# SOME POPULATION CHARACTERISTICS OF ORIBATID MITES IN STEPPE HABITATS

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ABSTRACT: Some characteristics of the reproduction mode (sex ratio, rate of gravid females, and mean number of eggs per female) were studied in 19 abundant species of oribatid mites in two steppe habitats of the Trans-Volga region, European Russia. Sex ratio close to 1:1 was found in 9 species, which show no significant changes in the reproduction intensity from May to August. Two more species, *Tectoribates ornatus* (Schuster, 1958) and *Microzetorchestes emeryi* (Goggi, 1898), reveal larger portion of females in the populations, yet showing seasonal changes in the population structure. *M. emeryi* is suspectedly a monovoltinous species with partially overlapping generations. In other 8 studied species males were not encountered despite the females were found to be gravid all during the summer. We consider the reproduction mode of these species as parthenogenetic (thelytokous). In our view no less than 27 thelitokous species making up 30% of the total number of oribatid mite species and up to 50% of the total abundance comprise both studied oribatid mite communities. Only parthenogenetic species form a soil strato-ecological group and a guild of true saprovores in steppe habitats.

Key words: oribatid mites, population sex structure, parthenogenesis, reproduction mode, community spatial structure, trophic guilds, steppe habitats

### INTRODUCTION

The sex ratio in populations of orbatid mites has been repeatedly studied, starting from the baseline paper by Grandjean (1941, cited by Luxton 1981a). As a rule, studies have considered only the adults, since sex determination of immatures based on morphological features is impossible. With respect to sex ratio, species are generally divided into four groups: (1) the number of males and females is approximately equal (ratio is near 1:1); (2) no males are present at all or females are hundreds times more abundant than males; (3) females are dozens of times more abundant than males; (4) sex ratio varies in a wide range in different local populations or in one population over time (Grandjean 1941; Luxton 1981a; Norton et al. 1988, 1993).

The first pattern is in a good agreement with a standard life strategy of Acariformes, when offspring are produced after mating of individuals of opposite sexes (Norton and Palmer 1991; Norton et al. 1993). In this case the genetic system represents diplodiploidy, i.e. both parents are diploid (Norton et al. 1993). The indirect fertilization thought the use of spermatophores is characteristic for oribatid mites, a direct contact of sexes is not necessary and likely exists as rare exception in a few species (Woodring and Cook 1962; Ghilarov 1970; Krivolutsky 1995).

The second pattern occurs among parthenogenetic species. Oribatid mites as a taxonomic group are distinguished by their exceptionally high rate of species with parthenogenesis (thelytoky) as a major reproductive strategy. Such species comprise about 10 per cent of the whole oribatid diversity; moreover there exist whole families and superfamilies where sexual reproduction is not known (Brachychthoniidae, Lohmanniidae, Camisiidae, Malaconothridae, Nanhermanniidae, Limnozetidae, Trhypochthonoidea, Parhypochthonoidea) (Norton and Palmer 1991; Palmer and Norton 1991; Norton et al. 1993; Olszanowski and Lembicz 1999; Maraun et al. 2003, 2004). Thelytoky is more frequently found among 'primitive' oribatids (cohors Enarthronota, Desmonomata, Mixonomata, Parhyposomata), but rare among the earliest Palaeosomata (except for members of Palaeacaridae, all are sexual) and highly occasional among the most derived Brachypylina (Norton et al. 1988; Norton and Palmer 1991; Palmer and Norton 1991; Norton et al. 1993; Krivolutsky 1995; Maraun et al. 2003).

A small portion of males in the population (near 1:80-1:100) may be the case of spanandry — presence of inert (not participating in reproduction) 'relic' males in thelytokous population (Norton and Palmer 1991; Norton et al. 1993).

Steady considerable predominance of females in the population (but their dominance is not so considerable) is characteristic for haplodiploidy, widespread among prostigmatic and astigmatic mites but scarcely known for Oribatida sensu stricto (Norton et al. 1993). Haplodiploidy here used sensu Norton et al. 1993: as the males are haploid while the females are diploid. Among oribatids such genetic system was supposed for genera *Humerobates* Sellnick, 1928 and *Orthogalumna* Balogh, 1961 (Helle et al. 1984 by: Norton et al. 1993).

The fourth mode corresponds to both thelytokous species with more or less notable number of spanandric males and species with the 'standard' sexual reproduction inclined to polygyny. Contrary to the earlier proposed assumption (Grandjean 1941; Luxton 1981a), there are no known 'intermediate' species combining (in different periods of time or in different populations) both reproduction strategies — thelytoky and any kind of sexual reproduction (Norton and Palmer 1991).

Generally, two reproduction strategies are prevalent among oribatid mites: sexual with diplodiploid genetic system and parthenogenetic (thelytokous) one.

Not much is known about the role of species with different reproduction strategies in oribatid communities. In a beech wood soil and lower litter (Denmark) the oribatid assemblage comprised 88 species including 33 reliably parthenogenetic and 4 possibly parthenogenetic species (about 38% of the whole assemblage) (Luxton 1981a). In another case, an extremely large component of species with asexual reproductive mode was found in oribatid assemblages in forests (New York State, USA); 67% of species, and 83% of individuals were asexual (Cianciolo et al., in press). There is no similar information for steppes and other semiarid open habitats.

It has been intimated that the portion of parthenogenes in communities is particularly high in extreme unstable habitats around the fumaroles (Ryabinin and Pan'kov 1987), inundated habitats, and disturbed environments like dumps, tillage, etc. (for short survey see Norton and Palmer 1991). It is underlined that the role of parthenogenetic species rises in deep soil layers, where they present the majority of species (Sitnikova 1962; Ryabinin and Pan'kov 1987; Luxton 1981a, b; Norton and Palmer 1991). Recently a negative correlation has been shown between asexuality and biological diversity of oribatid assemblages. Moreover, when considered separately, taxonomically clustered asexual oribatid mites were more strongly represented in more diverse plots than in depauperate ones, opposite from the expected pattern (Cianciolo et al., in press).

The ecological role of parthenogenesis as a reproductive mode for oribatids is still rather unclear. The correlation of the reproductive mode with other environmental peculiarities of species and the ecological roles of the species with different reproductive modes are poorly explored.

### MATERIAL AND METHODS

The main part of the material was collected in the ravine Kirilov Dol in the south of Samarskaya Oblast (N  $52^{\circ}03' \to 51^{\circ}20'$ ) situated in dry steppe landscape of the Trans-Volga Plain (the south-east of the European part of Russia).

A set of 45 samples was taken on 10 August, 1993 along a transect on a steppe part of the ravine slope. Three other sets of the samples were taken from 1 m<sup>2</sup> plots on 17 and 26 August, 1993, and on 9–10 June, 1994. For last three sets two plots were explored each time. One plot always was located on the plateau in a dry steppe dominated by Stipa lessingiana, Stipa capillata, and Galatella villosa (referred to as the "plateau" in the table), the other plot was located on the ravine slope in a true steppe dominated by Stipa tirsa and forbs with Phragmites *communis* (referred to as the "Slope" in the table). For each set the surface layer of soil 5 cm deep including turf and litter was sampled. Additionally, layers of soil at depth 5-10 and 10-15 cm were sampled in the plots. In total, 250 samples each of 125 cm<sup>3</sup> were examined.

To better characterize one species, *Microze-torchestes emeryi* (Goggi, 1898), additional sample sets from different steppe habitats were used. There are: 13 samples taken on 9 May, 1992 in the area near Kirilov Dol (N 51°55' E 50°53'); 26 samples taken on 15 September, 1992 in the 'Aituarskaya Steppe' Station of Orenburg Strict Nature Reserve (N 51°04' E 57°40'); 20 samples taken on 29 September, 1992 in the 'Burtinskaya Steppe' Station of Orenburg Strict Nature Reserve (N 51°16' E 56°40').

The taking of samples, extraction of mites and the following treatment were done using standard procedures. About 10200 individuals (including immatures) belonging to 90 species were examined.

The sex ratio (of adults only) was calculated for each set for the most abundant species except the species where defining sex without dissection was impossible.

#### RESULTS

For a number of species the sex ratio is close to 1:1 (Table 1). These are several "higher" oribatid mites (Poronota), such as *Oribatella similesuperbula* Weigmann, 2001, *Eupelops nepotulus* (Berlese, 1917), *Ceratozetes minutissimus* Willmann, 1951, *Ceratozetella sellnicki* (Rajski, 1958), *Semipunctoribates astrachanicus* (Shaldybina, 1973), *Liebstadia pannonica* (Willmann, 1953), *Peloribates europaeus* Willmann, 1935, and *P. pilosus* Willmann, 1935.

Two species, *Peloptulus gibbus* Mihelčič, 1957 and *Tectoribates ornatus* (Schuster, 1958), show no distinctive sex ratio, but there is a tendency to a

# Table

Sex ratio and some reproductive characteristics of females in the oribatid mite populations in the steppe habitats, South-East of the European part of Russia

Species	Dates	Sample set	Number of adults examined <sup>1</sup>	Sex ratio <sup>2</sup>	Portion of gravid females <sup>3</sup>	Mean ± SD number of eggs per one gravid female <sup>4</sup>
Peloptulus gibbus	1-10 June	plateau	26 (1)	0.64	0.42	$2.5 \pm 0.55$ (3)
	1-10 June	slope	35 (2)	0.51	0.33	$1.0 \pm 0.0$ (1)
	11-20 July	plateau	33 (5)	0.32	0.58	$1.54 \pm 0.69$ (3)
	11-20 July	slope	28 (2)	0.35	0.42	$1.5 \pm 0.76$ (3)
	21-31 August	plateau	47 (12)	0.20	0.46	$1.88 \pm 0.88$ (4)
	11-20 August	all steppe transect	34 (5)	0.38	0.28	$1.5 \pm 0.55$ (2)
Eupelops nepotulus	1-10 June	both plateau and slope	35(2)	0.43	0.75	1.60 ± 0.91 (4)
	21-31 August	slope	31 (4)	0.44	0.67	$1.5 \pm 0.71$ (3)
Ceratozetes minutissimus	11-20 July	slope	27 (3)	0.42	1.00	1.21 ± 0.43 (2)
	11-20 August	lower part of the transect (true steppe only)	144 (0)	0.51	0.64	1.06 ± 0.25 (2)
	21-31 August	slope	43 (0)	0.56	0.47	$1.00 \pm 0 (1)$
Ceratozetella sellnicki	11-20 August	all steppe transect	19 (0)	0.58	0.92	1.58 ± 0.67 (3)
Semi punctoribates	11-20 August	all steppe transect	35 (0)	0.49	0.72	3.31 ± 1.60 (6)
astrachanicus	21-31 August	slope	81 (0)	0.47	0.91	2.74 ± 1.02 (4)
Oribatella	11–20 August	all steppe transect	22 (0)	0.54	0.50	$1.20 \pm 0.45(2)$
similesuperbula	21-31 August	slope	36 (0)	0.61	0.57	1.67 ± 0.50 (2)
	1-10 June	plateau	20 (1)	0.21	0.87	$1.85 \pm 0.37$ (2)
	<u>1-10 June</u>	slope	25(1)	0.21	0.84	$1.81 \pm 0.66$ (3)
Tectoribates ornatus	11-20 July 11-20 July	plateau	30 (1) 11 (0)	0.24 0.27	0.70 0.50	$\frac{1.71 \pm 0.82 (3)}{1.50 \pm 1.00 (3)}$
	-	slope				$1.50 \pm 1.00$ (3)
	11-20 August	all steppe transect	39 (2)	0.38	0	_
	21–31 August	plateau	33 (1)	0.62	0	_
	21-31 August	slope	15(1)	0.21	0	_
Microzetorchestes emeryi*	1-10 May	additional sample set (in the vicinity of the Kirilov Dol site)	63(13)	0.12	0	_
	1-10 June	both plateau and slope	24 (0)	0.24	0.61	3.18 ± 1.33 (5)
	11-20 July	both plateau and slope	7 (2)	0.25	0	_
Peloribates pilosus	11-20 August	all steppe transect	23 (0)	0.70	0.29	2.0 (2)
	21-31 August	slope	49 (4)	0.56	0.80	$2.5 \pm 0.82$ (4)
Peloribates europeus	11-20 July	both plateau and slope	26 (4)	0.54	0.92	3.09 ± 1.45 (6)
	21-31 August	both plateau and slope	51 (5)	0.30	0.52	3.13±1.15(5)
Liebstadia pannonica	11-20 July	plateau	109 (4)	0.43	0.77	$1.78 \pm 0.59$ (3)
	11-20 July	slope	38 (0)	0.45	0.76	$1.75 \pm 0.68$ (3)
	21-31 August	plateau	96 (0) 75 (0)	0.54	0.84	$2.17 \pm 0.75$ (4) $2.10 \pm 0.72$ (3)
	21-31 August	slope	75 (0)	0.59	0.94	2.10 ± 0.72 (3)

Table continued

Species	Dates	Sample set	Number of adults examined <sup>1</sup>	Sex ratio <sup>2</sup>	Portion of gravid females <sup>3</sup>	Mean ± SD number of eggs per one gravid female <sup>4</sup>
Liebstadia pannonica	11-20 July	plateau	109 (4)	0.43	0.77	1.78 ± 0.59 (3)
	11-20 July	slope	38 (0)	0.45	0.76	$1.75 \pm 0.68$ (3)
	21-31 August	plateau	96 (0)	0.54	0.84	2.17 ± 0.75 (4)
	21-31 August	slope	75 (0)	0.59	0.94	2.10 ± 0.72 (3)
Protoribates cf. capucinus	1-10 June, 11-20 July, 11-31 August	the whole dataset	307	0	No data available	_
Epilohmannia cylindrica	1-10 June	slope	93	0	0.65	$1.65 \pm 0.73$ (3)
	11-20 July	both plateau and slope	42	0	0.62	1.15 ± 0.37 (2)
	11-31 August	the whole dataset	113	0	No data available	No data available
Rhysotritia ardua affinis	1–10 June, 11–20 July, 11–31 August	the whole dataset	54 (7)	0	_	_
Austrocarabodes foliaceisetus	1-10 June, 11-20 July, 11-31 August	the whole dataset	39 (3)	0	_	_
Parhypochthonius aphidinus	1–10 June, 11–20 July, 11–31 August	the whole dataset	7 (0)	0		_
Gehypochthonius rhadamantus	1–10 June, 11–20 July, 11–31 August	the whole dataset	27 (0)	0	_	_
Discoppia (Cylindroppia) cylindrica	1–10 June, 11–20 July, 11–31 August	the whole dataset	231 (10)	0	_	_
Microppia minus	21-31 August	plateau	43 (1)	0	_	-

<sup>1</sup> number of adults with unclear sex affinity is given in brakets; <sup>2</sup> portion of males in the total number of adults, with the sex defined;

<sup>3</sup> of all identified females; <sup>4</sup> maximum value is given in brackets.

\* Only the sample sets where adults were presented (see Discussion)

female domination in the population structure. In different sets the ratio varies from 1:5 to 1:1. It is of interest that in *T. ornatus* only one among the seven examined sets did not show considerable female predominance.

Only one species, *Microzetorchestes emeryi* (Goggi, 1898), exhibits a strong female predominance. Males were being present in the population but their number was much less than that of the females. For instance, in the first ten-day period of May the males comprised only 11.5% of the total number of adults (see Discussion).

A large group of species exhibits absence of males completely. They are as follows: *Epilohmannia cylindrica* (Berlese, 1904), *Rhysotritia ardua affinis* Sergienko, 1989, *Parhypochthonius aphidinus* Berlese, 1904, *Gehypochthonius rhadamanthus* Jacot, 1936, *Austrocarabodes foliaceisetus* D. Krivolutsky, 1969, *Microppia minus, Discoppia* (C.) cylindrica, Protoribates cf. capucinus and several others, which were not studied quantitatively (such as *Tectocepheus velatus*).

### DISCUSSION

# Seasonality of female predominance in populations

A steady considerable predominance of females in the population is regarded as one of the important indirect evidence of haplodiploidy (Norton et al. 1993). We found no references concerning genetic systems in the genus *Microzetorchestes* as well as in the family Zetorchestidae. Based on our sex ratio data we can expect haplodiploidy, but further research is necessary.

*M. emeryi* presents a unique example here. In the assemblages studied it is the only species demonstrating clear seasonal dynamics of age and sex structure in its population. In the local environment, *M. emeryi* may be considered a monovoltine species with a partial overlap of consecutive gener-

## Population characteristics of oribatids

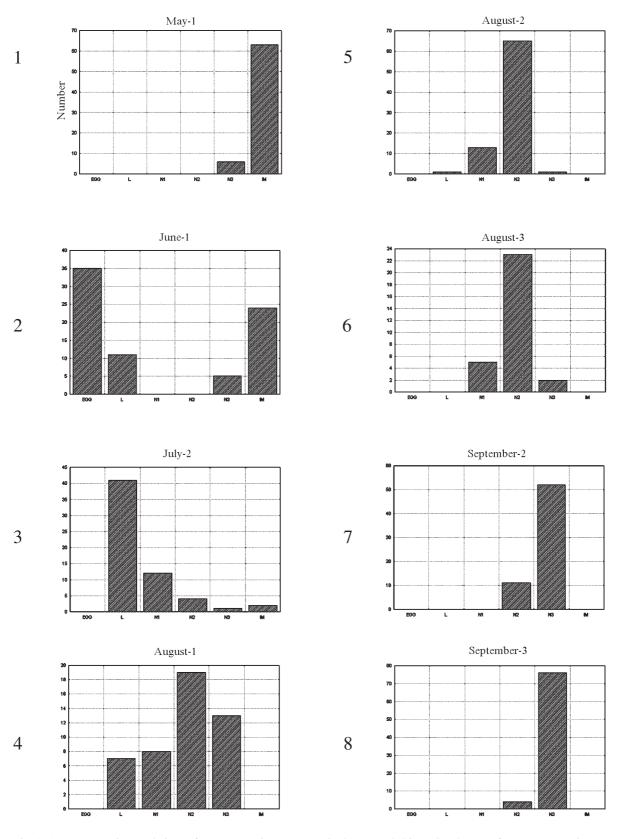


Fig. 1. Age structure in populations of *Microzetorchestes emeryi* in the steppe habitats, South-East of European Russia. Graph titles (1–8) indicate date of the census (month and its ten-day period).

EGG — eggs number in gravid females; L, N1, N2, N3 — Larvae, protonymphs, deutonymphs, tritonymphs; IM — imago (male, female, and individuals of undetectable sex in total).

Both graphs for September represent an additional data from other locations ( $N51^{\circ}16' E56^{\circ}40'$  and  $N51^{\circ}04' E57^{\circ}40'$ ) and should not be placed at the same data set, only illustrate the tendency.

The total sample is 489 individuals of *M. emeryi*. Namely: 1) May-1: 69; 2) June-1: 40; 3) July-2: 60; 4) August-1: 47; 5) August-2: 80; 6) August-3: 30; 7) September-2: 63; 8) September-3: 80.

ations (Fig.). From the mid ten-day period of July and especially from the beginning of August until the end of September (later periods were not studied) only immatures of *M. emeryi* were present (no adults), irrespective of the total number of individuals in the sample set. Moreover the number of adult individuals was highest in the first ten-day period of May and decreased to the middle of July. This decrease concurred with the appearance and increase of larvae and then protonymphs. Thus we suppose that only tritonymphs (or adults) overwinter. The time of oviposition continues from the end of May until mid-June. Only immatures survive from the end of July until the winter.

Female predominance was highest in the period when adults comprised the main part of the population. As the portion of adults in the population decreases the ratio changes: in the first ten-day period of June males accounted for 24% of all adults (and it was the maximum portion of males for this species). Possibly females die simultaneously after oviposition while the males have no similar death synchronization factor. Evidently the sex ratio 1:10 should be considered as the 'normal' one for the species. Therefore, this species would be a good one to study cytologically for the presence of haplodiploidy.

The genetic system in the genus *Tectoribates* is also not known. This genus belongs to the Achipteriidae, and there was presumed diplodiploidy noted in the family (*Achipteria punctata*) (Sokolov 1954, by Norton et al. 1993). However at least one family of Brachypylina (Galumnidae) is known to demonstrate various genetic systems in different genera (Norton et al. 1993). Besides, *Tectoribates* is also sometimes placed among Oribatellidae (Bernini 1974; Subia, 2004), for which we have no information about the genetic systems. So haplodiploidy can be suspected for the species, but it needs further testing.

Intriguingly *T. ornatus* also shows distinct seasonal dynamics of reproduction rate and sex ratio. The portion of gravid females in the population decreased from over 80% at the beginning of June to zero at mid of August (Table). So reproduction was at the peak in June but actually stopped in August. At the same time the sex ratio increased from 20% male to over 60%. Unfortunately data on this species are limited to summer only. Nevertheless the reproduction pattern in *T. ornatus* is assumed to be similar to that of *M. emeryi*.

Thus we may suppose in both taxonomically unrelated *T. ornatus* and *M. emeryi* the presence of

haplodiploidy as well as the strong seasonality of reproduction with female death synchronization.

## Absence of males in population

Males absence itself indicates the parthenogenetic (thelytoky) reproduction mode. The presence of immatures of different stages, including larvae, as well as gravid females in all populations at any time, serves as an additional evidence of thelytoky.

All but one species was previously recognized as thelytokous. For Tectocepheus velatus Michael, 1880 it was made by Fujikawa (1988, 1995), Hajmová and Smrž (2001); for other Tectocepheus (T. sarekensis, T. minor) — by Maraun et al. (2003), for Microppia minus (Paoli, 1908) by Luxton (1981a), for Discoppia (Cylindroppia) cylindrica (Perez-Iñigo 1965) - by Coetzee and Brink (2003), and for Oppiella nova (Oudemans, 1902) — by Woodring and Cook (1962). For the first time we assume thelytoky in Austrocarabodes. But this genus is closely related to the Carabodes, for some species of which thelytoky was already suspected (Reeves 1998; Norton et al. 1993). The evidence of thelytoky in Protoribates is of a particular interest. This is the representative of Brachypylina - Poronota (Circumdehescentiae), where thelytoky is rather uncommon. Nevertheless for this genus (and conceivably for the same species) thelytoky was already suspected (Norton et al. 1993, referred as *Xylobates*).

In the assemblages studied many other species may be thelytokous but they were not studied quantitatively. These include are R. ardua affinis Sergienko, 1989, Camisia horrida (Hermann, 1804), C. biverrucata (C.L.Koch, 1839), Nothrus biciliatus C.L.Koch, 1841, Trhypochthonius tectorum (Berlese, 1896), Tectocepheus velatus and presumably T. alatus Berlese, 1913, all species of Brachychthoniidae presented in this assemblage - Sellnickochthonius hungaricus (Balogh, 1943), S. meridionalis (Bernini, 1973), Brachychthonius impressus Moritz, 1976, B. hirtus Moritz, 1976, B. bimaculatus Willmann, 1936, B. cf. immaculatus Forsslund, 1942, Liochthonius muscorum Forsslund, 1964, L. cf. lapponicus (Tragardh, 1910), L. propinquus Niedbala, 1972, L. simplex (Forsslund, 1942), L. leptaleus Moritz, 1976, Verachthonius laticeps (Strenzke, 1951). We may assume thelytoky in it because this reproductive mode is the only one known in the respective genera and/or families (Norton and Palmer 1991; Palmer and Norton 1991; Hajmová and Smrž 2001).

# The role of parthenogens in oribatid communities

As a whole the examined oribatid assemblages include no fewer than 27 parthenogenetic (the-lytokous) species comprising nearly 32–33% of the species richness of each assemblage and nearly 50% of the total oribatid mite abundance in each assemblage (all periods taken together).

In all studied assemblages a large portion of thelytokous species belongs to a soil strato-ecological group, i.e. these are species having a mode of the vertical distribution in the lower layer of soil (10–15 cm deep, deepest layers not examined). Exceptions are R. ardua affinis and A. foliaceisetus, which belong in the surface (litter) strato-ecological group, as well as Microppia minus which belongs to the sub-surface strato-ecological group (Smelansky 1999). Even more interesting, the whole soil strato-ecological group in the studied assemblages consists of thelytokous species, namely are Epilohmannia cylindrica, Gehypochthonius rhadamanthus, Discoppia (C.) cylindrica, and Protoribates cf. capucinus. The oribatid mite assemblages in soil are constituted of mostly thelytokous species with only a small portion of species having other reproductive modes. The soil in these environments contained 5 to 25 species compared to 25-50 being encountered in the litter.

In these assemblages the gut content was analyzed quantitatively in 25 oribatid 'ecological species' (immatures and adults as different operational units, 17 taxonomical species) and qualitatively in several other species. The following trophic guilds were recognized: true saprovores, non-specialized sporovores, detritivores/hyphovores, specialized sporovores, and (specialized) sporovores 'feeding on surface' (Smelansky 2002). True saprovores feed on dead tissues of higher plants; non-specialized sporovores feed on any fungal and plant spores (pollen grains) and their guts contain dozens of morphological kinds of spores; detritivores/hyphovores feed fungal hyphae, very commonly this trophic mode combines with feeding detritus (including dead animal tissues as well); specialized sporovores feed on a very limited set of fungal spores including only 4-5 morphological kinds of spores in each mite species; the guts of sporovores 'feeding on surface' contain unusually high portion of pollen grains and spores of epiphytic fungi. Based on this analysis many thelytokous oribatids should be classified as true saprovores. In fact, the guild in total (for all assemblages) includes only 7 species, and all of them are thelytokous: *Epilohm*annia cylindrica, *Rhysotritia ardua affinis, Parhy*pochthonius aphidinus, Gehypochthonius rhadamanthus, Austrocarabodes foliaceisetus, Discoppia (C.) cylindrica, Protoribates cf. capucinus.

The true saprovorous guild contains only 7– 8% of the whole oribatid community (6 of 73 species in the slope assemblage and 4 of 57 species in the plateau assemblage). All other species feed on fungal material and/or detritus. Nevertheless thelytokous saprovores play a surprisingly important role in the deep soil. They are the main part of the soil strato-ecological group, and they comprise nearly all oribatid assemblage in the deepest soil layer (10–15 cm).

Thus the species having a parthenogenetic reproductive mode participate in community spatial and trophic structures in a very specific manner. The soil strato-ecological group and the trophic guild of true saprovores are formed exclusively of these species. At the same time, in other strato-ecological groups and other trophic guilds the role of parthenogenetic species is negligible. Their participation in surface (litter) and sub-surface strato-ecological groups and in trophic guilds of non-specialized sporovores and detritivores/hyphovores is minimal (less than 5% of species richness), while two guilds of species at all.

The studied oribatid mite assemblages break into 2 soil profile horizons by a line lying between 5 and 10 cm deep. The lower horizon includes almost only parthenogenetic (thelytokous) true saprovore species, while their participation in the upper soil levels is rather insignificant. The depth of the line is assumed to relate to the lower border of litter and turf while only mineral soil is presented deeper. As a habitat for oribatid mites, mineral soil is strongly different from litter and turf. We suspect the mineral soil is a highly patchy environment. The main food resource for oribatids here is dead roots. The soil matrix is very poor in food resources for oribatids while resource rich patches (dead roots) are scarce and isolated. Therefore asexual saprovore mites have a best fit to the soil environment while they have no preferences in litter and turf where sexual species are more successful competitors.

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