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Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae)

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Summary. During a 1-year-study in tropical Panama, prey of the social theridiid *Anelosimus eximius* was analysed at two locations and compared with the potential prey spectrum according to sweepnet catches, pitfall traps and bowl traps. Compared with other web-building spiders, *A. eximius* catch an unusually high number of large insects: about 90% are flying ants, beetles, lepidopterans, hemipterans, cockroaches and grasshoppers. This is the result of a communal strategy to overwhelm prey. Webs are maintained commonly, and several spiders attack an entangled insect simultaneously. More spiders participate on insects that are larger and struggle more. The ability to catch large prey insects is discussed as a major driving factor for sociality in spiders.

Introduction

Approximately 35000 species of spiders exist worldwide, but only 20 or 30 of them live in social groups. Curiously enough, these species are restricted to the tropics and belong to only six families (Shear 1970; Kullmann 1972; Buskirk 1981). In the last 20 years the behaviour of social spiders has been the subject of intensive studies. The main question asked has been *how* they manage to live in groups? Results differ only slightly between species: Individuals are tolerant of each other, communicate in many ways, practice to some degree division of labour, attack insects in cooperation and share prey items (Burgess 1979; references in Buskirk 1981). Several possible evolutionary routes to sociality have been discussed including enhanced parental care and an "urge for association" (Kullmann and Kloft 1968; Kullmann 1972), a tendency to aggregate (Shear 1970), and the mutual advantage of cooperative web building and predation (Brach 1977). The question *why* these spiders live in social groups has hardly been considered. It is remarkable that all social spiders in various families, though not related, share two characteristics: (1) They are exclusively web-building spiders (Witt 1975; Krafft 1982); (2) They occur mainly in the tropics where insects are abundant throughout the year. Exceptions to the latter point are *Stegodyphus* spp. (Eresidae) and *Mallos* spp. (Dictynidae) (e.g. Bradoo 1972; Jackson 1978). This suggests that prey availability is an important factor for the size of the territory of a spider (Riechert 1978) and for spider sociality. Since they all build extremely large webs, it is possible that preying on larger insects which cannot be caught by the web of one individual spider (e.g. grasshoppers, roaches etc.) is their ecological niche. This paper examines composition and length of the prey of the social theridiid *Anelosimus eximius* in tropical Panama and tests the hypothesis that social spiders prey on larger insects than solitary spiders of equivalent size. Apart from a short-term study in Ecuador (Tapia and de Vries 1980) and some occasional notes (Brach 1975; Christenson 1984), this is the first study on *A. eximius* which presents data on potential and actual prey collected during a whole year.

Methods

The taxonomy of *Anelosimus eximius* Simon (Theridiidae) has been studied by Levi (1956, 1963), with biological observations from Brach (1975), Tapia and de Vries (1980) (mistakenly identified as *A. jucundus*), Vollrath (1982), and Christenson (1984). *A. eximius* is a small spider (females 5–6 mm body length). It is widespread in neotropical forest of lowland to mid-elevation sites, but colonies are only locally abundant at forest edges or in treefall gaps. The web consists of a large sheet forming a bowl ranging from less than 0.5 m to more than 1.5 m in diameter (maximum 4 m, estimated volume of the bowl 0.05

to 0.5 m^3) and is suspended by vertical knockdown threads of several metres length. Some 1000 to 10,000 individuals may live in one web. Most webs were found on shrubs or trees 1–5 m above ground level.

Study sites. Populations of *A. eximius* were studied at two localities in Panama. 1. On Cerro Galera, a hill (50–100 m above sea level) near the Pacific coast which is covered with tropical humid forest, about 10 km west of the Panama Canal near Arraijan. This population was artificially introduced 5–10 years ago and consisted of five webs at the side of the road. During my investigations two of them were destroyed by falling branches or human activity and disappeared. The webs were medium sized (sheets 0.5 m high and up to 1 m wide). 2. El Valle, 100 km west of Panama City, is approx. 800 m above sea level in a premontane humid forest. The *A. eximius* population was concentrated on fern-covered banks and comprised about 150 webs; most of them medium-sized, one of them huge (4 m in length with suspension threads approx. 5–7 m long and a population of more than 10,000 individuals).

The El Valle population was observed monthly from August 1983 until February 1984. Prey insects and remains were collected from a total of approx. 50 medium-sized and large webs.

On Cerro Galera the potential and actual prey of the webs of *A. eximius* was analysed as follows:

Potential prey. Pitfall traps (white plastic beakers, 7 cm upper diameter, volume 200 ml) and bowl traps (yellow plastic bowls, 14 cm upper diameter, volume 500 ml) filled with 10% formaldehyde and detergent, were placed under 3 webs (2 different traps each) and emptied at 10-day intervals. For a discussion of trap selectivity, see Adis (1979) and Nentwig (1982b). Insects and spiders which avoid spider webs and the avoidance behaviour in general are discussed by Nentwig (1982a, 1983). After the traps had been emptied, insects were collected with a sweepnet from the vegetation (herbs and shrubs) between 2 webs up to a height of 2 m. At least 150 insects were collected, then identified to order/suborder and measured to the nearest mm.

Actual prey. At 10-day intervals from March 1983 to February 1984, all insects entangled in the webs and all prey remains were collected. Since the total prey number per collection was often low, the data presented here were aggregated over 1 year, so seasonal differences cannot be discussed. Actual and potential prey are compared by means of the Ivlev index of selectivity (Ivlev 1961), explained and discussed by Nentwig (1981).

Feeding experiments were made in Gamboa with spiders from El Valle in August and September 1983 under relatively natural conditions ("standard Gomboa conditions", Nentwig 1984). Seven groups of spiders, each comprising 10–13 adult females, were kept in plastic boxes (17 × 12 × 6 cm). Grasshoppers 4–28 mm in length (= 1 × to 4 × spiders size) were supplied daily. The following parameters were monitored: prey length, maximum number of attacking spiders and maximum number of feeding spiders within the first 5 min of the attack and of the feeding period.

Results

Prey composition

Potential prey according to the three different sampling methods is listed in Table 1. The main groups represented in the sweepnet results were ants, beetles and parasitic wasps, whereas dipterans comprised about 50% of the contents of the pitfall and yellow traps. The mainly phytophagous hemipterans were strongly represented in the sweepnet; epigeic Collembola were almost exclusively caught by the other methods. Many web-building spiders were caught exclusively by the sweepnet, but most other groups were distributed more or less evenly over all collecting methods.

The spiders actual prey (Table 1) consisted mainly of ants, beetles, lepidopterans, hemipterans, cockroaches, and grasshoppers. These groups comprise respectively 85% and 96% of the total for the two populations studied. There is a qualitative difference between the two colonies: Cerro Galera spiders caught more ants, wasps, bees and bugs; El Valle spiders caught more beetles and lepidopterans (differences significant, χ^2 test, $P < 0.02$). In El Valle no collections of the potential prey were made, so it is not possible to determine whether the differences in the composition of the actual prey are due to the availability of prey or, less likely, due to a different prey capture behaviour of the spiders. Comparing actual and potential prey of Cerro Galera with the Ivlev index of selectivity (Table 1), all these main prey groups show strong positive values, i.e. they are caught selectively. Highly positive values for Mantodea, Isoptera and Psocoptera, as well as the values for Acari and Opiliones, are statistically suspect due to the very low number of animals collected, and these results should be treated with some caution. Negative indices for parasitic hymenopterans, flies, midges and spiders are reliable and show that these groups avoid spider webs or are not caught by the web residents.

A combination of different traps is the best approach to establish the composition of potential prey (Nentwig 1981). *A. eximius* webs are built in the full vegetation, and traps on the soil (pitfall and bowl traps) perhaps contain disproportionate numbers of soil arthropods. The percentage difference (the sum of the % differences for all taxa of two traps) between trap and prey of all prey groups evaluates similarities between the three trap types and the actual prey. This shows the sweepnet data as best approximation to the spiders prey (77.5% accumulated difference), while pitfall traps (137.7%) and bowl traps (139.4%) differ more. But the Ivlev indices calculated only with the sweepnet data do not differ very much from those which are calculated with the average trap data (Table 1). The values of Formicoidea, Coleoptera and Cicadina are clearly less positive; the values of Thysanoptera and larvae are clearly more negative; the index for Orthoptera switched from slightly posi-

Table 1. The prey of *Anelosimus eximius* at two locations compared with trap data

	Actual prey (%)		Potential prey (%) at Cerro Galera			Ivlev index: actual prey Cerro Galera versus	
	Cerro Galera	El Valle	Sweep net	Pitfall trap	Bowl trap	Sweep net	All traps
Formicoidea	19.9	9.1	18.2	9.2	7.0	+0.04	+0.27
Wasps/bees	3.6	0.4	0.3	0.1	0.1	+0.85	+0.89
Parasitic hymenopterans	0.6		9.1	3.4	6.1	−0.88	−0.82
Coleoptera	17.8	35.0	12.9	10.3	8.1	+0.16	+0.41
Lepidoptera	2.1	11.0	0.8	0.2	0.2	+0.45	+0.68
Lepidoptera larvae[a]	0.9	0.8					
Brachycera	1.2		5.1	45.4	41.2	−0.62	−0.92
Nematocera	0.6		6.8	3.9	11.6	−0.84	−0.85
Diptera larvae[a]		0.4					
Heteroptera	17.2	10.6	5.2	1.9	1.9	+0.54	+0.70
Cicadina	7.6	12.9	6.8	1.0	4.4	+0.06	+0.30
Blattodea	12.7	10.6	0.3	0.1	0.2	+0.95	+0.97
Orthoptera	7.9	7.2	10.8	1.2	0.9	−0.16	+0.30
Mantodea	0.3		0.04	0.02	0.03	+0.76	+0.98
Isoptera	2.4	0.4	0.04	0.1	0.2	+0.97	+0.91
Psocoptera	0.9		0.1	0.1	0.2	+0.80	+0.74
Thysanoptera	0.3		0.5	0.2	0.3	−0.25	−0.05
Larvae[a]			1.5	1.0	0.4	−0.25	−0.04
Odonata		0.4					
Collembola		0.8	0.7	18.2	13.8		
Acari	0.6		2.2	1.0	0.8	−0.57	−0.38
Opiliones	0.3		0.1	0.03	0.04	+0.50	+0.67
Araneae	2.1	0.4	17.5	1.9	1.8	−0.79	−0.54
Undetermined	0.9						
Others[b]			0.9	0.7	0.8		
Total	331	263	4,761	12,190	25,174		

[a] Trap data (not specified to order, mainly Coleoptera and Lepidoptera larvae) versus prey data (only Lepidoptera and Diptera larvae) for index calculations

[b] Mainly Aphidoidea, Diplopoda and Isopoda, only a few Symphyta, Coccinea, Dermaptera, Phasmodea, Thysanura, Chilopoda, Scorpiones, and Pseudoscorpiones

tive to slightly negative; all other values remained more or less unchanged and none of these differences is statistically significant (χ^2 test). This indicates that the Ivlev index is not influenced too much by the selectivity of one trap type.

A total of 87% of all prey items were winged arthropods; 62% of all ants and 78% of all termites were winged. Among the beetles, four phytophagous families (Curculionidae, Chrysomelidae, Elateridae, Buprestidae) comprised nearly 50% of the total, two-thirds of the Lepidoptera were moths, one-third were butterflies. Heteroptera consisted of Pentatomidae (20%) and several large Reduviidae. Saltatoria were represented by Caelifera (64%) and Ensifera (36%) (including a few crickets).

Prey size

A. eximius prey consisted mainly of large insects (Fig. 1) with only a small percentage of prey items smaller than 4 mm and a considerable percentage of items longer than 10 or 20 mm. Selected taxonomic groups confirm this observation. Figure 2 compares the size of ants, beetles, bugs and cockroaches from the three collecting methods with the size of items from the spiders prey. In all cases, size distribution of trapped insects was similar for the three collecting methods, showing maxima smaller than 4 mm (only roaches are larger). In contrast, prey items were always larger. For Formicoidea, the larger size was mainly explained by the many winged specimens and the lack of smaller species in the spiders prey. The traps collected many immature stages of bugs and roaches, whereas the spiders caught only winged specimens.

Predatory behaviour

The spiders in an *A. eximius* colony attack prey items cooperatively. Groups of 30–50 or more spiders could often be observed subduing one large

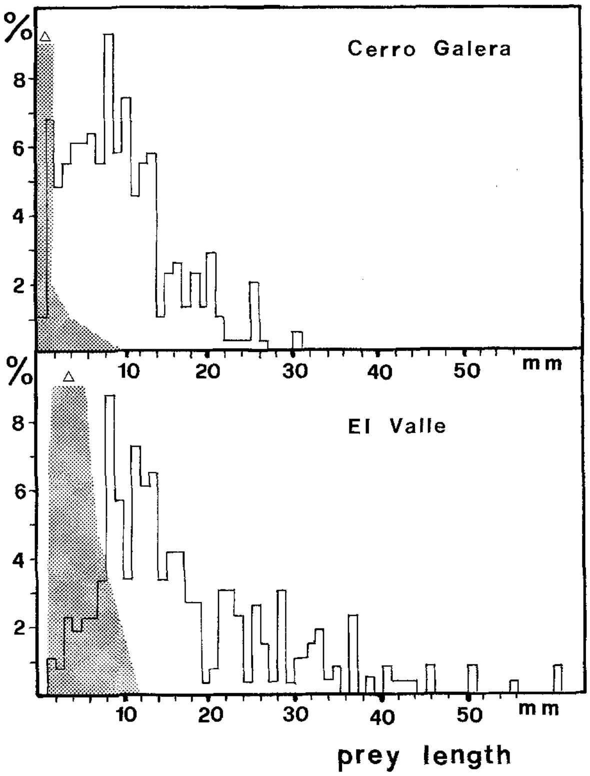

Fig. 1. Prey size of *A. eximius* at Cerro Galera ($n=311$, $\bar{x}$ 10.0 ± 9.5 mm) and near El Valle ($n=262$, $\bar{x}=16.8 \pm 11.2$ mm). The hatched area indicates the range of the body length of the prey for two nonsocial spider species: *Nephila clavipes* (Araneidae) at Cerro Galera (Nentwig 1985) and *Anelosimus jucundus* (Theridiidae) at El Valle (Nentwig and Christenson 1985), where prey size data were obtained by collecting all prey items and remains from the webs during a whole year (*Nephila*) or three times (*A. jucundus*)

grasshopper or butterfly. The stronger a prey item is and the longer it struggles, the more spiders approach and join the attacking group. Feeding experiments in the laboratory with small groups of 10–13 spiders yielded comparable results: all grasshoppers offered to the spiders could be subdued immediately but the larger an insect was, the more spiders attacked and fed on it (Table 2). The number of spiders attacking a prey item was lower (36.8±18.1% of the total experimental group) than the number of spiders feeding (55.2±23.0). The composition of the attacking and feeding groups was permanently changing.

Discussion

The social spider *A. eximius* catches especially large insects if compared with a variety of European and African Araneidae, Tetragnathidae, Linyphiidae, Theridiidae, Agelenidae, Pholcidae, Amaurobiidae, Dictynidae, and Filistatidae (Fig. 3). Most of these species are of the same size as *A. eximius,* some are larger. They build all kind of webs (sticky – non-sticky, cribellate – ecribellate). The extreme prey size is accomplished by means of the non-sticky threads of the barrier web which reach lengths of several metres and which are repaired and replaced at dusk and dawn. In this way the grouped spiders can maintain webs in open flyways where larger insects tend to fly. The "knockdown strands" stop flying insects whose struggling movements immediately attract some spiders. Small insects, however, are often ignored and escape within a short time after landing on the web (Brach 1975; own observation). *Drosophila* flies were ignored by a laboratory colony of spiders after their third molt (Brach 1975). The second and more important type of behaviour that allows this 5-mm spider to overwhelm insects up to 60 mm in length is the communal attack. More spiders participate in the attacks on larger prey and those that struggle longer. There is a correlation between the number of spiders that attack and the number that feed although this correlation does not necessarily imply more food per spider. Spiders might get the same amount of food on a larger number of small insects. My results agree with those of Dewar and Koopowitz (1970) for *Stegodyphus dumicola,* although Vollrath and Rohde-Arndt (1983) found no correlation between time spent attacking and time spent feeding. Communal or cooperative attacks on large prey items have been observed in several social spiders and appear to be the rule in this group (*Mallos gregalis:* Jackson 1979; two *Agelena* species: Pain 1964; Krafft 1966, 1969, 1970; several *Anelosimus* species: Brach 1975; Tapia and de Vries 1980; Vollrath and Rohde-Arndt 1983; Christenson 1984; several *Stegodyphus* species: Marshall 1898; Kullmann 1972; *Achaeranea disparata:* Darchen 1968; Bradoo 1972; *Achaeranea wau,* Lubin, personal communication).

If communal attacks are a prerequisite for subduing large prey, then one can expect that other social spiders catch large prey as well, and that solitary web-building spiders do not. In fact, this is the case. Figure 1 compares the prey size of *A. eximius* at Cerro Galera with that of a large orb-weaving spider, *Nephila clavipes* (Araneidae) (Nentwig 1985), and the prey size of *A. eximius* in El Valle with the congeneric *A. jucundus,* a spider with a less highly evolved social structure but of the same body length as *A. eximius* (Nentwig and Christenson 1985). In both cases the social *A. eximius* catches by far the larger prey. This size difference explains the large differences in the prey com-

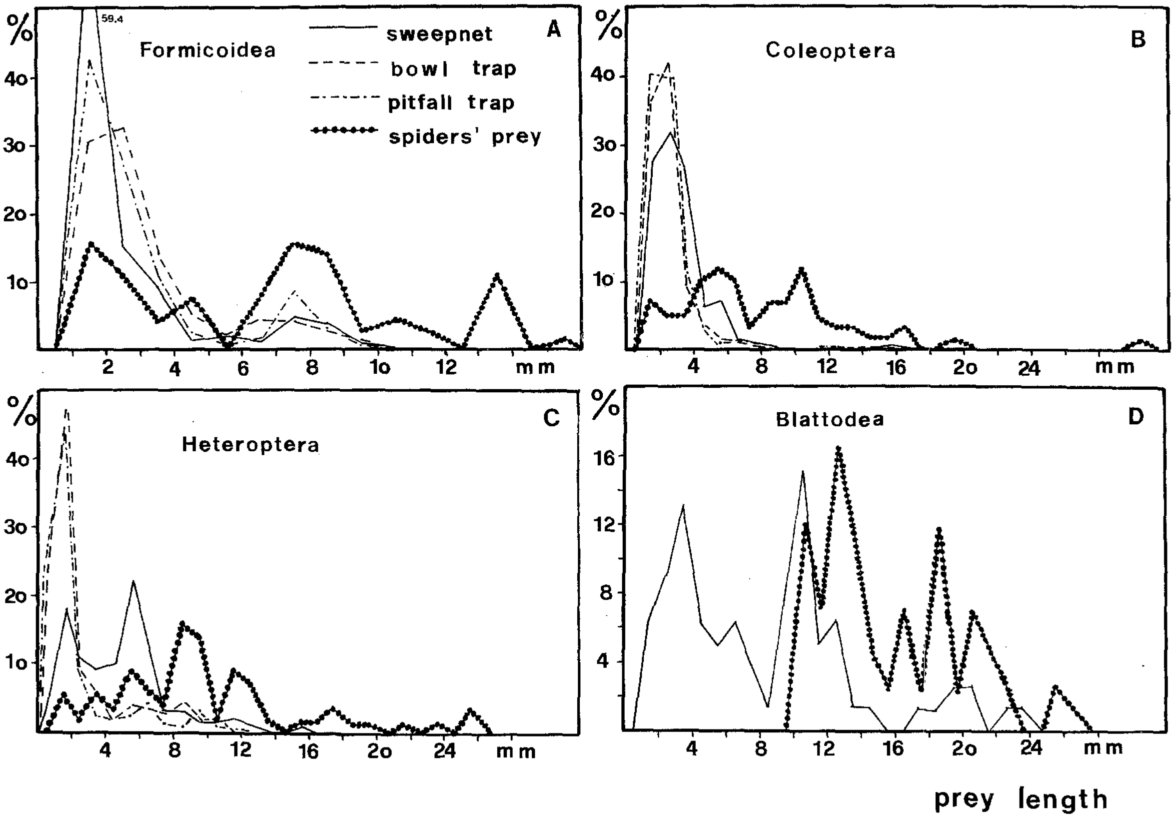

Fig. 2 A–D. Size distribution of selected taxa in the potential prey (sweepnet, bowl trap, pitfall trap) and actual prey of *A. eximius*. Lumped data of a 1-year collection, for total n see Table 1. **A** Formicoidea; **B** Coleoptera; **C** Heteroptera; **D** Blattodea (unbroken line = lumped results of the potential prey)

Table 2. Correlations (linear regressions) of *Anelosimus eximius* feeding experiments ($n = 46$, grasshoppers 4–28 mm as prey, 10–13 adult female spiders per experiment)

Variable 1	Variable 2	r	P
Prey length (mm)	n attacking spiders	0.54	<0.001
Prey length (mm)	% attacking spiders	0.53	<0.001
Prey length (mm)	n feeding spiders	0.56	<0.001
Prey length (mm)	% feeding spiders	0.55	<0.001
n attacking spiders	n feeding spiders	0.51	<0.001

position of *A. eximius* and *A. jucundus* in El Valle. Small arthropods such as Formicoidea, parasitic hymenopterans, Brachycera, Nematocera, Aphidoidea, Cicadina, and Acari are more numerously represented in the diet of *A. jucundus*, and comprise 75.2% of the diet. Of these insect groups, *A. eximius* caught only Formicoidea and Cicadina which made up only 22.0% of the diet. Large insects (wasps/bees, Coleoptera, Lepidoptera, Heteroptera, Blattodea, and Orthoptera) account for

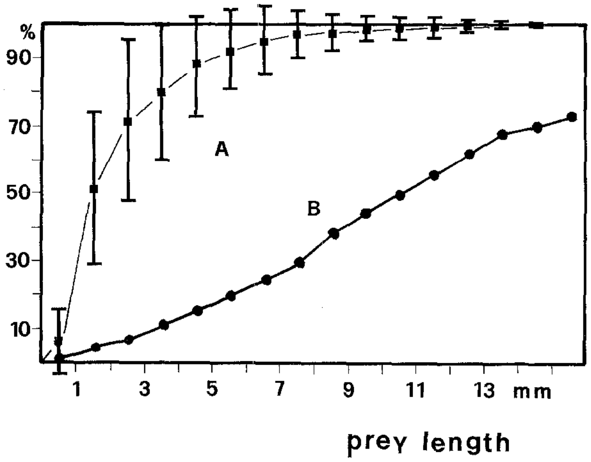

Fig. 3. Cumulative presentation of the prey size of 11 species or families of web-building spiders (curve A, mean ± SD of species data, n prey = 15,000, data from Nentwig 1983), compared with prey size of *A. eximius* (curve B, n prey = 573). The species are: *Zygiella x-notata*, several *Araneus* species (Araneidae), *Tetragnatha extensa* (Tetragnathidae), several Linyphiidae and Theridiidae species, *Coelotes terrestris*, *Tegenaria ferruginea* (Agelenidae), *Pholcus phalangioides* (Pholcidae), *Amaurobius ferox* (Amaurobiidae), 2 *Dictyna* spec. (Dictynidae), *Filistata nana* (Filistatidae)

74.8% of *A. eximius* prey but constitute only 22.5% of *A. jucundus* prey. Differences in the prey availability at the locations of the two species may account for some of this disparity. However, the main reasons appear to be these characteristics of *A. jucundus:* the smaller spider groups per web, fewer attacking individuals per prey item, smaller webs and shorter suspension threads.

Figure 3 shows the prey size of nonsocial web-building spiders as a cumulative percentage per size-class and compares it with the social *A. eximius*. The size range of prey items of nonsocial spiders is clearly different from that of *A. eximius*. The spider size is similar in both groups and can be neglected (*A. eximius* 5–6 mm, nonsocial spiders approx. 4–10 mm). Prey analysis of *A. eximius* (Tapia and de Vries 1980) or other social spiders yielded similar results (Jambunathan 1905; Fischer 1907; Diguet 1915; Chauvin and Denis 1965; Darchen 1968; Jackson 1979) but in all these cases data are not detailed enough to be compared in the manner of Fig. 3. However, comparing these incomplete data, Buskirk (1981) came to a similar conclusion. She demonstrated that spiders which cooperate in prey capture catch larger prey than spiders which do not. Enders (1975) compared the size of predator and prey on a larger scale and showed that most hunting spiders take smaller prey than web builders of comparable size. Since there are few reliable data on prey size in hunting spiders, his idea remains to some extent hypothetical. Mainly in view of this lack of information the graphs of Buskirk and Enders do not agree very well and there is also considerable discrepancy between them and predator-prey length correlations collected in recent years (Nentwig, in preparation). However, a very generalized assertion can be put forward: in relation to a spider's body size, prey size increases from hunting spiders through solitary web-building spiders to web-building social spiders with cooperative prey capture.

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