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Seasonal dynamics of mites (Acari) in pastures and meadows in Poland, with species analysis of Oribatida

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Original research

ABSTRACT

The study involved three pastures, grazed by geese, goats and fallow deer, and three nearby meadows (control plots) situated in north-central Poland. Samples of 150 cm³ each (6 cm of soil and 3 cm of lower parts of plants) were collected in spring, summer and autumn 2016 and 2017 in 10 replications, 360 samples in total. This material included 22.561 mites, among which Oribatida accounted for 69%, Mesostigmata for 21%, and other mites for 10%. At most study sites, both pastures and meadows, no significant seasonal differences in the abundance of Oribatida and Mesostigmata were seen. Such differences were only observed for the third category of other mites that were the most abundant in spring and usually the least abundant in autumn. Also species diversity of Oribatida differed between the seasons – in all pastures it was the highest in summer and the lowest in spring, while in all meadows it was the highest in spring and decreased towards autumn. Oribatid species were more affected by the habitats than by seasons, as some species were strongly associated with pastures (*Platynothrus peltifer*), other with meadows (*Achipteria coleoprata*, *Liebstadia similis*, *Metabelba pulverosa*, *Scheloribates laevigatus* and *Sellnickochthonius immaculatus*), and some (*Eupelops occultus* and *Tectocepheus velatus*) were abundant in both habitats. Although the effect of seasonality was weaker than that of the habitat, it was still perceptible. *Platynothrus peltifer* was most associated with autumn, *T. velatus* with spring, *E. occultus* with spring and summer and *L. similis* with summer.

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Keywords grazing; geese; goats; fallow deer; tapeworms

Introduction

Mites (Acari), and particularly Oribatida, are considered one of the most abundant arthropod groups in the soil (Walter and Proctor 2013). Their densities in meadows and pastures are comparable and range from several thousand to several tens of thousands of individuals per 1 m². For example, in north-central Poland, mean density of Oribatida in meadows in a growing season varied from 6.000 to 60.000 individuals/m² and they constituted 32–75% of all mites. Density of Mesostigmata in the same meadows ranged between 3.000–10.000 individuals/m² (Chachaj and Seniczak 2006; Szczukowska 2015; Seniczak *et al.* 2017; Pacek *et al.* 2020). Mite density in pastures depended on the grazing species (Chachaj and Seniczak 2006; Pacek *et al.* 2020). The highest density of Oribatida was observed in a goose pasture (57.000 individuals/m²), where they made up 83% of mites, and the lowest in a sheep pasture

(3.500 individuals/m²), where Oribatida made up only 38% of mites. Density of Mesostigmata ranged from 2.000 individuals/m² in a cattle pasture to 10.000 individuals/m² in a goose pasture (Chachaj and Seniczak 2006; Pacek *et al.* 2020). High abundance of oribatid mites in soils translates into their ecological importance (Walter and Proctor 2013). These mites play important roles in decomposition of soil organic matter, formation and changes in the soil properties, and they help with supporting plants with nutrients (Wasilewski 2006; Walter and Proctor 2013). In Poland, the number of oribatid species in pastures ranged between 19 and 22, and in meadows between 24 and 31 (Chachaj and Seniczak 2005). In the Czech Republic the number of oribatid species in cow pastures and meadows ranged between 15 and 30 (Hubert 2000). However, some oribatid species negatively affect domestic and wild animals, as they are intermediary hosts of tapeworms (e.g. Zbikowska-Zdun and Koczara 2013; Václav and Kalúz 2014; Roczeń-Karczmarz and Tomczuk 2016; Tomczuk *et al.* 2017). Mesostigmata are mostly predators, and play a positive role in ecosystems by controlling and regulating the density of saprophages, including oribatid mites (Walter and Proctor 2013).

Ecological investigations of the mite fauna in grasslands have focused mainly on the effects of fertilizing (Bolger and Curry 1980; Bielska 1986; Bielska and Paszewska 1995; Domek-Chruścicka and Seniczak 2005; Parfitt 2005; Sokółowska and Seniczak 2005; Graczyk *et al.* 2008, 2010; Wasieńska-Graczyk *et al.* 2009; Kruczyńska and Seniczak 2010; Seniczak *et al.* 2017), grazing (Hubert 2000; Clapperton *et al.* 2002; Seniczak *et al.* 2007a,b; Schon *et al.* 2008; Pacek *et al.* 2020), or ecotone zones (Bardgett and Cook 1998).

Grazing is a strong factor that can change seasonal dynamics of oribatid mites. It mainly depends on the weight of grazing animals, their behavior, hoof type (Greenwood *et al.* 1997; Parfitt *et al.* 2005) and the period of grazing, i.e. the longer the animals stay in the pasture, the more compact the soil becomes (Amiri *et al.* 2008). Since the compaction of soil worsens living conditions of mites, it can be expected that grazing affects mite communities (Chachaj and Seniczak 2006). In addition, grazing changes the composition of vegetation and root biomass between the seasons, and affects the content of organic matter in the soil, which together may alter microhabitat conditions for oribatid mites (Di *et al.* 2001; Altesor *et al.* 2006).

Farm animal feces affect chemical composition of soil and consequently seasonal dynamics of oribatid mites in different ways. For example, goose manure increases nitrogen and phosphorus content, while goat manure increases the level of potassium (Ligęza 2009; Uwah and Eyo 2014).

As majority of studies on acarofauna from grasslands have focused on one season only or presented averaged values from a few seasons (Clapperton 2002; Chachaj and Seniczak 2006; Schon *et al.* 2010), relatively little is known about seasonal changes in the mite communities in pastures and meadows. According to Norton (1994), the effect of seasons on oribatid communities in pastures is less pronounced because seasons are strongly associated with the availability of organic matter in the soil. This, in turn, is connected with life cycle of plants and circulation of matter in the environment, which can affect the abundance of Oribatida (Belnap and Lange 2001; Wasilewski 2006). Seasonal agrotechnical treatments may also influence Oribatida communities (Cookson *et al.* 1998; Vreeken-Buijs *et al.* 1998; Wickings *et al.* 2011; Wickings and Grandy 2013). Mowing of meadows or herbicide use can reduce abundance and species diversity of oribatid mites and change their age structure (Minor and Norton 2008), while moderate fertilizing can improve their living conditions (Beltman *et al.* 2003). However, significant differences in seasonal dynamics of oribatid species were more often observed in pastures than in meadows (Bedano *et al.* 2006; Chachaj and Seniczak 2006).

Studies on seasonal dynamics of Oribatida in pastures are particularly important in the regions seriously affected by tapeworm parasites with their resulting detrimental economic impact on farm animals (Denegri and Martinez 2007). There are at least 127 oribatid species known to be intermediary hosts of 27 species of anoplocephalid tapeworms (Denegri 1993). Denegri and Martinez (2007) demonstrated that increased number of oribatid mites in sheep pastures and rapid maturation of cysticercoids coincided with lambing season and lamb

weaning, leading to high lamb mortality. Knowledge of the seasonality of intermediary hosts can be used to help control tapeworms through the rotation of pasture plots.

Our aim was to study seasonal differences in the abundance of mites and, more specifically, oribatid communities, in pastures grazed by geese, goats and fallow deer, and in meadows (control plots) situated close to these pastures. Based on the literature mentioned above, we hypothesized that seasonal changes in mites and particularly in Oribatida, were more pronounced in the pastures than in the meadows.

Materials and methods

Study area

The study sites were three pastures and three meadows situated in north-central Poland (Figure 1). The pastures were grazed by geese (later referred to as GP, 52.4427° N, 18.0914° E), goats (GoP, 53.1046° N, 18.1048° E) and fallow deer (FP, 53.1743° N, 17.0146° E); the meadows were situated near each pasture (in the closest possible location) (control for geese, GM, 52.4655° N, 18.0804° E, goat – GoM, 53.1047° N, 18.1040° E and fallow deer – FM, 53.1746° N, 17.0133° E). All study plots were fenced. The pastures provided stable conditions and had a documented history of usage. The livestock density was established at the beginning of the study and did not change over time. It was expressed as LU/ha, (livestock unit per hectare), i.e. a unit of animal density on a pasture, based on the animal weight and food demand (Rozporządzenie Rady Ministrów 2010), and reached 31.27 LU/ha for geese, 21.12 LU/ha for goats, and 6.60 LU/ha for fallow deer. From early spring to mid-autumn the animals spent most of the day in the pastures. The meadows were extensively used and mowed twice a year.

Temperature and rainfall in the study years (2016–2017) were similar (Table 1). In all study plots the highest temperature and rainfall were registered in summer, while in spring and autumn they were similar. Data on the soil and vegetation in the study plots were published before (Pacek *et al.* 2020). Soil in GP was the richest in phosphorus and organic carbon, in GoP in potassium, and in FP in nitrogen. In two pastures (GP and FP) vegetation belonged to *Lolio-Plantaginetum* association, and in GoP it belonged to *Festuco-Brometea* class. Two meadows (GM and GoM) harbored plant association *Arrhenatheretum elatioris*, while the remaining one (FM) was covered with *Poa pratensis-Festuca rubra*.

Sampling and identification

Samples of soil and vegetation were collected from all experimental plots in spring (April), summer (July) and autumn (November) 2016 and 2017 in the grazing season. In each plot and season, the samples of 150 cm³ each were taken with a soil corer (to a depth of 6 cm and with 3 cm of lower parts of plants), in 10 replicates. In total, 360 samples were collected. The mites were extracted using high-gradient Tullgren funnels for 14 days and preserved in 75% ethanol. Oribatida were identified to species, including juvenile forms, using the key by Weigmann (2006) and other keys (Seniczak 1977, 1978, 1980a, 1980b, 1988, 1990; Seniczak and Klimek 1990; Seniczak and Seniczak 2008; Ermilov 2010; Pflingstl and Krisper 2011). Mesostigmata were sorted out using Lindquist *et al.* (2009), whereas the remaining acarofauna was treated together as ‘other mites’. Full names of oribatid species are used in Tables 3 and 4; in other tables and figures abbreviations are used.

Statistical analyses

Since weather conditions in two subsequent years were similar, the data from seasons from these two years were analyzed together. The oribatid communities were characterized by their abundance index (A , specimens/m²), number of species (S), and Shannon species diversity index (H') (Odum 1982). Basic statistical descriptors included mean values \bar{x} and standard



Figure 1 Location of the study plots. G – goose pasture and meadow, Go – goat pasture and meadow, F – fallow deer pasture and meadow.

Table 1 Temperature and rainfall in sampling seasons in goose pasture (GP) and corresponding meadow (GM), goat pasture (GoP) and corresponding meadow (GoM), and fallow deer pasture (FP) and corresponding meadow (FM), in spring (Sp), summer (Su) and autumn (Au).

Study plot	Factor	Year	Season		
			Sp	Su	Au
GP and GM	Temperature (°C)	2016	9.9	18.9	8.6
		2017	9	17.8	9.4
	Rainfall (mm)	2016	25.4	85.2	52.9
		2017	45	77.7	64.5
Go and GoM	Temperature (°C)	2016	9.6	18.6	8.8
		2017	9	18.2	9.7
	Rainfall (mm)	2016	29.8	97.1	60.8
		2017	44.3	93.8	82.9
FP and FM	Temperature (°C)	2016	9.2	17.9	8.7
		2017	8.7	17.6	9.4
	Rainfall (mm)	2016	19.2	65.8	30.3
		2017	33.7	111.8	59.9

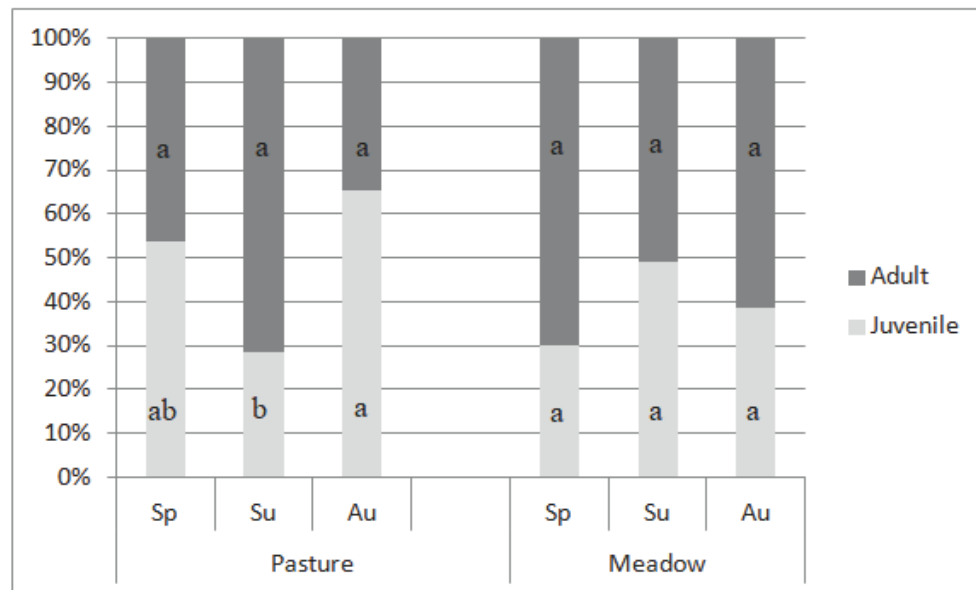


Figure 2 Age structure of Oribatida in spring (Sp), summer (Su) and autumn (Au); a, b – significant difference between seasons at $p \leq 0.05$; the same letter indicates that difference is not significant. Adult pasture p -value=0.236, juvenile pasture p -value=0.011, adult meadow p -value=0.156, juvenile meadow p -value=0.080.

deviation (\pm SD). For the remaining statistical analyses, the values were log-transformed $\log(x + 1)$ (Łomnicki 2010). Normality of the distribution was tested with Kolmogorov–Smirnov test, while equality of variance in different samples with Levene test. Multifactorial analysis of variance was used to find significant differences between the means, and in the case of significant differences Tukey’s post-hoc test was employed (Stanisz 2006). The analysis of the most numerous oribatid species, seasons and habitats was performed using detrended correspondence analysis (DCA) (Piernik 2008). INCOMPLETE DCA, instead of PCA, was carried out because gradient length was 5.0 indicating that unimodal models were more appropriate than linear models (Leps and Smilauer 2003), as the structure of the data had unimodal character (i.e., each species occurs in particular range of a given habitat parameter) (Hill and Gauch 1980). The level of significance for all statistical tests was $\alpha=0.05$. The statistical calculations mentioned above were carried out using MS Excel 2019 software (Microsoft 2019), STATISTICA 13.3 (Dell 2019) and MVSP 3.2 software (Kovach Computing Services 2019).

Results

Abundance and diversity of mite species

In total, 22.561 mites were extracted, in which Oribatida predominated (69% of all mites), followed by Mesostigmata (21%) and other mites (10%). Among oribatid mites, adult forms dominated (Figure 2), representing 51% of all mites. At most study plots, both in the pastures and meadows, total abundance of mites, of Oribatida as well as of Mesostigmata, did not differ significantly between the seasons. Only other mites were at all plots most abundant in spring and usually least abundant in autumn, and in all plots significant differences between some or all the seasons were found (Table 2).

Species diversity of Oribatida changed over seasons. In all pastures, it was the lowest in spring and the highest in summer, while in all meadows it was the highest in spring and

decreased towards autumn (Table 2). In total, 21 oribatid species were found in the studied grasslands (Tables 2–4), but only about half of them [*Platynothrus peltifer* (C.L. Koch, 1839), *Tectocephus velatus* (Michael, 1880), *Eupelops occultus* (C.L. Koch, 1835), *Liebstadia similis* (Michael, 1888), *Sellnickochthonius immaculatus* (Forsslund, 1942), *Punctoribates punctum* (C.L. Koch, 1839), *Trichoribates novus* (Sellnick, 1928), *Achipteria coleoprata* (Linnaeus, 1758), *Metabelba pulverosa* (Strenzke, 1953) and *Scheloribates laevigatus* (C.L. Koch, 1835)] were relatively abundant, at least in some plots. The abundance of juvenile Oribatida in pastures changed significantly over the seasons, being the lowest in summer and the highest in autumn (Figure 2), while no significant changes were observed in the meadows.

Juveniles of some species (*T. velatus*, *L. similis*, *E. occultus* and *P. peltifer*) showed greater abundance in certain seasons. For example, at a majority of plots juveniles of *T. velatus* were most abundant in summer and those of *P. peltifer*, in autumn. In most species, juveniles were absent in some seasons (Table 5).

Oribatid mites were more influenced by the habitat than by season (Figure 3). *Platynothrus peltifer* was strongly associated with pastures, five species (*A. coleoprata*, *L. similis*, *M. pulverosa*, *S. laevigatus* and *S. immaculatus*) showed stronger preferences for meadows, and

Table 2 Abundance of mites, adults and juveniles (A , in 10^3 individuals \cdot $m^{-2} \pm$ SD), number of species (S) and Shannon diversity index (H') of Oribatida in goose pasture (GP) and corresponding meadow (GM), goat pasture (GoP) and corresponding meadow (GoM), fallow deer pasture (FP) and corresponding meadow (FM) in spring (Sp), summer (Su) and autumn (Au).

Group	Season	Plot					
		GP	GM	GoP	GoM	FP	FM
Oribatida	Sp	38.8 ^a ±36.8	17.8 ^a ±10.8	3.2 ^a ±4.3	13.4 ^a ±10.2	8.0 ^a ±10.6	11.2 ^a ±10.7
	Su	39.5 ^a ±21.0	7.5 ^a ±24.3	4.8 ^a ±4.1	23.8 ^a ±20.7	7.9 ^a ±7.5	0.5 ^b ±0.5
	Au	91.3 ^a ±116.0	11.0 ^a ±11.1	5.5 ^b ±10.1	13.0 ^a ±12.6	12.1 ^a ±13.7	6.3 ^{ab} ±14.4
p -value		0.553	0.063	0.034	0.355	0.393	0.007
S	Sp	8	17	8	13	6	14
	Su	13	15	12	15	13	10
	Au	15	15	13	12	13	9
H'	Sp	0.67	1.96	1.04	1.78	0.71	1.66
	Su	1.58	1.88	1.6	1.7	1.62	1.63
	Au	1.2	1.8	1.52	1.64	1.27	1.38
Mesostigmata	Sp	2.1 ^a ±3.1	2.3 ^a ±3.0	4.6 ^a ±5.3	4.9 ^a ±6.1	5.6 ^a ±5.2	3.9 ^a ±5.3
	Su	10.5 ^a ±23.2	13.9 ^a ±19.5	13.5 ^{ab} ±22.5	7.9 ^b ±7.7	5.4 ^a ±7.1	8.8 ^a ±14.9
	Au	16.0 ^a ±20.0	12.5 ^a ±15.6	8.3 ^b ±5.3	7.5 ^{ab} ±11.1	6.1 ^a ±6.7	10.8 ^a ±14.0
p -value		0.162	0.492	0.044	0.028	0.936	0.182
Other mites	Sp	5.2 ^a ±8.7	5.7 ^a ±8.3	2.4 ^a ±6.9	4.2 ^a ±4.0	9.6 ^a ±19.8	10.3 ^a ±19.7
	Su	0.2 ^{ab} ±0.4	2.4 ^{ab} ±6.5	1.2 ^b ±4.2	2.1 ^{ab} ±2.6	0.2 ^b ±0.4	0.9 ^b ±1.8
	Au	1.2 ^b ±1.9	0.3 ^b ±0.5	<0.1 ^b ±0.5	0.2 ^b ±0.1	1.0 ^{ab} ±2.2	0.6 ^b ±1.7
p -value		0.033	0.024	0.007	0.023	0.022	0.014
Acari	Sp	46.2 ^a ±37.1	25.8 ^a ±17.8	12.1 ^a ±8.0	20.8 ^a ±14.7	23.3 ^a ±18.3	28.2 ^a ±26.7
	Su	50.3 ^a ±35.9	33.8 ^a ±43.2	20.5 ^{ab} ±22.7	32.9 ^a ±24.0	13.6 ^a ±13.3	10.1 ^b ±14.1
	Au	108.5 ^a ±131.4	23.8 ^a ±24.8	14.0 ^b ±15.8	20.4 ^a ±19.0	19.2 ^a ±29.1	17.8 ^{ab} ±24.9
p -value		0.255	0.081	0.032	0.555	0.356	0.047

^{a, b} – significant difference between seasons at $p \leq 0.05$; the same letter indicates that difference is not significant.

two other (*E. occultus* and *T. velatus*) were abundant both in the pastures and the meadows. Albeit to a lesser degree, seasons had an impact, too (Figure 4). *Eupelops occultus* was most associated with spring and summer in the pastures, *P. peltifer* with autumn in the pastures, and *L. similis* and *S. immaculatus* with summer in the meadows.

Table 3 Abundance (*A*, in 10³ individuals * m⁻² ± SD) of most numerous Oribatida (*A* > 0.5) adults and juveniles, in goose pasture (GP) and corresponding meadow (GM), goat pasture (GoP) and corresponding meadow (GoM), fallow deer pasture (FP) and corresponding meadow (FM) in spring (Sp), summer (Su) and autumn (Au).

Species	Season	Plot					
		GP	GM	GoP	GoM	FP	FM
<i>Platynothrus peltifer</i> (C.L. Koch, 1839) °	Sp	31.9 ^a ±34.9	0.3 ^a ±0.7	0.0 ^{ab} ±0.0	0.0 ^a ±0.0	3.1 ^{ab} ±4.2	0.2 ^a ±0.5
	Su	23.8 ^a ±15.6	0.1 ^b ±0.3	0.5 ^b ±0.6	1.5 ^a ±2.3	1.3 ^b ±1.8	<0.1 ^a ±0.1
	Au	74.8 ^a ±99.6	0.1 ^b ±0.3	1.7 ^a ±7.8	0.1 ^a ±0.3	5.6 ^a ±8.5	3.4 ^a ±12.0
<i>p</i> -value		0.453	0.005	0.025	0.248	0.042	0.231
<i>Tectocephus velatus</i> (Michael, 1880)	Sp	4.8 ^a ±6.3	0.9 ^a ±1.7	0.7 ^a ±0.8	0.8 ^a ±0.8	3.9 ^a ±7.6	4.8 ^a ±4.5
	Su	5.4 ^b ±8.1	2.4 ^a ±5.2	1.7 ^a ±1.7	0.7 ^a ±1.2	2.5 ^a ±3.7	0.1 ^b ±0.2
	Au	3.0 ^a ±4.6	1.3 ^a ±1.7	0.4 ^a ±0.7	0.5 ^a ±0.8	2.5 ^a ±3.7	1.0 ^b ±1.5
<i>p</i> -value		0.002	0.777	0.476	0.344	0.653	<0.001
<i>Eupelops occultus</i> (C.L. Koch, 1835)	Sp	1.0 ^a ±1.1	5.1 ^a ±4.0	1.5 ^a ±2.9	1.5 ^b ±2.1	0.5 ^a ±1.2	0.4 ^{ab} ±0.1
	Su	2.9 ^a ±3.5	1.1 ^a ±2.0	0.5 ^a ±1.0	1.2 ^a ±1.4	2.3 ^b ±2.5	<0.1 ^b ±0.1
	Au	3.1 ^a ±4.1	1.3 ^a ±2.8	1.2 ^a ±2.3	1.5 ^b ±2.7	2.2 ^{ab} ±2.6	1.5 ^a ±2.4
<i>p</i> -value		0.320	0.840	0.076	<0.001	0.021	0.007
<i>Liebstadia similis</i> (Michael, 1888) °	Sp	0.1 ^a ±0.3	2.3 ^a ±3.1	<0.1 ^a ±0.1	4.0 ^a ±6.0	0 ^a ±0.0	0.3 ^a ±0.5
	Su	0.5 ^a ±0.7	3.2 ^a ±6.1	0.2 ^a ±0.4	6.6 ^a ±8.9	0.1 ^a ±0.3	0.1 ^{ab} ±0.3
	Au	1.3 ^a ±1.5	1.1 ^a ±1.4	0.2 ^b ±0.5	3.2 ^a ±5.5	<0.1 ^a ±0.1	<0.1 ^b ±0.0
<i>p</i> -value		0.266	0.290	0.001	0.279	0.306	0.048
<i>Sellnickochthonius immaculatus</i> (Forsslund, 1942)	Sp	0.4 ^a ±1.2	3.7 ^a ±5.0	<0.1 ^a ±0.4	2.0 ^a ±3.8	0.1 ^a ±0.5	2.2 ^a ±5.9
	Su	1.5 ^a ±3.7	5.7 ^a ±16.4	1.0 ^a ±0.6	5.7 ^a ±13.3	0.1 ^a ±0.4	<0.1 ^a ±0.1
	Au	2.3 ^a ±7.1	0.7 ^a ±1.5	0.3 ^a ±1.1	2.5 ^a ±4.4	0.1 ^a ±0.4	<0.1 ^a ±0.1
<i>p</i> -value		0.269	0.326	0.461	0.291	1.000	0.080
<i>Punctoribates punctum</i> (C.L. Koch, 1839)	Sp	0.6 ^a ±1.0	0.3 ^a ±0.5	0.2 ^a ±0.4	2.0 ^{ab} ±3.1	<0.1 ^a ±0.1	0.1 ^a ±0.2
	Su	2.6 ^a ±2.9	0.7 ^a ±0.7	0.5 ^b ±0.6	1.0 ^a ±1.5	0.2 ^a ±0.3	<0.1 ^a ±0.1
	Au	2.3 ^a ±2.5	0.2 ^a ±0.4	0.6 ^b ±1.1	2.3 ^b ±3.6	0.2 ^a ±0.3	0.1 ^a ±0.2
<i>p</i> -value		0.162	0.332	0.015	0.014	0.178	0.812
<i>Trichoribates novus</i> (Sellnick, 1928)	Sp	0.0 ^a ±0.0	0.2 ^a ±0.3	0.4 ^a ±0.7	0.0 ^a ±0.0	0.0 ^a ±0.0	1.0 ^a ±1.4
	Su	1.9 ^a ±4.0	0.6 ^b ±1.0	0.1 ^b ±0.3	0.5 ^a ±0.9	0.3 ^a ±0.9	<0.1 ^b ±0.1
	Au	1.3 ^a ±1.7	0.2 ^a ±0.6	0.1 ^{ab} ±0.2	0.1 ^a ±0.3	0.3 ^a ±0.9	<0.1 ^b ±0.1
<i>p</i> -value		0.127	0.006	0.045	0.089	0.370	<0.001
<i>Achipteria coleoptrata</i> (Linnaeus, 1758) °	Sp	0.0 ^a ±0.0	2.3 ^{ab} ±2.8	0.4 ^a ±0.8	0.1 ^a ±0.2	0.0 ^a ±0.0	0.4 ^a ±1.2
	Su	<0.1 ^a ±0.1	0.3 ^a ±0.5	0.2 ^a ±0.4	0.3 ^b ±0.5	0.1 ^a ±0.2	0.0 ^a ±0.0
	Au	0.8 ^a ±1.4	0.6 ^b ±1.2	0.1 ^b ±0.4	0.0 ^a ±0.0	<0.1 ^a ±0.1	0.0 ^a ±0.0
<i>p</i> -value		0.173	0.018	0.006	0.002	0.361	0.162
<i>Metabelba pulverosa</i> Strenzke, 1953	Sp	0.0 ^a ±0.0	0.7 ^{ab} ±1.7	0.0 ^a ±0.0	0.5 ^a ±0.7	0.0±0.0	<0.1 ^a ±0.1
	Su	0.0 ^a ±0.0	1.0 ^a ±1.9	0.0 ^a ±0.0	1.1 ^a ±1.5	0.0±0.0	0.0 ^a ±0.0
	Au	0.2 ^a ±0.4	0.7 ^b ±1.4	<0.1 ^a ±0.1	0.1 ^a ±0.3	0.0±0.0	0.0 ^a ±0.0
<i>p</i> -value		0.374	0.012	0.097	0.789	1.000	0.374
<i>Scheloribates laevigatus</i> (C.L. Koch, 1835) °	Sp	0.0 ^a ±0.0	0.6 ^a ±1.3	0.0 ^a ±0.0	0.7 ^a ±1.1	0.0 ^a ±0.1	0.0±0.0
	Su	0.1 ^b ±0.2	0.3 ^a ±0.6	0.2 ^a ±0.4	1.7 ^a ±4.4	<0.1 ^a ±0.1	0.0±0.0
	Au	0.1 ^{ab} ±0.2	0.2 ^a ±0.4	<0.1 ^a ±0.1	0.8 ^a ±1.5	<0.1 ^a ±0.1	0.0±0.0
<i>p</i> -value		0.047	0.440	0.355	0.226	0.609	1.000

^{a,b} – significant difference between seasons at *p* ≤ 0.05; the same letter indicates that difference is not significant.

(°) – intermediate hosts of tapeworm (Denegri 1993; Roczeń-Karczmarsz and Tomczuk 2016; Tomczuk *et al.* 2017)

Table 4 Occurrence of oribatid families and species ($A < 0.5$) in goose pasture (GP) and corresponding meadow (GM), goat pasture (GoP) and corresponding meadow (GoM), fallow deer pasture (FP) and corresponding meadow (FM) in spring (Sp), summer (Su) and autumn (Au).

Species	Season	Plot					
		GP	GM	GoP	GoM	FP	FM
<i>Hypochothonius luteus</i> Oudemans, 1917	Sp						
	Su		*				
	Au						
<i>Rhysotritia duplicata</i> (Grandjean, 1963)	Sp	*					
	Su	+					
	Au	+					+
<i>Spatiodamaeus boreus</i> (Bulanova-Zachvatkina, 1957)	Sp		+				+
	Su		+				
	Au	+	+	*			
<i>Oppiella nova</i> (Oudemans, 1902) °	Sp		+	+			
	Su	*	+	*	*	+	*
	Au	*	+			+	
<i>Suctobelba</i> sp.	Sp		*		*	*	
	Su						
	Au						
<i>Scutovertex minutus</i> (C.L. Koch, 1836)	Sp						+
	Su			*			
	Au					*	+
<i>Galumna obvia</i> (Berlese, 1914)	Sp			*	+		*
	Su	+	+		+	+	
	Au		+	+	+	+	+
<i>Ceratozetes gracilis</i> (Michael, 1884) °	Sp	*	+		*		
	Su				*	*	
	Au	+	+		+		
<i>Trichoribates incisellus</i> (Kramer, 1897)	Sp						+
	Su						*
	Au						
<i>Liebstadia humerata</i> Sellnick, 1928	Sp		+		+		
	Su		*		+		
	Au						
<i>Scheloribates latipes</i> (C.L. Koch, 1844) °	Sp		+		+	+	+
	Su	+	+	+	+	+	*
	Au	+	+	+	+	+	

(+) – $A = 0.1 - 0.5$

(*) – $A < 0.1$

(°) – intermediate hosts of tapeworm (Denegri 1993; Roczeń-Karczmarz and Tomczuk 2016; Tomczuk *et al.* 2017)

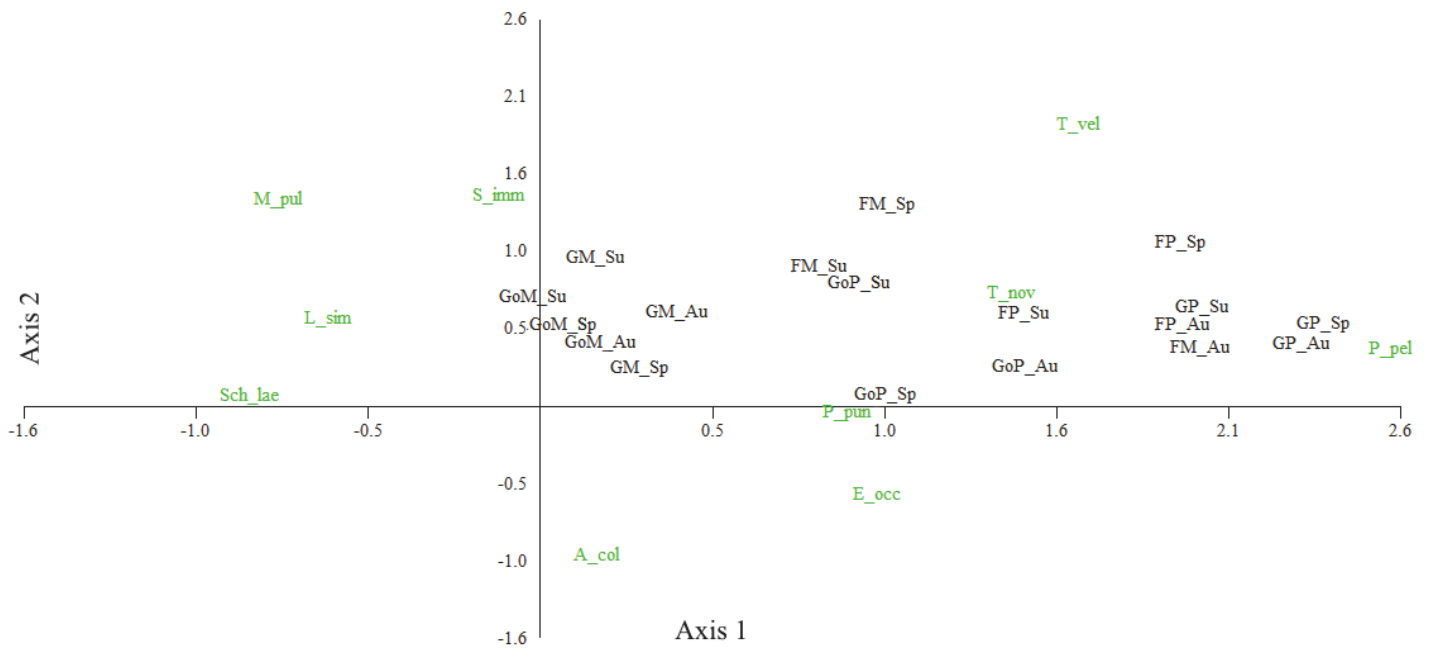


Figure 3 Detrended correspondence analysis (DCA) for most abundant ($A > 0.5$) oribatid species (adults and juveniles). Season, eigenvalues for axis 1 $\lambda = 0.59$ (58.3%), for axis 2 $\lambda = 0.07$ (7.4%). Goose pasture (GP) and corresponding meadow (GM), goat pasture (GoP) and corresponding meadow (GoM), fallow deer pasture (FP) and corresponding meadow (FM), in spring (Sp), summer (Su) and autumn (Au). A_col – *Achipteria coleoprata*, E_occ – *Eupelops occultus*, L_sim – *Liebstadia similis*, M_pul – *Metabelba pulverosa*, P_pel – *Platynothrus peltifer*, P_pun – *Punctoribates punctum*, S_lae – *Scheloriabates laevigatus*, S_imm – *Sellnickochthonius immaculatus*, T_vel – *Tectocepheus velatus*, T_nov – *Trichoribates novus*.

Seasonal changes in the goose pasture/ meadow

Both at the goose pasture and meadow the abundance of Oribatida and Mesostigmata did not differ significantly between the seasons. Only the abundance of other mites was significantly higher in spring than in autumn (Table 2). In all studied seasons, total density of mites, as well as of Oribatida, was higher in the pasture than in the meadow with differences being insignificant.

Platynothrus peltifer was the most numerous species in the pasture but its abundance did not differ significantly between the seasons. Only in some species significant seasonal differences were observed. In the pasture, *T. velatus* was more abundant in summer than in other seasons and *S. laevigatus* was more abundant in summer than in spring. In the meadow, *P. peltifer* was more abundant in spring than in other seasons, *T. novus* was more abundant in summer than in other seasons, *A. coleoprata* was more abundant in autumn than in summer, while *M. pulverosa* was more abundant in summer than in autumn (Table 3).

Seasonal changes in the goat pasture/ meadow

In the goat pasture, total density of mites and of their individual groups differed significantly between the seasons (Table 2). In this pasture, the density of Acari and of Mesostigmata was higher in autumn than in spring, density of Oribatida was higher in autumn than in the remaining seasons, while other mites were more abundant in spring than in summer and autumn. In the meadow, no seasonal differences were observed in total density of Acari and Oribatida but such differences were observed in Mesostigmata and other mites (Table 2). In many oribatid species significant seasonal differences were perceived. In the pasture, *P. peltifer* and *L. similis* were more abundant in autumn than in other seasons, *T. novus* and *A. coleoprata* were more abundant in spring than in other seasons, and *P. punctum* was more abundant in summer and autumn than in spring. In the meadow, *E. occultus* was more abundant in spring and autumn

Table 5 Abundance of juvenile forms (*A*, in 10^3 individuals * $m^{-2} \pm$ SD) of most numerous Oribatida (*A* > 0.5) in goose pasture (GP) and corresponding meadow (GM), goat pasture (GoP) and corresponding meadow (GoM), fallow deer pasture (FP) and corresponding meadow (FM) in spring (Sp), summer (Su) and autumn (Au).

Species	Season	Plot					
		GP	GM	GoP	GoM	FP	FM
<i>Platynothrus peltifer</i>	Sp	21.6 ^a ±33.7	0.3 ^a ±0.7	0.0 ^a ±0.0	0.0 ^a ±0.0	1.2 ^a ±2.2	0.2 ^a ±0.4
	Su	4.1 ^a ±4.3	<0.1 ^a ±0.1	0.2 ^a ±0.3	0.2 ^a ±0.7	0.8 ^a ±1.0	0.0 ^a ±0.1
	Au	62.0 ^b ±80.6	0.0 ^a ±0.0	1.4 ^a ±6.2	0.1 ^a ±0.3	0.7 ^a ±1.5	0.0 ^a ±0.1
<i>p</i> -value		0.002	0.718	0.418	0.208	0.589	0.073
<i>Tectocephus velatus</i>	Sp	0.9 ^a ±2.2	0.5 ^a ±0.9	0.3 ^b ±0.4	0.1 ^a ±0.2	1.9 ^a ±3.9	1.7 ^a ±2.7
	Su	1.7 ^a ±4.4	1.4 ^a ±4.4	0.9 ^a ±1.0	0.4 ^a ±0.8	0.5 ^a ±1.4	0.1 ^b ±0.2
	Au	1.1 ^a ±2.7	0.8 ^a ±1.6	0.1 ^a ±0.2	0.2 ^a ±0.3	0.5 ^a ±1.4	0.1 ^b ±0.3
<i>p</i> -value		0.671	0.554	<0.001	0.245	0.132	0.001
<i>Eupelops occultus</i>	Sp	0.0 ^a ±0.0	0.4 ^a ±1.1	0.2 ^a ±0.4	0.4 ^a ±0.5	0.1 ^a ±0.3	0.1 ^a ±0.3
	Su	0.9 ^a ±1.9	0.7 ^a ±1.4	0.2 ^a ±0.4	0.4 ^a ±0.9	0.2 ^a ±0.4	0.0 ^a ±0.0
	Au	0.3 ^a ±1.1	0.5 ^a ±1.2	0.0 ^a ±0.0	0.1 ^a ±0.2	0.2 ^a ±0.4	<0.1 ^a ±0.1
<i>p</i> -value		0.099	0.811	0.096	0.147	0.406	0.306
<i>Liebstadia similis</i>	Sp	0.0 ^{ab} ±0.0	0.6 ^a ±1.5	0.0 ^a ±0.1	1.9 ^a ±6.0	0.0 ^a ±0.0	0.2 ^a ±0.5
	Su	0.3 ^a ±0.5	2.5 ^a ±5.9	0.1 ^a ±0.3	4.7 ^a ±8.2	0.1 ^a ±0.3	0.1 ^a ±0.3
	Au	0.5 ^b ±0.9	0.2 ^a ±0.3	0.1 ^a ±0.4	0.8 ^a ±1.0	0.0 ^a ±0.1	0.0 ^a ±0.0
<i>p</i> -value		0.041	0.093	0.531	0.099	0.552	0.137
<i>Sellnickochthonius immaculatus</i>	Sp	0.0 ^a ±0.0	2.4 ^a ±3.3	0.0 ^a ±0.0	1.3 ^a ±2.4	0.0±0.0	0.0±0.0
	Su	0.3 ^a ±0.7	0.0 ^a ±0.0	0.2 ^a ±0.8	3.7 ^a ±8.9	0.0±0.0	0.0±0.0
	Au	0.2 ^a ±0.6	0.3 ^a ±0.9	0.1 ^a ±0.3	1.6 ^a ±3.0	0.0±0.0	0.0±0.0
<i>p</i> -value		0.211	<0.001	0.387	0.343	1.000	1.000
<i>Punctoribates punctum</i>	Sp	0.0 ^a ±0.0	0.0 ^a ±0.0	0.0 ^b ±0.1	0.1 ^a ±0.2	0.0 ^a ±0.0	<0.1 ^a ±0.1
	Su	0.8 ^b ±1.4	0.3 ^a ±0.6	0.4 ^a ±0.6	0.4 ^a ±0.8	<0.1 ^a ±0.1	<0.1 ^a ±0.1
	Au	0.7 ^{ab} ±1.0	0.1 ^a ±0.4	0.0 ^a ±0.1	1.1 ^a ±3.7	<0.1 ^a ±0.1	0.0 ^a ±0.0
<i>p</i> -value		0.016	0.123	0.001	0.432	0.609	0.609
<i>Trichoribates novus</i>	Sp	0.0 ^a ±0.0	0.0 ^a ±0.0	0.3 ^a ±0.7	0.0 ^a ±0.0	0.0 ^a ±0.0	0.8 ^a ±1.4
	Su	1.5 ^a ±4.0	0.3 ^b ±0.6	0.1 ^a ±0.3	0.5 ^b ±0.9	0.1 ^a ±0.3	<0.1 ^b ±0.1
	Au	1.2 ^a ±1.6	0.2 ^a ±0.6	0.1 ^a ±0.2	0.1 ^a ±0.3	0.2 ^a ±0.3	<0.1 ^b ±0.1
<i>p</i> -value		0.136	0.092	0.118	0.043	0.171	0.007
<i>Achipteria coleoprata</i>	Sp	0.0 ^a ±0.0	0.0 ^a ±0.1	0.4 ^a ±0.8	0.1 ^a ±0.2	0.0 ^a ±0.0	0.1 ^a ±0.4
	Su	0.0 ^a ±0.0	0.1 ^{ab} ±0.4	0.2 ^a ±0.4	0.3 ^{ab} ±0.5	0.1 ^a ±0.2	0.0 ^a ±0.0
	Au	0.1 ^b ±0.2	0.0 ^b ±0.1	0.1 ^a ±0.4	0.0 ^b ±0.0	0.0 ^a ±0.0	0.0 ^a ±0.0
<i>p</i> -value		0.042	0.468	0.174	0.018	0.130	0.374
<i>Metabelba pulverosa</i>	Sp	0.0 ^a ±0.0	0.1 ^a ±0.4	0.0±0.0	<0.1 ^a ±0.1	0.0±0.0	0.0±0.0
	Su	0.0 ^a ±0.0	0.5 ^a ±1.7	0.0±0.0	0.2 ^a ±0.5	0.0±0.0	0.0±0.0
	Au	0.1 ^a ±0.3	0.5 ^a ±1.0	0.0±0.0	<0.1 ^a ±0.1	0.0±0.0	0.0±0.0
<i>p</i> -value		0.162	0.411	1.000	0.428	1.000	1.000
<i>Scheloribates laevigatus</i>	Sp	0.0 ^a ±0.0	0.1 ^a ±0.2	0.0 ^b ±0.0	0.1 ^a ±0.3	0.0 ^a ±0.0	0.0±0.0
	Su	0.1 ^a ±0.2	0.1 ^a ±0.3	0.2 ^a ±0.4	0.2 ^a ±0.5	<0.1 ^a ±0.1	0.0±0.0
	Au	0.1 ^a ±0.2	0.0 ^a ±0.1	0.0 ^a ±0.0	0.0 ^a ±0.0	<0.1 ^a ±0.1	0.0±0.0
<i>p</i> -value		0.354	0.438	0.022	0.188	0.609	1.000

^{a, b} – significant difference between seasons at $p \leq 0.05$; the same letter indicates that difference is not significant.

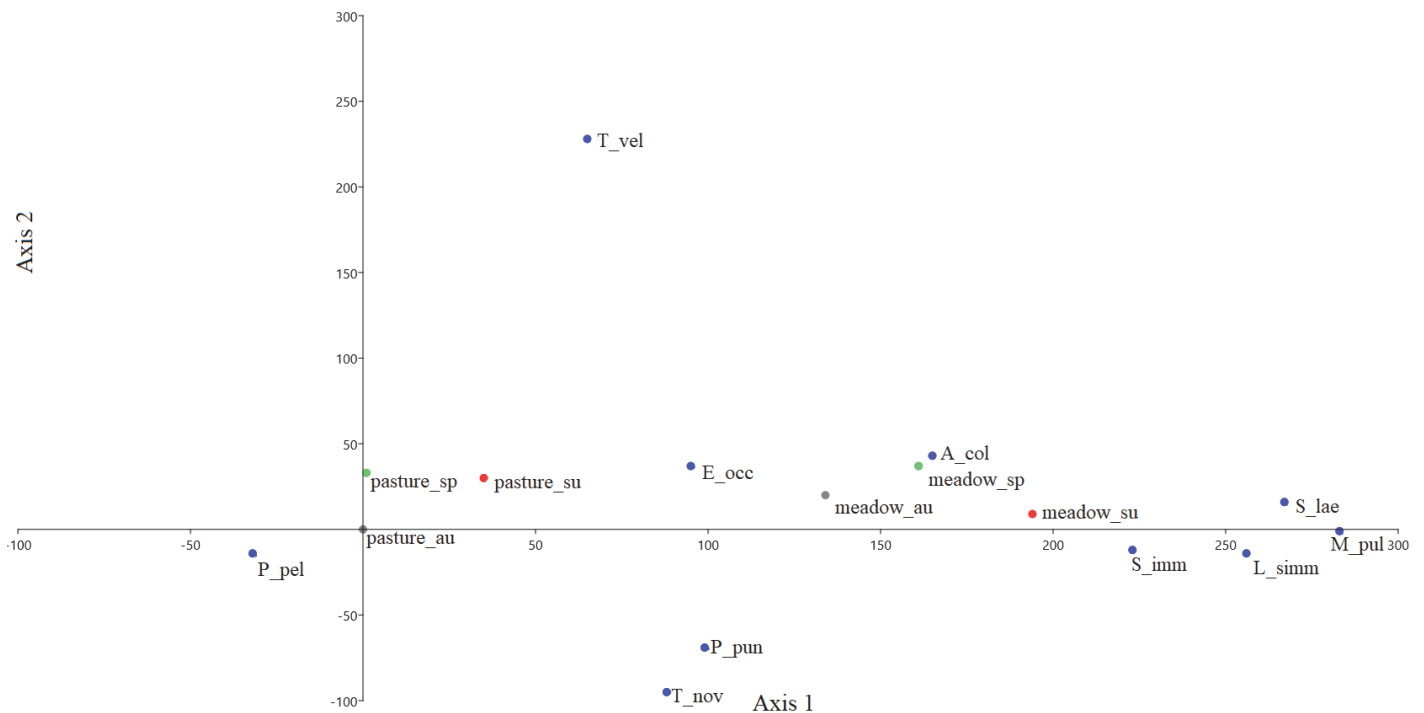


Figure 4 Detrended correspondence analysis (DCA) for most abundant oribatid species (adults and juveniles) with ($A > 0.5$). Study site eigenvalues for axis 1 $\lambda = 0.50$ (84.07%), for axis 2 $\lambda = 0.02$ (3.08%). Pasture and meadow in spring (sp), summer (su) and autumn (au). A_col – *Achipteria coleoprata*, E_occ – *Eupelops occultus*, L_sim – *Liebstadia similis*, M_pul – *Metabelba pulverosa*, P_pel – *Platynothrhus peltifer*, P_pun – *Punctoribates punctum*, S_lae – *Scheloribates laevigatus*, S_imm – *Sellnickochthonius immaculatus*, T_vel – *Tectocephus velatus*, T_nov – *Trichoribates novus*.

than in summer, *A. coleoprata*, in summer than in other seasons, and *P. punctum*, in autumn than in other seasons. Density of Mesostigmata in the goat pasture was significantly higher in autumn than in spring, and in the meadow, it was significantly higher in summer than in spring (Table 2).

Seasonal changes in the fallow deer pasture/ meadow

In the fallow deer pasture significant seasonal differences were observed only in other mites, which were more abundant in spring than in summer (Table 2). In the meadow, total density of Acari and of Oribatida was higher in spring than in summer, and density of other mites was higher in spring than in other seasons. Abundance of some oribatid species differed significantly between the seasons: in the pasture, *P. peltifer* was more abundant in autumn than in the remaining seasons, *E. occultus*, in summer than in spring; in the meadow, *T. velatus*, *L. similis* and *T. novus* were more abundant in spring than in other seasons, and *E. occultus* was more abundant in autumn than in other seasons.

Discussion

In this study, oribatid mites were more influenced by habitat than by season, which is consistent with the literature. Some authors (Clapperton 2002; Chachaj and Seniczak 2006; Schon *et al.* 2010) showed that in pastures grazed by cows and horses, the number of species and species diversity of Oribatida did not clearly change throughout the year. Studies on the impact of climate on Oribatida also showed that habitat factors can be more important than seasons (Corral-Hernandez 2006). Mowing of meadows or grazing and trampling of pastures

by domestic animals have such strong effects on oribatid communities (Maraun and Scheu 2000) that the effects of other factors, e.g. seasonality, can be less visible (Eitminavičiūtė 2006; Eitminavičiūtė *et al.* 2008). In addition, if humidity and temperature remain within the tolerance range of oribatid species, they have little effect on the abundance and structure of the mite communities (Maraun and Scheu 2000). Oribatid species with greater tolerance of environmental factors respond only slightly to short-term changes in the environment (e.g. amount of precipitation, temperature) and availability of food (Clapperton *et al.* 2002). Additionally, pastures and meadows are inhabited by species more tolerant to environmental factors such as drying and low or high temperature (Siepel 1996). Oribatida were shown to be less responsive to seasonal changes in root structure and plant productivity in grazed areas (Bardgett *et al.* 1996; Bardgett *et al.* 1998; Clapperton *et al.* 2002). Our results suggest that this also partly applies to mowed meadows. In contrary to that, in natural ecosystems, such as bogs, Oribatida respond clearly to seasonal changes, both in terms of their abundance and species diversity (Seniczak *et al.* 2019).

Although in our study some effects of seasons on the abundance of all mite groups were observed in the goat pasture, it needs to be emphasized that total density of mites was very low there. Goats negatively affect mite communities due to intensive grazing and trampling (Pacek *et al.* 2020), and also goat manure has a limiting effect on the oribatid fauna (Seniczak *et al.* 2017). In the meadows, there were no clear trends in the abundance of mites and Oribatida, which supports our hypothesis that seasonal effects are more pronounced in the pastures than in the meadows, probably due to regular disturbances in meadows caused by agrotechnical treatments (Siepel 1996; Cookson *et al.* 1998; Vreeken-Buijs *et al.* 1998; Wickings *et al.* 2011; Wickings and Grandy 2013).

Clear seasonal changes were seen in species diversity and in the number of species, which increased during the year in the pastures and decreased in the meadows. In the pastures, these changes could be caused by increased influence of grazing, which promotes fungivorous and parthenogenetic species of Oribatida (Rajski, 1967; Niedbała, 1980; Parfitt *et al.*, 2005; Amiri *et al.* 2008). Additionally, some oribatid species reacted clearly to seasonal changes, both in the pastures and the meadows (Table 3). Many oribatid species are sensitive to grazing, mowing and drying and therefore they may react more strongly to seasonal changes related to agrotechnical treatments and atmospheric factors (Rajski 1967; Olszanowski *et al.* 1996; Siepel 1996; Clapperton 2002; Maraun and Scheu 2000; Chachaj and Seniczak 2006).

Such species include e.g. *E. occultus*, *L. similis*, *T. novus*, *A. coleoprata* and *M. pulverosa*, that are sensitive to organic fertilizers and prefer natural meadows (Weigmann 2006; Szczukowska 2015). However, in our study, more tolerant species like *P. peltifer* and *T. velatus* reacted to seasonal changes. *Platynothrus peltifer* is a hygrophilous species (Travé 1963; Lebrun 1965) and prefers soils rich in organic matter (Rajski 1967; Niedbała 1980), and *T. velatus* shows a broad tolerance to many ecological factors (Rajski 1967; Siepel 1996). In these cases, the seasonal differences in abundance could be caused by the concentration of macroelements in the soil, the livestock species and plant cover (Pacek *et al.* 2020). In the goose pasture *P. peltifer* had favorable conditions in all investigated seasons, which could be the reason for lack of differences in its abundance between the seasons. Although the goose pasture had the highest livestock density, in autumn Oribatida achieved the highest abundance there. Geese have small body weight and are incapable of compacting the soil by trampling. Therefore, they did not affect the soil fauna in any negative way during the grazing season and the mites could reproduce and achieve their highest density. The goose pasture had also the most abundant plant cover as the animals did not eat some plant species, and the soil was well protected against drying and erosion. The goose pasture was also the richest in organic matter (Pacek *et al.* 2020) and water, thus providing very favorable conditions for *P. peltifer*.

Heavier animals, in particular ungulates like goats and fallow deer, strongly compact the soil to a depth of 5 cm and destroy its structure (Greenwood *et al.* 1997; Di *et al.* 2001; Parfitt 2005), thus decreasing the abundance and species richness of oribatid mites (Siepel 1996; Hubert 2000; Clapperton *et al.* 2002; Chachaj and Seniczak 2005; Seniczak 2007a; Schon *et al.*

2008). In the pastures of goats and fallow deer, mites, including Oribatida, were significantly less abundant than in the goose pasture (Pacek *et al.* 2020). However, also in the pastures grazed by goats and fallow deer, the mites and Oribatida were the most abundant in autumn, the difference especially noteworthy with regard to the goat pasture. In our study, livestock density did not clearly change the abundance of mites between seasons.

Platynocheilus peltifer, *L. similis*, *S. laevigatus* and less abundant in pastures *A. coleoprata*, *Oppiella nova* (Oudemans, 1902), *Ceratozetes gracilis* (Michael, 1884) and *Scheloriobates latipes* (C.L. Koch, 1844) are intermediary hosts of Anoplocephalidae, which pose serious problems on horse pastures (Denegri 1993; Roczeń–Karczmarz and Tomczuk 2016; Tomczuk *et al.* 2017). These species are of epidemiological significance where the problem of tapeworms exists. Additionally, *P. peltifer* was highly abundant in pastures, which increased the likelihood of contracting tapeworms in farm animals.

In conclusion, we can state that oribatid communities in pastures and meadows were more affected by habitat than by season. Mowing of meadows, grazing or trampling of pastures by domestic animals had strong effects on Oribatida. However, a seasonal effect on the mites was also observed. Studies of this kind expand our knowledge on the ecology of oribatid mites in pastures and meadows, and can have practical implications for the pasture management and tapeworm prevention.

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