



Original article

The life cycle, population dynamics, and contribution to litter decomposition of *Penthetria holosericea* (Diptera: Bibionidae) in an alder forest



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ABSTRACT

Soil sampling and pitfall traps were used to monitor *Penthetria holosericea* larvae and adults at approximately monthly intervals during 2001 in an alder forest near Cesky Krumlov (Czech Republic). Adult flies were detected only in late May and early June. The distribution of larval head widths indicated that there were seven larval instars and that the larvae spend most of their lives in the 6th instar. The mean (\pm SD) annual larval density was 140 ± 485 ind. m^{-2} , and the mean annual larval biomass was 0.56 ± 0.37 g (dw) m^{-2} . Larval abundance peaked in June (1078 ind. m^{-2}), and larval biomass peaked in August (1.3 g m^{-2}), which was before maximum litter fall in September and October. Larval food consumption relative to body mass was negatively correlated with body mass. Based on larval biomass and laboratory measurement of litter consumption, the annual consumption of litter by *P. holosericea* was estimated to be 137 g (dw) m^{-2} , which represents about 40% of the annual litter fall.

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1. Introduction

Substantial research has indicated that the maintenance of ecosystem functions depends on keystone species or particular functional groups [1,2]. It follows that a better understanding of the ecology of keystone species and the dominant species of important functional groups will increase our understanding of ecosystem functioning [3]. Despite this, the autecology of many dominant species representing important functional groups of soil organisms is underexplored.

The litter-transforming soil macro-arthropods are functionally important in some ecosystems [4,5]. They fragment litter and transform it into fecal pellets that form an important part of the soil profile [5]. This functional group includes diplopods, terrestrial isopods, and the larvae of certain insects (mainly dipterans) [4]. Among dipterans, bibionid larvae are important litter fragmenters [6–8] and are abundant in many ecosystems [9,10]. In the process of transforming litter into fecal pellets, bibionid larvae alter the

litter's chemical composition, microbial community, and rate of decomposition [6,11–16]. Some bibionid larvae may be pests of grasses and field crops [17].

Bibionidae are clearly important and although the morphology of the larvae has been well described [18,19], the life cycles and population dynamics of dominant bibionid species are poorly known. This is particularly true for the saprophagous larvae of *Penthetria holosericea* (Diptera: Bibionidae), even though many details concerning the physiology of its litter transformation and its interaction with soil microorganisms are known [13,14,20]. In this study, we describe the life cycle and population dynamics of *P. holosericea* in an alder forest. We also determine the rate at which larvae consume alder litter in a laboratory experiment. The data are then used to estimate the annual consumption of alder litter by *P. holosericea* larvae. We postulate following hypothesis: 1) larval mass specific consumption and assimilation efficiency will decrease with increasing body mass, as a consequence peak of consumption appear before peak of larval biomass 2) larval phenology will be synchronized with litter quality and the youngest larvae will use litter with the low CN ration and phenolic content. 3) bibionid larvae consume larger proportion of litter fall than is given in literature for millipedes.

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2. Materials and methods

2.1. Study site

The study was conducted in an alder (*Alnus glutinosa*) forest surrounding Kremelna Stream near Cesky Krumlov (48.8919053°N, 14.3376031°E), 470 m a.s.l., mean annual temperature 7 °C, mean annual precipitation 644 mm. The forest consists of mature alder trees that border the stream in a band that is about 50 m wide and 400 m long. The sandy soil contains gravel and was formed by alluvial deposits. In addition to *P. holosericea*, several species of millipedes and the isopod *Ligidium hyphorum* dominate the litter-fragmenting macroarthropods in this forest.

2.2. Sampling and processing of *P. holosericea* and leaf litter

In 2001, soil was sampled at approximately monthly intervals from February to November (20.Feb., 22.Mar., 26.Apr., 30.May., 13.Jun., 27.Jun., 24.Jul., 10.Aug., 13.Aug., 10.Sep., 4.Oct., 10.Oct., 4.Nov., 7.Nov., and 10.Nov.2001). On each sampling date, five circular soil samples (area 625 cm², depth 10 cm) were taken. Samples were transported to the laboratory and immediately extracted in a modified Tullgren apparatus [9]. The extracted organisms were fixed in 2% formaldehyde and then transferred into 80% ethanol. Larvae of *P. holosericea* were separated and examined with an eyepiece-mounted micrometer fitted to a stereomicroscope; body length and head width were measured to within 0.1 mm and 20 μm, respectively. The larvae were then dried at 60 °C for 24 h and weighed on an analytical balance (Sartorius Research R200D) to the nearest 0.1 mg. Very small larvae (<5 mm long) were pooled into groups of 3–5 larvae of the same size before they were weighed. If the sample contain 5 larvae or less all larvae were weighted, in larger samples 25% of larvae were weighted.

As the adults do not occur in soil but mainly exist on the litter surface and ground vegetation, pitfall traps was used to record the adults. On 20 February 2001, five pitfall traps filled with a solution of 10% glycerin and 8% formaldehyde plus a drop of detergent were deployed in the forest. On the same dates as indicated for soil sampling in the previous paragraph, the arthropods in the pitfall traps were collected, the solution in each pitfall trap was replaced, and the arthropods were transported to the laboratory where the *P. holosericea* larvae and adults were counted. Five randomly selected female adults from pitfall traps were dissected and the wing length was measures in similar way described for larval heads above. The abdomen was opened and number of eggs was counted.

Five litter traps were deployed in the forest on march Month 2001 after the snow melt Each litter trap consisted of a screen mounted in a wooden frame; the screen openings were 0.5 × 0.5 mm, and the screen area 0.25 m². The screens were horizontally oriented and located 50 cm above the soil surface in the same areas where the soil was sampled and the pitfall traps were placed. The litter on each litter trap was collected in the same terms as soil was sampled. The collected litter was dried at 60 °C for 24 h, weighed, and ground into a powder. Total carbon (C) and total nitrogen (N) content in the litter were determined using a Carlo Erba CNH elemental analyzer. The lignin content of the litter was determined as the fraction that remained undissolved in 72% H₂SO₄ (the Klason lignin method). Total soluble phenolics were extracted by methanol and quantified spectrophotometrically using Folin-Ciocalteu reagent [21].

2.3. Laboratory feeding experiment with *P. holosericea* larvae

Living *P. holosericea* larvae were collected by hand when the soil was sampled from June, till October of 2001 which means during

whole season where larvae were present in field. The larvae were placed in boxes with litter and were transported to the laboratory. The larvae collected on each sampling date were measured, and groups of three larvae of similar size were placed in each of three 5-cm-diameter Petri dishes. Each dish also contained about 1 g of moist, decomposing litter collected in the field. Field-moist litter was used because drying and rewetting of litter may affect its consumption by soil arthropods [22]. The dry weight of the added litter was determined with a separate sample. The Petri dishes containing larvae and litter were kept at 15 °C in the dark. After 1 week, the fresh weights of the remaining litter, of the larvae, and of larval feces were determined. The remaining litter, the feces, and larvae were then dried at 60 °C for 24 h and weighed. The C and N content of the litter was then determined as described earlier. This was done repeatedly in each sampling occasion.

2.4. Data processing

To estimate the number of instars for *P. holosericea* in the sampled alder forest, histograms for larval length and head width were plotted. The highest peaks in the histogram were assumed to be medians of individual instars. If peaks were close together, we determined whether the increment in size was significantly smaller than increments in the previous instars. If the increment was smaller, we assumed, based on Dyar's law [23], that the peak was formed by outliers of the previous instar.

Larval weight on each sampling date was calculated based on larval length of larvae from soil samples and on relationships between body mass and body length. Body length was plotted on body weight, and the data were assessed by nonlinear regression using Statistica 10.0; linear logarithmic and exponential functions were tested, and the function with the best fit was selected. The biomass of larvae per m² on each sampling date was calculated by multiplying larval population density and average body mass. To estimate litter consumption per g of larva in the laboratory, the dry weight of the litter consumed per dish (litter at the beginning minus litter at the end) was divided by the mean dry mass of the larvae. This was expressed as a daily rate by dividing by 7 days (the duration of the assay) and was expressed per g of larval biomass by dividing by larval biomass on that sampling date. Assimilation was calculated by subtracting the dry weight of feces from the dry weight of consumed litter and was expressed per g of larval mass per day. Relationships between body mass and the rate of mass-specific food consumption (g of litter consumed per g of larva per day) was fitted by nonlinear regression using Statistica 10.0; linear, logarithmic, and exponential functions were tested, and the function with the best fit was selected. Food consumption in the field was estimated by multiplying larval biomass per m² by the rate of mass-specific food consumption; this was estimated based on the average mass of individual larvae on each sampling date and the regression between body mass and the rate of mass-specific food consumption, for all summer dates we used equation based on filed survey in this study, in winter months data was temperature corrected based on [24].

Daily consumption (DC) of litter by larval population was calculated as follows:

$$DC = (a * msl + b) * LB * SC.$$

where msl is average mass of one larva in given time, a and b are coefficients of empirical equation that determine relationship between size (mass) of larvae and mass specific litter consumption, which will be determined in this study. LB is larval biomass in g m⁻² calculated as larval density multiplied by average mass of single larva ld*msl. SC is seasonal coefficient which is 1 for spring to

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