

Trophic niche and predatory behavior of the goblin spider *Triaeris stenaspis* (Oonopidae): a springtail specialist?

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Abstract. *Triaeris stenaspis* Simon 1891 is a parthenogenetic goblin spider that has been introduced into greenhouses all over Europe. Here we investigated its trophic niche and predatory behavior. Potential prey in the greenhouses included predominantly springtails, aphids, and other spiders. Out of ten potential prey types offered in the laboratory, *T. stenaspis* captured only three types, the primary one being springtails. The spider rarely caught the other two types, termites and crickets, and completely rejected beetles, ants, aphids, thrips, flies, spiders and mites. *Triaeris stenaspis* did not build webs for prey capture, but instead used the grasp-and-hold tactic. Prey-capture efficiency decreased with springtail body size, the spider using more than three bites to capture large springtails. Large springtails defended themselves by saltation with the spiders still attached to their backs. Our study supports the hypothesis that *T. stenaspis* is a specialized predator of springtails, being effective in the capture of this type of prey.

Keywords: Stenophagy, prey acceptance, capture behavior, prey

Spiders are mostly known as euryphagous predators, consuming a wide variety of prey (Nentwig 1987), but several spider species are prey specialists. Known examples of trophic specialists include myrmecophilous spiders of the genus *Zodarion* (Zodariidae) (e.g., Pekár 2004), oniscophilous spiders of the genus *Dysdera* (Dysderidae) (Řezáč et al. 2008), araneophilous spiders of the genus *Portia* (Salticidae) and *Palpimanus* (Palpimanidae) (Harland & Jackson 2001; Pekár et al. 2011), lepidopterophilous spiders of the genus *Mastophora* (Araneidae) (Yeagan 1988) and termitophilous spiders of the genus *Ammoxenus* (Ammoxenidae) (Dippenaar-Schoeman et al. 1996).

Trophic specialists possess various kinds of specific adaptations that are effective for their preferred prey. Pekár et al. (2011) documented specific behavioral and morphological adaptations in araneophilous *Palpimanus* spiders. Harland & Jackson (2001) identified a specific behavioral adaptation, “cryptic stalking”, in araneophilous *Portia fimbriata* Dolschall 1859, which prevents prey dangerous to spiders from identifying *Portia* as a predator. Researchers observed unique physiological adaptations in ant-eating spiders of genus *Zodarion* (Pekár et al. 2008; Pekár & Toft 2009), one being that they cannot metabolize alternative prey at all, or at most to a much more limited degree.

Goblin spiders (Oonopidae) occur throughout the temperate and tropical regions of the world, in habitats as diverse as deserts, savannahs, mangroves and rainforest (e.g., Jocqué & Dippenaar-Schoeman 2006). To date, arachnologists have described more than one thousand species, making goblin spiders one of the largest families among the Haplogynae (Platnick 2012). Yet very little is known about the trophic niche of oonopid spiders. Scientists have found oonopids in a variety of underground microhabitats such as ant nests (Jacobson 1933, Weber 1957), termite mounds (Benoit 1964) and caves (Harvey & Edward 2007), but also on the soil surface (Ubick 2005) and on tree bark and in the canopy (e.g.,

Fannes et al. 2008). All oonopid species appear to be active cursorial hunters, as they do not build prey-capture webs. They have been observed to feed on springtails, mites, firebrats, psocids, and other spiders (Bristowe 1948; Knoflach et al. 2009; Korenko et al. 2009; Hansen 1992). Researchers have even detected some oonopids scavenging insect remains on webs of larger spiders (Bristowe 1948; Knoflach et al. 2009). To date, rigorous analysis of the trophic niche of oonopids is lacking.

Triaeris stenaspis Simon 1891 seems to be indigenous to West Africa (Platnick et al. 2012) and, according to Platnick (2012), its range stretches from Central to South America, including Antilles and Europe. It has become a resident in Europe and is successfully surviving in heated greenhouses (Korenko et al. 2007). It is known to be parthenogenetic in Europe (Korenko et al. 2009).

Since greenhouses are rather poor in arthropod species diversity (Mahr et al. 2001), we expect *T. stenaspis* to be trophically specialized on an abundant prey. Based on knowledge from our previous study when *T. stenaspis* was successfully reared on a monotypic diet including only springtails (Korenko et al. 2009), we hypothesized that *T. stenaspis* prefers, or at least is adapted to, springtail prey. Such trophic specialization is either fixed across populations or is a plastic response of a population to locally abundant prey, as was recently found for *Oecobius* spiders (Liznarová et al. 2013). In the former case, specialized traits used for capture and utilization of prey occur in all populations and are leading to the evolution of species-specific adaptations for particular prey types. In the latter case, a predator does not possess specialized traits, but it can be locally specialized on profitable prey to enhance its versatility at a particular time and place. Our aim in this study was to investigate the trophic niche of *T. stenaspis*, namely the prey spectrum and the predatory behavior of this species in order to test our hypothesis on prey-specialization and to investigate whether it is effective in the capture of prey.

METHODS

On eight sampling dates during the autumn and winter 2006–2008, we collected all ground-dwelling arthropods occurring in the microhabitat of *T. stenaspis*' occurrence in the botanical garden of the Masaryk University in Brno (Czech Republic) to estimate the potential prey spectrum. Our team members hand-collected arthropods by lifting stones and rotten pieces of wood, inspecting the ground and plant roots underneath using a pooter, and then put the arthropods in tubes with ethanol and identified them to order in the laboratory. We only considered specimens of a total body size less than six mm as potential prey.

Altogether, we collected 60 adult females of *T. stenaspis* in the greenhouse in order to perform observations in the laboratory. The body length of spiders was very similar, ranging between 1.6 and 1.7 mm. We placed spiders singly in cylindrical containers (diameter 35 mm, height 40 mm) with a layer of plaster of Paris at the bottom, and kept them at room temperature, $22 \pm 3.5^\circ\text{C}$, to replicate conditions in the greenhouse. The plaster was moistened with a few drops of water to retain sufficient humidity. Spiders were fed springtails *Sinella curviseta* (Brook 1882) at 3–4 day intervals.

We tested the following 11 prey types of ground-living arthropods for acceptance: beetle imagoes (Curculionidae) (average body length = 1.93 mm, SD = 0.20), first instars of crickets *Acheta domestica* (Linnaeus 1758) (Gryllidae) (2.81 mm, SD = 0.46), aphids (Aphididae) (1.81 mm, SD = 0.25), thrips (Thysanoptera) (1.41 mm, SD = 0.15), mites (Trombididae) (0.87 mm, SD = 0.10), early instars of crab spiders of genus *Xysticus* (Thomisidae) (1.4 mm, SD = 0.38), ants *Tetramorium caespitum* (Linnaeus 1758) (Formicidae) (3.14 mm, SD = 0.20) and a mixture of springtail species (Collembola). Our team collected all of these prey from the soil in the greenhouse (1.06 mm, SD = 0.41). Termites *Reticulitermes* sp. (Isoptera), (3.54 mm, SD = 0.30), larvae and imagoes of *Drosophila melanogaster* Meigen 1830 (Diptera) (3.8 mm, SD = 0.54 for larvae and 2.4 mm, SD = 0.50 for imagoes) and springtails *Sinella curviseta* (Brook 1882) (1.45 mm, SD = 0.12) (Entomobryidae) came from laboratory cultures. The body length of prey was measured using an ocular ruler in the stereomicroscope before each trial.

Altogether we performed 150 trials over a period of 60 days to test prey acceptance. For each prey type, 12 individuals of adult female *T. stenaspis* were used. The order of tested prey was based on the availability of particular prey. Each tested spider was kept singly in a dish (diameter 35 mm, height 45 mm), which was marked by number, 1–60, in the order in which the individuals were collected. Twelve individuals from the set of 60 specimens were randomly (without replacement) selected for each prey type. When all individuals were used in the first round of tests, another 12 individuals were randomly (without replacement) selected from those that had already been used. Each individual was tested a maximum of two or three times. Each individual was used in the trial five days after being satiated with springtails. Individuals that did not feed during the day of satiation were not used in the next trial. At least six days elapsed between the repeated uses of the same individual.

Before each trial, spiders were placed singly in an experimental dish (diameter 35 mm, height 15 mm) with a

Table 1.—Relative incidence of potential prey types found on the soil in the greenhouse ($n = 148$).

Potential prey	Relative incidence
Isopoda	0.12
Myriapoda	0.02
Araneae (other than <i>Triaeris</i>)	0.09
Schizomida	0.07
Collembola	0.61
Ensifera	0.02
Formicidae	0.03
Coleoptera larvae	0.02
Other larvae	0.02

thin (2–3 mm) layer of plaster of Paris at the bottom. After five minutes of acclimatization, the potential prey was released into the experimental dish, and the occurrence of capture (incidence) was recorded. If the spider accepted the prey, or did not catch the prey within 120 minutes following encounter with prey, we terminated the trial.

The capture efficiency was studied in detail using *S. curviseta* springtails as prey. Thirty adult female spiders, selected randomly (without replacement) from the set of 60, were starved for five days and placed in arenas as described above. After five minutes of spider acclimatization in the dish, a springtail *S. curviseta* of body length between 0.5 mm–2 mm (prey-predator body length ratio = 0.3–1.2) was released. Spiders were selected randomly from the same experimental group as in the previous experiment. We recorded the attack latency, the capture behavior and the number of attempts required to capture springtails. The attack latency was the time between when the spider oriented itself toward the springtail and successfully completed the attack, (i.e., when prey was held in the chelicerae). We measured the body length of springtails before each experimental trial.

Statistical analyses were conducted within the R environment (R Development Core Team 2011). The relationship between prey size and attack latency, springtail size and number of attacks were analyzed using Generalized Linear Models with Gamma (GLM-g) or Poisson (GLM-p) error structure, respectively (Pekár & Brabec 2009). We used Generalized Estimating Equations with binomial error structure (GEE-b) to compare the incidence of captured prey assessed in a binary form. GEE is an extension of GLM used for repeated measurements by specifying correlation among measurements (Pekár & Brabec 2012). GEE was used since measurements were not independent due to repeated use of the same individual spiders.

RESULTS

The most abundant potential prey arthropods in the greenhouse ($n = 148$) were springtails (Entomobryidae) followed by aphids, other spiders, schizomids, ants, myriapods, coleopteran larvae, other larvae and crickets (Table 1). From 11 potential prey types tested in the laboratory, *T. stenaspis* accepted only springtails at high incidence rates (83%, $n = 42$, Fig. 1). Crickets and termites were rarely accepted (8%, $n = 12$, both prey types). The prey-predator body-length ratio of accepted prey was on average 0.6 (min–max = 0.3–1.1) in springtails, 1.2 in crickets, and 2.0 in termites. Mites, spiders, thrips, aphids, beetles, ants and flies

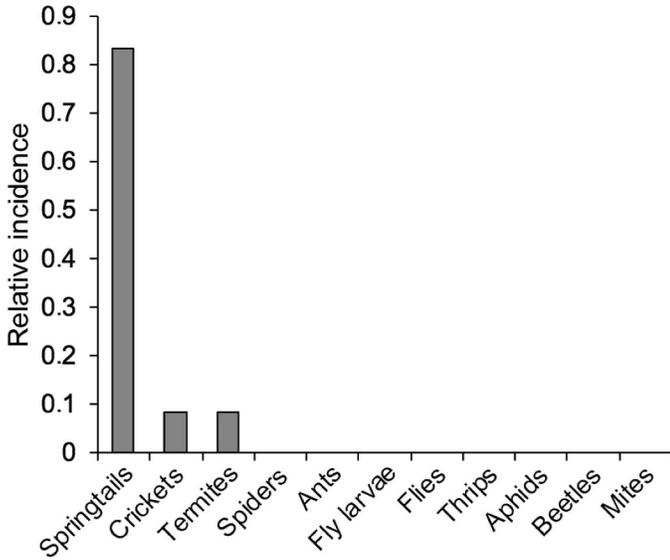


Figure 1.—Comparison of the relative capture incidence of 11 prey types.

(larvae and imagoes) were never accepted. The prey capture incidence thus differed among groups (GEE-b, $X^2_{10} = 45.7$, $P < 0.0001$).

Triaeris stenaspis did not build a web for prey capture; instead, it caught springtails and other prey using the grasp-and-hold tactic. After an attack, springtails attempted to escape by means of saltation. Ten percent of springtails jumped up with the spider attached to the springtail's back and hit the top of the experimental arena. All jumping springtails were large adults with a prey-predator ratio > 1.2 .

The attack latency increased significantly with prey size (GLM-g, $F_{1,23} = 6.4$, $P = 0.02$, Fig. 2). The number of attacks required for prey immobilization increased significantly with

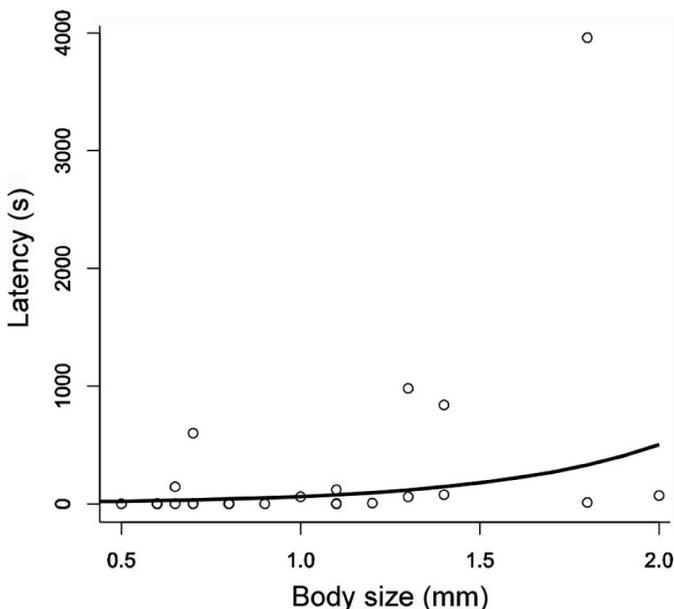


Figure 2.—Relationship between the attack latency and the springtail body size with estimated model.

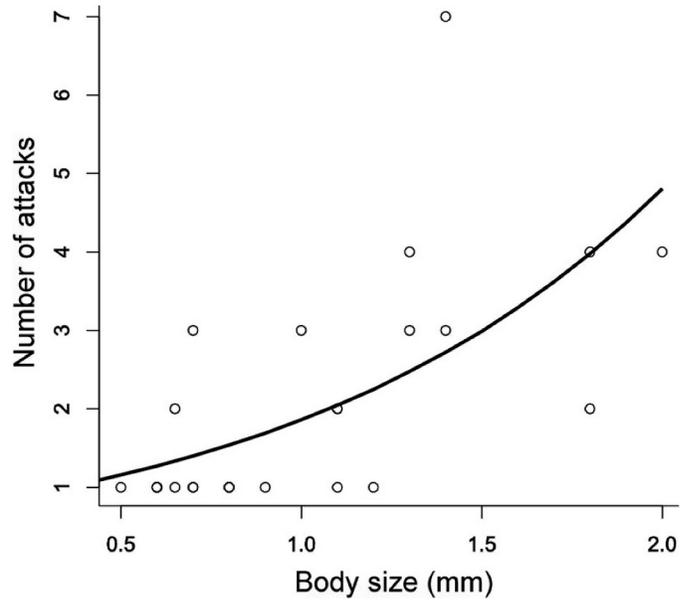


Figure 3.—Relationship between the number of attacks and prey size with estimated model.

prey size (GLM-p, $X^2_1 = 9.5$, $P = 0.002$, Fig. 3). *Triaeris stenaspis* required significantly fewer attacks to catch small springtails than to catch large springtails. The spiders made on average 1.4 attacks (SD = 0.71, $n = 17$) to catch small springtails (prey-predator ratio < 0.7), compared to 3.8 attacks (SD = 1.48, $n = 8$) to catch large springtails (prey-predator ratio > 0.7).

DISCUSSION

We found a moderate diversity of potential prey for *T. stenaspis* on the surface of the greenhouse soil. All of these arthropods were expected to be potential prey for *T. stenaspis*, at least at the life stage when of suitable body size. *Triaeris stenaspis* is a ground dweller that inhabits various structures of the soil and encounters all of these taxa. Although we did not record prey capture by *T. stenaspis* in the field, acceptance trials clearly indicate that *T. stenaspis* likely utilizes only a very small portion of available prey.

Little is known about the prey consumption of goblin spiders. There is only one report of the natural prey of *T. stenaspis*: Weber (1957) stated that it consumed *Cyphomyrmex costatus* (Mann 1922) ants and springtails. Our laboratory study confirmed the spiders feeding on springtails but not on ants. Since Weber (1957) observed only ant remnants in the spider surrounding, not the actual feeding on ants, we propose that *T. stenaspis* was not feeding on ants. Ants are dangerous prey and feeding on them requires morphological and behavioral specialization (e.g., Pekár et al. 2008, 2011). We have not observed any adaptation useful for capture of ants in this spider species. *Triaeris stenaspis* is thus likely myrmecophilous but not myrmecophagous.

In the laboratory, *T. stenaspis* consumed springtails almost exclusively and haphazardly preyed on other prey. Spiders uniformly used the grasp-and-hold predatory tactic to capture springtails, termites, and crickets. Several other spiders use this tactic (Nentwig 1987). The grasp-and-hold tactic seems efficient for the capture of mobile prey, because after a bite such prey could escape the spider. This is particularly

important for species capable of fast escape, such as springtails with furca.

The venom of *T. stenaspis* seems to be extremely effective in immobilizing springtail prey. Springtails with bodies larger than the spiders were not able to jump more than once. The spider injected the venom behind the head, near the central neural system, and the paralysis latency was only a few seconds. Thus *T. stenaspis* was able to immobilize the large springtail within a few seconds.

Most cursorial spider species prey on much smaller prey than themselves (Nentwig 1987). *Triaeris stenaspis* was able to catch springtails larger than itself, even capturing one termite double its size. The ability to capture much larger prey is typical for many stenophagous predators (e.g., Pekár et al. 2008) that possess various adaptations to capture their specific prey.

Springtails are consumed by many spider species either of cursorial or web-building habit, such as corinnids (Pekár & Jarab 2011), linyphiids (Sunderland et al. 1986; Nyffeler & Benz 1988; Alderweireldt 1994), lycosids (Hallander 1970; Gettmann 1978; Punzo 2006), salticids (Guseinov et al. 2004; Huseynov et al. 2005), theridiids (Ibarra- Núñez et al. 2001) and thomisids (Guseinov 2006). The spiders differ in the way they capture springtails. Although web-builders such as *Lepthyphantes* (Linyphiidae) rely on the use of webs, cursorial species such as *Erigone*, *Oedothorax* (both Linyphiidae) or *Mexcala* (Salticidae) grasp springtails with their forelegs and chelicerae (Alderweireldt 1994; Pekár & Haddad 2011). The linyphiid *Bathypantes simillimus* (L. Koch 1879) captures springtails by means of two different strategies (Rybak 2007): juvenile individuals rely on the web (a springtail gets entangled in a web by its hairs), while adult spiders grasp springtails with their chelicerae.

For spiders, many springtails are palatable prey, except for some species that are toxic (Toft & Wise 1999). Springtails, however, possess efficient defenses: species having furca can escape by jumping either from a web or from a spider's forelegs. For a predator that is of similar or smaller size, the springtails can jump after being grasped. Such "rodeo-riding" on the springtail may carry a high risk of injury to the spider. Springtails with a spider attached to their back jumped high enough to hit the lid of the experimental arena. This strong knock could cause serious injury to the spider's soft abdomen. However, three scuta located on both sides of the soft abdomen in *T. stenaspis* seem to prevent such injury. Whether the scuta can be considered morphological adaptations used for defense against prey remains to be investigated.

Our study found that springtails are readily accepted as prey by *T. stenaspis*, even when the prey is longer than the spider. It is yet to be discovered whether *T. stenaspis* is a collembolan specialist and whether such prey-specificity is a fundamental property of all populations of this species or only a case of local specialization. Although data gathered so far do not provide clear evidence for specific adaptations, we found a high efficiency of capture of collembolan prey. This efficiency is attributed to their powerful grasp-and-hold tactic and the fast-ensuing paralysis from the spider's bite. Riding the "rodeo" on the springtail back is a behavioral trait serving to avoid the loss of the escaping prey. Strong scuta on the spider abdomen could be a morphological trait that protects

the spider's soft parts against injury during "rodeo." The short paralysis latency suggests that the venom is used for fast immobilization and minimizing the duration of the dangerous "rodeo." Finally, in our previous study, we reared this spider species on a monotypic diet of springtails (Korenko et al. 2009); the spiders suffered low mortality, were able to develop completely and produce viable offspring. They also seem to possess physiological adaptations to utilize a monotypic springtail flesh. Whether these traits have evolved as an adaptation to collembolan prey remains to be proven.

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