

**Natural prey of the jumping spider *Menemerus semilimbatus* (Hahn, 1827) (Araneae: Salticidae), with notes on its unusual predatory behaviour**

**Естественная добыча паука скакунчика *Menemerus semilimbatus* (Hahn, 1827) (Araneae: Salticidae) с заметками о его необычном хищническом поведении**

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**ABSTRACT.** Prey composition and the hunting behaviour of the jumping spider, *Menemerus semilimbatus*, which inhabits stone walls was studied. Less than 10% of the specimens in the population studied were observed feeding. Adult males fed significantly less frequently than adult females and juveniles. Diptera, the dominant prey group, accounted for more than 70% of all prey consumed. No other single prey type was present in significant numbers. *M. semilimbatus* adopts a specialized predatory behaviour towards flies that is unusual for salticids. This behaviour depends on how the fly is orientated towards the spider. If the fly is facing away from the spider, *M. semilimbatus* approaches it directly. When the fly is facing the spider, *M. semilimbatus* keeps its distance and encircles it until the prey is facing away from the spider. Only then, will the spider start to approach the fly directly. The specific habitat of *M. semilimbatus* (stone walls), is characterized by a prevalence of Diptera, and was probably the crucial factor affecting the evolution of this unusual predatory behaviour in this species.

**РЕЗЮМЕ.** Изучался состав добычи паука скакунчика *Menemerus semilimbatus*, обитающего на каменном заборе. Доля питающихся особей в изученной популяции была низкой (< 10%). Взрослые самцы питались значительно реже, чем взрослые самки и неполовозрелые особи. Доминирующим типом добычи были Diptera, составляющие более 70% от всей добычи. Другие типы добычи были представлены в незначительном количестве. Примечательно, что *M. semilimbatus* использует специализированное хищническое поведение при охоте на мух, что нетипично для сальтицид. Это поведение зависит от ориентации мухи относительно паука. Если муха ориентирована задней частью своего тела относительно паука то *M. semilimbatus* приближается к ней по прямой линии. Когда же муха ориентирована передней частью тела к пауку, *M. semilimbatus* на дальней дистанции окружает ее до тех пор пока не окажется напротив задней части ее тела. Только после этого паук начинает приближаться по прямой линии. Специфическое местообитание *M. semilimbatus* (каменные стены), которые характеризуются преобладанием Diptera, по-видимому, является решающим фактором, обусловившим развитие необычного хищнического поведения у этого вида.

**KEY WORDS:** jumping spider, prey composition, predatory behaviour.

**КЛЮЧЕВЫЕ СЛОВА:** паук скакунчик, состав добычи, хищническое поведение.

## Introduction

Salticidae is the largest family of spiders, with nearly 5000 described species [Platnick, 2003]. The jumping spiders are characterized by a unique and highly developed visual system, which governs their peculiar and complex predatory behaviour. The salticid slowly creeps up to its prey until close enough for an attack, pauses, and then finally leaps at the prey [Richman & Jackson, 1991].

Recent studies have revealed a high diversity of predatory strategies in the Salticidae [e.g., Jackson & Pollard, 1996]. For some prey types salticids use highly specialized hunting behaviours, which differ from the standard technique. Prey specific predatory behaviour is especially pronounced in myrmecophagic and araneophagic jumping spiders, which specialize on ants and spiders respectively [Li & Jackson, 1996]. However, specialized prey-capture behaviours are observed with other prey types, although in a less pronounced manner [Edwards & Jackson, 1993].

Thus, the following question arises: why have some salticid species evolved specialized predatory techniques, while others have not? It seems reasonable to suggest that food resources available to a particular species in its environment might influence behavioural adaptations for catching specific prey. However, little is known about the natural prey of most jumping spiders. To my knowledge, the diets of only 11 salticid species have been studied quantitatively [Jackson, 1977, 1988a,b; Jackson & Blest, 1982; Dean *et al.*, 1987; Horner *et al.*, 1988; Young, 1989; Nyffeler *et al.*, 1990; Żabka & Kovac, 1996; Clark & Jackson, 2000; Bartos, 2002; Wesołowska & Jackson, 2003].

This paper studies the natural prey of the jumping spider *Menemerus semilimbatus* (Hahn, 1827), which is an epilitous species, occurring on cliffs, stony debris, fences and the external walls of buildings [Monterosso, 1958; Guseinov, in prep.]. This spider uses a specialized predatory behaviour towards flies. The behaviour of this species was not considered in recent reviews of predation in salticids [see Forster, 1982; Jackson & Pollard, 1996]. The main aim

of this study is to investigate the relationship between the predatory specialization of *M. semilimbatus* and its natural diet. The predatory behaviour of *M. semilimbatus* is described qualitatively, based on numerous field observations.

## Material and methods

The prey of *M. semilimbatus* were obtained from spiders inhabiting a stone wall in Mardakyan Village (Absheron Peninsula, Azerbaijan). Fifty-one surveys were conducted from 5 January to 27 December 1997 (on average once per week), which took approximately 93 hours in total. During each survey, the wall surface was thoroughly searched for *M. semilimbatus* and the mouthparts of each individual found were inspected using a lens of  $\times 4$  magnification, to prevent small prey being overlooked. Spiders with prey in their chelicerae were captured using a transparent cup, placed in separate vials containing 75% ethyl alcohol, and brought to the laboratory to identify the prey type (order) and to take body size measurements of both spider and prey. Spiders without prey were left in the field. The spiders collected were classified into the following groups: (1) adult males, which could be easily distinguished by their bicolour (black and white) palps (all other individuals of *M. semilimbatus* had white palps); (2) small juveniles, included all spiders less than 5 mm in length; (3) large juveniles and females, included all specimens larger than 5 mm, with white chelicerae. During most of the surveys (but not all) the numbers of individuals with and without prey were counted separately for each of these groups. Additionally, several prey items were collected during non-quantitative observations on the same wall. There was a food refuse dump near one end of the wall, which had a significant influence on the composition of the arthropod fauna inhabiting the adjacent part of the wall. Thus, observations made in this region (site B) were analyzed separately from the rest of the wall (site A).

Observations on the predatory behaviour of *M. semilimbatus* were made on a barn roof and an adjacent stone wall in my backyard in Mardakyan Village, between 1990 and 1996.

During this period I observed thousands of individuals of *M. semilimbatus* and witnessed many incidences of predation by these spiders.

## Results

### Feeding rate

A total of 1 157 observations of *M. semilimbatus* individuals was made during the study period; 774 in site A and 383 in site B. Fifty-one spiders were found with prey in site A (6.6%), and 45 in site B (11.7%). The difference in the percentage of feeding specimens between the two sites is significant ( $\chi^2 = 8.301$ ;  $df = 1$ ;  $P < 0.01$ ). In both sites, adult males fed significantly less frequently than juveniles and adult females; five males with prey from 219 observations (2.3%) vs. 45 juveniles and females with prey from 541 observations (8.3%) in site A ( $\chi^2 = 8.282$ ;  $df = 1$ ;  $P < 0.01$ ), and one male with prey from 97 observations (1.0%) vs. 26 juveniles and females with prey from 219 observations (11.9%) in site B ( $\chi^2 = 8.771$ ;  $df = 1$ ;  $P < 0.01$ ). In contrast, there was no significant difference in feeding rate between small juveniles and large juveniles and females; 17 small spiders with prey from 270 observations (6.3%) vs. 28 large spiders with prey from 271 observations (10.3%) in site A ( $\chi^2 = 2.384$ ;  $df = 1$ ;  $P > 0.1$ ), and 11 small spiders with prey from 67 observations (16.4%) vs. seven large spiders with prey from 84 observations (8.3%) in site B ( $\chi^2 = 1.614$ ;  $df = 1$ ;  $P > 0.1$ ).

### Prey composition

Seven prey items were lost whilst capturing the spiders. However, six additional prey items were collected during non-quantitative surveys. Thus, 95 prey items were included in the analysis (49 from site A and 46 from site B). These were distributed among eight arthropod orders; seven from the class Insecta and one from the class Arachnida (Table). Spiders observed near the food refuse dump captured representatives of only three orders, while those observed on the rest of the wall caught representatives of seven orders.

The dominant prey order was Diptera, which constituted over half of the total prey records

Table.  
Prey composition of *Menemerus semilimbatus*.

Таблица.  
Состав добычи *Menemerus semilimbatus*.

Prey order	Site A		Site B		Total	
	N	%	N	%	N	%
Diptera	28	57.1	43	93.5	71	74.7
Araneae	9	18.4	1	2.2	10	10.5
Lepidoptera	6	12.2	—	—	6	6.3
Homoptera	3	6.1	—	—	3	3.2
Hymenoptera	—	—	2	4.3	2	2.1
Thysanoptera	1	2.0	—	—	1	1.1
Ephemeroptera	1	2.0	—	—	1	1.1
Collembola	1	2.0	—	—	1	1.1
<b>Total</b>	<b>49</b>	<b>100.0</b>	<b>46</b>	<b>100.0</b>	<b>95</b>	<b>100.0</b>

from site A and more than 90% from site B. Most of the dipterans captured in site A were brachycerans (71.4%). In contrast, in site B nematoceran prey constituted the majority (55.8%), although brachycerans were also caught in considerable numbers (44.2%). Scatopsidae were the nematocerans eaten most frequently in site B, whereas in site A, Psychodidae were the dominant nematoceran prey. Among brachyceran prey, the Muscidae and Calliphoridae predominated. Other insect prey included Lepidoptera (five moths and one caterpillar), Homoptera (two aphids and one Coccinea male), Hymenoptera (one winged ant and one Apocryta) and one representative each of Thysanoptera, Ephemeroptera and Collembola.

Spiders (Araneae) were the second most abundant prey order in the diet of *M. semilimbatus* (10.5%). They were represented by individuals of six species from four families. Salticidae were the most common (50% of all spiders killed), followed by Theridiidae (20%), Philodromidae (10%), Filistatidae (10%) and an unidentified family (10%). Three cases of cannibalism were observed; one adult male of *M. semilimbatus* killed a juvenile, and in two other cases larger juveniles fed on smaller ones.

### Prey length

Eighty-three prey items were measured. Their length varied from 0.60 to 10.00 mm (mean  $\pm$  SD:  $3.79 \pm 2.30$ ) and represented a range of 12.0 to 228.6% ( $72.3 \pm 42.1$ ) of the size of their captors, whose length ranged from 2.25 to 9.50 mm ( $5.51 \pm 1.78$ ). The frequency of prey in relation to their length is shown in

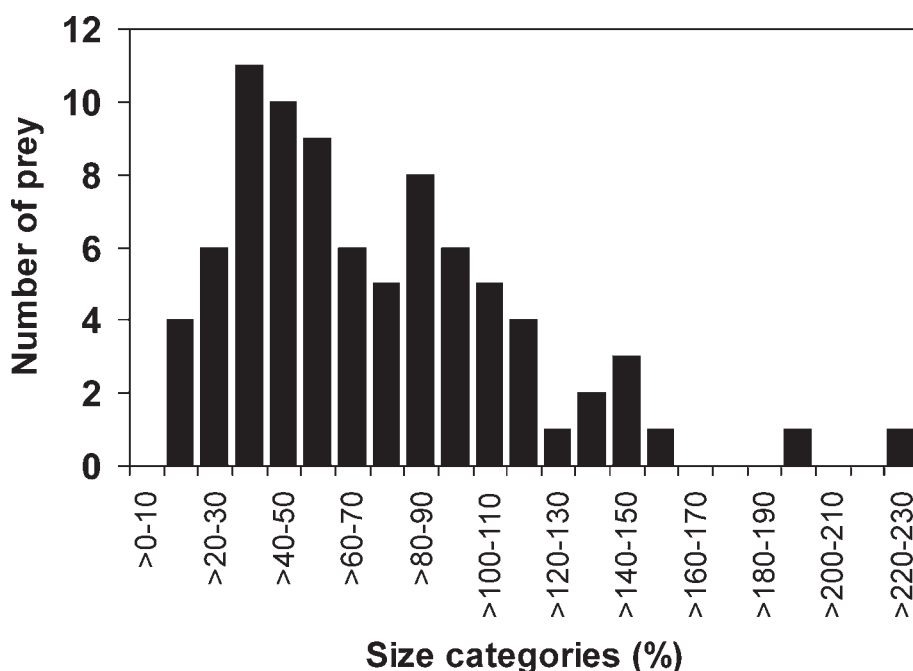


Fig. 1. Frequency of prey size of *Menemerus semilimbatus*.

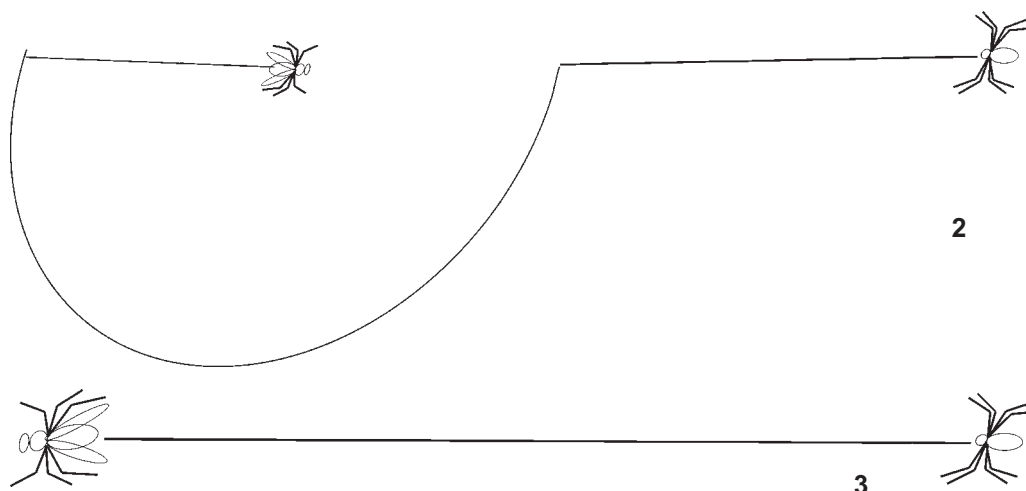
Рис. 1. Распределение добычи *Menemerus semilimbatus* по размерным классам.

Fig. 1. The most common were medium-sized arthropods (from 50 to 100% of spider body length), which accounted for 41.0% of the total prey measured. Small prey, less than half the size of the spiders, were present in a similar proportion (37.3%). Approximately one-fifth of the prey of *M. semilimbatus* (21.7%) consisted of large prey, which exceeded the size of the spiders. Most of these did not exceed 150% of their captor's length and only three were larger.

### Predatory behaviour

While hunting most kinds of arthropods *M. semilimbatus* adopted the typical predatory sequence of jumping spiders, which consists of three basic functional categories as described by Forster [1977]: (1) orientation: *M. semilimbatus* responded to the prey from a long distance (up to 1 m) by pivoting around to face their target; (2) pursuit: advancing towards the prey in a straight line with gradually decreasing speed; (3) attack: when the spiders were a few centimeters away from their prey, they paused, attached a drag-line to the substrate and then leapt on and seized their victims.

However, with flies *M. semilimbatus* used a different hunting behaviour. It differed from the standard technique by using a complicated pursuit behaviour, which consisted of three distinct phases (Fig. 2). The first phase, 'preliminary approach', was most similar to the typical pursuit of salticids with the only difference being that it ceased at a much further distance from the prey. If the spider was initially orientated towards the rear part of fly's body, then the preliminary approach was similar to the typical pursuit and ended in attack (Fig. 3). However, when the spider was orientated towards any other part of the fly's body, there was an incomplete pursuit (i.e., the preliminary approach). Then *M. semilimbatus* embarked upon the next phase, 'circling'. At a distance of approximately ten body lengths from the fly, the salticid began to circle the prey moving laterally until it faced the rear part of fly's body. When this position was achieved the spider proceeded to the third phase, 'orientated approach'. *Menemerus* again moved directly towards the fly, but more slowly than during the preliminary approach. The characteristic peculiarity of this



Figs 2–3. The pursuit route of *Menemerus semilimbatus* towards a fly: 2 — when the fly is facing the spider; 3 — when the fly is facing away from the spider.

Рис. 2–3. Маршрут преследования мухи *Menemerus semilimbatus*: 2 — когда муха ориентированна задней частью своего тела по отношению к пауку; 3 — когда муха ориентированна передней частью своего тела по отношению к пауку.

phase is that it was performed only towards specifically orientated flies. If a fly changed its position during the orientated approach then *M. semilimbatus* ceased this phase and began to circle the prey again. Moreover, before resuming their circling behaviour most spiders moved back from flies thereby increasing the predator–prey distance. The transitions between the different phases in this general predatory sequence of *M. semilimbatus* were distinct. The movements of the spiders during these various phases differed in speed and/or direction. Therefore, one can conclude that unlike typical salticids, the predatory sequence of *M. semilimbatus* consists of five distinct functional categories: orientation, preliminary approach, circling, orientated approach and attack.

## Discussion

The percentage of feeding individuals of *M. semilimbatus* on the majority of the wall (site A) was low (6.6%). The significantly higher rate of prey capture in the site near the food refuse dump was because the decaying organic waste provided a very favourable environment for various dipterans which reached high densities in this site. The low feeding rate is charac-

teristic of other salticids, e.g., *Pelegrina galathea* (Walckenaer, 1837) and *Phidippus audax* (Hentz, 1845) [Dean *et al.*, 1987; Young, 1989]. Jackson [1977] reported a much lower value (0.4%) for *Phidippus johnsoni* (Peckham et Peckham, 1883). However, most of the spiders he observed occupied nests under stones and were not involved in foraging activity. Given only individuals found in open places, a higher rate of prey capture would be expected for *P. johnsoni*, comparable to that of other salticids. Yet, Jackson [1977] observed that all spiders with prey were females and juveniles, and that no males caught prey, despite the fact that most were active. Likewise, in laboratory experiments on the feeding behaviour of *Phidippus audax*, Givens [1978] found that males fed less frequently than females. Both authors attributed their observations to the lifestyle of salticid males, which has mating as the highest priority, such that they feed opportunistically only when they encounter prey directly. In contrast, females and juveniles, which need a high intake of food for yolk production and growth respectively, spend much of their time searching or waiting for prey. My findings are consistent with this idea. The percentage of feeding male specimens of *M. semilimbatus* was signif-

icantly lower than that of females and juveniles. This tendency was similar both in the site with high prey availability and in the site with low prey availability.

*M. semilimbatus* is a polyphagous predator, which feeds on a wide range of arthropods. The predominance of Diptera in its diet is apparently due to the peculiar habitat of this spider. The stone walls are poor environments with limited food resources and extreme microclimatic conditions. Relatively few groups of arthropods are adapted to this habitat. Synanthropic flies that use the wall surfaces as resting sites are one of the most abundant components the local entomofauna [Klausnitzer, 1990]. Other abundant inhabitants of the stone wall were various species of jumping and web-building spiders. Therefore, it is not surprising that spiders constituted the second most abundant prey type in the diet of *M. semilimbatus*. Most spiders captured were typical wall dwellers, such as *Salticus mutabilis* Lucas, 1846, *Philaeus chrysops* (Poda, 1761), *Theridion melanurum* Hahn, 1831, *Filistata insidiatrix* (Forskål, 1775) and conspecifics, suggesting that the migration of arthropods from adjacent habitats (e.g., vegetation or ground litter) may be limited. Despite the fact that web-building spiders were quite abundant on the wall, they were rarely captured by *M. semilimbatus*. In all the cases that they were caught, they were consumed away from their webs. In one instance the prey was a male of *F. insidiatrix*, which might have been captured while searching for a female. Two other records were sub-adult females of *T. melanurum*. In fact, *M. semilimbatus* was never observed on the webs of other spiders. Instead, when it encountered webs, *M. semilimbatus* steered a wide path around their perimeter, thereby avoiding contact with the silk. Ants of the genus *Crematogaster*, were also very common on the wall. However, despite frequently watching passing worker ants, *M. semilimbatus* avoided attacking them. The only ant captured by *M. semilimbatus* was a winged one.

Experimental study of prey size preference in spiders has shown that most cursorial spiders, including salticids, do not accept prey exceeding 150% of their own body length. The preferred prey size tends to be equal to or less

than the size of the spider [Nentwig & Wissel, 1986]. My findings agree with this generalization. Most of the prey of *M. semilimbatus* (c. 80%) were smaller than the spiders, while those larger than their captors usually did not exceed 150% of the spider's length. It is likely that the largest prey of *M. semilimbatus* (in terms of prey/predator size ratio) was scavenged by the spider. It was a large blowfly consumed by a small juvenile and it did not look like fresh prey. Indeed, on several occasions I have observed *M. semilimbatus* attacking and attempting to ingest dead, dry flies.

Field observations indicate that *M. semilimbatus* is a versatile predator, which adopts different predatory behaviours towards flies and other prey. The specialized predatory technique used against flies is probably a modification of the standard prey-capture technique. The best evidence for this is that when a fly is initially orientated with the rear part of its body towards the spider, the salticid's predatory behaviour does not differ from the typical pattern. This also suggests that the major function of the specialized hunting behaviour of *M. semilimbatus* is to allow a specifically orientated approach to the prey.

Orientation movements during the pursuit of prey also occur in myrmecophagic salticids and in spiders of the genus *Phidippus* when they hunt caterpillars [Edwards & Jackson, 1993; Li & Jackson, 1996]. The main difference between the behaviours of these spiders and *M. semilimbatus* is that the former attack the prey on a particular part of the body, while the latter selects a specific direction from which to approach the prey. That is, unlike *Menemerus* other salticids circle their prey just prior to attacking them. The circling arc in these spiders is small and usually poorly discernible from other manoeuvres during pursuit. Thus the predatory behaviour of *Phidippus* is a subtle form of specialization [Edwards & Jackson, 1993]. In contrast, the predatory sequence of *M. semilimbatus* differs discernably from the standard technique and the degree of specialization is comparable to that of the araneophagic and myrmecophagic jumping spiders. In ant-eating salticids, striking modifications of predatory behaviour occur in orientation ('sudden activa-

tion') and attack ('stab-and-release technique') phases [Li & Jackson, 1996].

The literature data suggest that specialized hunting behaviour in Salticidae have evolved to overcome well-defended, dangerous prey, such as web-building spiders or worker ants [Jackson & Pollard, 1996]. Thus, it is interesting to speculate about why *M. semilimbatus* has evolved a specialized technique against flies, which are common prey for most spiders. Although flies present no hazard for *M. semilimbatus*, they can be considered difficult prey to catch. Spiders cannot rapidly chase flies because of their ability to fly. To catch such a prey *Menemerus* needs to stalk it carefully. However, flies have good eyesight and quickly detect even slow-moving predators. Finally, the open and brightly lit surfaces of walls make the spiders' task difficult by reducing their concealment.

To some extent similar problems face the araneophagic salticid *Portia fimbriata* (Dole-schall, 1859) when hunting other jumping spiders. Although salticids do not appear to be a dangerous prey for *Portia*, they have acute vision and are much more mobile than their pursuers. Apparently, like flies for *Menemerus*, salticids are difficult to catch for *Portia* [Li & Jackson, 1996]. To prevent this prey with a well-developed visual system from recognizing them as predators, *Portia* uses an unusually slow and mechanical gait, exaggerated by its general unanimal-like appearance, such that the predator resembles a piece of detritus blown by a gentle breeze [Jackson & Blest, 1982].

*M. semilimbatus* lacks a pronounced cryptic appearance, nor does it use a specific mode of locomotion. Instead, *M. semilimbatus* has adopted another way to approach the prey without being detected. Spiders choose a route of pursuit, which maximally reduces the probability of being detected by prey with good vision. Such a route involves approach from the rear. Thus, the specialized approach of *M. semilimbatus* may have evolved as a means of avoiding detection while approaching mobile prey with high visual acuity.

The key to understanding the evolution of predatory behaviour in *M. semilimbatus* is its habitat. As the present investigation has shown,

this habitat influences the predominance of flies among the prey of *M. semilimbatus*. At the same time, as discussed earlier, peculiarities of wall relief makes them unfavorable environments for hunting visually acute insects. On the other hand, the two-dimensional, flat surface of a wall enables spiders to choose any route of approach to the prey. Such behaviour would be impossible in a more complex and heterogeneous environment. For example, salticids occurring in arboreal habitats usually have no opportunity to approach the prey even by a simple direct path and frequently have to use opportunistic detour routes [Hill, 1979; Forster, 1982]. The combination of these factors related to habitat, influenced the evolution of this unusual predatory behaviour observed in *M. semilimbatus*.

*Menemerus* is a large genus with approximately 70 described species [Platnick, 2003]. However, little is known about their ecology and behaviour. Some African species were reported to be communal, living in large nest complexes [Jackson, 1986, 1999]. *Menemerus bracteatus* (L. Koch, 1879) from Australia builds nests under the bark of eucalypt trees and also exhibits some degree of sociality [Rienks, 2000]. The scarce data on habitats of some solitary *Menemerus* indicate that they commonly occur on cliffs, fences and external walls of buildings [Bhattacharya, 1936; Rakov & Logunov, 1996; Guseinov, in prep.], suggesting that these species might also use a specialized predatory behaviour towards flies. In light of this, the brief note by Bhattacharya [1936] on *Menemerus bivittatus* (Dufour, 1831) (cited as *Marpissa melanognathus*) is worthy of inclusion: "Their mode of capturing flies is marvelously skilful. The spider stalks the fly from a distance of about two feet or more. A fly is sitting on the floor, the spider advances towards it slowly, when close, it moves with still greater caution. It approaches still closer; if it finds the fly facing it; the spider changes its course and moving backwards in a wide circle approaches the fly from behind. It then crawls towards the prey and, when in easy reach, jumps on it". This brief description corresponds completely with my observations on the predatory behaviour of *M. semilimbatus*. Bhattacharya was probably

the first and, as far as I am aware, the only arachnologist who noted this peculiar type of hunting behaviour in jumping spiders. Laboratory investigations of various *Menemerus* species are required to establish whether this behaviour is characteristic of the genus and to clarify the details of this unusual predatory technique.

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