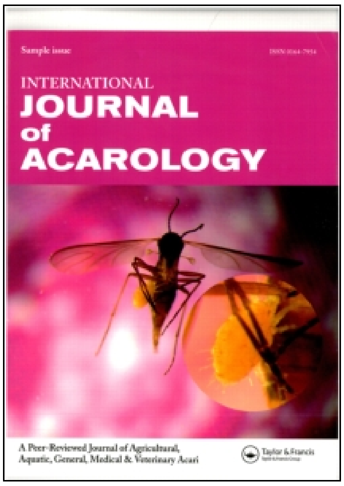

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Daria Bajerlein[a]
[a] Department of Animal Taxonomy and Ecology, Institute of Environmental Biology, Faculty of Biology, A. Mickiewicz University, Poznań, Poland

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SEASONAL ABUNDANCE AND INFESTATION OF DEUTONYMPHS OF *UROPODA ORBICULARIS* (MÜLLER, 1776) (ACARI: MESOSTIGMATA) PHORETIC ON COPROPHILOUS BEETLES (SCARABAEIDAE, GEOTRUPIDAE, APHODIIDAE, HYDROPHILIDAE, HISTERIDAE)

Daria Bajerlein
Department of Animal Taxonomy and Ecology, Institute of Environmental Biology, Faculty of Biology, A. Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland (e-mail: daria.bajerlein@amu.edu.pl)

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ABSTRACT – Seasonal abundance and rates of infestation of deutonymphs of *Uropoda orbicularis* (Müller, 1776) on various groups of coprophilous beetles (Scarabaeidae, Geotrupidae, Aphodiidae, Hydrophilidae and Histeridae) are reported. Beetles and mites were collected using pitfall traps placed in a pasture situated in western Poland. The results have shown that deutonymph infestation varies among beetle families, and that season is an important factor affecting mite infestation. The highest rates of infestation were recorded for Scarabaeidae and the lowest values for Hydrophilidae. Scarabaeidae were most numerous during late May/early June when deutonymph abundance was the highest which may explain why they carried the largest numbers of phoretic deutonymphs. Season affected *U. orbicularis* directly as well as indirectly, due to beetle abundance. Changes in beetle and phoretic deutonymph abundances were similar. Phoretic deutonymphs were observed early in the season on the first beetle specimens collected, however during autumn their numbers decreased markedly even though abundance of carriers was still high. The results have shown that phoretic mite abundance and infestation on carriers may be influenced by seasonal factors to a high degree. This fact should be taken into account by determining mite preferences towards their carriers.
Key words – Phoresy, mites, *Uropoda orbicularis*, coprophilous beetles, infestation, seasonal abundance, season influence.

INTRODUCTION

Phoresy refers to a relationship in which an individual of one species is transported by another species for a limited time, for the purpose of dispersal (Farish and Axtell, 1971). Phoresy is one of the most frequently occuring associations between mites and insects. This phenomenon has evolved in all orders of mites but not in ticks, and the nature of phoretic relationships varies between and within mite groups. In some cases phoresy may be accidental, while in others a high level of specificity may lead to very close associations, such as parasitism (Athias-Binche, 1984; Krantz, 1998). Phoresy is usually observed in mites inhabiting ephemeral and island-like microhabitats such as animal dung, carcasses or dead wood (Athias-Binche, 1993; Athias-Binche *et al.*, 1993; Mašán, 1994a). Under unfavorable biotic conditions such as reduced humidity, mites may leave a previous habitat using co-existing insects in order to disperse to a new habitat.

Phoresy has been reported in many taxonomic, faunistic, ecological and evolutionary studies. Taxonomic papers often include descriptions of phoretic instars of new mite species (Hirschmann, 1981; Mašán, 1994b; Wiśniewski and Hirschmann, 1996). Many faunistic papers include lists of phoretic mites and their carrier insects (Costa, 1966; Philips, 1984; Kofler and Schmölzer, 2000). In recent years experimental studies were conducted, to determine how mite infestation is influenced by the body size of the carrier

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(Kotiaho and Simmons, 2001), sex of the carrier (Lajeunesse *et al*., 2004) or frequency of its occurrence (Wallace, 1986). There is almost nothing known about the influence of season on the rates of infestation on mites, which is surprising since seasonal influences should be regarded as one of the most important factors affecting associations between species. A fundamental condition required for any interaction between two animals is the need to meet each other at the same time and at the same place. Thus, a study of temporal and spatial overlap of interacting species is essential in order to understand the nature of this interaction. Phoresy has rarely been studied using regular field observations. Only a few studies have attempted to describe the seasonal dynamics of phoretic mites such as macrochelid and parasitid mites associated with dung beetles (Wallace and Holm, 1985; Glida *et al*., 2003). Such studies are important because they can answer some basic questions concerning phoresy. In what part of the season do mites start to disperse phoretically and when they stop? How frequently does phoresy occur? To what degree does mite abundance depend on the abundance of their carriers? In what part of the season is the abundance of phoretic stages highest and lowest? These questions have almost never been examined in the case of mites of the family Uropodidae.

The main purpose of this study was to analyze *Uropoda orbicularis* infestation on different coprophilous beetle groups, with special reference to seasonal changes in the abundance of phoretic deutonymphs and their carriers. The hypothesis that season (the date of sampling) is an important factor affecting mite infestation on beetles was tested. *Uropoda orbicularis* is one of the most common phoretic uropodid mites and inhabits temporal microhabitats such as animal dung, dead wood and compost (Hirschmann and Zirngiebl-Nicol, 1969; Schelvis, 1994; Mašán, 2001). Its deutonymphs are phoretic on various species of coprophilous beetles (Faasch, 1967; Karg, 1989; Makarova, 1995; Kofler and Schmölzer, 2000; Mašán, 2001; Bajerlein and Błoszyk, 2004; Bajerlein and Przewoźny, 2005).

MATERIAL AND METHODS

Collection and identification of mites and insects – The field work was carried out on a pasture located about 20 km north-west of Poznań (Poland, Wielkopolska region, 52°31′N 16°43′E). The material was sampled using six pitfall traps baited with fresh cow dung, and emptied at seven day intervals between March 23 and November 26, 2003, and from April 3 to December 18, 2004. Pitfall traps were filled with 50% ethylene glycol solution. Beetles were stored in 75% ethyl alcohol and identified under a stereomicroscope using the keys of Stebnicka (1976), Mazur (1981), Freude *et al.* (1971), Hansen (1987, 1990), Heubauer (1989), Heubauer and Schödl (1998). Beetles were examined for phoretic deutonymphs, the number of pedicels was also quantified. Phoretic deutonymphs were identified using keys of Mašán (2001) and Karg (1989). The collected material is deposited in Natural History Collections, Adam Mickiewicz University, Poznań, Poland.

Statistical analysis – In this study a sum of deutonymphs and pedicels without mites was analyzed. The incidence of phoretic deutonymph infestation on beetles from the families Scarabaeidae, Geotrupidae, Aphodiidae, Hydrophilidae and Histeridae was calculated using the following parameters: prevalence (P), intensity (I) and density (D). Prevalence (P) was expressed as a percentage of beetle specimens infested among the total of all analyzed beetles. Intensity (I) was expressed as the mean number of cases of phoresy (a sum of deutonymphs and pedicels) per infested beetle. Density (D) was expressed as the number of cases of phoresy (a sum of deutonymphs and pedicels) per each collected beetle. Confidence limits for prevalence were calculated directly from the binomial distribution. For other parameters, the standard error (SE) of the mean was calculated. Density of phoretic deutonymphs shown in Figs. 2A and B was expressed as a mean density per trap. The curves of mite density shown in Figs. 2A and B were obtained by the Weighted Least Squares Method. Numbers of phoretic deutonymphs and beetles shown in Figs. 3–7 were expressed as a mean number of specimens per trap collected on a particular sampling date. Differences in mite density between beetles were tested using the Kruskal-Wallis test. *A posteriori* non-parametric test for multiple comparision of mean ranges was used. Density was chosen for analysis, because this parameter contains information about both prevalence and intensity. Spearman's rank correlation coefficient was calculated for the abundances of beetles from a particular family and the phoretic deutonymphs found on them. Calculations were made using Statistica 7.1. In both cases a 5% significance level was used.

RESULTS

A total of 32,064 beetles were collected representing 64 species, belonging to the families: Scarabaeidae, Geotrupidae, Aphodiidae, Hydrophilidae and Histeridae. On the beetles collected there were a total of 35,839

Table 1. Numbers of beetles collected (N), phoretic deutonymphs of *Uropoda orbicularis* (UOR) and pedicels without mites (PD).

	N	UOR	PD
Scarabaeidae	3,134	1,940	10,394
Geotrupidae	240	87	304
Aphodiidae	23,607	3,301	16,255
Hydrophilidae	3,672	191	386
Histeridae	1,411	297	2,684
Total	32,064	5,816	30,023

cases of phoresy: 5,816 deutonymphs of *Uropoda orbicularis* and 30,023 pedicels without deutonymphs. General information on the collected material are given in Table 1. Table 2 contains a list of all beetle species collected, their abundance, size, and whether they carried mites or not.

Infestation of phoretic deutonymphs on beetles from particular families – Beetles of the family Scarabaeidae were most frequently accompanied by phoretic deutonymphs. Cases of phoresy were recorded on more than half of the specimens from this beetle family (Fig. 1A). In contrast, only 5% of hydrophilids carried deutonymphs. Values of prevalence were relatively high on Histeridae and Geotrupidae, but phoretic deutonymphs infested only a small proportion of the Aphodiidae (Fig. 1A). Every infested beetle from the family Scarabaeidae carried an average of 7.2 deutonymphs (Fig. 1B). Histeridae, Aphodiidae and Geotrupidae were less intensively infested, and these three groups of beetles did not differ in deutonymph intensity. The lowest value of mite intensity was recorded for Hydrophilidae (I = 3.5) (Fig. 1B). The highest mite density (D = 3.9) was observed on Scarabaeidae and the lowest (D = 0.2) on Hydrophilidae (Fig. 1C). Histeridae had density of D = 2.1 mites and Geotrupidae (D = 1.6) and Aphodiidae (D = 0.8) carried less deutonymphs (Fig. 1C). Differences in mite density between the studied beetles were statistically significant (ANOVA Kruskal-Wallis: H = 4143.189, p < 0.000).

Seasonal changes in density of phoretic deutonymphs on carriers – The highest deutonymph density occurred in late spring, in May and June 2003 and in June 2004 (Fig. 2A and B). After this period, mite density gradually decreased and the level of infestation was lower during summer. A slight increase in deutonymph density was observed in early autumn (September) and mite loads on beetles were low in October and November (Fig. 2A and B).

Seasonal abundance of phoretic deutonymphs and beetles from particular families – Most scarabaeids were collected in spring. At this time, beetles showed a period of high abundance at the beginning of May 2003 and at the beginning of June 2004. A slight increase in scarabaeids abundance was also observed in early July. The number of phoretic deutonymphs on scarabaeids was very high, but in 2003 beetles carried more mites than in 2004. Deutonymphs showed three main periods of abundance, with the highest abundance at the begining of June (Fig. 3). The abundances of scarabaeids and phoretic deutonymphs were strongly correlated ($r_s = 0.9$, P = 0.000).

In both seasons, the number of geotrupid beetles was very low. A distinct increase in the number of specimens was observed in late summer and early autumn. At this time, the abundance of phoretic deutonymphs carried by geotrupids was highest (Fig. 4). A moderate correlation was observed for the abundances of geotrupids and phoretic deutonymphs ($r_s = 0.5$, P = 0.000).

Aphodiidae were the first and the last beetles to be observed each year. Numbers of aphodiids reached maxima in spring and autumn. The first peak of abundance was observed at the beginning of May in 2003 and at the end of April in 2004. In 2003, a slight increase in abundance was recorded in September and in the first part of October. A distinct peak in beetle abundance occurred in late October. During autumn in 2004, aphodiid abundance peaked twice, at the begining of October, and at the begining of November (Fig. 5). Phoretic deutonymphs were present on the first aphodiid specimens collected. The highest numbers of deutonymphs were recorded in spring. The first peak of mite abundance occurred at the same time as the peak of beetle abundance. An increase in deutonymph numbers was observed in late spring, although beetle abundance was low. The next period of deutonymph activity was observed at the begining of autumn, and was correlated with the increase in numbers of aphodiids. Abundance of deutonymphs was very low in late autumn, although distinct peaks of carrier abundance were seen (Fig. 5). A moderate correlation was observed for abundances of aphodiids and phoretic deutonymphs ($r_s = 0.5$, P = 0.000).

Hydrophilids were observed from April until the end of September, and some individuals were collected at the beginning of October (Fig. 6). Their abundance differed in 2003 and 2004. In 2003, a peak of hydrophilid abundance occurred in the middle of May. After this time, numbers of beetles increased three times during summer. In the 2004, two distinct peaks in beetle abundance occurred, at the beginning of June and in the middle of August. The number of phoretic deutonymphs on hydrophilids was low. In the 2003 a slight increase in their numbers was observed in May and at the end of

Table 2. List of beetle species collected with their abundance (N), body size (BS) and mean body size.

	N	BS (mm)
GEOTRUPIDAE		
1. *Anoplotrupes stercorosus* (Hartmann in Scriba, 1791)	16	12.0–19.0
2. *Geotrupes spiniger* (Marsham, 1802)	177	18.0–26.0
3. *Trypocopris vernalis* (Linnaeus, 1758)	47	12.0–20.0
		14.0–21.7*
SCARABAEIDAE		
1. *Onthophagus coenobita* (Herbst, 1783)	468	6.0–10.0
2. *Onthophagus fracticornis* (Preyssler, 1790)	83	7.0–10.0
3. *Onthophagus nuchicornis* (Linnaeus, 1758)	1,826	6.0–9.0
4. *Onthophagus ovatus* (Linnaeus, 1767)	584	4.0–6.0
5. *Onthophagus semicornis* (Panzer, 1798)	22	5.5–6.0
6. *Onthophagus similis* (Scriba, 1790)	150	4.0–7.0
7. *Onthophagus taurus* (Schreber, 1759)	1	6.0–11.5
		5.5–8.5*
APHODIIDAE		
1. *Aphodius ater* (De Geer, 1774)	6	4.0–6.0
2. *Aphodius coenosus* (Panzer, 1798)	7	4.5–5.0
3. *Aphodius contaminatus* (Herbst, 1783)	3	5.0–6.5
4. *Aphodius depressus* (Kugelann, 1792)	1	6.0–9.0
5. *Aphodius distinctus* (O. F. Müller, 1776)	11,085	3.5–5.5
6. *Aphodius erraticus* (Linnaeus, 1758)	2	6.0–8.5
7. *Aphodius fimetarius* (Linnaeus, 1758)	1,523	5.0–8.0
8. *Aphodius foetens* (Fabricius, 1787)	641	6.0–9.0
9. *Aphodius fossor* (Linnaeus, 1758)	11	10.0–13.0
10. *Aphodius granarius* (Linnaeus, 1767)	68	3.0–5.0
11. *Aphodius haemorrhoidalis* (Linnaeus, 1758)	28	3.5–5.0
12. *Aphodius luridus* (Fabricius, 1775)	10	6.0–9.0
13. *Aphodius porcus* (Fabricius, 1792)	25	4.5–5.0
14. *Aphodius prodromus* (Brahm, 1790)	9,570	4.0–7.0
15. *Aphodius pusillus* (Herbst, 1789)	10	2.5–4.5
16. *Aphodius rufipes* (Linnaeus, 1758)	53	10.0–13.0
17. *Aphodius rufus* (Moll, 1782)	123	5.0–7.0
18. *Aphodius sordidus* (Fabricius, 1775)	15	5.0–7.0
19. *Aphodius subterraneus* (Linnaeus, 1758)	413	6.0–7.5
20. *Oxyomus sylvestris* (Scopoli, 1763)	13	2.5–3.5
		5.1–7.2*
HYDROPHILIDAE		
1. *Cercyon analis* (Paykull, 1798)	1	1.7–2.5
2. *Cercyon haemorrhoidalis* (Fabricius, 1775)	130	2.5–3.2
3. *Cercyon impressus* (Sturm, 1807)	4	3.0–3.6
4. *Cercyon laminatus* (Sharp, 1873)	1	3.2–4.0
5. *Cercyon lateralis* (Marsham, 1802)	595	2.3–3.1
6. *Cercyon melanocephalus* (Linnaeus, 1758)	4	2.3–3.0
7. *Cercyon nigriceps* (Marsham, 1802)	8	1.5–2.0
8. *Cercyon castaneipennis* (Vorst, 2009)	5	3.2–4.2
9. *Cercyon pygmaeus* (Illiger, 1801)	1,233	1.4–1.8
10. *Cercyon quisquilius* (Linnaeus, 1760)	81	2.0–2.6
11. *Cercyon terminatus* (Marsham, 1802)	3	1.6–2.3
12. *Cercyon unipunctatus* (Linnaeus, 1758)	5	2.4–3.4

(*Continued*)

Table 2. (*Continued*).

	N	BS (mm)
13. *Cryptopleurum crenatum* (Kugelann, 1794)	2	2.1–2.4
14. *Cryptopleurum minutum* (Fabricius, 1775)	337	1.6–2.2
15. *Cryptopleurum subtile* (Sharp, 1884)	6	1.5–2.2
16. *Megasternum concinnum* (Marsham, 1802)	20	1.7–2.0
17. *Sphaeridium bipustulatum* (Fabricius, 1781)	89	4.0–5.7
18. *Sphaeridium lunatum* (Fabricius, 1792)	470	5.5–7.5
19. *Sphaeridium marginatum* (Fabricius, 1787)	297	4.0–5.7
20. *Sphaeridium scarabaeoides* (Linnaeus, 1758)	381	5.0–7.0
		2.6–3.5*
HISTERIDAE		
1. *Atholus bimaculatus* (Linnaeus, 1758)	8	2.5–4.0
2. *Atholus duodecimstriatus* (Schrank, 1781)	45	2.8–4.2
3. *Hister unicolor* (Linnaeus, 1758)	64	5.0–8.0
4. *Margarinotus bipustulatus* (Schrank, 1781)	1	4.9–7.0
5. *Margarinotus carbonarius* (Hoffmann, 1803)	819	3.0–4.2
6. *Margarinotus obscurus* (Kugelann, 1792)	4	3.4–5.5
7. *Margarinotus purpurascens* (Herbst, 1792)	20	3.5–4.5
8. *Margarinotus ventralis* (Marseul, 1854)	38	3.0–5.0
9. *Margarinotus* sp.	1	–
10. *Onthophilus punctatus* (O. F. Müller, 1776)	1	2.5–3.5
11. *Onthophilus striatus* (Forster, 1771)	1	1.7–2.5
12. *Saprinus aeneus* (Fabricius, 1775)	400	2.5–3.5
13. *Saprinus planiusculus* (Motschulsky, 1849)	7	3.4–5.5
14. *Saprinus semistriatus* (Scriba, 1790)	2	3.6–6.0
		3.2–4.9*
Total	**32,064**	

Note: Bolded species names indicate carriers of *U. orbicularis*. Body size of geotrupids, scarabaeids and aphodiids according to Stebnicka (1978), body size of hydrophilids according to Przewoźny (2009), body size of histerids according to Mazur (1981). Mean body size (marked with bold letters*)

July. In the next year, a distinct peak in deutonymph abundance occurred in early June, and after this time the number of mites was low (Fig. 6). A moderate correlation was observed for the abundance of hydrophilids and phoretic deutonymphs ($r_s = 0.5$, $P = 0.000$).

Histerid beetles were active during spring and summer, although in 2004 they appeared earlier than in 2003 (Fig. 7). In both 2003 and 2004, beetle abundance increased and decreased several times. Changes in phoretic deutonymph numbers were similar to changes in beetle numbers. Most deutonymphs carried by histerids were recorded during spring, and the least in summer (Fig. 7). A strong correlation was observed for abundances of histerids and phoretic deutonymphs ($r_s = 0.7$, $P = 0.000$).

DISCUSSION

Deutonymph infestation on beetles – The results obtained here have confirmed the hypothesis that season should be regarded as an important factor affecting mite infestation. Although deutonymphs of *U. orbicularis* use most of the co-occuring beetles as a mean of transport, infestation of deutonymphs varied among beetle families. At the end of May and the beginning of June, the number of phoretic deutonymphs was higher than the number of beetles, so deutonymph density on beetles reached their maximum at this time. Mite load was highest in each beetle family at the end of May and beginning of June. During autumn, phoretic activity of *U. orbicularis* decreased markedly, and all beetles collected in this period carried few mites. The seasonal changes in numbers of individuals follow different patterns in dung beetles (Hanski and Cambefort, 1991). In temperate regions, dung beetle communities are dominated by small species belonging to the genus *Aphodius*, particularly *Aphodius prodromus* (Brahm, 1790) and *Aphodius distinctus* (Müller, 1776) (see Table 2). Two seasonal peaks are evident in *A. prodromus* and *A. distinctus*, one in early spring and the other in the autumn. The beetles that appeared in spring are those who overwintered as

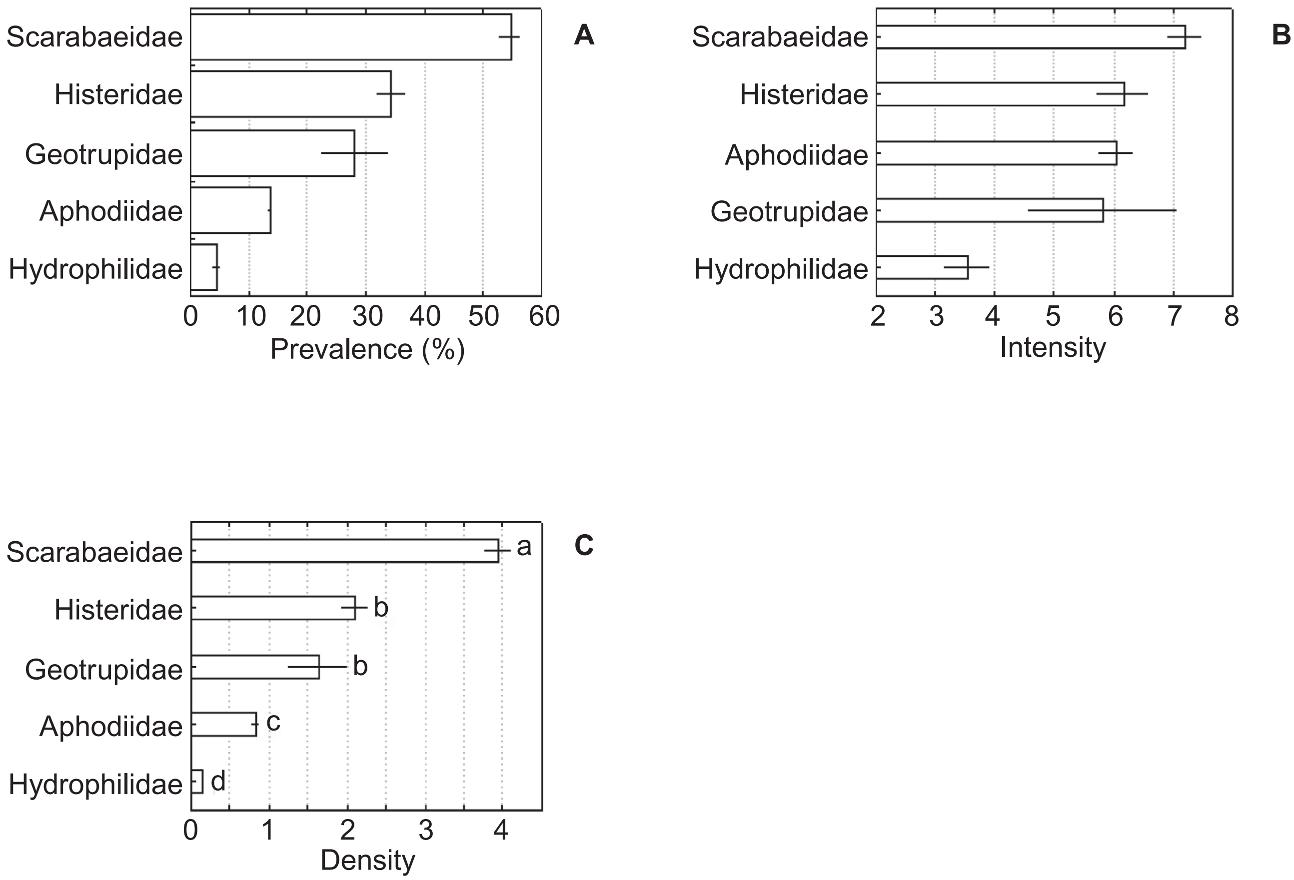

Fig. 1A–C. Values of infestation parameters: A – prevalence (value of prevalence with confidence limits), B – intensity (mean ± SE), C – density (mean ± SE) of *Uropoda orbicularis* on beetles from particular families. Different letters in the Fig. 1C denote significant differences between studied beetle groups in multiple comparisons ($P < 0.05$).

adults and those that appeared in autumn are those who overwintered as larvae. In late spring, *Aphodius* shows a definite decrease in abundance. At this time, the number of species and individuals of *Onthophagus* beetles (Scarabaeidae) increases, and they dominate during late May and June. The family Geotrupidae is represented by only a few species, collected in a low number (Bunalski, 1997; Bajerlein, 2004). Scarabaeids were active in the period when deutonymph abundance reached its maximum, but simultaneously the number of all beetles in the community was low. Therefore, the prevalence and abundance of mites was highest on scarabaeids. Also histerids carried dense loads of mites. Most histerids were collected in spring and for this reason they were one of the most intensively used carrier groups. Although the infestation level of deutonymphs on aphodiids was relatively low, they played an important role in transporting *U. orbicularis*. Aphodiids were present throughout the whole season, reaching their maximum numbers in spring and autumn. Aphodiids collected during the spring carried more mites than those collected during autumn.

Although these results focused on seasonal influences on deutonymph infestation, other factors affecting differential use of carrier species should also be taken into account. One of them may be the body size of the carrier. Bigger beetles may carry more mites and are more frequently infested by mites than smaller beetles (Wallace, 1986; Kotiaho and Simmons, 2001). This relationship may explain the low rate of infestation of deutonymphs on hydrophilid beetles. Hydrophilid beetles occurred throughout the whole season (hydrophilids are multivoltine), and they were common and easily accessible to the mites, but they were less intensively used, possibly as a result of the small body size of most species (mean size rage 2.6–3.5 mm, see Table 2). On the other hand, Geotrupidae, the biggest beetles in the present study, (mean size range 14–21.7 mm, see Table 2), had a lower prevalence than much smaller scarabaeids (mean size range 5.5–8.5 mm, see Table 2). The relatively lower prevalence

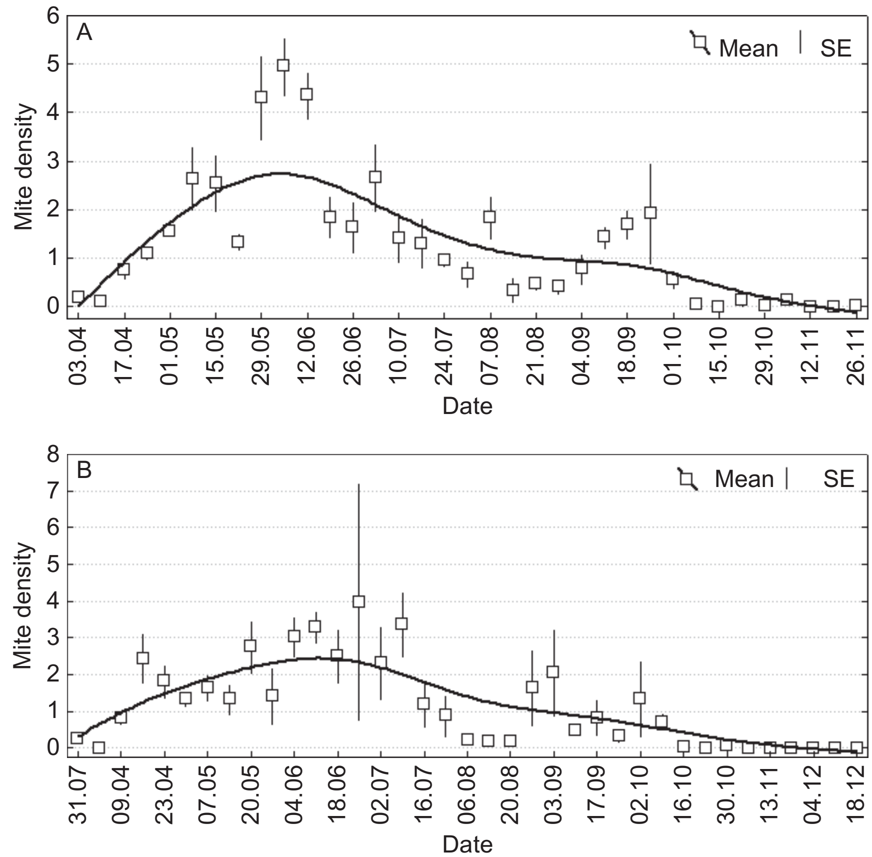

Fig. 2A, B. Density of *Uropoda orbicularis* on coprophilous beetles in 2003 (A) and 2004 (B).

of mites on geotrupids may be explained by the fact that geotrupids were not numerous in the studied community and most of them occurred only in late summer and in autumn when deutonymph abundance was low. In this case, it can be assumed that deutonymph infestation was probably more influenced by season then by body size of the carriers.

These results show that mite infestation may be influenced by seasonal factors to a high degree. Differences in mite infestation on carriers may reflect mite preferences towards specific carriers (Schwarz *et al.*, 1998). In the case of *U. orbicularis* and coprophilous beetles, the differences in infestation may have resulted mainly from seasonal changes in the abundance of beetles and mites. Therefore, seasonal factors should be taken into account when determining mite preferences towards their hosts, which requires a detailed study of the temporal distribution of both the phoretic mites and their carriers.

Seasonal abundance of phoretic deutonymphs and their carriers – Phoresy of *U. orbicularis* was observed throughout the whole season confirming that this phenomenon is a vital life strategy among mites living in dung. Fast ontogenetic development is an adaptation to living in rapidly changing environmental conditions. Faasch (1967) found that *U. orbicularis* is a multivoltine species with rapid developmental rates. Considering the frequency of migration, phoresy of *U. orbicularis* is facultative. This kind of phoresy may be caused by changes in abiotic factors and density-dependent factors (Athias-Binche, 1994). The fact that phoretic deutonymphs were present on the beetles collected at the start of the season may indicate that deutonymphs pass the winter with their carriers. Stewart and Davis (1967) observed that adult beetles hatching under laboratory conditions had attached uropodid deutonymphs.

Analysis of the seasonal dynamics of coprophilous beetles and the phoretic mites have shown that their abundances varied through time. Changes in deutonymph and beetle seasonal abundances were similar, indicating that *U. orbicularis* is dependent to a high degree on beetles for its dispersal. During the study I have not found phoretic deutonymphs of

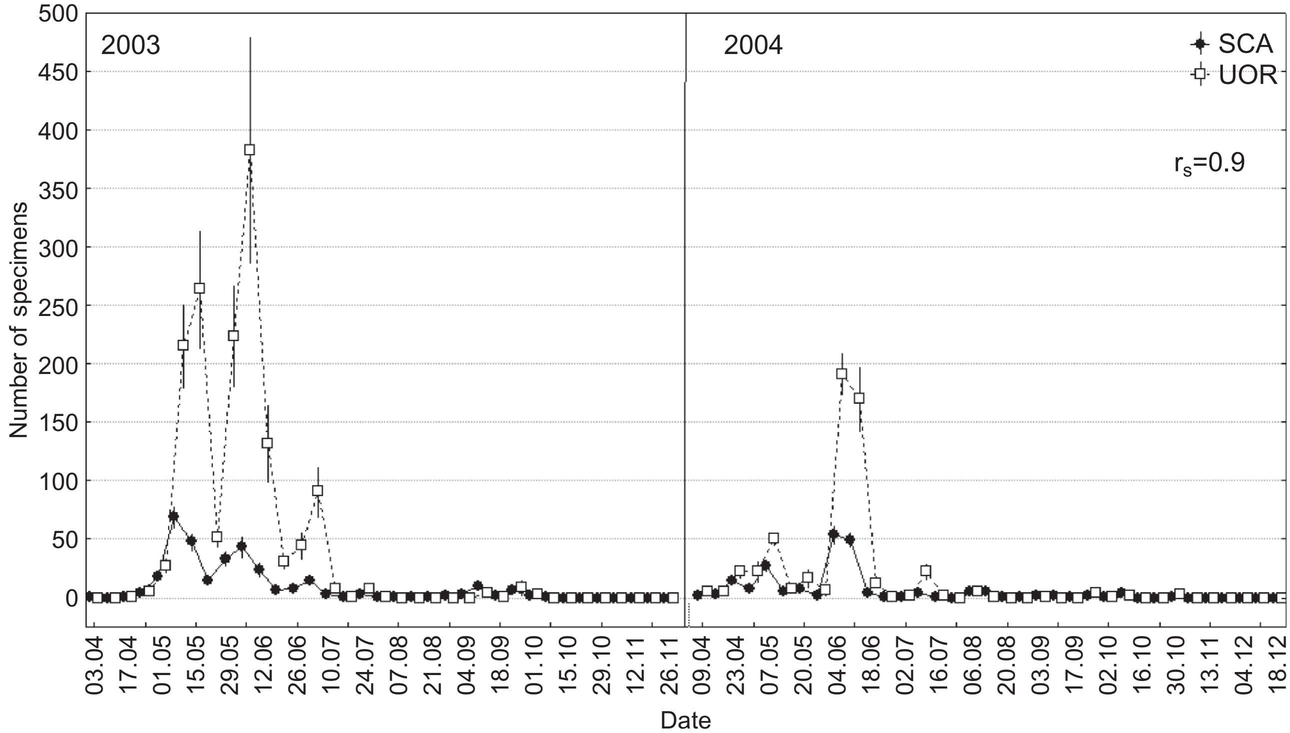

Fig. 3. Seasonal abundance (mean ± SE) of *Uropoda orbicularis* (UOR) and beetles from the family Scarabaeidae (SCA) (r_s – Spearman's rank correlation coefficient for abundance of scarabaeids and deutonymphs of *U. orbicularis*).

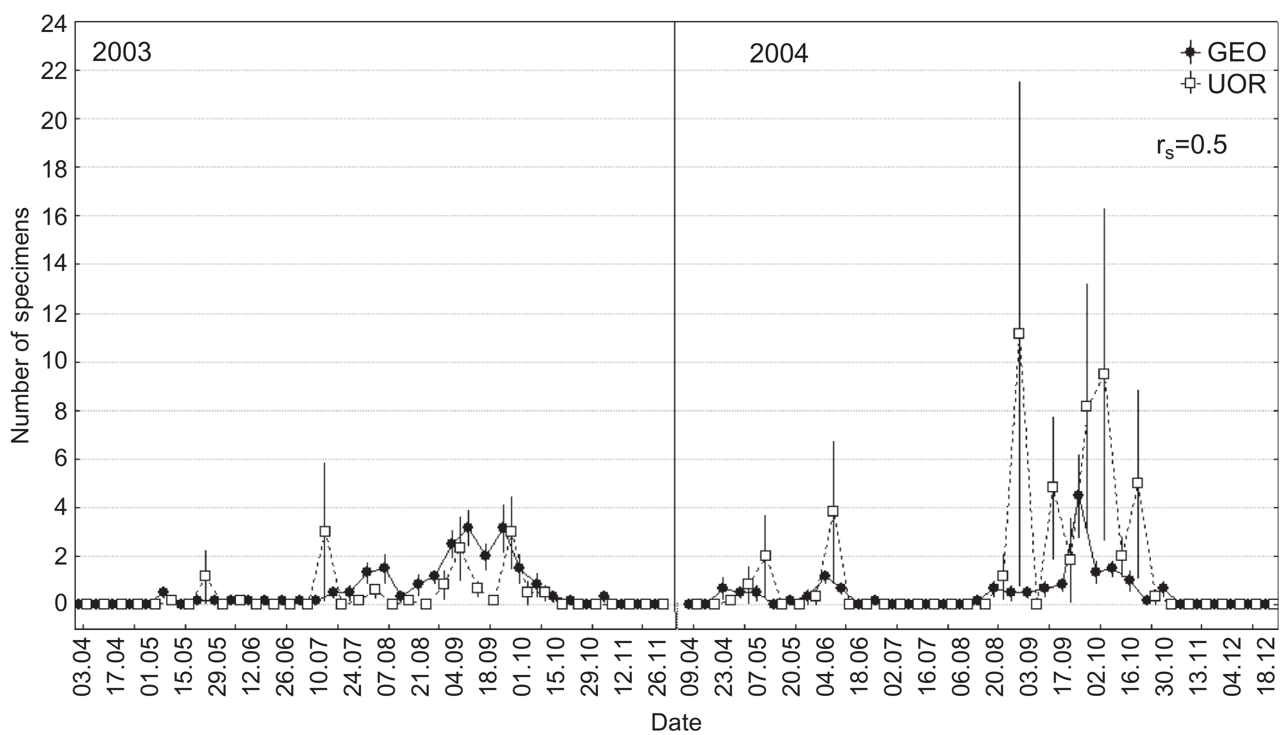

Fig. 4. Seasonal abundance (mean ± SE) of *Uropoda orbicularis* (UOR) and beetles from the family Geotrupidae (GEO) (r_s – Spearman's rank correlation coefficient for abundance of geotrupids and deutonymphs of *U. orbicularis*).

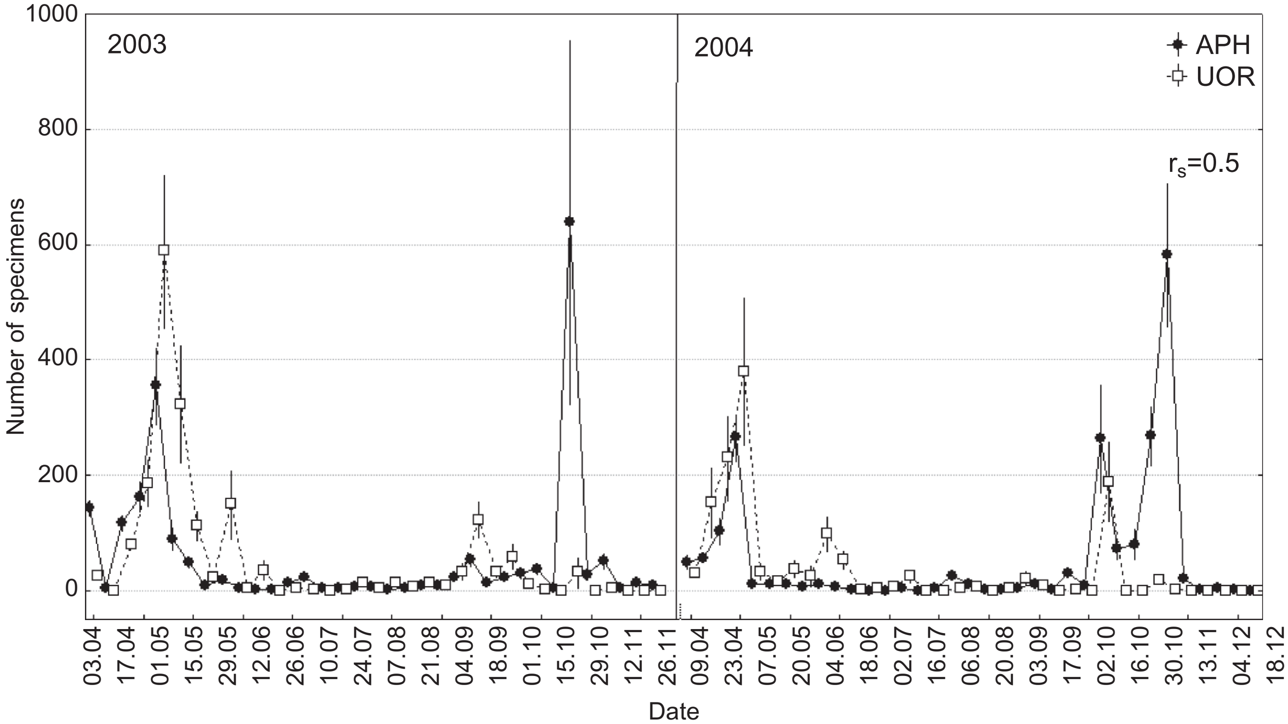

Fig. 5. Seasonal abundance (mean ± SE) of *Uropoda orbicularis* (UOR) and beetles from the family Aphodiidae (APH) (r_s – Spearman's rank correlation coefficient for abundance of aphodiids and deutonymphs of *U. orbicularis*).

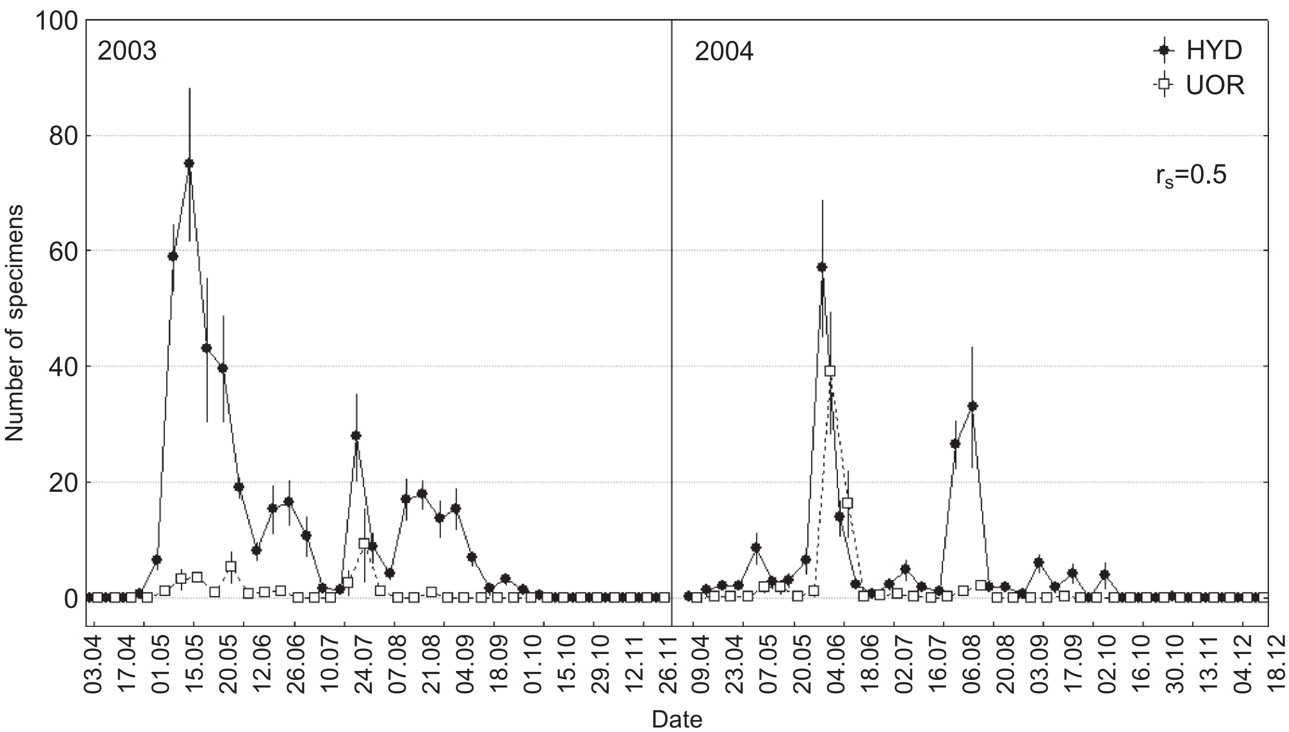

Fig. 6. Seasonal abundance (mean ± SE) of *Uropoda orbicularis* (UOR) and beetles from the family Hydrophilidae (HYD) (r_s – Spearman's rank correlation coefficient for abundance of hydrophilids and deutonymphs of *U. orbicularis*).

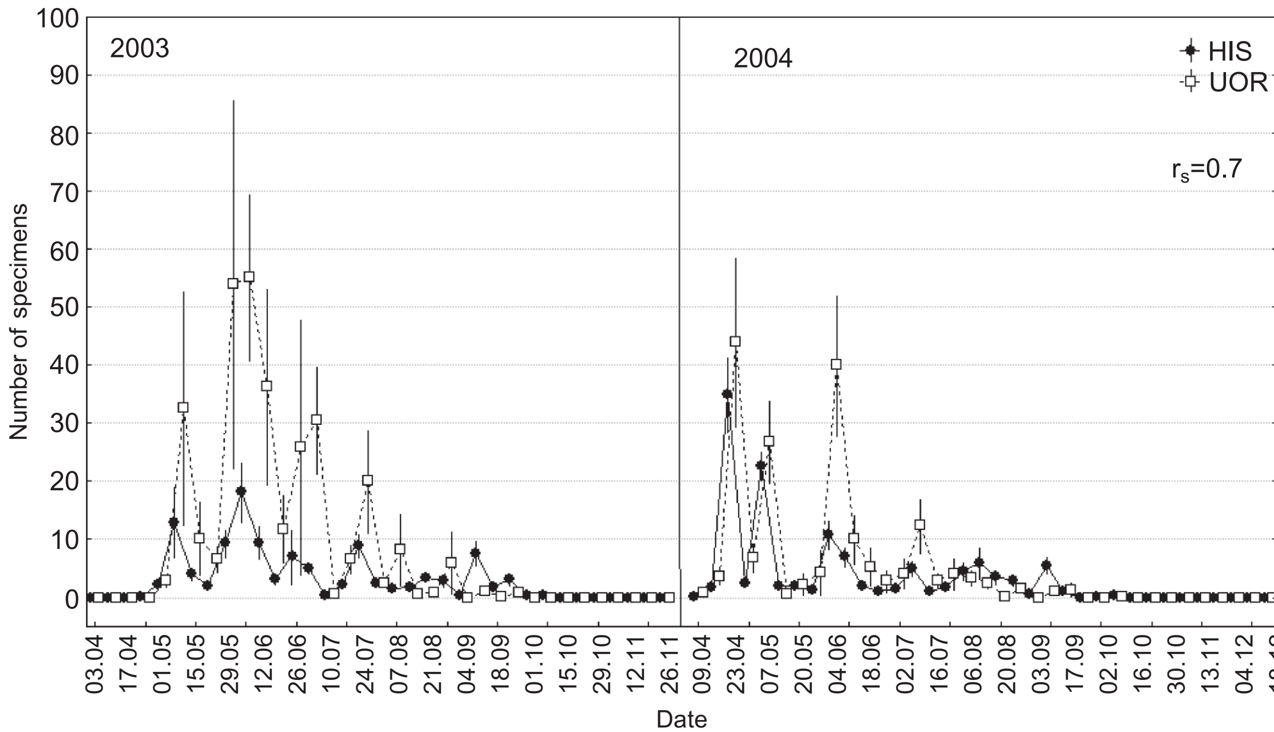

Fig. 7. Seasonal abundance (mean ± SE) of *Uropoda orbicularis* (UOR) and beetles from the family Histeridae (HIS) (r_S – Spearman's rank correlation coefficient for abundance of histerids and deutonymphs of *U. orbicularis*).

U. orbicularis attached to dipterans. The highest correlation coefficients were recorded between the abundances of phoretic deutonymphs and beetles from the families Scarabaeidae and Histeridae. This may be explained by the fact that beetles from these families were most abundant during spring when the number of deutonymphs was the highest. The lowest correlation coefficients were recorded between deutonymphs and aphodiids, geotrupids and hydrophilids. Relatively low correlation coefficient values between phoretic deutonymphs and Aphodiidae may have resulted from the fact that the number of aphodiids was very high during autumn, whereas the number of deutonymphs at that time was low. At this time the abundances of Aphodiidae and deutonymphs were not correlated. Aphodiidae were important carriers of *U. orbicularis* in spring, especially in April and the first part of May. At this time aphodiids were most numerous beetles in the studied community. The low value of the correlation coefficient between the abundance of phoretic deutonymphs and hydrophilids may have resulted from the fact that these beetles are too small to carry deutonymphs of *U. orbicularis*. Most species of coprophagous hydrophilid beetles did not transport deutonymphs of *U. orbicularis* (Bajerlein and Przewoźny, 2005). Low correlation coefficients between deutonymphs and geotrupids was probably caused by the fact that these beetles occurred in very low numbers. This study demonstrates that the abundance of carriers is not the only factor affecting the abundance of phoretic deutonymphs. In autumn, the abundance of phoretic deutonymphs decreased, indicating that at this time the phoretic activity of *U. orbicularis* was low, although the number of potential carriers was high. At the beginning of May and the end of June, abundance of phoretic deutonymphs was high but the numbers of beetles decreased markedly.These observations proved that phoresy of *U. orbicularis* on coprophilous beetles may be influenced by seasonal factors. It can be assumed that the abundance of phoretic deutonymphs observed on beetles is a function of their carrier abundance, size and *U. orbicularis* abundance, and that both carrier and *U. orbicularis* abundances may be influenced by season. Thus, season may have affected abundance of phoretic deutonymphs indirectly by carrier abundance as well as directly.

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