

EGG NUMBER VARIES WITH POPULATION DENSITY; A STUDY OF THREE ORIBATID MITE SPECIES IN ORCHARD HABITATS IN EGYPT

Mohamed A. KHALIL^{1*}, Abdel-Naieem I. AL-ASSIUTY¹ and Nico M. VAN STRAALLEN²

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¹ 1Department of Zoology, Faculty of Science, Tanta University 31527, Tanta, Egypt.
mohamed.khalil@science.tanta.edu.eg (*corresponding author), a_lassiuty@yahoo.com

² 2Department of Ecological Science, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands.
nico.van.straalen@falw.vu.nl

ABSTRACT — This study was done to investigate the relationship between the reproductive potential of oribatid mites (estimated by egg number) and their population density in different orchard habitats. We hypothesized that species with narrow feeding niches would be more susceptible to intraspecific competition and would show a decrease in egg number with increasing density, while general feeders would show egg numbers independent of density. To investigate these predictions, soils were sampled four times a year in orange, mango and date palm orchards at each of three sites in Al-Gharbia Governorate, Egypt. The number of mites extracted, the total number of eggs contained in their bodies and the gut contents were evaluated. The results show a significant difference between species in the way egg number varies with density. In *Scheloribates laevigatus*, a positive correlation between population density and egg number per individual is present. For *Xylobates lophotrichus*, however, a negative correlation was observed, while in the case of *Zygoribatula undulata*, no significant correlation between population density and egg number could be demonstrated. Gut contents showed that *S. laevigatus* has the widest trophic breadth, while *X. lophotrichus* is the most specialized feeder. We argue that the relationship between egg number and population density is shaped by differences in feeding habits: a specialized feeding habit is associated with a negative relationship between egg number and population density, whereas a broad trophic niche seems to be associated with a positive relationship between egg number and population density. This suggests that feeding habits have important population dynamic consequences in these soil-living invertebrates.

KEYWORDS — egg number; gut content; soil invertebrates; species traits; trophic niche

INTRODUCTION

In many terrestrial ecosystems oribatid mites are among the most abundant soil arthropods. They are assumed to be important agents in regulating microbial activity in litter decomposition (Seastedt, 1984; Moore and Walter, 1988; Khalil, 2005). The coexistence of such a great number of species in a relatively small area, combined with the fact that many of them seem to have similar feeding niches

has puzzled soil biologists for a long time. It has, however, been shown that the feeding habits of oribatid mites are more diverse than they seem on first sight, different species showing different arrays of digestive enzymes (Siepel, 1990), and different preferences for specific food items correlated with cheliceral size and shape (Kaneko, 1988).

We now know that the species richness of oribatid mites is supported by an equally high niche

diversity, along a variety of niche dimensions (Van Straalen, 1997). The trophic niche differentiation of oribatid mites is much greater than expected before, and this contributes to their high biodiversity (Schneider *et al.*, 2004; Erdmann *et al.*, 2007). The feeding attributes of soil arthropods and their microenvironmental preferences are also important factors for understanding successional changes of microarthropod communities during the decomposition processes (Takeda, 1995).

Despite the recognized importance of trophic niche differentiation, little information still exists on its relationships with life-history traits such as fecundity. A new trend in community ecology is to explain community structure from species traits (McGill *et al.*, 2006). For oribatid mites, an important species trait is the number of eggs contained in the body, which is an indicator of fecundity. In this way, joint studies of gut content and egg number can be used for the interpretation of oribatid mite community structure.

The gut contents of oribatid species are often characterized by specific items, such as fresh pollen (Behan-Pelletier and Hill, 1983). In other cases fungal spores dominate the gut contents of oribatid mites (Behan-Pelletier and Hill, 1978). Earlier studies by our group (Al-Assiuty *et al.*, 1993a,b) focused on the relationship between vegetational cover and abundance of oribatid mite species. We showed that vegetational type has a major influence on several, but not all, soil-living oribatid mites and that each species has a characteristic phenology.

In this paper we focus on the fecundity of oribatids. The hypothesis tested was that there is a species-specific relationship between egg number and population density. Species with specialized feeding habits are expected to be more susceptible to intraspecific competition at increasing densities and should thus show a decrease in egg number with density. The egg numbers of generalist feeders are expected to be independent of density or may even increase if a higher density was correlated with better habitat quality. Seasonal changes in oribatid abundance, egg number and gut content were measured to study these predictions.

MATERIALS AND METHODS

Study locations and sampling sites

Sampling was carried out in orchards of orange, mango and date palm in each of three areas in Al-Gharbia Governorate in the Nile delta of lower Egypt (see Fig. 1, Tanta: area 1, Al Mahalla Al Kobra: area 2, and Kafr Al Zayat: area 3). The soil was loamy at all sites, litter depth was shallow (no litter accumulation) and the pH (H₂O) was 7.01, 6.99, 7.5 for areas 1, 2 and 3, respectively. In each of four seasons, eighteen cores (10 x 10 x 8 cm depth) were taken randomly from the three chosen orchard soils at each site (six soil samples from each orchard) forming a total of 3 x 3 x 6 = 54 samples in each season. The oribatid mite fauna was extracted from the samples using modified Berlese funnels. Preparation and identification of species were undertaken as explained in detail elsewhere (Al-Assiuty *et al.*, 1993a).

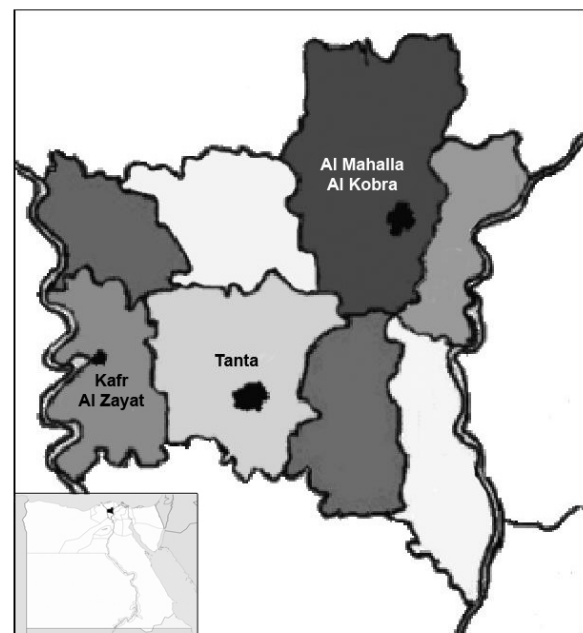


FIGURE 1: Map of Al-Gharbia Governorate in Egypt, indicating the three sampling areas (Tanta, Al Mahalla Al Kobra and Kafr Al Zayat). The inset shows the location of Al-Gharbia in Egypt. In each area, three orchards were sampled four times in a year. The same three types of orchard were selected in each area. The distance between locations varies from 19 to 38 km; the distance between sites within one location is 1-2 km.

Preparation of specimens for counting eggs

A total of 47 species of oribatid mite and eight species of Collembola were found. Three species of oribatid mite dominating the community at each site were selected for analysis of abundance and egg numbers per individual: *Scheloribates laevigatus* (Scheloribatidae, Grandjean, 1935), *Zygoribatula undulata* (Oribatulidae Thor, 1929) and *Xylobates lophotrichus* (Xylobatidae Balogh and Balogh, 1984). Eggs could be easily recognized in the cleared animals as explained elsewhere (Khalil *et al.*, 1999). Only adult animals were screened for egg number. For the two sexual species, *S. laevigatus* and *Z. undulata* (*X. lophotrichus* is parthenogenetic) males and females are difficult to distinguish in our microscopic procedure, hence the sex of these taxa was ignored.

Preparation of specimens for gut content

Oribatid mites were preserved in 70% alcohol and then transferred onto lactic acid for two weeks; this clears the specimens making the gut contents clearly visible. The gut contents were individually observed every season, dissected out on a slide and squeezed beneath a cover slip, then examined microscopically. In each season, about 250 individuals were examined for each species. Only adult animals were examined for gut contents. The number and the kind of food particles in the gut contents were assessed and classified (Schuster, 1956; Fujikawa, 1988).

Data analysis

A three-way analysis of variance (ANOVA) was applied to the abundance data per sample (Sokal and Rohlf, 1995), using time (four levels), vegetation type (three levels) and site (three levels) as factors, and six replicate samples per combination. The average egg number per species was evaluated by dividing the total number of eggs counted by the total number of individuals of a species; these data were pooled over the six samples per site. The relationship between egg number and population density was studied by plotting the data for each species at each sampling site in a correlation diagram. Pearson's correlation coefficient was calculated (Sokal and Rohlf, 1995). The gut content and egg number data were subjected to a nonparametric analysis (Kruskal-Wallis test) for comparisons between sites and vegetation cover. Trophic niche breadth (B) was estimated according to Levins's equation: $B = 1/\sum p_j^2$, where p_j is the fraction of items in the gut that are of food category j (Levins 1968).

RESULTS

A three-way ANOVA (Table 1) applied to the mean number of individuals per core revealed that in the case of *Scheloribates laevigatus* the effect of time, vegetation cover, site and the interaction site x vegetation cover were significant. For *Xylobates lophotrichus* the effects of time, vegetational cover and site, as well as the three-way interaction were

TABLE 1: Three-way analysis of variance for oribatid mite abundance as a function of time, sampling site and vegetation type.

Source of variation	df	<i>Scheloribates laevigatus</i>		<i>Xylobates lophotrichus</i>		<i>Zygoribatula undulata</i>	
		MS	F	MS	F	MS	F
Time	3	75.8	7.5*	63.5	5.0*	41.2	5.7*
Vegetation	2	118.9	11.8*	417.8	32.9*	114.8	15.9*
Site	2	14.7	1.5*	86.0	6.8*	37.6	5.2*
Time x Veg.	6	14.1	1.4 n.s.	17.1	1.3 n.s.	7.0	1.0 n.s.
Time x Site	6	16.2	1.6 n.s.	11.2	0.9 n.s.	0.6	0.1 n.s.
Veg. x Site	4	51.5	5.1*	133.1	10.2 n.s.	62.5	8.7 n.s.
Time x Veg. x Site	12	8.6	0.9 n.s.	16.2	1.3*	9.8	1.4 n.s.
Error	180	10.1		12.7		7.2	

df= degrees of freedom, F= F-statistic, MS = mean square, n.s. = not significant, * $p < 0.05$.

found to be significant but the other interactions were not significant. In the case of *Zygoribatula undulata*, time, vegetational cover and site showed a significant effect but no significant interaction among them was recorded.

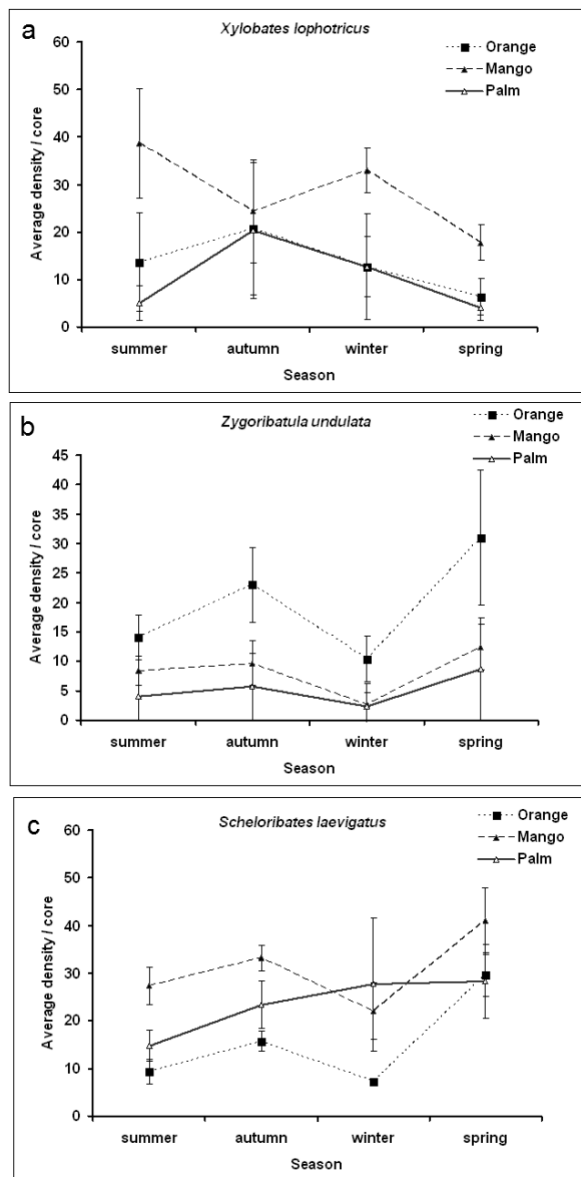


FIGURE 2: : Average population densities of the three studied species as a function of sampling time. Means are given with their standard errors. For each vegetation type, means were taken over three different sites (cf. Fig. 1) and three replicate samples within a site.

Overall, the ANOVA showed that vegetation

had a much stronger effect on the abundance of the mites than season and site. In addition, the factor time hardly interacted with vegetation and site (except for the marginally significant three-way interaction in the case of *X. lophotrichus*). So the mite populations are affected strongly by local conditions, which are dominated by vegetation type; on top of that they are affected by seasonal changes which are more or less the same for all vegetation types.

A graph of the seasonal population fluctuations reinforces these conclusions (Figure 2). To emphasize the effects of vegetation and season, the data were averaged over all sites for this purpose. *X. lophotrichus* and *S. laevigatus* can be seen to reach the highest densities under mango vegetation, while *Z. undulata* had the highest density under orange vegetation. The population peaks of the mites tended to fall in summer (*X. lophotrichus*) or spring (*Z. undulata* and *S. laevigatus*). In addition, *S. laevigatus* did not have strong seasonal dynamics; it fluctuated within a smaller range than the other species.

Regarding the relationship between population density and fecundity a varied pattern both within species and between species was observed. In the case of *Schelorbates laevigatus* a positive correlation was observed at site 1 and site 2 but no clear correlation could be seen at site 3, however, *Xylobates lophotrichus* showed no significant correlation between population density and its fecundity at site 1 but a negative correlation was observed at site 2 and site 3. In the case of *Zygoribatula undulata*, at site 1 a negative correlation was observed between population density and fecundity, but positive correlations were recorded at site 2 and site 3.

When the data for all sites, vegetational types and seasons were considered together a clear positive correlation between population density and fecundity was seen for *Schelorbates laevigatus* (Pearson correlation, $p < 0.05$). In the case of *Xylobates lophotrichus* the data showed a significant negative correlation (Pearson correlation, $p < 0.05$); in case of *Zygoribatula undulata* no significant correlation was observed (Figure 3).

Gut content analysis (Table 2) showed that every species had its characteristic affinity towards

the various food items. *S. laevigatus* had the widest trophic breadth, while *X. lophotrichus* appeared to be the most specialized feeder.

DISCUSSION

Soil invertebrate populations are influenced by soil factors in a species-specific way. Several workers have demonstrated a relationship between soil factors and microarthropod community composition (Al-Assiuty *et al.*, 1993a; Badejo and Akinwale, 2006; Khalil *et al.*, 2009; Hågvar, 1984; Van Straalen *et al.*, 1988; Wallwork, 1983). In our case the relationship between leaf-litter type and oribatid mite abundance was significant. The highest densities were usually found under mango, but in some cases date palm and orange vegetations supported larger mite populations than mango.

There were consistent differences between the three selected oribatid mites in the number of eggs per individual, as related to population size. Our results have demonstrated a positive correlation between the density of individuals and the egg number of *Scheloribates laevigatus*. This is linked to our observation that this oribatid should be considered a euryphagic species. Gut content analysis of *S. laevigatus* revealed that this species can feed on a number of resources such as fungal hyphae and spores from multicellular and unicellular fungi, and it has the greatest niche breadth. In an earlier study, Khalil *et al.* (1999) likewise argued that food availability supports fecundity in this species because the animal can feed on a large number of different food items.

In the case of *Xylobates lophotrichus*, a negative correlation between the density of individuals and the egg number was obtained. This can be explained by the fact that this species has a more specific food choice (stenophagic species); it had the smallest estimated niche breadth. When food is in short supply, intraspecific competition will result in food shortage and a reduction in egg number. Our results revealed that individuals of this species are restricted to particular resources such as algal cells. Similar results have been reported earlier (Al-Assiuty *et al.*, 1993b).

The third studied species, *Zygoribatula undulata*, was not a dominant species, but its egg number was highest. There was no clear relationship between population density and egg number in this species.

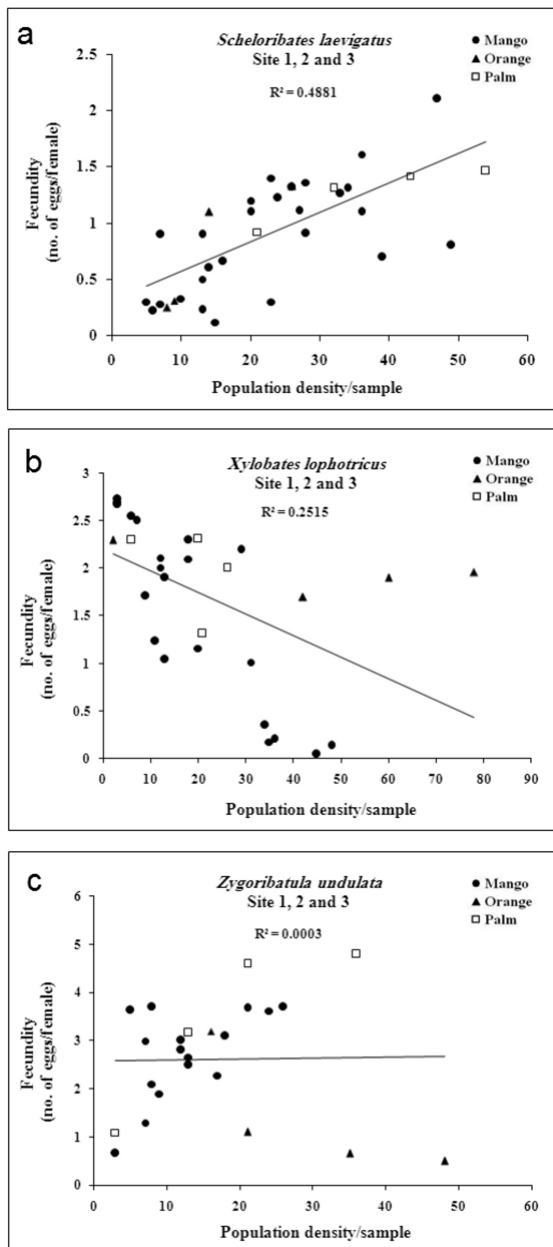


FIGURE 3: Relationship between population density and fecundity of the three studied species. The data (pooled over three samples per site) are for all sites, vegetation types and seasons together.

For this species site-specific effects seem to be of more importance.

Several oribatid mites are characterized by relatively long life cycles, high adult survival and low fecundity (Norton *et al.*, 1994). An experimental population established in microcosms suggested spatial variation in reproductive patterns between local populations (Søvik *et al.*, 2003). Furthermore, life-history patterns do not only depend on current conditions, but just as much on the season and the environment, through biotic and abiotic influences (Kaneko, 1989; Søvik, 2004). The causal relationships between life history parameters, such as generation time, mode of reproduction and numbers of eggs produced, are poorly understood (Domes *et al.*, 2007).

We realize that egg number may not directly reflect fecundity of oribatids since we do not know the residence time of eggs in the female. Also, we know that *S. laevigatus* and *Z. undulata* are bisexual, while *X. lophotrichus* is parthenogenetic. Therefore, egg numbers cannot be directly compared between species to indicate differential fecundity. However, we assume that egg numbers will be comparable within each species, in which case the correlations with density are still valid. Because our sampling covered four seasons in a year, possible intraspecific differences in phenology between the three habitats will disturb the average annual egg number to a lesser degree than a single observation. However, future investigations should find ways to elucidate the life-histories of the studied species, as this is essential for a complete understanding of the relationship between fecundity and habitat characteristics.

Gut content analysis of the studied species has demonstrated a variety of feeding habits. This conclusion agrees with Erdmann *et al.* (2007) who mentioned that the great differentiation of trophic niches of oribatid mites contributes to their high biodiversity. Badejo and Akinwale (2006) found that oribatid mite species responded differently towards different microhabitats and they concluded that gradients of light, microclimate and foliage quality effected oribatid mites in a complex way. Feeding preferences of mites are influenced greatly by the stage of leaf litter decomposition (Hubert *et al.*, 2000). In addition, the feeding activity of oribatid populations does not necessarily coincide with the peaks of their abundance (Hubert *et al.*, 2004).

It can be concluded that our basic hypothesis is confirmed: egg numbers of oribatid mites vary with population density in a species-specific manner. We suggest that this may be due to the feeding habits of the mites that mould intraspecific competition. Our data demonstrate that the species with the broadest trophic breadth is characterized by a positive relationship between egg number and population density, while the species with the narrowest trophic breadth showed a negative relationship. This suggests that the feeding habits of soil-living mites have important population dynamic consequences.

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TABLE 2: Gut contents (as proportions of diet) of the three studied oribatid species throughout the period of study.

Gut contents	<i>Zygoribatula undulata</i>	<i>Xylobates lophotrichus</i>	<i>Scheloribates laevigatus</i>
Fungus hyphae cylinder	0.6	-	0.12
Thick hyphae	0.01	-	0.2
Multicellular fungus spores	0.19	-	-
Unicellular fungus spores	0.2	-	-
Algal cells	-	1.0	-
Teleutospores of fungi	-	-	0.4
Black coloured granules	-	-	0.1
Trophic niche breadth (Levins's B)	2.29	1.0	4.33

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