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Sit-and-wait forager or aggressive spider predator: Araneophagic cases of orb-weaving spiders by crab spiders of the genus *Thomisus* (Araneae: Thomisidae)

Yuya Suzuki

Graduate School of Life and Environmental Science, University of Tsukuba, 1-1-1, Tennodai, Tsukuba-shi, Ibaraki, 305-8572 Japan. E-mail: sasaganiya1206@gmail.com

ABSTRACT. Observational cases of predation and consumption on web-building spiders by two crab spiders from Japan, *Thomisus labefactus* Karsch, 1881 and *T. kitamurai* Nakatsudi, 1943 are reported based on the data collected from non-peer reviewed articles, illustrated books and various sources on the internet. Prey of *Thomisus* spiders mainly comprised orb-weaving spiders (Aranaidae), most frequently *Nephila clavata* (L. Koch, 1878). This publication represents the first description of web-invasion and araneophagy of orb-weaver spiders by Thomisidae in a research paper.

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KEY WORDS. Araneophagy, crab spiders, dietary specialization, field observations, orb webs.

Фуражировщик-засадчик или агрессивный хищник на пауков: Случаи аранеофагии, или нападения на пауков-кругопрядов со стороны пауков-бокоходов рода *Thomisus* (Araneae: Thomisidae)

Юя Судзуки

Graduate School of Life and Environmental Science, University of Tsukuba, 1-1-1, Tennodai, Tsukuba-shi, Ibaraki, 305-8572 Japan. E-mail: sasaganiya1206@gmail.com

РЕЗЮМЕ. По литературным и интернет-данным описаны случаи охоты на пауков-кругопрядов и их поедания со стороны двух видов пауков-бокоходов из Японии, *Thomisus labefactus* Karsch, 1881 и *T. kitamurai* Nakatsudi, 1943. Добычей *Thomisus* обычно являются пауки-кругопряды Araneidae, наиболее часто *Nephila clavata* (L. Koch, 1878). Здесь впервые дано научное описание вторжения в сеть и аранеофагии со стороны Thomisidae.

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КЛЮЧЕВЫЕ СЛОВА. Аранеофагия, пауки-бокоходы, пищевая специализация, полевые наблюдения, круговые сети.

Although spiders are well known as insectivorous predators, some of them also eat other spiders (Nentwig, 1987). In spiders which do not build webs, such as the families Salticidae, Lycosidae, Oxyopidae, and Thomisidae, predation of other spiders does not unusually occur (Guseinov, 2006; Jackson, 1977; Huseynov, 2005, 2007a, b; Nentwig, 1986; Nyffeler, Benz, 1988). Capturing a spider is risky if the prey is larger than predator, because in general, capture success decreases with increase of prey-predator size ratio (Erickson, Morse, 1997). Thus, araneophagic (i.e., spider-eating) predators that hunt larger spiders tend to exhibit effective prey-capturing and defensive traits, such as spider-specific venom (Pekár *et al*., 2018) and a hardened carapace (Pekár *et al*., 2011). Capturing web-building spider is also risky and laborious, because the web functions both as a barrier and a "sensory system" that helps to detect invaders (Foelix, 2011). To overcome this defensive system, some araneophagic spiders employ "aggressive mimicry," luring prey by generating vibration on the threads of their prey's web (Jackson, Blest, 1982), while others perform "smokescreen tactics", utilizing noise by wind to mask a predator's stalking movement (Wilcox *et al*., 1996).

Spiders of the family Thomisidae, also known as crab spiders, do not build prey-capturing webs; instead, they subdue prey with two pairs of frontal legs and venom (Herberstein, Gawryszewski, 2013). Within this family, spiders of the genus *Thomisus* have been well recognized as sit-and-wait (or ambush) predators on flowers and used as model organisms for studying body-color camouflage and interactions between pollinators and predators (Théry, Casas, 2002; Heiling *et al*., 2004; Heiling, Herberstein, 2004). Primarily, prey of *Thomisus onustus* Walckenaer, 1805 comprises bees (Hymenoptera: Apidae), hoverflies (Diptera: Syrphidae), and ants (Hymenoptera: Formicidae) (Huseynov, 2007b). Though they sometimes eat other cursorial spiders (Huseynov, 2007b), web invasion and predation of web-builders have never been reported in a scientific research paper until now.

Recently, the author became aware of several cases of predation and consumption on web-building spiders by crab spiders reported outside the traditional scientific literature, i.e., in non-peer reviewed articles, illustrated books and various sources on the internet. These cases apparently contradicted the common assumption that *Thomisus* crab spiders hunt exclusively as sit-and-wait predators on flowers. Therefore, herein I describe observational cases of araneophagy in *Thomisus* spiders gathered from multiple sources and discuss the potential of this phenomenon for the further study of dietary specialization in spiders.

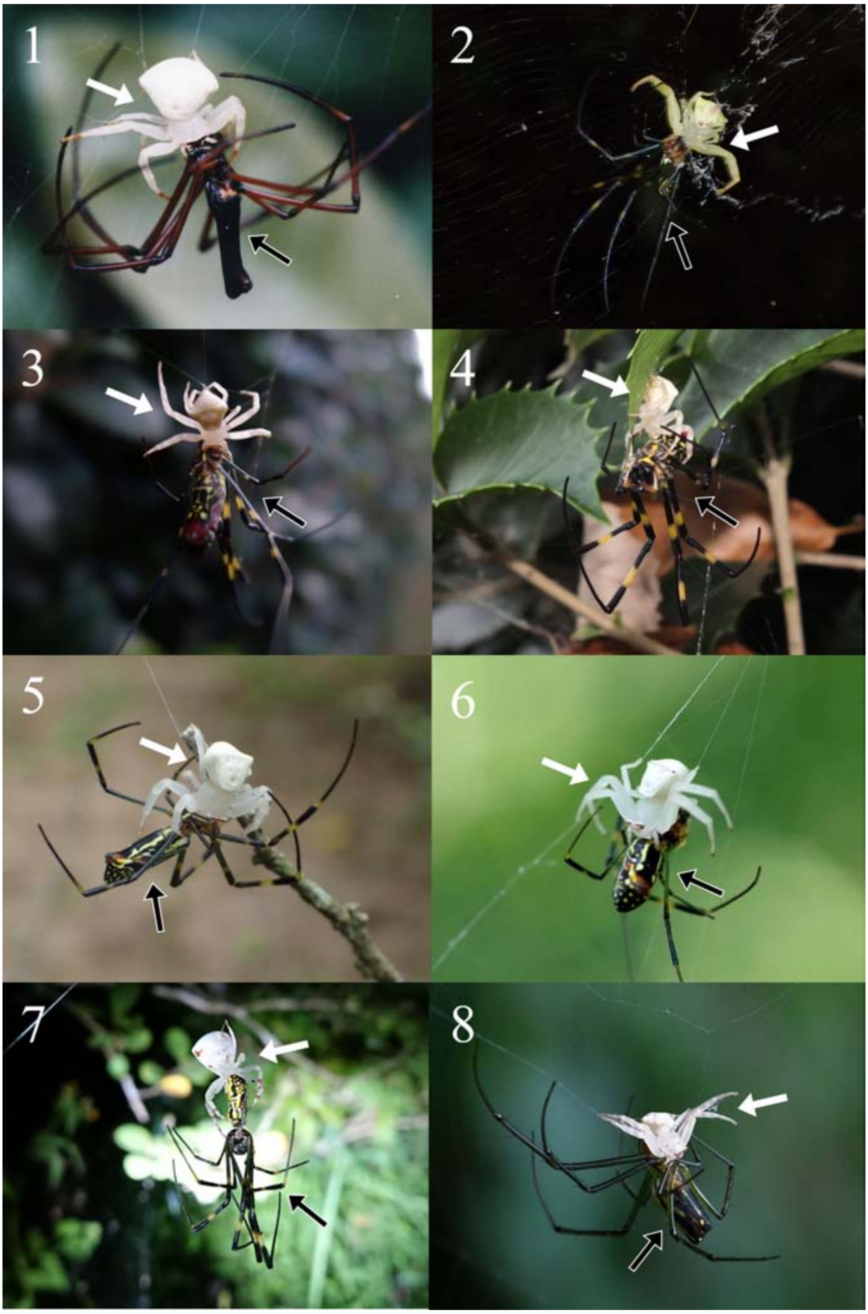
Information on araneophagy in *Thomisus* spiders was compiled from five sources: peer-reviewed articles (Acta arachnologica and Atypus; the journals published by the Arachnological Society of Japan), non-peer reviewed articles (Kishidaia; bulletin of Tokyo spider study group), an illustrated book (Ono, Ogata, 2018), posts on Twitter (Twitter, Inc.) and blogs on the internet. After information was found on Twitter profiles or blogs, I contacted their respective owners to ask for details of observations and obtain their consents to use the photographs. I documented data of the following categories: predator species, sex and maturity; prey species; prey web-type; location where predation or consumption was observed (i.e., on the prey's web or anywhere else); prey-capturing process (if available); position of bites and prey-predator body size relationship (PPSR). As all observational cases lacked actual measured values of body length, PPSR was calculated as ratio of prey body length (in pixels) and predator body length (in pixels) measured with image processing software (ImageJ). When information of prey-capturing process was not available, I considered whether these cases were predations or other interactions (e.g., kleptoparasitism or scavenging) based on the posture of the spiders and the freshness of prey's body.

In total, 11 cases of predation and consumption on web-builders by *Thomisus* spiders were collected (Table 1). Two of 11 cases were of *Thomisus kitamurai*, the species distributed on the south-western Japanese islands and ten were

Table 1. Araneophagic cases of *Thomisus* spiders.
Таблица 1. Случаи аранеофагии у пауков рода *Thomisus*.

ID	Predator species	Predator sex	Date	Locaility	Prey species	Place of predations	Position of bites	PPSR	Source of original information	No. of Fig.
a	*T. kitamurai*	f	26.07.1997	Nago-shi, Okinawa Pref.	*Nephila pilipes*	In the prey's web	Frontal side of prosoma	1.95	Shinkai *et al.*, 1998	1
b	*T. kitamurai*	m	8.06.2017	Amami-shi, Kagoshima Pref.	*Nephila clavata*	On the edge of the prey's web	Femur of leg1	1.61	Ono, Ogata, 2018	–
c	*T. labefactus*	f	9.08.2009	Kimitsu-shi, Chiba Pref.	*Neoscona melloteei*	Leaf	–	–	Shinkai, 2010	–
d	*T. labefactus*	f	9.08.2011	Toyota-shi, Aichi Pref.	*Nephila clavata*	Leaf	Abdomen	–	Ono, Ogata, 2018	–
e	*T. labefactus*	f	17.08.2015	Wakasano-cho, Aioi-shi, Hyogo Pref.	*Nephila clavata*	Leaf	Coxa of leg1	1.48	Twitter	–
f	*T. labefactus*	f	27.08.2016	Shinagawa-ku, Tokyo	*Nephila clavata*	On the prey's web	Sternum	1.57	Twitter	2
g	*T. labefactus*	f	12.11.2017	Maioka-cho, Yokohama-shi, Kanagawa Pref.	*Nephila clavata*	On the prey's web	Coxa of leg1	2.45	Blog	3, 4
h	*T. labefactus*	f	11.08.2018	Hanno-shi, Saitama Pref.	*Nephila clavata*	On the edge of the prey's web	Sternum	1.66	Twitter	5
i	*T. labefactus*	f	22.08.2018	Yokohama-shi, Kanagawa Pref.	*Nephila clavata*	On the edge of the prey's web	Coxa of leg4	1.54	Twitter	6
j	*T. labefactus*	f	10.09.2019	Iwata-shi, Shizuoka Pref.	*Nephila clavata*	On the edge of the prey's web	Abdomen	1.46	Twitter	7
k	*T. labefactus*	f	6.09.2019	Maioka-cho, Yokohama-shi, Kanagawa Pref.	*Leucauge celebesiana*	On the prey's web	Sternum	2.03	Blog	8

Abbreviations: PPSR — prey-predator size ratio; f — female adult; m — male adult. "–" in column of position of bite and PPSM indicates that data was not obtained from original sources. All the localities are of Japan.



Figs 1–8. Predation of web-building spiders by *Thomisus* spiders.

1 — *T. kitamurai* feeding *Nephila pilipes*; 2–7 — *T. labefactus* feeding juveniles of *Nephila clavata*; 8 — *T. labefactus* and *Leucauge celebesiana* bite each other. Photographers: T. Kamura (1); an anonymous Twitter user (2); H. Abe (3, 4, 8); J. Shimada (5); M. Wada (6); M. Yanagisawa (7). Whiter and black arrows represent predator and prey, respectively.

Рис. 1–8. Охота пауов рода *Thomisus* на пауков-кругорядов.

1 — *T. kitamurai*, поедающий *Nephila pilipes*; 2–7 — *T. labefactus*, поедающие ювенильных особей *Nephila clavata*; 8 — *T. labefactus* и *Leucauge celebesiana* кусают друг друга. Фотографии: T. Kamura (1); анонимный пользователь Twitter (2); H. Abe (3, 4, 8); J. Shimada (5); M. Wada (6); M. Yanagisawa (7). Белые и черные стрелки указывают, соответственно, хищника и добычу.

of *T. labefactus*, widely distributed on mainland Japan. One specimen of *T. kitamurai* was a male adult and the rest were female adults. The moment of predation was directly observed only in case (h) and the others were snapshots. In the former case, the predator was positioned on the tip of a branch and touched the edge of a frame thread of the prey's web. Then, the prey spider approached the predator and was caught by its forelegs (Fig. 5).

The latter cases were clearly distinguished from kleptoparasitism (e.g., feeding a same food with a host; Whitehouse, 1997) by the posture of spiders and the fact that no food item was between spider's mouths (Figs 1–8). These were also unlikely to be a consequence of scavenging dead spiders because all the prey spiders maintained fresh body color and markings (Figs 1–8).

Orb-weavers of the family Araneidae and Tetragnathidae were dominant among the victims of *Thomisus* spiders. Instances of predation on *Nephila clavata* (L. Koch, 1878) were most frequently recorded (n=8; Table 1), followed by *Nephila pilipes* (Fabricius, 1793), *Neoscona mellotteei* (Simon, 1895), and *Leucauge celebesiana* (Walckenaer, 1842). Prey spiders tended to be larger than their predators, as PPSR ranged from 1.46 to 2.45 (Table 1). Locations where predation was observed varied: on the edge of the prey's web (n=4), in the prey's web (n=4), and on leaves (n=3) (Table 1). Positions of bites concentrated on the prosomal region of prey's body (n=8/11), especially on the basal segments of the legs and sternum (Table 1). In case (g), a predator was hanging on threads of the web with its hindlegs and caught its prey by biting a coxa of a prey's leg (Fig. 3). The following day, the spider had already moved to the edge of the prey's web and was consuming the abdomen of prey under the leaf (Fig. 4).

This study reports on araneophagic cases of araneid and tetragnathid orb-weavers by two Japanese *Thomisus* crab spiders, which were previously assumed to be sit-and-wait predators. Two distinct modes of predation were hypothesized, based on the position in which predation occurred: (1) invading a prey's web by walking on its threads and capturing the prey on the web (e.g., case (g)); (2) waiting on the edge of the web and capturing the prey when it approached the predator (e.g., case (h)). As most cases were documented by snapshots, it was difficult to assess whether the observed locations of predation and positions of bites represent instances of first contact between predator and prey. Cases (g) indicate that crab spiders can vary the position of bites between the prosomal and abdominal parts of their prey (Figs 3, 4). The cases assessed herein did not provide any evidences that *Thomisus* spiders employ other specialized hunting behaviors, such as "smoke-screen tactics" or aggressive mimicry.

Based on previous research reporting that *T. labefactus* accepted various insects (Diptera, Homoptera, and Orthoptera) under rearing conditions (Miyashita, 1999), *Thomisus* spiders seem to be generalist predators, rather than spider-eating specialist. If no specific traits for dietary specialization have evolved in this genus, the observation that such generalized predators can apparently capture large web-building spiders in the web of their prey seems even more intriguing. *Thomisus* spiders are known as extremely powerful predators with an ability to subdue larger insects (Huseynov, 2007b). Thus, it might be possible that this prey-capturing ability may also be co-opted for more dangerous prey, that is, web-building spiders. Further studies are needed to examine the process of capturing behavior, how frequent these predations occur, and which nutritional factors make the crab spiders actively seek out web-building spiders as prey.

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