

A comparison of prey lengths among spiders

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Summary. Field observations and laboratory experiments were carried out to determine the influence of body length of preys on the acceptance rate by spiders. Feeding experiments with 13 spider species and a model prey (crickets) reveal a decreasing acceptance rate with increasing prey size. Prey sizes of 50–80% of the spiders' size yielded the highest acceptance rates, crickets of double the spiders' size were accepted by two species only. By fitting the acceptance rate Y versus prey size X by $Y(x) = Y(0)(1 - \beta x^2)$, two coefficients could be calculated: $Y(0)$, the size-independent palatability of the prey and β , a coefficient of size-induced refusal of the prey. These values describe the degree of specialisation towards (a) crickets and (b) large prey, respectively. Further comparison showed (a) that labidognath (= araneomorph) spiders do not necessarily subdue larger prey items than orthognath (= mygalomorph) spiders and (b) that webbuilding spiders are superior to non-webbuilding spiders in respect of catching large prey. A modified model of the generalized pattern of the length relations of predator and prey is given with special reference to spiders and compared to other polyphagous predator groups.

Most predators subdue their prey within certain size limits. Very large prey items cannot be overwhelmed and too small items are overlooked or rejected as well. Only a few studies on predacious invertebrates have been carried out (Holling 1964) and show that morphological patterns such as leg length or the width of the mouthparts effect these size limitations. Hespeneide (1973) and Enders (1975) gathered some of these data and presented a generalized model on the size, relations of several predator groups and their prey. Enders' addition of spiders into this model, however, is not carefully and detailed enough, as already mentioned by Nentwig (1985b). We present here results of field observations and laboratory studies of many spider species. The similarity and the degree of specialization, respectively, of their prey size pattern is investigated and this leads to a revised form of Enders' model.

Material and methods

The following spiders were investigated. Non-webbuilding spiders: *Avicularia* spec. (Theraphosidae); *Pisaura mirabilis* (Cl.) (Pisauridae); *Xysticus cristatus* (Cl.) (Thomisidae); *Evarcha arcuata* (Cl.) (Salticidae); *Tibellus oblongus*

(Walck.) (Philodromidae); *Selenops* spec. (Selenopidae); *Cupiennius salei* (Keys.) (Ctenidae); *Alopecosa cuneata* (Cl.) and *Pardosa lugubris* (Walck.) (Lycosidae). Webbuilding spiders: *Ischnothele guyanensis* (Walck.) (Dipluridae); *Tegenaria atrica* C.L.K. (Agelenidae); *Scytodes longipes* Lucas (Scytodidae); *Pholcus phalangioides* (Fuesslin) (Pholcidae); *Nephilengys cruentata* (F.) (Araneidae).

The common European spiders *Pisaura*, *Xysticus* and *Evarcha* were collected near the Biology Department, Marburg; *Pholcus* and *Tegenaria* were collected in buildings of Marburg. *Tibellus* was collected near Darmstadt, *Pardosa* near Koblenz, *Alopecosa* originates from Lyon, France. *Cupiennius* has been reared over a considerable time in several German universities (Melchers 1963), *Avicularia* was bred in captivity and originates from Brazil, *Selenops*, *Scytodes* and *Ischnothele* are Panamanian spiders, they were collected 1983 in Panama and have been reared successfully in Marburg. *Nephilengys* originates from Rio de Janeiro, Brazil. The spiders were caught as juvenile animals, raised from eggs (*Tegenaria*, *Pardosa*, *Alopecosa*, *Selenops*, *Nephilengys*), or had been kept in captivity for several generations (*Cupiennius*, *Avicularia*, *Scytodes*, *Ischnothele*). More background information on these spiders is given in Bristowe (1939, 1941), Melchers (1963), Foelix (1979), Nentwig (1985a, in preparation).

Experimental procedure. All spiders were kept in white plastic boxes (17 × 12 × 6 cm) with transparent tops. A wet cellulose sheet (4 mm thick) provided humidity and substrate (exception: *Pholcus*, *Scytodes* and *Tegenaria* which tolerate 40% RH). Temperature varied between 25° C (European spiders) and 30° C (tropical species). Depending on the availability of the species, the experiments were run in 1983 in Panama (*Scytodes*, Nentwig 1985a) and in Marburg from early 1984 to mid 1985. In most cases specimens of the last juvenile instars (both sexes) and adults (females only) were selected for feeding experiments. Only the experiments with large spiders (*Avicularia*, *Cupiennius*, *Nephilengys*) were made with earlier instars. During the first week spiders were fed with one small cricket (*Acheta domestica* (L.)) per day. Then the feeding experiment started. One cricket per spider per day was offered, the next day the remains or the refused crickets were replaced by a new cricket. A refused cricket was followed by a smaller item, an accepted cricket was followed by a larger item. This led to a feeding regime in which prey sizes tended to cluster around the optimum prey size and with acceptance rates of approx. 30–50% over the complete experiment. Crickets were of-

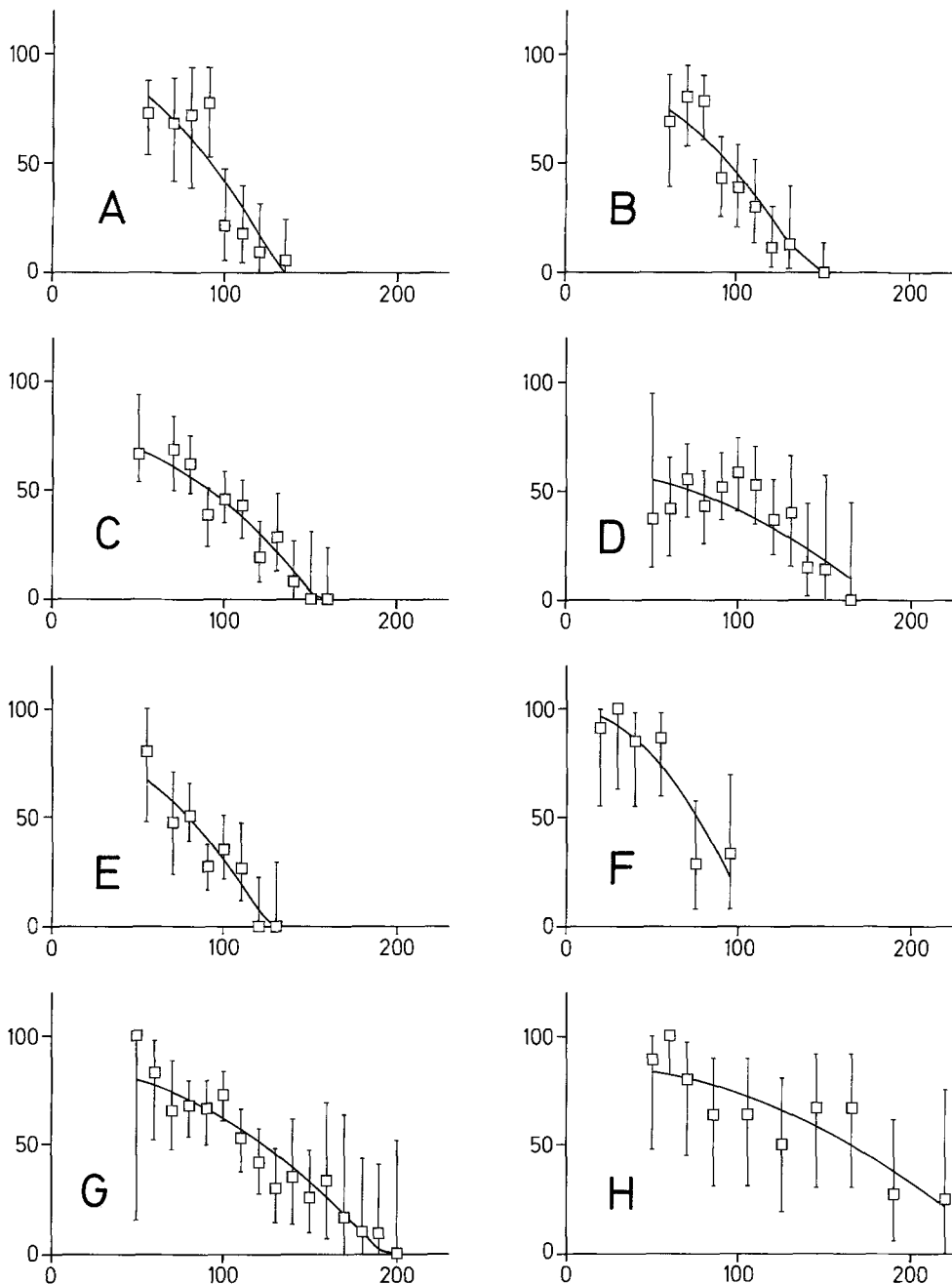


Fig. 1 A-H. Acceptance rates (% of accepted prey items) versus body length of the prey (measured as % of body length of the spider). The 95% confidence limits are shown. **A** *Pisaura*; **B** *Evarcha*; **C** *Tegenaria*; **D** *Pholcus*; **E** *Pardosa*; **F** *Tibellus*; **G** *Ischnothele*; **H** *Xysticus*

ferred in a size range of 50–230% of the spiders' length. Due to some prey specialisation (Nentwig in preparation) *Xysticus* and *Tibellus* rarely accepted crickets (24 and 17% acceptance rates). Flies of different body sizes (acceptance rates 87 and 71%) were offered to these spiders. We suggest that for the following considerations the behaviour of these spiders towards their "favourite" prey is comparable with that of the other spiders. The days in which a spider moulted and the days before and after moulting were not taken into consideration. The length of all crickets (without antennae and cerci) was measured to the nearest 0.5 mm; the length of the spiders (without chelicerae and spinnerets) was measured at intervals of approximately 3 days.

Evaluations. The acceptance rates (% of accepted prey items) of each spider species is plotted (Fig. 1) versus the

body size of the prey. This is given as percentage of the body size of the spider in order to compare spider species of different body sizes. For the determination of the confidence limits we assume that each spider species shows a certain probability to accept a prey item of the offered size class. Thus offering a number of preys of the same size class the acceptance rate will show a binomial probability distribution. This has been used to determine (e.g. Colquhoun 1971) the 95% confidence limits in Fig. 1.

A least mean square fit with $Y(x) = Y(0) - \beta x^2$ has been used which offers a reasonable fit for all species. It is evident that this function can be used only for the range of x shown in Fig. 1. For small values of x the acceptance rate $Y(x)$ has to decrease by biological reasons. The fitted values of $Y(0)$ and β are shown in Table 1. The deviation of $Y(0)$ from 100% describes the size independent acceptability or

Table 1. Fitted parameters of the prey size patterns in figure 1. $Y(x) = Y(0) - \beta x^2$ (arranged according to the decreasing values of $Y(0)$)

Spider	$Y(0)$ size-independent palatability of the prey (crickets) (%)	β coefficient of size- induced refusal of the prey (crickets)
<i>Cupiennius</i>	113	0.0037
<i>Scytodes</i>	108	0.0019
<i>Tibellus</i> ^a	100	0.0085
<i>Alopecosa</i>	99	0.0054
<i>Pisaura</i>	97	0.0056
<i>Evarcha</i>	91	0.0046
<i>Xysticus</i> ^a	87	0.0014
<i>Selenops</i>	87	0.0038
<i>Ischnothele</i>	86	0.0023
<i>Pardosa</i>	82	0.0052
<i>Tegenaria</i>	77	0.0033
<i>Avicularia</i>	69	0.0035
<i>Pholcus</i>	60	0.0018

^a flies as prey

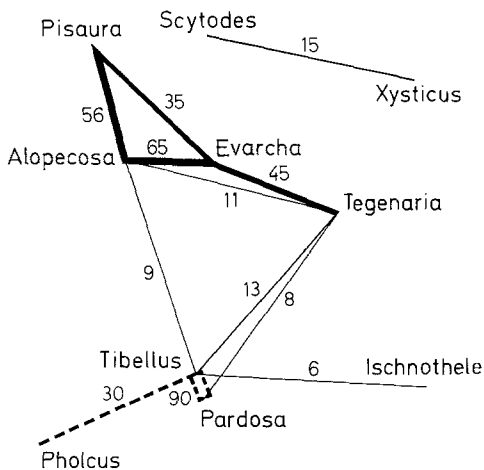


Fig. 2. Statistical similarity of the prey size patterns (see Fig. 1). The values of the measure of similarity P are given on the interconnections. The distances are chosen to be proportional to $100\% - P$. Values of P smaller than 5% are not shown

palatability of the prey. The coefficient β indicates how the acceptance rate declines with the increase of the prey size, which we call the coefficient of size induced refusal. The proportionality to x^2 means that the refusal is proportional to the visible area of the prey.

In order to examine if the differences of the fitted values or $Y(0)$ and β in Table 1 are significant the following statistics have been used. If one compares the results (accepted/refused) of the same size class of the preys for two different spider species one gets a 2×2 table of classification. The chi-square test may be used to determine the significance level of the difference of the species. A corresponding test has been used comparing all size classes. Starting with the null hypothesis that there is not difference between the two species we determined the expected frequencies for all size classes and used the chi-square test to find P , the level of significance, i.e. the probability that the seen difference of the species can result by accident. The higher the value

of P the higher the probability that there is no real difference between the two species. Therefore we take P as a measure of similarity.

In Fig. 2 the species are shown in a way that the nearer the points are the more similar the corresponding species are. As a measure of distance we have used $100\% - P$. The values of the measure of similarity P are written at the interconnections. Values of P smaller than 5% are not shown.

Results

All spiders accepted smaller prey items more readily than larger items and preferred prey sizes of less than 80–100% of their own size. Crickets of 50–80% of the spiders size yielded the highest acceptance rates (up to 100%); crickets of double the spiders' size were accepted only by *Scytodes* (ca. 30%) and *Xysticus* (acceptance rate of flies ca. 30%). For details see Fig. 1. Non-webbuilding spiders generally accept smaller items than webbuilding spiders. *Evarcha*, *Pisaura*, *Selenops*, both lycosids and *Avicularia* accepted no crickets larger than 150% of the spider's size. *Cupiennius* showed higher acceptance rates for many size classes; *Tibellus* preferred very small flies (<70% body size); *Xysticus*, at the opposite extreme, overwhelmed flies of more than 200% of its own size. Among webbuilding spiders *Tegenaria* and *Pholcus* caught the smallest prey items, while *Scytodes*, *Ischnothele* and *Nephilengys* were able to subdue crickets of more than 200% of their own size.

For a detailed comparison we use Table 1 which describes the parameters of the fitted functions in Figs. 1 and 2 which shows the statistical measure of similarity P . Therefrom the similarity of *Pisaura*, *Alopecosa* and *Evarcha* is obvious. *Pardosa* shows the same magnitude of β ; its difference in $Y(0)$ is reflected in Fig. 2, too. The values of $Y(0)$ and β indicate a certain similarity of *Evarcha* and *Tegenaria* which is statistically confirmed by Fig. 2. *Avicularia* resembles *Tegenaria* by the agreement of the β -values. A weak similarity of *Scytodes* and *Pholcus* is shown by the almost equal values of β . The similarities of *Tibellus* and *Pardosa*, *Scytodes* and *Xysticus*, *Tibellus* and *Pholcus*, respectively, indicated by Fig. 2 rest on the comparison for two or three size classes of the preys only. The corresponding curves in Fig. 1 would intersect each other just in the small range where data for both curves exist. There is no real similarity as the values of Table 1 indicate, too.

Field analyses of non-webbuilding spiders which just had caught a prey item yielded similar results: Salticids (several species) catch prey items (several groups) of $89 \pm 39\%$ ($N=45$) their own body size, lycosids $56 \pm 26\%$ (6), oxyopids $79 \pm 32\%$ (21), thomisids from flowers $171 \pm 68\%$ (11). The prey size of webbuilding spiders is easier to investigate and many data are available (Nentwig 1980, 1982, 1985b, c). For both spider groups field data generally yield a smaller size spectrum than the experimental data in the laboratory.

Discussion

The results of the feeding experiments show that the size of prey items which spiders can overwhelm is limited. Most crickets accepted were smaller than the spider; the optimum prey size is 50–80% of the spiders' own body size. Prey items of webbuilding spiders collected under natural condi-

tions show that most prey items are relatively small too (Nentwig 1980, 1982, 1985b, c). Comparable data for non-webbuilding spiders are rare but support these results as well (Buchli 1969, Edwards 1974, Jackson 1977, Nyffeler and Benz 1981). Gettmann (1976) could provoke attacking behaviour of *Pirata piraticus* (Lycosidae) with dummies of the four fold spider length, but the natural prey consisted always of small items.

There is only one important group of spiders which catch prey much larger than themselves: social spiders. By communal attacks on entangled items they can subdue insects of 10–20 times their own body size (Burgess 1979, Nentwig 1985b). Kleptoparasitic spiders (e.g. Theridiidae: *Argyrodes*) may steal large prey (Vollrath 1984). This aspect of their feeding biology, however, needs further investigations. Reports on salticids (Robinson and Valerio 1977) or flower-inhabiting thomisids (Hobby 1930, Morse 1979) feeding on prey items three times their own size or larger do not conflict with the results presented here. These records concern prey taxa such as dragonflies, butterflies or wasps; in this study we have dealt with crickets as model prey. There may be other predator – prey size relationships, but these are not a consequence of the preceding statements.

Our results allow two astonishing generalizations. First, webbuilding spiders are superior to non-webbuilding spiders in respect of catching large prey. The plesiomorph orthognath *Ischnothele*, one of the most “primitive” of spiders which builds catching webs, and the more recently evolved araneid orbweaver *Nephilengys* subdue crickets up to 200% of their own size. Both species have independently evolved an aggressive wrapping behaviour which enables them to catch a wide spectrum of difficult prey items (Eberhard 1967, Robinson et al. 1969, Nentwig 1986). *Tegenaria*, a funnel-web spider with an intermediate evolutionary position attacks its prey in the same manner as a wolfspider or a salticid. It jumps towards the cricket, bites it and holds it with its chelicerae. It scarcely uses its legs and does not use silk at all. For *Tegenaria* the silken sheet is only the substrate on which it hunts and which helps to hinder a rapid escape of entangled insects. All non-webbuilding spiders (with the possible exception of Theraphosidae) evolved from this line between *Ischnothele* (or mygalomorphs in general), *Tegenaria* and *Nephilengys*. They have reduced their webs independently several times and have thereby incurred two disadvantages: They can only attack smaller prey and they cannot subdue such a large spectrum of prey group (Nentwig, in preparation). There is only one

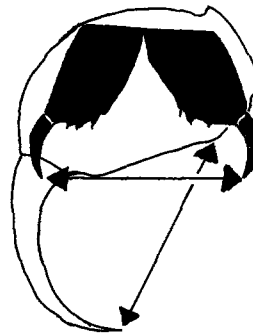


Fig. 3. Common scheme to explain the functional superiority of a labidognath spider with small chelicerae (black) to orthognath spiders (white) in subduing a prey item of the same size (arrow) (redrawn from Kaestner 1969)

prominent exception in the case of the first disadvantage: *Xysticus* has evolved enlarged legs I and II, which enable it to subdue larger prey items (this is probably valid for other Thomisidae too). The enlarged front legs of other spider families may have similar functions (e.g. the giant crab spiders, Heteropodidae) but our study shows that at least *Selenops* does not use its long legs to catch very large items. This “negative” evolutionary effect of web reduction in spiders is difficult to explain and we do not try to do so here.

Our second generalization derives from a comparison of orthognath spiders (= Mygalomorphae) with certain labidognath spiders (= Araneomorphae). The data of the non-webbuilding spiders (the orthognath *Avicularia* vs. labidognath lycosids, pisaurids or salticids) are rather similar; a comparison of webbuilding spiders (*Ischnothele* vs. *Tegenaria*) shows the orthognath *Ischnothele* to catch larger prey than the labidognath *Tegenaria*. Consequently, the ability per se of orthognath spiders to subdue large prey items is comparable to labidognath spiders (or even better). The evolutionary direction is clear: labidognath chelicerae derived from orthognath chelicerae. The common explanation of this step is, however, wrong. It is generally said that this should enable labidognath spiders to subdue larger prey items with their small chelicerae (e.g. Foelix 1979). A current illustration of this statement is given in Fig. 3, taken from Kaestner (1969: 680). The comparison between both chelicerae types as it is given in Table 2 (for the measurements of chelicerae, see Fig. 4) shows that size differences between chelicerae types of comparable efficiency are negligible. We will probably require revised functional explanations for this important step in the evolution of spiders.

The experimental data of this study combined with various field data (see references) and unpublished data allow

Table 2. A comparison of the chelicerae of orthognath and labidognath webbuilding and non-webbuilding spiders. All measurements in mm; letters refer to chelicerae sizes of Fig. 4 (see text)

Spider chelicerae type	<i>Avicularia</i> orthognath	<i>Ischnothele</i> orthognath	<i>Cupiennius</i> labidognath	<i>Tegenaria</i> labidognath	Δ^a (%)
web	—	+	—	+	
body length	11.1	11.1	11.0	11.0	
age	juvenile	adult	juvenile	subadult	
a. Length of basic segment	2.1	2.3	2.0	2.3	2
b. Width of basic segment	1.4	2.0	1.3	1.1	42
c. Length of fang	1.7	1.7	1.2	1.3	36
d. Diameter of fang	0.25	0.25	0.22	0.2	19
e. Length of longest tooth	0.13	0.22	0.18	0.1	25
f. Angular with	1.8	1.6	1.4	1.4	21

^a Δ (%) = orthognath measurement larger than labidognath measurements (average)

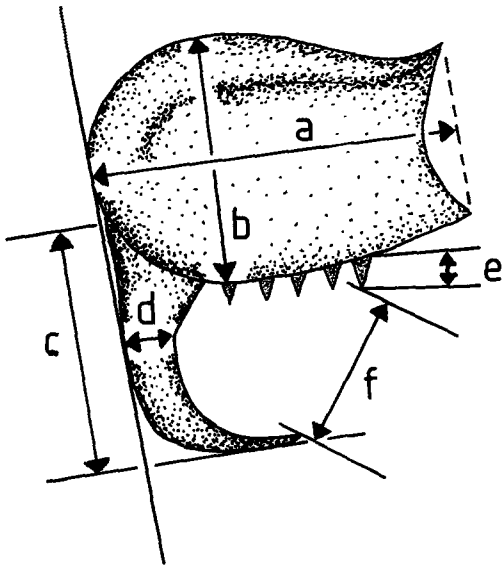


Fig. 4. Chelicerae measurements taken to compare the orthognath and labidognath type (see Table 2)

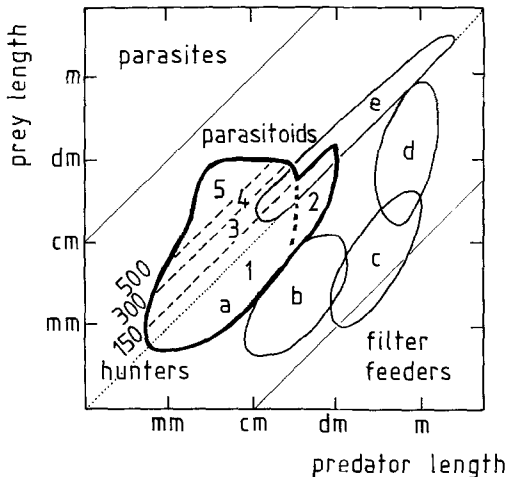


Fig. 5. Generalized pattern of the relative lengths of predator and prey. The surrounded areas indicate size relations for *a* spiders; *b* chewing insects; *c* insectivorous birds; *d* hawks, owls; *e* ants, dogs (pack hunters). Spiders are subdivided to 1 non-webbuilding spiders; 2 large mygalomorph spiders; 3 non-webbuilding spiders specialized on large prey items (e.g. some salticids or thomisids); 4 solitary webbuilding spiders; 5 social webbuilding spiders. The central dotted line indicates equality of size of predator and prey; the peripheral unbroken lines indicate prey (predator) one-hundredth length of predator (prey); the three broken lines indicate prey 150%, 300%, and 500% of the length of the predator (modified after Enders 1975)

us to modify the generalized model of the size of predator and prey from Hespeneide (1973) and Enders (1975) with special reference to spiders (Fig. 5). We assume that insects (as the major prey of spiders) are not larger than 10 cm and that non-mygalomorph spiders are not larger than approx. 4 cm. The largest mygalomorph spiders reach 9–10 cm body length and may prey on insects and other prey groups up to 150% of their body length. Non-webbuilding spiders which specialized on large prey items (e.g. some salticids or thomisids) subdue prey items up to 300% of their own body size. Solitary webbuilding spiders catch

items of not more than 500% of their own body size. Even the largest insects, however, can be overwhelmed by the communal attacks of social webbuilding spiders. These spiders (only a few species of 2–3 mm to less more than 1 cm body length) compensate their limited individual power by attacks where the number of attacking spiders is positively correlated with the size and power of their victims (Nentwig 1985b). Consequently, they subdue their prey nearly independently of their own body size. Compared to other predator groups spiders cover a much wider range (Fig. 5) with nearly two orders of magnitude for the length of predator and prey. This is achieved by different hunting manners which include specific overwhelming techniques, high evolved social behaviour and a variety of web types.

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