ADULT LIFESPAN OF SHEET WEB SPIDERS (ARANEAE, LINYPHIIDAE)

Boudewijn Heuts
Swammerdam Institute for Life Sciences, Faculteit der Natuurwetenschappen, Wiskunde en Informatica – Postbus 94215, 1090 GE Amsterdam, The Netherlands (b.a.heuts@uva.nl)

&
Tibor Brunt
Amsterdam Medical Centre, Faculteit Psychiatrie, Amsterdam, The Netherlands (tibor.brunt@gmail.com)

ABSTRACT
Adult lifespan of sheet web spiders (Araneae, Linyphiidae).
We investigated maximal and median adult lifespan in 61 linyphiid species that were caught in the field (as adult or subadult specimens) or were raised in the laboratory from wild-caught or laboratory-bred gravid females.
The results are thought to reflect the real adult lifespan potential we wanted to measure when spiders are not threatened by natural adverse factors in the field. Of some species, in particular of the genus *Walckenaeria*, we never succeeded to capture subadult specimens in the field.
The main result is that adult females live significantly longer than adult males which is in accordance with the literature. A second finding is that we now can demonstrate a significantly longer adult-stage-duration in small than in large linyphiid species, as well as a significantly longer lasting adult stage in species living at ground-litter level than in species living higher up in the vegetation.
When comparing the adult-lifespan of single species with each other we can demonstrate that some particular linyphiid species live a significantly longer time than others in their adult stage.

Key words: adult lifespan, linyphiid spiders

INTRODUCTION

Data on the adult lifespan of spiders are scarce. We shortly reviewed the available literature in Heuts & Brunt (2004). We now give many new adult lifespan data of linyphiid spiders and we include small samples of old data in the totals of each species (previous data in Heuts & Brunt 2004, 2006).

We investigated maximal and median adult lifespan in 61 linyphiid species which were caught in the field (as adult or subadult specimens) or were raised in the laboratory from wild-caught or laboratory-bred gravid females. Part of the adult lifespan data was obtained from field-caught adults living from the day of capture until death in captivity. The other part was obtained from young specimens that moulted to adult and died in captivity after having been caught in the field or after having been bred or raised in captivity. As most linyphiids cannot be recovered later on when discovered in the field due to their hidden webs in the leaf litter or low vegetation, their adult lifespan had to be measured in captivity. This probably reflects the actual adult lifespan potential we wanted to measure when spiders are not threatened by their natural adverse factors in the field.

MATERIAL AND METHODS

Adult and non-adult linyphiid spiders were caught in the field and then kept alive in captivity, or they were raised in laboratory containers from freshly caught gravid females or from their egg cocoons. Another part of the spiders was raised from egg cocoons deposited by laboratory-raised females which had been fertilized in captivity by various types of adult males, i.e. by freshly caught males from the field, or by laboratory-raised males that were probably closely related to the adult females.

Our main catching device consisted of manual grasping and spreading out of ground litter which had first been thrown into a plastic, white and opaque 'catching bucket'. For spiders living above ground level in the vegetation we used another method, i.e. pushing the upper rim of the catching bucket against the underside of low vegetation or bushes while at the same time beating with one hand in a downward direction. We recorded the time interval between the day of catching and the day of dying in captivity while noting the day of moulting to the adult stage in case of young field-caught or captivity-bred specimens. In some genera and species we never caught young (non-adult) specimens in the field (specified below at the end of this chapter).
Apart from physical and biotic factors (such as predation by birds or by other spiders) which reduce the lifespan of adult spiders in the field and which can easily be circumvented by keeping the spiders in captivity, there is possibly another interfering factor which may have distorted our adult lifespan data. It is e.g. possible that there are some linyphiid species that are only liable to be caught in the field after having spent the first part of their adult life below ground-litter level so that we could not obtain them alive by our catching method (manual

collection of ground litter). We, therefore, may have underestimated the actual adult lifespan of our linyphiid spiders. This may for instance. be the case for the species of the genus *Walckenaeria* (see tables 1 and 2), a genus from which we, unfortunately, never caught non-adult specimens in the field.

The nomenclature of the species is based on Roberts (1985, 1987, 1995, 1998) and Heimer & Nentwig (1999). Many generic names have been changed since the publications of Roberts (see Van Helsdingen 2009).

RESULTS

The main outcome of our experiments is that adult females live significantly longer than adult males, which is in accordance with the general notion in the spider literature (which, however, does not provide adequate quantitative data). Our significant female-male difference is based on the combined adult lifespan data of the 43 species (table 1) which provided data for both sexes. In 29 species the median adult lifespan was longer in females than in males, in contrast to the reverse in only 13 species (one species, *Troxochrus scabriculus,* was discarded in this analysis because females did not differ from males; $\chi^2 = 6.09$, $p < 0.02$). In 34 species the maximal adult lifespan was longer in females than in males, in contrast to the reverse in only 7 species with adult males living longer (two species, *Erigone atra* and *Porrhomma microphthalmum,* were discarded because the maximal adult lifespan of females did not clearly differ from males; $\chi^2 = 17.78$, $p < 0.001$). In our two earlier studies (Heuts & Brunt 2004, 2006) we could not demonstrate a significant difference in the compound adult lifespan data of a much smaller sample of different species.

A second result was that, in accordance with our two earlier papers (Heuts & Brunt 2004, 2006), we now demonstrate in a much larger sample of species a significantly longer lasting adult stage in small than in large linyphiid species ('small' average body size being less than 3.5 mm, versus 'large' body size being more than 3.5 mm; our *Centromerita bicolor* and *Centromerus sylvaticus* were rather large so that they were counted as large species). In the analysis we disregard species of which only one sex was tested (as indicated by horizontal stripes in table 1) except for including, nevertheless, the data of *Microlinyphia impigra* of which only females were available.

The 10 species that were categorized as "large species" were *Centromerita bicolor*, *Centromerus sylvaticus*, *Linyphia hortensis*, *Linyphia triangularis*, *Macrargus rufus*, *Microlinyphia impigra*, *Neriene clathrata*, *Neriene montana*, *Neriene peltata*, *Saaristoa abnormis.*

The 31 species that were categorized as "small species" were: *Bathyphantes approximatus*, *Bathyphantes gracilis*, *Ceratinella brevis*, *Collinsia inerrans*, *Dicymbium nigrum*, *Diplocephalus cristatus*, *Diplocephalus permixtus*, *Diplocephalus picinus*, *Diplostyla concolor*, *Entelecara acuminata*, *Entelecara erythropus*, *Erigone atra*, *Erigone dentipalpis*, *Gnathonarium dentatum*, *Gongylidium rufipes*, *Hypomma bituberculatum*, *Kaestneria dorsalis*, *Lepthyphantes leprosus*, *Lessertia dentichelis*, *Maso sundevalli*, *Micrargus subaequalis*, *Microneta viaria*, *Oedothorax apicatus*, *Oedothorax fuscus*, *Ostearius melanopygius*, *Porrhomma microphthalmum*, *Tenuiphantes tenuis*, *Troxochrus scabriculus*, *Walckenaeria acuminata*, *Walckenaeria atrotibialis*, *Walckenaeria cucullata*.

When now contrasting in table 1 the median adult lifespan of the 10 large species against the 31 small species in a two-tailed Mann-Whitney U test ($n_1 = 10$; $n_2 = 31$) it appears that their adult lifespans differed almost significantly from each other (species' median adult lifespan amounting to 3.52 and 4.61 months in large and small species respectively; U approx = 100; critical two-tailed U-value for $p < 0.05$ estimated at 102 from the incomplete tables of Siegel (1956) giving a p-value of approx. 0.05). When contrasting the 10 large and 31 small species with respect to their maximum adult lifespan (averaged maximal adult lifespan amounting to 6.72 and 10.45 months in the large and small species, respectively) it appears that the small and large species differed significantly from each other **(**$n_1 = 10$; $n_2 = 31$; $U = 80.5$, giving $p < 0.05$ in a two-tailed test ; critical 0.05-U-value estimated at approx. 90). Thus, the maximal adult lifespan of small linyphiid species was significantly longer than of large linyphiid species (about 1.55 times as long).

We further, demonstrate a significantly longer lasting adult stage in species living at ground-litter level than in species living higher up in the vegetation. In order to do this, we used median values of species in which both at least one male and one female had been tested. Thus, the male and female median value (see always table 1) were added and averaged for each species separately, first with respect to median , and secondly with respect to maximal, adult lifespan. In *Floronia bucculenta* e.g. the male-female-averaged median adult lifespan was 3.03 months, while the male-female-averaged maximal adult lifespan was 4.00 months, values which can quickly be calculated from the data in table 1.

The 12 species categorized as living higher up in the vegetation were the following: *Entelecara acuminata, Floronia bucculenta, Gnathonarium dentatum, Gongylidium rufipes, Hypomma bituberculatum, Kaestneria dorsalis, Linyphia hortensis, Linyphia triangularis, Maso sundevalli, Neriene clathrata, Neriene montana, Neriene peltata.*

The 26 species categorized as living at ground level were the following: *Bathyphantes approximatus, Bathyphantes gracilis, Centromerus sylvaticus, Ceratinella brevis, Collinsia inerrans, Dicymbium nigrum, Diplocephalus cristatus, Diplocephalus permixtus, Diplostyla concolor, Entelecara erythropus, Erigone atra, Erigone dentipalpis, Lepthyphantes leprosus, Lessertia dentichelis, Macrargus rufus, Micrargus subaequalis, Microneta viaria, Oedothorax apicatus, Oedothorax fuscus, Ostearius melanopygius, Porrhomma microphthalmum, Tenuiphantes tenuis, Troxochrus scabriculus, Walckenaeria acuminata, Walckenaeria atrotibialis, Walckenaeria cucullata.*

For some species the categorization was difficult , and hence, possibly arbitrary. Thus, one adult male of *Diplocephalus picinus* (categorized as ground-level-species) was observed in the field on a tree at a height of 160 cm. Adult males and adult females of both *Erigone atra* and *Erigone dentipalpis* (ground-level-species) were often observed on the outer side of buildings or in the vegetation at a height of at least 50 cm. This was also the case for *Porrhomma microphthalmum*. Ballooning males of *E. atra* , *E. dentipalpis* and *P. microphthalmum* often entered into houses.

When now contrasting the 26 linyphiid species living at ground-litter level against the 12 linyphiid species living higher up in the vegetation the contrast between median adult lifespan was highly significant. Thus, with an averaged adult lifespan of 2.80 months for vegetation-living species (N = 12), these species had a significantly shorter adult lifespan than had the ground-level species (N = 26) with their averaged lifespan of 4.71 months (two-tailed Mann-Whitney U-test giving an U = 65 which is much smaller than the estimated 0.05-critical U-value of approx. 90 in the incomplete tables of Siegel (1956); $p < 0.05$).

When comparing the adult lifespanof single species with each other (not the combined data of all investigated species) we now can demonstrate for the first time that some particular linyphiid species lived significantly longer than others in their adult stage. In table 2 it can be seen that the difference in adult lifespan is statistically significant in several cases when contrasting the males or the females of one species with those of the same, or of another, species. (1) One example is that adult male *Bathyphantes approximatus* lived significantly longer than the adult male of *Bathyphantes gracilis* (median adult lifespan 7.90 and 2.00 months respectively; number of tested individual males 3 and 9 respectively; Mann-Whitney U test giving U = 1, $p < 0.02$ in a two-tailed test). (2) Another example is that adult female *Lessertia dentichelis* lived significantly longer than adult female *Linyphia triangularis* (median adult-stage duration 8.75 and 1.33 months respectively; number of tested individual females 8 and 19 respectively; Mann-Whitney U test giving U = 4, $p < 0.001$ in a two-tailed test).

DISCUSSION

Maximal and average adult lifespan of linyphiid spiders was investigated by using field-caught and laboratory-raised specimens (tables 1 and 2).

As most linyphiids cannot be recovered later on when discovered in the field due to their hidden webs in the leaf litter or low vegetation, their adult lifespan had to be measured in captivity.

The data probably reflect the maximal adult lifespan potential when spiders are not threatened by natural adverse conditions. Apart from natural factors such as predation by birds, other spiders, pompilid wasps, larvae of parasitic Diptera (and perhaps by ants and beetles) that reduce the lifespan of adults in the field and that can easily be circumvented by keeping spiders in captivity, there is an unwanted factor that can have distorted our adult lifespan data. It is possible that there are some linyphiid species that are only liable to be caught in the field after having spent the first part of their adult life below ground-litter level so that we could not obtain them alive by our catching method (manual collection of ground litter). We, therefore, might have underestimated their actual adult lifespan. This might e.g. be the case for all the species of the genus *Walckenaeria* we tabulate, i.e. a genus from which we, unfortunately, never caught young (non-adult) specimens in the field. It might also be the case in the theridiid genus *Robertus* which are known as ”mole spiders”. This critical note should be kept in mind if one tries to measure the adult lifespan of small spiders living at ground level.

A final critical note is that our adult-lifespan data might be over-estimations for two other reasons (when disregarding predators that reduce lifespan in the field). (1) Our captive spiders were not exposed to sunshine, ultraviolet or other types of noxious radiations. (2) Our spiders probably received energy-richer types of food than they can obtain in the field, i.e. a mixture of live small and large dipteran species, egg yolk, chocolate and bread. However, our huge differences in lifespan between species (all of which received the same treatment) remain valid and are worthwhile to be considered here.

REFERENCES

Heimer, S. & W. Nentwig, 1991. Spinnen Mitteleuropas. Ein Bestimmungsbuch. 1-543. – Verlag Paul Parey, Berlin und Hamburg.

Helsdingen, P.J. van, 1999. Catalogus van de Nederlandse spinnen (Araneae). – Nederlandse Faunistische Mededelingen 10: 1-191.

Helsdingen, P.J. van, 2009. Spinnencatalogus. [Versie 2009.2; laatst bijgewerkt: 15.xii.2009. – http://www.naturalis.nl/spinnen
Heuts, B. & T. Brunt, 2004. Langlevende volwassen spinnen [Long lifespan of adult spiders]. - Nieuwsbrief SPINED 19: 13-18.
Heuts, B.A. & T. Brunt, 2006. Adulte en pre-adulte levensduur van dwergspin-soorten (Linyphiidae) hangt samen met hun habitat-hoogte boven grondniveau. - Nieuwsbrief SPINED 22: 9-12.
Roberts, M.J. 1985. The spiders of Great Britain and Ireland. Vol. 1 & 3. – Harley Books, Colchester.
Roberts, M.J. 1987. The spiders of Great Britain and Ireland. Vol. 2. – Harley Books, Colchester.
Roberts, M.J. 1995. Spiders of Britain & Northern Europe. – Harper Collins Publishers, London.
Roberts, M.J. 1998. Spinnengids (vertaling en bewerking door A. Noordam):. – Tirion, Baarn).
Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. xiii + 1-312. – McGraw-Hill Book Company, Inc., New York etc.

Table 1. Maximal (Max) and median (Me) adult lifespan in months and number (N) of tested linyphiid specimens. Species listed in alphabetic order. Horizontal stripes indicate no specimens available.

FIELD-CAUGHT SPIDERS AS ADULTS OR REACHING ADULTHOOD IN CAPTIVITY

	MALES			FEMALES		
	Max	Me	N	Max	Me	N
Allomengea vidua	----------			10.40	10.40	1
Bathyphantes approximatus	8.80	7.90	3	9.60	8.44	5
Bathyphantes gracilis	5.75	2.00	9	>11.65	4.50	19
Bolyphantes luteolus	0.44	0.44	1	----------		
Centromerita bicolor	5.80	4.10	7	8.00	3.89	18
Centromerus aequalis>	1.30	>1.30	1	----------		
Centromerus sylvaticus	6.20	4.72	9	6.82	3.37	11
Ceratinella brevipes	----------			3.60	2.56	2
Ceratinella brevis	0.13	0.13	1	0.93	0.93	1
Ceratinopsis stativa	----------			4.95	4.95	1
Cnephalocotes obscurus	4.25	4.13	2	----------		
Collinsia inerrans	4.52	2.73	2	13.25	13.25	1
Dicymbium nigrum	9.00	6.60	11	17.77	5.00	13
Diplocephalus cristatus	7.70	3.00	23	25.72	7.00	15
Diplocephalus permixtus	5.07	3.54	2	1.93	1.93	1
Diplocephalus picinus	3.48	1.93	9	>15.60	>3.73	8
Diplostyla concolor	15.70	7.00	17	19.83	>7.00	30
Drapetisca socialis	----------			4.95	4.95	1
Entelecara acuminata	3.23	1.55	16	8.37	3.70	13
Entelecara erythropus	>15.80	2.07	5	9.20	2.24	9
Erigone atra	11.30	4.50	13	>>10.50	5.37	18
Erigone dentipalpis	16.30	6.62	26	13.20	5.50	28
Floronia bucculenta	3.12	2.00	3	4.87	>4.06	4
Gnathonarium dentatum	11.10	6.90	6	>>22.20	8.75	11
Gongylidium rufipes	>10.30	5.80	18	>23.20	5.00	19
Hypomma bituberculatum	6.00	3.63	7	14.20	5.28	5
Kaestneria dorsalis	13.70	8.43	4	8.40	2.84	8
Lepthyphantes leprosus	3.00	2.50	2	>6.00	5.35	2
Lessertia dentichelis	>21.83	8.16	9	42.00	8.75	8
Linyphia hortensis	8.30	1.60	9	9.70	3.00	19
Linyphia triangularis	1.95	1.03	14	4.70	1.33	19
Macrargus rufus	8.53	7.14	7	6.70	6.70	1
Maso sundevalli	5.85	0.80	7	>7.60	2.90	12
Meioneta rurestris	6.30	2.95	6	4.83	2.54	10
Micrargus subaequalis	0.40	0.25	2	13.40	6.30	7
Microlinyphia impigra	----------			>0.78	0.50	3
Microlinyphia pusilla	----------			0.57	0.57	1
Microneta viaria	>>9.33	4.00	21	18.80	2.78	33
Neriene clathrata	8.70	3.39	12	24.70	6.00	18
Neriene montana	5.50	2.12	17	7.40	3.00	17
Neriene peltata	1.03	0.57	2	4.90	1.20	12
Oedothorax apicatus	3.00	1.00	3	8.57	5.62	2
Oedothorax fuscus	10.64	2.90	24	15.00	9.90	12
Ostearius melanopygius	9.63	9.63	1	11.27	7.00	9
Palliduphantes insignis	----------			6.67	6.34	2
Pocadicnemis pumila	----------			7.60	4.92	3
Porrhomma microphthalmum	28.67	3.90	5	>>22.50	5.26	8
Porrhomma pygmaeum	----------			10.80	7.08	6
Saaristoa abnormis	7.50	7.50	1	>10.00	6.00	12
Savignya frontata	----------			8.62	5.42	3
Tenuiphantes tenuis	11.20	3.59	12	>16.00	6.00	33
Tenuiphantes zimmermanni	----------			11.50	8.34	4
Troxochrus scabriculus	21.20	7.50	19	>23.87	7.50	17
Walckenaeria acuminata	5.70	5.07	3	4.72	4.15	5
Walckenaeria alticeps	>>4.20	>>42s0	1	----------		
Walckenaeria atrotibialis	0.83	0.83	1	7.70	7.09	3
Walckenaeria clavicornis	2.10	2.10	1	----------		
Walckenaeria cucullata	3.50	3.50	1	5.75	4.53	2
Walckenaeria nudipalpis	4.00	4.00	1	----------		
Walckenaeria unicornis	4.00	2.28	2	6.50	5.25	2
Walckenaeria vigilax	----------			6.90	2.33	3

Table 2. Adult lifespan (in months) of all the spider specimens of the linyphiid species listed in table 1. Male data in bold. The individual data are separated by slashes. Median adult lifespan is given in parentheses for each species and are underlined.

	MALES	FEMALES
Allomengea vidua:		10.40 (10.40)
Bathyphantes approximatus	**7.90/8.80/5.10 (7.90)**	9.60/7.50/8.44/8.33/9.10 (8.44)
Bathyphantes gracilis	**5.75/0.67/1.00/3.00/2.00/3.60 1.33(3056VIIachter)/1.95/3.31 (2.00)**	0.80/5.00/>>7.82/ 3.00/0.43/1.00/0.80/6.70/8.00 4.50/8.20/>11.65/1.70/4.00/ >>5.00/10.67/ 3.72/1.82/9.33 (4.50)
Bolyphantes luteolus	**0.44 (0.44)**	
Centromerita bicolor	**0.77/5.80/4.97/5.10/>>4.00/ 3.80/4.10 (4.10)**	1.50/1.83/2.50/2.83/2.50/>3.00 >3.50/3.63/3.87/3.90/4.00/4.50/ 4.70/>4.76/5.50/6.20/8.00/6.20 (3.89)
Centromerus aequalis	**>1.30 (>1.30)**	
Centromerus sylvaticus	**2.39/2.42/4.00/4.72/4.00/ 5.10/5.40/6.00/6.20 (4.72)**	1.20/>2.50/>3.37/ 6.37/1.63/2.22/2.92/3.50/5.41/ 6.27/6.82 (>3.37)
Ceratinella brevipes		3.60/1.53 (2.56)
Ceratinella brevis	**0.13 (0.13)**	0.93 (0.93)
Ceratinopsis stativa		4.95 (4.95)
Cnephalocotes obscurus	**4.25/4.00 (4.13)**	
Collinsia inerrans	**4.52/0.94 (2.73)**	13.25 (13.25)
Dicymbium nigrum	**3.27/5.07/5.12/5.25/5.50/6.60/ 7.23/7.50/9.00/8.83/9.00 (6.60)**	2.70/3.27/>3.50/3.90/4.32/3.90/ 5.00/6.00/8.20/8.23/9.12/9.27/ 17.77 (5.00)
Diplocephalus cristatus	**1.77/>2.50/2.00/6.50/6.00/3.00/ 3.50/4.33/0.63/6.00/1.65/>2.00/ 2.50/2.10/4.27/>7.70/0.87/2.10/ 3.30/2.60/3.60/5.25/5.73 (3.00)**	1.67/0.90/9.00/7.00/3.60/12.87/ >11.50/1.67/2.78/2.00/7.12/6.15/ 11.20/>10.83/25.72 (7.00)
Diplocephalus permixtus	**5.07/2.00 (3.54)**	1.93 (1.93)
Diplocephalus picinus	**0.44/1.30/>1.20/1.57/ 1.93/2.00/>2.00/3.48/ >2.23 (1.93)**	2.50/>2.00/3.36/2.66/>4.10/ >15.60/13.50/12.23 (>3.73)
Diplostyla concolor	**>1.33/2.00/2.25/2.81/3.23/ >3.50/3.80/4.70/7.00/7.33/ >7.50/8.00/8.10/8.25/>9.70/ 9.80/15.70 (7.00)**	0.50/1.37/2.00/2.30/2.33/4.00/ 4.83/5.00/5.93/6.00/6.10/7.00/ >7.00/7.90/>9.33/9.53/>9.67/ 11.50/>15.00/19.83/0.86/>2.60/ 2.60/8.00/8.56/8.33/>10.65/9.42/ >10.80/12.40 (>7.00, <7.90)
Drapetisca socialis		4.95 (4.95)
Entelecara acuminata	**0.20/0.40/0.70/1.00/1.00/ 1.43/1.67/1.75/3.20/3.23/ 0.79/0.80/2.00/2.40/2.20/ 2.38 (1.55)**	1.10/1.30/1.33/>4.00/>6.00/ 6.60/0.60/2.00/3.00/3.70/4.30/ >6.10/8.37 (3.70)
Entelecara erythropus	**0.67/>1.00/2.07/2.80/>15.80 (2.07)**	0.47/0.90/>0.90/1.10/2.24/2.80/ 4.22/6.40/9.20 (2.24)
Erigone atra	**0.43/2.33/3.10/4.50/6.00/ >7.10/7.67/0.93/2.55/2.65/ (**	1.10/1.17/1.27/1.80/2.40/3.42/ 3.50/4.57/7.27/7.80/9.72/1.77/ >10.50 (5.37)

(Table 2, continued)

Erigone dentipalpis	**0.58/0.87/2.50/3.00/4.07/4.30/ 5.27/5.40/5.50/6.00/6.50/ 6.57/6.67/6.70/7.80/8.00/ >8.27/8.30//8.33/9.00/16.30/ 3.02/9.30/11.60/10/42/9.20 (6.62)**	0.07/0.44/1.43/1.53/1.63/1.53/ 2.73/3.10/3.57/3.63/3.72/5.00/ 6.00/6.23/8.10/8.63/8.67/9.60/ 1.20/4.65/6.67/6.95/7.93/8.18/ 8.80/9.70/12.30/13.20 (5.50)
Floronia bucculenta	**1.88/2.00/312 (2.00)**	3.88/>4.00/4.11/4.87 (> 4.06)
Gnathonarium dentatum	**1.50/1.15/6.60/7.26/8.00/ 11.10 (6.90)**	>3.50/3.70/4.60/7.50/8.75/9.45/ 10.30/11.65/14.16/18.46/>22.20 (8.75)
Gongylidium rufipes	**2.50/2.83/3.00/>3.00/>5.30/ >6.50/8.00/8.10/>9.40/9.67/ 3.82/>4.00/5.30/5.47/6.12/ 8.81/>9.77/>10.33 (5.80)**	0.42/>1.00/>2.63/>3.40/>4.10/ >5.20/6.00/>9.00/14.67/>23.20/ >0.73/2.00/2.80/3.00/5.00/6.00/ 6.00/6.43/7.10 (5.00)
Hypomma bituberculatum	**0.43/1.27/>2.80/4.33/3.63/ 4.33/6.00 (3.63)**	>1.00/>4.33/5.28/>5.90/14.20 (5.28)
Kaestneria dorsalis	**1.68/6.70/10.15/13.70/ (8.43)**	0.60/>2.33/>2.60/2.82/2.85/ 3.67/6.26/8.40 (2.84)
Lepthyphantes leprosus	**>2.00/3.00 (2.50)**	4.70/>6.00 (5.35)
Lessertia dentichelis	**>4.00/>4.50/>5.00/>6.00/ >8.16/10.00/>12.00/>14.00/ >21.83 (8.16)**	3.60/5.50/>6.00/>>7.50/10.00/ 17.00/>18.00/42.00 (8.75)
Linyphia hortensis	**0.22/1.00/1.14/1.50/1.60/3.00/ 3.00/3.03/8.30 (1.60)**	>0.97/1.20/>1.67/>3.00/>3.20/ 4.40/>5.00/5.33/0.48/0.60/1.14/ 1.40/2.00/2.50/3.00/3.03/3.10/ 3.22/9.70 (3.00)
Linyphia triangularis	**0.63/0.83/0.63/1.00/1.03/ 1.03/0.60/0.87/1.28/1.30/ 1.43/1.50/>1.70/1.95 (1.03)**	0.44/0.77/0.83/0.93/1.00/0.93/ 1.30/1.33/2.60/3.00/>3.65/4.70/ 1.00/1.30/2.12/2.72/2.76/4.50/ >4.60 (1.33)
Macrargus rufus	**1.44/2.10/5.30/7.14/8.00/ 8.20/8.53 (7.14)**	6.70 (6.70)
Maso sundevalli	**0.67/0.70/0.80/0.55/1.33/ 1.50/5.85 (0.80)**	1.00/1.00/2.00/2.00/2.40/2.90/ 2.90/3.18/3.20/5.40/5.67/ >7.60 (2.90)
Meioneta rurestris	**0.50/1.00/1.10/4.80/4.87/ 6.30 (2.95)**	0.27/>0.77/1.57/>2.00/>2.50/ >2.57/2.80/3.36/>3.80/ 4.83 (2.54)
Micrargus subaequalis	**0.10/0.40 (0.25)**	0.67/3.00/>3.48/6.30/9.90/ 12.30/13.40 (6.30)
Microlinyphia impigra		>0.78/>0.23/0.50 (0.50)
Microlinyphia pusilla		0.57 (0.57)
Microneta viaria	**1.07/1.30/1.33/1.47/1.50/ 1.80/2.00/2.20/3.10/3.57/ 4.00/4.00/>4.00/4.50/5.80/ 6.10/6.30/6.33/6.47/6.57/ >9.33 (4.00)**	0.87/0.87/1.23/1.40/1.50/1.63/ 2.00/2.00/2.23/2.30/2.30/2.50/ 2.90/3.00/3.00/3.27/4.30/4.90/ 5.30/7.43/8.00/9.00/9.67/ 13.65/1.00/1.53/1.63/2.30/ 2.78/3.03/4.56/>8.50/18.80 (2.78)
Neriene clathrata	**0.73/1.14/3.00/6.50/6.90/ 7.00/0.62/1.00/2.70/3.77/ 4.46/8.70 (3.39)**	4.10/5.00/>8.80/10.12/10.50/ 1.26/2.20/3.10/3.40/3.47/4.00/ 4.20/>6.00/>6.00/6.72/10.10/ >11.20/24.70 (6.00)

(Table 2, continued)

Neriene montana	**1.00/>1.32/1.60/2.00/2.00/ 2.00/2.12/2.60/5.07/1.40/ 1.73/2.40/2.67/3.10/3.92/ 4.00/5.50 (2.12)**	1.07/>1.30/>2.00/2.20/2.90/ 3.00/>3.40/>6.30/7.00/1.00/ >2.00/2.80/3.00/3.50/>5.00/ 6.75/7.40 (3.00)
Neriene peltata	**1.03/0.10 (0.57)**	0.17/1.44/1.57/4.90/0.40/0.87/ 0.93/>1.00/1.20/1.20/>1.80/ 2.50 (1.20)
Oedothorax apicatus	**3.00/0.08/1.00 (1.00)**	8.57/2.67 (5.62)
Oedothorax fuscus	**>0.47/>0.33/0.48/1.00/1.10/ 2.00/2.60/3.20/3.40/6.73/ 7.00/7.50/8.00/8.80/10.64/ 0.37/0.40/0.83/1.18/1.78/ >3.00/7.00/7.40/>9.70 (2.90)**	5.95/>8.60/10.63/12.50/>4.18/ 7.33/8.20/8.60/11.00/11.53/ 12.30/15.00 (9.90)
Ostearius melanopygius	**9.63 (9.63)**	>2.20/6.00/>6.00/7.00/>7.00/ 8.40/9.63/11.27/7.90 (7.00)
Palliduphantes insignis		6.67/6.00 (6.34)
Pocadicnemis pumila		3.80/4.92/7.60 (4.92)
Porrhomma microphthalmum	**1.60/2.78/3.90/12.00/28.67 (3.90)**	0.42/0.83/1.80/2.18/8.33/8.77/ 13.10/>22.50 (5.26)
Porrhomma pygmaeum		4.40/4.70/6.25/7.90/>9.60/ 10.80 (7.08)
Saaristoa abnormis	**7.50 (7.50)**	0.10/0.64/1.00/>2.00/6.00/ >6.00/>6.00/6.30/6.22/8.10/ 9.42/>10.00 (6.00)
Savignya frontata		0.17/5.42/8.62 (5.42)
Tenuiphantes tenuis	**0.67/1.40/1.70/1.90/2.43/ 2.67/4.50/6.27/7.48/7.83/ 8.40/11.20 (3.59)**	>0.83/2.00/2.50/4.00/4.00/4.50/ 5.00/6.00/>6.00/6.73/>6.93/ 7.20/7.50/>7.73/9.33/0.32/ >1.67/>2.00/2.33/2.95/3.31/ 4.50/4.67/5.50/6.20/>6.60/ >7.00/9.03/>11.00/12.50/ >13.15/13.50/>16.00 (6.00)
Tenuiphantes zimmermanni		7.00/7.67/9.00/11.50 (8.34)
Troxochrus scabriculus	**>0.20/2.00/2.00/2.32/7.50/ 7.50/>7.67/8.50/10.00/11.00/ 21.20/1.21/1.60/6.50/7.50/ 8.40/9.42/10.80/>11.30 (7.50)**	2.90/3.20/3.30/4.20/7.70/10.00/ 10.00/17.70/18.00/3.70/5.40/ 5.63/5.90/>>7.50/>>9.33/10.68/ >23.78 (7.50)
Walckenaeria acuminata	**3.43/5.07/5.70 (5.07)**	0.20/1.80/4.15/4.20/4.72 (4.15)
Walckenaeria alticeps	**1.40/>>4.20 (2.80)**	
Walckenaeria atrotibialis	**0.83 (0.83)**	5.00/7.09/7.70 (7.09)
Walckenaeria clavicornis	**2.10 (2.10)**	
Walckenaeria cucullata	**3.50 (3.50)**	3.30/5.75 (4.53)
Walckenaeria nudipalpis	**4.00 (4.00)**	
Walckenaeria unicornis	**0.55/4.00 (2.28)**	4.00/6.50 (5.25)
Walckenaeria vigilax		1.50/2.33/6.90 (2.33)