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Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae)

Yasuaki Murakami
Department of Biology, Faculty of Science, Kyushu University, Fukuoka 812, Japan

Summary. *Argiope amoena* is a common web spider in southwestern Japan. Surveys were made of prey size by use of prey traps and by direct observations, and of potential prey size by use of the sweeping method. The web size, web mesh size, spider size, and spider's effective size on prey capture were also measured. Hymenoptera, Coleoptera, and Hemiptera were important as prey for female *A. amoena* which is far larger than male. Small insects such as dipterans, which are numerous in the surrounding vegetation, were excluded as prey of the female. It seems that small insects pass through the web mesh. *A. amoena* caught prey nearly twice its own length. The upper limit of prey size coincided with the distance between the first and third legs of *A. amoena;* these legs are used for prey handling and silk-wrapping. It seems that large insects above the upper limit escape by defeating the spider or by breaking the web.

Introduction

Most predators have an optimum prey size range, and prey which are smaller or larger than this range are ignored or not easily captured. For example, Holling (1964) showed that the prey size of the praying mantid *Hierodula crassa* is determined by the grasping mechanism of the foreleg. Thus, if one considers a particular predator, the proximate causes of prey size determination can be found in physiological and structural features.

Among the insect-feeding predators, web spiders are characterized by the use of a web to capture prey, and there are many published accounts of their feeding biology (Brown 1981; Enders 1975; Kajak 1965; LeSar and Unzicker 1978; Nentwig 1980; Robinson and Robinson 1970, 1973; Turnbull 1960, 1973; Uetz et al. 1978). Studies of prey size selection are very restricted, and there exists some confusion among them. For example, LeSar and Unzicker (1978) suggested that heavy-bodied insects are totally excluded as prey, but Nentwig (1980) stated that the web spiders select larger prey. LeSar and Nentwig were exclusively concerned with the relationship between the actual prey size and the potential prey size. The predator size and the web measurements were not studied in these papers. But as Brown (1981) showed, spider size and web measurements are indispensable to the study of prey size selection.

In this paper, the spider size, web size, web mesh size, and spider's effective size on prey capture are investigated as factors that determine the prey size of *Argiope amoena*.

Methods

Study areas

Studies were carried out in hedgerows of *Cryptomeria japonica* D. Don (Taxodiaceae) surrounding an orchard of 2,275 m^2 in area, and in the adjacent grassland on the east side of the orchard, in Shimobaru, Fukuoka, Japan. The hedgerow was 2–2.5 m high, 98.7 m long and 1.0 m wide, and contained 135 Cryptomeria trees. The grassland was dominated by *Solidago altissima* L. (Compositae), and *Miscanthus sinensis* Andress (Gramineae). Less abundant species were also widespread, including *Rubus hirstus* Thunb. (Rosaceae) and *Pleioblastus variegatus* Makino (Gramineae). There were 125 orange trees of 0.5–2.0 m in height in the orchard. The undergrowth of the orchard was dominated by *Artemisia princeps* Pamp. (Compositae), and *Boehmeria grandifolia* Weddell (Urticaceae) was also found in a very limited area. Near the orchard, there was grassland to the east, farmlands of melon, watermelon, and eggplant to the north, paddyfields and a radish farm to the west, and another orange orchard to the south.

Additional experiments were made in a hedgerow of *C. japonica* surrounding a peach orchard 600 m from the orange orachard, and in a pine wood of the Experimental Station of Faculty of Agriculture, Kyushu University, Hakomatsu, Fukuoka.

Sampling techniques.

A belt transect (2 m by 260 m) was made along the hedgerow of the orange orchard and along the small paths in the grassland. Webs of *A. amoena* found by walking along the transect were marked by a piece of red cloth attached to the nearest plants during June 2 to August 4. The location of each web, its height above ground, and its diameter were recorded. The number of sticky silk lines along the radii was also counted to measure the mesh size of web in a way similar to that described by Uetz et al. (1978). The spider on the web was photographed dorsally from a fixed distance of 23 cm, and the carapace width and the body length were measured from the photograph. After taking the photograph, the spider on the web was marked with colored enamel paint. Each spider was distinguished by different colors and positions of marks. Similar measurements were also made from October 1978 to March 1979 in the hedgerow of the peach orchard and from April to June 1978 in the pine wood.

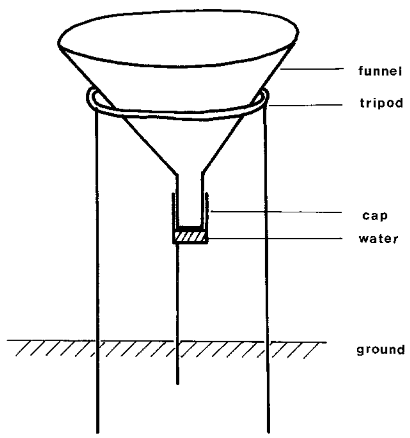

Fig. 1. Prey trap used in the present study

Estimates of daily food consumption were made by direct observations of 7 females during 12 h on 12 and 13 July. By walking the transect every 15 min, individual spiders were checked and it was recorded whether they were feeding or not. The prey on which they were feeding was classified into the taxonomic order, and the body length of the prey was recorded. The prey was not identified into categories below order because identification was very difficult in the field. The same observations were also made in the additional experiments, for 22 males and 10 females on 25 and 27 May, 1978 and for 19 males and 6 females on 8 and 11 June, 1978.

The discarded prey remnants that *A. amoena* threw down from the web were gathered by use of a prey trap from 14 June to 10 August when all the spiders died off (Fig. 1). A tripod (70 cm in height) with legs partly buried in the soil was set at an appropriate height under a female spider's web. A funnel (30 cm in diameter and 43 cm in height) was put on the tripod. The end of the tube of the funnel was closed with a small cap filled with water into which discarded prey items dropped by the spider fell. These were removed at intervals of 1–5 days and were preserved in ethanol for later identification. The samples were dried in an oven at 60° C for 48 h and each sample was examined under a binocular dissecting microscope. It was possible to identify most prey cadavers to family and often to lower taxonomic divisions. The head, elytra, and thorax of Coleoptera served to identify the fragmented remains of those insects. Hemipteran remains were characterized by the presence of a proboscis on the head, and the shape and color of the fragments were a further guide to separation. The number of prey items was calculated by counting elytra, wings, heads, and other hard parts. Prey length was measured directly from the samples, or taken from Inoue et al. (1959), Nakane et al. (1963) and Asahina et al. (1965), or partly calculated using the relationship between wing length and body length. Prey traps were set for 29 females of 2.17–8.92 mm in carapace width. Among them, 18 individuals were adults, 5 were sub-adults and 6 were older juveniles.

A sweep net (45 cm in diameter) was used to collect insects from surrounding vegetation on 5 and 20 July to compare with insects found in the diet of the spider. Each sample contained 100 sweeps. The sample insects were put into 75% ethanol for later identification and body length measurement.

Results

Life cycle of A. amoena

A female of *A. amoena* produces several egg sacs during her life. Spiderlings emerge from the first egg sac in late July. They grow to 1.3–2.9 mm in carapace width before overwintering. In winter, from late November until early March, they do not make webs. They overwinter on branches of trees or on stems of grasses without eating anything. They start their development again in the following spring and by the middle of May most of the males become sub-adults (1.6–3.0 mm in carapace width). The first adult males appear in late May, about 20 days earlier than the first females. The adult female (6.3–8.9 mm in carapace width) is far larger than the adult male (2.3–3.3 mm in carapace width). Mating occurs in early June. In late June, the female produces her first egg sac. Most of the females die by early August, while the males die by late June.

Prey of female A. amoena

Table 1 shows the insect species captured over 192 web-days recorded by use of prey traps. Among the insects caught by the spiders, Hymenoptera, Coleoptera, and Hemiptera were largest in number. Among Hymenoptera, ants and honey bees were most numerous, but as ants were small compared to honey bees, the latter constituted the major part of prey biomass. Many species of Coleoptera were caught by the spider, and scarabs (Scarabaeidae) were more numerous and larger in size (15.06 ± 5.24 mm in body length; mean $\pm 95\%$ confidence interval; $n = 29$) than other Coleoptera caught (6.23 ± 1.26 mm in body length; $n = 52$). Among Hemiptera, *Petaphora maritima* (Cercopidae) was large in number. Figure 2 shows the number of individuals

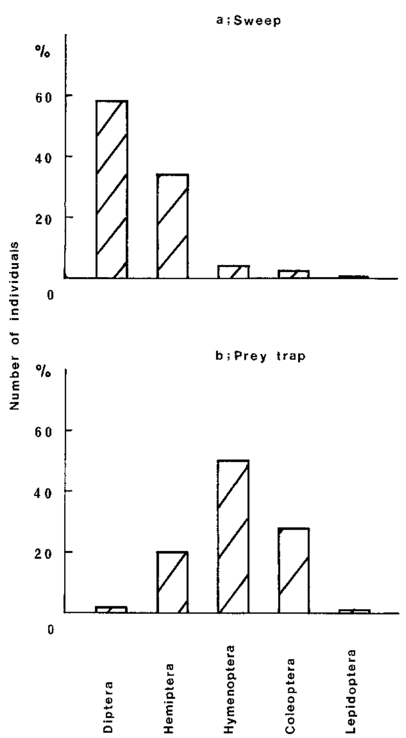

Fig. 2a, b. The number of individuals of 5 important orders of insects found in **a** the sweep samples and **b** the diet of female *A. amoena*

Table 1. List of the prey species, body length and number of individuals

Order	Prey species	Body length	Number of individuals
Hymenoptera	Tenthredinidae gen.sp.	7.8	1
	Ichneumonidae gen.sp.1	10.4	1
	Ichneumonidae gen.sp.2	15.4	1
	Ichneumonidae gen.sp.3	5.4	1
	Formicidae gen.sp.1	8.5	18
	Formicidae gen.sp.2	5.4	58
	Scoliidae gen.sp.	18.2	1
	Polistes chinensis	16.0	1
	Pompilidae gen.sp.1	17.7	2
	Pompilidae gen.sp.2	13.9	1
	Pompilidae gen.sp.3	15.4	1
	Sphecidae gen.sp.	13.2	1
	Lasioglossum sp.	7.6	1
	Halictidae gen.sp.1	8.6	2
	Halictidae gen.sp.2	9.4	1
	Apis cerana	12.0	110
	Bombus sp.1	18.0	1
	Bombus sp.2	15.0	1
	Hymenoptera fam.gen.sp.		8
Coleoptera	*Anoplogenius cyanescens*	9.0	1
	Harpalidae gen.sp.1	10.0	7
	Harpalidae gen.sp.2	8.0	4
	Histeridae gen.sp.	5.0	1
	Staphylinidae gen.sp.1	4.0	2
	Staphylinidae gen.sp.2	4.0	1
	Staphylinidae gen.sp.3	4.0	1
	Lachnosterna kiotonensis	18.0	6
	Maradera japonica	8.5	2
	Protaetia brevitarsis	24.0	4
	Popillia japonica	10.0	9
	Anomala testaceipes	17.0	2
	Anomala sp.	22.0	1
	Oxycetonia jucunda	14.0	3
	Caccobius sp.	7.0	1
	Scarabaeidae gen.sp.		1
	Elateridae gen.sp.1		1
	Elateridae gen.sp.2		1
	Elateridae gen.sp.3		1
	Attagenus japonicus	4.0	5
	Soronia fracta	8.5	1
	Microlanguria jansoni	4.2	1
	Harmonia axilidis	7.5	1
	Coccinella septempunctata	8.0	1
	Propylaea quatuordecimpunctata	4.5	2
	Epirachna vigintioctopunctata	6.5	5
	Coccinellidae gen.sp.	4.0	1
	Paraglenea fortunei	13.0	1
	Aulacophora femoralis	7.5	3
	A. nigripennis	6.5	5
	Chrysomelidae gen.sp.	6.0	1
	Coleoptera fam. gen.sp.		5
Hemiptera	*Platypleura kaempferi*	22.0	1
	Petaphora maritima	10.0	38
	Ricaniidae gen.sp.1	7.0	1
	Ricaniidae gen.sp.2	7.0	1
	Aphididae gen.sp.		2
	Homoeocerus unipunctatus	13.5	2
	Riptortus clavatus	15.5	1
	Coptosoma punctissimum	5.1	5
	Eysarcoris guttiger	5.2	1
	Cretus sp.		1
	Hemiptera fam.gen.sp.		4
Orthoptera	*Gastrimargus marmoratus*	45.0	1
Diptera	Tipulidae gen.sp.	10.0	1
	Syrphidae gen.sp.	6.0	1
	Muscidae gen.sp.	7.0	1
	Diptera fam.gen.sp.		1
Odonata	*Pantala flavescens*	46.0	1
Lepidoptera	*Pieris rapae crucivora*	19.0	1
	Deilephila elpenor lewisii	34.0	2
Araneae	Araneae fam.gen.sp.		4
Unidentified			25
Total			387

of insects of the five most important taxonomic orders captured by sweeping the surrounding vegetation (Fig. 2a) and found in the diet of female *A. amoena* (Fig. 2b). The individuals belonging to these orders constituted 92.2% of the total number of insects found in the diet. From the sweep samples (Fig. 2a), Diptera (59.0%) and Hemiptera (34.3%) were larger in number than Hymenoptera (4.0%), Coleoptera (2.7%) or Lepidoptera (0.1%). In the diet sample (Fig. 2b), Hymenoptera (49.7%) constituted by far the largest number of prey. Coleoptera and Hemiptera were 28.1% and 19.9% respectively. Diptera (1.7%) and Lepidoptera (1.0%) were very rare. These figures show that female *A. amoena* does not capture prey in proportion to the number of insects available in the surrounding vegetation. She prefers Hymenoptera and Coleoptera but rejects Diptera. Generally, the dipterans are small in size.

Figure 3 shows the size frequency distribution of insects in the surrounding vegetation (Fig. 3a) and in the diet of female *A. amoena* (Fig. 3b). Very small insects below 5 mm in body length were abundant while large insects above 10 mm were very rare in the sweep samples (Fig. 3a). More than 50% of the diet was composed of insects above 10 mm (Fig. 3b). In the diet, insects of 10–15 mm were most numerous and small insects below 5 mm were very few compared to those from the samples by sweeping. Thus female *A. amoena* seem to select the larger insects from those in the surrounding vegetation as prey. This result agrees with Brown (1981) studying the prey of female adult *Argiope trifasciata*.

Web size, web mesh size and prey handling length of A. amoena

The web size increased with the carapace width of spider (Fig. 4). A linear relationship was obtained between these two variables ($y = 96.10x - 87.89$, $r^2 = 0.88$; $n = 106$). Figure 5 shows the relationship between the carapace width and the web mesh size (the web radius/the number of sticky lines per radius). Web mesh size increased with carapace

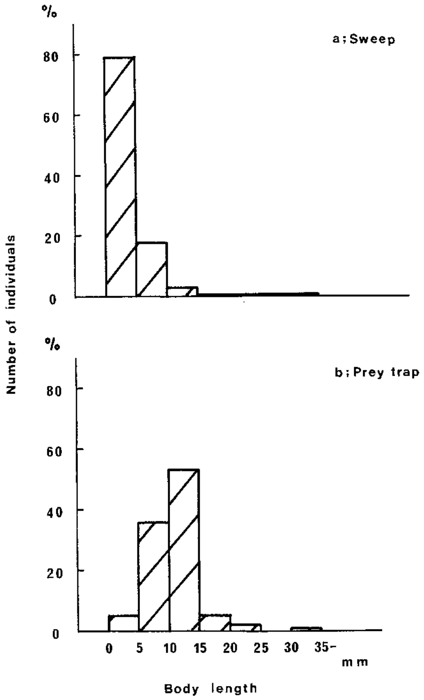

Fig. 3a, b. Size frequency distribution of insects in **a** the sweep samples and **b** the diet of female *A. amoena*

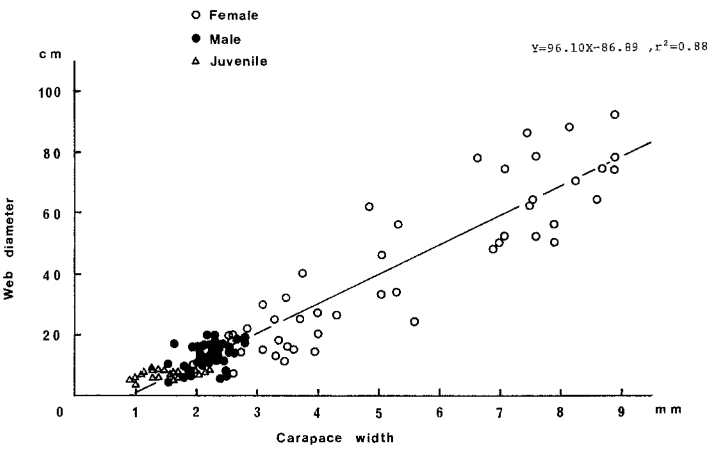

Fig. 4. The relationship between carapace width and web diameter

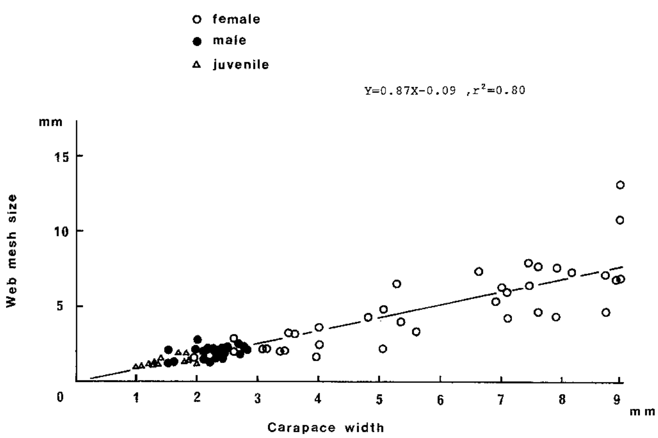

Fig. 5. The relationship between carapace width and web mesh size

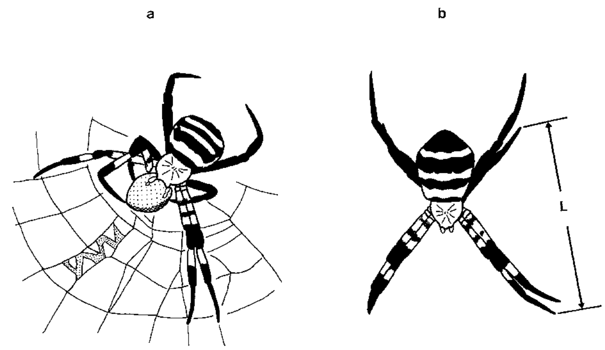

Fig. 6a, b. The posture of *A. amoena* while **a** handling prey and **b** resting

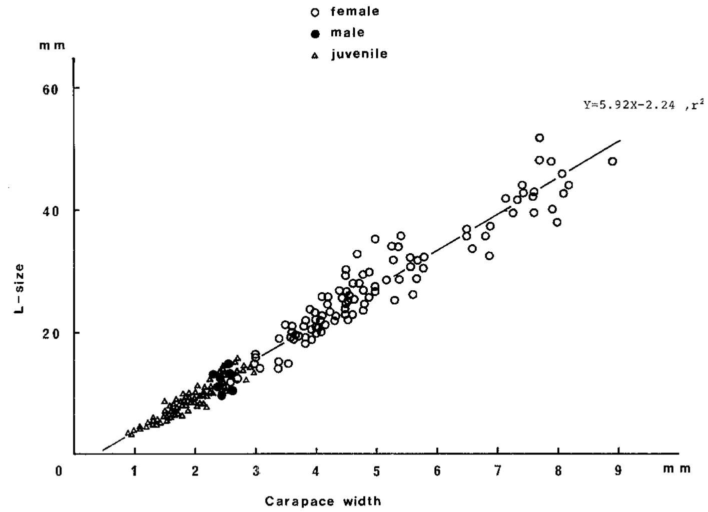

Fig. 7. The relationship between carapace width and L-size

width of the spider. A linear relationship was obtained between these two variables ($y=0.87x-0.09$, $r^2=0.80$; n = 83). The female is larger than the male and therefore both female web mesh size and web size were also larger.

Figure 6 (drawn from photographs) shows the postures of *A. amoena* while handling prey and resting. *A. amoena* uses the first and third legs for prey capture, silk wrapping, and prey holding. The distance *L* between first and third legs as shown in Fig. 6b was measured from the photographs taken while spider was resting. The author calls this 'L-size' for convenience. Figure 7 shows the relationship between carapace width and L-size ($y=5.92x-2.24$, $r^2=0.95$; n = 203). L-size increased with carapace width of the spider.

Figure 8 shows the relationship between carapace width and prey size. With increase of the carapace width the prey size and its range increased. The two staight lines drawn in Fig. 8 are those in Fig. 5 (lower) and Fig. 7 (upper). These lines approximately coincide with the lower and upper limits of the prey size for each spider size. These relations are probably due to the fact that prey species smaller than the lower limit pass through the web mesh, whilst larger prey species than the upper limit defeat the spider or destroy the web, that is, *A. amoena* cannot wrap prey items larger than its L-size and therefore the prey escapes.

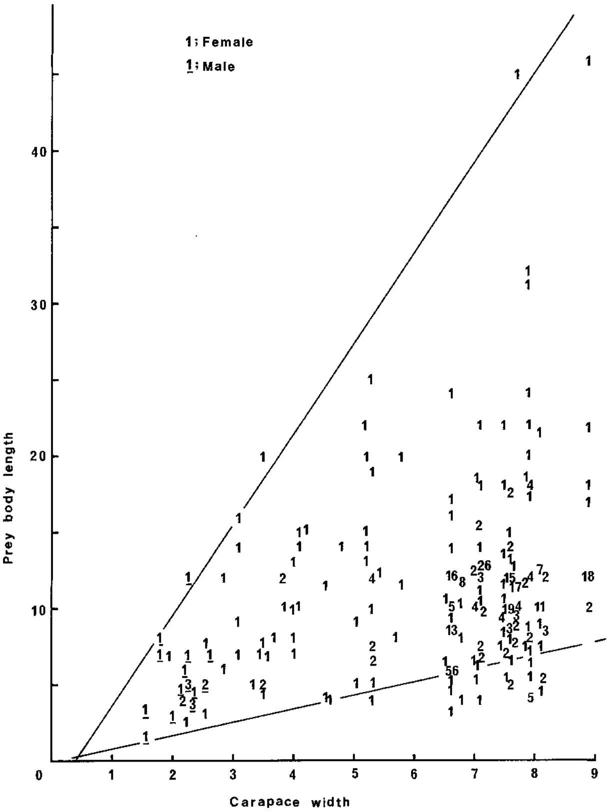

Fig. 8. The relationship between carapace width and prey body length. The two straight lines in the Figure are those in Fig. 5 (lower) and Fig. 7 (upper). The numbers in the Figure mean the number of prey animals

Discussion

Web spiders are truly polyphagous predators. Many workers have investigated the food habits of the web spider in field populations (Brown 1981; Buskirk 1975; Enders 1977; Kajak 1965; LeSar and Unzicker 1978; Nentwig 1980; Riechert and Tracy 1975; Robinson and Robinson 1970, 1973; Turnbull 1960; Uetz et al. 1978; Wise 1975, 1979) though studies of prey size are very restricted.

LeSar and Unzicker (1978) studied the small web spider *Tetragnatha laboriosa* (Tetragnathidae) and suggested that utilization of prey is essentially non-selective, except that heavy-bodied insects are totally excluded as prey. Nentwig (1980) studied the prey selectivity of seven species of sheet web spiders. He obtained the opposite result, i.e., the spiders select larger prey. However it is important to examine the components that determine prey size selection by spiders. Brown (1981) showed that *Argiope trifasciata* feeds preferentially on larger items, and that web radius, web height, and spider body length are important in prey size selection. In the present study, female *A. amoena* also ate larger items (Fig. 3), and when the spider was small, the prey size and its range were also small (Fig. 8). The largest prey were *Gastrimargus marmoratus* (45 mm) (Locustidae) and *Pantala flavescens* (46 mm) (Libellulidae). The body length of these insects coincides with the upper limit of prey size as determined by L-size. Enders (1975) stated that a congeneric web spider, *A. aurantia,* caught prey as large as twice its body length. In **A.** *amoena,* the body length was related to carapace width as $y = 2.64x + 0.22$ ($r^2 = 0.85$; n = 250). Therefore the upper limit approximately coincides with twice of the body length of *A. amoena.* Tibial length is one of the factors limiting prey size in the praying mantid *Hierodula crassa* Giglio-Tos (Holling 1964). The L-size is considered to be the effective length determining prey capture of *A. amoena.* Turnbull (1960, 1973) stated that some insects, for example Scarabaeidae, may be powerful enough to break through Linyphiidae webs. The prey difficulty must be discussed on the basis of relative size of prey and predator. Many scarabaeid insects of 10–24 mm in body length were found in the diet of *A. amoena* and were smaller than the upper limit.

In web spiders including two argiopid spiders, prey size was related to web mesh size (Uetz et al. 1978). Web mesh size seems to determine the lower limit of the prey size (Fig. 8). Smaller prey species than the lower limit pass through the web mesh. Turnbull (1960, 1973) and Nentwig (1980) pointed out that soft bodied, fragile, or wind-drifting insects are vulnerable to web capture. It was observed that small insects such as dipterans were sometimes caught on the web but not fed upon.

Many insects intermediate between the lower and upper limit of size were fed upon. Hymenoptera provide good examples, and among them, the honey bee *Apis cerana* was most abundant in the diet. Nentwig (1980) showed that pollinating insects, predators and parasites avoided the sheet web of seven species of linyphiid-like spiders. In contrast, *A. amoena* fed on many pollinating insects as well as predators and parasites. Even three species of pompilid wasp that usually hunt spiders were fed upon. The orb-web of *A. amoena* may be suited to capture these strongly flying insects as well as stout-bodied insects like scarabaeids. Some spiders temporarily fed on many winged ants. It seems that some ant nests were located near the web. Robinson et al. (1973) reported a similar incident, stating that the capture of ants probably coincided with the ant's nuptial flight.

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