

## UNIDIRECTIONAL AND TRANSITIVE PREDATORY RELATIONSHIPS OF SPIDER SPECIES IN ONE-ON-ONE ENCOUNTERS (ARACHNIDA: ARANEAE)

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### ABSTRACT

[Unidirectional and transitive predatory relationships of spider species in one-on-one encounters (Arachnida: Araneae)]

Inter-specific predation ('inter-specific araneophagy') among spiders is very common in the field.

We investigated the transitivity (defined hereafter) of inter-specific predatory dominance relationships among 60 spider species belonging to 16 families in the laboratory in one-on-one encounters between specimens of unlike species (dyads). Inter-specific predatory dominance (killing-dominance) of one over another species was only assigned if the killing specimen was smaller than the killed specimen (smaller prosoma and shorter and thinner first legs of the killing than of the killed specimen, while disregarding opisthosoma (abdomen) size). The transitivity of predatory-dominance-relationships was statistically significant (as demonstrated in our earlier study on much fewer species). The definition of transitivity of dominance relationships among three different species is that species A shows dominance over species C if A is dominant over B and B dominant over C.

The inter-specific dominance (predatory) relationships were not only significantly transitive, but also significantly unidirectional (as in the pioneer studies of the 'peck-right' order among individuals of the same species in fowl and fish groups).

An example of an unidirectional killing(predatory)dominance-relationship between two different species is that smaller specimens of species A have the power to kill larger specimens of species B, whereas smaller specimens of species B cannot kill larger specimens of species A (definition of unidirectionality in the case of only two involved species). We are not aware of published accounts on the statistical significance of the unidirectionality of the inter-specific predatory relationships among spiders in the field or in the laboratory.

Highly-killing-dominant species of spiders showed shorter killing(predation)-latency times than less dominant species in the laboratory. Hence, the high dominance of a particular species could be predicted from its short killing-latency-time.

The stickiness of the silk, some predatory techniques (with or without using threads and/or wrapping up of the prey), and morphological characteristics of the legs are discussed in an attempt to explain the high dominance of a few of the highly dominant investigated species.

Key words: anatomy, araneophagy, body size, inter-specific predation, killing dominance, killing-latency-time, spiders, transitivity, unidirectionality.

### INTRODUCTION

Inter-specific predatory relationships (killing-dominance relationships) were demonstrated to be transitive in our earlier laboratory study of one-on-one encounters between spiders of a few different species (Heuts & Brunt 2001). However, the transitivity was based on inter-specific dominance relationships that were not clearly shown to be unidirectional. We now test *unidirectionality*, i.e. we ask whether species that can kill (and eat) a larger spider of another species, are never killed in return by smaller specimens of that other species. We, further, now test our hypothesis of *transitivity* of the inter-specific predatory dominance relationships on a much larger sample of spider species and families than in our earlier study. We, again, ask whether or not species A will kill specimens of species C being larger than itself when species A has shown to be capable of killing larger specimens of species B and when B has shown to be capable of killing larger specimens of C.

If we find unidirectionality of inter-specific predation on allospecific spider victims having a larger body size than the killing spider, this unidirectionality is comparable to the absolute 'peck-right' found in the pioneer studies on birds and fish (e.g. Schjelderupp-Ebbe 1922; Braddock 1945, 1949). These vertebrates showed absolute unidirectionality ('peck-right') in dyadic encounters within small groups of their own species. Always the same individuals gave way to (were dominated by) other individuals while never dominating in return.

We now include, further, the latency times before spiders were killed and correlate them to the inter-specific dominance relations. Short killing times may be typical of highly dominant species, but not necessarily so. If so, inter-specific dominance positions of spider species might be predicted from their tendency to kill spiders after a short or long time.

Exclusive or obligatory araneophagy (spider-eating) has often been observed both in the field and laboratory in Mimetidae and several Theridiidae (Foelix 1982, Jackson & Whitehouse 1986, Whitehouse 1987, Suter & al. 1989, Heuts & Brunt 2001). In captive and wild non-exclusively araneophagic spiders inter-specific araneophagy is also very common (e.g. Bilsing 1920; Rovner 1968; Hallander 1970; Kiritani & al. 1972; Jackson & Blest 1982; Gunnarsson 1985; Jackson & Rowe 1987; Sunderland 1996; Samu & al. 1996; Jackson & Wilcox 1998; Watson 1998; Crooke 2002). Intra-specific araneophagy (cannibalism) is also common, both in the field and laboratory (e.g. Rovner 1968; Sunderland 1996; Samu & al. 1996; Watson 1998).

We end up with briefly discussing an obvious question deserving further research, i.e. what makes a spider species capable of killing other spider species larger than itself? What is the role of behavioural and anatomical factors apart from web characteristics?

## MATERIAL AND METHODS

Spiders of 60 different European species from 16 families were kept isolated in plastic petri-dishes (9 cm diameter, 1.5 to 2.0 cm depth) and larger plastic boxes of at least 5 cm depth. Both types of transparent containers served as arena for one-on-one encounters in the laboratory (the larger containers for spiders with a large body size; similar test situations in Sunderland & al. 1994; Heuts & Lambrechts 1999; Heuts & Brunt 2001, 2004; Heuts & al. 2001). The containers 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 from the start of 2000 to October 2005. Natural and/or artificial light was present from 7 am to 21 pm. Live and/or crushed fruitflies and houseflies were given once or twice a week depending on the temperature but were absent during the first test day. After the second moult following emergence from the egg-sac the young and older spiders often only ate from the crushed flies (see also Bilde & Toft, 2001, mentioning the high quality of fruitfly food).

Part of the species could not be bred from gravid females caught from the wild (Heuts & Brunt, not published). Three linyphiid species were easily bred in large numbers, i.e. *Gnathonarium dentatum*, *Saarioa abnormis*, and *Micrargus subaequalis*. Seven linyphiid species were bred in much smaller numbers, i.e. *Bathypantes gracilis*, *Diplostyla concolor*, *Erigone dentipalpis*, *Gongylidium rufipes*, *Microneta viaria*, *Oedothorax fuscus*, and *Pocadicnemis pumila*. Nine linyphiid species were rarely or very rarely bred, i.e. *Bathypantes approximatus*, *Diplocephalus cristatus*, *D. picinus*, *Linyphia hortensis*, *Meioneta rurestris*, *Neriere montana*, *N. peltata*, *Tenuiphantes zimmermanni*, and *Walckenaeria acuminata*. Thirteen species outside the linyphiid family were bred in large numbers, i.e. *Achaearanea tepidariorum*, *Enoplognatha ovata*, *Neottiura bimaculata*, *Steatoda grossa*, *Theridion impressum*, *T. melanurum*, *Pholcus phalangoides*, *Pachygnatha clercki*, *P. degeeri*, *Tegenaria atrica*, *Clubiona phragmitis*, *C. reclusa*, and *Pardosa amentata*. The remaining species that were rarely bred or very rarely, were *Zygiella x-notata*, *Nuctenea umbratica*, *Larinioides cornutus*, *Theridion tinctum*, *Ero furcata*, *Amaurobius similis*, *Evarcha falcata*, *Clubiona comta* and *Marpissa muscosa*.

For spider species identification we followed Roberts (1985,1987,1995).

Small spiders were tested after having been kept singly in the containers for at least 30 minutes (up to more than two months). A test consisted of bringing together two spiders into a container. One of the two was resident in it and might have constructed a web during its isolation before introduction of the other spider (“intruder”). In all these resident/intruder tests the webs were removed except for the web part occupied by the resident. In approx. half of the tests two spiders were introduced simultaneously into a new container without webs (two “intruders” whose introduction times were at most one minute apart). Preliminary tests had shown that predation times did not significantly differ between two-intruder dyads and one-resident-one-intruder dyads. Resident linyphiid spiders did not significantly differ from intruder linyphiid spiders in probability of killing the other spider (Heuts, unpublished data). In other spider families, however, residents did significantly differ from intruders, i.e. the residents had a higher killing-dominance (Suter & Keiley 1984; Hammerstein & Riechert 1988; Jackson & Cooper 1991; Heuts & al. 2001). In order to exclude that the differences between spider species would still be confounded by resident-intruder asymmetries we assigned residence and intruder status randomly to the species.

After having put two spiders together they were observed during at least 5 minutes. If at that time they still had not touched each other or had not come within each other’s reach, the observation was continued for another 5 minutes during which vibrations were administered to their container in order to stimulate running and probability of meeting. This method was successful in more than 90 % of such tests. At that time the observation was aborted except for cases of continued observation if at the end of the 10 minutes the spiders were at approx. 1.5 body lengths distance from each other or less and, in fact, were often clearly responding to each other or were even attacking. Observation was resumed approx. 1 hour later for 1 minute in order to check for possible inflicted lesions (leg loss) or araneophagy. A similar short control observation was inserted on the next day before noon and on each of the following days up to the 10<sup>th</sup> day (9 days after the spiders had been put together). If at that time the two spiders were still alive they were separated (often in view of other experiments) or they were left together and were observed at least once every 2 or 3 days until one of them had been killed. We counted only unambiguous cases of killing (with at least partial consumption of the victim in more than 96 % of the tests). We excluded cases where a spider was found dead without any body lesion (visible under 10 x magnification) while having extremely curved legs (not pressed against the body as in the “feigning-death-position”). However, incompletely poisoned spiders that had been bitten briefly were included as killed spiders in the data because they were readily recognizable by their motionless extended legs or by retracted trembling legs and because they were almost always searched for and bitten again (definitively killed) by the killing spider within the next one or two days.

There were only two clear cases of two spiders killing each other among several thousands of kills, i.e. (1) a *Walckenaeria acuminata* adult female and an *Euophrys lanigera* adult male; (2) a juvenile female *Achaearanea tepidariorum* and a very young *Textrix denticulata* of unknown sex.

Killing spiders survived for a time not importantly different from that of untested isolated spiders.

Only nonparametric statistical tests (Siegel 1956) were applied and are specified in the Results section and tables (two-tailed critical significance level  $\alpha = 0.05$ ). Parametric tests were avoided, e.g. because the predation latency times did not show a normal distribution.

## RESULTS

### *Unidirectionality of inter-specific killing-dominance*

Unidirectional inter-specific killing-dominance of species A over species B was defined as the capacity of A killing at least once a specimen of B having three main body-size measures larger than A (while discarding abdomen size), whereas species B was never able to kill a larger specimen of species A. The three main body-size measures were prosoma length, length of the legs of the first pair, and thickness of these legs.

There were 22 different types of two-species-pairs that were tested each at least twice and that each time showed an identical killing-dominance outcome (table 1). In this list of 22 species-pairs there were 12 different *species* involved and each of these species showed at least twice an identical killing-dominance outcome, i.e. they showed a statistically significant degree of unidirectionality at the species level (Sign test;  $N = 12$ ,  $x = 0$ ,  $p < 0.001$ ; table 1). For each of the 22 two-species combinations there was at least one control test, i.e. a spider of the dominant species was tested against a smaller instead of a larger spider of the non-killing-dominant species. In all these (more than 22) control tests the killing-dominant species killed the non-dominant species when the latter had a smaller body size.

We conclude that statistically significant unidirectionality of inter-specific killing-dominance in spiders is demonstrated here.

### *Transitivity of inter-specific killing-dominance*

“Transitivity of (inter-specific) killing dominance” was assigned if species A was dominant over species B, species B dominant over C, and species A also dominant over C, thereby forming a closed loop with three species. In contrast, a triangularity-supporting (transitivity-contradicting) outcome in this closed loop of three species would be that C would be dominant over A.

A necessary condition for accepting true transitivity was a preceding demonstration of statistically significant unidirectionality characterizing the investigated species group as a whole (demonstrated in the previous section of the Results but not demonstrated by Heuts & Brunt 2001).

In order to restrict the high number of closed loops that can directly be deduced from the data in table 2 (loops comprising three or more species), we chose at random a species from the series of killed ‘inferior’ species at the right of each killing-dominant species (table 2) and then put the killing-dominant species at the beginning of a possibly closed loop. Thus, for the killing-dominant species *Theridion tinctum* e.g. the randomly assigned inferior species was *Diplostyla concolor*. It appeared that *T. tinctum* killed a larger *Steatoda grossa* that on its turn, in another dyad of two newly tested spiders, killed a larger *D. concolor* that on its turn killed a larger *Zygiella x-notata*. The loop was closed by testing *T. tinctum* against *Z. x-notata* and finding that *T. tinctum* killed a larger *Z. x-notata*, i.e. the transitivity hypothesis was supported for this case. The triangularity hypothesis, on the contrary, would have been supported if *Z. x-notata* would have killed a larger *T. tinctum*.

A more complex example was found for the highly killing-dominant species *Theridion blackwalli* at the beginning of a closed loop and *Amaurobius similis* as the randomly chosen killed species in the loop. Here the killing-dominance sequence was *T. blackwalli* → *T. tinctum* → *S. grossa* → *Enoplognatha ovata* → *A. similis* and the loop was closed by *T. blackwalli* killing a larger *A. similis* (support for the transitivity hypothesis). However, there was more than one closed loop here, i.e. there were four additional closed loops: (1) *T. blackwalli* → *T. tinctum* → *S. grossa* and *T. blackwalli* closing this loop by killing a larger *S. grossa* (transitivity support); (2) *T. blackwalli* → *T. tinctum* → *S. grossa* → *E. ovata* and *T. blackwalli* closing the loop by killing a larger *E. ovata* (transitivity support); (3) *T. tinctum* → *S. grossa* → *E. ovata* and *T. tinctum* closing the loop by killing a larger *E. ovata* (transitivity support); (4) *S. grossa* → *E. ovata* → *A. similis* and *S. grossa* closing the loop by killing a larger *A. similis* (transitivity support). The fifth and last theoretically possible closed loop in this complex example of five species is *T. tinctum* → *S. grossa* → *E. ovata* → *A. similis* while the loop would be closed by *T. tinctum* killing a larger *A. similis* (possible support), or the reverse, i.e. *A. similis* killing a larger *T. tinctum* (possible contradiction of the transitivity hypothesis). Neither of both outcomes was found in several tests between *T. tinctum* and *A. similis*. Hence, there were in total 5 loops supporting the transitivity hypothesis in the five species versus none contradicting it. In addition to the 6 loops in this example there were 8 other (randomly selected) loops in which transitivity was tested. Each of these 8 additional loops supported the hypothesis of transitivity. Hence, there were in total  $5 + 8 = 13$  supports for transitivity versus no contradiction, i.e. a statistically significant degree of transitivity in the species selected from table 2 ( $p < 0.001$  in a two-tailed Sign test;  $N = 13$ ,  $x = 0$ ).

The additional eight not yet specified randomly selected closed loops supporting transitivity were: (1) *S. grossa* → *E. ovata* → *A. similis* → *Larinioides sclopetarius* → *Araneus diadematus*, while *S. grossa* closed the loop by killing (a larger) *A. diadematus*. This 5-species-loop included 4 “sub-loops”, i.e. (1a) the sub-loop *S. grossa* → *E. ovata* → *A. similis* → *L. sclopetarius* while *S. grossa* closed the sub-loop by killing a larger *L. sclopetarius* “in two steps”, i.e. *S. grossa* killed a larger *Achaearanea tepidariorum* that on its turn, in another

dyad, killed a larger *L. sclopetarius*; (1b) the sub-loop *A. tepidariorum* → *L. sclopetarius* → *A. diadematus* while *A. tepidariorum* closed the sub-loop by killing a larger *A. diadematus*; (1c) the sub-loop *S. grossa* → *E. ovata* → *A. similis* while *S. grossa* closed the sub-loop by killing a larger *A. similis*; (1d) the sub-loop *S. grossa* → *E. ovata* → *A. similis* → *L. sclopetarius* while *S. grossa* closed the sub-loop by killing a larger *L. sclopetarius*; (2) = the 6<sup>th</sup> out of the eight additional loops: *D. concolor* → *Tenuiphantes tenuis* → *Z. x-notata* while *D. concolor* closed the loop by killing a larger *Z. x-notata*; (3) = the 7<sup>th</sup> additional loop: *Gnathonarium dentatum* → *Oedothorax fuscus* → *Z. x-notata* while *G. dentatum* closed the loop by killing a larger *Z. x-notata*; (4) = the 8<sup>th</sup> additional loop: *Walckenaeria alticeps* → *Gongylidium rufipes* → *Neriene clathrata* while *W. alticeps* closed the loop by killing a larger *N. clathrata*.

It is concluded that statistically significant unidirectionality and transitivity (non-triangularity) of killing-dominance among 60 spider species (tables 1 and 2) has been demonstrated.

#### *Correlation between inter-specific killing-dominance and predation latency time*

There was a statistically significant positive correlation between inter-specific killing-dominance position and quickness of killing when only the eight species were considered that formed the longest possible chain of species connected to each other by killing-dominance between adjacent species ( $p < 0.05$ ; table 3). When all species were considered instead of only eight, it appeared that killing-dominant species killed significantly quicker than inferior species (table 4;  $\chi^2 = 9.00$ ,  $p < 0.01$ ).

## DISCUSSION

Do the significantly unidirectional and transitive inter-specific killing-dominance relationships as demonstrated in our laboratory (tables 1, 2, and 3) have any relevance for araneophagy in the field in the sense that highly killing-dominant species would outcompete less dominant species? We could not demonstrate this for e.g. the highly killing-dominant *Theridion blackwalli* and *T. tinctum* because in the micro-habitat of *T. blackwalli* (rain-protected horizontal outdoor fences on buildings) the less killing dominant species occupying the same microhabitat (*T. hemerobium*, *T. melanurum*, *Steatoda bipunctata*, *L. sclopetarius*, *Tegenaria atrica*, and *Dictyna arundinacea*) were capable of remaining present there during at least four years. In a similar way, the less killing-dominant species *P. phalangioides*, *L. sclopetarius*, *A. similis*, *S. bipunctata*, *Z. x-notata*, and *Salticus scenicus* that occupied the micro-habitat of *T. tinctum* on the outside of buildings, were not outcompeted by *T. tinctum*. The reason might simply be that the species differ so much from each other in adult body size that only a very small proportion of the (in adulthood) larger non-killing-dominant species, such as *L. sclopetarius* for example, can be killed by *T. blackwalli*. However, this small proportion of additional spider prey might have provided sufficient reproductive benefit to *T. blackwalli* and *T. tinctum* for evolving and consolidating their araneophagic specializations in killing techniques combined with their extreme web stickiness. In fact, we hit upon an adult female *T. tinctum* consuming a slightly larger juvenile *L. sclopetarius* in the field.

What makes a spider species highly killing-dominant over other spider species, i.e. how has it evolved its killing skills? A plausible cause may be the capability of producing very sticky threads by which other spiders are immediately immobilized, as suggested in our earlier study (Heuts & Brunt 2001). Hence, highly killing-dominant species should, in general, produce more sticky threads than the less dominant species. But, of course, behavioural factors could also play a role because the threads must be moved towards the victim before immobilizing it by wrapping as is typical for the highly killing-dominant theridiids and pholcids. But other highly or moderately killing-dominant species (like mimetids of the genus *Ero*, the clubionid *Clubiona phragmitis*, the salticid *Evarcha falcata*, and linyphiids of the genus *Walckenaeria*) kill their prey by quickly biting it while not losing grip and without any wrapping up the victim before biting. In a somewhat similar way some theridiids like the top-dominant *T. blackwalli* and *T. tinctum* deliver a very quick and premature killing bite after only a very short period of casting threads with extremely fast leg movements and then start to wrap their prey, unlike other theridiids that first wrap the prey with much slower leg movements before biting it.

The part of the web that was left intact in our tests, apparently cannot have played a role because the introduced spider was never caught due to entanglement in this web remnant but always as a result of being bitten or being caught in freshly produced threads. So, further studies on thread stickiness, speed of thread-casting leg movements and speed of approach when trying to apply a killing bite, might show whether they can predict killing-dominance. The prediction might even be based on purely anatomical factors because we demonstrated that the highly killing-dominant *Walckenaeria* genus has significantly heavier and relatively shorter forelegs than a random sample of other, generally less killing-dominant, linyphiid species (Heuts & Brunt, 2005). In that study we, further, demonstrated a significantly higher degree of araneophagy in *Walckenaeria* than in a large group of other linyphiid species.

Apart from specific physiological factors (web stickiness) and behavioural factors (killing technique) we found that quickness of inter-specific killing, i.e. a short predation latency time, predicted inter-specific killing-dominance position (tables 3 and 4). Thus, the quickest killing species were significantly more killing-dominant

than the slower killing species. It should be easy to test this relationship in the natural situation because inter-specific predation in the field (araneophagy) has been reported very often (references in the Introduction).

The importance of our results for a natural situation can be evaluated by experiments in which spiders with undamaged webs would be tested interspecifically in the field. But such tests are only relevant to species that make elaborate webs, thus excluding e.g. many salticid, thomisid, lycosid, and some tetragnathid and linyphiid species. Even within some genera like the typically elaborate-web-building tetragnathid genus *Tetragnatha* there are several “wandering” species that subdue their prey when walking around in the field (Binford 2001).

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#### SAMENVATTING

In het wild komt inter-specifieke predatie bij spinnen vaak voor (spinnen van ongelijke soort die elkaar doden en opeten, d.i. 'inter-specifieke araneofagie').

Wij onderzochten de transitiviteit (zie definitie hieronder) van inter-specifieke dominantie(predatie)verhoudingen tussen 60 spinnensoorten van ongelijke soort die behoorden tot 16 verschillende families en die elkaar doodden en opeten in het laboratorium bij ontmoetingen tussen telkens twee individuen van een verschillende soort. Inter-specifieke dominantie (dodingsdominantie) van een soort over een andere soort werd alleen toegekend indien de dodende spin kleiner was dan de gedode spin (kleiner prosoma en kortere en dunnere poten van het eerste paar poten bij de dodende dan bij de gedode spin, zonder rekening te houden met de grootte van het opisthosoma (abdomen)). De transitiviteit van de dodingsdominantie-verhoudingen was statistisch significant (zoals in onze eerdere studie met een veel kleiner aantal soorten). Een voorbeeld van transitiviteit van dominantieverhoudingen tussen drie verschillende soorten is dat soort A dominant is over soort C indien A dominant is over B en B dominant over C (definitie van transitiviteit).

De inter-specifieke dodingsdominantie-verhoudingen waren niet alleen significant transitief, maar ook significant unidirectioneel zoals in dominantieverhoudingen tussen individuen van dezelfde soort in een groep ("pik-orde" van kippen en vissen in baanbrekende ethologische studies). Een voorbeeld van een unidirectionele dodingsdominantie-verhouding tussen twee verschillende soorten is dat kleinere individuen van soort A in staat zijn om grotere individuen van soort B te doden en op te eten, terwijl kleinere individuen van soort B nooit in staat zijn om grotere individuen van soort A te doden en op te eten (definitie van unidirectionaliteit). Het aantonen van de statistische significantie van de unidirectionaliteit van de inter-specifieke predatie bij spinnen in het wild of in het laboratorium is ons niet bekend uit de literatuur.

Sterk dodingsdominante spin-soorten vertoonden in het laboratorium significant kortere dodings(predatie)-latentietijden dan minder dominante spin-soorten. De sterke dodingscapaciteit van een soort kon dus voorspeld worden uit zijn snel doden (korte dodings-latentietijd).

De kleverigheid van de webdraden, enkele predatie-technieken (met of zonder gebruik van webdraden en/of het inwikkelen van de prooi), en morfologische kenmerken van de poten worden besproken met het oog op een mogelijke verklaring voor de sterke dominantie van enkele van de onderzochte soorten.

Table 1. Unidirectionality tests: Species pairs in which an identical killing-dominance between the two species was found at least twice, versus species pairs in which the killing-dominance was not identical in repeated tests. Killing-dominance was defined as killing and eating a larger specimen of another species (larger with respect to prosoma and leg size while disregarding abdomen size)\*.

Identical killing-dominance	Non-identical killing-dominance
<p><i>Theridion blackwalli</i> → <i>Zygiella x-notata</i>  <i>Theridion tinctum</i> → <i>Tetragnatha montana</i>  <i>Theridion tinctum</i> → <i>Achaearanea tepidariorum</i>  <i>Theridion tinctum</i> → <i>Linyphia hortensis</i>  <i>Theridion tinctum</i> → <i>Zygiella x-notata</i>  <i>Steatoda grossa</i> → <i>Larinioides sclopetarius</i>  <i>Steatoda grossa</i> → <i>Araneus diadematus</i>  <i>Steatoda grossa</i> → <i>Linyphia hortensis</i>  <i>Steatoda grossa</i> → <i>Linyphia triangularis</i>  <i>Steatoda grossa</i> → <i>Neriere montana</i>  <i>Steatoda bipunctata</i> → <i>Diplocephalus cristatus</i>  <i>Clubiona phragmitis</i> → <i>Amaurobius similis</i>  <i>Walckenaeria acuminata</i> → <i>Larinioides sclopetarius</i>  <i>Walckenaeria acuminata</i> → <i>Zygiella x-notata</i>  <i>Walckenaeria unicornis</i> → <i>Zygiella x-notata</i>  <i>Gnathonarium dentatum</i> → <i>Neriere clathrata</i>  <i>Gnathonarium dentatum</i> → <i>Oedothorax fuscus</i>  <i>Gnathonarium dentatum</i> → <i>Zygiella x-notata</i>  <i>Diplocephalus cristatus</i> → <i>Zygiella x-notata</i>  <i>Diplocephalus concolor</i> → <i>Tenuiphantes tenuis</i>  <i>Gongylidium rufipes</i> → <i>Zygiella x-notata</i>  <i>Troxochrus scabriculus</i> → <i>Zygiella x-notata</i></p>	never found in any of the 22 species-pairs
Total: 22 species pairs	versus 0 species pairs ( $\chi^2$ -test, df = 1, p < 0.001)

There are 12 different killing *species* in the 22 pairs (from *Theridion blackwalli* to *Troxochrus scabriculus*). Each of these 12 species killed specimens of another species surpassing them in size in at least two tests without ever being killed in return by (another individual of) the alien species they had killed (not shown in the table). This demonstrates a significant degree of unidirectionality at the species level in addition to the significance obtained with the 22 species pairs (two-tailed Sign test, N = 12, x = 0; p < 0.001).

\* Sex of the species is not specified because a statistically significant difference in killing capacity between males and females (adults and subadults) was never found (except for *Steatoda grossa*: see Table 3). In the larger species *Achaearanea tepidariorum*, *Steatoda grossa*, *Steatoda bipunctata*, *Larinioides sclopetarius*, *Araneus diadematus* and *Zygiella x-notata* also younger stages of unknown sex were tested.

Table 2. Complete list of species that in spite of smaller body size of the tested specimens killed larger specimens of other species\*.

KILLING species	KILLED species
<i>Theridion blackwalli</i> :	<i>Theridion tinctum</i> , <i>Steatoda grossa</i> , <i>Achaearanea tepidariorum</i> , <i>Enoplognatha ovata</i> , <i>Amaurobius similis</i> , <i>Theridion hemerobium</i> , <i>Theridion melanurum</i> , <i>Zygiella x-notata</i> , <i>Dictyna arundinacea</i>
<i>Theridion tinctum</i> :	<i>Steatoda grossa</i> , <i>Ero</i> sp., <i>Enoplognatha ovata</i> , <i>Pholcus phalangioides</i> , <i>Achaearanea tepidariorum</i> , <i>Tetragnatha montana</i> , <i>Theridion melanurum</i> , <i>Theridion sisypium</i> , <i>Theridion varians</i> , <i>Achaearanea lunata</i> , <i>Zygiella x-notata</i> , <i>Centromerita bicolor</i> , <i>Linyphia hortensis</i> , <i>Pachygnatha clercki</i> , <i>Clubiona</i> sp.
<i>Theridion melanurum</i> :	<i>Steatoda grossa</i> males
<i>Steatoda grossa</i> :	<i>Ero tuberculata</i> , <i>Enoplognatha ovata</i> , <i>Achaearanea tepidariorum</i> , <i>Tetragnatha montana</i> , <i>Amaurobius similis</i> , <i>Larinioides sclopetarius</i> , <i>Tegenaria atrica</i> , <i>Pachygnatha degeeri</i> , <i>Segestria bavarica</i> , <i>Araneus diadematus</i> , <i>Diplostyla concolor</i> , <i>Linyphia hortensis</i> , <i>Linyphia triangularis</i> , <i>Neriene montana</i> , <i>Meta segmentata</i> , <i>Pisaura mirabilis</i> , <i>Theridion melanurum</i>
<i>Steatoda grossa</i> males:	<i>Amaurobius similis</i> , <i>Tegenaria atrica</i> , <i>Tetragnatha montana</i>
<i>Steatoda bipunctata</i> :	<i>Tetragnatha montana</i> , <i>Larinioides sclopetarius</i> , <i>Erigone dentipalpis</i> , <i>Diplocephalus cristatus</i> , <i>Dictyna arundinacea</i>
<i>Enoplognatha ovata</i> :	<i>Amaurobius similis</i> , <i>Tegenaria atrica</i> , <i>Theridion varians</i>
<i>Achaearanea tepidariorum</i> :	<i>Steatoda grossa</i> males, <i>Larinioides sclopetarius</i> , <i>Araneus diadematus</i> , <i>Theridion melanurum</i> , <i>Tetragnatha nigrita</i> , <i>Meioneta rurestris</i> , <i>Entelecara acuminata</i> , <i>Neriene montana</i> , <i>Pisaura mirabilis</i>
<i>Pholcus phalangioides</i> :	<i>Tetragnatha montana</i> , <i>Theridion melanurum</i>
<i>Ero</i> sp.:	<i>Enoplognatha ovata</i>
<i>Amaurobius similis</i> :	<i>Larinioides sclopetarius</i> , <i>Segestria senoculata</i>
<i>Larinioides sclopetarius</i> :	<i>Araneus diadematus</i>
<i>Larinioides cornutus</i> :	<i>Araneus diadematus</i>
<i>Pachygnatha clercki</i> :	<i>Neriene montana</i> , <i>Pisaura mirabilis</i>
<i>Scotophaeus blackwalli</i> :	<i>Tegenaria atrica</i>
<i>Clubiona phragmitis</i> :	<i>Amaurobius similis</i> , <i>Tegenaria atrica</i> , <i>Neriene montana</i>
<i>Clubiona corticalis</i> :	<i>Pisaura mirabilis</i>
<i>Textrix denticulata</i> :	<i>Pirata piraticus</i>
<i>Xysticus cristatus</i> :	<i>Trochosa terricola</i>
<i>Evarcha falcata</i> :	<i>Marpissa muscosa</i>
<i>Diplostyla concolor</i> :	<i>Tenuiphantes tenuis</i> , <i>Zygiella x-notata</i> , <i>Bathyphantes gracilis</i> ,
<i>Gnathonarium dentatum</i> :	<i>Neriene clathrata</i> , <i>Oedothorax fuscus</i> , <i>Zygiella x-notata</i> , <i>Erigone dentipalpis</i> , <i>Tenuiphantes zimmermanni</i>
<i>Diplocephalus cristatus</i> :	<i>Zygiella x-notata</i>
<i>Oedothorax fuscus</i> :	<i>Zygiella x-notata</i>
<i>Troxochrus scabriculus</i> :	<i>Zygiella x-notata</i>
<i>Gongylidium rufipes</i> :	<i>Zygiella x-notata</i> , <i>Neriene. clathrata</i>
<i>Erigone atra</i> :	<i>Zygiella x-notata</i>
<i>Erigone dentipalpis</i> :	<i>Tenuiphantes zimmermanni</i>
<i>Bathyphantes approximatus</i> :	<i>Zygiella x-notata</i>
<i>Tenuiphantes tenuis</i> :	<i>Zygiella x-notata</i>
<i>Walckenaeria acuminata</i> :	<i>Larinioides sclopetarius</i> , <i>Zygiella x-notata</i> , <i>Araneus diadematus</i> , <i>Neriene clathrata</i>
<i>Walckenaeria unicornis</i> :	<i>Zygiella x-notata</i> , <i>Centromerita bicolor</i>
<i>Walckenaeria alticeps</i> :	<i>Neriene clathrata</i> , <i>Gnathonarium dentatum</i> , <i>Gongylidium rufipes</i>

- In *S. grossa* data from recognizable males were separated from other specimens because they differed in killing-dominance capacity as it appeared that *Ac. tepidariorum* females were killing-dominant over *S. grossa* males, whereas *Ac. tepidariorum* females were killed by smaller *S. grossa* females. In all the other species the data of all age and sex classes were combined.
- The genus *Ero* was not determined at species level and comprised the species *E. cambridgei*, *E. furcata*, and *E. tuberculata*.



Table 3. Significant positive correlation between killing superiority (degree of inter-specific-killing-dominance) and killing time (quickness of inter-specific predation) of 8 spider species. Killing superiority of a particular species is calculated as a ratio, i.e. the number of species by which it was killed divided by the number of species it killed. Killing superiority (dominance) was only assigned to a species if it killed larger spiders of another species (larger prosoma, longer and thicker legs while disregarding the abdomen)\*.

	Number of superior and number of inferior species given as a ratio (killing-dominance rank in parentheses)	Median killing time in hours (rank in parentheses and based on the inverse of the median killing time)	Number of dyads on which the median killing times were based
<i>Theridion. blackwalli</i>	0/9 (1)	0.95 (2)	28
<i>Theridion tinctum</i>	1/15 (2)	0.38 (1)	54
<i>Steatoda grossa</i>	2/17 (3)	1.80 (3)	88
<i>Achaearanea tepidariorum</i>	3/9 (4)	36.00 (7)	45
<i>Steatoda grossa</i> males	2/3 (5)	7.50 (4)	9
<i>Amaurobius similis</i>	2/2 (6)	84.00 (8)	17
<i>Larinioides sclopetarius</i>	3/1 (7)	12.63 (6)	26
<i>Araneus diadematus</i>	4/0 (8)	10.44 (5)	8

Spearman correlation coefficient ( $r_s$ ) between killing-dominance rank en the inverse of the predation-time rank is + 0.6904762 (rounded to + 0.69 gives  $p < 0.05$  at a two-tailed significance level): species with high dominance ranks kill significantly quicker than species with low dominance ranks

\* The spider species were selected from Table 2 because they formed the longest possible chain of species connected to each other showing unidirectional killing dominance between adjacent species in the chain. *Steatoda grossa* males (with swollen pedipalps, adults or subadults) were listed as a “separate species class” because they showed clearly less killing capacity than other *Steatoda grossa* (females and young stages of unknown sex) e.g. because *Achaearanea tepidariorum* was capable of killing larger *Steatoda grossa* males, whereas it was killed itself by smaller *Steatoda grossa* females. The median killing (predation) time of a particular species was calculated on its latency times when killing various other spider species of various age and sex classes

Table 4. Difference between the median predation latency time (in hours) shown by killing-dominant species and the median predation time shown by inferior species, when preying upon all sorts of spiders (genus abbreviations as in table 1). "Killing-dominant" species were those that had killed at least once a larger-sized specimen of each of the inferior species listed to its right side. The times were mediated separately for each killing-dominant species and each killed (inferior) species (numbers in parentheses) irrespective of age and sex\*.

KILLING-DOMINANT species		LARGER-SIZED INFERIOR species			
<i>Theridion blackwalli</i>	0.95 (28)	<i>Theridion tinctum</i>	0.38 (55) -		
		<i>Steatoda grossa</i>	1.80 (97) +		
		<i>Enoplognatha ovata</i>	17.17 (61) +		
		<i>Achaearanea tepidariorum</i>	96.00 (45) +		
		<i>Amaurobius similis</i>	84.00 (17) +		
		<i>Theridion hemerobium</i>	57.75 (4) +		
		<i>Theridion melanurum</i>	8.25 (20) +		
		<i>Zygiella x-notata</i>	60.00 (3) +		
		<i>Theridion tinctum</i>	0.38 (54)	<i>Steatoda grossa</i>	1.80 (97) +
				<i>Achaearanea tepidariorum</i>	96.00 (45) +
<i>Enoplognatha ovata</i>	17.17 (61) +				
<i>Ero</i> sp.	>8.85/<11.00 (10) +				
<i>Pholcus phalangioides</i>	0.17 (72) -				
<i>Tetragnatha montana</i>	7.75 (14) +				
<i>Theridion melanurum</i>	8.25 (20) +				
<i>Theridion varians</i>	44.25 (5) +				
<i>Zygiella x-notata</i>	60.00 (3) +				
<i>Centromerita bicolor</i>	20.25 (5) +				
<i>Steatoda grossa</i>	1.80 (97)	<i>Linyphia hortensis</i>	252.00 (10) +		
		<i>Pa. clercki</i>	96.50 (16) +		
		<i>Clubiona</i> sp.	252.00 (10) +		
		<i>Ero tuberculata</i>	>5.00/<12.00 (3) +		
		<i>Enoplognatha ovata</i>	17.17 (61) +		
		<i>Achaearanea tepidariorum</i>	96.00 (45) +		
		<i>Amaurobius similis</i>	84.00 (17) +		
		<i>Larinioides sclopetarius</i>	12.63 (26) +		
		<i>Araneus diadematus</i>	10.44 (8) +		
		<i>Tegenaria atrica</i>	32.95 (60) +		
<i>Ero</i> sp.	>8.85/<11.00 (10)	<i>Diplostyla concolor</i>	64.50 (16) +		
		<i>Linyphia hortensis</i>	252.00 (10) +		
		<i>Linyphia triangularis</i>	63.25 (10) +		
		<i>Neriene montana</i>	17.80 (20) +		
		<i>Theridion melanurum</i>	8.25 (20) +		
		<i>Pachygnatha degeeri</i>	0.98 (5) -		
		<i>Meta segmentata</i>	2.42 (10) +		
		<i>Pisaura mirabilis</i>	7.35 (7) +		
		<i>Segestria bavarica</i>	12.00 (5) +		
		<i>Tetragnatha montana</i>	.75 (14) +		
<i>Achaearanea tepidariorum</i>	36.00 (45)	<i>Enoplognatha ovata</i>	17.17 (61) +		
		<i>Steatodagrossa</i> -males	7.50 (9) -		
<i>Enoplognatha ovata</i>	7.75 (14)	<i>Theridion melanurum</i>	8.25 (20) -		
		<i>Meioneta rurestris</i>	45.00 (5) +		
		<i>Entelecara acuminata</i>	7.25 (3) -		
<i>Pholcus phalangioides</i>	0.17 (72)	<i>Amaurobius similis</i>	84.00 (17) +		
		<i>Tegenaria atrica</i>	32.95 (60) +		
		<i>Theridion varians</i>	44.25 (5) +		
<i>Steatoda grossa</i> -males	7.50 (9)	<i>Tetragnatha montana</i>	7.75 (17) +		
		<i>Theridion melanurum</i>	8.25 (20) +		
		<i>Amaurobius similis</i>	84.00 (17) +		
<i>Amaurobius similis</i>	84.00 (17)	<i>Tetragnatha montana</i>	7.75 (14) +		
		<i>Tegenaria atrica</i>	32.95 (60) +		
		<i>Larinioides sclopetarius</i>	12.63 (26) -		
<i>Theridion melanurum</i>	8.25 (20)	<i>Segestria senoculata</i>	109.50 (2) +		
<i>Steatoda bipunctata</i>	24.52 (21)	<i>Steatoda grossa</i> males	7.50 (9) -		
<i>Larinioides cornutus</i>	102.50 (10)	<i>Tetragnatha montana</i>	7.75 (14) -		
		<i>Larinioides sclopetarius</i>	12.62 (26) -		
		<i>Erigone dentipalpis</i>	108.00 (5) +		
		<i>Diplocephalus cristatus</i>	1.18 (10) -		
		<i>Larinioides sclopetarius</i>	12.62 (26) -		

<i>Pachygnatha clercki</i>	96.50 (16)	<i>Neriene montana</i>	17.80 (20)	-
<i>Scotophaeus blackwalli</i>	4.00 (9)	<i>Pisaura mirabilis</i>	7.35 (7)	-
<i>Clubiona phragmitis</i>	5.87 (27)	<i>Tegenaria atrica</i>	32.95 (60)	+
<i>Clubiona corticalis</i>	485.85 (4)	<i>Amaurobius similis</i>	84.00 (17)	+
<i>Textrix denticulata</i>	106.95 (9)	<i>Neriene montana</i>	17.80 (20)	+
<i>Xysticus cristatus</i>	31.37 (12)	<i>Pisaura mirabilis</i>	7.35 (7)	-
<i>Evarcha falcata</i>	0.12 (18)	<i>Pirata piraticus</i>	2.77 (3)	-
<i>Diplocephalus cristatus</i>	1.38 (11)	<i>Trochosa terricola</i>	0.67 (5)	-
<i>Diplostyla concolor</i>	45.00 (17)	<i>Marpissa muscosa</i>	7.50 (11)	+
<i>Gnathonarium dentatum</i>	4.07 (6)	<i>Zygiella x-notata</i>	60.00 (3)	+
<i>Oedothorax fuscus</i>	4.99 (6)	<i>Zygiella x-notata</i>	60.00 (3)	+
<i>Gongylidium rufipes</i>	26.12 (20)	<i>Zygiella x-notata</i>	60.00 (3)	+
<i>Erigone atra</i>	102.63(6)	<i>Zygiella x-notata</i>	60.00 (3)	-
<i>Bathyphantes approximatus</i>	7.87 (5)	<i>Zygiella x-notata</i>	60.00 (3)	+
<i>Troxochrus scabriculus</i>	13.50 (7)	<i>Zygiella x-notata</i>	60.00 (3)	+
<i>Tenuiphantes tenuis</i>	9.67 (9)	<i>Zygiella x-notata</i>	60.00 (3)	+
<i>Walckenaeria acuminata</i>	5.75 (20)	<i>Larinioides sclopetarius</i>	12.63 (26)	+
<i>Walckenaeria unicornis</i>	72.00 (11)	<i>Zygiella x-notata</i>	60.00 (3)	+
	72.00 (11)	<i>Araneus diadematus</i>	10.44 (8)	+
		<i>Zygiella x-notata</i>	60.00 (3)	-
		<i>Centromerita bicolor</i>	20.25 (5)	-

\* Some inferior species are not included because they never killed a spider. Recently tested species in which e.g. *W. alticeps* killed other spiders were not included in this table (see Table 2). Genera abbreviations as specified in table 2\*.

Plus-signs indicate a shorter median predation time shown by a killing-dominant than by an inferior species and minus-signs indicate a longer median time shown by a killing-dominant species. There are 20 plus signs versus 10 minus signs if each killing species provides only one (mediated) sign: difference between 20 and 10 marginally significant ( $\chi^2 = 3.33$ ;  $0.05 < p < 0.10$ ). When counting all plus and minus signs (thereby giving more weight to some than to other species) the plus-minus-contrast is 44 versus 20 and highly significant ( $\chi^2 = 9.00$ ;  $p < 0.01$ ), i.e. killing-dominant species killed significantly quicker than inferior species.



## KOMENDE CONGRESSEN

Dit jaar werd het congres van de Society of European Arachnology (SEA) in Bern gehouden. Of was het een colloquium? Daar was enige discussie over. De voorkeur gaat bij de meesten toch uit naar de term congres. Dat waren het vroeger ook, later werden het opeens colloquia. Nu weer congres is er democratisch besloten. Een modeverschijnsel? Het maakte natuurlijk helemaal niets uit, de opzet is dezelfde: het samenkomen om anderen te vertellen over resultaten van onderzoek, daarover te discussiëren, collega's te ontmoeten. Dat laatste is zeker een heel belangrijk onderdeel. Het congres in Bern kan zeker geslaagd worden genoemd en dat was niet in de laatste plaats te danken aan de perfecte organisatie. Ik heb nooit en congres meegemaakt waar zo weinig wijzigingen in het programma voorkwamen, wat natuurlijk niet alleen aan de organisatie is te danken, maar ook aan de deelnemers die allen waren komen opdagen.

Inmiddels kunnen er twee nieuwe congressen worden aangekondigd.

Van 16-21 augustus 2009 zal het 25<sup>e</sup> congres van ESA plaatsvinden in Alexandroupolis in het noordoosten van Griekenland met Maria Chatzaki als voorzitter van het organisatie comité. Het lijkt mij een goede keuze om het niet in Athene te doen, waar het in die tijd van het jaar heet en stoffig is en vol smog. Nadere gegevens: <http://www.european-arachnology.org/society/news.shtml>

Voor 2010 staat een congres van de International Society of Arachnology op het programma. Het zal worden gehouden in Siedlce in Polen. We hadden daar al eerder een Europees congres, in (1996).

