PROSOMA SHAPE AND ARANEOPHAGY IN LINYPHIIDAE AND OTHER SPIDER FAMILIES (ARACHNIDA: ARANEAE)

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ABSTRACT

Adult males of linyphiid spider genera with a domed masculine prosoma shape and/or with a protuberance on the prosoma, showed a marginally significant higher killing potential (predation on spiders of various families surpassing the individuals of the killing genera in three body size measures) than did adult males of linyphiid genera possessing a flat prosoma shape. If the domed-prosoma linyphiid genera awere statistically contrasted to the total of flat-prosoma linyphiid genera and non-linyphiid genera always characterized by a flat prosoma) the difference was highly significant, i.e. the adult domed-prosoma linyphiid males killed significantly more often spiders surpassing them in size than did the flat-prosoma adult males of linyphiid and non-linyphiid genera combined.

It is hypothesized that the superior killing power of domed-prosoma genera is partly due to the domed shape of the prosoma. There may be factors closely linked with a domed prosoma that give a killing advantage to these genera, such as chelicerae morphology, behavioural manoeuvrability or killing technique, specific poisons, etc. We, further, hypothesize that the height of the dome (which was not included in measuring prosoma size) is not a decisive factor in killing advantage. If dome height would be a key factor, also the adult males of genera or species with an extreme dome height (like e.g. *Entelecara acuminata*) should have shown a high killing potential, but they did not. However, the adult males (and also often the adult females) of genera with a less extreme dome height, notably *Walckenaeria* and *Gnathonarium*, showed a very high killing potential, most clearly so *Walckenaeria unicornis* males and *Gnathonarium dentatum* females.

Key words: Araneae, spiders, Linyphiidae, domed prosoma, araneophagy

INTRODUCTION

Araneophagy (cannibalism and killing and eating of allospecific spiders) has often been reported in spiders in the field and laboratory. Brunt & Heuts (2008) mention some relevant studies, e.g. Bilsing (1920), Crooke (2002), Foelix (1982), Gunnarsson (1985), Hallander (1970), Heuts & Brunt (2001), Jackson & Blest (1982), Jackson & Rowe (1987), Jackson & Whitehouse (1986), Jackson & Wilcox (1998), Kiritani et al. (1972), Rovner (1968), Samu et al. (1996), Sunderland (1996), Suter & Keiley (1984), Suter et al. (1989), Watson (1998), Whitehouse (1987).

In the present laboratory study we ask if there is possibly a relationship between the intensity of inter-specific araneophagy and the shape of the prosoma when allospecific spiders are presented as prospective victims to adult males of linyphiid genera possessing a 'domed' prosoma. A heightened (domed) prosoma with or without a small protuberance on its front side is typical for many linyphild genera and is not found in other spider families. We hypothesize that a domed prosoma (or other morphological and/or behavioural pecularities that are closely linked with a domed prosoma but were not measured) increases the inter-specific killing power of the owner of such a prosoma. The hypothesis is based on the remarkably high killing power of linyphild species of the genus Walckenaeria most of which have a domed prosoma, often with a small protuberance. They often killed allospecific spiders (mainly young araneids) that surpassed them in three main body size measures, i.e. prosoma size (length x width without taking into account prosoma height and chelicerae), leg length, and leg thickness. We wanted to know if other domed-prosoma linyphild genera, such as Erigone, Hypomma, Oedothorax, and Troxochrus, also have a high killing power. If so, a domed prosoma (or domed-prosoma-linked characteristics) may have given a selective advantage during evolution by increasing the amount of food obtained by araneophagy. If part of the domed-prosoma genera would not show the high killing power of Walckenaeria, this would imply that a domed prosoma is not the only decisive factor in producing killing power. It would also imply that the height of the dome may be disregarded and skipped when measuring prosoma size (as we did in the present study by including only length and width). The possible importance of a prosoma protuberance on the dome for killing power can be investigated by comparing adult males of Walckeneria species that possess a clearly narrowed protuberance having its base on the prosoma top (such as in W. unicornis) with those species that do not possess it (such as the species W. atrotibialis and W. nudipalpis). Outside the genus Walckenaeria we did not carry out a sufficiently high number of tests (presentations of larger-sized allospecific spiders) in order to investigate the possible role of a prosoma protuberance. We e.g. did not have the disposal of adult males of Oedothorax apicatus that like many Walckenaeria adult males have a typical protuberance on their prosoma front part.

Our hypothesis of a high killing potential in domed-prosoma adult males also predicts that adult males of other spider families than linyphiids (always with a flat prosoma) will not kill spiders surpassing them in the three used size measures. The result is presented in a tabulated form (Table 1) together with the data of the linyphiid males. Species are only included in the tabulated data if both adult males and adult females of a species were

tested with allospecific spiders of superior body size. Like in linyphiids, adult females of non-linyphiids were also often tested with spiders surpassing them in size but they are not included in the tabulated data.

MATERIAL AND METHODS

Spider species that are commonly found in the Netherlands, were kept isolated in plastic petri-dishes (9 cm diameter, 1.5 to 2.0 cm depth) and in larger (transparent or opaque) round or quadrangular plastic boxes (diameter and depth at least 11 cm and 5 cm respectively). These containers served as test arena in the laboratory (similar test situations in e.g. Sunderland et al. 1994; Heuts & Brunt 2001, 2005; Brunt & Heuts 2008). The petri-dishes and boxes had wet filter paper (c. 4 x 4 cm) and a dry leaf or twig on the bottom. Temperature varied between 12 and 31° C depending on the season. Tests were carried out between 1995 and February 2009. Natural and/or artificial light was present from 0700 to 2100. Live and/or crushed flightless fruitflies and houseflies were given once or twice a week depending on the temperature but were absent during the first test day.

We consulted Roberts (1985, 1987, 1998), Van Helsdingen (1999), and Heimer & Nentwig (1991) for the genus and species determination of the spiders. We used non-parametric statistical tests (Siegel 1956) that are mentioned in Table 1 (critical two-tailed p < 0.05).

The killing potential of a test spider (ability to subdue an allospecific spider with a body size surpassing the size of this test spider, usually resulting in araneophagy) was assessed by introducing the allospecific spider into the container of the test spider that was resident in it since at least one hour up to several months. The resident test spiders usually had constructed a web at the time of the test. The only linyphild genus that rarely constructed a web with enough silk to detect the web without magnification, was *Walckenaeria*. In earlier observations we found that resident test spiders that had constructed their own web, did not differ in killing potential from resident test spiders that had not, nor from test spiders of which the web had been destroyed immediately before the test by the experimenter.

We only mention species of which both resident adult males and resident adult females had received an intruder allospecific spider in their test container ('arena') that surpassed their own size. We took three size measures of the resident test spiders and introduced allospecific spiders: (1) prosoma size measured as length x width on the dorsal side without including the chelicerae; (2) average length of the eight legs; (3) average thickness of the eight legs.

RESULTS AND CONCLUSIONS

Adult males of the genus Hypomma and Troxochrus which possess a quite high (domed) prosoma (Table 1), showed a high killing potential as they each killed and ate once an allospecific spider (young stage of Zygiella xnotata) that surpassed them in the three used body size measures (prosoma length x width, leg length, and leg thickness). Adult males of the genus Walckenaeria which possess a less domed prosoma than Hypomma or Troxochrus, showed an even higher killing potential when preving upon young Z. x-notata surpassing them in size (predation shown by several adult Walckenaeria unicornis males). The similarly less domed-prosoma adult males of Gnathonarium dentatum and Diplocephalus cristatus also preyed upon a larger Z. x-notata (shown once by each of these two species). These genera (Hypomma, Troxochrus, Walckenaeria, Gnathonarium, and *Diplocephalus*) gave support to our hypothesis of a high killing potential in adult males with a domed-prosoma. However, there were two genera in which adult males with a flat (not domed) prosoma (Gongylidium and Centromerus) were also capable of subduing an allospecific spider surpassing them in size (Table 1; the victim species, Z. x-notata, that was killed by one G. rufipes and one C. sylvaticus, is not shown in the table). These two unexpected results in view of our hypothesis (lower killing potential in flat- than in domed-prosoma males) were, however, largely overriden by the sixteen other linyphild flat-prosoma genera in which the adult males never killed spiders surpassing them in size in spite of several tests on each genus and each species (Table 1). When, further, also taking into account the five domed-prosoma genera in which the adult males did not kill larger-size spiders (genera Entelecara, Oedothorax, Erigone, Dicymbium, and Floronia) we show that the positive relationship (correlation between domed prosoma and high killing potential in linyphilds) is marginally significant in a two-tailed test (Table 1).

If also the 39 investigated non-linyphiid genera are included (always with a flat prosoma; lower part of table 1) we demonstrate a statistically very significant higher killing potential in the adult males of domed-prosoma linyphiid genera than in the adult males of flat-prosoma linyphiid and non-linyphiid genera combined.

We conclude that if the real size of the prosoma would have been taken into account (i.e. its volume while including height, not only its surface measured as length x width) our hypothesis might still be supported. One reason is that the adult males of genera or species with a highly domed prosoma (such as *Entelecara* or *Erigone*) did not (apparently could not) kill spiders surpassing them in prosoma surface and in longer and thicker legs, whereas the adult males of other genera (especially so *Walckenaeria*, often with a small protuberance on the domed prosoma) could do so (three different adult males). Are the small protuberances on the prosoma perhaps important, e.g. because they might be closely linked with other non-measured characters that increase the killing potential? We do not believe that such a protuberance-related factor plays a decisive role because e.g. the domed-prosoma species of *Troxochrus* and *Gnathonarium* both of which lack a prosoma-protuberance, were able to kill

Table 1. Killing power ('araneophagic power') of **adult males versus adult females** in linyphiid and non-linyphiid spider genera with a **flat prosoma** shape (FLAT), versus those with a **domed prosoma shape** with or without a prosoma **protuberance** (DOMED) which type of prosoma is only found in linyphiids. A high killing power is defined as the capacity to kill (prey upon) allospecific spiders of larger size than the own size (LARGER-SIZE-SPIDER) in the laboratory. Larger size is defined as having a larger prosoma (measured on the dorsal side as length x width without counting the chelicerae) and larger (longer and thicker) legs. The number of linyphiid genera are given in the upper part of the table and the number of non-linyphiid genera in the lower part. A genus is only included in the table if in at least one species of the genus both adult males and adult females had frequently been tested with larger-sized allopspecific spiders.

LINYPHIID GENERA

	Number of DOMED genera	Number of FLAT genera
Adult males killed LARGER-SIZE-SPIDER (adult females did so, or did not)	R 5 *	2 ***
Adult males did NOT kill LARGER-SIZE- (adult females did so, or did not)		16 ****
	n = 0.065	

0 = 0.005

(0.05 two-tailed Fisher exact probability test)

* Genera Walckenaeria, Gnathonarium, Troxochrus, Diplocephalus, Hypomma
** Genera Erigone, Oedothorax, Entelecara, Dicymbium, Floronia,
*** Genera Gongylidium, Centromerus
*** Genera Neriene, Bathyphantes, Tenuiphantes, Porrhomma, Diplostyla, Saaristoa, Micrargus, Linyphia, Microlinyphia, Meioneta, Maso, Centromerita, Lessertia, Lepthyphantes, Kaestneria, Microneta

NON-LINYPHIID GENERA

	Number of DOMED genera	Number of FLAT genera
Adult males killed LARGER SPIDER (adult females did so, or did not}	0	0
Adult males did NOT kill LARGER SPIDE (adult females did so, or did not)	R 0	39 ****

p not significant

***** Genera Steatoda, Enoplognatha, Theridion, Robertus, Ero, Pachygnatha, Larinioides, Clubiona, Xysticus, Pirata, Segestris, Trochosa, Textrix, Heliophanus, Salticus, Pardosa, Pholcus, Tegenaria, Achaearanea, Marpissa, Psilochorus, Anelosimus, Pisaura, Zygiella, Scotophaeus, Tetragnatha, Haplodrassus, Amaurobius, Philodromus, Meta, Nuctunea, Zora, Hasarius, Zelotes, Neoscona, Dictyna, Micaria, Neoscona, Ozyptila (Oxyptila)

	TOTAL OF LINYPHIID AND NON-LINYPHIID GENERA	
	Number of DOMED genera	Number of FLAT genera
Adult males killed LARGER SPIDER (adult females did so, or did not)	5	2
Adult males did NOT kill LARGER SPIDER (adult females did so, or did not)	5	55
	$p < 0.001 \ (\chi^2 = 14.9987)$	

spiders surpassing them in size. Is the size of the chelicerae (which we did not include in prosoma size) perhaps important? Quite probably not chelicerae length because genera or species with extremely long chelicerae in adult males and/or adult females (such as *Linyphia* and *Tetragnatha*) never killed spiders surpassing them in body size in spite of many laboratory tests. Is chelicerae thickness important? Probably it is not in adult males (e.g. in the genus *Pachygnatha* and *Meta* where adult males did not kill spiders surpassing them in size) but it may be

important in e.g. adult females of some non-linyphild genera such as *Pachygnatha* with its very thick chelicerae (females disregarded in Table 1). Of course, behavioural factors are important for killing power. We only mention here running speed and/or running acceleration as possible factors, and the locus of the killing bite ('killing technique'). We often observed very high running acceleration in adult *Walckenaeria* males with a domed prosoma (with or without a protuberance). Further, several *Walckenaeria* species (both adult males and adult females) typically applied their killing bite on a vulnerable body locus of their spider victims (prosoma or opisthosoma). This was at the same time a locus that made it impossible for the victim spiders to apply a counterbite.

Detailed results of adult *female* linyphiid and non-linyphiid species are not given in table 1. We only shortly mention here non-linyphiid species if both adult males and adult females were tested in a species with spiders surpassing them in size (both sexes always with a flat prosoma). As expected, the adult male non-linyphiids never killed allospecific spiders surpassing them in body size, whereas the adult females of several non-linyphiid species killed such large spiders, i.e. *Steatoda grossa, S. bipunctata, Enoplognatha ovata, Robertus lividus, Theridion blackwalli, T. tinctum, T. melanurum, Ero tuberculata, Pachygnatha clercki, Larinioides cornutus, L. sclopetarius, Clubiona phragmitis, and Xysticus cristatus.*

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REFERENCES

Bilsing, S.W. 1920. Quantitative studies in the food of spiders. - Ohio Journal of Science 20: 215-260.

- Brunt, T.M. & B.A. Heuts 2008. Unidirectional and transitive predatory relationships of spider species in one-on-one encounters (Arachnida; Araneae). Nieuwsbrief SPINED 25: 18-28.
- Crooke, R.J. 2002. Araneophagy in *Pholcus phalangioides* (Fuesslin 1775). Newsletter of the British arachnological Society 93: 2-3.
- Foelix, R.F. 1982. Biology of spiders. Harvard University Press, Cambridge.
- Gunnarsson, B. 1985. Interspecific predation as a mortality factor among overwintering spiders. Oecologia 65: 498-502.
- Hallander, H. 1970. Prey, cannibalism and microhabitat selection in the wolf spiders *Pardosa chelata* O.F. Müller and *P. pullata* Clerck. Oikos 21: 337-340.
- Heimer, F. & W. Nentwig 1991. Spinnen Mitteleuropas. Ein Bestimmungsbuch. Verlag Paul Parey.
- Helsdingen, P.J. van 1999. Catalogus van de Nederlandse spinnen (Araneae). Nederlandse Faunistische Mededelingen 10: 1-191.
- Heuts, B.A. & T.M. Brunt 2001. Transitive predatory relationships of spider species (Arachnida, Araneae) in laboratory tests. - Behavioural Processes 53: 57-64.
- Heuts, B. & T. Brunt 2005. Araneophagie en poot-anatomie bij *Walckenaeria* soorten (Arachnida, Araneae). [Araneophagy and leg anatomy in Walckenaeria species] Nieuwsbrief SPINED 20: 35-38.
- Jackson, R.R. & A.D. Blest 1982. The biology of *Portia fimbriata* a web building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. Journal of Zoology, London 196: 255-293.
- Jackson, R.R. & R.J. Rowe 1987. Web-invasion and araneophagy by New-Zealand and Australian pholcid spiders. New Zealand Journal of Zoology 14: 139-140.
- Jackson, R.R. & M.E.A. Whitehouse 1986. The biology of New Zealand and Queensland pirate spiders (Araneae, Mimetidae): aggressive mimicry, araneophagy, and prey-specialisation. Journal of Zoology, London A 201: 279-303.

Jackson, R.R. & R.S. Wilcox 1998. Spider-eating spiders. - American Scientist 86: 350-357.

- Kiritani, K., Kawahara, S., Sasaba, T. & Nakasuji, F. 1972. Quantitative evaluation of predation by spiders on the green rice leafhopper *Nephotettix cincticeps* Uhler, by a sight-count method. Research in Population Ecology 13: 187-200.
- 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.
- Rovner, J.S. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck)(Araneae, Linyphiidae). Zeitschrift für Tierpsychologie 25: 232-242.
- Samu, F., Sunderland, K.D., Topping, C.J. & Fenlon, J.S, 1996. A spider population in flux: selection and abandonment of artificial web-sites and the importance of intraspecific interactions in *Lepthyphantes tenuis* (Araneae: Linyphiidae) in wheat. – Oecologia 106: 228-239.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. - McGraw-Hill Book Company Inc., New York.

- Sunderland, K.D. 1996. Studies on the population ecology of *Lepthyphantes tenuis* (Araneae: Linyphiidae). Bulletin SROP/WPRS 19: 53-68.
- Sunderland, K.D., Ellis, S.J., Weiss, A., Topping, C.J. & Long, S.J. 1994. The effects of polyphagous predators on spiders and mites in cereal fields. Proceedings BCPC Conference, Pests and Diseases, 1994: 1151-1156.

Suter, R.B. & M. Keiley 1984. Agonistic interactions between male *Frontinella pyramitala* (Araneae, Linyphiidae). – Behavioural Ecology and Sociobiology 15: 1-7.

- Suter, R.B., Shane, C.M. & Hirscheimer, A.J. 1989. Spider vs. spider: *Frontinellina pyramitela* detects *Argyrodes trigonum* via cuticular chemicals. Journal of Arachnology, Research Notes 17: 237-240.
- Watson, P.J. 1998. Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). – Animal Behaviour 55: 387-403.
- Whitehouse, M.E.A. 1987. Spider eat spider. The predatory behaviour of *Rhomphaea* sp. from New Zealand. Journal of Arachnology 15: 355-362.

SAMENVATTING

Adulte mannetjes-spinnen van Linyphiidae-genera met een koepelvormig prosoma en/of met een smal uitsteeksel vooraan op het prosoma, vertoonden een marginaal significant grotere kans dan adulte mannetjes van Linyphiidae-genera met een vlak prosoma zonder uitsteeksel, om spinnen van andere soorten te doden die hen overtroffen in drie lichaamsmaten (prosomalengte x breedte gemeten aan de rugzijde, zonder de chelicerae mee te tellen; gemiddelde lengte van de acht poten; gemiddelde dikte van de poten). Indien de dodingskans van de mannetjes van genera met deze koepelvorm (10 Linyphiidae-genera) vergeleken werd met de dodingskans bij alle geteste genera met een vlak prosoma (18 Linyphiidae-genera en 39 genera uit 17 andere families (17 niet-Linyphiidae-families: Theridiidae, Mimetidae, Tetragnathidae, Araneidae, Clubionidae, Lycosidae, Segestriidae, Agelenidae, Salticidae, Pisauridae, Pholcidae, Gnaphosidae, Amaurobiidae, Dictynidae, Philodromidae, Thomisidae, Zoridae) dan Linyphiidae die altijd een vlak prosoma hebben), dan was de dodingskans van deze 10 koepelvormgenera (mate van predatie [araneophagie] op grotere spinnen dan zijzelf) zelfs zeer significant groter dan de dodingskans bij de overige genera (vlak-prosoma-Linyphiidae en niet-Lyniphiidae samengenomen).

We nemen voorlopig aan dat het superieure vermogen van de mannetjes van de genera met een koepelvormig prosoma om grote spinnen te doden, slechts voor een deel te wijten was aan het feit dat de hoogte van het prosoma en de chelicerae-grootte niet meetelden in onze lichaamsgroottevergelijkingen tussen dodende en gedode spinnen. Indien prosoma-hoogte altijd een beslissende factor zou zijn bij de dodingskans, dan zou ook de geteste soort *Entelecara acuminata* (waarvan de adulte mannetjes een extreem hoog prosoma hebben) een hoge dodingskans moeten vertoond hebben, hetgeen niet het geval was. Adulte mannetjes van *Walckenaeria unicornis* daarentegen (die een minder hoog prosoma hebben dan *E. acuminata*) hadden een hoog dodingsvermogen. Ook andere adulte mannetjes (en wijfjes) met een minder hoog prosoma dan *E. acuminata*, zoals adulten van *Gnathonarium dentatum*, hadden een hoog dodingsvermogen.

NIEUWE VINDPLAATS VAN OZYPTILA RAUDA SIMON, 1875

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ABSTRACT

Ozyptila rauda Simon was found in the eastern part of the country, Prov. of Guelre, in grassland. The species can be added to the Dutch fauna. Earlier records of this species were already corrected at an earlier date.

Key words: Dutch fauna, Ozyptila rauda

In 1996 werd *Ozyptila rauda* Simon voor het eerst uit ons land vermeld (Van Helsdingen 1996) naar aanleiding van een inventarisatie van de Wrakelberg bij Voerendaal. Later bleek dat de determinatie onjuist was (volgens Janssen 1992) en dat op de kalkgraslanden in België en Zuid-Limburg de verwante soort *Ozyptila pullata* (Thorell) voorkomt, die tot de karakteristieke spinnensoorten van dat biotoop kon worden gerekend. De naam werd naar aanleiding daarvan uit de Nederlandse Spinnencatalogus (Van Helsdingen 2009b) en dus ook van de naamlijst en het overzicht van de verspreiding over de provincies geschrapt, en vervangen door *Ozyptila pullata* (Thorell).

Ozyptila rauda komt echter wel degelijk in ons land voor en kan dus weer worden toegevoegd. Ivo Raemakers verzamelde deze soort in de Rijnwaarden bij Herwen, provincie Gelderland, in bloemrijk grasland, tussen half juni en half oktober, in totaal 13 3° en 3 9° . Het materiaal is opgenomen in de collectie van het Nationaal Natuurhistorisch Museum te Leiden. De soort kan dus nu weer aan onze catalogus worden toegevoegd (Van Helsdingen 2008).

Ozyptila rauda is wijdverspreid in Europa. Hij ontbreekt in Groot-Brittannië en Ierland, is niet bekend uit Zweden en Finland, maar werd uit de meeste andere landen gemeld, met nadruk op Centraal- en Zuid-Europa (maar hij ontbreekt blijkbaar in Griekenland). Voor meer gedetailleerde verspreidingsgegevens, zie Fauna Europaea (Van Helsdingen 2009).

LITERATUUR

Helsdingen, P.J. van 1996. Nieuwe soorten voor Nederland. - Nieuwsbrief SPINED 10: 7-8.

Helsdingen, P.J. van 2009. Araneae. In: Fauna Europaea Database (Version 2009.1). (http://www.european-arachnology.org) Helsdingen, P.J. van 2008. Spinnencatalogus. [Versie 2008.2] – (http://www.naturalis.nl/spinnen)

Janssen, M. 1992. Oxyptila pullata (Thorell, 1875) (Araneae, Thomisidae) in België. – Arabel, Nieuwsbrief Belgische Arachnologische Vereniging 7(1): 9.