2019. Journal of Arachnology 47:202–208

Prey acceptance and conditional foraging behavior in the cribellate-web spider *Titanoeca quadriguttata* (Araneae: Titanoecidae)

Yun-Yun Tsai[1,2] and **Stano Pekár**[1]: [1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic. E-mail: pekar@sci.muni.cz; [2]Department of Biomedical Science and Environmental Biology, Faculty of Life Science, Kaohsiung Medical University, Kaohsiung, Taiwan.

Abstract. Spiders employ a wide range of foraging strategies and some are known to use conditional foraging behavior, which is tailored to the type of prey attacked. Little is known about the prey capture behavior of cribellate titanoecid spiders. Here, we investigated the fundamental trophic niche and predatory behavior of a cribellate-web spider, *Titanoeca quadriguttata* (Hahn, 1833). Juvenile spiders were collected under stones in a quarry and used in the experiment. We offered each individual nine prey types (spider, springtail, termite, cricket, cockroach, beetle, fly, moth, and ant) and observed the frequencies of capture and consumption, and the foraging behavior. We found that *T. quadriguttata* accepted many prey types, and thus, that its fundamental trophic niche was wide. The hunting behavior differed among prey types, depending on the size and potential danger of the prey. Two capture behaviors were used to overcome prey on the web. For dangerous and some large prey, such as spiders and crickets, the spider bit its victim and immediately retreated, whereas for innocuous and small prey, such as springtails and flies, the spider bit its victim and held it in the chelicerae. Attacks were administered to different body parts of prey. For example, ants were always bitten on the head, and crickets were bitten on the legs. We conclude that *T. quadriguttata* is an euryphagous generalist predator which uses conditional prey capture behavior to catch a variety of prey types.

Keywords: Fundamental trophic niche, conditional behavior, generalist predator, cribellate spider

Spiders are the main predators of insects in many ecosystems (Nyffeler & Birkhofer 2017). They have evolved an enormous variety of foraging modes based on either a web-building or wandering habit. The former habit has been further classified into four guilds on the basis of the shape and function of the web: sensing-web weavers, sheet-web weavers, space-web weavers, and orb-web weavers (Cardoso et al. 2011). Spiders belonging to different guilds are expected to employ specific foraging strategies (Dias et al. 2009). These different foraging strategies are the result of an arms race between prey and predators (Dawkins & Krebs 1979; Brodie & Brodie 1999). Various anti-predator behaviors exhibited by prey have imposed selection pressures on predators to evolve effective prey capture strategies. As a result, for example, orb-web spiders mainly capture flying prey, tube-web hunters and wandering spiders tend to subdue epigean prey, and sheet-web spiders mostly hunt arboreal arthropods (Michalko & Pekár 2016). Yet, such differences may to some extent be due to occurrences in different microhabitats (Nyffeler et al. 1989).

Many web-building spiders have evolved ecribellate sticky silk to build webs for prey capture. However, a number of species use cribellate silk to build webs for prey capture. The cribellate web may have a similar design to the ecribellate web, but is made of non-sticky silk in which prey is entangled instead of becoming stuck to the threads. This mechanism of capture has been studied for a long time (Opell 1994, 1995; Hawthorn & Opell 2003), but the main mechanisms involved in prey capture were revealed only recently. Capillary forces induced by epicuticular waxes of prey constitute the main adhesive mechanism leading to capture in cribellate webs (Bott et al. 2017). It also has been shown that a cribellate web is more efficient in prey capture than a web employing sticky silk under dry conditions (Amarpuri et al. 2015; Elettro et al. 2015).

Most spiders are euryphagous generalist predators (Pekár & Toft 2015), exhibiting conditional foraging tactics to catch different prey types. For example, a salticid spider, *Yllenus arenarius* Simon, 1868 (Bartos 2007; Bartos & Szczepko 2012), used prey-specific capture behavior towards different prey with high and low escape risk. They stalked prey with slow movement or employed 'movement masking' behavior to carefully approach prey with high escape risk. The spitting spider, *Scytodes pallida* Doleschall, 1859, regulated the amount of its spit according to prey size and struggling intensity (Clements & Li 2005). Surprisingly, a similar response was also found in the web-building (orb-web) spider, *Nephila pilipes* (Fabricius, 1793) (Araneidae). This species changed its web structure as a response to different prey types (Tso et al. 2005). However, the use of conditional foraging strategies in cribellate-web spiders remains unknown.

Cribellate spiders have been reported to catch a wide range of prey types which are mostly insects and other spiders (Pekár et al. 2012). Although most cribellate spiders are euryphagous predators, they seem to prefer some taxa in nature. For dictynids, the most numerous prey is dipterans (Bilsing 1920; Heidger & Nentwig 1984; Laing 1988; Hagley & Allen 1989; Miliczky & Calkins 2001); for eresids, it is either coleopterans (Nørgaard 1941; Chandra 1987) or hymenopterans (Henschel & Lubin 1992; Voss et al. 2007); for desids, the main prey are amphipods (Lamoral 1968); for uloborids of the genus *Philoponella* Mello-Leitão, 1917, the main prey are hymenopterans, coleopterans, and lepidopterans (Breitwisch 1989; Binford & Rypstra 1992), and of the genus *Uloborus* Latreille, 1806, the main prey are dipterans (Muma 1975) or hemipterans (Nyffeler et al. 1989).

In our study, we focused on the cribellate-web spider *Titanoeca quadriguttata* (Hahn, 1833), (Titanoecidae) which belongs to the space-web weavers and is widespread in Europe (World Spider Catalog 2018). We investigated its fundamental

Table 1.—Relative frequencies of attack and consumption by *Titanoeca quadriguttata* towards nine prey types.

Prey type	No. of trials	Attack frequency	Consumption frequency
Spider	28	0.96	0.93
Springtail	24	0.79	0.79
Termite	27	1.00	1.00
Cricket	27	0.89	0.89
Cockroach	24	0.83	0.83
Beetle	23	0.78	0.70
Fly	24	1.00	1.00
Moth	25	0.88	0.84
Ant	24	1.00	1.00

trophic niche and foraging behavior using nine potential prey types. We recorded its attack and consumption rates and investigated in detail its predatory behavior. As this species lives under rocks, we expected it to be a euryphagous predator that mainly preys on epigean insects. Because the different prey types used varied in size and defensive ability, we predicted that *T. quadriguttata* would exhibit a conditional foraging behavior according to the size of each prey and its dangerousness.

METHODS

Study species.—*Titanoeca quadriguttata* lives in stony habitats and builds webs under logs and stones (Růžička 2000). Adult females are about 6 mm long, and adult males are about 4.5 mm long. We collected these spiders by hand under stones in the Hády Quarry, Brno, Czech Republic in October 2017. Altogether, 28 specimens at different juvenile developmental stages were collected (mean prosoma length = 1.57 mm, SE = 0.04). All spiders were fed with a fly (*Drosophila melanogaster*) after arrival at the laboratory.

Collected spiders were placed into 2 ml Eppendorf tubes with a punctured lid and kept at room temperature (23 °C), at a RH of 43%, and under a natural LD regime. In all spider individuals, we measured the width and length of the prosoma after each molt using an ocular micrometer within a stereomicroscope. Once spiders reached adulthood, which typically occurred towards the end of the experiment, their sex was recorded.

All voucher specimens were deposited at the collection of the Terrestrial Invertebrate Research Group, Department of Botany and Zoology, Masaryk University, Brno, Czech Republic.

Experimental design.—The experiment was performed with spiders five days after satiation with fruit flies. Spiders were placed singly in a Petri dish (diameter 4 cm) in a room with a temperature of 23 °C. Moisture in the Petri dish was maintained with a few drops of water provided at 3-day intervals.

Nine prey types selected among the potential prey were offered to the spiders. Prior to the trial, we measured the total body size of each prey individual using a ruler. The following prey types were used: spiders (*Mangora* sp. O. Pickard-Cambridge, 1889 (Araneae: Araneidae), mean = 2.2 mm), springtails (*Sinella curviseta* Brook, Collembola, 1.35 mm), and insects including termites (*Reticulitermes* sp., Isoptera, 4.5 mm), crickets (*Acheta domestica* Linnaeus, Orthoptera, 4.3 mm), cockroaches (*Symploce pallens* (Stephens), Dictyoptera, 3.5 mm), beetles (*Callosobruchus maculatus* Fabricius sp., Coleoptera, 2.8 mm), fruit-flies (*Drosophila melanogaster* Meigen, Diptera, 1.8 mm), moths (*Ephestia kuehniella* Zeller, Lepidoptera, 10.3mm), and ants (*Lasius* sp., Hymenoptera, 3.5 mm). Among these prey types, spiders and ants were classified as dangerous prey, because they are also predators and have the potential to attack *T. quadriguttata*. Crickets were categorized as dangerous prey because in our preliminary experiments they bit spiders. All other prey types were classified as innocuous. All prey types besides spiders were taken from laboratory breeding cultures. Spiders used as prey were collected by sweeping nearby vegetation cover.

The trial started when one prey type was released into the Petri dish occupied by a spider. If the spider did not attack the prey within 15 minutes, the prey was replaced by one of a different type. If the spider did not catch the second prey, the trial was terminated. Then, we waited for one or two more days and repeated the trial with the same prey type. Once a spider attacked the prey, it was allowed to feed on it for one hour in order to maintain a similar satiation level after each prey type. The same spider individual was used in a new feeding trial 2-3 days after its last successful feeding. Every individual was fed with all prey types in a randomized order; thus, nine feeding trials were to be conducted with every individual. However, six spiders died before all prey could be tested, reducing the number of trials per prey type below 28 (Table 1).

The web of *T. quadriguttata* was mainly placed on the bottom of the dish, and some radial threads reached the dish margins. The web almost covered the whole dish (diameter 4 cm); therefore, when the prey was placed into the dish, it was immediately on the web. The spider was typically positioned in the center of the web. The web was so dense that the prey became easily entangled.

In every trial, we recorded whether the prey was attacked and consumed. The attack rate was used to calculate the standardized Levins' index (Hurlbert 1978). In addition, 10 spider individuals were randomly chosen to record details of the prey capture behaviors employed for all prey types using a video camera (Canon Legria HF R606) and a macro conversion lens (Raynox DCR-250). Videos were mainly used to record the behavior of the first attack. From the video footage, we recorded the strategy spiders used to attack their prey, and which body part of the prey was attacked by spiders during the first attack. According to our previous observations, five different prey body parts could be the potential target of spider attack: antennae, head, thorax, abdomen, and legs. We merged the antennae and head into the same category because spiders always bit on the basal segment of the antenna, which was very close to the head.

Data analysis.—The standardized Levins' index (B_A) of niche breadth (Hurlbert 1978) was used to calculate the fundamental trophic niche. The experimental design was randomized incomplete block so we tested for the presence of temporal autocorrelation in the data. As it turned out to be negligible, a Generalized Linear Model with binomial error structure (GLM-b) was used (Pekár & Brabec 2016). The model formula included the following explanatory variables as main effects: relative body size (spider prosoma/total prey body), prey type, and prey dangerousness. The response variables were the attack frequency (on different body parts) and capture strategy. Bonferroni correction ($\alpha = 0.0125$) was applied because tests on different body parts were not independent. All analyses were performed within the R environment (R Core Team 2017).

RESULTS

Fundamental trophic niche.—Spiders attacked all prey types offered (Table 1). The attack and consumption frequencies for juvenile males ($n = 14$) were both 0.91, whereas for juvenile females ($n = 14$), the attack frequency was 0.95 and the consumption frequency was 0.91. The frequencies between juvenile male and female were very similar.

The breadth of the trophic niche with a value almost reaching 1 ($B_A = 0.93$) indicates that *T. quadriguttata* is an euryphagous predator.

Prey capture behavior.—Prey capture began when the prey became entangled in the web. Some prey types (flies, termites, springtails, and spiders) could hardly move once they had become entangled, whereas others (crickets, cockroaches, beetles, moths, and ants) struggled emphatically, some of them even moving on the web for a while. A few spiders produced more threads during the hunting process when the prey was dangerous or struggled very extensively.

Hunting behavior was different for different prey types, depending on the size and potential danger of the prey. We distinguished two capture strategies: bite-and-retreat (i.e., spiders bit the prey and immediately retreated) and bite-and-hold (i.e., spiders bit and held the prey in their chelicerae). The frequency of use of each capture strategy was not significantly related to spider/prey body size ratio (GLM-b, $\chi^2_1 = 0.3$, $P = 0.58$) but was significantly different among prey types (GLM-b, $\chi^2_8 = 41.3$, $P < 0.0001$, Fig. 1a). The bite-and-retreat strategy was used significantly more frequently (0.57 vs. 0.11) on dangerous prey, such as crickets and spiders, than on innocuous prey, such as termites, springtails, flies, and moths (GLM-b, $\chi^2_1 = 14.3$, $P = 0.0002$). Cockroaches and beetles were frequently captured by bite-and-hold strategy; however, if they struggled a great deal, the spider used bite-and-retreat strategy (Fig. 1a).

The attack was administered to different body parts of prey (Fig. 1b). If the prey was a spider, cricket, or beetle, the first bite was mainly administered to the legs (Figs. 2a-c). If the prey was a termite, cockroach, or ant, the first bite was mainly administered to the head (Figs. 2d-f). If the prey was a moth, the spider mainly bit the thorax (Fig. 2g). As for springtails and flies, the spider grabbed the whole body in its chelicerae (Figs. 2h, i).

The frequencies of attacks on head, legs and thorax were not significantly related to spider/prey body size ratio (GLM-b, $\chi^2_1 < 2.49$, $P > 0.11$) but were significantly different among prey types (GLM-b, $\chi^2_8 > 26.2$, $P = 0.001$, Fig. 1b). The frequency of attacks on the head was not significantly different between dangerous and innocuous prey (GLM-b, $\chi^2_1 = 2.9$, $P = 0.08$). The frequency of attack on the legs was significantly greater (0.74 vs. 0.28) on dangerous prey than on innocuous prey (GLM-b, $\chi^2_1 = 13.4$, $P = 0.0002$). In turn, attacks on the thorax were significantly more frequent (0.20 vs. 0.0) on innocuous prey than on dangerous prey (GLM-b, $\chi^2_1 = 7.4$, $P = 0.006$). The frequencies of attacks on the abdomen were significantly related to spider prosoma/total prey body size ratio (GLM-b, $\chi^2_1 = 12.7$, $P = 0.0004$, Fig. 3): it was higher when the spider was larger than the prey. However, the frequencies of attacks on the abdomen were not significantly different among prey types (GLM-b, $\chi^2_8 = 10.6$, $P = 0.22$) or between dangerous and innocuous prey (GLM-b, $\chi^2_1 = 0.1$, $P = 0.87$).

DISCUSSION

Our results show that *T. quadriguttata* is an euryphagous generalist predator which uses conditional prey capture behavior to catch a variety of prey types. Although the attack and consumption rates were very high on all prey types, termites, flies, and ants were the most commonly accepted prey in the laboratory.

There was no preference for epigean insects as even flying insects (flies, moths) were often captured by spiders. That titanoecids exhibit a generalist feeding niche has also been documented by a study from Brazil where a species of the genus *Goeldia* Keyserling, 1891 was feeding predominantly on lepidopterans, coleopterans, dipterans and mites under natural conditions (Almeida-Silva et al. 2009).

Various capture tactics were used for different prey types, which indicates that these spiders can distinguish different prey on the basis of mechanical (e.g., Suter 1978), visual (e.g., Nelson & Jackson 2007), or chemical cues (e.g., Persons & Rypstra 2000), and employ versatile behavior in predation. This plasticity is especially well known in jumping spiders (Jackson & Pollard 1996). Also, several studies have shown that web-weavers can distinguish prey and adjust their foraging behavior (Robinson & Mirick 1971; Olive 1980; Sandoval 1994).

In our study, two foraging strategies were used by *T. quadriguttata* to catch different prey, the bite-and-retreat and the bite-and-hold strategy, and they were used differently among prey types. For dangerous prey (like spiders or crickets), spiders tended to use the bite-and-retreat strategy. Spiders bit their victims several times and immediately retreated to wait for the venom to take effect. Feeding only started when the prey became immobilized. A similar strategy was reported for dictynids (Jackson 1977) and for *Trichonephila clavipes* (Linnaeus, 1767) (Araneidae) (Robinson & Mirick 1971; cited as *Nephila clavipes*). Such strategy allows spiders to avoid potential counter-attack by the prey. With respect to innocuous prey (like springtails and worker termites), spiders were more likely to employ the bite-and-hold strategy. This strategy was similar, for example, to the basket-like manner of holding prey described in some zodariid spiders (Pekár & Lubin 2009) and the pluck-out strategy for orb-weaver (Robinson 1975; Olive 1980). Spiders bit their victims and kept hold of them in their chelicera. Innocuous prey were not aggressive, so spiders treated them with less caution.

Ants are dangerous prey, yet *T. quadriguttata* used the bite-and-hold strategy to subdue them. Even tiny juveniles caught ants using this strategy. Our observations may indicate, therefore, that *T. quadriguttata* is well adapted to this prey

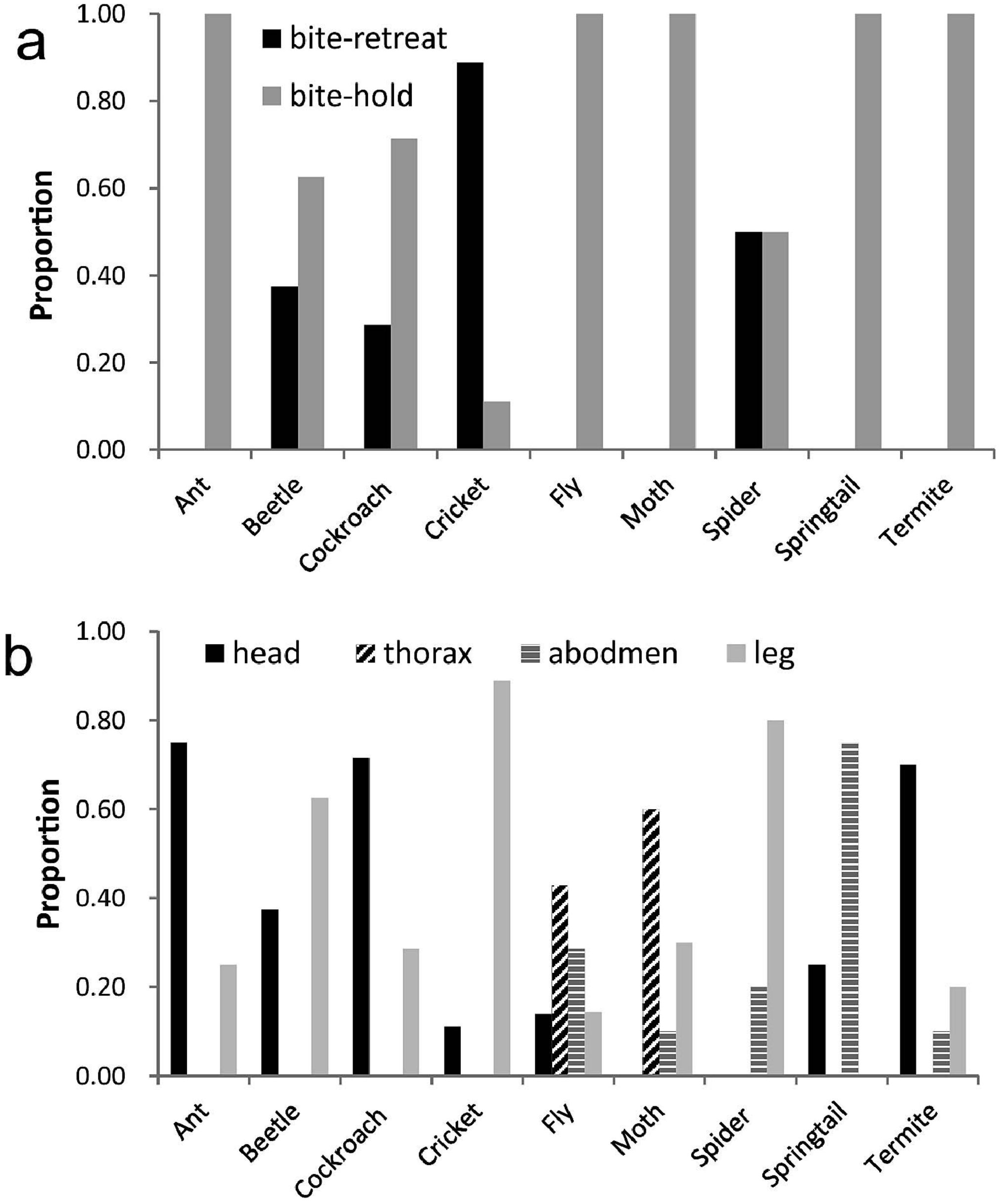

Figure 1.—Comparison of the relative frequencies of two foraging strategies (a) and the first attack on four body parts (b) used by *Titanoeca quadriguttata* (n=10) for nine prey types.

type. *Titanoeca quadriguttata* can always be found under stones in rocky habitats, so it has a high possibility to encounter ants. Indeed, the food composition of a spider is related to its habitat. For example, some thomisids often hunt on flowers and thus catch mostly pollinators (Nentwig 1986). Similarly, species living under stones should particularly target ants (e.g., Nørgaard 1956).

Besides the use of two different foraging strategies, we also observed that the first attack was delivered to different prey body parts. This might be due to two reasons: increasing the capture success or balancing nutrition intake if bite-and-hold strategy was used. From the first point of view, different prey possess different morphology and aggressiveness, thus, spiders need to bite on the right place to inject the venom or to avoid the counter-attack (García et al. 2016). From the perspective of nutrient balance, various body regions within an individual contain different concentration of nutrient, for example, there are more lipids in the abdomen and more proteins in the thorax (Wilder 2011). As a result, it has been shown that some spiders can regulate the nutrient intake from a single prey item by exploiting different body parts (Pekár et al. 2010).

Attacks on the head were frequently used for ants, termites and cockroaches. This tactic seems to limit counter-attack from the prey by pushing its head downward. It could also accelerate paralysis because the head includes the ant's brain (Pekár 2004). The attack on head was also found in other ant-eating spiders (Jackson & Van Olphen 1991; Li et al. 1999; Huseynov et al. 2005). Termite workers do not possess defensive abilities, yet the spiders also attacked them on head. However, other studies have shown that spiders also attack

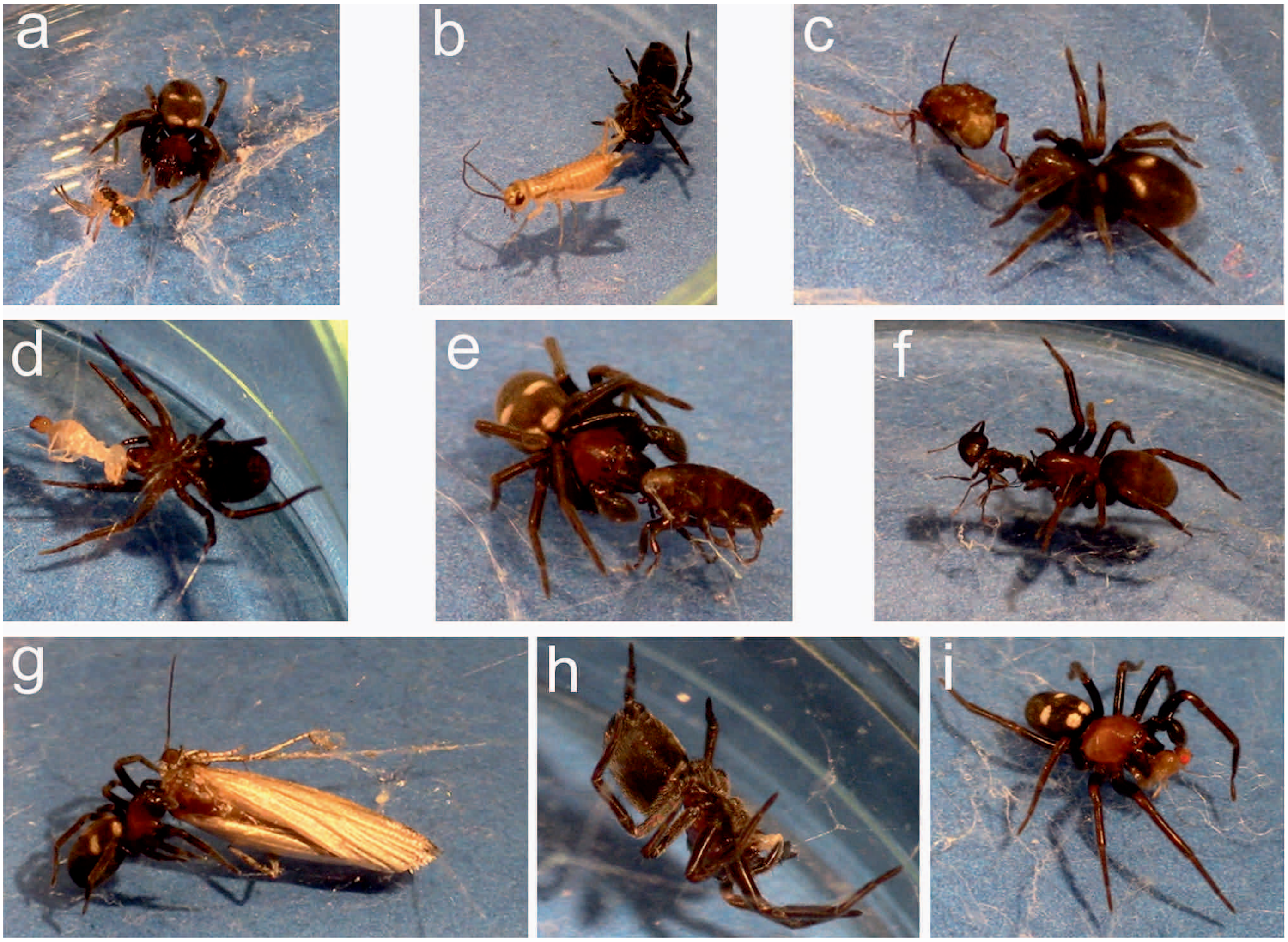

Figure 2.—Picture of the first attack administered to different body parts in nine prey types. Spider (a), cricket (b) and beetle (c) were attacked on the leg; termite (d), cockroach (e) and ant (f) were attacked on the head; moth (g) was attacked on the thorax; and springtail (h) and fly (i) were grabbed by the whole body.

termite workers from the rear (Wesołowska & Haddad 2002; Petráková et al. 2015).

Attacks on legs were frequently carried out on other dangerous prey, such as spiders and crickets. Biting on the appendage allowed spiders to retreat faster from the dangerous counter-attack. But attacks on the thorax were more often carried out on innocuous prey, such as moths and flies. Interestingly, attacks on the abdomen were not different among prey types, but were more frequently used when the body size ratio between spider prosoma and total prey body was over 1.2. The most common cases in our experiment happened on springtails and flies. These prey have tiny and soft bodies, and it seemed that spiders simply masticated them on the obvious body region. Beetles were innocuous prey but were often bitten on the leg, presumably because venom could not be injected through the hard exoskeleton covering the whole body (Nentwig 1987).

Moths represent innocuous prey to *T. quadriguttata* because the spiders were able to overcome specimens which were bigger than themselves. Even small juveniles captured moths which were almost eight times longer than the prosoma of the spider. The prey/predator body size ratio seems to be an unimportant factor with respect to decision making in foraging. This may be because cribellate threads can entangle Lepidoptera more efficiently than the sticky threads of the ecribellates (Eisner et al. 1964; Nentwig 1982). The scales on the wings of Lepidoptera would not decrease the trapping efficiency of cribellate thread due to the different mechanism of cribellate thread. Moreover, the strong capillary forces of cribellate threads (Bott et al. 2017) may explain the prolonged retention of prey on such threads (Strohmenger & Nentwig 1987) and the ability of cribellate spiders to capture fairly large prey.

Cribellate spiders are reported to catch a wide range of prey types, and the capture behavior is also very diverse. Most cribellate species use the sit-and-wait strategy, but deinopids are active ambushers (Austin & Blest 1979). Some species, such as uloborids, use silk to wrap the prey (Binford & Rypstra 1992), others, such as *Titanoeca*, do not.

In conclusion, *Titanoeca quadriguttata* used conditional foraging on the whole range of prey types offered in lab experiments. This indicates that their foraging could be even

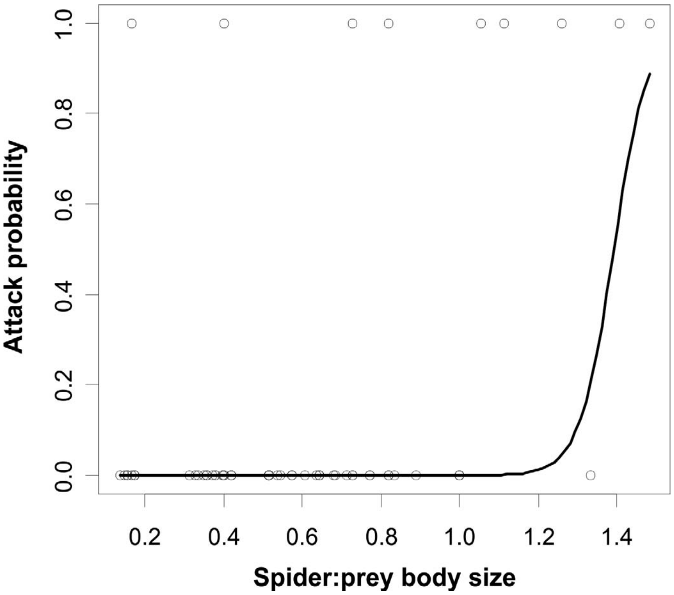

Figure 3.—Relationship between the relative spider/prey body size (i.e., spider prosoma to prey total body) and the probability of attack on the abdomen of nine prey types. Estimated logit model is shown.

more generalistic than in other cribellate web-builders. However, field studies are needed to demonstrate if the realized trophic niche of these spiders is wide, as well. More investigations on different species are also needed to find whether the versatility of foraging strategies differs among the foraging guilds of spiders.

ACKNOWLEDGMENTS

We would like to thank E. Líznarová, O. Michálek, and J. Raška for their help with collecting spiders in the field; and Z. Varadínová for the provision of the cockroach culture.

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Manuscript received 3 October 2018, revised 22 December 2018.