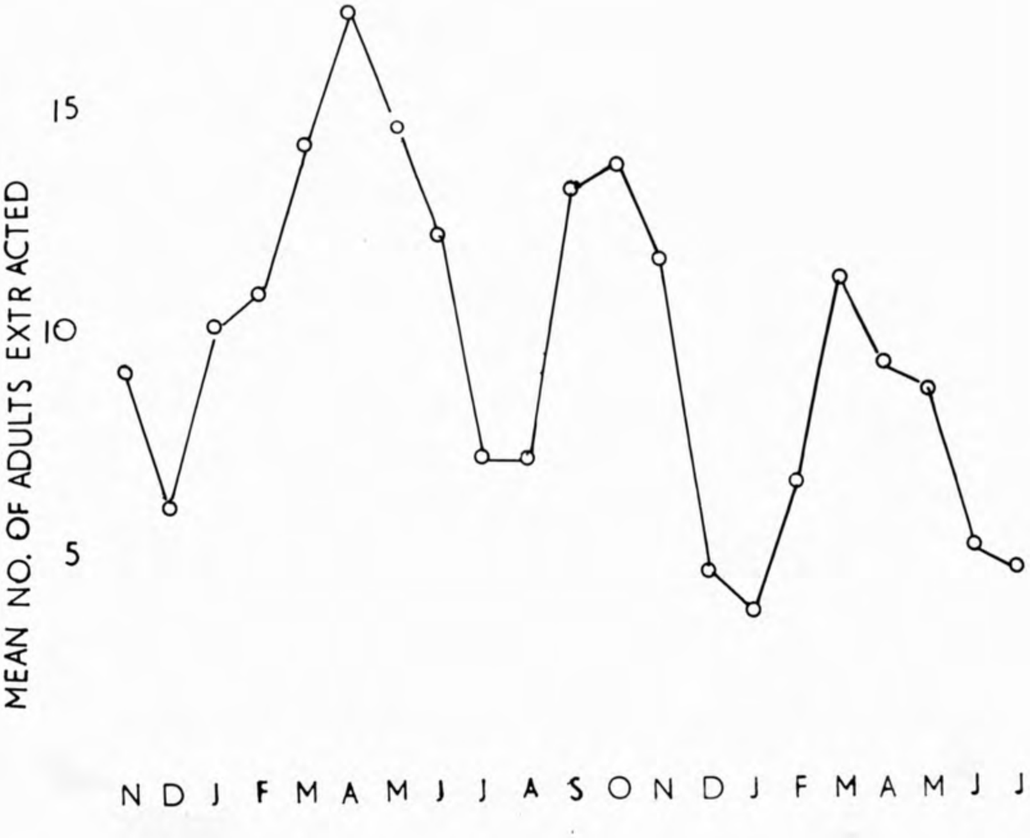


FIG. 1.1. Seasonal variation in the population of adult <u>Cylindroiulus punctatus</u> extracted from litter.

FIG. 1.2. Seasonal variation in the population of immature instars of <u>Cylindroiulus punctatus</u> extracted from litter.

year. One of these occurs in the spring, whilst the other occurs in the autumn. It is difficult to find such peaks with the immature instars, though their numbers per quadrate decreased in winter months, but in the summer of 1963 the population of immature instars remained very low.

2. Qualitative analysis of the population.

Some information about the sex ratio in the natural population of C.punctatus may be obtained from the results on litter sampling. The data presented in Table 1·2 shows the total number of adults obtained from ten samples each month and the percentage of males and females in each month's total. (Fig. 1.3).

Table 1.2. Sex distributions of the adults of Cylindroiulus punctatus (Leach) in the litter samples extracted.

Month	Total number of adults.	Percentage of Males.	Percentage of Females.
Nov'61	90	44.6	55.4
Dec.	60	41.6	58.4
Jan'62	100	45.0	55.0
Feb.	108	41.7	58.3
Mar.	160	46.8	53.2
Apr.	170	55.8	44.2
May	144	65.8	34.2
June	120	64.1	35.9
July	70	64.2	35.8
Aug.	76	47.3	52.7
Sept.	130	57.6	42.4
Oct.	146	52.0	48.0
Nov.	114	43.8	56.2
Dec.	44	43.1	56.9
Jan'63	36	38.8	61.2
Feb.	64	40.6	59.4
Mar.	110	40.9	59.1
Apr.	92	58.6	41.4
May	86	63.9	36.1
June	50	70.0	30.0
July	44	56.8	43.2

On the basis of monthly analysis it can be seen that during November 1961 to March 1962 a large number of females were present in the population. This picture was reversed in the following seven months, with males

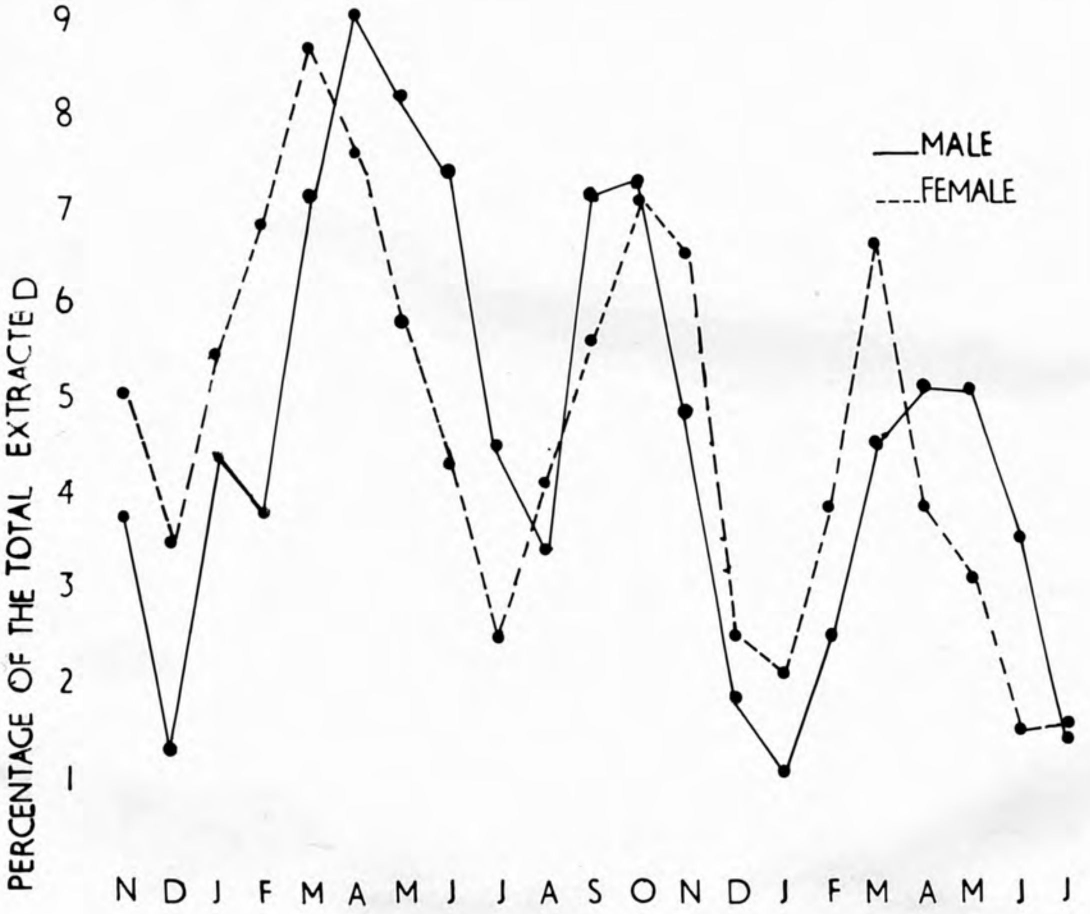


FIG. 1.3. Sex distribution in the adult population of _Cylindroiulus punctatus_ extracted from litter in different seasons.

appearing in large numbers in the samples, except in August 1962. There was an increase in female population again from November 1962 to March 1963, and this was followed by a peak in male population in the next four months. On a yearly basis, two peaks occur in the number of females in the litter population. One of them at the beginning of the year, from January to March, whilst the other occurs between October to December. The male peak occured in between these two phases. The number of male and female in the litter for every three months of 1962 have been calculated from Table 1.2 and are shown below.

Table 1.3. Distribution of male and female of *Cylindroiulus punctatus* (Leach) in litter in different periods of 1962.

Period	Total No.of males.	Total No.of females.	% of the total	
			Male	Female
Jan.-Mar.	110	208	34.7	65.3
Apr.-June	258	176	59.4	40.6
Jul.-Sept.	158	120	56.8	43.2
Oct.-Dec.	145	159	47.6	52.4

A considerable number of immature instars were obtained in each sample. Different instars were identified by counting the number of podous segments and total length, as was suggested by Blower (Private communication). The following key was used in identifying various instars.

Table 1.4. Characteristics of different instars of _Cylindroiulus punctatus_ (Leach).

Instar	No. of podous ring.	No. of apodous rings.	Range of total length.mm.
I	3	4	1.0- 1.3
II	6	5	1.3- 2.5
III	11	5-7	3.0- 3.5
IV	16-18	5-7	3.2- 5.2
V	21.25	6-8	5.4- 7.5
Males			
VI	29-31	6-7	6.5- 9.4
VII	34-38	6	9.0-11.6
VIII	41-44	3-4	13.8-16.0
Females			
VI	29-31	6-7	7.5- 9.0
VII	35-38	5	9.5-12.0
VIII	40-43	3-4	13.5-16.5
IX	42-48	2-3	16.5-19.0
X	45-50	4	19.2-21.0
XI	49-54	2	20.0-22.5
XII	51-56	2	23.5-24.5
XIII	54-58	3	25.5-27.2

Sex differentiation begins at the sixth instar. Both the male and female reach maturity at the eighth instar. The male ceases moulting after this stage, but the female continues to moult.

In the following analysis of the population of immature instars the total number of each instar obtained from ten samples per month is given.

Table 1.5. Distribution of immature instars of *Cylindroiulus punctatus* (Leach) in the litter.

Month	Total number of various instars present in the samples extracted.				
	Fourth instars	Fifth instars	Sixth instars	Seventh instars	Total
Nov'61	24	2	31	6	63
Dec.	20	3	17	5	45
Jan'62	31	20	23	4	78
Feb.	20	35	6	16	77
Mar.	5	43	7	30	85
Apr.	5	40	5	45	95
May	0	43	4	41	88
June	0	37	5	52	94
July	0	19	3	40	62
Aug.	0	5	35	10	50
Sept.	10	0	75	12	102
Oct.	27	0	60	5	93
Nov.	30	0	30	5	65
Dec.	11	0	7	0	18
Jan'63	2	4	3	2	11
Feb.	10	0	8	7	25
Mar.	5	35	5	25	85
Apr.	0	15	0	11	26
May	0	17	2	14	33
June	0	10	4	30	44
July	0	4	0	30	34

It becomes clear from Table 1·5 that fourth instars were present in the litter from September to March, fifth instars from January to July and sixth instars throughout the year - with the majority in August to September. Seventh instars were also present in the litter throughout the year with the largest number in March to July. Very few of the first three instars were obtained from these samples throughout the period of investigation.

II. Litter, humus and soil sampling.

(pp 15-16)

I. Measurement of physical conditions.

Hydrogen-ion concentrations of randomly selected samples from each of the three zones of the woodland floor are shown below. The analyses were done on different days and the figures indicate the range obtained with respect to eight samples per day.

Table 1.6. pH values of randomly collected samples from different layers of woodland floor.

Day no.	Litter layer	Humus layer	Soil layer
1	4.1-4.8	4.3-4.0	4.2-5.1
2	4.1-4.5	4.2-4.8	4.3-5.2
3	4.3-4.5	4.2-5.0	4.5-5.2
4	4.3-5.0	4.2-4.7	4.5-5.5
5	4.4-4.8	4.5-5.0	4.5-5.5
6	4.5-4.8	4.5-5.0	4.3-4.5
7	4.2-4.5	4.5-5.5	4.2-4.8

Though the pH values indicated wide range of variation in the samples, the litter layer appeared more acid than the humus and soil layers. The mean temperatures in these three zones in different months are presented in the following table. These figures are based on ten readings.

Table 1.7. Variation in the temperature (°C) of the three zones of the woodland floor.

Month	Mean temperature °C in (+S.E.)		
	Litter layer	Humus layer	Soil layer
Mar.	6.9±1.7	4.6±1.5	6.1±2.5
Apr.	8.2±1.2	6.6±2.4	8.5±1.2
May	13.5±2.5	12.7±3.0	11.7±2.3
June	16.2±2.5	15.0±2.8	14.2±2.5
July	16.1±1.2	15.8±1.8	14.8±2.4
Aug.	14.5±2.4	15.5±2.3	14.2±1.4
Sept.	13.6±2.5	12.8±1.5	11.8±1.2
Oct.	14.0±3.2	14.8±2.4	15.1±1.6
Nov.	8.2±1.2	10.2±1.8	7.6±2.3
Dec.	4.5±1.5	6.0±1.4	6.7±2.0
Jan.	1.8±0.9	3.0±1.2	4.4±1.5
Feb.	4.0±1.8	4.4±1.5	4.8±1.9
Mar.	6.2±1.8	6.0±1.8	7.4±2.3
Apr.	7.3±1.7	6.5±0.6	6.0±1.8
May	11.5±2.1	9.2±1.7	7.2±2.3
June	13.5±2.5	11.4±1.8	10.4±1.9
July	15.2±3.5	13.3±2.8	11.6±2.5

Temperatures in the different zones were, of course, dependent on the concomitant air temperatures and were also influenced by the precipitation and the amount of heat they absorbed from the sunlight. The canopy of vegetation in certain parts also influenced the temperature in different zones. However, it can be seen from the previous table that there was a winter range of temperature which increased with depth and a summer range of temperature which decreased with depth.

2. <u>Quantitative analysis of the population</u>.

Tables 1·8 and 1·9 show respectively the number of adult and immature instars obtained from the three zones of the woodland floor. (Figs. 1.4 to 1.6).

Table 1.8. Monthly variation in the numbers of adult *Cylindroiulus punctatus* (Leach) extracted from samples from three zones of woodland floor.

Mean (±S.E.) number of adults per quadrate of one foot square sample.

Month	No. of samples.	Litter layer.	Humus layer.	Soil layer.
Mar'62	4	15.0±1.5	11.7±1.8	10.0±1.0
Apr.	4	17.5±1.8	11.0±1.0	8.0±1.5
May	4	16.2±1.3	5.7±1.8	4.0±0.8
June	4	13.0±0.8	4.5±0.6	2.5±0.8
July	4	8.0±1.2	5.2±1.2	3.7±1.4
Aug.	4	6.2±2.0	2.5±1.5	2.0±0.5
Sept.	4	11.0±0.6	6.5±1.2	3.7±1.5
Oct.	4	12.0±1.5	8.7±1.5	7.2±1.3
Nov.	4	9.2±2.3	8.0±1.5	7.5±1.5
Dec.	4	4.5±1.2	5.5±1.2	8.5±1.5
Jan'63	4	3.7±1.5	5.0±0.8	10.0±2.3
Feb.	4	5.5±1.2	7.0±0.8	8.7±1.4
Mar.	4	9.2±2.3	9.0±1.2	10.2±1.5
Apr.	4	10.0±0.9	7.0±1.5	7.7±2.5
May	4	7.0±1.4	5.0±1.3	3.5±1.4
June	4	5.7±1.8	2.7±1.4	2.0±1.0
July	4	5.0±1.5	3.0±1.7	2.0±1.9

Friedman two way analysis of variance by ranks shows a significant difference ($P \geq 0.05$) exists in the number of adults extracted from different zones in various months.

Table 1.9. Monthly variation in the number of immature instars of <u>Cylindroiulus punctatus</u> (Leach) extracted from samples from three zones of woodland floor.

Mean (±S.E.) number of immature instars per quadrate of one foot square.

Month	No. of samples.	Litter layer.	Humus layer.	Soil layer.
Mar'62	4	5.2±1.5	4.2±1.2	1.2±0.8
Apr.	4	4.0±0.9	3.2±1.2	1.0±0.5
May	4	6.2±1.7	3.7±1.5	1.5±0.5
June	4	7.5±1.6	5.0±1.2	2.0±0.7
July	4	5.0±1.4	2.7±1.5	1.2±0.8
Aug.	4	2.5±1.6	2.0±0.4	1.0±0.08
Sept.	4	3.0±1.2	2.5±0.9	1.5±0.9
Oct.	4	4.5±1.9	2.0±0.5	1.0±0.05
Nov.	4	2.5±0.8	1.5±0.5	1.0±0.07
Dec.	4	2.0±0.5	1.7±0.7	0.75±0.01
Jan'63	4	2.5±1.8	3.7±1.5	2.0±0.8
Feb.	4	2.0±0.8	3.0±1.1	1.2±0.6
Mar.	4	2.0±0.6	2.5±1.3	1.0±0.6
Apr.	4	3.0±1.1	2.0±1.2	0.75±0.02
May	4	3.7±1.9	2.5±1.4	1.2±0.7
June	4	5.0±1.5	2.7±0.7	1.2±0.8
July	4	6.2±1.5	3.7±1.2	1.5±0.6

Figures for different layers in different months appeared to be significant when tested by Friedman two way analysis of variance by ranks ($P \geq 0.05$). It can be seen from Table 1.8 that in winter a large number of adults were obtained from the two lower zones, whereas, in spring and summer, more of them

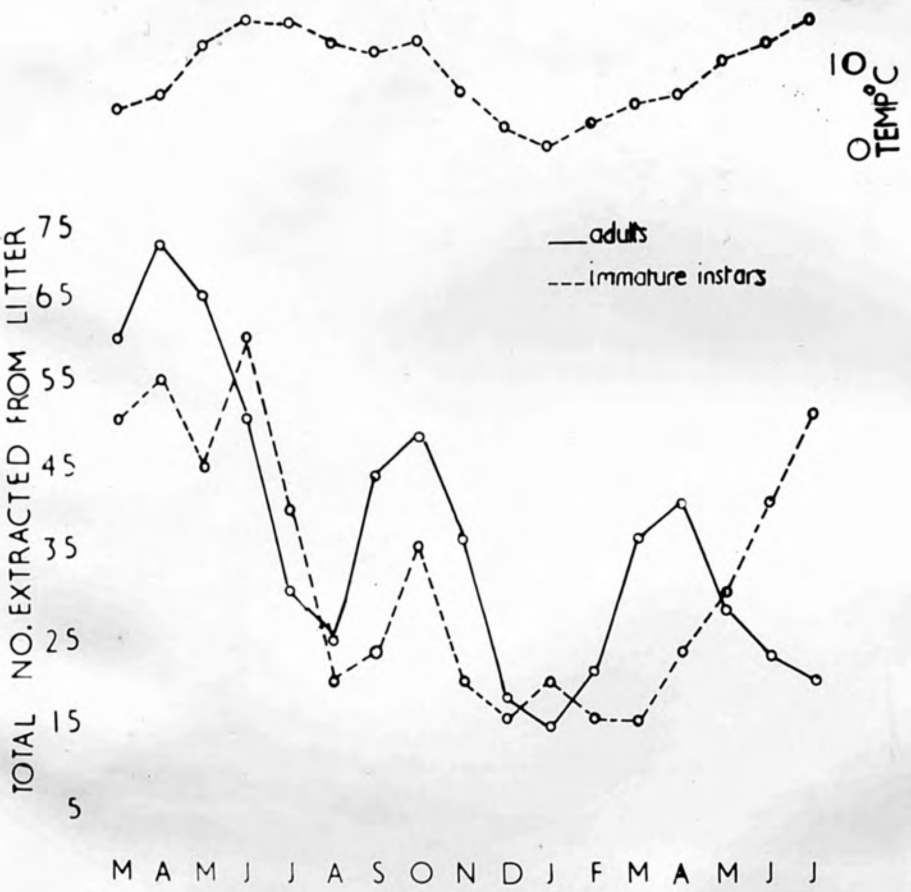


FIG. 1.4. Relationship between litter temperature and litter populations of adult and immature instars of Cylindroiulus punctatus in different seasons.

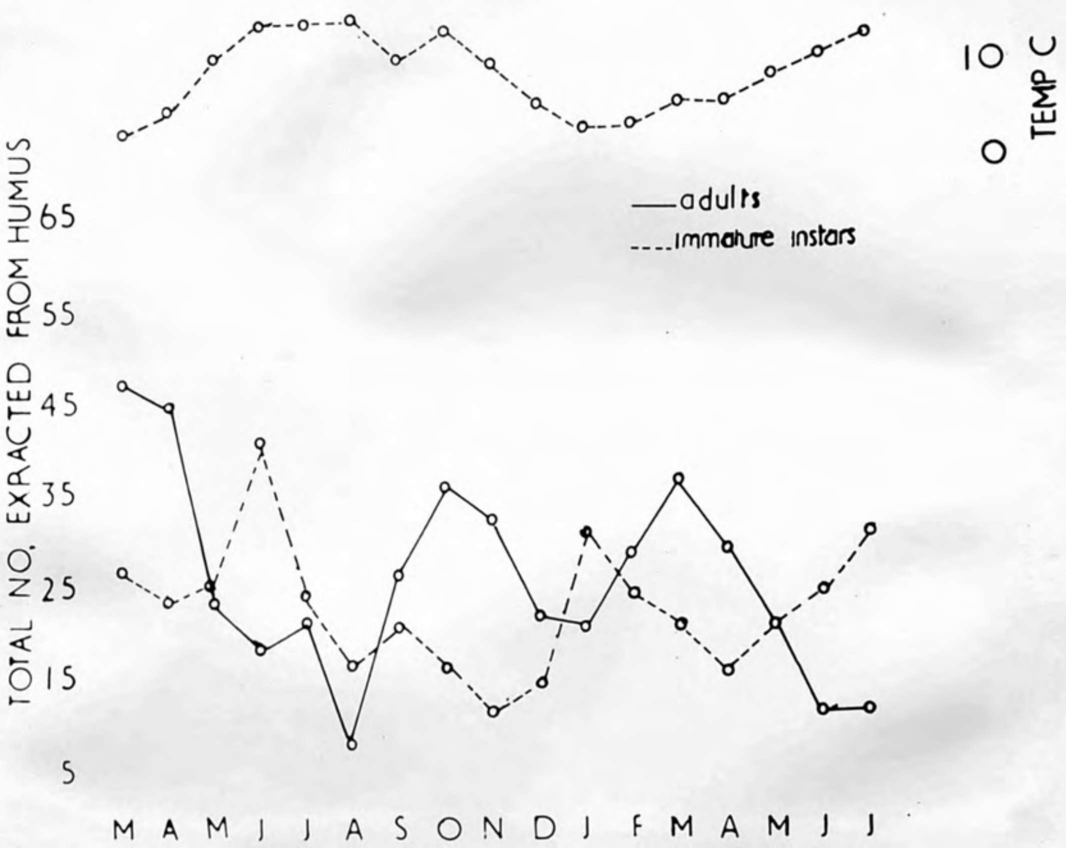


FIG. 1.5. Relationship between humus temperature and the populations of adult and immature instars of Cylindroiulus punctatus in humus in different seasons.

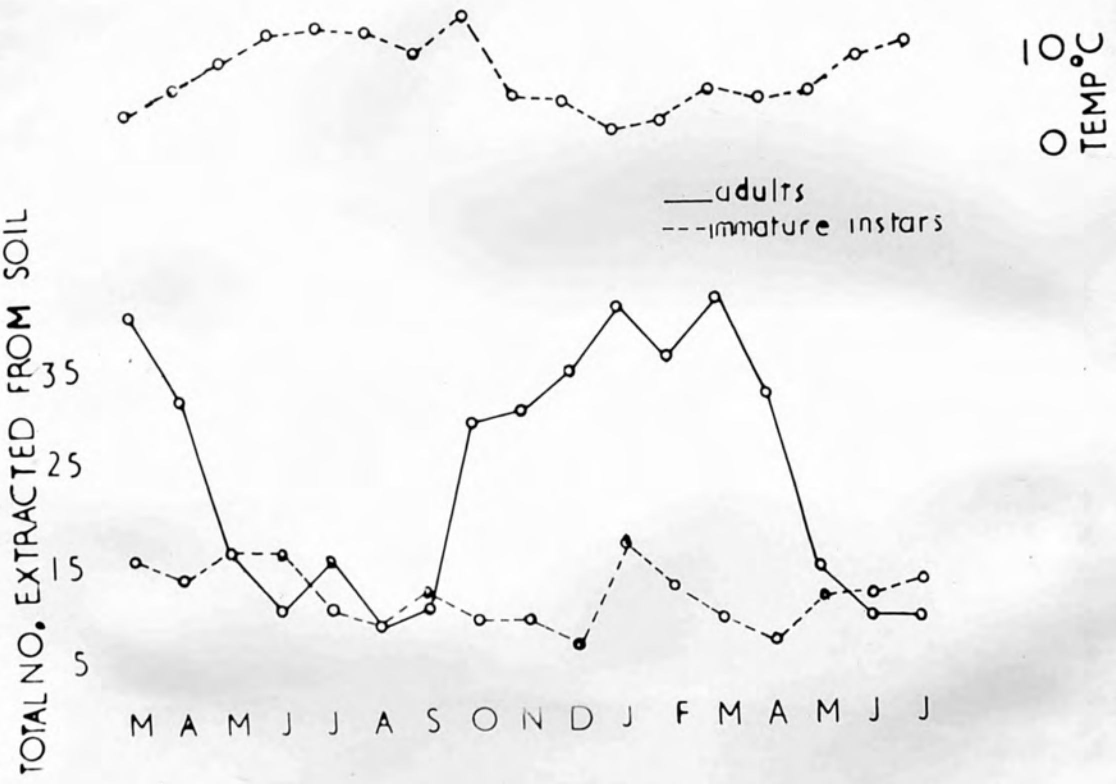


FIG. 1.6. Relationship between soil temperature and soil populations of adult and immature instars of _Cylindroiulus punctatus_.

were extracted from the upper zone consisting of litter. Table 1·9 shows relatively few immature instars were obtained from soil zones in different months and that their vertical distribution is mostly restricted between the humus and soil layers. Thus, a large number of immature instars were obtained from humus layer in winter, and from the litter in spring and summer.

3. Qualitative analysis of the population.

Percentage analysis of the sex of the adults, sampled from the three zones, is presented in Table 1·10, and it can be seen from this table that the sex ration in these populations follows the same general trend noted earlier.

Table 1.10. Sex distributions of the adults of <u>Cylindroiulus punctatus</u> (Leach) in samples from different zones of woodland floor.

T Total number of adults.
M% Percentage of males.
F% Percentage of females.

Month	Litter layer			Humus layer			Soil layer		
	T	M%	F%	T	M%	F%	T	M%	F%
Mar'62	60	41.6	68.4	47	43.5	56.5	40	50.0	50.0
Apr.	72	62.5	37.5	44	52.5	47.5	32	61.2	58.8
May	65	53.8	46.2	33	62.8	37.2	16	52.4	47.6
June	52	53.8	46.2	18	58.3	41.7	10	60.0	40.0
July	32	56.2	43.8	21	56.0	44.0	15	58.0	42.0
Aug.	25	56.0	44.0	10	60.0	40.0	8	50.0	50.0
Sept.	44	54.5	45.5	26	53.7	46.3	15	56.0	44.0
Oct.	46	45.8	54.2	25	48.5	51.5	29	48.2	51.8
Nov.	37	50.0	50.0	32	42.7	57.3	30	43.6	56.4
Dec.	18	44.5	55.5	22	45.4	54.6	34	47.2	52.8
Jan'63	15	44.6	55.4	20	40.0	60.0	40	43.6	56.4
Feb.	21	47.7	52.3	28	35.8	64.2	35	41.8	58.2
Mar.	37	41.8	58.2	36	45.4	54.5	41	38.5	61.5
Apr.	40	62.5	37.4	28	50.0	50.0	41	54.5	45.5
May	28	58.2	41.8	20	42.7	57.3	14	50.0	50.0
June	23	65.2	34.8	11	51.2	48.8	8	52.5	47.5
July	20	60.0	40.0	12	53.4	46.6	8	50.0	50.0

Distribution of various immature instars in the samples from different zones are shown in the following table.

Table 1.11. Distribution of the immature instars of <u>Cylindroiulus punctatus</u> (Leach) in samples from different zones of woodland floor.

Total number of various immature instars present												
Month	Litter layer				Humus layer				Soil layer			
instar	IV	V	VI	VII	IV	V	VI	VII	IV	V	VI	VII
Mar'62	10	23	7	11	3	11	5	8	0	2	5	8
Apr.	8	25	11	12	0	4	9	10	0	0	6	8
May	5	20	5	15	0	12	4	9	0	5	2	9
June	0	25	5	30	0	20	6	14	0	7	1	8
July	0	15	5	20	0	8	4	10	0	0	2	8
Aug.	0	4	12	4	0	4	10	2	0	0	4	4
Sept.	8	2	10	4	4	0	8	8	0	0	8	4
Oct.	12	3	15	6	4	1	8	3	2	1	4	1
Nov.	10	1	5	4	6	0	4	2	0	1	6	1
Dec.	4	1	9	2	4	1	8	1	0	0	5	1
Jan'63	10	8	1	1	4	12	2	12	0	2	4	10
Feb.	7	7	1	1	4	2	8	10	0	0	4	8
Mar.	8	4	2	2	3	1	8	8	0	0	2	6
Apr.	3	12	1	8	2	7	3	4	0	0	0	6
May	0	12	6	12	0	8	4	8	0	2	1	7
June	6	12	2	20	1	12	2	9	0	4	0	6
July	0	20	8	22	0	10	6	14	0	4	2	6
Total	91	194	105	174	35	112	99	133	2	28	56	101

It is to be noted that the monthwise distribution of various immature instars follows the same general pattern noted in connection with the analysis of populations from litter. Percentage composition of each instar in the total population of immature instars extracted from these three zones is presented in the following table. It would appear from this table that fourth to seventh immature instars are fairly well represented in the litter samples, and the same is more or less true with the humus layer. However, the fourth instars are less represented in the humus layer. In the soil layer, the seventh instars are present in large numbers, the fourth instar practically being unrepresented.

Table 1.12. Numbers of the various immature instars of <u>Cylindroiulus punctatus</u> (Leach) present in the samples from different zones of woodland floor.

Zone	Total no. extracted	Percentage of various instars in the population.			
		Fourth instar	Fifth instar	Sixth instar	Seventh instar
Litter	564	16.1	34.3	18.4	30.8
Humus	379	9.2	29.5	26.1	35.0
Soil	187	1.0	14.9	29.9	54.0

III. Day and night sampling.

Results from day and night samples are presented in the following tables.

1. Quantitative analysis of the population.

The mean number of adults and immature instars calculated from the results of four samples per month, collected in the day and at night, is tabulated below.

Table 1.13. Monthly variation in the number of adult *Cylindroiulus punctatus* (Leach) extracted from litter sampled by day and at night.

Month	No. of samples.	Mean (±S.E.) no. per quadrate of one foot square.	
		Day samples	Night samples
Mar'62	4	10.5±2.5	12.0±1.2
Apr.	4	15.0±1.0	21.0±2.5
May	4	16.5±2.5	22.5±1.8
June	4	10.0±0.9	16.5±1.5
July	4	9.5±1.2	13.5±1.6
Aug.	4	8.5±1.0	10.0±0.9*
Sept.	4	9.0±1.1	10.5±1.1*
Oct.	4	11.0±1.3	14.0±1.2
Nov.	4	5.0±0.8	6.0±0.8*
Dec.	4	4.5±1.1	4.0±0.7*
Jan'63	4	5.0±0.5	6.0±0.6*
Feb.	4	7.5±1.5	7.0±1.1*
Mar.	4	8.5±1.2	11.5±1.3
Apr.	4	13.2±2.0	17.5±1.5
May	4	11.5±1.2	15.5±1.2
June	4	10.0±0.9	14.5±1.3
July	4	9.8±1.0	11.5±1.1

A "t test" applied to the data on day and night samples for different months separately indicates significant difference exists between these samples ($P \geq 0.05$) from March to August in 1962 and again from March to July in 1963. In other months (marked with asterisks) a significant difference did not exist.

Table 1.14. Monthly variation in the number of various immature instars of <u>Cylindroiulus punctatus</u> (Leach) extracted from litter sampled by day and at night.

Month	No. of samples	Mean (±S.E.) per quadrate of one ft.sq.	
		Day samples.	Night samples.
Mar'62	4	9.0±1.2	12.5±1.5
Apr.	4	10.5±1.3	12.5±1.3*
May	4	7.5±1.2	10.5±1.2*
June	4	12.5±1.3	12.5±1.5*
July	4	5.5±0.5	7.0±1.0*
Aug.	4	6.0±1.2	10.5±1.2
Sept.	4	5.0±0.9	6.0±1.4*
Oct.	4	5.0±1.0	11.5±1.5*
Nov.	4	3.5±1.2	8.5±2.4
Dec.	4	3.5±1.4	7.0±3.5
Jan'63	4	3.0±0.8	6.0±1.5
Feb.	4	7.0±1.5	6.0±1.2*
Mar.	4	5.0±1.3	7.5±1.5
Apr.	4	7.0±1.9	10.5±2.3
May	4	5.5±1.2	7.0±1.8*
June	4	4.5±1.4	8.5±3.2
July	4	4.0±1.2	5.5±1.2*

The data from different months was also tested by the "t test". Significant difference ($P \geq 0.05$) existed in the day and night samples of different months - except those marked with asterisks.

2. Qualitative analysis of the population.

In the following two tables sex analysis of the adults and the distribution of various immature instars are presented.

Table 1.15. Sex distributions of the adults of Cylindroiulus punctatus (Leach) in day and night litter samples.

T Total number of adults.
M% Percentage of males.
F% Percentage of females.

Month	Day samples.			Night samples.		
	T	M%	F%	T	M%	F%
Mar'62	42	43.6	56.4	48	42.0	58.0
Apr.	60	58.2	41.8	84	49.0	51.0
May	75	53.7	46.3	90	56.5	43.5
June	40	58.2	41.8	66	47.4	52.6
July	38	55.6	44.4	50	65.3	34.7
Aug.	34	52.6	47.4	40	58.5	41.5
Sept.	36	50.0	50.0	42	52.3	47.7
Oct.	44	43.5	56.5	56	50.0	50.0
Nov.	20	40.0	60.0	24	46.3	53.7
Dec.	18	42.0	58.0	16	50.0	50.0
Jan'63	30	41.8	58.2	24	47.5	52.5
Feb.	30	51.2	48.8	28	45.7	54.3
Mar.	34	46.5	53.5	46	43.5	56.6
Apr.	52	52.7	47.5	70	53.8	46.2
May	46	58.6	41.4	62	65.3	34.7
June	40	61.3	38.7	58	53.5	46.5
July	38	51.5	48.5	46	55.5	44.4

Table 1.16. Distribution of the immature instars of <u>Cylindroiulus punctatus</u> (Leach) in day and night litter samples.

Total no. of various instars in Day and Night samples.

D = Day
N = Night

Month/	IV		V		VI		VII	
Instar	D.	N.	D.	N.	D.	N.	D.	N.
Mar'62	6	7	10	20	10	8	10	15
Apr.	5	7	20	15	7	13	10	15
May	6	7	10	12	4	10	10	13
June	0	0	15	15	15	10	20	25
July	0	0	6	7	8	10	8	11
Aug.	0	0	8	12	10	6	6	24
Sept.	10	8	2	2	8	10	0	4
Oct.	12	15	0	5	8	20	10	16
Nov.	8	10	2	6	4	10	0	18
Dec.	9	7	1	2	3	6	1	13
Jan'63	6	8	2	2	2	5	2	9
Feb.	9	7	4	5	5	8	5	4
Mar.	4	5	8	10	5	6	5	9
Apr.	0	3	15	10	10	5	10	22
May	0	5	8	9	6	4	6	10
June	2	3	6	11	8	5	8	15
July	0	0	9	7	5	3	5	12

It is clear from these tables that the sex ratio and the distribution of different instars in these samples follow the same general trend noted earlier in connection with the sampling of litter. With the adults, significant difference occurs between the numbers obtained from the day and night samples in summer and spring, but with the immature instars the picture was somewhat different. Table 1.16 shows that various instars, except the seventh ones, were present in the day and night samples in more or less equal numbers. A significant difference between day and night samples usually occured at a time when there was a great difference in the distribution of seventh instars in the night samples.

Discussion.

The analyses of the litter population from the three sampling areas indicate that the adults of Cylindroiulus punctatus were present in the litter throughout the year, though in different numbers. There were two distinct peaks in the population of adults, one in spring and another in autumn. There is also evidence of a seasonal vertical migration of the adults. It would appear from results that in winter the adults gradually move from litter into humus and soil layers of the woodland floor. In spring, a reversal of the vertical movement occurs with more adults coming into litter from the lower layers. To a great extent, the vertical migration is related to the temperatures of the three layers. In winter, the humus and soil layers maintain higher temperatures than that of the litter, whereas in the spring and summer the soil layer shows a lower temperature than the two upper layers. In winter, C. punctatus migrates into the soil layer to avoid the relatively cooler surrounding of the litter layer. During spring and summer, the adults come up into the litter, where the temperature is higher than in either the humus or the soil layer. Dowdy (1944) also noted similar tendencies in invertebrates, including millipedes, to undergo periodic vertical migrations and correlated them with the temperature fluctuations. Schmidt (1952), however, believes that vertical migration in millipedes occurs in response to dry conditions.

The results from day and night samples indicate that in spring and summer, more adults were present in the night samples than in the day samples. This would suggest the abilities of the adults to make diurnal vertical movements through the profile of the woodland floor. It is impossible to say if all the adults from humus and soil layers were making these movements, but there cannot be any question that some of them were appearing in the litter at night and then retreated into lower zones before day break. The presence of this diurnal vertical movement makes the conception of three distinct populations of C. punctatus in soil, litter and humus layers rather doubtful, though in winter the results show that these populations were more stabilized in the three layers. On the basis of the results given in the present investigation, it may be suggested that a large number of adults stay in the lower zones of woodland during spring and summer days, and at night when the air temperature goes down and the relative humidity of the air rises, these adults come up from the lower zones into litter. Relatively small numbers of adults obtained from humus and soil layers during spring and summer would also indicate the tendencies of the adults to stay close to the surface of the litter, so that they could easily come into litter at night. Drift (1951) also records that millipedes become active on the surface of the litter at night. In winter large numbers of adults were present in the soil layer and no significant difference was noticable in the results from day and night samples of the litter. This would suggest that very little vertical movement occured during this period and that the populations in the three zones were more "stabilized".

The distribution of various immature instars in the litter population of C. punctatus followed the same general pattern in all the study areas. Only fourth, fifth, sixth and seventh instars were present in the litter, humus and soil samples. There was also evidence of the immature instars undergoing seasonal vertical movements through the woodland floor, but it can be seen from table 1.12 that only a few individuals of fourth and fifth instars were able to move below the humus layer. These instars are mostly present in the litter layer, and their numbers gradually decrease in the humus and soil layers. In fact, only the seventh instars are seen to be capable of making diurnal vertical movements, and a significant difference in the numbers of immature instars obtained from day and night samples occurs only when the seventh instars are unevenly distributed in the samples.

SECTION II

Population dynamics of Cylindroiulus punctatus (Leach) in oak logs.

Introduction.

A survey of available literature shows that while a considerable work has been done on the ecology of the insect fauna in the tree stumps, there is practically no reference to the ecology of the diplopods in tree stumps and logs. Blackman and Stage (1924) have studied the succession of insect fauna in hickory. Food relations of insects in pine stumps have been studied by Richards (1926), and Krogerus (1927) investigated the biology of insects associated with pine stumps in Finland. Savely (1939) has described the ecology of certain wood boring beetles in oak and pine logs, while the insect fauna associated with beech stumps has been discussed by Derksen (1941). Ecology of insect fauna in the pine stumps in England has been discussed by Wallace (1953). Recently, Rudinsky (1962) has reviewed the existing information on the ecology of bark beetles. Apart from insects, the activities of woodlice on aspen trees have been described by Den-Boer (1961). However, Blower (1958) mentions a number of species of diplopods living in the fallen tree stumps and logs, and Manton (1954, 1961) has studied extensively diplopod burrowing techniques in the wood. The present study deals with the ecology of Cylindroiulus punctatus (Leach) in oak logs and seeks to discover the role of this habitat in its life cycle.

Methods.

The field work was carried out in Areas D and E mentioned earlier.

A. Measurement of physical conditions inside logs.

1. Temperature.

Temperature recordings below the bark were made with thermocouples, constructed in the manner described by Macfadyen (1957). The galvanometer was calibrated against known temperatures. At the time of recording the bark temperatures, the air temperatures were also noted with the help of a quick registering mercury thermometer.

II. Moisture.

Samples of bark with wood (4 inches long and 1 inch in diameter) were removed from the logs in the field and were brought to the laboratory in air tight tins. Each sample was then weighed as soon as possible and was then dried at 105^{0}C. until constant weight for the sample was obtained.

III. Relative humidity.

The relative humidity in the sub-cortical spaces within the logs where the millipedes live was measured colorimetrically by small pieces of cobalt thiocyanate paper, a technique developed by Solomon (1945, 1957). Papers were kept in the sub-cortical spaces for about two hours and were then quickly immersed in liquid paraffin. In the laboratory, the papers were placed on a piece of white opal glass and were covered with another piece of clear glass. Next they were matched in a comparator. Since the matching was done at temperatures different from field, allowances were made for this from a table of corrections. The efficiency of this method was checked by exposing the papers to known humidities in the laboratories. In every case the papers were exposed in triplicate. Very close agreement was obtained from the replications (usually ± 3% relative humidity).

IV. Wood density of the rotteness of the logs.

A general idea of the "rotteness" of the logs was obtained by piercing a needle through the bark and noting the resistance that the bark offers to the needle. From this an idea of the "relative rotteness" of the logs was obtained. However, a better idea of the state of decay of the logs was obtained from the determination of the bulk density of the wood (Cartwright and Findlay, 1946). As the decay of the logs progresses the bulk density decreases, with very little change in the bulk volume i.e. the volume enclosed by the outer surface of the wood. A measurement of the bulk density will, therefore, give an indication of the amount of the decay that the log has undergone. The bulk density of a piece of wood is equivalent to the weight of the oven dry wood/bulk volume.

The bulk volumes of wood samples were determined by a method described by Campbell (1932). Fine sand is packed in a 25 ml. graduated cylinder and the volume is read after slightly tapping the top of the cylinder to settle the sand. The wood sample is next immersed in the sand and the difference between the first and second readings gives the bulk volume of the wood. Five readings were taken for each sample and the mean was used in the determination of the bulk density. The bulk volume can be estimated to 0.1 ml. The bulk density of each wood sample used in the moisture determination was worked out by the above method.

Every week ten wood samples were taken from the logs and examined for millipedes. From the determinations of the percentage of moisture content and bulk densities of these samples, an idea of the state of decay of the logs was obtained.

B. Sampling technique.

Every week one log was examined from each of the study areas. Sometimes more than one log was present in the same quadrate. In such cases, all the stumps in the quadrate were arbitarily numbered and the numbers were written down on cards. Next, one of these cards was drawn and the log bearing the number was sampled. If no millipedes were found in a log, a second selection was made. The logs without millipedes were usually not sufficiently decayed. Otherwise, all the logs in the study areas were considerably decayed.

Each log was sampled by dividing the whole surface into a number of six inch units extending round the upper and lower sides of the logs. A number of millipedes in the upper and lower sides of the sampling units were recorded separately. After recording the millipedes beneath the bark, the central "wood" was also examined.

Results.

A. Measurements of physical conditions inside logs.

I. Temperature.

Diurnal changes in the temperature inside a number of logs, recorded in various months, are graphically presented in Figs.2·1–2·4 It can be seen from these figures that the bark temperature varies considerably from the air temperature, though the latter has great influence on the diurnal variation in the temperature inside the bark. Thus, with the rise in the air temperature the bark temperature also tends to go up, and at night when the temperature of the air drops, there is also a corresponding decrease in the bark temperature. Graham (1925), Savely (1939), Haarløv and Peterson (1952) and Macfadyen (1957) also made similar observations in tree logs.

Graham (1925) states that temperature inside the bark does not only depend on air temperature, but also on several other factors. Chief of these are the intensity of solar radiation, colour and thickness of the bark and the incidence of the sun's ray on the bark surface. Fig.2·5 shows the difference in the temperature fluctuation in logs in open and in shaded area beneath a large oak tree.

It is clear from this figure that bark temperature in the logs in the shaded area fluctuate less than the logs in the open. Bark temperature of the logs exposed to direct sunlight for several hours in summer show that solar radiation has remarkable

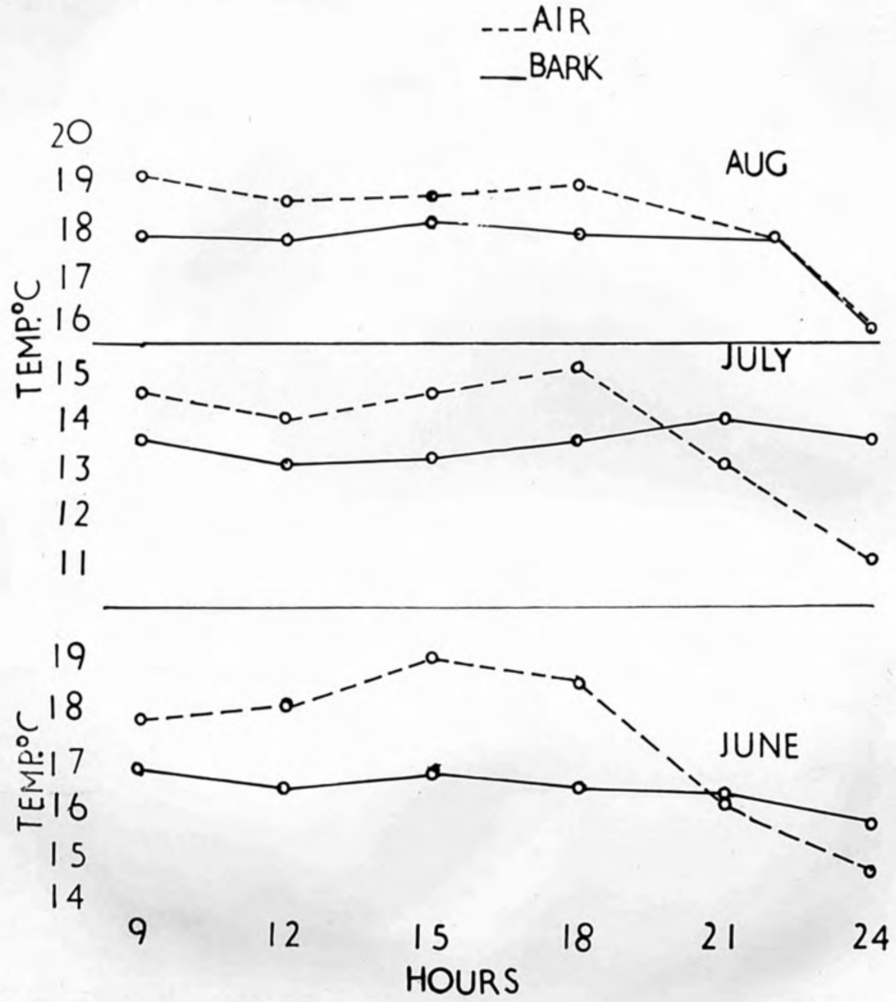


FIG. 2.1. Diurnal changes in air temperature and temperature inside the bark of oak logs on 5th June, 12th July and 15th August 1962.

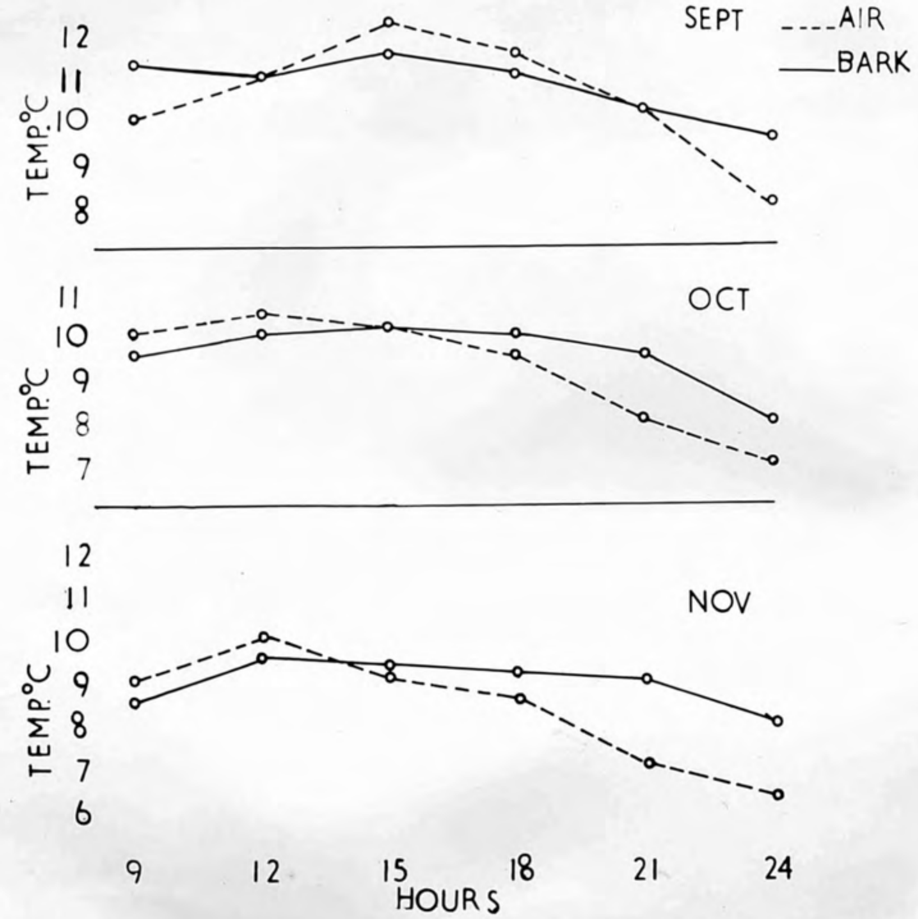


FIG. 2.2. Diurnal changes in air temperature and temperature inside the bark of oak logs on 10th September, 8th October and 12th November 1962.

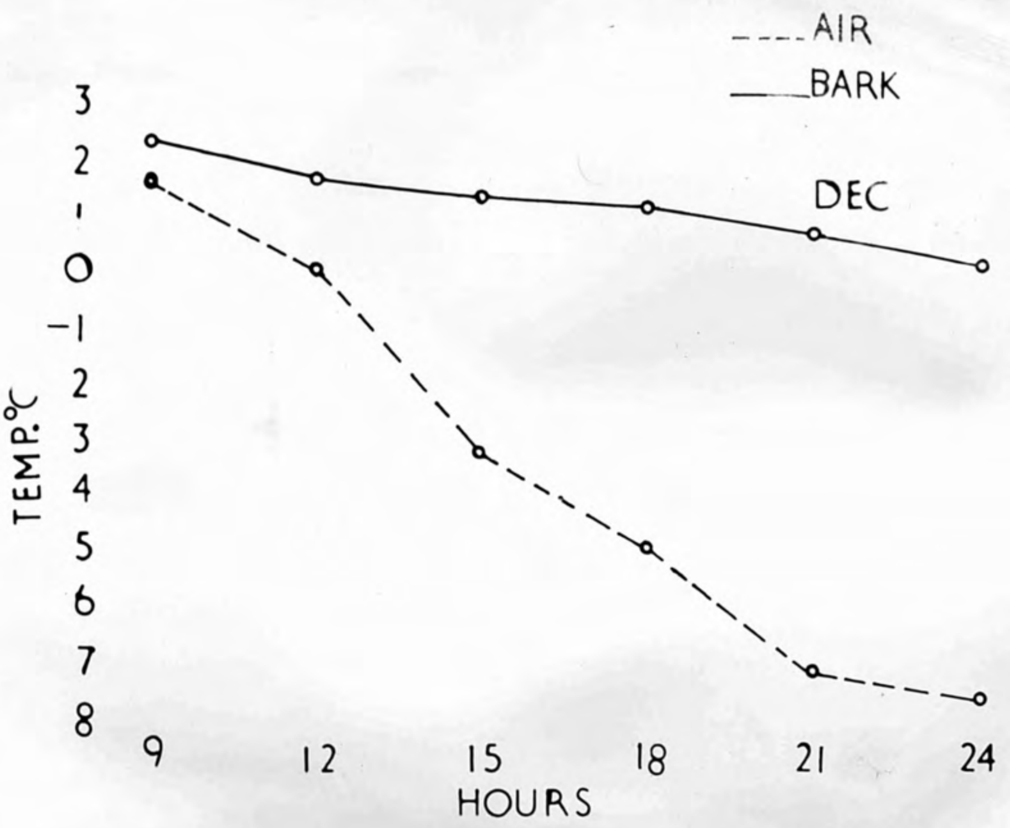


FIG. 2.3. Diurnal changes in air temperature and temperature inside the bark of oak logs on 23rd December 1962.

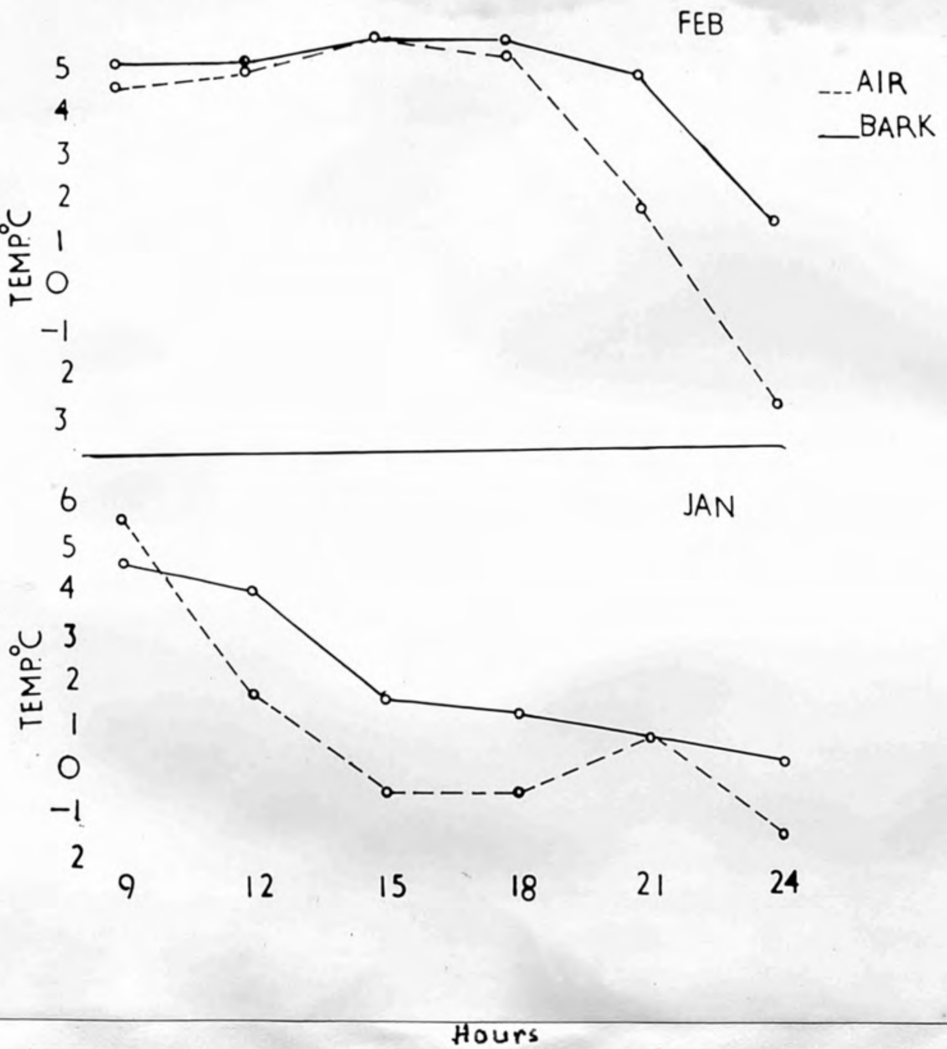


FIG. 2.4. Diurnal changes in air temperature and temperature inside the bark of oak logs on 13th January and 12th February 1963.

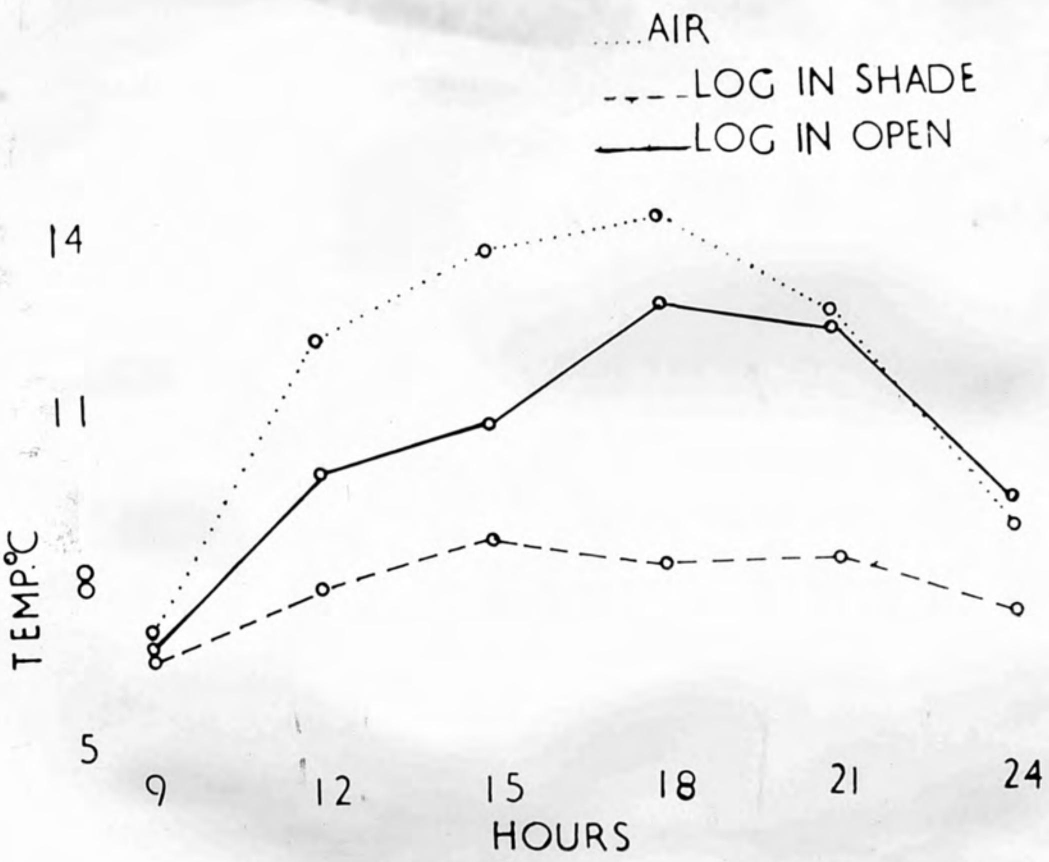


FIG. 2.5. Diurnal changes in air temperature and temperature inside the bark of oak logs in the open ahd in the shade.

effects in controlling the bark temperature. Bark temperature in logs exposed to direct sunlight was higher than those in the shade. The results obtained are very similar to those reported by Craighad (1920), Graham (1925), Gottlieb (1928) and Patterson (1930).

Bark temperature in the logs varies with air temperature at all seasons of the year. The average bark temperature is higher in summer than in winter. Usually, the bark temperature in summer tends to remain below the air temperature during the day, particularly if the sun is bright. At night, when the air temperature drops steadily, the bark temperature usually remains higher than the air temperature. In winter, however, the bark temperature tends to remain above the air temperature. Savely (1939) states that when the rotten oak stumps are covered with snow, the temperature inside the stumps did not go below $-1.5^{o}C$, even when the air temperature reached $-10^{o}C$. In the present study, it has been observed that when the air temperature goes several degrees below freezing point, the bark temperature usually stays above freezing point. However, when the air temperature remains below freezing point continuously for several days, as it did in December 1962 and January 1963, the bark temperature also reached freezing point. Savely (1939) made similar observations in pine stumps.

These recordings of the bark temperatures in the field give general indications of the temperature relations in oak logs. Diurnal and seasonal cycles of temperature fluctuations are very common, but these are considerably influenced by the location of the stumps and the weather.

II. Moisture.

Cartwright and Fidlay (1946) have studied the effects of decay on the density and moisture content of the wood. Savely (1939) found that the moisture content in the pine stumps he studied was seldom less than 50 percent. It has been noted in the present investigation that the moisture content of the oak logs, even under the same state of "rotteness", vary considerably depending on the location of the logs. Logs exposed to direct sunlight usually have low moisture content, whereas those in shaded areas have higher moisture content. Table 2.1 shows the moisture content of samples taken from upper side of logs in shaded and open area.

Table 2.1. Moisture content (percentage) of samples taken from oak logs in open and shaded areas.

	Percentage of moisture contents in samples from	
Sample no.	Open area.	Shaded area.
1	66	79
2	69	74
3	65	75
4	66	76
5	67	78
6	68	76
7	68	74
8	70	76
9	60	76
10	65	76

Samples taken from the lower side of the logs, in contact with the ground, usually showed higher moisture content than those from the upper side of the logs. The variations were greater in logs in the open than those in the shaded areas.

Table 2.2. Moisture content of samples taken from upper and lower sides of oak logs under same condition of decay.

	Percentage of moisture content of			
	Logs in open.		Logs in shade.	
Sample no.	Upper side.	Lower side.	Upper side.	Lower side.
1	63	68	73	89
2	69	65	78	82
3	63	68	68	73
4	66	70	78	84
5	63	68	75	80
6	67	76	74	75
7	64	65	65	70
8	60	73	85	89
9	69	78	76	80
10	65	75	72	76

Moisture content of the logs goes up immediately after the rainfall and no great difference exists in the moisture content of the samples from upper and lower sides of the logs during this period. When the same logs are again subjected to daylight for a few days difference in the moisture content in samples from upper and lower surface became evident again. Table 2.3 shows the moisture content of the samples that were taken from one end of a large oak log after rainfall and again after the remaining part of the same log had been in the sun for three days. The rain continued intermittently for two days and this was followed by three days of clear sunshine.

Table 2.3. Moisture content of samples taken from upper and lower sides of oak logs after rainfall and after exposure to direct sunlight.

	Percentage of moisture content after			
	Rainfall		Sunshine	
Sample no.	Upper side.	Lower side.	Upper side.	Lower side.
1	78	80	65	70
2	76	78	66	70
3	78	80	69	73
4	76	75	65	79
5	76	73	67	75

Throughout spring and summer, samples taken from oak logs on days without any rainfall, showed an average moisture content of 70.5±3.5 percent for the lower surface, and 68.5±2.3 percent for the upper surface. In winter, when the logs were covered with snow, no difference was noticeable in the moisture contents of the samples taken from the upper and lower sides of the logs. (86.4±3.5 percent for both sides).

The results presented here show the variation in moisture contents of some of the representative logs from which collections were made. It is worth noting that in spring and summer the moisture content of the logs appears to be lower than in winter and that logs in the shade show higher moisture content than those in the open. In winter, little difference exists in the moisture contents of the logs in the open and those in the shade.

III. Relative humidity.

The relative humidity in the sub-cortical spaces below the bark (where the millipedes live and oviposit) of rotten oak logs was always very high, averaging 95.5±4.5 percent (N=500). There was not much variation in the relative humidity of these spaces in different seasons of the year. However, it was thought that the moisture content of the logs might have some influence on the relative humidity in small spaces within the logs. Relative humidity in a number of logs with different moisture content was therefore determined. It may be mentioned that millipedes were not present in the logs with low moisture content. Nevertheless, the determinations of moisture content and relative humidity were carried out to find out the relationship between the two. The results are presented in Table 2.4.

Table 2.4. Moisture content and relative humidity in small spaces in oak logs.

Moisture content. (Percent)	Relative humidity. (Percent)	Number of observations.
20.0	60.0±3.4	10
30.0	75.0±2.8	10
40.0	85.0±3.4	10
50.0	90.0±2.8	15
60.0	95.0±3.5	15
70.0	100	15
80.0	100	15
90.0	100	15
100	100	10

Hawley and Wise (1926) state that wood containing over 50 percent moisture content will raise the humidity of an enclosed space within to saturation point. Savely (1939) also made similar observations in pine stumps. According to Becker (1943) moisture content above 28 percent will raise the relative humidity of an enclosed space inside the log to saturation point. From the data presented here, it would appear that air inside an enclosed chamber inside the log tends to get satured as the moisture content rises.

IV. Bulk density and determination of the rottenness of logs.

Like relative humidity, the bulk density of the logs is also correlated to the moisture content. The results are tabulated below.

Table 2.5. Relationship between the bulk density and moisture content of samples taken from oak logs.

Bulk density.	Moisture content. %	Number of observations.
1.0	50±4.8	150
0.8-0.9	60±3.5	150
0.7	70±5.0	150
0.6	80±4.5	145
0.4-0.5	85±4.0	150
0.2-0.3	90±6.1	150

It appears from this table that as the logs undergo decay, their moisture content tends to go up and this in its turn reduces the bulk density. The general relationship between moisture content, relative humidity and bulk density of the logs can be seen from Fig.2.6 . For the purpose of the present study, a scale of "rottenness" of the oak logs has been developed on the basis of the data incorporated in Tables 2.4 and 2.5 and is shown overleaf.

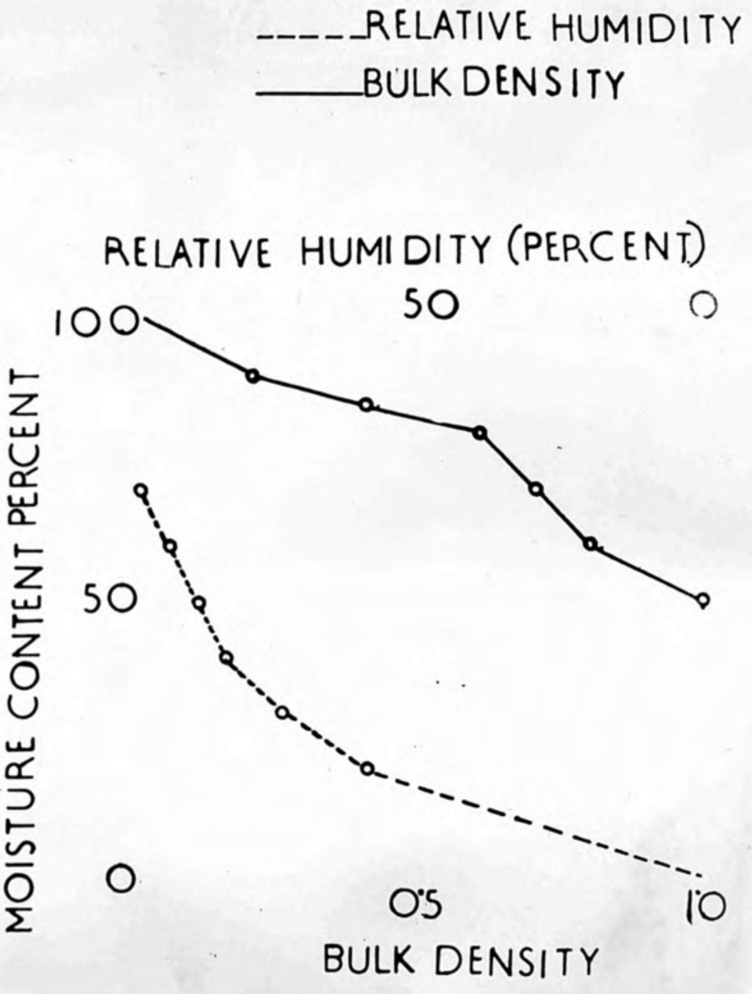


FIG. 2.6. Relationship between moisture content, bulk density and relative humidity in oak logs.

Table 2.6. Scale of "rottenness" of oak logs.

Index	Moisture content%	Relative humidity	Bulk density	Remarks.
R.1	40	85	1.0	Slight.
R.2	50-60	90-95	1.0-0.8	Medium.
R.3	70	100	0.7	Extreme.

B. Sample analysis from Area D.

I. Quantitative analysis of the population.

The oak logs that were examined in this area were more or less in the same state of "rottenness". (R_3) The number of adults and immature instars obtained from the regular sampling of the logs is tabulated overleaf. (Table 2.7 and Figs. 2.7 and 2.8).

Table 2.7. Numbers of adults and immature instars of *Cylindroiulus punctatus* (Leach) beneath the bark of oak logs in different months.

Month	No. of logs sampled.	Mean length (± S.E.) of the logs in inches.	Mean radius (± S.E.) of the logs in inches.	Mean (± S.E.) no. of adults per log	Mean (± S.E.) no. of immature instars per log.
Dec'61	4	50.0±1.8	5.0±0.5	15.0±1.5	7.2±2.5
Jan'62	4	49.2±0.8	4.2±0.5	16.0±1.8	4.5±1.5
Feb.	4	53.2±1.5	5.3±1.0	17.7±2.5	5.0±1.3
Mar.	4	48.5±3.5	4.2±0.8	23.2±3.0	7.2±2.5
Apr.	4	57.7±4.2	5.1±0.5	24.7±5.2	14.5±3.5
May	4	58.7±4.5	5.3±1.2	90.0±9.5	26.5±5.8
June	4	55.0±2.5	2.7±0.5	67.2±5.5	25.7±3.5
July	4	50.0±4.5	3.7±1.2	38.5±5.2	17.0±3.5
Aug.	4	41.5±5.0	4.0±1.0	23.7±4.5	13.0±4.5
Sept.	4	51.2±3.5	5.0±1.2	16.2±2.5	9.2±1.5
Oct.	4	54.7±2.5	4.7±1.2	18.0±2.5	4.7±1.3
Nov.	4	52.0±3.0	4.0±0.8	11.7±2.5	2.7±0.5
Dec.	4	45.0±4.5	4.0±0.8	10.5±2.5	7.5±1.5
Jan'63	4	45.0±3.5	3.0±0.5	14.5±3.5	7.7±1.3
Feb.	4	43.2±5.0	3.7±1.2	13.5±2.5	7.5±1.5
Mar.	4	49.2±4.5	4.2±0.8	16.5±3.4	8.0±2.0
Apr.	3	48.3±2.5	4.0±0.5	16.6±2.5	8.6±1.5
May	3	61.6±4.7	4.3±2.5	33.6±2.5	14.3±1.5
June	2	57.5±2.8	4.0±0.8	33.2±8.5	13.5±3.5
July	2	55.0±0.5	4.2±0.8	25.0±8.6	12.0±3.0

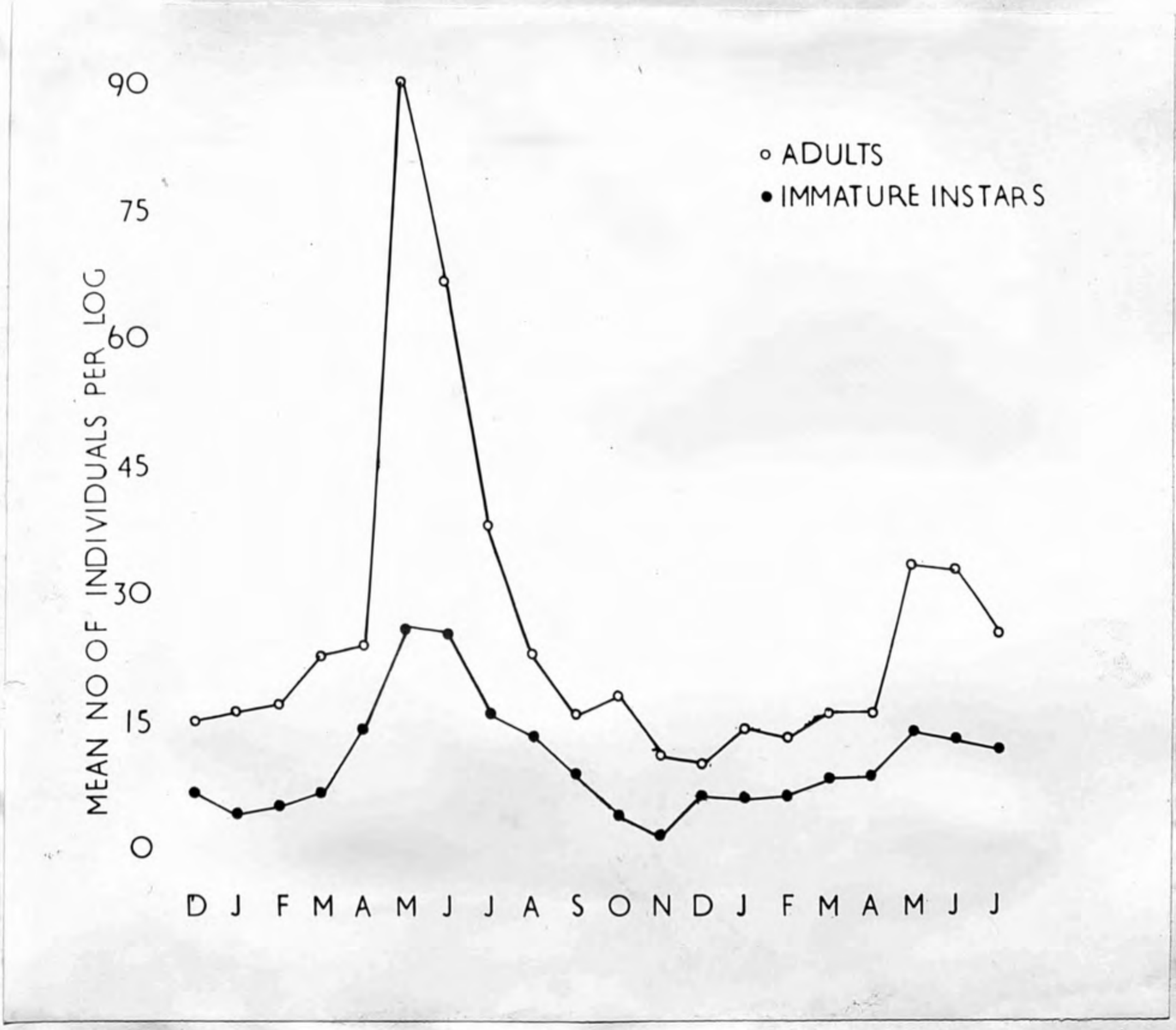


FIG. 2.7. Seasonal variation in the populations of adult and immature instars of Cylindroiulus punctatus in oak logs.

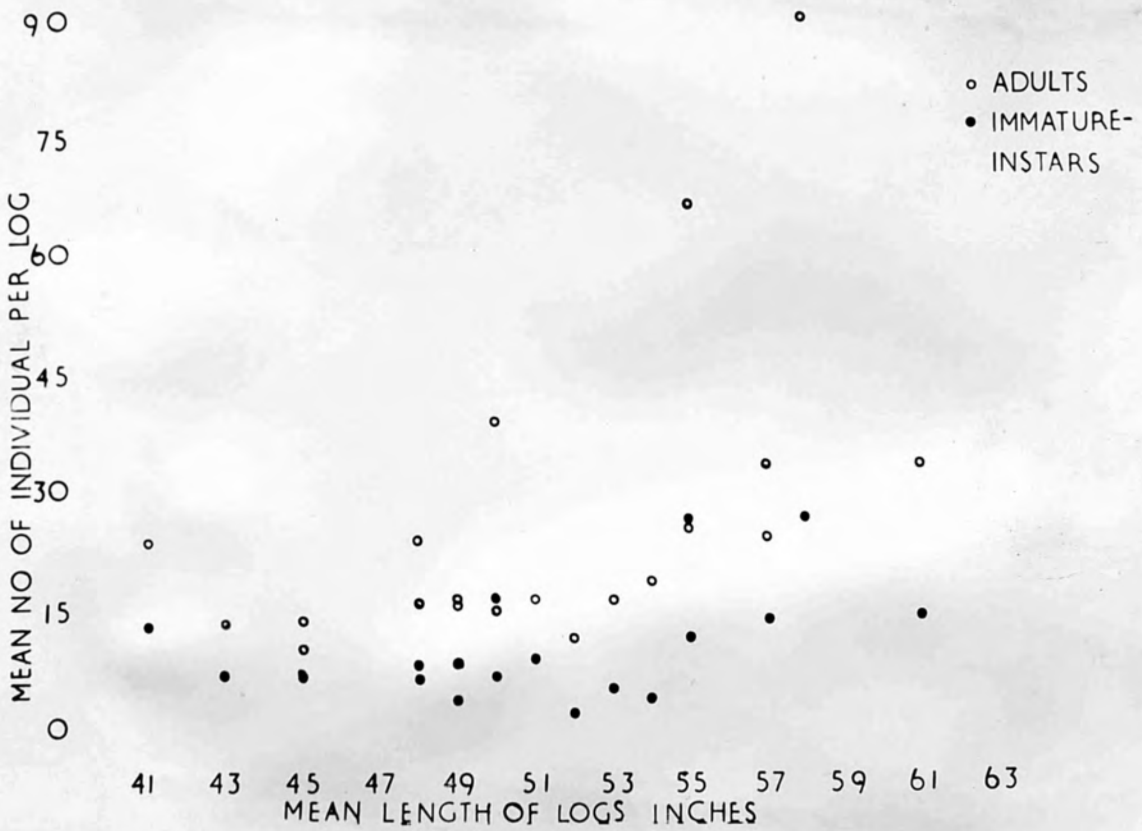


FIG. 2.8. Relationship between the lengths of oak logs and the numbers of adult and immature instars of Cylindroiulus punctatus in them.

It can be seen from this table that no linear relationship exists between the size of the log and the number of millipedes (both adults and immature instars) obtained from them. A statistical analysis of the variance applied to the number of adults and immature instars in different logs in various months show significant difference exists in their populations in oak logs in different months.

Table 2.8. Analysis of the variance applied to the distribution of the adults and immature instars of Cylindroiulus punctatus (Leach) in oak logs in different months.

Source of variation	Sum of squares	Degrees of freedom.	Mean square	Variance ratio.	P
		A. Adults			
Between months.	26232.9	19	1380.6		
Between number sampled.	29113.6	73		2.57	= 0.05
Residual.	2880.6	54	53.3		
		B. Immature instars			
Between months	3170.4	19	166.8		
Between number sampled.	3993.5	73		1.09	= 0.05
Residual.	823.1	54	15.2		

2. Qualitative analysis of the population.

Percentage of the males and females in the total adult population of the adults in the logs sampled each month is given below.

Table 2.9. Sex distributions of the adults of Cylindroiulus punctatus (Leach) beneath the bark of oak logs.

Month	Total no. of adults in logs.	No. of logs sampled.	Percentage of Males.	Percentage of Females.
Dec'61	60	4	56.4	43.6
Jan'62	64	4	58.2	41.8
Feb.	71	4	51.3	48.7
Mar.	93	4	51.2	48.8
Apr.	99	4	52.0	48.0
May	360	4	41.3	58.7
June	269	4	44.7	55.3
July	154	4	48.0	52.0
Aug.	95	4	45.4	54.6
Sept.	65	4	46.4	53.6
Oct.	72	4	51.7	48.3
Nov.	47	4	50.0	50.0
Dec.	42	4	51.6	48.4
Jan'63	58	4	47.4	52.6
Feb.	54	4	54.8	45.2
Mar.	66	4	57.5	42.5
Apr.	50	3	47.6	52.4
May	101	3	37.5	62.5
June	76	2	41.5	58.5
July	50	2	42.7	57.3

Table 2.10 shows the total number of various instars present in the logs sampled each month.

Table 2.10. Distribution of immature instars of *Cylindroiulus punctatus* (Leach) beneath the bark of oak logs.

Month	No. of logs sampled.	Total number of				
		First instars	Second instars	Third instars	Fourth instars	Seventh instars
Dec'61	4	0	0	8	14	7
Jan'62	4	0	0	0	15	3
Feb.	4	0	0	0	14	6
Mar.	4	0	0	0	19	10
Apr.	4	35	0	0	0	23
May	4	65	26	0	0	15
June	4	32	60	0	0	11
July	4	26	30	0	0	12
Aug.	4	16	20	10	0	6
Sept.	4	0	11	24	0	2
Oct.	4	0	9	10	0	0
Nov.	4	0	0	5	6	0
Dec.	4	0	0	8	15	7
Jan'63	4	0	0	10	17	4
Feb.	4	0	0	0	24	6
Mar.	4	0	0	0	23	10
Apr.	3	18	0	0	0	8
May	3	22	10	0	0	11
June	2	12	9	0	0	6
July	2	10	8	0	0	6

It can be seen from Table 2.9 that in the adult population the percentage of males was higher during January to April 1962, and again during October to December. The peak in the female population occured in between these two periods. Table 2.10 indicates the presence of first instars in the logs during April to August, second instars from May to October, third instars from August to January and the fourth instar from November to March. Seventh instars were noted throughout the year except in October and November.

3. Aggregation.

In the course of sampling the logs, it was noted that millipedes were always present in small groups or clumps beneath the bark. The distance between the aggregating groups varied from log to log and, in many cases, more than one aggregation was noted within the same sampling unit in the log. The distance between the aggregating groups varied from three inches to twelve inches. Again, in many logs, only one individual was recorded from a sampling unit. These individuals will be referred to as the "splitary" individuals as opposed to the "aggregating" individuals. Results are presented in Table 2.11.

During the breeding season, in each aggregation, immature instars were also noticed. Closer examination revealed in many cases the immature instars stay a little distance ($\frac{1}{2}$ - 2 inches) away from the main group of aggregating adults. Aggregating adults stay in close physical contact with each other, and, in some cases, they were found staying twisted round each other.

Table 2.11. Occurance of "solitary" and "aggregating" adults of _Cylindroiulus punctatus_ (Leach) beneath the bark of oak logs.

Percentage of aggregations of different numbers.													
Month	Solitary	2	3	4	5	6	7	8	9	10	11	12	13
Dec'61	18.3	23.3	30.0	20.0	6.6	0	0	0	0	0	0	0	0
Jan'62	9.3	28.1	23.4	31.2	7.7	0	0	0	0	0	0	0	0
Feb.	14.0	28.0	21.5	22.5	14.0	0	0	0	0	0	0	0	0
Mar.	3.2	8.6	22.5	17.2	26.8	12.8	0	8.6	0	0	0	0	0
Apr.	8.0	20.0	27.0	16.0	15.0	6.0	7.0	0	0	0	0	0	0
May	0	0	0	0	2.7	1.6	0	11.1	7.5	36.2	0	30.8	10.8
June	0	0	0	0	1.8	2.2	10.3	12.2	6.8	40.8	12.6	8.9	4.4
July	0	5.1	9.7	15.5	12.9	7.7	13.6	10.3	11.6	12.9	0	0	0
Aug.	0	4.2	12.9	37.8	31.5	6.3	7.3	0	0	0	0	0	0
Sept.	7.6	27.6	32.3	24.6	7.6	0	0	0	0	0	0	0	0
Oct.	10.9	24.6	32.8	21.8	0	0	9.5						
Nov.	42.5	38.2	12.7	9.1	0	0	0	0	0	0	0	0	0
Dec.	47.2	52.8	0	0	0	0	0	0	0	0	0	0	0
Jan'63	17.2	30.1	20.6	13.7	17.2	0	0	0	0	0	0	0	0
Feb.	18.5	29.6	16.6	14.3	9.2	11.0	0	0	0	0	0	0	0
Mar.	7.5	42.4	22.7	12.1	15.1	0	0	0	0	0	0	0	0
Apr.	10.0	12.0	18.0	16.0	10.0	0	0	16.0	0	0	0	0	0
May	1.9	1.9	8.9	23.7	9.1	17.8	27.7	7.9					
June	1.2	3.6	3.9	10.5	26.3	23.6	0	31.5		0	0	0	0
July	8.0	12.0	12.0	8.0	20.0	12.0	28.0	0	0	0	0	0	0

It is to be noted that solitary adults were not found inside the bark during May to August in 1962, and in June and July of 1963 they were present in very low percentage. In other months of both these years a large percentage of solitary adults was recorded. The largest number of adults in an aggregation was found to be thirteen. Aggregating groups of five or more individuals were mostly found in May to August, a time when solitary adults were present in low frequency or were totally absent.

4. Patterns of population distribution.

In many oak logs sampled, C.punctatus population was mostly concentrated on either end of the logs rather than in the centre. In some cases no millipedes were recorded from the central part of the logs, though they were present in large numbers on either end of the logs. However, most of the logs examined in May, June, July and August revealed the presence of aggregating groups of adults all along the lengths of the logs. During this period, the aggregations of immature instars were also noticed all along the length of the logs.(Fig. 2·9).

It is, however, worth noting in this connection that inside the deep "wood" of the logs, more millipedes were present in the central part than in the two ends. In only fourteen logs millipedes were found in the deep "wood" in addition to those beneath the bark. (Table 2.12). In others they were present only beneath the bark. No immature instars were found in the deep "wood".

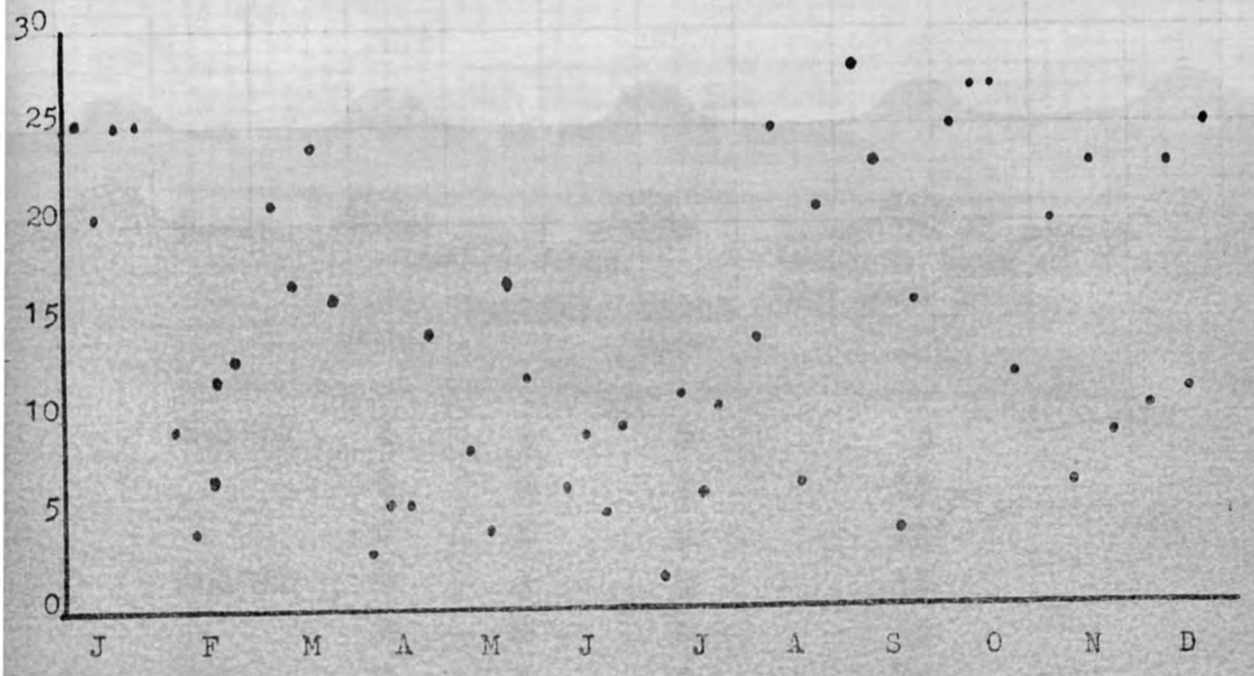


Fig. 2.9. Seasonal variation in the distribution of Cylindroiulus punctatus along the length of the oak logs.

Table 2.12. Distribution of adult Cylindroiulus punctatus (Leach) beneath the bark and inside the deep "wood" of some oak logs.

Month	Total no.of adults inside wood.			Total no.of adults beneath bark of the same logs.
	Left side	Central	Right side	
Dec'61	6	3	0	15
	0	4	1	17
	0	6	2	11
Jan'62	2	4	3	15
	0	6	0	16
Feb.	0	5	0	15
June	0	8	3	77
Aug.	4	0	2	30
Oct.	0	5	3	15
Nov.	2	5	0	13
	0	6	0	9
Dec.	2	5	0	13
	2	3	1	9
Feb'63	0	3	1	7
Total	18	63	16	

It was not possible to sample the deep "wood" in the similar way as the bark. Nevertheless, it is interesting to note that 60 percent of the total number of adults obtained from the deep "wood" were in the central part of the "wood". It may also be noticed that the adults were found inside the deep "wood" of some logs in winter only, with the exception of one in June and one in August.

It has been mentioned earlier that the lower side of the logs, lying in contact with the ground, usually show higher moisture content than the upper side, exposed to direct sunlight. Analysis of C.punctatus populations from these two sides of all the logs examined in various months, indicate a higher percentage of the population were present in the lower side of the logs. The results are tabulated overleaf.

Table 2.13. Distribution of adult <u>Cylindroiulus punctatus</u> (Leach) beneath the bark of oak logs on the upper and lower sides.

Month	Total no. of adults in logs.	No. of logs examined.	Percentage of total number of adults in logs present on	
			lower side	upper side
Dec'61	60	4	55.0	45.0
Jan'62	64	4	56.2	43.8
Feb.	71	4	56.3	43.7
Mar.	93	4	55.4	44.6
Apr.	99	4	53.5	46.5
May	360	4	57.2	42.8
June	269	4	42.3	57.7
July	154	4	56.4	43.6
Aug.	95	4	52.6	47.4
Sept.	65	4	60.0	40.0
Oct.	72	4	55.5	44.5
Nov.	47	4	65.9	34.1
Dec.	42	4	76.1	23.9
Jan'63	58	4	67.2	32.8
Feb.	54	4	57.4	42.6
Mar.	66	4	51.5	48.5
Apr.	50	3	58.0	42.0
May	102	3	60.0	40.0
June	76	2	54.0	46.0
July	50	2	56.0	44.0

Distribution of the immature instars on either side of the logs sampled follow the same general pattern as noted with the adults.

Table 2.14. Distribution of the immature instars of <u>Cylindroiulus punctatus</u> (Leach) beneath the bark of oak logs on upper and lower sides.

Month	Total no. of immature instars in logs.	No. of logs examined.	Percentage of total number of immature instars in logs present on	
			Lower side.	Upper side.
Dec'61	28	4	52.1	47.9
Jan'62	18	4	53.4	46.6
Feb.	20	4	54.2	45.8
Mar.	29	4	52.4	47.6
Apr.	58	4	50.0	50.0
May	106	4	51.3	48.7
June	103	4	54.5	45.5
July	68	4	55.3	44.7
Aug.	42	4	54.5	45.5
Sept.	37	4	52.5	47.5
Oct.	19	4	51.0	49.0
Nov.	11	4	65.3	34.7
Dec.	30	4	67.2	32.8
Jan'63	31	4	60.0	40.0
Feb.	30	4	54.7	45.3
Mar.	32	4	52.3	47.7
Apr.	26	3	54.0	46.0
May	43	3	53.5	46.5
June	27	2	52.3	47.7
July	26	2	54.5	45.5

5. Diurnal sampling of the logs.

Population of C. punctatus in the oak logs was noted in four phases of twenty-four hour cycle (Williams 1959) in order to find out whether nightly activities of these millipedes take them in and out of the logs all the time. If there is a mass exodus into the litter at night, fewer animals can be expected in the logs sampled at random at night. Similarly, of millipedes were moving into the bark at certain times, random sampling of the logs would also indicate that.

These observations were carried out in February, May, August and November of 1962. The logs selected for these observations had a length of 18.0±1.5 inches, with a radius of 3.0±0.5 inches. At four phases of 24 hour cycles in different months, two logs were examined. Each of these logs was numbered arbitarily and these were written down on cards. Selection of the logs for examination in different phases were done in the same way, as described before. Logs for sampling at night were selected in the day and an appropriate marker was placed on the logs to identify them at night. The results are tabulated below.

Table 2.15. Variation in the number of adult *Cylindroiulus punctatus* (Leach) beneath the bark of oak logs, sampled in various phases of twenty four hour cycles.

Time of sampling.	Number sampled.	Mean (±S.E.) no. of adults in logs in different months.			
		Feb.	May	Aug.	Nov.
4 P.M.	2	5.1±0.5	6.0±0.2	3.5±0.2	2.0±0.2
8 P.M.	2	6.0±0.2	7.5±0.3	4.0±0.3	3.0±0.3
Midnight	2	6.2±0.2	10.5±1.5	4.5±0.2	3.0±0.5
4 A.M.	2	5.0±0.4	8.0±1.2	3.5±1.0	4.5±1.1
8 A.M.	2	5.4±1.2	7.2±0.8	4.0±0.7	3.0±0.5
Noon	2	5.0±0.5	5.0±0.5	4.2±0.8	4.0±0.6
	P =	< 0.05	$= 0.05$	< 0.05	< 0.05

It can be seen from this table that a significant difference in population occured only in logs sampled in May. In that month more C.punctatus were obtained from the logs sampled at midnight. It is, however, difficult to say definitely if this in-crease in population in logs at night occured due to the movement of the millipedes from litter into the logs during this period, since the initial population was not known. It is worth noting, however, that in May a general increase in the population of C.punctatus in the logs usually occurs. Within the limits of these observations it may also be suggested that millipedes possibly did not move in and out of the logs during the night in different months, except in May.

6. Relationship between log population and litter population of C.punctatus.

In order to get some idea about the relationship between the population of C.punctatus in logs and surrounding litter, a simultaneous sampling of these two habitats was carried out. Every month one log (in addition to the regular four logs sampled per month) and one foot square litter surrounding the log was sampled. The length of the logs sampled was 48.5±1.5 inches with a radius of 4.0±0.5 inches. These logs were sorted out earlier and care was taken not to select them during the course of regular sampling of the logs. An identifying mark was placed on each of these logs to recognize them from the other logs in the area. The results are shown overleaf.

Table 2.16. Population of the adult and immature instars of <u>Cylindroiulus punctatus</u> (Leach) in oak logs and litter.

Month	Total no.of adults in one log.	Total no.of immature instars in one log.	Total no.of adults in litter sample.	Total no.of immature instars in litter sample.
Dec'61	14	10	10	5
Jan'62	10	6	8	8
Feb.	11	9	10	7
Mar.	20	12	15	12
Apr.	25	15	20	14
May	45	30	10	20
June	54	27	15	10
July	49	35	10	8
Aug.	25	20	8	7
Sept.	20	10	24	10
Oct.	15	10	20	18
Nov.	12	8	11	8
Dec.	8	12	6	3
Jan'63	10	11	5	4
Feb.	14	9	8	7
Mar.	18	8	13	11
Apr.	23	10	23	19
May	31	22	10	8
June	44	30	18	7
July	35	22	10	11

Population trends, as evident from the results of the simultaneous sampling of logs and litter, appear to follow the same general pattern as noted earlier. Two peaks occur in the litter population, one during April to June and the other during September to October. In the population of C.punctatus beneath the bark of logs, the peak occurs in May-July. It is, however, interesting to note that the first peak in the litter and log occur almost at the same time, and that the second peak in the litter occur concurrently with the decrease in the population of C.punctatus in the logs.

7. Rate of "colonization" of oak logs.

The purpose of this experiment was to test the extent of seasonal variation of C.punctatus population in oak logs from its "rate of colonization" of these logs from the surrounding litter. If these millipedes had a higher tendency to move into the bark in certain seasons, this can be roughly estimated from the higher percentage invading the logs during this period.

The field work for these experiments was carried out in an area with very thick oak litter, located about half a mile east of Area D. Twelve "branches" were collected from an old rotten oak tree. These branches will be referred to as logs in this discussion. The length of all these logs was 48.0 inches, with a radius of 4.5±0.8 ins. Each of these "logs" was in the same state of "rottenness" and they were tested for the presence of C.punctatus before being used in the experiments. This was achieved by keeping the logs under water for about twenty minutes. All living organisms began to float on the water surface within fifteen minutes of immersion. The logs were then scattered at random in the experimental area, by dividing the latter into twenty quadrates (each covering an area of four feet square) and then selecting the quadrates for the location of the logs by using a table of random numbers. each month one of these logs was examined, and the selection was made at random by the method described earlier. The logs were placed in the experimental area in November 1961 and observations were made from January 1962 to December 1962. The results are tabulated below.

Table 2.17. Rate of "colonization" of the oak logs by *Cylindroiulus punctatus* (Leach).

Month	Total no.of adults in one log examined.	Total no.of immature instars in the log examined	No.of six inch strips populated.
Jan'62	11	0	3
Feb.	13	0	4
Mar.	22	0	6
Apr.	43	0	6
May	58	0	8
June	51	0	7
July	43	37	7
Aug.	45	40	7
Sept.	32	16	6
Oct.	18	13	5
Nov.	21	24	6
Dec.	12	14	3

All the adults were released in the litter after counting them in the logs examined, so that the total population of C.punctatus in this area was least disturbed. The instars were taken to the laboratory. It can be seen from the table that the largest number of adults were obtained in the log examined in May and this was followed by the one examined in June. Similar trend has also been noted in regular monthly samplings. Immature in-stars were noted for the first time in July and they continued to appear until the end of the year. Only the first four instars were obtained from these samples. Seventh instars were not found. Distribution of the immature instars followed the same general pattern as noted earlier, i.e. first instars were found in the log in July and August, second instars extended from July until October, third instars from August to December and the fourth instars in November and December.

It was thought that the removal of logs from the experimental area in different months might have altered the natural conditions in the field to a certain extent, and secondly, removal of one log every month obviously reduces the chances of C.punctatus to invade the same number of logs all the time. For example, twelve logs were available in January and six in July. Under such conditions, heavy concentration of the population can be expected in the remaining logs if the adults were all the time moving into them. This was found to be true. In spite of the peak of the population in the logs sampled in May and June, population inside the logs in July to September was relatively high. After this there was a remarkable decrease in the population of C.punctatus in the remaining logs.

It is also to be noted from Table 2.17 that the number of six inch strips in the logs invaded by C.punctatus varied considerably in different months, and the number of strips populated was closely related to the total number of millipedes present below the bark of the log examined. Thus, in May eight strips were populated, indicating that the log was populated by C.punctatus all along its length. In December only three strips were populated.

8. Invasion of oak logs by "marked" adults.

The increased tendency of the adult C.punctatus to move into the bark in certain seasons of the year was further tested by using previously "marked" millipedes of this species, and recording their appearance in the logs offered in different months. This experiment was carried out in a specially selected area on the South-East side of the Royal Holloway College compound. Eight rotten oak logs, with loose bark (length 24.5±1.5 inches, radius 4.8±1.5 inches) were arranged on the perimeter of a rough circle, leaving a space of about six feet between the adjacent members. The logs were tested for the presence of millipedes before using them in the experiment and the testing method was the same as described earlier. Outside the main circle containing the logs, another circle at a distance of six feet from the main circle, was marked off. In this circle pit fall traps were sunk in positions corresponding to the space in between the logs in the main circle. One hundred adult C.punctatus collected from the litter were marked with a white lacquer by a very find brush. After the lacquer had dried the millipedes were set free at the centre of the circle and the logs were examined every week, when the bark was carefully removed and replaced again after observations. Marked specimens of C.punctatus were released in the last week of March 1962, and the logs were examined regularly for the next sixteen weeks, covering April, May, June and July 1962. The "marked" millipedes, after their recovery from the bark, were always released at the centre of the main circle, so that all the time the same number of "marked" adults were available in the litter for invading the logs. (unmarked adults obtained were also released at the centre). Only fifteen marked adults were obtained from the pit fall traps throughout the period of observation.

Table 2.18. Recapture of the "marked" adults of Cylindroiulus punctatus (Leach) in oak logs.

Recovered during (weeks)	Month covered	Total No.of "marked" adults available in litter.	Total No.of "marked" adults obtained from logs.	No.of unmarked adults obtained from logs.
1-4	April	100	18	34
5-8	May	100	25	63
9-12	June	100	14	55
12-16	July	100	9	38

Though it was not possible to find out if the same marked individuals were coming back into the logs all the time, it is interesting to note that maximum numbers of "marked" adults were obtained from the logs during the weeks covering May. It may also be noticed that the largest number of unmarked adults were also obtained from the logs during the same period.

This experiment was repeated, using different sets of 100 marked millipedes, in the corresponding months of 1963. The number of "marked" adults recovered from the logs was 25, 53, 42 and 22 respectively for April, May, June and July. The largest number of unmarked adults was also obtained in May.

C. Sample analysis from Area E.

Population analysis of adult and immature instars of C.punctatus in oak logs sampled at Area E is shown overleaf.

Table 2.19. Numbers of adult and immature instars of *Cylindroiulus punctatus* (Leach) beneath the bark of oak logs in different months.

Month	No. of logs sampled.	Mean length (±S.E.) of the logs in inches.	Mean radius (±S.E.) of the logs in inches.	Mean no. (±S.E.) of adults per log	Mean (±S.E.) of immature instars per log.
June'62	4	47.5±4.5	4.0±1.5	74.5±4.0	37.2±3.4
July	4	50.5±2.6	4.5±1.4	45.7±2.3	14.2±3.3
Aug.	4	45.5±4.3	4.3±1.8	33.0±6.3	14.0±4.8
Sept.	4	45.5±3.2	4.7±1.5	18.2±1.6	5.7±1.6
Oct.	4	42.7±1.6	4.3±1.4	23.6±3.6	7.2±0.8
Nov.	4	49.5±2.8	4.5±1.0	29.0±3.9	16.7±3.4
Dec.	4	48.5±4.9	4.5±1.5	21.2±3.5	19.2±1.9
Jan'63	4	51.5±2.8	4.5±2.1	28.2±1.3	10.2±2.4
Feb.	4	33.3±9.5	4.2±1.8	18.2±2.5	15.0±3.5
Mar.	4	35.0±4.4	5.0±1.5	24.5±2.8	13.2±1.9
Apr.	4	40.5±5.1	4.5±2.2	25.0±3.5	19.5±2.5
May	4	42.4±3.8	4.2±1.6	52.0±5.2	36.5±6.8

The population changes in these oak logs follow the same pattern noted at Area D. First instars were noted from June to August, Second instars from July to October, third instars from August to January and the fourth instars from November to April. Seventh instars were obtained throughout the period of sampling.

Discussion.

Regular sampling of the oak logs indicate that a definite increase in the adult population of *C. punctatus* occurs in them in May and June. Since the logs sampled were selected at random every month and their lengths and radii did not vary much, the peak of the population can be regarded as real. The population of *C. punctatus* beneath the bark of oak logs begins to increase slowly from March, reaching a peak in May-June. Noticable decrease in the population occurs in September and onwards. It may be noticed that this peak of the adult population in the logs in May-June approximately coincides with the peak in the population of the adults in the litter. However, there was no peak in the population in the logs in autumn as was noted in litter. Another interesting point is the proportion of females in the adult population of *C. punctatus* in litter and logs. While there is an increased percentage of females in the logs in May to July, there is a corresponding decline in the female population in the litter during this period. Analysis of the population of immature instars indicates that only the first four and the seventh instars were present in the logs.

It may be noted that the first instars appeared in the logs at the time when there was an increase in the adult population, particularly of the females. Eggs were also found in the logs during July. On the basis of these observations, it may be suggested that adults move into the bark during April-June for breeding. It has already been noted in section I that adults come up in litter during spring, and it may be possible that some of these adults move into the logs. This also explains the occurance of simultaneous peaks in the adult population in the logs and litter during the same period. The absence of eggs and the first three instars in the litter sampled, would also suggest that they can only develop beneath the bark of the logs.

The second peak of the adult population in the litter occurs when there is a decrease in the adult population beneath the bark. It seems that some of the adults coming out of the bark into the litter at the end of the breeding season, increase their numbers in the litter.

The increased tendency of the adults to move into the bark during the spring is also supported by the observations made by using "marked" adults. A higher percentage of marked adults were recovered from inside the logs during May-June than any other time of the year. Simultaneous sampling of the logs and the litter from their immediate vicinities also indicates that an increase in the adult population in the logs is associated with a decreased adult population in the logs and vice versa.

Adults stay beneath the bark of the logs in small aggregations. The aggregating tendency appears to be greatest during May to August, when groups of five or more individuals were obtained in large numbers from the logs. During this period, "solitary" adults were not found inside the logs. To a great extent, these "aggregations" appear to be sex centred, since aggregations of only males or only females were not obtained. Increased attraction between the adults during the breeding season reduces the chances of occurance of the "solitary" adults during this period. Aggregating adults were noted all along the lengths of the logs sampled during May-August, whereas in other months, they were mostly concentrated on two cut ends of the logs. It is likely that the heavy population of the adults during this period results in the spreading of the aggregations all along the length of the logs. It is difficult to suggest why large numbers of adults are not found in one aggregation, but two possible explanations can be offered. In the first place, in each aggregation room must be found for the females to oviposit and for the first three instars to develop there. Secondly, the presence of large numbers of adults in an aggregation and the resulting accumulation of faeces may produce toxic substances detrimental to immature instars and the adults. Formation of many aggregations, each with a small number of adults, may have therefore, great survival value both for the adults and the immature instars.

In most cases, the aggregations of adults and immature instars were found beneath the bark of the oak logs sampled. Only in a few logs sampled in winter, some adults were found inside the deep "wood" of the logs. It is difficult to say whether the adults noted in the deep wood actually migrated there from beneath the bark, since in all these logs a considerable number of adults were also obtained from the bark.

Adults and immature instars, whenever present beneath the bark, fed on soft sub-cortical tissues of the bark. Faeces were found in the aggregations and microscopic examination of the faeces revealed the presence of these materials in them.

Considering all the evidence together, it may be suggested that Cylindroiulus punctatus migrates from litter into the bark of rotten logs during April to July, with maximum numbers of adults moving into the bark during May-June. Adults probably mate here and the females lay eggs in the sub-cortical space below the bark. The first four instars develop here and the fourth instars migrate from the bark into the surrounding litter. The presence of fourth instars both in the logs and in the litter suggests their migration from one habitat to another, and this occurs from logs into litter because its preceeding stages are found in logs only. Fifth to seventh instars are found in litter only. Some of the seventh instars move back again into the logs while others stay in the litter. Since no sixth instars were noted inside the logs, there cannot be any doubt that the seventh instars come inside the logs from the litter. It is interesting that the peak in the populations of seventh instars and adults inside the logs, occurs during the same period. It is possible that some of the seventh instars, after their development from sixth instars, were migrating into the bark with the adults.

Simultaneous sampling of the litter and logs indicate that there is always a permanent adult population of C. punctatus in both these habitats. Since physical conditions in these two habitats are somewhat identical, and enough food is available in both places, adults can be expected to thrive well in them. However, it may be asked, if conditions are identical in both the habitats, why some of the adults should migrate from litter into bark for breeding. This behaviour has arisen in connection with the need for the protection of the eggs and the first three instars. This species does not construct any nest for the protection of the eggs or show any "parental care" for the earlier instars. The sub-cortical space beneath the bark, where the eggs are laid not only protects the eggs from the effects of fluctuating environmental conditions, but also against predation by other animals. The first three instars also find food and protection beneath the bark. But why the fourth to sixth instars should develop in litter is difficult to explain, possibly a change of diet at these stages provides growth stimulating substances for further development.

SECTION III

Experimental studies on the life cycle of *Cylindroiulus punctatus* (Leach).

Introduction.

Considerable information exists in the literature on the biology of millipedes and the works of Attemps (1926), Verhoeff (1928, 1932), Schubart (1934) and Brolemann (1935) may be mentioned in this connection. In recent years, life cycles of different species of the family Iulidae have been described by Drift (1957), Sahli (1958), Halkka (1958) and Blower (Private communication). However, very little work has been done on the life histories of millipedes from an experimental point of view. In this section, it is proposed to present some of the observations made in connection with an experimental approach on the life cycle of Cylindroiulus punctatus.

Methods.

A. Field Work.

The field work mentioned in the present section was carried out in various parts of the Royal Holloway College grounds. Observations on the duration of various larval instars were made on some specially selected logs of different tree species. The spaces beneath the bark of these logs, where C.punctatus oviposit, and the development of the first three instars takes place, have been described in the present work as "oviposition sites". On each of these logs, three "oviposition sites" were selected and these sites were examined for various instars every third day. During these examinations, the bit of bark covering the "oviposition sites" was removed, and after identifying various instars in these sites with the help of a hand lens, the bark was carefully re-places back in its former position again.

The rate of larval development in the field has been traced in the logs of the following tree species, and the conditions in which they were located are also mentioned below.

A. Oak log (_Quercus robur_ L) located in predominantly oak litter.

B. Oak log (_Q.robur_ L) placed in predominantly beech litter.

C. First instars transferred from oak log to a beech log (_Fagus sylvatica_ L). Both the logs were located in oak litter.

D. Beech log (_F.sylvatica_ L) in predominantly beech litter.

E. Beech log (_F.sylvatica_ L) in oak litter.

F. First instars transferred from beech log to an oak log. Both logs located in beech litter.

The lengths of all these logs were thirty inches, with a diameter of three inches. All these logs were more or less in the same state of "rottenness".

Preference for the selection of the "oviposition sites" was tested in the field by offering _C.punctatus_ five logs of each of the following tree species in both oak and beech litter.

1. Oak (_Quercus robur_ L).
2. Birch (_Betula verrucosa_ Ehrhart).
3. Beech (_Fagus sylvatica_ L).
4. Austrian pine (_Pinus nigra_ Arnold).

The lengths of all these logs were 25 inches, with a diameter of 4.5±1.5 inches. These logs were scattered at random in the experimental areas by the method described in Section II. All these logs were tested for <u>C.punctatus</u> before putting them in the field.

B. <u>Laboratory observations</u>.

All laboratory observations reported here were made in a constant temperature room at 23°C. The rate of larval development was followed by maintaining a culture of first instars inside the bark of an oak log placed in an earthenware trough with plenty of oak litter around. Subsequent instars, as soon as they appeared, were transferred to different oak logs of the same length as before, and were placed inside separate troughs. In the cultures of fifth, sixth and seventh instars, a piece of oak log was provided. Since all the instars were maintained separately, it was possible to find out the time taken by the majority of the population of each instar to moult into the next instar. All these cultures were examined every third day.

Experiments on the effects of different relative humidities on mating were done by keeping the experimental animals inside desiccators and the desired humidities were produced by different concentrations of potassium hydroxide solutions. The mating preference of the males for the females of different instars was tested by keeping the experimental animals in a large crytallizing dish and 100% relative humidity was maintained within the dish.

Results.

1. Rate of larval development in field observations. (Fig. 3.1).

The rate of development of the first four instars was traced in three "oviposition sites" on the logs of different tree species under various conditions referred to under "methods - field work". The results are presented below.

Table 3.1. Rate of larval development of the immature instars of Cylindroiulus punctatus (Leach) in the logs of different ~~tree~~ species of tree under various conditions.

Conditions	Mean time (± S.E.) in days, taken to pass from one instar to another.		
	Instars		
	1-2	2-3	3-4
A.	30.0±5.6	36.5± 8.6	83.0 ± 7.8
B.	35.3±7.4	34.3±10.2	94.5± 5.5
C.	38.0±5.2	58.3± 9.5	131.6±15.8
D.	35.0±2.5	39.0± 3.8	86.6± 3.5
E.	33.0±3.0	37.5 ± 3.5	86.0 ± 6.3
F.	39.0±2.5	51.6 ± 7.5	133.0±12.5

The rate of development could not be followed beyond the fourth instars, because most of them moved out of the bark as soon as this stage was reached. It was also difficult to keep a record of the exact number of various instars present in the "oviposition sites" at the time of examination, but the figures presented above are based on observations on fifty individuals.

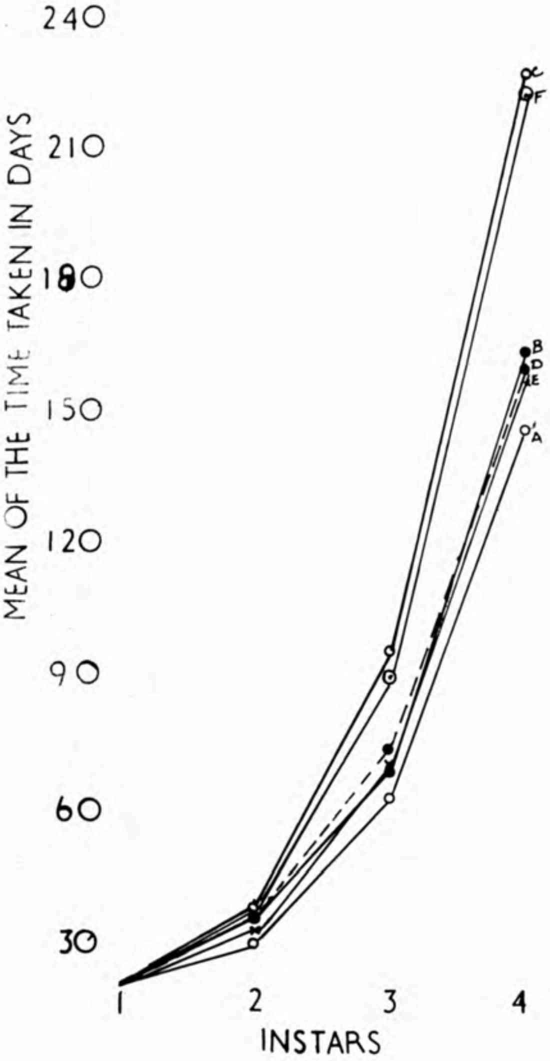


FIG. 3.1. Rate of larval development of the first four instars of <u>Cylindroiulus punctatus</u> in the field under different conditions.

Condition A. Oak log located in oak litter.
Condition B. 1 Oak log in beech litter.
Condition C. First instars transferred from oak log to beech log. Both logs in oak litter.
Condition D. Beech log in beech litter.
Condition E. Beech log in oak litter.
Condition F. First instars transformed from beech log to oak log. Both logs in beech litter.

2. Host preference for "oviposition sites".

The logs used in this experiment were put in oak and beech litter in the middle of March 1962, and the logs were examined for C.punctatus in the middle of May 1962. The sampling of the logs continued for five days and the logs were selected (one of each species every day) at random, by the method described in Section II.

Table 3.2. Preference for the logs of various tree species by Cylindroiulus punctatus (Leach) in oak litter.

Log of the tree species examined.	No.of logs examined.	Mean(± S.E.) of male.	Mean(± S.E.) of female.	Mean(±S.E.) no. of immature instars.
Oak	5	7.2±3.5	9.0±2.6	16.0±7.5(1)*
Birch	5	5.4±1.8	6.2±3.4	8.0±5.4(1)*
Beech	5	6.4±2.3	8.8±5.2	7.2±3.0(11)**
Austrian pine	5	1.2±0.7	2.0±0.9	0

Table 3.3. Preference for the logs of various tree species by Cylindroiulus punctatus (Leach) in beech litter.

Log of the tree species examined.	No.of logs examined.	Mean(± S.E.) no.of male.	Mean(± S.E.) no.of female.	Mean(± S.E.) no. of immature instars.
Oak	5	7.2±2.5	8.0±3.8	11.0±6.5(1)*
Birch	5	8.5±2.3	7.4±3.5	15.0±6.2(1)*
Beech	5	10.4±2.8	10.2±4.5	13.5±5.8(1)* 6.6±3.5(11)**
Austrian pine	5	3.0±0.5	3.5±1.0	0

* (1) First instar.
** (11) Second instar.

Friedman two way analysis of variance by rank indicates that a significant difference ($P \geq 0.05$) exists in the total population of adults in the logs of various tree species in both the oak and beech litter.

B. Laboratory observations.

1. Mating.

Effects of relative humidities on the frequencies of mating were observed by keeping five pairs of millipedes in each of the des~~s~~iccators with different relative humidities. The observations were continued for ten hours and pairs were removed immediately after mating. During mating, the mating adults twist round each other and the mating lasted from fifteen minutes to seventy five minutes in different cases.

Table 3.4. Mating of Cylindroiulus punctatus (Leach) in different relative humidities at 23°C.

Percentage of relative humidity produced.	Number of pairs found mating.					
	March	April	May	June	July	Total
30	0	0	0	0	0	0
40	0	0	0	0	0	0
50	0	0	0	2	1	3
60	0	3	2	2	0	7
70	0	0	2	2	2	6
80	0	3	4	2	1	10
90	1	2	3	1	0	7
100	0	2	4	4	0	10
Total	1	10	15	13	4	

It can be seen from this table that in May the largest number of adults were found mating, and this was followed by the numbers in June. There was considerable increase in the number of mating pairs, when the relative humidities offered were above fifty percent. It may be noted that the largest numbers were found mating during the period (May) of active migration of adults in the field into the logs.

The mating preference of the males for the females of various instars is shown below. These experiments were carried out in May and June and were repeated ten times each month, using different sets of animals. During each experiment, one male and one female of each of the instars 8 - 12 were used.

Table 3.5: Mating preference of the male *Cylindroiulus punctatus*(Leach) to females of various instars.

Month	No. of experiments performed.	Total number of females of various instars mated. 8th Instar	9th Instar	10th Instar	11th Instar	12th Instar
May	10	1	2	3	1	1
June	10	0	2	4	0	2
Total	20	1	4	7	1	3

Within the limits of these experiments, there is evidence that the females belonging to advanced instars are more preferred by the males than the females belonging to earlier instars.

2. Rate of larval development. (Fig. 3.2).

In the laboratory it was possible to trace the development of the eighth instars (sexually mature stage) from the culture of first instars. The results are presented below.

Table 3.6. Rate of development of *Cylindroiulus punctatus* (Leach) from first to eighth instars at 23 C and a relative humidity of 95.0±3.0%.

Instars	Number reared	Mean (± S.E.) time in days.	Location.
1-2	85	13.5 ± 2.5	Inside the bark of the log.
2-3	54	18.5 ± 3.7	"
3-4	37	60.0 ± 7.5	"
4-5	31	78.2 ± 8.6	Part in log, part in litter.
5-6	24	105.8±12.6	Mostly in litter.
6-7	18	95.5±10.5	"
7-8	11	230.8±24.6	Part in log, part in litter.

There was considerable larval mortality in this experiment and only 12.9% of the first instars developed into eighth instars. Unfortunately, the exact days of the laying of the eggs and the hatching of the first instars were not known, but the time taken by the first instars to develop into mature eighth instars varied between 532.3 to 672.3 days. However, it may be mentioned in this connection, that some of the eighth instars reared in

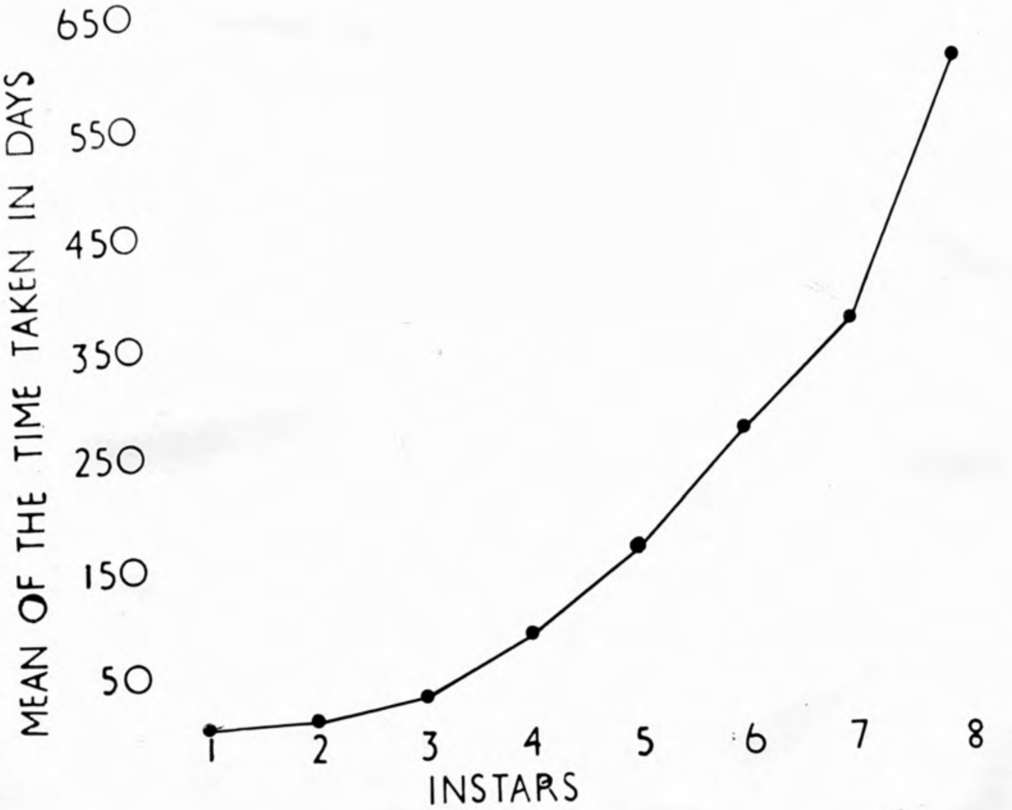


FIG. 3.2. Rate of larval development of *Cylindroiulus punctatus* in the laboratory at a constant temperature of 23°C.

the laboratory in 1962 mated in June 1963, and three of these females laid eggs beneath the bark of an oak log provided in the culture. The number of eggs laid were 35, 56 and 78 respectively, and these eggs took 15-25 days to hatch. Some of the first instars took 15-20 days to develop into second instars, and the latter took 21.26 days to reach the third instar. Some of these third instars moulted into fourth instars in 50-56 days.

It can be seen from Table 3.6 that there is a more or less progressive increase in the time taken by each instar to pass from one stage to another as they become more advanced. The seventh instars took the longest time to develop into eighth instars, whereas the first instars took the least time to moult into second instars.

3. Burrowing technique into the logs.

Manton (1954, 1961) has discussed in detail the diplopod burrowing technique and the functional significance of various body muscles in connection with burrowing. Since migration of the adults into the bark is somewhat associated with breeding behaviour some of the laboratory observations on the burrowing behaviour of C. punctatus are mentioned here. These observations were made in a constant temperature room at 23°C. The small head of the adult is first put into a crevice on the outer surface of the soft bark of the oak log provided. This was very soon followed by the collum which was also thrust forward into the crevice. Some of the trunk segments also took part in this initial "thrusting movement", but after a while the trunk segments came out of the crevice leaving the head and the collum inside. Inside the crevice, the head and collum were possibly "bulldozing" through the soft sub-cortical tissues, since the parts of the body segments outside the crevice were making wriggling movements all the time. Within the next few minutes the rest of the body slowly crept into the bark through the crevice which became larger.

After the burrowing adult had moved inside the bark, ten more adults were released on the surface of the log. These adults wandered on the surface of the log for some time, and after detecting the large hole on the surface, already made, four of the adults moved into it. Of the remaining six, three took up their positions within another crevice on the bark, whilst the rest stayed on the cut end of the log.

Discussion.

The rate of development of the first four instars of C.punctatus in logs of different species in the field appears to fall within a close range. However, the rate of development of these instars in oak and beech logs, when the latter were situated in oak and beech litter respectively, appeared to be slightly higher than the others.

When the first instars were transferred from the logs where they hatched from the eggs to logs of different species of trees, their rate of development was lowered. Second and third instars, similarly treated, also took more time to moult into third and fourth instars respectively.

On the basis of the present observations, it may be suggested that first and subsequent instars possibly develop a sort of "host specificity" to logs of a particular species of tree in which they developed from the eggs. Thus, the first three instars reared in oak logs all the time, took 126.5 - 171.5 days to develop into fourth instars, but when they were transferred from oak log to beech log they took 197.4 - 258.4 days. Possibly some sort of "plant substances" act as agents in regulating the rate of development of the first four instars inside the log and it seems that their effects are established with the first instars. Among the insects the role of these "plant substances" in the evolution of the specificity of host plants has been discussed by Fraenkel (1959 a,b.).

It has already been mentioned in Section II that fifth and sixth instars possibly require some sort of "growth stimulating" substances from the litter to undergo further development. It is likely that the first three instars have also developed specificity for the "growth stimulating" substances to be found inside the logs of different species of trees. The seventh instars, however, do not show any preference for either of these habitats and can develop equally well in both these habitats. The influence of the litter on the developmental rate of the instars seems to vary, depending on whether it is made up of freshly fallen leaves or decomposing leaves. Drift (1951) reported a significant difference in the developmental rate of millipedes reared in F_1 and F_0 layers of beech forest.

Experiments in the field indicate that *C. punctatus* prefers logs of deciduous trees to resinous trees as "oviposition sites". It is also interesting that *C. punctatus* has a tendency to prefer the logs of those species of tree, in whose leaf litter they were located. Field experiments show that a large number of adults migrated into the logs of oak when these logs were located in oak. Similar results were also obtained when the experiments were carried out with beech logs located in beech litter. It may be that *C. punctatus* reared in oak or beech litter would show a strong preference for the logs of these species of tree for "oviposition sites", though there is no evidence to suggest that logs of other species of tree in oak or beech litter would be rejected. It is difficult to explain why *C. punctatus* shows a slightly higher preference for the logs in whose leaf litter they underwent earlier development. It is possible that millipedes become habituated to a particular species of tree through their constant contact during larval development with its logs and litter, and develop a preference for these logs as oviposition sites. Yamamoto and Fraenkel (1960) found that the specificity of tobacco horn-worm which oviposits only on solanaceous plants is partly regulated by the stimulus imparted by different solanaceous plants. This stimulus, possibly peculiar to each species of plant, has been termed by them as an "orientation stimulus". Whether or not this stimulus also operates with millipedes, is difficult to say. Possibly certain stimuli like thigmostimuli and chemostimuli are also invovled in the selection of the logs, but more evidence is needed to confirm this.

It has been noted in Section II that the migratory habit of the adult C.punctatus into the bark for oviposition has arisen for the protection of the eggs and the first four instars. The stimulus which activates the females to seek "oviposition sites"in the logs may be described as the "reproductive stimulus". During the period of migration (March to June), the eggs become fully developed and are laid after the female has found a suitable"oviposition site".

The simultaneous sampling of the logs and litter suggest that the whole life cycle of C.punctatus in the field is completed in about three years. But in the laboratory, under a constant temperature of 23^{0}C and under constant darkness, it was possible to reduce the life cycle to about two years. It is possible that, among other factors, constant conditions of temperature, humidity and light maintained in the laboratory quickened the whole life cycle in the laboratory, than in the field, where these conditions are everchanging.

Section IV.

Experimental studies on the behaviour of *Cylindroiulus punctatus* (Leach).

I. Feeding habits and food preference of Cylindroiulus punctatus. (Leach.

Introduction.

Food and feeding habits of millipedes have received considerable attention of various workers. Latzel (1884), Vom Rath (1891), Sorauer (1913), Verhoeff (1914) have discussed the feeding biology of different species of millipedes. Brade-Birks (1930), Cloudsley-Thompson (1950) and Kinkel (1955) have dealt extensively on the food of Blaniulus guttulatus (Bosc), because of the agricultural importance of this species. Chandler (1939), and Lyford (1943) noted the preference of millipedes for leaves with high calcium content. Importance of millipedes in humus formation through the feeding of leaf litter has been discussed by Hoffman (1931), Lyford (1943), Kuhnelt (1950), Drift (1951), Schmidt (1952), Kubiena (1953, 1955) and Gere (1956). Barlow (1957) has made a comparative study of the feeding behaviour of three species of millipedes, while the physiology of digestion has been discussed by Wegelin (1959) and Nielsen (1962).

In the present investigation, attempts have been made to discover whether *Cylindroiulus punctatus* shows any preference for certain substances as food, and to observe the feeding behaviour under different external conditions.

Methods.

A. Food preference test.

Evidence of the choice of food by *Cylindroiulus punctatus* came from the laboratory tests on food preference. Five large crystallizing dishes were covered with glass plates and the relative humidity within them was maintained between 95 - 100% by means of a small dish of water kept at the centre, and also by a moist filter paper fixed on the inner surface of the lid. Humidities inside the crystallizing dishes was monitored from time to time by means of cobalt thiocyanate paper (Solomon 1945, 1957). Equally spaced around the circumference of each dish were placed four different foods: small pieces of wet and rotten bark of oak, a rotten and wet oak leaf, a piece of dry and hard oak wood (with bark removed) and a green oak leaf. These substances were attached to circular plaster of paris bases.

In each dish, ten defaecated millipedes were introduced through a hole on the covering glass, which was later plugged with plasticene. The number of animals on each food substance was noted every 60 seconds for twelve consecutive hours, and the presence of a millipede on a food substance was considered as evidence of feeding. Some of the millipedes were seen to be on no food substance at all, but were moving around the floor. These might have been in the process of seeking suitable food, and have been described in the results as "undecided".

These experiments were carried out in a constant temperature room at 23°C. and to ensure complete darkness the crystallizing dishes were covered by means of cardboard boxes. The millipedes on each food substance were counted by light from a torch with a red lens. These experiments were repeated five times, using different sets of animals and in different months.

B. Effect of constant diet on food preference.

The set up of the experiment was the same as before. The millipedes (ten) used in these experiments were fed with rotten oak wood for a week and then they were offered a choice of a piece of potato or rotten bark, and the number present on either of the food substances was recorded at 8 a.m. noon, 8 p.m. and midnight for seven successive days.

C. Rate of feeding in males and females.

The rate of feeding of males and females was found out by providing defaecated animals of either sex with an oak leaf and the amount of leaf consumed in one night was noted. Each animal was kept separately in a small petridish with the leaf, and high humidity (95 - 100%) inside the petridishes was maintained by moist filter paper fastened on the inner surface of the lid. Five males and five females were kept separately in the constant temperature room at 23°C. in complete darkness. Another series of five males and females were kept separately outside the laboratory to the fluctuating temperature, humidity and light of nature.

D. Variation in the feeding activity in 24 hour cycle.

Some idea about the feeding activity of the males and females was obtained by counting the number of faeces produced in different times of the day and night. Two series of observations were carried out simultaneously: one being in the constant temperature room at 23°C. and in complete darkness, while the other was kept outside the laboratory. In each series five defaecated males and five defaecated females were used, and each of them was kept separately inside a small petridish with a piece of potato. High humidity inside the petridishes was maintained by moist filter paper attached to the inner surface of the lid. The millipedes were put inside the petridishes at about 7 a.m. Faeces produced were counted at 8 a.m., noon, 8 p.m. and midnight.

E. Variation in food selection in 24 hour cycle.

Variation in food selection was determined by offering Cylindroiulus punctatus a combination of foods and examining the contents of faeces for the remains of food consumed at different times of day and night. The experimental set up was the same as in "A", and the foods offered were small piece of rotten bark, a piece of rotten oak leaf, moss and a piece of potato. Two series were run simultaneously. One in the constant temperature room at 23°C. and in complete darkness and the other outside the laboratory in the varying conditions of temperature, humidity and light. Ten defaecated millipedes were introduced in each of these sets and the number of faeces produced was noted at 8 a.m., noon, 8 p.m. and midnight for five consecutive days.

F. Effect of temperatures on feeding activity.

Effects of temperature on the feeding activities was studied at 15°C., 20°C., 25°C. and 30°C. in complete darkness. In each of these temperatures five defaecated males and five defaecated females were kept separately in petridishes. A piece of potato was put inside each petridish and humidity inside the petridishes was maintained between 95 - 100% by means of moist filter paper attached on the inner side of the lid. The experiments were carried out in a thermostatically controlled oven. The piece of potato and the filter paper inside the petridishes were replaced every morning and the number of faeces produced was counted at the end of every twenty four hours for ten successive days at 10 a.m.

G. Effect of the removal of antennae on food selection.

The antennae of *Cylindroiulus punctatus* are provided with a number of sensory hairs, which are said to help in chemoreception. In many preliminary experiments on food preference, it was frequently noted that the animals move their antennae to and fro before moving in any direction or before selecting any food. It was, therefore, decided to find out if the sensory organs on the antennae play any part in the selection of the food. In this experiment fifteen defaecated animals were used: five of them had both antennae removed, five had one antenna removed while the rest had both the antennae in position and these will be considered as "control". The antennae were removed twenty four hours before starting the experiments after the animals had been made motionless by putting them inside deep freeze for a few minutes before the removal of the antennae with the help of a pair of scissors.

Both the "control" and "experimental" animals were placed inside a 6" petridish and were given a choice between a piece of rotten bark of oak and a rotten oak leaf. The relative humidity inside the petridish was maintained at 95 - 100% and the experiments were carried out in the constant temperature room at 23°C. in complete darkness.

At the end of twenty four hours, the position of the "experimental" and "control" animals were noted with respect to the food. This experiment was repeated five times using different sets of animals. The animals used in these experiments were collected from the litter, and immediately after collection they were defaecated for 48 hours in the constant temperature room at 23°C. in constant darkness, and the relative humidity inside the container varied between 95 - 100%. In some experiments, conducted in winter, millipedes from stock culture maintained at the constant temperature at 23°C. were used.

Results.

A. Food preference tests.

In the following table position records of 250 millipedes (covering five experiments, each with five sets of ten animals) on different food items is presented.

Table 4.1. Position records of <u>Cylindroiulus punctatus</u> (Leach) on different foods.

Month.	Mean (± S.E) No. on rotten bark.	Mean (± S.E) No. on rotten leaf.	Mean (± S.E) No. on dry wood.	Mean (± S.E) No. on green leaf.	Mean (± S.E) No. undecided.
1961.					
Nov.	22.0 ± 4.5	22.0 ± 3.5	1.0 ± 0.5	3.0 ± 0.8	2.0 ± 1.0
1962.					
Feb.	22.0 ± 5.5	18.0 ± 4.5	4.0 ± 1.2	1.0 ± 0.5	2.0 ± 1.5
May.	25.0 ± 8.5	18.6 ± 7.5	2.0 ± 0.8	1.4 ± 1.2	3.0 ± 1.4
Aug.	25.0 ± 7.5	22.0 ± 5.4	0.8 ± 0.04	1.2 ± 0.5	1.0 ± 0.5
Nov.	20.0 ± 8.5	23.0 ± 8.5	2.0 ± 0.5	2.0 ± 1.1	3.0 ± 1.5
1963.					
Feb.	19.0 ± 7.5	24.5 ± 9.5	2.6 ± 1.2	1.6 ± 0.8	2.0 ± 0.8
May.	24.2 ± 7.8	23.6 ± 8.5	0.6 ± 0.05	1.0 ± 0.8	0.6 ± 0.05
Aug.	22.2 ± 9.5	21.6 ± 8.4	1.6 ± 0.8	2.4 ± 1.4	2.2 ± 0.5

Similar experiments were done using the bark and leaves of birch and beech. The results were similar.

It may be noticed that the largest number of animals were recorded on either rotten bark or rotten leaf. No significant difference exists between the numbers present on these two food substances.

B. <u>Effect of constant diet on food preference</u>.

The position of 50 millipedes, in five experiments each with ten animals, on different food items is tabulated below.

Table 4.2. Food preference of Cylindroiulus punctatus (Leach) after a period on constant diet.

Day.	Hrs.	Mean (± S.E) No. on potato.	Mean (± S.E) No. on bark.	Mean (± S.E) No. undecided.
1.	8 a.m.	6.0 ± 1.5	4.0 ± 1.0	0
	Noon.	5.0 ± 1.2	4.0 ± 1.5	1.0 ± 0.5
	8 p.m.	6.0 ± 2.0	4.0 ± 1.5	0
	Midnight.	4.0 ± 2.0	4.0 ± 1.5	2.0 ± 1.2
2.	8 a.m.	5.0 ± 1.5	5.0 ± 1.5	0
	Noon.	5.0 ± 2.0	5.0 ± 2.0	0
	8 p.m.	5.0 ± 2.0	4.0 ± 1.2	1.0 ± 0.5
	Midnight.	6.0 ± 1.8	4.0 ± 1.5	0
3.	8 a.m.	4.0 ± 1.2	6.0 ± 1.5	0
	Noon.	5.0 ± 1.5	5.0 ± 1.5	0
	8 p.m.	3.0 ± 0.8	5.0 ± 1.0	2.0 ± 1.5
	Midnight.	4.0 ± 1.2	4.0 ± 1.5	2.0 ± 1.2
4.	8 a.m.	3.0 ± 1.2	6.0 ± 2.0	1.0 ± 0.5
	Noon.	3.0 ± 1.5	7.0 ± 3.5	0
	8 p.m.	3.0 ± 2.0	7.0 ± 2.5	0
	Midnight.	3.0 ± 1.8	7.0 ± 2.5	2.0 ± 1.2
5.	8 a.m.	3.0 ± 1.2	7.0 ± 3.5	0
	Noon.	4.0 ± 1.4	6.0 ± 2.5	0
	8 p.m.	5.0 ± 1.5	4.0 ± 1.2	1.0 ± 0.5
	Midnight.	3.0 ± 1.2	6.0 ± 0.8	1.0 ± 0.5
6.	8 a.m.	4.0 ± 1.5	5.0 ± 1.5	1.0 ± 0.5
	Noon.	4.0 ± 2.0	5.0 ± 1.0	1.0 ± 0.5
	8 p.m.	5.0 ± 2.5	4.0 ± 1.5	1.0 ± 0.4
	Midnight.	6.0 ± 2.0	4.0 ± 1.4	0
7.	8 a.m.	7.0 ± 3.5	3.0 ± 1.2	0
	Noon.	7.0 ± 2.5	3.0 ± 1.5	0
	8 p.m.	8.0 ± 3.5	2.0 ± 1.2	0
	Midnight.	8.0 ± 2.5	1.0 ± 0.5	1.0 ± 0.5

It can be seen from this table that at the end of the third day more millipedes were recorded on bark ~~potato~~ than on potato ~~rotten bark~~, but this preference was reversed towards the end of the experiment.

C. Rate of feeding in males and females.

In the following table, the amount of leaf consumed by males and females in a night is shown.

Table 4.3. Rate of feeding of the males and females of *Cylindroiulus punctatus* (Leach) under different conditions.

Month.	Constant temp. of 23^{o}C. & constant darkness, with R.H. 95 - 100%.		Varying conditions of temperature, light & relative humidity in the field.	
	Mean (± S.E) sq. mm. of leaf consumed overnight by:			
	Males.	Females.	Males.	Females.
1962.				
Feb.	0.17 ± 0.05	0.19 ± 0.08	0.08 ± 0.03	0.07 ± 0.05
May.	0.37 ± 0.08	0.40 ± 0.10	0.28 ± 0.07	0.25 ± 0.10
Aug.	0.30 ± 0.07	0.27 ± 0.08	0.23 ± 0.08	0.24 ± 0.07
Nov.	0.21 ± 0.10	0.19 ± 0.09	0.19 ± 0.07	0.21 ± 0.09
1963.				
Feb.	0.20 ± 0.05	0.17 ± 0.08	0.10 ± 0.06	0.07 ± 0.04
May.	0.39 ± 0.11	0.36 ± 0.07	0.32 ± 0.08	0.29 ± 0.11.
Aug.	0.34 ± 0.10	0.36 ± 0.09	0.29 ± 0.08	0.30 ± 0.04.

In none of the tests for different months, does a significant difference exist in the amount of food consumed by the males and the females. However, it seems that the feeding activities of the males and the females increase in May and then slowly decrease in subsequent months. It may also be noticed that the feeding rates of males and females were higher in all the experiments conducted in constant temperature, darkness and humidity.

D. Variation in feeding activity in 24 hour cycle.

Mean number of faeces produced by males and females, in different periods under different external conditions are presented in the following two tables.

Table 4.4. Variation in the feeding activity of *Cylindroiulus punctatus* (Leach) under fluctuations of temperature, light and humidity.

Month.	Mean (± S.E) number of faeces produced by five individuals:			
	7 a.m. - 8 a.m.		8 a.m. - Noon.	
	Males.	Females.	Males.	Females.
1962.				
Feb.	0	0	0	0
May.	0	0.2 ± 0.01	1.8 ± 0.6	1.0 ± 0.05
Aug.	0	0	1.0 ± 0.03	1.6 ± 0.05
Nov.	0	0	0	0
1963.				
Feb.	0	0	0	0
May.	0	0	2.0 ± 0.5	3.6 ± 1.2
Aug.	0	0	0	0
	Noon - 8 p.m.		8 p.m. - Midnight.	
1962.				
Feb.	1.6 ± 0.5	1.0 ± 0.05	2.4 ± 0.08	2.4 ± 0.1
May.	5.6 ± 1.5	5.0 ± 1.3	6.0 ± 1.5	5.0 ± 1.4
Aug.	5.0 ± 1.4	4.6 ± 1.2	4.6 ± 1.3	4.8 ± 1.5
Nov.	2.6 ± 0.8	0	4.8 ± 1.5	5.0 ± 1.8
1963.				
Feb.	0	2.0 ± 0.5	1.6 ± 0.6	0
May.	4.0 ± 1.5	4.0 ± 1.8	5.6 ± 1.8	6.0 ± 2.1
Aug.	3.6 ± 1.2	3.0 ± 1.6	5.0 ± 1.6	4.6 ± 1.8

Table 4.5. Variation in the feeding activity of Cylindroiulus punctatus (Leach) under constant temperature of 23°C. in constant darkness with a relative humidity of 95 - 100%.

Month.	Mean (± S.E) number of faeces produced by five individuals:			
	7 a.m. - 8 a.m.		8 a.m. - Noon.	
	Males.	Females.	Males	Females.
1962.				
Feb.	0	0	0	0.4 ± 0.01
May.	0.4 ± 0.02	0.6 ± 0.03	1.0 ± 0.8	3.0 ± 0.5
Aug.	0.3 ± 0.02	0	1.6 ± 0.8	3.0 ± 0.8
Nov.	0	1.0 ± 0.02	1.6 ± 0.5	1.0 ± 0.03
1963.				
Feb.	0	0	0	0
May.	1.0 ± 0.04	0.6 ± 0.03	2.0 ± 0.5	2.6 ± 0.6
Aug.	1.0 ± 0.04	1.2 ± 0.05	1.6 ± 0.7	1.0 ± 0.08
	Noon - 8 p.m.		8 p.m. - Midnight.	
1962.				
Feb.	4.0 ± 0.8	5.0 ± 0.4	5.6 ± 0.8	5.0 ± 0.5
May.	6.2 ± 1.5	5.8 ± 1.3	6.6 ± 1.3	7.6 ± 2.4
Aug.	5.0 ± 0.3	6.0 ± 1.2	6.0 ± 0.9	6.5 ± 1.2
Nov.	4.6 ± 1.1	5.0 ± 1.0	5.4 ± 1.2	5.0 ± 0.8
1963.				
Feb.	3.4 ± 0.5	3.0 ± 0.4	5.2 ± 1.3	5.4 ± 0.6
May.	7.0 ± 1.3	5.8 ± 1.1.	8.0 ± 1.5	7.6 ± 1.6
Aug.	7.0 ± 1.7	6.0 ± 1.7	5.6 ± 1.3	6.0 ± 1.5

It may be noticed from these tables that feeding activity increases considerably in May, and in the experiments conducted in this month, faeces were produced in all the phases of the twenty four hour cycle. In both the series of experiments, conducted in other months, more faeces were obtained at the two night phases (4 p.m. - 8 p.m. and 8 p.m. - midnight) than the two phases of the day (4 a.m. - 8 a.m. and 8 a.m. - noon). However, production of faeces started earlier in the series kept under constant temperature, humidity and light. No significant difference occurs in the number of faeces produced by males and females.

In one experiment, conducted in May 1963, five defaecated Cylindroiulus punctatus were kept in a large petridish with a piece of potato in the constant temperature room, in total darkness. Total number of faeces produced by them was counted at 8 a.m., noon, 8 p.m. and midnight for five successive days. The piece of potato and the filter paper was changed every morning at 6 a.m. The results are presented in the following table.

Table 4.6. Feeding rhythm of Cylindroiulus punctatus (Leach) under a constant temperature of 23°C. under constant darkness with a relative humidity of 95 - 100%.

Hour.	Total number of faeces obtained.				
	1	2	3	4	5 days.
8 a.m.	8	59	62	75	49
Noon.	19	12	15	10	17
8 p.m.	40	30	21	22	28
Midnight.	45	50	40	35	40

This experiment also shows more faeces were produced in the two phases of the night and that feeding and the production of faeces continued throughout the night, as was evident from the large number of faeces obtained in the mornings (8 a.m. of 2nd to 5th day.

E. Variation in food selection in 24 hour cycle.

In the following table the percentages of the total number of faeces examined in which the remains of particular food substances found are given.

Table 4.7. Analysis of the faeces of *Cylindroiulus punctatus* (Leach) collected at different times.

Time of collection.		Number examined.	Percentage of the total faeces with: Wood fragments dominant.	Leaf fragments dominant.	~~Dominant~~ substances unidentified.
8 a.m.	E.	255.	70.	25.	5.
	C.	185.	55.	42.	3.
Noon.	E.	267.	63.	37.	0.
	C.	285.	40.	35.	25.
8 p.m.	E.	315.	48.	40.	12.
	C.	396.	43.	45.	12.
Mid-night.	E.	380.	43.	41.	16.
	C.	412.	45.	40.	15.

E. = Millipedes kept in the varying temperature, light and humidity in the field.

C. = Millipedes kept in constant temperature of 23°C. in constant darkness with a relative humidity of 95 - 100%.

It can be seen from the results that faeces produced by <u>Cylindroiulus punctatus</u> in all the periods, under the two experimental conditions, contained both wood and leaf fragments. However, in the faeces produced in different hours under constant environmental conditions, wood and leaf fragments were present in almost equal frequency. A Friedman two way analysis of variance by ranks, shows that no significant difference exists between the number of faeces containing these two substances. In the case of specimens subjected to varying temperature, light and humidity, only wood fragments were present in the majority of the faeces examined at 8 a.m. and noon. But in the faeces examined at 8 p.m. and midnight, both the wood and leaf fragments were present in almost equal amounts. There was an increase in the percentage of faeces containing "unidentifiable substances" (may be fragments of moss or potato) at night. It would appear that a variety of food substances are eaten after dark, and possibly constant environmental conditions induced <u>Cylindroiulus punctatus</u> to take varieties of food earlier than those kept under fluctuating conditions.

F. Effect of temperatures on feeding activity.

An idea of the feeding activity of Cylindroiulus punctatus may also be obtained from the number of faeces produced by them at different temperatures, when suitable food is available. In the following table, the production of faeces by the males and females at different temperatures is shown. Experiments under different temperatures were not run simultaneously, but they lasted from the fourth week of September to the middle of November 1962.

It appears from the table that the largest number of faeces were produced by both males and females in the temperatures below, and at, 20°C. It may also be suggested, that within the limits of these experiments, the rate of faeces production slowly increases from 15°C. reaching a maximum at 20°C. and is followed by a slow decrease in the subsequent temperatures. At 30°C. very few faeces were produced. The increased or decreased rate of faeces production under different temperatures was further tested by subjecting same sets of five males and five females to different temperatures and counting the number of faeces produced by them overnight. These animals were kept in the constant temperature room at 23°C. when temperatures inside the thermostat were being changed.

Table 4.8. Feeding activity of <u>Cylindroiulus punctatus</u> (Leach) under different temperatures.

Day.	Mean (± S.E) number of faeces produced by five individuals of both sexes.			
	15°C.		20°C.	
	Male.	Female.	Male.	Female.
1.	7.2 ± 1.3	6.5 ± 2.0	11.5 ± 2.3	12.2 ± 1.5
2.	8.5 ± 2.3	7.0 ± 1.5	10.8 ± 1.5	12.6 ± 1.8
3.	5.6 ± 1.2	6.8 ± 1.8	12.4 ± 2.5	14.0 ± 1.9
4.	6.0 ± 2.1	5.8 ± 1.2	8.8 ± 1.2	12.0 ± 2.5
5.	7.4 ± 1.5	6.4 ± 1.1	10.6 ± 1.8	8.5 ± 1.2
6.	5.6 ± 0.8	7.6 ± 2.1	12.6 ± 3.5	8.5 ± 2.0
7.	6.6 ± 1.2	7.0 ± 1.5	8.6 ± 1.5	9.0 ± 1.5
8.	5.6 ± 1.3	4.8 ± 1.2	7.6 ± 1.2	8.0 ± 1.2
9.	6.8 ± 1.8	6.8 ± 1.3	8.6 ± 1.5	7.6 ± 1.4
10.	5.2 ± 1.2	4.8 ± 1.2	10.4 ± 1.8	8.6 ± 1.5
	25°C.		30°C.	
	Male.	Female.	Male.	Female.
1.	5.0 ± 0.8	4.5 ± 1.2	2.0 ± 0.8	2.0 ± 0.6
2.	4.5 ± 0.7	4.0 ± 0.8	1.8 ± 0.6	3.0 ± 0.8
3.	6.8 ± 1.2	6.4 ± 1.5	2.2 ± 0.9	1.8 ± 0.5
4.	4.5 ± 0.8	4.6 ± 1.2	1.8 ± 0.8	0
5.	5.6 ± 1.2	5.0 ± 0.8	2.6 ± 0.9	1.6 ± 0.6
6.	4.6 ± 0.8	5.6 ± 1.2	1.8 ± 0.7	2.0 ± 0.5
7.	5.0 ± 0.5	6.0 ± 1.2	1.6 ± 0.5	2.0 ± 0.5
8.	4.6 ± 1.0	5.0 ± 1.4	0	0
9.	5.0 ± 1.2	6.4 ± 1.3	2.0 ± 0.8	1.8 ± 0.5
10.	4.6 ± 1.0	3.8 ± 1.2	2.6 ± 1.0	2.0 ± 0.8

Table 4.9. Feeding activity of the same set of male and female Cylindroiulus punctatus (Leach) under different temperatures.

Temp. °C.	Treatment.	Mean (± S.E) number of faeces produced. Males.	Females.
15.	24 hrs.	8.6 ± 2.6	9.8 ± 3.4.
20.	24 hrs.	15.6 ± 3.5	18.4 ± 5.2.
25.	24 hrs.	6.0 ± 1.4	7.4 ± 2.3.
30.	24 hrs.	2.2 ± 0.8	1.8 ± 0.5.

The results agree with what was noted earlier using different sets of Cylindroiulus punctatus in various temperatures, i.e. more faeces were produced at 20°C than at the other temperatures.

G. Effect of the removal of antenna on food selection.

It would appear from the results presented following that Cylindroiulus punctatus with both the antennae, can easily detect food and very few of them were found "undecided" in their selection for food. But with specimens, with one or both antennae removed, majority were "undecided" with a few reaching the food provided.

Table 4.10. Food selection by <u>Cylindroiulus punctatus</u> (Leach) with and without antenna.

Condition of the experimental animals.	Mean (± S.E) No. on rotten bark.	Mean (± S.E) No. on rotten leaf.	Mean (± S.E) No. undecided.
Both antennae removed.	0.8 ± 0.02	1.0 ± 0.5	3.2 ± 1.5
One antenna removed.	0.8 ± 0.05	0.6 ± 0.2	3.6 ± 1.4
Control.	2.4 ± 1.5	2.6 ± 1.2	1.0 ± 0.6

It is interesting to note that the removal of one or both antennae had similar effects on the behaviour of the experimental animals. But whether these animals failed to reach the foods because of the removal of antenna or due to the depressing effects induced by their removal is difficult to say.

Discussion.

The food of millipedes seems to vary. Brade-Birks (1930), Cloudsley-Thompson (1950), and Kinkel (1955) mention that the food of *Blaniulus guttulatus* consists of rotting plant materials, though this species also attacks living plants. According to Brade-Birks, *Diploiulus* (= Cylindroiulus) *londinensis* var. *Coeruleocinctus* (Wood) mostly lives on rotting vegetation and occasionally turns to living plants. He also mentions that *Cylindroiulus silvarum* occurring beneath the bark of dead trees, mainly feeds on wood. *Schizophyllum sabulosum* and *Tachypodoiulus niger* have been described by Blower (1955) as feeding on aerial parts of living vegetation. My experiments on the food preference of *Cylindroiulus punctatus* indicate that this species prefers rotten bark or rotten leaves, to fresh bark or leaves, though it has been found to feed well on potato. In these experiments, at no time of the year was there a significant difference between the numbers feeding on rotten bark or rotten leaves. Barlow (1957) also noted in the millipedes he studied, a preference for rotting leaves and rotting wood to green leaves and living wood.

In the course of the present investigation it has also been observed that C. punctatus does not show any special preference for the bark or leaves of birch, beech or oak when given a choice, as long as they are rotten. Schmidt (1952) found that the selection of leaves by the iulids and glomerids he studied, was not absolutely dependent on the state of decomposition of the leaves and Lyford (1943) records that D. (= Cylindroiulus) londinensis chooses leaves with high calcium content. However, in the present experiments, C. punctatus did not accept freshly fallen green leaves of oak, birch or beech.

It has been observed that when C. punctatus was kept on a constant diet for some time, it developed a tendency to change its food for a while, when alternate food was provided. Whether this behaviour also persists in nature is difficult to determine, as C. punctatus is common both in mixed litter of oak, birch and beech, and also in homogenous litter of each of these three.

In a mixed litter it has access to leaves of various species of tree: but its lack of specificity for leaves of any species of tree would indicate that *C. punctatus* feeds on different leaves with equal preference. The fact that *C. punctatus* does not show any special preference for the rotting bark and leaves of one species of tree is of prime importance in the ecology of this species, since it means that it can live in the litter beneath a variety of deciduous trees.

During the period of active feeding, faecal pellets are mostly produced within about two hours of feeding, but this time varies, depending partly on the physiological state and feeding activity of the individual animal. Examination of the faeces produced in different phases of the twenty-four hour cycle gives a fair indication of the feeding activity of *C. punctatus*. In all experiments, more faeces were produced at night, and in these faeces, remains of a greater variety of food substances were found, than in those produced in the day. However, *C. punctatus* kept in the laboratory under constant temperature, darkness and humidity, began their feeding activity earlier than those kept in continuously changing conditions of temperature, darkness and humidity in the field. *C. punctatus* begins its feeding activity after darkness, when the air temperature goes down and the relative humidity of the air rises. It is likely that constant environmental conditions, particularly darkness, induced *C. punctatus* to begin its feeding activity earlier than those under "fluctuating" conditions.

Kinkel (1955) mentions that *Blaniulus guttulatus* when kept on a protein free diet began to eat the legs off their fellows as well as their own legs. Examination of the gut contents of *C. punctatus* from laboratory cultures and also of individuals freshly captured from the litter sometimes revealed the presence of collembola and remains of other arthropods. It is however, difficult to say if these animal remains and collembola were actually eaten by *C. punctatus* or if they were ingested indirectly along with the litter consumed.

Barlow (1957) states that digestion in millipedes is incomplete and substances consumed by them were recovered practically unaltered from the faeces, although he also points out that some proteases must be present in the digestive tracts of the millipedes. However, Randow (1924) claims that only fat and starch digesting enzymes were present in the guts of the millipedes he examined. Recently, Nielsen (19$\overset{62}{\underline{26}}$) has reported that the millipede Cylindroiulus silvarum lacks the enzymes for hydrolyzing plant polysaccharides. Preliminary microchemical tests, made in the course of the present investigation, indicate that cellulose, lignin or starch are not digested by C. punctatus to any measureable extent, though substances containing these were readily accepted as foods. It is possible that bacteria and other micro-organisms taken in by C. punctatus along with rotten leaves and bark set up enzyme activities which may help in digestion.

II. Humidity preference of *Cylindroiulus Punctatus* (Leach)

Introduction.

The importance of environmental humidity as a survival factor for the millipedes has long been known. Shelford (1913) observed that the millipede *Fontaria corrugata* was stimulated by dry air and in an atmosphere with higher humidity the species was less active, becoming quiescent in the moist air. Cloudsley-Thompson (1951a) studied the humidity responses of *Blaniulus guttulatus* and *Paradesmus gracilis* and concluded that no klinokinetic, klinotactile or orthokinetic reactions occur in them, though there were tendencies for them to come towards the damper side of the humidity gradient. Perttunen (1953) studied in detail the reactions of *Orthomorpha gracilis*, *Iulus terrestris* and *Schizophyllum sabulosum* to differences in the relative humidities of the air. He observed both the orthokinetic and klinokinetic reactions in *Orthomorpha* and noticed the seasonal variation in the humidity preference in *Schizophyllum sabulosum*. Barlow (1957) has investigated the humidity responses of *Cylindroiulus silvarum*, *Schizophyllum sabulosum* and *Iulus scandinavius*, and noticed interspecific and intraspecific differences in the intensity of attraction towards high humidity. From all these accounts the importance of humidity as a limiting factor in the distribution of the millipedes becomes clear and in the present investigation it is purposed to examine the responses of Cylindroiulus punctatus and to correlate them with its distribution in nature.

Method:

The apparatus used in the experiments was the choice chamber or alternate chamber of Gunn and Kennedy (1936). It consisted of a glass dish, 18 cm. in diameter and 4.5 cm. in depth, divided into two by a glass and wax partition and covered by means of a circular glass plate. The desired humidities were maintained by keeping different concentrations of potassium hydroxide in water in the two halves. The arena was provided by a floor of muslin stretched over a perforated zinc gauze and attached to the sides by a ring of plasticine. The whole apparatus was covered by a large crystallizing dish, resting on a glass plate, and the junctions were sealed with vaseline to ensure they were air tight.

The humidity responses of Cylindroiulus punctatus was also observed by offering at the same time a multiple choice of 70%, 80%, 90% and 100% relative humidities. The apparatus used for this purpose was the same as before: under the arena were placed five small dishes with required strengths of potassium hydroxide in water to produce different humidities. 100% humidity was produced by distilled water. In both sets of apparatus the relative humidities produced were checked by means of cobalt thiocyanate paper. (Solomon, 1945, 1957).

The experiments, involving both the alternate and multiple choices of humidities, were repeated five times using different sets of animals each time, in April, July, October and January. With the alternate chamber, the males and females were tested separately. In each of these experiments, ten millipedes were introduced into the arena through a hole on the covering glass plate and the positions of the animals were recorded every 60 minutes for twelve consecutive hours. The hole was plugged with plasticine after inserting the animals. The millipedes used were collected from the litter the day before the experiment and were kept in the constant temperature room at 23°C. overnight, with a relative humidity of 95 - 100% inside the container. In the experiments done in January, the millipedes collected several days before, had to be used. But they were kept in the same conditions in the C.T. room before using in the experiments.

All the experiments were carried out in a constant temperature room at 23°C. and the apparatus was covered by a large cardboard box to ensure complete darkness.

The results given for each month represent the observations of 600 position records in five experiments, each of twelve hours duration.

Results:

The results of different tests are tabulated following. In all the tests, involving the multiple and alternate choice of humidities, there was a prevailing preference for the highest humidities in the gradients. Changes in the speed of locomotion were readily observable as the animals were passing from one humidity to another. Usually within an hour the experimental animals became motionless in the humidity of their choice. Halts, turns and testing movements, typical of kineses and taxes, were displayed at the time of the selection of a humidity, but once the animal became settled in a particular humidity, these movements were not frequently performed.

Table 4.11. Position record of adult Cylindroiulus punctatus (Leach) in alternate chamber with paired humidities.

No. of adults recorded between:

	30% R.H.	40% R.H.	50% R.H.	60% R.H.	70% R.H.	80% R.H.	90% R.H.	100% R.H.
				<u>Apr.</u>				
M	265	335	280	320	300	300	270	330
F	300	300	280	320	250	350	280	320
				<u>July.</u>				
M	270	330	310	290	280	320	260	340
F	290	320	270	330	270	330	280	320
				<u>Oct.</u>				
M	210	390	220	380	250	350	200	400
F	180	420	190	410	250	350	200	400
				<u>Jan.</u>				
M	150	450	180	420	150	450	200	450
F	140	460	200	400	200	400	190	410

M = Males: F = Females.

Table 4.12. Position record of adult Cylindroiulus punctatus (Leach) with with multiple choice of humidities.

No. of adults recorded at:

Month.	70% R.H.	80% R.H.	90% R.H.	100% R.H.
April.	70	90	230	210
July.	120	140	180	160
October.	70	80	200	250
January.	60	80	140	320

Discussion.

It can be seen from tables 4.11 and 4.12 that both males and females of Cylindroiulus punctatus show a preference for high humidity in all the seasons of the year. However, the degree of attraction towards higher humidities shows some variation in the experiments conducted in different months. In experiments with alternate choice of humidities conducted in October and January, a very high percentage of adults were found preferring highest of any two humidities offered. In the experiments conducted in April and July the figure was somewhat lower. When the multiple choice of humidities was offered, preference for the highest humidity (100%) was also very much pronounced in October and January. Perttunen (1953), and Barlow (1957) also noticed a seasonal variation in the humidity preference of the millipedes they studied.

The strong preference for high humidities, exhibited by Cylindroiulus punctatus in laboratory experiments can be explained in terms of the distribution of the species in nature. It inhabits wooded areas with dense cover of litter. The floral canopy provides a comparatively humid environment by inhibiting the evaporation of water in two ways. In the first place, it decreases the amount of sunlight which penetrates the ground level. Secondly, the air at this level is cooler, and consequently has less evaporating power than the air in direct sunlight. Vegetation also restricts air current, thereby reducing the amount of water vapour which is conducted away. Besides, the adults are also found in aggregations in the subcortical spaces of the logs where the relative humidity of the air is very high. Animals living under such conditions can be expected to develop a strong preference for high humidity. However, very little evidence was found of a seasonal change in the relative humidity in the subcortical spaces or in the litter, to account for a corresponding change in the humidity preference of <u>Cylindroiulus punctatus</u>. Possibly physiological conditions of the millipedes in different seasons also regulate their humidity responses. Preference for high humidity during winter (October and January) has great survival value for <u>Cylindroiulus punctatus</u> in nature since in a moist environment latent heat of water tends to prevent a rapid subzero drop in temperature.

Section V.

Studies on the life cycle of Polydesmus angustus Latzel.

Introduction.

Polydesmus angustus Latzel is one of the most common millipedes on the leaf litter of the woodland, and Nielson (1963) has described this species as one of the primary decomposers of the litter. Broleman (1935) and Blower (1958) have given a general account of the biology of Polydesmoidea, and life histories of various species have been described by Effenberger (1909), Evans (1910), Voges (1916), Miley (1927), Seifert (1932), Causey (1943), Eaton (1943), and Davenport, Wotten and Cushing (1952). Pflugfelder (1932) has described the segment formation in Platyrrheus amaurus, and the behaviour of different species has been studied by Cloudsley-Thompson (1951a), Perttunen (1953), and Barlow (1958).

As far as I am aware, life history of none of the polydesmid millipedes has been studied from an experimental point of view. In the present section, results of an experimental study on the life history of Polydesmus angustus Latzel are being reported.

Methods.

A. Field observations on life history.

A number of "colonies" of Polydesmus angustus on moss cushions in the woodland around the college compound were regularly examined for the presence of different larval instars. Large numbers of nests with eggs were also noticed here. Additional information on the relative abundance of various larval instars in the litter were obtained from regular extraction of litter by Berlese funnels. Advanced instars (5th, 6th and 7th) were also trapped in the pitfall traps at different times of the year. By pooling together all these data some information about the life cycle of the species in the nature was obtained.

B. Experimental studies on the life history.

Adults were kept in the laboratory in large petridishes filled with litter collected from the natural habitats. The litter was regularly sprinkled with water and occasionally fresh litter was added. Some of the cultures were maintained in a constant temperature room at 23°C. and were kept in constant darkness by covering them with a large cardboard box (CT). Another series was maintained at the room temperature (varying from freezing point to 32°C. in different seasons of the year) with varying conditions of light (RT). Humidity inside the petridishes varied between 95 - 100%.

In order to determine the duration of different instars, individuals belonging to different instars were isolated as soon as they appeared in the cultures and maintained separately under conditions in which they first appeared.

In the constant temperature room the cultures were maintained in oak, beech and birch litter. Effects of diet on the development were studied by transferring different instars from one food medium to another, and these experiments were carried out in a constant temperature room at 23°C. in complete darkness with a humidity of 95 - 100%.

C. Humidity preference:

Experiments on mating in different humidities were done in the constant temperature room. The experimental animals were kept inside dessicators and desired humidities were produced by different concentrations of potassium hydroxide in water. Humidity preference was studied in the choice chamber apparatus in the constant temperature room at 23°C.

Results.

A. Life history: field observations.

The relative abundance of the different instars in the litter is shown in the figure 5·1 . Nests with eggs were noticed in April to June, though many were constructed before this period, though not seen in the experimental area. Females were seen crawling around these nests or staying very near them. Blower (1958) has stated that the life histories of the Polydesmids are completed in about twelve months. From figure 5·1 it would appear that the development from 1st to 7th instars is completed in about twelve months, but from the hatching of the eggs to the emergence of the sexual adults possibly more than twelve months is required.

B. Life history: laboratory studies:

1. Mating.

Before mating, the male approaches the female from behind and slowly moves along the dorsal surface of the female, the latter by this time comes to lie below the male with her ventral side in contact with the ventral side of the male. The legs of the anterior segments of the male are used to clasp the female by the sides of her keel. Usually the mating

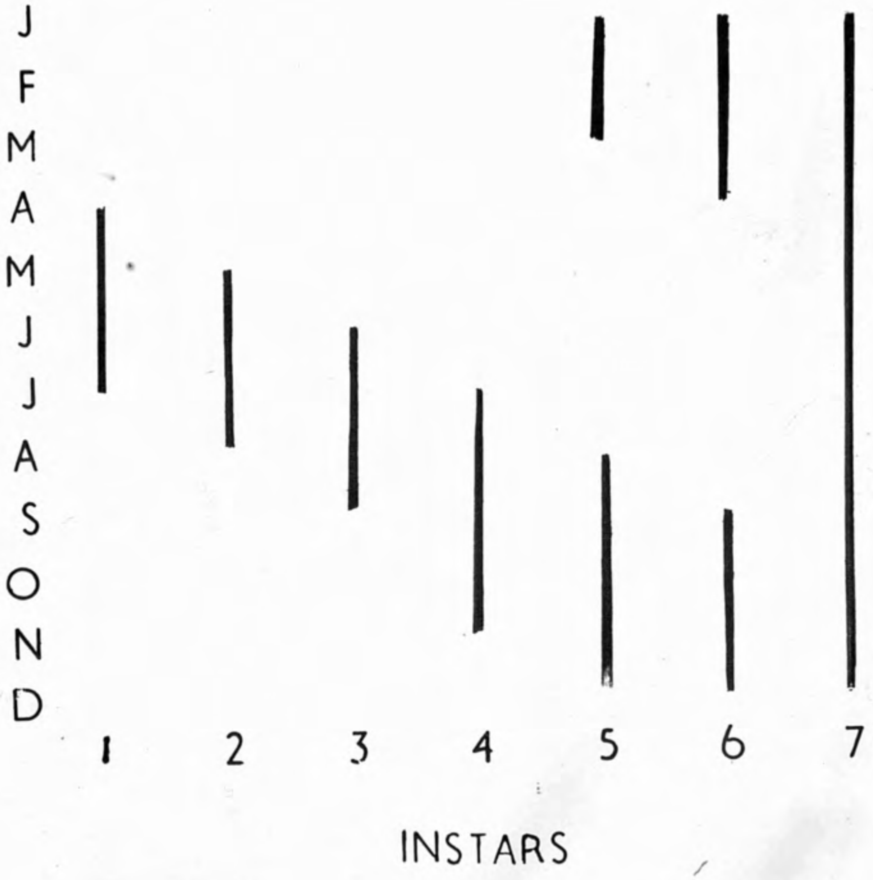


FIG. 5.1. Seasonal occurrence of different instars of <u>Polydesmus angustus</u> in litter.

lasts for considerable time, varying from 55 minutes to twelve hours in different pairs. Fertilized females do not mate again in the same year. In the constant temperature room at 23°C. mating was observed during January to July, but at room temperature it took place between different pairs in March - June.

Attempts were made to observe the effects of different humidities on the frequencies of mating between different pairs. The results presented in the following table show that most of the pairing occured in high relative humidities. The experiment was repeated five times spreading over five months, using different sets of animals every time.

Table 5.1. Mating of Polydesmus angustus in different relative humidities at 23°C.

Percentage. of RH produced.	No. of pairs found mating. (Out of ten pairs in each humidity). March.	April.	May.	June.	July.	Total.
30.	0	0	2	2	1	5
40.	2	4	2	3	4	15
50.	2	5	5	4	3	19
60.	4	3	4	5	6	22
70.	5	7	8	7	8	35
80.	9	8	8	8	7	40
90.	8	8	7	9	8	40
100.	6	7	7	7	7	34

Figures underlined indicate that some of the females from these groups laid eggs.

2. Oviposition and nesting behaviour:

The time between mating and egg laying showed considerable variation. In a few cases the females failed to lay any eggs though they were seen mating. Table 5.2 shows some observations regarding the time between mating and egg laying.

Table 5.2. Time passed between mating and egg laying in Polydesmus angustus Latzel in the constant chamber room at 23°C. in total darkness with a relative humidity of 95 - 100%.

Mating seen on	Eggs laid on	Time taken days	Eggs laid at
Jan 7,'62.	April 22,'62.	105	Day.
Mar 30,	April 19,	20	Day.
Apr 28,	June 17,	50	Night.
May 5,	May 20,	15	Night.
June10,	June 30,	20	Day.
Jul 12,	July 31,	19	Night.
Aug 7,	Aug 30,	23	Night.
Jun 12,'63*	June 26,'63	14	Night.
Jun 20,*	July 10,	20	Night.
Jun 28,*	July 21,	23	Day.
Jul 5,*	July 26,	21	Night.
Jul 15,*	Aug 10,	26	Day.
Mar 21,	April 10,	20	Day.
Apr 5,	April 30,	25	Day.
May 11,	June 5,	25	Night.
Jun 4,	June 22,	18	Night.
Jul 25,	Aug 8,	14	Night.

* These adults were reared in the laboratory.

Since the majority of the eggs were laid between 14 - 25 days after mating, it may be assumed that two weeks passed between mating and the laying of the eggs.

It may be possible that the females which mated but did not lay eggs, had immature ova or the males with whom they mated lacked mature spermatozoa. But the fact that the freshly emerged mature adults readily mated and laid eggs minimizes this possibility. Same pairs of males and females mated in the laboratory both in 1962 and 1963 and both times eggs were laid. It is possible that the females that mated but did not lay were the older ones with less or no fecundity at all.

Just before oviposition, the females become restive, possibly in search of suitable sites for nest construction preparatory to egg laying. In the cultures, the females were seen walking round and round the edges of the crystallizing dishes in which they were kept. They constantly flicked their antennae during such movements. Sometimes they would stop this movement for a while, apparently after detecting a suitable site. If, after close inspection the site was not found suitable for nest construction, the females resumed their movements.

What factors determine the selection of the nesting sites are difficult to say, but these sites usually appeared to be on slightly concave surfaces. In the field, the nests were found on the moss cushions, and also on the surface of tree logs on the ground.

After the selection of a suitable site, the female begins to move slowly round the site selected. As she does so, she leaves behind a blob of excrement which dries quickly as it comes into contact with the air. These faeces are held together by a sticky substance which also comes out of the rectum. Eventually this sticky substance spreads all over the faeces making them rather "muddy". In about ten to forty minutes, the concave spot is surrounded by a sort of rampart. Sometimes the female adds bits of leaves on the surface of the rampart to make it indistinguishable from the surroundings. Soon after, the female lies across the nest and eggs are laid one after another, sticking together as they drop. The female rests on the nest for some time after laying the eggs and from a dorsal view the whole egg mass appears like a bouquet.

Soon after laying the eggs, the female begins to construct the upper part of the nest to cover the egg mass. The construction of the upper part takes place rather slowly. Only the posterior part of the animal makes slow movements around the rim of the nest leaving a blob of excreta in a similar manner as before. The anterior part of the female's body rests in the surrounding litter and makes very slow movements. The whole nest is completed in about one to one and a half hours, and when finished, it looks like a chimney with a broad base and gradually tapering upper end. The average diameter of the nests at the broad base is 7 mm., the height being 10 mm.

The females do not leave immediately after the nest is completed, but stay round it for several days. Sometimes she covers the whole nest with bits of leaves and crawls slowly all over the surface. When the females were forcibly removed from these positions, they quickly returned to the nests and regained their former positions round the nests. If the nests were damaged they were quickly repaired by the females. During the whole process of nest construction, the males stayed passive. Attempts were made to replace the females crawling round the nests by males. In no case did the males stay round the nest and sometimes they retreated so quickly that they actually damaged the nest.

When the females were removed after they had laid eggs and before they had constructed the "chimney" part of the nest, those eggs failed to hatch. The temperature inside a number of nests in different locations was measured by means of a thermocouple and is shown in the table 5.3.

Table 5.3. Temperature inside the nests of <u>Polydesmus angustus</u> Latzel.

Location of nests.	Outside temp. °C.	Nest temp. °C.
Field.	22.5	14.4
	19.0	17.5
	18.8	14.0
	20.5	16.2
	17.5	14.6
Constant temp. room.	23.0	17.5 *
		17.0 *
		17.0 *
		19.0 **
		19.5 **
Room temp.	18.5	15.6 **
	20.0	15.8 **
	19.5	14.0 *
	19.0	14.5 *
	20.5	15.0 *

* Temperature measured soon after construction.
** Temperature measured one day after construction.

It would appear that the temperature inside the nests is slightly affected by the outside temperature, though the range of temperature inside the nests was between 14.0 - 19.5°C. with the outside temperature varying from 17.5 to 23°C. Noticeable difference also existed in the nest temperature measured soon after, and one day after, finishing its construction. The latter observation was further confirmed by measuring the nest temperature for twelve consecutive hours. For this purpose the thermocouple prober was kept fixed inside the nest all the time, and the temperature was read at the appropriate hours. The results shown in the table 5.4 are the mean of five observations on five different nests all constructed in the constant temperature room.

Table 5.4. Variation in the nest temperature of <u>Polydesmus angustus</u> Latzel.

Recording time. (Hours after construction).	Recorded temp. °C.
Soon after construction.	15.0 ± 1.5
1.	15.5 ± 2.0
2.	16.0 ± 1.8
3.	16.0 ± 2.0
4.	17.0 ± 2.5
5.	17.0 ± 2.5
6.	17.5 ± 1.9
7.	18.0 ± 2.5
8.	18.0 ± 2.5
9.	18.0 ± 2.0
10.	19.0 ± 1.5
11.	19.5 ± 1.5
12.	20.0 ± 1.4

In the next four days the temperature in these nests was recorded at intervals of three hours and the reading was between 19.0 - 20.5°C.

Out of 48 nests constructed in the constant temperature room, 10 females died after completing the nests. Out of these 10 nests, eggs in six did not hatch, since no first instars were observed in the cultures. Males removed immediately after mating, or during any phase of the nest building, seemed to have no effect on the nest building behaviour of the females. Removal of the females from the culture where they mated to new sites, had no effect on their nesting behaviour. The females removed from one culture to another during their initial "seeking behaviour" for nesting sites, continued this behaviour in new places only after a little pause and eventually laid eggs. In the same culture more than one nest was constructed by different females.

3. Nature of the eggs and number laid.

Eggs are white in colour and adhere together by means of a sticky substance. They are roughly spherical in outline, average diameter being 0.35 - 0.45 mm. The eggs are very rich in yolk. The number of eggs counted in different nests is shown in the table 5.5.

Table 5.5. Number of eggs in the nests of *Polydesmus angustus* Latzel.

Number of eggs counted in some nests located at:		
Field.	RT.	CT.
125	128	135
150	145	125
175	211	145
225	227	153
246	238	251

Apparently, the number of eggs laid is a matter of individual variation. The number of eggs laid by the same females in two successive years are shown below.

Table 5.6. Number of eggs laid by same females of <u>Polydesmus angustus</u> Latzel in successive years. (All in CT room).

Number of eggs laid: 1962.	1963.
175.	135.
118.	97.*
201.	178.
225.	180.*
185.	142.

* Mated with the same males as in the year before.

Three females which were reared from the eggs laid in 1962, laid 211, 275 and 238 eggs respectively. There is a slight indication in the table 5.6 that the fecundity of the females decreases with age.

4. Hatching and Post embryonic development.

Some information about the time passed between the egg laying and hatching may be obtained from table 5.7. To study the post embryonic development, different cultures were examined every day for the presence of various instars. There was therefore little chance of overlooking any stage of development or the time taken to develop from one instar to another.

Table 5.7. Time (days) between egg laying and appearance of first instars of Polydesmus angustus Latzel.

Nest no.	Field.	Constant temp. room at 23°C.
1.	43	12
2.	35	16
3.	46	28
4.	52	19
5.	43	33
6.	40	29
7.	42	25
8.		30
9.		26
10.		22
Mean.	43.0	23.0.

The eggs laid by three females which were reared in the laboratory took 15, 20 and 25 days respectively to hatch. These females were kept in the constant temperature room. The observations would indicate that the eggs in the field took longer to develop than those in the constant temperature room in constant darkness.

The first instar larvae came out of the basal end of the nests and all of them appeared to come out from the same point. The females, which in many instances were staying round the nests at the time of the emergence of the first instar larvae, possibly made the apertures in the nests through which the larvae came out. In some cases, the removal of the female after the completion of the nests, prevented the emergence of the first instars, otherwise the first instar larvae came out of their own accord from the basal part of the nests. However, these individuals appeared to be slightly older, as was evident from their guts filled with black humus. Under normal circumstances, immediately after hatching the first instar larvae appear to be transparent white in colour and move around the surface of the nests. Within one to four hours after their emergence they start feeding on humus and other substances from the surface of the nests. As a result, their guts become dark very soon. After feeding, the first instar individuals started moving at random all over the cultures, and sometimes even moved on the backs of the adult males and females when they were present in the cultures.

When the first instar larvae emerged more or less at the same time from different nests in the same culture, for a time they stayed on the surfaces of their respective nests. But soon after feeding, the larvae from different nests intermingled freely with each other all over the culture.

The removal of the females after the emergence of the first instar larvae, had no effect on the further development of the instars.

5. Moulting.

Polydesmus angustus undergo seven moults before developing into sexually mature adults. The basic plan of moulting is very similar in all the instars. Prior to moulting, the individuals become 'inactive', in the sense that they make very slow movements. Each individual constructs its own moulting chamber with bits of humus and leaves which are held together by the secretions of the salivary glands. The individual then creeps inside this chamber and seals the opening from inside. More than one individual in the same chamber was not uncommon, though individuals belonging to different instars were never found in the same moulting chamber. In the cultures it was frequently observed, that, if parts of the original nests were present at the time of moulting, many individuals went back into them for moulting.

Miley (1927) has described the whole process of moulting. During this time, the old cuticle splits laterally above the articulation of the legs. The animal then creeps out of the old skin near the junction of the head with the first trunk segment.

In cultures, immediately after moulting, the newly moulted individuals started coming up on the surface of the humus and fed actively on it.

6. Gonopod development.

The pattern of gonopod development is very similar to other Polydesmoid millipedes. Sexual dimorphism begins from the fourth instar and at this stage, in the males, a dome shaped structure appears in the place of the 8th pair of legs. In the two succeeding instars, this dome shaped structure becomes more complicated, larger and three jointed. In the seventh instar, the three joints of the "dome" become considerably larger with the proximal segment sinking into a pit in the sternite. After the final moult, the gonopod is further modified.

7. Characteristics of different instars.

The segment numbers and the measurements of different instars are tabulated below. The individuals measured (more than 150 for each instar) were reared in the constant temperature room at 23°C.

Table 5.8. Segment numbers and measurements of various instars of Polydesmus angustus Latzel.

Instars.	No. of Segments.	Mean total length (±S.E) mm.	Mean maximum width (±S.E) mm.	No. of pairs of legs. Male.	Female.
1.	7	1.3 ± 0.23	0.35 ± 0.09	3	3
2.	9	2.1 ± 0.42	0.54 ± 0.12	6	6
3.	12	3.8 ± 0.38	0.94 ± 0.16	11	11
4.	15	5.7 ± 0.96	1.25 ± 0.18	16	17
5.	17	6.7 ± 0.34	1.83 ± 0.34	22	23
6.	18	12.7 ± 0.41	2.30 ± 0.27	26	27
7.	19	17.8 ± 0.57	3.40 ± 0.23	28	29

8. Rate of larval development under different external stimuli.

The rate of development of various instars was studied in the constant temperature room at 23°C. in complete darkness (CT) and also under varying conditions of temperature and light (RT). The following results are presented.

Table 5.9. Rate of larval development of various instars of <u>Polydesmus angustus</u> Latzel under different external stimuli.

Instars.	Mean (± S.E) of time in days taken to pass from one instar to another.			
	N.	CT.	N.	RT.
1-2	100	9.6 ± 3.2	100	15.5 ± 2.5
2-3	93	23.8 ± 6.8	89	28.4 ± 7.3
3-4	87	31.0 ± 5.4	75	35.6 ± 6.4
4-5	83	25.0 ± 7.3	70	34.2 ± 3.8
5-6	79	21.4 ± 3.8	65	38.7 ± 4.5
6-7	69	20.0 ± 3.5	58	27.5 ± 6.5
7-8	43	34.2 ± 7.3	38	42.5 ± 6.2

In the field, whole life cycles are completed in about 12 - 14 months, but under constant conditions of temperature and darkness, life cycles are considerably reduced. It may also be noticed, that those reared under varying conditions of temperature and light took more time to develop into adults than those under constant conditions. These observations were continued on the same group under both the conditions, and it can be seen that percentage of survival was higher in the group kept under constant conditions of temperature and darkness.

In the following table, the effect of altered external stimuli on the rate of larval development of various instars is shown.

Table 5.10. Rate of larval development of Polydesmus angustus Latzel, under altered external stimuli. Instars transferred from constant temperature and darkness to varying conditions of temperature and light.

Instar transferred.	No. transferred.	No. developed into adults.	Mean (± S.E) days taken to develop into adults from 1st instar.
1.	20	8	245.6 ± 28.6
2.	20	11	232.5 ± 21.5
3.	20	10	236.8 ± 18.4
4.	20	9	221.5 ± 15.7
5.	20	17	178.6 ± 12.4
6.	20	15	174.5 ± 8.5
7.	20	18	164.5 ± 9.5

It appears from this table that transference of 5th, 6th and 7th instars from original conditions in which they were reared to new conditions, had no effects on the duration of the rest of the life cycle. They took more or less the same time to develop into adults as they would have taken in the constant temperature and darkness. The first four instars, when similarly treated, took about the same time to develop into adults as the individuals reared throughout under varying conditions of temperature and light.

The rate of development of 15 males and 15 females under different external stimuli are shown in the table 5.11.

Table 5.11. Rate of larval development of male and female <u>Polydesmus angustus</u> Latzel, under different external stimuli.

Instars.	Mean (± S.E) of the time in days, taken to pass from one instar to another.			
	CT.		RT.	
	Males.	Females.	Males.	Females.
4-5	23.4 ± 8.5	22.6 ± 3.4	35.6 ± 8.5	36.2 ± 3.5
5-6	25.0 ± 4.7	25.4 ± 3.5	33.8 ± 4.5	29.0 ± 3.8
6-7	22.6 ± 8.5	19.6 ± 4.5	28.6 ± 5.8	25.3 ± 3.7
7-8	39.6 ± 8.2	32.5 ± 5.4	45.5 ± 5.8	40.2 ± 3.8

It appears that under different external stimuli, the females tend to develop earlier than the males.

9. <u>Effect of diet on development</u>.

The effect of diet on the developmental rate was studied by transferring various instars from oak (control series) to birch and beech litter, and noticing the time taken by these instars to develop into adults. Thirty individuals of different instars were transferred from oak to each of the birch and beech litter. The results presented in table 5.12 would indicate that duration of the life cycle was greatly reduced when the diet of first five instars was changed at any level of development. Such treatment had least effect on the duration of the rest of the life cycle of 6th and 7th instars.

Table 5.12. Rate of larval development of <u>Polydesmus angustus</u> Latzel, on different diets, at a constant temperature of 23°C. in complete darkness, with a relative humidity of 95 - 100%.

	Mean (± S.E) days taken to develop into adults from first instar.			
Instars transferred from oak litter. (30 of each instar).	Transferred to birch litter.	No. developed into adults.	Transferred to beech litter.	No. developed into adults.
1.	225.5 ± 18.5	20	242.0 ± 15.5	23
2.	248.2 ± 24.2	22	258.5 ± 23.4	21
3.	245.0 ± 25.6	18	250.6 ± 25.6	20
4.	240.5 ± 18.5	18	245.3 ± 24.3	15
5.	237.7 ± 24.6	17	243.8 ± 18.9	18
6.	170.4 ± 19.8	23	178.2 ± 21.2	26
7.	168.5 ± 18.7	26	170.0 ± 18.4	22

Time taken by first instars to develop into adults when maintained in homogenous oak, birch or beech litter separately throughout the entire period of development is shown in the following table.

Table 5.13. Rate of larval development of Polydesmus angustus Latzel, on the same diet, at a constant temperature of 23°C. in complete darkness, with a relative humidity of 95-100%.

Food medium.	No. of first instars kept.	No. developed into adults.	Mean (± S.E) days taken to develop into adults from first instar.
Oak litter.	30.	17.	168.5 ± 18.6
Birch litter.	30.	12.	174.8 ± 22.6
Beech litter.	30.	10.	180.2 ± 12.8

Another effect of the change of diet was on the size of the adults. The results shown in the table 5.14 indicate that adults with entire developmental stage maintained in the same food, appear larger than others subjected to a change of diet during larval development.

Table 5.14. Length of the adult Polydesmus angustus Latzel, reared in different food media, at a constant temperature of 23°C. in complete darkness, with a relative humidity of 95 - 100%.

Reared in	Mean length (± S.E) mm.	Number measured.
Oak litter	25.7 ± 3.7	43.
Beech litter	26.9 ± 4.8	49.
Birch litter	26.5 ± 3.5	45.
*Oak litter to birch litter.	18.5 ± 4.5	25.
*Oak litter to beech litter.	22.6 ± 3.2	28.

* Includes adults with any instar, except 6th and 7th transferred.

Adults, having 6th or 7th instars transferred to different food media, appeared to have more or less same lengths (25.5 ± 4.8 : N= 45) as the adults maintained in the same food medium throughout their larval development. The physiological reason for the slow development, when diet is altered at certain stages of development has not been worked out, nevertheless it is interesting to note that slow development associated with altered diet also leads to the development of small sized adults.

C. Humidity preference of the newly emerged and old adults.

The tests for the humidity preference by the adults of Polydesmus angustus indicate a strong preference for the high humidity in the gradients. Since large numbers of adults were all reared in the laboratory, it was decided to see if any real difference existed between the humidity preference of the freshly emerged and relatively older adults. The choice of humidities offered were 60% - 70%, 70% - 80%, 80% - 90% and 90% - 100%. For each pair of humidities, ten different sets of animals were used. Since this species of millipede is particularly sensitive to humidity, the experimental animals took up their positions in the preferred humidity within ten to thirty minutes after starting the experiment. The results in the table 5.15 represent the total number of animals noted in different humidities during twelve consecutive hours of observation.

Table 5.15. Humidity preference by the old and freshly emerged adults of Polydesmus angustus.

RH.%	60 - 70.		70 - 80.		80 - 90.		90 - 100.	
	No. of adults found in each humidity gradient.							
Older adults.	2	8	3	7	5	5	4	6
Freshly emerged adults.	0	10	0	10	2	8	3	7

Unfortunately, the experiments could not be repeated owing to the lack of large numbers of freshly emerged adults to be used in the experiments. It is however, interesting to note that the freshly emerged adults show a stronger preference for high humidities than the older ones.

Discussion.

The basic plan of development of Polydesmus angustus Latzel is very similar to that of other Polydesmoids. The number of post cephalic segments in the adults and various instars appear to be the same in all the polydesmoids. The constant number of segments between and within the species, at various stages of development has been described as modal variation (Maynard Smith 1960). The number of segments added during successive moults of Polydesmus angustus is 2, 3, [illegible] 3, 2, 1, 1, as in other species of Polydesmoidea and can be explained in terms of the "multiplicative mechanism" (Maynard Smith 1960). This assumes a constant ratio between the rate of segment formation and moulting at a given time. Which factors are regulating the multiplicative process during the various phases of development is difficult to say, nevertheless, it is interesting to note that in spite of the constancy in the number of post cephalic segments, the individuals of various instars show considerable variation in their measurements.

Food seems to play an important part in regulating the duration of the life cycle and the ultimate size of the adults in different cultures. Adults reared in the same food substance from first to seventh instar, took not only less time to develop, but were relatively larger than those which were subjected to a change of diet during various stages of development. Apart from food, external stimuli have considerable effect on the duration of the life cycle. Animals reared in the constant temperature and in constant darkness took less time to develop than those in the room temperature or subjected to constant light throughout the development. Larval mortality was also highest in the latter conditions. It is apparent that the animals reared in a constant environment and on the same kind of food grew larger in size and took less time to develop. The laboratory observations can readily be applied to explain the rather "prolonged" period of the life cycle in the field. Here the temperature, humidity and light are ever changing, and the litter on which the earlier instar thrives is not always homogenous. These ever changing biotic and abiotic factors possibly interact together to increase the duration of the life cycle and indirectly lead to the enormous variation in the size of the adults.

It may be argued that the limitation of space to which the various instars were subjected during the laboratory studies might have influenced the life cycle. But it appears that the limitation of space had more effect on the larval mortality than on the duration of the life cycle. Animals reared in large or small areas took the same time to develop, though in the latter case the larval mortality was higher. Since in all the experiments on larval mortality plenty of food was available, it may be assumed that the competition which ensued in a limited space was apparently a struggle for a suitable site for moulting. In an unlimited space, migration may lead to survival and will lessen the chances of intraspecific competition.

Regarding the size variation of the adults, it has already been pointed out that individuals reared in the same food medium grew relatively larger than those whose food was altered during the course of larval development. Though the physiological effect of diet on the adult size has not been worked out, it is worth mentioning in this connection that large sized adults (mean length ± S.E = 27.5 ± 8.7 : N = 275) were mostly trapped from areas with homogenous oak litter. Adults from mixed litter were smaller in size (mean length ± S.E. = 20.6 ± 5.4 : N = 259).

The size variation between the adults from the two habitats can be explained on the assumption that the animals from the homogenous litter fed on oak litter only during their larval development and finally emerged as large sized adults. In heterogenous litter the mixed diet possibly had its effect on the size of the adults in this population.

It has been noted in section III that in Cylindroiulus punctatus oviposition and development of the first three instars take place beneath the bark of fallen tree logs in the litter. But in Polydesmus angustus the oviposition and the entire larval development take place in the litter. The nesting behaviour of the females of Polydesmus angustus is associated with the protection of the eggs until they hatch. The females of Cylindroiulus punctatus do not exhibit such nesting behaviour, since their eggs are given natural protection beneath the bark.

The simple and short life cycle of Polydesmus angustus makes the species more abundant in the woodlands than Cylindroiulus punctatus. The numerical superiority of the species together with its "monohabitat" nature makes it one of the most important agents for the breaking down of the woodland litter. Cylindroiulus punctatus, on the other hand, takes longer to develop and is found in two habitats. This reduces the numerical strength of its adults in the litter: consequently all its adults may not be available at any time for the breaking down of the litter.

Section VI

Studies on the distribution, diurnal and seasonal activity of *Cylindroiulus punctatus* (Leach), *Tachypodoiulus niger* (Leach) and *Polydesmus angustus* Latzel.

Introduction.

Twenty-four hour rhythms of activity are well known in the animal kingdom. Recently Cloudsley-Thompson (1961) and Harker (1961) have reviewed existing information on the rhythmic behaviour of animals. Park, Lockett and Myers (1931) in a study of a large number of nocturnal invertebrates, including the millipede Polydesmus serratus noted that all the nocturnal species have a definite period of activity, with a peak occuring towards midnight. Park (1935) noticed the presence of an "inherent nocturnal rhythm" in the tropical millipede, Spirobolus marginatus and claimed that this rhythm persisted even during the period of starvation. Cloudsley-Thompson (1951b) has studied the diurnal cycle of rhythmic activity in British and two African species of millipedes, and concluded that this behaviour is primarily a response to light and darkness, but is also correlated with the stimulus of falling temperature. However, later observation was made in the laboratory, and no field observations have been directed to test at which phases of twenty-four hour cycle animals in their natural communities become most active. Barlow

(1957, 1958) has studied the seasonal activity of different species of millipedes by trapping the population, and Williams (1958, 1958) has used mechanically operated traps to study the activity of various invertebrates. One of the purposes of the present study was to find out the phases of the twenty-four hour cycle, in which Cylindroiulus punctatus, Tachypodoiulus niger and Polydesmus angustus become active in their natural habitats. A second reason for the present investigation was to make a comparative study of the seasonal variation in the population of these three species as evident from trapping, and their distribution in different biotopes with distinct ecological features.

Methods.

A. Diurnal activity.

The term activity has been referred to in this work to indicate the locomotor activities of the three species of millipedes. The population was trapped in the field by means of pitfall traps. The traps used were the jam jars, 10 cm. in diameter and 18 cm. in depth. They were covered by pieces of asbestos sheets, leaving sufficient space between the roof and the rim of the jar to allow millipedes to crawl through it into the jar. Ten such jars were sunk below litter in each of the areas F-K around Royal Holloway College ground. Six traps, one from each of the areas F-K were examined for millipedes in the following six phases of a twenty-four hour cycle (Williams, 1958) in different months.

Phase I. Midnight to one hour before sunrise.
Phase II. One hour before sunrise to one hour after.
Phase III. One hour after sunrise to noon.
Phase IV. Noon to one hour before sunset.
Phase V. One hour before sunset to one hour after.
Phase VI. One hour after sunset to midnight.

B. Seasonal activity.

An idea of the seasonal variation in the population of the three species was obtained from the examination of 60 above mentioned pitfall traps every day throughout the period of investigation. The traps were examined every morning and the millipedes were returned to litter after recording their numbers and identification.

C. Distribution.

The distribution and seasonal population variation of the three species were studied in the four biotopes (biotopes A, B, C and D), described in the section on "Descriptions of study areas and field sampling methods" as areas L-O. 25 traps were laid in each of these biotopes. Each of these biotopes was divided into a number of quadrats and the positions of the traps in these quadrats were determined by using a table of random numbers.

Results.

A. Diurnal activity.

In the tables 6.1 - 6.3 the total numbers of Cylindroiulus punctatus, Tachypodoiulus niger and Polydesmus angustus trapped, in the six phases of the twenty-four hour cycle in different months, is shown. The observations were made once in every month of 1962.

Table 6.1. Diurnal cycle of locomotor activity of Cylindroiulus punctatus (Leach).

Phase.	Total number obtained from 6 traps in different months.											
	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
I.	8.	6.	12	31	27	15	11	8	12	7	4	3
II.	0	0	0	6	4	0	3	0	0	0	0	0
III.	0	0	0	0	0	0	0	0	0	0	0	0
IV.	0	0	0	0	0	0	0	0	0	0	0	0
V.	0	0	3	4	3	2	0	0	0	0	0	0
VI.	4	3	5	11	9	5	3	2	4	6	2	0

Table 6.2. Diurnal cycle of locomotor activity of Tachypodoiulus niger (Leach).

Phase.	Total number obtained from six traps in different months.											
	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
I.	9	5	10	21	33	21	8	12	8	11	3	5
II.	0	0	4	2	7	4	0	0	0	0	0	0
III.	0	0	0	0	0	0	0	0	0	0	0	0
IV.	0	0	4	2	4	5	0	0	0	0	0	0
V.	0	0	6	5	7	6	0	0	0	0	0	0
VI.	7	11	9	14	11	8	7	6	8	12	5	0

Table 6.3. Diurnal cycle of locomotor activity of Polydesmus angustus Latzel.

Phase.	Total number obtained from six traps in different months.											
	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
I.	4	3	6	11	13	8	9	9	5	6	0	0
II.	0	0	0	0	5	4	6	0	0	0	0	0
III.	0	0	0	0	0	0	0	0	0	0	0	0
IV.	0	0	0	0	0	0	0	0	0	0	0	0
V.	0	0	0	0	0	1	2	0	0	0	0	0
VI.	3	6	7	8	4	7	3	1	4	6	3	0

It can be seen from these tables that all the three species are active in the phases I and VI of the twenty-four hour cycle in all the months, though largest numbers were trapped in the phase I. A few

Cylindroiulus punctatus were trapped in the phase II in April, May and July, and some more in the phase V during March to June. During May to July, some *Polydesmus angustus* were trapped in the phase II and only a few in the phase V in June and July. *Tachypodoiulus niger* were trapped in the phases II, IV and V during March to June.

B. *Seasonal activity*.

Total number of animals of the three species of millipedes trapped in different months from areas F-K is shown in the fig. 6.1 and table 6.4.

Table 6.4. Weather conditions and total number of various species trapped in different months.

Month.	Average min. temp °F.	Total rainfall. (inches)	Total No. of *C.punctatus* trapped.	Total No. of *P.angustus* trapped.	Total No. of *T.niger* trapped.
Nov.61	38.7	2.12	44	43	55
Dec.	35.6	3.03	71	15	10
Jan.62	44.1	3.31	50	51	30
Feb.	38.1	0.33	91	80	50
Mar.	40.0	1.30	85	155	68
Apr.	51.9	1.58	237	202	118
May.	58.8	6.94	270	296	250
Jun.	53.1	0.40	115	105	345
Jul.	54.0	4.10	33	98	350
Aug.	54.1	2.65	41	45	100
Sep.	53.4	1.30	99	58	80
Oct.	47.6	0.69	118	45	50
Nov.	42.6	2.23	75	38	30
Dec.	34.5	2.54	37	26	10
Jan.63	27.6	1.24	25	37	20
Feb.	39.0	3.35	54	55	15
Mar.	49.7	2.21	82	128	60
Apr.	45.7	4.10	187	214	110
May.	47.5	3.43	230	214	270
Jun.	56.0	2.41	75	93	345
Jul.	56.2	1.32	23	45	360

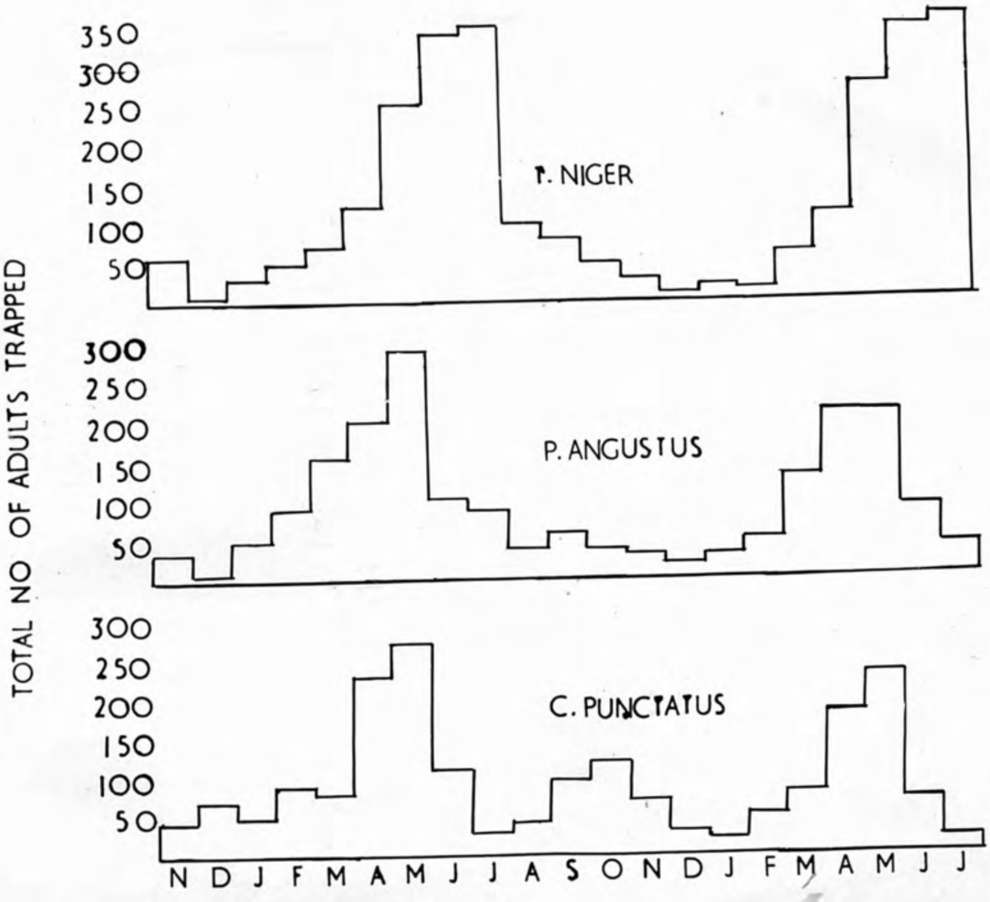


FIG. 6.1. Seasonal variation in the total adults of Cylindroiulus punctatus, Tachypodoiulus niger and Polydesmus angustus trapped.

Considering the activities of the three species throughout the period of investigation, there are some well marked periods, during which largest numbers of adults of species were trapped. It can be seen from fig. 6.1 that two distinct peaks occur in the activities of *Cylindroiulus punctatus* population in the litter, one from April to June and the other in September and October. With *Polydesmus angustus*, there has been a steady increase in the number trapped from January onwards, reaching a maximum in May, and this was followed by a sharp decrease in their numbers in the following months of the year. Largest numbers of *Tachypodoiulus niger* were trapped during May to July. The pattern of activities of the three species followed a similar trend in both the years studied. It appears that as the temperature slowly rises at the end of winter, there is a gradual increase in the number of the different species trapped, increasing to a maximum in the spring and then the number trapped decreases slowly, except in *Cylindroiulus punctatus* which shows a second peak in autumn.

Attempts were made to determine the correlations between the number of different species trapped and temperature, and also between the number trapped and rainfall, by applying rank correlation method of Kendall (1955). In this calculation the total number of different species trapped in four weeks of each month was compared with corresponding weekly minimum temperature and total rainfall. The results for different months are presented below.

Table 6.5. Coefficient of correlation between number of different species of millipedes trapped, and temperature and rainfall.

Tt. rank correlation coefficient of temperature.
Tr. rank correlation coefficient of rainfall.

Month.	C.punctatus.		T.niger.		P.angustus.	
	Tt.	Tr.	Tt.	Tr.	Tt.	Tr.
Nov.61	0.66	0.65	0.44	0.35	0.66	0.60
Dec.	0.20	0.33	0.18	0.16	0.60	0.28
Jan.62	-0.66	0.34	0.29	-0.17	0.33	-0.20
Feb.	0.68	0.66	0.31	0.36	0.65	-0.26
Mar.	0.50	0.33	0.65	0.41	0.66	0.28
Apr.	0.16	0.66	0.50	0.32	0.35	0.35
May.	0.10	0.66	0.66	0.22	0.66	0.28
Jun.	-0.16	0.50	0.41	0.15	0.83	-0.15
Jul.	0.50	-0.66	0.66	0.41	0.66	0.28
Aug.	0.83	0.50	0.50	0.35	0.61	-0.17
Sep.	0.33	0.27	0.55	0.31	0.64	0.46
Oct.	0.35	0.37	0.31	0.19	0.82	0.50
Nov.	-0.16	-0.33	0.52	-0.21	0.56	0.15
Dec.	-0.32	0.33	0.55	0.30	0.65	0.33
Jan.63	0.33	0.37	0.52	0.33	0.66	0.28
Feb.	0.22	0.66	0.45	0.33	0.68	0.48
Mar.	0.42	0.40	0.65	0.41	0.45	0.23
Apr.	0.28	0.33	0.55	0.33	0.66	0.36
May.	0.16	0.66	0.75	0.33	0.33	0.28
Jun.	0.33	0.37	0.38	0.85	0.27	0.41
Jul.	-0.18	0.15	0.45	0.87	0.22	0.38

It is to be noted that the coefficient of correlation between number trapped and temperature or rainfall varies from month to month in the three species studied. Activity, as evident from trapping, is sometimes positively and sometimes negatively correlated with fluctuations in temperature and rainfall.

C. Distribution.

Total number of the three species trapped in the four biotopes in different months is presented in the following table.

Table 6.6. Total number of the three species of millipedes trapped in different biotopes.

CP = *Cylindroiulus punctatus*.
TN = *Tachypodoiulus niger*.
PA = *Polydesmus angustus*.

Month.	Biotope A.			Biotope B.			Biotope C.			Biotope D.		
	CP	TN	PA	CP	TN	PA	CP	TN	PA	CP	TN	PA
Jan.	23	28	12	11	15	8	5	7	4	3	8	0
Feb.	8	5	6	7	11	3	3	7	2	0	6	0
Mar.	37	25	35	33	21	12	10	16	10	8	19	2
Apr.	75	45	61	55	47	45	16	34	8	4	21	3
May.	64	58	58	49	61	43	28	56	10	10	39	0
Jun.	43	55	45	31	52	40	28	48	14	11	42	6
Jul.	25	31	32	18	25	31	12	33	8	7	38	4
Aug.	12	26	25	17	24	22	8	28	11	5	30	0
Sep.	25	24	18	10	28	20	10	25	8	6	21	3
Oct.	18	26	15	10	31	13	8	23	6	8	20	6
Nov.	10	26	8	8	21	10	8	16	5	8	15	0
Dec.	10	15	7	11	10	6	8	19	7	0	10	0
	350	364	322	260	347	253	146	312	93	70	289	24

It is clear from the preceding table that the adults of the three species were trapped in large numbers from biotopes A and B, which are wooded areas rich in litter. This condition lowers the temperature in the habitat by cutting down the sun rays by the canopy of vegetation and also prevents the rapid evaporation of water. All the three species seem to prefer such moist and humid habitats. In the biotope C, which is rather an open area, Cylindroiulus punctatus and Polydesmus angustus were trapped in smaller numbers than Tachypodoiulus niger. In the biotope D, which is a plot of grassland, Tachypodoiulus niger was trapped in large numbers in all the months. In fact Tachypodoiulus niger seems to be present in all the biotopes sampled in large numbers, whereas Cylindroiulus punctatus and Polydesmus angustus were mostly present in biotopes A and B. The table also gives a measure of cyclic changes in activity of the three species in different habitats.

Discussion.

Drift (1951) mentions that millipedes characteristic of the lower soil horizon, become actibe on the surface at night. Present investigation also indicates that the three species of millipedes, Cylindroiulus punctatus, Tachypodoiulus niger and Polydesmus angustus become active in the litter layer in the phases I and VI of a twenty-four hour cycle. Weather records of different phases indicate that largest numbers of adults of the three species were trapped in those two phases when the air temperature was low and the relative humidity of the air was high. It is possible that stimuli of falling air temperature and increased humidity of the air provide a stimulus to make these active at night, though other factors like darkness and length of the day may be equally effective. However, it may be recalled here that in some months, some adults of the three species were trapped at a time when it was not completely dark. This was particularly true with Tachypodoiulus niger which was trapped in phases II, IV and V during March to June.

It is possible that during this period the species develops a strong resistance to dry conditions, to become active in the day, and it is known that certain species of millipedes show a seasonal variation in their humidity preference (Perttunen 1953). The fact that all the species anticipate the daylight by diminishing activity before dawn, would suggest the presence of an intrinsic rhythmicity in behaviour.

It appears from the results presented that there is no constant correlation between activity, as measured in numbers trapped, and temperature and rainfall. Barlow (1958), in his results did not find any valid indication of the influence of either temperature or rainfall on the changes in the activity of the millipedes he studied, though an association of these factors with the activity was evident. However, certain biological factors, like the reproductive state of the animal may be partly responsible for the monthly fluctuations in the number of these three species trapped.

Food may be one of the major factors influencing the locomotor activities of the three species. At nightfall, when air temperature drops and the relative humidity of the air is high, these animals leave their day time shelter and wander about in the litter in search of suitable food. It is possible that during this movement, millipedes were trapped in the two night phases. However, it is not clear why millipedes have to move about in search of food when they are present on the food substances.

The "breeding cycle" of the animals may also be responsible for the initiation of locomotor activities in large numbers of adults in the population of *Cylindroiulus punctatus*, *Tachypodoiulus niger* and *Polydesmus angustus*. It may be noticed that the greatest activity of *Cylindroiulus punctatus* occurs at a time of active migration of the adults into the sub-cortical spaces of the logs for breeding. The second peak of activity occurs in the autumn, when some of the adults again migrate from the logs back into litter. It is possible that large numbers of adults were trapped during these two periods of migration between the two habitats.

Similarly, the largest numbers of Polydesmus angustus were trapped during the breeding period of this species (April to June). Though the life cycle of Tachypodoiulus niger has not been worked out, it is possible that the largest number of adults of this species were trapped during its breeding period. Since the "breeding activity" of the animals is controlled by internal physiological processes, it is possible that all the sexually mature adults in the population will be affected by the operation of this factor, rather than by the feeding urge. During the "breeding cycle", a large number of adult Cylindroiulus punctatus can be expected to become active prior to moving into the logs or in search of mates. Similarly adult Polydesmus angustus becomes active in search of mates and suitable sites for oviposition.

It may be argued that a sudden increase in the number of adults trapped may reflect an increase of freshly developed adults in the population of millipedes. The relatively simple and shorter life cycle of Polydesmus angustus makes it possible for the adults to develop from eggs laid the year before. It is therefore possible that some of the freshly developed adults of *Polydesmus angustus* were trapped during April to June. The life cycle of *Cylindroiulus punctatus* is more complex and extends for about three years in the field. Nevertheless, it is possible that some freshly developed adults were added to the population during the period of greatest activity. No data on the life cycle of *Tachypodoiulus niger* is available. It is, therefore, difficult to speculate anything about this species.

Regarding the distribution of the three species, *Tachypodoiulus niger* has a wider distribution than the other two. *Cylindroiulus punctatus* is mostly found in wooded areas with thick litter around. Such a habitat is ideal for this species, since oviposition sites beneath the bark are easily available, and the fourth instar can move into litter from log to undergo further development. Food also plays an important part in regulating the distribution of the three species. Both *Cylindroiulus punctatus* and *Polydesmus angustus* eat rotten leaves and bark of deciduous trees, and therefore they are mostly restricted to areas which offer the maximum amount of these foods.

Tachypodoiulus niger has been reported to feed on both rotten and green leaves, and is more widely distributed.

It can be seen that both climate and biological factors appear to influence the biology of the three species of millipedes discussed here.

SUMMARY OF THE DISCUSSIONS.

Cylindroiulus punctatus inhabits both litter and rotten logs of deciduous woodland floor. The importance of these two habitats in the biology of C. punctatus can be appreciated from the fact that it spends part of its life cycle beneath the bark of logs and part in the litter. C. punctatus shows two peaks of activity in the litter, one in the spring and the other in autumn. The spring activity coincides with the time of the migration of C. punctatus inside the bark of logs for oviposition. The second peak in autumn occurs at the time when some of the adults from the logs move back into the litter. C. punctatus lays eggs beneath the bark of logs and the first four instars undergo their development here. The fourth instars move out of the bark into surrounding litter, where they moult three times to develop into seventh instars. Seventh instars are found both inside the logs and in the litter, where they moult into mature eighth instars.

Laboratory tests indicate that C. punctatus does not show any significant preference for either rotten leaves or rotten bark. Experiments also show that it has the same preference for the rotten leaves or bark of oak, birch and beech, but rejects the fresh green leaves of these plants. In the field this species is found in areas rich in homogenous oak litter as well as in areas with mixed litter. In the laboratory experiments, C. punctatus was found to be capable of detecting changes in humidity and always exhibited a stronger preference for high humidities. The laboratory observations can be related to the distribution of C. punctatus in the field. It is mostly found in those parts of woodland which are rich in both logs and litter. Apart from providing suitable sites for oviposition and the development of the first four instars, such conditions also maintain moist and humid surroundings, so essential for the millipedes.

In the litter, C. punctatus is commonly found with Polydesmus angustus which shows a single peak of activity in litter during its breeding period. The life cycle of P. angustus is much more simple than that of C. punctatus. P. angustus constructs nests in which females lay eggs and all the instars undergo development in the litter. In the field, the life cycle of C. punctatus is completed in about three years, whereas that of P. angustus takes about 12-14 months. However, in the laboratory, at a constant temperature of 23°C. and under constant darkness, the life cycles of both the species are considerably reduced.

Tachypodoiulus niger differs remarkably from the two other species of millipedes both in its distribution and feeding habits. This species has been recorded from areas rich in decaying vegetation and also from grasslands. It has been noted on living aerial parts of green trees and it possibly feeds on green leaves too.

It may be mentioned that in the litter sampled in 1962, T. niger was less numerous than either C. punctatus or P. angustus. Food does not seem to be the most important factor controlling the populations, since the feeding habits and the foods of these three species are somewhat different: some other biological factors must be operative here. However, the population regulating factors in millipedes have not been studied in the present work, but it is a subject that calls for further investigation.

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APPENDIX 4.

The pattern of distribution of Cylindroiulus punctatus in a number of upright oak stumps was noted. The sampling was done for every five inches from the ground level right up to the tip of the trunk. A total of nine rotten oak trunks were examined.

Table 1. Total number of <u>Cylindroiulus punctatus</u> (Leach) obtained at different heights in vertical oak trunks. (Figures represent total of nine trunks).

Range of height.	No.of Males.	No.of Females.	Total no. of adults.
(inches)			
0-5	83	81	164
5-10	69	54	123
10-15	48	44	92
15-20	22	29	51
20-25	28	25	53
25-30	27	26	53
30-35	19	13	32
35-40	17	22	39
40-45	11	13	24
45-50	10	14	24
50-55	6	8	14
55-60	6	4	10
60-65	0	0	0
65-70	1	0	0
70-75	0	0	0
75-80	0	1	1
80-85	1	1	1
85-90	0	0	0
90-95	0	0	0
95-100	1	2	3
100-105	0	0	0
105-110	1	1	2

Results from six rotten and upright apple trunks are tabulated below.

Table 2. Total number of <u>Cylindroiulus punctatus</u> (Leach) obtained at different heights in vertical apple trunks.

Range of height.	No. of Males.	No. of Females.	Total no. of adults.
(inches)			
0-5	38	41	79
5-10	16	22	38
10-15	10	11	31
15-20	10	7	17
20-25	14	12	26
25-30	12	16	28
30-35	13	9	22
35-40	18	10	28
40-45	9	6	15
45-50	7	5	12
50-55	0	0	0
55-60	0	0	0
60-65	0	0	0
65-70	0	0	0
70-75	4	3	7
75-80	2	1	3
80-85	1	0	1

Table 3. Number of <u>Cylindroiulus punctatus</u> (Leach) at different heights in beech trunks. (Figures represent total of four trunks).

Range of height.	No. of Males.	No. of Females.	Total no. of adults.
(inches)			
0-5	15	17	32
5-10	13	15	28
10-15	7	10	17
15-20	10	12	22
20-25	14	6	20
25-30	15	10	25
30-35	12	13	25
35-40	10	12	22
40-45	8	7	15
45-50	11	6	17
55-60	7	10	17
60-65	9	8	17
65-70	8	6	14
70-75	7	5	12
75-80	0	2	2
80-85	1	1	2
85-90	1	0	1
90-100	1	1	2
100-105	1	0	1
105-108	0	1	1

Table 4. Number of <u>Cylindroiulus punctatus</u> (Leach) obtained at different heights in elm trunks.

Range of height.	No. of Males.	No. of Females.	Total no. of adults.
(inches)			
0-5	21	15	36
5-10	16	17	33
10-15	28	18	46
15-20	16	14	30
20-25	17	12	29
25-30	10	12	22
30-35	7	11	18
35-40	11	10	21
40-45	8	7	15
45-50	6	4	10
50-55	7	5	12
55-60	5	4	9
60-65	4	4	8
65-70	2	2	4
70-75	2	1	3
75-80	1	0	1
80-85	1	2	3
85-90	1	1	2
90-95	0	0	0
95-100	0	1	0
100-105	2	1	3
105-110	2	1	3
110-115	1	1	2
115-120	0	1	1
120-125	1	1	2
125-130	0	1	1

Table 5. Number of *Cylindroiulus punctatus* (Leach) obtained at different heights of a cricket bat willow trunk.

Range of height.	No. of Males.	No. of Females.	Total no. of adults.
(Inches)			
0-5	6	8	14
5-10	7	5	12
10-15	4	6	10
15-20	7	5	12
20-25	4	1	5
25-30	2	2	4
30-35	3	2	5
35-40	0	0	0
40-45	0	1	1
50-55	0	0	0
55-60	3	2	5
60-65	1	0	1
65-70	2	1	3

In addition to the above samplings a number of oak trunks were examined for the presence of millipedes, while they were being cut down. The maximum height of their occurrence in an oak stump was to be 19 feet above the ground. All this data agree one point and that is that the largest numbers were recorded in the lower end of the trunk and their number is reduced progressively towards the upper end of the trunk. Further, the young instars were noted only on the lower end of the trunks and nothing on the upper side of the trunk.

It seems likely that the adults moved into the trunks from the surrounding litter, since the latter, in most cases, was remarkably rich in the millipede population. In all cases young instars were found in the lower end of the trunk, and this is significant. Since some of the young instars need to go back into the litter to complete their development, it would be advantageous for them to stay nearer the litter. At the same time, it opens the question - why the adults move up and stay towards the upper end of the trunks - when the the availability of the food is uniform both in the upper and lower ends of the trunks. It may be assumed that the lower ends of the trunks being nearer the litter will naturally have a higher millipede population than the upper end, and that the animals at the upper end have taken up their positions there in the course of their diurnal activity. To test this vertical movement along the trunk, a series of observations was made on four selected aggregations on an oak trunk. The distances between these four aggregations on the south side of the trunk, and their positions, are shown in the following diagram. The aggregations were observed every two hours, by carefully removing the bark, and the number of individuals in each aggregating group was noted. The formation and the breaking down of the aggregations was supposed to give a fair indication of the vertical movement of the individuals constituting the groups, since the aggregating groups are situated one above another along the vertical axis of the trunk.

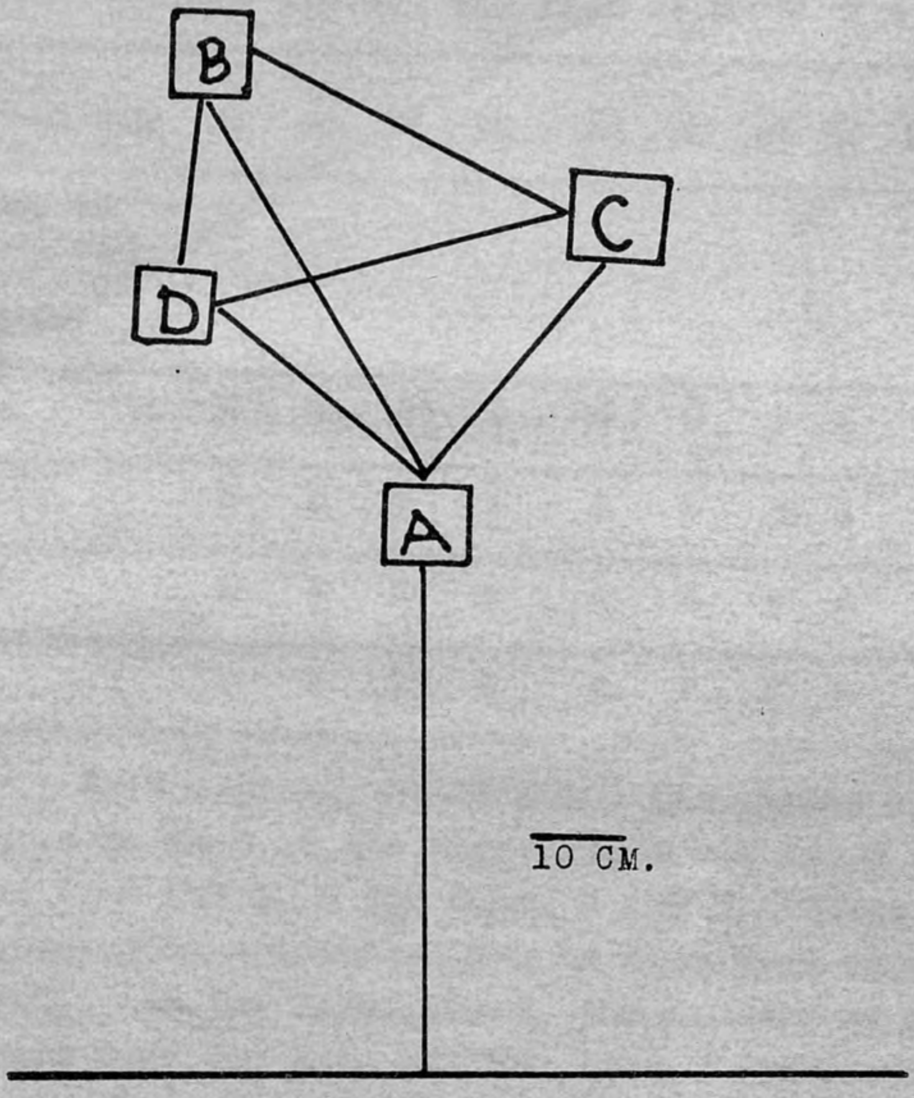

Fig. 1. Positions and distances between the aggregating groups A,B,C and D.

Table 6. Formation of aggregating groups of <u>Cylindroiulus punctatus</u> on a vertical oak stump.

Hrs. of observation.	9	11	13	15	17	19	21	23	1	3	5
Temp. °C.	6.0	5.0	6.5	9.5	11.0	12.0	8	7	6.5	3.5	4.0
Air humidity	44	42	34	30	28	30	49	60	68	74	71
No. of individuals in group.											
A	6	6	6	6	6	6	5	6	4	3	5
B	6	6	6	6	5	5	3	4	4	2	4
C	4	4	4	4	4	4	4	4	2	2	2
D	7	7	7	7	7	7	5	3	4	4	6

Next morning, at 11 a.m., the number of individuals in each of the aggregation was found to be 4 for A, 4 for B, 2 for C and 5 for D. Several interesting deductions can be made from this experiment. In the first place, the centers of aggregations were the same all the time, irrespective of the number of individuals making up the aggregating groups. Unfortunately, all the members of the aggregations could not be marked in this experiment, so that it becomes difficult to say if there has been any interchange between the members of the four aggregating groups. Nevertheless, it becomes clear that the aggregating groups break down and reform in the course of diurnal activity. Since the aggregating groups are arranged one above the other along the vertical plane of the trunk, it may be assumed that the millipedes may be able to make some vertical movement along the trunk surface.