SOIL ORGANISMS **90** (1) · April 2018 pp. 13–21

Sex ratios of oribatid mite assemblages differ among microhabitats

Katja Wehner*, Michael Heethoff and Adrian Brückner

Ecological Networks, Technische Univeristät Darmstadt, Schnittspahnstraße 3, 64287 Darmstadt, Germany

* Corresponding author, e-mail: kdwehner@gmx.de

Received 8 January 2018 | **Accepted** 2 March 2018

Abstract

This study investigates sex ratios of oribatid mite species and oribatid mite assemblages in different forest microhabitats (dead wood, grass sod, moss, lichen litter, tree bark) to identify possible factors driving sex ratio dynamics. We considered 46,320 individuals belonging to 47 species, and analyzed data on numbers of sexual and parthenogenetic species as well as individuals across microhabitats using paired t-tests and generalized linear mixed effect models. Most species (75 %) were sexual, with females comprising 43 % to 89 % of samples. In twelve out of 35 sexual species sex ratios differed significantly among microhabitats, the sex ratio of most species (23) remained constant. Parthenogenetic species of Enarthronota, Mixonomata, Nothrina and *Quadroppia quadricarinata* comprised of 100 % females, but in *Oppiella nova*, and *Tectocepheus* spp. spanandric males were found (1–3 %). Sex ratios of oribatid mite assemblages were generally female-biased and differed significantly among microhabitats. The highest proportions of females were found on tree bark (~ 72 %) and grass sod (~ 69 %) and the lowest were in lichens (~ 53 %). The mechanism of sex determination in oribatid mites and factors influencing the distortion of primary sex ratios are poorly known, so explanations for the observed patterns remain speculative. Since field observations are mostly infeasible, complex long-term laboratory studies on egg deposition, egg development and development of males and females under different conditions in different species are needed.

Keywords Sex ratios | oribatid mites | microhabitats | litter | dead wood | moss | grass sod | lichen | tree bark

1. Introduction

Theories on sex ratio evolution are manifold, starting with the Fisher theorem proposing equal sex ratios with equal resource investment in both sexes (Fisher 1930). Exceptions to this prediction, i.e. sex ratios distorted towards males or females, have been explained by many unpredictable influences, such as local mate competition (Hamilton 1967), geographical or temporal variation (Charnov et al. 1981), maternal condition advantages (Charnov 1982, Nager et al. 1999), food stress (Myers 1978) or sex-ratio-distorting endosymbiotic bacteria (Weeks 2003). A full explanation of sex ratio pattern – both equal and distorted – requires some preconditional knowledge (Myers 1978, Nager et al. 1999, Kokko & Jennions 2008): How is sex determined? Are there different mortality rates of males and females prior to and after birth (primary sex ratios)? Is the production of one sex more expensive than the other? What is the future success of the different sexes?

In oribatid mites – a group of decomposer microarthropods comprising about 11,000 described species worldwide (Subias 2017) – a surprisingly high percentage of species reproduces parthenogenetically. While only 1 % of all animal species are obligate parthenogens, nearly 10 % of oribatid mites have abandoned sex, comprising female-only lineages as thelytokous automicts (Bell 1982, Norton & Palmer 1991, Norton et al. 1993, Heethoff et al. 2009). How this mode of reproduction could persist over evolutionary timescales – oribatid mites are at least 360 million years old (Shear et al. 1984, Norton et al. 1988, Schaefer et al.

ISSN 1864-6417 (print) · **ISSN** 2509-9523 (digital)

2010) – is still enigmatic. Most oribatid mite species are diploid (usually 2n = 18, Heethoff et al. 2006) regardless of the reproductive mode, but sex determination remains unresolved (they lack sex chromosomes) and our information on cytological mechanisms of parthenogenesis (automixis with terminal fusion) relates to very few species (Taberly 1987, Wrensch et al. 1994, Heethoff et al. 2006, 2009, Laumann et al. 2008, Bergmann & Heethoff 2012, Bergmann et al. 2018). In sexual oribatid mite species fertilization indirectly occurs via spermatophores that are deposited on the ground by the males and taken up by females usually without individual contact (Norton et al. 1993, Walter & Proctor 1999).

The current study focuses on the overall distribution of sex ratios among species in oribatid mite communities occupying different forest microhabitats. In general, different kinds of sex ratio patterns are known in oribatid mites, comprising groups with an approximately equal sex ratio, those where males are absent or extremely rare, and those species with sex ratios varying widely among local populations or within a population over time (see Smelansky 2006 and references therein). However, most studies of sex ratios have related to either single species or to species in a single microhabitat, such as litter or moss (e.g., Steinberger et al. 1990, Hubert 2000). Since many oribatid mites occur in more than one forest microhabitat (Wehner et al. 2016), the sex ratio of oribatid mite assemblages or even that of a certain species may vary according to different microhabitat-specific conditions (e.g. resource availability). To test this idea we examined the distribution of sex ratios of oribatid mites in a German forest, according to both species and species assemblages in different forest microhabitats.

2. Material and methods

Samples of litter, dead wood and moss (ten replicates each, taken haphazardly in an area of 30 m × 30 m) were taken in November 2016 from an oak-mixed forest in State Forest 2043 A in Mörfelden-Walldorf (N49°58`30.8424/E8°33`1.0332; 96 m a.s.l.), about 15 km north of Darmstadt, Hesse, Germany. The site is moderate subcontinental and mesotrophic, the surface is flat and covered with sand. The main tree population – pine (*Pinus sylvestris*), birch (*Betula pendula*), oak (*Quercus robur*), beech (*Fagus sylvatica*) and spruce (*Picea abies*) – has an approximate age of 67 years. The shrub-layer consists of 35-year-old beech, oak, sorbus (*Sorbus* sp.), birch, pine, willow (*Salix* sp.), cherry (*Prunus* sp.), maple (*Acer* sp.), elm (*Ulmus* sp.), lime (*Tilia* sp.) and common hornbeam (*Carpinus betulus*). This data were provided by the forest management plan of the Forestry office Groß-Gerau.

Oribatid mites were extracted for 48 hours using a modified Kempson heat extractor (Kempson et al. 1963) and stored in 75 % ethanol. Adult mites were determined to species level under a microscope using the key of Weigmann (2006). Gender was determined according to the presence of an ovipositor or spermatopositor in females and males, respectively. Only those species that could be sexed without ambiguity were included in the analyses; therefore, excluded are Brachychthoniidae, species of Phthiracaridae and Euphthiracaridae (except *Rhysotritia duplicta* and *Microtritia minima*), Suctobelbidae and dark pigmented genera such as *Carabodes* and *Hermannia*. Taxonomic classification was adapted from Weigmann (2006), Norton & Behan-Pelletier (2009), Schatz et al. (2011), and Subias (2004, 2017).

To complement this sampling, data from additional microhabitats – tree bark, lichen and grass sod – were taken from Wehner et al. (2016). Those samples were taken in November 2015 in neighboring forests in Groß-Gerau, Raunheim and Rüsselsheim, which are about 10 km apart from each other and about 15 km apart from the forest in Mörfelden. Samples (four to five replicates) were similarly taken as in this study and oribatid mites were extracted in the same extractor using the same method. Differences in oribatid mite abundances and diversity were only present among microhabitats but not among locations (for more details see Wehner et al. 2016).

2.1. Statistics

In a first step, we analyzed the differences among the pooled numbers of sexual and parthenogenetic species as well as individuals across microhabitats using paired t-tests. Second, to access whether sex ratios of a given species differ among microhabitats, we used a generalized linear mixed effect model (GLMM) using a binomial error distribution and logit as link-function. Hence, we fitted ‘sex ratio’ as a binomial response variable of counted females and total number of counted mites to weighted different sample sizes and ‘microhabitat’ as well as ‘species’ as fixed explanatory variables. To account for different spatial dependencies, we used ‘location’ and ‘site ID’ as crossed random effects. Third, to analyze the sex ratios of oribatid mites found in different microhabitats, we again fitted the binomial variable ‘sex ratio’ (fixed effect) in a GLMM with ‘microhabitat’ as a fixed explanatory variable as well as ‘species’ and ‘location’ as nested and ‘site ID’ as crossed random effects. The random factors were fitted to account for different oribatid community composition across sites and spatial as well as within-species dependencies in one sample. We used marginal and conditional $r^2_{(GLMM)}$ as coefficients describing the proportion of variance explained by the fixed factor and by fixed and random factors, respectively (Nakagawa & Schielzeth 2013).

All statistical analyses were performed with R 3.3.2 (R Core Team 2014), using the packages ‘car’ (Fox & Weisberg 2011), ‘DHARMa’ (Hartig 2017), ‘effects’ (Fox 2003) ‘MuMIn’ (Barton 2017), ‘multcomp’ (Hothorn et al. 2008), ‘nlme’ (Pinheiro et al. 2016) and ‘lme4’ (Bates et al. 2015).

3. Results

In total, gender of 46,320 adult oribatid mites belonging to 47 species were investigated. The majority of species we interpreted sexually (75 %), but all studied Enarthronota (*Eniochthonius minutissimus, Hypochthonius rufulus*), Mixonomata (*Microtritia minima, Rhysotritia duplicata*) and Nothrina (*Camisia spinifer, Nanhermannia nana, Nothrus palustris, Nothrus silvestris, Platynothrus peltifer*) as well as three species of Brachypylina (*Oppiella nova, Qudadroppia quadricarinata, Tectocepheus* spp.) were parthenogenetic (Tab. 1). We defined species to be sexually at presence of at least 5 % males.

The sex ratios of all species across all habitats were mostly female biased. However, sex ratios in sexual species

Table 1. Sex ratios [% females] of 47 oribatid mite species (adult individuals) in the microhabitats dead wood, grass sod, lichen, litter, moss, and tree bark. p(model estimate) = significance value for differing sex ratios among microhabitats; NA = not applicable; ns = not significant; * = P ≤ 0.05; ** = P ≤ 0.01; *** = P ≤ 0.001. **Bold** names indicate parthenogenetic reproduction.

	dead wood	**grass sod**	**lichen**	**litter**	**moss**	**tree bark**	**p**
	sex ratio	sex ratio	sex ratio	sex ratio	sex ratio	sex ratio	
Enarthronota							
***Eniochthonius minutissimus* (Berlese, 1903)**	100	-	100	100	100	-	NA
***Hypochthonius rufulus* (Koch, 1835)**	100	-	-	100	100	-	NA
Mixonomata							
***Microtritia minima* (Berlese, 1904)**	100	-	-	100	100	-	NA
***Rhysotritia duplicata* (Grandjean, 1953)**	100	-	-	100	100	-	NA
Nothrina							
***Camisia spinifer* (Koch, 1835)**	-	-	100	-	100	-	NA
***Nanhermannia nana* (Nicolet, 1855)**	100	-	-	100	100	-	NA
***Nothrus palustris* (Koch, 1839)**	100	-	-	100	100	-	NA
***Nothrus silvestris* (Koch, 1839)**	100	100	100	100	100	-	NA
***Platynothrus peltifer* (Koch, 1839)**	100	100	-	100	100	-	NA
Brachypylina							
Achipteria coleoptrata (Linné, 1758)	69	-	-	62	66	-	***
Achipteria nitens (Nicolet, 1855)	84	-	-	71	72	-	ns
Adoristes ovatus (Koch, 1839)	53	-	56	58	58	-	ns
Autogneta longilamellata (Michael, 1885)	57	-	-	-	68	-	ns
Berniella sigma (Strenzke, 1951)	56	-	-	-	65	-	**
Ceratoppia bipilis (Hermann, 1904)					48	-	ns
Chamobates cuspidatus (Michael, 1884)	59	-	48	48	49	-	***
Cymberemaeus cymba (Nicolet, 1855)	-	-	-	-	76	57	ns
Dissorhina ornata (Oudemans, 1900)	48	-	-	62	57	-	*
Dometorina plantivaga (Berlese, 1895)	56	-	-	-	64	78	ns

Table 1. Continued.

	dead wood sex ratio	**grass sod** sex ratio	**lichen** sex ratio	**litter** sex ratio	**moss** sex ratio	**tree bark** sex ratio	**p**
Eueremaeus oblongus (Koch, 1835)	-	-	69	-	61	-	ns
Eupelops plicatus (Koch, 1836)	-	72	-	-	56	-	ns
Euzetes globulus (Nicolet, 1855)	-	-	-	-	81	-	ns
Galumna lanceata (Oudemans, 1900)	60	-	50	-	53	-	**
Galumna obvia (Berlese, 1914)	-	-	-	-	59	-	ns
Gustavia microcephalia (Nicolet, 1855)	-	-	-	-	63	-	ns
Liacarus coracinus (Koch, 1841)	47	-	-	-	62	-	ns
Liebstadia similis (Michael, 1888)	-	60	-	-	59	-	*
Medioppia subpectinata (Oudemans, 1900)	59	-	60	59	62	-	ns
Metabelba pulverosa Strenzke, 1953	70	-	-	67	73	-	ns
Multioppia laniseta (Moritz, 1966)	60	-	-	58	51	-	ns
Oppia denticulata (G. & R. Canestrini, 1882)	50	-	-	-	63	-	ns
Oppiella falcata (Paoli, 1908)	63	-	-	-	74	-	*
***Oppiella nova* (Oudemans, 1902)**	99	98	100	98	99	-	NA
Oribatella quadricornuta (Michael, 1880)	43	-	-	-	63	-	*
Oribatula tibialis (Nicolet, 1855)	89	-	67	-	66	-	ns
Peloptulus phaenotus (Koch, 1844)	59	68	-		65	-	ns
Pergalumna nervosa (Berlese, 1914)	50	-	-	71	66	-	ns
Punctoribates punctum (Koch, 1839)	-	61	-	-	56	-	ns
***Quadroppia quadricarinata* (Michael, 1885)**	100	-	-	100	100	-	NA
Scheloribates laevigatus (Koch, 1835)	43	-	-	-	70	-	ns
Scheloribates latipes (Koch, 1844)	-	-	55	-	69	-	*
Scheloribates pallidulus (Koch, 1841)	-	-	50	-	71	-	**
***Tectocepheus* spp. (Berlese, 1813)**	99	97	99	99	99	-	NA
Trichoribates novus (Sellnick, 1928)	-	61	-	-	54	-	**
Xenillus clypeator Robineau-Desvoidy, 1839	83	-	-	-	60	-	ns
Xenillus tegeocranus (Hermann, 1804)	-	-	-	-	62	-	ns
Zygoribatula exilis (Nicolet, 1855)	61	-	60	50	61	55	***

ranged from 43% females in dead wood populations of *Scheloribates laevigatus* to 89% females in *Oribatula tibialis* (Tab. 1). In twelve out of 35 sexual species sex ratios differed significantly among microhabitats, that of most species (23) did not (see Tab. 1 for significance levels). In parthenogenetically reproducing species males were entirely absent in all sampled Enarthronota, Mixonomata and Nothrina, and in the brachypyline species *Q. quadricarinata*. However, in *O. nova* and *Tectocepheus* spp. up to 3% males were found (Tab. 1).

The number of sexual species exceeded those of parthenogens in all microhabitats (paired t-test: t = -5.46, P = 0.003; Fig. 1A), with the highest richness in moss and the lowest on tree bark. Yet, pooled numbers of sexual and parthenogenetic individuals were the same (paired t-test: t = -1.16, P = 0.29; Fig. 1B). All microhabitats were dominated by sexual species, ranging from about 75% in litter to 100% on tree bark (Fig. 1C, dark bars) but when focusing on individuals a different pattern was observed. In all microhabitats except tree bark the proportion of sexual individuals was lower than the proportion of sexual species (Fig. 1C, light bars). In lichen only about 30 % of the individuals were sexual, dead wood and moss had approximately equal proportions of sexual and parthenogenetic individuals (58 % vs. 42 %, respectively) and grass sod and litter were biased towards sexual reproduction.

Sex ratios of pooled oribatid mite assemblages in different microhabitats were generally female-biased and differed significantly (GLMM: Wald-$\chi^2 = 30.49$, $n = 563$, $df = 5$, $p < 0.0001$; $r^2_{GLMM(m)} = 0.008$, $r^2_{GLMM(c)} = 0.03$; Fig. 2). The highest proportions of females were found in populations on tree bark (~ 72 %) and grass sod (~ 69 %) and lowest were found in lichen assemblages (~ 53 %).

4. Discussion

While all microhabitats were dominated by sexual species, the number of sexual individuals was only higher than those of parthenogenetic individuals in litter. In dead wood and grass sods numbers of sexual and parthenogenetic individuals were similar, but lichens were even dominated by parthenogenetic individuals. Thus, lower number of parthenogenetic species was compensated by the higher individual abundances per species which has been reported earlier in litter habitats and explained by the potentially faster reproductive ability of usually smaller parthenogens (Maraun et al. 2003, Domes et al. 2007, Wehner et al. 2014).

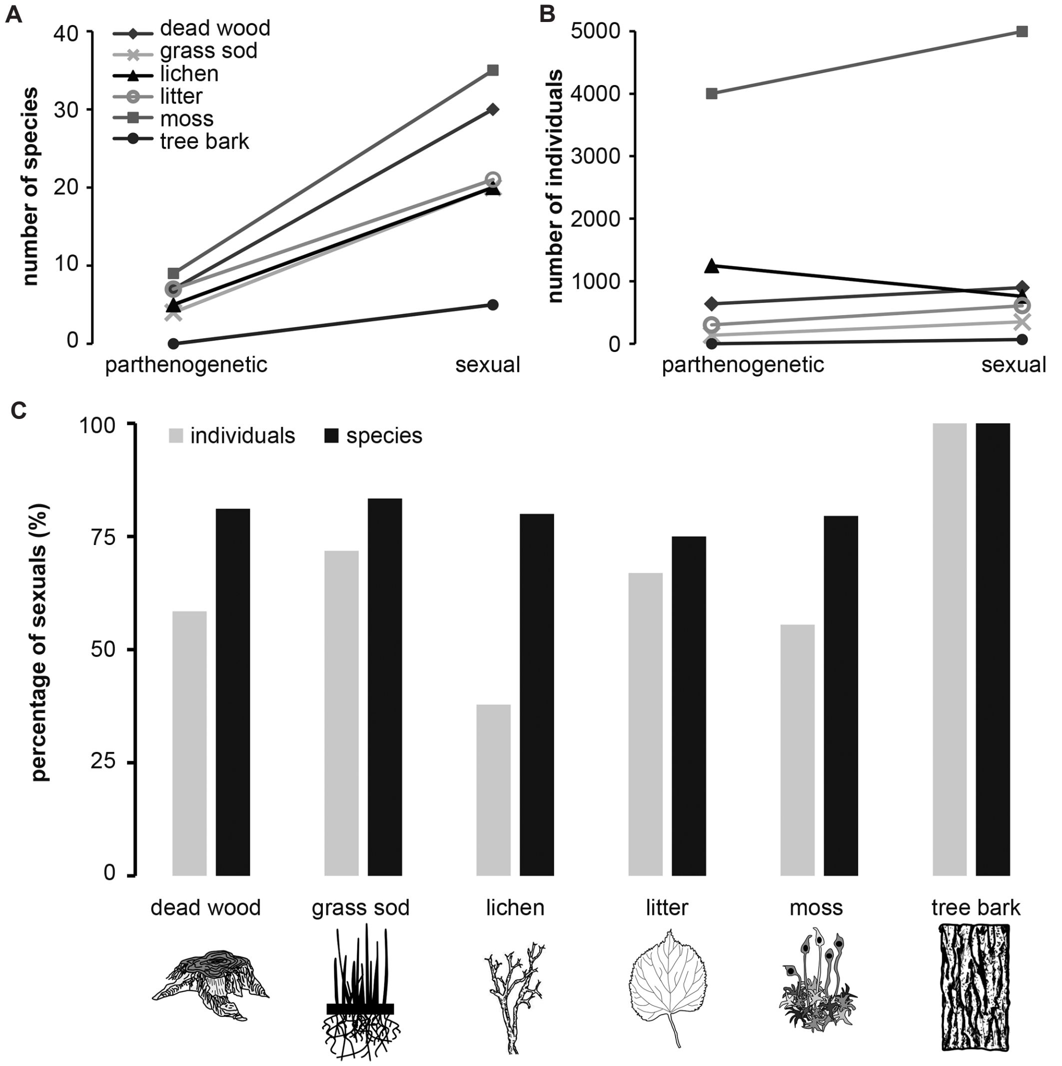

Figure 1. Summarized numbers of sexual vs parthenogenetic species (**A**) and individuals (**B**), respectively, and percentages (**C**) of sexually reproducing individuals (light bars) and sexual species (dark bars) in the microhabitats dead wood, grass sod, lichen, litter, moss, and tree bark.

The observed female-biased sex ratios across sexual oribatid mite species and microhabitats confirm earlier studies (e.g., Grandjean 1941, Webb & Elmes 1979, Domes et al. 2007, Wehner et al. 2014, 2016, Smelanzky 2006). Some species, e.g., *Adoristes ovatus, Chamobates cuspidatus*, had approximately equal sex ratios with proportions of females ranging from 48 % to 58 %. However, in most sexual species, e.g., *Achipteria coleoptrata, Metabelba pulverosa*, proportions of females were higher than 60 % and in most species (64 %) sex ratios did not differ among microhabitats.

Whether the sex ratios in our samples reflect primary sex ratios, i.e. the ratio at fertilization, or have been modified after fertilization or egg deposition, remains unknown. Potential modifying factors include gender-specific differences in mortality during development or during adult lifespan (probably also differing among species), and sex ratio distorting endosymbionts (Frey & Leong 1993, Weeks et al. 2003). Observed female-biased sex ratios in sexual oribatid mites also may be due to differences in dispersal activity, which could influence 'catchability' (Frey & Leong 1993).

However females are produced, female-biased sex ratios are common. In other sexual arthropods (e.g., spiders) they have been explained by the condition of the mother; she responds to a decline in her fitness by skewing the sex ratio of her eggs towards females, since daughters are more likely to survive than sons (Nager et al. 1999); it is probably more effective to produce more females than males. A single male can fertilize several females, so less males than females are necessary. Thus, highly female-biased sex ratios of oribatid mite species on tree bark – a microhabitat inhabited by rather specialized oribatid mites showing rather low abundance

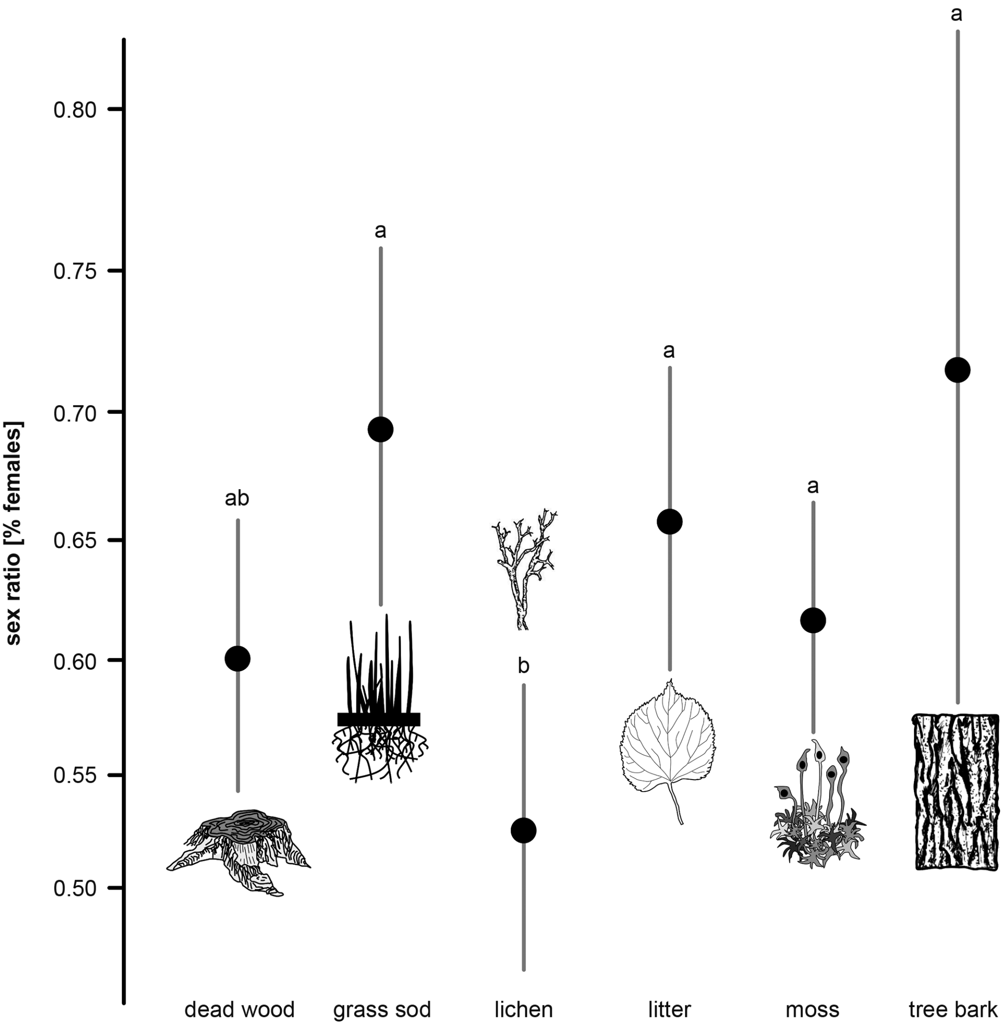

Figure 2. Average sex ratio [% females] of sexual oribatid mite species found in a respective microhabitat. Different letters indicate significant differences (Tukey pairwise contrast; $P \leq 0.05$). Circles represent means; lines are standard errors.

and diversity – may be due to generally harder survival conditions, with mothers adjusting their reproduction toward more female offspring. Also food stress seems possible since resources quality on tree bark may be low (which may also explains the absence of parthenogens on tree bark; Scheu & Drossel 2007). However, such arguments do not explain female-biased sex ratios in other microhabitats (e.g., moss), and any explanation is hampered by our ignorance of sex determination and maternal influence in oribatid mites.

In most parthenogenetically reproducing species – especially in Enarthronota, Mixonomata and Nothrina – no males were found, which is the typical pattern (Norton & Palmer 1991, Norton et al. 1993, Cianciolo & Norton 2006). On the other hand, very low numbers of males were found in *Oppiella nova* and *Tectocepheus* spp., both belonging to Brachypylina. These rare, so-called spanandric males are occasionally, but regularly reported in the literature (e.g., Grandjean 1941, Taberly 1988, Palmer & Norton 1992, Wehner et al. 2014, 2016). In the few studied cases, their spermatophores have been proven to be sterile and ignored by females, and they seem to have no effect on genetic diversity (Grandjean 1941, Taberly 1988, Palmer & Norton 1992). Why they persist over evolutionary timescales and why they are not found in all parthenogenetic oribatid species is still unknown.

In conclusion, the basic mechanisms and external factors that influence sex ratios of sexual oribatid mite populations in different microhabitats remain poorly known and needs further investigation. However, field observations of such basic information as spermatophore deposition, the frequency at which females take them up, egg deposition and juvenile development are mostly infeasible. Experiments to demonstrate adaptive adjustment of sex ratios are also difficult since there are many potentially confounding factors influencing sex ratio determination as well as practical problems. Most oribatid mite species are difficult to culture in the laboratory due to long generation times and lack of knowledge about special preferences for food and microclimatic conditions (Weigmann 1975, Tràvnìcek 1989, Ermilov et al. 2008). Furthermore, most oribatid mite species cannot be sexed without killing the individual, since sexual dimorphism is minimal (Behan-Pelletier 2015). Nevertheless, complex long-term laboratory studies are needed to elucidate sex ratio adjustment, gender-specific mortality rates and reproductive success.

5. Acknowledgements

We thank Klaus Velbecker from the Forestry Office of Groß-Gerau for providing information on forest characteristics. We thank Bernhard Domes and Dirk Wehner for supporting the fieldwork and Sebastian Schmelzle, Romina Schuster, Cristina Munoz-Sanchez, Cristina Marín Montaner, Sebastian Kruse, Timo Smit and Andrea Hilpert for their help during sample processing. We are most thankful to Roy A. Norton for his guidance and helpful comments on the manuscript. Finally we thank two anonymous reviewers for carefully reading and commenting on an earlier draft of the manuscript. AB was supported by a scholarship of the German Nation Academic Foundation (Studienstiftung des deutschen Volkes).

6. Competing financial interests

The authors declare no competing financial interests.

7. References

Barton, K. (2017): MuMIn: Multi-Model Inference. – R package version 1.40.0. [https://CRAN.R-project.org/package=MuMIn].

Bates, G., M. Maechler, B. Bolker & S. Walker (2015): Fitting linear mixed-effects models using lme4. – Journal of Statistical Software **67**(1):1–48 [doi:10.18637/jss.v067.i01].

Behan-Pelletier, V. M. (2015): Review of sexual dimorphism in brachypyline oribatid mites. – Acarologia **55(2)**:127–146.

Bell, G. (1982): The Masterpiece of Nature. The Evolution and Genetics of Sexuality. – University of California Press, California.

Bergmann, P. & M. Heethoff (2012): Development of the internal reproductive organs in early nymphal stages of *Archegozetes longisetosus* Aoki (Acari, Oribatida, Trhypochthoniidae) as obtained by synchrotron X-ray microtomography (SR-µCT) and transmission electron microscopy (TEM). – Soil Organisms **84**:459–470.

Bergmann, P., M. Laumann, R. A. Norton & M. Heethoff (2018): Cytological evidence for automictic thelytoky in parthenogenetic oribatid mites (Acari, Oribatida): Synaptonemal complexes confirm meiosis in *Archegozetes longisetosus*. – Acarologia, accepted.

Charnov, E. L. (1982): The Theory of Sex Allocation. – Princeton University Press, Princeton.

Charnov, E. L., R. L. Los-den Hartogh, W. T. Jones & J. van den Assem (1981): Sex ratio evolution in a variable environment. – Nature **289**: 27–33.

Cianciolo, J. M. & R. A. Norton (2006): The ecological distribution of reproductive mode in oribatid mites, as related to biological complexity. – Experimental and Applied Acarology **40**: 1–25.

Domes, K., S. Scheu & M. Maraun (2007): Resources and sex: soil re-colonization by sexual and parthenogenetic oribatid mites. – Pedobiologia **51**: 1–11.

Ermilov, S. G., M. Łochysńka & Z. Olszanowski (2008): The cultivation and morphology of juvenile stages of two species from the genus *Scutovertex* (Acari: Oribatida: Scutoverticidae). – Annales Zoologici **58**(2): 433–443.

Fisher, R. A. (1930): The Genetical Theory of Natural Selection. – Clarendon Press, Oxford.

Fox, J. (2003): Effect displays in R for generalised linear models. – Journal of Statistical Software **8**(15): 1–27 [http://www.jstatsoft.org/v08/i15/].

Fox, J. & S. Weisberg (2011): An {R} Companion to Applied Regression, Second Edition. – Thousand Oaks CA: Sage [http://socserv.socsci.mcmaster.ca/jfox/Books/Companion].

Frey, D. F. & K. L. H. Leong (1993): Can microhabitat selection or differences in 'catchability' explain male-biased sex ratios in overwintering populations of monarch butterflies? – Animal Behaviour **45**(5): 1025–1027.

Grandjean, F. (1941): Statistique sexuelle et parthénogenèse chez les Oribates (Acariens). – Comptes Rendus des Seances de l' Academie des Sciences **212**: 463–467.

Hamilton, W. D. (1967): Extraordinary sex ratios. – Science **156**(3774): 477–488.

Hartig, F. (2017): DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.1.5. [https://CRAN.R-project.org/package=DHARMa].

Heethoff, M., P. Bergmann & R. A. Norton (2006): Karyology and sex determination of oribatid mites. – Acarologia **46**: 127–131.

Heethoff, M., R. A. Norton, S. Scheu & M. Maraun (2009): Parthenogenesis in oribatid mites (Acari, Oribatida): evolution without sex. *in* I. Schoen, K. Martens & P. van Dijk, editors. Lost Sex – The Evolutionary Biology of Parthenogenesis. – Springer Press: 241–257.

Hothorn, T., F. Bretz & P. Westfall (2008): Simultaneous inference in general parametric models. – Biometrical Journal **50**(3): 346–363.

Hubert, J. (2000): Seasonal changes of abundance, sex ratio and egg production of *Scheloribates laevigatus* (Acari: Oribatida) in the soil of a meadow in the Czech Republic. – Acta Societatis Zoologicae Bohemicae **64**: 37–56.

Kempson, D., M. Llyod & R. Ghelardi (1963): A new extractor for woodland litter. – Pedobiologia **3**: 1–21.

Kokko, H. & M. D. Jennions (2008): Parental investment, sexual sexual selection and sex ratios. – Journal of Evolutionary Biology **21**(4): 919–948.

Laumann, M., P. Bergmann & M. Heethoff (2008): Some remarks on the cytogenetics of oribatid mites. – Soil Organisms **80**: 223–232.

Maraun, M., J. A. Salamon, K. Schneider, M. Schaefer & S. Scheu (2003): Oribatid mite and collembolan diversity, density and community structure in a moder beech forest (*Fagus sylvatica*): effects of mechanical perturbations. – Soil Biology and Biochemistry **35**(10): 1387–1394.

Myers, J. H. (1978): Sex ratio adjustment under food stress: maximization of quality or number of offspring? – The American Naturalist **112**(984): 381–388.

Nager, R. G., P. Monaghan, R. Griffiths, D. C. Houston & R. Dawson (1999): Experimental demonstration that offspring sex ratio varies with maternal conditions. – Proceeding of the National Academy of Sciences **96**: 570–573.

Nakagawa, S. & H. Schielzeth (2013): A general and simple method for obtaining R^2 from generalized linear mixed-effects models. – Methods in Ecology and Evolution **4**: 133–142.

Norton, R. A. & S. C. Palmer (1991): The distribution, mechanisms, and evolutionary significance of parthenogenesis in oribatid mites. In: R. Schuster & P. W. Murphy (eds). – The Acari: Reproduction, Development and Life-History Strategies. – Chapman and Hall, London: 107–136.

Norton, R.A. & V. Behan-Pelletier (2009): Suborder Oribatida. – In: G. W. Krantz & D. E. Walter (eds): A Manual of Acarology. – Third Edition. Lubbock, Texas: Texas Tech University Press: 430–564.

Norton, R. A, P. M. Bonamo, J. D. Grierson & W. A. Shear. (1988): Oribatid mite fossils from terrestrial Devonian deposit near Gilboa, New York. – Journal of Paleontology **62**: 259–269.

Norton, R. A., J. B. Kethley, D. E. Johnston & B. M. OConnor. (1993): Phylogenetic perspectives on genetic systems and reproductive modes in mites. In: D. L. Wrensch & M. A. Ebbert (eds): Evolution and Diversity of Sex Ratios. – Chapman and Hall, New York: 8–99.

Palmer, S. C. & R. A. Norton (1992): Genetic diversity in thelytokous oribatid mites (Acari: Acariformes: Oribatida). – Biochemical Systematics and Ecology **20**: 219–231.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar & R Core Team (2016): Nlme: linear and nonlinear mixed effects models. – R package version 3.1–128, [http://CRAN.R-project.org/package=nlme>].

R Development Core Team (2014): R version 3.0.3. R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria.

Schaefer, I., R. A. Norton, S. Scheu & M. Maraun (2010): Arthropod colonization of land – Linking molecules and fossils in oribatid mites (Acari, Oribatida). – Molecular Phylogenetics and Evolution **57**(1): 113–121.

Schatz, H., V. M. Behan-Pelletier, B. M. OConnor & R. A. Norton (2011): Suborder Oribatida van der Hammen, 1968.

In: Z.-Q. Zhang (ed.): Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. – Zootaxa **3148**: 141–148.

Shear, W. A., M. Bonamo, J. D. Grierson, W. D. I. Rolfe, E. L. Smith & R. A. Norton (1984): Early land animals in North America: evidence from Devonian age arthropods from Gilboa, New York. – Science **224**: 492–494.

Smelansky, I. E. (2006): Some population characteristics of oribatid mites steppes habitats. – Acarina **14**(1): 123–130.

Steinberger, Y., J. A. Wallwork & M. Halimi (1990): Sex ratios and egg production of *Zygoribatula* spp. (Acari, Cryptostigmata) in the Negev Desert of Southern Israel. – Acarologia **31**(1): 85–91.

Subías, L. S. (2004, 2017): Listado sistemático, sinonímico y biogeográfico de los ácaros oribátidos (Acariformes, Oribatida) del mundo (1758-2002). – Graellsia **60**:3–305. Actualized in February 2017: 1–598 [http://bba.bioucm.es/cont/docs/RO_1.pdf, doi:10.3989/graellsia.2004.v60.iExtra.218].

Taberly, G. (1987): Recherches sur la parthénogenèse thélytoque de deux espèces d`acariens oríbates: *Trhypochthonius tectorum* (Berlese) et *Platynothrus peltifer* (Koch). III. Etude anatomique, histologique et cytologique des femelles parthénogenétiques. – Acarologia **28**: 389–403.

Taberly, G. (1988): Recherches sur la parthénogenèse thélythoque de deux espèces d’acariens oribatides: *Trhypochthonius tectorum* (Berlese) et *Platynothrus peltifer* (Koch). IV Observations sur les mâles ataviques. – Acarologia **29**: 95–107.

Tràvnìcek, M. (1989): Laboratory cultivation and biology of mites in the family Liacaridae (Acari: Oribatida). – Acta Universitatis Carolinae – Biologica **33**: 69–80.

Walter, D.E. & H. C. Proctor (1999): Mites: Ecology, Evolution, and Behaviour. – University of New South Wales Press.

Webb, N. R. & G. W. Elmes (1979): Variations between populations of *Steganacarus magnus* (Acari; Cryptostigmata) in Great Britain. – *Pedobiologia* **19**: 390–401.

Weeks, A. R., R. Velten & R. Stouthamer (2003): Incidence of a new sex−ratio−distorting endosymbiotic bacterium among arthropods. – Proceedings of the Royal Society of London B **270**: 1857–1865.

Weigmann, G. (1975): Labor- und Freilanduntersuchungen zur Generationsdauer von Orbatiden (Acari: Oribatidei). – Pedobiologia **15**: 133–148.

Weigmann, G. (2006): Hornmilben (Oribatida). In: Dahl (ed.) – Tierwelt Deutschlands **76**. – Goecke and Evers, Keltern.

Wehner, K., S. Scheu & M. Maraun (2014): Resource availability as driving factor of the reproductive mode in soil microarthropods (Acari, Oribatida). – PlosOne **9(8)**: e104243 [doi:10.1371/journal.pone.0104243].

Wehner, K., R. A. Norton, N. Blüthgen & M. Heethoff (2016): Specialization of oribatid mites to forest microhabitats – the enigmatic role of litter. – Ecosphere **7**(3) [doi10.1002/ecs2.1336].

Wrensch, D. L., J. B. Kethley & R. A. Norton (1994): Cytogenetics of holokinetic chromosomes and inverted meiosis: keys to the evolutionary success of mites, with generalizations on eukaryotes. In: M. A. Houck (ed.): Mites: Ecological and Evolutionary Analysis of Life-history Patterns. – Chapman and Hall, New York: 282–343.