Studies in the ecology of two species of woodlouse

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STUDIES IN THE ECOLOGY OF TWO SPECIES OF WOODLOUSE

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INTRODUCTION

The broad objective of the project is to contribute to an understanding of some of the factors affecting the distribution and abundance of two animal species, namely the woodlice, Trichoniscus pusillus pusillus (Brandt) and Philoscia muscorum (Scopoli) (Crustacea: Isopoda). These were chosen as subjects as they are readily accessible, common and abundant litter and soil animals, some aspects of whose ecology have been investigated previously.

In short, what was attempted was to characterise the habitat and distribution of the two species in a woodland and adjoining grassland area near Durham, and to see to what extent the distributions and favoured habitats overlapped and to what extent they differed.

T. pusillus occurs throughout the British Isles occupying a great range of habitats, even acid moorland, and inhabits both the woodland and grassland sites that were studied. P. muscorum also occurs all over the British Isles but sparsly in the north of England and Scotland. It is characteristic of hedgerows and grassland and not normally of woodland, although it does occur in the latter, including the woodland site of this project, in the locality of Durham.

Elton (1949) used the term "habitat" to describe an area which seems to possess a certain uniformity with regard to physiography, vegetation or some other quality considered important by the investigator and the definition is applied in the present work.

A species may occupy a range of different habitats in different parts of its area (i.e. geographical range) and within each habitat it has a position in the space, time, and functional relationships of the community that occupies that habitat. The species' place in a community in relation to other species is its niche.

The term niche has been used to mean two different things: a sub-division of the habitat and the "role" of the species in a community. Hutchinson (1958) redefined the niche and developed the concept of niche hyperspace. For each environmental variable there is a range of values that allow a species to survive and reproduce. Such values of two variables will describe an area, of three a volume, and additional variables an n-dimensional hypervolume (the fundamental niche of the species). The centres of the different species' hypervolumes are dispersed in niche hyperspace.

Many difficulties would be met in determining in full the fundamental niche of a species. It has an infinite number of dimensions and not all environmental variables can be linearly ordered and measured. The interactions with other organisms, such as predators and parasites, will be harder to measure than many physical variables such as temperature. The model also refers to a single instant in time, but values of variables will change.

The distribution of a species will often be limited directly by an environmental variable when the maximum or minimum tolerable value is exceeded, such as when there is an excess of humidity or a shortage of water. At other times, it appears that a species further limits its own distribution by habitat selection. The larva of the European corn borer (Pyrausta nubilalis Hübn.) will feed on a wide variety of plants but occurs mainly on corn (maize) because the ovipositing female is most attracted by an odour produced by the corn plant (Schoonhoven, 1968). However, it is still due to the variation of a factor in the environment that the stimulus occurs in some places and not others and ultimately limits the distribution.

The behaviour of animals and variation in the environment cannot be separated as causes of distribution as this implies spontaneous behaviour in the absence of stimuli.

In regular distributions, the animals are spaced apart more evenly than in a random distribution and may in part be the result of intraspecific competition or, at least, avoidance between individuals. Contagious distributions are those where the individuals are more aggregated than in a random distribution, to a greater or lesser extent in response to environmental variation.

Distribution may be considered as a facet of abundance, the limit of the distribution of a species being where abundance falls to zero, and the factors that affect the distribution may also affect the abundance.

Standen (1972) obtained figures of abundance for T. pusillus in deciduous woodland and found a high degree of aggregation in the distribution. Sutton (1968), in a study of the population dynamics of T. pusillus and P. muscorum in limestone grassland, obtained data on the abundance of both species throughout the year. He also found that after growth of juveniles and breeding of T. pusillus had been curtailed during drought conditions in 1964, an extended breeding programme and improved survival of the young the following year re-established the former abundance.

In the present work, the environmental variables within the species' habitats are considered to fall within the following major categories: food, water and temperature relations, shelter, competitors and predators (parasites apparently being uncommon in woodlice).

Samples were taken from different habitats at the grassland and woodland sites and the T. pusillus and P. muscorum were extracted. A study was made of a number of the variables of the habitats investigated through a combination of field notes taken at each sample location and analysis of the samples after extraction. Multivariate analysis was then used to see how the numbers of woodlice were related to the variables.

The activity of possible predators and competitors was studied by pitfall-trapping and a simpler form of analysis.

Some aspects of feeding behaviour of T. pusillus and P. muscorum were studied by experiment and the development of P. muscorum in woodland and grassland assessed by measurements of those collected in the sampling programme and of young reared in cultures.

CHAPTER 1

PREVIOUS WORK RELEVANT TO THE ECOLOGY OF WOODLICE

1.1 Food

Woodlice are usually regarded as primary decomposers as much of their food is dead plant material. Living material was considered a minor component of their diet until Paris and Sikora (1965) demonstrated that *Armadillidium vulgare* Latreille fed on ^{32}P-labelled plants and was able to switch from living to dead material as resources changed. Woodlice also feed on their own faeces, to which extent they are secondary decomposers. Woodlice need relatively large quantities of copper (Weiser, 1966) but cannot obtain it from most types of food. Copper, in a form that can be assimilated, is probably made available through bacterial activity in the faeces, and it is possible that other trace requirements are met in the same manner. Other items of diet include living bacteria and fungi (Ing, 1967) and animal remains.

Much of the litter in natural habitats may be unavailable as food at a given time, due to distasteful substances, low water content, cuticle thickness or other factors. Leaves with high tannin contents are unacceptable until the substances have been leached out by rain, while species with low tannin contents, such as *Fraxinus* spp. and *Acer pseudoplatanus* L. are acceptable much sooner after leaf fall (Standen, 1963). Edwards and Heath (1963) noted that beech and oak leaves that did not darken appreciably after leaf fall began to be fragmented by litter animals far sooner than those which darkened rapidly. The darker "sun" leaves had a much greater percentage of both polyphenols and sugars than did "shade" leaves (Heath and King, 1964; Heath and Arnold, 1966). As the water soluble polyphenols were removed by weathering, the litter became more palatable to arthropods.

Tannins inhibit microbial activity, which appears to be necessary before the leaves are eaten by woodlice. Thus tannin may detract from the palatability of leaves. If this is the case, the woodlice cannot be considered primary decomposers in the strictest sense, as they are not the first organisms to feed on the litter (Sutton, 1972).

Healey (1963), working on *T. pusillus*, found both species and age of leaf of importance in preference tests. A summary of preferences is listed chronologically.

Age of Litter	Species preferred
up to 5 weeks	Variable, nothing readily acceptable
6 weeks - 3 months	Sycamore
4 - 7 months	Ash
over 12 months	Sycamore or oak (The ash was avoided in these last experiments, probably due to myxobacterial growth.)

Litter unacceptable to woodlice for a period after leaf fall may be eaten by other decomposers before reaching an age suitable for the former.

The proportion of ingested food that is assimilated varies considerably. Hubbell et al (1965) found that material is retained in the gut, and assimilation is greater, when food is scarce. When food is abundant, large quantities of up to about 3% body weight will be processed but a smaller proportion of ingested food assimilated.

In summary, woodlice feed mainly on dead plant material with preferences of type and age of leaf. They can utilise a variety of food as resources change and can assimilate a greater proportion of ingested food when it is scarce. However, despite their flexibility, it cannot be considered impossible that woodlice are subjected to shortages of edible food in the natural habitat.

1.2 Water and temperature relations

Isopod species have evolved a range of degrees of independence from the aquatic habitat, from the littoral Ligia, susceptible to rapid dessication in a dry atmosphere and with low temperature tolerance, to the terrestrial Armadillidium, capable of surviving dry air and high temperatures for several hours (Edney, 1951a, 1951b, 1954).

Isopods lack the epicuticular layer of wax possessed by many other arthorpods and tend to have much higher transpiration rates than most of the latter. Without a relatively impermeable integument (and water-economical respiration, excretion, etc.), the other obvious way in which small animals can avoid dessication in terrestrial environments is to avoid dry places and remain most or all of the time in a humid environment as a result of physiological orienting mechanisms (Cloudsley-Thompson, 1954). The intensity (and sometimes nature) of response of woodlice to temperature, humidity and light changes with the intensity of the stimulus, with the physiological state of the animal, and in phase with the animal's diurnal and possible seasonal rhthyms (Waloff, 1942; Cloudsley-Thomspon, 1952, 1954; Warburg, 1964).

Most of the work on the water and temperature relations of isopods has been experimental and many of the assumptions as to their ability to withstand dry air and high temperatures and regulate body water content and heat have not been confirmed by field observations. The excretion of woodlice does not normally compensate for water-uptake in saturated air and so there is a need to emerge into the open at night and lose excess water by evaporation (Boer, 1961). Observed vertical migrations, up trees and walls (Brereton, 1957; Boer, 1961) may be directly attributable to evaporation requirements.

Brereton (1957) described the distribution of woodland isopods in an oak-ash-sycamore wood near Oxford and the changes in distribution over daily and seasonal cycles. T. pusillus was found to retreat under stones in winter and move into dead wood and litter during summer. No significant seasonal change was found in the distribution of P. muscorum, as they remained under stones and litter throughout the year.

Sutton (1968) showed that T. pusillus is not resistant to frost when confined in growth pots to the upper layers in the field. P. muscorum kept in this way all survived. Normally T. pusillus is able to escape frost by vertical migration (Healey, 1963) and is always scarce in the litter during periods of frost. Sutton also showed that T. pusillus migrated deep into the soil during drought conditions in the summer of 1964, while P. muscorum remained in the litter. He does not accept the simple explanation that T. pusillus is more susceptible to dessication than P. muscorum on account of its smaller size, as young P. muscorum are no larger than adult T. pusillus but do not migrate into the soil. P. muscorum showed marked tolerances in laboratory culture and in field observations of far drier conditions than those preferred in tests (Edney, 1954).

Sutton concluded that P. muscorum survives extremes of climate through physiological flexibility, while T. pusillus avoids such extremes through ecological flexibility, of which avoidance of mortality by vertical migration is a component.

1.3 Shelter

Shelter, as an independent environmental entity can be refuge from climatic extremes, predators, parasites and destruction of habitat by trampling or mowing. It is difficult to determine the difference between shelter and food when considering litter-dwelling animals. Moist leaves will provide food and shelter from dessication, grass tussocks may provide food and shelter from predators. Shelter is also a qualitative commodity. A stone that traps a small volume of water-saturated air may provide a refuge from dessication at high temperatures but may not protect from frost. It seems likely that shelter may be one of the factors causing contagious (aggregated) distribution.

1.4 Competitors

It is not known how intra- and interspecific competition affect woodlice populations.

1.5 Predators

A wide variety of animals are known to eat woodlice under laboratory conditions but there is little evidence as to which of these predate on woodlice in the wild. Shrews and toads will readily eat woodlice and little owls, hedgehogs, slow-worms and frogs will accept them. Carabid and staphylinid beetles, spiders, harvestmen and centipedes are mong the invertebrates that eat them under laboratory conditions.

The nocturnal and retiring habits of woodlice make observation of predation in the field very difficult. Rudge (1968) has established through analysis of gut contents that the shrew (Sorex araneus L.) will sometimes eat large quantities of woodlice. To identify predators that take only liquid food, such as spiders, other methods can be employed. Potential prey can be labelled with radio-isotopes which are detectable in predators though this method involves disturbing the prey. Paris and Sikora (1967) used this method and found lycosid spiders and a species of ground cricket ate small numbers of Armadillidium vulgare. Another method is the application of serological techniques. The woodlice proteins will last for some time in the gut of the predator and there is no need to disturb the study area until the predators are removed and their gut contents tested. Using this method, Sutton (1968) found that woodlice were eaten by lycosid spiders, centipedes and shrews.

The spider Dysdera is one predator that has been studied. The genus has two British representatives which are quite common in Southern England. The poison is very toxic to woodlice and the tegumental glands of the latter, which in some species secrete a repellent fluid (Gorvett, 1956) are ineffective.

1.6 Parasites

Woodlice have few parasites (Thomspon,1934) though Porcellio scaber Latreille has a far greater number and variety than other species. None are known in P. muscorum.

CHAPTER 2

METHODS

2.1 Site Descriptions

The woodland sites studied were both situated in Hollingside Wood, on the southern outskirts of Durham (grid references 276 407 and 275 404 for first and second site respectively), on lightly acid podsol. Both sites were situated at about 60 metres altitude on shallow (15^{o}) sloping ledges on a steeper slope facing east-south-east at the first site and east at the second. The wood is mainly mixed-deciduous with small areas of larch (*Larix decidua* Miller), which occurs at the first woodland site.

The predominant species of tree in the wood are beech (*Fagus sylvatica* L.) Oak (*Quercus*) and sycamore (*Acer pseudoplatanus* L.) with birch (*Betula*), holly (*Ilex*) and ash (*Fraxinus*) of minor occurance, although the latter does not occur at either of the sites studied.

At both sites there are substantial areas covered by bramble (*Rubus*) and by *Holcus mollis* L. Some areas have little or no field or ground layer. Bluebells (*Endymion non-scriptus* (L.) Garcke) are scattered throughout all three areas in both sites, forming dense patches in the second site. Woundwort (*Stachys sylvatica* L.) was common amongst the *Holcus* at the first site. Bracken (*Pteridium aquilinum* L.) was common and dispersed throughout both sites and *Dryopteris* also occurred, although infrequently.

Indexes of tree cover were not prepared as they would depend on the size of the area considered (although the contribution of each species to the litter was assessed in detail later in the work.

The grassland site is situated adjacent to Hollingside Wood (grid reference 274 403) and is part of the University of Durham field station. There is a lightly acid brown-earth soil profile which may have been deteriorating since sheep grazing finished in 1965. Part of the site is left unmown and is covered by tussocks of *Dactylis glomerata* L., *Phleum pratense* L. and *Arrhenatherum elatius* (L.) S. & C. Presl. In the mown area, *Phleum pratense*, *Holcus lanatus* L. and *Poa* spp. are of importance although no species are predominant in this very mixed vegetation which also includes *Anthoxanthum odoratum* L., *Dactylis glomerata* (not in clear tussocks), *Cirsium arvense* (L.) Scop., *Heracleum sphondylium* L. and *Plantago lanceolata* L.

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MAP of the locality of the study,
showing the first (1) and second (2) woodland sites,
together with the grassland site (3).

2 .2 Identification of *T. pusillus* and *P. muscorum*

The two species were generally readily recognisable on account of several characteristics but in the case of specimens that had lost all traces of pattern in the preservative, or were damaged or extremely small, it was necessary to examine them under a binocular microscope to determine the species. In practice, all those specimens considered to be *T. pusillus* were checked in this way.

T. pusillus (of which *T. pusillus pusillus* is the form occuring in the north and west of Britain) is a small species reaching 5mm. in body length with a reddish brown colour. *P. muscorum* reaches 1cm. in body length and has a bronze colouring, with a darker head and a median dorsal stripe along the body.

When viewed with a microscope, the flagella (the terminal parts of the antennae) of *T. pusillus* are seen to consist of four indistinct segments ending in a fine brush, whereas the flagella of *P. muscorum* are seen to comprise three distinct segments with no brush. Also, the telson of *T. pusillus* has a concave apical margin but that of *P. muscorum* is triangular.

2.3 Sampling

a) Fieldwork. The sampling programme followed a general plan: the sample unit area was $1/20m^2$ and for the early samples a square container, from which the base had been removed, was used. Samples were taken from different habitats within the woodland (the areas characterised by dominance of *Rubus*, of *Holcus* and by absence of vegetation) and from mown and unmown areas of the grassland site, where a distinction was later drawn between the tussocks and the gaps between them.

For taking woodland samples, the container was pressed to the ground and the litter, förna and humus layers scooped from the open top into a large polythene bag and labelled. As the material was removed, the container sank down, ensuring that a constant area was taken through the depth of the sample. Impeding *Rubus* stems and fallen branches were removed before sampling and when large pieces of buried wood were encountered the sample was abandoned. Notes were taken of the depth of leaf litter, shading, proximity of trees and any feature of particular interest. Grassland samples were dug out with a spade, using the container to gauge size. All litter samples were accompanied by a sample of the underlying soil, sealed and labelled in a polythene bag.

Following consideration of the results from samples of the first woodland site, sampling was continued at woodland site 2 after high densities of P. muscorum had been observed there during searches over the previous week. The first ten samples taken at site 2 were not in accordance with the division into three habitats applied previously, as they included single samples taken from an area with much fallen wood and an area with a dense stand of Endymion.

For the final sampling, it was considered necessary to use a more efficient method for obtaining samples. A cylindrical container with a basal area of $1/20m^2$ and diameter of 25.2cm was adapted by removing the base and attaching a rim of mild steel onto which a serrated flange was filed. The cylinder could be turned with force even into the grassland, obtaining accurate samples from which it was expected few P. muscorum could escape.

As there was insufficient extraction equipment to deal with these last sixty samples, sampling from each habitat was divided between two occasions.

Table 2a summarises the sampling programme.

b) Extraction. The samples were weighed in the polythene bags or sacks and placed in large Berleze funnels heated with 100 watt bulbs. The grassland samples remained as entire cores and were inverted or turned on the sides , enabling animals to pass down with minimum impediment. The animals were collected in jars containing a dilute copper sulphate solution as a fungicide. The jars were removed after six days and replaced by clean jars, the funnels remaining heated until the samples were sorted, preventing them from absorbing moisture. No woodlice, and rarely any other animals, were collected in the replacement jars.

Sutton (1968) tested the efficiency of the Kempson-Lloyd-Ghelardi heat and light extractor in extracting T. pusillus and P. muscorum and found efficiencies of 90% and 83-93% respectively. The apparatus used in the present work allowed a considerable amount of soil and humus to pass through and so efficiencies were probably lowered for T. pusillus and young P. muscorum, due to the difficulty in seeing the smallest individuals.

c) Collection of data. The following data were collected from woodland samples:

a) Number of T. pusillus per sample

b) Number of P. muscorum per samples

c) Shading: noted subjectively on 1(light)-3(dark) scale.

Date		WOODLAND		Date	GRASSLAND			
		Site 1						
	Rubus	Holcus	Litter		Mown		Unmown	
29.4.75	7	7	7	1.5.75	7		7	
20.5.75	3	3	3					
		Site 2						
21.5.75		Mixed 10						
	Rubus	Holcus	Litter			Gap		Tussock
20.6.75	5	5	5	21.6.75	5	5		5
7.7.75	5	5	5	5.7.75	5	5		5
TOTALS	20	20	20		17	10	(7)	10

TABLE 2a

Numbers, timing and distribution of samples taken

d) Depth of litter: noted subjectively to nearest 1.25cm(½"). Depth could vary over the sample, in which case an average was assessed.

e) Soil water content: soil samples were weighed and dried in an oven for three days at 75°C. The water content is expressed in the results as a percentage of the original total wet weight.

f) Predominance at sample location of Rubus: scored as 1 or 0 for analysis.

g) Predominance at sample location of Holcus: scored as 1 or 0 for analysis.

h) Dry weight of grass litter. Attached stems and leaves were trimmed off and included.

i) Dry weight of leaf litter.

j)k)l)m) Score of quantities of beech (Fagus), oak (Quercus), sycamore (Acer) and holly (Ilex) leaves: 3=most abundant, 2=half the quantity of the most abundant, 1=presence.

n) Dry weight of wood

o) Dry weight of bracken

p) Dry weight of the whole sample

q) Water content of the whole samples, expressed in the results as a percentage of the original fresh weight.

r) Dry weight of F & H layers, the residual weight after all litter components had been sorted. The F (fermentation) and H(humified) layers are those in which the litter is in various stages of partial decomposition. Together with the litter (L) layer, they comprise the AO horizon.

The data a)b)e)h)i)n)p)q)r) listed above were recorded from the grassland site and samples, with two additional data:

s) Mowing: 1=grass mown, 0=grass unmown.

t) In unmown area: 1=tussock, 0=gap.

2.4 Pitfall trapping

a) Fieldwork. Pitfall traps were used at the second woodland site to provide further evidence of the distribution and activity of T. pusillus and P. muscorum in relation to environmental factors, and of the distribution and activity of potential predators and competitors. Thirty-five 1-lb jam jars were positioned in the ground one metre apart in a single file transect, their rims flush with the top of the F layer and notes were taken of the nature of the vegetation within ½m. radius of each jar. A small quantity of extremely dilute detergent in water was poured into each jar, ensuring the death of incoming animals. No preservative, which may have had a repellent effect, was added.

A 24-hour trial run commenced 15.30 BST on 22.5.75. Jars were recovered for sorting in the same order in which they were laid out, clean jars being left inverted in the holes, ready to be upturned for the next run. The contents of the removed jars were preserved in 70% ethyl alcohol in labelled containers. Due to the very low numbers collected, it was decided to extend the trapping period and further pitfall trapping was conducted over periods of six days. Accumulation of debris and decay of animals would have rendered the contents unsortable if left longer. The first six day period ran from 31.5.75 to 6.6.75, a second period from 6.6.75 to 12.6.75. Attempts to retrieve a third batch failed when the jars were tampered with. After several attempts to recover a batch intact failed, the jars were removed for two weeks before being put back on 10.7.75. These were concealed better than previously and were recovered intact.

Characteristics of the vegetation surrounding each jar were recorded on 2/3.8.75 in far greater detail than the notes taken earlier (on 22.5.75). There had been little change during the trapping except for a decline in *Endymion* and an increase in trampling of the bare litter areas.

b) *Collection of data*. The contents of the pitfalls were sorted and the following data a)-h) recorded. Vegetation data i)-t) were scored on subjective (0=low-3=high) scales twice at each jar in the transect. The first value applied to an area within a ¼m. radius of the jar, the second to an area within ½m. radius of the jar.

a) Number of *T. pusillus*

b) Number of *P. muscorum*

c) Number of *Oniscus asellus* L.

d) Number of *Porcellio scaber*

e) Number of Staphylinid beetles greater than 6mm. body length.

f) Number of Carabid beetles greater than 1cm. body length.

g) Number of *Sorex* shrews

h) Number of *Glomeris marginata* Villers

i)j) *Rubus* cover

k)l) Fern cover. Most fern cover was due to *Pteridium* but subscores were recorded for less frequent *Dryopteris*.

m)n) *Endymion* cover

o)p) Grass cover

q)r) Total aerial cover (*Rubus*, ferns and dense erect grasses).

s)t) Quantity of leaf litter.

2.5 Feeding experiments

a) The first experiment commenced on 25.5.75 and was designed to test the preference by and acceptability to T. pusillus of five species of plant. Twelve plastic containers (9cm. diameter and 8cm. depth) were prepared with 2cm. depth of non-nutrient, tap water agar poured into each and allowed to set. Leaves, in the early stages of decay, of Acer pseudoplatanus, Betula, Fagus and Quercus were collected, which were considered the principal possible items of diet of T. pusillus and P. muscorum in Hollingside Wood. Six 1cm. squares were cut from leaves of each species. Six rectangles of $1cm.^2$ area were cut from leaves of the grass, Dactylis glomerata, a possible item of diet at the grassland site. Not all the principal grasses occurring at the grassland site could be included in the one experiment. One segment of each of the five species of plant was put in each container, the five species being spaced evenly near the perimeter. Five adult T. pusillus were placed in the centre of each container. The lids were replaced and the containers stored in a constant temperature cabinet at 18°C.

The proportion of each species of leaf eaten since the experiment commenced was assessed at 24-hour intervals on a 1-5 scale:

1 = first signs of damage to segment
2 = more than ¼ eaten
3 = more than ½ eaten
4 = more than ¾ eaten
5 = almost completely eaten

b) An experiment with the same aims and design was set up on 25.5.75 using P. muscorum collected in Hollingside Wood.

Assessment of quantities eaten since commencement of the experiment was more accurate than in experiment a), as P. muscorum ate from the edge of segments, without reducing the thickness. A 20 point scale (of 5% steps) was used.

c) A replicate of experiment b) was commenced on 25.6.75 with the modification of using P. muscorum collected from the grassland site. In addition to furthering the aims of experiment b), it was considered possible that a significant difference would be observed between the behaviour of the two collections of P. muscorum.

d) An experiment was conducted to assess the quantity of leaves of different species eaten daily by P. muscorum. Nine dishes prepared with 2cm. of agar were utilised. Several pieces of each species of tree leaf used in the experiment were cut from adjacent to the midrib; the grass leaves used were cut into equal segments along their length.

For each species, one of each pair of tree leaf segments was used as food in the experiment. The other segments were dried at 110°C in an oven for two days and then weighed collectively. Alternate segments of grass leaves were similarly treated. Leaves from nine species were used: Acer, Betula, Fagus and Quercus and the grasses Arrhenatherum elatius, Dactylis glomrata, Holcus mollis, Holcus lanatus and Phleum pratense. The segments of each species to be used as food were spaced out in a container. It was anticipated that the provision of several segements of each species of leaf would ensure several days' supply of food in edible condition.

Five P. muscorum collected from Hollingside wood were placed in the centre of each container holding tree leaf segments, and five collected from the grassland site into each container with grass leaf segments. The tree and grass leaf containers were set up on 12.7.75 and 13.7.75 respectively.

Each container was to have been checked daily until a substantial proportion of the food was eaten, at which stage the animals were to be removed and the remaining food picked out, dried for two days at 110°C and weighed. A high death rate in all containers resulted in the termination of the experiment on 30.7.5. The total dry weight of the remaining segments of each species of plant is expressed in the results as a percentage of the total dry weight of the replicate halves.

2.6 Developmental studies of P. muscorum

a) The head widths of P. muscorum collected from the Berlese funnels during the sampling programme were measured with a micrscope fitted with a micrometer eyepiece. The width of the head capsule was taken to be a suitable measure of size by Standen (1973) working with T. pusillus, as it is well sclerotised and resistant to swelling and shrinkage.

Detached head capsules were included, damaged were not. For each measurement, sex and presence or absence of eggs were recorded (except where the body was absent). The data from all woodland P. muscorum were pooled, as were those from the grassland.

b) P. muscorum collected from the woodland site 2 were kept in culture. As young were born they were accumulated in a separate container. Two plastic containers were prepared with 2cm. depth of agar. One was provided with a copious supply of leaves of all major grass species growing at the grassland site, the other with many leaves of the major tree species found at the woodland site.

On 17.7.75, forty of the young P. muscorum (aged up to 4 days) were picked up with a moist brush and placed in each container. The lids were replaced and the containers left in a constant temperature cabinet at 18°C without disturbance, except for checks that a sufficient number were surviving. Forty days later, on 26.8.75, the surviving P. muscorum in each container were removed, and killed and preserved in 70% alcohol. The widths of head capsules of the two collections were measured using a microscope with micrometer eyepiece.

CHAPTER 3

RESULTS AND ANALYSIS

3.1 Sampling Programme

The accumulated data of the numbers of woodlice and values of different environmental variables are reproduced in full in tables 3a-3l in the appendix. Due to the large quantity of data compiled, it was decided to analyse in detail only the last sixty samples (tables 3g-3l). These were considered more useful than earlier samples as they were taken with the new sampler and contained the majority of all P. muscorum collected.

These data were analysed to determine the nature of the distribution and subjected to multivariate analysis to determine which environmental variables account for most variation in the numbers of T. pusillus and P. muscorum.

a) Analysis of the nature of the distributions of T. pusillus and P. muscorum in the different sites and habitats.

A random distribution, in which there is an equal chance of an organism occupying any point in space and the presence of one individual does not influence the distribution of another, is described by the Poisson series. When plotted, the Poisson series gives a curve which is described completely by one parameter, as the variance (S^2) is equal to the mean ($\bar{x}$). The goodness of fit of a set of data to the Poisson distribution may be tested by a X^2 test on the observed and expected values

$$X^2 = \frac{S\ (N-1)}{\bar{x}}$$

where S^2 = variance, N = number of samples and $\bar{x}$ = mean. If the distribution is Poisson the X^2 values calculated will be within the 0.95 and 0.05 limits. If the X^2 value does not conform with the Poisson expectation, it will be found that the index of dispersion = $X^2 \div (N-1)$ will approximate to unity. A value of zero for the index would imply that the animals were regularly distributed and a value significantly greater than one (as tested by χ^2 above) implies a contagious distribution.

A breakdown is given of the distributions within different areas in table 3m. In each case the Null Hypothesis that the distribution is Poisson must be rejected.

	χ^2	P	Index of dispersion
T. pusillus			
30 samples from woodland habitats: bramble litter & grass	1494.63123	<.001	51.54
20 samples from litter and bramble areas	572.811094	<.001	30.15
30 grassland samples	222.43	<.001	7.67
20 samples from unmown area	102.29	<.001	5.38
10 tussock samples from unmown area	51.53	<.001	5.73
10 gap samples from unmown area	49.54	<.001	5.50
P. muscorum			
30 samples from woodland habitats: bramble litter & grass	83.00	<.001	2.86
20 samples from litter and bramble areas	39.93	<.01	2.10
30 grassland samples	487.71	<.001	16.82
20 samples from unmown area	272.64	<.001	14.35
10 tussock samples from unmown area	55.08	<.001	6.12

TABLE 3m

χ^2 values, and corresponding P values, from tests of dispersion of T. pusillus and P. muscorum in areas and habitats studied, together with the χ^2 index of dispersion, derived from each value of For Null Hypothesis, see 3.1.

b) Analysis by multiple regression of the effect of environmental variables on numbers of T. pusillus and P. muscorum.

(I) Computing Procedure. The results were analysed using a stepwise regression computer programme BMDO2R (described more fully in Biomedical Computer Programs (1973)) which "computes a sequence of multiple linear regression equations in a stepwise manner. At each step one variable is added to the regression equation. The variable added is the one which makes the greatest reduction in the error sum of squares. Equivalently, it is the variable which has the highest partial correlation with the dependent variable partialed on the variables which have already been added; and equivalently, it is the variable which, if it were added, would have the highest F value ..."

The output before the regression is performed includes a) means and standard deviations of the variables and b) a co-relation matrix.

The output at each step of the regression includes a) the multiple R and the standard error of the estimate, b) for each variable in the equation, the regression coefficient, the standard error and the F to remove and c) for each variable not in the equation, the tolerance, the partial correlation coefficient and the F to enter. (The significance of each entry in the equation is found by entering the F value in the tables of the F distribution for the chosen level of significance. 95% was taken as the minimum acceptable level of significance and, additionally, it is recorded when values exceed the 99% level.)

The output after the regression is performed includes a) a list of residuals and plots of residuals versus input variables and b) a summary table.

A preliminary run was entered for each group of samples and a correlation table obtained. Separate runs, with T. pusillus or P. muscorum as the dependent variable and all independent variables as free variables (i.e. free to enter the equation), provided a general view of which were the important variables.

The correlation matrices contain many high values, largely due to two variables being similar. Using the correlation matrix for 30 woodland samples as an example, the presence or absence of grass is correlated with the dry weight of grass and the dry weight of tree leaf litter is correlated with the depth of litter (table 3n). Other high correlations are due to a cause and effect relationship; for instance, the heaviest shading was always due to a dense cover of bramble and the dry weight of tree leaf litter may be correlated with the dry weight of wood because the latter serves to obstruct the litter which therefore accumulates. Some pairs of variables are significantly negatively correlated, largely due to the presence of one occurring mainly in the absence of the other. There is, for example, little leaf litter in the grass habitat.

	(Number) T. pusillus	(Number) P. muscorum	(Predominance) Rubus	(Predominance) Grass	(Dry weight) Grass	(Dry weight) Tree Leaves	(Proportion of Litter) Beech	Oak	Sycamore	Holly
	1	2	3	4	5	6	7	8	9	10
1	1.000	0.181	0.002	-0.059	-0.005	0.246	0.193	0.055	-0.094	0.309
2		1.000	0.240	-0.541	-0.534	0.489	0.119	0.302	0.019	0.248
3			1.000	-0.500	-0.485	-0.015	-0.149	0.390	0.095	-0.177
4				1.000	0.971	-0.630	-0.149	-0.613	0.095	-0.354
5					1.000	-0.597	-0.111	-0.569	0.061	-0.343
6						1.000	0.278	0.458	0.018	0.659
7							1.000	-0.182	-0.713	0.210
8								1.000	0.074	0.217
9									1.000	0.067
10										1.000

	(Dry weight) Wood	(Dry weight) Bracken	Depth of Litter	Water content Soil	(Intensity) Shading
	11	12	13	14	15
1	-0.096	-0.161	0.122	0.242	0.114
2	0.251	0.281	0.470	0.165	0.160
3	0.105	0.298	0.209	-0.242	0.853
4	-0.541	-0.035	-0.730	-0.314	-0.426
5	-0.526	-0.129	-0.723	-0.279	-0.414
6	0.591	-0.162	0.773	0.527	-0.064
7	0.074	-0.296	0.186	0.211	-0.222
8	0.490	-0.093	0.511	0.193	0.440
9	0.028	0.421	-0.072	-0.051	0.081
10	0.156	-0.125	0.270	0.504	-0.113
11	1.000	0.086	0.738	0.426	0.115
12		1.000	-0.017	-0.181	0.235
13			1.000	0.306	0.178
14				1.000	-0.120
15					1.000

TABLE 3n. Correlations between variables of the last 30 samples, second woodland site. Figures given are values of the correlation coefficient r.

	(Number) *T. pusillus*	(Number) *P. muscorum*	(Predominance) Rubus	(Dry weight) Tree Leaves	Beech	Oak	Sycamore	Holly	(Dry weight) Wood	(Dry weight) Bracken
	1	2	3	4	5	6	7	8	9	10
1	1.000	0.255	-0.051	0.460	0.117	0.100	0.341	0.488	-0.079	-0.295
2		1.000	-0.042	0.231	0.099	-0.056	0.074	0.073	-0.093	0.340
3			1.000	-0.495	-0.420	0.135	0.314	-0.436	-0.258	0.449
4				1.000	0.347	0.091	0.188	0.606	0.397	-0.303
5					1.000	-0.850	-0.426	0.275	0.064	-0.091
6						1.000	0.353	-0.000	0.249	-0.101
7							1.000	0.206	-0.221	0.106
8								1.000	-0.051	-0.203
9									1.000	-0.123
10										1.000

	Depth of Litter	(Dry weight) Whole Sample	Water content Soil	(Dry weight) F & H layers	(Intensity) Shading	Water content whole sample Unadjusted	Water content whole sample Adjusted
	11	12	13	14	15	16	17
1	0.128	-0.135	0.345	-0.163	0.156	-0.003	0.243
2	0.106	-0.145	-0.007	-0.422	-0.093	0.139	0.218
3	-0.273	-0.474	-0.500	-0.438	0.816	-0.412	-0.568
4	0.617	-0.255	0.443	0.162	0.478	0.180	0.417
5	0.242	0.487	0.257	0.474	-0.514	-0.163	0.206
6	0.123	-0.376	-0.019	-0.414	0.275	-0.395	0.004
7	-0.200	-0.260	-0.027	-0.265	0.257	-0.269	-0.047
8	0.020	0.063	0.457	0.028	-0.312	-0.074	0.109
9	0.641	0.332	0.348	0.236	-0.173	0.509	0.314
10	-0.297	-0.441	-0.293	-0.436	0.338	-0.290	-0.342
11	1.000	0.424	0.124	0.345	-0.223	0.130	0.182
12		1.000	0.192	0.993	-0.377	-0.135	0.235
13			1.000	0.143	-0.305	0.465	0.697
14				1.000	-0.345	-0.189	0.193
15					1.000	-0.374	-0.515
16/17						1.000	1.000

TABLE 3o. Correlations between variables of the 1st 20 bare litter and bramble habitat sample second woodland site. Figures given are values of the correlation coefficient r.

	(Number) T. *pusillus*	(Number) P. *muscorum*	(Dry weight) Grass	(Dry weight) Tree Leaves	(Dry weight) Wood	Water content Soil	Tussock/ Gap type habitat
	1	2	3	4	5	6	7
1.	1.000	0.288	0.187	0.470	0.055	-0.035	0.101
2		1.000	0.781	-0.222	0.117	-0.726	0.773
3			1.000	-0.386	0.226	-0.823	0.900
4				1.000	-0.030	0.377	-0.478
5					1.000	-0.065	0.168
6						1.000	-0.850
7							1.000

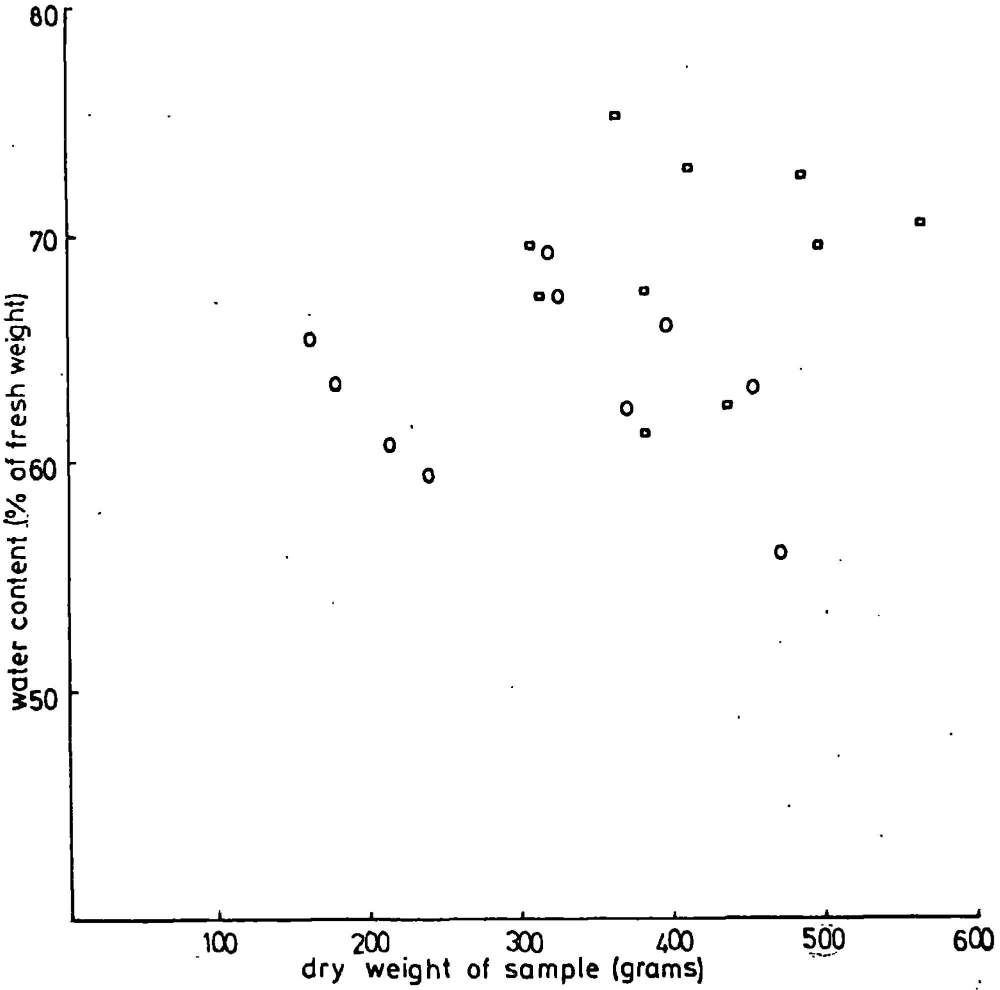
TABLE 3p. Correlations between variables of the last 20 samples, grassland site. Figures given are values of the correlation coefficient r.

A variable entering the regression equation may lower the F value of another with which it is highly correlated. In such circumstances, only one of the correlated variables should have the status of a free variable. Variables can be deleted from the regression equation by means of a control/delete card.

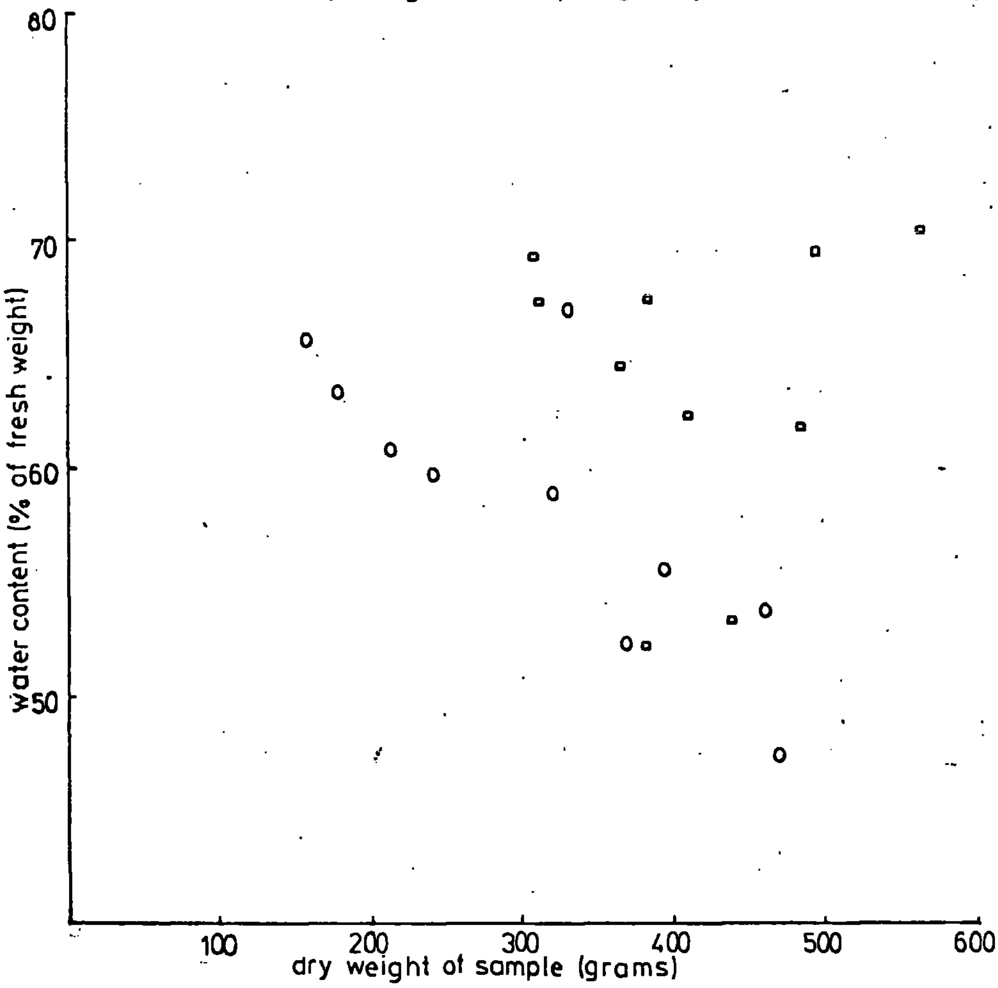
All independent variables were plotted against T. pusillus and P. muscorum and some with other independent variables, on scatter diagrams to aid interpretation of their relationships. The only data altered in any way before they were entered into the multiple regression were the water contents of the soil samples. The second thirty samples were adjusted so that they had the same mean as the previous samples. This seemed legitimate as the values had small standard deviations and were unlikely to be of much use when separated into two distinct ranges. The water contents of the whole litter and bramble samples were tried in the analysis with both original and similarly adjusted values. Viewed separately (diagrams 3a and 3b), the points for bramble and litter, when plotted as a function of dry weight of whole sample, form two different patterns. When the water contents of the samples are plotted in the unaltered form, those of the bramble samples describe a straight line relation between water content and dry weight of sample, whilst those of the litter samples form a scattered cloud. When the adjusted values of water contents of the samples are plotted against the dry weight of the whole samples, the scatter of points of the bramble samples breaks into two components, largely coinciding with the two batches of samples taken, and the scatter of points relating to the litter samples becomes vertically compressed. The significance of these distributions is considered in later discussion.

From study of the correlation matrices and from the negative effect of grass areas in the woodland site on the distribution of P. muscorum, it was decided that the grass habitat was somewhat set apart from the other two main woodland habitats studied, and the regression was run firstly including, and then excluding, the ten grass habitat samples. This scheme was also necessary to bring in three variables which it was only possible to measure in the litter and bramble habitats: dry weight of whole sample, water content of whole sample and dry weight of F & H layers.

The samples from the mown area at the grassland site were devoid of woodlice (except for one P. muscorum) and were excluded from the final runs.



3a



3b

DIAGRAMS 3a and 3b. Scatter diagrams showing the relationship between the water content of samples (expressed as a percentage of total fresh weight) and the dry weight of samples. The adjusted values of water content are used in 3a, the unadjusted in 3b. (see section 3.1). Squares represent samples from the bare litter habitat, circles from bramble.

(II) Results of stepwise regression

WOODLAND

a) <u>T. pusillus</u>

<u>30 SAMPLES</u>

(i) No variable entered the regression equation with a significant value. The dry weight of tree leaf litter became significant when the dry weight of wood entered the equation.

STEP 2

(constant=58.12598)

	coefficient	standard error	F to remove	Significance Level
dry weight of tree leaf litter	3.23013	1.52699	4.4747	95%
dry weight of wood	-2.26282	1.34199	2.8432	insignif.

R^2 = 0.1500 (increase in R^2 since step 1 = .0895)

<u>20 SAMPLES</u> (grass habitat samples excluded)

(ii) STEP 1

(constant=30.74059)

	coefficient	standard error	F to remove	Significance Level
dry weight of tree leaf litter	2.61784	1.19074	4.8334	95%

R^2 = 0.2117

STEP 2

(constant=85.77475)

	coefficient	standard error	F to remove	Significance Level
dry weight of tree leaf litter	3.94283	1.22177	10.4145	99%
shading	41.94522	18.47749	5.1532	95%

R^2 = .3951 (increase in R^2 = .1834)

b) <u>P. muscorum</u>

<u>30 SAMPLES</u>

(i) STEP 1

(constant=2.90000)

	coefficient	standard error	F to remove	Significance Level
Habitat grass	-2.69999	0.79305	11.5910	99%

R^2 = 0.2928

(ii) With habitat grass deleted:

(constant=2.86200)

	coefficient	standard error	F to remove	Significance Level
dry weight of grass	-0.29487	0.08828	11.1565	99%

$R^2 = 0.2849$

(iii) With dry weight of grass and habitat grass deleted:

STEP 1

(constant=0.76385)

dry weight of tree leaf litter	0.14618	0.04934	8.7760	99%

STEP 2

(constant=0.22313)

dry weight of tree leaf litter	0.16410	0.04625	12.5894	99%
dry weight of bracken	0.063931	0.26712	5.7280	95%

$R^2 = 0.3719$ (increase in $R^2 = .1333$)

<u>20 SAMPLES</u>

No variables were significant in the equation at step 1.

(i) With the adjusted values of sample water contents in use:

STEP 1

(constant=6.39030)

dry weight of F & H layers	-0.01039	0.00497	4.3742	not signif.

$R^2 = 0.1955$

STEP 2

(constant=-3.55105)

dry weight of F & H layers	-0.01181	0.00489	5.8351	95%
water content of sample	0.05759	0.10425	2.2850	not signif.

$R^2 = .2908$ (increase in $R^2 = .0953$)

(ii) With the original water contents of samples used:

STEP 2

(constant=5.58181)

dry weight of F & H layers	-0.01157	0.00487	5.6500	95%
dry weight of tree leaf litter	0.10083	0.06729	2.2451	not signif.

$R^2 = .2984$ (increase in $R^2 = .0939$)

GRASSLAND

a) *T. pusillus*

30 SAMPLES

(i) STEP 1

	(constant=0.61699) coefficient	standard error	F to remove	Significance Level
dry weight of tree leaf litter	3.58831	0.86643	17.1520	99%

R^2 = .3799

STEP 2

(constant=-2.24124)

dry weight of tree leaf litter	3.98934	0.75947	27.5918	99%
dry weight of grass	0.06501	0.02012	10.4416	99%

R^2 = .5528 (increase in R^2 = .1729)

STEP 3

(constant=0.90593)

dry weight of tree leaf litter	3.5018	0.95917	13.6227	99%
dry weight of grass	0.05715	0.02266	6.3601	95%
mown area	-1.63430	2.10472	0.6029	insignif.

R^2 = .5629 (increase in R^2 = .0101)

20 SAMPLES

(i) STEP 1

(constant=2.87068)

dry weight of tree leaf litter	2.72252	1.20523	5.1028	95%

R^2 = .2209

STEP 2

(constant=-1.19035)

dry weight of tree leaf litter	3.69256	1.19892	9.4858	99%
dry weight of grass	0.05846	0.02792	4.3833	insignif.

R^2 = .3806 (increase in R^2 = .1597)

STEP 3

(constant=-1.38696)

	coefficient	standard error	F to remove	Significance Level
dry weight of tree leaf litter	3.77335	1.30458	8.3059	95%
dry weight of grass	0.04809	0.06130	0.6155	insignif.
tussock/gap	1.08496	5.77825	0.0366	insignif.

R^2 = .3820 (increase in R^2 = .0014)

b) <u>*P. muscorum*</u>

<u>30 SAMPLES</u>

(i) STEP 1

(constant=-1.83521)

dry weight of grass	0.20032	0.02889	48.0806	99%

R^2 = .6320

STEP 2

(constant=0.01223)

dry weight of grass	0.18620	0.02930	40.3865	99%
mown/unmown area	-3.89665	2.35346	2.7414	not signif.

R^2 = .6659 (increase in R^2 = .0339)

(ii) With mown/unmown deleted:

STEP 2

(constant=-4.01582)

dry weight of grass	0.20775	0.02851	53.1060	99%
dry weight of tree leaf litter	1.71510	1.07611	2.5431	not signif.

R^2 = .6637 (increase in R^2 = 0.0317)

<u>20 SAMPLES</u>

(i) STEP 1

(constant=.014912)

dry weight of grass	0.18925	0.03566	28.1573	99%

R^2 = .6100

STEP 2

(constant=-0.47200)

dry weight of grass	0.10854	0.08144	1.7752	not signif.
tussock/gap	7.89505	7.17197	1.2118	not signif.

R^2 = .6360 (increase in R^2 = 0.0259)

3.2 Pitfall trapping

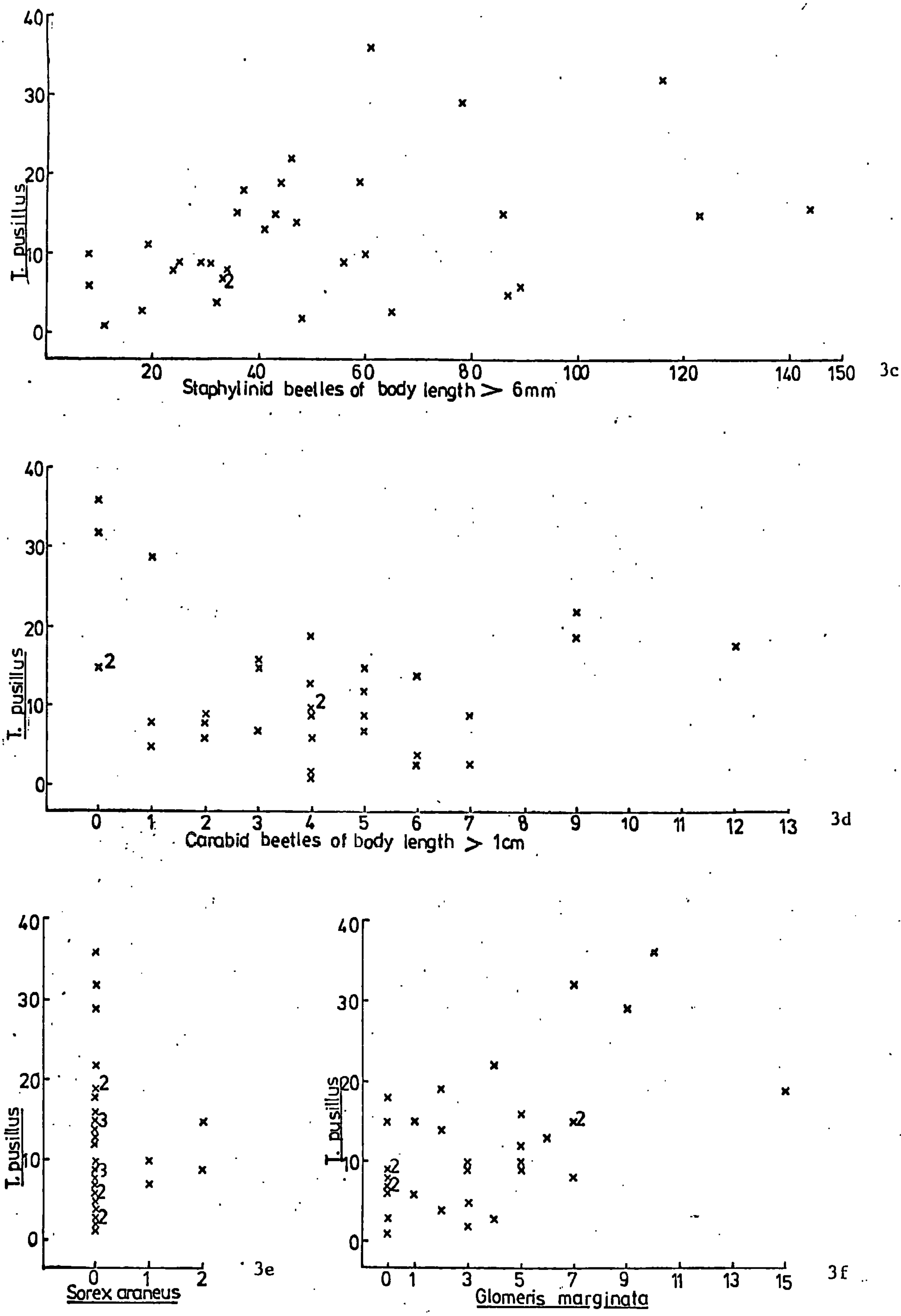
The total numbers of T. pusillus and P. muscorum collected in each jar are plotted against the numbers of predators and pill-millipedes in diagrams 3c–3j. Jar 1 and jar 35 are omitted from all consideration of results as there is a bilateral interference from neighbouring jars affecting all jars in the transect except these two. The total numbers of Porcellio scaber and Oniscus asellus collected over the whole trapping period were too low to analyse meaningfully.

There is need for caution in the interpretation of pitfall data. The numbers of any species of animal collected are affected by the size of the population, the activity of the animals and the likelihood of them falling into a trap when they encounter one. The way in which a trap is set will affect the results, as will the type of vegetation. It is quite possible that, during the short trapping period in the present work, certain species of animal were not active. The data are analysed here only to form a general picture of the relative dispersion of the woodlice and other animals around the transect. There is probably also a large amount of error due to the diversity of the vegetation. The vegetation and structure of the transect area is portrayed diagrammatically (diagram 3k), using the data for the area within ½ metre of each trap, beneath which is a histogram of the numbers of each species of animal along the transect.

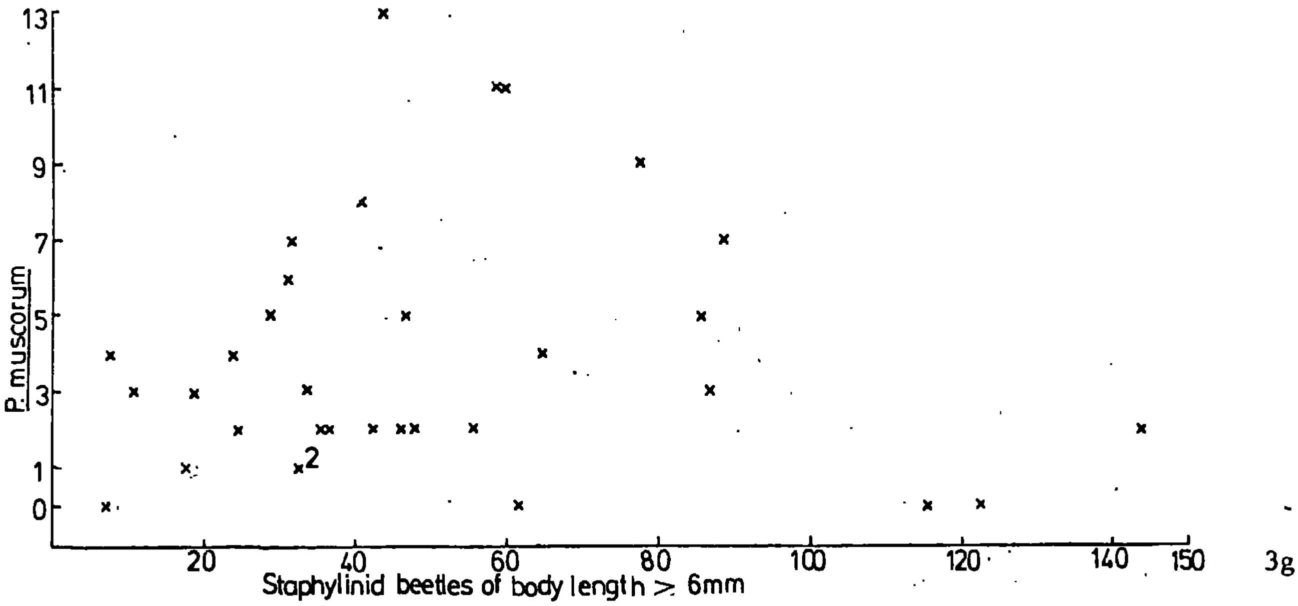
In diagram 3c, there is some degree of correlation and value significance between the numbers of T. pusillus and Staphylinid beetles. The scatter of points is very wide and it is likely that a portion of this correlation is due to there being a large quantity of many forms of potential prey for staphylinids at those locations where there were most T. pusillus (hence, there would be an attraction for the staphylinids whether or not T. pusillus was predated), and also due in part to some jars being better set to trap litter dwellers generally.

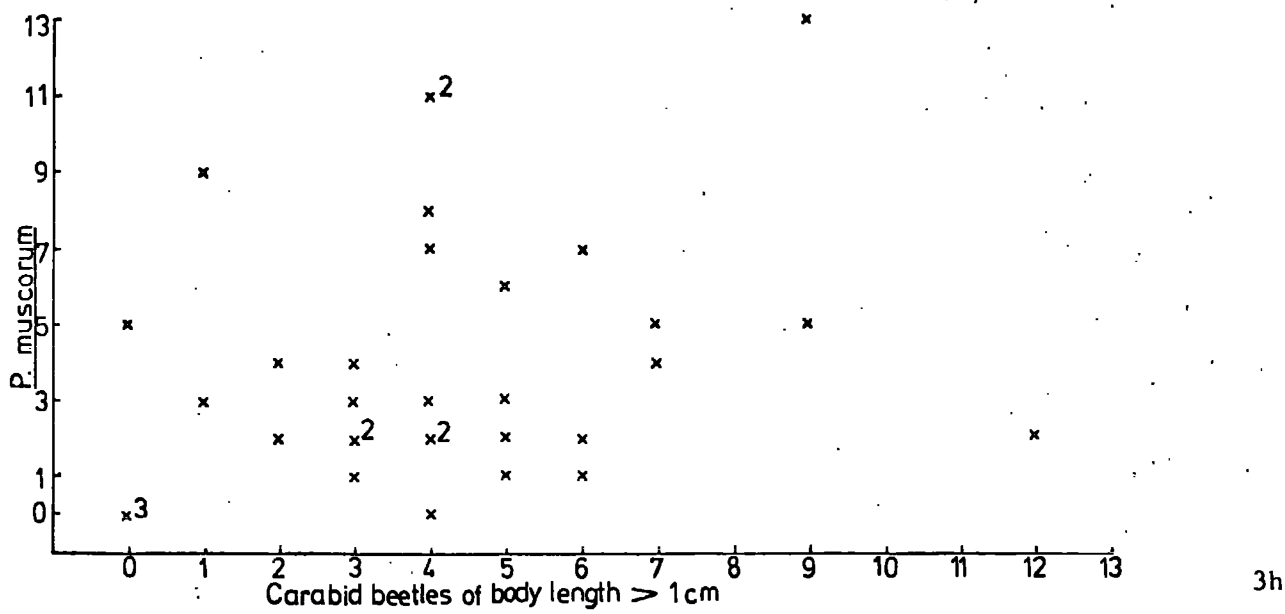
There is no clear relation between numbers of T. pusillus and numbers of carabid beetles (diagram 3d) and numbers of shrews (diagram 3e) but some degree of correlation does emerge between T. pusillus and Glomeris marginata (diagram 3f).

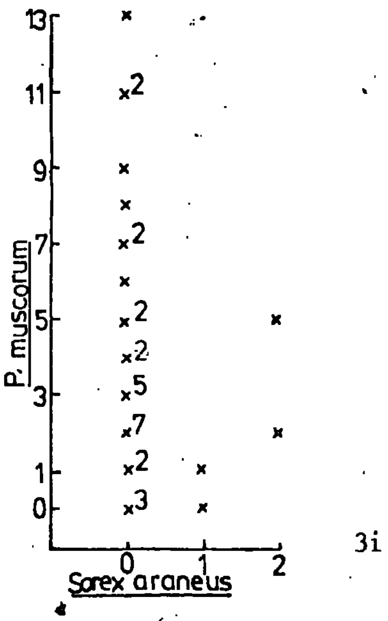
None of the plots of numbers of P. muscorum against numbers of other animals show a relationship between the two species (diagrams 3g–3j).

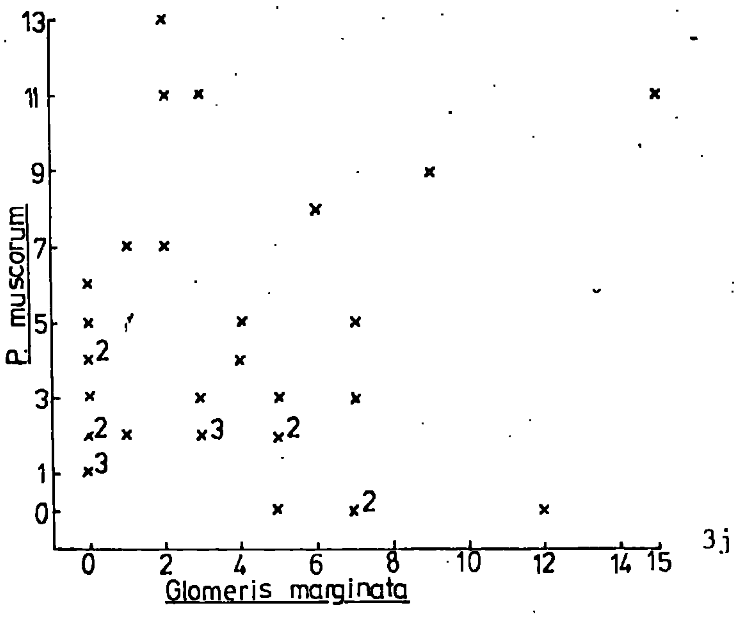


DIAGRAMS 3c to 3f. Scatter diagrams showing the relationship between the numbers of T. pusillus and four other types of animal collected in pitfall traps. Each plotted point represents one trap.

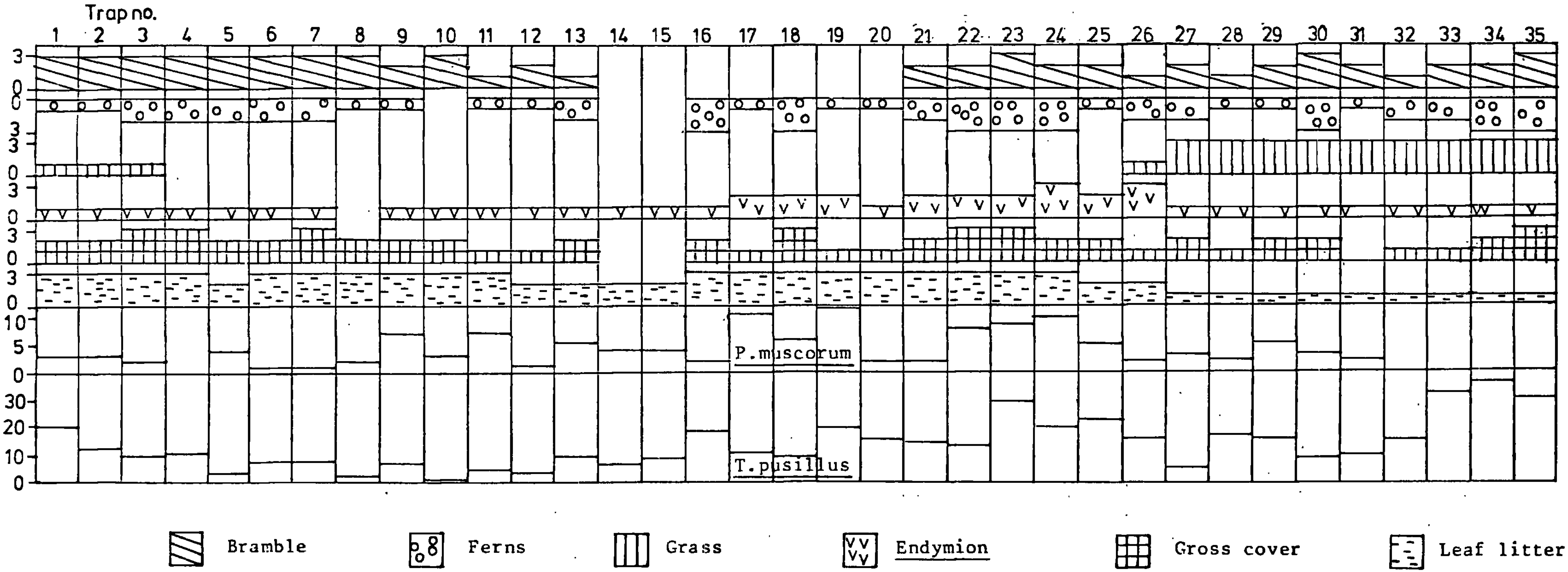








DIAGRAMS 3g-3j. Scatter diagrams showing the relationship between the numbers of P. muscorum and of four other types of animal collected in pitfall traps. Each plotted point represents one trap.



Vegetation: vertical scales represent score assessed at each pitfall trap (see section 2.4)

Woodlice: vertical scales represent number of animals collected in each pitfall trap

DIAGRAM 3k showing the structure of the vegetation around, and the number of woodlice collected in, each pitfall trap

3.3 Feeding Experiments

As there was difficulty in assessing the quantities of food eaten in the T. pusillus preference feeding experiment, the results are not analysed to the same extent as those of the experiments using P. muscorum. Diagram 3L summarises the quantity of each species consumed (taken as averages over the six replicates) over a 23-day period. Further results are not included as the condition of the food would have been altered by decomposition over a longer period of time, if it had not been already. In order to plot the diagram, the five stages of progressive consumption were equivalated to 5%, 25%, 50%, 75% and 95%.

It can be seen that the grass was consumed at a greater rate than the tree leaf species, of which sycamore was the preferred species, although only 40% had been consumed by the end of the experiment.

The results of the preference feeding experiments, using P. muscorum from the woodland site in the first six replicates and P. muscorum from the grassland site in the second six, are summarised in diagrams 3m and 3n. In addition, the amounts of each of the five species of leaf consumed during the experiments are summarised in diagrams 3o-3x. It can be seen from these diagrams that different average proportions of the different leaf species had been eaten by the end of the experiment. The situation is complicated by the fact that different quantities of each species were eaten in the different replicates. The average total quantities of grass and sycamore eaten in the first six replicates are both very high but the rate at which they were eaten differs. After one day, only an average of about 3% of the grass in each replicate was eaten, compared with an average of 55% of the sycamore. After two days, 18% of the grass was eaten and 77% of the sycamore. It can also be seen from diagrams 3o-3x that leaf species that were not, on average, totally consumed were in fact eaten much more readily in some replicates than in others. For example, the beech in the second experiement (diagram 3r) is totally consumed in four days in replicate 5 and yet is barely eaten in replicate 3. The amount of beech in this former replicate eaten after two days, exceeds the average quantity eaten after the same period of oak, the species that appears to be favoured in diagram 3n.

The results of the quantitative feeding experiments are listed in table 3q.

When an animal was found dead in a container, it was considered for simplicity not to have eaten at all during the previous day and the number of feeding days reduced by one.

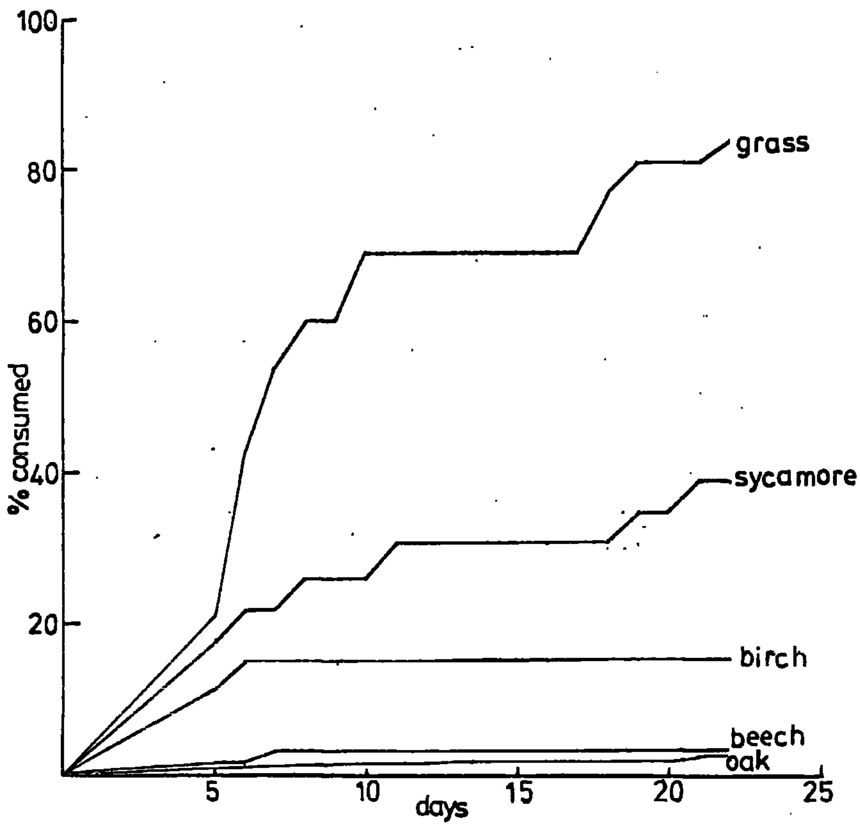
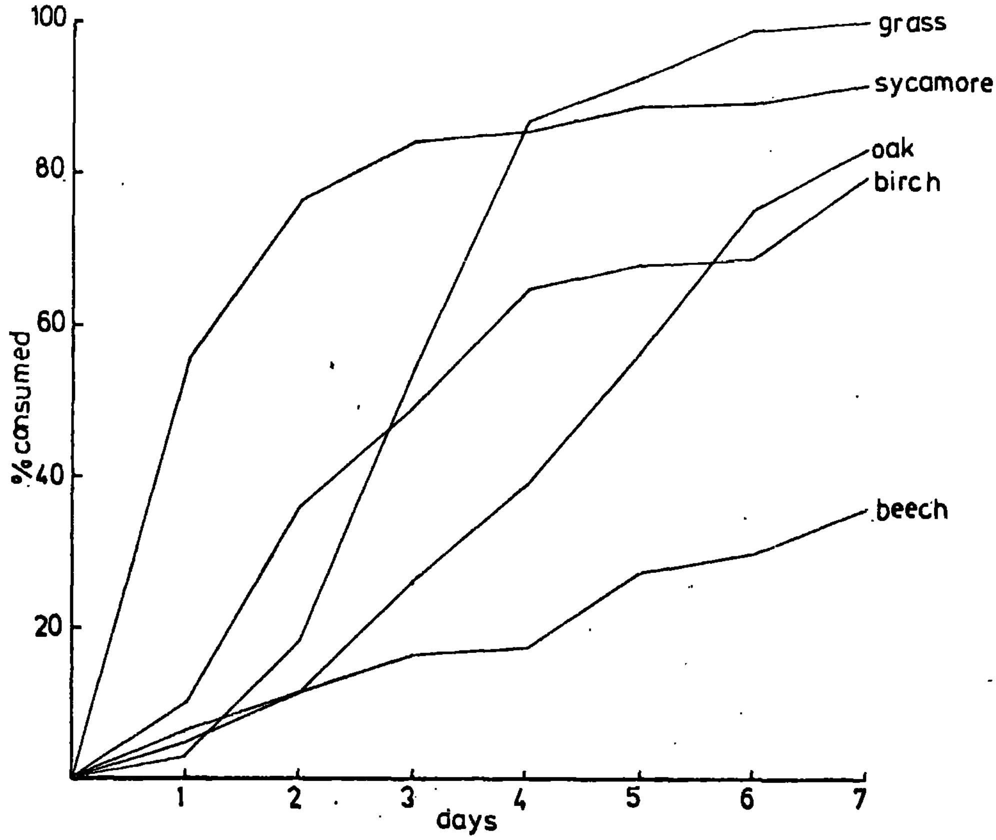
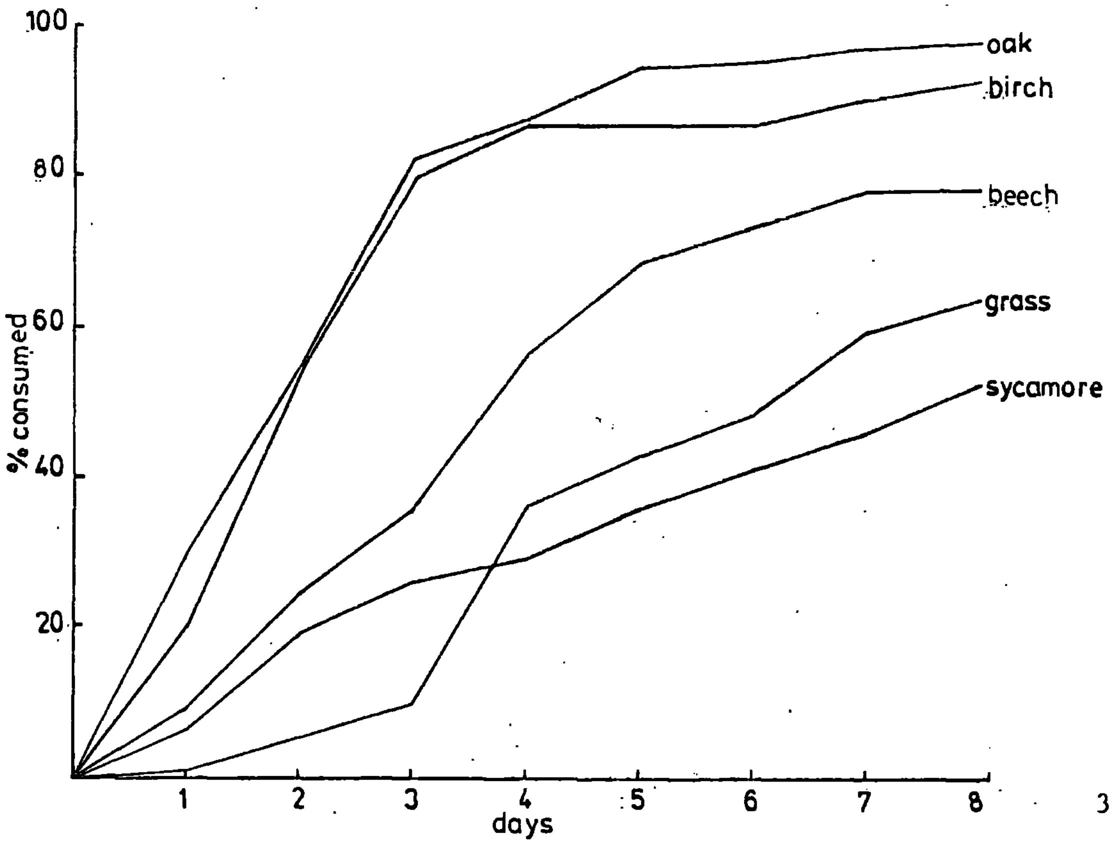


DIAGRAM 3L. Graph showing the average daily accumulative total percentages eaten by five T. pusillus of segments of five different leaf species over a period of 23 days. The averages are calculated from 6 replicates.

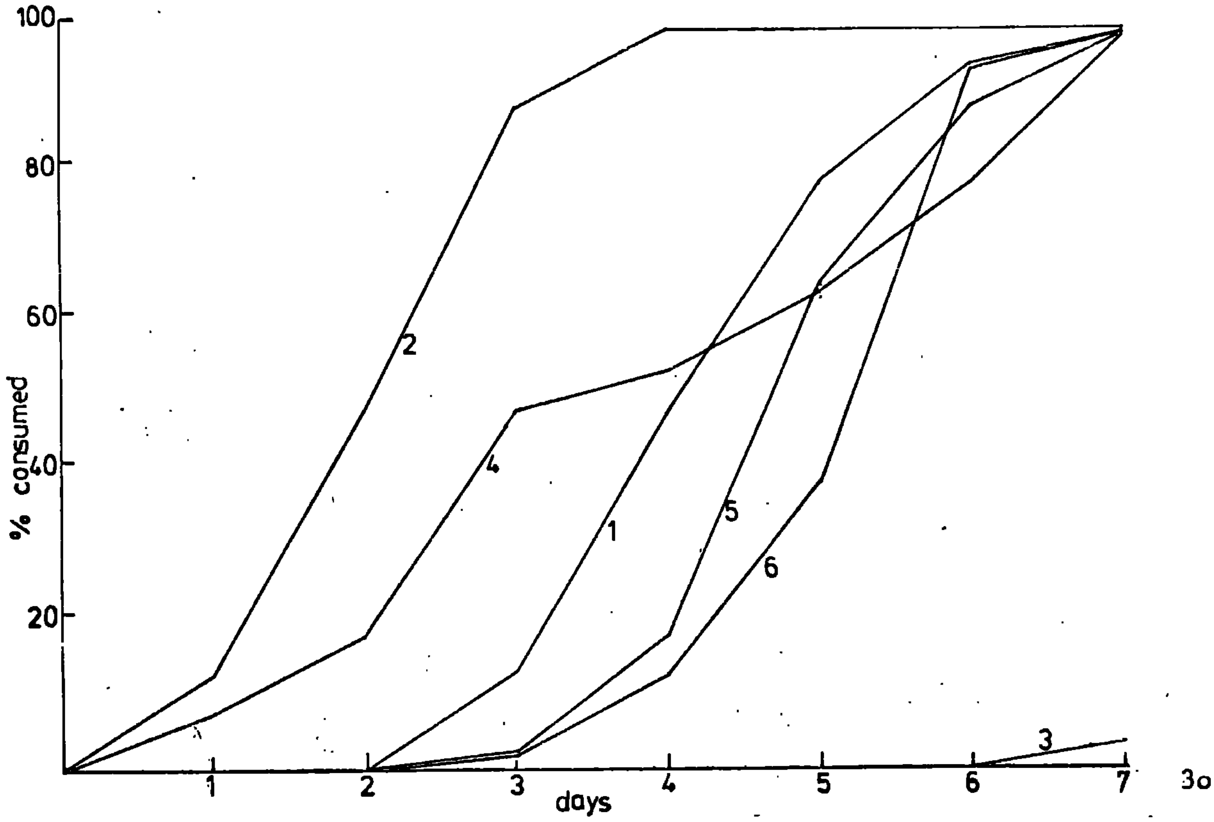


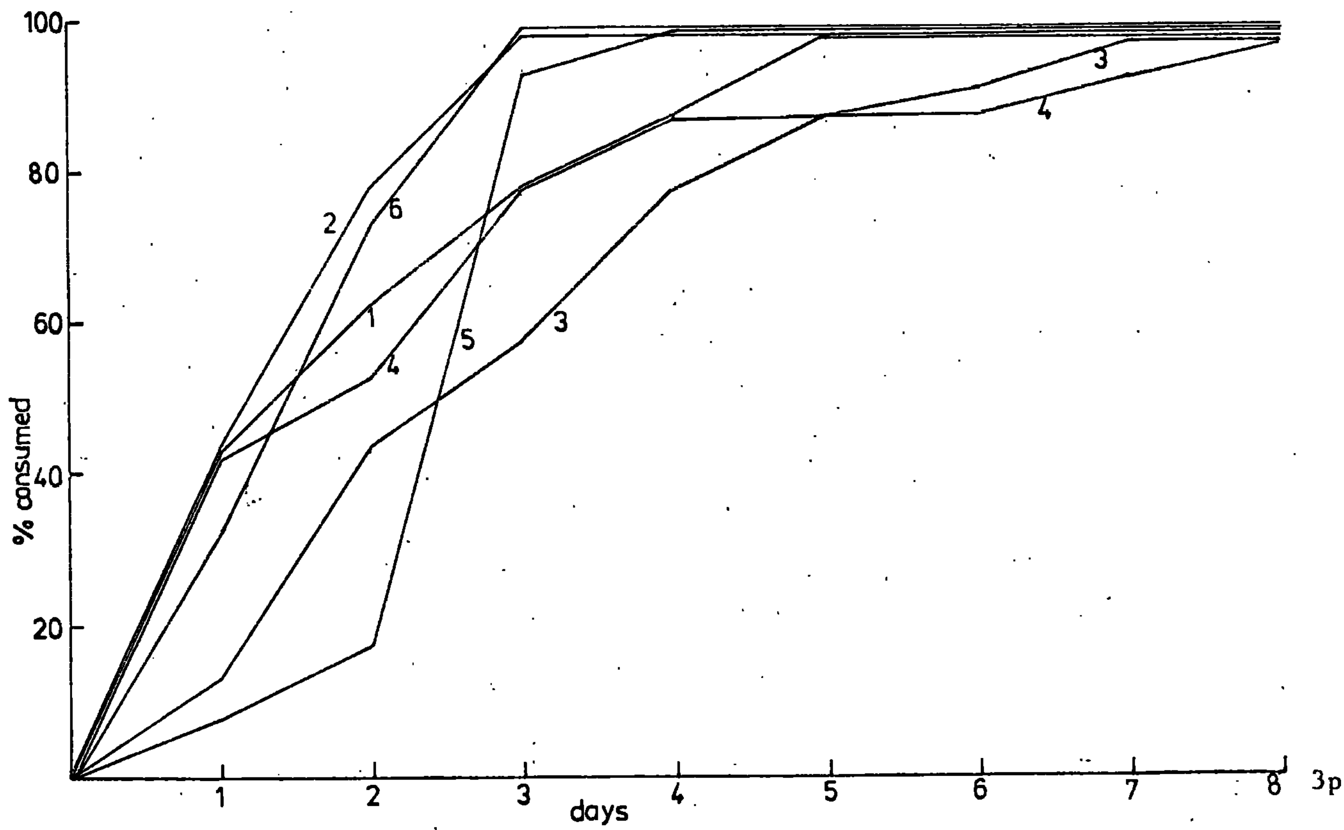
3m



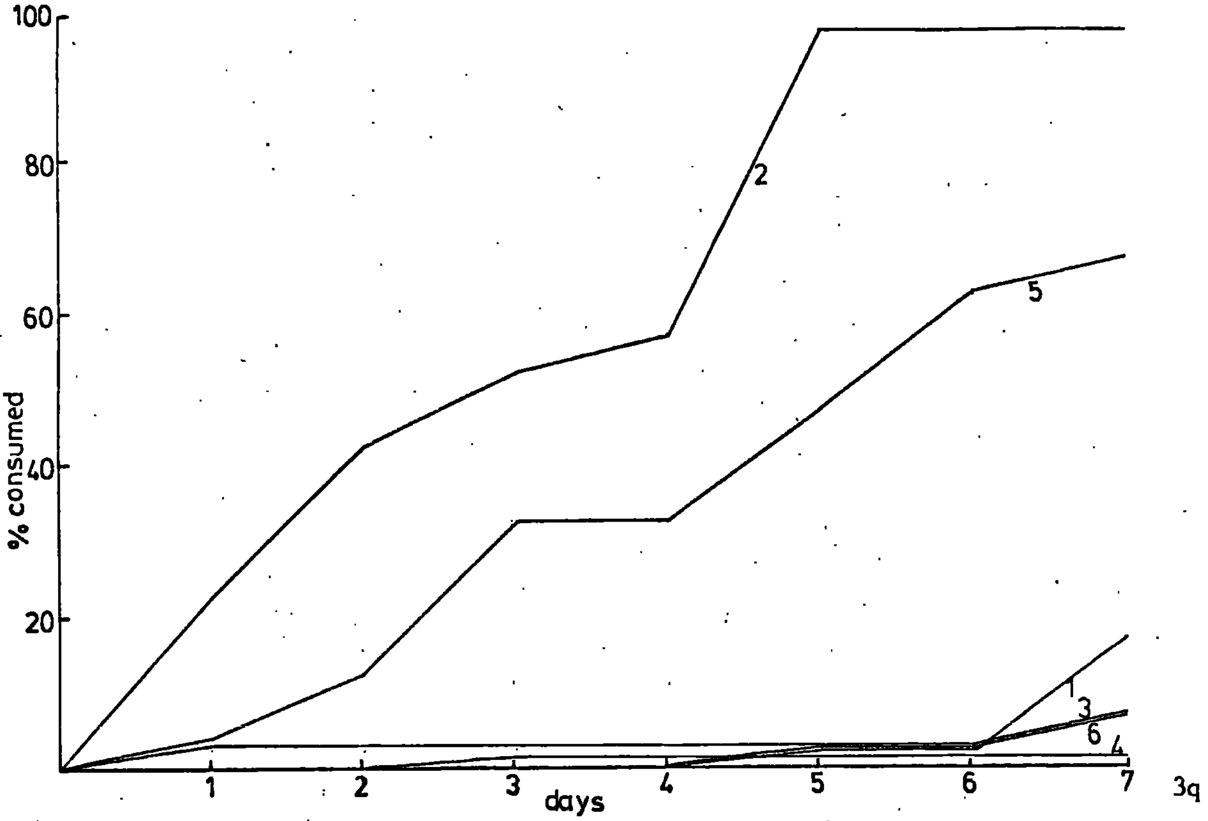
3n

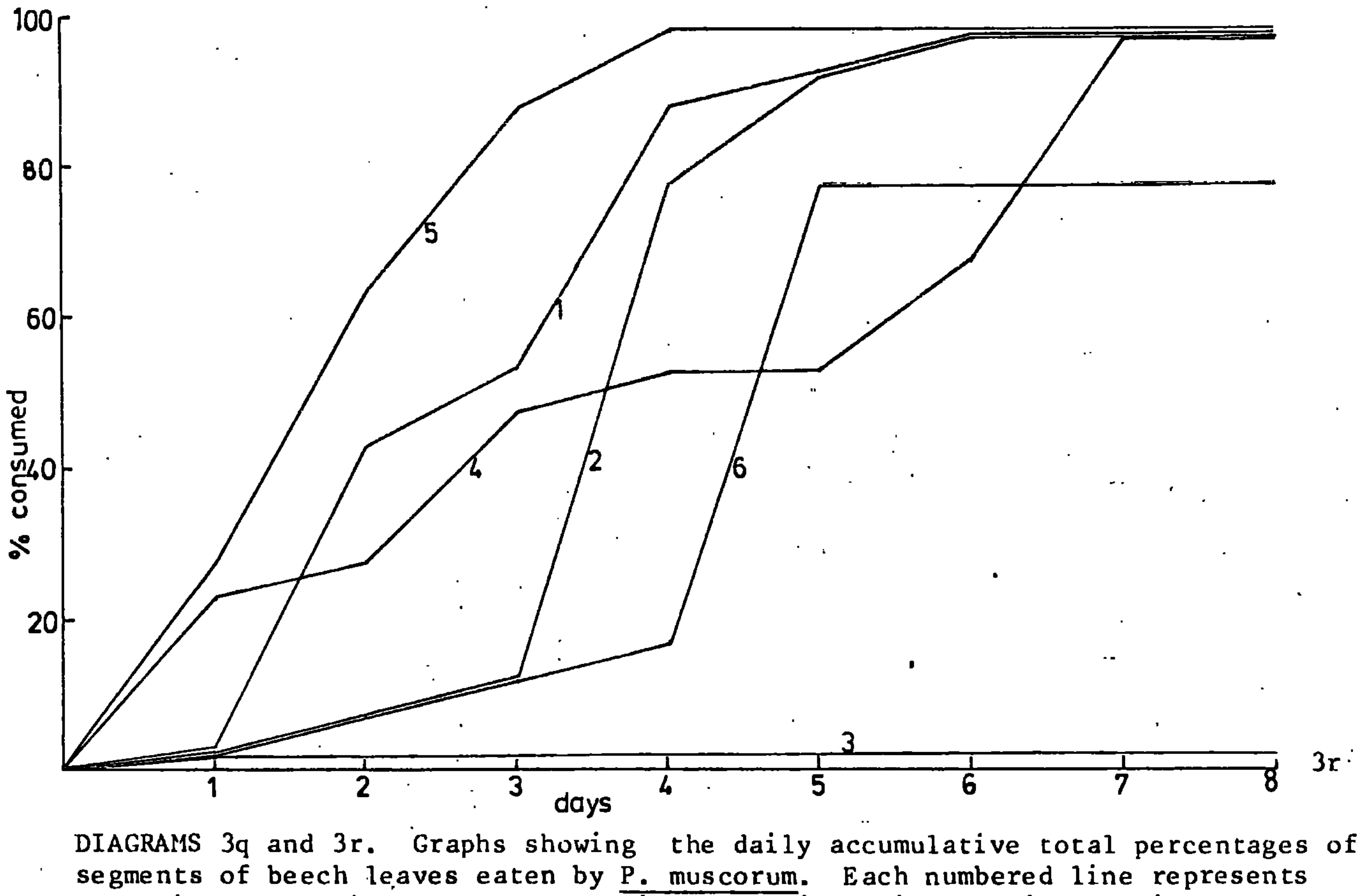
DIAGRAMS 3m and 3n. Graphs showing the daily, accumulative, total percentages (averaged over 6 replicate experiments) eaten by P. muscorum of segments of 5 species of leaf. 3m depicts experiments using P. muscorum collected from the woodland and 3n specimens from grassland.



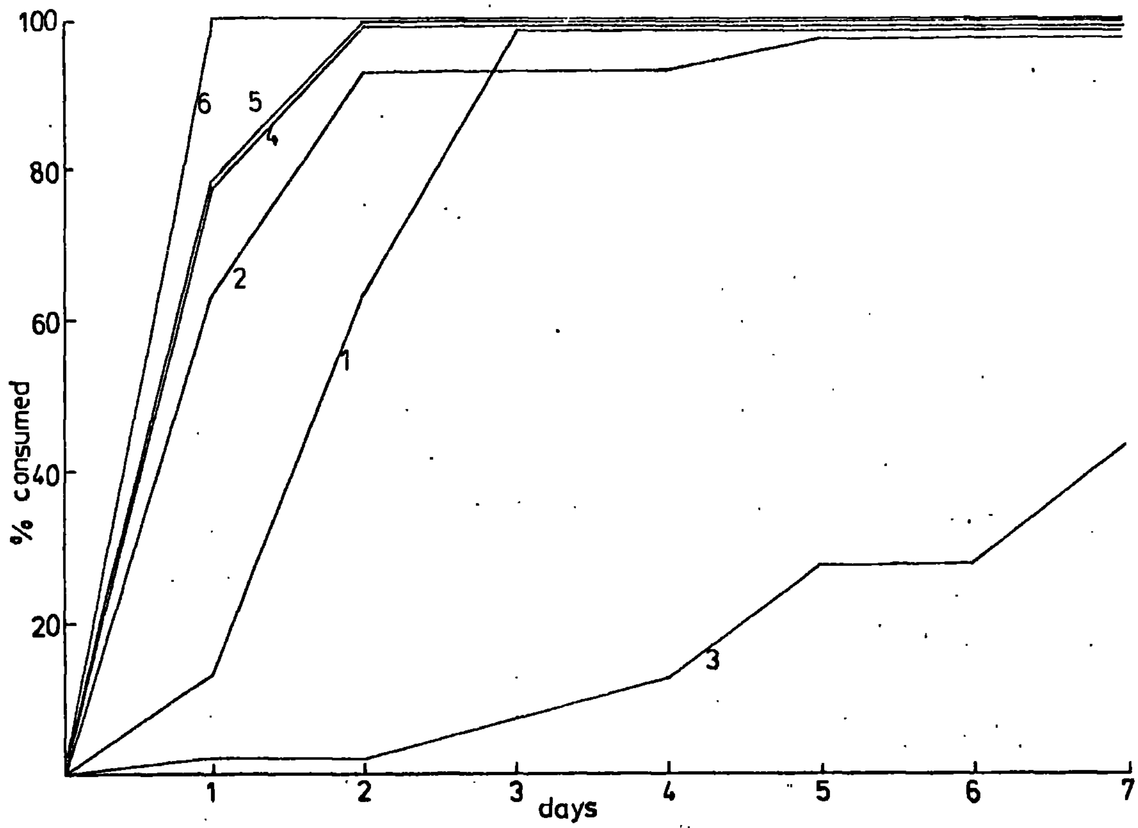


DIAGRAMS 3o and 3p. Graphs showing the daily accumulative total percentages of segments of oak leaves eaten by P. muscorum. Each numbered line represent a replicate experiment, those in graph 3o using specimens collected from woodland and those in 3p specimens from grassland.

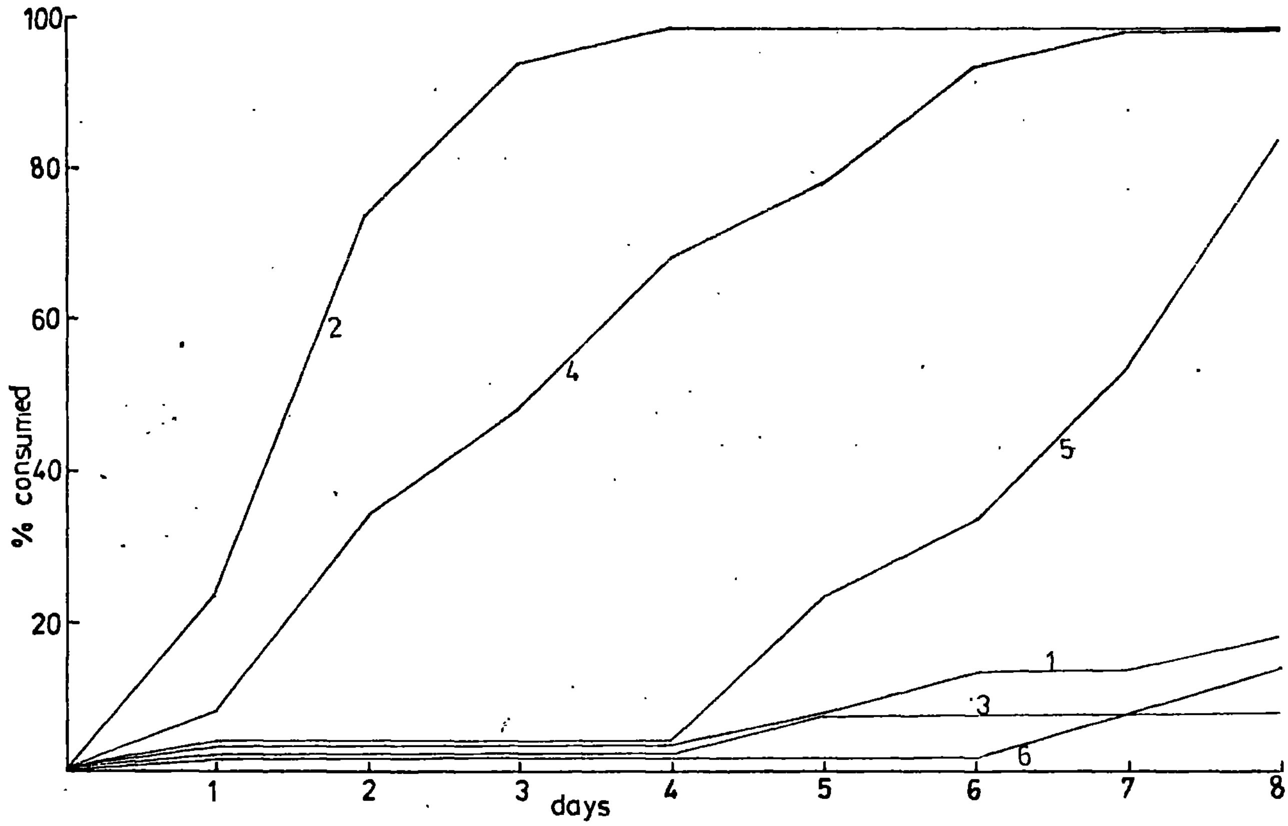




DIAGRAMS 3q and 3r. Graphs showing the daily accumulative total percentages of segments of beech leaves eaten by P. muscorum. Each numbered line represents a replicate experiment, those experiments depicted in 3q using specimens collected from woodland and those in 3p specimens from grassland.

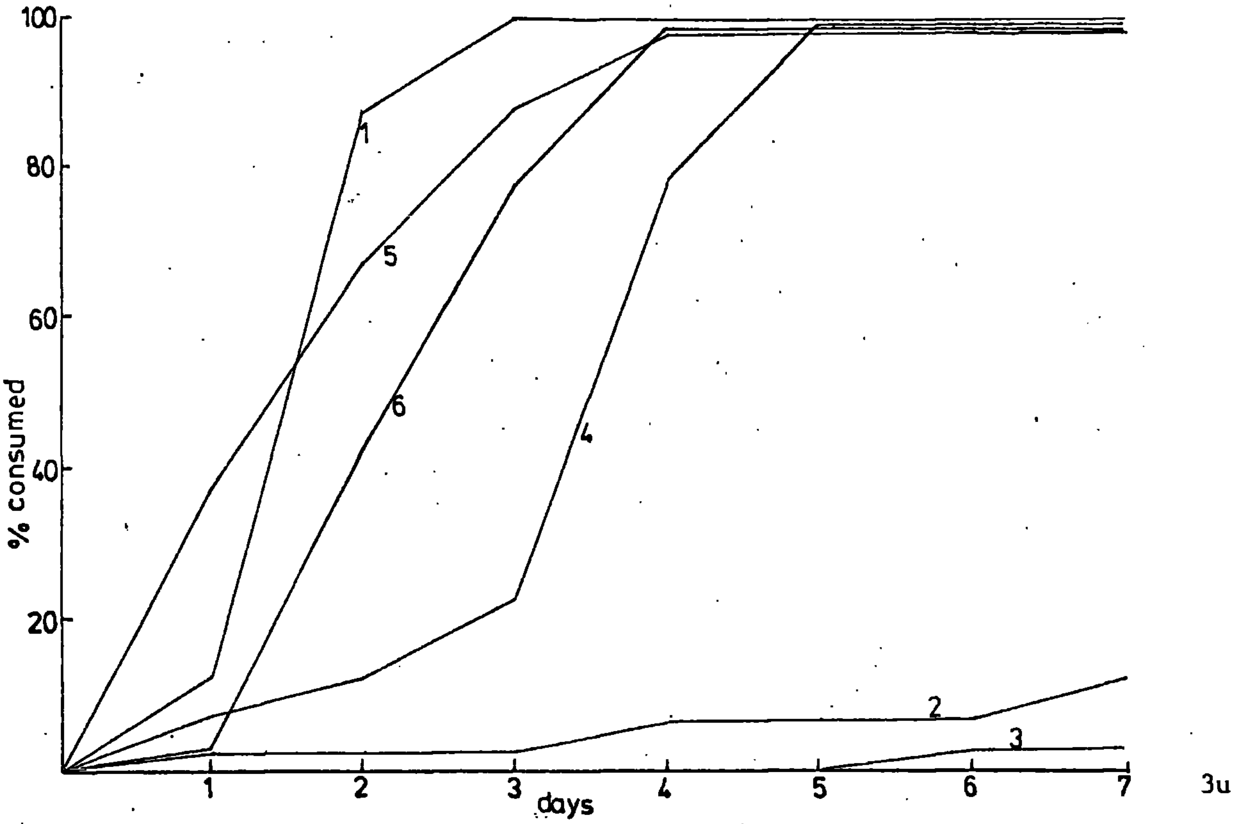


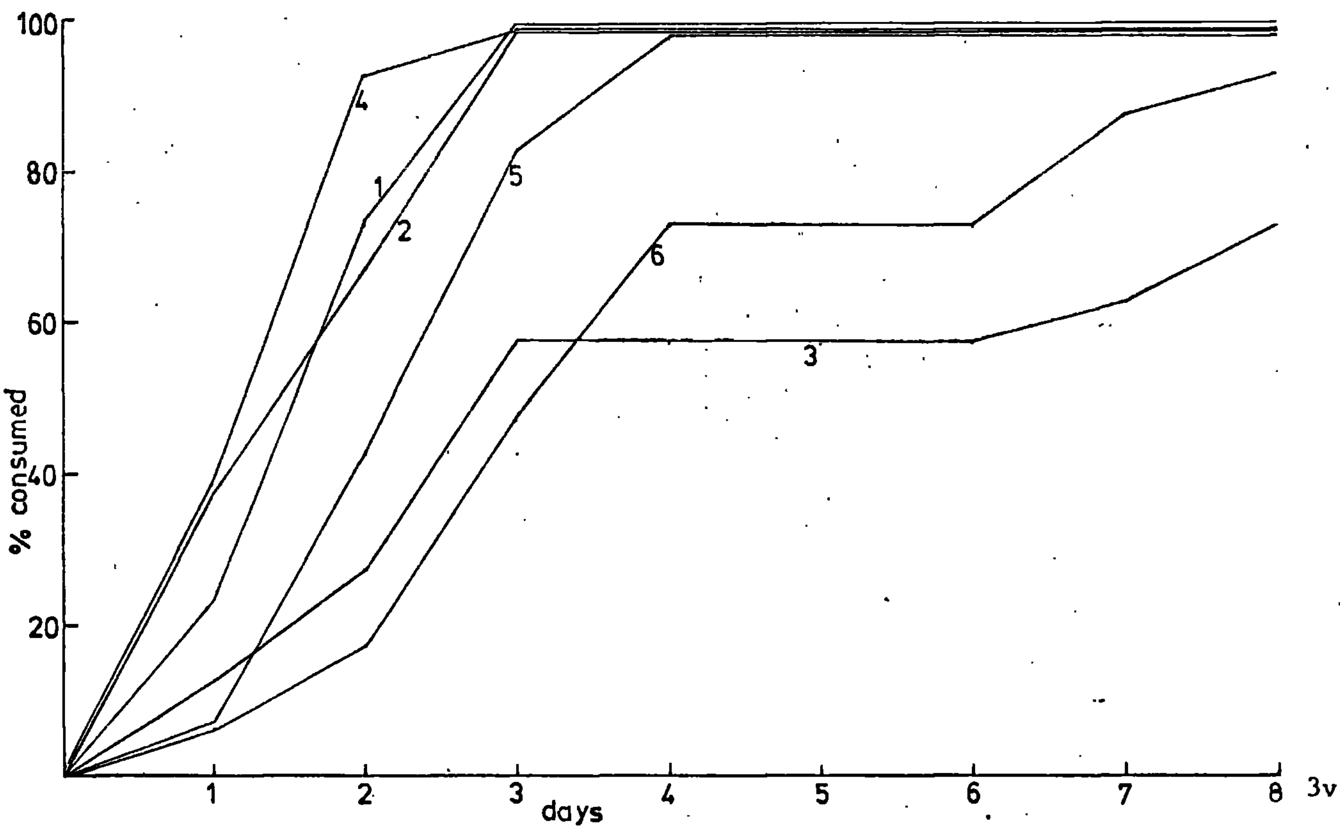
3s



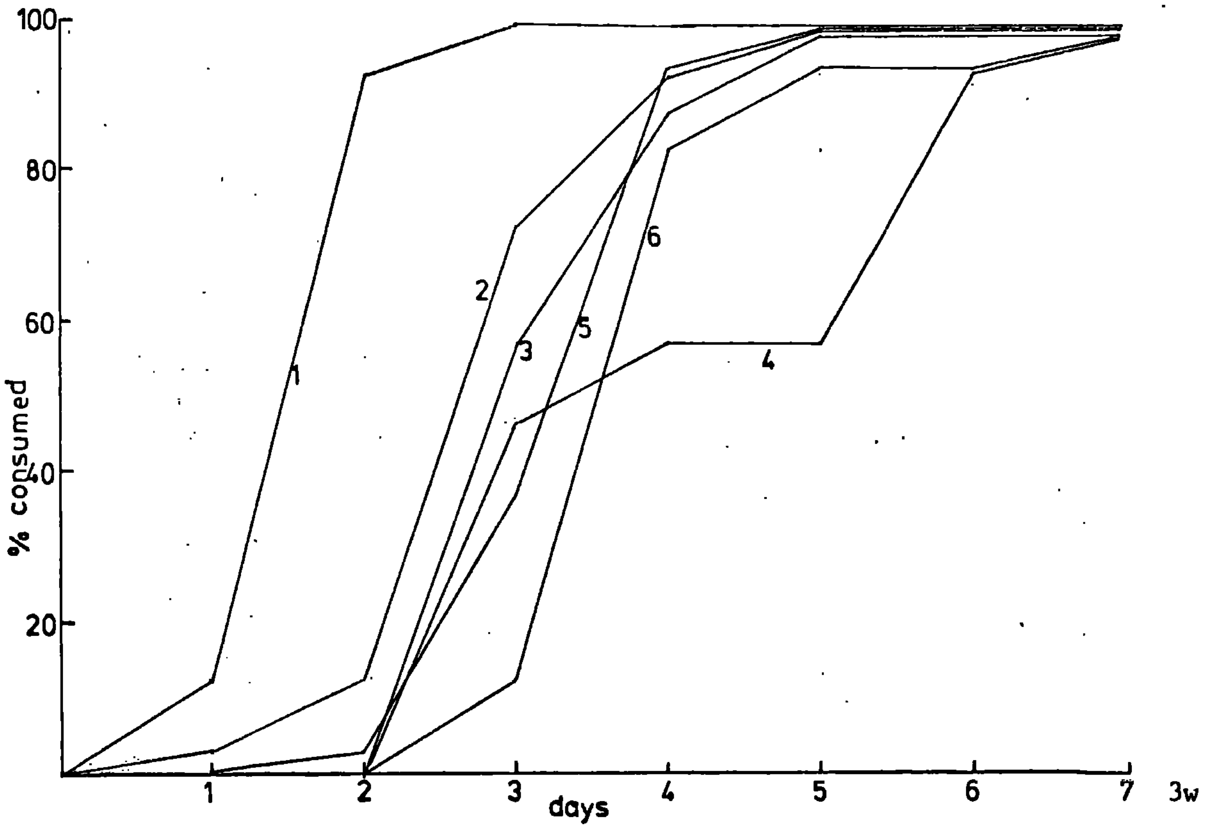
3t

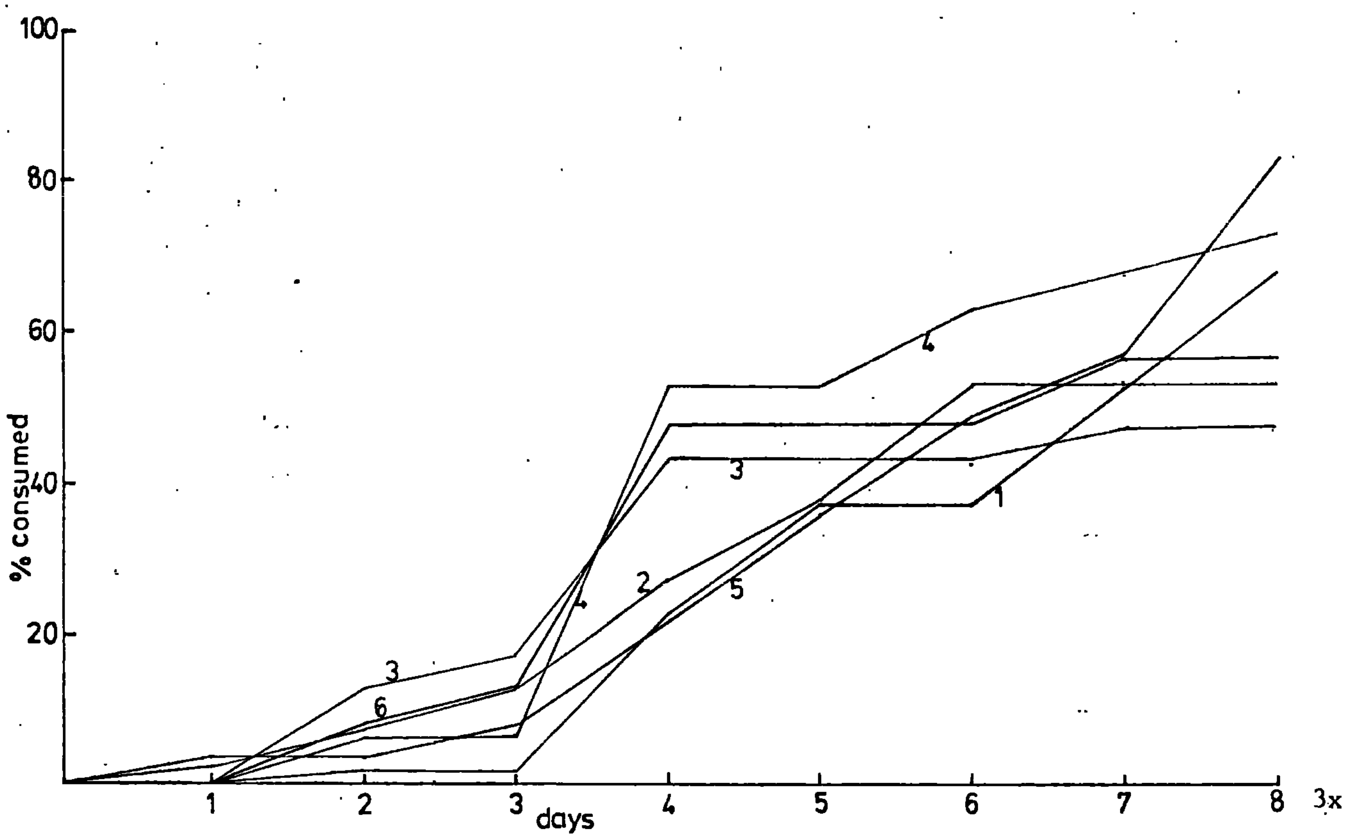
DIAGRAMS 3s and 3t. Graphs showing the daily accumulative total percentages of segments of sycamore leaves eaten by P. muscorum. Each numbered line represents a replicate experiment, those in 3s using specimens collected from woodland and those depicted in 3t specimens from grassland.





DIAGRAMS 3u and 3v. Graphs showing the daily accumulative total percentages of segments of birch leaves eaten by P. muscorum. Each numbered line respresents a replicate experiment, those experiments depicted in graph 3u using specimens from woodland and those in 3v specimens from grassland.





DIAGRAMS 3w and 3x. Graphs showing the daily accumulative total percentages of segements of grass leaves eaten by P. muscorum. Each numbered line represents a replicate experiment, those depicted in graph 3w using specimens collected from woodland and those in 3x specimens from grassland

	Dry weight (m.g.) of segments at beginning of expt.	Dry weight (m.g.) of segments at end of expt.	% eaten	duration of expt. (days)	no. of feeding days (see script)	no. died
<u>Holcus mollis</u>	7.7	3.2	58	17	81	4
<u>Holcus lanata</u>	14.1	4.5	68	17	82	3
<u>Dactylis glomerata</u>	24.7	17.6	29	17	83	2
<u>Arrhenatherum elatius</u>	31.1	24.2	22	17	83	2
<u>Phleum pratense</u>	25.6	12.5	50	17	81	4
<u>Acer pseudoplatanus</u>	56.6	33.0	41	18	83	7
<u>Betula</u>	39.6	15.4	61	18	87	3
<u>Fagus</u>	50.2	37.8	24	18	84	6
<u>Quercus</u>	45.4	12.3	73	18	86	4

TABLE 3q.

Results of quantitative feeding experiment. For details see section 3.3.

3.4 Developmental Studies

The head-width measurements of the P. muscorum from the samples are arranged in diagrams 3y and 3z, each column representing a size class. Peaks in the histogram represent different stadia.

The stadia of each of the woodland and grassland animals were separated into those with head widths of 5.5 micrometer units and bigger, and those smaller than this measurement. A χ^2 test was used to test the Null Hypothesis that any difference in the relative proportion of animals from each site, in the above size classes, was due to chance. A contingency table (table 3r) was constructed and the expected (e) values calculated from the marginal totals of observed (o).

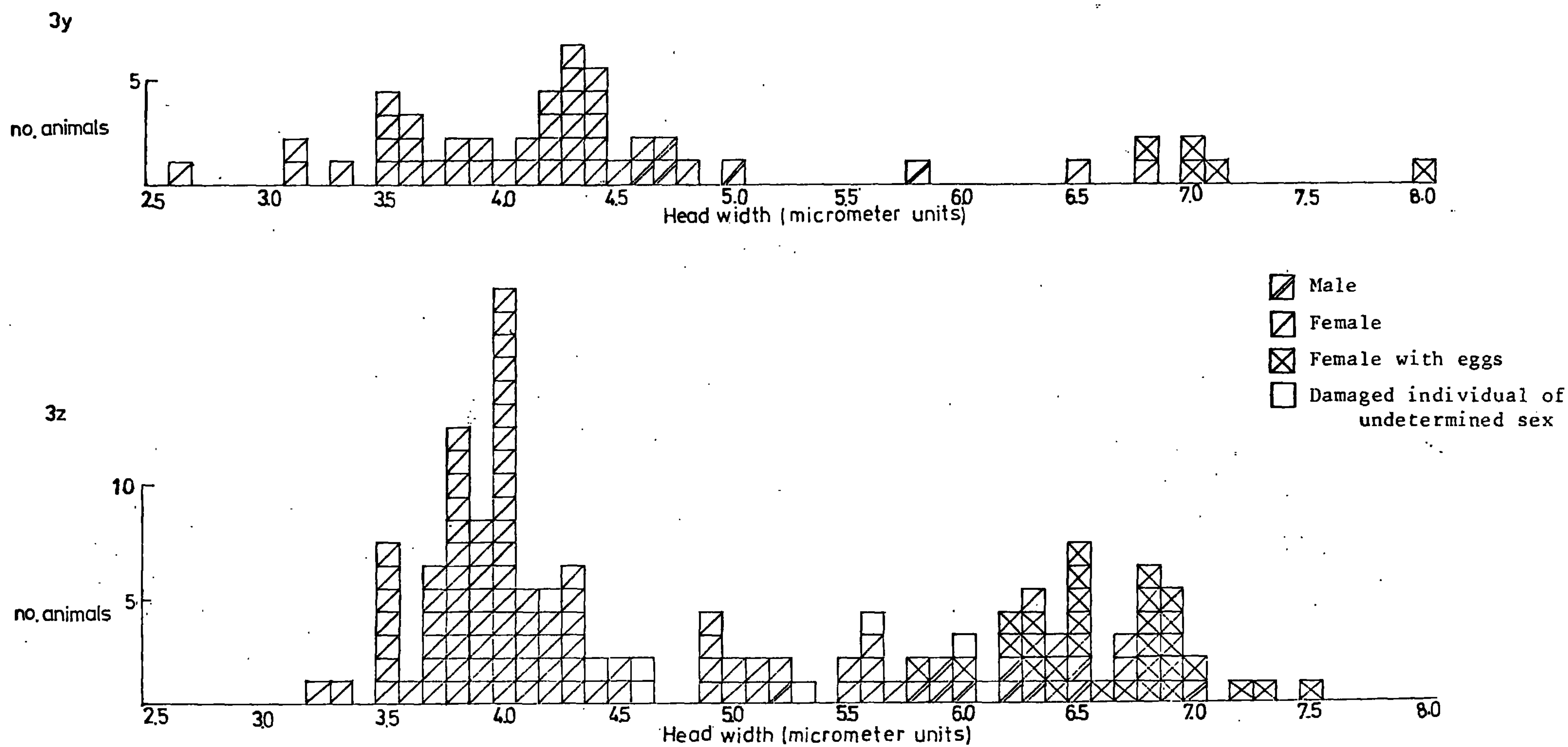
TABLE 3r	Woodland	Grassland	Total observed
Smaller than 5.5 micrometer units:			
observed	40	87	127
expected	32.254	94.746	
5.5 micrometer units and larger:			
observed	8	54	62
expected	15.746	46.254	
TOTAL (observed)	48	141	189

$$\chi^2 = \Sigma \frac{(O-E)^2}{E} = 7.60 \text{ with one degree of freedom}$$

The value of P is less than 0.01 and the difference in the size class structure of the populations is highly significantly greater than would be expected to occur by chance.

The head width was also taken as a measure of the size of individuals to assess the relative development of young P. muscorum in the culture experiment. The means and standard error of each group of animals are very similar but survival was greater in the woodland culture.

	Survival out of 40	Mean head width	Standard error of mean
Woodland	28	8.07	.104
Grassland	21	8.09	.133



DIAGRAMS 3y and 3z. Histograms showing size-distribution of samples of P. muscorum from woodland (3y) and grassland (3z), using the head width as a measure of size. In both diagrams 10 micrometer units = 2.4mm.

A χ^2 test was used to test the Null Hypothesis that any difference in the relative proportion of animals surviving in each group was due to chance. A contingency table was used, in the manner described for the previous test, to calculate the expected values from the marginal totals of the observed values.

The resulting χ^2 value of 2.58 has (with one degree of freedom) a P value of between 0.95 and 0.05 and the Null Hypothesis is maintained.

A tetest was applied to test the Null Hypothesis that the difference between the two mean values of head widths is due to chance.

$$t = \frac{\bar{x}_1 - \bar{x}_2}{S\sqrt{\{(1/n_1+1/n_2)\}}} = .103980 \text{ with 47 degrees of freedom}$$

where $\bar{x}_1$ = mean for first (woodland) group, $\bar{x}_2$ = mean for second (grassland) group, S = standard deviation (taken over all individuals) and n_1 and n_2 are number of first and second group of samples respectively.

The value of P is greater than .10 and the Null Hypothesis is maintained.

CHAPTER 4

DISCUSSION

4.1 Sampling Programme

a) Woodland site

The distribution of T. pusillus, deduced from the last thirty samples, possesses a high degree of contagion. The index of dispersion falls in value from 51.54 to 30.12 when only the samples from the litter and bramble areas are considered, but it would be uncautious to suggest there is a more contagious dispersion in the grass habitat on the evidence of only two peaks in numbers in the latter.

The stepwise regression programme produced no significant result at step 1 but at step 2 the dry weight of tree leaf litter is significant at the 95% level (with a positive coefficient), where there is an interaction with the dry weight of wood. The two variables together have an R^2 value of .1500 (i.e. they account for 15% of the variation in numbers of T. pusillus). It is interesting that the coefficient of the dry weight of wood is negative (although the calculation is not significant at the 95% level), as the dry weight of tree leaf litter and dry weight of wood are significantly positively correlated (table 3n). As a result of this correlation, the two variables are, to a small extent, accounting for the same variation in numbers of T. pusillus, although overall the effect of the dry weight of wood on the numbers of animals is negative. It appears, therefore, that the dry weight of tree leaf litter is of some importance in affecting the distribution of T. pusillus and that the wood has no direct significant effect but tends to occur most where the quantity of leaf litter is greater.

When twenty samples from the litter and bramble areas are subjected to regression analysis, the (dry weight of) tree leaf litter enters the step 1 equation with a positive coefficient and at the 95% significance level. Shading enters the step 2 equation with a positive coefficient and 95% significance level and the coefficient and significance level of the tree leaf litter both increase from the step 1 values. The two variables together account for 39.5% of the variation in numbers of T. pusillus, an increase in R^2 from step 1 of .1834. From table 3o, it can be seen that the heaviest shading is due to the presence of bramble, and yet this latter is significantly negatively correlated with tree leaf litter. It would be expected that bramble stems would impede the movement of fallen leaves and cause them to settle. That there is in actuality less leaf litter accumulated under the bramble than in the bare litter areas means little without knowledge of the speed with which leaves decompose and are eaten in the two habitats. A cover of bramble may also impede the movement of air and thus maintain an enclosed humid atmosphere over the ground. Although the samples with highest water content (expressed as a percentage of total fresh weight - see the distribution in relation to y-axis in diagram 3b) are from the litter habitat, there may be a steeper and longer gradient of moisture through the depth of these samples, due to the drying effects of moving air and insolation at the surface, and to a greater depth of the underlying F and H layers. This last character was not measured directly, but is likely related to the whole weight of the samples (see distribution of points in relation to the x-axis in diagrams 3a and 3b). Drier conditions in the surface layers in the bare litter habitat would limit the activity of the animals and the palatability of the tree leaf litter, effectively reducing the useful proportion of the litter. On balance, the shading provided by bramble increased the R^2 to an extent that more than compensated for the lesser quantities of tree leaf litter. Whatever the differences between the bare litter and bramble habitats, the mean numbers of animals per sample are remarkably similar, being 64.2±S.E.13.6 and 59.9±S.E.13.9 respectively.

The whole argument concerning the interaction between the weight of the tree leaf litter and shading is conjectural beyond the statement that these two variables account for more variation in the numbers of <u>T. pusillus</u> per sample than the other variables considered.

From the low R^2 values obtained, it is evident that no explanation of the cause(s) of aggregation can be formulated. Reasons for this may include the neglect of variables that affect T. pusillus, the method by which those variables included in the study were recorded, the low sample number, the unit area of the samples and the method of analysis. Considering the size of the animal,iit is possible that a smaller unit sample area and a larger number of samples would be necessary to determine the dispersion in any detail. In such a study, the details of the environment such as the nature of individual leaves or small pockets of high humidity may assume importance.

The distribution of P. muscorum in the second woodland site is mainly restricted to the bare litter and bramble habitats, as only two individuals were collected from the grass habitat. The χ^2 test of dispersion for the twenty samples from the bare litter and bramble habitats results in a χ^2 of 39.93, the P (probability) value of which lies between .01 and .001 and the index of dispersion is 2.1. The distribution therefore shows a degree of contagion less than that found in the distribution of T. pusillus.

In the stepwise regression on the thirty woodland samples, the predominance of grass (i.e. the quality by which the grass habitat samples were defined) entered the step 1 equation, with a negative coefficient, at the 99% significance level, as would be expected due to the virtual absence of P. muscorum in the grass habitat. When this variable was deleted in the following run, the dry weight of grass entered the step 1 equation at the same high significance level and produced an almost identical R^2. The above two variables are both significantly negatively correlated with both dry weight of tree leaf litter and depth of litter and thus the former variables are accounting in part of the same variation in the numbers of P. muscorum as the latter variables. When the variables grass habitat and dry weight of grass are both deleted from the equation, the dry weight of tree leaf litter enters the step 1 equation (at the 99% significance level, with an R^2 of.24) and bracken enters at step 2 at the 95% significance level, increasing the R^2 value to .37. Both variables have a positive coefficient and some of the variation accounted for must correspond to that accounted for by the grass variables.

The importance of the tree leaf litter to a litter dweller is manifest and need not be discussed at length here, but the importance of dry weight of bracken to P. muscorum is harder to understand. No significant negative correlation exists between bracken and habitat grass or dry weight of grass (table 3n), so it is unlikely that a spurious regression has been generated by deleting the two latter variables. Neither is bracken significantly correlated to any variable except the score of oak. There is therefore nothing to indicate whether bracken, as a component of the litter, is directly affecting the distribution of P. muscorum or whether they are linked through a second variable.

In the stepwise regression on the twenty samples from the bare litter and bramble habitats, the dry weight of F & H layers enters the step 1 equation with a negative coefficient and below the 95% significance level. When the adjusted values of water contents of the samples are used in the analysis, they enter the step 2 equation with a positive coefficient and below the

95% significance level, increasing the significance of the dry weight of F and H layers to the 95% level and the amount of variation accounted for to 29%. This is despite a significant (at 95% level) positive correlation (table 3o) between the two variables. By comparing the two scatter diagrams 3a and 3b, it can be seen that a complex relationship exists between the whole sample dry weight and sample water contents and the former can be taken as being nearly equivalent to weight of F and H layers (table 3o). The date at which the first half of the samples were taken followed a period of fairly low rainfall (see table 4a) which continued past the dates when the second half were taken, over two weeks later (none of the July rain having fallen by then). The driest samples were accordingly amongst the second batches taken, but altering the values of the second batches so that the means equal those of the first batches, in order to negate the effect of the dry weather, results in breaking a nearly straight-line spread of points for bramble (diagrams 3a and 3b). The unadjusted spread of bramble points probably reflects the truer relationship between dry weight and water content of samples, the cover having prevented much evaporation of water from the litter surface. No clear relationship exists between the dry weight and water content of the bare litter habitat samples, whether or not adjusted values of water content are used, and the cloud of points is basically separate from those representing the bramble samples, the latter being drier and lighter. The combining of the bare litter and bramble habitat data is masking the relation between water content and whole weight in the bramble habitat samples, and the role of the adjusted water content of samples in the stepwise regression must be suspect, if not useless.

When the original values of water content of samples are used in the regression analysis, the dry weight of tree leaves enters the step 2 equation (at below 95% significance) increasing the R^2 from .0939 to .2894 (and the water content of samples has a very low F to enter value). Thus, as determined by the methods of this study, the dry weight of the F and H layers and the dry weight of tree leaf litter account for 29% of the variation in numbers of P. muscorum in the part of the study area in which it is distributed, but there are insufficient samples to fully understand the relation between dry weight of F and H layers and the water content of the sample. As with T. pusillus, the mean number of animals per sample in the bare litter and bramble habitats are very similar, being 3.0±S.E..87 and 2.8±S.E..73 P. muscorum respectively.

	Monthly mean temperature °C	Total monthly rainfall mm.
Average 1916-1950:		
April	7.4	43.2
May	10.1	51.3
June	13.2	45.7
July	15.3	70.9
1975		
April	7.7	76.5
May	7.9	49.6
June	13.1	24.8
July	15.9	61.5

TABLE 4a. Details of rainfall and temperature recorded in Durham

The distribution of T. pusillus and P. muscorum in the grassland site is basically restricted to the unmown area, as there were no T. pusillus and only one P. muscorum collected from the last ten samples from the mown area in early July, and only one and three individuals of these species respectively during the earlier sampling at the beginning of May, before mowing in the current year. Little extra understanding of the factors accounting for the distribution of the two species was gain from the stepwise analysis by including the mown area samples, but it would be bad practise to decide a priori that any particular variable was the 'obvious' cause of the absence of woodlice from these samples. Without the analysis of variation within the unmown habitat, one may have considered the "mown/unmown area" variable to account for most variation in the numbers of woodlice; (this was not the case).

The distribution of T. pusillus in the last twenty samples from the unmown area shows a high degree of contagion, the index of dispersion being 5,38 and the χ^2 value, from the test of dispersion over 102 (with a P value of <.001). This is not due to the woodlice occuring in only the tussock or gap samples as the mean number of animals in the tussock and gap samples is 7.5±S.E.1.87 and 6.3±S.E. 1.88 respectively and the index of dispersion 5.73 for the tussock and 5.50 for the gap. The distributions in the two types of sample are remarkably similar in view of the significantly greater quantities of leaf litter in the gap samples and of grass in the tussock samples (see tables 3j and 3k), and of the differences in the physical environment that must exist.

From the results of the stepwise regression analysis on thirty samples, it is evident that the dry weight of tree leaves accounts for 38% of the variation in numbers of T. pusillus (step 1) and the dry weight of grass another 17% (step 2). Both coefficients are positive and both F values equivalent to 99% significance. The mown/unmown variable (step 3) contributes little more to the R^2 but reduces the significance level of the dry weight of grass. The differences of dry weight of tree leaf litter and particularly of dry weight of grass are therefore a nearly complete description of the differences between the mown and unmown areas (in terms of the variables included in the analysis) that account for variation in the numbers of T. pusillus. (The dry weights of grass and of tree leaves do not, however, fully describe the contribution of grass and tree leaf litter to the habitat, without some indication of pattern, species, seasonality and condition.) When only the twenty samples from the unmown area are included in the regression analysis, the dry weight of leaf litter enters step 1, with a positive coefficient, at the 95% significance level and produces an R^2 of .2209.

The weight of grass enters at step 2 with a fairly high but not significant F value and a positive coefficient and the F value of the dry weight of tree leaf litter improves as there is some degree of negative correlation (though not significant at the 95% level - see table3p) between these two variables. There is an increase in R^2 of .1597, so that 38% of the variation in numbers of T. pusillus is thus accounted for. When the variable "tussock/gap" enters the step 3 equation, the F value of the dry weight of grass is greatly reduced but the F value of the dry weight of tree leaf litter to a far lesser extent. The larger interaction between the tussock/gap variable and the dry weight of grass indicates that the variation in numbers of T. pusillus accounted for by the latter was partly a variation between numbers in tussock and gap samples. The dry weight of leaf litter, the F value of which is altered less by the entry of the tussock/gap variable into the equation at step 3, is mainly accounting for variation between individual samples, not between the types of sample.

The virtual absence of P. muscorum from the mown area at the grassland site restricts meaningful analysis of distribution to the twenty samples from the unmown area, as was the case with T. pusillus.

The χ^2 test of dispersion in the twenty samples from the unmown area results in a χ^2 value of over 272, with a P value of <.001, and the index of dispersion is 14.35. In contrast to the distribution of T. pusillus, P. muscorum is mainly restricted to the ten tussock samples, as there was only one animal in the gap samples. This does not account for all the contagion in the distribution as the χ^2 value from the test of dispersion on the ten tussock samples is 55.08 (with a P value of <.001) and an index of dispersion of 6.12.

In the stepwise analysis of the thirty grassland samples, the dry weight of grass enters the step 1 equation with a positive coefficient and at the 99% significance level, producing an R^2 of .6659. When the variable "unmown" enters the step 2 equation (with a negative coefficient and significance below the 95% level), the R^2 is only increased by .0339 and the F value of the dry weight of grass remains high (at the 99% significance level). Of the variables entered in the analysis, it is the dry weight of grass that is accounting for the most variation in the numbers of P. muscorum, and a fraction of this is the same as some of the small amount accounted for by the "mown/unmown area" variable.

When the twenty samples from the unmown area are analysed by stepwise regression, the dry weight of grass enters the step 1 equation with a positive coefficient and at the 99% significance level, the resulting R^2 being .6100. The "tussock/gap" variable enters the step 2 equation (with a positive coefficient and below the 95% significance level) only increasing the R^2 by 0.0259, and greatly reducing the F value of the dry weight of grass. The latter is therefore accounting for much of the same variation as that accounted for by the "tussock/gap" variable.

Thus, the dry weight of grass accounts for 61% of the variation in numbers of P. muscorum in the twenty samples from the unmown area of the grassland site and this variation includes most of that between the tussock and gap samples.

4.2 Pitfall trapping

It was noted in section 3.2 that the numbers of animals collected from the different pitfalls are affected by several factors. There is a source of error in the distribution of each species of animal due to the diversity of the vegetation and, in comparing the distribution of two species, the errors are compounded.

From examination of diagram 3k, which shows the variation in numbers of animals and in the nature of the vegetation and litter, it is seen that the numbers of T. pusillus collected from each jar is less in the area of the transect of jars 8-15, where total cover varied from 0 to 2 (for coding, see section 2.4) and litter between 2 and 3, than in the adjacent areas, where on one side (jars 2-7) cover was higher, varying from 2 to 3, and on the other side (jars 16-26) where there was patchy cover varying from 1 to 3 and a fairly continuous growth of Endymion non-scriptus. In both these adjacent areas, the amount of leaf litter tended to be higher than that around jars 8-15. This evidence, if it is to be trusted, supports that from the stepwise regression on twenty woodland samples (see section 4.1), where it was found that the amount of leaf litter and degree of shading accounted for some of the variation in numbers of T. pusillus, and adds the further point that the quantities of leaf litter in the bare litter (i.e. lacking aerial cover) habitat tend to be greater where there is some growth of Endymion non-scriptus. The area with a dense cover of bramble (jars 2-7) does not, in general, contain such large numbers of animals as the jars 16-26, although they do tend to increase in number into the bramble (i.e. towards jar 1).

The spread of number of T. pusillus from jars 27-34 indicates a more aggregated distribution than that in the other general areas of the transect described. There are, within the series of eight jars, three totals of 9 animals and lower, and two of 32 and higher, together with three intermediate numbers. This area generally corresponds to that from which the ten woodland "grass habitat" samples were taken and amongst which there were two high peaks in numbers of T. pusillus (section 4.1). The exclusion of these ten samples from calculations reduced the index of dispersion. The evidence from the pitfall data that T. pusillus exists in the grass area with a distribution more contagious than elsewhere is as sparse as that obtained from analysis of the ten samples and, additionally, more subject to error. Despite this, it is interesting that there is some agreement between the samples taken earlier and the pitfalls.

A conspicuous feature of the spread of numbers of P. muscorum in the transect (as seen in diagram 3k) is the total absence of animals in jars 32-34, which are situated in part of the transect area where grass predominates. There were, however, a collection of numbers of P. muscorum comparable with those in other areas of the transect, in the jars 27-31, which are also in the grassed area. Some of these animals may have ventured into the marginal grass areas from the adjacent area, where there was a greater quantity of litter, with interspersed Endymion, and greater cover, but the distances involved would be large: up to 5 metres. It is possible that the occurrence of P. muscorum in some of the jars in the grass area is, in part, due to the variation in the environment. The part of the grass area where P. muscorum were collected in the jars has a tendency to greater total cover but the differences, over the low number of jars being considered, are not large.

The average cover over an area may be of less importance to P. muscorum than the presence of discrete incidences of a high degree of cover, such as that of jar 30 where the bramble and ferns both achieve the highest score (although they are so disposed that the score of total cover is intermediate).

The highest peaks in the numbers of P. muscorum all occur in jars within the part of the transect (jars 16-26) characterised by deep litter (amongst which Endymion is common) and by a very patchy cover of bramble and ferns. (The importance of the dry weight of bracken in the litter, as a free variable in the analysis of the samples (section 4.1) is reflected in this instance by the living plants.) There are no major trends in the distribution between jars 2 and 15. This corresponds with the rather equal total numbers of P. muscorum collected from the ten litter and ten bramble habitat samples in the earlier work.

Taking into account the margin of error that must exist in the data, the only correlations worthy of note between woodlice and other animals are those between the numbers of T. pusillus and the numbers of Staphylinid beetles (of body length greater than 6mm) and of the pill millipede, Glomeris marginata, which have r values of .676 and .608 respectively (both values have a corresponding P value of $<.001$). It can be seen from diagrams 3c and 3f that there is nothing unusual about the scatter of points.

The correlation between T. pusillus and Staphylinids may indicate a real predator/prey relationship or merely that they occur in the same places, possibly those areas where other species of prey live. If the beetles are feeding to a large extent on litter-dwellers, then other prey species may have similar requirements to T. pusillus. Alternatively, the correlation may not reflect even similar distributions in T. pusillus and the Staphylinid beetles but that some jars trapped more animals generally, possibly because the rims were set at slightly different heights in the litter.

The correlation between T. pusillus and pill millipedes may also be due to such spurious results but it is likely that these two types of animal, which have similarities of ecology, will live in similar places. If this is the explanation of part of the high correlation, it is unlikely that competition, if it exists, is affecting the distribution of either species.

4.3 Feeding experiments

It can be seen from diagram 3L that T. pusillus ate a greater proportion of the total grass (over 80%) than of the other species of leaf offered and at a faster rate, particularly during the first 10 days of the experiment. The changes in rates were not as abrupt as they appear in the diagram, as the percentages eaten of each piece of leaf were assessed in wide stages and there will be no apparent change after a stage is reached until it is completed.

About 40% of the sycamore was consumed and 15% of the birch, whilst oak and beech were barely eaten at all.

It is interesting that the animals should so readily eat the grass segments, not only because the grass is a species alien to specimens of T. pusillus collected from the woodland, but, additionally, because it makes the importance of the tree leaf litter in the stepwise analysis of the unmown area grassland samples (see section 4.1) seem less that of a food reserve. The experiment only compares the relative palatability of leaves of different species collected at one time of year, although it has been shown to change seasonally. Another source of error is due to the variation between leaves of the same species. It seems also that components of the experiment were not in scale, there being either too much food or too few animals for a complete set of results to be obtained before possible changes could occur in the leaf segments, due to microbial decomposition.

The results of the experiments with P. muscorum show that the order in which the different species of leaf were eaten differed greatly when the experiments using specimens from the woodland and from the grassland are compared. The difference seems remarkable when it is considered that specimens from woodland ate more of the grass (which was a grassland species) than of any other species and, that the specimens from the grassland ate greater quantities of three tree species than of the grass species.

The results are less remarkable when examined closer, as the average quantities plotted in diagrams 3m and 3n are comprised of diverse components. When the plotted line for sycamore is studied in diagram 3m, the impression is given that almost all of it was eaten during the experiment. When the plots of the percentages consumed of the individual sycamore segments are examined, it is seen that in five replicates almost 100% was eaten by the end of the experiment, but only some 45% was eaten in replicate 3. There is much diversity of this type in the results and it seems most likely that this is due to the different condition of the segments of the same plant species.

There is, however, still some indication of preferences being made in the experiment. In the first experiment, using P. muscorum from the woodland, the average total quantity of sycamore eaten was slightly lower than that of grass, which approaches 100%. The rate at which the segments of sycamore were eaten was much greater than the rate of consumption of the grass segments (e.g. after the first day, only a few percent of the grass segments had been eaten but 55% of the sycamore). The difference in rate of consumption, despite the fact that even more grass was eaten by the end of the experiment than sycamore, shows that the latter is in some way the preferred food.

It appears that both the species and condition of leaves are important in the choice of food of P. muscorum. It is interesting to note that when animals in the first experiments (using P. muscorum from woodland) had apparently eaten nearly all the edible leaf segments, they finally ate small quantities of three beech segments that previously had been almost totally avoided. That texture is important in the palatability of leaves, is evident from direct observation of the animals, when it was seen that the P. muscorum met with difficulty in breaking away fragments of oak leaves.

The proportion of the litter attributable to different species of leaf did not emerge in the stepwise analysis programme as being important in accounting for variation in the numbers of T. pusillus and P. muscorum (see section 4.1). This may have been due to the way in which the work was conducted. With so many litter samples to sort, the method of scoring the relative proportions of different leaves (see section 2.4) had to be devised beforehand, but this did not result in a very diverse collection of scores and so little variation in the numbers of animals could be thus accounted for.

The quantitive feeding experiment did not provide a measure of the quantities that P. muscorum will eat of the different species of leaf offered, as it became evident after a few days that many of the leaf segments remaining in the experiment were being avoided or only slightly eaten. An interesting point in the results is that the animals in the containers with grass litter survived as well as those in the containers with woodland leaves (table 3q), despite the fact that the latter had consumed, in general, much larger quantities of food (as measured in milligrams dry weight). The implication of these results is either that P. muscorum is assimilating a greater proportion of the grass consumed than of the tree leaves, or, that the total biomass of the P. muscorum in the containers with grass litter was less than in those containers with tree leaves.

4.4 Developmental studies

It was found that a significantly greater proportion of the P. muscorum from the grassland are in larger size classes than of those P.muscorum collected from the woodland (tables 3y and 3z), and the difference is taken to indicate a greater proportion of animals in the later stadia in the grassland population (as expansion in size is restricted to the periods following each moult). The differences between the populations may be due to a greater survival or faster growth and recruitment of the grassland animals into the later stadia or to a greater rate of recruitment into the earlier stadia in the woodland animals, and may be heightened by differential mortality of the young in the grassland or of the adults in woodland. It is possible that at the time of sampling, the population at one or both of the sites did not have a stable age distribution.

The choise of sample locations may have biased the results as the young and old animals may not have identical requirements and distributions.

The average growth of young P. muscorum in separate cultures provided with grass and with tree leaves (section 3.4) did not differ significantly over the period of the experiment (although it is possible that they were in different stages of the moulting cycle at the end of the experiment). There is no evidence here that the age-distributions of woodland and grassland site populations differ because of faster development into adult stadia in the grassland site. The greater survival of animals in the tree leaf culture may have had some effect on the quantity of food available, but in consideration of the large amounts of litter in both containers, this seems improbable.

SUMMARY

1) A study was made of the distributions of T. pusillus and P. muscorum in a woodland and in a grassland site near Durham, and an attempt made to determine the environmental variables most affecting the distribution observed. Data were obtained from Berlese-extracted samples from each site, from pitfall traps in the woodland site and from laboratory feeding and growth experiments.

2) The distributions of T. pusillus and P. muscorum in the woodland site both showed a high degree of contagion. Few P. muscorum were collected from samples taken from the grass area within this woodland site, but a greater number from pitfalls near the edge of the grass area. The distribution of P. muscorum was still contagious when samples from the grass area were excluded from the calculations.

3) Of the variables of the samples that were included in stepwise regression analysis, the dry weight of tree leaf litter and dry weight of wood accounted for 15% of the variation in numbers of T. pusillus, when all the last thirty samples were considered and the dry weight of tree leaf litter and shading accounted for 39.5% of the variation when only the twenty samples from the bramble and bare litter habitats were considered.

4) In the twenty samples from the bramble and bare litter habitats, the dry weight of the F and H layers and of tree leaf litter accounted for 29% of the variation in numbers of P. muscorum.

5) Grassland distribution of both T. pusillus and P. muscorum were basically restricted to the unmown part of the grassland site, that of P. muscorum further restricted to the grass tussocks. Both distributions were highly contagious in this area and that of P. muscorum still showed contagion when only the tussock samples were considered.

6) The dry weight of tree leaf litter and the dry weight of grass together accounted for 38% of the variation in numbers of T. pusillus in the unmown grass area.

7) The dry weight of grass accounted for 61% of the variation in numbers of P. muscorum in the unmown grass area.

8) The pitfall traps provided further information basically in agreement with the data from the woodland samples and showed a particular type of habitat to favour both species of woodlice, namely the areas with deep litter and discontinuous cover.

9) Significant correlations exist between the numbers of T. pusillus in the pitfalls and the numbers of staphylinid beetles greater than 6mm in body length and of pill millipedes.

10) Both the condition and type of leaves are important in food preferences of P. muscorum, so that, for example, segments of the same leaf species were eaten at very different rates in replicate experiments. When both sycamore and grass were in an edible condition, sycamore was eaten at a greater rate.

11) In an quantitative feeding experiment, P. muscorum from the grassland site survived on a much smaller quantity (grams dry weight) of grass than the amount of tree leaf litter eaten by P. muscorum from the woodland site.

12) A significant difference in size-class structure was found between the woodland and grassland populations of P. muscorum, the latter having proportionately more individuals of the larger of the size classes defined.

13) No significant difference was found between the rates of development of young P. muscorum in separate cultures provided with tree leaf litter and with grass litter.

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APPENDIX

Raw Data

Tables 3a to 31 include the raw data collected in the sampling programme. For details of the numbers, distribution and timing of the programme, see table 2a in section 2.3.

Number of *T. pusillus*	1	5	10	0	0	13	19	13	49	7
Number of *P. muscorum*	0	0	0	0	0	0	0	0	0	0
Shading in situ	2	2	2	2	2	2	2	2	2	2
Depth of tree leaf litter in cms.	5.00	5.00	10.00	3.75	5.00	10.00	7.50	6.25	7.50	3.75
Water content of soil (as % total fresh weight)	53	72	71	42	44	61	57	64	63	68
Bramble (*Rubus*) habitat	0	0	0	0	0	0	0	0	0	0
Grass (*Holcus*) habitat	0	0	0	0	0	0	0	0	0	0
Dry weight of tree leaf litter in grams	7.1	8.0	7.6	7.6	9.9	3.2	7.2	4.3	5.1	13.3
Dry weight of wood in grams	2.4	32.4	4.5	3.4	1.9	15.0	2.8	27.6	11.7	29.5
Dry weight of bracken (*Pteridium*) in grams	0	0	0	0	0	0	0	0	1.2	.6
Dry weight of whole sample	217	211	250	226	235	255	300	432	419	260
Water content of whole sample (as % of total fresh weight)	62	77	75	50	58	77	60	78	77	72
Dry weight of F & H layers in grams	207.4	170.4	238.2	215.1	223.2	236.2	290.4	399.8	400.8	216.6

TABLE 3a. Raw data obtained from samples taken at the first woodland site: litter.

Number of *T. pusillus*	10	11	1	4	0	0	2	2	1	2
Number of *P. muscorum*	0	0	0	0	0	0	0	1	0	0
Shading in situ	2	1	2	1	1	1	2	2	2	2
Depth of tree leaf litter in cms.	2.50	1.25	3.75	2.50	3.75	2.50	1.25	2.50	2.50	2.50
Water content of soil (as % of total fresh weight)	67	46	50	51	69	76	56	69	46	74
Bramble (*Rubus*) habitat	0	0	0	0	0	0	0	0	0	0
Grass (*Holcus*) habitat	1	1	1	1	1	1	1	1	1	1
Dry weight of tree leaf litter in grams	2.4	2.5	3.0	5.9	1.1	1.7	1.8	2.3	1.6	3.2
Dry weight of grass litter in grams	2.2	5.6	7.9	9.0	12.5	7.0	14.2	15.2	11.1	7.3
Dry weight of wood in grams	0	0	0	0	0	1.9	1.7	2.9	3.1	2.9
Dry weight of bracken (*Pteridium*) in grams	0	0	3.4	1.5	1.4	1.4	0	2.5	1.3	.5

TABLE 3b. Raw data obtained from samples taken at the first woodland site: grass.

Number of *T. pusillus*	10	6	33	62	39	27	15	20	17	5
Number of *P. muscorum*	1	0	0	1	0	0	0	1	1	0
Shading in situ	3	3	3	3	3	3	3	3	3	3
Depth of tree leaf litter in cms.	5.00	2.50	7.50	7.50	6.25	7.50	10.00	6.25	7.50	6.25
Water content of soil (% of total fresh weight)	69	47	59	80	30	46	40	56	28	35
Bramble (*Rubus*) habitat	1	1	1	1	1	1	1	1	1	1
Grass (*Holcus*) habitat	0	0	0	0	0	0	0	0	0	0
Dry weight of tree leaf litter in grams	11.6	7.7	2.9	4.0	7.6	7.8	18.0	6.8	6.7	4.5
Dry weight of wood in grams	2.88	7.5	3.3	4.4	7.5	7.6	6.1	14.7	19.1	17.5
Dry weight of bracken (*Pteridium*) in grams	.95	0	0	0	0	0	0	.2	0	0
Dry weight of whole sample in grams	161	76	198	118	245	159	168	237	201	187
Water content of whole sample (% of total fresh weight)	71	62	76	75	67	71	71	76	63	67
Dry weight of F & H layers in grams	145.1	60.5	192.1	109.5	230.0	144.1	144.4	215.8	175.2	164.9

TABLE 3c. Raw data obtained from samples taken at the first woodland site: bramble

Number of <u>T. pusillus</u>	1	0	0	0	0	0	0
Number of <u>P. muscorum</u>	0	2	0	0	1	0	0
Water content of soil (as % of total fresh weight)	25	26	24	29	25	24	24
Dry weight of whole sample in grams	1315	649	687	907	728	729	527
Water content of whole sample (as % of total fresh weight)	31	42	41	38	40	46	35
Dry weight of litter and F & H layers in grams	39.1	36.6	27.5	36.8	49.3	59.3	47.0

TABLE 3d. Raw data obtained from samples taken at the first grassland site: mown

Number of *T. pusillus*	1	2	43	3	4	2	5
Number of *P. muscorum*	0	9	37	3	0	0	0
Water content of soil (as % of total fresh weight)	28	27	26	27	27	31	28
Dry weight of grass litter in grams	15.6	28.5	99.4	22.8	8.8	3.1	16.7
Dry weight of whole sample in grams	1221	1692	1912	2350	1632	867	1557
Water content of whole sample (as % total fresh weight)	46	39	42	33	38	48	36
Dry weight of F & H layers	27.8	64.4	146.1	59.9	20.7	9.2	33.4

TABLE 3e: Raw data obtained from samples taken at the first grassland site: unmown

Number of *T. pusillus*	64	72	9	15	19	14	13	35	5	17
Number of *P. muscorum*	0	0	4	1	1	3	0	0	0	0
Shading in situ	3	3	3	2	2	2	2	2	2	2
Depth of tree leaf litter in cms.	6.25	5.00	2.50	3.75	6.25	5.00	7.50	5.00	2.50	2.50
Water content of soil (as % total fresh weight)	47	57	50	75	46	62	70	46	42	38
Bramble (*Rubus*) habitat	0	1	0	0	0	0	0	0	0	0
Grass (*Holcus*) habitat	0	0	0	0	0	0	0	0	1	1
Dry weight of grass litter in grams	0	0	0	0	0	0	0	0	5.6	6.5
Dry weight of tree leaf litter in grams	7.5	6.4	11.9	9.7	10.1	23.8	26.4	9.6	3.8	1.9
Dry weight of wood in grams	3.2	4.1	5.0	9.8	11.1	19.2	34.6	7.2	.3	.6
Dry weight of bracken (*Pteridium*) in grams	3.2	.8	.3	.6	.6	.2	.3	3.8	1.3	.1
Dry weight of whole sample in grams	337	256	215	226	303	241	360	203	-	-
Water content of whole sample (as % total fresh weight)	63	74	39	74	73	72	72	74	-	-
Dry weight of F & H layers in grams	322.8	244.4	197.9	206.4	281.4	198.1	298.8	182.2	-	-

TABLE 3f. Raw data obtained from samples taken at the second woodland site: 10 mixed samples

Number of *T. pusillus*	129	36	7	28	130	78	5	93	50	86
Number of *P. muscorum*	6	3	0	1	1	4	1	9	2	3
Shading in situ	2	2	2	2	2	2	2	2	2	2
Depth of leaf litter	6.25	7.50	3.75	2.50	3.75	3.75	2.50	5.00	3.75	6.25
Water content of soil (as % of total wet weight)	59.0	45.9	69.1	32.1	68.1	26.3	31.3	31.7	48.7	43.1
Bramble (*Rubus*) habitat	0	0	0	0	0	0	0	0	0	0
Grass (*Holcus*) habitat	0	0	0	0	0	0	0	0	0	0
Dry weight of tree leaf litter in grams	34.1	15.9	7.2	4.5	16.5	12.0	11.3	13.0	13.7	28.1
Quantity of beech (*Fagus*)	3	3	3	3	3	3	3	3	3	3
Quantity of oak (*Quercus*)	2	2	1	1	2	1	1	1	1	2
Quantity of sycamore (*Acer*)	1	0	0	0	1	1	1	1	1	1
Quantity of holly (Ilex)	1	0	0	0	1	1	1	0	0	1
Dry weight of wood in grams	27.3	39.8	24.2	6.5	15.3	7.0	10.1	7.4	17.0	14.1
Dry weight of bracken (Pteridium) in grams	.6	.9	.2	.2	.3	1.4	2.0	.7	1.5	.2
Dry weight of whole sample in grams	307	495	566	382	316	381	439	411	363	485
Water content of whole sample (as % of total fresh weight)	69.3	69.6	70.4	67.6	67.3	52.5	53.4	62.7	64.6	61.8
Dry weight of F & H layers in grams	244.5	438.2	534.0	370.6	283.9	360.2	415.3	389.8	330.8	442.3

TABLE 3g. Raw data obtained from samples taken at the second woodland site: litter habitat

Number of T. pusillus	25	16	142	36	33	6	11	25	14	244
Number of P. muscorum	1	0	1	0	0	0	0	0	0	0
Shading in situ	2	2	2	2	2	2	2	2	2	2
Depth of leaf litter	2.5	1.25	2.5	1.25	1.25	1.25	1.25	1.25	1.25	1.25
Water content of soil (as % of total wet weight)	39.2	38.6	41.4	38.8	41.7	23.7	38.7	28.4	27.0	30.5
Bramble (Rubus) habitat	0	0	0	0	0	0	0	0	0	0
Grass (Holcus) habitat	1	1	1	1	1	1	1	1	1	1
Dry weight of grass litter in grams	6.9	8.7	8.1	6.3	6.9	8.3	11.9	9.6	9.8	11.2
Dry weight of tree leaf litter in grams	1.2	.4	1.3	.1	1.0	.5	4.5	3.8	.9	.8
Quantity of beech (Fagus)	2	1	3	3	3	3	3	3	3	3
Quantity of oak (Quercus)	0	0	1	0	0	1	1	1	0	0
Quantity of sycamore (Acer)	3	3	1	0	0	1	1	1	0	0
Quantity of holly (Ilex)	0	0	0	0	0	0	0	0	0	0
Dry weight of wood in grams	18.0	0	1.0	.2	2.0	1.4	8.5	13.1	.6	.2
Dry weight of bracken (Pteridium) in grams	5.4	1.7	2.6	1.1	1.4	0	.2	0	0	0
Dry weight of whole sample in grams	608	715	472	350	239	280	222	247	223	151
Water content of whole sample (as % of total fresh weight)	61.0	52.0	62.5	68.0	71.4	42.4	56.6	54.8	51.6	62.4

TABLE 3h. Raw data obtained from samples taken at the second woodland site: grass habitat

Number of *T. pusillus*	25	28	39	47	65	59	133	58	135	10
Number of *P. muscorum*	4	7	5	1	1	4	4	1	1	0
Shading in situ	3	2	3	3	3	3	3	3	3	2
Depth of leaf litter	5.0	2.5	2.5	3.75	3.75	3.75	2.5	5.0	3.75	5.0
Water content of soil (as % of total wet weight)	48.4	38.5	35.2	48.0	35.8	35.0	62.4	29.9	40.1	28.6
Bramble (*Rubus*) habitat	1	1	1	1	1	1	1	1	1	1
Grass (*Holcus*) habitat	0	0	0	0	0	0	0	0	0	0
Dry weight of tree leaf litter in grams	3.2	9.3	3.9	8.2	5.4	10.2	10.9	11.4	7.8	12.6
Quantity of beech (*Fagus*)	3	3	2	2	2	3	3	3	3	3
Quantity of oak (*Quercus*)	1	1	3	3	3	1	1	1	1	1
Quantity of sycamore (*Acer*)	0	1	1	2	1	1	1	1	1	1
Quantity of holly (*Ilex*)	0	0	0	0	0	0	1	0	0	0
Dry weight of wood in grams	14.9	10.1	8.9	23.9	7.8	15.3	11.0	13.3	9.3	12.2
Dry weight of bracken (*Pteridium*) in grams	2.7	2.9	2.7	1.2	.9	5.1	1.3	.4	.4	1.2
Dry weight of whole sample in grams	242	159	178	330	216	370	319	470	398	458
Water content of whole sample (as % of total fresh weight)	59.9	65.7	63.4	67.0	60.9	62.3	69.2	56.0	66.0	63.5
Dry weight of F & H layers in grams	221.3	137.0	162.9	296.8	201.6	339.1	296.1	444.4	380.5	431.9

TABLE 3i. Raw data obtained from samples taken at the second woodland site: bramble habitat

Number of <u>T. pusillus</u>	1	11	7	8	6	4	24	7	1	6
Number of <u>P. muscorum</u>	3	28	15	35	24	8	21	9	12	11
Water content of soil (as % of total wet weight)	23.9	21.6	20.8	19.2	19.8	15.7	19.9	20.7	19.3	16.3
Dry weight of grass litter in grams	60.1	77.9	54.9	108.5	98.4	135.3	110.3	88.3	61.5	50.3
Dry weight of tree leaf litter in grams	.5	.4	.2	1.9	1.2	.2	2.5	.9	1.0	1.1
Dry weight of wood in grams	.7	0	0	.3	.3	0	.9	.4	0	.1
Dry weight of whole sample in grams	2053	1953	1453	2566	1824	2570	1314	2984	1508	1679
Water content of whole sample (as % of total fresh weight)	31.1	30.3	29.9	27.3	29.7	31.5	26.6	23.3	30.9	33.4
Dry weight of F & H layers in grams	40.5	85.7	184.4	197.0	62.0	170.4	92.8	69.1	79.3	62.5
Mown/Unmown	0	0	0	0	0	0	0	0	0	0
Tussock/Gap	1	1	1	1	1	1	1	1	1	1

TABLE 3j. Raw data obtained from the samples taken at the second grassland site: tussock habitat.

Number of <u>T. pusillus</u>	2	9	15	0	6	17	4	7	0	3
Number of <u>P. muscorum</u>	0	0	0	1	0	0	0	0	0	0
Water content of soil (as % of total wet weight)	26.6	26.4	27.1	25.0	32.6	20.3	21.4	22.4	21.3	20.0
Dry weight of grass litter in grams	11.6	6.1	3.2	9.5	4.6	2.5	7.9	1.0	2.5	3.8
Dry weight of tree leaf litter in grams	1.0	2.5	1.2	1.3	1.3	4.7	1.1	2.5	2.1	2.0
Dry weight of wood in grams	0	0	0	.8	0	0	.6	0	.3	0
Dry weight of whole sample in grams	906	445	389	679	298	443	227	93	488	479
Water content of whole sample (as % of total fresh weight)	32.4	35.3	38.0	36.5	43.3	29.7	41.3	33.1	27.1	22.7
Dry weight of F & H layers in grams	10.3	17.3	19.3	33.6	13.8	17.0	13.9	4.7	20.2	11.0
Mown/Unmown	0	0	0	0	0	0	0	0	0	0
Tussock/Gap	0	0	0	0	0	0	0	0	0	0

TABLE 3k. Raw data obtained from samples taken at the second grassland site: gap habitat

Number of T. pusillus	0	0	0	0	0	0	0	0	0	0
Number of P. muscorum	0	0	0	0	0	0	1	0	0	0
Water content of soil (as % of total wet weight)	26.2	24.2	23.8	27.0	28.2	29.2	27.2	23.5	23.4	26.1
Dry weight of grass litter in grams	27.2	25.6	35.7	12.3	16.3	14.3	13.7	15.1	28.8	26.3
Dry weight of tree leaf litter in grams	.3	.3	.1	.5	0	.7	1.0	.1	.1	.6
Dry weight of wood in grams	0	0	0	0	.1	0	.7	.3	.6	.9
Dry weight of whole sample in grams	725	696	783	982	696	1097	585	841	620	1483
Water content of whole sample (as % of total fresh weight)	35.9	36.0	32.3	33.1	36.1	29.4	31.6	29.2	32.8	24.8
Dry weight of F & H layers in grams	24.0	40.1	31.4	34.2	16.5	35.1	32.4	39.1	34.2	28.6
Mown/Unmown	1	1	1	1	1	1	1	1	1	1
Tussock/Gap	0	0	0	0	0	0	0	0	0	0

TABLE 31. Raw data obtained from samples taken at the second grassland site: mown area habitat