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RESEARCH

Diurnal activity of terrestrial arthropods in the High Arctic

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Abstract

At high latitudes, where the sun does not set over the horizon for a significant part of the summer, living organisms cannot regulate diurnal rhythms on the basis of photoperiod. In such regions, are other factors acting as zeitgebers or are the animals in these regions arrhythmic? The objectives of this study were to determine whether diurnal rhythms of locomotor activity are pronounced in model groups of terrestrial arthropods under natural conditions of constant light and to determine whether factors such as light, temperature, humidity, and wind influence this activity. Using pitfall traps, we have studied the diurnal activity of springtails, soil mites, dipterans, spiders, and beetles on Shokalsky Island, Kara Sea, Western Siberia (72.92°N 74.33°E). It was revealed that the continuous light regime in the Arctic does not eliminate the daily periodicity of activity of terrestrial arthropods. Periodicity was observed both at the whole community level and at the level of model groups and species. For the majority of the taxa studied, there was a daily peak of activity that occurred in the first half of the day. The general rhythm observed in different taxonomic groups indicates that the activity is regulated by some external factors. Although the rhythms identified apparently correlate with light level, temperature, and thermal preference, it remains difficult to determine the leading factor driving activity in the field.

Keywords Polar day · White night · Spiders · Springtails · Diurnal rhythms · Thermal preference

Introduction

Diurnal (circadian) rhythms are characteristic of all living organisms and are detected as fluctuations with a period of approximately 24 h at the level of populations, organisms, organs, or cells that persist in the absence of external signals (Aschoff 1960; Danilevsky et al. 1970; Tyshchenko 1977; Cloudsley-Thompson 1987, 2000; Jones et al. 2018; Mah et al. 2020). Of the variety of circadian rhythms, the dynamics of locomotor activity (mobility, flight) have been best studied. The main reason for this appears to be the relative ease of its registration (Aschoff 1960; Daan and Aschoff 1975; Cloudsley-Thompson 1987). The diurnal rhythms of activity have been registered in mammals, birds, amphibians, insects, arachnids, and other animal groups (Dondale et al. 1972; Daan and Aschoff 1975; Seyfarth 1980; Dolmen 1983; Nakamuta 1987; Cloudsley-Thompson 2000; Chiu et al. 2010; Vazquez et al. 2019). The distribution pattern of diurnal activity is one of the most important features of animal behavior that is relevant to a number of ecological and physiological phenomena (Nakamuta 1987; Ortega et al. 1992; Bayram 1995; Ortega-Escobar 2002; Vazquez et al. 2019). For example, differentiation of daily activity can contribute to the segregation of ecological niches in species of similar life forms living in the same biotope, as was shown on springtails of the Taimyr Peninsula *Corynothrix borealis* (Tullberg, 1877) and *Isotoma* sp. (Babenko 1993). In summer, in the semi-desert of the northern cis-Caspian region, where the amplitude of daily temperature fluctuations is very large, diurnal vertical migrations of chortobiont spiders and weevils make it possible to avoid unfavorable environmental factors and reduce intraspecific competition (Mikhailov 1985; Piterkina 2006; Khruleva et al. 2012).

In most terrestrial animals, the activity is regulated by the endogenous circadian clock (Nakamuta 1987; Suter 1993; Ortega-Escobar 2002; Jones et al. 2018; Vazquez et al. 2019). The mechanism of the circadian clock is usually studied in the laboratory under controlled temperature and

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light conditions, as these factors are attributed the leading role in synchronizing circadian rhythms with the environment (Aschoff 1960; Vazquez et al. 2019). However, the uniformity of laboratory conditions can become a source of distortions in actual behavior (Vanin et al. 2012; Helm et al. 2017). Studying organisms in natural environments, where their behavior is subject to stimuli that cannot be accounted for in laboratory (Helm et al. 2017), can improve the predictability of the responses of organisms and communities to environmental changes. Arctic communities can be convenient natural laboratories for conducting this kind of experiments. The environmental parameters here go beyond what is considered normal for most organisms, making abiotic factors decisive (Danks and Oliver 1972; Chernov 2008a, b). Additionally, the relative simplicity of community organization makes it easier to establish cause-and-effect relationships. Despite this, it remains unclear how circadian activity manifests itself under these conditions.

The main signaling factor that stimulates seasonal and diurnal rhythms is attributed to photoperiod (Danilevsky 1961; Danilevsky et al. 1970; Tyshchenko 1977; Denlinger et al. 2017). It would be logical to assume that the photoperiodic response is of less importance in circumpolar regions where the sun does not set over the horizon for much of the summer. At the same time, high-latitude inhabitants have a unique opportunity to compensate for the short duration of the warm season by maintaining continuous activity under conditions of constant light. Thus, the seasonal lack of daily rhythmicity in Svalbard ptarmigan (*Lagopus muta hyperboreus* (Sundevall, 1845)) (Reierth and Stokkan 1998) and in the subspecies of reindeer (*Rangifer tarandus platyrhynchus* (Vrolik, 1829) and *R. t. tarandus* L.) are seen as the adaptations to polar day and polar night (van Oort et al. 2005). Yet, there are cases that are just the opposite. Black-capped marmots (*Marmota camtschatica bungei* Katschenko, 1901) and arctic ground squirrels (*Urocitellus parryii* Richardson, 1825) maintain daily rhythms of behavior and physiology under polar day conditions, presumably thereby minimizing the costs of thermoregulation (Semenov et al. 2001; Williams et al. 2012, 2017).

Results from the studies of terrestrial arthropods are also inconsistent. When studying the activity of springtails under polar day conditions on Disko Island (West Greenland), a distinct increase in the activity of *Sminthurides malmgreni* (Tullberg, 1877) during the daytime was observed (Kristensen and Vestergaard 1975). Similar studies in Svalbard revealed acyclic behavior in this species, as well as in *Ceratophysella longispina* (Tullberg, 1877) (listed as *Hypogastrura hirsuta* Valpas, 1967), while the other seven species of springtails had "definite periodicity" (Solem and Sendstad 1978). Arrhythmic behavior was also detected in the ground beetle *Carabus violaceus* L. occurring beyond the Arctic Circle when its specimens were kept on a polar day in natural light conditions (Hempel and Hempel 1955). However, in a later similar experiment, opposite results were obtained (Neudecker 1971). The identified cases of arrhythmia in beetles and springtails, in our opinion, are probably an artifact provoked by the irregularity of food and water intake in the first case (Hempel and Hempel 1955) and a change in methodology in the second year of study in the latter (Solem and Sendstad 1978).

In Lapland, bumblebees (Stelzer and Chittka 2010) and spiders (Koponen 1972) showed stable diurnal rhythms of activity on a polar day, with a maximum around noon and a minimum at night. There is at least one study describing the diurnal dynamics of the whole complex of chortobiont invertebrates (at least its main groups) at high latitudes (Chernov and Rudenskaya 1975). The authors demonstrated that distinct vertical diurnal migrations of various invertebrates (springtails, oribatid mites, true flies, grasshoppers, spiders, beetles, etc.) in grass, as well as unique features of these rhythms in individual species, occurred in all natural zones from deserts to tundra. Yet, the maximum increase in activity usually shifts to night time, even under constant light conditions (Chernov and Rudenskaya 1975). It is worth mentioning that the objects of the latter study were chortobiont invertebrates and their vertical migrations, while the objects of the previously listed works were herpetobiont invertebrates and their horizontal movements. This probably explains the difference in the results obtained.

The following papers have considered humidity, temperature, and/or light levels among the putative causes of diurnal phenomena under polar day conditions. It has been repeatedly emphasized that the light level on a polar day during the day, even in sunny weather, differs by orders of magnitude, and the diurnal variation in ambient temperature is no less significant for poikilothermic animals (Syrjämäki 1968; Kristensen and Vestergaard 1975; Solem and Sendstad 1978; Babenko 1993; Chernov and Matveyeva 1997; Stelzer and Chittka 2010). Relative humidity also fluctuates throughout the day, with its course reversing that of temperature (Kristensen and Vestergaard 1975). Its dynamics presumably stimulates vertical migrations of chortobiont invertebrates (Chernov and Rudenskaya 1975) and is considered one of the possible mechanisms determining niche segregation in springtails (Babenko 1993). A synergy of several factors cannot be ruled out (Babenko 1993; Solem and Sendstad 1978; Stelzer and Chittka 2010). Yet, all these assumptions have not been statistically confirmed in any of the aforementioned studies.

The majority of these papers put the emphasis on just one taxonomic group sharing similar ecological preferences, and yet the ambiguity of the findings prompted us to conduct our own study. The aim of the present study is to determine the extent to which diurnal rhythms of locomotor activity are expressed in model groups of terrestrial arthropods under natural conditions of constant light and to determine whether environmental factors influence this activity. The most common and abundant groups of terrestrial arthropods in the (sub)Arctic—springtails, soil mites, dipterans, spiders, and beetles—were chosen as model groups (Danks 1981; Chernov 1992, 2002; Chernov et al. 2014; Potapov et al. 2023). Pitfall traps were chosen as the primary collecting method, which is recognized as universal for collecting herpetobiont invertebrates (reviewed by Skvarla et al. 2014). Such traps are also used in polar landscapes as a primary or supplementary method of recording mass Diptera families (e.g., Standen 2000; Greenslade et al. 2012; Sorokina and Khruleva 2012; Shamshev et al. 2020; Stur and Ekrem 2020), since representatives of many "flying" taxa are represented here by brachypterous and wingless forms due to limited opportunities for active flight (Roff 1990; Chernov and Makarova 2008). Many mite species (e.g., oribatids of the families Ceratozetidae and Ameronothridae or the prostigmata of the family Rhagidiidae) reach high numbers in Arctic landscapes and mainly on soil surface or in moss-lichen cushions (Makarova 2000; Søvik 2004; Zacharda and Kučera 2006, 2010; Gudleifsson and Bjarnadottir 2008; Fischer et al. 2016; Ermilov et al. 2019; Bizin et al. 2021); they are easily captured by pitfall traps as well. Finally, pitfall traps were used by our predecessors when recording the daily activity of springtails (Kristensen and Vestergaard 1975; Solem and Sendstad 1978; Babenko 1993) and spiders (Koponen 1972), thereby allowing us to compare the results obtained. The effectiveness of pitfall traps is determined by both animal activity and population density, the latter of which can be considered constant over a short period of time. Therefore, the number of animals caught by pitfall traps was adopted as an indication of their activity (Kristensen and Vestergaard 1975; Gudleifsson and Bjarnadottir 2008).

A specific protocol was developed for this study (see "Materials and Methods" and Online Resource 1 for a detailed description), following which continuous daily activity counts of model groups of terrestrial arthropods were conducted. Several major factors that are thought to be responsible for the existence of rhythms have been recorded in parallel. These factors included both the "obvious" ones, such as light, temperature, humidity, and the less evident ones, such as wind. Accounting for the latter factor was necessary to rule out its involvement in the increase in the number of individuals in traps as a result of passive transfer. This study is the first to consider simultaneously several groups of the Arctic's most abundant and diverse terrestrial invertebrates. Therefore, two hypotheses have been tested here: (1) the entire community, as well as model groups and dominant terrestrial invertebrate species, adhere to a circadian periodicity in their activity when there is no alternation of day and night and (2) the observed periodicity is related to environmental factors.

Materials and methods

Study region

Shokalsky Island (72°58′ N, 74°27′ E) is located in the southern part of Kara Sea, to the north of Yavai Peninsula, representing the northwestern point of Gyda Peninsula (Fig. 1a). The entire territory of the island and the adjacent mainland territories belong to the Gydansky National Park. The average annual temperature here is between −10 °C and −12 °C, and the mean temperature of the warmest months (July and August) is + 5 °C; the snowless period lasts from 55 to 70 days (Kalyakin et al. 2000). The island lies in the northern part of the Arctic tundra subzone (Yurtsev 1994). The vegetation is mostly represented by the willow-shrub-moss, sedge, and cotton-grass tundras (Rebristaya 2002). There is a prominent strip of marshes on the seaside accumulative plain. A more detailed description of the study area

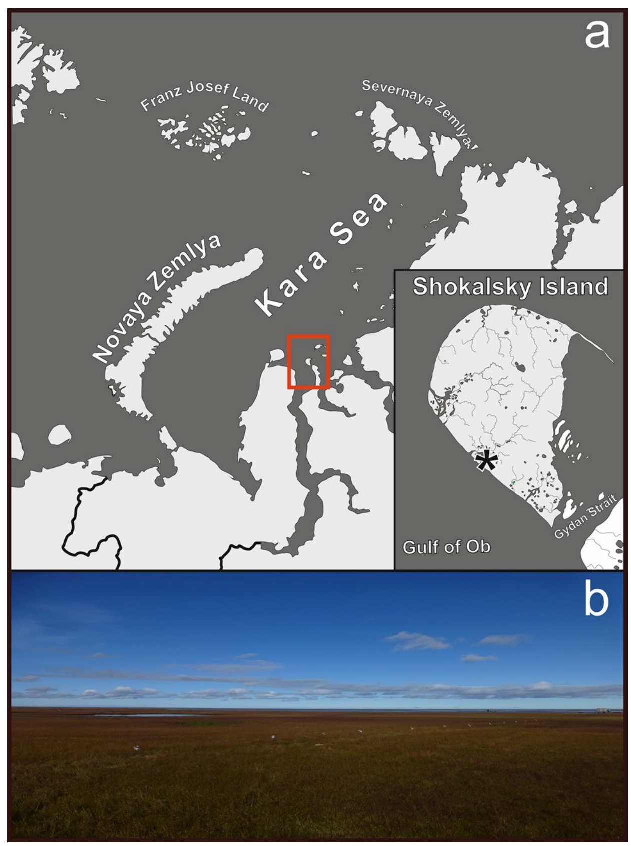

Fig. 1 Studied locality: **A** Map of Kara Sea region with the position of Shokalsky Island. The study region is marked with an asterisk. **B** Experimental site on the sea marsh

is given in the papers on the beetle and spider fauna of the island (Makarov et al. 2018; Nekhaeva 2018).

Experimental Site

The work was conducted on the sea marsh in the Pereprava river delta (Fig. 1b). The flat sea coast is flooded during the highest tides, storms and water level fluctuations caused by long-lasting winds. During our stay on the island (23 days), this happened once. For this reason, the experimental site was situated on the furthest part of the seashore away from the sea (approximately 250 m from the sea and 150 m from the river). The plant association on the experimental site was formed predominantly by meadow-grass (*Poa* sp.) and tussock grass (*Deschampsia borealis* (Trautv.) Roshev.), with individual patches of pendant grass (*Arctophila fulva* (Trin.) Anderss.); a thick moss cover (*Dicranum* sp.) was developed on the soil surface. The grass height is approximately 15–20 cm.

Collection procedure

Specimens were collected using pitfall traps (plastic transparent 200-ml cups with a mouth diameter of 65 mm); the preservative was 4–8% formalin with a detergent added to reduce surface tension. Soil breakdown during trap setting can contribute to increased catch in the following two days (the so-called "digging-in effect") (Joosse and Kapteijn 1968). For this reason, traps were set up two days before the start of the surveys, filled with preservative and covered with lids to prevent animals from entering them. In total, thirteen traps were set in a row at a distance of 1.5 m from each other. Walking disturbances, as well as trap checks, can also stimulate invertebrate activity and therefore increase catches (Joosse and Kapteijn 1968). To minimize these effects, traps were set at regular intervals, and to facilitate the removal of traps from the ground, two cups were placed one inside the other (so that one was non-removable and the other removable).

Traps were checked in two series of surveys; each series was two days long (August 7–8 and 16–17). The material was collected six times per day at 4:00–8:00–12:00–16:00–20:00–00:00 local time (UTC + 5 h). Each trap had a serial number and was processed individually. The detailed protocol of the work is given in Online Resource 1.

Environmental factors

In 2016, the polar day (the period when the sun does not set beyond the horizon) lasted on Shokalsky Island from May 5 to August 7. Before its start and after its end, "white nights" (when the sun is no more than 6–7° below the horizon) can be observed on the island. It is never completely dark at this time of year.

Light level and wind speed (at heights of 0.2 and 2 m above the soil surface) were measured with a handheld light meter CEM DT-1308 and a handheld anemometer Mastech MS6250 every time before we checked traps. Air temperature and humidity near the soil surface were monitored using a Thermochron revizor TCR-G-U-X measuring system (Electronic instruments, Russia). One logger was set on the soil surface near the traps line. An additional temperature logger was set in a plastic pipe at a height of 2 m. In all cases, the loggers were hidden from direct sunlight. Temperature and humidity data were logged hourly and averaged across 4 h which preceded the sampling. All information about environmental factors is presented in the Online Resource 2.

Material processing and species identification

After the expedition, invertebrates were sorted into taxonomic groups in the laboratory using a Carton SPZ50 stereomicroscope (magnification 6.7–50x). The materials collected have been deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (spiders), the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow (springtails and mites), and the Natural History Museum of the University of Oslo, Norway (rove beetles). Two of us (A. Babenko and A. Nekhaeva) conducted the species identification of springtails and spiders, respectively. The following sources were used to identify the springtails—Fjellberg (1998, 2007), Bretfeld (1999), Potapov (2001), Thibaud et al. (2004), Jordana (2012), and for the spiders Holm (1956), Palmgren (1976), Eskov (1989), Marusik and Tanasevitch (2003), Marusik et al. (2016), Nekhaeva et al. (2019), and Marusik and Nekhaeva (2020).

Statistical processing and data presentation

All collected individuals, regardless of their instars, were included in activity calculations. Species activity was calculated from reliably identified individuals only. No data transformations were performed prior to calculations. We used the scaling to max = 1 only for visualization (Figs. 5, 6, Online Resource 3, 4, 5), because of the strong differences between the abundance of taxa.

The activity analysis was performed at 3 scales: all taxa, main orders, and dominant species. The periodicity was estimated by spectral analysis (Shumway and Stoffer 2017). The selected frequency for testing was 1/6 because we did six samples per day. Spectral density ratio (SDR) was calculated as the ratio of the power spectral density (PSD) at the frequency of interest to the average PSD over a range of frequency of interest. Here we interpret SDR as signal to noise ratio and SDR is greater than 1 if periodicity exists. Fisher's *F* test was used to test the significance of the obtained result.

Having proved periodicity, the time-stamped data were presented as unbroken time series and disintegrated into its components (trend, periodicity, and residuals) using the additive model (Mastitskiy 2020). We ignored the 7-day break between survey series and combined the two time periods into one. We consider this assumption acceptable, and most importantly, more preferable than its alternative—conducting two statistical tests on a limited set of data. All these methods are sufficient to work with our data, because they assume and control for temporal reference rather than being subject to autocorrelation.

We checked for multicollinearity among the measured factors using the Spearman rank correlation test. The significance of the results was assessed using adjusted *p* values by Benjamini and Hochberg (1995) method.

We rejected a null hypothesis in all the statistical tests when *p* value reached 0.05 or less. Calculations were performed in the R statistical programming environment v. 4.3 (R Core Team 2023). All data, code, and outcome are available at the public repository: github.com/ANSozontov/polar_2023.

Results

Environmental factors

The weather was predominantly clear and sunny during the first series of surveys (August 7–8) and cloudy during the second series (August 16–17) (Online Resource 2). White nights began on 8 August, which affected light levels. Thus, its minimum intensity at night on August 7–8 was 330 and 360 lx and on August 16–17 it was already 22 and 33 lx (Online Resource 2). However, the onset of white nights did not affect the dynamics of illuminance and air temperature. For all days, the illuminance reached maximum values at noon and minimum values at midnight (Fig. 2a, b). Only on August 7, due to fog at noon, maximum light level occurred at 16:00. The air temperature near soil surface differed between the series and, according to the hourly logs, on average it was 10.7 ± 0.5 °C and 9.3 ± 0.4 °C for the first and second series, respectively. At daytime, the surface air layer warmed thoroughly. The maximum temperatures reached + 18 °C and + 15 °C for the first and second series, respectively (Online Resource 2, Fig. 2c, d). At night and early in the morning, the minimum temperatures dropped to + 5 °C to + 2.5 °C. During the study period, wind speeds at a height of 20 cm did

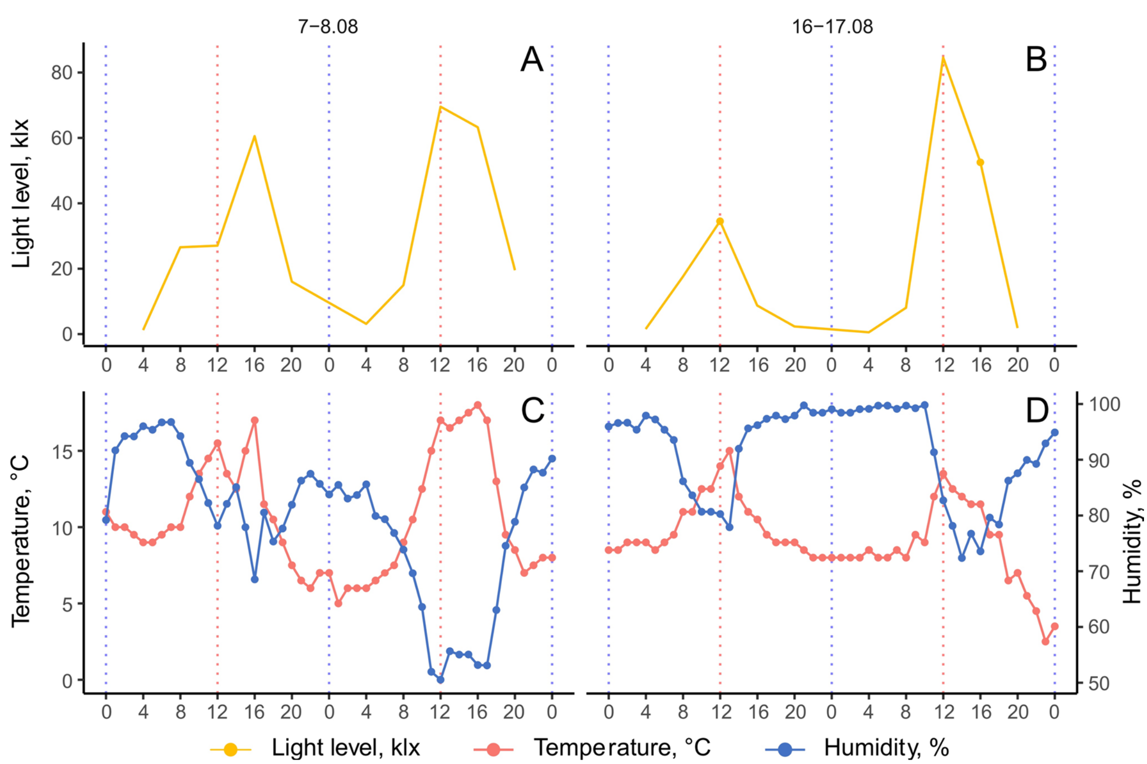

Fig. 2 Changes in light level (**A**, **B**) and temperature and relative air humidity (**C**, **D**) on August 7–8 and 16–17. Survey time mapped along X-axis

Table 1 Taxonomic composition and abundance of the specimens collected during the surveys (including juveniles)

Taxon	I series	II series	Total
Collembola	1784	4768	6552
Acari	141	120	261
Araneae	101	63	164
Diptera	89	43	132
Staphylinidae	17	13	30
Aphidoidea	9	12	21
Coleoptera larvae	9	7	16
Hymenoptera	2	2	4
Dytiscidae	0	3	3
Total	2152	5031	7183

not exceed 4 m/s, although at a height of two meters the strongest gusts reached 8 m/s.

Taxonomic diversity and abundance of collected arthropods

A total of 7183 specimens of invertebrates were caught in the traps. Springtails, spiders, soil mites, and dipterans were the most abundant (Table 1), with springtails comprising the vast majority of collected specimens (6552 specimens, 91%).

Among the 16 collembola species collected during the study (Table 2), the most dominant was *Isotomurus chaos* (5312 specimens). Next in abundance were *I. stuxbergi* (377 specimens), *Brachystomella parvula* (244 specimens), and *Pachyotoma crassicauda* (241 specimens). We found from ten to forty specimens of *Scutisotoma subarctica*, *Hypogastrura sensilis*, *Desoria tshernovi,* and *Sminthurides malmgreni*. The remaining species were represented by singletons (Table 2). Six spider species were collected (Table 2), of which the most dominant were *Masikia caliginosa* (72 specimens) and *Erigone psychrophila* (33 specimens).

Diurnal activity of terrestrial arthropods

Arthropods diurnal activity is shown in Fig. 3 as decomposed time series (tiles “trend,” “periodic,” and “random”) along with original data (tile “observed”). In each survey series, we recorded daytime increases in terrestrial arthropod activity. The average activity reached maximum and minimum values at noon and midnight, respectively (Fig. 4). Here, we detected four times greater periodicity than noise (SDR = 4.14). Therefore, we reject a null hypothesis about the absence of diurnal periodicity of activity at the high level of significance ($p < 0.001$) (Table 3).

The activity of individual arthropod groups was periodic as well (Fig. 5, Online Resource 3). This is

Table 2 Species composition and abundance of the collected collembolan and spider specimens

Taxon	I series	II series	Total
Collembola			
Brachystomella parvula (Schäffer, 1896)	88	156	244
Ceratophysella czelnokovi Martynova, 1978	–	8	8
Desoria tshernovi (Martynova, 1974)	1	21	22
Desoria violacea (Tullberg, 1877)	–	2	2
Folsomia bisetosa Gisin, 1953	1	–	1
Folsomia quadrioculata (Tullberg, 1871)	3	5	8
Friesea quinquespinosa (Wahlgren, 1900)	2	–	2
Hypogastrura sensilis (Folsom, 1919)	6	25	31
Hypogastrura tullbergi (Schäffer, 1900)	3	2	5
Isotomurus chaos Potapov et Babenko, 2011	1457	3855	5312
Isotomurus stuxbergi (Tullberg, 1877)	88	289	377
Pachyotoma crassicauda (Tullberg, 1871)	70	171	241
*Parisotoma reducta (*Rusek, 1984)	1	–	1
Scutisotoma subarctica (Gisin, 1950)	6	40	46
Sminthurides malmgreni (Tullberg, 1877)	11	2	13
Sminthurides schoetti Axelson, 1903	1	–	1
Araneae			
Erigone psychrophila Thorell, 1871	21	12	33
Gibothorax tchernovi Eskov, 1989	6	2	8
Hilaira glacialis (Thorell, 1871)	3	9	12
Hilaira incondita (L. Koch, 1879)	1	–	1
Masikia caliginosa Millidge, 1984	48	24	72
Pachygnatha sp.	–	1	1

particularly true for Collembola, as they made up the vast majority of the animals collected (up to 91%). On average, their activity peaked at noon (Fig. 4). The SDR of their periodicity was 4.08 and the aperiodicity hypothesis is to be rejected ($p < 0.001$). Spiders and mites showed less pronounced diurnal periodicity of their activity (SDR = 3.34 and 1.97, p value = 0.036 and 0.045, respectively) (Table 3). The average activity of spiders reached its maximum value at noon, in contrary, for mites it was minimal at this time (Fig. 4). Yet, there is no convincing evidence to reject the null hypothesis of no periodicity in dipterans (Table 3).

The activity of dominant species was also periodic (Fig. 6, Online Resource 4). The average activity of *I. chaos*, *B. parvula, P. crassicauda,* and *M. indistincta* reached maximum values at noon (Fig. 4). For all these species, SDR was found to be greater than 1 and thus the hypothesis that they do not have a diurnal periodicity of activity should be rejected (Table 3). At the same time, no periodicity was detected for the spider *E. psychrophila* and the collembola *I. stuxbergi* (Table 3).

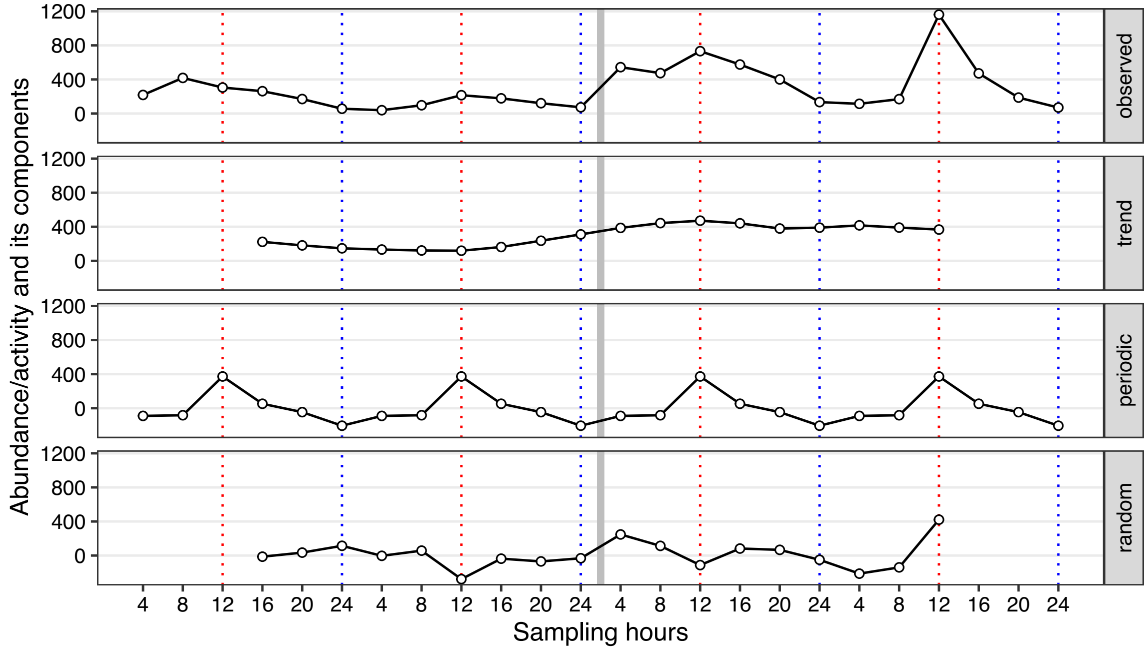

Fig. 3 Time series of diurnal arthropods activity and its components (trend, periodicity, residuals). Red line marks noon, blue line marks midnights, and gray line marks the boundary between survey series

Diurnal activity and environmental factors

All the measured factors are interconnected to varying degrees (Fig. 7). Therefore, some of them were excluded from further analyses and only relative air humidity, wind at 20 cm height from the soil surface, light level, and temperature at the soil surface were retained. Despite the correlation between some of them, in our opinion these factors are the most significant in relation to invertebrate activity.

Apparently, weak trends in activity increase with light level can be noted for all taxa studied except Acari (Fig. 8). A positive relationship between activity and temperature was observed in dipterans and spiders (*M. indistincta* in particular), and for collembolans (both in general and in dominant species) activity was greatest at average values of this factor (Figs. 8, 9). An increase in absolute humidity had a negative effect on the activity of spiders and dipterans, while its low values, apparently, limit the activity of springtails. It appears that wind had no effect on arthropod activity during our work.

Discussion

As expected, springtails, soil mites, spiders, and dipterans formed the bulk of the material collected (Table 1). Beetles were underrepresented in our samples. This could be due to the fact that their greatest activity on Shokalsky Island was shown to be in zonal tundra communities (Makarov et al. 2018) rather than marshes where our daily surveys were conducted.

The results suggest that so-called 'digging-in effect' has generally been avoided. Only dipterans and soil mites showed maximum activity during the first 4 h of traps operation (Online Resource 3, tile "observed"). Moreover, the number of springtails collected in the series II (August 16–17) of our study was more than 2.5 times higher compared to the series I (August 7–8) (Table 1). This difference in activity might be due to significant changes in atmospheric pressure caused by weather changes. A similar response to changes in atmospheric pressure was noted in laboratory experiments with springtails active on snow (Zettel 1984). The weather on August 16–17 was indeed cloudy and rainy, while August 7–8 was mostly sunny. Increased humidity and drizzle precipitation on August 16–17 could also have contributed to an increase in the activity of these hygrophilous animals; however, it had inverse effect on the activity of spiders, mites, and dipterans. Similar results were obtained in field experiments in North American broadleaf forests, where springtails were more active in plots receiving increased precipitation than in the drought plots, while spiders showed the opposite results (Lensing et al. 2005). However, the authors note that the overall reaction of the spiders was mainly due to the activity of cursorial spiders from the family Gnaphosidae. A negative correlation of spider catches with precipitation is also known for web-building spiders (mainly from the family Linyphiidae) in the Finnish boreal forest (Niemelä et al. 1994).

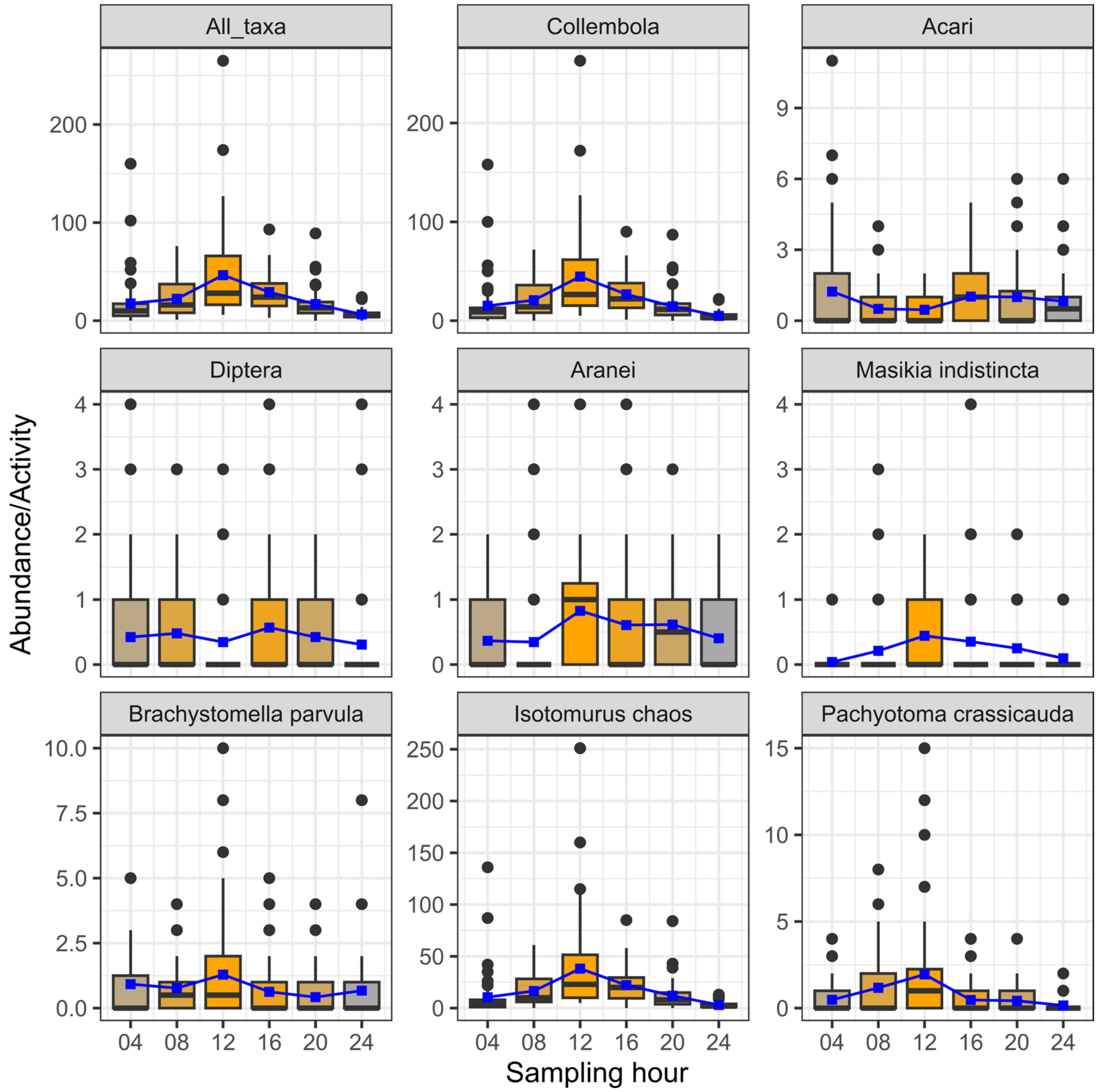

Fig. 4 Activity of terrestrial arthropods at different times of the day. The horizontal line in the boxplot references the median value. The box encompasses the interquartile range from the first to third quartile, and the whiskers accounts for minimum and maximum values within 1.5 interquartile ranges from the box boundaries. Points beyond the whiskers are outliers. Average activity values are marked in blue. Data over both time periods were used

Using spectral analysis, we have shown that under continuous daylight hours in the Arctic the rhythms of locomotor activity of terrestrial arthropods show circadian periodicity at the community level (Table 3, Fig. 3). Daily periodicity of activity was also revealed in most model taxonomic groups (i.e., springtails, spiders, soil mites), the dominant collembolan species (*I. chaos*, *B. parvula*, *P. crassicauda*) and the spider *M. indistincta* (Table 3, Figs. 5, 6). To date, it has been impossible to confirm periodicity in dipteran activity (Table 3). Increasing the number of traps used could increase the power of analysis, but would significantly complicate their maintenance. For this reason, we would recommend the use of yellow pan traps to record the daily activity of dipterans, which should be more effective. In addition, it is difficult at this stage to interpret the results for the second most abundant springtail species, *I. stuxbergi* (Table 3). This species can be asynchronous, but it cannot be ruled out that its activity could be bimodal (Online Resource 5); the method used, which is designed to the search for 24 h periodicity, did not reveal it. Further research should also consider these options.

To identify the periodic component in arthropod activity, we combined data from two survey series into a continuous time series to avoid double statistical testing of sparse data. Although the gap in our case was short, future work should probably strive for continuous and longer counts. The

Table 3 Spectral analysis of diurnal activity arthropods

Taxa	Individuals	SDR	*F*	*p* value
Total	7183	4.14	> 1000	< < 0.001***
Orders				
Collembola	6552	4.08	> 1000	< < 0.001***
Acari	261	1.97	26.2	0.045*
Araneae	164	3.34	34.2	0.036*
Diptera	132	1.47	9.7	0.103
Dominant species				
Isotomurus chaos	5312	4.44	> 1000	< < 0.001***
Isotomurus stuxbergi	378	0.99	75.1	0.018
Brachystomella parvula	244	1.23	38.4	0.032*
Pachyotoma crassicauda	241	3.22	316.5	0.005**
Masikia indistincta	72	5.15	23.0	0.050*
Erigone psychrophila	33	0.76	0.47	0.572

*$p \leq 0.05$, **$p < 0.01$, ***$p < 0.001$

average activity values also confirm that arthropods were most active during the daytime hours with a maximum at midday (Fig. 4). Previous studies have shown similar trends in the circadian activity rhythms of springtails (Kristensen and Vestergaard 1975; Solem and Sendstad 1978) and spiders (Koponen 1972) despite a polar day in the (sub)Arctic, which has also been confirmed in bumblebees (Stelzer and Chittka 2010) and non-biting midges (Syrjämäki 1968). The daily dynamics of activity of most tundra anthophils is also unimodal, with the time of maximum activity in many species shifted toward noon (Chernov and Matveyeva 1997). Only soil mites stand out from the general picture—their activity increased in the evening and night time and was lowest at midday (Figs. 4, 5). Intense night migrations to the upper parts of the grass stand were also observed for oribatid mites in the tundra zone of the Taimyr Peninsula under 24 h lighting (Chernov and Rudenskaya 1975). Thus, Arctic arthropods do not appear to maintain continuous activity during the 24 h daylight period, although they are potentially capable of doing so. The thermal activity window of polar terrestrial arthropods is comparable to that of temperate and tropical insects. At the same time, the temperature threshold for activity of polar arthropods is shifted toward lower temperatures, and some of them are able to move even at subzero temperatures (Burn and Lister 1988; Block 1990; Marshall and Chown 1995; Coulson et al. 1995; Hodkinson 2003; Everatt et al. 2013). Some researchers suggest this allows invertebrates to make the most of a short growing season (Block 1990; Marshall and Chown 1995; Everatt et al. 2013). However, daily activity data show that this is not always the case. During our study, the minimum

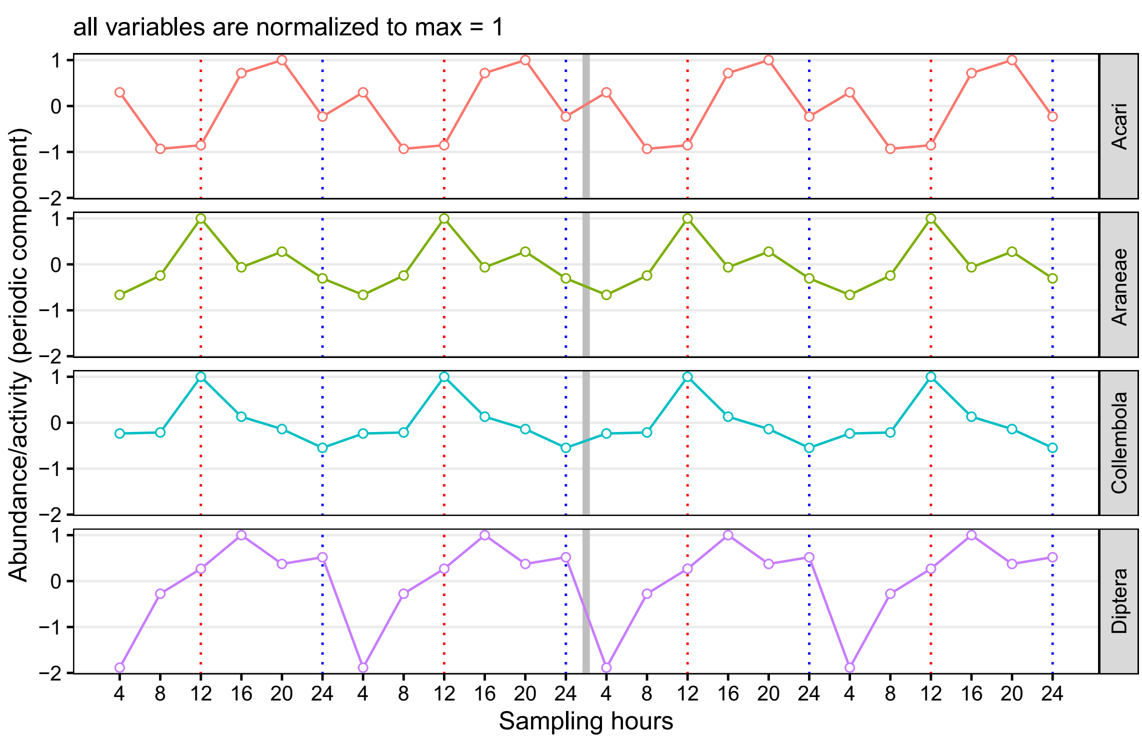

Fig. 5 Periodicity component of time series of diurnal arthropods activity (by orders). Red line marks middays, blue line marks midnights, and gray line marks the boundary between survey series. Note: all raw variables data were normalized to max = 1

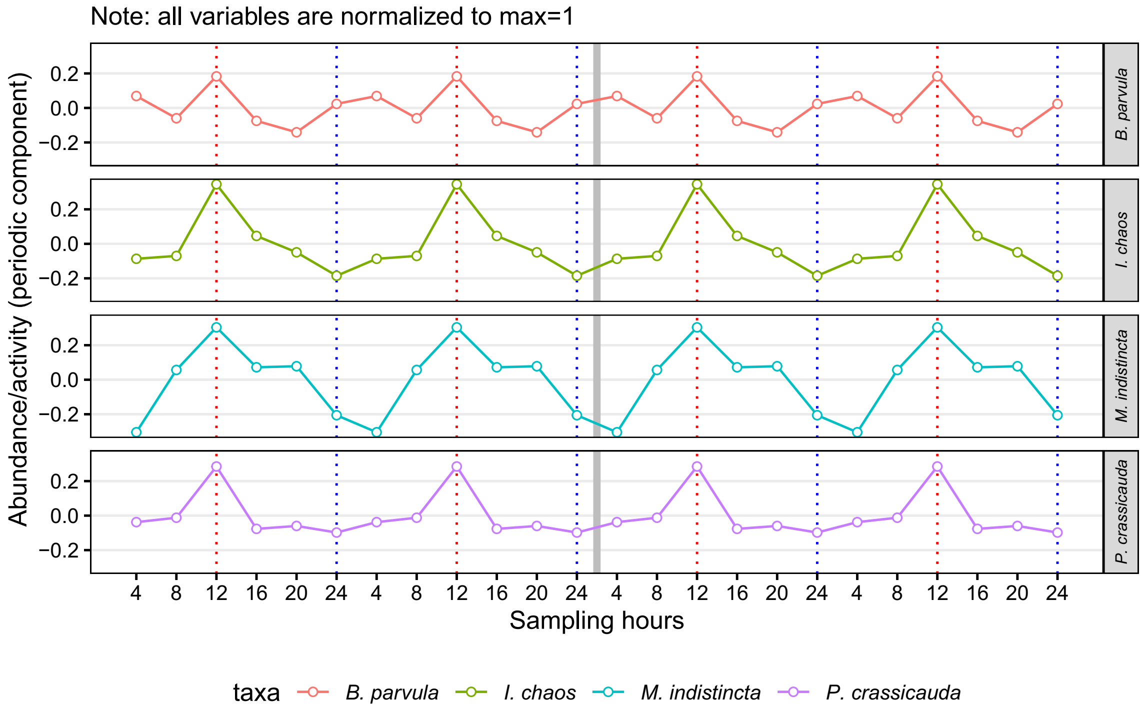

Fig. 6 Periodicity component of time series of dominant species diurnal activity. Red line marks middays, blue line marks midnights, and gray line marks the boundary between survey series. Note: all raw variables data were normalized to max = 1

temperature was + 2.5 °C (recorded on August 17 at 23:00); however, terrestrial arthropods were most active only during certain daytime hours.

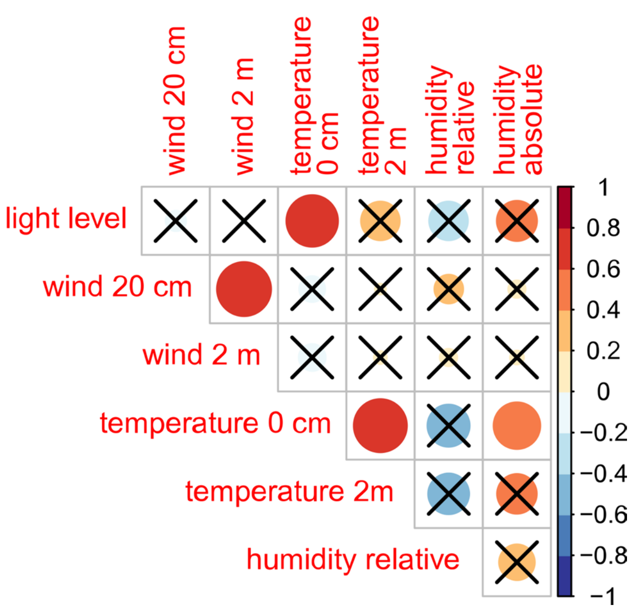

Fig. 7 Correlation matrix of measured factors. The Spearman coefficient value is shown on the scale on the right. The significance level (α) = 0.05. Statistically non-significant correlations are crossed out

The similarity of results in different taxonomic groups (maximum activity during the day and minimum at night) could indicate that under continuous daylight conditions in these regions, the locomotor activity of most terrestrial arthropods is entrained by some external cues. The ability of light and temperature to influence circadian rhythms has been repeatedly demonstrated under laboratory and semi-natural conditions (Yoshii et al. 2009; Peschel and Helfrich-Förster 2011; Helfrich-Förster 2020; George and Stanewsky 2021), and their values in the field vary significantly throughout the day despite continuous illumination. Therefore, it can be speculated that even during a polar day, these factors could be among the main drivers for the synchronization of activity rhythms with environmental conditions. We only have data on the absolute values of light levels for every 4 h (Fig. 2, Online Resource 2), but the pattern and maximum levels correspond to those in other areas of the Arctic. In the Arctic tundra of the Taimyr Peninsula in July, the maximum light level at noon reaches 50,000–100,000 lx; at night these indicators drop 10 times (Chernov and Matveyeva 1997). On Svalbard, light levels also ranges from 6000 to 64,000 lx (Solem and Sendsrad 1978). Our study was carried out in August, when the light intensity at these latitudes drops significantly (Chernov and Matveyeva 1997). The minimum light levels were 330 and 22 lx on August 7–8 and 16–17 respectively, but the maximum on these days reached 70,000 and 85,000 lx (Fig. 2,

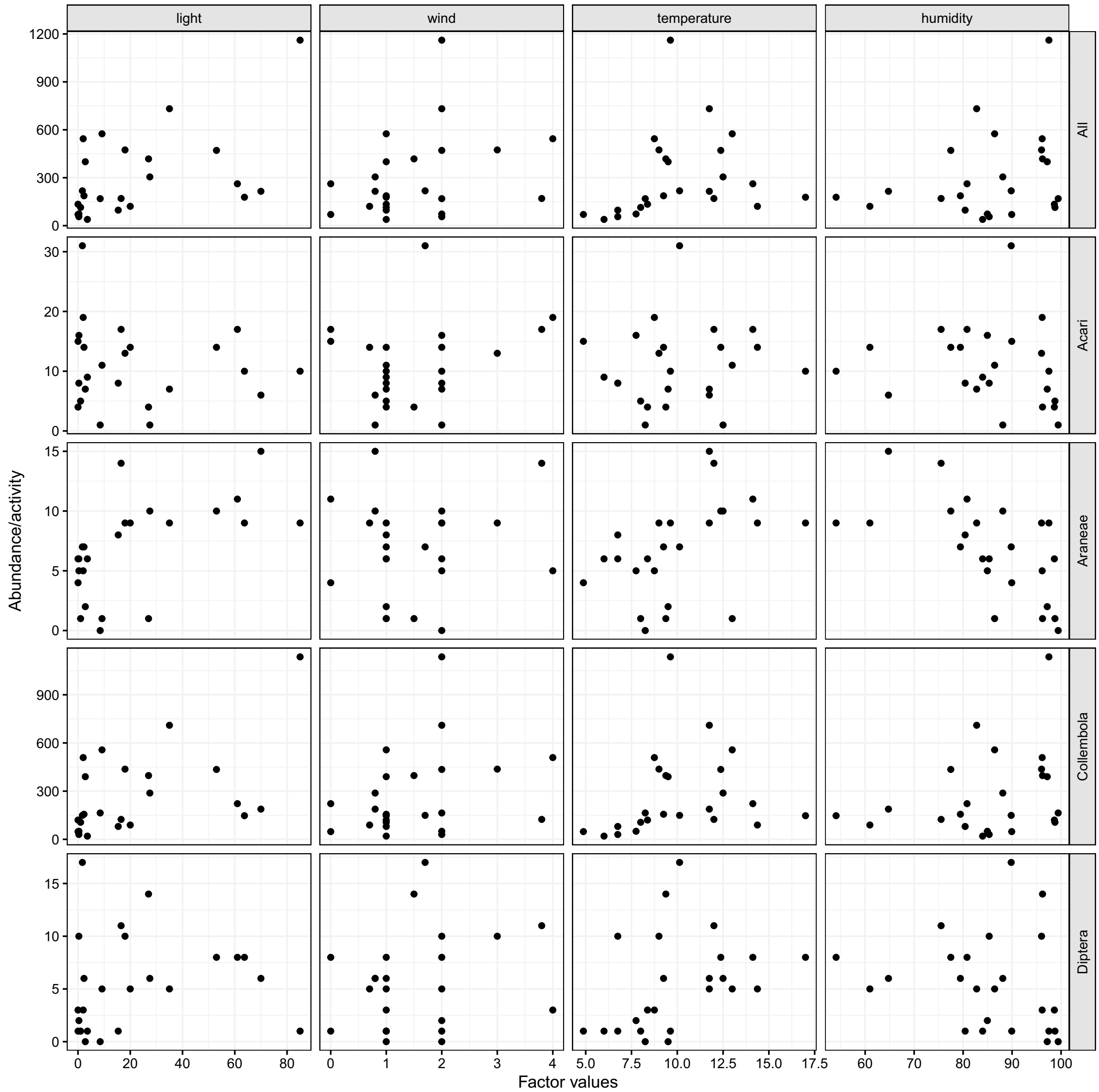

Fig. 8 Scatterplot of different invertebrate taxa activity (Y) depending on environmental factors (X)

Online Resource 2). Typically, light level is highest around midday, but weather conditions may shift the peak position (Solem and Sendsrad 1978). We observed this on August 7 when the light level at 12:00 was lower than at 16:00 due to fog (Fig. 2).

Since many factors were correlated to varying degrees under natural observation conditions (Fig. 7), it is difficult to isolate their particular influence on activity at this stage of research. However, we can note some trends in changes in activity under the influence of various factors. Wind did not appear to change activity (Figs. 8, 9), and increasing absolute humidity had a negative effect on spider and dipteran activity (Fig. 8). This observation correlates well with the aforementioned decrease in the abundance of spiders and dipterans in cloudy weather on August 16–17 (Table 1). It is known that light stimulates the activity of surface-dwelling springtail species, while soil-dwelling species avoid it (Zettel and Zettel 1987; Zettel 1984; Salmon and Ponge 1998). All common springtail species collected during our study live on the soil surface or in the upper layer of litter, so a certain increase in their activity along with the light intensity seems natural (Figs. 8, 9). The increase in the activity of spiders is also associated with light level, but we cannot exclude that it could occur following a change in the activity of their prey—springtails and dipterans (Fig. 8). For example, the diurnal activity of wolf spiders (Lycosidae) in East Greenland positively correlates with the activity of collembolans *Desoria tolya* Fjellberg 2007 (in that study, the species is listed as *Isotoma violacea*) on the snow (Fox and Stroud 1986). Polar arthropods become more active as

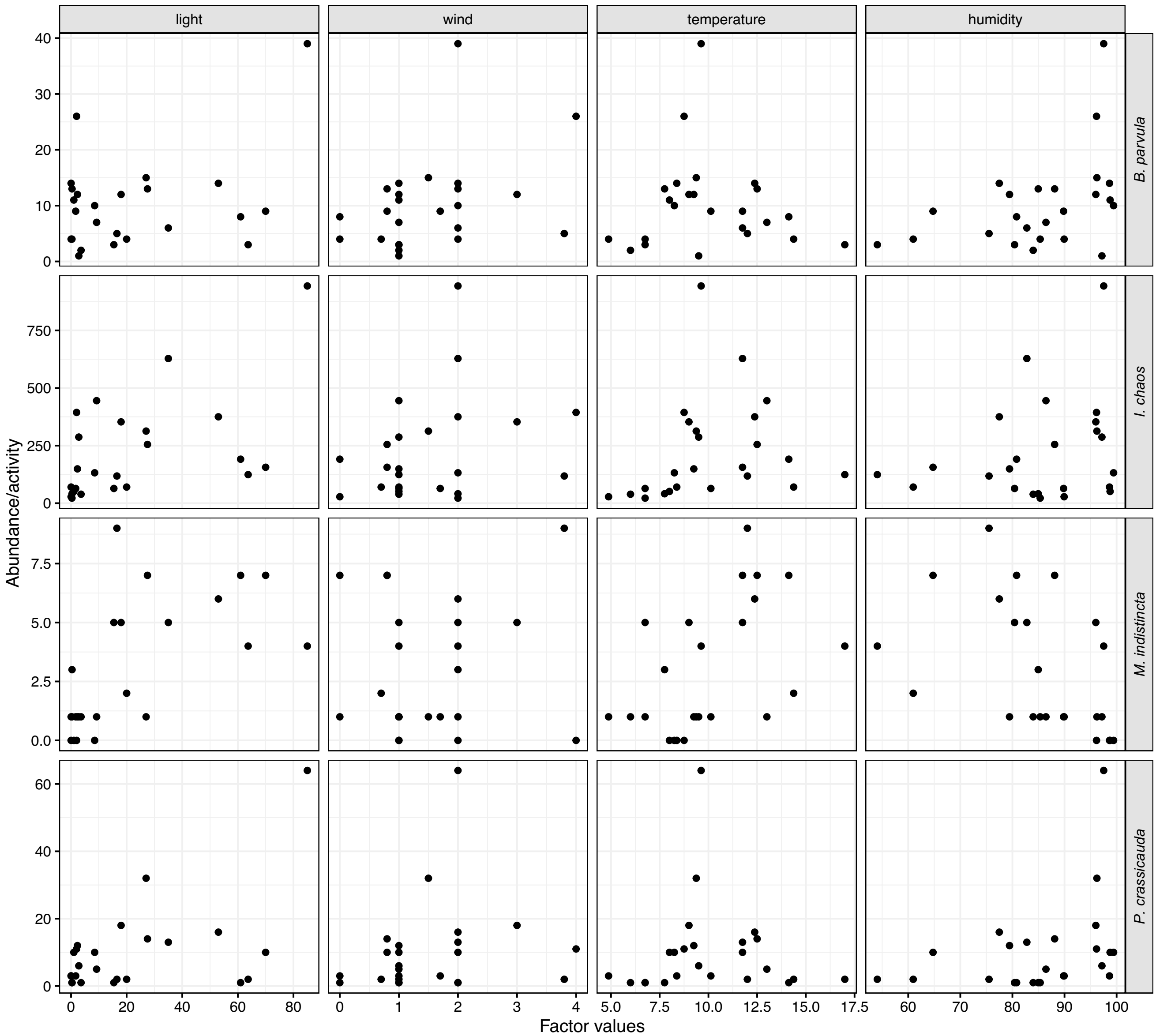

Fig. 9 Scatterplot of dominant species activity (Y) depending on environmental factors (X)

temperatures increase (Coulson et al. 1995; Marshall and Chown 1995; Everatt et al. 2013). The activity of most taxa studied appears to be related to changes in temperature (Figs. 8, 9). Only the activity of soil mites does not show any connection with any of the factors we selected (Fig. 8). This might explain the differences in the daily activity of mites compared to other arthropod groups (increased activity in the evening and at night) (Figs. 4, 5). Perhaps the activity of mites is correlated with soil temperature, where diurnal temperature variation is more even, and maximum warming occurs later compared to air (Babenko 1993; Chernov and Matveyeva 1997). For the predatory Antarctic mite *Hydrogamasellus racovitzai* (Trouessart, 1903), a weak negative relationship between activity and soil temperature was found (Burn and Lister 1988). Presumably due to this, mites might be active at night and have the opportunity to hunt springtails *Cryptopygus antarcticus* Willem, 1901, which become less mobile and more accessible to it (Burn and Lister 1988). On the coastal marshes of Shokalsky Island, herbivorous (in a broad sense) mite species predominate (Bizin and Makarova 2024). Their evening and night activity may help reduce competition with springtails for food resources.

Scatterplots (Figs. 8, 9) show that the greatest activity of springtails was observed at average temperatures (from + 7.9 to + 15.9 °C). Thermal preferences (the region in the temperature gradient chosen by most individuals of a species (Babenko 1993)) may be one possible reason for limiting daily activity to certain times of the day. The temperature range we noted overlaps with the known absolute values of thermal preferences of springtails in the Arctic tundra of the Taimyr Peninsula (from + 9.4 °C to + 19.5 °C) (Babenko 1993), where the average long-term July temperature corresponds to that on Shokalsky Island (Chernov and Matveyeva 1997). Since thermal preferences are subject to seasonal changes and can vary depending on acclimatization conditions (Babenko 1993; Balashov et al. 2011; Hayward et al. 2003), it can be expected that daily activity of arthropods after and before wintering will be observed at a lower temperature range, and the nature of daily activity will remain unchanged. Perhaps this is where the lower-temperature threshold for activity mentioned above appears.

To distinguish between the effects of factors in the field, we propose continuous daily activity recordings during the snowless season. At this time, the length of the day successively changes from short to long (polar day) and vice versa. This approach would cover the full range of weather and light conditions (including minimal changes in light intensity around the solstice) and to track how (and whether) daily activity changes throughout the season. If changing the length of the day affects the nature and duration of activity, it would indicate that activity is entrained by light. Data from different regions may also help distinguish the effects of factors on activity in natural conditions.

Conclusion

Our experiment clearly showed that under conditions of continuous daylight in the Arctic, the locomotor activity of terrestrial arthropods still has a certain periodicity. We assume that most taxa of terrestrial arthropods under these conditions do not "stretch" their activity throughout the day to compensate for the short duration of the warm season. In Arctic ecosystems, the influence of abiotic factors is of primary importance (Danks and Oliver 1972; Chernov 2008a, b) and it can be assumed that light, temperature, and thermal preference are the main factors that limit the activity of arthropods to daytime hours. Long-term continuous observations of diurnal activity under conditions of varying day length and during abrupt weather changes are likely to help distinguish the effects of these interrelated factors.

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Author contributions AN conceived and designed research. In the discussion with AB the project was improved. AN and MB conducted the field work. AB identified springtails. AN identified spiders and wrote the first draft of the manuscript. AS designed and performed data analysis. AB, MB, and AS contributed to reviewing and editing of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets generated during and analyzed during the current study are available at the public repository: github.com/ANSozontov/polar_2023.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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