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THE ECOLOGICAL SIGNIFICANCE OF ACTIVITY PATTERNS IN THE WOODLOUSE PORCELLIO SCABER LATR. (Isopoda)

by

P. J. DEN BOER

(*Zoological Laboratory, State University of Leiden, Netherlands* [1])

CONTENTS

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[1] The present address of the author is: Biological Station (Dept. of the Laboratory of Plant Taxonomy and Geography, Wageningen), Wijster (Dr.), Netherlands.

1. INTRODUCTORY REMARKS

1. INTRODUCTION [1.1.]

1.1.1. Autecology is generally considered to deal with the relations of an organism to its environment (ODUM, 1953: p.3 and 7). Because autecological studies should start not from the environment but from the organism, it is more correct to say: Autecology deals with the manner in which and the extent to which an organism fits into an environment (see also: VAN DER KLAAUW, 1951).

Of the many possible environments the natural ones are to be studied first, since the relations of an organism to unnatural, abnormal, or artificial environments can only be understood in comparison with its relations to natural environments.

1.1.2. When speaking of the manner in which and the extent to which an organism fits into a natural environment, two aspects of adjustment can be distinguished, *viz.*:

a. Passive adjustment.
b. Active adjustment.

a. By passive adjustment is understood the manner in which and the extent to which an organism as a whole endures the influences of the environment.

a.a. The qualitative aspects of passive adjustment are concerned with the way in which an organism fits into an environment through morphological structures and physiological processes (ecological morphology: VAN DER KLAAUW, 1948; and ecological physiology).

a.b. The quantitative aspects of passive adjustment are concerned with the extent to which an organism as a whole endures the influences of the environment (physiological autecology). These aspects are usually studied by determining in both natural and artificial environments (*i.e.* in the laboratory) the limits of tolerance and the optimum value of the most important environmental factors for a number of vital functions. These aspects are generally studied in relation to numbers and/or distribution and dispersal.

b. By active adjustment is understood the manner in which and the extent to which an organism as a whole reacts to influences of the environment. Unlike passive adjustment, which can be studied in both plant and animal organisms, the aspects of active adjustment are characteristic for animal organisms only.

b.a. The qualitative aspects of active adjustment are concerned with the way in which an animal organism fits into the environment with patterns of activity and behaviour (ecological ethology).

b.b. The quantitative aspects of active adjustment can be described as the extent to which an animal organism as a whole reacts to influences of the environment (ethological autecology). These aspects have usually been studied in artificial environments in the laboratory only (preferendum apparatuses). For a good understanding of the results of preferendum experiments in the laboratory, however, it is first necessary to study the quantitative aspects of active adjustment to a natural environment by the animal. Some knowledge of these aspects is very important in relation to studies on numbers and/or distribution and dispersal (see *e.g.* ANDREWARTHA and BIRCH, 1954).

By studying the quantitative aspects of the activities of an animal species our concept of adjustment to the natural environment can be greatly changed, as I hope to demonstrate in the case of the woodlouse *Porcellio scaber* Latr.

2. LITERATURE ON ASPECTS OF PASSIVE ADJUSTMENT TO AN ENVIRONMENT IN WOODLICE [1.2.]

1.2.1. Many authors have shown that from a morphological and physiological point of view woodlice on the whole are very badly equipped for life on land.

Respiration takes place by gills which must be kept continuously wet, and only a number of species have additional pseudotracheae (corpora alba) (VERHOEFF, 1917a, 1920a; REINDERS, 1933), which are quite obviously an adaptation to terrestrial life. In damp air cutaneous respiration is also possible, but this is greatly inhibited by water-loss in dry air (EDNEY and SPENCER, 1955).

The cuticle lacks an external wax layer (BURSELL, 1955) and is very permeable to water, so that the animals lose considerable amounts of water even at high air humidities (*e.g.*: Relative Humidity (R.H.) 85%) (WALOFF, 1941; EDNEY, 1949, 1951a; AUZOU, 1953).

As in most water animals, the main N-excretion product is ammonia (DRESEL and MOYLE, 1950). The eggs and young larvae can only develop in the fluid contained in the marsupium (VERHOEFF, 1917b, 1920b).

1.2.2. On the other hand, woodlice are able to take up water from wet surfaces very easily (SPENCER and EDNEY, 1954) and to extract water from their food (KUENEN, 1959). They are able to survive comparatively large fluctuations in the osmotic pressure of their body-fluids (WIDMANN, 1936). For short periods they can sustain high temperatures in the environment by transpiring large amounts of water (EDNEY, 1951b, 1953).

1.2.3. The structure of the respiratory organs and the rate of desiccation by water-loss in the different species are more or less correlated with the moistness of the habitats in which the respective species are usually found (MILLER, 1938; MEINERTZ, 1944). Most authors are agreed that woodlice can only live in moist to very moist surroundings (in the litter of woods, in cellars, and under stones, fallen trees, decaying materials, *etc.*).

1.2.4. An excellent review of the literature dealing with different aspects of passive adjustment to the environment in woodlice is given by EDNEY (1954). He wonders why these animals which are so badly equipped for life in land habitats can be found in dense populations in nearly every part of the world, and concludes that woodlice must have at their disposal very sensitive reaction-mechanisms which enable them to maintain themselves in very moist surroundings.

3. FORMULATION OF THE PROBLEM OF THE PRESENT INVESTIGATION [1.3.]

As part of a long-term investigation on different ecological aspects of woodlice which is being carried out at the Zoological Laboratory of the University of Leiden under the guidance of Prof. D.J. KUENEN, two students, A.B. STAM and P.W. LEENHOUTS, studied the natural environments of three species of woodlice in the dune area „Meijendel" in 1952. In the course of their observations they discovered that the three species of woodlice present in the area, *Porcellio scaber* Latr., *Armadillidium vulgare* (Latr.), and *Philoscia muscorum* (Scop.), show a remarkable activity. At night many specimens can be observed in motion and leaving the woods in which they pass the day. We had not expected these activities, for there is plenty of appropriate food in the places where they can be found during the day.

A good understanding of the reasons for these activities could be important for our views on the question of how woodlice fit into their natural environments. Hence, the problem of the present investigation can be formulated as follows: "What is the ecological significance of activity patterns in woodlice?" The investigation itself was formulated in four phases: first, to study these activities in an environment natural to the animals; second, to formulate a working hypothesis to explain the observed phenomena in ecological terms; third, to provide direct proof of the validity of the working hypothesis, and lastly, to attempt to reproduce these activities in the laboratory under controlled conditions.

In the present paper only the work on *Porcellio scaber* Latr. will be discussed. The observations on other species will be published separately. In 1955 and 1956 a number of observations were made both in the field and in the laboratory on the activities of males and females separately and of young and old individuals separately. Although some interesting differences were found between the activities of males and females and of young and old individuals, the findings do not influence the conclusions and suggestions given in this paper, and the data will therefore also be published separately.

4. AREA IN WHICH PORCELLIO SCABER WAS STUDIED UNDER NATURAL CONDITIONS [1.4.]

Observations on the activities of *P. scaber* were made in a wooded part of the dune area "Meijendel", named "Bierlap". Meijendel is very suitable for ecological fieldwork because of its proximity to Leiden (see map, Fig. 1), its relatively large area (± 1600 ha), and its great diversity of environmental conditions. In addition, Meijendel has been used since 1874 as a water reservoir for The Hague and consequently receives special protection.

The Bierlap is situated in the centre of Meijendel and consists of a large, flat depression with groups of trees (mainly birches and aspens)

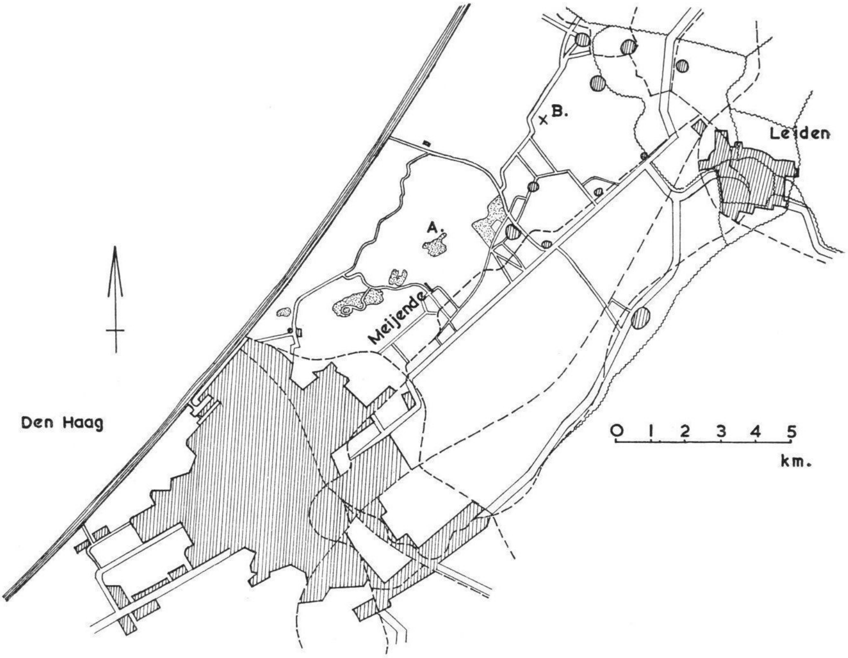

Fig. 1. Situation of the dune area "Meijendel" between Den Haag and Leiden (about 52°5′ N and 4°20′ E).
A = the Bierlap area; B = the meteorological station "Valkenburg".

of various sizes mixed with open areas which are covered by a dense growth of *Calamagrostis epigejos* (L.) Roth. and other grasses (see map, Fig. 2). Since about 1895 this part of the dunes has not been either inhabited or cultivated (Boerboom, 1958a).

A narrow path, 50 cm wide, runs through the eastern part of the Bierlap. Observations on the activities of *P. scaber* were made primarily on this path and in two aspen woods, the "first" aspen wood (A) and the "second" aspen wood (B) in the neighbourhood of this path (see map, Fig. 2).

P. scaber is a very abundant species, not only in the Bierlap but in the whole dune area of Meijendel; for laboratory experiments it was possible to collect many thousands of specimens during a single day in summer or autumn.

Fig. 2. The Bierlap area (after Boerboom, 1958b, modified).
A = "first" aspen wood; B = "second" aspen wood; a–e = path;
------ = track;
-·-·-·- = fence;

▨ = wooded areas (mainly birches)
▦ = aspen wood;
▥ = growth of *Calamagrostis epigejos*
⁘ = scattered trees (mainly birches)
░ = young aspen trees;
○ = bushes (*Hippophaë rhamnoides*).

5. LITERATURE ON ACTIVITIES IN WOODLICE [1.5.]

Study of the literature on woodlice revealed that only a few authors report observations on locomotory activities in woodlice under more or less natural conditions.

1.5.1. CLOUDSLEY–THOMPSON (1951) counted the number of specimens of *Armadillidium vulgare* (Latr.) which were active on a section of road. The greatest number appeared to be active in the morning. This author does not discuss the question of why woodlice are active; he is mainly interested in the diurnal rhythms and in the factors which stimulate and arrest activity. He studied these phenomena in the laboratory by means of actographs and preferendum apparatuses. He concluded that there must be an innate 24-hour rhythm, which is controlled by the diurnal light-darkness periodicity. Activity is stimulated by the falling of darkness and not by changes in temperature or humidity, and is stopped by daybreak, while the amount of activity can be influenced by temperature and/or humidity (1952, 1956a, 1956b, 1958). He found that in the dark, humidity responses are weaker than in the light and he supposes that this change in humidity responses enables the animals to move about at night (1952, 1956b).

1.5.2. COLE (1946) mentions that specimens of *Trachelipus rathkei* (Brandt) left their shelters under oak boards at night to walk around, but not all individuals did so, for considerable numbers could be found under the boards during the entire night.

FRITSCHE (1934) observed *Porcellio scaber* Latr. moving about during the day; he mentions that in 1897 VOSSELER saw large numbers of *Porcellio wagneri* Brandt walking in the sunshine.

STANDEN (1921) found large numbers of woodlice during the day on stones and on vegetation after a period of heavy rains.

A comparable observation was made by ABBOTT (1918) who during the day found many specimens of *Porcellio scaber* on green plants (up to 4–5 feet above the ground) in a period when the ground was extremely wet and partly flooded.

COLE (1946) also mentions that he found specimens of *Trachelipus rathkei* at a height of 4 feet above the ground on a day when the ground was extremely wet.

FRITSCHE (1934) observed that specimens of *Porcellio scaber* can be found in places at a considerable distance above the ground, whereas *Oniscus asellus* L. is never found in such places.

The only author who studied the activities of woodlice in a natural environment to some extent is LE GAY BRERETON (1957). During 1953 and 1954 he observed the activities of *Porcellio scaber* at night in a garden at Oxford and in Wytham Great Wood near Oxford. The results of the investigations of LE GAY BRERETON, which are of special interest to the present work, will be discussed in Chapters 2 and 3.

1.5.3. Many authors have made laboratory studies of the reactions and orientations of woodlice to differences in light-intensity (TORREY and HAYS, 1914; ABBOTT, 1918; MÜLLER, 1925; BUDDENBROCK and SCHLIEPER, 1926; HENKE, 1930; DIETRICH, 1931; BROOKS, 1942; FISCHBACH, 1954), to gradients of air humidity (ALLEE, 1926, 1931; GUNN, 1937; WALOFF, 1941; BROOKS, 1942; CLOUDSLEY-THOMPSON, 1956b), to gradients of air temperature (BARLOW and KUENEN, 1957) and to gravity (HENKE, 1930; FISCHBACH, 1954). Since these experiments are on the whole unconnected with activities of woodlice under natural conditions their results will not be discussed.

6. HUMIDITY OF THE AIR [1.6.]

1.6.1. Air humidity can be an important ecological factor for terestrial plants and animals, because it influences the amount of water-loss by transpiration. Thus, when considering air humidity in ecological investigations generally we should express this factor in terms of the evaporative power of the air. Two measures for air humidity are in use, *viz.*:

a. Relative Humidity (R.H.): the amount of water vapour present in comparison with the amount at saturation at the same temperature and atmospheric pressure; this is expressed as the percentage of saturation.

b. Saturation Deficit (S.D.) or Vapour-pressure Deficit: the difference between the water vapour pressure at saturation and the actual vapour pressure at the same temperature and atmospheric pressure; this is expressed in mm of mercury.

From these definitions it is obvious that S.D. is related more to the evaporative power of the air than R.H. (see also: EDNEY, 1957, Chapter 1).

Botanists express the evaporative power of the air more directly as the Suction Pressure (= Diffusion-pressure Deficit) of the air (VAN DEN HONERT, 1948), which is proportional to saturation deficit rather than to relative humidity, *e.g.*: the evaporative power of the air is higher at R.H. 80 % and temperature 20° C (S.D. = 3.7 mm and Suction Pressure = 297.5 atm) than at R.H. 80 % and temperature 10° C (S.D. = 1.9 mm and Suction Pressure = 287.4 atm) at the same atmospheric pressure.

In agreement with these considerations, in the present investigation, correlations with S.D. were always stronger than the corresponding correlations with R.H. (in the present paper only the correlations with S.D. are given).

1.6.2. A number of different hygrometers were tested and compared. When sufficient precautionery measures are taken, the readings of different types of psychrometers and electrical hygrometers agree quite well. Since most electrical hygrometers can only be used in either wholly stationary or flowing air preference was given to the Assmann psychrometer which generates its own constant air-current and gives the most reliable results.

In the present investigation only the Assmann psychrometer was used to measure S.D. Unfortunately, this instrument cannot be used for measuring S.D. in small spaces (*e.g.* shelters of woodlice) and up to the present no reliable hygrometer has been constructed for this purpose.

Hair hygrometers could not be used at all because these instruments must be recalibrated after each change in temperature. Moreover the indications of the instruments are not reproducable even in a thermo-hygrostat. Deviations of 30–40 % R.H. were not exceptional, especially in very moist air.

Hygrographs with hair-bundles can be used to get a rough idea of the trend of the R.H. during a 24-hour period, but only if the temperature does not fluctuate greatly. The absolute value of the R.H. indications of the instrument is not reliable, however, because considerable deviations were found (especially under very moist conditions).

7. STATISTICAL METHODS USED [1.7.]

1.7.1. When making quantitative observations under natural conditions, nothing or little is known about the mathematical distribution form of the populations studied. Thus, when working up the quantitative results of field observations it is necessary to use methods of estimation or test, which are not dependent upon the mathematical distribution form of the populations, *i.e.* it is necessary to use rank-order tests.

On the other hand, if we replace variate values by rank-numbers we standardize the scale of the variate and consequently there will be some loss of special information. In my case, however, as in many other practical situations, the power of rank-order tests has been surprisingly high and I am therefore certain that little has been lost by employing ranking methods.

Moreover, since I am not interested in the absolute value of my quantitative estimations but only in their being larger or smaller than other estimations, it is more logical, from a theoretical point of view, to use the rank-numbers of my estimations than to use the corresponding variate values.

The following statistical methods have been used in the present investigation:

1.7.2. Wilcoxon's two-sample test. In all cases in which the homogeneity of two samples of quantitative estimations had to be tested, Wilcoxon's test could be used (Van der Vaart, 1950; Wabeke and van Eeden, 1955). In all such cases the difference between the two samples is only given by the value of p (probability with a two-sided critical region) and in some cases by the value of $x = \frac{U - \frac{1}{2}mn}{\sigma_n}$ as well (in the null case x is a normally distributed variable with mean 0 and standard deviation 1).

1.7.3. Rank correlations. To test whether or not there is a correlation between two samples of quantitative estimations, the rank correlation method of M.G. Kendall is used (Kendall, 1955). These correlations are given in this paper by the value of τ and the value of the corresponding p (probability with a two-sided critical region); in some cases $x = \frac{S}{\sigma_s}\left(= \frac{\bar{\tau}}{\sigma_{\bar{\tau}}}\right)$ is also given (x normally distributed; mean 0 and stand. dev. 1).

1.7.4. In a number of cases we are faced with the question of whether a correlation of A with B is really due to the correlations of each with a third quality C. By means of the method of partial rank correlation (Kendall, 1955: Chapter 8) it is possible to correct the correlation of A with B for the effect of C, by considering sub-populations in which the variation of C is eliminated. Conclusions from such corrected correlation-coefficients must be drawn with a certain amount of caution. Moreover, it is not possible to test the significance of partial τ.

1.7.5. When the numbers of active specimens in different parts of the year (or in different years) are correlated with some other quality (*e.g.* temperature), unknown fluctuations of population density in the course of the year (or in the course of a number of years) may mask the real relationship. A better approximation of this relationship can be obtained by splitting up the original period into k shorter periods and by calculating the correlation-coefficient τ_i for each period i separately, after which the coefficients τ_i are combined again. By this means the masking effect of fluctuations of population density is reduced to the much smaller effect within each period i separately. The resulting correlation-coefficient $\bar{\tau}$ is the arithmetical mean of the different τ_i's $\left(i.e.\ \bar{\tau} = \sum \frac{\tau_i}{k}\right)$.

The significance of $\bar{\tau}$ can be tested as follows: $\mathrm{var}\,(\tau_i) = \frac{2(2n_i + 5)}{9n_i\,(n_i - 1)}$ (without ties) (KENDALL, 1955, p. 71); from this follows:

$$\mathrm{var}\,(\bar{\tau}) = \frac{1}{k^2} \sum \mathrm{var}\,(\tau_i) = \frac{1}{k^2} \sum \frac{2(2n_i + 5)}{9n_i(n_i - 1)} = \frac{1}{k^2} \sum \frac{\frac{1}{18} n_i(n_i - 1)(2n_i + 5)}{\{\frac{1}{2} n_i(n_i - 1)\}^2}.$$

$\sigma_{\bar{\tau}} = \sqrt{\mathrm{var}\,(\bar{\tau})}$; $x = \frac{\bar{\tau}}{\sigma_{\bar{\tau}}}$, in the null case normal (mean 0 and stand. dev. 1). When ties of small extent are present, the above formula is still a good approximation.

1.7.6. When observationed frequencies in a distribution must be compared with frequencies which may be expected according to an assumed hypothesis, the Chi-square test (χ^2) is used. In such cases the difference is given by the value of p (probability with a two-sided critical region) and in most cases by the value of χ^2 as well.

In all tests 0.05 is chosen as a level of significance.

1.7.7. In Chapters 3 and 5 it will be noticed that the τ values of rank correlations on which conclusions are based are not very high (about 0.25–0.60). In field studies of the relations between the amount of activity of an animal population and the value of a particular meteorological factor, many unknown factors will have a masking effect on the real relationship, so that the observations will show considerable dispersion. In such cases correlations with high τ values cannot be expected (see also 8.3). If enough observations are made, the p value will indicate whether or not it is probable that a correlation exists, whereas the τ value gives an idea of the amount of correlation which may be observed in the field in spite of the disturbing effects of many factors.

2. THE DAY-HABITAT OF PORCELLIO SCABER

When studying the activities of animals at night it is necessary to know where the animals can be found when they are inactive, *i.e.*: to know something about their day-habitat.

1. DATA FROM THE LITERATURE [2.1.]

Many authors have discussed the places where woodlice can be found during the day, *e.g.*: HEROLD, 1925, 1928, 1929, 1930; MILLER, 1938; MEINERTZ, 1944, 1950; COLE, 1946; *etc.*

2.1.1. All species are found in places where the animals are well protected against desiccation, but there are differences in the moistness of the places which are preferred by the different species. Several authors have pointed to the series: *Ligia*, *Philoscia*, *Oniscus*, *Porcellio*, *Cylisticus*, *Armadillidium*, in which the moistness of the preferred places decreases from *Ligia* to *Armadillidium*. This habitat-selection is correlated with resistance to desiccation (MILLER, 1938; EDNEY, 1951a) and with the structure and function of the respiratory organs (MILLER, 1938; MEINERTZ, 1944).

COLE (1946) mentions that more specimens of *Trachelipus rathkei* (Brandt) could be found under oak boards on moist ground than under boards on dry ground. Woodlice are considered by COLE to be typical cryptozoic animals, *i.e.* animals which mainly live in a hiding-place.

2.1.2. MEINERTZ (1944), who examined 3000 localities in Denmark for the presence of woodlice, gives a detailed description of the places in which *Porcellio scaber* Latr. was to be found during the day. From his observations it is clear that *Porcellio scaber* is mainly found in places where there are moist shelters. One gets the impression that in relatively dry localities the animals can only find a moist shelter in or under compact or large masses of material, whereas in moister localities they can also find adequate shelter in or under less compact materials. The curious preference of *Porcellio scaber* for the base of walls which was found by MEINERTZ wil be discussed later (3.2.2).

2.1.3. LE GAY BRERETON (1957) has studied the places where *Porcellio scaber* can be found during the day-period in Wytham Great Wood near Oxford. In winter it was found in large numbers in the moss layer at the base of trees, especially oak, ash, and sycamore. Moreover, many specimens were found at eye-level in shelters under the "flakey" bark of large sycamore trees. Only a few specimens were found in the litter. In summer this species was also found at the base of trees and in shelters at eye-level in a number of tree species but in much smaller numbers than in winter. LE GAY BRERETON supposes that in summer the animals move into shelters in the upper parts of the trees (see 3.4.2). In summer only a few specimens were found in the litter.

2. DAY-HABITAT OF THE POPULATIONS USED FOR ACTIVITY OBSERVATIONS [2.2.]

2.2.1. In the two aspen woods in the Bierlap dune area in which activity observations were made, a number of samples from soil and litter were taken and examined in 1953. For this purpose the vegetation, litter, and soil with roots (to a depth of 5 cm) were removed from a surface of 50 × 50 cm. In each sample the number of specimens of *P. scaber* was determined and in a number of these samples the dry weight of the following parts was estimated: vegetation, roots, coarse litter (parts larger than 5 mm), and fine litter (parts smaller than 5 mm).

Nineteen samples were taken from the centre of the "first" aspen wood (see map, Fig. 2), eight samples from the W-border, four from the N-border, and one from the E-border of this wood; from the "second" aspen wood twelve samples were taken (the second aspen wood is much smaller than the first, and no distinction was made between samples taken from the centre and samples taken from the borders). In the first aspen wood eight samples were also taken at the base of trees, *viz.* six from the centre and two from the W-border of this wood.

TABLE I

Number of specimens in samples taken from the two aspen woods

first aspen wood						second aspen wood	
centre of the wood		borders of the wood		at the base of a tree		date	number of specimens
date	number of specimens	W-border		centre of wood			
		date	number of specimens	date	number of specimens		
July 16 **A**	1 0 2 2	July 24 **C**	5 6 11 16	August 27 **N**	17 3	August 3 **G**	0 1 0 0
July 28 **D**	2 8 0 0	July 29 **F**	14 4 11 14	Septem-ber 1 **P**	14 3 17 24	August 6 **H**	2 1 3 1
July 29 **E**	8 2 1 0	N-border		W-border of wood		August 11 **J**	1 0 0 0
		date	number of specimens	date	number of specimens		
August 13 **K**	0 3 0	July 16 **B**	5 4 0 1	August 27 **O**	115 39		
August 18 **M**	3 2 1 12	E-border					
		date	number of specimens				
		August 13 **L**	6				

2.2.2. Table I gives the figures for the number of specimens found in each of these 52 samples.

In general, more specimens were found in samples from the borders – especially the W-border of the first aspen wood – than in samples from the centre (the W-border is the only border which is limited sharply by a straight path made of concrete tiles; the other borders merge gradually into a vegetation of tall grasses and young aspen trees and cannot be traced sharply; see map, Fig. 2). When tested with Wilcoxon's two-sample test these differences are significant for different groups of samples (Table II); only the difference between A, K and B, L is not significant.

TABLE II

p value of the difference between two groups of samples

groups of samples (see Table I) *a*	*b*	*p value of the difference between a and b*
A, D, E, K, M	C, F, B, L	$p = 0.0037$
A, D, E, K, M	C, F	$p = 0.0006$
D, E	C, F	$p = 0.00019$
A, K	B, L	$p = 0.202$

Significantly more specimens were found in samples from the base of a tree than in samples without a tree: for the groups K, M as compared with N, P we find $p = 0.0182$. When a sample was taken from the W-border of the first aspen wood as well as from the base of a tree, it was found to contain a very large number of specimens (group O).

In agreement with my observations in the first aspen wood, Le Gay Brereton (1957) has also observed that in Wytham Great Wood more specimens are found at the base of a tree than in the litter (2.1.3).

The mean number of specimens per sample amounts to 4.5 for the first aspen wood (mean of 32 samples) and to 0.75 for the second aspen wood (mean of 12 samples). This difference is significant: for the groups A, D, E, K, M, C, F, B, L as compared with the groups G, H, J we find $p = 0.00614$.

2.2.3. Other properties which were determined only for samples of groups K, M, L, N, P, O, H, J are generally not correlated with the numbers of specimens they contained. With the rank correlation method (1.7.3) the following correlations could be estimated:

a. with the dry weight of coarse litter: $\tau = +0.183$, $p = 0.2380$;
b. with the dry weight of fine litter: $\tau = -0.290$, $p = 0.0588$;
c. with the dry weight of coarse + fine litter: $\tau = -0.042$, $p = 0.8026$;
d. with the dry weight of vegetation: $\tau = -0.306$, $p = 0.1212$;
e. with the dry weight of roots: $\tau = +0.137$, $p = 0.3788$.

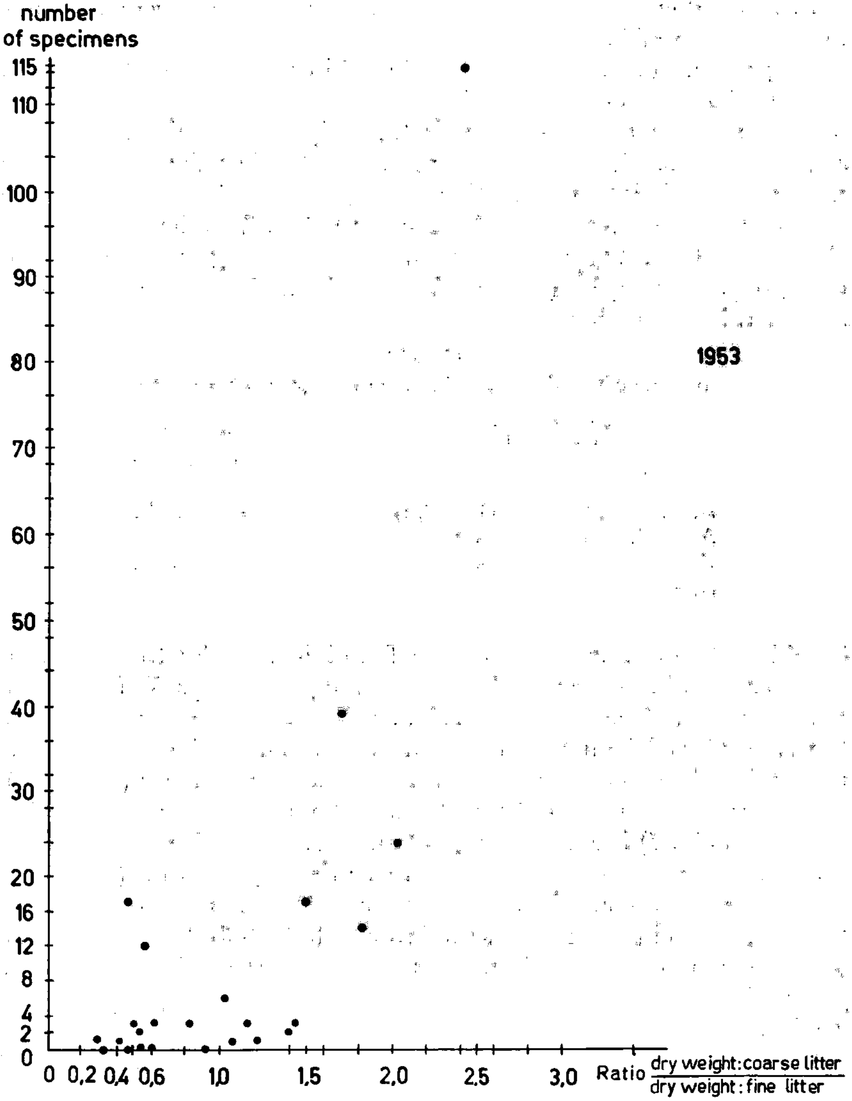

Fig. 3. Relation between the ratio: $\frac{\text{dry weight: coarse litter}}{\text{dry weight: fine litter}}$ and the number of specimens in samples taken from the litter of two aspen woods.
$\tau = +\ 0.471$, $p = 0.00214$

The number of specimens may be negatively correlated with the dry weight of fine litter. Since specimens were generally found under the larger bits of the litter, it was supposed that the percentage of coarse litter may be an important factor. In agreement with this the number of specimens was significantly correlated with the ratio: $\frac{\text{dry weight of coarse litter}}{\text{dry weight of fine litter}}$ (Fig. 3: $\tau = +\ 0.471$, $p = 0.00214$).

2.2.4. The day-habitat of woodlice must certainly be considered as mainly a shelter against the relative dryness of the day-period, and it is thus obvious that the more coarse elements the litter contains the more shelter there can be found in it. A good illustration of this phenomenon is given by four samples taken from a small wood which consists of old black poplars (*Populus nigra* L.) situated in another part of the dunes (Table III).

TABLE III

Number of specimens in four samples

sample	*number of specimens*	*dry weight in mg of:* *coarse litter*	*bits of bark and wood in coarse litter*	*fine litter*	*coarse + fine litter*	*ratio:* $\frac{\text{coarse litter}}{\text{fine litter}}$
N1	19	377	0	312	689	1.21
N2	77	521	172	230	751	2.27
N3	14	234½	0	216½	451	1.09
N4	148	628	127	261	889	2.41

The significant difference in the number of specimens in samples from the first aspen wood (4.5 ind./sample) and in samples from the second aspen wood (0.75 ind./sample; see 2.2.2) is probably due to the unfavourable ratio of coarse to fine litter in the second aspen wood (the ratio: $\frac{\text{dry weight: coarse litter}}{\text{dry weight: fine litter}}$ is almost significantly smaller ($p = 0.0650$) for samples of the groups H, J than for samples of the groups K, M, L).

3. OTHER OBSERVATIONS ON THE DAY-HABITAT OF PORCELLIO SCABER [2.3.]

2.3.1. In the four years (1953–1957) during which I studied *P. scaber* in the dune area of Meijendel, I found it by day mainly in the following places:

a. In cavities and under the loose bark of dead or dying trees (in some cases many hundreds of specimens together).

b. Under fallen trees, under the loose bark, and in the decaying wood of fallen trees and of tree stumps.
c. Under branches, bits of bark, and decaying wood only when these materials lay in the litter of woods.
d. In the litter of deciduous woods, especially those of black poplars and aspens (with a preference for the base of trees and the borders of the wood).
e. At the base of brick walls (Water Company pump houses).

No specimens or only very few can be found during the day in the open dunes, in open areas with a dense vegetation, in areas with only scattered trees, in small bushes of creeping willows (*Salix repens* L.) and thorn bushes (*Hippophaë rhamnoides* L.). In large bushes *P. scaber* can be found frequently, although usually not in great numbers.

In other localities (in the neighbourhood of Leiden) great numbers of *P. scaber* are found: under stones; in heaps of stones, rubbish, and compost; in dunghills; under planks, boards, and other materials.

In 1954 some observations on *P. scaber* were made in Finland (Tvärminne). Specimens of this species were found in exactly the same kind of day-habitats as in Holland and also in and under heaps of *Fucus* spec. which had been washed ashore.

2.3.2. For specimens which have found a day-habitat in cavities and under the loose bark of dead or dying trees, the species of tree clearly does not play a part. As far as I can judge, the only important factor is whether or not a suitable shelter is present. In Meijendel specimens have been found in cavities and under the loose bark of *Populus nigra* L., *Populus tremula* L., *Betula verrucosa* Ehrh., *Sambucus nigra* L., and *Crataegus monogyna* Jacq.; in Finland of *Pinus* spec., *Betula* spec., and *Alnus* spec. Because in Meijendel many black poplars and aspens are dying, a large number of suitable shelters is present especially in these trees, so that it is easy to collect many hundreds of specimens by breaking open a number of them.

According to LE GAY BRERETON (1957), *P. scaber* has a preference for special tree species. The order of preference is beech (*Fagus sylvaticus* L.), sycamore (*Acer pseudo-platanus* L.), oak (*Quercus robur* L.), ash (*Fraxinus excelsior* L.), silver birch (*Betula verrucosa* Ehrh.), while in Scotch pine (*Pinus silvestris* L.) and larch (*Larix decidua* Mill.) no specimens were found. The differences in preference between the tree species are not significant, however. The order of preference found by LE GAY BRERETON is no doubt an order of suitability as shelters.

2.3.3. Specimens of *P. scaber* cannot be found in every place which looks to us at first like a good shelter. Some special conditions must be fulfilled to make a shelter a suitable day-habitat. For a dead or dying tree, these conditions are:

a. The shelter must be moist but not wet; a certain amount of water must be absorbed in the decaying wood or in the bark, but excess water must not be present.

b. The cavity must be narrow, so that a woodlouse which creeps into it can be in touch with the substratum with both its dorsal and ventral sides. As a result of this, the loose bark of a dead or dying tree presents much more suitable shelters than cavities in the wood.

c. The openings which connect the shelter with the open air must be as narrow as possible.

When in 1956 observations were made in artificial shelters in trees, care had to be taken that these conditions were continuously fulfilled.

4. GENERAL CONCLUSIONS [2.4.]

2.4.1. A review of the data given in this chapter makes it obvious that only one factor really determines the suitability of a shelter for *P. scaber* (and probably for most other woodlice as well). This factor is the moistness of the shelter. Under natural conditions woodlice are only protected against desiccation in shelters which are situated in comparatively large masses of water-absorbing materials. Air humidity in the shelter is buffered better at a high level if the surface of the shelter walls is large with respect to the content of the shelter (*i.e.* when the shelter is narrow) and if the exchange of air with the open air is minimal (*i.e.* when the entrances into the shelter are very small and few in number). On the other hand, for woodlice the entrances to a shelter must be easy to find (*i.e.* these entrances must extend over relatively long distances), so that fissure-shaped entrances are the best possible type. From this it will be clear that the best shelters are offered by the loose bark of dead or dying trees and by compact objects which lie flat on the ground, such as planks, fallen trees, heaps of rubbish, stones, *etc.*

2.4.2. I do not believe that woodlice require unknown capacities to enable them to find suitable shelters. Mainly as a result of their very strong thigmotactic tendencies they will arrive quite easily at a fissure-shaped shelter after a period of activity. Their hygrotactic tendencies (GUNN, 1937; WALOFF, 1941; BROOKS, 1942; CLOUDSLEY–THOMPSON, 1956b) and negative phototactic tendencies (see *e.g.*: TORREY and HAYS, 1914; MÜLLER, 1925; DIETRICH, 1931) may also play a part in the finding of a suitable shelter. Inside the shelter woodlice are able to restrict their water-exchanges with the surrounding air by bunching (ALLEE, 1926, 1931).

3. DIRECT OBSERVATIONS ON ACTIVITIES IN A NATURAL ENVIRONMENT

1. OBSERVATIONS ON "HORIZONTAL ACTIVITY" [3.1.]

3.1.1. When preparing to observe in August 1953, the first problem was to find a method for measuring the activity of a *P. scaber*-population. As such a relative measure we chose the number of specimens which could be seen moving about on a certain area of ground at a given moment.

This number of specimens depends on both the density and the amount of activity of the population concerned. In consequence, it can only be used as a relative measure of the amount of activity of this population when the fluctuations in density are much smaller than the fluctuations in amount of activity within the period of investigation.

Since it may be accepted that the populations of *P. scaber* on which the observations were made (the populations inside of two aspen woods) are relatively well isolated, migration will have no great influence on the density of these populations. Other causes of density fluctuations (reproduction, mortality) are likely to manifest themselves in woodlice only in the course of long periods of time. Therefore, when the observations are made after the reproduction period within a period of one or two months it may be assumed that the number of specimens active on a certain area gives a reasonable indication of the amount of activity, although fluctuations in the density of the population concerned may confuse the results to some extent.

3.1.2. The area in which the amount of activity is to be measured must be easy to observe. A stretch of path consisting of 415 concrete tiles, 100 × 50 cm each, appeared to be very suitable for this purpose: woodlice moving about at night did not alter their behaviour at all when crossing the path; moreover, one tile at a time could be observed at once by means of a high-powered paraffin lamp (Tilley).

The path runs through the following types of terrain (see map, Fig. 2):

a. tiles 1–70: mostly bare sand with patches of grasses, mosses, and lichens, and some small bushes.

b. tiles 71–145: at the very edge (W-border) of a dense aspen wood, the "first" aspen wood (A).

c. tiles 146–250: an open area covered by *Calamagrostis epigejos* (L.) Roth. and some other grasses.

d. tiles 251–331: an aspen wood with an undergrowth of grasses, the "second" aspen wood (B).

e. tiles 332–415: an open area covered by *Calamagrostis epigejos* (L.) Roth. and large groups of thorn bushes (*Hippophaë rhamnoides* L.).

During the period July 27 – September 30, 1953 the *P. scaber* individuals present at about 11:00 p.m. on the 415 m long path were counted on 44 nights. On 36 of these nights temperature and humidity of the air were also measured at about 1½ m above the path by means of an Assmann psychrometer.

3.1.3. The mean number of specimens per observation period and per tile for each of the surrounding vegetation types is given in Table IV.

TABLE IV

Mean number of specimens on different parts of a stretch of path

type of terrain	*tiles*	*mean number of specimens per count and per tile*	*type of terrain*	*tiles*	*mean number of specimens per count and per tile*
a	1–70	1.3	d	251–331	1.1
b	71–145	3.5	e	332–415	0.6
c	146–250	1.4			

In 2.2.2 we saw that in the second aspen wood population density is significantly smaller than in the first aspen wood; in accordance with this, significantly fewer specimens were active ($p < 0.000066, x = 4.95$) in the second aspen wood than at the border of the first aspen wood.

Moreover, it is evident from the Table that active specimens were not only observed at the border of the first and inside the second aspen wood but also outside the woods. Since I am certain that in areas a and c (tiles 1–70 and 146–250 respectively) no suitable shelters are present and in area e (tiles 332–415) only a few if any, nearly all specimens observed must have come from the two aspen woods.

If this is the case, more individuals should have been observed in the immediate vicinity of the aspen woods than at greater distances from these woods. The number of specimens observed indeed decreases with the distance from the first aspen wood (under the young aspen trees no suitable shelters are present, see Fig. 4), whereas with the second aspen wood this phenomenon is less clear (Fig. 4).

3.1.4. The small number of active specimens observed in the centre of the second aspen wood is surprising. The observations were all started at 11:00 p.m. This means that the observations were made 2½ hours after dark towards the end of July and 4½ hours after dark in September. During the whole period, however, the same phenomenon was observed, so the most justifiable conclusion is that population density was much smaller in the centre of the second aspen wood than

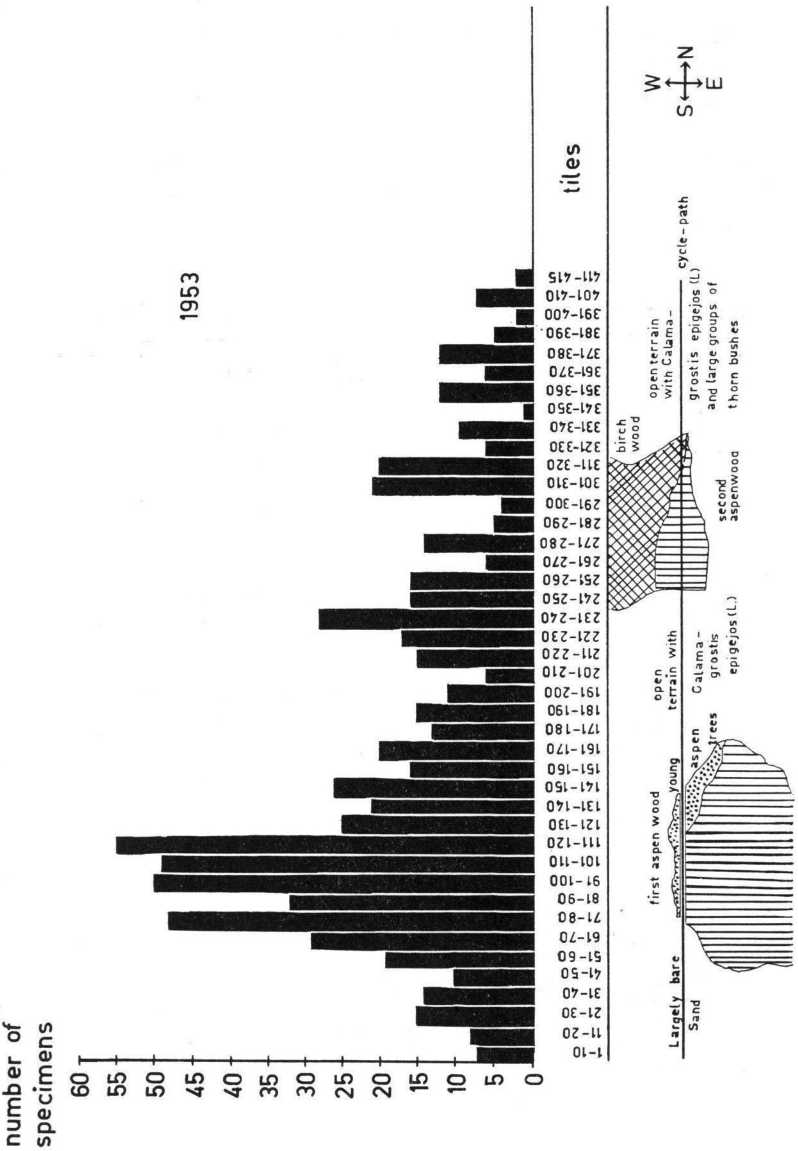

Fig. 4. Distribution of active specimens on the path (total number per ten tiles, summarization of 44 observations).

at the borders. It will be recalled that we reached the same conclusion for the first aspen wood (2.2.2).

In my opinion, this difference in population density between centre and borders of the two aspen woods is caused by the activities of the animals. Specimens which move about outside the woods sooner or later will have to look for shelters. The first shelters these animals are able to find are situated at the borders of the woods, so that more specimens will arrive at shelters at the borders of a wood than at shelters in the centre. This difference will become larger if the animals have a preference for moving outside the woods during the night.

3.1.5. When making the observations it became evident that only on certain nights could a number of active specimens be found at greater distances from the two aspen woods. As a relative measure for the distance the animals cover outside the woods the relation was chosen between the number of specimens observed at 0–40 m from the W-border of the first aspen wood (on tiles 80–41 and 131–170) and the number of specimens observed at 40–80 m from the W-border of the first aspen wood (on tiles 40–1 and 171–210; see Fig. 4), *i.e.* the ratio:

$$\frac{\text{number of specimens on tiles 80–41} + \text{131–170}}{\text{number of specimens on tiles 80–1} + \text{131–210}} \times 100\,\%.$$

This ratio is significantly correlated with S.D. ($\tau = +0.285$, $p = 0.0188$; see Fig. 5) and not significantly with air temperature ($\tau = +0.201$, $p = 0.0950$). Possibly the correlation with temperature is indirect and due to the correlation between temperature and S.D. ($\tau = +0.436$, $p = 0.00030$). After correction for this correlation (1.7.4) between temperature and S.D. there remains only $\tau = +0.089$, whereas for the correlation with S.D. there remains $\tau = +0.224$ after the same correction.

Because observations on tiles 171–210 may be confused by specimens coming from the second aspen wood, the ratio:

$$\frac{\text{number of specimens on tiles 80–41}}{\text{number of specimens on tiles 80–1}} \times 100\,\%$$

may give a more reliable measure. This ratio too is significantly correlated with S.D. ($\tau = +0.360$, $p = 0.00736$) and also significantly with temperature ($\tau = +0.292$, $p = 0.030$). After correction of the latter correlation for the correlation between temperature and S.D. there remains $\tau = +0.161$, whereas for the correlation with S.D. there remains $\tau = +0.270$ after this correction.

3.1.6. If woodlouse individuals move about during the whole night as is generally accepted, it may be expected that four hours after dark

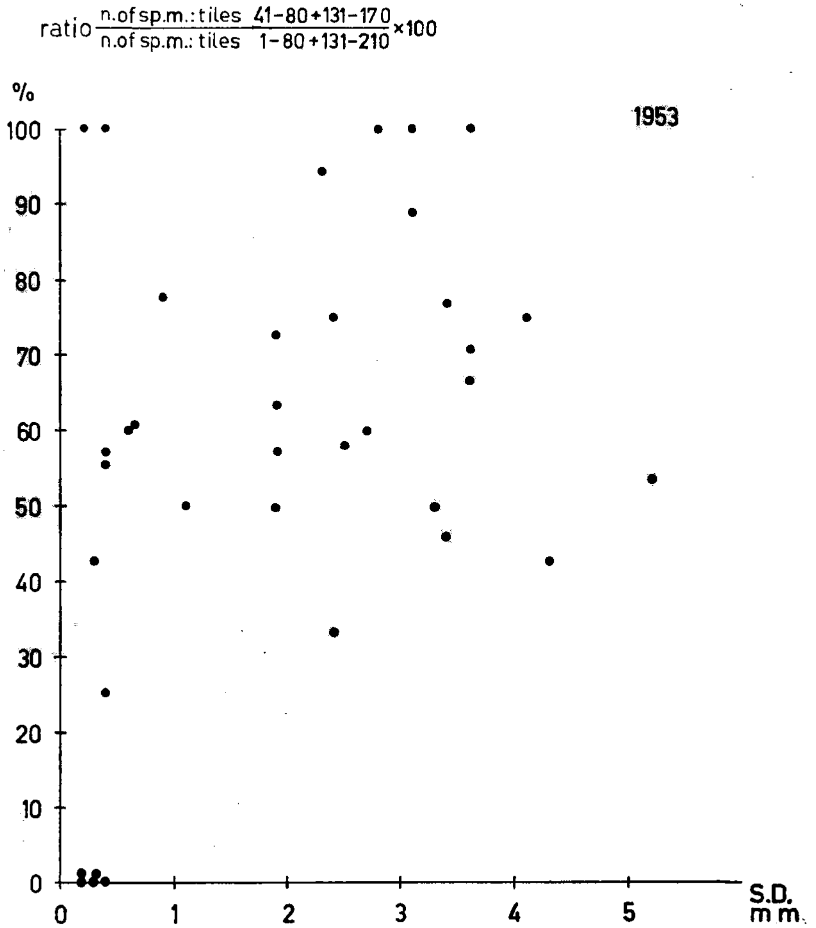

Fig. 5. S.D. and the relation between the number of specimens moving about at distances between 40 and 80 m from the first aspen wood (on tiles: 1–40 and 171–210) and the number moving about at distances between 1 and 40 m from the first aspen wood (on tiles: 41–80 and 131–170); single observations.
$\tau = +0.285$, $p = 0.0188$

more specimens of *P. scaber* will be found at greater distances from their shelters (the two aspen woods) than three hours after dark, *i.e.*: the above ratios will be larger for observations made in the period August 4–August 28 (2½–3½ hours after dark) than for observations made in the period August 31–September 29 (3½–4½ hours after dark). Such differences, however, were not found ($p = 0.3078$ and $p = 0.5754$ respectively) in my observations. Moreover, if activity lasted during the whole night the correlations found between the above ratios and S.D. could only mean that the animals move faster when air humidity is higher (there is no significant difference between the S.D. values in the period August 4 – August 28 and the S.D. values in the period August 31 – September 29: p = 0.8135).

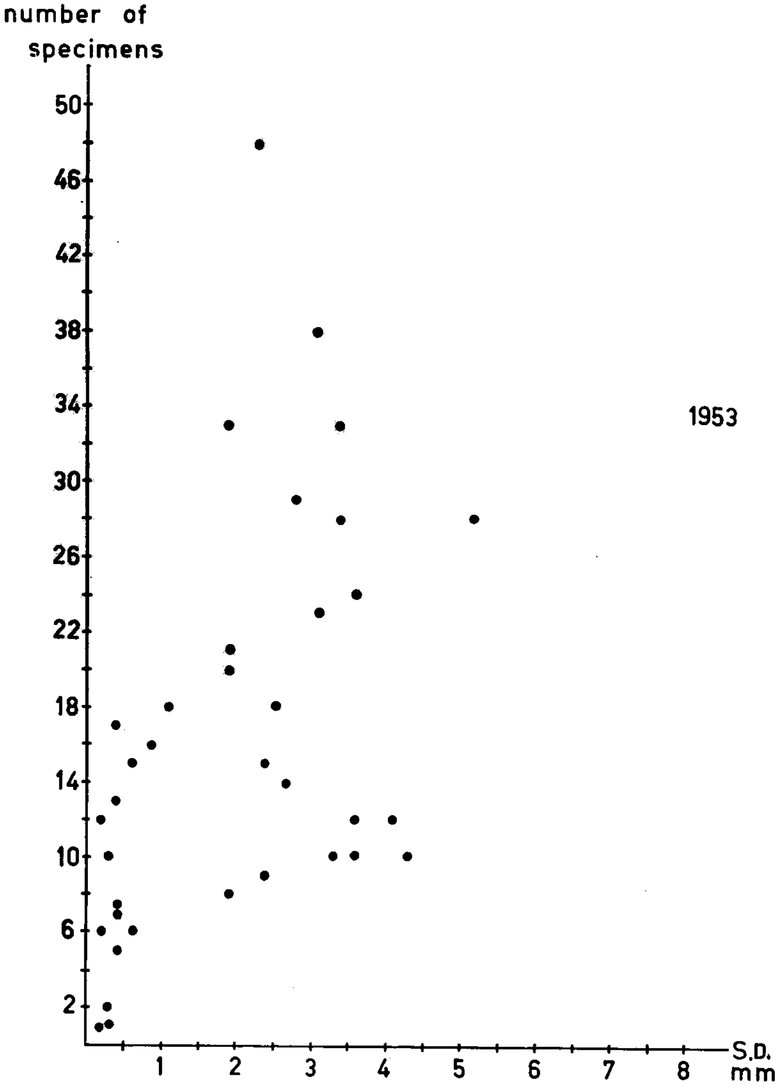

Fig. 6. Relation between the amount of horizontal activity (single observations) and S.D.
$\tau = + 0.398$, $p = 0.00096$

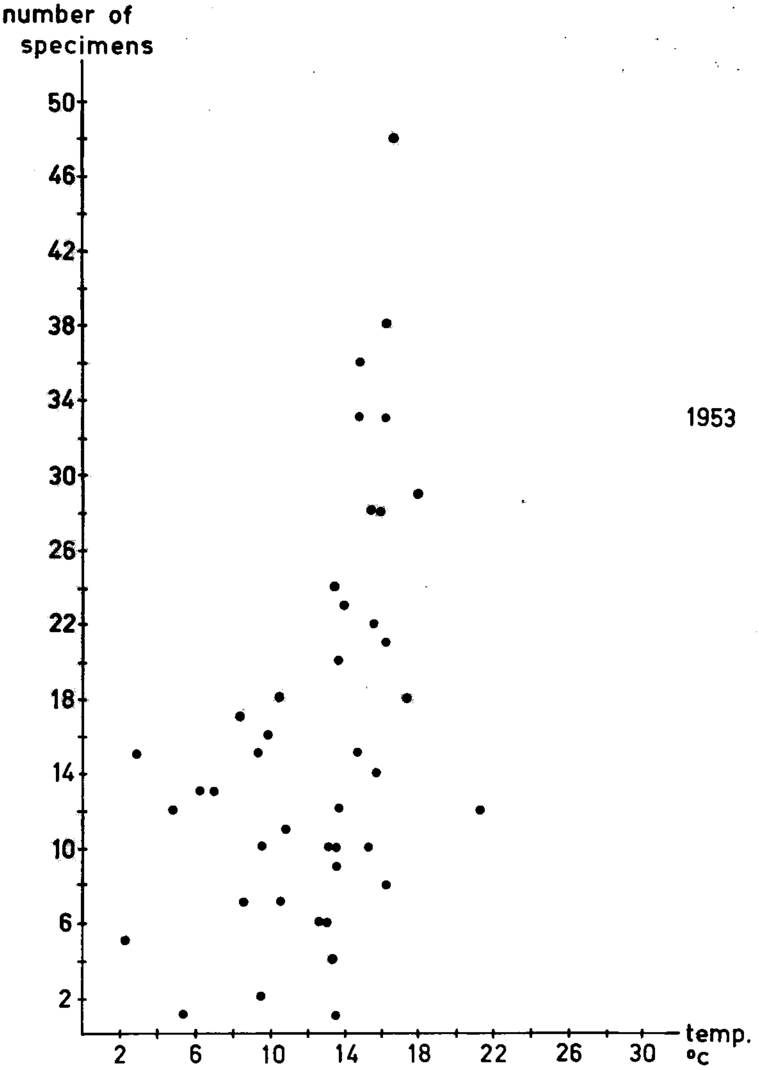

Fig. 7. Relation between the amount of horizontal activity (single observations) and temperature.
$\tau = +0.425$, $p = 0.00036$

In my opinion, individuals of *P. scaber* do not move about during the whole night but only during part of the night. Every moment in the course of a night a number of specimens will become active and other specimens will end their activities and seek shelter (more arguments for this will be given in 3.3.7 and 3.3.8). Thus, the correlations with S.D. must indicate that the individual period of activity lasts longer when air humidity is higher. The correlations with temperature possibly indicate that the individual period of activity lasts longer when air temperature is lower.

3.1.7. If this is true, many active specimens would have been observed on the path as a whole when S.D. was small, that is to say there must be a negative correlation between numbers and S.D. It was therefore very startling to find a positive and significant correlation between the number of active specimens observed on the path and S.D. ($\tau = +0.398$, $p = 0.00096$; see Fig. 6) and a positive and significant correlation between the amount of activity and temperature ($\tau = +0.425$, $p = 0.00036$; see Fig. 7). These correlations can only be understood after the observations on another form of activity, the so-called "vertical activity" (as opposed to the "horizontal activity" which is discussed here) have been discussed. In 3.2.5 we will return to this subject.

3.1.8. Only the results of single observations (one observation on each night) on horizontal activity have been given so far. These results would gain in significance if it could be demonstrated that one observation made at about 11:00 p.m. gives a representative measure for the amount of activity during the whole night.

For this purpose the number of active specimens on the path was counted each hour between nightfall and daybreak during eight nights in 1953. Apart from the small numbers at nightfall and at daybreak, the amount of activity did not alter very much during any given night, so the number of active specimens at about 11:00 p.m. does give a reasonable measure for the amount of activity during the whole night (Fig. 8).

The reliability of the single observations can be illustrated by comparing for these eight nights the correlation between the amount of activity at about 11:00 p.m. and S.D. ($\tau = +0.444$, $p = 0.1310$) or temperature ($\tau = +0.519$, $p = 0.1032$) at the same hour with the correlation between the mean amount of activity per count/per night and the mean S.D. ($\tau = +0.444$, $p = 0.1310$) or the mean temperature ($\tau = +0.571$, $p = 0.062$) per count/per night. Moreover, these correlations agree very well with the correlations found for the 36 single observations and which are given in 3.1.7. These correlations can not be expected to be significant, since they have been calculated from only eight pairs of observations.

The amount of activity on the path was also measured during eight entire nights in 1954, but the numbers of active specimens were so small that in my opinion calculations with these values on the possible correlations with S.D. and temperature are not justifiable.

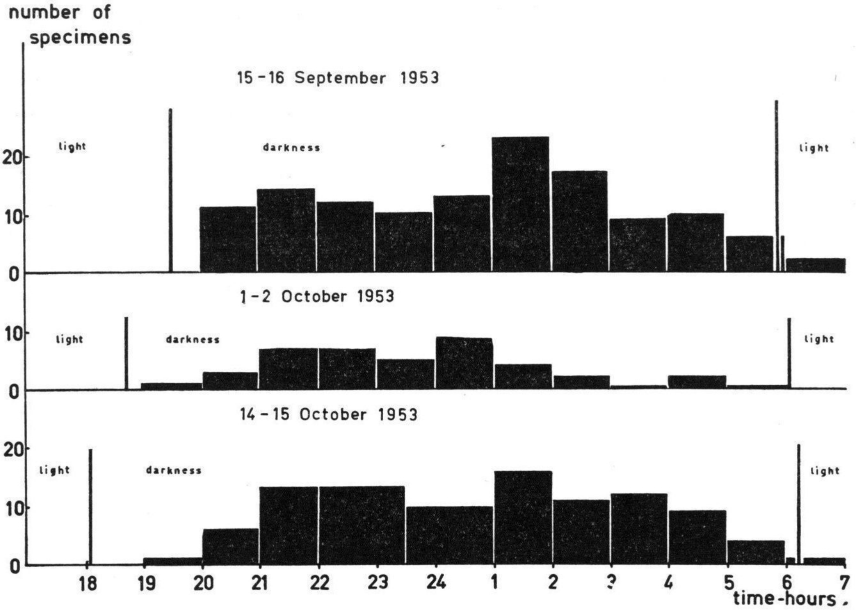

Fig. 8. Amount of horizontal activity at various counts during one night.

3.1.9. In 3.1.6 it was suggested that individuals are only active during part of the night and that the period of activity is longer the higher the humidity of the air and, possibly, the lower the temperature of the air. During the observation nights the humidity and temperature of the air did not vary very much in the course of one night (sea-climate), and therefore the ratio:

$$\frac{\text{number of specimens on tiles } 80\text{–}41 + 131\text{–}170}{\text{number of specimens on tiles } 80\text{–}1 \quad + 131\text{–}210} \times 100\ \%$$

will not differ essentially for different parts of the night. To test the correctness of this supposition this ratio was calculated separately from observations made during the first three hours (group a), from observations made between 4 and 7 hours after dark (group b), and from observations made during the last three hours of these five nights (group c). Only five out of eight nights could be used because during the other three nights the numbers of specimens observed on the path were too small. These three groups of ratios were compared. No significant differences could be found.

2. OBSERVATIONS ON "VERTICAL ACTIVITY" [3.2.]

3.2.1. In the course of 1953 it was observed that at night specimens of *P. scaber* moved about not only outside the woods and on the litter but also on the trunks of trees. This form of activity appeared to have two origins. First, specimens climb up the trees from the litter; this form of activity will be called: "vertical activity". Second, part of the specimens which have found a shelter in cavities and under the loose bark of dead or dying trees move about on these trees; this form of activity will be called: "activity on trees".

As a measure of the amount of these activities we chose the number of specimens observed at a given moment between the base and about two meters above the ground on the trunk of 16 trees which were selected at random from the two aspen woods. The amount of these activities was measured each hour during entire nights in 1953 (8 nights), 1954 (12 nights), and 1955 (4 nights).

Only the observations on "vertical activity" will be discussed here, the "activity on trees" being reserved for 3.3. Six of the 16 trees were entirely sound and contained no shelters, so that the number of speci-

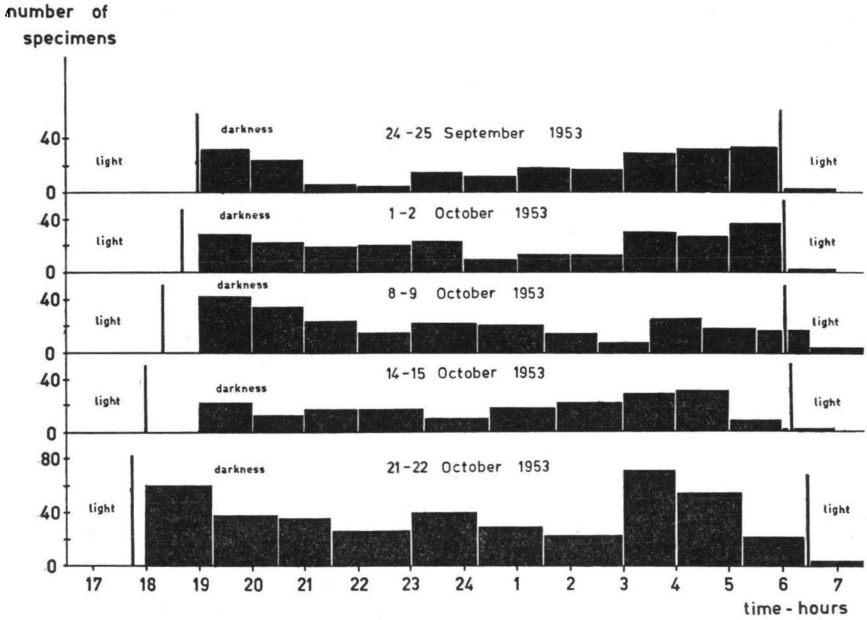

Fig. 9. Amount of vertical activity at various counts during one night.

mens observed on them gives a measure of the amount of vertical activity.

3.2.2. The number of specimens observed on all of these six trees did not vary very much in the course of a night (Fig. 9). It was remarkable that as soon as darkness had fallen relatively large numbers of specimens could be observed on the trees. These "early" specimens must have had their day-habitat very close to the observation-trees. In 2.2.2 it was mentioned that the base of a tree is a preferred day-habitat in *P. scaber*. Thus, it is clear that the specimens observed at nightfall on the six trees mentioned above had their day-habitats at the base of the observation-trees. Just as specimens which have been active outside a wood will find the most accessible shelters at the borders of this wood, specimens which have been active on the trunk of a tree will find the most accessible shelters at the base of this tree (if no shelters are present in the tree itself). Since vertical activity is a frequent phenomenon, more specimens will find a shelter at the base of a tree than anywhere else on the forest floor, so that population density around the base of a tree will be larger than elsewhere in the litter (2.2.2). The large numbers of specimens at the base of brick walls (2.1.2 and 2.3.1) are probably also due to vertical activity. Vertical activity on the brick walls of a Water Company pump house was observed.

3.2.3. It was important to establish whether the same specimens were observed on the trees at each count during a night. On a number of occasions, therefore, each animal present on the observation-trees was marked with a quick-drying paint (shellac-solution in alcohol with pigment). After one hour only about 5 % of the marked specimens was seen on the same trees.

The 95 % of the marked specimens which had disappeared after one hour must either have climbed higher up the trees or have returned to the litter. In 3.3.7 I will return to this subject.

3.2.4. In connection with the correlations found between the amount of horizontal activity and S.D. or temperature (3.1.7), it is important to know how the amount of vertical activity is correlated with these factors.

The following correlations with S.D. have been found:

1953: $\tau = -0.577$, $p = 0.0768$ ($n = 8$);
1954: $\tau = -0.259$, $p = 0.3078$ ($n = 11$);
1955: $\tau = -0.667$, $p = 0.334$ ($n = 4$).

The observations made in 1954 were spread over the whole year, so that fluctuations in population density will have had a large and masking effect on the real correlations (see 3.1.1). By combining the three

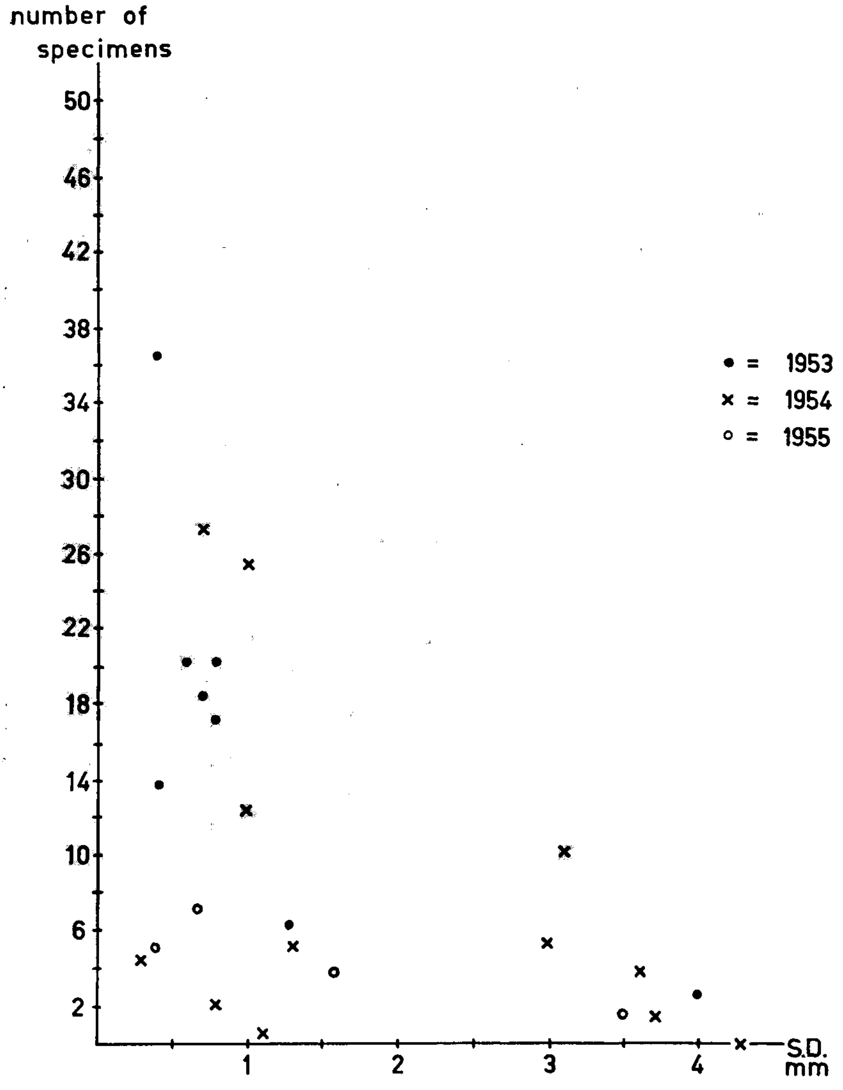

Fig. 10. Relation between the amount of vertical activity and S.D. (each point represents the mean of observations during one night).
$\tau = -0.411$, $p = 0.00830$

years in the same rankings we get a significant negative correlation: $\tau = -0.411$, $p = 0.00830$ (Fig. 10).

Since it may be expected that there were considerable differences in mean population density between the years 1953, 1954, and 1955, a better approximation of the real correlation can probably be obtained by combining the three individual coefficients (1.7.5), in which case: $\bar{\tau} = -0.501$, $p = 0.0146$.

With temperature the following correlations were found:

1953: $\tau = +0.111$, $p = 0.7114$ ($n = 8$);
1954: $\tau = -0.418$, $p = 0.0872$ ($n = 11$);
1955: $\tau = +1.00$, $p = 0.084$ ($n = 4$);
1953 + 1954 + 1955 in the same rankings: $\tau = -0.112$, $p = 0.4778$.

The individual coefficients for 1953, 1954, and 1955 combined: $\bar{\tau} = +0.264$, $p = 0.1970$.

When the correlation between the amount of vertical activity (1953 + 1954 + 1955 in the same rankings) and temperature is corrected for the correlation between temperature and S.D. ($\tau = +0.319$, $p = 0.0340$), only $\tau = +0.022$ remains, whereas for the correlation with S.D. we have $\tau = -0.399$ after this correction.

Thus, we may conclude that a negative and significant correlation exists between the amount of vertical activity and S.D., while no correlation is present between the amount of vertical activity and temperature.

3.2.5. If the amount of vertical activity is larger when S.D. is smaller and the amount of horizontal activity is larger when S.D. is larger, we can assume a relation between the two forms of activity. Such a relation might be, for instance, that a greater portion of the specimens which become active climb into the trees (so that a smaller portion of these specimens move about on soil and litter) when air humidity is higher. It is not yet clear, however, why a strong and positive correlation exists between the amount of horizontal activity and temperature (3.1.7 and 3.1.8) and no correlation between the amount of vertical activity and temperature (3.2.4). In 4.2.6 an attempt will be made to explain these phenomena.

A relative measure of the possible relation between vertical and horizontal activity is given by the ratio:

$$\frac{\text{mean amount of vertical activity per count/per night}}{\text{mean amount of vertical + horizontal activity per count/per night}} \times 100\,\%,$$

estimated for each night separately. The following correlations with this ratio are found for the eight entire nights in 1953:

S.D.: $\tau = -0.444$, $p = 0.1310$; temperature: $\tau -0.571$, $p = 0.062$.

During eight nights in 1954 combined observations on vertical and horizontal activity were also made. In spite of the very small amount of horizontal activity in 1954 and of vertical activity in some of these nights as well, the above ratio gives some indication of the relation between the two forms of activity. For 1954 the following correlations with this ratio were found:

S.D.: $\tau = -0.291$, $p = 0.398$; temperature: $\tau = -0.291$; $p = 0.398$.
For 1953 + 1954 in the same rankings is found:
S.D.: $\tau = -0.502$, $p = 0.00830$ (Fig. 11); temperature: $\tau = -0.385$, $p = 0.0424$.
For the individual coefficients for 1953 and 1954 combined we find:
S.D.: $\bar{\tau} = -0.368$, $p = 0.0434$; temperature: $\bar{\tau} = -0.431$, $p = 0.0182$.

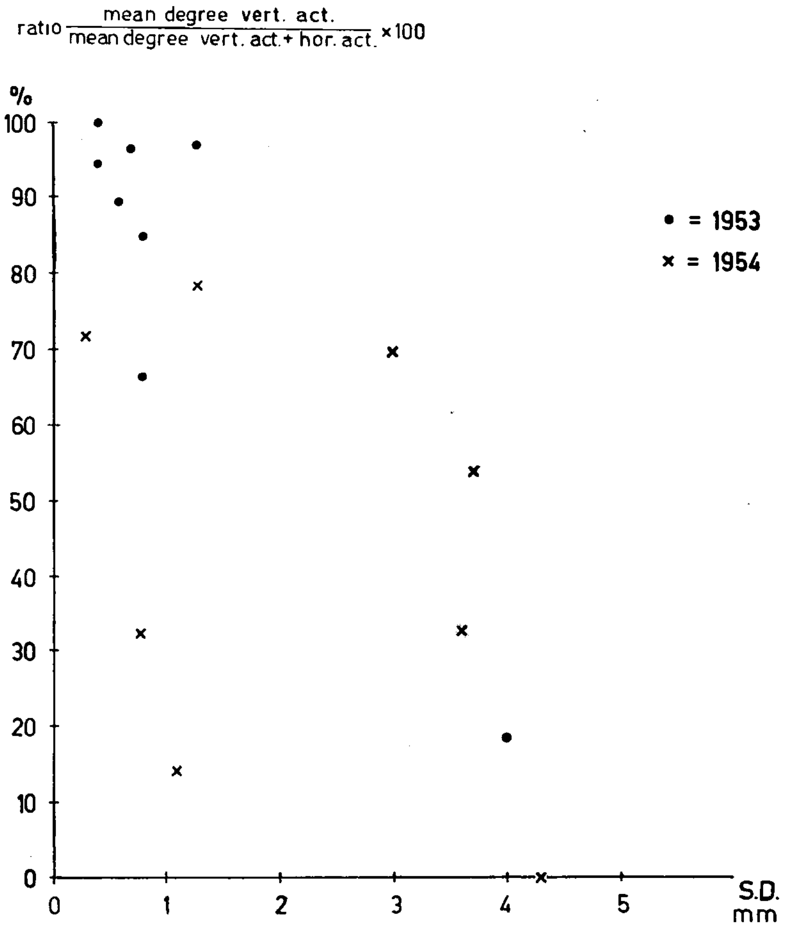

Fig. 11. S.D. and the relation between the mean amount of vertical activity and the mean amount of horizontal activity, both measured during the same nights. $\tau = -0.502$, $p = 0.00830$

Perhaps the correlation with temperature is partly due to the correlation between temperature and S.D. ($\tau = +0.598$, $p = 0.00174$). After correction (1953 + 1954 in the same rankings) for this correlation between temperature and S.D. we get $\tau = -0.122$, while for the correlation with S.D. we have $\tau = -0.367$ after this correction. Of course, the correlation with temperature is also due to the positive correlation between the amount of horizontal activity and temperature (3.1.7 and 3.1.8).

3. OBSERVATIONS ON "ACTIVITY ON TREES" [3.3.]

3.3.1. Six other trees among those mentioned in 3.2.1 each contained several shelters in which large numbers of specimens passed the day. As soon as darkness had fallen many specimens left these shelters and moved about on the trees. By counting the number of specimens active on these six trees together each hour throughout a night, a measure of the amount of this form of activity was obtained. Specimens from the litter also climb up these trees, but generally there is little need to correct for vertical activity because the amount of activity on trees is 10–20 times as large as the amount of vertical activity. Correlations with corrected values for the amount of activity on trees do not differ essentially from correlations with uncorrected values.

3.3.2. If we suppose that the behaviour of specimens from shelters in the litter does not differ from the behaviour of specimens from shelters in trees, we may consider the activity on trees to give a general picture of the activities of *P. scaber.* In that case the amount of activity on trees (corrected for vertical activity) gives an approximation for the same form of activity (the activity as a whole) as the amount of horizontal + vertical activity. Thus, there should be a strong correlation between both approximations for the activity as a whole. The following correlations were found:

1953: $\tau = +0.572$, $p = 0.062$ ($n = 8$);
1954: $\tau = +0.572$, $p = 0.062$ ($n = 8$);
1953 + 1954 (in the same rankings): $\tau = +0.542$, $p = 0.00398$ (Fig. 12).

The amount of activity on trees naturally gives a direct and consequently a much better approximation of the activity as a whole than the amount of horizontal + vertical activity, which activities are expressed in two different measures with an unknown quantitative relation.

3.3.3. In 3.2.5 we saw that the relation between the amount of horizontal and the amount of vertical activity is correlated with S.D.

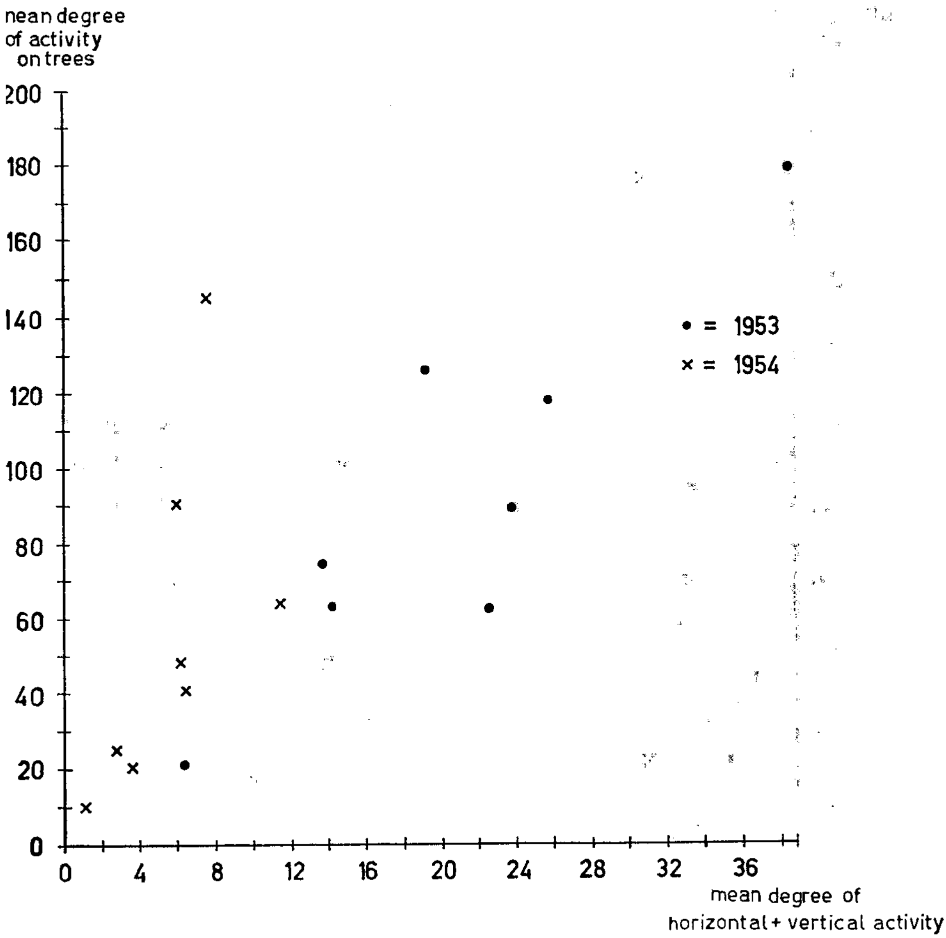

Fig. 12. Relation between the amount of activity on trees (corrected) and the mean amount of horizontal + vertical activity, all measured during the same nights. $\tau = +0.542$, $p = 0.00398$

The question now arises whether the activity as a whole (*i.e.* the amount of activity on trees) is also correlated with S.D. The following correlations with S.D. were found:

1953: $\tau = -0.444$, $p = 0.1676$ ($n = 8$) (corrected for vertical activity: $\tau = -0.370$, $p = 0.2584$);
1954: $\tau = -0.354$, $p = 0.1310$ ($n = 12$) (corrected: $\tau = -0.354$, $p = 0.1310$);
1955: $\tau = -1.00$, $p = 0.084$ ($n = 4$) (corrected: $\tau = -1.00$, $p = 0.084$);

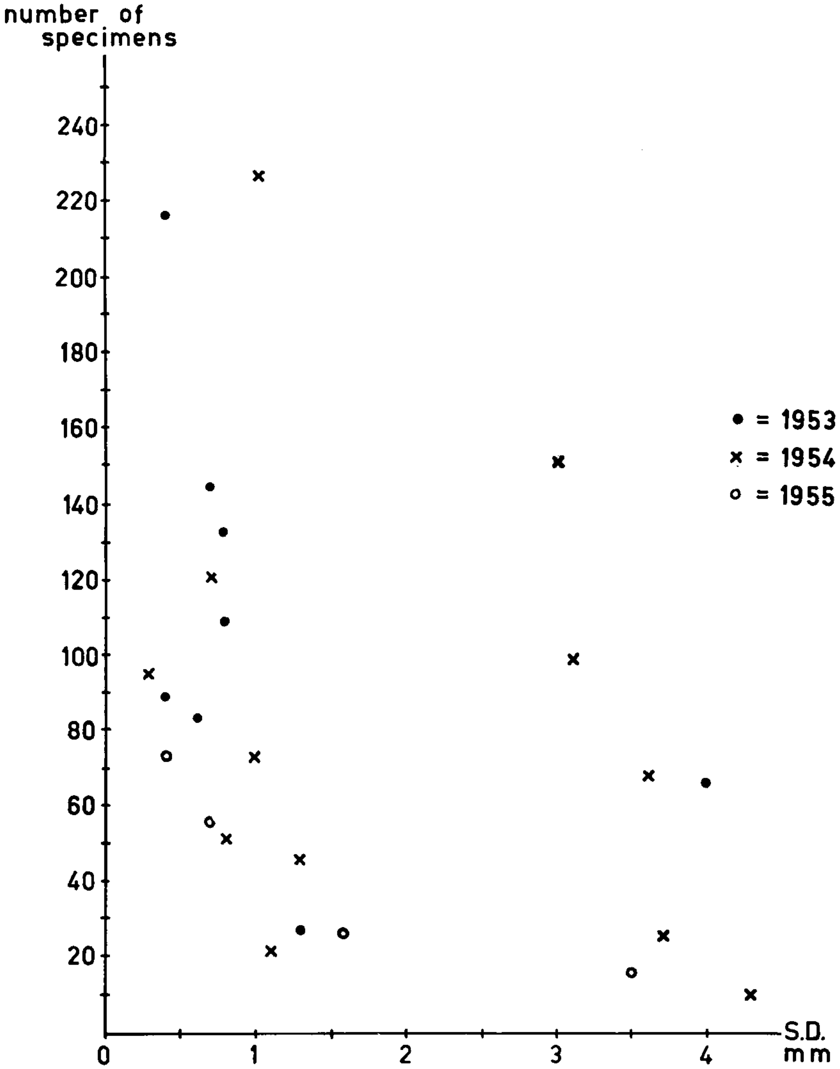

Fig. 13. Relation between the mean amount of activity on trees and S.D. (each point represents the mean of observations during one night).
$\tau = -0.393$, $p = 0.00880$

1953 + 1954 + 1955 in the same rankings: $\tau = -0.393$, $p = 0.00880$ (Fig. 13) (corrected for vertical activity: $\tau = -0.353$, $p = 0.0192$). The individual coefficients for 1953, 1954, and 1955 combined: $\bar{\tau} = -0.599$, $p = 0.00328$ (corrected: $\bar{\tau} = -0.575$, $p = 0.00480$).

The following correlations with temperature were found:

1953: $\tau = 0.00$, $p = 1.00$ ($n = 8$);
1954: $\tau = -0.273$, $p = 0.2420$ ($n = 12$);
1955: $\tau = +0.667$, $p = 0.334$ ($n = 4$);
1953 + 1954 + 1955 in the same rankings: $\tau = -0.069$, $p = 0.6528$.
The individual coefficients for 1953, 1954, and 1955 combined: $\bar{\tau} = +0.131$, $p = 0.5962$.

Thus, we may conclude that a negative and significant correlation exists between the amount of activity on trees and S.D., whereas no correlation is present between the amount of activity on trees and temperature.

3.3.4. In 3.1.6 we saw indications that the individual period of activity on the path is longer when S.D. is smaller. Probably this applies not only to individuals which move about on soil and litter but to all active individuals. In that case the negative correlation between the amount of activity on trees and S.D. can be caused partly (or wholly) by a longer individual period of activity when air humidity is higher. A temperature effect on the length of the individual period of activity is not clear in the case of activity on trees (3.3.3).

3.3.5. Hence, the amount of vertical activity is double-negatively correlated with S.D.: not only is the individual period of activity longer when S.D. is smaller, but also a greater portion of the active specimens climb up the trees when S.D. is smaller. As a consequence, the quantitative effect of S.D. must be proportionally larger on vertical activity than on activity on trees, *i.e.* the ratio:

$$\frac{\text{mean amount of vertical activity}}{\text{mean amount of vert. act.} + \text{act. on trees}} \times 100\,\%$$

must be larger when air humidity is higher. Such a correlation with S.D. does indeed exist: $\tau = -0.349$, $p = 0.0204$ (Fig. 14). The amount of horizontal activity is also double-correlated with S.D.: the individual period of activity is longer when S.D. is smaller, but, on the other hand, a smaller proportion of the active specimens move about on soil and litter when S.D. is smaller. Thus, the two S.D. influences must have an opposite effect, but since a significant positive correlation between the amount of horizontal activity and S.D. is found (3.1.7 and 3.1.8), the latter S.D. influence must be much more important than the former.

3.3.6. On some nights the number of specimens observed on the six trees together did not vary much in the course of the night, but on other nights these numbers were markedly higher during the first hours

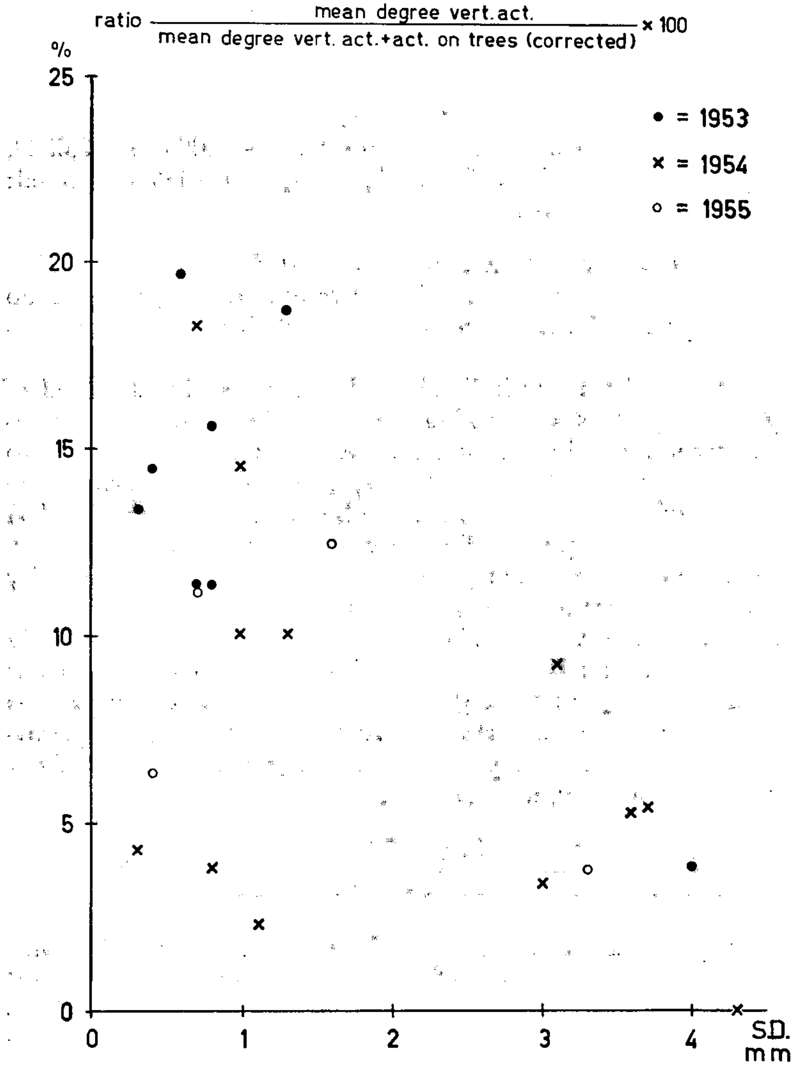

Fig. 14. S.D. and the relation between the mean amount of vertical activity and the mean amount of activity on trees (corrected), both measured during the same nights. $\tau = -0.349$, $p = 0.0204$

after dark than during the rest of the night (Fig. 15) [1]. It was found that the numbers of specimens observed during the first hours of a night are larger as compared with the numbers during the rest of this night when air humidity is higher, *i.e.* a negative and significant correlation exist between S.D. and the ratio:

$$\frac{\text{mean number of specimens during first three counts of each night}}{\text{mean number of specimens during the remaining counts of each night}};$$

for 1953 + 1954 + 1955 in the same rankings, $\tau = -0.367$, $p = 0.0146$. This phenomenon will be discussed in 4.2.4.

3.3.7. At a number of counts during two nights in 1953 each animal present on the observation-trees was marked (see 3.2.3). After one hour only about 2 % of the specimens marked at the previous count was re-observed on the same trees. The animals which had disappeared after one hour could have gone in one of three ways:

a. they may have climbed higher up the trees;
b. they may have left the trees and gone to the litter;
c. they may have returned to their shelters in the observation-trees.

To study this phenomenon, 16 trees, each[1] containing many shelters, were selected from the first aspen wood. After a number of provisional observations in 1954, these trees were divided in 1955 into 4 groups of 4 trees, *viz.*:

a. Before each observation night a ring of tree-banding grease was applied to the base of each of the 4 trees in order to prevent specimens from leaving or climbing up these trees in the course of the observation night.

b. In another group of 4 trees the ring of tree-banding grease was applied to the trunk about two meters above the ground in order to prevent specimens from climbing higher up in these trees in the course of the observation night.

c. In a third group of 4 trees a ring of tree-banding grease was applied both to the base and to the trunk about two meters above the ground, so that each active specimen could be observed continuously during its whole period of activity.

d. In 4 trees no rings were applied.

In the course of nine nights the number of active specimens was counted hourly on each of these 4 groups of 4 trees separately.

When comparing the numbers of active specimens observed at hour-

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[1] The same phenomenon was observed during the night of August 18/19, 1954 on the island of Brännskär (Skären-Archipelago near Tvärminne, Finland), where hourly counts of the amount of activity on trees were made on five pines (*Pinus* spec.). The phenomena of horizontal and of vertical activity were also observed.

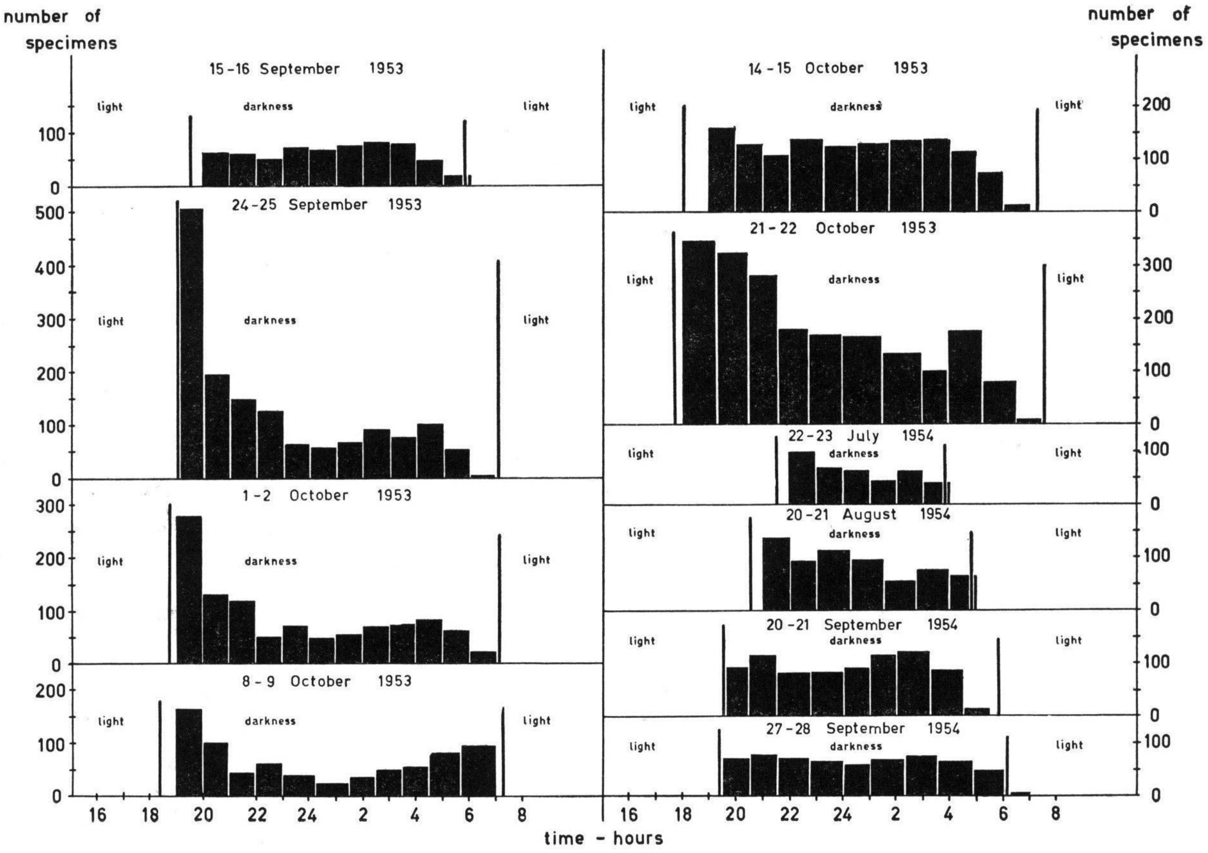

Fig. 15. Amount of activity on trees at various counts during one night.

ly intervals in the course of a night on the 4 groups of 4 trees, it could be expected that distinct differences in the trend of these numbers between the different groups of trees would be found. Such differences were not found, however; as a whole, the results are not at all clear.

More information can be obtained from observations made on three of these nights when all active specimens observed on these 4 groups of 4 trees were marked each hour with a different colour. The percentage of specimens marked on the different groups of trees re-observed after one hour (summarized for the whole night) is given in Table V.

TABLE V

Percentage of marked specimens re-observed after one hour on four groups of four trees

date	June 23/24, 1955				August 4/5, 1955				September 28/29, 1955			
group of trees	a	b	c	d	a	b	c	d	a	b	c	d
number of marked specimens	98	176	186	143	326	306	703	216	469	332	1700	340
mean number of marked specimens re-observed after one hour	21	25	32	6	49	39	66	21	59	32	191	31
mean % of marked specimens re-observed after one hour	21	14	17	4	15	13	9	10	13	10	11	9

None of the differences in percentage between any two groups of trees is significant: a, b: $p = 0.3270$; a, c: $p = 0.3270$; a, d: $p = 0.0818$; b, c: $p = 0.7718$; b, d: $p = 0.3370$; c, d: $p = 0.6170$ ($n = m = 17$; each hour separately).

Since there are no clear differences between the percentages of marked specimens re-observed after one hour on the different groups of trees, we must conclude that all the specimens have disappeared from all groups of trees in about the same way, *i.e.* have returned to their shelters (the only way in which specimens are able to disappear from trees of group c).

Thus, it seems from these experiments that the period of activity of the greater majority of active specimens lasts about one hour (see also 6.4.6). This conclusion agrees very well with the supposition (made in

3.1.6) that specimens moving about on the path are active only during part of the night.

3.3.8. In spite of this result, I have observed some cases of specimens climbing higher than two meters up the trees and other specimens leaving the trees.

It may be that the distance the animals cover on the trunk of a tree (vertical activity) is in some way comparable with the distance the animals cover upon the path (horizontal activity), *i.e.* perhaps specimens only climb up the trees higher than two meters when air humidity is very high. Indeed, the phenomenon was most obvious during some very humid nights in 1953 and it may generally not be very important quantitatively.

Individuals which leave the trees are most probably seeking a shelter; if such individuals are prevented from leaving a tree by a ring of tree-banding grease, they will seek a shelter in the trunk of this tree. Thus, the quantitative result will be the same in both cases.

Besides the great majority of active specimens which show a very short period of activity, I regularly observed individuals which remained on the trunk of a tree for a considerable space of time (some hours).

3.3.9. After two nights during which all active specimens were marked (August 4/5 and September 28/29), the rings of tree-banding grease were kept in place in order to estimate what proportion of the total tree-dwelling populations had been active during these nights by making observations on other nights. The results are given in Table VI.

Trees of group c might provide an ideal situation for estimating population density with the help of the "Lincoln Index". In this case the index should be of the form:

$$\frac{\text{specimens marked (active specimens)}}{\text{specimens not marked (non-active specimens)}} = \frac{\text{marked specimens subsequently seen}}{\text{unmarked specimens subsequently seen}}.$$

From group c in Table VI it can be concluded that about half of the tree-dwelling population became active during the nights of marking, if we assume that the specimens which become active during one night (marked specimens) were distributed at random in the original tree-dwelling population. In other words: this conclusion is based on the assumption that the population of active specimens during the observation night is independent of the population of active specimens during the night of marking. This can be checked as follows: during the night of marking all active specimens were marked, red at the first count, green at the second, yellow at the third count, *etc.*; the distribution of

TABLE VI

Percentage of marked specimens observed during two counts of a night after the night of marking (only two counts directly after the falling of darkness)

date of marking	August 4/5	September 28/29	
date of observation	August 5/6	Sept. 30/Oct. 1	October 4/5
group of trees	% of marked specimens from total number observed during two counts; between brackets the number of marked ind.		
a	45 (111)	33 (51)	24 (33)
b	51 (104)	17 (28)	12 (14)
c	56 (271)	55 (279)	40 (229)
d	28 (52)	23 (17)	17 (13)
Total	48 (538)	42 (375)	32 (289)

active specimens over the different counts during this night can now be compared (as the expected distribution) with the distribution of marked specimens over the different colours at each count during the observation night. The differences with expectation are significant: August 4/5 and 5/6: $\chi^2 = 57.55$ ($v = 4$) $p < 0.01$; Sept. 28/29 and Sept. 30/Oct. 1: $\chi^2 = 98.85$ ($v = 8$), $p < 0.01$; Sept. 28/29 and Oct. 4/5: $\chi^2 = 70.00$ ($v = 8$), $p < 0.01$. Thus, we may not conclude that the marked specimens have wholly redistributed themselves after the night of marking and consequently conclude that about half of the tree-dwelling population has become active during the nights of marking. It is obvious from these experiments, however, that a relatively great proportion of a tree-dwelling population becomes active during a night and that many (but not all) specimens which have been active during a given night become active again during the following nights. On the other hand, it is also clear that the periods of inactivity last much longer than the periods of activity (see 3.3.7).

4. OBSERVATIONS BY LE GAY BRERETON (1957) ON ACTIVITIES OF PORCELLIO SCABER [3.4.]

Because LE GAY BRERETON (1957) is the only author who has studied the activities of *P. scaber* under natural conditions, it is important to discuss the results of his observations here. He studied only the activity on trees.

3.4.1. During 5 nights in 1953 LE GAY BRERETON counted at two-hour intervals the numbers of specimens present on a number of tree trunks between ground-level and eye-level. The observations were made during three nights in a garden at Oxford and during two nights at Wytham Great Wood near Oxford. The numbers of specimens observed were generally small (mean number per count and per night: 0.3–15.5).

The observed numbers increased till about 11 p.m. (G.M.T.) and decreased after about 1 a.m. LE GAY BRERETON concludes that the animals come out from their shelters at nightfall, move about on the trunks in increasing numbers until about midnight, and disappear gradually until by daylight they are all in their shelters again. Since he did not mark the individuals observed at each count, LE GAY BRERETON was not able to observe that the individual period of activity only lasts a very short time (see: 3.2.3 and 3.3.7).

Since LE GAY BRERETON only counted every two hours and in general the numbers counted are small, it is difficult to compare the trend of his numbers of active specimens with my observations (3.3.6, Fig. 15).

During each count LE GAY BRERETON measured R.H. and temperature, and he concluded that there is no clear relationship with temperature and R.H. changes, which is in accordance with the conclusions reached by CLOUDSLEY–THOMPSON (1952) from his laboratory experiments ("the locomotory rhythm is correlated primarily with alternating light and darkness, and not with fluctuating temperature or humidity").

Like LE GAY BRERETON, I did not find any relationship with temperature or humidity changes within any one night. In fact, according to the working hypothesis given in Chapter 4, such a relationship was not to be expected.

3.4.2. Throughout 1953 and 1954 LE GAY BRERETON made monthly counts of the number of specimens present on four trees in a garden at Oxford at 11 p.m. (G.M.T.) on several nights; his Table 5 gives the mean number of specimens per month with mean temperature and mean R.H. per month. From this Table it is clear that active specimens were present throughout the year, although only few specimens were observed in January 1954 (mean temperature at night: 1.8° C), in February 1954 (mean temperature at night: 3.0° C), and in December 1954 (mean temperature at night: 4.4° C). More active specimens were observed in December 1953 (mean temperature at night: 8.8° C), which agrees with the observation of a considerable number of active specimens in the first aspen wood during the night 9/10 December 1953 (mean temperature: 7.1° C). From the experiment with artificial tree-shelters (Chapter 5, Fig. 17) it could be concluded that some unmarked specimens still arrived in the tree-shelters at mean night temperatures of about 3–5° C (Fig. 17, November 1956).

Although I did not systematically study the activities of *P.scaber* in winter, I have the impression that *P.scaber* does not hibernate, but only becomes inactive if the temperature falls below zero, which is affirmed by LE GAY BRERETON's observations and by experiments in the laboratory (7.2.2). (For the influence of higher temperatures (8–16° C) on the amount of activity, see 4.2.6).

According to WIDMANN (1936), *P.scaber* looks for other shelters in winter depending on temperature. In the first aspen wood it was indeed observed that tree-shelters were left when the temperature fell below 3–5° C. LE GAY BRERETON also observed that in winter *P.scaber* generally is not found in tree-shelters or only in tree-shelters at eye-level ("flakey" bark of large sycamore trees, 2.1.3), whereas in summer many specimens were found in shelters in the upper parts of the trees.

It would be interesting to study the relations between shelter-selection and temperature, especially in view of the annual cycle in the osmotic-pressure of the haemolymph as found by WIDMANN (1936) (see 6.1.3).

The main conclusion drawn by LE GAY BRERETON from his Table 5 is that the number of specimens active on tree trunks is high in spring and autumn and low in summer. Because these low numbers in summer coincide with low numbers of specimens in shelters at the base of trees and at eye-level in the trunks of trees (2.1.3), LE GAY BRERETON concludes that in spring the animals are active in the neighbourhood of their winter-shelters, that in summer the population shifts to the upper parts of the trees, and that in autumn the animals return again to the base of the trees. He tried to prove this hypothesis of "vertical migration" by comparing the numbers of specimens present in September 1954 in shelters at a height of 18 feet (*i.e.* at the first big fork of the trees) and those present in shelters at the base. For 14 oak trees and 3 ash trees, 117 specimens were found at 18 feet and only 10 at the base. In another case, 174 specimens were found in the upper parts of the trees and only one below.

3.4.3. It is interesting now to compare LE GAY BRERETON's findings on "vertical migration" with my findings in Meijendel. Since in the first aspen wood almost no suitable shelters were found at more than two meters above ground-level (the aspen trees are small with the first forks at about $1\frac{1}{2}$–$2\frac{1}{2}$ meters above ground-level), the animals could not shift into shelters above the upper observation-level (3.2.1). According to the discussion in 3.2.5, it could be expected that during a period with very humid nights specimens will continuously have a strong tendency to show vertical activity and, in consequence, the chances of arriving at shelters in the upper parts of the trees will become greater if there is a succession of humid nights, *i.e.* during a period with very humid nights specimens will gradually shift into shelters in the upper parts of the trees. Because LE GAY BRERETON's observation-trees are very tall (the first big fork at a height of 18 feet), he could observe this phenomenon.

If this supposition is correct, in the Oxford region many humid nights must have succeeded each other during the months of May, June, July, and August 1953. Because the data for 1954 are much less convincing, I am not sure that in 1954 the phenomenon of "vertical migration" occurred to the same extent (perhaps only during the months August and September). This phenomenon cannot be analysed further here because no more data are available for the moment.

5. GENERAL CONCLUSIONS [3.5.]

In this chapter the direct observations on the activities of *P. scaber*, made in the dune area "Meijendel" (especially the Bierlap area), are discussed. We have seen that three forms of activity must be distinguished, *viz.*:

a. "Horizontal activity" shown by specimens which move about on soil and litter and which often leave the woods.
b. "Vertical activity" shown by specimens which climb into trees.
c. "Activity on trees" shown by specimens which have left shelters in the trunks of trees and which move about on these trunks.

The amount of most forms of activity is mainly influenced by air humidity (S.D.), whereas air temperature is of no importance or only of minor importance (see 4.2.6). Only the amount of horizontal activity is positively correlated with air temperature (3.1.7 and 3.1.8). The amount of activity as a whole (activity on trees) is larger when air humidity is higher; this phenomenon may be caused (partly or wholly) by a longer period of activity when S.D. is smaller (3.3.4). As for horizontal activity, it was found that the distance the animals cover outside the woods is greater when S.D. is smaller and it is supposed that this means that the individual period of activity is longer when air humidity is higher (3.1.5 and 3.1.6).

Active specimens tend to climb up trees more when air humidity is higher, so that the amount of horizontal activity is positively and the amount of vertical activity is negatively correlated with S.D. (3.2.5).

More specimens become active during the first hours of a night as compared with the numbers active during the rest of the same night, when air humidity is higher (3.3.6).

More than 80 % of the active part of a *P. scaber* population shows a period of activity which lasts about one hour (3.3.7). A relatively great proportion of a tree-dwelling population becomes active during one night. Many (but not all) specimens which have been active during one night become active again during the following nights. The periods of inactivity last much longer than the periods of activity (3.3.9).

The activity patterns of *P. scaber* have a clear influence on the distribution of the animals over a wood:

a. As a consequence of horizontal activity outside of woods, more specimens will be found during the day at the borders of a wood than in the centre (3.1.4).
b. As a consequence of vertical activity, more specimens will be found during the day at the base of trees than elsewhere in the litter (3.2.2).

In 3.4 the observations made by LE GAY BRERETON (1957) on activities of *P. scaber* are discussed. It was concluded that a "vertical migration" as found by LE GAY BRERETON in the summer of 1953 is a striking phenomenon only if vertical activity occurs on tall trees with suitable shelters at a considerable distance above ground-level. This phenomenon illustrates the fact that the form in which the activity patterns arise and the extent to which they influence the distribution of the animals over the observation-area depends on the structure of this area.

4. A WORKING HYPOTHESIS FOR UNDERSTANDING THE ACTIVITY PATTERNS

1. TO WHAT END DO SPECIMENS OF PORCELLIO SCABER BECOME ACTIVE AT NIGHT? [4.1.]

4.1.1. If we consider to what end an animal leaves its shelter and becomes active, the answer will in most cases be to feed. Hence, we must examine to what extent we may consider the activity patterns found to be feeding-activities. In the first place we must know on what substances *P. scaber* feeds under natural conditions.

4.1.2. Because relatively large pieces of food pass the mandibles of woodlice and digestion often appears to have little visible influence on the substances consumed, large intact pieces of food can be recovered from the faeces. By feeding woodlice in the laboratory with only one kind of food for several days it can be determined what state different kinds of food are in after having passed through the digestive tract of a woodlouse (unpublished work by P. LEENHOUTS). These determinations made it easy to recognize the various food remnants in the faeces of *P. scaber*. A more extensive description of this method is given by BARLOW (1957), who used it to study food preferences in three species of Diplopods.

Such faeces-analyses showed that a great many substances are consumed by *P. scaber*: nearly all kinds of dead plant materials (litter, decaying wood, decaying fruits *etc.*,), a number of dead animal materials (dead insects, dead or dying woodlice, the shed cuticles of woodlice), a number of living plant materials (mosses, lichens, grasses, algae, fungi) and in the laboratory: potatoes, carrots, and moist filter paper. These faeces-analyses give the impression that the animals feed on any organic material they meet except living animals.

4.1.3. Food preferences do not seem to play an important part in this species. This conclusion is based on the following findings: the faeces of specimens from the litter of an aspen wood contained mainly pieces of decaying aspen leaves; the faeces of specimens from tree-shelters contained mainly remnants of decaying wood and moulds; the faeces of specimens from *Fucus*-heaps (Tvärminne, Finnland) contained mainly pieces of *Fucus*-tissues; *etc.* Moreover, with a diet of most of these materials – especially litter, decaying wood, potatoes, and carrots – *P. scaber* can be bred successfully in the laboratory.

Since shelters of *P. scaber* are usually situated in the midst of food (litter, decaying wood, bark, *etc.*) these animals need not become active to feed. Moreover, specimens of this species generally feed both during the day and at night and both inside and outside a shelter, as was found during the experiments described in 4.1.5 and 4.1.6 (see also BAKKER, 1956). Thus, the activity patterns found probably have nothing to do with feeding. To determine the relation between feeding and activity, some experiments were done in the laboratory.

4.1.4. To measure the amount of activity under controlled conditions, the following experimental set-up was used: an artificial wooden shelter with woodlice was set on a zinc platform consisting of a circular box placed upside down in a larger circular box (Fig. 16B). This gave a kind of circular trap with smooth, sheer walls around the platform. Woodlice leaving the wooden shelter and moving about fell into the circular trap, so that the amount of activity could be given by the percentage of specimens trapped during a certain period. After each count the trapped animals were put back into the wooden shelter. Such an apparatus could be placed in each cell of a serial thermo-hygrostat (Fig. 16A) to provide a comparison of the amount of activity at different temperatures and/or humidities of the air. In most experiments the wooden shelters were filled with moist flower-pot shards

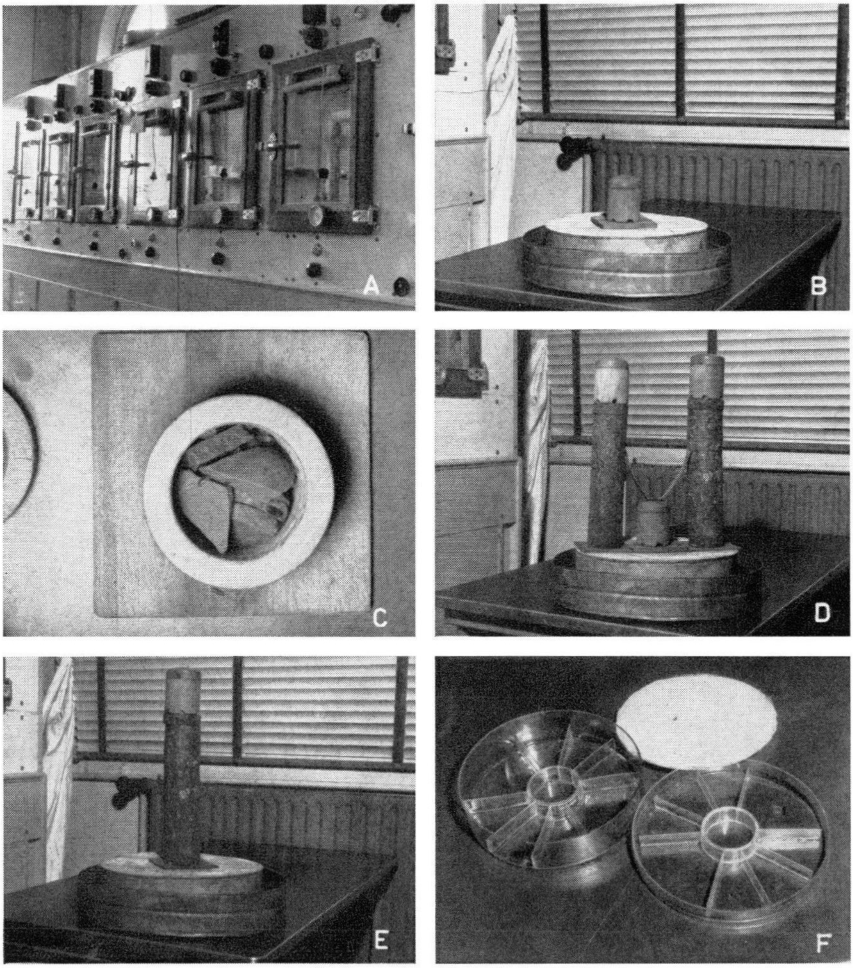

Fig. 16. For explanation see text (A, B, C: 4.1.4; D: 7.1.5; E: 7.1.9; F: 6.4.1).

(Fig. 16C) in order to approximate the conditions given in 2.3.3 and 2.4.1.

4.1.5. In 1955 two experiments were started with this apparatus:

a. During 21 periods of 24 hours (September 7 – October 8) the amount of activity was measured each day at 2° C, 5° C, 10° C, 15° C, and 20° C (S.D. was held as near to 0 mm as possible). The wooden shelters were filled with decaying aspen leaves (food inside the shelters) and a number of decaying aspen leaves were also put down in the trap. Each shelter contained 50 specimens of *P. scaber.*

b. During 24 periods of 24 hours (October 18 – November 19) the same experiment was repeated except that the wooden shelters were filled with moist flower-pot shards (no food inside the shelters).

The results of both experiments are given in Table VII.

TABLE VII

Mean amount of activity in two experiments (with and without food inside the shelters)

	mean amount of activity (%) *per 24 hours*									
temp.	2° C		5° C		10° C		15° C		20° C	
exp.	a	b	a	b	a	b	a	b	a	b
1st week	6.0	10.8	1.0	10.4	34.0	28.8	78.0	50.8	80.0	42.4
2nd week	5.2	2.0	3.2	4.4	18.0	27.6	44.0	31.2	70.4	21.6
3rd week	3.6	0.4	1.6	1.6	21.0	22.0	32.0	26.4	11.0	20.0
4th week	1.6	4.0	5.2	4.0	19.6	16.0	40.8	27.2	22.0	19.2
5th week	2.6	4.4	4.6	6.0	20.0	10.0	26.6	23.6	7.6	24.0
total	3.6	4.4	3.4	5.2	21.6	20.8	42.4	32.0	34.8	25.4

A significant difference between the amount of activity in experiment a and that in experiment b was found only at 15° C: 2° C, $p = 0.5222$; 5° C, $p = 0.7414$; 10° C, $p = 0.6818$; 15° C, $p = 0.0278$ and 20° C, $p = 0.8104$. This difference at 15° C, however, cannot have anything to do with feeding-activities, because the amount of activity was larger for the set-up with food in both the wooden shelter and in the trap. Thus, we may conclude that the amount of activity is not increased by the absence of food inside the shelters.

4.1.6. In 1957 another experiment was started with the apparatus described in 4.1.4. At 15° C and S.D. = 1 mm, the amount of activity was measured each day in the following three combinations during 39 periods of 24 hours (January 15 – March 9):

a. Decaying aspen leaves (food) in both the wooden shelter and the trap.
b. Decaying aspen leaves (food) in the wooden shelter and moist flower-pot shards (no food) in the trap.
c. Moist flower-pot shards (no food) both in the wooden shelter and in the trap.

Each shelter contained 100 specimens of *P. scaber.* Table VIII gives the mean amount of activity (%) per 24 hours for each week and for each of the three combinations separately and the value of p for the difference between two combinations for each week ($n = m = 5$; each day separately).

TABLE VIII

Mean amount of activity in three experiments (with and without food in the trap and/or in the shelter)

	mean amount of activity (%) per 24 hours			*p value of the difference between:*		
	comb. a	*comb. b*	*comb. c*	*comb. a and b*	*comb. a and c*	*comb. b and c*
1st week	79.2	88.2	77.4	0.420	0.840	0.220
2nd week	39.2	64.4	48.6	0.075	0.123	0.151
3rd week	24.2	14.6	33.0	0.220	0.151	0.012
4th week	25.0	16.7	37.5	0.200	0.200	0.043
5th week	10.2	7.0	32.0	0.420	0.007	0.007
6th week	7.4	7.6	30.6	0.690	0.007	0.007
7th week	5.4	3.6	16.2	0.921	0.056	0.016
8th week	10.8	11.4	10.8	0.841	0.690	1.000
total	25.2	26.9	35.7			

The Table clearly shows that the amount of activity is not influenced by the presence or absence of food outside the shelter (trap), (combinations a and b), when only the shelter contains food. In combinations a and c the total absence of normal food1) (c) has some influence on the amount of activity, but only after four weeks is this influence clearly demonstrable. Curiously, in combinations b and c the total absence of normal food (c) significantly influences the amount of activity after two weeks. Although the results of this experiment are not wholly

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[1] Some abnormal food is always present in the form of dead or dying specimens and of faeces; this cannot be very important, however, since during the experiment it appeared that no faeces or very small amounts were produced in combination c, whereas large amounts were produced in combinations a and b.

clear, it seems as though a total absence of normal food during a short period (one or two weeks) does not influence the amount of activity. Since under natural conditions woodlice are nearly always surrounded with food, it may be assumed that a total absence of food for even one or two weeks will never occur.

Moreover, mortality was not influenced by the total absence of normal food during a period of five weeks (mean mortality per week, comb. a: 10.5 %; comb. b: 11.2 % and comb. c: 11.4 %), and only slightly, but not significantly, influenced during a period of eight weeks (mean mortality per week, comb. a: 8.4 %; comb. b: 10.2 % and comb. c: 15.6 %. Differences: comb. a and b, $p = 0.574$; comb. b and c, $p = 0.278$; comb. a and c, $p = 0.117$).

On the basis of the results of these two experiments (4.1.5 and 4.1.6), we may conclude that the presence or absence of food inside or outside the shelters does not influence the amount of activity within a period of one or two weeks. Thus, we cannot consider the activity patterns found (3) to be feeding-activities.

4.1.7. If *P. scaber* does not become active to feed, it might be supposed that its activities have something to do with reproduction. This possibility need not be considered further, however, because during the reproduction season (June, July, August) the amount of activity does not increase in either sex; in September and October the amount of activity is even larger than in June, July, and August in both sexes.

4.1.8. Besides the possibilities discussed and discarded in the preceding sections, I believe only the following reasonable explanation to remain:

After a certain period of time the shelter in which specimens of *P. scaber* hide somehow becomes unsuitable, and the animals tend to move out. Since the animals regularly return to the same shelters and only some of the specimens present leave their shelters during any given night, this unsuitability cannot be a direct property of the shelter itself. We must look for the source of this unsuitability rather in a gradual change in the animal itself under the effects of a stay inside a shelter. In 2.4.1 we saw that the day-habitat of woodlice is primarily characterized by a very high humidity, and thus there is an inclination to suppose that a stay at a very high humidity after some time becomes unfavourable to the animals. In other words, a very high humidity may influence the water-balance of the animals unfavourably. Since many authors have found that woodlice lose considerable amounts of water in air of medium humidity in consequence of a very permeable cuticle (1.2.1), it may be supposed that the cuticle is also permeable to water in the other direction, *i.e.* at very high humidities water vapour from the surrounding air could be easily absorbed through the cuticle, when the vapour pressure in the air is higher than the vapour pressure of the body-fluids. To this increase of water-content must be added the water extracted from the food (KUENEN, 1959) and metabolic water.

4.1.9. Of course it cannot be excluded that woodlice may be able to lose the excess of water by "normal" excretion and thus we must consider what is known about excretion and excretory organs in woodlice.

There is no evidence at all regarding the amount of water lost by excretion. In *Asellus aquaticus* (L.) the segmental glands of the second maxillae are the main excretory organs (TER-POGHOSSIAN, 1909; NEEDHAM, 1942). Glands of the same structure, but much less developed, are found in terrestrial Isopoda (TER-POGHOSSIAN, 1909). Perhaps still other organs should be suspected of having an excretory function, but there is little experimental evidence on this subject. Some water is certainly also lost in the faeces (see also: KUENEN, 1959). Thus, strictly speaking, we do not know whether or not specimens of *P. scaber* are able to lose the excess of water in their bodies by "normal" excretion, but from observations in the laboratory (6.2.8) it became clear that they are unable (or only partly able) to do so. If we therefore suppose for the moment that water-excretion mainly takes place by transpiration through the cuticle (1.2.1), the activities of *P. scaber* can be understood in terms of the following working hypothesis: The activities of *Porcellio scaber* are a means of losing by transpiration the excess of water which has accumulated in the bodies of the animals during a stay inside a very moist shelter.

2. SIGNIFICANCE OF THE HYPOTHESIS FOR EXPLAINING THE ACTIVITY PATTERNS FOUND [4.2.]

4.2.1. The first phenomenon observed which agrees with the working hypothesis is the very short period of activity (3.3.7). From data in the literature (WALOFF, 1941; EDNEY, 1949, 1951a, 1954; AUZOU, 1953) and from unpublished experiments made in the Zoological Laboratory at Leiden, it is known that *P. scaber* loses large amounts of water by transpiration during a stay of 1–2 hours in air of medium humidity (50 %–85 % R.H.). Because it is certain that the rate of water-loss in air of medium humidity is much higher than the rate of water-uptake inside a humid shelter, it may be expected that the periods of inactivity last much longer than the periods of activity (3.3.9).

4.2.2. If specimens of *P. scaber* become active to lose water by transpiration, it is clear that a number of properties of these activities are mainly influenced by the evaporative power of the air (*i.e.* by S.D., see 1.6.1). It is evident now that the same amount of water will be transpired faster when air humidity is lower, so that the period of activity must be longer when air humidity is higher (3.1.6 and 3.3.4).

4.2.3. When air humidity at ground level is extremely high, *e.g.* after a period of heavy rains, the animals are unable to transpire water by moving about at this level and so they must look for localities where air humidity is lower. Air humidity is usually highest near the soil-surface and decreases with increasing distance above the ground. Inside a wood air humidity is lowest (during the greater part of the night as well) somewhere between the two transpiring surfaces, *i.e.*: between the litter with the vegetation on the forest floor and the roof of foliage formed by the tops of trees (GEIGER, 1950: p.317–320). Thus, the phenomenon of vertical activity (3.2) can be considered a search for localities where air humidity is low enough to allow adequate transpiration.

It is also clear now that the amount of vertical activity will be larger (and, in consequence, the amount of horizontal activity will be smaller) when air humidity (strictly speaking: the humidity of the air at the ground-level) is higher (3.1.7, 3.1.8, 3.2.4, and 3.2.5).

The phenomenon of "vertical migration" as found by LE GAY BRERETON (3.4.2) can thus be considered as the result of a long period with a large amount of vertical activity, *i.e.* of a long period with very humid nights (3.4.3).

4.2.4. Since woodlice seldom become active during the day-period under normal conditions (there are some exceptions in *Armadillidium vulgare* (Latr.): CLOUDSLEY–THOMPSON, 1951 and in *Ligia oceanica* L.: EDNEY, 1954) as a consequence of their negative phototactic tendencies, it may be expected that in a number of cases some accumulation of individuals which require activity will occur during the day-period. These accumulated specimens will become active very soon after dark. In accordance with this, it is often found that the numbers of specimens active on trees are markedly higher during the first hours after dark than during the rest of the night (3.3.6). The mean S.D. during the observation period can hardly be expected to influence the ratio:

$$\frac{\text{mean number of specimens during first 3 counts of each night}}{\text{mean number of specimens during the remaining counts}}$$

so that the significant correlation found (3.3.6) cannot be a direct one. The amount of accumulated specimens which must become active will depend rather on air humidity (strictly speaking: the humidity of the air inside the shelters) during the whole period of inactivity preceding the observation period of each specimen.

Hence, it is very probable that the significant correlation found (3.3.6) is indirect and due only to a strong correlation between the mean S.D. during the observation period and the mean S.D. during the mean period of inactivity preceding the observation period. That such a strong correlation may exist can be illustrated by S.D. observations at the Valkenburg meteorological station (at a distance of about 5 km, see map, Fig. 1). Between the mean of S.D. values from the three-hour interval data recorded at Valkenburg during each observation period and the mean of S.D. values for the preceding day-period (for many specimens the period of inactivity lasts no longer than one day-period, see 3.3.9) a correlation is found in which $\tau = +0.730$ and $p < 0.000066$ $(x = 4.86)$.

Between the above ratio and the mean S.D. during the day-period preceding each observation period only a correlation with $\tau = -0.503$ is needed to give a correlation with $\tau = -0.367$ (3.3.6) between this ratio and the mean S.D. during the observation period, because of the strong correlation between both S.D. values (method of partial rank correlation, see 1.7.4). In the absence of more data on this subject, this problem can not be analysed further here.

4.2.5. On the basis of the working hypothesis it may be expected that more specimens will become active during an observation period after a period with very high air humidities than after a period with lower air humidities (strictly speaking, the humidity of the air inside the shelters must be considered). Thus, the amount of activity as a whole (= activity on trees) must not only be negatively correlated with the air humidity during the observation period (length of the period of activity, 3.3.3 and 3.3.4), but also with the mean S.D. during the mean period of inactivity preceding the observation period. In 5.1.8 the data on this point are given and discussed.

Because the amount of vertical activity depends not only on the percentage of active specimens which climb up the trees, but also on the amount of activity as a whole, we can expect not only a correlation with the air humidity during the observation period (3.2.4), but also a negative correlation with the mean S.D. during the mean period of inactivity preceding the observation period. The relevant data are given and discussed in 5.1.6.

Something similar can be supposed for the amount of horizontal activity: the amount of horizontal activity must be negatively correlated with mean S.D. during the mean period of inactivity, but positively correlated with mean S.D. during the period of activity (3.1.7 and 3.1.8). No data on this subject are yet available, however.

4.2.6. In the light of the working hypothesis, it can be expected that temperature influences the rate of water-loss and water-uptake (diffusion of water vapour) and in this way may have some effect on the length of the individual periods of activity and of inactivity. Although the correlations given in 3.1.5 suggest such an effect (3.1.6), in general the data do not suggest an effect of temperature on the length of the individual periods of activity (3.3.3). This may be due to the small differences between the mean temperatures of the various observation nights (nearly all values measured lay between 8° C and 16° C; see also 7.2.5).

If temperature has some influence on the length of the individual periods of inactivity (rate of water-uptake), it is likely that the amount of horizontal activity and the amount of vertical activity are indirectly influenced by temperature in two ways:

a. The amount of activity as a whole will be larger when the mean length of the individual periods of inactivity is smaller, *i.e.* when temperature is higher during the mean period of inactivity (approximated by the day-period preceding each observation period). Some data on this point are given in 5.1.7. Because a strong correlation exists between the mean temperature during each observation night and the mean temperature during the preceding day-period (1953 + 1954 + 1955 in the same rankings ($n = 29$): $\tau = + 0.740$, $p < 0.000066$ ($x = 5.50$); data from the Valkenburg meteorological station), a positive though indirect correlation may still be expected between the amount of activity as a whole and temperature during the observation night.

b. Because a significant and positive correlation exists between mean temperature and mean S.D. during the observation nights (1953 + 1954 + 1955 in the same rankings: $\tau = + 0.319$, $p = 0.0340$), some indirect effect of temperature on the amount of horizontal and vertical activity may be expected. Hence, the amount of horizontal activity will be larger when temperature is higher (via the correlation between temperature and S.D.) and the amount of vertical activity will be smaller when temperature is higher.

Thus, for the amount of horizontal activity these two indirect temperature effects (a and b) reinforce each other and may cause the significant and positive correlations between the amount of horizontal activity and temperature given in 3.1.7 and 3.1.8. For the amount of vertical activity these two indirect temperature effects must have an opposite effect and may be the cause of the absence of correlation between the amount of vertical activity and temperature (3.2.4) (see also: 7.2.3).

4.2.7. Summarizing, it can be concluded that the activity patterns

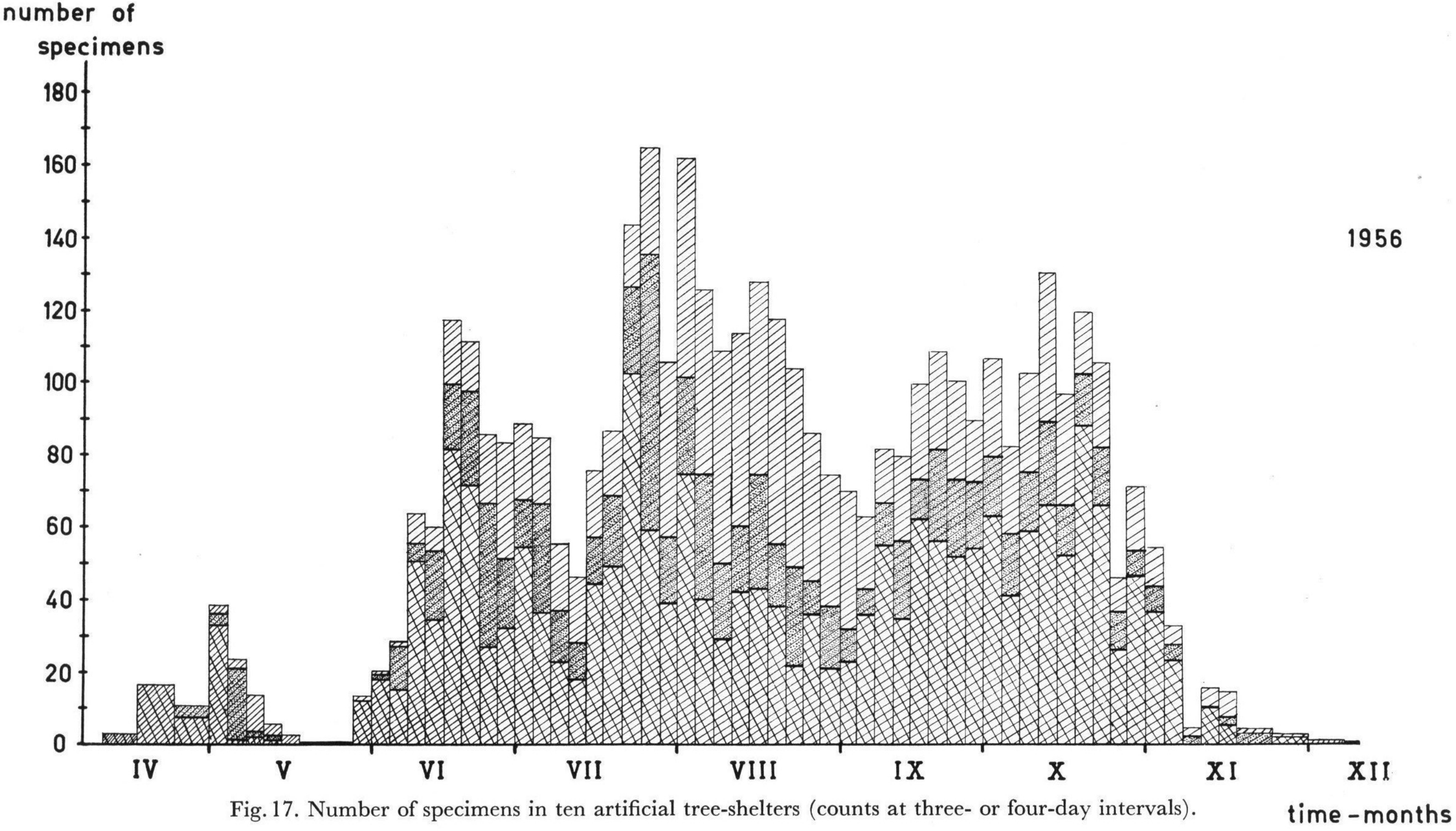

Fig. 17. Number of specimens in ten artificial tree-shelters (counts at three- or four-day intervals).

▨ = total number of specimens

▨ = unmarked specimens (from total number of specimens)

▨ = specimens marked at previous count (from total number of specimens) found can be understood in terms of the working hypothesis. On the other hand, it is clearly very important to collect still more information on these activity patterns under natural conditions, because a number of phenomena are not yet clear. The relation between the length of the period of inactivity and humidity in particular deserves further investigation (5.1).

5. INDIRECT OBSERVATIONS ON THE ACTIVITIES OF TREE-DWELLING POPULATIONS

1. MIGRATION INTO AND OUT OF TREE-SHELTERS [5.1.]

5.1.1. On April 3, 1956 in the first aspen wood ten trees without natural shelters were each provided with an artificial shelter. For this purpose a rectangular piece of bark was detached from the tree which could be put back and secured by two cords. Behind this piece of bark a hole with a radius of 15 mm was bored into the bole, and a hollow copper cylinder, closed at one end (radius: 15 mm; length: 60 mm) and filled with pieces of decaying wood was inserted. The cylinder had a projecting rim which completely closed off the hole. By leaving some space around the piece of bark and seeing to it that the shelter was sufficiently moist but not wet, these artificial shelters functioned as suitable tree-shelters (see also: 2.3.3; in agreement with the conditions given there, only a few specimens were present in the copper cylinders and most specimens were found behind the pieces of bark).

All the animals present in such an artificial tree-shelter could be collected easily by removing the piece of bark and the cylinder from the tree. On each Tuesday and Friday between April 5th and December 11th, 1956, the number of specimens present in each of the ten artificial shelters was counted. At each count the specimens which had arrived since the previous count were marked with paint (quick-drying shellac-solution, with different colour for each count). After counting and marking, the animals were put into the cylinder which was then returned to the hole and covered by the piece of bark.

5.1.2. From Fig. 17 it is clear that during spring, summer, and autumn unmarked specimens continuously arrived in the tree-shelters and marked specimens continuously left these shelters, *i.e.* during the greater part of the year there was an uninterrupted exchange between tree-dwelling and litter-dwelling populations. The very small numbers of specimens present in the artificial tree-shelters during the month of May, 1956, coincided with a dry period without any rainfall.

The number of unmarked specimens which was found at each count in the tree-shelters (migration into tree-shelters) must be regarded as a result of vertical activity (3.2), whereas the percentage of marked specimens which had disappeared from the tree-shelters (migration out of tree-shelters) must be regarded as a result of activity on trees (3.3).

5.1.3. As in Chapter 3, correlations with S.D. or temperature should be calculated, but since S.D. and temperature were not measured in the first aspen wood in 1956 the necessary data are not available. Fortunately, a very strong correlation was found between the S.D. values (and temperature values) of the climate of the first aspen wood and the S.D. values (and temperature values) of the macro-climate of the Valkenburg meteorological station (at a distance of about 5 km, see map, Fig. 1). The correlation between the mean S.D. value of each observation night in 1953, 1954, and 1955 (Chapter 3) measured in the first aspen wood and the mean of the S.D. values from Valkenburg are as follows:

1953: $\tau = +0.604$, $p = 0.0574$ ($n = 8$);
1954: $\tau = +0.636$, $p = 0.00578$ ($n = 12$);
1955: $\tau = +0.500$, $p = 0.0872$ ($n = 9$);
1953 + 1954 + 1955 in the same rankings: $\tau = +0.649$, $p < 0.000066$ ($x = 4.72$).

A very strong correlation also exists between the temperature values of the climate of the first aspen wood and the temperature values of the macro-climate of Valkenburg. The following correlations could be calculated for the observation nights in 1953, 1954, and 1955 (Chapter 3):

1953: $\tau = +0.857$, $p = 0.00174$ ($n = 8$);
1954: $\tau = +0.870$, $p = 0.000118$ ($n = 12$);
1955: $\tau = +0.761$, $p = 0.00634$ ($n = 9$);
1953 + 1954 + 1955 in the same rankings: $\tau = +0.805$, $p < 0.000066$ ($x = 6.02$).

Thus, it may be assumed that the data for the climate of the first aspen wood can be approximated by the corresponding data on the macro-climate of the Valkenburg station.

5.1.4. If the percentage of the specimens showing vertical activity which arrive in tree-shelters is mainly governed by chance, *i.e.* if the amount of migration into tree-shelters depends mainly on the amount of vertical activity, the former should show about the same correlations with temperature and S.D. as the latter.

Before calculating these correlations, however, we must remember that when studying the amount of activity, fluctuations in population density must be held as small as possible (3.1.1). Hence, because fluctuations in the litter-populations (especially of the populations at the base of the observationtrees) may have a masking effect on the calculated correlations, the best approximation of the real relationship can be obtained by splitting up the period between June 5th and November 6th (see Fig. 17) into n smaller periods and by combining the n correlation-coefficients for the individual periods (1.7.5).

This masking effect is nicely illustrated by comparing the correlations between the amount of migration into tree-shelters and the mean of S.D. values during the period after the previous count (mean S.D. of the whole period), a. for one period (all the 45 counts in one ranking): $\tau = -0.165$, $p = 0.1236$; b. for 5 periods of one month each (5 coefficients combined): $\bar{\tau} = -0.279$, $p = 0.0232$ and c. for 10 periods of 14 days each (10 coefficients combined): $\bar{\tau} = -0.409$, $p = 0.00578$ (Fig. 18).

Between the amount of migration into tree-shelters and mean temperature of the whole period the following correlations are found: 45 counts in the same rankings: $\tau = +0.045$, $p = 0.6744$; the individual coefficients for every month combined: $\bar{\tau} = -0.021$, $p = 0.8650$; the individual coefficients for every 14-day period combined: $\bar{\tau} = +0.107$, $p = 0.4716$.

Thus, we may conclude that the amount of migration into tree-shelters is, like the amount of vertical activity (3.2.4 and 4.2.6), negatively correlated with S.D. and not correlated with temperature. The amount of migration into tree-shelters may thus be considered a relative measure of the amount of vertical activity.

5.1.5. Because the amount of migration into tree-shelters and also of vertical activity may be only indirectly correlated with air humidity and more directly with the moistness of the litter, the correlation between the amount of rainfall (in mm) during the period after the previous count and the amount of migration into tree-shelters was calculated for 45 counts. A correlation of $\tau = +0.015$, $p = 0.9044$ was found for the 45 counts in the same rankings and a correlation of $\bar{\tau} = +0.085$, $p = 0.5686$ after combining the individual coefficients for every 14-day period. Thus, we may conclude that the amount of migration into tree-shelters (and probably also the amount of vertical activity) is not correlated with the amount of rainfall.

5.1.6. In 3.2.5 it was supposed that a greater part of the specimens which become active at night will climb up the trees when air humidity is higher. This means that the amount of vertical activity must be correlated with S.D. during the period of activity (at night; 3.2.4). On the other hand, it may be expected that more specimens will become active at night when the air humidity inside the shelters has been

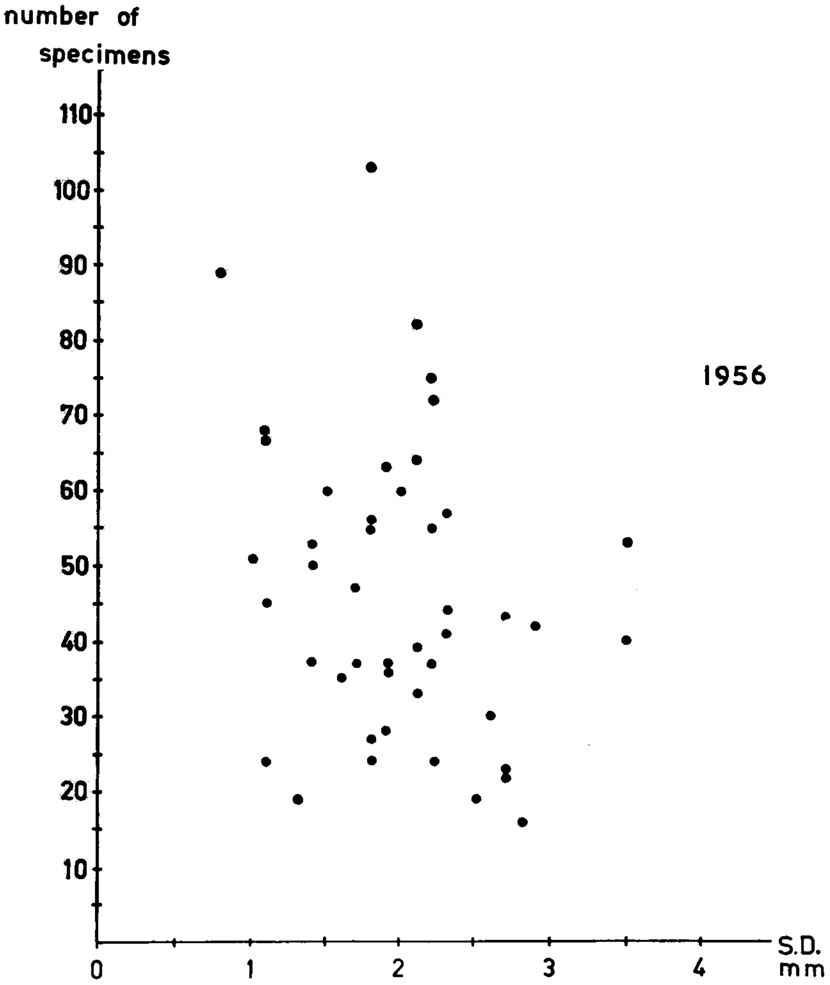

Fig. 18. Relation between the amount of migration into tree-shelters (measured at three- or four-day intervals) and S.D.

Total observations: $\tau = -0.165$, $p = 0.1236$
Sum of separate months: $\bar{\tau} = -0.279$, $p = 0.0232$
Sum of separate 14-day periods: $\bar{\tau} = -0.409$, $p = 0.00578$

higher (4.2.5). This means that the amount of activity as a whole, and thus also the amount of vertical activity, must be correlated with S.D. during the periods of inactivity (4.2.5). Unfortunately, it was impossible to measure S.D. inside the shelters. Referring to the discussions in 2.4, however, we may expect that the air humidity inside a shelter will generally be high and often near to saturation, but that it will fluctuate to some extent with S.D. of the open air (see also 7.1.8). Since at night air humidity is always much higher than during the day (GEIGER, 1950, p.94–97), the diffusion of water vapour from a shelter will be much stronger during the day than at night; consequently changes in S.D. inside a shelter will be caused mainly by S.D. of the air during the day. Thus, the mean of S.D. values of the air during the day can be expected to give a relative measure of the humidity level inside the shelter during the whole period of inactivity.

It may be then expected that the amount of vertical activity is correlated both with the mean of S.D. values during the periods of activity (mean S.D. of nights) and of inactivity (mean S.D. of days). For the amount of migration into tree-shelters the following correlations are found:

a. With mean S.D. of nights: 45 counts in the same rankings: $\tau = -0.161$, $p = 0.1326$; the individual coefficients for every month combined: $\bar{\tau} = -0.157$, $p = 0.2006$; the individual coefficients for every 14-day period combined: $\bar{\tau} = -0.287$, $p = 0.0526$.

b. With mean S.D. of days: 45 counts in the same rankings: $\tau = -0.133$, $p = 0.2150$; the individual coefficients for every month combined: $\bar{\tau} = -0.183$, $p = 0.1362$; the individual coefficients for every 14-day period combined: $\bar{\tau} = -0.310$, $p = 0.0366$.

These correlations are not high, but no better could be expected since mean S.D. of the whole period must be regarded a combination of both mean S.D. of days and mean S.D. of nights and thus it should give a stronger negative correlation with the amount of migration into tree-shelters (which is a combination of the results of the two S.D. influences) than each of the mean S.D. values separately (see also: 5.1.4). With temperature, the following correlations were found:

a. With mean temperature of nights: 45 counts in the same rankings: $\tau = +0.070$, $p = 0.5092$; the individual coefficients for every 14-day period combined: $\bar{\tau} = +0.147$, $p = 0.3222$.

b. With mean temperature of days: 45 counts in the same rankings: $\tau = +0.035$, $p = 0.7490$; the individual coefficients for every 14-day period combined: $\bar{\tau} = +0.030$, $p = 0.8414$.

Thus, we may conclude that the amount of migration into tree-shelters is correlated with neither mean temperature of nights nor with mean temperature of days.

5.1.7. If the amount of migration out of tree-shelters (%) depends mainly on the amount of activity on trees, the former should show about the same correlations with S.D. and temperature as the latter. When the amount of migration out of tree-shelters is correlated with mean S.D. of the whole period, we find for 45 counts in the same rank-

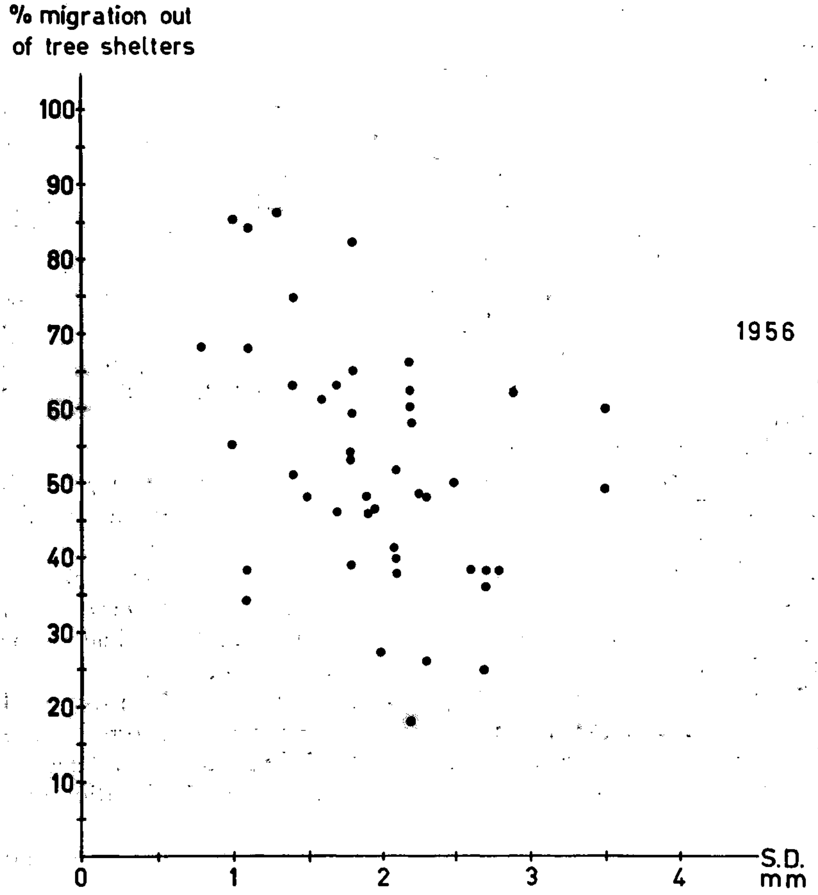

Fig. 19. Relation between the amount of migration out of tree-shelters (in % of the number of specimens present at the previous count) and S.D.
$\tau = -0.278$, $p = 0.00932$

ings: $\tau = -0.278$, $p = 0.00932$ (Fig. 19); with mean temperature of the whole period: $\tau = -0.193$, $p = 0.0688$. When correcting the correlation with temperature for the correlation between temperature and S.D. ($\tau = +0.253$, $p = 0.0182$) there remains $\tau = -0.132$, and for the correlation with S.D. there remains $\tau = -0.241$ after the same correction.

Thus, it can not be excluded that temperature may have some effect on the amount of migration out of tree-shelters. Because in 3.3.3 no correlation was found between the amount of activity on trees and mean temperature during the periods of activity, it may be that only mean temperature of days is correlated with the amount of migration out of tree-shelters (see 5.1.8). On the other hand, the amount of migration out of tree-shelters like the amount of activity on trees, is negatively correlated with S.D. (3.3.3).

5.1.8. In 3.3.4 it was supposed that the negative correlation between the amount of activity on trees and S.D. may be caused by a longer period of activity when air humidity is higher. In that case it can hardly be expected that during the periods of activity S.D. will have a large effect on the amount of migration out of tree-shelters (such an effect would have to be that the chance of disappearing from the trees is larger when the period of activity lasts longer). In accordance with this, only a small correlation was found between the amount of migration out of tree-shelters and mean S.D. of nights: $\tau = -0.169$, $p = 0.1164$.

In 4.2.5 we concluded that the amount of activity on trees must be larger when air humidity during the periods of inactivity has been higher. In that case a correlation can be expected between the amount of migration out of tree-shelters and mean S.D. of days (5.1.6). Such a correlation does indeed exist: $\tau = -0.299$, $p = 0.00480$.

Since the amount of migration out of tree-shelters is about equally correlated with mean S.D. of the whole period and with mean S.D. of days, the correlation between mean S.D. of nights and the amount of migration out of tree-shelters will not be very important and consequently it can be said that the length of the periods of activity does not have a clear effect on the chance of disappearing from the trees. With temperature, following correlations were found:

a. With mean temperature of nights: $\tau = -0.151$, $p = 0.1556$. When this correlation for the correlation between mean temperature of nights and mean S.D. of nights ($\tau = +0.152$, $p = 0.1556$) is corrected, there remains $\tau = -0.129$, while for the correlation with S.D. there remains $\tau = -0.149$ after the same correction.

b. With mean temperature of days: $\tau = -0.210$, $p = 0.0488$. When this correlation for the correlation between mean temperature of days and mean S.D. of days ($\tau = +0.396$, $p = 0.00017$) is corrected, there remains $\tau = -0.102$, while for the correlation with S.D. there remains $\tau = -0.240$ after the same correction.

It is therefore not clear whether or not temperature is correlated with the amount of migration out of tree-shelters (5.1.7) and the supposition made in 4.2.6 cannot yet be evaluated.

The effect of temperature on the activities of *P. scaber* is not clear, either from the data discussed in Chapter 3 or from the data discussed in this chapter. It is evident, however, that if temperature has some

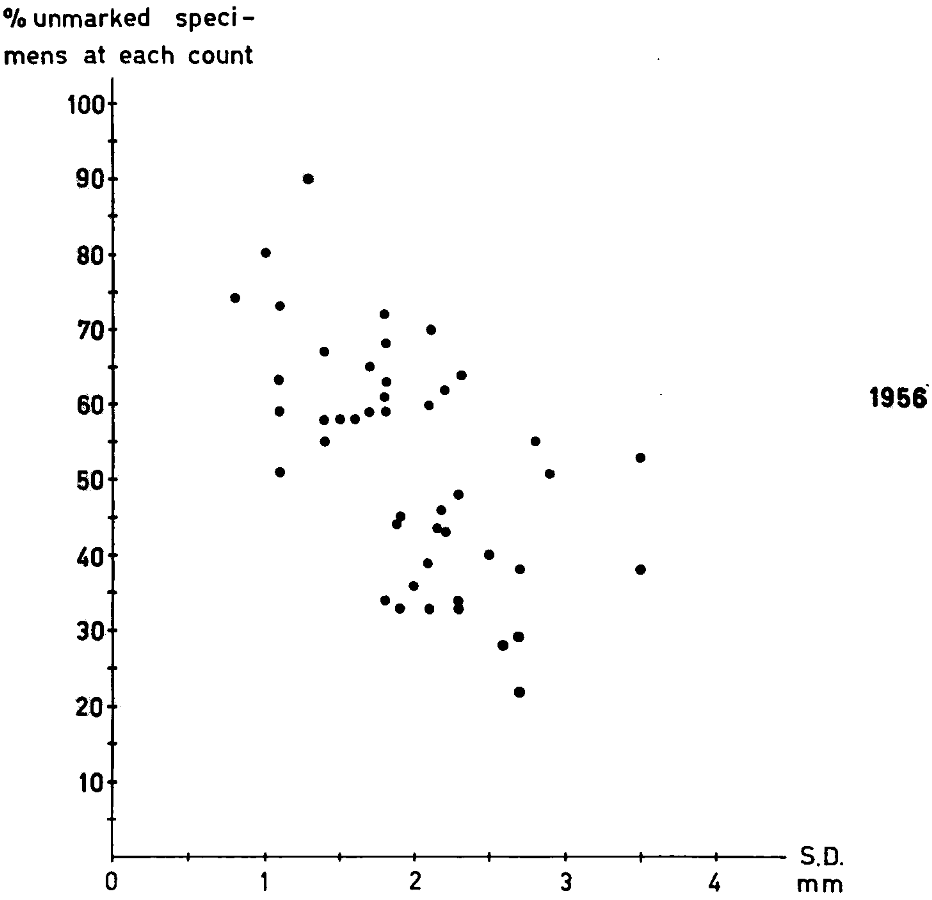

Fig. 20. Relation between the rate of exchange between tree-dwelling and litter-dwelling populations (migration into and out of tree-shelters) and S.D.
$\tau = -0.456$, $p < 0.000066$

direct effect, under natural conditions this effect is only of minor importance as compared with the effect of S.D. Temperature may only have some direct or indirect effect on the amount of horizontal activity (3.1.7 and 3.1.8). Only temperatures near to the freezing-point have an observable effect on activity (see 3.4.2).

5.1.9. Since the percentage of unmarked specimens present inside the tree-shelters is determined both by the amount of migration into tree-shelters and the amount of migration out of tree-shelters, it gives a measure of the rate of exchange with the litter-dwelling populations.

On the basis of the preceding discussions, the rate of exchange may be expected to be strongly correlated with mean S.D. of the whole period and with mean S.D. of days; somewhat less strongly with mean S.D. of nights; and only very weakly or not at all with mean temperature of the whole period and the amount of rainfall. The following correlations are found:

a. with mean S.D. of the whole period: $\tau = -0.456$, $p < 0.000066$ ($x = 4.27$) (Fig. 20);
b. with mean S.D. of days: $\tau = -0.412$, $p = 0.000096$;
c. with mean S.D. of nights: $\tau = -0.314$, $p = 0.00318$;
d. with mean temperature of the whole period: $\tau = -0.194$, $p = 0.0658$;
e. with the amount of rainfall: $\tau = +0.067$, $p = 0.5222$.

We may therefore conclude that the rate of exchange with litter-dwelling populations is mainly governed by air humidity and somewhat more so by the humidity of the air during the periods of inactivity (amount of activity as a whole) than by that during the periods of activity (amount of vertical activity).

5.1.10. While making the observations it struck me that during the autumn of 1956 large numbers of unmarked specimens were found in the artificial tree-shelters of four trees at the W-border of the first aspen wood, while in the shelters of the remaining trees which were situated more in the centre of this wood much smaller numbers of unmarked specimens were found during the same period. To investigate this phenomenon the percentage of the total number of unmarked specimens which were found at each count in the shelters of the four trees at the W-border of the first aspen wood was correlated with different factors. The following correlations were found:

a. with mean temperature of the whole period: $\tau = -0.022$, $p = 0.8414$;
b. with mean S.D. of the whole period: $\tau = -0.093$, $p = 0.3898$;
c. with time: $\tau = +0.447$, $p < 0.000066$ ($x = 4.29$) (Fig. 21).

We may therefore conclude that in the course of the year the amount of migration into tree-shelters (and also the amount of vertical activity) at the W-border of the first aspen wood becomes larger as compared with that in the centre of this wood. Since no other differences between the activities of tree-dwelling populations at the W-border and in the centre of the first aspen wood were found, this phenomenon must be caused by a trend in the activities of the litter-dwelling populations in the course of the year.

Now, in 2.2.2 we saw that population density is larger at the

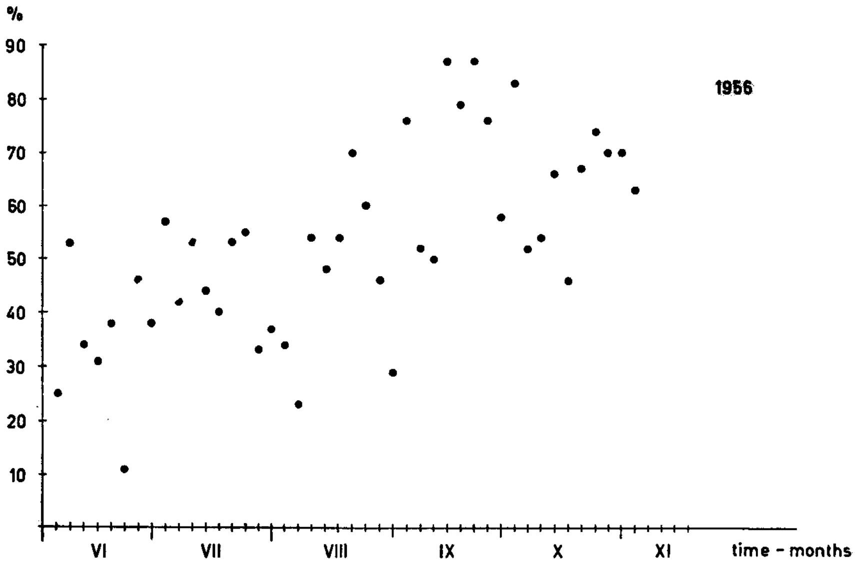

Fig. 21. Percentage of the total number of unmarked specimens found at each count in four out of the ten artificial tree-shelters (the four shelters in trees at the W-border of the first aspen wood) and time.
$\tau = + 0.447$, $p < 0.000066$

W-border than in the centre of the first aspen wood and that this difference is caused by horizontal activity outside of the wood (3.1.4). Because horizontal activity is shown by the litter-dwelling population during most of the year, the difference between population density at the W-border and in the centre of the first aspen wood must increase in the course of the year. Thus, it is clear that this trend in the density of the litter-dwelling populations must be the cause of the trend in the amount of migration into tree-shelters which was discussed above.

5.1.11. In 5.1.2 we saw that in the first aspen wood there was an uninterrupted exchange between tree-dwelling and litter-dwelling populations and in 5.1.9 it was found that the rate of exchange strongly depends on air humidity. If the large majority of the tree-dwelling populations is found in shelters at a considerable distance above the litter (as was the case during the LE GAY BRERETON's observations in 1953, see 3.4.2 and 3.4.3) the rate of exchange between tree-dwelling and litter-dwelling populations may expected to be less than was found in the first aspen wood (the chance of disappearing from the trees may be expected to become smaller if the distance between the tree-shelters and the litter is larger). Thus, LE GAY BRERETON

(1957) may be right when he assumes that in his observation areas the rate of exchange between tree-dwelling and litter-dwelling populations, and therefore between the populations of different trees, will not be large.

5.1.12. Summarizing, it may be concluded that a continuous exchange occurs between tree-dwelling and litter-dwelling populations (5.1.2). In agreement with the working hypothesis given in 4.1.9, it has been found that the amount of activity is larger when air humidity during the individual periods of inactivity has been higher. For the litter-dwelling populations this means that not only the activity as a whole, but also the amount of vertical activity (migration into tree-shelters) will be larger when air humidity during the individual periods of inactivity has been higher (5.1.6; see also 4.2.5). For the tree-dwelling populations this means that the amount of activity on trees (migration out of tree-shelters) is larger when air humidity during the individual periods of inactivity has been higher (5.1.8; see also 4.2.5). In agreement with 3.2.4, it was found that the amount of vertical activity (migration into tree-shelters) is larger when air humidity during the periods of activity is higher (5.1.6). In agreement with the discussions in 3.2 and 3.3, it appeared that air temperature has little effect on these activity patterns (5.1.8).

As a consequence of horizontal activity outside of the first aspen wood (3.1.4) in the course of the year, the difference between population density at the W-border and in the centre of this wood becomes larger by a growing accumulation of specimens in shelters at the borders of the wood. Due to this phenomenon, in the course of the year the amount of vertical activity (migration into tree-shelters) at the W-border becomes larger as compared with that in the centre of the wood (5.1.10).

The rate of exchange between tree-dwelling and litter-dwelling populations strongly depends on air humidity (5.1.9), but it may be expected that it is also influenced by the distance between the inhabited tree-shelters and the litter (LE GAY BRERETON, 1957) (5.1.11).

2. THE DIFFERENCES BETWEEN 3-DAY AND 4-DAY PERIODS [5.2.]

5.2.1. In 5.1.1 it was mentioned that on each Tuesday and Friday between April 5th and December 11th, 1956, the number of specimens present in each of ten artificial tree-shelters was counted. This means that the amount of migration into tree-shelters and the amount of migration out of tree-shelters were measured and totalled for three nights on each Friday (3-day period) and for four nights on each Tues-

TABLE IX

Correlations with S.D. for indirect observations on the amount of activity

	3-day and 4-day periods in the same rankings (5.1)			3-day periods only			4-day periods only		
	mean S.D. of the whole period	mean S.D. of nights	mean S.D. of days	mean S.D. of the whole period	mean S.D. of nights	mean S.D. of days	mean S.D. of the whole period	mean S.D. of nights	mean S.D. of days
correlation between the amount of migration into tree-shelters and S.D.									
45 counts in the same rankings	$\tau = -0.165$ $p = 0.1236$ (5.1.4)	$\tau = -0.161$ $p = 0.1326$ (5.1.6)	$\tau = -0.133$ $p = 0.2150$ (5.1.6)	$\tau = -0.327$ $p = 0.0384$	$\tau = -0.266$ $p = 0.0950$	$\tau = -0.242$ $p = 0.1310$	$\tau = -0.095$ $p = 0.5686$	$\tau = -0.134$ $p = 0.4122$	$\tau = -0.053$ $p = 0.7566$
5 periods of one month each combined	$\bar{\tau} = -0.279$ $p = 0.0232$ (5.1.4)	$\bar{\tau} = -0.157$ $p = 0.2006$ (5.1.6)	$\bar{\tau} = -0.183$ $p = 0.1362$ (5.1.6)	$\bar{\tau} = -0.456$ $p = 0.0324$	$\bar{\tau} = -0.246$ $p = 0.2584$	$\bar{\tau} = -0.133$ $p = 0.5352$	$\bar{\tau} = +0.046$ $p = 0.8258$	$\bar{\tau} = -0.094$ $p = 0.6600$	$\bar{\tau} = -0.027$ $p = 0.8966$
10 periods of 14 days each combined	$\bar{\tau} = -0.409$ $p = 0.00578$ (5.1.4)	$\bar{\tau} = -0.287$ $p = 0.0526$ (5.1.6)	$\bar{\tau} = -0.310$ $p = 0.0366$ (5.1.6)						
correlation between the amount of migration out of tree-shelters (%) and S.D.									
45 counts in the same rankings	$\tau = -0.278$ $p = 0.00932$ (5.1.7)	$\tau = -0.169$ $p = 0.1164$ (5.1.8)	$\tau = -0.299$ $p = 0.00480$ (5.1.8)	$\tau = -0.308$ $p = 0.0536$	$\tau = -0.107$ $p = 0.5156$	$\tau = -0.430$ $p = 0.00736$	$\tau = -0.118$ $p = 0.4778$	$\tau = -0.138$ $p = 0.3954$	$\tau = -0.071$ $p = 0.6672$
correlation between the rate of exchange with litter-dwelling populations and S.D.									
45 counts in the same rankings	$\tau = -0.456$ $p < 0.000066$ $(x = 4.27)$ (5.1.9)	$\tau = -0.314$ $p = 0.00318$ (5.1.9)	$\tau = -0.412$ $p = 0.000096$ (5.1.9)	$\tau = -0.489$ $p = 0.00188$	$\tau = -0.288$ $p = 0.0702$	$\tau = -0.519$ $p = 0.00108$	$\tau = -0.406$ $p = 0.0114$	$\tau = -0.256$ $p = 0.1118$	$\tau = -0.232$ $p = 0.1470$

day (4-day period). Since it was expected that the values estimated after 3-day periods would show about the same correlations with S.D. and temperature as the values estimated after 4-day periods, it might have seemed unnecessary to calculate these correlations for 3-day and 4-day periods separately (5.1). It was therefore very startling to find that correlations with S.D. were generally much stronger for 3-day periods than for 4-day periods (Table IX).

Correlations with temperature did not differ clearly for 3-day and 4-day periods and therefore these correlation-coefficients are not given here.

From Table IX it can be seen that we would have reached the same conclusions if, in 5.1, we had considered the correlations for 3-day periods only, instead of the correlations for 3-day and 4-day periods in the same rankings (see 5.1.12). It may be assumed, therefore, that the discussions in 5.1 are not altered appreciably by considering the curious differences between the correlations with S.D. for 3-day periods and for 4-day periods.

5.2.2. To examine the differences between 3-day and 4-day periods we will now consider the variations of population numbers in an artificial tree-shelter during several successive nights.

On each Tuesday or Friday a number of unmarked specimens were found in each tree-shelter (5.1.1). These specimens were marked and put back in the tree-shelter. During the first night after marking, a part a_1 of these specimens will become active. A part v_1 of these active specimens will leave the tree and for the greater part will find a new shelter at the base of the tree (3.2.2) while a part $s_1 = 1 - v_1$ will return to the tree-shelter.

During the second night after marking, a part a_2 will become active. A part v_2 of these active specimens will leave the tree (and arrive at the base of the tree), whereas a part $s_2 = 1 - v_2$ will return to the tree-shelter. But now a complication arises: a part a_2' of the marked specimens at the base of the tree will become active during that second night also. A part d_2 of these specimens will show horizontal activity and disperse over the litter, but a part $1 - d_2$ will show vertical activity. Besides a part v_2' of these vertically-active specimens which will return to the base of the tree, a part $s_2' = 1 - v_2'$ of these marked specimens will turn up again in the tree-shelter. Thus, part of the marked specimens which have left the tree during the first night after marking will return to the tree-shelter during the second night (remigration into tree-shelters).

During the third night after marking this remigration into tree-shelters will be still more important quantitatively because part of the specimens which have left the tree during the first *and* during the second night will return to the tree-shelter during the third night. During the fourth night after marking, the effect of remigration into tree-shelters will be larger again than during the third night, *etc.*, until during the nth night the amount of remigration into tree-shelters will be of about the same magnitude as the amount of migration out of tree-shelters of specimens of the same group (the same colour-mark) (see 5.2.3). Hence, after a 4-day period the quantitative effect of remigration into tree-shelters will be greater (the effect of remigration during the second + third + fourth night) than after a 3-day period (the effect of remigration during the second + third night).

Since both the amount of migration out of tree-shelters and the amount of remigration into tree-shelters (vertical activity) are negatively correlated with S.D. (5.1), remigration into tree-shelters diminishes the effect of S.D. on the amount of migration out of tree-shelters (remigration into tree-shelters decreases the absolute value of the regression-coefficient of the correlation between the amount of migration out of tree-shelters and S.D.). This masking effect of remigration into tree-shelters will of course be larger after 4 nights than after 3 nights, and so a larger correlation-coefficient may be expected for 3-day than for 4-day periods (Table IX).

The same can be said about the masking effect of remigration out of tree-shelters (of unmarked specimens) on the correlation between the amount of migration into tree-shelters and S.D. The expected differences between 3-day and 4-day periods were also found in this case (Table IX).

As a consequence of the masking effect of remigration, the correlation-coefficients with S.D. calculated from indirect observations (Table, IX, even for 3-day periods) may generally be expected to be smaller than those calculated from direct observations (Chapter 3).

5.2.3. The phenomenon of remigration is sometimes clearly illustrated by the number of the specimens, marked at a special count, which has disappeared from the tree-shelters after different numbers of nights (as measured at some successive counts). In a number of cases at a special count a greater number of the specimens, marked at one special date (with one special colour), were observed in the tree-shelters than at the previous count. These cases are given in Table X.

In these cases during one or two nights the amount of remigration into tree-shelters has been even greater than the amount of migration out of tree-shelters of specimens of the same group (marked with the same colour, *i.e.* from the same date of marking) [1]. In agreement with

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[1] The chance of making errors when counting the animals was very small since all specimens were removed from the tree-shelters at each count (see: 5.1.1) and each counted specimen was immediately set apart.

TABLE X

Migration out of tree-shelters in a number of cases

date of marking	number of specimens marked	number of specimens disappeared after		
		3 days (3-day period)	7 days	10 days
10–7	24	14	20	**18**
17–7	45	**26**	**39**	**37**
4–9	24	**17**	**22**	**19**
23–10	67	**57**	**56**	64
6–11	24	**21**	**20**	**19**

date of marking	number of specimens marked	number of specimens disappeared after		
		4 days (4-day period)	7 days	11 days
24–8	23	**14**	**18**	**17**
21–9	57	**36**	**50**	**49**

the discussions in 5.2.2, it can be seen from Table X that the effect of remigration into tree-shelters was larger after 10 or 11 days than after 7 days, and also larger after 7 days than after 3 or 4 days (at all 45 counts after 3 or 4 days the amount of remigration into tree-shelters was smaller than the amount of migration out of tree-shelters).

Mr. J. C. Smit of the Institute for Theoretical Biology at the University of Leiden was kind enough to construct a mathematical model which enabled me to estimate the quantitative role of remigration into tree-shelters in the differences between 3-day and 4-day periods. Since it is unnecessary for the questions under discussion to go further into the problem here, this model will be published separately. For the moment it suffices to mention that with the help of the model it was possible to show that the quantitative effect of remigration into tree-shelters was indeed such as to give a smaller correlation between S.D. and the amount of migration out of tree-shelters for 4-day periods than for 3-day periods.

6. WATER-BALANCE AND ACTIVITY

To give a direct proof of the correctness of the working hypothesis (4.1.9) it is necessary to demonstrate the occurrence of two processes:

a. That *P. scaber* takes up water during a stay in air with a high humidity.

b. That *P. scaber* goes in search of lower air humidities after having taken up a considerable amount of water and goes in search of high air humidities (shelter) after having lost a considerable amount of water.

1. DATA FROM THE LITERATURE [6.1.]

6.1.1. In a paper on the causes and effects of bunching, ALLEE (1926) gives the following data:

a. Specimens of *Cylisticus convexus* (de Geer), *Porcellio scaber* Latr., *Oniscus asellus* L., *Trachelipus rathkei* (Brandt), and *Armadillidium vulgare* (Latr.) may form a bunch in an environment or on a substratum which is not too moist. When the air humidity is too low or the substratum too moist, no bunching occurs and an existing bunch disintegrates.

b. At 22° C bunches can exist continuously for three days, but at 33°–36° C for only 18 hours. At fluctuating room-temperature bunches usually exist for a long period. At very low temperatures bunches persist even on a very moist substratum.

c. Bunches are more lasting in the dark than in the light.

d. Specimens of *Oniscus asellus* and *Cylisticus convexus* in a bunch take up or lose less water than isolated specimens under the same conditions: after 18 hours, specimens of *O. asellus* in a bunch showed 12 % and isolated specimens 21 % increase of body weight; under less humid conditions the increase of body weight amounted to 0.3 % for specimens in a bunch and 1.0 % for isolated specimens; after 24 hours specimens of *C. convexus* in a bunch showed 2.3 % and isolated specimens 9–12 % increase of body weight. With lower air humidities the increase of body weight changed into a decrease with relatively equal differences between specimens in a bunch and isolated specimens.

6.1.2. Unlike ALLEE (1926, 1931), AUZOU (1953) mentions that specimens of *Oniscus asellus* are unable to take up water from saturated air, whereas specimens of *Porcellio scaber* are able to do so. According to EDNEY (1951a) specimens of a great number of species of woodlice increase in weight during a stay in saturated air after a preliminary stay in dry air. Only *Armadillidium vulgare*, *Armadillidium nasatum* Budde-Lund, and *Ligia oceanica* (L) are also able to restore their body weight in air with 98 % R.H. after a preliminary stay in dry air. Graphs in this paper show that specimens of still other species increased in weight in air with 98 % R.H. after a preliminary stay of 23 hours in air with 50 % R.H., but EDNEY remarks that the results of these experiments are very variable. Another paper (SPENCER and EDNEY, 1954) states that no specimens of the species studied (*Ligia oceanica*, *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*) are able to take up water from air with 98 % R.H. after a preliminary stay of one hour in air with 0 % R.H., but there is no mention of the results of the experiments published by EDNEY (1951a) three years earlier.

According to these authors it is useless to study the possibility of water-uptake in woodlice in air with very high humidities, because condensation of water on the bodies of the animals and drinking of condensation-water cannot be prevented. In my case, however, such a study could be very useful, because I am not interested in how water is taken up, but whether or not water is taken up.

6.1.3. When water is taken up into the body of a woodlouse, the osmotic pressure of the haemolymph may be expected to decrease. Thus, changes in the osmotic pressure of the haemolymph may inform us whether water is taken up or lost.

WIDMANN (1936) mentions that in all species studied by him the osmotic pressure of the haemolymph increased in autumn (October), reached a maximum in winter (November-March), decreased again in spring (April, May), and reached a minimum in summer (May-September). In *Porcellio scaber*, for instance, he found in winter a lowering of the freezing-point: d = 1.680° C (= 0.908 mol.) and in summer: d = 1.545° C (= 0.835 mol.). WIDMANN supposes this cycle in the osmotic pressure of the haemolymph to be caused by temperature and to result in the animal's going into winter-shelters in autumn and leaving of these shelters in spring.

A stay of some months in a dry environment resulted in an increase of the osmotic pressure of the haemolymph in *P. scaber*: dry, d = 1.346° C (= 0.727 mol.) and control, d = 1.324° C (= 0.716 mol.). After a stay of only 15 days in a dry environment the increase was even larger in *Ligia oceanica*: dry, d = 3.273° C (= 1.769 mol.), control, d = 2.820° C (= 1.524 mol.) and in another experiment: dry, d = 3.185° C (= 1.721 mol.), control, d = 2.69° C (= 1.454 mol.).

Using a new method for the determination of the freezing-point, PARRY (1953) was able to measure the effect of different air humidities on the osmotic pressure of the haemolymph in individual specimens of *Ligia oceanica*. Such an influence was evident from her experiments.

6.1.4. Data on reactions of woodlice as a consequence of the condition of the water-balance are very scarce in the literature. WALOFF (1941) mentions that specimens of *Oniscus asellus* placed in a preferendum apparatus which consisted of a dark, dry part and a light, humid part, moved to the dark, dry part (negative phototactic reaction), but after a stay of 20–200 min in the dark, dry part they moved to the light, moist part. I agree with WALOFF that the latter reaction must be considered a hygrotactic reaction stimulated by water-loss. It is evident that the negative phototactic tendencies were inhibited by water-loss in these experiments. Cloudsley–Thompson (1952) also observes that specimens of *Oniscus asellus* showed stronger hygrotactic and weaker negative phototactic reactions if they were more desiccated. Abbott (1918) mentions that specimens of *Porcellio scaber* showed weaker negative phototactic reactions if they had lived in a dry environment. In *Oniscus asellus* this phenomenon could not be established. According to Abbott (1918), all woodlice react to desiccation with an increase of activity. Henke (1930) mentions that the negative phototactic tendencies in *Armadillidium vulgare* can easily be inhibited by a stay of 24 hours in a dry environment, by starving, by a sudden increase of temperature, and by a stay in a wholly unnatural environment (*e.g.* a glass container).

2. WATER-UPTAKE AND WATER-LOSS [6.2]

Since it is not clear from the literature whether or not specimens of *P. scaber* take up water during a stay in very humid air (6.1.1 and 6.1.2), it was necessary to investigate this subject.

6.2.1. In the following experiments the proportional change of body weight in specimens of known initial weight after a stay in air with fixed humidity is used as a measure of the amount of water-uptake or water-loss. The following method was used: After being weighed each individual was separately placed (in its weighing-jar) in a glass jar with glass top and rubber ring which was then closed as quickly as possible and placed in a constant temperature cabinet (20° C). A saturated salt-solution was present under the unstoppered weighing-jar in order to maintain an atmosphere with known humidity inside of each glass jar. After 24 hours the glass jar was opened and the weighing-jar was stoppered instantly, after which the animal in it could be weighed again and its change of body weight determined. Before starting the experiments each empty and unstoppered weighing-jar was kept for 24 hours in the closed glass jar, so that the air in it could reach equilibrium with the humidity maintained by the saturated salt-solution. The animals used in the experiments were kept for 24 hours in a container with some moist flower-pot shards but without food, in order to avoid the disturbing effect of defaecation during the experiment.

Provisional experiments were made using 25 males of different sizes. Humidities were kept constant with distilled water (R.H. $= 100$ %, S.D. $= 0$ mm) and saturated solutions of K_2SO_4 (R.H. $= 97$ %, S.D. $= 0.65$ mm), KNO_3 (R.H. $= 93$ %, S.D. $= 1.4$ mm), Na_2CO_3

(R.H. = 91 %, S.D. = 1.6 mm), and KCl (R.H. = 85 %, S.D. = 3.0 mm). The humidity of the air to which each individual was actually exposed in these experiments could not be controlled precisely because a number of factors (distance above the solution, height and width of the weighing-jar, transpiration by the animal, *etc.*) will cause deviations from the values given in Chemical Tables (moreover, all Tables do not give the same values). It may be assumed, however, that the humidity inside the weighing-jar showed about an equal relation to the expected humidity, irrespective of the salt-solution used in each glass jar. Thus, the humidity values given here must be considered approximate values.

After a stay of 24 hours at 20° C and a fixed humidity, the change of body weight in these 25 males appears to be strongly and significantly correlated with S.D.: $\tau = -0.829$, $p < 0.000066$ ($x = 5.20$) (Fig. 22A). Moreover, in saturated air (over distilled water) all specimens obviously increased in weight. (N.B. In many of the laboratory experiments it was found that S.D. = 0 mm could only be reached and maintained during very short periods (even when distilled water was nebulized in a thermostat); so by saturated air, almost-saturated air is generally meant).

6.2.2. When making these experiments, considerable condensation sometimes occurred in the weighing-jars over distilled water, so that in these cases the increase might not be due to an increase in weight of the animal. These experiments were therefore repeated, using many empty control jars at the same time. Moreover, the preliminary experiments showed that the proportional change of body weight is different in specimens of different size, therefore in these experiments only males of 20–30 mg were used [1].

Since it may be assumed that the ability to take up water is larger when the animals are more desiccated, the specimens used in these experiments were kept in air with medium humidity (without food), for 24 hours before the experiments.

To study the possibility of water-uptake in particular a number of KCl-solutions of different concentration were used to maintain a fixed high humidity in each glass jar. The solutions were renewed each week. Following solutions of KCl were used: 0.0 g/l (S.D. = 0 mm); 22.2 g/l (S.D. = 0.17 mm); 74.3 g/l (S.D. = 0.55 mm); 148.6 g/l (S.D. = 1.11 mm) and 223.8 g/l (S.D. = 1.68 mm). The experiments were made in a thermostat at 20° C.

After correcting the values for the proportional change of body weight of each individual for the change of weight of its weighing-jar

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[1] My thanks are due to Mr. C. VAN DEN HOEK for making these experiments for me.

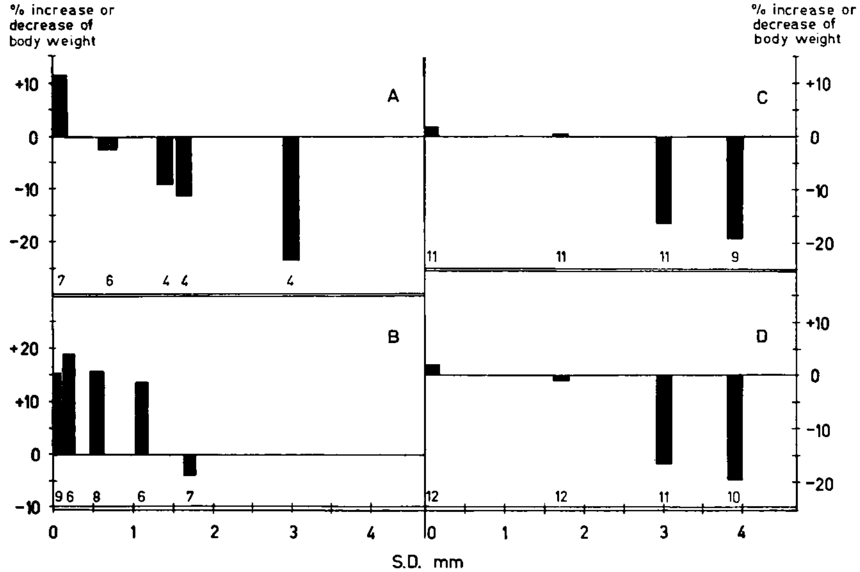

Fig. 22. Mean proportional increase or decrease of body weight of a number of specimens kept for 24 hours in air with constant humidity and temperature (20° C) after a preliminary exposure for 24 hours:
A: to moist air (25 males of various weight): $\tau = -0.829$, $p < 0.000066$
B: to laboratory air (36 males of 20–30 mg): $\tau = -0.376$, $p = 0.00424$
C: to S.D. of 0.65 mm (42 males of 30–60 mg) : $\tau = -0.753$, $p < 0.000066$
D: to S.D. of 0.65 mm (45 females of 30–60 mg): $\tau = -0.798$, $p < 0.000066$

(based on 60 control experiments) it becomes evident that during a stay of 24 hours the males in the present experiments took up water even in unsaturated air (Fig. 22B).

When comparing Fig. 22A and 22B it becomes clear that the ability to take up water is indeed larger when the animals have previously been more desiccated.

The proportional change of body weight is significantly correlated with S.D.: $\tau = -0.376$, $p = 0.00424$ (Fig. 22B). After a stay of 48 hours the proportional increase of body weight was still 3–6 % higher than after 24 hours, while a correlation of $\tau = -0.336$, $p = 0.0308$ is found between the proportional change of body weight and S.D. Although these correlations are not strong, in combination with 6.2.1 and 6.2.3 these experiments show that water can be taken up even from unsaturated air.

6.2.3. In connection with the experiments to be discussed in 6.3, a number of experiments were also made by K. BAKKER (unpublished) on the relation between the proportional change of body weight and humidity. To make it possible to start the experiments with specimens of about the same water-content, the animals were kept for 24 hours in glass jars above a saturated solution of K_2SO_4 (S.D. = 0.65 mm) without food.

To prevent any influence of changes in the weight of the weighing-jars, after each experiment the individual to be weighed was quickly put into a weighing-jar which had not yet been used in the experiment. While this arrangement has the advantage that no control experiments with empty jars were required, it has the disadvantage that the animals are certain to lose some water during the manipulations before weighing (see also 6.2.8). Thus, the values found for the amount of water-uptake must be considered minimum values.

To maintain a fixed humidity in the glass jars at 20° C, distilled water (R.H. = 100 %, S.D. = 0 mm) and saturated solutions of Na_2CO_3 (R.H. = 91 %, S.D. = 1.6 mm), KCl (R.H. = 85 %, S.D. = 3.0 mm), and NH_4Cl (R.H. = 79 %, S.D. = 3.9 mm) were used.

After a stay of 24 hours at a fixed humidity, the change of body weight in 42 males is strongly and significantly correlated with S.D.: $\tau = -0.753$, $p < 0.000066$ ($x = 6.54$) (Fig. 22 C). About the same correlation was found for 45 females: $\tau = -0.798$, $p < 0.000066$ ($x = 7.15$) (Fig. 22D). In saturated air (over distilled water) a small but significant increase of body weight was found in both sexes: ♂♂, $\chi^2 = 7.36$, $p < 0.01$ ($v = 1$); ♀♀, $\chi^2 = 5.33$, $p \approx 0.02$ ($v = 1$).

6.2.4. It is clear that *P. scaber* is able to take up water from saturated air and sometimes also from unsaturated air (when desiccated). Since it is known that in dry air water is lost by evaporation through the cuticle (EDNEY, 1951a), it may be expected that water-uptake in saturated or nearly-saturated air also takes place through the cuticle. Thus, the amount of loss or uptake of water (in % of body weight) must be about directly proportional to the ratio: $\frac{\text{surface}}{\text{volume}}$. For animals of a simple body-shape (like woodlice), it may be assumed that in specimens of the same species body volume is directly proportional to body weight (W) and in consequence body surface is about directly proportional to $W^{\frac{2}{3}}$ (see also EDNEY, 1951a). Thus, the ratio: $\frac{\text{surface}}{\text{volume}}$ can be approximated by: $\frac{W^{\frac{2}{3}}}{W} = W^{-\frac{1}{3}}$.

To test this supposition, the amount of water-uptake was determined in males of different sizes after a stay at 20° C in saturated air (over distilled water, using the experimental set-up described in 6.2.2).

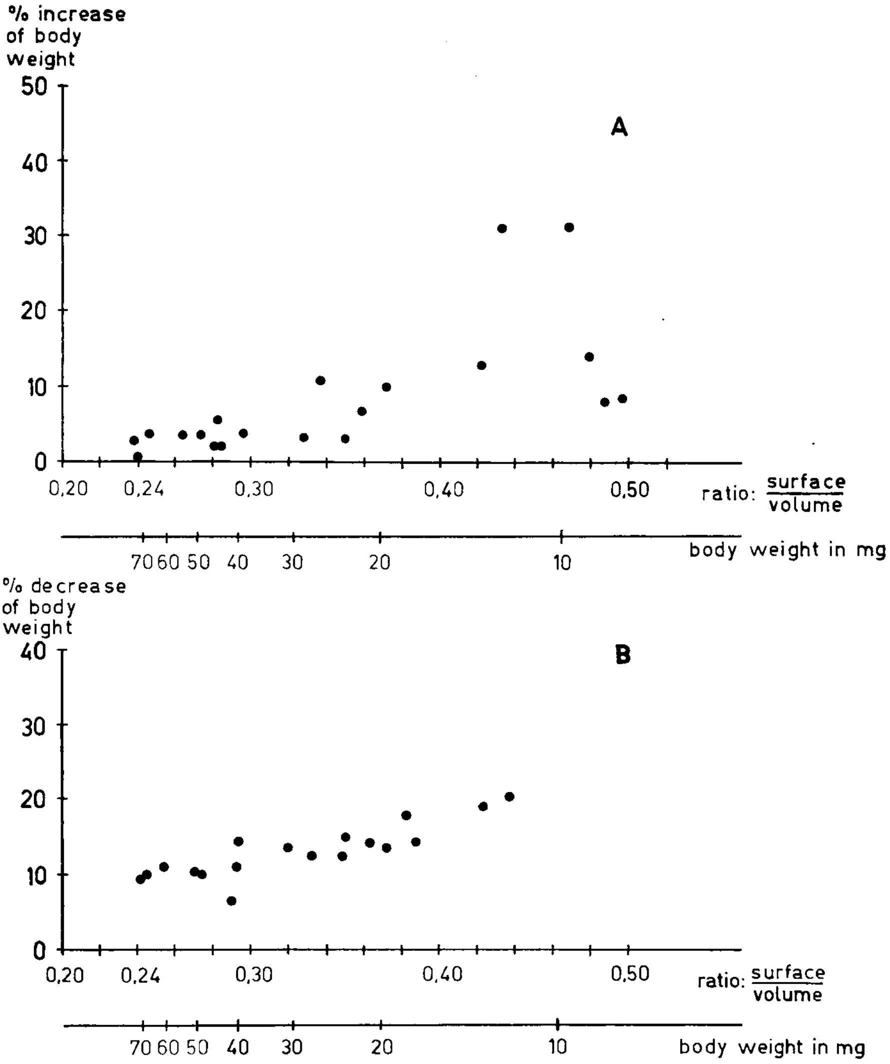

Fig. 23.

A. Proportional increase of body weight in males of various sizes kept for 24 hours in saturated air (temperature = 20° C).

$\tau = +0.547$, $p = 0.00084$

B. Proportional decrease of body weight in males of various sizes kept for 24 hours in air with S.D. = 1.68 mm (temperature = 20° C).

$\tau = +0.712$, $p < 0.000066$

After a stay of 24 hours, the proportional increase of body weight is strongly correlated with the ratio: $\frac{\text{surface}}{\text{volume}}$: $\tau = +0.547$, $p = 0.00084$ (Fig. 23A). After a stay of 48 hours, about the same correlation was found ($\tau = +0.621$, $p = 0.000144$). During the same period the amount of water-loss was determined in males of different sizes after a stay at 20° C in air with S.D. = 1.68 mm. Between the proportional decrease of body weight and the ratio: $\frac{\text{surface}}{\text{volume}}$ a correlation of $\tau = +0.712$, $p < 0.000066$ ($x = 4.09$) was found after a stay of 24 hours (Fig. 23B) and a correlation of $\tau = +0.752$, $p = 0.000144$ after a stay of 48 hours.

From Fig. 23 it can be seen that the amount of water-uptake and the amount of water-loss are about directly proportional to the ratio: $\frac{\text{surface}}{\text{volume}}$. It may therefore be assumed that both water-uptake and water-loss take place through the cuticle.

It is possible that in this connection a bunch may be considered one very large specimen, in which case ALLEE's findings (6.1.1) that water-uptake and water-loss are reduced in specimens in a bunch agree well with my views.

6.2.5. That the amount of water-uptake and water-loss depends on the condition of the water-balance and on the relation between surface and volume is illustrated by experiments done by K. BAKKER (unpublished). In these experiments three groups of eight males (group A: 8 ♂♂ of 70–100 mg; group B: 8 ♂♂ of 35–45 mg; group C: 8 ♂♂ of 16–26 mg) successively stayed for a number of hours in air of different humidities, in the following order: 7 hours at S.D. = 3.9 mm; 21 hours at S.D. = 1.6 mm; $24\frac{1}{2}$ hours at S.D. = 0 mm; 19 hours at S.D. = 3.0 mm; 26 hours at S.D. = 0.65 mm; 26 hours at S.D. = 0 mm; 23 hours at S.D. = 3.9 mm; 20 hours at S.D. = 1.6 mm and 48 hours at S.D. = 0 mm. After each period the proportional change of body weight was determined (experimental set-up as in 6.2.3).

Fig. 24 clearly illustrates that proportionally more water is taken up if the animals were more desiccated during the previous period and *vice versa*. Moreover, the fluctuations of water-content in these experiments were stronger in small than in large specimens. The differences in change of body weight between males of group A and males of group C are significant (per. 1 : $p = 0.000155$; per. 2: $p = 0.00031$; per. 3: $p = 0.0345$; per. 4: $p = 0.00166$; per. 5: $p = 0.000583$; per. 6: $p = 0.04545$; per. 7: $p = 0.00408$; per. 8: $p = 0.04800$. Per. 9: could not be determined because too few specimens remained).

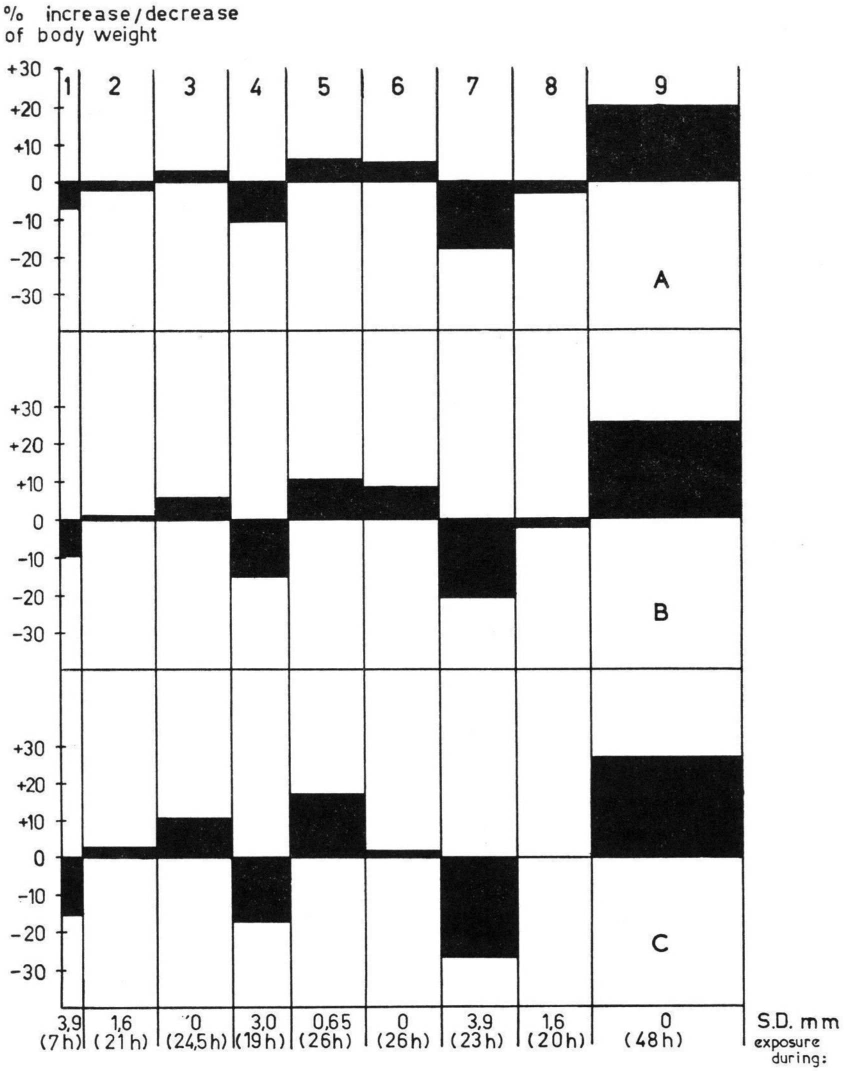

Fig. 24. Proportional increase or decrease of body weight in males of three size-groups after successive exposures to air with constant humidity (different during each exposure) and temperature (20° C).
A: eight males with initial weight: 70–100 mg
B: eight males with initial weight: 35–45 mg
C: eight males with initial weight: 16–26 mg

These fluctuations of water-content in *P. scaber* under the influence of air humidity are similar to the fluctuations of osmotic pressure in *Ligia oceanica* (L.) under the same influence found by PARRY (1953).

6.2.6. The question now arises whether water-uptake and water-loss are physical processes governed by the osmotic pressure of the haemolymph and the structure of the cuticle only, or processes which the living animal can influence.

Some information on this subject may be obtained by comparing the amount of water-uptake and water-loss in living and in recently-dead specimens. During the experiments discussed in 6.2.1, 6.2.2, 6.2.3, and 6.2.7, some specimens died soon after the beginning of an experiment. The change of body weight of these specimens can be compared with the values for living specimens of the same size-group derived from the same experiments. These data (from experiments at 20° C only) are given in Table XI.

TABLE XI

Percentage change of body weight in living and in recently-dead specimens

size-group	*S.D. (mm)*	*stay of ... at 20° C*	*living specimens*	*dead specimens*	*number of dead ind.*
20–30 mg	0	24 hours	+15%	+10%	1
20–30 mg	0	24 hours	+23%	+ 6%	2
20–30 mg	0	48 hours	+33%	+12%	2
50–80 mg	0	48 hours	+19%	+ 5%	2
20–30 mg	0.55	48 hours	+21%	−10%	1
20–30 mg	1.11	24 hours	+14%	− 6%	2
20–30 mg	1.11	48 hours	+19%	−17%	2
20–30 mg	1.68	24 hours	− 4%	−14%	1
25–35 mg	1.6	20 hours	− 2%	− 9%	2
20–30 mg	1.68	48 hours	− 4%	−19%	5

From the Table it is evident that at S.D. = 0 mm the % increase of body weight is smaller in dead specimens than in living ones and that at S.D. = 1.68 mm the % decrease of body weight is larger in dead specimens than in living ones. At S.D. = 0.55 mm and S.D. = 1.11 mm water-uptake occurs in living specimens, whereas water-loss takes place in dead specimens. It seems that water-uptake and water-loss are primarily physical processes (they also occur in dead specimens), but that the quantitative relation of these processes with the humidity of the surrounding air is modified in living individuals, *i.e.* in living specimens water-loss is reduced in favour of water-uptake.

As far as physical water-uptake is concerned, water can only be taken up if the osmotic pressure of the haemolymph is higher than the suction-pressure of the surrounding air. According to WIDMANN (1936), in *P.scaber* the lowering of the freezing-point of the haemolymph lies between 1.16° C and 1.60° C (0.63 mol. and 0.86 mol.); this means that water can only be taken up by osmosis from air with S.D. smaller than 0.4–0.5 mm.

6.2.7. Now, since water-uptake is partly governed by physical processes and is partly an active process of the living animal, it is important to know what relation exists between the amount of water-uptake and temperature. In order to study this factor the amount of water-uptake was determined in males weighing 30–35 mg after a stay at a constant temperature of between 2° C and 25° C in saturated air (over distilled water; experimental set-up as in 6.2.2)[1]. Six constant temperatures were used in these experiments: 2° C, 5° C, 10° C, 15° C, 20° C and 25° C. After 24 hours a significant and positive correlation was found between the proportional increase of body weight and temperature ($\tau = +0.477$, $p < 0.000066$, $x = 4.29$; Fig. 25A). After a stay of 48 hours a nearly equal correlation was found ($\tau = +0.341$, $p = 0.00244$; Fig. 25B).

Like many wholly or partially biological processes, water-uptake shows an optimum for temperature (Fig. 25); especially after 48 hours the amount of water-uptake at 25° C is much smaller than at 20° C ($p = 0.0426$; $n = 6$, $m = 8$). An optimum for temperature between 15° C and 25° C or between 10° C and 20° C is also found for most activities of *P.scaber* when studied in the laboratory (7.2.2 and 7.2.5).

6.2.8. In 4.1.9 the question arose of whether or not specimens of *P.scaber* are able to lose the excess of water in their bodies by "normal" excretion. We have seen that during a stay in saturated or nearly-saturated air specimens of *P.scaber* increased in weight. This means that the amount of water taken up must be larger than the amount of water lost by "normal" excretion during the same period. Obviously "normal" excretion does not keep up with water-uptake under these conditions, and it may be assumed that a similar process takes place during a stay in a very moist shelter.

In the experiments discussed in 6.2.1, 6.2.2, and 6.2.7, "normal" excretion may have played a part since its quantitative influence is not separated from the calculated proportional increase of body weight (amount of water-uptake). In the experiments discussed in 6.2.3 and 6.2.5, a possible influence of "normal" excretion is eliminated by putting each individual into a new weighing-jar when weighing, and yet

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[1] My thanks are due to Mr. C. VAN DEN HOEK for making these experiments for me.

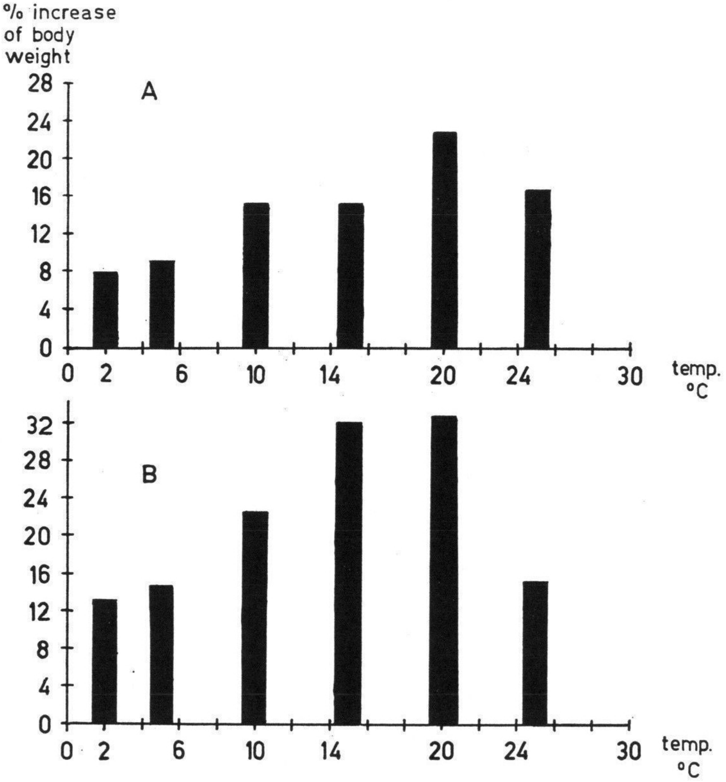

Fig. 25. Mean proportional increase of body weight of males (30–35 mg) kept in saturated air with constant temperature.
A: for 24 hours: $\tau = +0.477$, $p < 0.000066$
B: for 48 hours: $\tau = +0.341$, $p = 0.00244$

water-uptake was observed in these experiments too (especially in 6.2.5). Moreover, in 6.3 it will be shown that there is a significant correlation between the proportional change of body weight and the water-content of the haemolymph.

If "normal" excretion cannot keep up with water-uptake under very moist conditions, a stay in saturated air must eventually become unfavourable for the animals. In agreement with this, unpublished results from the Zoological Laboratory at Leiden showed that the mean duration of life was shorter when the animals were continuously exposed to saturated air than when they were exposed to a S.D. of about 0.8 mm (at 25° C).

It has also been observed by the writer that after a long stay in saturated air some of the recently-dead specimens were markedly elongated and showed considerable distance between the segments. It seems plausible to assume that in such cases the animals had died as a result of excessive water-uptake.

3. WATER-BALANCE AND WATER-CONTENT OF THE HAEMOLYMPH [6.3.]

6.3.1. To determine whether a proportional change of body weight (6.2) really indicates that water is lost from or is taken up into the body, K. BAKKER estimated the refractive index of the haemolymph after a known change of body weight (unpublished). It can be assumed that in specimens of the same species, collected from the same locality, which have lived under the same uniform conditions in the laboratory, the composition of the haemolymph will be more or less identical, so that at a constant temperature the refractive index of the haemolymph will mainly depend on its water-content (see 6.3.2).

With the experimental set-up described in 6.2.3 (previous stay of 24 hours over a saturated solution of K_2SO_4 (S.D. = 0.65 mm) at 20° C) the proportional change of body weight was estimated after an exposure of 24 hours to air with a certain humidity. By means of a small pipette, 1–2 mm^3 of haemolymph was extracted from the body by inserting the pipette between the second and third thoracic segment into the dorsal part of the body (dorsal sinus). This sample of the haemolymph was brought between the prisms of a refracto-meter (Abbe) and the refractive index measured.

6.3.2. In this way a highly significant correlation was found between the proportional change of body weight in 46 males after exposure for 24 hours to air with a certain humidity and the refractive index of the haemolymph: $\tau = -0.489$, $p < 0.000066$ ($x = 4.74$) (Fig. 26). In 49 females a correlation is found of $\tau = -0.583$, $p < 0.000066$ ($x = 5.87$).

Now, we know that there is a statistical relation between the refractive index of the haemolymph and the proportional change of body weight. Since it may be assumed that there is also a relation between the osmotic pressure and the refractive index of the haemolymph, it is very probable that the osmotic pressure of the haemolymph mainly depends on its water-content.

To make certain that the refractive index may be used as a relative measure of the water-content of the body as well, the water-content of the body (percentage of body weight) was also estimated by other

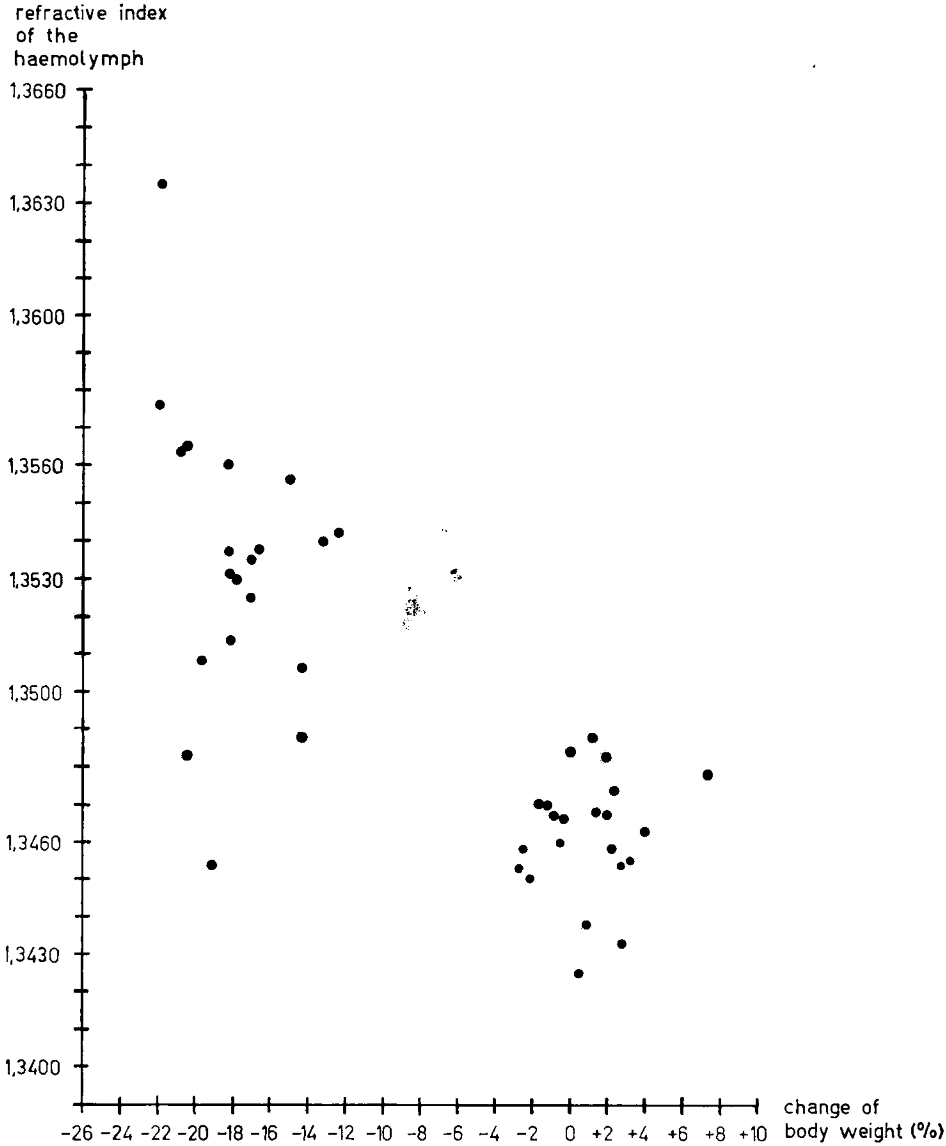

Fig. 26. Relation between the proportional change of body weight and the refractive index of the haemolymph in 46 males kept for 24 hours in air with a certain humidity. $\tau = -0.489$, $p < 0.000066$

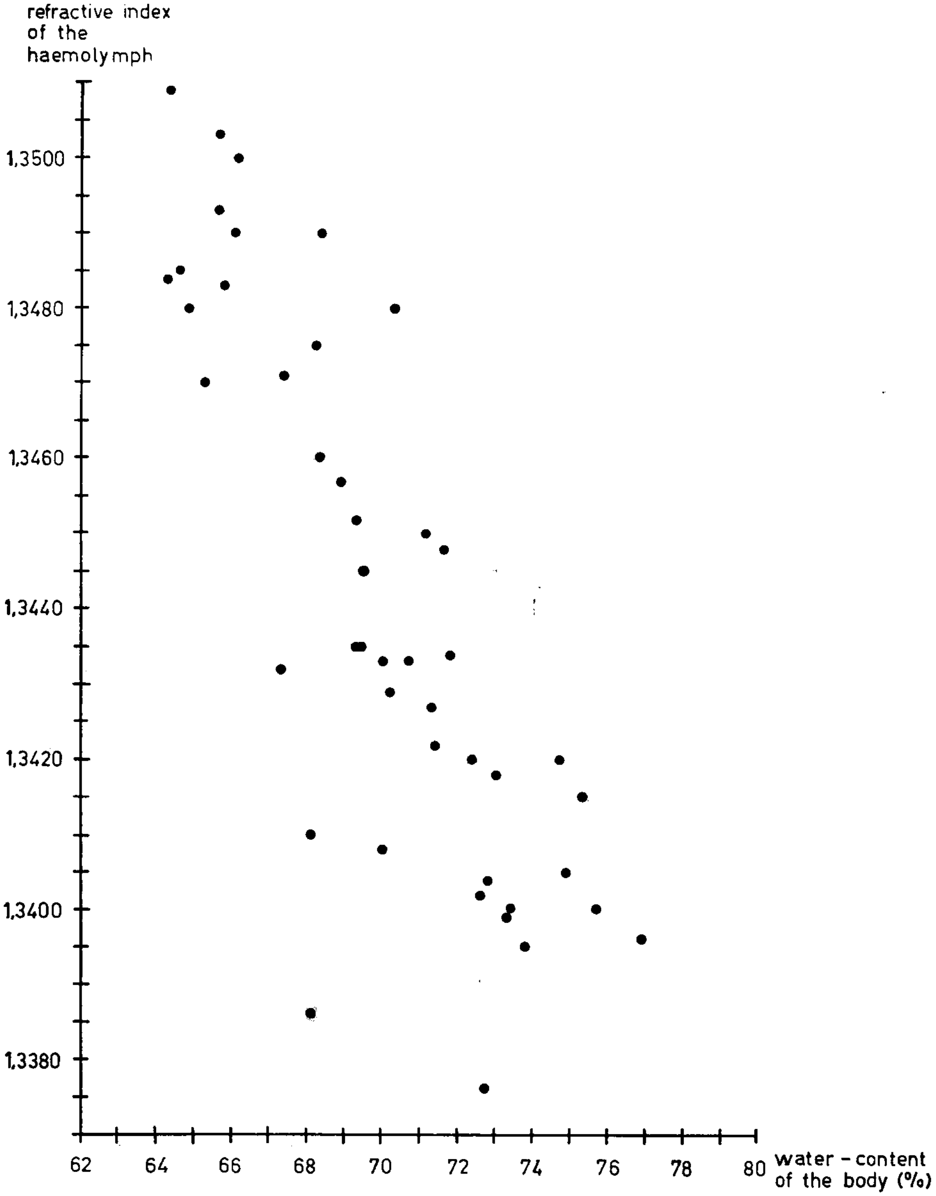

Fig. 27. Relation between the water-content of the body (% of body weight) and the refractive index of the haemolymph in 45 males kept for 24 hours in air with a certain humidity.
$\tau = -0.628$, $p < 0.000066$

experimental methods. As a result of these experiments, a highly significant correlation was found between the water-content of the body and the refractive index of the haemolymph: for 45 males, $\tau = -0.628$, $p < 0.000066$ ($x = 6.05$) (Fig. 27); for 48 females, $\tau = -0.585$, $p < 0.000066$ ($x = 5.79$). Thus, in these experiments the refractive index could be used as a reliable relative measure of the water-content of the body. We may now conclude that in the present experiments (6.2) the proportional change of body weight could be used as a relative measure of the amount of water-loss or water-uptake.

4. WATER-BALANCE AND ACTIVITY [6.4.]

Having shown that water is taken up by specimens of *P. scaber* during a stay in saturated or nearly-saturated air, we have still to demonstrate that the preference for lower or higher air humidities is influenced by the condition of the water-balance.

6.4.1. For this purpose comparisons were made between the preference for moist or dry air of specimens which had taken up water and specimens which had lost water [1].

To provide experimental specimens of approximately the same water-content, the animals were all placed in glass jars over a saturated solution of Na_2CO_3 (R.H. = 91 %, S.D. = 1.6 mm) at 20° C for 24 hours. Half of the specimens were then placed in jars over distilled water (in the Tables = A) to take up water („moist" individuals) and the other half in jars over a saturated solution of KCl (in the Tables = B) (R.H. = 85 %, S.D. = 3.0 mm) to lose water ("dry" individuals) (see 6.2.1).

To be able to compare the humidity preferences of "moist" and "dry" individuals, they were placed in a humidity gradient apparatus (Fig. 16 F). This gradient apparatus was constructed by taking a large, glass culture-dish and dividing the lid and half of the bottom radially with plastic strips into eight sections. Saturated salt solutions were placed in the watertight sections of the bottom to produce two equal gradients of five humidities in each half of the dish. In order to produce an equal experimental area at each humidity, sections 1 and 5, which produced the lowest and highest humidity respectively, were made larger than the other sections (see Fig. 16 F). The experimental animals could move about on a false bottom of cloth gauze resting on the plastic partitions of the bottom sections. When the lid was in place, its sections corresponded vertically to the sections of the bottom, with a space of

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[1] My thanks are due to Miss. H. ANDRÉ DE LA PORTE for making these experiments for me.

about five mm left between the partitions of the lid and the false bottom. The lid of the dish made an airtight closure with the bottom.

Animals were introduced into the apparatus through a small hole in the lid of the dish above the section with the highest humidity. The hole could be plugged with a rubber stopper (see also: BARLOW, 1957, p. 363). The following humidities were produced in the sections of the dish (see 6.2.1): 1. R.H. = 100 % (distilled water), 2. R.H. = 93 % (saturated solution of KNO_3), 3. R.H. = 85 % (KCl), 4. R.H. = 79 % (NH_4Cl) and 5. R.H. = 75 % ($NaNO_3$).

To avoid the effect of bunching, not more than five specimens were placed in each gradient apparatus at the same time and in a number of experiments only one specimen at a time was used. At 10, 25, 40, 55, 70, 85, 100, 115, and 130 min after the beginning of the experiments, the positions of the animals in the gradient apparatus were recorded. A number of experiments were made at the same time and each type of experiment was repeated several times. For each type of experiment the mean percentage of specimens (from the total number used in the experiment) present at each observation at the "dry" side (in the sections with R.H. = 75 % and R.H. = 79 %) of the gradient apparatus and at the "moist" side (in the sections with R.H. = 100 % and R.H. = 93 %) was calculated. These data are given in Tables XII–XV. Specimens present in the sections with R.H. = 85 % were not included in the calculations.

6.4.2. The first series of experiments (with 5 specimens in each experiment) were made in the light with "moist" and "dry" individuals (n and m = number of experiments with "moist" (n) or "dry" (m) individuals). The results are given in Table XII.

TABLE XII

Experiments in the light

	Mean % of specimens present					
	at the "dry" side			*at the "moist" side*		
	A ("moist" ind.)	*B ("dry" ind.)*	*p value of difference between A en B*	*A ("moist" ind.)*	*B ("dry" ind.)*	*p value of difference between A and B*
I. after 21 hours in A, or 21 hours in B	11%	5%	p = 0.2802	83%	87%	p = 0.6456
II. after 45–50 hours in A, or 21 hours in B	12%	5%	p = 0.0250	69%	87%	p = 0.0024

I: n = m = 26 (130 ind.); II: n = 12 (60 ind.), m = 26 (130 ind.).

It is clear that after having taken up water during a stay of 21 hours in saturated air, in the light ,,moist" individuals do not show a demonstrably stronger preference for the "dry" side of the gradient apparatus than "dry" individuals, while after a stay of 45–50 hours in saturated air this preference is significantly stronger in "moist" than in "dry" individuals under the same conditions.

Since under natural conditions activities occur in the dark, all other experiments were made in the dark. Light was only admitted to permit determination of the position of each individual at the times of observation.

6.4.3. The results of the experiments in the dark are given in Table XIII (5 specimens in each experiment).

TABLE XIII

Experiments in the dark

	Mean % of specimens present					
	at the "dry" side			*at the "moist" side*		
	A ("moist" ind.)	*B ("dry" ind.)*	*p value of difference between A and B*	*A ("moist" ind.)*	*B ("dry" ind.)*	*p value of difference between A and B*
I. after 21 hours in A, or 21 hours in B	18%	5%	$p < 0.000066$ $(x = 4.52)$	77%	87%	$p = 0.0022$
II. after 45–50 hours in A, or 21 hours in B	20%	5%	$p = 0.00062$	74%	87%	$p = 0.0192$
III. after 71 hours in A, or 21 hours in B	15%	5%	$p = 0.00026$	77%	87%	$p = 0.00152$
IV. after 163 hours in A, or 21 hours in B	17%	5%	$p < 0.000066$ $(x = 4.77)$	71%	87%	$p < 0.000066$ $(x = 4.31)$

I and II: $n = m = 40$ (200 ind.); III: $n = 20$ (100 ind.), $m = 40$ (200 ind.); IV: $n = 46$ (230 ind.), $m = 40$ (200 ind.).

Table XIII shows that after a stay of 21 hours or longer in saturated air, "moist" individuals always show a significantly stronger preference for the "dry" side of the gradient apparatus than "dry" individuals under the same conditions. After a stay of 21 hours in saturated air the preference for high air humidities is stronger in the light (6.4.2, Table XII) than in the dark (Table XIII), which possibly agrees with the findings of CLOUDSLEY-THOMPSON (1952, 1956^{a}) (see also 1.5.1).

The preference for the "dry" side of the gradient apparatus does not clearly become stronger when the stay in saturated air has lasted longer than 21 hours. This is in agreement with the conclusion reached in 3.3.9 that for many specimens the period of inactivity does not last longer than 24 hours.

6.4.4. In 6.2.4 we saw that the amount of water-loss and of water-uptake is larger in small than in large specimens. Thus, we may expect that after a stay of 21 hours in saturated air, small specimens will have taken up relatively more water than large specimens, and hence small specimens will show a stronger preference for the "dry" side of the gradient apparatus than large specimens. To test this supposition, the preference for the "dry" or the "moist" side of the gradient apparatus was compared for "moist" and "dry" individuals of different size-groups. The results are given in Table XIV (one specimen in each experiment).

TABLE XIV

Experiments in the dark with specimens of different weight

after 21 hours in A, or 21 hours in B	*Mean % of specimens present ......*					
	at the "dry" side			*at the "moist" side*		
size-group	*A ("moist" ind.)*	*B ("dry" ind.)*	*p value of difference between A and B*	*A ("moist" ind.)*	*B ("dry" ind.)*	*p value of difference between A and B*
I. < 30 mg	27%	5%	p = 0.000192	64%	81%	p = 0.00222
II. 30–40 mg	24%	5%	p = 0.000074	68%	84%	p = 0.00200
III. 40–50 mg	29%	4%	p = 0.00410	68%	92%	p = 0.00236
IV. 50–60 mg	17%	3%	p = 0.0138	78%	93%	p = 0.0258
V. 60–70 mg	19%	3%	p = 0.0376	75%	92%	p = 0.0574
VI. 70–80 mg	12%	3%	p = 0.2984	85%	92%	p = 0.3898
VII. > 80 mg	9%	5%	p = 0.1470	86%	88%	p = 0.5686

I: n = 20 ind., m = 40 ind.; II: n = m = 30 ind.; III, IV and VII: n = m = 20 ind.; V: n = 20 ind., m = 15 ind.; VI: n = 15 ind., m = 11 ind.

The Table nicely illustrates that in "moist" individuals the preference for the "dry" side of the gradient apparatus is weaker when the animals are heavier. In accordance with this, a significant though small correlation is found between the ratio: $\frac{\text{surface}}{\text{volume}}$ (6.2.4) of the "moist" individuals used in these experiments and their preference for the "dry" side of the gradient apparatus ($\tau = +0.215$, $p = 0.00042$).

6.4.5. After a stay of 21 hours in saturated air, "moist" individuals heavier than 70 mg do not show a significantly stronger preference for the "dry" side of the gradient apparatus than "dry" individuals (Table XIV). It may be expected, however, that when the stay in saturated air has lasted much longer than 21 hours, this preference will also be significantly stronger in "moist" individuals heavier than 70 mg than in "dry" individuals. The data given in Table XV (in which the preferences of specimens lighter than 30 mg are compared with those of specimens heavier than 80 mg) show that this is indeed the case (one specimen in each experiment).

6.4.6. In 3.3.7 we saw that in most specimens the periods of activity do not last longer than about one hour. It may therefore be expected that in the present experiments "moist" individuals will only stay at the

TABLE XV

Experiments in the dark with specimens lighter than 30 mg and with specimens heavier than 80 mg

	Mean % of specimens present					
	at the "dry" side			*at the "moist" side*		
	A ("moist" ind.)	*B ("dry" ind.)*	*p value of difference between A and B*	*A ("moist" ind.)*	*B ("dry" ind.)*	*p value of difference between A and B*
	in specimens < 30 mg					
I. after 21 hours in A, or 21 hours in B	27%	5%	$p = 0.000192$	64%	81%	$p = 0.00222$
II. after 45–50 hours in A, or 21 hours in B	20%	5%	$p = 0.00794$	74%	81%	$p = 0.1416$
III. after 163 hours in A, or 21 hours in B	30%	5%	$p < 0.000066$ $(x = 4.70)$	57%	81%	$p < 0.000066$ $(x = 4.14)$
	in specimens > 80 mg					
IV. after 21 hours in A, or 21 hours in B	9%	5%	$p = 0.1470$	86%	88%	$p = 0.5686$
V. after 45–50 hours in A, or 21 hours in B	23%	5%	$p = 0.0114$	67%	88%	$p = 0.0818$
VI. after 163 hours in A, or 21 hours in B	12%	5%	$p = 0.0376$	67%	88%	$p = 0.00288$

I, II and III: $n = 20$ ind., $m = 40$ ind.; IV and V: $n = m = 20$ ind.;
VI: $n = 12$ ind., $m = 20$ ind.

"dry" side of the gradient apparatus during part of the experimental period (130 min). Since in many of these experiments each specimen was marked with a different colour, the mean length of the stays at the "dry" side of the gradient apparatus could be calculated for "moist" and for "dry" individuals. The results of these calculations for all specimens together were, "moist" individuals: 45.1 min and "dry" individuals: 25.8 min. From the data in 3.3.7 the mean length of the individual periods of activity can be roughly estimated at 64 min.

Specimens generally stay at the "moist" side of the gradient apparatus for the greater part of the experimental period, so that the chance of observing a specimen at the "moist" side of the gradient apparatus is much larger than the chance of finding a specimen at the "dry" side (Tables XII–XV).

6.4.7. It was also possible to calculate the percentage of marked specimens which had visited the "dry" side of the gradient apparatus in these experiments (had become active). For specimens $<$ 30 mg: "moist" individuals: 81 % (out of 69 ind.) and "dry" individuals: 35 % (out of 40 ind.). For specimens $>$ 80 mg: "moist" individuals: 60 % (out of 60 ind.) and "dry" individuals: 40 % (out of 20 ind.). For all specimens together: "moist" individuals: 69 % (out of 234 ind.) and "dry" individuals 32 % (out of 136 ind.) (compare also: 3.3.9).

In agreement with ABBOTT's results (1918) (see 6.1.4) it was found in all experiments discussed in 6.4 that "dry" individuals were more active than "moist" individuals.

5. GENERAL CONCLUSIONS [6.5.]

The experiments discussed in this chapter support the working hypothesis given in 4.1.9.

It has been shown that specimens of *P. scaber* take up water from saturated or nearly-saturated air (6.2.1, 6.2.2 and 6.2.3) and that this results in an increasing preference for lower air humidities (for becoming active) and *vice versa* (6.4.3). These preferences are weaker in the light than in the dark (6.4.2).

Water-uptake occurs through the cuticle, as shown by the fact that during the same period the proportional increase of body weight is greater in small than in large specimens (6.2.4 and 6.2.5); and, as a consequence, the preference for lower air humidities is stronger in small than in large specimens under these conditions (6.4.4 and 6.4.5).

The amount of water-uptake increases with temperature up to about 15–20° C (6.2.7). Water-uptake seems to be governed primarily by physical processes (osmotic pressure of the haemolymph), but in living individuals water-loss is reduced in favour of water-uptake (6.2.6). In saturated or nearly-saturated air, "normal" excretion cannot keep up with water-uptake, so that water is accumulated in the body (6.2.8) and the osmotic pressure of the haemolymph decreases (6.3).

Both from direct observations in the field and from experiments in the laboratory the mean length of the individual periods of activity could be estimated (about 45–64 min) (6.4.6).

After a stay of 21 hours in saturated air, at least 60 % of the experimental specimens show a preference for lower air humidities (6.4.7).

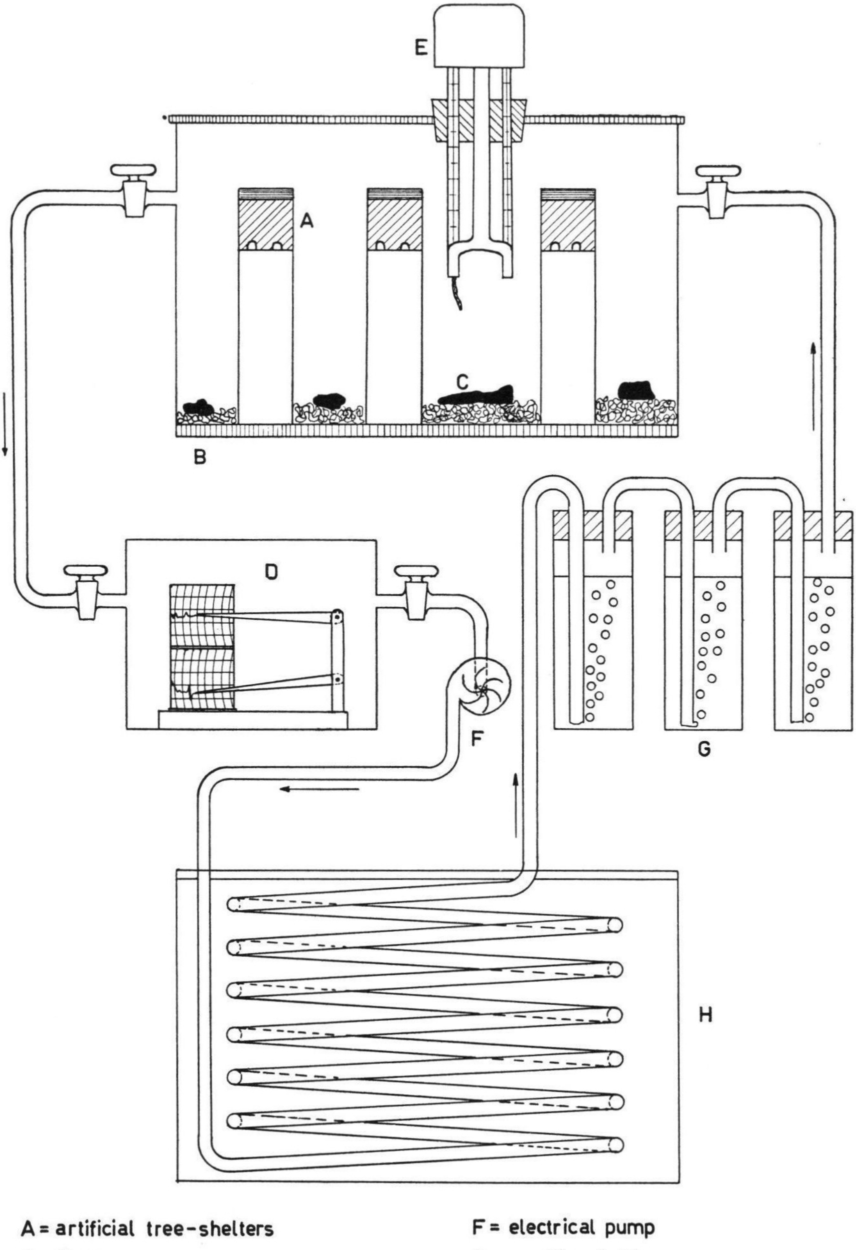
7. ACTIVITY PATTERNS UNDER EXPERIMENTAL CONDITIONS

Having shown that the working hypothesis formulated in Chapter 4 gives an explanation of the activity patterns observed under natural conditions, the picture can be completed by trying to reproduce the natural activity patterns under experimental conditions.

1. EXPERIMENTS ON THE EFFECT OF HUMIDITY [7.1]

According to Chapters 3 and 5, the qualitative and quantitative aspects of activity are primarily determined by the humidity of the air both inside and outside the shelters. Laboratory experiments were therefore designed to compare the amounts of activity accompanying a number of different and fixed levels of saturation deficit, holding other environmental factors as constant as possible.

7.1.1. In one experiment the amount of migration into tree-shelters (as a relative measure of the amount of vertical activity, see 5.1.4) per night of a group of one thousand specimens was studied during successive and alternating periods (one or two weeks) with low or high air humidities. The experimental set-up is given in Fig. 28. Six small "trees" (about 30 cm high) each provided with an artificial tree-shelter (A) were placed in a large glass container (for a tree with shelter see Fig. 16E). A layer of aspen litter (B) with shelters (C) was brought onto the bottom of the container. By means of an electric pump (F) a constant air-current was conducted through the container. The air passed a thermo-hygrograph (D), a water-thermostat (H) by which the air temperature could be brought to about 15° C, and



A = artificial tree-shelters
B = litter
C = shelters in litter
D = thermo-hygrograph
E = electrical psychrometer (Assmann)
F = electrical pump
G = washing-bottles
(distilled water or $CaCl_2$ - solution)
H = water - bath.

Fig.28. For explanation see text (7.1.1).

through three washing-bottles (G) by which the saturation deficit of the air could be held within certain limits. To maintain high air humidities, the washing-bottles were filled with distilled water and for lower humidities they were filled with $CaCl_2$-solutions. By means of the thermo-hygrograph large deviations in temperature or humidity could be recorded. Such large irregularities rarely occurred during the period of the experiment: temperature generally fluctuated between 15° C and 19° C and S.D. generally did not fluctuate more than 1.0 mm per week (only during the second half of the experimental period did some irregularities occur). Through a hole in the lid of the container (closed with a large cork) an Assmann psychrometer (E) could be brought into the container by which temperature and S.D. inside the experimental chamber could be measured.

7.1.2. On February 26, 1957 one thousand specimens of *P. scaber* (collected in Meijendel) were brought onto the litter of the container. During successive and alternating periods of one or two weeks, the S.D. of the air-current was held at a high or at a low level. Each morning at 9 o'clock the number of specimens in the "tree-shelters" was counted, after which they were put back onto the litter. At the same time the temperature and S.D. of the air inside the experimental room were measured with the Assmann psychrometer. The flower-pot shards inside the "tree-shelters" and the litter were held in a moist condition during the whole experimental period. The experiment was continued until May 23, 1957.

At the end of the experimental period about half of the specimens had survived. If we assume that mortality was distributed regularly over the whole of the experimental period (from other experiments in the laboratory it was evident that this is generally the case), the amount of migration into tree-shelters per 24-hour period can be expressed as a percentage of the population present.

If the amount of migration into tree-shelters per 24-hour period is correlated with S.D., a negative and highly significant correlation is found: $\tau = -0.384$, $p < 0.000066$ $(x = 4.96)$ (Fig. 29). Because during the second half of the experimental period there were some irregularities with unknown effect, the first half of the experimental period gives the most reliable results. For that period a strong negative and highly significant correlation is found: $\tau = -0.600$, $p < 0.000066$ $(x = 5.16)$ (Fig. 29).

The results of this experiment, by which the effect of S.D. could be studied without the interference of other environmental factors, agree well with the results of corresponding observations made in Meijendel (see 5.1.4).

7.1.3. From direct observations during this experiment it was again

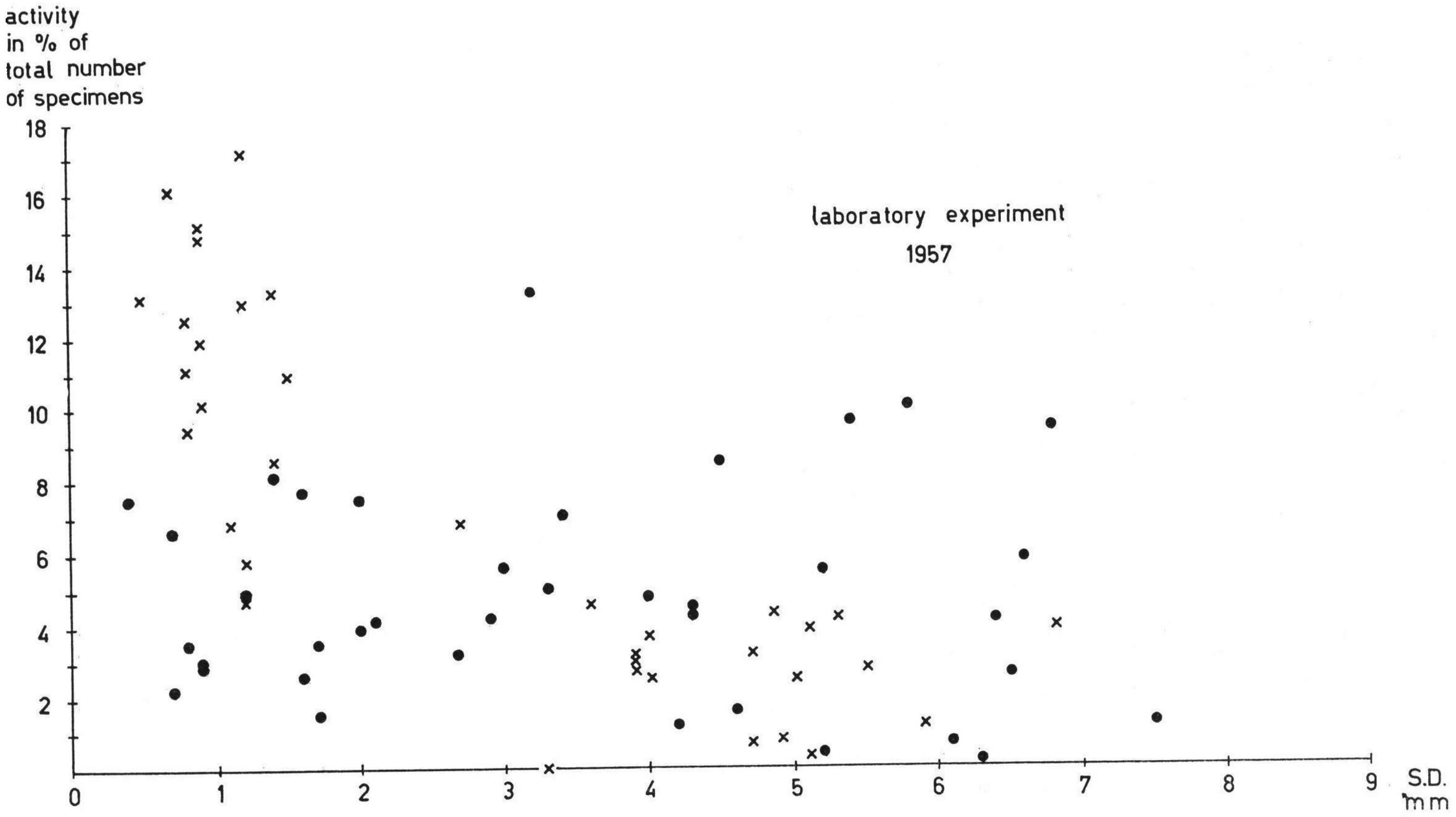


Fig.29. Relation between the amount of migration into tree-shelters (% activity per 24-hour period) and S.D.
Total observations: $\tau = -0.384$, $p < 0.000066$. Observations during first half of experimental period (×): $\tau = -0.600$, $p < 0.000066$

clear that vertical activity must be considered a search for localities where air humidity is low enough to allow an adequate transpiration (see 4.2.3). Since the litter was continuously held in a moist condition it may be accepted that the animals were unable to transpire water by horizontal activity only. With high humidities of the air-current (S.D. = 0.5–1.5 mm) it must have been difficult for the animals to transpire water even by vertical activity. It may be expected that under these conditions adequate transpiration was mainly possible at the upper parts of the "trees" where the air-current was most pronounced. In agreement with this expectation, with high humidities of the air-current specimens preferably moved about upon the upper parts of the "trees" and upon the "tree-shelters".

With low humidities of the air-current (S.D. = 4.0–7.0 mm) a steep humidity-gradient must have existed between the moist litter and the level of the dry air-current. It may be accepted that under these conditions adequate transpiration was possible at even a small distance above the litter. In agreement with this expectation, with low humidities of the air-current many specimens moved about upon the lower parts of the "trees" up to about 5 cm above the litter.

7.1.4. All other experiments were made in 6 cells of a serial thermohygrostat (Fig. 16A). In each cell the amount of activity of a group of specimens at a fixed level of temperature and air humidity was measured during a number of 24-hour periods. During the experiments discussed in this section (7.1), the air temperature was continuously held at 15° C in all cells, while in each cell a different but fixed level of S.D. was maintained. At each count, temperature and S.D. inside the closed cell were measured with an electrical Assmann psychrometer, which could be read through a double glass window in the door of the cell (Fig. 16A) (temperature and S.D. were measured after the cell had been closed for more than one hour). In all experiments the amounts of activity per 24-hour period were averaged for each week.

7.1.5. To study the relation between horizontal activity and vertical activity (3.2.5) under experimental conditions, the following modification of the set-up described in 4.1.4 was used (July 29–September 30, 1957): at each side of the wooden shelter a small "tree" provided with an artificial tree-shelter was placed (Fig. 16D). The wooden shelter on the platform as well as the "tree-shelters" were filled with moist flower-pot shards. The circular trap was provided with some decaying aspen leaves. At the beginning of the experiment, 57 specimens (collected in the Botanical Garden at Leiden) were put into each platform-shelter (Fig. 16C).

Specimens leaving the platform-shelter and showing horizontal activity were collected in the circular trap, while part of the specimens showing vertical activity arrived in the tree-shelters (migration into tree-shelters). In this way in each of six cells of the thermo-hygrostat the amount of horizontal activity and the amount of migration into tree-shelters during the previous 24-hour period could be periodically measured (9:00–10:00 a.m.). After each count all specimens were put back into the platform-shelters. The S.D. in the respective cells was maintained between the following limits: cell 1: 0.5–0.8 mm; cell 2: 0.6–1.2 mm; cell 3: 1.3–2.0 mm; cell 4: 2.1–2.6 mm; cell 5: 3.1–3.8 mm; cell 6: 4.1–5.1 mm.

Once a week the flower-pot shards in each shelter were replaced by freshly moistened ones (when necessary the shards were also moistened in the course of the week) and the total number of living specimens in each cell was counted.

7.1.6. When the amount of horizontal activity (averaged for each week) is correlated with S.D. (averaged for each week), a positive correlation is found: $\tau = +0.335$, $p = 0.00194$ (Fig. 30) and with the individual coefficients for each week ($n = 6$) combined: $\bar{\tau} = +0.467$, $p = 0.00108$. This result is wholly in agreement with the results from observations on horizontal activity in Meijendel (3.1.7 and 3.1.8).

But if we look more closely at Fig. 30 it becomes clear that the positive correlation is only evident for high air humidities. If we therefore calculate the correlations between the amount of horizontal activity and S.D. for high and for low humidities separately, we find: cell 1–3 (S.D. = 0–2.0 mm: $\tau = +0.502$, $p = 0.00124$ and cell 4–6 (S.D. = 2.1–5.2 mm): $\tau = -0.125$, $p = 0.4716$. If we now compare Fig. 30 with Fig. 6 (3.1.7) we are struck by the very great similarity between the two Figures. Although for the observations made in Meijendel the correlations with S.D. were not separately calculated for high and low humidities (the drawing of a line between high and low humidities under natural conditions would be much more arbitrary than in these experiments), it will be evident that both for observations made under natural conditions and for those made under experimental conditions the amount of horizontal activity is only positively correlated with S.D. at high air humidities.

In 3.2.5 it was found that horizontal and vertical activity are the two aspects of the activities of the same *P. scaber*-population. Hence, if the amount of horizontal activity is only positively correlated with S.D. at high air humidities, the amount of vertical activity must only be negatively correlated with S.D. at high air humidities. If we look at Fig. 10 (3.2.4) we find that this is probably the case (although the evidence is not conclusive).

The observed phenomenon can be understood with the help of the working hypothesis: only at high air humidities is it necessary for

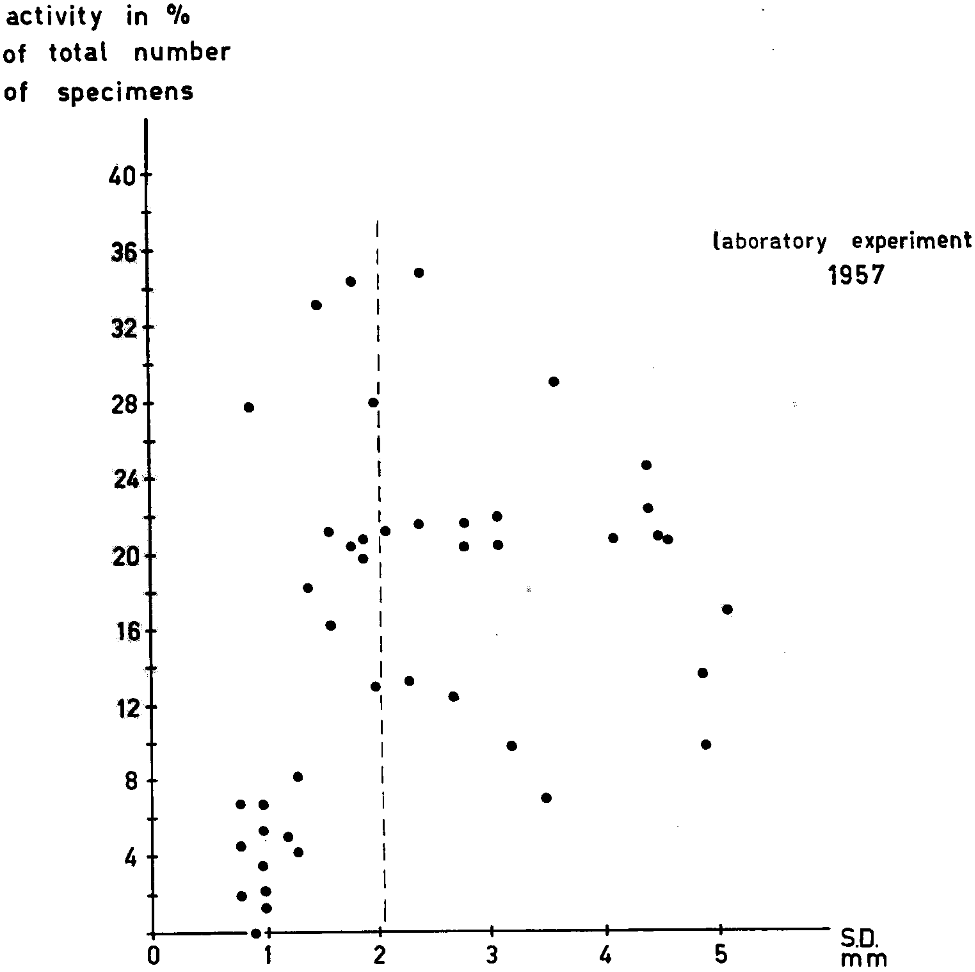


Fig.30. Relation between the amount of horizontal activity (% activity averaged for each week) and S.D.

Total observations: $\tau = +0.335$, $p = 0.00194$

Observations at S.D. between 0 and 2.0 mm: $\tau = +0.502$, $p = 0.00124$

Observations at S.D. between 2.1 and 5.2 mm: $\tau = -0.125$, $p = 0.4716$

active specimens to climb up the trees to find localities where adequate transpiration is possible and hence only with high air humidities is it to be expected that the phenomena of vertical and of horizontal activity are causally connected with saturation deficit. The causal connection of these two forms of activity with S.D. does not gradually in-

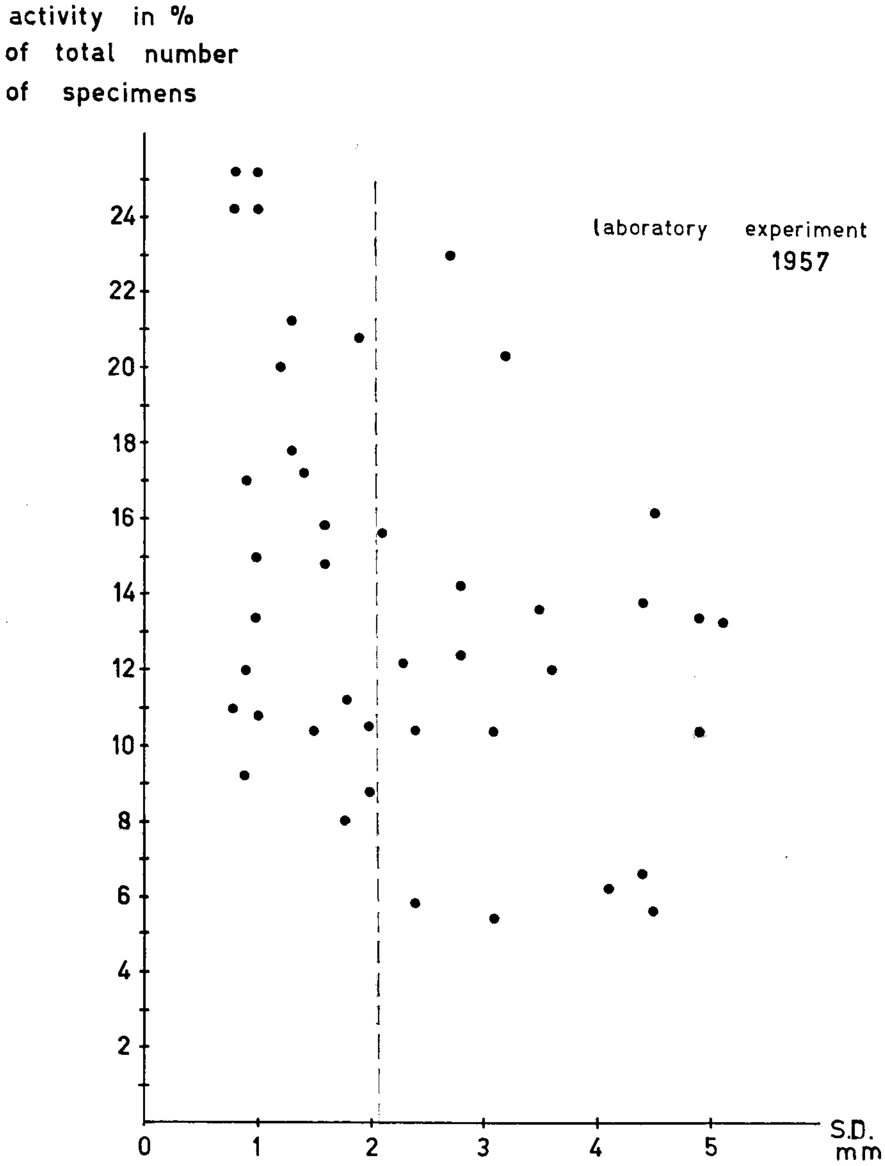


Fig.31. Relation between the amount of migration into tree-shelters (% activity averaged for each week) and S.D.

Total observations: $\tau = -0.292$, $p = 0.00672$

Observations at S.D. between 0 and 2.0 mm: $\tau = -0.313$, $p = 0.0456$

Observations at S.D. between 2.1 and 5.2 mm: $\tau = -0.081$, $p = 0.6456$

crease when air humidity is higher, but there seems to be a critical level of humidity above which the effect of humidity on the behaviour of active specimens becomes quantitatively directed (Fig. 30).

If these suppositions are correct, in the above experiment the amount of migration into tree-shelters (as a relative measure of the amount of vertical activity) should show a negative correlation with S.D. at high air humidities and no correlation at low air humidities. For cell 1–3 (S.D. = 0–2.0 mm) we find: $\tau = -0.313$, $p = 0.0456$ and for cell 4–6 (S.D. = 2.1–5.2 mm): $\tau = -0.081$, $p = 0.6456$ (Fig. 31), which agrees with expectation.

With 6 cells taken together (S.D. = 0–5.2 mm) we find: $\tau = -0.292$, $p = 0.00672$ and with the individual coefficients for each week combined: $\bar{\tau} = -0.377$, $p = 0.0083$. This result agrees with the findings under natural conditions (5.1.4). From Fig. 18 it is not clear, however, that only with high air humidities does a correlation exist between the amount of migration into tree-shelters and S.D., but many factors may have masked this phenomenon here (*e.g.*: the very indirectness of the S.D. values used (5.1.3 and 5.1.4: mean of S.D. values estimated at the Valkenburg station during both the night- and the day-periods after the previous count), and remigration out of trees, 5.2.2).

The quantitative directness of both aspects of activity under the influence of S.D. with high air humidities (0–2 mm) versus the absence of this directness with lower air humidities is nicely illustrated by Fig. 32, where the relation between the amount of vertical activity (measured as the amount of migration into tree-shelters) and the amount of horizontal activity

$$\left(\frac{\text{amount of migration into tree-shelters}}{\text{amount of horizontal activity}}\right)$$

is plotted against S.D. for this experiment. Between S.D. = 0 mm and S.D. = 2 mm the relation is strongly correlated with S.D.: $\tau = -0.547$, $p = 0.00044$ and between S.D. = 2.1 mm and S.D. = 5.2 mm the relation is not correlated with S.D.: $\tau = +0.049$, $p = 0.7948$.

7.1.7. In 4.2.5 it was postulated that more specimens will become active after a period of high air humidities than after a period of lower air humidities, because we may accept that the air humidity inside a shelter is influenced by the humidity of the open air (5.1.6). In 5.1.8 data are discussed which affirm this supposition. In 1958 an attempt was made to prove this supposition by an experiment in the laboratory (September 8– October 20). The same experimental set-up was used as that described in 4.1.4 and shown in Fig. 16B. Fifty specimens (collected in Meijendel) were put into the wooden shelter. Each morning

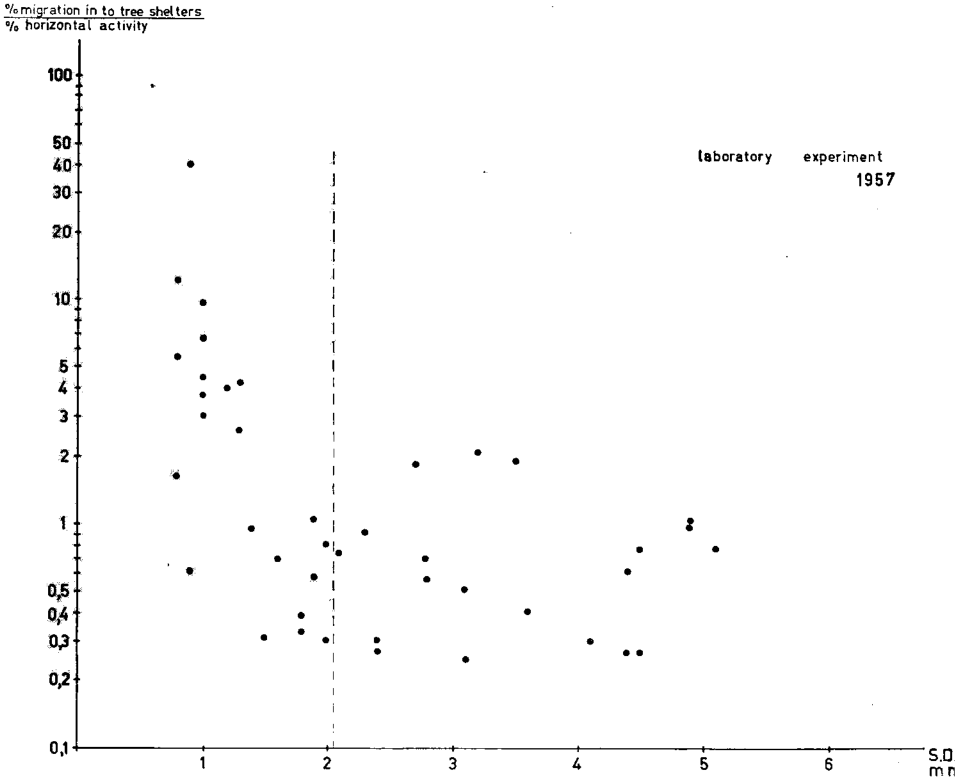


Fig.32. S.D. and the relation between the amount of migration into tree-shelters (Fig.31) and the amount of horizontal activity (Fig.30).
Total observations: $\tau = -0.409$, $p = 0.00014$
Observations at S.D. between 0 and 2.0 mm: $\tau = -0.547$, $p = 0.00044$
Observations at S.D. between 2.1 and 5.2 mm: $\tau = +0.049$, $p = 0.7948$

between 9 and 10 o'clock the trapped specimens were counted and put back into the wooden shelter. Two of these units were placed in each of six cells of the serial thermo-hygrostat.

The flower-pot shards in the wooden shelter of one set-up in each cell were moistened each day with distilled water during the whole experimental period in order to maintain the air humidity inside the shelter at a very high level and to make it as independent of the air humidity outside the shelter as possible (series A). The shards in the wooden shelter of the other set-up in each cell were not moistened but only replaced by freshly moistened ones once a week (to prevent the shelter from becoming unsuitable). In this way it could be expected that the air humidity inside the shelter was influenced to some extent by the humidity of the air outside the shelter during the greater part of each week (series B). In the cells with low air humidities it was indeed noticed that the shards discoloured towards the end of each week as a result of drying.

The set-up of series A and the set-up of series B exchanged places weekly inside the same cell. S.D. inside the respective cells was maintained between the following limits: cell 1: 0.9–1.1 mm; cell 2: 0.9–1.5 mm; cell 3 :1.9–2.3 mm; cell 4: 2.2–3.3 mm; cell 5: 3.2–3.8 mm; cell 6: 3.3–4.1 mm. The number of living specimens in each set-up was counted once a week.

7.1.8. When the amount of activity (averaged for each week) is correlated with S.D. (averaged for each week), we find for series A: $\tau = -0.024$, $p = 0.8494$ (Fig. 33) and for series B: $\tau = -0.420$, $p = 0.00044$ (Fig. 34). Thus we may conclude that the amount of activity is smaller when the air humidity inside the shelter has been lower. If the humidity of the air inside the shelter more or less depends on the humidity of the open air (series B and under natural conditions), we find that the amount of activity is smaller when the humidity of the open air has been lower (series B, Fig. 34 and 5.1.8). If the humidity of the air inside the shelter is artificially kept at a high level, no correlation is found between the amount of activity and the humidity of the open air (series A, Fig. 33), which proves that the mean length of the individual periods of inactivity (*i.e.*: the amount of activity) depends on the humidity of the air inside the shelter. These results agree wholly with the working hypothesis.

If we look more closely at Fig. 34 it becomes evident that the amount of activity is only negatively correlated with S.D. at low air humidities (S.D. = 2.1–4.2 mm): with S.D. = 0–2.0 mm we find: $\tau = -0.083$, $p = 0.7566$ and with S.D. = 2.1–4.2 mm: $\tau = -0.679$, $p < 0.000066$ ($x = 4.41$). This must be due to the fact that under the experimental conditions only a considerable difference in humidity between shelter and air could influence the S.D. value in the shelter sufficiently, because water-vapour will not be lost very easily from a wooden shelter with small entrances placed in stationary air. Hence, this does not imply that under natural circumstances S.D. values between 0 and 2 mm would not affect the amount of activity in *P. scaber.*

Calculating the correlations between the amount of activity and S.D. for high and for low air humidities separately in series A does not modify our conclusions: S.D. = 0–2.0 mm: $\tau = +0.014$, $p = 1.000$; S.D. = 2.1–4.5 mm: $\tau = -0.096$, $p = 0.5620$ (Fig. 33).

7.1.9. To study the effect of air humidity on the amount of migration out of tree-shelters under experimental conditions (October 19–

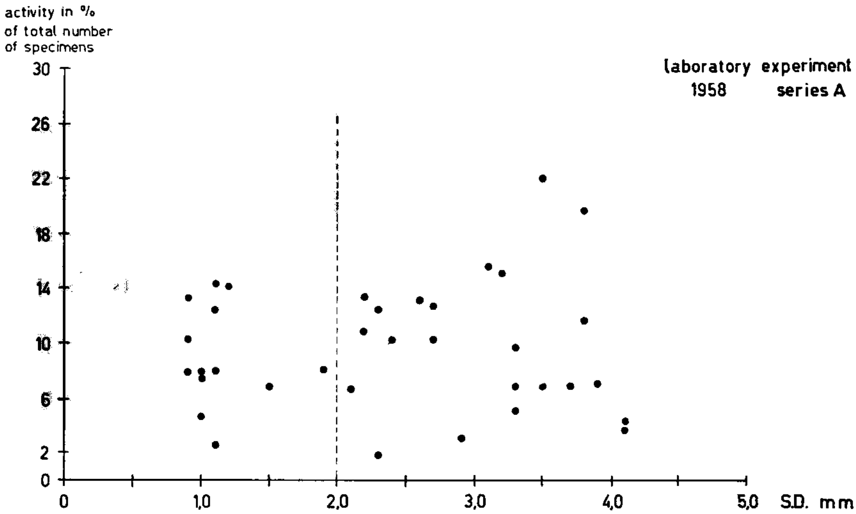


Fig.33. Relation between the amount of activity as a whole (% activity averaged for each week) and S.D.; shelters moistened daily.

Total observations: $\tau = -0.024$, $p = 0.8494$

Observations at S.D. between 0 and 2.0 mm: $\tau = +0.014$, $p = 1.000$

Observations at S.D. between 2.1 and 4.2 mm: $\tau = -0.096$, $p = 0.5620$

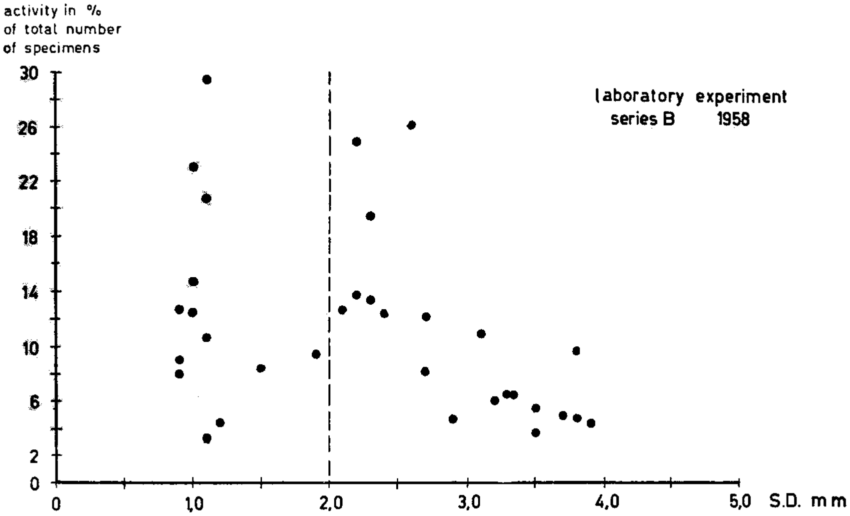


Fig.34. Relation between the amount of activity as a whole (% activity averaged for each week) and S.D.; shelters moistened weekly.

Total observations: $\tau = -0.420$, $p = 0.00044$

Observations at S.D. between 0 and 2.0 mm: $\tau = -0.083$, $p = 0.7566$

Observations at S.D. between 2.1 and 4.2 mm: $\tau = -0.679$, $p < 0.000066$

November 29, 1957) the set-up described in 4.1.4 was used except that the wooden shelter was not placed on the platform but on a "tree" (Fig. 16E). The shelters were filled with moist flower-pot shards and 100 specimens (collected in the neighbourhood of Leiden) were put into each one. Such a set-up was placed in each of six cells of the serial thermo-hygrostat. Once a week the shards were replaced by freshly moistened ones and the total number of living specimens in each cell was counted. Each morning between 9 and 10 o'clock the trapped specimens were counted and put back into the artificial tree-shelter. S.D. in the respective cells was maintained between the following limits: cell 1: 0.9–1.2 mm; cell 2: 1.0–1.3 mm; cell 3: 1.6–2.3 mm; cell 4: 2.6–3.6 mm; cell 5: 3.6–4.1 mm; cell 6: 4.9–5.6 mm.

When the amount of migration out of tree-shelters (averaged for each week) is correlated with S.D. (averaged for each week) no correlation is found: $\tau = -0.070$, $p = 0.5892$ (Fig. 35). If we look more closely at Fig. 35, it appears that with high air humidities the relation between the amount of migration out of tree-shelters and S.D. shows a

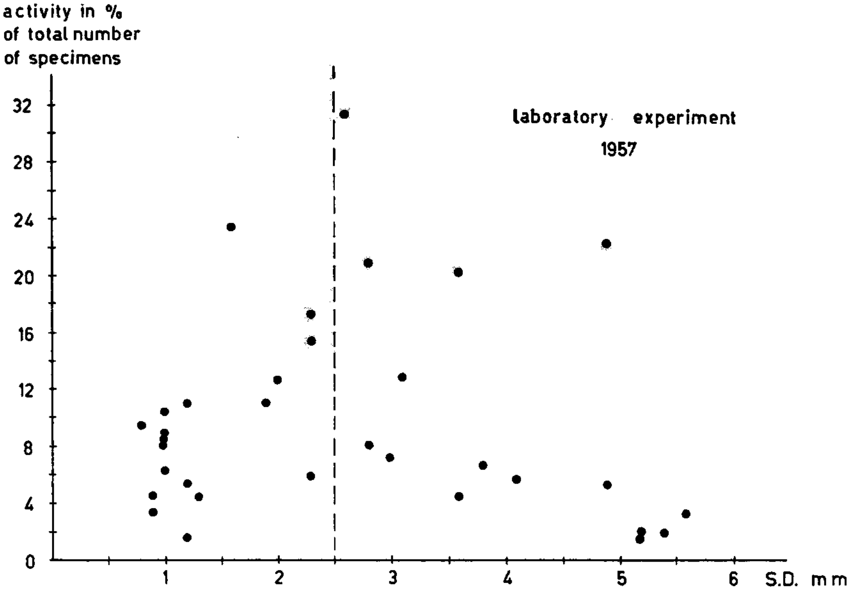


Fig. 35. Relation between the amount of migration out of tree-shelters (% activity averaged for each week) and S.D.

Total observations: $\tau = -0.070$, $p = 0.5892$

Observations at S.D. between 0 and 2.5 mm: $\tau = +0.348$, $p = 0.0574$

Observations at S.D. between 2.6 and 5.7 mm: $\tau = -0.585$, $p = 0.00328$

trend opposite to that with low air humidities. If we therefore calculate the correlations between the amount of migration out of tree-shelters and S.D. for high and for low humidities separately, we find: cell 1–3 (S.D. = 0–2.5 mm): $\tau = +0.348$, $p = 0.0574$; cell 4–6 (S.D. = 2.6–5.7 mm): $\tau = -0.585$, $p = 0.00328$ (Fig. 35).

The negative correlation with low air humidities points to the phenomenon discussed in 7.1.8 for series B with low air humidities, *i.e.* the amount of activity as a whole is smaller when the humidity of the air is lower.

With high air humidities the absence of a correlation between the amount of activity (migration out of tree-shelters) and S.D. would be expected on the basis of the discussions given in 7.1.8 (series B). In my opinion the positive correlation found (although not yet significant) may be the result of a reappearance in the artificial tree-shelter of the greater part of the specimens which show vertical activity. With direct observation it was noticed that with high air humidities a number of specimens show vertical activity by climbing up the wooden shelter and moving about upon it. This was noticed in experiments with set-up B, set-up D, and set-up E (Fig. 16). For this reason in set-up D the platform-shelter was connected with the "trees" by strips of cardboard to enable the animals to reach the "trees" (Fig. 16. D). In 7.1.6 it was shown that only with high air humidities is the amount of vertical activity negatively correlated with S.D. and therefore the amount of "other" activity (*i.e.*: horizontal activity, but in this case the greater part of migration out of tree-shelters) is positively correlated with S.D.

The positive correlation with high air humidities is unquestionably also due to the particularities of the experimental set-up: specimens which have moved about upon the tree-shelter (vertical activity) are "caught" so to speak, when moving down again, by the small ridge between the surface of the "tree" and the outer surface of the shelter and are strongly inclined to move along this ridge, as was noticed several times by direct observation. In this way a large proportion of these specimens will find an entrance into the shelter and re-enter it. Under natural conditions the greater part of the specimens which have climbed up the trees will not find an entrance into a tree-shelter when moving down again and therefore this circumstance will not appreciably influence the amount of migration out of tree-shelters under natural conditions. With set-up B the numbers of specimens which collect in the circular trap are less clearly influenced by this mechanical circumstance than with set-up E (Fig. 16) (compare the correlations with high air humidities in 7.1.8 and 7.1.9). This may be due to the absence of a ridge between the shelter and the wooden support in set-up B (Fig. 16B;

see also 7.2.4), but it is also possible that the lack of correlation between S.D. and the amount of activity with high air humidities in the experiments described in 7.1.8 (Figs. 33 and 34) is due to an unfavourable distribution of the S.D. values at which the observations were made (nearly all observations with high air humidities are made at S.D. values close to 1.0 mm (see Figs. 33 and 34).

2. EXPERIMENTS ON THE EFFECT OF TEMPERATURE [7.2]

According to Chapters 3 and 5, temperature has no distinct effect on the amount of acitivity. It is possible that only the amount of horizontal activity is clearly correlated with temperature (3.1.7 and 3.1.8). Since it was found in 6.2.7 that temperature influences the rate of water-uptake and in this way may influence the length of the individual periods of inactivity indirectly, temperature should have some influence on the amount of activity as a whole (length of the individual periods of inactivity). Therefore, an attempt was made to study the influence of temperature under experimental conditions.

7.2.1. All experiments were made with a number of cells of the serial thermo-hygrostat (Fig. 16A). In four experiments (1955a, 1955b, 1956a and 1956b) set-up B as described in 4.1.4 and shown in Fig. 16B was used, and in one experiment (1957a) set-up D as described in 7.1.5 and shown in Fig. 16D was used. The shelters were filled with decaying aspen leaves only in experiment 1955a; in all other experiments the shelters were filled with moist flower-pot shards. Once a week the shards were replaced by freshly moistened ones (or the aspen leaves by new ones) and the total number of living specimens in each set-up was counted. Trapped animals (and in experiment 1957a also the animals in tree-shelters) were counted daily.

In all experiments the air humidity inside the cells was maintained at a high level; in experiments 1955a and 1955b it was kept close to saturation by regularly pouring distilled water on large sheets of filter-paper; in experiments 1956a and 1956b at about S.D. = 1.0 mm and in experiment 1957a at about S.D. = 1.5 mm. Saturation deficit usually did not deviate more than 1.0 mm and temperature more than 0.2° C from the desired value.

7.2.2. In experiment 1955a the amount of activity was measured during 5 weeks (September 7–October 8) and also in experiment 1955b (October 17–November 19), at 2° C, 5° C, 10° C, 15° C, and 20° C. At the beginning of both experiments 50 specimens (collected in Meijendel) were put into each shelter. For each temperature the mean amount of activity (%) per 24-hour period averaged for the whole

TABLE XVI

p value of the difference between the amounts of activity at two temperatures

p value of the difference between	*experiment*					
					1957a	
	1955a	*1955b*	*1956a*	*1956b*	*migration into tree-shelters*	*horizontal activity*
2° C and 5° C	$p = 0.9442$ $(n = 20, m = 21)$	$p = 0.4296$ $(n = m = 24)$				
5° C and 10° C	$p < 0.000066$ $(x = 4.92)$ $(n = 20, m = 21)$	$p < 0.000066$ $(x = 4.86)$ $(n = m = 24)$	$p = 0.00158$ $(n = m = 35)$	$p < 0.000066$ $(x = 5.88)$ $(n = m = 34)$	$p = 0.1470$ $(n = m = 15)$	$p = 0.00244$ $(n = m = 15)$
10° C and 15° C	$p < 0.000066$ $(x = 4.09)$ $(n = m = 21)$	$p = 0.1802$ $(n = m = 24)$	$p < 0.000066$ $(x = 6.92)$ $(n = m = 35)$	$p = 0.1362$ $(n = m = 34)$	$p < 0.000066$ $(x = 4.21)$ $(n = m = 15)$	$p = 0.00096$ $(n = m = 15)$
15° C and 20° C	$p = 0.0574$ $(n = 21, m = 20)$	$p = 0.4328$ $(n = m = 24)$	$p = 0.0500$ $(n = m = 35)$	$p = 0.4066$ $(n = m = 34)$	$p = 0.2302$ $(n = m = 15)$	$p = 0.07114$ $(n = m = 15)$
20° C and 25° C			$p = 0.0264$ $(n = 35, m = 25)$			

experimental period is given in Fig. 36A (1955a) or in Fig. 36B (1955b). In both experiments the mean amounts of activity at 2° C and 5° C do not differ significantly, whereas the difference between 5° C and 10° C is highly significant (Table XVI).

In experiment 1955a the mean amount of activity at 15° C is significantly greater than at 10° C, while in experiment 1955b this difference is not significant (Table XVI). In experiment 1955a the mean amount of activity at 20° C is almost significantly smaller than at 15° C, while in experiment 1955b this difference is not at all significant (Table XVI). We may thus conclude that between 2° C and 5° C the amount of activity is very small and is not influenced by temperature. In agreement with the discussions in 3.4.2, a small amount of activity can still be observed at these low temperatures. Between 5° C and 10° C the amount of activity is clearly influenced by temperature. Between 10° C and 20° C the influence of temperature is not clear from these experiments. Somewhere between 10° C and 20° C the optimal temperature for the amount of activity is reached, but it looks as if the value of this optimal temperature varies. Perhaps between 10° C and 20° C the amount of activity is more influenced by other factors (*e.g.* small fluctuations in air humidity) than by temperature (see also 7.2.4).

In experiment 1956a the amount of activity was measured during 7 weeks (September 24– November 9) and also in experiment 1956b (May 7–June 22), at 5° C, 10° C, 15° C, 20° C and 25° C (25° C only in experiment 1956a). At the beginning of experiment 1956a, 80 specimens (collected in Meijendel) and at the beginning of experiment 1956b, 50 specimens (collected in Meijendel) were put into each shelter. For each temperature the mean amount of activity (%) per 24-hour period averaged for the whole experimental period is given in Fig. 36 C (1956a) or Fig. 36 D (1956b).

The same conclusions may be drawn from these experiments as from experiments 1955a and 1955b (Table XVI). In experiments 1956a and 1956b the optimal temperature for the amount of activity is reached not between 10° C and 20° C, but somewhere between 15° C and 25° C (Fig. 36 C and D).

I am unable to explain why the mean amount of activity is generally much greater in experiments 1956a and 1956b than in experiments 1955a and 1955b (Fig. 36 A–D); this might be caused by the different level of the air humidity inside the cells in 1955 (S.D. $\rightarrow 0$) and 1956 (S.D. $= 1.0$ mm). It would be worthwhile to study the relations between the amount of activity and temperature at different air humidities.

7.2.3. In experiment 1957a the amount of horizontal activity and the amount of migration into tree-shelters were measured during 3 weeks

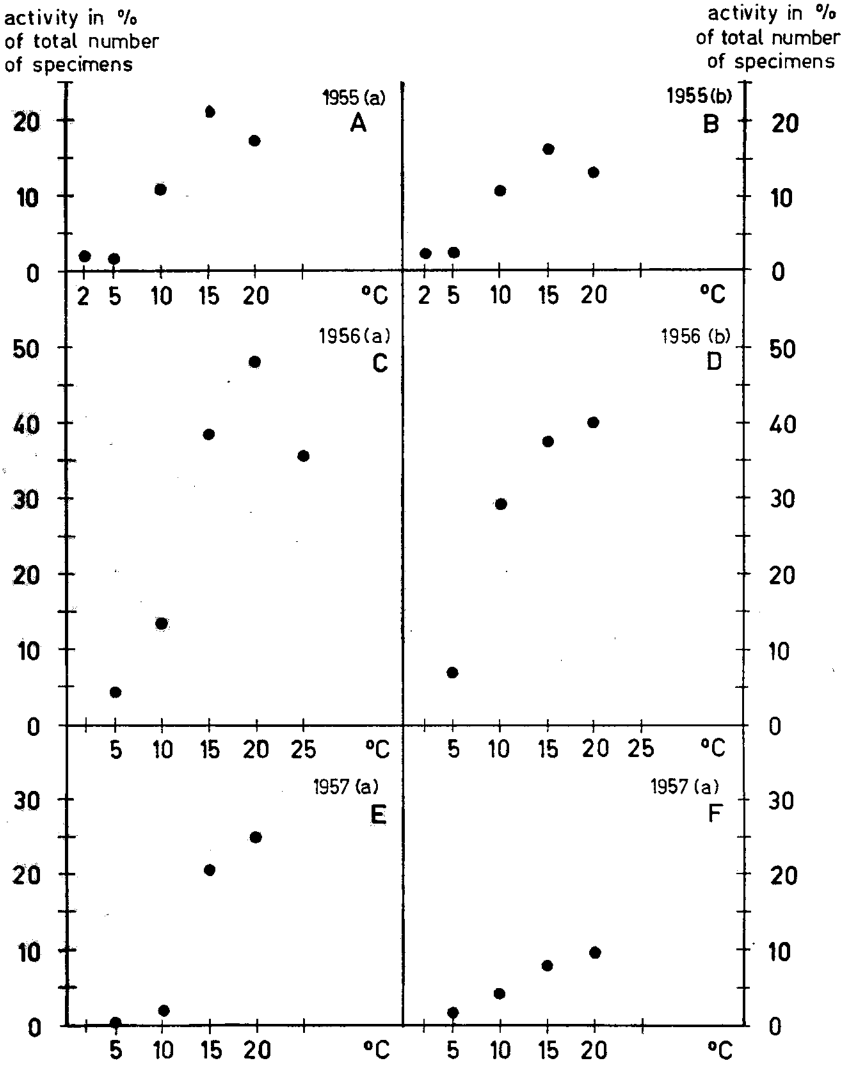


Fig.36. Relation between the amount of activity (% activity averaged for the whole experimental period) and temperature.
A, B, C, and D: amount of activity as a whole
E: amount of migration into tree-shelters
F: amount of horizontal activity

(December 3–December 23) at 5° C, 10° C, 15° C and 20° C. At the beginning of the experiment, 60 specimens (collected in Meijendel) were put into each platform-shelter. The mean amount of migration into tree-shelters (%) per 24-hour period averaged for the whole experimental period is given for each temperature in Fig. 36 E. The mean amount of migration into tree-shelters at 5° C and at 10° C does not differ significantly nor does the mean amount of migration into tree-shelters at 15° C and at 20° C; at 15° C, however, the mean amount of migration into tree-shelters is significantly larger than at 10° C (Table XVI).

Possibly it may be concluded from these results that temperature is only correlated with the amount of vertical activity (and the amount of migration into tree-shelters) between 10° C and 15° C, but in my opinion it is preferable to conclude that somewhere between 10° C and 15° C there is a critical temperature below which vertical activity is only a quantitatively unimportant phenomenon and above which vertical activity occurs to a quantitatively important extent. Below and above this critical temperature the amount of vertical activity (and the amount of migration into tree-shelters) is uncorrelated with temperature. If we assume that this critical temperature is generally situated close to 10° C, our supposition agrees with the findings under natural conditions: because the greater part of the observations on vertical activity are made at temperatures above 10° C (76 %), it could not be expected that significant correlations between temperature and the amount of vertical activity (3.2.4) or the amount of migration into tree-shelters (5.1.4) would be found.

The mean amount of horizontal activity (%) per 24-hour period averaged for the whole experimental period is given for each temperature in Fig. 36 F. The mean amount of horizontal activity at 5° C and at 10° C differs significantly, just as the mean amount of horizontal activity at 10° C and at 15° C; only the mean amount of horizontal activity at 15° C and at 20° C does not differ significantly (Table XVI).

Thus, we may conclude that at least between 5° C and 15° C the amount of horizontal activity is correlated with temperature. Since the greater part of the observations under natural conditions were made at temperatures between 5° C and 15° C (see Fig. 7; 3.1.7) it could be expected that a significant correlation between the amount of horizontal activity and temperature (3.1.7) would be found, and hence the observations made under experimental conditions agree with those made under natural conditions.

7.2.4. Now that we have discussed the dependence of the amount of vertical activity (migration into tree-shelters) and the amount of horizontal activity on temperature (7.2.3), it is possible to formulate a reasonable explanation for the results given in 7.2.2. In 7.1.9 it was mentioned that with high air humidities a number of specimens begin to show vertical activity. Since it may be assumed that with set-up B (Fig. 16 B) a number of these specimens will be trapped but also that some specimens will certainly re-enter the shelter, in these experiments vertical activity will introduce a disturbance.

Between 5° C and 10° C the mean amount of vertical activity (migration into tree-shelters) is very small (Fig. 36 E) and smaller than the mean amount of horizontal activity (Fig. 36 F) (at 5° C this difference is not significant: $p = 0.3174$, but at 10° C it is significant: $p = 0.0208$) and thus it may be expected that in experiments 1955a, 1955b, 1956a, and 1956b the amount of activity as a whole is mainly determined by the amount of horizontal activity. In agreement with this supposition, in all these experiments (7.2.2) the difference between the mean amount of activity at 5° C and at 10° C is significant, as is the difference between the mean amount of horizontal activity at 5° C and at 10° C (7.2.3).

Above 10° C the mean amount of migration into tree-shelters (vertical activity) is significantly greater than the mean amount of horizontal activity: at 15° C: $p = 0.00188$; at 20° C: $p = 0.00022$ (Fig. 36 E and F), and thus it may be expected that the disturbance will have a noticeable effect. In some experiments the effect of this disturbance is clearly not very large (1955a, 1956a), in other experiments it is clearly large enough to mask the relationship between temperature and the amount of activity as a whole (1955b, 1956b).

7.2.5. Although many more experiments on the influence of temperature would be necessary to complete the picture, I am inclined to suppose that between 5° C and an optimal temperature somewhere between 10° C and 20° C the amount of activity as a whole is greater when temperature has been higher during the individual periods of inactivity. This agrees with the findings in 6.2.7 and with the working hypothesis, because it may be expected that the rate of water-uptake is influenced by temperature. Above the optimal temperature other factors obviously play a part: possibly higher temperatures are harmful to the physiological condition of the animals (in 6.2.7 it was found that the amount of water-uptake is significantly smaller at 25° C than at 20° C and at 25° C mortality is much greater than at 20° C, *e.g.* in experiment 1956a after 6 weeks at 15° C, 50 % of the specimens had died, at 20° C, 70 %; and at 25° C, 98 %).

It is still not clear why under natural conditions no correlation is found between the amount of activity on trees (as a measure of the amount of activity as a whole) and temperature (3.3.3), while it cannot be excluded that the amount of migration out of tree-shelters (as a measure of the amount of activity on trees) is correlated with temperature (5.1.7). Perhaps under natural conditions the rate of water-uptake is influenced more by fluctuations in the humidity than by fluctuations in the temperature of the air inside the shelter, so that the length of the individual periods of inactivity is primarily determined by the air humidity inside the shelter. In the laboratory experiments fluctuations in the air humidity inside the shelter were largely eliminated, so the effect of differences in temperature could be found.

3. OTHER RESULTS FROM LABORATORY EXPERIMENTS [7.3]

7.3.1. When looking at Table VII (4.1.5) it becomes clear that in both experiments 1955a and 1955b the mean amount of activity tends to decrease with time. This is not only the case for experiments 1955a and 1955b, but for all experiments with set-up B (Fig. 16B). In the experiments discussed in 7.1.7 the phenomenon occurred mainly in series B with high air humidities (Table XVII), the situation being very confused on this point in series A.

TABLE XVII

Mean percentage of activity during a number of weeks at different air humidities

series B	*mean amount of activity (%) per 24-hour period averaged for each week*					
S.D.(mm)	0.9–1.1	0.9–1.5	1.9–2.3	2.7–3.3	3.2–3.8	3.3–4.1
1st week	29.4	22.9	24.9	4.7	6.0	5.4
2nd week	20.7	9.0	19.4	10.9	3.6	9.6
3rd week	10.7	14.7	12.6	8.1	4.3	6.4
4th week	8.4	4.4	9.4	12.1	26.1	12.3
5th week	12.4	3.3	13.3	0?	0?	6.4
6th week	12.6	8.0	13.7	4.7	0?	4.9
total	15.7	10.4	15.5	6.8	6.2	7.5

Because experiments 1955a, 1955b, 1956a, and 1956b were all done with high air humidities, it looks as though the decrease of the mean amount of activity with time occurs mainly with high air humidities (see Table XVII).

In the experiment discussed in 7.1.5 and 7.1.6 (set-up D, Fig. 16 D) this phenomenon is noticed especially in the mean amount of horizontal activity with high air humidities (Table XVIII, first 7 weeks).

TABLE XVIII

Mean percentage of two forms of activity during a number of weeks at different air humidities

	mean amount of acticity (%) per 24-hour period for each week											
S.D.(mm)	0.5–0.8		0.6–1.2		1.3–2.0		2.0–2.6		2.3–3.2		3.1–3.8	
	I	II	I	II	I	II	I	II	I	II	I	II
1st week	11.0	6.8	10.4	33.2	10.4	34.8	23.0	12.4	9.8	17.4	12.0	29.0
2nd week	20.0	5.0	17.0	27.8	8.0	20.4	12.2	13.2	18.0	12.6	16.2	20.8
3rd week	25.2	6.8	15.8	16.2	8.8	28.0	14.2	20.4	15.2	2.0	6.2	20.8
4th week	24.2	2.0	17.2	18.2	11.2	34.4	12.4	21.6			13.8	22.4
5th week	10.8	3.6	21.2	8.2	12.0	20.8	10.4	20.4			10.4	9.8
6th week	13.4	1.4	17.8	4.2	20.8	19.8	5.8	21.6			6.6	24.6
7th week	9.2	0?	25.2	4.6	14.8	21.2	5.4	22.0			5.6	20.8
8th week			24.2	5.4	15.6	21.2	13.6	7.0			13 4	13.6
9th week			15.0	2.3	10.5	13.0	20.3	9.8			13.3	17.0
total	16.3	3.7	18.3	13.6	12.5	24.0	12.9	16.6	14.3	10.7	10.8	19.9

I = migration into tree-shelters II = horizontal activity

From Table XVIII it is clear that the decrease of the mean amount of horizontal activity with time at high air humidities tends to coincide with an increase of the amount of migration into tree-shelters (at least as far as the first 7 weeks are concerned).

Hence, it seems as though the tendency to show vertical activity gradually increases with time with high air humidities. This unquestionably means that under these conditions it is very difficult for the animals to transpire water, so that it may be expected that the percentage of specimens which are searching for localities with lower air humidities by showing vertical activity increases with time. As a consequence of this phenomenon, the percentage of specimens which show horizontal activity will decrease with time (if the mean amount of activity as a whole does not greatly alter with time).

In 7.2.4 we discussed the disturbing effect of specimens which show vertical activity in experiments with set-up B. It may be expected that the disturbing effect of this vertical activity will increase with time and generally this will mean that with time an increasing number of specimens will re-enter the shelter and a decreasing number of specimens will be caught in the trap. In agreement with 7.2.4 the phenomenon is more obvious (although not conclusively so) with high temperatures than with low temperatures (*e.g.* see Table VII; 4.1.5).

Under natural conditions these phenomena will not often occur because air humidity will continuously fluctuate under such circumstances. Hence, these phenomena must be due to the experimental conditions (air humidity almost constant during the whole experimental period).

7.3.2. In experiment 1956a most specimens were marked in such a way that individuals could be distinguished. As a result, it became clear that the individual length of the period of inactivity fluctuates highly: at 5° C between 48 and 144 hours (mean 90 h); at 10° C between 25 and 114 hours (mean 52 h); at 15° C between 18 and 69 hours (mean 37 h); at 20° C between 17 and 67 hours (mean 29 h); at 25° C between 20 and 75 hours (mean 31 h). Even in each individual, short periods of inactivity alternated irregularly with long periods of inactivity.

4. GENERAL CONCLUSIONS [7.4]

In this chapter some experiments on the effect of humidity or temperature of the air on the amount of different forms of activity are discussed. The results of these experiments do not contradict the working hypothesis (Chapter 4), and they are also in general agreement with corresponding findings under natural conditions.

In a number of experiments, however, the results are clearly influenced by the experimental conditions, especially with high air humidities. Aberrant activity patterns are caused by: stationary air with high humidities (7.1.8); constant air humidity during a long period (7.3.1); the possibility of climbing up the wooden shelter in experiments with set-up B (Fig. 16B), especially with high air humidities (7.2.4); the ridge between the surface of the "tree" and the outer surface of the shelter in experiments with set-up E (Fig. 16E; 7.1.9). Thus, only the experimental set-up described in 7.1.1 was adequate (Fig. 28), except for the ridge between "tree" and tree-shelter. These characteristics of the experimental conditions illustrate that the form and amount in which the activity patterns arise depend on the structure of the shelters and of the habitat in which the activities occur (see also 3.4.3).

Two experiments showed that the amount of migration into tree-shelters (as a measure of the amount of vertical activity) is larger when the air humidity is higher (7.1.2 and 7.1.6), and one experiment showed that the amount of horizontal activity is larger when air humidity is lower (7.1.6). Moreover, it appeared that only with high air humidities is the amount of these forms of activity correlated with S.D., and the same phenomenon was shown to occur under natural conditions (at least with regard to the amount of horizontal activity). This phenomenon could be understood with the help of the working hypothesis (7.1.6).

Another experiment proved that the mean length of the individual periods of inactivity (measured as the amount of activity) depends on the humidity of the air inside the shelter; it was also shown that under normal conditions the humidity inside the shelter is influenced by the humidity of the open air (7.1.8).

One experiment showed that the amount of migration out of tree-shelters (like the amount of activity as a whole) is smaller when air humidity (via the humidity of the air inside the shelter) is lower, at least with low air humidities (7.1.9).

Experiments in the laboratory suggest that the amount of activity as a whole is correlated with temperature (7.2.2), which agrees with the working hypothesis and with the findings in 6.2.7 (rate of water-uptake). Under natural conditions, however, this temperature effect generally is not found (3.3.3 and 5.1.7). Probably in some experiments the experimental set-up (vertical activity) had a masking effect on the relation between temperature and the amount of activity as a whole (7.2.4).

Under both natural conditions (3.1.7 and 3.1.8) and experimental conditions the amount of horizontal activity is positively correlated with temperature. It is supposed that vertical activity (and migration into tree-shelters) mainly occurs above a critical temperature between 10° C and 15° C (7.2.3). Below and above this critical temperature the amount of migration into tree-shelters (and of vertical activity) is not correlated with temperature, which agrees with findings under natural conditions (3.2.4 and 5.1.4).

8. GENERAL DISCUSSION AND SUMMARY

1. PORCELLIO SCABER AND THE LAND HABITAT [8.1]

8.1.1. In 1.2 the literature on aspects of passive adjustment to an environment in woodlice is discussed. From a morphological and physiological point of view woodlice are on the whole very badly equipped for life on land, but since they can be found in dense populations in nearly every part of the world woodlice must be able to maintain life in land habitats (EDNEY, 1954). Most animals depend for their adjustment to an environment not only on morphological structures and physiological processes (passive adjustment), but also on patterns of activity and behaviour (active adjustment), so it is logical to suppose that woodlice are able to live in land habitats principally through active adjustment. EDNEY (1954) expresses himself along the same lines. The literature on activities in woodlice (1.5) does not provide a basis for this supposition, with the exception of a paper by LE GAY BRERETON (1957) which did not reach me until my investigations were finished.

8.1.2. The present paper has attempted to show that *P. scaber* is able to live in land habitats by mainly active adjustment. Many authors have shown that woodlice lose considerable amounts of water by transpiration with low or moderate air humidities (1.2.1) and quickly die as a result of desiccation under such conditions. In Chapter 6, Section 2, it is shown that specimens of *P. scaber* take up water from saturated or nearly-saturated air and that the amount of water-uptake is larger when the animals were initially more desiccated. Since "normal" excretion seems not to compensate for water-uptake under these conditions (6.2.8), a stay during a long period in saturated or nearly-saturated air becomes unfavourable for the animals.

Air humidity in most land habitats continuously fluctuates between wide limits or is more or less buffered at a very high level (shelters, see 2.4.1), and therefore specimens of *P. scaber* can only live in land habitats by moving at intervals from a habitat with a very high air humidity to a habitat with a lower air humidity and *vice versa*. Besides a regulation of the water-balance by physiological processes (*e.g.*: excretion, water-uptake), *P. scaber* can accomplish regulation by activity patterns.

8.1.3. In Chapter 4, Section 1, it was shown that under normal conditions specimens of *P. scaber* do not become active to feed or to reproduce, and it was concluded that they become active to lose by transpiration the excess of water which has accumulated in their bodies during a stay inside a very moist shelter. Since specimens of *P. scaber* feed on a great many organic materials (4.1.2), both inside and outside the shelters, and the same activity patterns are shown both before, after, and during the reproduction period by both sexes (4.1.7), the active regulation of the water-balance must be considered the most important factor in determining the form and amount of the activities shown by *P. scaber*.

Hence, it may be expected that the activity patterns of *P. scaber* are qualitatively and quantitatively controlled both by the condition of the water-balance and by the air humidity. In Chapter 6, Section 4 it is proved that the preferences for lower (becoming active) or higher (looking for shelters) air humidities depends on the condition of the water-balance. This is why the activity patterns described in Chapters 3 and 5 must be considered activities directed to a recovery of the disturbed water-balance, and these activity patterns must thus be quantitatively determined by the air humidity, as was indeed found.

8.1.4. Because the becoming-active of specimens of *P. scaber* must be considered a search for localities where air humidity is low enough to allow adequate transpiration, the distribution and accessibility of such localities must greatly influence the form in which the activity patterns occur.

Specimens which have found a shelter in the litter at the border of a wood can move out of the wood to find localities with lower air humidities (horizontal activity, 3.1). Trees, buildings, and walls make it possible to find localities with lower air humidities above ground-level (vertical activity, 3.2). If suitable tree-shelters are present, many specimens will find a new shelter above ground-level as a consequence of this form of activity (migration into tree-shelters, 5.1). Specimens which become active from tree-shelters (activity on trees, 3.3) may be expected to climb higher up the trees (if possible) during very humid nights. If the trees are very tall and suitable shelters are still present at a considerable height above ground-level, it may be expected that during a period with many very humid nights specimens will gradually shift into shelters at a considerable distance above ground-level (LE GAY BRERETON's "vertical migration", 3.4.2 and 3.4.3). Part of the specimens which become active from tree-shelters will disappear from the trees (migration out of tree-shelters, 5.1).

Especially with small trees, the phenomena of vertical activity (migration into tree-shelters) and migration out of tree-shelters will cause a continuous exchange between tree-dwelling and litter-dwelling populations (5.1.2). All these forms of activity are quantitatively correlated with the humidity of the air both inside the shelter (during the individual periods of inactivity) and outside the shelter (during the individual periods of activity) and must be considered the results of an interaction between the tendency of the animals to an active regulation of the water-balance and the structure of the habitat in which the activities occur and the shelters are situated. This interaction may lead to quantitatively very complicated situations, as illustrated by the discussions in 5.2 for natural conditions and by the discussions in 7.1.8, 7.1.9, 7.2.4, and 7.3.1 for experimental conditions.

8.1.5. Summarizing, we may conclude that the success of *P. scaber* in fitting into land habitats, in spite of its inadequate equipment for life on land from a morphological and physiological point of view is mainly due to activity patterns directed to an active regulation of the water-balance. These activity patterns not only result in a moving away from unfavourable conditions and in a search for more favourable conditions, but they also contribute to an effective dispersal of the species. Because *P. scaber* does not show "shelter-fidelity", the search for suitable shelters during each period of activity will result in a thorough dispersal throughout the area in which suitable shelters are present (*e.g.:* a wood) and – especially during very humid nights – also outside of this area (see 3.1.5 and 3.1.6).

By the very nature of the distribution of suitable shelters within an adequate area, the distribution of specimens will show a typically patchy pattern. This pattern is not a stable one but will be changed after each period of activity in a way which depends on the environmental conditions (especially air humidity) during each period of activity. If environmental conditions show a trend during a certain period, the changes in the pattern of distribution will also show a trend (see *e.g.:* 5.1.10 (trend during the greater part of the year), 3.4.2 and 3.4.3).

8.1.6. The extent to which population density in *P.scaber* is influenced by environmental factors was not investigated by me, but some indications may be drawn from the present study. It seems likely that the accessibility of suitable shelters will largely determine the chance to survive in active specimens. Long periods with low air humidities will increase mortality by diminishing the number and the accessibility of suitable shelters. After winters with a period of relatively low temperatures, the numbers of *P.scaber* to be found in Meijendel were greatly reduced, *e.g.* after the winters 1953–'54 and 1955–'56 (see also 8.2.1). Temperatures above 20–25° C may also be supposed to increase mortality (see 8.2.1). It is not known what part is played by predation: shrews and hedge-hogs may also have some effect on the density of the population.

2. HABITAT-SELECTION IN PORCELLIO SCABER [8.2]

The necessity for active regulation of the water-balance has its consequences for habitat-selection in *P.scaber*. An adequate habitat for P.*scaber* must contain both suitable shelters and localities where water can be lost by transpiration under different conditions of humidity.

8.2.1. In experiments in the laboratory it was found that temperatures above 20–25° C are harmful to the animals (7.2.5 and 6.2.7), so that it may be assumed that under natural conditions *P.scaber* is not usually exposed to temperatures above 20–25° C.

Very low winter temperatures may also be harmful, as was observed after the severe winter of 1955–'56: from specimens which had found a shelter under a heap of rubbish in the Botanical Garden at Leiden only the specimens under the centre of the heap were still alive, all other specimens having died. In agreement with this observation, Dr.

E. Palmén told me that in the neighbourhood of Tvärminne (Finland), *P. scaber* is mainly found in the vicinity of *Fucus*-heaps, in the centre of which it is protected against low temperatures in winter.

Thus, in an adequate habitat *P. scaber* must be protected against low winter temperatures and against temperatures above 20–25° C. In general, the suitability of a habitat will depend upon the mean trend of temperature and humidity of the air over a number of years, the presence and accessibility of suitable shelters and of localities where adequate transpiration is possible. The presence or absence of adequate food will seldom if ever play a part, since *P. scaber* feeds on nearly all kinds of organic material. For The Netherlands this means that adequate habitats must be available in woods and, if suitable shelters are present, also in large thickets, small groups of trees, and in gardens, farms, parks, *etc.* (also near buildings, 3.2.2).

8.2.2. In Chapter 2 the day-habitat (shelters) of *P. scaber* is discussed. The numbers of specimens found in different samples taken from the litter of the first aspen wood depend not only on the presence of suitable shelters (2.2.3), but also on other factors, *e.g.* the chance that any suitable shelter at all is found by active specimens (3.1.4, 3.2.2, 5.1.10). The chance that suitable shelters are found by specimens which have been active on the trunk of a tree will be greater for shelters at the base of this tree than for shelters elsewhere in the litter (3.2.2). The numbers of specimens which have left a tree during the previous periods of activity will largely determine the numbers of specimens found in shelters at the base of this tree during any day-period. In the same way, the chance that suitable shelters are found by specimens which have been active outside of a wood will be greater for shelters at the borders of this wood than for shelters in the centre (3.1.4). Because this form of activity occurs during the greater part of the year, the difference between population density at the borders and in the centre of a wood must become larger in the course of a year as a result of this phenomenon. Also, at the borders of a wood more specimens will be found in shelters at the base of a tree than elsewhere in the litter. The combination of these two phenomena gives: the difference between the numbers of specimens present in shelters at the base of trees at the borders and in the centre of a wood will become larger in the course of the year (see 2.2.2, Table I, group 0) and the same applies to the numbers of specimens present in tree-shelters at the borders and in the centre of a wood (5.1.10). On tall trees many specimens may shift into shelters in the upper parts of the trees during humid periods (3.4.2 and 3.4.3).

Thus, in *P. scaber* the selection of day-habitats is strongly influenced by the form and amount of the activity patterns and not by the presence of suitable shelters alone. Since the form and amount in which the activities occur are the results of an interaction between air humidity and the structure of the habitat (8.1.4), the selection of day-habitats in *P. scaber* is indirectly correlated with the trend in air humidity and the structure of the habitat in which the activities occur.

8.2.3. From data in the literature (2.1.1: COLE, 1946 and MEINERTZ, 1944) and my own observations (2.3), it is clear that the suitability of a day-habitat largely depends on the moistness of the shelter (see also 2.4.1). It is not known whether the moistness of a shelter is directly perceived by the animals when looking for a shelter or is only perceived via the change in the water-balance during the stay in a shelter. In both cases it will sometimes be necessary to look for another shelter if the shelter dries up during the day-period. Possibly specimens moving about in the sunshine, which I sometimes observed (see also 1.5.2: FRITSCHE, 1934), are specimens looking for a new shelter. During the experiment with artificial tree-shelters in 1956 (Chapter 5) it was observed that the shelters were left within three days when they dried up; this was especially evident during the month of May when the shelters dried up rapidly (5.1.2, Fig. 17).

A number of authors have noticed that woodlice were active during the day period during or after a period of heavy rains (1.5.2: STANDEN, 1921; ABBOTT, 1918; COLE, 1946). The same phenomenon was observed by me in the first aspen wood in 1956 (*Philoscia muscorum* (Scop.) and *Porcellio scaber* Latr.). This undoubtedly means that the shelters are also left when water enters the shelters.

Hence, we may assume that specimens of *P. scaber* do not only become active to lose water by transpiration, but also when the shelter becomes more directly unsuitable (dried-up or partly flooded).

For the supposition that the moistness of a shelter is only perceived via the change in the water-balance during the stay in a shelter, it is not necessary to suppose that woodlice must have sense-organs to directly perceive air humidity. In the former case all forms of activity would depend on the condition of the water-balance.

3. INDIVIDUAL VARIABILITY IN THE AMOUNT OF ACTIVITY [8.3]

In the present paper the τ-values of rank correlations on which conclusions are based often are not very high. To provide a better justification of the conclusions drawn, it is worth-while to discuss these correlation-coefficients.

8.3.1. In the present paper an attempt has been made to prove that the amount of activity depends on the condition of the water-balance, which in its turn again depends on air humidity. The correlation between air humidity and the condition of the water-balance is certainly influenced by the structure of the tissues situated between the haemolymph and the open air. It may be expected that the permeability of these tissues and of the cuticle for water vapour will not be the same in each individual (see also 6.2.6), and this factor will therefore introduce some variability into the relation between air humidity and the condition of the water-balance. The influence of this factor seems not to be very large, however, since in 6.2.1 a correlation of $\tau = -0.829$ and in 6.2.3 a correlation of $\tau = -0.753$ or $\tau = -0.798$ was found between the proportional change of body weight and S.D..

8.3.2. Since water-exchange between the haemolymph and the open air occurs via the cuticle, the proportional change of body weight must be correlated with the ratio: $\frac{\text{surface}}{\text{volume}}$ (6.2.4). For the proportional increase of body weight (S.D. $\rightarrow$ 0) we found: after a stay of 24 hours: $\tau = +0.547$ and after a stay of 48 hours: $\tau = +0.621$; for the proportional decrease of body weight (S.D. = 1.68 mm) we found: after a stay of 24 hours: $\tau = +0.712$ and after a stay of 48 hours: $\tau = +0.752$ (6.2.4).

Since the condition of the water-balance determines whether a specimen becomes active or looks for a shelter, in 6.4.4 it was found that the ratio: $\frac{\text{surface}}{\text{volume}}$ of "moist" individuals is correlated with their preference for the "dry" side of the gradient apparatus ($\tau = +0.215$). Obviously the link between the proportional increase of body weight ($\tau = +0.547$) and becoming active to look for a locality where adequate transpiration is possible ($\tau = +0.215$) brings much variability into the relation.

Thus, it is clear that there is considerable individual variability on this point (see also 7.3.2) and therefore strong correlations between the amount of activity and S.D. cannot be expected.

In the field, many unknown factors will have a masking effect on the real relationship between the amount of activity and air humidity, and it may be expected that stronger correlations will be found under experimental conditions (Chapter 7) than under natural conditions. Moreover, direct observations in the field (Chapter 3) may be expected to give stronger correlations than indirect observations (Chapter 5). The data do not contradict these expectations. This is more evident if we keep in mind that under experimental conditions only more or less indirect observations were made. I feel certain that direct observations under experimental conditions would give still stronger correlations.

Under natural conditions differences in the suitability of different shelters will influence the length of the individual periods of inactivity and under both natural and experimental conditions the length of the individual periods of inactivity will also be influenced by the exact position of each individual inside the shelter. These factors will bring much variability into the length of the individual periods of inactivity (7.3.2) and will contribute to the lowering of the correlation-coefficients.

8.3.3. Although many correlations are not strong, the conclusions drawn are more convincing because the results from all groups of observations (8.1) reinforce each other. Moreover, the working hypothesis could be proved directly (Chapter 6). The observations on the day-habitat of *P.scaber* (Chapter 2 and 8.2.2) and a number of incidental observations also fit into the picture given in 8.1.

9. ABSTRACT

From the literature it is known that woodlice are badly equipped for life on land, but because they can generally be found in dense populations they must be able to maintain life in land habitats. In 1952 it was found that in the dune area "Meijendel" near Den Haag woodlice show remarkable nocturnal activities, and it was supposed that these activities had something to do with their adjustment to the habitat. In 1953 an investigation into the ecological significance of activity patterns in the woodlouse *Porcellio scaber* Latr. was started in two aspen woods in "Meijendel".

It was found that the amount of different forms of activity and the quantitative relations between these forms are correlated with air humidity. The duration of the individual periods of activity depends on air humidity and is for the great majority of active specimens about one hour. The activity patterns of *P.scaber* have a distinct effect on the distribution of the animals over a wood (day-habitat) and contribute to an effective dispersal of the species. The suitability of a day-habitat for *P.scaber* depends on its moistness, since it must essentially be considered a shelter against the relative dryness of the day-period. Generally the best shelters are offered by the loose bark of dead or dying trees and by compact objects lying flat on the ground.

The observations made under natural conditions may be generally understood by the working hypothesis: "The activities of *P.scaber* are a means of losing by transpiration the excess of water which has accumulated in the bodies of the animals during a stay inside a very moist shelter". An experiment with artificial tree-shelters under natural conditions has yielded new data which confirm the hypothesis.

With experiments in the laboratory it could be shown that specimens of *P. scaber* take up water from saturated or nearly-saturated air and that this results in an increasing preference for lower air humidities (for becoming active) and *vice versa.* Water-uptake occurs through the cuticle and the amount of water-uptake increases with temperature up to about 15–20° C. It is apparent that in saturated or nearly-saturated air, "normal" excretion cannot compensate for water-uptake, so that water is accumulated in the body.

The activity patterns of *P. scaber* must be considered an active regulation of the water-balance, by which the animals move at intervals from a habitat with a very high air humidity (shelter) to a habitat with a lower air humidity (locality for adequate transpiration) and *vice versa.* It could be shown that at high humidities the animals have a greater tendency to move upwards. They then reach places where the evaporative power of the air is greater and transpiration of water is thus increased.

The results from experiments in the laboratory on the effect of humidity or temperature on the amount of activity agree with corresponding findings under natural conditions. A number of unexpected results of these experiments demonstrate that the form and amount in which the activity patterns arise depend on the structure of the shelters and of the habitat in which the activities occur.

Habitat-selection in *P. scaber* depends on the mean trend of temperature and humidity of the air during a number of years and on the presence and accessibility of suitable shelters and of localities where adequate transpiration is possible.

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