Diurnal epigeic activity of terrestrial isopods (Isopoda: Oniscidea)

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Abstract

Diurnal epigeic activity of woodlice in a floodplain forest and nearby clear-cut areas was studied during late spring and early autumn of 2005 by pitfall trapping technique. A total of 100 traps was being checked every three hours. In total, 6 species of isopods were trapped, but only *Trachelipus rathkii* and *Protracheoniscus politus* were found being dominant. The species *P. politus* and *Porcellium conspersum* showed specific significant patterns of their epigeic activity depending on day-time.

Keywords – circadian rhythm, diel activity, floodplain forest, woodlice

Introduction

Soil is inhabited by a huge number of invertebrate species. For these species, the soil fauna, the soil represents a refugium. Out of the soil, the environment is less suitable for them: there is too much light, and humidity and temperature are rather unstable. For these reasons, many species of the soil fauna show specific patterns of epigeic activity – they are more active during periods of time with more favourable conditions, i.e. during spring and autumn in an annual rhythm and/or during night in a diurnal rhythm.

Circadian rhythms of epigeic activity have been recognised not only for surface-dwelling animals that adjust their activity to the prevailing light conditions, but also for troglobiotic species that live in a constantly dark environment (Koilraj *et al.*, 2000). Generally, woodlice mainly show epigeic activity during the night (Cloudsley-Thompson, 1959) with various exceptions, for example twilight activity (Ammar & Morgan, 2005). According to Cloudsley-Thompson (1952), the diurnal epigeic activity is primarily correlated with light-dark changes, but not with other conditions (humidity, temperature) that may change over the course of the day, although there are intrinsic physiological mechanisms (a kind of timer) for the maintenance of a rhythm in permanent darkness, too (Cloudsley-Thompson, 1956a). This intrinsic timer is apparent in behaviour of *Hemilepistus reaumurii* (Milne-Edwards 1840), but not of *Oniscus asellus* Linné 1758 (Cloudsley-Thompson, 1952). An endogenous timer was found to control activity in *Armadillidium vulgare* (Latreille 1804) (Smith & Larimer, 1979), and its development during ontogenesis was described for *Tylos granuliferus* Budde-Lund 1885 (Ondö, 1954).

Besides light, other environmental stimuli have been investigated for their ability to control diurnal rhythms of woodlice. The most important of them for starting locomotory activity are humidity (Paris, 1963; Ilosvay, 1982) and temperature (Cole, 1946). Air temperature has been recognised as important for epigeic activity of myriapods, too (Banerjee, 1967; Tuf *et al.*, 2006). Probably the most interesting trigger for activity has been studied by Moore (1983), who found that *A. vulgare* infected by an acanthocephalan parasite is more active, runs farther and rests less time than non-infected ones.

Diurnal epigeic activity of terrestrial isopods, an ecologically significant element of the epigeic macrofauna, was studied in a floodplain forest and nearby clear-cut areas during spring and autumn.

Material and Methods

The locality is situated in the Litovelské Pomoraví Protected Landscape Area, a natural landscape surrounding the meandering Morava river (Central Moravia, Czech Republic) by a

Table 1. Diurnal epigeic activity of terrestrial isopods during late spring (May-June) and early autumn (September-October). Catches of individuals by 60 traps during 18 days at different times of the day (3:00 means that animals were caught from 0:00 to 3:00), grey columns mark night time.

Spring	Forest							
	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00
Ligidium hypnorum (Cuvier, 1792)	-	-	-	-	-	-	-	1
Hyloniscus riparius (C.L. Koch, 1838)	1	-	1	1	-	-	-	-
Trichoniscus pusillus Brandt, 1833	-	-	-	-	-	-	-	-
Porcellium conspersum (C.L. Koch, 1841)	-	-	8	7	7	2	1	1
Protracheoniscus politus (C.L. Koch, 1841)	7	14	14	8	1	-	3	5
Trachelipus rathkii (Brandt, 1833)	1	1	1	-	-	-	-	1

Autumn	Forest							
	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00
Ligidium hypnorum (Cuvier, 1792)	0.7	1.4	1.4	0.7	-	0.7	-	2.2
Hyloniscus riparius (C.L. Koch, 1838)	-	-	-	-	-	-	-	-
Trichoniscus pusillus Brandt, 1833	-	-	-	-	-	-	-	-
Porcellium conspersum (C.L. Koch, 1841)	-	-	-	-	-	-	-	-
Protracheoniscus politus (C.L. Koch, 1841)	1.4	1.4	2.2	-	-	-	3.6	0.7
Trachelipus rathkii (Brandt, 1833)	7.9	7.9	5.8	2.2	2.9	0.7	8.6	9.4

Spring	Clear-cut							
	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00
Ligidium hypnorum (Cuvier, 1792)	7.5	1.5	3	-	-	-	3	3
Hyloniscus riparius (C.L. Koch, 1838)	-	3	-	-	-	-	-	-
Trichoniscus pusillus Brandt, 1833	3	-	-	-	-	-	-	-
Porcellium conspersum (C.L. Koch, 1841)	-	1.5	-	-	-	-	-	-
Protracheoniscus politus (C.L. Koch, 1841)	-	-	1.5	-	-	-	-	-
Trachelipus rathkii (Brandt, 1833)	4.5	4.5	3	-	-	1.5	-	4.5

Autumn	Clear-cut							
	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00
Ligidium hypnorum (Cuvier, 1792)	1.1	-	1.1	-	-	-	-	-
Hyloniscus riparius (C.L. Koch, 1838)	-	-	-	-	-	-	-	-
Trichoniscus pusillus Brandt, 1833	-	1.1	-	-	-	-	-	-
Porcellium conspersum (C.L. Koch, 1841)	-	-	-	-	-	-	-	-
Protracheoniscus politus (C.L. Koch, 1841)	-	-	-	-	-	-	-	-
Trachelipus rathkii (Brandt, 1833)	2.2	4.3	6.5	4.3	3.2	-	3.2	4.3

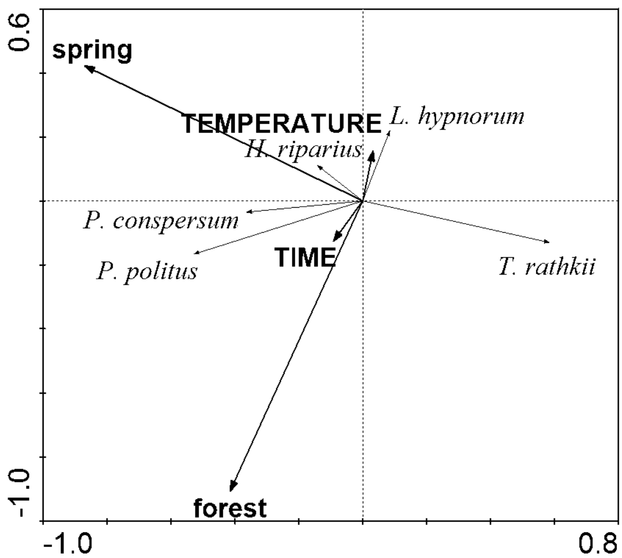

Figure 1. RDA ordination plot, showing epigeic activity of woodlice species in relation to habitat (*forest vs. clear-cut*), time of the day (*time*), season (*spring vs. autumn*), and *temperature*. For description of model and significance of environmental variables see Tabs 2 and 3.

Table 2. Summary of the explained variability of RDA plot

Axis	**1**	**2**	**3**	**4**
Eigenvalues	0.242	0.020	0.009	0.000
Species–environment correlations	0.692	0.302	0.220	0.080
Cumulative percentage variance of species data	24.2	26.2	27.1	27.1
Cumulative percentage variance of species–environment relation	89.2	96.7	99.9	100.0

Sixty traps were spread over the forest habitat, whereas 40 traps were placed in a clear-cut area in transect lines with three meters distance spacing. The experiment was carried out in late spring (May 20th to June 7th, 18 days) and early autumn (September 23rd to October 18th, 25 days) 2004. The traps were checked every three hours during these seasons (i.e. at 3.00, 6.00, 9.00, 12.00, 15.00, 18.00, 21.00, and 24.00). Soil surface temperature was measured in both localities using data-loggers Minikin TH (Environmental Measuring Systems Brno, www.emsbrno.cz). Redundancy Analysis and Generalised Additive Models for the evaluation of results were created using the software CANOCO for Windows 4.5© (ter Braak & Šmilauer, 1998), the illustrations were created in CanoDraw for Windows 4.0©. The model was evaluated using Monte-Carlo permutation tests (4999 permutations).

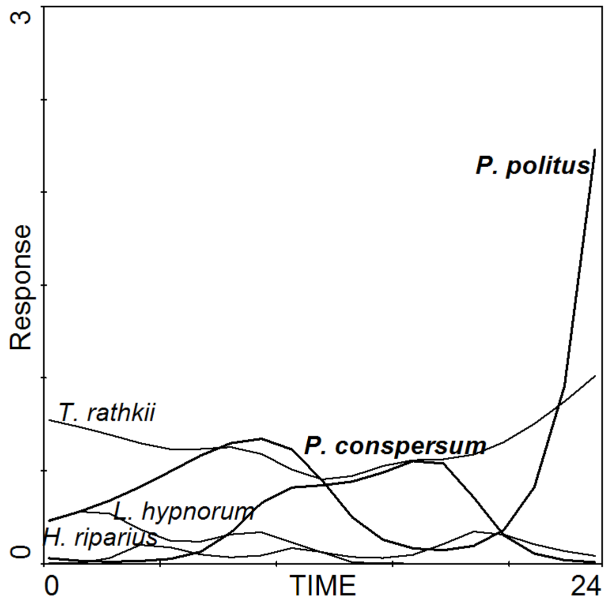

Figure 2. Epigeic activity (Response) of terrestrial isopod species in relation to time of the day. For significance of model for individual species see Tab. 4.

Results

In total, 231 individuals of six species of terrestrial isopods were trapped. Dominant species were *Trachelipus rathkii* and *Protracheoniscus politus*.

Terrestrial isopods were mostly active throughout the day at both seasons and localities. However, in the clear-cut area during spring, woodlice were not active from 9.00 to 15.00 (Tab. 1). Individual species showed this pattern of behaviour generally too, although there were several exceptions. *Ligidium hypnorum* and *T. rathkii* were active during night and twilight in spring, *P. politus* was active during twilight mainly, and *Porcellium conspersum* was active mainly during the day in spring. A comparison of activity at different sites shows that *P. politus* and *P. conspersum* were active mainly in the forest and *L. hypnorum* and *Trichoniscus pusillus* were active mainly in the clear-cut area. During spring, higher numbers of isopods were caught than in autumn (131 vs. 93 ind. caught into 60 traps during 18 days), and this pattern was most evident in the catches of *P. conspersum* that was not found in autumn. The dominant species, *T. rathkii*, was more active in autumn.

RDA (Fig. 1, Tab. 2) was significant (first axis $F = 50.457$, $p = 0.0002$; all axes $F = 14.705$, $p = 0.0002$) and explained 27 % of species data variability. The most important environmental variables were the nominal variables season (*spring*) and locality (*forest*). *Time* was significant but less important, and *temperature* was not significant, albeit only marginally not so (Tab. 3). Similar results were obtained in other analyses, when excluding the variables *temperature* or *time*; in the latter case, *temperature* proved significant.

Table 4. Significance of time of the day for epigeic activity of terrestrial isopod species.

species	Deviance	F	P	AIC
L. hypnorum	91.32	1.35	0.239966	105.165
H. riparius	29.63	1.85	0.110987	36.470
P. conspersum	91.04	5.00	0.000131	106.328
P. politus	145.24	2.72	0.017544	158.257
T. rathkii	159.53	0.532	0.221699	172.308

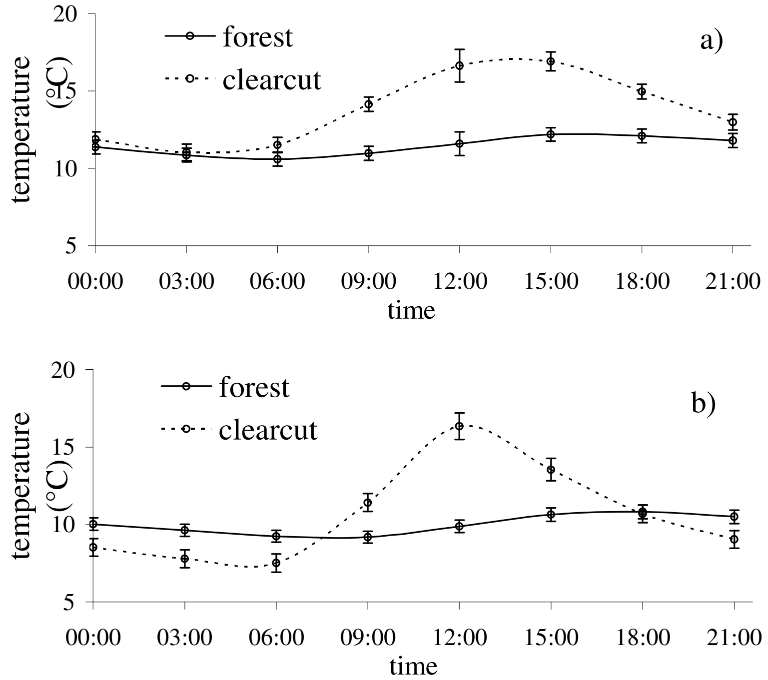

Figure 3. Mean temperature regime during the study period: a) late spring (May-June 2005), b) early autumn (September-October 2005) (mean ± SE).

As the models for individual species (*T. pusillus* was excluded for low number of individuals) shows, time of the day is an important factor to influence epigeic activity of *P. politus* and *P. conspersum* (Fig. 2, Tab. 4). *P. politus* was most active before dusk and after dawn, whereas, oppositely, *P. conspersum* was most active during the day. The activity of *P. politus* was highest in the forest in spring; from 6.00 to 12.00, the temperature was slowly increasing (Fig. 3). The major activity of *P. conspersum* was measured in the forest in spring from 10.00 to 17.00, i.e., during increasing temperature, too.

Table 3. Significance of environmental variables in RDA model to prediction of activity of woodlice

Variable	Var.N	LambdaA	P	F
spring	3	0.19	0.000	37.02
forest	4	0.06	0.000	13.10
time	2	0.01	0.049	2.48
temperature	1	0.01	0.053	2.44

We observed –albeit non-significant– differences between sexes for *T. rathkii* and *P. politus*. Thus, females of *P. politus* were active at a mean temperature 11.2 ± 2.0 °C, whereas males were active at a mean temperature of 10.5 ± 2.2 °C; *T. rathkii* females at 10.8 ± 2.3 °C and males at 10.4 ± 3.0 °C. A bigger difference (non-significant though) was evident between the activities of gravid and non-gravid females of *P. politus* (gravid at 11.9 ± 2.1 °C vs non-gravid at 10.8 ± 1.9 °C).

Discussion

Terrestrial isopods lose water by transpiration through their entire integument (Gunn, 1937), and their responses to humidity (hygrokinesis) are controlled by the intensity of dessication (Waloff, 1941). To avoiding dessication, they stay in damp and humid environment under stones, fallen leaves, logs or bark or in crevices in soil during daytime. They leave these habitats during night when temperature falls and relative humidity increases (Cloudsley-Thompson, 1959). The most desiccating species are the most photonegative ones, with strict nocturnal activity. Thus, among e investigated species were likely of *Philoscia muscorum* (Scopoli 1763), *O. asellus*, *Porcellio scaber* Latreille 1804 and *A. vulgare*, *P. muscorum* is the most nocturnal one and *A. vulgare* the least (Cloudsley-Thompson, 1956b).

The typical duration of activity is about one hour for *P. scaber* (den Boer, 1961). In shelter, woodlice absorb water from air humidity through their cuticle, that is lost again after leaving shelter. Within about one hour, they lose a critical amount of water (Waloff, 1941; Edney, 1951) and they must hide in shelter with higher relative air humidity again.

The majority of the recorded variability in activity of woodlice was explained by habitat type (forest *vs* clear-cutt) and season (spring *vs* autumn). An influence of these factors is not surprising, differences between densities of woodlice in different biotopes are well known (e.g. Farkas *et al.*, 1999), and their changes in abundances and activity during year are well known, too (e.g. Hornung & Warburg, 1995; Zimmer & Brauckmann, 1997). Nevertheless, beside these factors, time of the day is significant, too. Thus, *P. politus* was mainly active in twilights and in the morning. The activity of this has also been studied in Hungarian beech forests in summer (Ilosvay, 1982). Although several specimens were caught during daytime, the peaks of activity were at dusk and at midnight at a humidity of 75-80 %. Based on big catches in forests during winter, Ilosvay (1982) supposed that temperature is not an important factor for their activity. According to our results, too, time of the day was more important than temperature for the activity pattern of this species. Its activity before dusk and in the morning could be related to higher air humidity on the soil surface due to dew, as its activity started with increasing of temperature. *Porcellio scaber* was active after dusk and before dawn, i.e. at times of highest relative air humidity (lowest saturation deficit respectively), too (den Boer, 1961).

The other species with a significant diurnal pattern of activity was *P. conspersum* with strict daylight activity. According to the argumentation that *A. vulgare* is more resistant to desiccation than other species (Edney, 1951) and that it is active in the morning hours (Cloudsley-Thompson, 1951), we conclude that *P. conspersum* is most resistant to dessication of the species found. This species shows a primitive level of volvation. Its activity occurred at temperatures of ca 15 °C, recorded during the warmest spring days in forest, similar to midday wandering of *H. reaumurii* during winter months, when temperature and humidity are suitable at noon (Ammar & Morgan, 2005). Similarly, a positive correlation between temperature and horizontal activity was found for *P. scaber* (den Boer, 1961).

Temperature and locomotory activity relation can be a clue for an explanation of lower catches in autumn than in spring. Paris (1965) studied locomotory activity of *A. vulgare* in summer and winter in California. He found that woodlice were more active in summer (they walked 13 m per 12 hours) than in winter (10 m per 6 days), probably due to differences in temperature; the lowest temperatures in both seasons in California were comparable with temperatures measured by us. Occasional prolongation of this species' activity from night to morning was caused by high humidity during nights (Paris, 1963).

Low catches of some species were probably caused by their generally low epigeic activity, inhabiting upper soil layers (family Trichoniscidae). Other species can be sedentary. For example, Brereton (1957) re-caught tagged specimen of *P. scaber* on the same tree after six months. Another interesting observation related to low numbers of isopods is the evidence for that individual woodlice are not active every night (or day, respectively), as documented by den Boer (1961) through marking of *P. scaber* specimens.

The females of dominant species were active at higher temperatures than males, and gravid females of *P. politus* were more active at the higher temperatures that those non-gravid. Although these differences were not significant, they seem to be plausible, because the developmental time of the brood is affected by temperature. Dangerfield & Hassall (1994) found female-biased sex ratios under a cryptozoic board (with higher temperature than in soil) for *A. vulgare* and *P. scaber*. The activity of gravid females of *P. politus* in our study can be a result of their tendency to search actively for sites with more favourable conditions for brood development.

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