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Contribution to the life history and morphology of the water mite *Panisellus thienemanni* (Acari, Hydrachnidia: Hydryphantidae)

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Original research

ABSTRACT

The crenobiontic water mite *Panisellus thienemanni* (K. Viets, 1920) is a rare species confined to Europe, occurring in predominantly shaded helocrenes. Larvae of this species are known to utilize two species of springtails (Collembola) within the family Tomoceridae as a host. With only sparse published data available of *P. thienemanni*, this paper provides an up-to-date status of its distribution in the Netherlands, and presents new data on the morphology, life cycle, and host-parasite relationship. We report the first record of the species using a host within the family Isotomuridae (Collembola), i.e. *Isotomurus fucicola* Schött, 1893. The finding was part of a survey in a shaded helocrene spring in the eastern part of the Netherlands, carried out in 2011 and 2012. We particularly looked at the host species being used by larvae of *P. thienemanni* at the site, the number of larvae attached to an individual springtail, and the attachment site of the host. Furthermore, we compared some morphological characteristics of adult males and females with descriptions in literature. We briefly discuss the not yet fully understood life cycle of *P. thienemanni* based on existing data, and our own observations.

Keywords life cycle; phenology; parasite-host relationship; Collembola; dispersal

Introduction

Panisellus thienemanni (K. Viets, 1920) is a spring-dwelling water mite with an interesting life cycle, using springtails (Collembola) as their host (Boehle 1996). With legs lacking swimming setae, *P. thienemanni* adults and deutonymphs have a crawling mode of locomotion. The species has a characteristic arrangement of dorsal and postero-ventral sclerites (Figure 1).

By using adult and juvenile stages of Collembola as hosts (Boehle 1996), *P. thienemanni* can be considered as one of the few exceptions to the rule by not resorting to flying insects.

Springtails infected by larvae of *P. thienemanni* (Figure 2) can be found from April-June (Boehle 1996; Wohltmann in Martin and Stur 2006).

Panisellus thienemanni has a scattered distribution throughout Europe, probably due to rare studies on spring habitats. The current state of knowledge of the distribution of *P. thienemanni* in the Netherlands is presented in Figure 3. Up till recently, *P. thienemanni* was only known from a single site in the Netherlands, a helocrene spring on a shaded, sloping bank of a headwater stream in the very east of the country (Mosbeek, N 52°26.741′ E 6°51.760′, Province of Overijssel) (Smit *et al.* 2012). In 2019 the first author also encountered the species in an area with seepage outflow on the shaded bankside of a stream in the southern part of the Netherlands (Tongelreep, Province of Noord-Brabant, N 51°20.449′ E 5°29.060′, 22 Mar. 2019, 1 ♂, 2 ♀♀, 1 deutonymph).

Figure 1 Dorsal view of an adult of *Panisellus thienemanni* showing the characteristic arrangement of sclerotized plates. Photo Rink Wiggers.

In 2011 and 2012 we actively searched for *P. thienemanni* adults, deutonymphs and parasitized springtails in the helocrene springs adjacent to the Mosbeek. This paper describes the results of the survey, with special emphasis on the life cycle of the mite, selected hosts, and morphology.

Figure 2 The springtail *Tomocerus minor* with unengorged larvae of *P. thienemanni*. Larvae typically attach themselves to the soft cuticle on the dorsomedial side of the reduced prothorax. Photo Christophe Brochard.

Figure 3 Records of *P. thienemanni* in the Netherlands.

Material and methods

Description of the sampling site

The sampling site is a helocrene spring, situated on the face of the stream bank of the Mosbeek, a small headwater stream near the hamlet of Hezingen (Province of Overijssel). The site is shaded by black alder (*Alnus glutinosa*), with an undergrowth of plants like wood club-rush (*Scirpus sylvaticus*), large bittercress (*Cardamine amara*), marsh marigold (*Caltha palustris*), water horsetail (*Equisetum fluviatile*), stinging nettle (*Urtica dioica*), and several moss species. The bankside is partially saturated with groundwater, with seepage outflow forming some trickles (Figure 4). Locally precipitation of iron oxide takes place.

Sampling

Sampling of water mites was carried out in the spring and autumn of 2011. A small shovel sampler as described in Bijkerk (2010) was used. A sample consisted of several shovel samples from the site. Sampling of springtails was carried out in the spring of 2012. Fifteen pitfall traps (Figure 5) containing some fixative (formaline, 6%) and a drip of detergent for breaking

Figure 4 Impression of the study area, 14 Apr. 2019: face of the headwater stream bank of the Mosbeek at Hezingen, with trickles seeping down towards the stream. Photo Rink Wiggers.

the surface tension, were placed at regular intervals on the slope of the bankside and collected again after twelve days (in place from 5 Apr. 2012 to 17 Apr. 2012). When collecting the pitfall traps, an additional shovel sample adjacent to every pitfall trap was taken for sampling water mites.

Abiotic parameters

To measure conductivity, acidity, and temperature of the groundwater discharged to the surface, groundwater monitoring wells were placed next to every pitfall trap (Figure 5). After twelve days, measurements were carried out in the monitoring wells. The electric conductivity, pH, oxygen saturation and concentration, temperature, and oxidation-reduction potential were determined.

Processing of samples, identification and measurements

All samples were taken back to the laboratory. In order not to miss the small mites while sorting, all shovel samples were divided into different fractions by gently washing the samples through a stack of sieves with different mesh sizes (mesh width bottom sieve: 300 μm). The fractions of the washed samples were sorted and water mites were stored in Koenike-fluid. When encountered, also infected springtails were collected and stored in ethanol (70%). Springtails from the pitfall traps were sorted and preserved in ethanol (70%).

Identification of mites and springtails was executed using a stereo microscope and a compound microscope. Measurements on adults and nymphs of *P. thienemanni* were executed using a calibrated compound microscope with graticule.

Figure 5 In the spring of 2012 fifteen pitfall traps were placed at the site, consisting of a container with some preservative buried in the ground and a rain cover placed on top. Next to each pitfall a groundwater monitoring well was placed for abiotic measurements. Photo Rink Wiggers.

Results

Abiotic factors

The electric conductivity, pH, oxygen saturation and concentration, temperature, and oxidation-reduction potential of the groundwater measured in the 15 groundwater monitoring wells are shown in Table 1. The groundwater coming to the surface at the site can be described as weakly acidic. Groundwater temperature measured in the monitoring wells was very constant. Electric conductivity ranged from 203-450 µS/cm, with higher measurements at higher altitudes on the face of the stream bank.

Table 1 Acidity (pH), electric conductivity (EC), oxygen saturation (O_2 (%)), oxygen concentration (O_2 (mg/l)), temperature (T), and oxidation-reduction potential (ORP) of the groundwater measured in the 15 groundwater monitoring wells.

	Range	Mean
pH	5.9-6.8	6.3
EC (µS/cm)	203-450	289.5
O_2 (%)	6-40	29.7
O_2 (mg/L)	0.6-4.4	3.3
T (°C)	8.4-9.2	8.8
ORP	105.7-148.4	127.4

Table 2 Other species of water mites encountered at the sampling site.

Family	Species
Anisitsiellidae	*Bandakia concreta* Thor, 1913
Axonopsidae	*Ljania bipapillata* Thor, 1898
Hydryphantidae	*Parathyas pachystoma* (Koenike, 1914)
	Tartarothyas romanica Husiatinschi, 1937
Lebertiidae	*Lebertia* (*Brentalebertia*) *minutipalpis* K. Viets, 1920
	Lebertia (*Lebertia*) *glabra* Thor, 1897
	Lebertia (*Mixolebertia*) *stigmatifera* Thor, 1900
Mideopsidae	*Xystonotus* (*Xystonotus*) *willmanni* (K. Viets, 1920)
Sperchontidae	*Sperchon* (*Sperchon*) *squamosus* Kramer, 1879
	Sperchon (*Sperchon*) *thienemanni* Koenike, 1907

Invertebrate assemblage

A complete list of other spring dwelling water mite species found at the sampling site is presented in Table 2. The assemblage of other invertebrates found at the site is also typical for helocrenes. Examples of encountered species are the beetles *Agabus guttatus* (Paykull, 1798) and *Hydroporus discretus* Fairmaire & Brisout, 1859, the stoneflies *Nemoura dubitans* Morton, 1894 and *Nemurella pictetii* Klapálek, 1900, and the chironomids *Krenopelopia binotata* (Wiedemann, 1817) and *Heterotanytarsus apicalis* (Kieffer, 1921). Wiggers *et al.* (2019) provide a full list of macro-invertebrates found at the site.

Morphology

Measurements of the idiosoma length and width, and number of acetabula (Ac) anterior and posterior to the genital plates of males, females and deutonymphs are presented in Table 3. The designation of the gender of adult specimens is based on the number of Ac anterior to each genital plate (one in males, two in females), which seems to be the most reliable feature (Figure 6). We found two aberrant adult specimens with the number of Ac anterior to the left genital plate being dissimilar to the number anterior to the right plate. These specimens have not been included in the measurements.

Adults, deutonymphs and larvae

The number of collected specimens of adult males and females, deutonymphs, and the presence or absence of larvae for each sampling date is presented in Table 4. We found adult males and females as well as deutonymphs in April and September. Adults and deutonymphs were mainly collected from groundwater saturated patches of moss. In all samples, females were found in greater numbers than males, most convincingly in autumn due to a higher number of

Table 3 Morphological features of adult males and females and deutonymphs of *P. thienemanni*: range (average) of idiosoma length and width, number of acetabula anterior and posterior to genital plate.

		Idiosoma		Number of Ac bordering genital plate	
	n	length (µm)	width (µm)	posterior	anterior
male	10	820-980 (900)	530-610 (580)	3-6 (4.5)	1
female	14	930-1050 (1000)	600-690 (640)	4-8 (6)	2
deutonymph	4	560-700 (660)	370-500 (440)	1	1

Figure 6 Genital field of a female (left) and male (right) of *P. thienemanni*. Males possess only one genital acetabulum anterior to each genital plate, whereas in females a pair of acetabula is present anterior to each plate (red arrow). Photo Christophe Brochard.

adults collected compared to in spring. The main part of the females caught in April were still ovigerous and carried 2-9 eggs (average 6; n=6).

The number of deutonymphs found was low. Larvae attached to collembolans were only observed in spring.

Sampling effort and method of sampling differed between the sampling dates. Therefore, statements on the difference in number of specimens caught between dates cannot be made.

Table 4 Number of males, females, and deutonymphs of *P. thienemanni* collected as well as the presence or absence of larvae for each sampling date.

Sampling date	Males	Females	Deutonymphs	Larvae
10 Apr. 2011	4	8	0	present
28 Sep. 2011	5	18	3	absent
17 Apr. 2012	0	4	1	present

Table 5 Species and total number (Ntot) of collembolans caught during 12 days in 15 pitfall traps at the sampling site as well as the number (Ninf) and percentage (%inf) of specimens infected with larvae of *P. thienemanni* (April 2012).

Family	Species	Ntot	Ninf	%inf
Entomobryidae	*Entomobrya corticalis* (Nicolet, 1841)	4	0	0
	Entomobrya nivalis (Linnaeus, 1758)	3	0	0
	Lepidocyrtus lignorum (Fabricius, 1775)	1663	0	0
Isotomidae	*Desoria cf trispinata* (MacGillivray, 1896)	88	0	0
	Isotoma viridis Bourlet, 1839	29	0	0
	Isotomurus fucicola Schött, 1893	1	1	100
	Isotomurus plumosus Bagnall, 1940	296	0	0
Tomoceridae	*Tomocerus flavescens* (Tullberg, 1871)	82	5	6.1
	Tomocerus minor (Lubbock, 1862)	56	2	3.6

Infected springtails, number of larvae and attachment site

The total number of Collembola species caught in the pitfall traps, as well as the number and percentage of specimens with larvae of *P. thienemanni* attached to their body are shown in Table 5. In the pitfall traps we found nine species of springtails, of which three could be observed hosting larvae of *P. thienemanni*. The main two species hosting larvae were *Tomocerus flavescens* and *T. minor* (Tomoceridae). Of *T. flavescens* (n = 82) 6.1% of the specimens were infected, of *T. minor* (n = 56) 3.6%. Only a single specimen of *Isotomurus fucicola* (Isotomidae) was caught, and also hosted a larva. Of the remaining six species caught, no specimens could be observed hosting larvae, even not in the most abundant species, *L. lignorum* and *I. plumosus*.

The number of *P. thienemanni* larvae found attached to specimens of encountered host species caught in the pitfall traps and shovel samples are presented in Table 6. The number of larvae attached to an individual springtail ranged from 1-7 (n of springtails = 23, mean: 1.9). Larvae were exclusively found attached to the soft, reduced dorsal section of the prothorax. Occasionally we observed unengorged larvae clutched to the ventral side of the thorax and abdomen. However, these larvae were not fixed to the host's integument.

Discussion

Habitat

Both Dutch sites are shaded faces of stream banks with seepage outflow. At our study site, *P. thienemanni* could only be observed in samples of groundwater-soaked mosses on the bankside of the stream, and not in the main headwater itself. Also the known German sites are all shaded, weakly seeping helocrenes, which never dry out completely (personal communication Reinhard Gerecke). Andreas Wohltmann (personal communication) found *P. thienemanni* exclusively in wet mosses, which corresponds with our observations. The occurrence in shaded places

Table 6 Observed number of *P. thienemanni* larvae (range and mean) attached to the dorsal side of the prothorax for each springtail species.

Infected springtail species	n	Number of attached larvae of *P. thienemanni*
Tomocerus minor	15	1-4 (1.7)
Tomocerus flavescens	7	1-7 (2.3)
Isotomurus fucicola	1	1
total Collembola	23	1-7 (1.9)

only, implies that *P. thienemanni* depends on a stable thermal regime and can be considered a stenothermic species, which was classified in the past as "cold-stenothermic", a term which is not really fitting to a habitat which is relatively warm in the winter.

Sexual dimorphism

To distinguish adult males morphologically from females the number of Ac anterior to each genital plate can be used best. This feature mainly worked out, but we found two aberrant specimens with the number of Ac anterior to one genital plate being dissimilar to the number anterior to the other plate (1 versus 0 and 1 versus 2). Idiosoma length and width of both specimens would categorize them as males.

The position of the pregenital plate as well as the position of the setae on the genital plate as features to separate male and female as mentioned in Viets (1936) appeared unreliable in our specimens.

The number of Ac posterior to each genital plate we observed in adults varies and differs slightly from the number Di Sabatino *et al.* (2010) are reporting. They mention 4-6 posterior Ac, whereas we found 3-6 in males and 4-8 in females.

In general, females are larger than males but ranges of idiosoma length and width overlap.

Life cycle and phenology

Panisellus thienemanni is likely to be univoltine. Oviposition takes place in early spring, possibly in March-April. Oviposition and the subsequent hatching of larvae clearly takes place over a period of time. The main part of adult females caught at the study site on 17 Apr. 2012 could still be observed with eggs, whereas larvae were also present.

Hatching of larvae possibly starts as early as the end of March, since infected springtails were already observed on 10 Apr. 2011. It may well carry on until the end of spring, but this needs further investigation. Before attaching to a host, the bright red and terrestrial larvae are able to crawl freely in the moss (own observation in collected sample).

The larvae we found attached to springtails in our April samples, were not or not fully engorged. Combined with the presence of ovigerous females, this indicates that the time of sampling was at the beginning of the period host-seeking larvae were present. Boehle (1996) found infected hosts from the beginning of April until the middle of June. The length of the idiosoma of the larvae he observed increased from 0.2 mm to at most 0.7 mm when fully engorged. The larvae left their host after approximately three weeks and subsequently metamorphosed into deutonymphs in 20 days. This period of time seems temperature related. For the protonymphal stage, Wohltmann (unpublished data) observed a duration of an average of 50 days at a temperature of 15 °C before the active deutonymphs emerged. At 20 °C the protonymphal stage lasted on average 27 days. Considering the restricted seasonal presence of larvae, we assume only a single peak of emergence takes place. From these observations, we conclude that the development from larva to deutonymph takes place in the same year. From the scant data available, it is unclear when deutonymphs metamorphose into adults. At our study site, deutonymphs were at least still present on 28 Sep. 2011. In the temperate zone, deutonymphs of water mites typically feed and grow throughout the summer, and adults appear in late summer or early autumn and mate almost immediately (Proctor *et al.* 2015). However, since we also found a deutonymph the following spring (17 Apr. 2012), it can be inferred that not all deutonymphs metamorphose into adults before the winter. Part of the population seems to pass the winter in this stage. Another three records of deutonymphs found in March, April and May in the Netherlands, Luxembourg, and the Czech Republic (this publication; Martin 2006; personal communication Ian Smith; see below) are in line with this observation. This phenomenon of overwintering deutonymphs is not uncommon and has also been reported for other members of Hydryphantidae (Böttger and Völkl 1987; own observation). Those deutonymphs of *P. thienemanni* overwintering, might enter a reproductive diapause after turning into adults and partake in the following reproduction period.

Feeding behaviour of the deutonymphs is not known. Wohltmann (in Martin 1998) found that without nourishment deutonymphs were able to survive for four months.

As documented for other species within the Hydryphantidae and other early derivative groups (Witte 1991; Proctor 1992), sperm transfer in *P. thienemanni* is likely to take place without bodily contact (dissociated sperm transfer). Males deposit spermatophores on a substrate, while uptake of sperm packets by females takes place afterwards. In the temperate zone inseminated females of water mites typically overwinter and lay fertilized eggs the following spring (Martin 2010; Proctor *et al.* 2015), which possibly also applies to *P. thienemanni*.

Both adult males and females were found in both spring and autumn samples. This observation contradicts with the supposition of Martin and Rückert (2011) that *P. thienemanni* is an early spring species. Also Gerecke *et al.* (2009) mention records from Italy in samples from spring habitats taken in August, September, and October. The female-biased sex ratio observed might be explained by males having a shorter lifespan (Gerecke 2006), a phenomenon also observed in other species (Ullrich 1976).

Martin (1998, 2004) managed to feed a kept adult male with chironomids, which could be the main food source of adults and deutonymphs.

Parasite-host relationship

Panisellus thienemanni is probably highly host-specific to a limited number of springtail species. The dorsal side of the prothorax is the attachment site exclusively used by the larvae. Belonging to an early derivative family (Hydryphantidae), the species' specific site selection is striking. In many representatives of early derivative families, attachment sites are selected accidentally. Highly specific attachment sites are found to be more common in species of higher evolved families (Martin 2004). In many of these species, larvae are preparasitically attending their host awaiting the process of host ecdysis, during which they attach for feeding. This behaviour often correlates with aggregation of mite larvae at particular regions of the host's body. Such preparasitic attendance has also been observed in terrestrial Parasitengona (Johnstonianidae, Calyptostomidae, see e.g. Wohltmann 2000) and Hydryphantoidea (Lanciani 1971), again correlated with attachment site specificity. Further research is needed to confirm if larval attachment of *P. thienemanni* is likewise preceded by preparasitic attendance.

Springtail adults and nymphs of the genus *Tomocerus* are mainly selected (Boehle 1996; personal communication Andreas Wohltmann; this study). The three parasitized species we observed, *T. flavescens*, *T. minor* and *I. fucicola*, all belong to the Entomobryomorpha. Species within this large order are all exhibiting a reduced, not fully sclerotized prothorax. This feature enables the larva to attach itself onto the soft, membranous integument. Moreover, this obvious site specificity might be stimulated due to the site being out of reach by brushing movements of the host's legs (Wohltmann 2000). In line with Boehle (1996), the infected springtails we found were parasitized by a single larva. Occasionally higher numbers were found, with a maximum of seven. Wohltmann (personal communication) found 1-6 larvae on a single host. Boehle (1996) reported a maximum of four, a number found to be lethal to the host. As he observed, attached larvae are positioned in a fashion that their swelling idiosoma is supported by their host's head.

The range of host species selected by larvae of *P. thienemanni* seems limited. This narrow host range may be determined by different factors. *Panisellus thienemanni* is likely to exhibit a narrow niche breadth within its heterogeneous macrohabitat. Positive co-occurrence of *P. thienemanni* and a suitable host species due to overlap in habitat requirement therefore may be restricted. Of the three parasitized host species, *Tomocerus flavescens* and *T. minor* are common, drought sensitive, surface-dwelling species. In damp forests they can be abundantly found in leaf litter and mosses. In spring habitats their niche is rather broad and evidently overlaps with that of *P. thienemanni* larvae. Therefore, exposure of these species to mite larvae is comparatively high. Also *Isotomurus fucicola*, a much rarer species, apparently prefers very

wet conditions along the shore of different waterbodies (Fjellberg 2007) and in spring habitats may tend to prefer similar sites as *P. thienemanni*.

Isotomurus plumosus is also a species found in wet habitats. Interestingly, no parasitized specimens of this species were found, although caught in substantial numbers at the study site. This apparent lack of susceptibility may be influenced by specific morphological, physiological, or behavioural host traits preventing successful settlement of larvae. *Isotomurus plumosus* is clearly a smaller species compared to the encountered host species and might therefore be an unsuitable host for development of *P. thienemanni* larvae.

Some of the unparasitized springtail species caught, exhibit a different habitat preference compared to *P. thienemanni*. For example, *Entomobrya corticalis* and *E. nivalis* can be mainly found on trees, where they live underneath bark or on mosses and lichens (Berg and Aptroot 2003). A host-parasite association between these species and *P. thienemanni* therefore seems highly unlikely.

The relatively high number of unengorged larvae encountered, as well as the presence of ovigerous females, implies our sampling was carried out at the beginning of the hatching period. The percentage of parasitized springtails determined by us reflects the situation at that period and is likely to underestimate the percentage expected at a later time in spring.

Smith and Oliver (1986) observed a larva, which they ascribed to the genus *Thyas* (currently *Parathyas*), attached to the thorax of *Tomocerus* sp. The record stems from a site in the Czech Republic, 1972. At the time of their research, larvae of *P. thienemanni* as well as their host species were not yet known. A request to reexamine the material resulted in a rectification, the Czech larvae found at the time on *T. flavescens* in fact belong to *P. thienemanni* (personal communication Ian Smith). No other cases of water mite species using springtails have been observed, making this host-parasite relationship of *P. thienemanni* and springtails unique among this group.

Low interspecific competition might be an advantage for *P. thienemanni*, since no other water mites utilize springtails. Furthermore, springtails are very abundant in spring habitats. However, there are some cases of terrestrial mites, with larvae known to parasitize on springtails (e.g. Greenslade & Southcott 1980; De Oliveira *et al.* 2016; Felska *et al.* 2018).

Dispersal

The main part of water mite species select flying insects as hosts. Besides providing the larvae with haemolymph for growth and development, the host facilitates dispersal of the mite. Selecting a flying insect therefore seems advantageous for dispersal.

Whereas springtails are not capable of flying, they have other means to reach a new site. Although springtails are mobile, dispersal by active locomotion is of minor importance, and they mainly rely on passive dispersal. However, successful aerial dispersal of wind-borne springtails has been proven (Hawes *et al.* 2007). Considering the predominantly sheltered biotopes of *P. thienemanni*, we expect this mode of transport of co-occurring, bottom-dwelling springtails of minor significance. Springtails inhabiting such biotopes are likely to be poorly dispersive.

Springs can be considered insular environments (Cantonati *et al.* 2006). Consequently, crenobiontic mites show a disjunct distribution, with populations assumed to be rather isolated (Blattner *et al.* 2019). Successful inter-population dispersal might therefore be very limited and depends predominantly on the dispersal abilities of the selected host. To reduce the high risk of being transferred to unsuitable habitats, it might be even advantageous for crenobionts to greatly reduce dispersal to prevent population decline. As for *P. thienemanni*, using poorly dispersive collembolans as hosts might therefore be a strategy to remain at the well-suited natal location.

Crenobiontic species with limited dispersal abilities and low inter-population migration rates show restricted gene flow, resulting in high genetic diversity between populations and

the potential for speciation (Blattner *et al.* 2021). To better understand the degree of isolation between populations of *P. thienemanni,* a population genomic analysis will be of great value.

Despite their supposedly limited dispersal abilities, possible modes of dispersal of infected springtails cannot be regarded obsolete. Water is another dispersal agent, springtails can be regularly found on floating debris or driftwood. Furthermore, many springtails have hydrophobic cuticles that enable them to survive on water surfaces (Moore 2002). Considering the already mentioned high risk of ending up in an unsuitable habitat when depending on passive long-distance dispersal, we expect dispersal of *P. thienemanni* will be more successful at a local spatial scale. Downstream drift of infected collembolans could be one of the mechanisms facilitating this (see Schuppenhauer *et al.* 2019). Further research is needed to confirm if this mode of transport is of significance.

Besides using collembolans, *P. thienemanni* is not known to occasionally resort to other, winged hosts with better dispersal abilities. However, usage of other hosts cannot be ruled out, since studies on the species are very limited.

The two only known populations *of P. thienemanni* in the Netherlands appear to be isolated. Directly downstream from the study site, the hydrologic condition of the headwater deteriorates, with dry banksides without groundwater discharge due to groundwater regulation. Consequently, settlement after dispersal further downstream seems highly unlikely. The isolated Dutch populations of *P. thienemanni* might therefore be surviving relicts of the once more widespread forested and undrained headwater systems. Currently restoration measures are in progress at both sites to increase discharge of seepage (Duursma 2020; Zekhuis 2020).

Acknowledgements

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