Predatory Behavior of *Meta reticuloides* YAGINUMA (Araneae : Tetragnathidae)

Makoto YOSHIDA¹⁾

吉田 真¹⁾: ヤマジドヨウグモの捕食行動

Abstract: The predatory behavior of *Meta reticuloides* YAGINUMA was studied, and the natural prey of the species were collected from its webs. This species employed four predatory sequences, seize-pull out, bite-pull out, bite-wrap and wrap-bite. Wrap-bite sequence, not observed in *Metleucauge* (YOSHIDA, 1989a), was employed to ants, stink bugs, a large crane fly, bees and wasps, which may be large and/or potentially dangerous prey for *M. reticuloides*. Attack-wrapping was occurred after prey-touching by legs I (and palps?). The prey, which were entangled with the sticky spirals of the webs, were sometimes carried by pulling from the hub, using legs I and II. "Pulling the prey from the hub" is not observed in *Metleucauge* (YOSHIDA, 1989a). The ability of attack wrapping of *M. reticuloides* remains probably because it sometimes captures large and/or potentially dangerous prey.

Meta and the related genera have many primitive morphological characters, and resemble some genera of Theridiidae, a family of Araneoidea (LEVI, 1980). So these genera can be regarded as a primitive group of Araneidae (LEVI, 1980: He included Tetragnathidae in the Araneidae at that time), or of Tetragnathidae (LEVI, 1986: He divided Araneidae again into two families, Araneidae and Tetragnathidae, with the latter including *Meta* and the related genera). Of these genera, *Metleucauge* does not use immobilization wrapping at all, but immobilizes their prey only by biting (YOSHIDA, 1989a). It is probably a primitive character in spiders as a whole, but may be a derived character within Araneidae-Tetragnathidae (that is, the ancestor of these families could probably perform immobilization wrapping). If the lack of immobilization wrapping is a primitive behavioral character (EBERHARD, 1967: ROBINSON *et al.*, 1969), we would be able to state that *Metleucauge* has both morphological and behavioral primitive characters.

I report here on the predatory behavior of *Meta reticuloides*. This species, in contrast to *Metleucauge*, sometimes uses immobilization wrapping. I compare the predatory behavior of this species with that of *Metleucauge*, and discuss the evolution of the predatory behavior in Metinae.

1) Department of Biology and Geology, Faculty of Science and Engineering, Ritsumeikan University, Kyoto, 603 Japan

立命館大学 理工学部 生物地学教室

Materials and Methods

The investigation was done in 1987 at Mt. Kiyosumi in Chiba Prefecture, and in 1987–1989 at Mt. Hiei in Kyoto City. *M. reticuloides* matured in autumn, made their horizontal orb-webs at damp cliffs or above mountain streams. I observed the predatory behavior of the adult females (6–9 mm in body length) both with natural prey and with the fairly large prey given by me for several hundred hours. The latter prey was collected using a sweep-net near the study area. The observation on the predatory behavior in a web was done less than twice in order to avoid the satiation of spiders. The body length of both the spiders and the prey was estimated by eye. Natural prey captured in the webs were collected, identified in the laboratory, and their body length was measured.

Results

1. Predatory behaviors

The following behaviors were observed in the context of predatory sequences. They can be divided into two groups as follows:

A) The behaviors observed also in *Metleucage* (YOSHIDA, 1989a)

Jerking: This consists of a rapid pulling of the radii with the first pair of legs. But, *M. reticuloides* jerked less often than *Metleucauge* (I observed the behavior only several times in *M. reticuloides*).

Approach to prey: Running or walking from the hub to the capture site along the radial thread(s).

Touch: Repeated touching or tapping of the prey with legs I (and palps?) before prey immobilization. But, as shows later, touching occurred in both unsuccessful and successful prey capture sequences, different from *Metleucage* (YOSHIDA, 1989a).

Seizing in jaws: Seizing and holding the prey in the chelicerae.

Biting: Biting the prey with the chelicerae. The jaws are used in “seizing” and “biting”, but the time required for “seizing” was very short, whereas the time required for “biting” was several times longer than that for seizing. So, I intend to distinguish “seizing” from “biting”. Biting was used not only to immobilize the prey but also after prey-immobilization.

Wrapping: *M. reticuloides* used wrapping not only after prey immobilization (post immobilization wrapping: observed also in *Metleucauge*: YOSHIDA, 1989a) but also to immobilize the prey (immobilization wrapping). Wrapping after prey immobilization occurred at three sites: at the capture site, during transportation to the hub, and at hub itself. *M. reticuloides* was different from *Argiope argentata*, because it never rotated the prey around a radius while wrapping (“rotisserie” wrapping of EBERHARD, 1982).

Pulling out: Pulling the prey from the web, using the jaws.

Cutting out: Cutting the web in order to remove the prey from the web.

Carrying on silk: Carrying the prey to the feeding site, suspended on a silk line from the spinnerets.

B) The behaviors not observed in *Metleucauge*

Waiting (Hesitating): *M. reticuloides* often showed the behavior. For example, the spider ran to the prey, but did not attack it soon, as if the spider could not know whether it was a dangerous prey or not, and she could not decide whether she should attack it or not. Waiting (Hesitating?) were observed mainly if the prey was ants, and occurred in several contexts of predatory sequences, such as before immobilization biting, between immobilization biting and post immobilization wrapping, or between immobilization wrapping and cutting out of the web.

Pulling from the hub: Pulling the immobilized prey by legs I (and II?) from the hub. This behavior was mainly observed if the prey was entangled with the viscid spirals of the web in the process of transportation suspended on a silk line.

2. Predatory sequences employed

Four predatory sequences (Seize-Pull out, Bite-Pull out, Bite-Wrap, Wrap-Bite) were observed.

Seize-Pull out (SP): Spiders ran to the prey, seized it in the jaws and pulled it from the web. Spiders then carried the prey in the jaws to the hub. In most cases, spiders returned by dropping from the web, hanging with the dragline attached to the hub, and then climbed quickly to the hub along the dragline (“drop and climb up” behavior).

Bite-Pull out (BP): This sequence resembles SP, the above sequence, but it includes the behavior unit “biting”. Spiders usually bit some parts of a large prey first for a fairly long time (more than several seconds), and then they changed the biting sites successively. As a result, the prey was crushed gradually into a ball. Then the spider pulled it from the viscid spirals with the jaws. The prey were carried either by “drop and climb-up” mentioned above, or carrying along a radial thread.

Bite-Wrap (BW): The prey were immobilized by “biting”. After immobilization biting, spiders first wrapped the prey with silk usually while it was still in the jaws. Then they wrapped further after releasing it from the jaws. Then spiders cut out all the entangling silk lines, in order to remove the prey from the web. In most cases, the prey were carried to the hub suspended on a silk line, but in some cases, the prey were entangled with spirals and radii on the way to the hub, then spiders pulled the prey from the hub, using their legs I. Spiders sometimes carried the prey by “drop and climb-up”.

Wrap-Bite (WB): The prey were immobilized by “wrapping”, and then spiders usually bit the prey for more than 10 seconds. Cutting out the web and carrying method was as same as “Bite-Wrap” sequence.

3. Frequency of sequences and efficiency of predation with different types of prey

M. reticuloides captured 61.4% of the prey restrained by the web (Table 1). Diptera and Lepidoptera were captured effectively. On the contrary, Orthoptera was captured only once.

Table 1 Frequency of attack sequences with different types of prey of *Meta reticuloides*.

Prey type	Attack sequences employed				Total prey captured (%)	Total prey not captured (%)
	Seize-Pull out	Bite-Pull out	Bite-Wrap	Wrap-Bite		
Diptera	4	5	33	1	43(93.5)	3(6.5)
Hemiptera						
Stink bugs	0	0	7	2	9(45.0)	11(55.0)
Leafhoppers	0	0	4	0	4(57.1)	3(42.9)
Hymenoptera						
Ants	0	0	6	7	13(36.1)	23(63.9)
Bees & Wasps	0	1	2	4	7(46.7)	8(53.3)
Lepidoptera	1	0	8	0	9(100.0)	0(0.0)
Orthoptera	0	0	1	0	1(14.3)	6(85.7)
Total	5	6	61	14	86(61.4)	54(38.6)

Of four attack sequences, Bite-Wrap was most frequently used (70.9% of the captured insects). Leafhoppers, Lepidoptera and Orthoptera were not immobilized by wrapping at all, on the contrary, 55.5% of Hymenoptera were captured by Wrap-Bite sequence. There are statistically significant differences in the frequency of sequences employed between Hymenoptera and the other three orders (χ^2 -test: $<P(0.001)$ between Hymenoptera and Diptera, $<P(0.05)$ between Hymenoptera and Hemiptera, and $<P(0.02)$ between Hymenoptera and Lepidoptera). On the contrary, there is not statistically significant difference among Diptera, Hemiptera and Lepidoptera.

Fig. 1 shows the relation between the relative body length (prey/spider) and the sequences employed. In the capture of Diptera, the sequences seemed to be dependent on prey size. The spider employed Bite-Pull out and Bite-Wrap mainly to smaller Diptera, on the contrary, employed Bite-Wrap mainly to larger Diptera (χ^2 -test: $<P(0.02)$, calculated by Table 2).

But, all of the Lepidoptera were captured by Bite-Wrap sequence, regardless of the relative body size of the prey (Fig. 1). And in the capture of Hymenoptera, it was not dependent on relative prey size whether the prey was captured by biting attack or wrapping one (χ^2 -test:

Fig. 1 Frequency of attack sequences in relation to prey size. Relative body length means the ratio of the body length of prey to that of spider. Dip: Diptera, Sti: stink bugs, Lea: leaf hoppers, Ant: ants, B&W: bees and wasps, Lep: Lepidoptera, Ort: Orthoptera, NC: the prey was not captured by the spider, SP: Seize-Pull out, BP: Bite-Pull out, BW: Bite-Wrap, WB: Wrap-Bite.

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Table 2 Relation between the frequency of attack sequences and the relative prey size, in the capture of Diptera.

	Relative body length (prey/spider)			Total
	0-0.5	0.5-1.0	1.0-	
Seize-Pull out & Bite-Pull out	5	3	1	9
Bite-Wrap	0	13	20	33

Table 3 Relation between the frequency of attack sequences and the relative prey size, in the capture of Hymenoptera.

	Relative body length (prey/spider)			Total
	0-0.5	0.5-1.0	1.0-	
Bite-Pull out & Bite-Wrap	4	4	1	9
Wrap-Bite	7	3	1	11

<P(0.90), calculated by Table 3).

Fig. 2 shows the details in the process of prey immobilization by spiders. *M. reticuloides* approached almost all prey restrained by the web (136/140=97.1%). Then, spiders attacked their prey using the jaws ([5+62]/136=49.3%), or returned to the hub after the trial to bite the prey, leaving it at the capture site (3/136=2.2%), or returned to the hub (5/136=3.7%), or touched their prey probably because to get more informations about them (61/136=44.9%). The prey bitten were pulled from the web with the jaws or wrapped with silk. The half of the spiders which touched the prey returned the hub, leaving them at the capture site (30/61=49.2%). Of the spiders which touched the prey, 11.5% (7/61) attack-bit their prey, and 16.4% (10/61) returned to the hub, or attack-bit, or attack-wrapped, after the trial to bite. 14.8% (9/61) attack-wrapped them and 6.6% (4/61) hesitated to attack the prey probably because the spider could not get enough informations about them. In one case (1/61=1.6%) the prey, an ant, bit the leg I of the spider when the latter touched the former. The spider shook itself from the ant, and escaped to the hub.

Table 4 shows the relation between whether prey-touching occurred or not and which sequences were employed. Seize-Pull out and Bite-Pull out always occurred without prey-touching, on the contrary, Wrap-Bite always occurred after prey-touching. Bite-Wrap was used both

Fig. 2 Response of spiders to the 140 prey insects restrained by the web. Arrows show the chain between two behavioral units. Solid and broken arrows show successful attack sequences and unsuccessful attack sequences, respectively. Numerals and the breadth of lines show the frequency. The lines drawn under the behaviors (Seizing in jaws, Bite, Wrapping) show that they were used in order to attack their prey. Bite-Wrap sequence and Wrap-Bite one are shown by Bite* → Wrap* and Wrap* → Bite*, respectively.

without touching and after touching. But, Bite-Wrap and Wrap-Bite, different from Seize-Pull out and Bite-Pull out, occurred in various contexts of the prey capture process, shown in Fig. 2.

Table 5 shows that the percentage of prey captured without prey-touching is high in Lepidoptera and Diptera. On the contrary, that percentage is low in Hymenoptera. There are statistically significant differences in the frequency of prey capture without or after prey-touching between Hymenoptera and the other three orders (χ^2 -test: $<P(0.001)$ between Hymenoptera and Diptera, $<P(0.05)$ between Hymenoptera and Hemiptera, $<P(0.001)$ between Hymenoptera

Table 4 Frequency of prey-touching behaviour after the spider approached the prey.

	Attack sequences employed				Not captured	Total
	Seize-Pull out	Bite-Pull out	Bite-Wrap	Wrap-Bite		
Spider touched the prey	0	0	8	14	39	61
Spider did not touch the prey	5	6	53	0	11	75
Total	5	6	61	14	50	136

Table 5 The number and percentages of the prey captured by spiders without and after prey-touching.

Prey type	Prey captured		Percent of prey captured
	Without touching (%)	After touching (%)	
Diptera	38(88.4)	5(11.6)	93.5
Hemiptera			
Stink bugs	5(55.6)	4(44.4)	45.0
Leafhoppers	4(100)	0(0)	57.1
Hymenoptera			
Ants	4(30.8)	9(69.2)	36.1
Bees & Wasps	2(28.6)	5(71.4)	46.7
Lepidoptera	9(100)	0(0)	100.0
Orthoptera	1(100)	0(0)	14.3
Total	63(73.3)	23(26.7)	61.4

and Lepidoptera).

4. Frequency of carrying methods in relation to prey size and to attack sequences

Table 6 shows the frequency of carrying methods in relation to the relative prey size. "Carrying in jaws" was used apparently to smaller prey than "Carrying with silk" and "Carrying with silk and Pulling from hub", though the ranges overlapped (χ^2 -test: $<P(0.001)$). This species sometimes left its prey at the capture site.

Table 7 shows the relation between attack sequences and carrying methods. In the case of "Seize-Pull out" and "Bite-Pull out", all the prey were carried in the jaws. This means that "pull out the prey from the web" always results in "Carrying in jaws". In the case of "Bite-Wrap" and "Wrap-Bite", various carrying methods were used, though "Carrying with Silk" was most frequently used. "Leaving Prey at Capture Site" occurred also in the case of "Bite-Wrap" and "Wrap-Bite".

Table 6 Frequency of carrying methods in relation to the relative prey size. CwS and PfH: Carrying with Silk and Pulling from Hub. See the text in detail. Leaving the Prey: Leaving the prey at the capture site.

Carrying methods	Relative body length (prey/spider)								Total
	0-0.5	-1.0	-1.5	-2.0	-2.5	-3.0	-3.5	-4.0	
Carrying in jaws	12	9	2	0	0	0	0	0	23
Carrying with silk	2	23	6	5	2	1	0	0	39
CwS and PfH	0	2	0	1	2	1	0	1	7
Leaving the prey	4	2	0	0	0	0	0	0	6
Total	18	36	8	6	4	2	0	1	75

Table 7 Relation between attack sequence and carrying method. CwS & PfH: Carrying with Silk and Pulling from Hub.

Attack sequence employed	Carrying method			Leaving prey at capture site	Total
	In jaws	With silk	CwS & PfH		
Seize-Pull out	5	0	0	0	5
Bite-Pull out	6	0	0	0	6
Bite-Wrap	7	35	6	3	51
Wrap-Bite	5	4	1	3	13
Total	23	39	7	6	75

5. The prey collected in the webs of *M. reticuloides*

Table 8 shows the prey collected between August and October in the webs of *M. reticuloides*. Though the number of prey collected was very small, main prey was apparently small Diptera. All the dipteran insects belonged to Nematocera.

Table 8 Natural prey of *Meta reticuloides*. The prey were collected from the webs.

Prey type	Body length of prey in mm			Total
	0-1.5	1.5-3.0	3.0-	
Diptera	70	6	4	80
Ephemeroptera	0	0	2	2
Hemiptera (winged aphid)	1	0	0	1
Lepidoptera (larva)	0	0	1	1
Unidentified	0	1	1	2
Total	71	7	8	86

Discussion

M. reticuloides employs four predatory sequences, Seize-Pull out, Bite-Pull out, Bite-Wrap and Wrap-Bite. Which sequence the spider employs depends partly on the kind of prey, and partly on prey size. For example, leafhoppers are always immobilized by Bite-Wrap sequence (though the data is fragmentary), Diptera and Lepidoptera are also immobilized mainly by Bite-Wrap. It is worthy of notice that Lepidoptera and Diptera restrained by the webs are captured effectively, and that these insects are captured almost without prey-touching. The prey collected in the webs of *M. reticuloides* consists mainly of small Diptera such as midges. So, small nematoceros flies are apparently main prey of *M. reticuloides*. As Lepidoptera was not collected in the webs of the spiders, so it seems not to be the prey of *M. reticuloides*. But, I collected the prey insects mainly in daytime, nocturnal moths may be sometimes captured by the spiders. So, whether Lepidoptera is the main prey or not, is to be investigated in future.

Though *M. reticuloides* makes its webs in various habitats, I collected the prey in the webs of *M. reticuloides* made mainly above mountain streams, because the density of the webs there was far higher than in other habitats such as damp cliffs. Nematoceros flies, especially midges, are also main prey of *Metleucauge* above mountain streams (YOSHIDA, 1989a). So, nematoceros flies seem to be the common main prey for the species whose web is made above mountain streams. At damp habitats apart from mountain streams, the prey items may be

different from them above mountain streams. For example, moths, winged ants, or winged aphids may be captured, as often observed in the webs of *Leucauge magnifica* (YOSHIDA, unpublished data).

Orthoptera may be not a normal prey of *M. reticuloides* because of the low capturing efficiency. Stink bugs, (wingless) ants, bees and wasps may also be not normal prey of *M. reticuloides*, because of the low capturing efficiency and of the frequent use of prey-touching. Attack-wrapping was used against ants, bees and wasps, stink bugs and a large diptera. It may suggest that attack-wrapping is used against unfamiliar and/or large prey.

LEVI (1980) divided *Meta* into three genera, *Meta*, *Metellina* and *Metleucauge*. There are three species of *Metleucauge* and two species of *Meta* in Japan (YAGINUMA, 1986). There are three major differences between the attack behavior of *M. reticuloides* and that of three Japanese species of *Metleucauge* as follows: 1) *M. reticuloides* sometimes immobilizes its prey by wrapping, but *Metleucauge* does not, 2) The former sometimes carries its prey by a combination of "Carry with silk" and "Pulling from hub", but the latter does not, and 3) Prey-touching occurs only in unsuccessful attack sequences in *Metleucauge*, but it occurs in both successful and unsuccessful attack sequences in *M. reticuloides*. It is worthy of notice that attack-wrapping observed in *M. reticuloides* occurs only after prey-touching.

"Pulling from hub" used by *M. reticuloides* can be observed also in *Gasteracantha mammosa* (YOSHIDA, 1989b), but its function is not known. The difference in the function of prey-touching and the ability of attack-wrapping seen in *M. reticuloides* may be explained by the fact that the habitat of this species is not being limited to mountain streams. *Metleucauge* usually makes its web above mountain streams, but *M. reticuloides* makes its web in various habitats, such as at damp cliffs and above mountain streams. In other habitats except mountain streams, large and/or potentially dangerous prey may be restrained by the webs, and attack wrapping may be very effective to immobilize such type of prey. In order to prove the hypothesis, at first, the prey of *M. reticuloides* must be collected in various habitats and it should be ascertained that there are fairly many large and/or dangerous prey in them. By which sequences the spider attacks such prey should be ascertained.

EBERHARD (1982) listed various patterns of attack behavior in Araneidae. The list shows that there are a subfamily (Nephilinae) which does not use attack-wrapping and two subfamilies (Tetragnathinae and Metinae) which use attack-wrapping. In Araneinae, several tribes (Gasteracanthae, Micratheneae, etc.) do not use attack-wrapping and the other tribes (Argiopeae, Araneae, etc.) use attack wrapping. So, all the species belonging to the same subfamily or the same tribe show the same behavior, that is, they use attack-wrapping or not.

In Metinae, *Leucauge* spp. and *Chrysometa* spp. use attack-wrapping (EBERHARD, 1982). In addition to these species, *Meta reticuloides* also uses attack-wrapping, shown by this paper. On the contrary, three Japanese species of *Metleucauge* do not use attack-wrapping at all. As *Meta* and *Metleucauge* are the related genera (LEVI, 1986), this difference in attack behavior is very important to throw light on the evolution of attack-behavior in Metinae. More information

is necessary about the attack-behavior of *Metellina* and other species of *Meta*.

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摘 要

ヤマジドヨウグモの捕食行動を調べた。このクモは日本産のオオドヨウグモ属の3種(タニマノドヨウグモ, メガネドヨウグモ, キタドヨウグモ)とは異なり, 網にかかったアリ・ハチ・カメムシなどに対して, しばしば糸の投げ掛けによって攻撃した(攻撃ラッピング, または固定ラッピング)。また, 糸でぶらさげてコシキの近くまで運んだ餌が網にからまった場合に, からまった糸を切って再び糸でぶらさげてコシキまで運ぶのではなく, 糸を切らないでクモがコシキから餌を引き寄せるという, 特異な行動が見られた。オオドヨウグモ属が攻撃ラッピングをまったく行わないのに, ヤマジドヨウグモがそれを行なうのは, おそらく両者の生息場所の違いによる餌相の違いに関連しているものと思われる。

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