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# Multiple environmental factor analysis in habitats of the harvest mite *Neotrombicula autumnalis* (Acari: Trombiculidae) suggests extraordinarily high euryoecious biology

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**Abstract** The harvest mite *Neotrombicula autumnalis* (Trombiculidae) has become a great nuisance in various vegetated areas in Germany over the last 15 years. According to reports of dermatologists, this species appears to have propagated and spread significantly. Moreover, cases of severe trombidiosis or trombidiosis-like skin reactions have been noticed at unusually early times of the year. Due to the lack of scientific studies, little is known about the ecology of *N. autumnalis* and its distribution, and preferred habitats cannot be predicted. A four-year study was conducted to identify trombiculid foci in different areas of Bonn in order (1) to determine the timing of larvae appearance in different years, (2) to identify the factors that lead to high larvae abundances at the mite foci ('multiple factor analysis'), and (3) to develop an ecological control strategy. By means of the 'tile catch method' (TCM) which turned out to be most appropriate to collect data on the distribution and abundances of trombiculid mites, larvae of *N. autumnalis* were caught from mid July until the end of October/beginning of November. The distribution of the mites was patchy, supporting the hypothesis that certain factors cause a concentration in foci. Most of the mite foci had a fixed location for at least three years. Efforts to isolate nymphs and adults in larger quantities to gain knowledge about their preferred soil areas and soil depths failed. Only some nymphs of *N. autumnalis* could be found living 10–40 cm deep in the soil. Due to the restriction that the nymphs and adults can only rarely be isolated in the ground, the analysis of environmental factors was executed based on abundances of questing larvae on the soil surface. The detailed analysis of soil-physical, soil-chemical and meso-faunistic factors could not finally explain the unequal distribution of the mites, although the porosity of the soil had a statistically significant slight influence on the abundance of larvae, and soil pH bordered significance, also suggesting a slight

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influence. Furthermore, soil temperatures during the winter seasons in three subsequent years appeared too high to affect the harvest mite. The field experiments suggest that *N. autumnalis* and particularly its larval stages are extremely euryoecious (meaning tolerating very different environmental conditions). Further studies are necessary: additional investigations on the influence of certain abiotic environmental factors on *N. autumnalis*, the search for factors underlying the rhythmicity of its life cycle ('zeitgeber'), and the reasons and mechanisms for heterogeneous distribution of soil fauna in general. Ecological control of the mite is, in principle, possible but only after identifying the foci and ascertaining their approximate dimensions with the TCM. This control strategy is the most promising one, albeit very laborious, emphasising the need of further research on the ecology of the harvest mite.

**Keywords** Host fauna · Long-term measurements · Mite foci · Multiple survey · Soil physics · Trombiculids

## Introduction

Mites of the family Trombiculidae are widespread ectoparasites of vertebrates. In central Europe, *Neotrombicula autumnalis* Shaw is the most abundant trombiculid species. The larval stages (chiggers) of *N. autumnalis* parasitise mammals, birds and humans, causing pruritic dermatitis called trombidiosis or trombiculosis (Mumcuoglu and Rufli 1983; Varma 1993). In contrast, the (deuto-)nymphal and adult stages are soil-dwelling predators and are supposed to feed on other arthropods and their eggs (Minter 1957; Varma 1993). In the Cologne-Bonn-area, western Germany, dermatologists have noticed a growing number of severe cases of trombidiosis for the last 15 years. Contrary to the literature data (e.g., Storch and Welsch 1997), they have recognised trombidiosis-like skin reactions not only in summer and autumn but also in early spring and in winter.

The study presented was planned to clarify such puzzling phenomena by collecting more detailed information on the ecology and biology of indigenous trombiculids. Moreover, it was intended to disentangle the confusing mixture of biological data imputed to the harvest mite though originally belonging to different mite species. Additionally, preliminary investigations revealed that sites infested by larvae of the harvest mite (called 'mite islands' by Williams 1946) are quite clearly defined in size, and larvae could not be detected in the immediate vicinity of these 'islands'. We refer to such a site as 'mite focus' or 'larvae focus'. It was the predominant purpose to find out which environmental factors are responsible for the patchy distribution of the trombiculid larvae and which factors influence their population dynamics and life cycle. As private gardens and public areas, e.g. kindergartens (Hassler and Kimmig 2002), are heavily contaminated, a pest control strategy forgoing the use of pesticides was intended as well. Therefore, a multiple survey of biotic and abiotic factors with special emphasis on various soil parameters was carried out at several mite foci. As far as is known, this study is the first dealing with a detailed investigation of the soil physics with regard to trombiculid mites. To tackle the questions, field investigations were indispensable, as the special conditions inside the naturally grown soil layers can hardly be imitated in the laboratory. Nonetheless, we tried to work out laboratory experiments with controlled factors but we failed to rear field-collected chiggers further than the (deuto-)nymphal stage (Schöler 2003) using the slightly modified methods of Jones (1951), Minter (1957), Simonová (1977), and Struppe (1994).

## Materials and methods

### Sampling of larvae

A quantitative collection of larvae of harvest mites was conducted using a variation of the plate method described by Williams (1946) and Hubert and Baker (1963): white ceramic bathroom tiles, 15 × 15 cm, were placed on the ground guaranteeing firm contact with the substrate (Fig. 1). The distribution of larvae foci in complete gardens was surveyed with a random grid of approximately one tile per 0.7 $m^2$ and checked successively for larvae after 15–25 min. Larvae that climbed onto the tiles were collected by dabbing them off with a moist brush of soft hair. A much narrower grid was used at the so-called 'sites of long-term measurements' (see below). At these sites, nine tiles were regularly placed on the ground with 10 cm or less in between.

In order to evaluate the reliability and reproducibility of the 'tile catch method' (TCM), a test of quantitative catches was done, also to reveal the most fruitful time period of tile exposure (data not shown). It proved to be a method to reproducibly record quantitative differences in larvae abundances at different sites and, therefore, was considered sufficiently exact to correlate numbers of collected chiggers with environmental factors.

To assess the timing of first appearance of larvae, a 'funnel trap' was developed. This kind of trap offers the possibility of an accumulative catch of larvae at a given site: a funnel of semi-transparent white plastic, 12 cm in diameter, was installed upside down on a larvae focus. As the larvae are positively phototropic and negatively geotropic (Jones 1950a, b), they were expected to be attracted by the white plastic funnel cone and to climb up its wall until they accumulate at the upper end of the funnel. The traps were set up on the sites of the long-term measurements and were checked twice a week.

**Fig. 1** The 'tile catch method' (TCM) with a narrow grid as applied at the sites of long-term measurements

## Sampling of post-larval stages

In April 2001, trombiculid mites, especially post-larval stages, were searched for in soil samples. Using the method of Cockings (1948), which was modified by Richards (1950) and Daniel (1961, 1969), 3-l soil samples were taken from different depths (0–10 cm, 10–20 cm, 20–30 cm, 30–45 cm) from a total of 30 sites. The soil material of these samples represented the remainders of each soil layer left over after the samples for the investigation of the soil physics were drawn. This sampling was done in order to find out how deep the post-larval stages dwell in early spring. Possible findings would, on one hand, give a clue on the population of mites inside the soil and, on the other hand, in which depth the mites spend the winter season. The predominant developmental stage found would, very likely, be the hibernating stage. However, as not a single mite could be found, these investigations were not repeated in the following year.

Since larvae abundance is directly connected to the egg masses (app. 400 eggs per female (Storch and Welsch 1997)), the 'on soil surface abundances' of larvae were used in regard to environmental factors in the statistical analysis. It was hypothesised that the larvae abundance on the soil surface would be the result of the integration of all the environmental factors influencing the population of harvest mites inside the soil (biased only by the influences of the soil surface conditions on the larvae). Therefore, the different quantities of larvae on the soil surface could be tested against the different factors in the analysis.

## Environmental factors

Environmental factors were measured at the mite foci, in an attempt to explain the different abundances of trombiculid larvae. For each site, the biotope characteristics (herbaceous border, undergrowth of shrubs, flowerbed or lawn) were recorded and the surface was characterised by the organic matter and its covering vegetation (see below for methodology).

Additionally, there were two other groups of factors determined: one group of factors was characterised by the fact that they could only be assessed once at each site because their measurement destructed the soil integrity.

The other group of factors was measured throughout the whole study period at the 'sites of long-term measurements' (soil temperatures, water tension/matric suction inside the soil, soil surface conditions).

### *Physical and chemical properties of the soil*

The soil pore size categorised as coarse, medium-sized and fine pores was measured in undisturbed soil samples using sample rings (100 $cm^3$) (Eijkelkamp Co., Giesbeek, The Netherlands) and pressure plate extractors (Extractor Cat. # 1200, Soil Moisture Equipment Co., Santa Barbara, California, USA) as described by Richards and Fireman (1943). Coarse pores were divided into 'narrow' (10–50 μm) and 'wide' (over 50 μm) because continuous wide coarse pores may serve as pathways for trombiculid larvae. Medium-sized pores (0.2–10 μm) may be regarded as important to the mites as they are responsible for the capacity of the soil to keep water available to plants and animals (Harrach 1978; Scheffer and Schachtschabel 1998). From the pore data the bulk density and other mathematically related data were calculated according to the equations of Richards and Fireman (1943): density of solid particles and total volume of pores (porosity).

The samples taken with the sample rings were also used to measure the air permeability of the soil. A Grover–Tanner apparatus (self-constructed by the Department of Crop Science and Plant Breeding, University of Bonn, following the guidelines of Kmoch and Hanus 1965) was used to measure the time a piston needed to press a certain amount of air through the soil probes. The data were then used to calculate the 'aer' coefficient following the equation of the above authors. This method indirectly determines the vertical continuum of pores. Six ring samples each were taken from four soil depths (0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm) at 73 mite foci that differed in their larvae abundances. The samples were drawn in April and at the beginning of May 2001 and 2002. The determination of the larvae abundances took place in the preceding summer.

After sampling the soil with the sample rings, the remaining soil material of each of the $50\times 50 \times 10$ $cm^3$ soil layer was taken out, mixed and used to measure the pH-value following the method of Kordatzki (1948). Additionally, in 2002 the salinity of the soil in the respective layers was measured via electrical conductivity following the method of Hoffmann (1991). Measurements in the laboratory were done with a pH-meter (pH 537, WTW Co., Weilheim, Germany) and a conductometer (LF 2000/C, WTW Co.).

*Soil fauna*

Prior to drawing the ring samples for the investigation of the soil physics, two parallel soil probes of each soil depth (0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm) were taken by a soil column cylinder auger (Eijkelkamp Co.) of 40 cm length, containing eight cylinders of 100 $cm^3$ each, to obtain data on the soil fauna at each mite focus. The samples were put into a Berlese–Tullgren apparatus (self-constructed by the Department of Soil Sciences, University of Bonn, according to the construction plans of Dunger and Seifert 1997) using heat and desiccation to expel the animals from the samples. Determination of the fauna was done following Karg (1993, 1994) and Moritz (1993) for Gamasida, and Bruckner and Kalusche (1990) and Dunger (1997) for Collembola and other soil fauna.

*Chigger host fauna*

In September 2000 and 2001 surveys of the chigger host fauna were carried out. A combination of three different live traps to catch mammals of the size of shrews up to rabbits was used at mite foci that differ in abundance of trombiculid larvae. Each trapping period lasted three days and four nights. A total of 112 sites were surveyed in nine gardens. The majority of these sites were investigated for the soil parameters mentioned above. The mammal species, their numbers and the numbers of parasitising trombiculid mites (infestation quantity) were recorded.

The surveys were conducted in September, as this time of the year would provide the highest abundance of most of the mammal species (Boye et al. 1996; Niethammer and Krapp 1978, 1982, 1990) that are known to be trombiculid hosts (Elton and Keay 1936; Garben et al. 1978).

Statistical analysis

The factors measured only once were analysed statistically: the size distribution of pores and porosity, pH-values, salinity and air permeability of the soil were analysed for each soil layer of a mite focus with regard to the larvae abundance on the soil surface in a

multiple linear regression analysis using the SPSS 10.0 software package (SPSS Inc., Chicago, USA). If statistical limits were reached regarding a possible interference of one factor and the larval abundance, a single linear regression with the respective factor was done as well. The same procedure was applied to the data of the mammal host frequency and their mite infestation. Additionally, the data from each garden were analysed separately if more than five sites were surveyed.

The soil fauna data (abundance of collembolans and gamasids) were analysed with regard to the distribution of the different species or taxonomic groups in the four depth-levels (two samples per site versus each site in a one-way analysis of variance (ANOVA)). Additionally, the pooled data of each column sample was used to perform a regression analysis on the larvae abundance on the surface.

### Long-term measurements

The second set of environmental factors was measured regularly over a period of three years at eight mite foci (four pairs) in four gardens located in different areas of the city of Bonn ('sites of long-term measurements'). Each pair of sites represented a different microbiotope: herbaceous border, undergrowth of shrubs, flowerbed, and transition between flowerbed and lawn. The two foci of each pair had a distance of one to two metres to each other and were characterised by a significant difference in the abundance of chiggers in the summer of 1999 when the sites for the long-term measurements were selected. The following factors were determined: the matrix suction of the water (positive value of matrix potential) was measured at each mite focus with six mechanical tensiometers (Ecotech Co., Bonn, Germany), two each at a soil depth of 30, 60 and 90 cm, as well as one absorbent block (Watermark soil water potential sensor, WMSM type, Irrometer Company, Inc., Riverside, California, USA) at 5 cm deep in the centre of each site. Water tension in the soil was recorded from May to November three times a week in 2000 and two times a week in 2001 and 2002. With the same frequency, the soil temperatures were measured at 5, 30, 60 and 90 cm depth. A manual digital thermometer (Greisinger Electronic Co., Regenstauf, Germany) was used in three gardens.

In the fourth garden, a data logger (Campbell Scientific Ltd., Loughborough, UK) with PTC-thermistor-sensors (Driesen and Kern Co., Bad Bramstedt, Germany) could be installed at the pair of sites to measure the temperatures continuously over a three years' period saving a set of data every 30 min. These continuous data were also used for a comparison of the winter temperature courses in the different study years.

The precipitation was measured with a rain gauge directly at those eight sites over the whole study period. The respective data were captured together with the matric suction from May to November and once per week from November to May.

This set of environmental factors was believed to be of importance to all developmental stages of the harvest mite. Only the abundances of larvae on the soil surface were measurable (see above 'sampling of post-larval stages'). Nonetheless, the abundances of edaphic stages had to remain obscure, since measurements were planned to last over three years covering different climatic conditions. Searching for edaphic stages would have destroyed the soil integrity at the mite foci. Therefore, only annual counts of larvae on the soil surface were possible.

On the soil surface where the larvae accumulate to wait for an appropriate host, the following factors were recorded at each of the eight sites from May to November in order to measure the living conditions and to evaluate the ecological potential of the larvae. The maximum temperature was measured with a manual mechanical $T_{max}$-thermometer posi-

tioned in the centre of each site and read each visit when the matric suction was measured. The soil surface moisture was measured using the finger test method according to Schlichting et al. (1995). Categories from 1 (very moist) to 8 (dry) were established. The cover of the sites by vegetation up to a height of 15 cm or by organic matter was measured every second week in percentage value of the whole site surface by estimation (±5%) using the estimation tables given by Rowell (1997).

The data of the maximum temperature, soil surface moisture and site cover were combined for a climatic condition assessment to describe the soil surface climate for the time period when the larvae appear on the surface ('larvae season'). A direct climate measurement right at the soil surface was not possible for technical reasons.

In the climatic condition assessment, the environmental factors were assigned to a certain category that was selected when the respective values were in their majority over or below the limits given in Table 1. Subsequent to this classification, the category values of the cover of the site and the soil moisture were doubled to emphasise the importance of these factors for the relative air humidity in contrast to the maximum temperatures which might have influenced the site for only a very short period of time. As mechanical $T_{max}$-thermometers were used, the actual duration of the maximum temperatures could not be ascertained. The category values of the three factors were added up to the 'climate condition index' that was used to compare sites and larvae abundances.

## Results

### Trombiculid species

It was shown with the help of classical morphological taxonomy (Brennan and Goff 1977; Kepka 1964; Krantz 1986; Vercammen-Grandjean 1960) and comparative DNA-sequence analysis (Schöler and Kampen unpublished) that the only trombiculid species encountered in this study was *N. autumnalis*.

### Characteristics of larvae foci and population dynamics

Thirty-nine different gardens in the Bonn city area were surveyed for foci of trombiculid larvae in the course of 118 inspections carried out from spring 1999 until autumn 2002. More than 500 foci were investigated—187 of them for two or three subsequent years, thus producing some general information about the larvae population dynamics:

**Table 1** Limits to assign the environmental factors 'soil moisture on the surface', 'cover of soil surface' and '$T_{max}$' to the appropriate assessment number to calculate the 'climate condition index'

| Surface soil moisture (following the categories 1 = moist to 8 = very dry) | Cover of soil surface (%) | Maximum temperature $T_{max}$ (°C) | Assessment number |
|---|---|---|---|
| ≤4 | 100–70 | <25 | 3 (high) |
| 5 and 6 | 70–30 | 25–35 | 2 (medium) |
| 7 and 8 | 30–0 | >35 | 1 (low) |

- Bites on the skin of the investigator resembling a trombidiosis-like reaction and chiggers themselves were never observed before mid-July. The latest larvae were seen by the middle (2000) or end (2001) of October or even at the beginning of November (1999). The highest number of larvae was found at the beginning or in the middle of September each year.
- The level of mite infestation could not be correlated with the type of garden in terms of care and attention, spatial relation between lawn, flowerbeds and borders, or with a certain type of vegetation or morphology of the soil surface.
- No correlation could be found between the level of infestation and the city area or adjoining biotopes like woods, the river Rhine or creeks, or excessively sealed surfaces.
- Within a given garden, the foci of larvae infestation were spread irregularly and patchy.
- The solar radiation and moisture conditions at a focus as well as the level of cover by vegetation or organic matter did not show any correlation with the larvae abundance on the surface.
- Generally, the foci had a fixed location for the whole three-year study period. A new focus with a high level of infestation could only rarely be found in the subsequent year. In contrast, owing to the accuracy of the TCM, there was some local fluctuation of foci of very small catches (2–3 mites).
- The foci had a size of 0.3–0.5 $m^2$ with the highest larvae abundance in the centre.
- Larva activity were more or less the same throughout the whole daytime without a specific maximum.
- The number of larvae at each focus increased over the four-year study period; only in one garden a great reduction of numbers of larvae could be found at every focus in summer 2000.

In one garden, the surface soil layer of the lawn was removed up to 15 cm depth in spring 2001. Interestingly, this activity did not seem to have an influence on the mite population: the survey in August 2001 revealed the same mite foci with similar larvae abundances as in the year before.

## Larvae foci in correlation to physical and chemical properties of the soil

The physico-chemical survey of the soil at the larvae foci did not give a definite explanation for the patchy distribution of the foci in the gardens. Only some interesting phenomena and statistically conspicuous results shall be mentioned. Seventy-three foci with an infestation level between 0 and 50 larvae collected by the TCM were surveyed. The

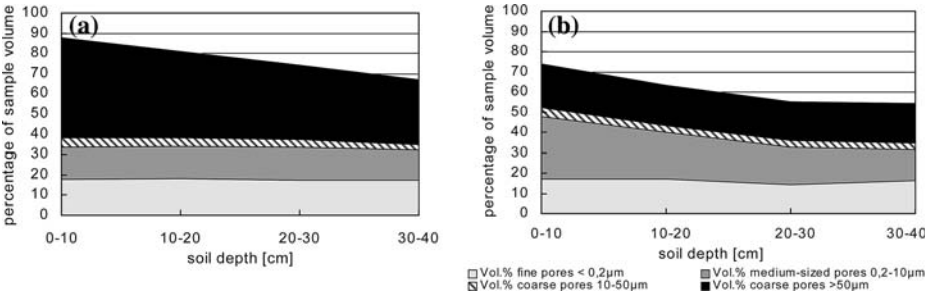


**Fig. 2** Average percentages of the different pore size fractions in the soil sample volume ($n = 6$) at two sites with similar numbers of larvae collected by the 'tile catch method' (TCM) (**a**: 7 larvae, **b**: 8 larvae). Mark the great differences in coarse and medium-sized pore contents between the two sites

percentage of medium-sized pores of the complete porosity of the soil was quite different among the sites as is illustrated in Fig. 2 for two sites with similar larvae abundances. Surprisingly, some other foci with a very high percentage of medium-sized pores in the 20–40 cm soil layers (data not shown) were characterised by little larvae abundances (only 1 to 2 animals) on the surface.

On the other hand, the linear regression analysis of the soil data for the medium-sized pore-fraction at 10–20 cm depth revealed a significant positive proportional correlation ($r^2$=0.88, corrected $r^2$=0.74) between this pore-fraction and the larvae abundance on the soil surface. However, the standard error about the regression line is high (9.68) and the further statistical test shows a bad residue explanation (Durbin–Watson statistic = 1.14).

The pH-values were relatively homogeneous at most of the study sites (varying approximately 0.6 around pH 7). However, in a single garden that showed a very small infestation with larvae throughout the whole study period values between pH 4.83 and 5.05 were measured. Nevertheless, the analysis neither produced significant results nor results reaching statistical limits. On the other hand, considering the data of another huge garden investigated at 10 sites increasing pH-values showed a minor, yet statistically significant, proportional correlation ($r^2$=0.52, corrected $r^2$=0.46) with increasing larvae abundances on the soil surface (SD = 7.61, Durbin–Watson statistic = 2.25).

The air permeability coefficient was also very different from site to site and reduced in soil samples of deeper layers. The correlation between permeability and coarse pores is not necessarily proportional. Although the percentage of coarse pores was quite high sometimes (absolutely and relatively), the air permeability was not and vice versa. It was hypothesised that high air permeability in concert with a high amount of coarse pores may form a positively influencing factor which although of importance to all soil-dwelling stages of the mite would play a special role with regard to the up- and downward movement of larvae inside the soil. But neither the air permeability nor the coarse pore measurements revealed a statistically significant influence on the larvae abundances.

The bulk density at the sites reached values between 0.81 and 1.68 g/cm$^3$. Although some sites showed a relatively high soil compaction, an influence on the larvae abundances (mirroring the population of harvest mite inside the soil) could not be detected. Furthermore, the other related physico-chemical properties of the soil measured in the study (porosity, density of solid particles giving a hint on the amount of organic matter, salinity) showed neither statistically conspicuous values nor significant results that could be correlated with the abundance of larval harvest mites.

## Larvae foci in correlation to the soil fauna

It was hypothesised that the abundance of Collembola whose eggs are preyed upon by post-larval trombiculid stages (Minter 1957; Simonová 1977), and of Gamasida, which are predators of both collembolans and (supposed by the authors) trombiculid mites, would influence the population dynamics of the harvest mite and, consequently, influencing the larvae abundance, too. In order to measure this influence, 159 soil samples were analysed for gamasids and collembolans.

The gamasid genera *Pergamassus* (Parasitidae), *Veigaia* (Veigaiaidae), *Amblyseius* (Phytoseiidae), *Geholaspis* (Macrochelidae) and *Hypoaspis* (Hypoaspididae) were regarded as mite- and collembolan-predators. In contrast, *Rhodacarus coronatus*, *Rhodacarellus silesiacus*, *Minirhodacarus minimus* (all of them Rhodacaridae) as well as the genera *Dendrolaelaps* (Rhodacaridae) and *Alliphis* (Eviphididae) were assigned to the group of collembolan-, but not mite-predators.

Collembolans were determined to the family-level and belonged to the Isotomidae, Entomobryidae, Onychiuridae and Sminthuridae.

The statistical analysis of the data showed significantly more collembolans and mite-feeding gamasids in the depth of 0–10 cm than in deeper soil layers. In contrast, the data of the collembolan-feeding gamasids did not show any significance. The regression analysis of the data did not reveal any correlation of the occurrence of gamasids to the abundance of larval harvest mites on the soil surface.

Surprisingly, also nymphs of *N. autumnalis* were found in different soil layers: 1 nymph in 0–10 cm, 7 nymphs in 10–20 cm (five of them in one single sample), 1 nymph in 20–30 cm and 1 nymph in 30–40 cm.

## Larvae foci in correlation to mammal hosts

This survey covers the analysis of data from 116 sites. Altogether 114 micro-mammals were caught, carrying approximately 5,700 larvae. The hedgehogs were most heavily infested: mite patches were sometimes so dense that single mites could not be distinguished. Thirteen hedgehogs carried a load of approximately 4,200 larvae, 47 Muridae (*Apodemus*- and *Mus*-species) carried 360 larvae, 5 Arvicolidae (*Microtus* sp.) were infested by 717 larvae and 47 Soricidae (*Crocidura* sp.) by 405 larvae. Mammal host abundance and specific mite infestation level did not show any statistically significant correlation to the larvae abundance at the mite foci.

## Long-term measurements

The observation of the course of larvae abundance at the long-term measurement sites for four years led to some information about the population dynamics of the harvest mite, although dynamic processes could not be ascribed to certain developmental stages. Figure 3 shows the development of the larvae abundances at two sites in a flowerbed 2 m apart from each other. The appearance of larvae on the soil surface in the middle or at the end of July and the disappearance in the middle or at the end of October was comparable in the two sites. At site Ka1, larvae were observed 10 days earlier in 2001 than in the other years. Surprisingly, at every site devoid of larvae in 1999, chiggers were caught in 2000 and in subsequent years but in lower numbers than at the neighbouring sites. Figure 3 shows the exceptional situation where nearly the same numbers of larvae were found at both sites in the summer of 2002 although, at site Ka2, hardly any chigger was collected in 1999. At sites where a larvae infestation was detectable in 1999 (such as Ka1), relatively

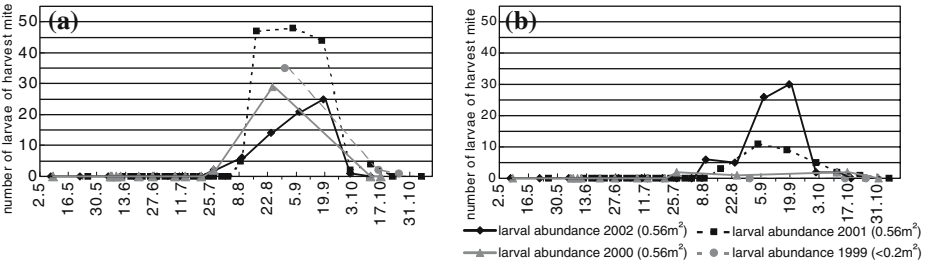


**Fig. 3** Population dynamics of larval harvest mites on the soil surface at two neighbouring sites (**a**: Ka1, **b**: Ka2)

high numbers of larvae were caught in every year. Figure 3a shows a representative example for all sites: in general, a relative decline in larvae abundance took place in the year 2000 whereas the highest number of larvae was registered in the summer of 2001. But as larvae were collected on a smaller area in 1999 (1 tile) than in the following three years (9 tiles), it is very likely, in fact, that in 1999 the larvae abundance was highest.

Soil matric suction correlated with population dynamics

In summer, the matric suction of the soil sometimes reached extreme values at a depth of 5 cm for a longer period of time, whereas in 30 cm the values were high but without extreme peaks. The three summer periods were quite different with respect to the matric suction levels and it is interesting to learn that the highest abundance of larvae on the surface was found in the driest summer-period. Figure 4a–c show examples for matric suction measurements at 5 and 30 cm depth and for the precipitation at the site Ka1 in the years 2000–2002. The development of matric suction values was very different between the two depths during the growing season of subsequent years. A suction of 300 hPa means that nearly all medium-sized pores of the soil are filled with water. It becomes obvious that this value is by far exceeded in spring and summer 2001 (Fig. 4b) when the suction reached extremely high values at 5 cm depth in August, indicating a rather dry soil. In 2002, the measurements revealed a more fluctuating matric suction at both depths sometimes with high values, but only for short time periods (Fig. 4c). On the other hand, the matric suction at both depths was very moderate in the year 2000 meaning that the soil was moist throughout the growing season (spring to autumn) although plants take up greater quantities of water (Fig. 4a).

Soil temperature correlated with population dynamics

At the mite foci, the soil temperatures at 5 cm depth quite frequently reached values above 20°C and very rarely above 25°C in summer, being reduced quickly by rainfall (data not shown). No obvious influence of the soil temperature on the larvae abundances was found. However, the smooth and moderate (always below 20°C) temperature courses at 30 cm soil depth and also in deeper soil layers that were similar in all three years from spring to autumn could be a key factor that influences and synchronises the developmental cycle of the harvest mite (see discussion).

The measurements of the winter soil temperatures were executed to find a correlation with the larvae abundance in the subsequent summer season. Generally, the winter seasons in the Bonn area and the whole Rhine Valley are relatively mild. Therefore, temperatures below 0°C were hardly measured in layers deeper than 5 or 10 cm. Even in the relatively cold winter of 1999/2000 (data not shown), conditions of frost at 20 cm soil depth were only measured during four periods: two of them just below 0°C (lasting 2–3 days), the third (4 days) reaching −1.5°C, and the fourth (8 days) reaching −2.5°C. The respective temperatures at 5 cm depth were 1–2 degrees lower, but never below −4°C. No effect of that relatively cold winter could be found on the time of first appearance of larvae in the following summer season, but interestingly, a decline of larvae abundance was detected at various mite foci (e.g. Fig. 3; see above mentioned decline in a complete garden). However, this phenomenon could not be generalised.

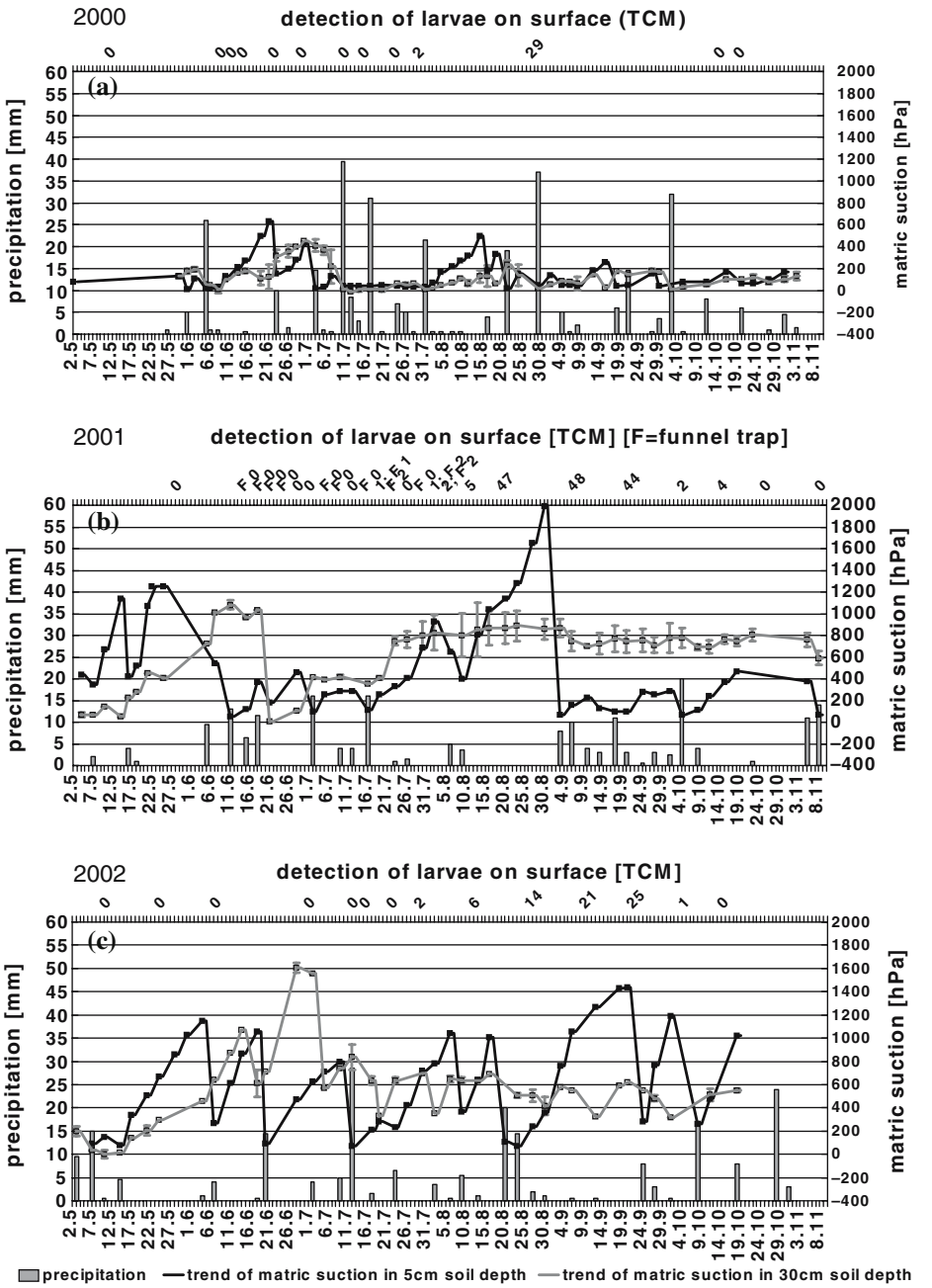


**Fig. 4** Matric suction data for the soil depths of 5 and 30 cm at the site Ka1 in the summer seasons of 2000 (**a**), 2001 (**b**) and 2002 (**c**). The bars show the amount of precipitation fallen in between two visits

**Table 2** Climate condition indices of the soil surface at the sites of long-term measurements

| | Site | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Gr1 | | Gr2 | | Ka2 | | Ka1 | | Wa2 | | Wa1 | | Schu2 | | Schu1 | | | |
| Climate indices of first and second half of larvae season 2000 | 14 | 15 | 14 | 15 | 14 | 10 | 7 | 12 | 12 | 10 | 10 | 8 | 10 | 9 | 11 | 9 | | |
| Sum of indices 2000 | 29 | | 29 | | 24 | | 19 | | 22 | | 18 | | 19 | | 20 | | | |
| Maximum abundance of larvae found in 2000 | 12 | | 12 | | 2 | | 29 | | 4 | | 9 | | 15 | | 37 | | | |
| Climate indices of first and second half of larvae season 2001 | 13 | 15 | 10 | 13 | 9 | 13 | 7 | 13 | 6 | 13 | 8 | 13 | 8 | 11 | 6 | 11 | | |
| Sum of indices 2001 | 28 | | 23 | | 22 | | 20 | | 19 | | 21 | | 19 | | 17 | | | |
| Maximum abundance of larvae found in 2001 | 26 | | 11 | | 11 | | 48 | | 12 | | 39 | | 15 | | 56 | | | |
| Climate indices of first and second half of larvae season 2002 | 14 | 13 | 14 | 12 | 12 | 15 | 10 | 11 | 11 | 8 | 11 | 8 | 11 | 9 | 10 | 7 | | |
| Sum of indices 2002 | 27 | | 26 | | 27 | | 21 | | 19 | | 19 | | 20 | | 17 | | | |
| Maximum abundance of larvae found in 2002 | 24 | | 5 | | 30 | | 25 | | 13 | | 13 | | 7 | | 51 | | | |

The table lists the appropriate maximum abundance of larvae detected by the 'tile catch method' (TCM). To improve data resolution, the larvae season lasting from mid July to mid October was divided into two parts

### Soil surface conditions correlated with population dynamics

The 'climate condition indices' were used to give a quantitative, comparable value for the air humidity and temperature conditions in the micro-habitat of the trombiculid larvae. Table 2 shows the results of these assessments for the larvae seasons of the three-year study period at all eight long-term measurement sites.

It turned out to be difficult to correlate any conditions in the second half of the larvae season with a high larvae abundance: As the life cycle per se supports a higher larvae abundance in the second half of the larvae season compared to the first part (at the beginning or in the middle of September the highest amount of chiggers were found), possible minor influences of surface conditions (negative as well as positive) on larvae abundance were obscured. No influence of the soil surface climate conditions on the maximum abundance of larvae was detected. There is no evidence for the hypothesis that favourable climate conditions (high air humidity and relatively low and constant temperatures) lead to a high abundance of larvae over a certain period of time thereafter (e.g., 'plateau formation' in 2001, see Fig. 3b).

Interestingly, extreme $T_{max}$-values recorded at various sites (35 or even 40°C at numerous occasions) and a $T_{max}$ of 49°C (at the site Ka1 at the end of July 2000) did not have any noticeable influence on the number of larvae collected.

## Discussion

### Collection methodology

Assuming that the problems arising with the growing abundance of *N. autumnalis* in private gardens or even in public areas will make more research on pest control necessary, it is important to have a reliable and 'easy-to-use' collection method. In the present study, the method originally used by Williams (1946) was tested and improved. The TCM represents an efficient and easy survey method for larvae that is indispensable for pest control but it bears the disadvantage that it is very time consuming. It is also very unlikely

to collect all chiggers occurring at a given site, as the larvae do not accumulate on the tiles. However, as could be demonstrated, a reliable and reproducible detection of mite foci and a comparison of sites with regard to the relative abundance levels are possible. The 'funnel trap'-method turned out to be very useful for the investigation of the population dynamics at a given mite focus. However, it is not a method to survey the larvae distribution in a greater area in general. It may be set up very quickly and is, therefore, more 'easy-to-use' than the light traps of Cockings (1948) and Jones (1950a) and also much cheaper in terms of materials used. Both, the TCM and the funnel trapping, are very appropriate for further ecological and biological investigations on trombiculid larvae.

On the other hand, isolating trombiculids that live in the soil is laborious (Cockings 1948; Daniel 1961; Takahashi et al. 2004). The quantitative collection method for the post-larval stages or even larvae inside the soil ('floating method') as described by Cockings (1948) and modified by Richards (1950) and Daniel (1961, 1969) has to be improved, especially when only a small amount of soil can be surveyed or when a relatively sparse larvae abundance is encountered. Since the acceptance to dig in lawns, flowerbeds and their borders is limited in private gardens, the amount of soil material that can be surveyed for mites is usually relatively small. The above authors did not mention data of mite abundance found with the floating method in a certain amount of soil. However, further work will have to improve the breaking of clods, if the clay content of the soil is high, and the handling of the foam that is forming on the soil–water mixture in order to make the spotting of mites easier.

Coincidentally, we were able to isolate nymphs with the Berlese–Tullgren apparatus usually used to catch animals that live in relatively high numbers in the soil. The results of the present study together with the extensive data of Daniel (1961) strongly support the hypotheses that the nymphs are the predominant hibernating developmental stage under temperate climate (e.g. Central Europe) and that (when the soil temperatures are rising in spring) they concentrate in certain soil layers (10–20 cm; at least 5 individuals/100 $cm^3$).

## Characteristics of the mite foci

Regarding the question whether or not *N. autumnalis* has a characteristic habitat with respect to living conditions on the soil surface or inside the soil, a great, confusing mixture of data exist in the literature (Vitzthum 1930; Keay 1937; Toldt 1946; Jones 1950a; Gasser and Wyniger 1955; Daniel 1961; Vater 1981; Struppe 1994). In the present study, no clear evidence for preferred (micro-)biotopes or a characteristic harvest mite habitat could be found. In fact, Daniel's idea of the harvest mite having a tremendous 'ecological potency' (1961) is supported.

Jones (1950a), Garben et al. (1978), and Struppe (1994) found a patchy distribution of *N. autumnalis* larvae foci on the soil surface that is confirmed by the findings presented here. Beside this, a more or less constant location of foci for at least three years could be demonstrated. Jones (1950a) mentioned that larvae of the harvest mites do not show activity below 10°C in tubes in the laboratory. In this study, single larvae were observed busy crawling on the lawn at 6°C ground-level air temperature. Additionally, Jones (1950a) and Gasser and Wyniger (1955) found a maximum activity of the larvae in the afternoon. The results of the present study do not substantiate these observations but are in line with those of Struppe (1994) who found the larvae eagerly and consistently crawling throughout the day. Especially when looking at potential hosts, it would appear that an activity maximum in the afternoon would be anticyclic to the activity of most micro-mammal species (Boye et al. 1996; Niethammer and Krapp 1978, 1982, 1990).

Seasonal appearance of larvae and possible other nuisance species

Another misunderstanding on the side of affected persons is associated with the origin of the bites: In congruence with other reports of larvae abundance, the trombiculid larvae appeared on the soil surface at a certain time period of the year (Jones 1950a; Garben et al. 1978; Struppe 1994). Toldt (1946) is the only one who mentioned ''trombiculid-like'' free-living larvae in late March/April in Austria.

However, trombidiosis-like skin reactions are often diagnosed on patients outside the normal chigger season from July to November. In fact, due to a vast variety of individual immunogenic reactions towards chigger bites as well as similar appearances of papules on the skin caused by different ectoparasites (personal observations), single bites can rarely be attributed to the ectoparasite responsible unless it is caught in action. Therefore, other arthropods than trombiculid larvae may be responsible for the dermatoses. Several species of mites (including fur mites of pets) belonging to the families Dermanyssidae, Pyemotidae, and Macronyssidae, for instance, may infest humans and cause itching bite reactions especially on children (Qadripur and Kant 1996; Mumcuoglu and Rufli 1983; Rodríguez-Casado et al. 2004). In springtime, people are often attacked by avian fleas when cleaning nest boxes. Thysanopterians have been recognised 'biting' under high air humidity conditions (Waisman 1968; Mumcuoglu and Volman 1988; personal observation), and even mosquitoes spending the winter season inside houses and cellars should be taken into account (Eichler 1954).

Multiple factor analysis at the mite foci

Despite the extensive data collection and multiple factor analysis, definite reasons for the patchy distribution of the larvae foci on the soil surface could not be found. One may argue that laboratory experiments with controlled factors are more reliable. So far, it is not possible to breed *N. autumnalis* for generations which is indispensable to test the impact of environmental factors on the survival of the mite under constant and controlled conditions. Additionally, measuring the conditions inside an artificial soil set-up with appropriate sensors might lead to biased data as well. We believed that, for this kind of study, fieldwork would be much more appropriate because it mirrors the conditions 'in situ' much better than artificial laboratory experiments. Additionally, most of the soil parameters that were measured are relatively constant: e.g. under natural conditions soil pH-value, salinity and pore fractions are not changing quickly at a given site. In our study, the porosity at the mite foci was measured reliably as each soil layer was taken out nearly completely with the sample rings. Temperature and moisture were measured constantly in the long-term measurements. Though punctually, the levelling effects inside the soil have led to representative data in a small circle around the sensors that were established in different soil layers in the centre of the mite foci. At those sites, we could measure changes of the factors over a three-year period believing that these sets of data would be sufficient to analyse the influences of these factors on the harvest mite. However, the minor impact of the medium-sized pores and the pH-value inside the soil on the abundance of the harvest mite support the hypothesis that *N. autumnalis* (all developmental stages) is eurypotent as these environmental factors strongly influence most animals in the soil (Edney 1977; Topp 1981; Gisi et al. 1997). On the other hand, it is quite confusing that the data of the medium-sized pores revealed an anti-proportional correlation between the abundance of larvae caught on the surface and the amount of pores in the soil depth of 20–40 cm—which is regarded as

the major dwelling depth of the harvest mites (especially of post-larval stages). Therefore, it should be questioned whether the choice of the selected factors or the scale on which they were measured were inappropriate. As Anderson (1977) already conjectured for many studies in soil ecology, it is possible that the relevant factors were not covered in the present study or that they were not measured with sufficient accuracy. It is also a matter of fact, that in a multiple investigation an interference of the measurements cannot completely be avoided. Therefore, for example, the measurements of the surface conditions leading to the 'climate condition indices' are important but might have been inaccurate. Nevertheless, the indices and especially the experiments of Jones (1950b) showed the larvae being able to stand high temperatures (above 40°C) and low air humidity. While Jones found that the larvae endure an air humidity less than 50% for only 10–20 h, the present study demonstrated that an air humidity of 30% and even lower did not influence the animals at least for a couple of hours. Edney (1977), Topp (1981), and Salin et al. (1999) described mechanisms how arthropods manage the loss of water through transpiration in extreme situations that may apply to the harvest mite as well.

In case the harvest mite has a wide tolerance range for different abiotic factors, our study set-up was not able to detect the borders of these ranges. Nevertheless, there are clues to the fact that not only the larval stages but probably also the post-larval stages are eurypotent and euryoecious. This hypothesis is strongly supported, for instance, by the fact that both the larvae and the post-larval stages foraging inside the soil have to traverse very dry soil layers in spring and summer as shown by the measurements of the matric suction.

Taking into consideration the facts regarding the air humidity mentioned above, the larvae as well as the post-larval stages must be suspected to take up water from the soil air. This hypothesis is supported by Vannier (1983) and Verhoef (1995). Verhoef also mentioned that soil-dwelling animals are normally not able to endure water loss. Besides this, no literature data are available to discuss an influence of high matric suction on the egg development in spring and early summer.

According to the mammal survey, it was hypothesised that mammals are important to the population dynamics at the mite foci as they carry off questing larval mites and introduce engorged larvae. High frequencies of mammal hosts as well as high infestation quantities would therefore lead to a so-called high 're-infestation potential' for the mite focus that could support the growth of the mite population in the following year(s) or introduce the mite to areas that may not have formerly been mite foci. The results of the study presented do not support this hypothesis. However, it may in fact be true with regard to the possible life span of adult trombiculids of three or more years: *Leptotrombidium pallidum*, for instance, lived for 970 days under laboratory conditions (Takahashi et al. 1993); additionally, according to DeBach and Smith (1947), oscillations of host and parasite population densities are normal and sometimes considerably shifted in time. Accordingly, the influence of hosts is only detectable by a long-term investigation that would have to cover at least three subsequent years. However, in the present study, the factor 'hosts' does not seem to be a key factor determining the distribution and density of *N. autumnalis*. Nevertheless, the availability of hosts has an essential influence on the life cycle of trombiculid mites (Varma 1993; Azevedo et al. 2002). On the other hand, the effects of the control of potential hosts in order to control the larvae abundance are also questionable, as the reduction of hosts in a certain area (e.g. by traps) would cause a constant immigration of new (larvae infested) animals (see Harrison 1956 and Wilkinson 1979 for details).

The role of birds and bats as hosts can be neglected in this context since they are never as heavily infested by harvest mites as certain mammal species living on the ground (Elton and Keay 1936; Daniel 1961; Dusbábek 1963; Garben et al. 1978; Literák et al. 2001).

In summary, the environmental factor 'hosts' needs to be surveyed for a longer period of time to receive sufficient information on its influence on the population dynamics of the trombiculids. However, it does not seem to be a key factor determining the distribution and density of *N. autumnalis*.

Interestingly, we found a seasonally regular appearance and disappearance of larvae throughout the study years. Wohltmann (2001) and Wohltmann et al. (2001) mentioned the importance of a synchronisation in the life cycle for the sexual partners of a parasite species and for an optimal coordination with the host activity. The authors found that the diapause of developmental stages serve to achieve this synchronisation. The soil temperature is probably an important factor to synchronise the development of the harvest mite as it changes similarly and steadily every year whereas the other important abiotic factor in the soil, the moisture, fluctuates much more in subsequent years as represented by the matric suction data. However, as the developmental cycle of *N. autumnalis* appears to be very steady over the years, the soil temperature is likely to be the most important time-giver ('zeitgeber') for its endogenous rhythm. This hypothesis is supported by studies by van Peenen et al. (1976).

## Patchy distribution

The mayor environmental factors influencing all developmental stages of the mite were investigated. Apart from that, investigations on the abundances of female mites, their distribution inside the soil, and their behaviour regarding egg deposition would very likely lead to substantial results regarding the patchy distribution of the harvest mite. But since the abundances of post-larval stages at the mite foci had to remain obscure due to inappropriate sample methodologies, investigations rely on the abundances of larvae. Regarding the patchiness, environmental conditions are influencing egg hatching and the living of the freshly hatched larvae until they reach the soil surface that much that, in fact, a combined investigation on female mites, egg deposition, hatching of larvae and abiotic and biotic factors would be the optimal research set-up. However, using the data of many foci with different larvae abundances (being the integrated outcome of the combined influences of the above mentioned ecological factors), it was expected that the statistical analysis led to substantial results. Nonetheless, why is there a lack of definite results?

One aspect could be that the influences of the patchiness of female mites or egg deposition sites are greater than all the other factors. If so, then special emphasis has to be laid on the improvement of the isolation of post-larval stages in future studies.

Additionally, besides the mentioned deficiencies regarding the investigations of the hosts' influences, it is suspicious that an influence of the other soil fauna on the population dynamics of *N. autumnalis* could not be detected. As the interactions of soil organisms are diverse (Topp 1981; Schaefer 1995; Gisi et al. 1997), it is possible that any correlation between the data of the chigger mites and the other soil fauna was concealed due to methodological reasons in the present study. Generally, the soil fauna—similar to the mite foci on the soil surface—is spread very heterogeneously (e.g. Verhoef 1995; Geißen et al. 1997). Schaefer (1995) mentioned a control of collembolans by predators. It is likely that predators and the abundance of prey organisms influence the abundance and distribution of *N. autumnalis* in a similar way. More research on predator–prey relationships may lead to a key factor of the patchy distribution of the mite foci. The role of this factor becomes even

more interesting if the observations of Ernsting (1977) are taken into consideration: the author found that the population of collembolans is forced into a stable patchy distribution through the influence of predators. This seems to be caused by reduced intraspecific concurrence between collembolans due to the influence of the predators (Remmert 1992). A computer-based model of Breckling and Reuter (1999) led to the same results. However, due to some random processes in their simulation, the authors couched a so-called 'self-organised heterogeneity of the distribution of organisms'. If this model actually mirrors the natural situation, the research on the influence of certain biotic and abiotic factors on the location of a harvest mite focus would be dispensable, as coincidences would cause confusion results.

Another problem to explain why the mite foci show a patchy distribution or why there are more chiggers at nearly every focus from year to year could be a situation in which the 'migration' of the harvest mite into urban areas is still in progress. Older publications always mentioned trombidiosis being a problem in rural areas. Migrations of micro-mammals into urban areas have been observed during the last years (personal communication R. Hutterer, Zoological Research Institute and Museum Alexander Koenig, Bonn). Perhaps a similar migration takes place regarding the harvest mite forced by their hosts. If so, then the above-mentioned phenomena are possibly caused by the fact that not all potential habitats and niches have yet been fully occupied by the harvest mite. This hypothesis is supported by the investigations of Haitlinger (1986) and Gregoire-Wibo and Snider (1977).

## Impact of cold winter seasons

Despite some phenomena in the present study in summer 2000, it is very unlikely that the soil temperatures in winter have any influence on the harvest mite population in the Bonn area. Topp (1981), Vannier (1998), and Gisi et al. (1997), beside others, mentioned that a great variety of soil animal genera are able to endure temperatures below the freezing point. Correspondingly, Daniel (1961) postulated an only minor influence of cold temperatures on the migration of the harvest mite inside the soil, and Kepka (1958) found a 'freezing tolerance' in the trombiculid *Euschöngastia xerothermobia*. On the other hand, Eichler (1964) observed that the harvest mite causes lesser nuisance in a summer following a cold winter. The data obtained during the wintertime of the study presented did not reveal critical temperature values, especially, in the deeper soil layers where the nymphs and adult mites are assumed to spend the winter. Nevertheless, it is very likely that cold periods in winter directly or indirectly (e.g., via the influence on prey organisms or hosts) affect the population of the harvest mite. Cold winter periods were not covered by the present study and were extremely seldom in the last decade in the Rhine Valley.

## Pest control

The data described do not allow the identification of a specific environmental factor that could be manipulated to reduce larvae abundances at the mite foci. This suggests that the larvae as well as the post-larval stages are extraordinarily euryoecious and eurypotent. Typical habitats cannot be specified and, therefore, the whole garden or park could be affected. With regard to a possible pest control strategy, the experimental use of acaricides or pesticides that are questionable per se from an ecological point of view did not solve the problem of massive larvae occurrences in gardens (Sy 1986). However, any kind of

poisoning of the post-larval and euedaphic trombiculid stages would probably only be successful if a huge amount of active agent is used which bears the risks of affecting the soil fauna in an unexpected way. In other studies, for instance, gamasid mite species were even more numerous after such a treatment (Karg 1967; Krogh 1995), the target organism was the only one deriving benefit (Wood 1995; Wallwork 1976), or unpredicted changes in the faunal composition occurred (Halopainen and Rikala 1995). Besides, the use of acaricides is quite expensive.

As a control strategy, it is suggested to survey the mite foci with the 'TCM' followed by a simple pest control strategy: pouring boiling water in large quantities onto the mite foci. The high temperatures inside the soil will kill all meso- and micro-faunal life. The harvest mite will only very slowly re-infect these treated foci, as they are patchily distributed and isolated from each other, whereas the other soil fauna will return much quicker.

Another promising strategy to reduce the abundance of larval harvest mites could be the use of the gamasid species *Amblyseius cucumeris* and *A. agrestis*, as suggested for a biological pest control in the field by Karg (1994).

However, it generally turned out to be quite difficult and laborious to reduce the nuisance caused by harvest mites, and even the application of pest control measures does not guarantee a success. Therefore, for the time being the use of repellents seem to be the best method to reduce trombiculid annoyance in infested areas. In this field, recent research brought about successful approaches (Lerdthusnee et al. 2003; Smal et al. 2004).

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