Some aspects of the ecology of Woodlice

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SECTION I.

Introduction

Ecology has been defined by Odum (1962) as the "study of the structure and function of ecosystems". He suggests that a great deal of attention has been focused on the structural, descriptive approach, whereas few studies of the functions of ecosystems have been attempted. Odum (1962) further states that by structure he means : (a) the composition of the biological community, including species, numbers, biomass, life history and distribution in space of populations, (b) the quantity and distribution of abiotic materials such as nutrients and water, and (c) the range of conditions of existence, such as temperature and light. Function was defined as : (a) the rate of biological energy flow through the ecosystem, i.e. rates of production plus rates of respiration, (b) the rates of biogeochemical cycling, e.g. nutrient flow, and (c) biological or ecological regulation.

The two approaches to the study of ecosystems are both necessary. The structural approach serves to describe the existence of organisms and materials. Odum (1962) and Macfadyen (1964) have stressed that, although biomass in different ecosystems may be widely different, the energy flow produced may be very similar. Strict comparisons of numbers alone are therefore of limited use when one wishes to fully understand the working of ecosystems. The functional approach, whereby rates of energy flow per unit area of habitat per unit time are measured for various organisms, will enable strict comparisons to be made both within and between ecosystems. Only Watson (1966) has worked on this functional approach to woodlice. He calculated that Oniscus asellus and Porcellio scaber ingested 10.11g dry weight per annum, assimilated 3.025g and egested 7.081g dry weight.

From these figures the implicit importance of woodlice in many terrestrial habitats can be judged. Bocock (1963) found that Glomeris marginata consumed about 5% of the total annual litter fall in woodlands, and woodlice are far more abundant (Heeley 1941, Cole 1946, Brereton 1957, Sutton 1968). Macfadyen (1963) found that earthworms dominate mull soil types but are partially replaced by isopods in some cases.

Woodlice appear to have very few predators, and appear to be generally distasteful. Gorvett (1956) showed this distastefulness to result from secretions of the tegumental glands and suggested that these glands, which do not occur in aquatic isopods, had evolved in terrestrial species as a defence mechanism. Paris (1963) confirms that Carabid beetles, Salamanders, and Lizards will eat them. The present study showed that the wolf spider Trochosa terricola (Thor.) and the harvestman Lacinius ephippiatus (Koch) did eat them, but Iguanas, hens, rats, and mice did not.

Woodlice probably make their greatest contribution to energy flow in the ecosystem, not as food for higher trophic levels, but by their production of a fecal substrate, i.e. by the mechanical breakdown of litter, not so much by being preyed upon by other organisms.

Woodlice came onto land to take over an available niche in spite of the hazards of dessication, and many studies have been made of various aspects of their biology. In spite of this interest, very few studies have dealt with the population ecology of these common organisms. The only comprehensive studies are those by Paris & Pitelka (1962). Paris (1963) worked on Armadillidium vulgare (Latrielle) in California, Brereton (1956) combined laboratory and field studies to obtain data on Porcellio scaber. Sutton (1968) compared the population dynamics of Trichoniscus pusillus and Philoscia muscorum. All these studies were made on grassland.

The present study attempts to compare the ecology of four species of woodlice in four different habitats. This topic was chosen because of the importance of these organisms in promoting energy flow in ecosystems and for the need of more knowledge of their ecology in the field. A second factor in choosing this study is the fact that woodlice offer some unique advantages for teaching. They are readily accessible in the field for sampling and collecting, even in urban areas, and they are of a convenient size for observation and experimental work. Finally, a body of knowledge on other aspects of the biology of terrestrial woodlice, especially their environmental physiology, forms a valuable background for field studies.

Because of the very limited time available for this project no reliable explanations can be given for population size and control. The work does, however, point the way to further research.

The study areas

Samples were taken from four different half-acre sites. These four were chosen for their contrasting positions, relief, flora, and soil types.

1. St. Margaret's Churchyard. Plate IV. Map reference 259421 is in the centre of Durham City, at an altitude of 200 feet on a S.E. 40 degree slope. The site has a brown earth soil profile overlying glacial deposits although this is continually being altered by the depositing of rubbish from neighbouring allotments. There is a thick covering of vegetation comprising :

	Domin (1960) scale of abundance
Melandrium dioicum (Wiegel)	1
Aethusca cynapium L.	1
Rumex acetosa L.	1
Fraxinus excelsior L.	3
Sombucus nigra	6
Acer campestre L.	7
Dactylis glomerata L.	2
Festuca ovina L.	2

2. Great High Wood. Plate I. Map reference 275404. This is part of the University wood on the outskirts of the city at an altitude of 200 feet on a E.N.E. 70 degree slope. It has a brown podsolic profile. There was little pre-vernal vegetation, but a

Plate I Great High Wood

Plate II Field Station

fairly thick covering of a few species in early summer comprising :

	Domin scale of abundance
Anthoxanthum puelli L.	1
Deschampsoa flexuosa L. (Trin.)	1
Digitalis purpurea L.	2
Dryopteris dilatata (Hoffm.) A Gray ...	6
Melandrium dioiciim (Wiegel)	1
Mnium hornum	2
Acer campestre L.	5
Fagus sylvatica L.	2
Aesculus hippocastanum L.	2

3. Field Station. Plate II. Map reference 274403. This is part of the University field station being disused grassland which had been grazed by sheep up to four years ago. It is on the opposite slope of Houghall Wood at an altitude of 150 feet on a w.s.w. slope of 60 degrees. It has a brown earth soil profile. The vegetation forms a thick mat made up of the previous permanent pasture,grasses and plants that have invaded the area since it was managed. The ground is uneven with many Cocksfoot tussocks interlaced with runs of the vole Microtus agrestis L.

	Domin. scale of abundance
Achillea millefolium L.	1
Aethusca cynapium L.	1
Bellis perennis L.	1
Dactylis glomerata L.	6

Plate III Sherburn Hill Quarry

Plate IV St. Margaret's Churchyard

	Domin. scale of abundance
Fagus sylvatica L.	2
Festuca ovina L.	1
Cractaegus monogyna L.	3
Holcus lanatus L.	1
Lolium perenne L.	3
Phleum pratense L.	2
Plantago lanceolata L.	2
Potentilla erecta L. (Rauschel) ...	1
Rubus spp. L.	3
Rumex acetosa L.	3
Urtica doicia L.	2

4. Sherburn Hill Quarry. Plate III. Map reference 334418.

This is a disused Magnesium limestone quarry 4 miles east of Durham city, at an altitude of 450 feet, facing S.S.E. It has a well-drained calcareous soil giving a Rendzina soil profile, with a very rich flora and fauna.

	Domin. scale of abundance
Achillea millefolium L.	1
Cardius crispus L.	2
Chloroccum spp.	1
Ctenidium moluscum	3
Crataegus monogyna L.	1
Festuca ovina L.	7
Koeleria gracilis	5

		Domin. scale of abundance
Linum catharticum L.	... ...	1
Lotus corniculatus L.	... ...	5
Plantago lanceolata L.	... ...	2
Plantago maritima L.	... ...	3
Prunella vulgaris L.	... ...	1
Rubus fruticosa L.	... ...	3
Thymus drucei Ronn.	... ...	4
Urtica dioica L.	... ...	2
Vicia cracca L. ...	... ...	1

The Species

Trichoniscus pusillus (Brandt, 1833)

This species exists in two forms, one diploid and bisexual (Trichoniscus pusillus provisorius, Racovitza) and the other parthenogenetic and triploid (Trichoniscus pusillus pusillus, Brandt.) with very few males. Only the latter form was found which confirms Healey (1963) who did not find T.p.provisorius north of the river Humber, and Vandel (1934) who believed that this sub-species only occurred as far north as Lancashire. This species measures up to 4mm. It is fast moving, very susceptible to dessication, and lives deep in litter and soil in winter and during drought. It is abundant in moist woodland litter and grassland. It has small broods with an average of six which are large in size, being well supplied with yolk. It has a slow brood development (Healey 1941) and is the earliest species in the year to breed. Its breeding period extends longer than any other of the species studied.

Philoscia muscorum (Scopoli 1963)

This species measures up to 10mm and after Trichoniscus is the next most susceptible to dessication. It is most abundant in disused grassland habitats. Philoscia has a rapid brood development and close succession of moults. The eggs are large, richly supplied with yolk, but small in number, with an average of thirteen.

Oniscus asellus (Linne 1761)

This is the largest species studied, measuring up to 15mm and is the most abundant. It is found in moist situations, especially under logs and stones. The development of the embryo is uniform throughout the breeding season, and the average size brood is thirty.

Porcellio scaber (Latrielle 1804) Budde-Lund 1908.

This species is equal to Oniscus in size, reaching 15mm in length. It changes its habitat according to the season, being found under logs, stones, and at the base of trees in winter, and beneath loose bark on living trees in summer.(Brereton 1957). The development of the embryo is uniform throughout the breeding season and the average size of brood is twenty-four. Other species found, all in Sherburn Hill Quarry, were :

Haplophthalmus mengii (Zaddach) 1884. Only recorded in two other sites in Britain (Sutton, personal communication).

Porcellio spinicornis (Say 1818). A species restricted to calcareous soils.

Trichoniscus pygnaeus (Sars 1899). The smallest of the British woodlice.

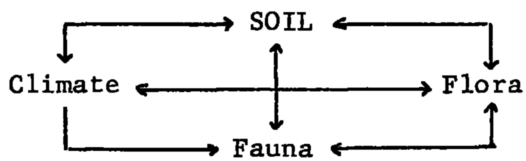
The oniscomorph millipede Glomeris marginata (Villiers) is also very common.

SECTION II.

The importance of soil properties as possible controlling factors

The most important soil properties are those which act uniformly over a long period and thus bring about a definite effect which influences selectively the fauna. Much has been written recently on Soil Biology (Kevan, 1955; Kuhnett, 1961; Macfadyen, 1963), and all agree that the controlling factors are temperature, moisture content, air, and to a lesser extent, vegetation, Although botanists stress the importance of the pH and mineral status as controlling factors, zoologists appear much less concerned.

In ecology the general interdependence of the great complex of factors should not be neglected. This can be illustrated :



The relation between vegetation and soil seems to be studied according to a set procedure which logically is :

(a) Qualitative vegetation and soil surveys, to establish the basic trends of vegetation development and stability and the related general soil properties.

(b) The study of the available soil nutrients and mineral cycling via autecological and detailed synecological studies.

This is the work pioneered by Tansley (1917) and Braun-Blanquet (1932) and into this scheme faunal studies should fit.

The present study, by detailed soil analysis, attempts to see if the edaphic factors are partly responsible for controlling populations of woodlice and determining their choice of habitat.

Methods

Random samples were taken from the top 5cm of soil and litter in all four sites. These samples were air-dried and tested by the following standard techniques :

Total N by Kjeldahl digestion

Organic C by digestion with potassium dichromate and sulphuric acid

P and K extracted by a mixture of 0.5 M acetic acid and 0.5 M ammonium acetate

Exchangeable Ca determined by leaching with neutral N ammonium acetate

pH by eletric meter

The amount of lime required to make the land suitable for agricultural crops was determined.

Because woodlice were quite rare in the Great High Wood, a detailed soil profile was studied in order to establish the influence of soil structure and drainage on the topsoil. Where the woodlice mainly live a soil profile pit was dug one foot square, twenty inches deep with smooth clean sides.

Table 1.

Results of soil analysis

	Organic C %	Total N %	extractable P.p.p.m.	extractable K.p.p.m.	pH	Ca.m equiv./100gms	L.R. cut/acre
Field Station	6.1	0.39	1.0	155	5.4	12.1	60
Great High Wood	28.9	1.43	6.2	94	4.0	11.6	120
St.Margaret's Churchyard	8.3	0.42	28.0	250	6.3	16.9	20
Sherburn Hill Quarry	5.9	0.38	3.5	106	8.4	62.5	0

Soil profile descriptions. Great High Wood

Soil horizon	Profile	Description
A_o	2 - 2½"	Matted layer of leaf mould. Moist, black in colour, plastic. Black mor soil. Fair crumb structure.
A_1	2½ - 4"	
A_2	4 - 6"	Sandy loam, 10% clay. Very few earthworms. Some evidence of leaching.
A_3	6 - 10"	Mottled orange/brown, some humic material, friable, free draining. Some rounded pebbles.
B_1	10 - 18"	Sandy loam, lighter in colour, moist, slightly leached. Washed down humus.

Discussion

The results for St. Margaret's Churchyard are probably inflated because of coal and ashes in the sample and this would interfere with the determinations.

The results from Great High Wood are the abnormal ones. The C : N ratio is unusually high whilst the other sites are near to the normal of 12 : 1 (Dowdeswell, 1959). The importance of N content probably lies in the fact that it serves as a nutrient for the organisms taking part in the decomposition although too much could be toxic. There is ample litter (carbon) from the deciduous trees and the influence of tannins in the litter slows down composition (Bocock, 1963). The key factor, however, must be the very low pH of the soil. This slows up microbiol activity and decomposition and is enhanced by the high Precipitation : Evaporation ratio on a cold, steep, north-facing slope.

Carbonic and other acids in the soil water can be neutralised to some extent by the secretions of the calciferous glands which are found in the bodies of several species of woodlice, millipede, centipede and earthworm. But there must obviously be some source of calcium if adequate replenishment of these glands is to be effected. Great High Wood had the lowest soil calcium content of all four sites.

Calcium probably influences woodlice in three ways :

(a) by controlling pH

(b) as an essential item of diet since all species have the integument calcified to a greater or lesser degree (Heeley, 1941)

(c) by effecting permeability of body tissue as calcium ions have a strong influence in controlling the passage of solutes through living membranes

In complete contrast Sherburn Hill Quarry site has a very high pH and calcium content. The latter reflects a balance between leaching and weathering in the soil. This habitat has a very abundant flora and fauna. A quarry is normally thought of as having a pioneer succession but where the fauna is so abundant it may act to hold back plant succession.

The Field Station was grazed by sheep up to 1955. The grassland has probably deteriorated since as no manure is being returned to the soil. The results show this habitat to have a poor nutrient status.

It is interesting to note that the habitats with most species and species abundance were the Quarry and the Churchyard. These sites had free drainage, adequate organic matter, neutral to calcareous reaction, high calcium content, and good aspect.

The soil profile of Great High Wood shows it to be a brown podsolic soil. Podsols are associated with : high acidity, high percentage of exchangeable hydrogen, with low percentage exchangeable calcium and the soil being wet and cold.

From these results it seems quite likely that the structure and nutrient status of the soils can partly control the abundance of woodlice and possibly the invertebrates living in them.

SECTION III.

Behaviour studies

(a) The interaction of micro-climate and diurnal rhythms

The conquest of land by arthropods illustrates a number of fundamental points of behaviour in the response of the animals to stimuli provided by the bioclimatological conditions of their physical environment. The terrestrial arthropods can be divided on an ecological basis into two main groups. The first includes Isopods, Diplopods and Chilopods which in dry air lose water rapidly by transpiration through their integuments, Cloudsley-Thompson (1956); Edney (1957). Consequently they are restricted by reflex behaviour mechanisms to damp, dark habitats which they leave only at night when the temperature falls and the relative humidity of the atmosphere increases (Cloudsley-Thompson 1952).

The second group includes most insects and arachnids: these are comparatively independent of moist surroundings because their integument possesses an impervious layer of wax which prevents dessication (Wigglesworth 1950).

The following trials were carried out in an attempt to interpret the distribution of terrestrial isopods in terms of their psychological responses and behavioural reactions.

Materials and Methods

Handling. It was realised that handling could have considerable effects upon their behaviour. The mechanical pressure, temperature, grease from sweat pores, could all be involved. The effects of such handling could take several forms.

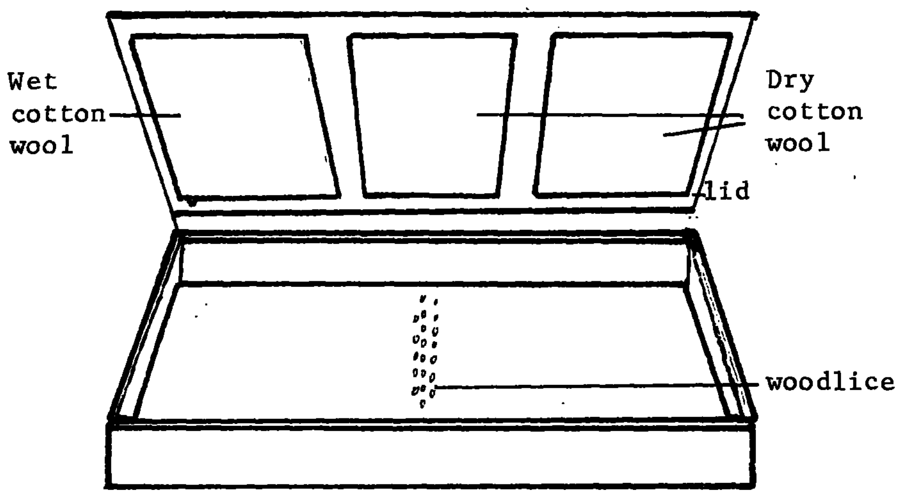
(a) complete suspension of activity (death feigning)

(b) temporary increase in activity (escape response)

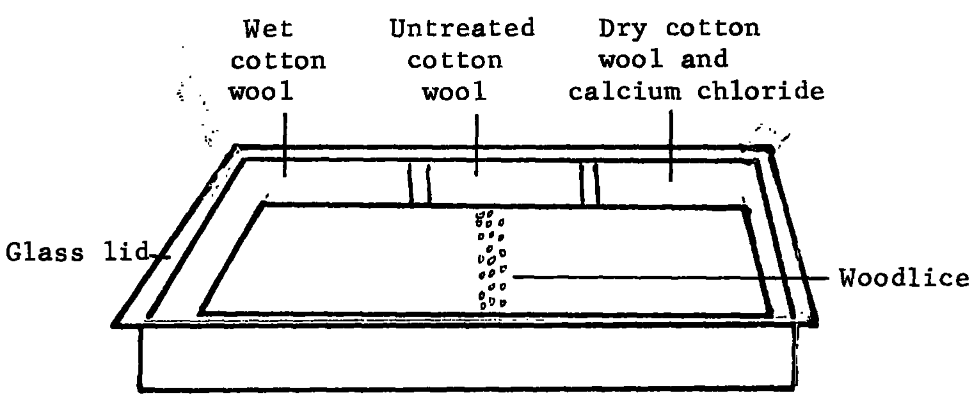
(c) complex interaction with the photic responses

Because these factors could confound results, animals were put into test environments well before commencement of observations. This would, it was assumed, allow time for any handling effect to dissipate.

Surgical dishes 30x20x4cms were set up as shown in Figs.1 and 2. One was covered with a hardboard lid which has a thick layer of cotton wool pasted on the underside in three broad strips. The strip at one end only was well moistened with water. Twenty woodlice were placed in a line in the centre of the dish and the lid replaced, After one hour, and at subsequent half-hourly intervals, the numbers in each half of the dish were noted. This was repeated five times and the results expressed as the percentage showing a positive response. A second variable, that of light, was introduced (Fig.2). In this design, cotton wool was fixed to the walls of the dish and the dish covered with a glass plate. The cotton wool on the walls at one end was well



(a)



(b)

Figs. 1 and 2. Method for investigating the distribution of woodlice in humidity gradients

(a) in darkness

(b) in light

moistened and the experiment repeated as before.

These trials were carried out in test runs with all four species and finally with Oniscus asellus and Philoscia muscorum in laboratory conditions with a temperature at 20°C.

Results Table II

(a) Oniscus asellus

Environmental conditions	% R.H.	Nos. showing positive response	Nos. showing negative response	Total
Dark/Damp	92	79	21	100
Dark/dry	44	4	96	100
Light/damp	74	98	2	100
Light/dry	66	0	100	100

(b) Philoscia muscorum

Dark/damp	92	91	9	100
Dark/dry	44	44	56	100
Light/damp	74	74	26	100
Light/dry	66	66	34	100

Discussion

These simple choice chamber trials show that the intensity of the humidity response of woodlice is less in darkness than in light.

The order into which the selected species fall in respect of humidity requirements in nature coincides with that found independently by experiments in dishes in the laboratory.

Philoscia 91%, showed a stronger response than Oniscus, 79% (χ^2 = 5.6. P = $<$0.025). Edney (1954) correlated species abundance with relative humidity and suggested the following optimum humidities :

Trichoniscus pusillus 84%. Philoscia muscorum 80%. Oniscus asellus 77%. Porcellio scaber 71%.

These experimental results can be related to the nocturnal activity of the species. Woodlice were often to be seen wandering in dry places at night, and during the day time were found regularly under logs, stones, and in litter; dark situations where environmental conditions are relatively constant. If nightfall involved only a reduction of the factors which normally operate to restrict them to their day time habitats, it seems unlikely that they would have any reason to leave them. The endogenous diurnal rhythm or physiological "clock", however, will encourage movement at nightfall when they are especially sensitive and easily disturbed. Field observations by Brereton (1957) on Porcellio scaber have indicated a shortening in the activity period as days lengthen to midsummer and also lack of any clear relationship between activity and changes in temperature and humidity.

The decrease in the intensity of the humidity response at night enables woodlice to walk in dry places where they are never found active by day, and the increased photo-negative response after they have been conditioned to darkness ensures that they get under cover at daybreak and thus avoid predation and dessication.

The results show that Philoscia muscorum is the most strongly photo-negative, with Oniscus asselus next, and the preliminary trials showed that Porcellio scaber came last.

The trials with Trichoniscus pusillus failed as the organisms died within a few minutes due to dessication. These results are in agreement with Edney (1954).

(b) Aggregation in Woodlice

It is well known that many species of woodlice from large aggregations under the influence of environmental conditions and a number of behavioural studies have been concerned with this problem (Allee 1926, Gunn 1937, Walof 1941). Allee (1926) was the first to show experimentally that this behaviour results in a reduction of water loss and so may have survival value.

There appear to be two types of aggregation between which the earlier literature does not distinguish, namely "bunching" and "grouping". When they bunch, woodlice pile up on each other forming an aggregation for a considerable time. In the present study Oniscus asellus were known to have stayed bunched for up to four hours. This behaviour is described by Allee (1926) who showed that bunching produces a drop in respiratory rate. He also showed that a low temperature induced bunching and a high one reduced it, but that the relative humidity of air affects it even more markedly. Edney (1960) states that bunching results in a reduction of water loss and increased survival in dry air and that the mechanism of the aggregation is still uncertain and may be a form of social behaviour brought about by thigmokinesis. The aquatic Asellus spp.

are poor swimmers and flood waters are likely to carry them downstream. Under these conditions the animals cluster together, hanging onto the substratum and to each other and so are better able to resist the current. All individuals behave alike and this results in bunching formation without differentiation of behaviour and without organization. However, this formation is a preliminary to social organization and these temporary groups may be the first step towards it.

In grouping, animals come to lie close together, sometimes with their isopods touching or lateral plates overlapping, but not necessarily with antennae in contact. This happens under low shelter such as logs and stones but also in vessels in the laboratory.

Bunching can reduce water loss but it appears that grouping cannot present the same advantage since each kind of aggregation may occur under low as well as high air humidity. It seems that aggregation is not a direct humidity response. The results obtained by Friedlander (1965) suggest that aggregations may be partly due to the attraction of mechanical contact with each other and show that Oniscus asellus can distinguish between different surface roughness. Allee records partial success in controlling the site of bunching by fixing a recently killed woodlouse to the floor of a container although woodlice do not aggregate around dead bodies. Woodlice may well be sensitive to chemical stimuli but there is no evidence in this particular instance. Cloudsley-Thompson (1956) showed that

Oniscus was sensitive to chemical stimulus as they discriminated in favour of water as apposed to one per cent sucrose solution using chemo-receptors in the terminal antennal segments.

The present study is an attempt to investigate the nature and mode of action of stimuli which induce aggregation.

Method

Specimens of Oniscus asellus were obtained from St. Margaret's Churchyard on the day of the tests, where they were frequently seen to be aggregated. Specimens of Philoscia muscorum were collected from the Field Station where they had never been seen to aggregate.

All the tests were carried out in 150mm x 75mm crystalising dishes floored with damp filter paper. Tests were made in laboratory conditions at 21°C and in an illuminated cold room at 10°C. Amputations were completed an hour before the test.

I. Assessment of Aggregation Behaviour in different conditions

The tendency of Oniscus asellus and Philoscia muscorum to aggregate was measured by placing ten animals at a time into a crystalising dish. At 30 minute intervals over a period of 5 hours from 10am to 3pm the number of aggregated animals was recorded. Any assemblage of two or more animals in physical contact was counted as an aggregation. After each recording the aggregations were gently dispersed with a fine damp brush. The following trials were completed :

(a) Control : R.H. 80%. Temperature 21°C.

(b) R.H. 95%. Temp. 10°C.

(c) R.H.100%. Temp. 21°C.

(d) Normal control conditions with antennae amputated. This did not appear to affect the animals in any way.

(e) Chemical stimuli of own kind. This test was designed to see if the species were attracted to chemicals emanating from them. Two animals were ground up with distilled water and the supernatant liquid tested against distilled water by placing the liquid on one half of the filter paper only. There was a 1cm gap left between the two halves of filter paper.

II. Effect of physical contact stimuli on aggregation.

Pieces of plasticine given a rough surface of gravel and measuring 2cm x 1cm x 1cm were prepared. Four obstacles were placed around the sides of a crystalising dish and one in the centre. The test was carried out as for I above.

Results

Table III. Aggregation experiments

(i) *Philoscia muscorum*

	Conditions	Total woodlice aggregated out of 100
(a)	Control. Normal animals at 85% R.H. 21°C. ...	7
(b)	100% R.H. 21°C. normal animals	0
(c)	95% R.H. 10°C. normal animals	10
(d)	Animals with antennae amputated at 85% R.H. 21°C.	0
(e)	Normal animals with obstacles in dish. 85% R.H. 21°C.	0
(f)	Choice H_2O/supernatant	0

(ii) *Oniscus asellus*

	Conditions	Total woodlice aggregated out of 100	χ^2	p
(a)	Control. Normal animals at 85% R.H. 21°C.	94	-	-
(b)	100% R.H. 21°C. normal animals	88	4.3	0.05
(c)	95% R.H. 10°C. normal animals	73	14.0	0.001
(d)	Animals with antennae amputated at 85% R.H. 21°C.	71	39.0	0.001
(e)	Normal animals with obstacles in dish. 85% R.H. 21°C.	70	39.02	0.001
(f)	Choice H_2O/supernatant	67	46.44	0.001

Discussion

It appears from these results that considerable aggregation occurs in Oniscus asellus under all conditions. In Philoscia muscorum there was no significant aggregation agreeing with field observations. As Philoscia is nore susceptible to dessication than Oniscus (Edney 1954) it would be to its advantage to aggregate. Aggregation has evolved for the advantage of the group, yet in spite of its greater need for a higher humidity, Philoscia appears to have lost the advantages which occur in most isopods of an essentially aquatic group. This mechanism, when carried over to terrestrial habitats, helps in avoiding the peril of excessive water loss. Low humidity is an ecological condition under which aggregation, with subsequent reduction of water loss by evaporation, has a survival value. The aggregation is not primarily a humidity reaction as Oniscus, even in 100 per cent saturated air, were 87 per cent aggregated, and at 85 per cent saturation caused only a 7 per cent rise.

The fact that antennae-less Oniscus (result d) aggregated less than normal ones suggests that the antennae contain some of the sense organs which are sensitive to stimuli associated with aggregation. Cloudsley Thompson (1956) showed that sensitivity to humidity is not controlled from the antennae. In fact no humidity receptors have been identified. Tactile receptors account for result (e) where Oniscus was induced to aggregate around obstacles. The presence of the obstacles increased the total number of aggregations because the woodlice were no longer dependent on each other's bodies for rough surfaces to aggregate against.

Result (f), where both species had a choice between liquid extract of crushed animals or distilled water, give conflicting results. Oniscus appeared agitated at first and took some time to aggregate with a consequent lower aggregation than any of the other trials. After the first two half-hourly counts it did not move onto the supernatant side again. In Philoscia the animals seemed to prefer the supernatant side. This is most interesting and needs to be followed up in future work.

SECTION IV.

Feeding trials

Much has been written about the omnivorous habits of isopods (Heeley 1941, Brereton 1956, Gere 1956, Paris 1963. However, only Paris, Heeley (1963) and Watson (1966) have attempted food preference experiments. Paris' and Watson's work is important because they conducted preliminary experiments to eliminate foods not eaten in the field. From those foods most readily eaten they were able to list a table of preference by conducting laboratory experiments where the numbers feeding on each food were compared. Watson further conducted his research under near natural conditions and out of 40 foods tried found that Oniscus asellus and Porcellio scaber preferred Urtica sp. and Onopordum sp. Of the foods available all the year round in the habitat, Querus sp. and Acer sp. were most preferred. The advantage of Heeley's work is that the age at which leaves become preferred was established for Trichoniscus. This was found to be Ash and Sycamore leaves which were decomposing and which were six months old. Macfadyen (1961) emphasised the need for more food preference studies on soil invertebrates so that 'bottle-necks' in the energy flow picture might be recognised.

In the present work at attempt is made to establish which of the twelve most common foods found in the four habitats the four species preferred.

Temporary slides were made of faecal pellets in order to confirm what the animals were eating and how much they altered the food consumed.

Methods

Leaves of Quercus petrea, Acer pseudo-platanus, Fúgus sylvaticus and Aesculus hippocatanum were collected in nylon bags and labelled. These were placed in litter and lightly covered over until they were required for use the following April. In April fresh green leaves of these trees and Fraxinus excelsior were collected, as was the calcifuge moss Mnium hordum, the grass Dactylis glomerata and the algae Pleurococcus spp. and Chlorococcum spp. The leaves were air-dried for 24 hours in a well ventilated room. Discs 2cm in diameter were cut with a cork borer from each of the leaves selected for the experiment and were then thoroughly wetted with distilled water. Petri dishes floored with moist filter paper were used for the experiments. Four different leaf discs were then placed in each dish and these were repeated for all four species. Adult animals were collected from the field the previous day and starved for 20 hours. Five animals were placed in each dish. Dunger (1958) criticised this method, previously used by Drift (1950) and Gere (1955), as starving could induce increased feeding activity. However, as the feeding trial lasted for seven days, it was thought that the error would be slight. The trials were kept in an illuminated cold room at 10°C, R.H. 95%, which was considered to be as near natural conditions as possible. During the third day of the trial hourly counts were made to establish the number of animals on the leaves. At the end of the week the number of faecal pellets on the leaves was counted and the percentage of leaf discs eaten was established. Table 4 summarises the results obtained.

Table IV.

Preliminary feeding trials

	Ash		Sycamore		Beech		Horse chestnut		Moss		Cocksfoot		Pleurococcus		Chlorococcum		Oak		Sycamore		Beech		Horse chestnut	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
Trichoniscus pusillus	8	0	2	0	4	0	0	0	18	0	15	0	2	0	1	0	1	4	1	0	9	4	2	2
					x		x		x		x						x		x				x	
Philoscia muscorum	17	3	0	7	0	3	0	1	8	4	0	1	0	3	1	0	1	0	1	1	3	0	0	2
	x		y						y								y		x				x	
Oniscus asellus	14	4	6	6	0	6	2	2	1	3	6	2	2	2	0	0	13	0	1	1	1	0	5	1
			y	100%			x		x										x				x	
Porcellio scaber	0	2	12	1	0	0	3	0	26	19	0	2	2	0	0	0	3	0	4	1	0	0	13	4
			y				y		y	85%			x				x		x				x	

Table IV. Summary of results of feeding trials :

a = number of animals on leaves

b = number of faecal pellets on leaves

x = less than 5% leaf eaten

y = more than 5% leaf eaten unless otherwise stated

From these results it can be deduced that different species of woodlice have food preferences : with all species eating new Moss and old Horse chestnut and Sycamore, whereas some foods did not appear to be touched. A second trial was carried out in crystalising dishes with the seven most preferred foods in them. The number of animals was doubled to 10 per dish. The trial, otherwise, was run as before.

Table V. Feeding Trials

	Ash new	Sycamore old	Sycamore new	Horse chestnut old	Horse chestnut new	Oak old	Moss
	b	b	b	b	b	b	b
Trichoniscus	6	2	4	2	4	7	7
pusillus	x				x	y	y
Philoscia	28	4	7	13	3	3	30
muscorum	y 95%	x		x	x		y
Oniscus	8		8	12	2	31	36
asellus	y 80%	y	y 100%	y	y	y	y
Porcellio	46	4			2	4	26
scaber	7 95%	x		x	x		y

Micro-photographs were taken of parts of faecal pellets of woodlice (Plates 5, 6, 7, 8) and these show quite clearly that woodlice alter the food that has passed through the gut very little. The food has not been subjected to digestive processes for long as part of the food is still green in the pellet, and nuclei, which are easily broken down, are clearly visible. It appears that woodlice feed on soft cellulose material as tracheids and vegetable fibres are left and not woody material. From the feeding trials and these photographs, moss seems to be a favourite food.

The following plant remains are clearly visible and the following parts can be identified.

Plate 5. Leaf of moss, lateral root, tracheid, vascular tissue

Plate 6. Leaf of moss showing thin cell walls with nuclei visible

Plate 7. Algal spores and fungal lymphae

Plate 8. Root tip or bud scales. Tracheid

In plates 5, 7, 8, humus and grit are discernible. More work needs to be done on this subject and it should not be difficult to construct a key for faecal pellet analysis. Chemical tests would show if material was lignin, cutin, or cellulose. Animals could be confined in dishes on one food type and their faeces analysed and this would help to confirm analysis of pellets from nature.

Discussion

It is felt that little significance can be given to the number of animals on leaf discs, or the number of faecal pellets, as the animals appear to use the leaf discs as resting places.

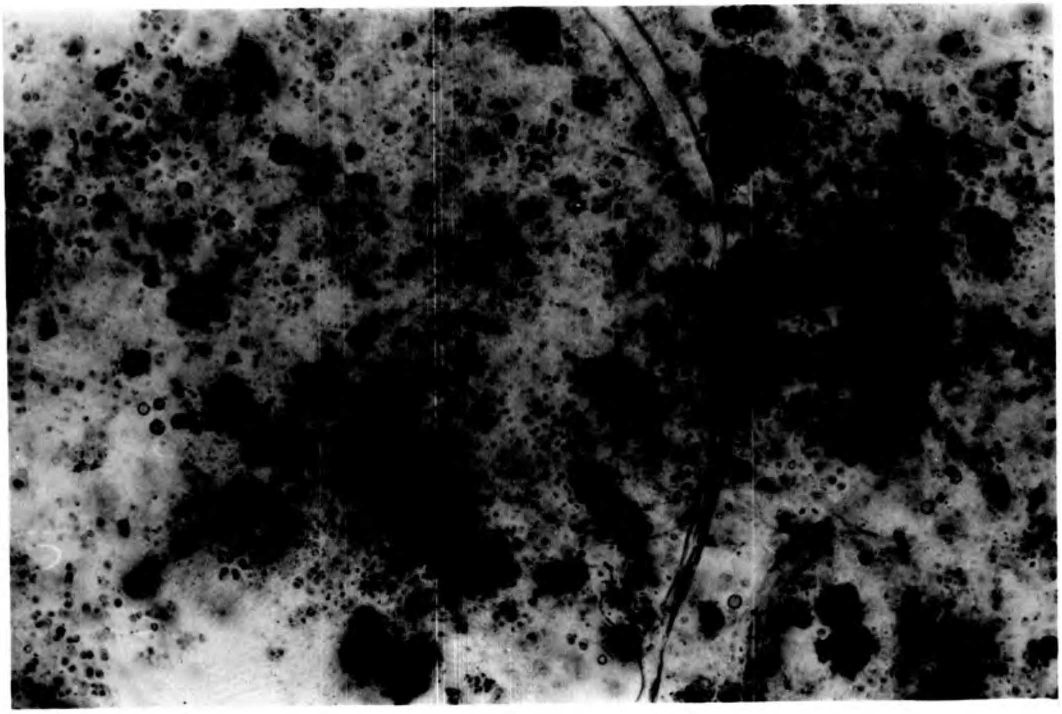
The results given in Table IV were used to eliminate the foods not eaten and the second trial used to determine the order of preference, Table V. The most popular foods for all four species were Fraxinus excelsior, Mnium hordeum and Horse chestnut. There was some variation in order of preference. Oniscus asellus preferred Sycamore. The results are contrary to Healey (1963) and Watson (1966) who found that old leaves were preferred although fresh green material

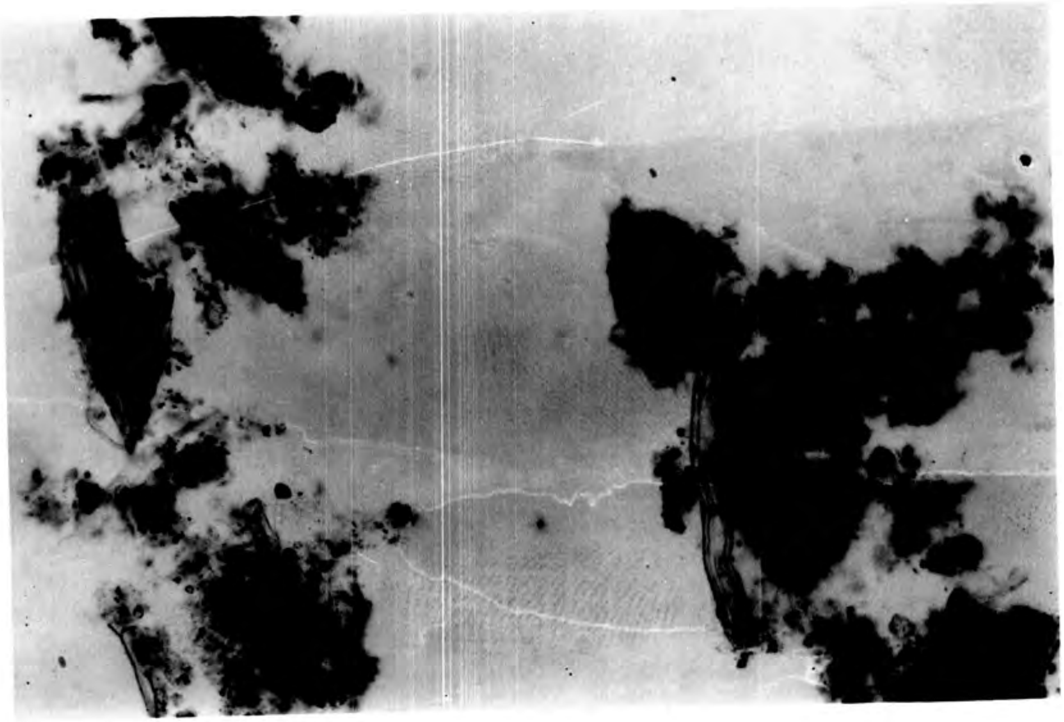
Plate V — Micro-photograph of faecal pellet of woodlice showing leaf of moss, lateral root, tracheid, vascular tissue.

Plate VI — Micro-photograph of faecal pellet of woodlice showing plant cell walls with nuclei.

Plate VII. Micro-photographs of faecal pellet of woodlice showing algal spores and fungal hyphae.

Plate VIII. Micro-photograph of faecal pellet of woodlice showing root tip or bud scales, tracheid.





was attempted. Paris & Pitelka (1962) suggested Armadillidium vulgare may function as a grazing animal as well as a scavenger in grassland. This could certainly be the case with Philoscia muscorum which were frequently found amongst grass tussocks.

Preference could be related to the toughness of the leaves. Oak and Beech have very thick cuticles whereas Ash and Horse chestnut, which were preferred, have relatively thin cuticles and decompose more rapidly. Healey (1963) suggests that woodlice may have a sense of taste and this could influence a choice of food.

There is a need for more research to see if food is a factor affecting population numbers. There was no evidence in this study that animals were short of food. They appear to utilise what is available. In Sherburn Quarry, for example, woodlice ate the only food available on the quarry wall, namely Chlorococcum sp. Brereton (1956) says that Porcellio scaber prefers Pleurococcus sp. on trees, but in the trials Pleurococcus was ignored and Mnium nordeum, which grows at the base of trees, was readily eaten. The conclusion which must be drawn seems clear : where a favourite food is available isopods utilise it as a principal food source, but in its absence they turn to other dietary items. The very diversity of their diet is probably part of their success story.

SECTION V

Population studies

Previous population studies have been made on several species of woodlice. Hatchet (1947) studied a population of Cylisticus convexus and was concerned to find the age-composition of the population and to investigate breeding biology. Brereton (1957) made a thorough study of several species but especially Porcellio scaber and included day and night activity studies. Paris (1962) and Paris & Pitelka (1963) worked on Armadillidium vulgare and assessed the roles of food, enemies and weather in population regulation. Their views are similar to Andrewartha & Birch (1954) who state that weather is the primary population regulating factor, whereas Brereton favours competition as the main regulating factor. Views expressed by Milne (1962) who considered that intra specific competition is the only perfectly regulating process, coming into action at high densities when the ultimate capacity of an environment was exceeded.
Healey (1963) working on Trichoniscus pusillus succeeded in determining both density and distribution of this species with most of the additional material needed for a life-table.

The desirability of additional research on the population ecology of woodlice derives, in part, from the abundance and hence the importance of these organisms in many terrestrial habitats.

The present study attempts to determine the abundance of four common species of woodlice in four different habitats from winter through to early summer and to calculate the biomass, egg production and growth of the populations. An all night observation was made in Sherburn Quarry in an attempt to work out activity patterns of woodlice on the quarry wall.

Methods

(a) Sampling

In the Great High Wood and the Field Station sampling was based on a grid system and using random numbers drawn from a box. The field station had a metre square grid of seventy 6" x 6" tiles laid out, and ten of these were sampled on each occasion. The woodland was laid out in metre squares by means of strings. In the quarry and churchyard there were abundant stones available, and ten of these were sampled randomly on each occasion. As they were sampled, a spot of paint was put on the stone to avoid re-sampling on another occasion. The ten sample units taken on each date were cores of soil, litter and living plant material taken with a thin walled steel cylinder of 4" diameter and to a depth of 4". Thus there were 123 cores to the square metre. The sampling interval was about 21 days during the season of growth and reproduction, with longer intervals in the colder months. Woodlice found on the underside of stones and logs were collected by hand or by pooter.

(b) Extraction

Samples were brought back to the laboratory in canvas bags and sorted by hand on a specially constructed white topped table and under strong illumination. The animals were killed and preserved in 70% alcohol (Edney 1954). During preliminary surveys Tulgren funnels were used for extraction but these crude extractors were found to be less efficient than hand sorting although the latter method is tedious and time-consuming. Neither method is very accurate but hand sorting was used consistently for samples from all four sites.

(c) Examination

Numbers of eggs in the brood pouches were counted using a microscope and dissecting needles. Head width measurements of the animals extracted were taken by the use of a microscope with a micrometer eyepiece. They were preferred to body-length measurements because these can vary between wide limits depending upon the contraction of the body at death (Sutton 1968) 1 micrometer unit = 0.5mm.

(d) Biomass

The total catch of each species from each habitat was washed with distilled water, having been killed in alcohol, allowed to dry for 2 minutes on filter paper, and then weighed on a balance accurate to 0.01mg.

(e) Climate

On each sampling date the relative humidity and temperature were recorded for each habitat (Appendix Table 5) and relevant information from the University Observatory monthly return was extracted (Appendix Table 6). The prevailing climatic conditions are greatly ameliorated in a woodland and the insulating effect of litter on the soil is well known (Drift 1951). This is why micro-climate studies are more important than general climatic conditions.

Results

(a) Population studies

Density - The numbers collected, given as total extracted from 10 core samples, are given in Tables I - IV. Estimates of density are also given in Tables I - IV as numbers/m^2, to aid comparison with estimates for other invertebrates. Numbers for *Philoscia* are comparable with those of Sutton (1968) and those for *Porcellio* to those of Brereton (1957), but the numbers for *Trichoniscus* are far below those of Sutton whose numbers rose to over 2000/m^2. Those could possibly be due to inferior extraction techniques. *Philoscia* was the least common of the four species with densities ranging from 12m^2 - 132m^2, although in hand searches it was easily seen because of its markings, rapid movements and less retiring habits. *Porcellio* had all disappeared from litter by the end of June and was later frequently found under bark on trees and under loose stones on the quarry wall. This is in agreement with Brereton (1957) who rarely found Porcellio in litter or moss in summer. There are no comparative figures for Oniscus. This large animal was very common with densities up to $756m^2$. The difference in biomass between Trichoniscus and Porcellio/Philoscia is much less than in population density, because of the much greater size of the latter. Comparison of density and biomass figures show that the size structure of the population was changing since the two did not rise and fall together. This is possibly due to the change in growth of populations and is discussed in the next section.

Size structure and biomass - The head width measurements, shown as a percentage of the total number sampled (Figs. 3 - 6) show an upward progression through the size classes in Trichoniscus and this, it is assumed, must represent growth. The animals being small in winter, gradually increasing in size in May and June, with young woodlice appearing in July. It is difficult to explain the changes in the other species. Oniscus appears to decrease in size in early summer and then increases later. This could be due to mortality of older adults and this could also apply to Philoscia. It would be an advantage if laboratory and field raised woodlice could be marked, then measured and weighed monthly, in order to acquire more conclusive results.

Climate - The climate appears to have a considerable effect on the animals, especially the small Trichoniscus. The start of the year was unusually mild (Appendix Tables 5 & 6) but February and March were both cold and wet. In March the temperature was $4^{o}F$. below normal and there were 27 ground frosts. This seems to have driven Trichoniscus deeper into the soil and litter because there was a drop in the numbers found at this time (Fig.II) which shows its ecological flexibility by vertical migration.

The other outstanding feature was the very dry warm period in July when the rainfall was the lowest for five years. This appears to have had a particularly dramatic effect on Trichoniscus (Fig.I) and Oniscus (see Fig.IV) especially in the quarry which is normally well drained and dry.

The warmest and driest habitat was the field station (see Table 5 in the Appendix) but it is difficult to find any correlation with populations of woodlice there.

Response to more profound seasonal changes is shown by the fact that in winter all species were scarce and are only found in crevices, holes and deep in the soil in a semi-lethargic state.

Embryo production - The breeding season, defined as 'the period during which females with brood pouches occur' (Sutton 1968) is shown as far as possible in Figs. 3-6 where total embryo production is given. Trichoniscus breeds earliest in the year and occupies the largest developmental period within the brood pouch whilst those species breeding later, Porcellio and Oniscus, occupy a shorter

Fig. III.

Embryo production, density (per $^{10}/123\ m^2$) and size distribution of Trichoniscus pusillus in each sample for four habitats. Size classes are given in micrometer units. The number in each size class is shown as a percentage of the sample total (~~mm = 100%~~)

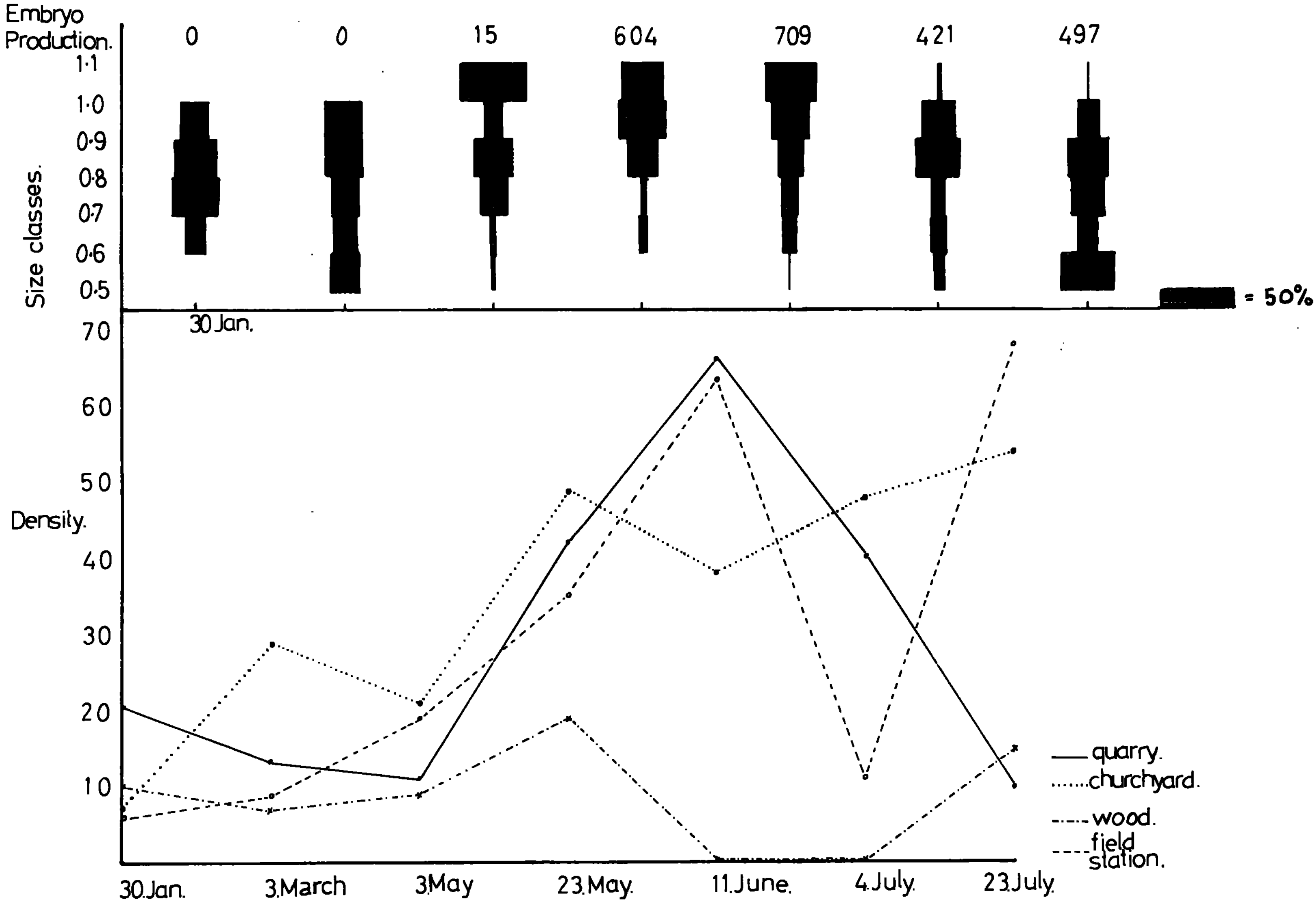

Embryo Production.
0
0
15
604
709
421
497
Size classes.
1·1
1·0
0·9
0·8
0·7
0·6
0·5
= 50%
30 Jan.
Density.
70
60
50
40
30
20
10
30.Jan.
3.March
3.May
23.May.
11.June.
4.July.
23.July.
quarry.
churchyard.
wood.
field station.

Fig. IV.

Embryo production, density (per $^{10}/123\ m^2$) and size distribution of <u>Oniscus asellus</u> in each sample for two habitats. Size classes are given in micrometer units. The number in each size class is shown as a percentage of the sample total ~~(mm = 100%)~~

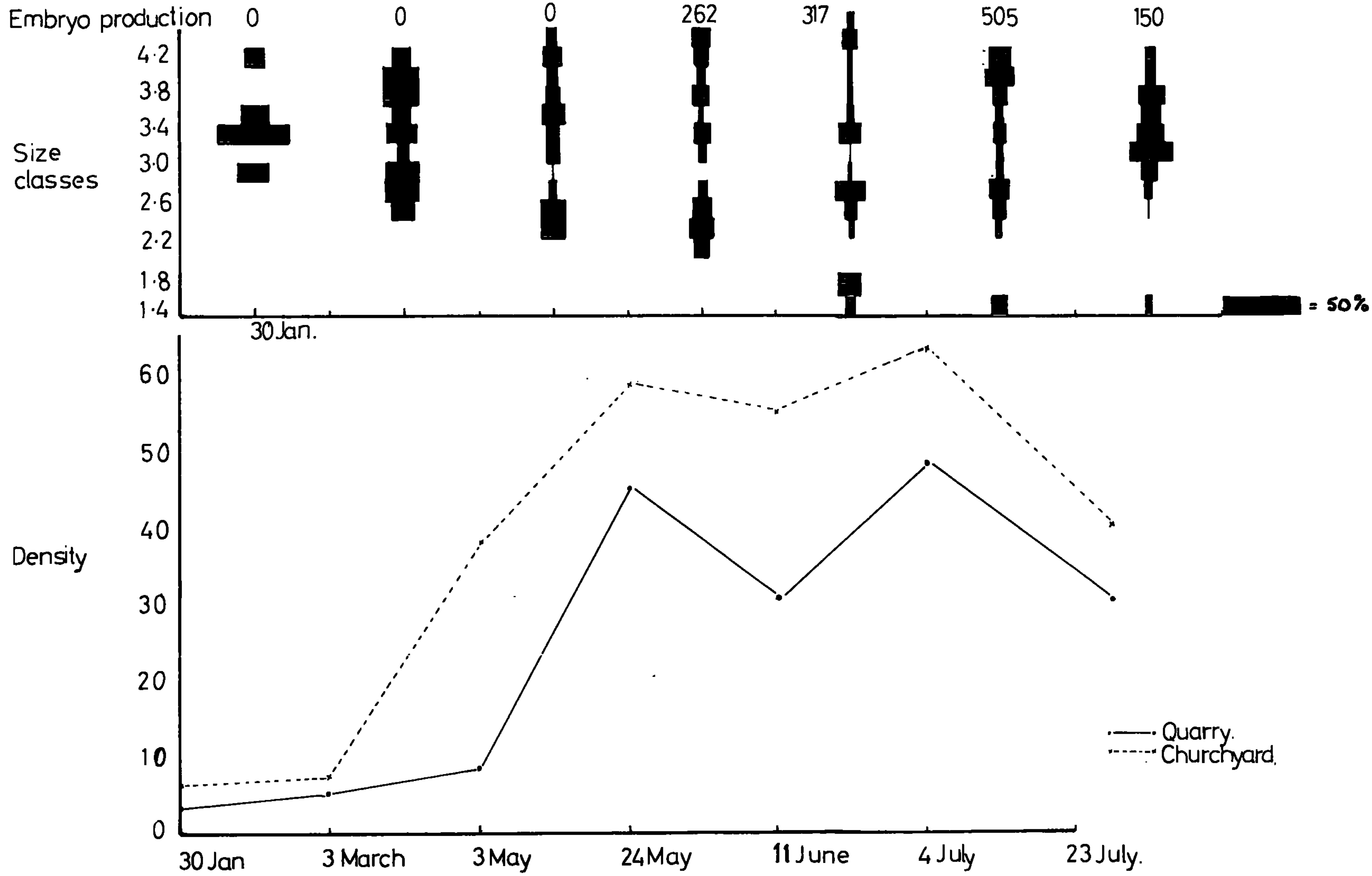
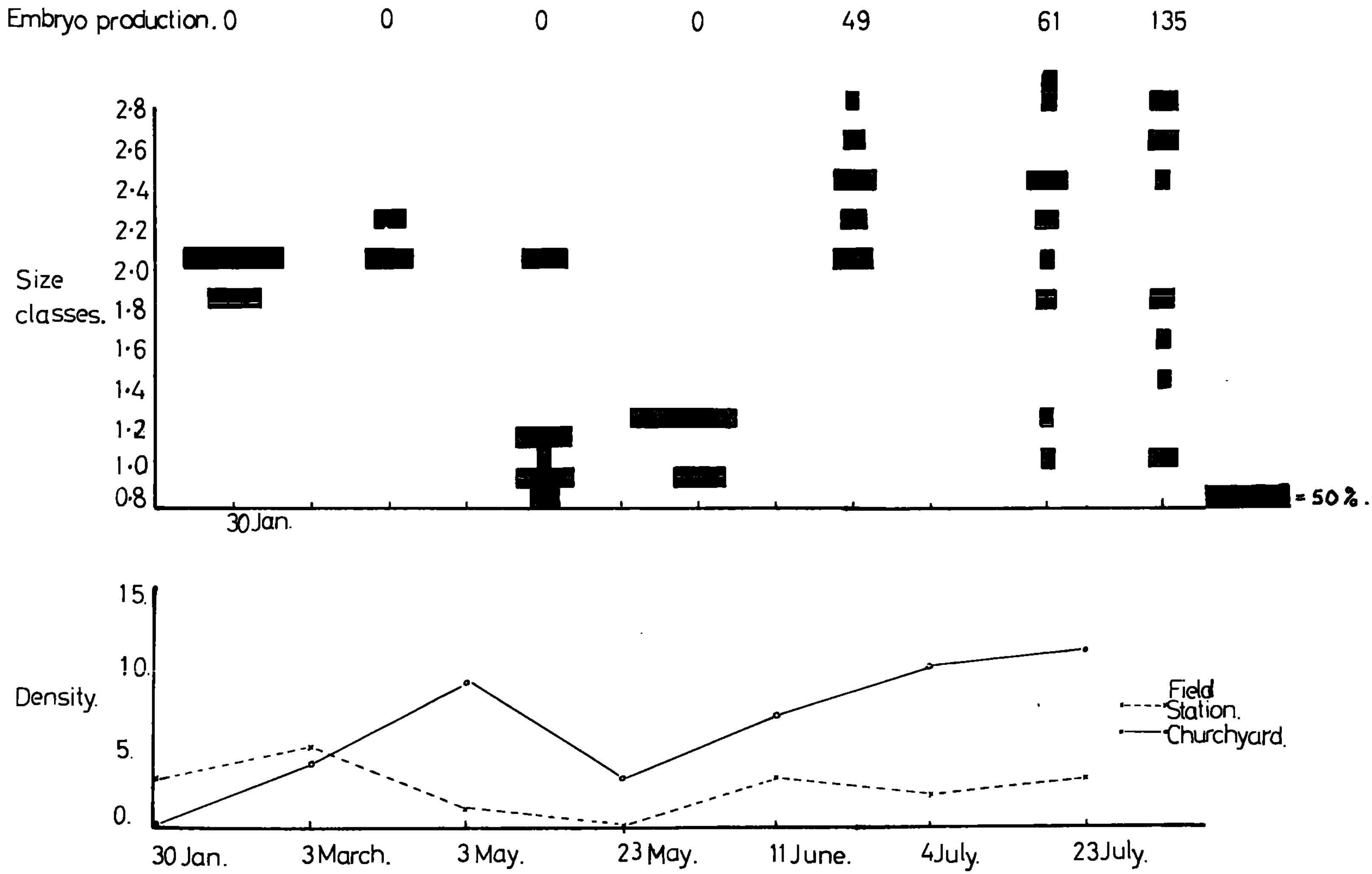

Embryo production
0
0
0
262
317
505
150
Size classes
4·2
3·8
3·4
3·0
2·6
2·2
1·8
1·4
= 50%
30 Jan.
Density
60
50
40
30
20
10
0
30 Jan
3 March
3 May
24 May
11 June
4 July
23 July.
Quarry.
Churchyard.

Fig. VI.

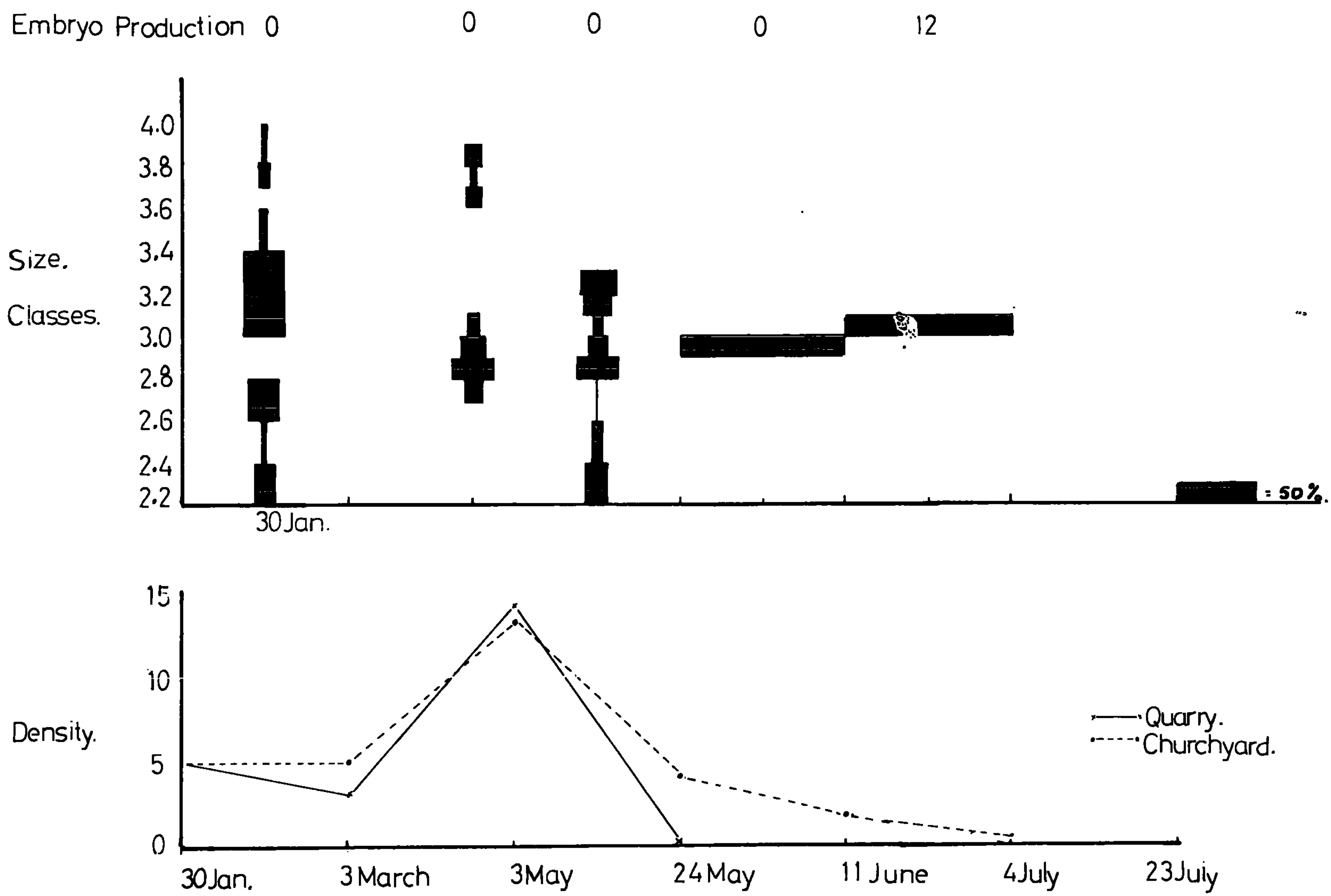
Embryo production, density (per $^{10}/123\ m^2$) and size distribution of *Philoscia muscorum* in each sample for two habitats. Size classes are given in micrometer units. The number in each size class is shown as a percentage of the sample total (~~mm = 100%~~)



Embryo production. 0
0
0
0
49
61
135
Size classes.
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
30 Jan.
= 50 %.
Density.
15.
10.
5.
0.
30 Jan.
3 March.
3 May.
23 May.
11 June.
4 July.
23 July.
Field Station.
Churchyard.

Fig. V.

Embryo production, density (per $^{10}/123\ m^2$) and size distribution of Porcellio scaber in each sample for two habitats. Size classes are given in micrometer units. The number in each size class is shown as a percentage of the sample total (~~mm = 100%~~)


Embryo Production 0
0
0
0
12
Size.
Classes.
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
30 Jan.
= 50%.
Density.
15
10
5
0
Quarry.
Churchyard.
30 Jan.
3 March
3 May
24 May
11 June
4 July
23 July

developmental period and hence the latter tend to "catch up" with the earlier breeding species. Philoscia which normally breeds latest in the year occupies the shortest total breeding period as they only produce one brood.in the year, which develops rapidly, and so they complete their breeding season at approximately the same time as the other species.which produce two broods per year (Heeley 1941). Trichoniscus has a small brood size with an average of siz compared with the other species (Oniscus 30, Porcellio 14, Philoscia 13), but the eggs are larger in size and richer in yolk. This small brood size is counteracted by the fact that it is the earliest in the year to breed and its breeding activity extends over a longer season than the others.

(b) Night activity study

During field work in Sherburn Hill Quarry it was observed that there were a number of woodlice under small rocks and in crevices on the quarry wall. This population was sampled and was found to be made up of three species, namely : Porcellio scaber, Porcellio spinicornis and Oniscus asellus. P. spinicornis is restricted to calcareous soils and can, therefore, be said to be a calcicole (Sutton pers.comm.). Brereton (1956) found that Porcellio scaber left woodland litter, its winter habitat, and spent the summer in trees feeding on the algae, Pleurococcus spp. Night observations were undertaken on 10th June to establish the activity pattern and populations of the species on the quarry wall.

Method

Two quadrats $1/4m^2$ and $\frac{1}{2}m^2$ were marked on the quarry wall with "Sticktight" at a height of 4f. and 10f. respectively in order to restrict the movements of woodlice in these areas. The $\frac{1}{2}m^2$ quadrat included a large area of bird droppings. A third $1/4m^2$ quadrat was established around an area of algae and all animals within the quadrat removed in order to establish if the algae grew more abundantly in the absence of woodlice. During the night observations the temperature and relative humidity were recorded. Woodlice activity was recorded every 45 minutes throughout the night from 10 p.m. - 4 a.m. A torch with a yellow filter was used for observational work and this did not appear to affect the animals.

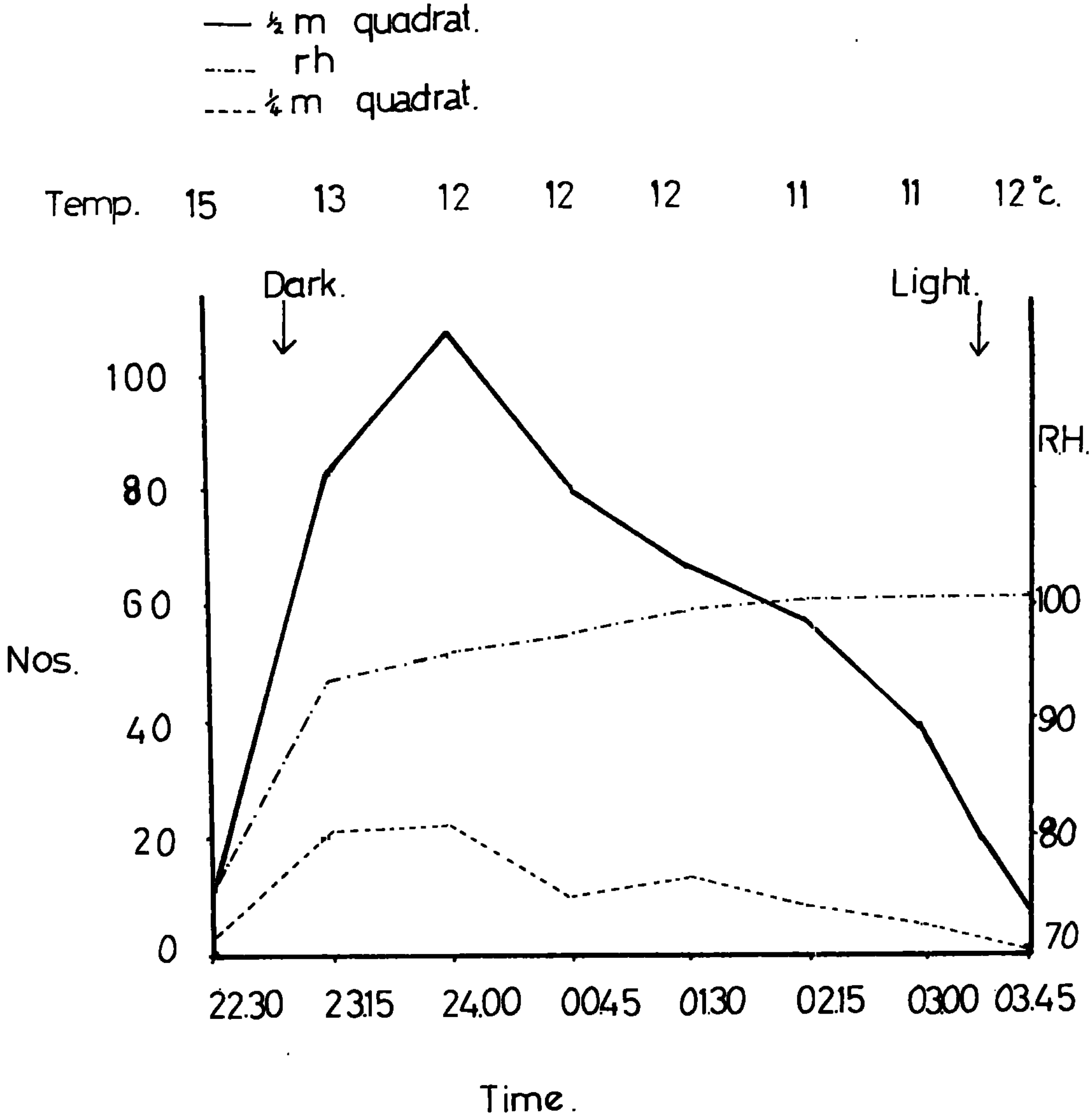
At 11.30 p.m. 51 woodlice were marked with a spot of quick drying paint in order to establish the total population using the Lincoln Index method (Bailey 1951, Southwood 1966). The same time the following night animals were recaptured. 10 woodlice were marked with a spot of green paint in an attempt to establish distance travelled and to see if woodlice returned to the same crevice.

Results

FigureVIIshows the relative humidity, temperature, hours of darkness and activity of woodlice in the quadrat. By 10.30p.m. it was quite dark and 13 woodlice were observed on the bird droppings in the large quadrat. They were motionless and appeared to be

Fig. VII.

Nocturnal activity of woodlice in two quadrats in Sherburn Hill quarry correlated with R.H. and temperature.


— ½ m quadrat.
-·-·- rh
---- ¼ m quadrat.
Temp. 15 13 12 12 12 11 11 12°c.
Dark.
Light.
Nos.
R.H.
100
80
60
40
20
0
100
90
80
70
22.30 23.15 24.00 00.45 01.30 02.15 03.00 03.45
Time.

grazing. By 12.03 a.m. 108 animals were recorded and this was the maximum number observed active that night. This is contrary to Brereton (1957) who recorded the peak of activity for Porcellis scaber as 11 p.m. There was a rapid rise in humidity up to this time. By 4.15 a.m. there were no woodlice to be seen and it was really light.

Using the Lincoln Index method of population estimation 51 woodlice were marked on the first night, 78 were recaptured at the same time the following night, of which 14 were marked. The population was estimated as being :

$$\frac{51 \times 78}{14} = 284$$

On the third successive night at 11.30 p.m. all the animals visible were caught with the following results :

Species	Density $\frac{1}{2}m^2$	
Oniscus asellus	8	
Porcellio scaber	32	
Porcellio spinicornis	62	Total 103

Discussion

From these results it appears that light "triggers off" the behaviour response of woodlice to become active at night and seek shelter at dawn, although activity probably increases with the rise in humidity. However, under conditions of suitable R.H. woodlice are quite active in laboratory conditions.

It is interesting to note that Oniscus asellus is able to climb to a height of 10f. and all the animals were young males. Porcellio scaber appears to move upwards in summer in a quarry as it does in a wood (Brereton 1957) as no animals were found on the quarry floor after 23rd May, and 32 were found in $\frac{1}{2}m^2$ on the wall on 10th June. P.spinicornis, which is restricted to calcareous soil, was the most abundant on the wall but was never found on the floor. The food the woodlice appeared to be eating was bird droppings and the green algae Chlorococcum spp. The patch of algae in the third quadrat, from which woodlice were restricted, deteriorated during the summer months, possibly because of the warm dry conditions.

The numbers of woodlice captured and the numbers estimated by the Lincoln Index method are considerably different. This points to the fact that animals do not necessarily remain out all night but have waves of activity. It would be interesting to determine if the different species have different times of feeding. This could be done by capturing all the animals, marking each species with different colours, and subsequently releasing them. Another possible reason for this discrepancy in numbers is that the Lincoln Index method is inaccurate.

With all capture - recapture methods the following assumptions are important :

(i) the marks are not lost or do not become indecipherable

(ii) marking and disturbance of the animals do not seriously affect their subsequent behaviour

(iii) the natural availability of the sub-population from which the sample is taken is the same as that of the whole population

(iv) there are no births, deaths, emigrations or immigrations.

By recapturing 24 hours later, by using small spots of paint which were harmless to the animals, and as the animals were restricted to ½m^2 quadrat, these factors were kept to a minimum. The maximum distance any of the green marked woodlice were observed to move was 45cms although the general impression gained was that woodlice outside the quadrats were very active and travelled considerable distances. Of the 10 woodlice originally marked, 6 returned to the same crevice, suggesting that woodlice may possibly have some 'homing' instinct.

Although these results are both small and tentative, they are original and most interesting. They point the way to further research.

General discussion

There were two courses open to the ancestors of the terrestrial arthropods : to evolve an impervious integument and all the physiological adjustments that accompany it; or, like woodlice, to remain in moist surroundings by means of behavioural responses, including nocturnal habits. There seems, however, to be a third factor. The leaf litter and humus (Ao horizon) of the soil where woodlice chiefly occur are subjected both to drought and to periodic flooding. Nocturnal activity could be an adjustment by which excess is eliminated. This ability to gain and lose water probably outweights the advantage of possessing an impervious cuticle (Cloudsley-Thompson, 1952 Boer, 1961). Neverthless, woodlice are poorly adapted to life on land because of their pronounced susceptibility to dessication. In general terrestrial isopods are scavengers of dead organic matter. Considered in the light of their abundance these animals must play a significant role in the trophic dynamics of many land habitats, by hastening decomposition of dead vegetation. The invasion of land by woodlice probably represented an occupation by them of an ecological niche less efficiently used by previous occupants.

The four species studied occupied different ecological niches possibly because of their different requirements for humidity, but also, probably, for food. The differences in distribution show some micro-geographical separation of the species although there is considerable overlap. P. scaber prefers to climb vertically in summer but overlaps considerably with O. asellus in winter in living under logs and stones for shelter. This appears to contradict Gause's hypothesis of one species one niche (Odum 1959) but more research would probably show that they are different particularly in their food requirements. P. muscorum showed a marked preference for litter, especially grassland litter. T.Pusillus also preferred litter but it appeared to be more often in older, decomposed litter. It is, therefore, possible to look at a habitat and predict what species of woodlice are likely to be found there.

Much more work needs to be done on these abundant animals. Hypotheses have been put forward for the population regulation of woodlice (Paris 1963; Brereton 1956), but more work on the climatic, edaphic and biotic factors of control are necessary, as all appear to influence the abundance of woodlice. The present study suggests that the soil pH and supply of calcium must be important factors. More research would help to tease apart these influencing factors, and it is regretted that more time has not been available for such work.

SUMMARY

1. The role of soil, food and climate in the ecology of four abundant species of woodlice (*Trichoniscus pusillus*, *Oniscus asellus*, *Porcellio scaber*, *Philoscia muscorum*) in four habitats, were studied during the first seven months in 1969.

2. Variations in soil properties, especially pH and calcium status, were correlated with differences in woodlice abundance.

3. *Oniscus asellus* was found to aggregate in a variety of environmental conditions, but *Philoscia muscorum* did not. This has survival value for *O. asellus* but could be a possible handicap for *P. muscorum* as it is more susceptible to dessication.

4. The intensity of the humidity response was less in darkness than in light and this can be correlated to the nocturnal ecology of the species.

5. Although certain foods were preferred (*Fraxinus excelsior*, *Mnium hordeum*, *Aesculus hippocastanum*) woodlice are able to utilise many foodstuffs according to their availability. This is one reason for their abundance and success. They are important for promoting energy flow in ecosystems.

6. The sampling methods used gave seasonal changes in numbers partly due to the movements of animals. For example *T.pusillus* migrated vertically into the soil in winter and entered the Ao horizon of the soil in Spring. *Trichoniscus pusillus* was the only species

present and quite abundant in all habitats (up to 686 m^2). *Oniscus asellus* was abundant in the churchyard and quarry (up to 756 m^2). *Philoscia muscorum* and *Porcellio scaber* were the least abundant (up to 132 m^2 and 168 m^2 respectively). The breeding season started in *T. pusillus* in early May and the last species to start breeding was *P. scaber* in early June.

ACKNOWLEDGMENTS

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APPENDIX

Table 1. Trichoniscus pusillus pusillus; density and biomass (per $\frac{10}{123}$ m^2) the sample size and equivalent density figures per m^2

(a) Sherburn Hill Quarry

Sample date	Density T.p.pusillus	Biomass (g) T.p.pusillus	Density per m^2 T.p.pusillus
30 Jan	21	.027	252
3 Mar	17	.021	228
3 May	11	.012	132
24 May	44	.065	528
11 June	66	.121	792
4 July	40	.103	480
23 July	10	.010	120

(b) Field Station

Sample date	Density T.p.pusillus	Biomass (g) T.p.pusillus	Density per m^2 T.p.pusillus
30 Jan	6	.006	72
3 Mar	9	.034	108
3 May	18	.039	216
24 May	35	.065	420
11 June	58	.074	686
4 July	40	.060	480
23 July	10	.034	120

(c) Great High Wood

Sample date	Density T.p.pusillus	Biomass (g) T.p.pusillus	Density per m^2 T.p.pusillus
30 Jan	10	.010	120
3 Mar	7	.007	84
3 May	9	.024	108
24 May	18	.061	216
11 June	0	0	0
4 July	0	0	0
23 July	15	.022	180

Table 1 (Contd.)

Sample date	Density	Biomass (g)	Density m^2
	(d)	St. Margaret's Churchyard	
30 Jan	7	.004	84
3 Mar	28	.028	336
3 May	21	.022	252
24 May	48	.094	576
11 June	36	.083	432
4 July	44	.081	528
23 July	48	.090	576

Table 2. Oniscus asellus; density and biomass (per $\frac{10}{123}$ m^2) the sample size and equivalent density figures per m^2

(a) Sherburn Hill Quarry

Sample date	Density	Biomass (g)	Density m^2
30 Jan	3	.184	36
3 Mar	5	.212	60
3 May	7	.250	84
24 May	45	3.043	540
11 June	30	1.456	360
4 July	47	2.316	564
23 July	30	1.181	360

(b) St. Margaret's Churchyard

Sample date	Density	Biomass (g)	Density m^2
30 Jan	6	.219	72
3 Mar	7	.239	84
3 May	37	1,770	444
24 May	58	2.498	686
11 June	55	1.744	650
4 July	63	2.988	756
23 July	40	1.654	480

Table 3. Porcellis scaber; density and biomass (per $\frac{10}{123}$ m^2) the sample size and equivalent density figures per m^2

(a) Sherburn Hill Quarry

Sample date	Density	Biomass (g)	Density m^2
30 Jan	5	.201	60
3 Mar	3	.079	36
3 May	14	.388	168
24 May	0	0	0
11 June	0	0	0
4 July	0	0	0
23 July	0	0	0

(b) St. Margaret's Churchyard

Sample date	Density	Biomass (g)	Density m^2
30 Jan	5	.211	60
3 Mar	5	.219	60
3 May	13	.417	156
24 May	4	.179	48
11 June	2	.057	24
4 July	1	.037	12
23 July	0	0	0

Table 4. *Philoscia muscorum*; density and biomass (per $\frac{10}{123}$ m^2) the sample size and equivalent density figures per m^2

(a) St. Margaret's Churchyard

Sample date	Density	Biomass (g)	Density m^2
30 Jan	0	0	0
3 Mar	4	.171	48
3 May	9	.227	108
24 May	3	.126	36
11 June	7	.166	84
4 July	10	.269	120
23 July	11	.340	132

(b) Field Station

Sample date	Density	Biomass (g)	Density m^2
30 Jan	3	.088	36
3 Mar	5	.120	60
3 May	2	.066	24
24 May	0	0	0
11 June	3	.208	36
4 July	2	.138	24
23 July	3	.257	36

Table 5. Micro-climate in the four habitats

	Sherburn Hill Quarry		Great High Wood		St.Margaret's Churchyard		Field Station	
	Temp. °C	RH %	Temp. °C	RH %	Temp. °C	RH %	Temp. °C	RH %
30 Jan	2	85	7	100	8	85	9	96
3 Mar	3	85	4	85	3	90	6	80
3 May	9	92	9	90	9	78	10	95
24 May	8	80	11	75	11	68	12	70
11 June	8	94	20	74	15	76	24	74
4 July	11	85	12	95	14	85	16	96
23 July	18	93	22	90	23	90	24	85

Table 6. Summary of Meteorological readings at Durham University Observatory

	Total rainfall (ins.)	Days rain fell	Mean temp. (C.)	No ground frosts	R.H. %
Jan	1.88	18	4.1	18	95
Feb	3.48	17	0.2	22	77
Mar	3.38	19	2.1	27	94
Apr	1.78	16	6.4	18	73
May	4.01	26	9.4	3	85
June	3.07	13	13.1	1	88
July	1.74	11	15.9	0	64