GENUS-SPECIFICITY OF ARANEOPHAGY OF LINYPHIID SPIDERS AND SPIDERS OF OTHER FAMILIES (ARACHNIDA, ARANEAE)

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ABSTRACT
Genus-specificity of araneophagy of linyphiid spiders and spiders of other families (Arachnida, Araneae).
We found genus specificity of predation by spiders on other spiders in captivity which surpass them in body size (araneophagy). Adult specimens of three species of the linyphiid genus *Walckenaeria* which were successively tested for araneophagy (in the laboratory) in the order of first species discovery in the field in their natural habitat, showed a consistently high level of killing potential (predation on allospecific spiders which surpassed them in body size: genus-specific araneophagy of high intensity). The body size was measured by prosoma size on the dorsal side without the chelicerae, and by average leg length and average leg thickness. This consistently high genus-specific araneophagy of *Walckenaeria* was not shown by eight other linyphiid genera. In three other spider families than linyphiids where at least two species per genus could be tested (Theridiidae, Araneidae, Clubionidae; adult females of the genera *Theridion*, *Steatoda*, *Larinioides*, and *Clubiona*) also showed a consistently high level of predation on allospecific spiders surpassing them in size as the genus *Walckenaeria* had shown. Apart from the genera-dependent capacity to kill large spiders, there were differences between the adult males and females in their killing capacity. In the theridiids, araneids, and clubionids, i.e. in non-linyphiid genera, only females managed to kill allospecific spiders surpassing them in size, whereas in *Walckenaeria* the males could do this in two out of the three tested species. We conclude that high araneophagic capacity is significantly less genus-specific across nine genera of the linyphiid family than across four genera of three other spider families (theridiids, araneids, and clubionids).

Key words: Araneae, spiders, Linyphiidae, genus specificity of araneophagy

INTRODUCTION

There are several reports in the literature on genus-specific behaviour of spiders. Tarsitano & Jackson (1992) mention a genus-specific tendency in the salticid genus *Portia* to initiate detours to motionless prey, in contrast to salticid species of four other genera (*Euryattus* sp., *Euophrys parvula*, *Marpissa marina*, *Trite auricoma*, *Trite planiceps*) which are more inclined to stalk to motionless prey without first making detours. Species of the genus *Portia* are, further, typically web-invading araneophagic spiders which have a preference for salticid prey, in contrast to the four other investigated salticid genera which are cursorial hunters of insects. Foelix (1982: 199) when reviewing the literature mentions that some *Tegenaria* species show 'type 1' of copulation while other *Tegenaria* species and other members of the agelenid family show 'type 3' of copulation. Hence, there is apparently no genus-specific way of copulating in the genus *Tegenaria*. However, Foelix (1982: 157) also mentions that salticids show genus-specific types of use of certain legs when jumping, i.e. the genus *Sitticus* uses the fourth pair of legs for jumping, the genus *Evarcha* uses the third pair, and the genus *Salticus* uses the third and fourth pair of legs. Rovner (1973) mentions a generic difference in sexual behaviour between the lycosid genera *Schizocosa* and *Lycosa*.

Genus-specific behaviour studies have to be distinguished from studies on morph-specific behaviour in polymorphic spider species, e.g. the courtship behaviour of the salticid species *Maevia inclemens* (Clark & Uetz 1993, Clark & Morjan 2001) and risk-related behaviour of the salticid *Portia labiata* (Jackson & Pollard 2002). At the (high) taxonomic level of spider families there are many statements on family-specificity of behaviour (e.g. in Foelix 1982 when reviewing the literature). Thus, tetragnathids, for instance, typically build obliquely oriented webs with few radii, in contrast to the vertically oriented webs with many radii of araneids. Foelix (1982) further mentions that the members of the lycosid family show no response to their mirror image, in contrast to the members of the salticid family who readily respond to their mirror image.

MATERIALS AND METHODS

Spider species which are commonly found in the Netherlands, were caught in the field and 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 or 8 cm, respectively). These containers served as test arena in the laboratory. For details not mentioned hereafter we refer to Heuts & Brunt (2009). There was a similar test situation in Sunderland & al. (1994), in Heuts & Brunt (2001, 2005, 2009), and in 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 31º 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 fruit-flies and house-flies were given once or twice a week depending on the size of the spiders and the temperature but were absent during the first test day.

Theridion (*Sardinidion*) *blackwalli* (the recently changed genus name *Sardinidion* is accepted by Van Helsdingen 2009 on the basis of publications by J. Wunderlich) was the only rather rare species which was tested and included in the tabulated data. We consulted Roberts (1985, 1987, 1995), and Heimer & Nentwig (1991) for

the genus and species determination of the spiders. We used non-parametric statistical tests (Siegel 1956) which are mentioned in table 2 (critical two-tailed $p < 0.05$).

The killing potential (ability to subdue an allospecific spider with a body size surpassing the size of the tested spider, usually resulting in araneophagy) was investigated by introducing the allospecific spider ('prospective victimized spider') into the container of the test spider which 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 linyphiid genus which rarely constructed a web with enough silk to be detected without magnification, was *Walckenaeria*. In earlier observations we found that resident test spiders which had constructed their own web, did not differ in killing potential from resident test spiders which had not, nor from test spiders of which the web had been destructed immediately before the test by the experimenter.

We only mention genera of which there was at least one species in which both resident adult males and resident adult females had received several times an intruder allospecific spider of superior size in their test container ('arena'). 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

The generic specificity of the capacity of spiders to prey upon other spiders which surpass them in body size (allospecific victims which were killed and eaten; araneophagy shown by the smaller specimen in dyadic encounters in laboratory test arenas) depended on the spider family to which the genera belonged (table 2). High generic specificity was attributed to a genus if the two, or three, first wild-caught and tested species belonging to that genus had the capacity to kill at least one spider of superior size. Low generic specificity was attributed to a genus if the two, or three, first caught and tested species of that genus did not show the same high (or low) killing capacity, i.e. one species killing at least once an allospecific spider of superior size while the other species could never kill such larger spiders in spite of several tests. There was a significantly weaker degree of genus specificity in a group of nine linyphiid genera than in a group of four genera (*Theridion*, *Steatoda*, *Larinioides*, *Clubiona*) which belonged to other families than linyphiids. When not contrasting linyphiids to other families but, instead, doing the statistical test across linyphiid genera only, it appeared that the group of nine linyphiid genera (*Walckenaeria* and eight other linyphiid genera) possessed a statistically significant low level of araneophagy ($p < 0.05$; Sign test, $N = 9$, $x = 1$). The high degree of genus specifity in the four non-linyphiid genera could not attain statistical significance because four genera is not sufficient in an across-genera significance test. *Walckenaeria* (with three species) was the only linyphiid genus in which there was genus specificity as found in the four genera of the other families (three species being not sufficient for attaining significance within the *Walckenaeria* genus). The similarity between *Walckenaeria* and the (adult) females of the genera of the families other than linyphiids was expected because in earlier experiments (Heuts & Brunt 2001, 2005) *Walckenaeria* had shown a surprisingly high capacity to kill large-sized allospecific spiders approaching the extremely high killing capacity of the adult females of the theridiid genera *Theridion* and *Steatoda*.

Apart from the family-dependent genus specifity to kill large spiders, there were differences between the adult males and females in their killing capacity. A difference with *Walckenaeria* was that in the theridiids, araneids, and clubionids (non-linyphiid genera) only females managed to kill spiders surpassing them in size, whereas in *Walckenaeria* the males could do this in two out of the three tested species. The high killing capacity of female linyphiids in some of the species pairs was similar to the high female killing capacity found in the non-linyphiid genera. However, in these non-linyphiid genera the two species members included in the different genera were always both capable of killing allospecific spiders of superior size (lower part of table 1 specifying the non-linyphiid genera).

We conclude that genus specificity of araneophagic capacity in our spiders was family-dependent. More specifically, the across genera consistently high, or consistently low, capacity to subdue spiders of superior size was significantly weaker in the linyphiid family than it was in a group of three other tested spider families (Theridiidae, Araneidae, Clubionidae).

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Table 1. First and later discovered (and tested) spider species belonging to identical genera which killed and ate at least once an allospecific spider surpassing them in three body size measures ('large victims'). Data separated for adult males and adult females which showed this type of araneophagy. The species are arranged from left to right according to sequence of first capture from the wild and first test showing araneophagy on a large victim-spider. The linyphiid data are shown above and the data of other families below in the table. The three size measures were prosoma size (prosoma length x width measured at the dorsal side without including the chelicerae), average leg length, and average leg thickness. If a later tested species of a genus also killed at least once a large victim like an earlier tested species of that genus had done, this is indicated by a plus sign (+; one instance of support for our hypothesis 'consistently high degree of araneophagy across species within a genus'). If, on the contrary, the later tested species of a genus did not kill a large allospecific spider unlike the first tested species of the genus had done, this is indicated by a minus sign (-; one instance of contradiction of our hypothesis). A minus sign is also assigned if the first tested species did not kill a large spider, whereas a later tested species of the same genus did kill a large victim spider surpassing it in body size. Genera of which neither the first, nor the later, tested species killed a large spider are not included in the table. In several genera adult males never killed a spider surpassing them in size (e.g. in none of the families other than linyphiids). Species which killed a large spider are underlined. The species *Theridion blackwalli* is still retained here in the genus *Theridion* (following the old nomenclature). It is not yet placed into the genus *Sardinidion* as proposed by J. Wunderlich and accepted by Van Helsdingen (2009).

LINYPHIIDAE

Adult males	**Adult females**
Walckenaeria *unicornis* → *alticeps* +	*Walckenaeria* *acuminata* → *unicornis* +
	Bathyphantes *gracilis* → *approximatus* -
Diplocephalus *cristatus* → *picinus*	*Diplocephalus* *cristatus* → *picinus* -
	Erigone *atra* → *dentipalpis* -
	Entelecara *acuminata* → *erythropus* -
	Linyphia *hortensis* → *triangularis* –
	Neriene *montana* → *clathrata* → *peltata* –
	Tenuiphantes *tenuis* → *zimmermanni* –
	Porrhomma *pygmaeum* → *microphthalmum* –

Total of the genera for males and females:
Walckenaeria : plus versus minus = 2 versus 0;
Other linyphiid genera: plus versus minus = 0 versus 8 :

2	0
0	8

two-tailed Fisher exact probability test: $0.05 < p < 0.10$
(the genus *Walckenaeria* showed a marginally significant larger consistency in its predation on allospecific spiders of superior size than showed the other eight linyphiid genera)

(*Table 1, continued*)

OTHER FAMILIES THAN LINYPHIIDAE

Adult males	**Adult females**
0 (adult males never killed a large spider)	*Steatoda* *grossa* → *bipunctata* +
	Larinioides *sclopetarius* → *cornutus* +
	Clubiona *phragmitis* → *reclusa* +
	Theridion *melanurum* → *tinctum* -→ *blackwalli* +

Table 2. Calculations on the data of table 1. 'Support' of our hypothesis means that a later tested species of a genus also killed at least once a large victim like an earlier tested species of that genus had done. This is indicated by a plus sign in table 1 (one instance of support for the hypothesis). 'Contradiction' of the hypothesis either means that a later tested species of a genus did not kill a large allospecific spider unlike the first tested species of the genus had done, or it means that the first tested species of a genus did not show such a kill while the later tested species did. This is indicated by a minus sign in table 1 (one instance of contradiction of the hypothesis).

Linyphiid genera: 1 genus (*Walckenaeria*) supported our hypothesis of generic specificity and the 8 other linyphiid genera contradicted this hypothesis (*Diplocephalus, Bathyphantes, Erigone, Entelecara, Linyphia, Neriene, Tenuiphantes, Porrhomma*)**:**

$N = 9$; $x = 1$; $p < 0.05$: Sign test, two-tailed
(significant absence of genus-specificity in the 9 linyphiid genera)

Genera of **families other than linyphiids** (Theridiidae: *Steatoda*, *Theridion*; Araneidae: *Larinioides*; Clubionidae: *Clubiona*): 4 genera supported the hypothesis and no genus contradicted it:

$N = 4$; $x = 0$: $p > 0.05$: Sign test, two-tailed
(trend towards genus-specificity in 4 genera belonging to 3 other families than lyniphiids; 4 genera is too few for attaining significance)

DIFFERENCE between LINYPHIID and OTHER genera

	SUPPORT	CONTRADICTION
Linyphiid genera:	1	8
Other genera:	**4**	**0**

Fisher exact probability test (two-tailed): $p < 0.02$ (significantly weaker genus specificity of high killing-potential level in linyphiid than in other genera)

ALL GENERA COMBINED

5 genera supported the hypothesis of genus specificity, whereas 8 genera contradicted the hypothesis: $N = 13$; $x = 5$; $p > 0.05$: Sign test, two-tailed (not significant). **Conclusion**: There was no overall statistically significant genus specificity of high killing-potential in the 13 genera from the four tested families (Linyphiidae, Theridiidae, Araneidae, Clubionidae).

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