

VORACIOUS MALE SPIDERS THAT KILL ADULT FEMALES OF THEIR OWN SPECIES (GENERA *WALCKENAERIA*, *DIPLOSTYLA*, *NERIENE*, *META*, ARANEAE)

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ABSTRACT

In contrast to the popular belief that adult female spiders often kill and eat their adult male partners in the context of copulation, we present a few instances of adult male spiders killing and eating adult females of their own species in the laboratory. However, in line with the popular belief, we also found a few instances of adult females killing adult males of their own species. In spite of the fact that our experiments during the last decade focused on *inter*-specific killing among spiders of unlike species, we found some adult males killing and eating their conspecific adult females when we tried to get offspring from females fertilised in the laboratory. In addition to data of male-killing-female and female-killing-male, we further, present instances of adult and younger male spiders killing and eating male and other conspecifics. We also give such data for females. Our laboratory data ask for an explanation of the possible reproductive benefit in the males that miss the chance of getting own offspring (own gene replicates) from the conspecific females they treat as a prey item. We give three reasons that can explain why male spiders benefit from killing females of their own species by referring to sociobiological explanations. Key words: Araneae, *Diplostyla*, inclusive fitness, intra-specific cannibalism, *Meta*, *Neriene*, sociobiology, spiders, spiteful behaviour, *Walckenaeria*

INTRODUCTION

There is a popular belief in the spider literature that adult female spiders often prey upon their male partners immediately after copulation (see e.g. Foelix, 1996). Roberts (1998: 22) mentions another type of cannibalism, i.e. killing among very young brother and sister spiders, especially so in large clutches, but he does not specify spider species. He further mentions (p. 25) that adult males of *Argiope* may be killed and eaten by the female with which they are copulating without, however, specifying whether this occurs in the field and/or in captivity. Foelix (1996: 199) gives critical details as follows: "The supposed aggressiveness of the female spider toward the male is largely a myth. When a female is ready for mating, there is little danger for the male. If the male courts at the wrong time, however, he may well be attacked and eaten by the female..... Only in some exceptional cases does the male fall victim to the female, for example, in certain *Argiope* and *Cyrtophora*. The infamous black widow (*Latrodectus mactans*) does have a bad reputation, but – quite contrasting to popular belief – the male usually withdraws..... In some *Latrodectus* species the males live for several weeks in the female's web and may even feed on her prey.....".

We here present, in contrast to the popular belief, a few observations of adult *male* spiders *killing and eating* adult females of their own species and size in the laboratory, probably outside a copulatory context (table 1). Besides this, and in accordance with the popular belief, instances of adult female spiders that killed and ate adult conspecific males, were also found (table 2) and were somewhat more frequent.

During the last decade of our research in the laboratory on *inter*-specific behaviour of spiders we conducted only few experiments on *intra*-specific behaviour (e.g. in trials to get offspring by putting together an adult male with an adult female of the same species). We, further, observed *intra*-specific behaviour when rearing brother-sister groups from the same clutch. In spite of this restricted research on *intra*-specific behaviour, we nevertheless found instances of adult males killing and eating adult females of their own species (including one field observation on *Meta*). In earlier experiments we often observed brother-sister cannibalism besides *inter*-specific predation among young spiders in the laboratory (Heuts & Brunt, 2001, 2005; Heuts & al. 2001). There are many other studies on cannibalism in spiders but they did not report on adult males killing adult conspecific females (see e.g. Rovner 1986, Hallander 1970, Samu & al. 1996, Croke 2002).

In linyphiids there are many species with adult males as large, or even slightly larger, than adult females (e.g. *Bathyphantes approximatus*, *Centromerus aequalis*, *Ostearius melanopygius*, *Microneta viaria*: see Heimer & Nentwig 1991; Roberts 1985, 1987, 1998). However, in these numerous "large-male"-linyphiid species the adult males were never seen to kill adult conspecific females in spite of many one-on-one male-female tests. These species clearly differed from the few "large male"-linyphiid species in which, in spite of only few one-male-one-female tests, adult males did kill adult conspecific females, i.e. the species *Walckenaeria cucullata*, *Diplostyla concolor*, and *Neriene clathrata*.

In tables 3 to 12 we present instances of male-female-cannibalism among unlike age classes and we, further, present instances of male-male and female-female cannibalism.

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 or 8 cm respectively). These containers served as arena for one-to-one encounters in the laboratory (similar test situations in Sunderland & al. 1994; Heuts & Lambrechts 1999; Heuts and Brunt 2001, 2004, 2005; Heuts & al. 2001).

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 2007. Natural and/or artificial light was present from 07.00 to 21.00. 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. Small wild-caught and young laboratory-bread spiders received crushed flies that were eagerly accepted (see also Bilde & Toft, 2001, who mention the high quality of fruitfly food).

We followed Helsdingen (1999), Heimer & Nentwig (1991), and Roberts (1985, 1987, 1998) for nomenclature and the determination of the spiders.

We used non-parametric statistical tests e.g. for testing whether or not, females were killed by males after a shorter time than that males were killed by females (Siegel 1956; critical two-tailed $p < 0.05$) We discarded parametric tests because of the non-normal distribution of the killing-latency-times (times given in the tables).

RESULTS

In the intra-specific predation of adult spiders on adults of their own species (cannibalism) we first distinguish between two categories: (1) adult males kill adult females, and (2) adult females kill adult males. We, furthermore, distinguish between ten other categories in which the victims of cannibalism were either or not adult and were either killed by adult, or by younger, individuals of their own species. These ten other categories of cannibalism are specified in tables 3 to 12.

Adult males kill and eat adult conspecific females

There may be a positive correlation in the spider species between the capacity of their adult males to kill adult females of their own species and the tendency of these species to frequently kill alien species (*inter-specific* predation) even if the killed specimens slightly surpass the killing spiders in body size. This may, further be positively correlated with short killing-latency times after two spiders have been put together. It was most clearly the case in *Walckenaeria cucullata* (see table 1) where an adult male of 2.40 mm body length killed and ate an adult female of his own species (having a body length of 2.25 mm) after a short time (0.55 hours). This *W. cucullata* male had already killed and eaten an adult female *Diplocephalus cristatus* after a short time (0.27 hours)

Table 1. Adult male spiders killing (and usually eating) adult conspecific females of approximately their own size in the laboratory (except for a *Meta segmentata* adult male that was observed in the field at an unknown time after he killed his conspecific adult female). Approximate killing-latency times (in hours) are given for each species. Species in which there was a large difference in size between the killing adult male and the conspecific adult female victim were not found.

<i>Walckenaeria cucullata</i>	0.55	median killing-latency time = 34.50
<i>Diplostyla concolor</i>	34.50	
<i>Nerienne clathrata</i>	84.00	
<i>Meta segmentata</i>		

on the day he had been caught from the field. It may be assumed that the *W. cucullata* male was hungry at the moment he killed the *D. cristatus* female because quite generally spiders that were freshly caught in our catching-bucket often killed and ate other spiders that happened to be present in the bucket. However, when the *W. cucullata* male was tested once more approximately one month later with his conspecific adult female, he was probably not hungry because during the preceding month he had been isolated while receiving numerous fruit-flies as prey. Hence, the *W. cucullata* male probably killed his conspecific female in spite of not being hungry. Other adult male *W. cucullata* were only rarely tested in the laboratory with spiders as a possible prey item, but adult female *W. cucullata* often killed and ate alien spider prey. Adult male and adult female linyphiids, in general, did not importantly differ from each other in their capacity to kill relatively large alien spiders, nor in the time interval before such spider prey was killed (Heuts, unpublished data). We, therefore, assume that also adult male *W. cucullata* give support to our positive-correlation hypothesis.

Another species, like *W. cucullata*, clearly gave support to the positive correlation between inter-specific killing skill, intra-specific killing of adult females by adult males, and short killing-latency times, i.e. *Diplostyla concolor* where an adult male killed and ate a like-sized adult female of his own species (after 34.50 hours; table 1). This *D. concolor* male received two live fruit-flies as soon as he had been brought to the laboratory on the day he had been caught. This was done in order to make sure he would not be hungry on the next day when receiving his conspecific adult *D. concolor* female as a potential prey item. In spite of probably not being hungry, the *D. concolor* male killed and ate the female after 34.50 hours (he was not tested another time). Many other adult male

D. concolor (and also adult females) were tested in the laboratory with all sorts of spiders that were often killed and eaten.

The third species in which an adult male killed and ate a conspecific adult female of nearly his own size in the laboratory was *Neriene clathrata* (killing-latency time = 84.00 hours: see table 1). He was tested with the female *N. clathrata* immediately after he had been brought to the laboratory on the day of catching (and, thus, was assumed to be hungry). He was not tested another time with a spider as a possible prey item. Many adult male and adult female *N. clathrata* were tested with all sorts of other spiders as possible prey items, but, in contrast to *W. cucullata* and *D. concolor*, our *N. clathrata* rarely killed and ate spiders or did so after long latency times of more than ten days. Hence, *N. clathrata* did not give support to the positive-correlation hypothesis. In the Discussion section we explain why controlling the hunger state (degree of satiation) is important in the light of modern sociobiological theories.

In the field we found a fourth case of an adult female killed and eaten by an adult male of her own species, i.e. an adult male *Meta segmentata* that was already eating the female when we spotted him, probably in a copulatory context. In the laboratory our adult and younger male and female *M. segmentata* were only tested with spiders of alien species. They often killed them and did so after a short time. Hence, *M. segmentata* gave support to our hypothesis.

In another species (*Theridion tinctum*) the positive correlation between the skill of adult males to kill adult conspecific females, frequent killing of large alien spider prey, and killing other spiders after a short time (see the data in Heuts & Brunt, 2001) was doubtful because we did not test adult male *T. tinctum* with adult conspecific females. We only found a very young female that was killed and eaten by an adult male *T. tinctum* after a time that was appreciably longer than in *W. cucullata*, i.e. 30.00 hours (table 7).

In contrast to the species mentioned above, there was a very large number of species (Linyphiidae and many other spider families) in which male-female- or female-male-killing (adults of the same species) was *never* seen in spite of many test trials, or in which there was a long killing latency-time of more than 10 days. This was most clearly the case for *Microneta viaria*, *Bathyphantes approximatus*, *Lessertia dentichelis*, *Centromerita bicolor*, *Centromerus sylvaticus*, *Dicymbium nigrum*, *Diplocephalus cristatus*, *Diplocephalus picinus*, *Tenuiphantes tenuis*, *Erigone atra*, *Erigone dentipalpis*, *Gongylidium rufipes*, *Kaestneria dorsalis*, *Lepthyphantes leprosus*, *Linyphia hortensis*, *Linyphia triangularis*, *Maso sundevalli*, *Meioneta rurestris*, *Neriene montana*, *Oedothorax fuscus*, *Porrhomma microphthalmum*, *Troxochrus scabriculus*, *Achaearana lunata*, *Anelosimus vittatus*, *Steatoda bipunctata*, *Pachygnatha clercki*, *Pachygnatha degeeri*, *Tetragnatha montana*, *Amaurobius similis*, *Dictyna arundinacea*, *Micaria pulicaria*, *Philodromus aureolus*, *Philodromus cespitum*, *Philodromus dispar*, *Hasarius adansoni*, *Heliophanus cupreus*, *Marpissa muscosa*, *Salticus scenicus*, *Pardosa amentata*, *Pirata piraticus*, *Tegenaria domestica*, *Tegenaria ferruginea*, *Textrix denticulata* and *Zora spinimana*.

Besides lacking to show male-female or female-male cannibalism (adult specimens), these species showed in general long latency times before killing alien species *inter-specifically*, this in contrast to the generally shorter killing-latency-times of the earlier mentioned species in which we showed cannibalism of adult males killing adult females.

Adult females kill adult conspecific males

There were a few cases of adult females killing adult conspecific males in the laboratory. Thus, an adult female *Saaristoa abnormis* killed an adult male after 1776.00 hours without eating him (table 2). There were five more species in which an adult female killed an adult conspecific male, i.e. *Floronia bucculenta*, *Ero tuberculata*, *Theridion melanurum*, *Zygiella x-notata*, and *Xysticus cristatus* (see the killing-latency-times in table 2).

Table 2. Adult female spiders killing adult conspecific males of approximately their own size in the laboratory. Approximate killing-latency times (in hours) are given for each species. In one species (*Xysticus cristatus*) the killing adult female was much larger than the male. An asterisk indicates that the spider victim was only killed and not eaten.

<i>Saaristoa abnormis</i> *	1776.00	median killing-latency-time = 123.00
<i>Floronia bucculenta</i>	126.00	
<i>Ero tuberculata</i>	36.00	
<i>Theridion melanurum</i>	3124.00	
<i>Zygiella x-notata</i>	60.00	
<i>Xysticus cristatus</i>	120.00	

Differences in killing-latency-time between males and females killing conspecific spiders

There are no statistically significant differences between the killing-latency-times if the times of adult male spiders killing adult female conspecifics in table 1 are contrasted to the times of adult females killing adult male conspecifics in table 2 (two-tailed Mann-Whitney-U-test with a critical p-value of 0.05; $n_1 = 3$, $n_2 = 6$, $U = 2$; Siegel 1956). In a similar way, contrasting the killing-latency times of other age- or sex-categories (table 3 versus table 4, table 5 versus table 6, table 7 versus table 8, table 9 versus table 10, and table 11 versus table 12) never resulted in a statistically significant difference.

When contrasting in table 1 and table 2, in table 3 and table 4, etc. the number of observed instances of killing (instead of contrasting the killing-latency times) there were, again, no significant differences.

Even when pooling all the killing-latency-times of the males in the six tables referring to males and contrasting them to the times of the females (in their six relevant tables) the times of the males ($n_1 = 15$; median = 72.00 hours) did not significantly differ from those of the females ($n_2 = 22$; median = 60.00 hours; $U = 161$, $p > 0.10$).

Behavioural characteristics of Walckenaeria when killing intra- and interspecifically, in contrast to other linyphiid genera

The behaviour of our adult male *Walckenaeria cucullata* that preceded the killing and eating of the adult female *W. cucullata* was different from the behaviour of other linyphiid genera before killing intra- or inter-specifically. Thus, similar to seven other species of *Walckenaeria* investigated in our earlier study (Heuts & Brunt 2005; *W. acuminata*, *W. atrotibialis*, *W. alticeps*, *W. clavicornis*, *W. nudipalpis*, *W. unicornis*, and *W. vigilax*) our *W. cucullata*-male slowly walked venter-down on the bottom of the petri-dish with slowly waving forelegs in a *Clubiona*-like fashion while approaching a prospective spider prey. When arrived at close distance he suddenly accelerated and grasped the spider victim with its fangs without loosing hold in spite of the victim's struggling movements (apparently unsuccessful attempts to counter-bite) and without wrapping the victim in silk (like other linyphiid species neither do). It seems that *Walckenaeria* species in general are very skillful in capturing spider prey because the prey is grasped at the prosoma, never at the distal part of a leg, thereby preventing that they would be bitten in return. The typically very strong acceleration of running speed during the short decisive attack phase of *Walckenaeria* species seems to be an important factor in aiming at an opportune and vulnerable body part of their spider victims. A very strong running acceleration that is in sharp contrast to their slow introductory approach of prey and to their equally slow "exploratory" running in small containers, is also shown by *Walckenaeria* species when touched with a brush. This contrast in running speed is generally not shown by other linyphiid genera (except for some species like e.g. *Bolyphantes luteolus*: see Heuts 2007).

DISCUSSION

How can we explain that adult male spiders sometimes prey upon adult females of their own species (as we found in *Walckenaeria cucullata*, *Diplostyla concolor*, *Neriene clathrata* when tested in the laboratory, and in a *Meta segmentata* male in the field)? In theory, it is possible that the killed adult females were infertile and that this was somehow perceived by the killing males. Thus, an infertile female can only contribute to the fitness of a conspecific male by whom she is killed and eaten by the food she so offers to the male. Hence, an experiment in which adult female spiders are artificially made infertile (by some chemical treatment?) and are offered to conspecific adult males, might show that such females are killed indeed, in contrast to control females that are artificially treated by a different chemical treatment that does not affect the reproductive potential of the females. So far, we did not consult the spider literature for such possible chemical substances but we guess they might exist. Of course, our laboratory environment might have induced non-adaptive behaviour in the males, although we regard this as improbable because different spider species generally show their species-specific behaviour patterns (such as species-specific copulation postures) in laboratory settings (see e.g. Foelix, 1996 and his references).

Another possibility is that the female-killing males are themselves infertile. By killing all conspecific females they happen to encounter, the males prevent that fertile but not closely-related males of their own species would fertilize the females and get offspring that might compete (e.g. compete for food) with the offspring of the close relatives of the infertile killing males. In this way the infertile males can increase their inclusive fitness by giving advantage to (decreasing the competition of) e.g. their brothers, sisters, nephews, etc. The female-killing behaviour of the males can be understood and described more specifically by the sociobiological term "spiteful behaviour" (see e.g. Alcock 1993, p. 507; Trivers 1985, p. 57-61). Thus, with spiteful behaviour, there is at the same time a disadvantage to the killed young female spiders and a disadvantage to the killing males (risk of being bitten in return and a low risk of succumbing to these return bites). But, anyhow, in spiteful behaviour the damage inflicted to the females (very probable death) is larger than the damage inflicted to the males (low risk of receiving dangerous counter-bites). Spiteful behaviour of old adult male spiders that kill conspecific females can

also be regarded as "making the best of a bad job" (i.e. can be regarded in another sociobiological terminology) because the male gains more from killing a young conspecific female than he gains from not killing her, although both options (killing versus not killing) provide little reproductive benefit or inclusive fitness to a male that is in a "bad" situation because of his old age. Now we can also explain or understand why the adult males of two of our tested species (*Walckenaeria cucullata* and *Diplostyla concolor*) killed their conspecific adult females in spite of having been satiated first with fruit-fly prey. Satiated spiders normally do not catch prey, but when encountering conspecifics as a possible prey, they should catch and kill conspecifics that are not close relatives in order to increase their own inclusive fitness.

CONCLUSIONS

The frequency of adult males cannibalising adult conspecific females in the laboratory was approximately the same as the reverse frequency, i.e. the frequency of adult females cannibalising adult conspecific females. In addition to this, the latency times preceding this cannibalism in one-male-one-female encounters between adult conspecifics were quite similar in males and females. These findings do not give support to the popular belief that adult females often kill and eat adult conspecific males in a copulatory context, both in the field and in captivity.

Table 3. Adult males killing adult conspecific males (further explanation as in tables 1 and 2).

<i>Diplocephalus cristatus</i>	1648.00	median killing-latency-time = 960.00
<i>Diplostyla concolor</i>	34.50	
<i>Gongylidium rufipes</i> *	5520.00	
<i>Heliophanus cupreus</i> *	6.90	
<i>Zygiella x-notata</i> *	960.00	

Table 4. Adult females killing adult conspecific females (further explanation as in tables 1 and 2).

<i>Bathyphantes gracilis</i>	696.00	median killing-latency-time = 27.50
<i>Neriene clathrata</i>	1224.00	
<i>Neriene peltata</i>	13.00	
<i>Neriene peltata</i>	528.00	
<i>Linyphia triangularis</i>	7.50	
<i>Linyphia triangularis</i>	276.00	
<i>Tetragnatha montana</i>	3.45	
<i>Enoplognatha ovata</i>	22.00	
<i>Enoplognatha ovata</i>	1.00	
<i>Larinioides cornutus</i>	33.00	

Table 5. Adult males killing younger conspecific males (further explanation as in tables 1 and 2).

<i>Entelecara acuminata</i>	264.00	median killing-latency-time = 72.00
<i>Steatoda grossa</i> *	7.50	
<i>Achaearanea tepidariorum</i> *	72.00	

Table 6. Adult females killing younger conspecific females (further explanation as in tables 1 and 2).

<i>Gongylidium rufipes</i>	12.00	median killing-latency-time = 36.00
<i>Neriene montana</i>	68.25	
<i>Theridion varians</i>	36.00	

Table 7. Adult males killing younger conspecific females (further explanation as in tables 1 and 2).

<i>Neriene clathrata</i>	84.00	median killing-latency-time = 57.00
<i>Theridion tinctorum</i>	30.00	

Table 8. Adult females killing younger conspecific males (further explanations as in tables 1 and 2).
[Not found]

Table 9. Adult males killing very young conspecifics of unknown sex (further explanation as in tables 1 and 2).

<i>Pirata piraticus</i>	864.00	median killing-latency-time = 864.00
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Table 10. Adult females killing very young conspecifics of unknown sex (further explanation as in tables 1 and 2).

<i>Oedothorax fuscus</i>	12.00	median killing-latency-time = 60.00
<i>Neriene montana</i>	68.25	
<i>Neriene montana</i>	3.72	
<i>Salticus scenicus</i>	60.00	
<i>Salticus scenicus</i>	170.00	

Table 11. Young (not adult) males killing young male or young female conspecifics or very young conspecifics of unknown sex (further explanation as in tables 1 and 2).

<i>Araneus diadematus</i>	35.00	median killing-latency-time = 35.00
<i>Araniella cucurbitina</i>	156.00	
<i>Pachygnatha clercki</i>	720.00	
<i>Enoplognatha ovata</i>	< 24.00	
<i>Enoplognatha ovata</i>	12.00	

Table 12. Young (not adult) females killing young male or young female conspecifics or very young conspecifics of unknown sex (further explanation as in tables 1 and 2).

<i>Neriene montana</i>	372.00	median killing-latency-time = 33.34
<i>Enoplognatha ovata</i>	33.67	
<i>Enoplognatha ovata</i>	33.00	
<i>Enoplognatha ovata</i>	504.00	
<i>Steatoda bipunctata</i>	4.00	
<i>Araneus diadematus</i>	348.00	
<i>Araneus diadematus</i>	12.12	
<i>Pirata piraticus</i>	2.77	

ACKNOWLEDGMENTS

We wish to thank Klaas de Boer (Swammerdam Institute for Lifesciences, University of Amsterdam) for providing several spiders.

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MICHAEL SAARISTO
(1938-2008)

Op 27 april 2008 overleed Michael Saaristo op 69-jarige leeftijd. Hij was als conservator verbonden aan het Zoölogisch Museum in Turku, waar hij ook woonde. Hij overleed na een jarenlange slopende ziekte.

We kenden hem als een aardige, bescheiden man met een enorme werklust. Vanaf het begin ging zijn belangstelling uit naar de Baldakijnspinnen (Linyphiidae), waarvan hij een aantal soorten kritisch bekeek en vooral de anatomie van de genitalia in detail bestudeerde. De eerste publicatie die ik van hem kon vinden ging over het genus *Maro* (1971). Er zouden er vele vergelijkbare studies volgen. In 1978 kwam er een eerste publicatie over spinnen van de Seychellen en ook daarvan zouden er nog vele volgen. Vooral de laatste jaren schreef hij veel over de spinnen van dat gebied. Hij was ook sterk geïnteresseerd geraakt in de Oonopidae en wijdde daar verschillende publicaties aan.

Persoonlijk zal ik zijn naam steeds blijven verbinden aan de herindelings van de soorten van het toen nog omvangrijke genus *Lepthyphantes*. Samen met Alexei Tanasevitch durfde hij het in 1996 aan om dat omvangrijke genus, met vele soortgroepen en vele soorten die niet in groepen leken te passen, op te splitsen in aparte genera. Zoals gebruikelijk was er eerst wel enige weerstand, maar inmiddels is de nieuwe indeling algemeen geaccepteerd. We zijn nu allemaal gewend aan de nieuwe generieke indeling.

Door verschillende auteurs zijn soorten naar Michael Saaristo vernoemd. Millidge vernoemde in 1978 het genus *Saaristoa* naar hem. Zo leeft deze bescheiden, maar zeer productieve arachnoloog in ons werk voort.

Een In Memoriam met een complete bibliografie zal binnenkort worden gepubliceerd in *Arthropoda Selecta*.

