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Trophic niche and capture efficacy of an ant-eating spider, *Euryopis episinoides* (Araneae: Theridiidae)

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Abstract. In this study, field and laboratory observations of the feeding ecology (natural diet, prey acceptance, prey capture behavior and capture efficacy) of the theridiid *Euryopis episinoides* Walckenaer, 1847 were combined to reveal its trophic niche and capture efficacy and to test the hypothesis that this species is an ant-eating specialist. Natural prey was investigated from individuals collected in southern Portugal and was found to contain only ants of several species. Prey acceptance experiments revealed that spiders accepted several prey types occasionally, but ants, termites, and fruit flies were accepted with a high frequency. Prey capture behavior was similar for four tested prey types (Formicinae and Myrmicinae ants, termites, and fruit flies). Hunting usually started with a wrapping sequence when the spider threw the silk from its spinnerets onto the prey while circling around it. Then the spider bit the prey and wrapped it in more silk. Afterwards the spider waited for some time until the venom paralyzed the prey. Finally, the spider attached the immobilized prey to its spinnerets and carried it away before feeding. Wrapping time, number of bites, and waiting time differed among the four prey types, with the longest wrapping time, the highest number of bites, and the longest waiting time recorded during the capture of Myrmicinae ants. We conclude that *E. episinoides* is an ant-eating specialist possessing an effective capture strategy for the capture of ants. Yet, *E. episinoides* spiders maintain the ability to capture alternative prey.

Keywords: Ants, diet breadth, myrmecophagous, trophic specialization

Spiders are among the most abundant predators in terrestrial ecosystems and have diversified enormously with respect to foraging habits (Cardoso et al. 2011). The majority of spider species seem to be euryphagous, or oligophagous with a slightly restricted diet (Nentwig 1987), while only a few species are stenophagous, feeding on a few prey types. Most spider species prefer to hunt prey which is innocuous (Pekár et al. 2012) so that prey capture poses no risk to them, but some spiders also catch dangerous prey, such as other spiders (e.g., Whitehouse 1987), ants (e.g., Pekár 2004; Jackson & Nelson 2012), or termites (e.g., Eberhard 1991). Spiders which frequently hunt dangerous prey have evolved various adaptations to avoid being injured or even killed by such prey during prey capture (Pekár & Toft 2015).

Typically, ants, as dangerous prey, are avoided by most euryphagous spiders (e.g., Huseynov et al. 2008). However, some spider species have become specialized on ants; indeed, myrmecophagy is the most frequent type of stenophagy in spiders (Pekár et al. 2011). Predominantly myrmecophagous spiders are found in a number of families, particularly of the cursorial guild (Cushing 2012; Pekár & Toft 2015). For example, many species of the genus *Zodarion* Walckenaer, 1826 (Zodariidae) feed only on ants and reject other prey types (Allan et al. 1996; Pekár 2004; Pekár et al. 2005, 2008).

Myrmecophagous spiders often use specialized capture strategies to subdue ants (Cushing 2012; Jackson & Nelson 2012). For example, cursorial myrmecophagous spiders rely mainly on venom during ant capture (Jackson & Nelson 2012). Ant-eating spiders from the families Zodariidae or Salticidae typically employ an attack-and-release strategy, which minimizes the time spent in close proximity with the ant (Li et al. 1999; Jackson & Li 2001; Pekár 2004; Huseynov et al. 2008). Web-building spiders from the family Theridiidae use sticky silk when hunting prey, which is very effective particularly for the capture of crawling prey such as ants (Nørgaard 1956; Nentwig 1987). A passing ant becomes stuck to the end of the trip line, which is equipped with highly adhesive gumdrops (Hölldobler 1970; MacKay 1982; Nyffeler et al. 1988). Web-building myrmecophagous spiders situate their webs close to places with high ant densities. They often build their webs over ant foraging trails (Nørgaard 1956; MacKay 1982; Cushing 2012) or even directly over ant nest entrances (Hölldobler 1970; MacKay 1982).

Myrmecophagous spiders occur near ants and must be adapted to moving among them safely. *Zodarion* spiders build igloo-like shelters from detritus under rocks that are situated in close proximity to ant nests and serve as safe places when they are not hunting (Jocqué 1991; Pekár & Král 2001). Both *Zodarion* spiders and myrmecophagous crab spiders of the species *Aphantochilus rogersi* O. P.-Cambridge, 1871 (Thomisidae) carry the paralyzed ant as a shield to protect themselves from attack by passing ants (Castanho & Oliveira 1997; Pekár & Král 2002).

In this study, we focused on *Euryopis episinoides* (Walckenaer, 1847) from the family Theridiidae, which occurs in the Mediterranean area and Asia (World Spider Catalog 2017). Although most theridiid species are web-builders, spiders of the genus *Euryopis* Menge, 1868 do not build webs for prey capture (Carico 1978). Instead, they cast silk threads onto the prey directly from their spinnerets. After the prey is entangled in the silk and cannot escape, they give one or more bites to paralyze it. A similar capture strategy was observed in spiders of the genera *Oecobius* Lucas, 1846 (Oecobiidae) and *Hersilia* Audouin, 1826 (Hersiliidae) (Bristowe 1930; Glatz 1967).

Observations concerning the prey of *Euryopis* species are mainly anecdotal in nature. According to them, *Euryopis* spiders prey mostly on ants. For example, Levi (1954) listed observations of several *Euryopis* species preying on ants; Berland (1933) reported that *E. episinoides* captured *Crematogaster* ants; Carico (1978) observed *E. funebris* (Hentz, 1850) adult females feeding mainly on *Camponotus castaneus* Latreille, 1802, and immature specimens feeding on a variety of ant species; Gertsch (1979) observed females of *E. texana* Banks, 1908 preying upon small ants; Porter & Eastmond (1982) frequently observed the close association of spiders of *E. coki* Levi, 1954 with *Pogonomyrmex* ants.

Here, we tested the hypothesis that *E. episinoides* is stenophagous and specialized on ants. We studied its natural diet, prey acceptance, prey capture behavior, and capture efficacy.

METHODS

Studied species.—We collected individuals of *Euryopis episinoides* together with their silken retreats constructed under stones in Lagoa do Santo André, Alentejo, Portugal (38°05′54.9″N, 8°46′53.7″W) in May 2011. After transfer to the laboratory in the Czech Republic, we kept live individuals singly in plastic tubes (diameter 5 mm, height 50 mm) with a layer of gypsum at the bottom. The tubes were plugged with rubber foam and maintained under controlled conditions (26 °C, L:D = 16:8). The gypsum was moistened with a few drops of water at four-day intervals.

Natural prey analysis.—The silken retreats of *E. episinoides* spiders contained small bundles of prey remnants (carcasses), as, after feeding, these spiders usually place prey carcasses in the same spot (Pekár, pers. observ.). We collected seven prey bundles and placed them separately in plastic tubes with ethanol. In the laboratory, we counted the number of prey individuals in each prey bundle and identified each prey individual to species level using the identification key by Collingwood & Prince (1998).

Prey acceptance experiment.—In this experiment, we observed the spiders' capture success with different prey types. We used 11 prey types from ten arthropod orders, namely fruit flies (*Drosophila melanogaster*, Diptera, mean body length 2 mm), termites (workers of *Reticulitermes grassei*, Isoptera, 3.5 mm), springtails (*Sinella curviseta*, Collembola, 4 mm), crickets (*Gryllus assimilis*, Orthoptera, 5 mm) and cockroaches (*Paratemnopteryx couloniana*, Blattodea, 5 mm) from laboratory reared cultures; spiders (*Xysticus* C. L. Koch, 1835 sp., Thomisidae, Araneae, 3.5 mm), beetles (Curculionidae, Coleoptera, 3 mm), bugs (larvae of Miridae, Heteroptera, 3.5 mm), ants (workers of *Messor barbarus*, 7 mm, *Myrmica rubra*, 5 mm, *Lasius niger*, 3 mm, Hymenoptera) and thrips (Thysanoptera, 1 mm) from the field. As a predator, adult females of *E. episinoides* spiders (mean body length 3 mm) were used.

Before the start of the experiment, we placed *E. episinoides* spiders ($n = 45$) individually in Petri dishes (diameter 40 mm). We left the spiders in the Petri dishes for one hour prior to releasing one live prey individual into each dish. We recorded whether the spider attacked and captured the prey. If the spider did not attack the prey within 15 min, we removed the prey from the dish and introduced another prey type. If the spider did not attack any prey during the experiment, it was not included in the analysis and the experiment with such an individual was repeated four days later. We used a randomized incomplete block design so that each prey type was used with at least ten spider individuals in a random order.

The breadth of the fundamental trophic niche was estimated by means of the standardized Levin's index (B_A), which varies between 0, when the niche breadth is minimal, up to 1, when the species does not discriminate among prey types (Hurlbert 1978). Values of B_A higher than 0.6 indicate a wide trophic niche, and values below 0.4 indicate a narrow niche (Novakowski et al. 2008).

Prey capture behavior.—In this experiment, we observed the predatory sequence with different prey types. We used adult female spiders as predators. As prey, we used prey types that were accepted in prey acceptance experiment with the probability higher than 50%. We used ants from two ant subfamilies, Formicinae (*Lasius niger*, $n = 11$) and Myrmicinae (*Messor barbarus*, $n = 14$); termites (*R. grassei*, $n = 10$); and fruit flies (*D. melanogaster*, $n = 12$). Before the start of the experiment, we placed spiders individually in Petri dishes (diameter 40 mm). We left the spiders in the Petri dishes for one hour before releasing one live prey individual into each dish. The following prey capture behavior was recorded on a video camera (Canon Legria HF R56). These recordings were then analysed and used to construct a kinematic diagram of prey capture behaviors.

We distinguished the following behavioral events: *encounter*—when the spider first encountered the prey; *wrap*—the spider circled around the prey while throwing a few strands of silk on it; *bite*—the spider bit the prey; *wait*—the spider retreated from the prey and waited for a while at a safe distance; *attach*—the spider attached the immobilized prey to its spinnerets; *carry* – the spider dragged the immobilised prey away; *feed*—the spider started to consume the prey. The sequences and frequencies of hunting behavior that followed *encounter* and ended with the successful subduing of the prey (*feed*) were used to construct flow diagrams with transition frequencies for selected prey types. The transition frequencies for the first step (i.e., encounter to wrap) were estimated from the total number of spider individuals used with a particular prey. The transition frequencies for all following steps were estimated from the number of individuals that had gone through the previous step; thus, the sum of the transition frequencies from one step to another was 1.

From the predatory sequence for each prey species, we estimated an entropy index using the Shannon formula (Lehner 1998). This index allowed us to compare the stereotypy of prey capture behavior among different prey types, where a lower value meant more stereotyped behavior while a higher value indicated a more complex hunting sequence.

Capture efficacy.—During the prey capture behavior experiment, we also measured the time taken by the spider to wrap the prey in silk; the total number of bites; and the waiting time (i.e., time between biting and the beginning of feeding).

Data analyses.—We performed all analyses in R (R Development Core Team 2010). The probability of prey acceptance was compared among prey types using Generalised estimating equations with the binomial distribution (GEE-b). GEE is an extension of GLM for correlated data such as repeated measurements on the same individuals (Pekár & Brabec 2018). An exchangeable correlation structure was used. Wrapping time and waiting time were compared among prey types using Generalised linear models with the gamma distribution (GLM-g) due to the heteroscedasticity of the data. Number of bites was compared among prey types using

Table 1.—List of prey items found in seven bundles in the retreat of *Euryopis episinoides* females in Lagoa do Santo André, Alentejo, Portugal.

Bundle #	Prey species	number of individuals
1	*Tapinoma erraticum*	13
2	*Messor marocanus*	1
	Tapinoma erraticum	15
3	*Aphaenogaster senilis*	1
	Tapinoma erraticum	15
4	*Aphaenogaster senilis*	1
	Tapinoma erraticum	11
5	*Messor marocanus*	2
	Tapinoma erraticum	25
6	*Tapinoma erraticum*	9
7	*Tapinoma erraticum*	1

GLM with Poisson distribution (GLM-p) (Pekár & Brabec 2016).

RESULTS

Natural prey.—The analysis of seven prey bundles collected from the retreat of *E. episinoides* female spiders revealed 94 prey items in total. All individuals were ants belonging to three species (Table 1): the majority of the prey (94.6%) were *Tapinoma erraticum* (Dolichoderinae, mean body size 3–4 mm); the remaining individuals were *Messor marocanus* (6–8 mm, Myrmicinae), and *Aphaenogaster senilis* (6–7 mm, Myrmicinae).

Prey acceptance.—The probability of prey acceptance in the laboratory differed significantly among the 11 used prey types (GEE-b, $X^2_{10} = 141908$, $P<0.0001$, Table 2): *E. episinoides* spiders accepted only termites, ants, and fruit flies in more than 50% of cases. Termites and ants of both subfamilies were accepted with significantly highest probabilities (contrasts, $P<0.0001$). Crickets were accepted in 40% of cases, but the acceptance probability did not differ significantly from fruit flies (contrasts, $P = 0.13$). The other prey types were accepted significantly less frequently (contrasts, $P<0.001$). Springtails and bugs were accepted in less than 10% of cases, and beetles, cockroaches, spiders, and thrips were rejected. Levin's index of fundamental trophic niche breadth (B_A) was 0.38, indicating a narrow niche.

Prey capture behavior.—*Euryopis episinoides* began hunting with a specific hunting posture, with the first three pairs of legs placed on the ground and the hind legs lifted up in the air alongside its elevated abdomen (See Video 1, showing capture and handling of a *Messor* ant by a *Euryopis episiniodes* female, online at http://dx.doi.org/10.1636/JoA-S-17-102.s1). At the same time, it drew a new short thread of silk from its spinnerets each time it lifted its abdomen. Once the prey moved close enough to the threads, the spider began throwing the silk from its spinnerets onto the prey while circling around it, its abdomen pointing at the prey (Fig. 1A). Usually the hunting sequence continued with the spider biting the prey (Fig. 1B) and wrapping it in more silk; then, the spider waited for some time until the prey was motionless. Finally, the spider began to feed or attached the immobilized prey to its spinnerets and carried it away before feeding.

There were some differences in prey capture sequence among four prey types, i.e., termites, fruit flies, Formicinae and Myrmicinae ants (Fig. 2). Both Formicinae and Myrmicinae ants were always bitten at least once during the prey capture sequence, while termites and fruit flies were often not bitten at all, the spiders start the feeding on them immediately after wrapping.

The Shannon entropy index of behavioral sequences was 2.05 for Formicinae, 2.64 for Myrmicinae, 2.22 for termites, and 0.83 for fruit flies, indicating that fruit flies were hunted in the most stereotyped way, while other prey types required more complex hunting behavior.

Capture efficacy.—The wrapping time differed among prey types (GLM-g, $F_{3,99} = 34.2$, $P<0.0001$): the wrapping of Myrmicinae ants was much longer than the wrapping of other prey types (contrasts, $P<0.0001$, Fig. 3A). The number of bites during prey capture also differed among used prey types (GLM-p, $\chi^2_3 = 20.4$, $P<0.0001$): significantly more bites were used in the capture of Myrmicinae ants than in the capture of other prey types (contrasts, $P<0.04$, Fig. 3B). The waiting time also differed among prey types (GLM-g, $F_{3,\ 99} = 14.3$, $P<0.0001$): the longest waiting time was recorded during the capture of Myrmicinae ants (contrasts, $P<0.04$) and the shortest during the capture of fruit flies (contrasts, $P<0.01$, Fig. 3C).

Table 2.—Frequency of acceptance of different prey types by *Euryopis episinoides* females in laboratory experiments; n = number of observations.

Prey order	Family/Genus/Species	Acceptance frequency (%)	*n*
Araneae	Thomisidae	0.0	42
Collembola	*Sinella curviseta*	6.5	31
Blattodea	*Paratemnopteryx couloniana*	0.0	16
Isoptera	*Reticulitermes grassei*	95.2	21
Orthoptera	*Gryllus asimilis*	40.0	15
Thysanoptera		0.0	17
Heteroptera	Miridae	3.7	27
Hymenoptera	Myrmicinae (*Messor* sp., *Myrmica* sp.)	85.3	34
	Formicinae (*Lasius* sp.)	89.6	48
Coleoptera	Curculionidae	0.0	26
Diptera	*Drosophila melanogaster*	52.4	42

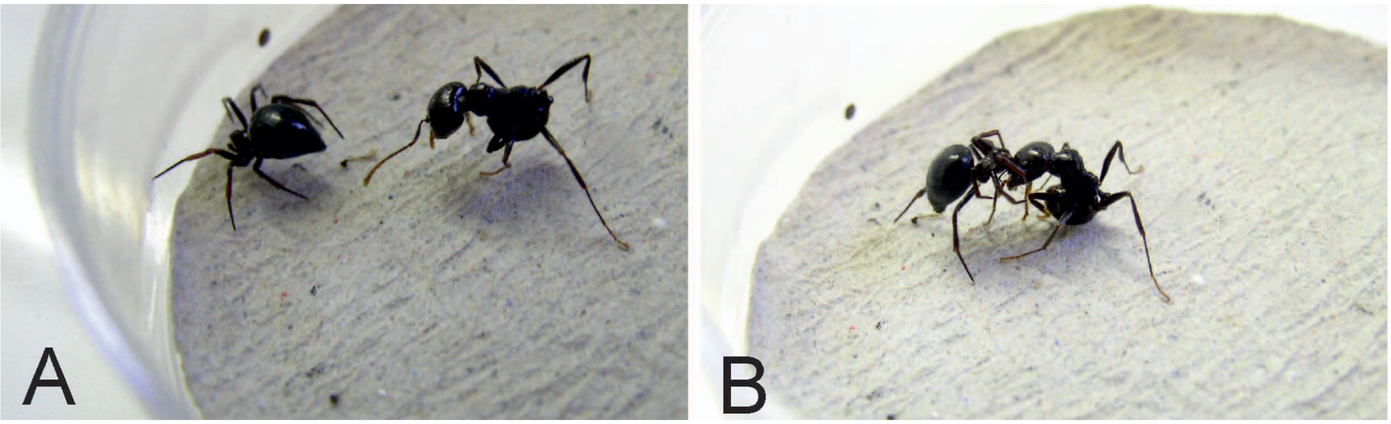

Figure 1.—*Euryopis episinoides* spider attacking a *Messor* ant. (A) Throwing silk from spinnerets. (B) Biting into the base of the antennae.

DISCUSSION

The analysis of natural prey revealed that the realized trophic niche of *E. episinoides* is narrow, as it includes only ants, which is well in agreement with observations on other *Euryopis* species (Berland 1933; Levi 1954; Allred 1969; Carico 1978; Porter & Jorgensen 1980; MacKay 1982). Thus, it would be tempting to consider *E. episinoides* as specialized myrmecophagous spiders. Yet, a narrow diet may also be observed in unspecialized predators if the habitat is dominated by a single prey type (Pekár et al. 2011; Monzó et al. 2013).

We analyzed the natural prey of *E. episinoides* only from a single site. It is possible that *E. episinoides* feeds on other prey types in other localities. Nonetheless, ants are very abundant prey in many terrestrial habitats (Hölldobler & Wilson 1990) and it seems from previous observations that *Euryopis* spiders prefer microhabitats with high ant abundances (Carico 1978; Porter & Eastmond 1982). As they are able to capture ants successfully, we believe that ants constitute the only – or, at least, the main – component of their diet at other sites, as indicated by previous observation (Berland 1933).

Yet, our acceptance experiments revealed that the fundamental trophic niche of *E. epsinoides* is wider than the realized niche, as it included some prey types other than ants. According to Levin's index, however, the fundamental trophic niche is still narrow, similar to other prey specialists (e.g., Michálek et al. 2017). We expected termites to be accepted, as this prey type is frequently accepted by other myrmecophagous spider species (Pekár 2004). Termites probably produce a signal similar to that of ants (e.g., a similar movement pattern)

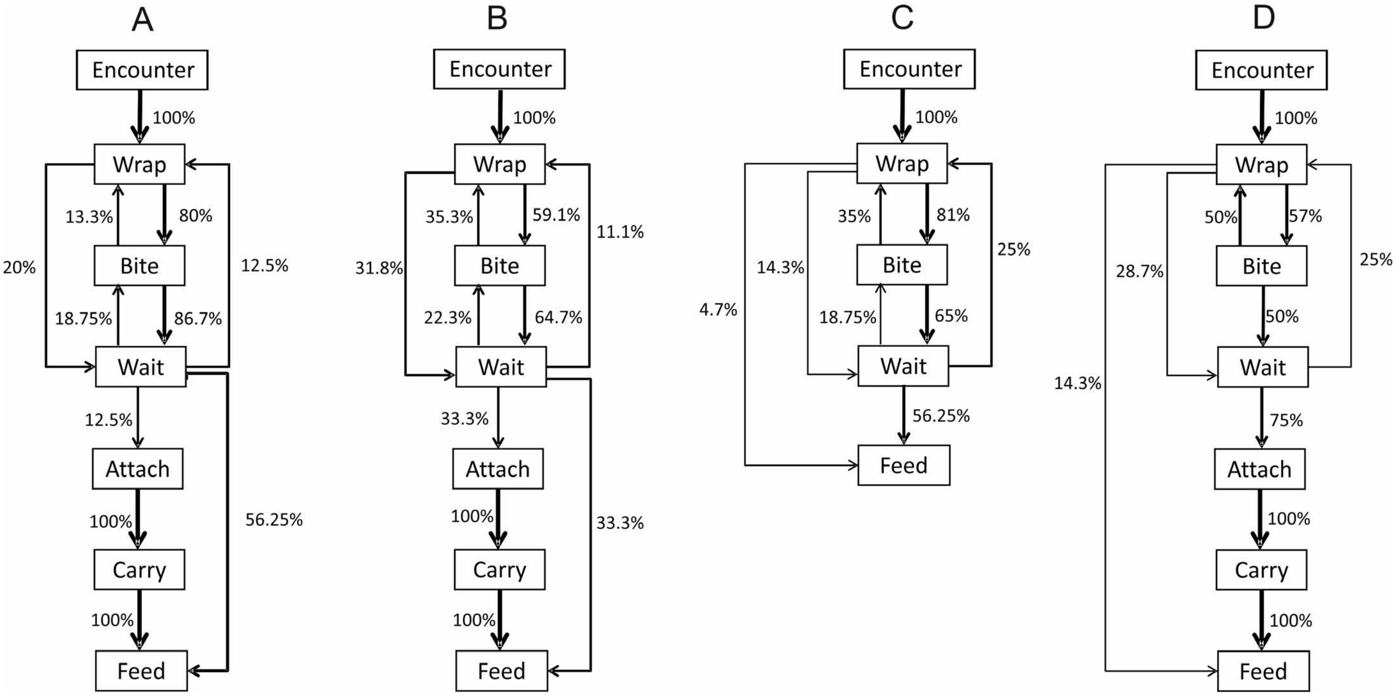

Figure 2.—Kinematic diagrams of the prey capture behavior of *Euryopis episinoides* used against four prey types with the relative frequencies of transitions. (A) Formicinae ants ($n = 11$); (B) Myrmicinae ants ($n = 14$); (C) termites ($n = 10$); (D) fruit flies ($n = 10$). The transition frequencies between events are also indicated by the width of the line.

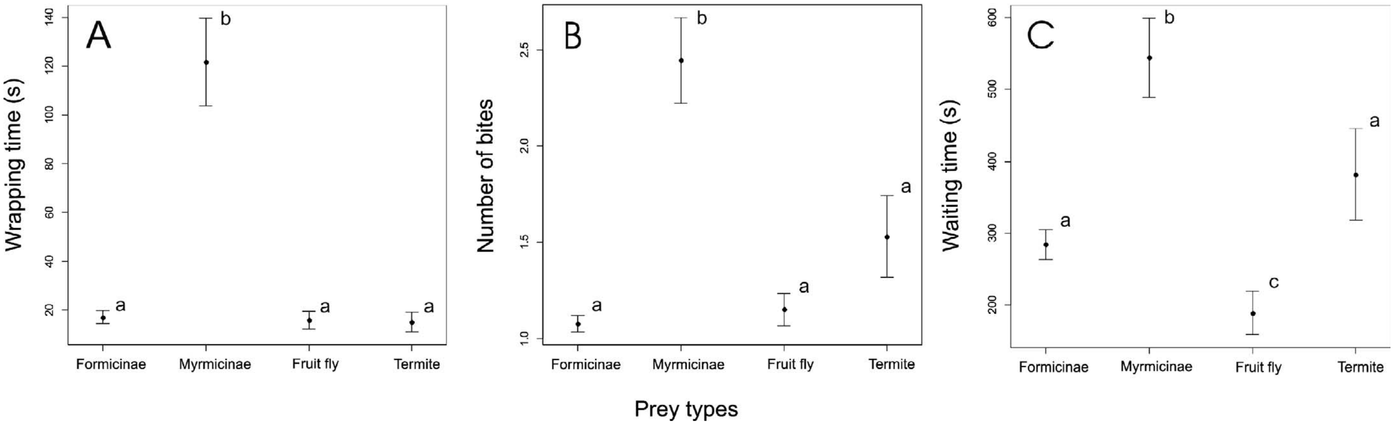

Figure 3.—Comparison of the wrapping times (A), numbers of bites (B), and waiting times (C) of *Euryopis episinoides* for four different prey types: Formicinae ants ($n = 39$), Myrmicinae ants ($n = 27$), fruit flies ($n = 20$), and termites ($n = 17$). Points are means, whiskers are SE. Different lower case letters next to whiskers indicate significant differences among prey types.

and are therefore accepted. Surprisingly, fruit flies were captured with quite a high frequency; nevertheless, we believe that flies are seldom captured in nature because the capture strategy of *E. episinoides* is adapted for crawling insects (Carico 1978). This is supported with a relatively high capture frequency of crickets. On the other hand, other crawling insects, namely cockroaches, were not captured at all. That is, the spiders attempted to catch them but they were too quick and went outside the spider's hunting range. *Euryopis episinoides* also approached beetles, bugs and thomisid spiders, but as soon as they touched them, they ceased hunting. Thrips were not even approached by *E. episinoides*, as they were probably too small to be considered as suitable prey. Overall, therefore, the results concerning both realized and fundamental trophic niche suggest that *E. episinoides* spiders are myrmecophagous; that is, they are at least able to feed on ants.

The question remains, however, as to whether *E. episinoides* is specialized in the capture of ants. A stenophagous specialist *sensu* Pekár & Toft (2015) exhibits a variety of adaptations that enhance efficiency in the utilization of preferred prey. Furthermore, prey-specific adaptations are found primarily when predators hunt exceptionally dangerous prey (Brodie & Brodie 1999). Hereafter, we will deal in more detail with traits of *E. episinoides* that might be specifically tuned to ants.

Due to their restricted diet range, specialists have become adapted to recognizing a narrow range of prey cues (Dukas & Kamil 2001). The predatory behavior of *E. episinoides* is driven by olfactory cues from prey deposited on the substrate. It was found that these spiders have an innate olfactory preference for ants (Pekár & Cárdenas 2015). Such selective attention may be beneficial as it may help the spider to prepare for the use of a specific foraging strategy and both increase prey capture efficiency and decrease the risk when hunting dangerous ants. Chemical cues from preferred prey have been found to be important also in other myrmecophagous spiders (Clark et al. 2000).

The ability to recognize the prey type before initiation of the hunting sequence may be important if the predator uses versatile strategies that are tuned to a particular prey type (Jackson & Nelson 2012). The hunting sequence may be distinctively different for different prey types (Jackson 1992). Most myrmecophagous salticids capture ants using specific prey capture tactics but use other tactics to catch other prey (Jackson & Olphen 1991; Jackson & Li 2001). One myrmecophagous salticid, *Anasaitis canosa* (Walckenaer, 1837), even distinguishes ants of different size and accordingly uses different hunting tactics (Edwards et al. 1974). The hunting behavior of *E. episinoides* differed for four different prey types. In trials with fruit flies and termites, the prey was sometimes only wrapped in silk. Probably, the wrapping was sufficient to immobilize the prey and the spider did not need to invest any venom. The fact that the fruit fly hunting sequence had the lowest value on the Shannon entropy index indicates that this prey was hunted in the most stereotyped way, while other prey types required more complex hunting behavior.

However, greater differences among prey types were revealed when we looked into the investment of silk, venom, and handling time. The wrapping and waiting times were longest, and the number of bites the highest during the capture of Myrmicinae ants (*Messor*), which were the biggest prey used and probably also the most dangerous. In contrast, the capture of smaller Formicinae (*Lasius*) ants required a similar investment of venom, silk, and time as the capture of innocuous fruit flies. *Lasius* ants were probably optimal for *E. episinoides* spiders, as they were similar in body size to *T. erraticum* ants, which were found to be the most abundant prey of *E. episinoides* in nature. Termites were wrapped only for a short time, but their capture involved repeated bites and a long waiting time for paralysis, probably due to reduced efficacy of the venom in non-preferred prey (Pekár et al. 2018).

Even if a specialized predator is able to catch alternative prey, feeding on such prey may have a negative effect on its fitness. Our previous study (Líznarová & Pekár 2016) with *E. episinoides* revealed that fruit flies do not provide a suitable food source. Specifically, the fitness of *E. episinoides* reared on alternative prey was markedly reduced (Líznarová & Pekár 2016). Probably, the presence of metabolic adaptations to ants constrains the utilization of alternative prey. The ability of *E. episinoides* to capture and feed on alternative prey is probably advantageous only for a short period of preferred prey scarcity.

Our results revealed that *E. episinoides* is stenophagous, capturing only ants in their natural habitat. Further, we found that *E. episinoides* was able to capture Formicinae ants with a similar efficiency as for innocuous alternative prey, indicating that it is adapted to ants. Their capture strategy even allows them to catch ants more than two times bigger than themselves, which is another indication of specialization (Pekár et al. 2014). All these findings taken together suggest that *E. episinoides* spiders possess specialized adaptations and thus can be considered as myrmecophagous specialists.

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