Seasonal vertical distribution of pseudoscorpions in beech litter*

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Summary

Three species of pseudoscorpion, *Chthonius ischnocheles* (Hermann), *Neobisium muscorum* (Leach) and *Roncus lubricus* L. Koch, were present on a beech site in Oxfordshire (Gabbutt, 1967). During 1968 Tullgren extraction of separate samples of litter, humus and soil revealed that spatial, temporal and ontogenetic differences occur in the distribution of these three species (Wood, 1971). Although each of the species was extracted from all three layers there was (a) movement upwards during the spring and downwards during the autumn, and (b) a vertical zonation of the species, with overlap, throughout the year. Differences in the seasonal return migration cycle of each species are examined and discussed.

Introduction

The evidence for seasonal movements of pseudoscorpions within the soil profile is limited. Goddard (1976) studied three species from litter, humus and soil on a beechwood site in the Chilterns but few pseudoscorpions were taken from soil. One species, *Allochernes dubius* (O. P.-Cambridge) was at such low density as to warrant its exclusion from further analysis. *Chthonius orthodactylus* (Leach) provided some evidence of a winter migration into the humus from the litter but this was not observed in *Neobisium muscorum* (Leach). By contrast Gabbutt (1970) observed a winter increase in the numbers of *N. muscorum* in the soil on a sycamore/ash site in

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Cheshire. The purpose of the present paper is to record more substantial evidence of seasonal movements by three species, *N. muscorum, Chthonius ischnocheles* (Hermann) and *Roncus lubricus* L. Koch in litter in an Oxfordshire beechwood community (Wood, 1971).

Site and methods

The site in Lambridge Wood, near Henley-on-Thames, Oxon, (Grid Ref. SU 746839) has been described by Gabbutt (1967).

The soil on the site was a black, basic rendzina (pH 7.6-7.8) 3-6 cm deep covering flint and chalk. Above this was a humus layer consisting of partially decomposed fibrous material up to 6 cm thick, and above this a 12 cm layer of beech leaves.

Samples of litter, humus and soil were taken during the period November 1967 — August 1968, and the pseudoscorpions extracted by using the same Tullgren funnels and techniques previously employed by Gabbutt (1967). Each sample was approximately 0.5 m² in area, but the number of samples varied slightly according to the availability of funnels. Litter, humus and soil were sampled and extracted separately. Normally 24 samples of litter and 12 each of humus and soil were taken at about noon on each of the nine visits to the wood during this period. Extraction time varied between 15 and 20 days.

Climate and microclimate

The meteorological records of the Royal Air Force station at Benson, eight miles from the site, were analysed for the period 1960-1969. The results (Table 1) show that the year can be arbitrarily divided into four temperature regimes, each with a range of 5°C in the average monthly temperature. This was 0°-5°C during December, January and February, 5°-10°C during March, April and November, 10°-15°C during May, June, September and October, and 15°-20°C during July and August. Thus average monthly temperatures rise or fall by approximately 5°C every two months throughout the year with the single exception of November when a fall of 5°C is accomplished during the month.

Temperatures were measured in Lambridge Wood at midday, the aim being to discover the relationship between these readings and the data from R.A.F. Benson. For this purpose thermometers were placed

at the surface of the litter and within litter, humus and soil. The resulting microclimatic records can be divided arbitrarily into three types of temperature regime:– (1) temperature gradients (positive) when temperature decreased with depth, (2) temperature gradients (negative) when temperature increased with depth, and (3) temperature gradients (neutral) when there was a 1°C or less difference between the temperature at the surface of the litter and in the soil. For instance, in specific instances, in July there was a positive gradient from 14.5°C to 20°C from soil to surface; in December there was a negative gradient from 5°C to 1°C and in June there was a neutral gradient from 11°C to 12°C.

In general (Table 1) over the year monthly average temperatures of 0°-5°C and 5°-10°C lead to midday temperature gradients which are negative (November-April) and those of 15°-20°C result in temperature gradients which are positive (July-September). The change from negative to positive gradients in the spring appears to take place slowly during May and June; microclimatic records show a mixture of negative, positive and neutral gradients. The transition from positive to negative gradients in the autumn is much faster and takes place during October. It is possible that the potential heat gain at the woodland floor is reduced by the spring leaf flush and that heat loss is accelerated by the autumn leaf fall.

	Average monthly temperature (°C)	Temperature gradient
January	0-5	–
February	0-5	–
March	5-10	–
April	5-10	–
May	10-15	0
June	10-15	0
July	15-20	+
August	15-20	+
September	10-15	+
October	10-15	0
November	5-10	–
December	0-5	–

Table 1: The relationship between the average monthly temperature at R.A.F. Benson and the temperature gradient from the soil to the surface of the litter at Lambridge Wood (positive gradient = +; neutral gradient = 0, negative gradient = –. (For further explanation see text).

Phenology

Before considering the disposition of the instars at different levels in the soil profile, it is necessary to set these against the background of the seasonal changes in density.

Pseudoscorpions construct silken chambers for the purposes of moulting, hibernation and brooding (Godfrey, 1910; Kew, 1929). The present evidence (Gabbutt, 1970) suggests that individuals encased in such chambers are not extracted in Tullgren funnels. The data presented here, therefore, refer only to the free-living population. The numbers per m^2 (Figs. 1-15) represent overall estimates of density derived from those for each instar in each of the three layers (i.e. data from litter, humus and soil are combined).

Neobisium muscorum

A preliminary study of this species by Gabbutt & Vachon (1965) on two sites in Devon and one in Cheshire preceded the investigation of the Lambridge site (Gabbutt, 1967). Recently Goddard (1976) has provided further information from the Chilterns (Buckinghamshire). All showed populations at comparatively low density with the possibility on the more favourable sites of two generations a year in June/July and again in October.

In the present study (Figs. 1-15) the total population is again low compared with the other two species Chthonius ischnocheles and Roncus lubricus. The June peak of protonymphs can be identified (Fig. 1) and there is a suggestion, in both the August and November collections, that the protonymphs might have peaked in September-October. This speculation is reinforced by the relatively high density of deutonymphs in November (Fig. 2). The majority of the overwintering population is composed of protonymphs (Fig. 1) and deutonymphs (Fig. 2) and only post-winter growth materially increases tritonymphal density (Fig. 3) and male density (Fig. 4) during April-July. Female density (Fig. 5) remains low throughout the year.

Chthonius ischnocheles

The main outline of the life-cycle has been given by Gabbutt & Vachon (1963) and Gabbutt (1967). The data presented here (Figs. 6-10) are consistent with this previous work.
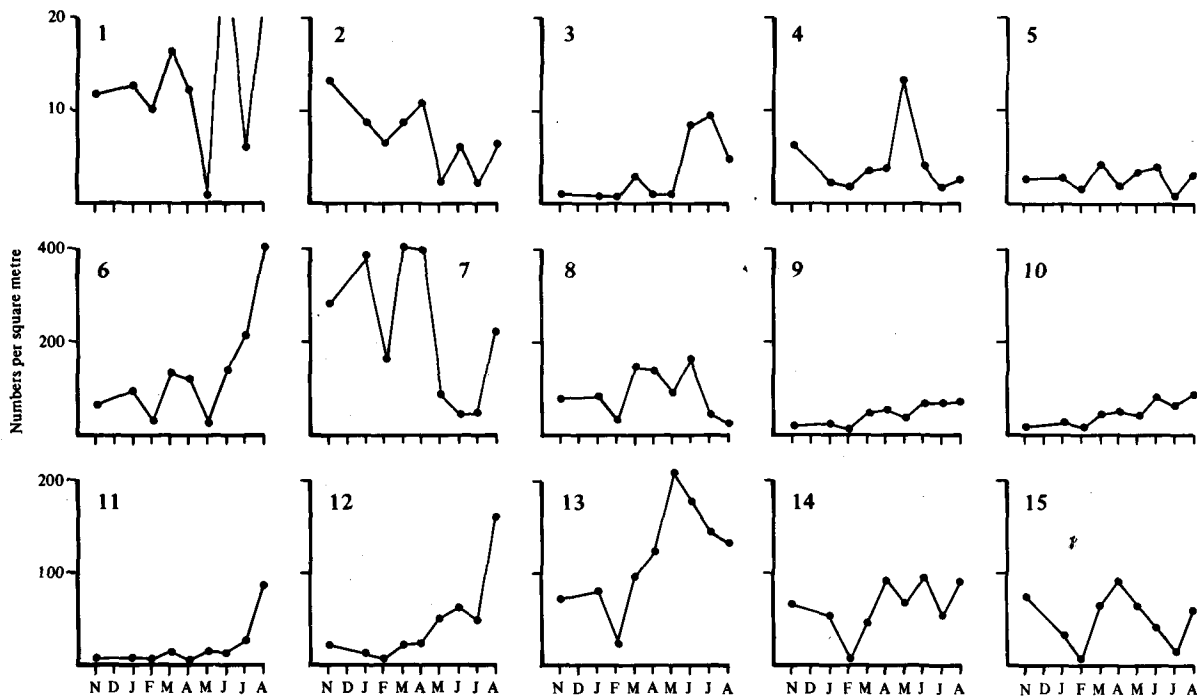
Figs. 1-15: The numbers per m² of pseudoscorpions collected at Lambridge Wood, November 1967 — August 1968. *N. muscorum:* 1 protonymph; 2 deutonymph; 3 tritonymph; 4 male; 5 female. *C. ischnocheles:* 6 protonymph; 7 deutonymph; 8 tritonymph; 9 male; 10 female. *R. lubricus:* 11 protonymph; 12 deutonymph; 13 tritonymph; 14 male; 15 female. Note the different scales on the y-axis of the graphs for the three species.

The new generation appears as protonymphs (Fig. 6) during July-September. As pre-winter growth occurs, increasing numbers of deutonymphs (Fig. 7) and tritonymphs (Fig. 8) appear during August-November. Although all three instars are present, the bulk of the overwintering nymphs (60-70%) are deutonymphs during October-April (Fig. 7). The apparent winter decrease in the density of nymphs (e.g. February) may reflect the propensity of a proportion of each instar to build silken chambers for hibernation and/or moulting. These are vacated the following spring (e.g. March) and the re-appearing individuals only then become susceptible to Tullgren extraction. When growth is resumed, post-winter, successive peaks of protonymphs, deutonymphs and tritonymphs occur in March-April (Fig. 6), March-April (Fig. 7) and June (Fig. 8) respectively as the generation proceeds to maturity. Overwintering males (Fig. 9) and females (Fig. 10) from previous, or more remote, generations leave their hibernation chambers

and rejoin the free-living population from March onwards. The old and the new adults reach peak densities during June-August (Figs. 9-10).

Roncus lubricus

Previous work on this species at the same site (Gabbutt & Vachon, 1967) was based only on litter samples. The present data (Figs. 11-15) clarify some of the interpretational problems inherent in the original study.

Protonymphs (Fig. 11) were collected at low density throughout most of the year, but the new generation is heralded by increasing numbers of this instar during July and August. The inability of Gabbutt & Vachon (1967) to collect many protonymphs from litter is not now surprising since, as will become clear later, 96-100% of all protonymphs were taken from humus and soil during this period (Fig. 26). Pre-winter growth results in high numbers of both deuto-

nymphs (Fig. 12) and tritonymphs (Fig. 13) in August but it is not thought likely that any substantial part of the population achieve maturity in late autumn. Although all three instars overwinter, the tritonymphs (Fig. 13) form the bulk of the nymphal population (70-85%) at this time. The lowest nymphal density occurs in February and this may mark the time when the majority of nymphs are in hibernation and/or moulting chambers. Their emergence from such chambers probably accounts for the increasing numbers of deutonymphs (Fig. 12) and tritonymphs (Fig. 13) during April and May, since there is no evidence of a breeding period at this time; the protonymphs maintain their pre-winter levels. The increase in the density of males (Fig. 14) and females (Fig. 15), during March and April, can be attributed partly to overwintering adults from previous generations leaving their hibernation chambers and partly to maturation in the latest generation. Adult density is high during April and the sex ratio is approximately 1:1.

The subsequent reduction in female density (Fig. 15), without a parallel reduction in male density (Fig. 14), during the period June to August, probably reflects the building of silken chambers for the purpose of brooding, since the distorted ratio is only observed prior to the appearance of the new generation of protonymphs (Fig. 11) in August.

Vertical distribution

In Figs. 16-30 the numbers of a particular instar present in each of the three layers (litter, humus and soil) are expressed as a percentage of the total numbers of the instar extracted on a particular date.

Neobisium muscorum

Since the density of this species is low for most of the year perhaps not too much significance should be attached to changes in the percentage numbers of each instar in each of the layers. It is clear, however, that at least some of the protonymphs (Fig. 16) and deutonymphs (Fig. 17) are to be found in the humus rather than the litter during November to May, and tritonymphs (Fig. 18), males (Fig. 19), and females (Fig. 20) occasionally occur in humus and soil in March to May. However, throughout the study period over 82% of all instars were extracted exclusively from the litter. The overall picture is of a litter

species which shows little evidence of seasonal movement into humus and soil. This does not preclude the possibility of upward and downward movements within the litter as a seasonal phenomenon in this species.

Chthonius ischnocheles

The percentage number of protonymphs (Fig. 21) decreases in the litter and increases in the humus (to 60%) during the period November to March with low numbers (20%) being maintained in the soil at this time. This situation is reversed during the period March to July when the percentage numbers dramatically increase in the litter (to 80%) and decrease in the humus and soil. Latterly this percentage increase takes place (Fig. 21) as the density of protonymphs increases (Fig. 6). However, despite the high density of protonymphs in August (Fig. 6) there is a decrease in the percentage numbers in the litter and an increase in the humus layer (Fig. 21).

The percentage number of deutonymphs (Fig. 22) decreases in the litter and increases in the humus (to 65%) from November to February, with a corresponding reversal of this situation from February to June when 85% of all deutonymphs were extracted from the litter. In contrast to the protonymphs, the increase in the percentage numbers of deutonymphs in the litter occurs at a time when deutonymphal density is falling sharply (Fig. 7) especially during the period April to June. As deutonymphal density recovers during August (Fig. 7) there is an increase in the percentage number in the humus (Fig. 22).

A similar pattern is exhibited by tritonymphs (Fig. 23) with the percentage increase in numbers in the humus (to 50%) and the soil (to 30%), during November to March, being reversed during March to August as more and more of the tritonymphs accumulate in the litter (85%). The percentage increase in the litter numbers at this time takes place as tritonymphal density increases during March to June and decreases during June to August (Fig. 8).

The percentage number of males (Fig. 24) and females (Fig. 25) decreases in the litter and increases in the humus (to 65%) during November to March, and then increases in the litter (to 85%) and decreases in the humus during March to July. Their occurrence in litter during this period coincides with increasing male (Fig. 9) and female density (Fig. 10) but,

despite high adult density, August is marked by an increase in the percentage numbers in humus (Figs. 24, 25). Males and females behave in the same way, there are no sexual differences in the seasonal distributional pattern.

Thus in *C. ischnocheles* all instars exhibit the same seasonal pattern in their distribution. The movement downwards, beginning in July/August is completed the following February/March when each of the instars is distributed approximately 25% in litter, 60% in humus and 15% in soil. The reverse movement upwards, commencing in February/March and complete in July/August, results in each instar being distributed approximately 85% in litter, 10% in humus and 5% in soil. The percentage number of each instar in the soil is comparatively low at all times of the year (Figs. 21-25) and thus the main seasonal movement is between litter and humus. It is characterised by the absence of an ontogenetic component, in contrast to *R. lubricus* (q.v.). The distribution patterns of all the instars of *C. ischnocheles* show remarkable similarities. Furthermore the seasonal movement is independent of instar density; increases or decreases in this parameter occur with both the upward and the downward movements.

Roncus lubricus

The percentage number of protonymphs (Fig. 26) increases in the soil and decreases in the humus from November to February, but perhaps not too much significance should be attached to this apparent downward movement since protonymphal density (Fig. 11) is consistently low during this period. Thereafter about 80% of all protonymphs are present in the soil and almost all the remainder in the humus (Fig. 26). This also represents the situation in August, the only occasion when protonymphal density is high (Fig. 11).
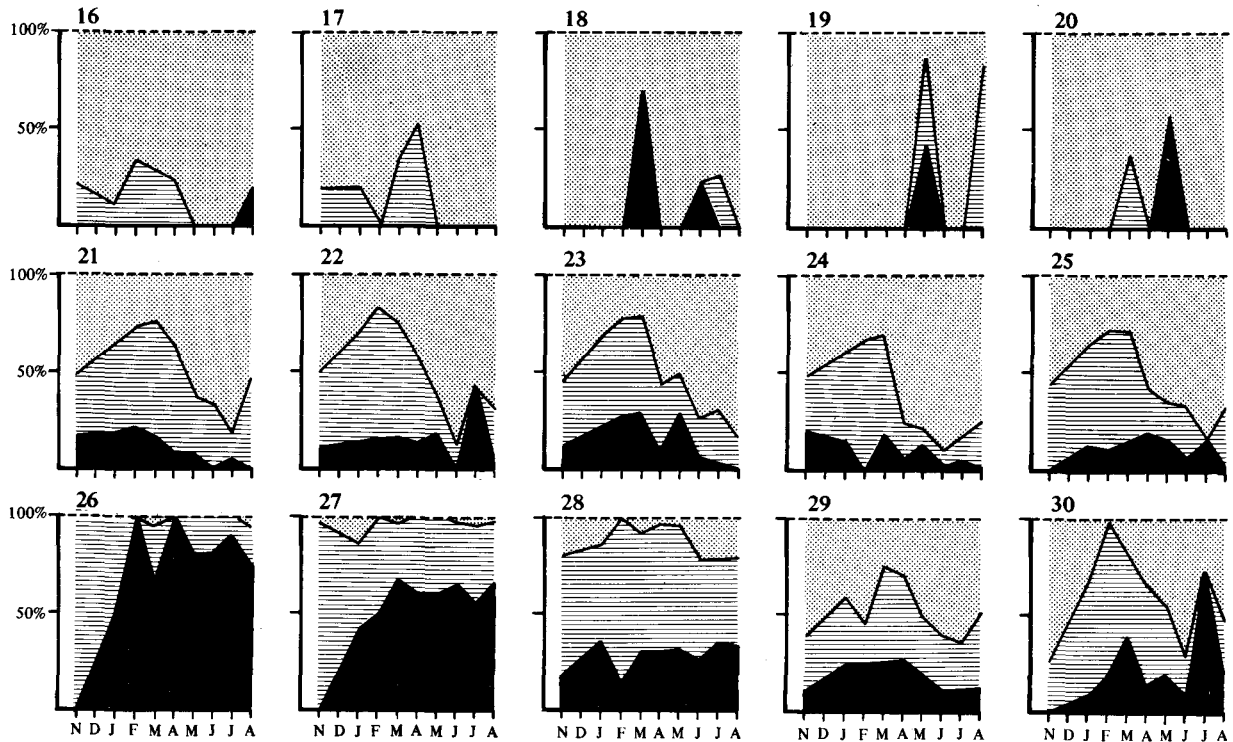
The percentage number of deutonymphs (Fig. 27) decreases in the humus and increases in the soil (to 60%) from November to March, and continues at this level until August when deutonymphs reach peak density (Fig. 12). The percentage number of deutonymphs taken from litter was rarely more than 5% in any month, and those in humus averaged 35% from March to August.

The percentage number of tritonymphs in the soil (Fig. 28) remained fairly constant at about 30%

throughout the year. The majority of tritonymphs (60%) were taken from humus during the period November to May, at a time when tritonymphal density was increasing (Fig. 13). A modest increase in the percentage of tritonymphs in the litter (to 20%) occurred during May to August as tritonymphal density suffered a decline (Fig. 13).

The percentage number of males (Fig. 29) decreases in the litter and increases in the humus and soil from November to March, at a time of low male density (Fig. 14). This situation is reversed during March to July (Fig. 29) when the percentage number of males increases in litter (to 65%) and correspondingly decreases in humus and soil at a time of high density (Fig. 14). Since the percentage number in the soil rarely exceeds 20% at any time of the year, the major changes in male distribution are between litter and humus. A similar pattern emerges for the female (Fig. 30) with two notable differences. In February there are no females in the litter and a much higher percentage of females (Fig. 30) than males (Fig. 29) in the humus. In July there is a marked discrepancy between the sexes, with only 13% of males but 73% of females in the soil. This downward movement into the soil (Fig. 30) may herald the building of silken chambers by females for the purpose of brooding. It is particularly significant that the density of females declines at this time (Fig. 15) and that one month later, in August, there is a considerable increase in protonymphal density (Fig. 11) and that this input of a new generation is virtually confined to the soil (Fig. 26).

All instars show some evidence of a seasonal movement downwards in the autumn, but the movement upwards in the spring was obvious only in the adults. This seasonal movement is superimposed on a partial spatial separation of instars. The protonymphs (Fig. 26) are almost entirely (80%) confined to the soil for most of the year and this is particularly true when they are at maximum density in the autumn (Fig. 11). Whilst over 50% of deutonymphs (Fig. 27) are to be found in the soil during the winter and spring, there are significant numbers always present in the humus. In tritonymphs (Fig. 28) even fewer are found in the soil and the majority (60%) are present in the humus. This tendency to appear in the higher layers is accentuated in adults where the majority of both males (Fig. 29) and females (Fig. 30) move

Figs. 16-30: The percentage number of each instar within the litter (stippled), humus (hatched) and soil (black) at Lambridge Wood, November 1967 – August 1968. *N. muscorum:* 16 protonymph; 17 deutonymph; 18 tritonymph; 19 male; 20 female. *C. ischnocheles:* 21 protonymph; 22 deutonymph; 23 tritonymph; 24 male; 25 female. *R. lubricus:* 26 protonymph; 27 deutonymph; 28 tritonymph; 29 male; 30 female.

seasonally between litter and humus. Thus, the onto-genetic progression from protonymphs to adults is correlated with a decreasing tendency to appear in the soil and an increasing tendency to be found in the litter.

Discussion

In reviewing migratory behaviour, Baker (1978) defines a return migration as "migration to a spatial unit that has been visited previously", with the spatial unit being delimited according to the descriptive re-quirements of each particular study. In the present case it is convenient to recognise the litter, humus and soil layers each as separate 'spatial units'.

There is now clear evidence in *C. ischnocheles* (Figs. 21-25) and *R. lubricus* (Figs. 26-30) of a return migration cycle with an annual periodicity. This is set in the context of a life-cycle in which the longevity of

the adults is at least two years (Gabbutt, 1969). In both species a large part of the population moves downwards to lower layers in the autumn and winter, and surviving individuals return to upper layers the following spring and summer.

The evidence for *N. muscorum* is much less con-vincing, partly because the sampling technique only recognised three layers and partly because the popula-tion of this species was at low density. A return migration cycle almost exclusively within the litter layer cannot be discounted, and there is some support for this view since at least some of the protonymphs (Fig. 16) and deutonymphs (Fig. 17) appear to spill over into the humus during the winter period. God-dard (1976) was unable to observe a winter migration to the deeper layers in this species at a nearby site, but she was also using a sampling technique which did not sub-divide the litter layer. Whatever the am-

biguities posed by this species on sites in southern England it is clear the *N. muscorum* shows a return migration within the soil profile on more northerly sites (Gabbutt & Vachon, 1965; Gabbutt, 1970).

Although at least two species exhibit return migration cycles there are significant spatial differences which separate, at least partially, the three species seasonally between litter, humus and soil. In general terms *N. muscorum is predominantly a litter species* throughout the year; *C. ischnocheles* moves between litter and humus and *R. lubricus* between humus and soil. For instance as protonymphs of *R. lubricus* (Fig. 26) gradually vacate the humus at mid-winter to enter the soil, they are replaced by increasing numbers of protonymphs of *C. ischnocheles* (Fig. 21) as they move from litter to humus.

Superimposed on these broad spatial differences are both temporal and ontogenetic effects. As far as the former are concerned the protonymphs of both *C. ischnocheles* (Fig. 6) and *R. lubricus* (Fig. 11) reach maximum density in August or shortly thereafter. By contrast the majority of the protonymphs of *N. muscorum* (Fig. 1) appear in June. The appearance of similar instars is thus separated in time.

The return migration cycle of *C. ischnocheles* (Figs. 21-25) is clear cut and remarkably consistent in that all the instars behave in the same way. The cycle change in the percentage of each instar in each of the three layers is very similar throughout the year. By contrast *R. lubricus* shows ontogenetic differences. The majority of protonymphs (Fig. 26) and deutonymphs (Fig. 27), e.g. in March, are to be found in the soil whilst there is an increasing tendency for tritonymphs (Fig. 28), males (Fig. 29) and females (Fig. 30) to be extracted from humus. Later on in the year when protonymphs and deutonymphs are almost exclusively in humus and soil, the majority of adults are to be found in litter. Unlike the younger instars, the return migration cycle of adults of *R. lubricus* is very similar both in timing and resulting distribution to that of *C. ischnocheles.*

Changes in vertical distribution can only tentatively be attributed to a long period seasonal return migration cycle, since a sampling periodicity of approximately one month has been used. The optimum level for the species may be seasonal and the same for all instars (*C. ischnocheles*), so that each is nearer the surface in the summer than in the winter. Alter-

natively the adults may be nearer the surface than the nymphs at all times of the year (*R. lubricus*), when an upward ontogenetic component is superimposed on the up and down seasonal migration. This is by no means the only interpretation, but until it is known whether pseudoscorpions undergo a daily return migration the matter remains speculative. However, if a daily return migration should occur, similar to that *known to occur in earthworms* (Gerard, 1967), then seasonal effects in pseudoscorpions might be a function of variations in the distance component, the timing and the periodicity of a daily return migration. For instance, the influence of season might be for the distance component of the daily migration to be greater in winter than in summer.

An interesting feature of the seasonal distribution of all instars of *C. ischnocheles* is that the peaks of occurrence away from or at the surface are in February/March and June/July respectively (Figs. 21-25). At these times the microclimatic temperature gradients (Table 1) are respectively negative and positive. The subsequent seasonal movements upwards and downwards continue to take place when there are reversals in the temperature gradients during May/June and again in October (Table 1). On this basis temperature may be a contributory but not a critical factor. Perhaps the June/July timing of the beginning of a downward migration and the February/March timing of the beginning of an upward migration, a situation closely analogous to the movements of some zooplankton (Baker, 1978), indicates that day-length is a significant factor, at least in summer.

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