2021. Journal of Arachnology 49:268–271

SHORT COMMUNICATION

Fundamental trophic niche of two prey-specialized jumping spiders, *Cyrba algerina* and *Heliophanus termitophagus* (Araneae: Salticidae)

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Abstract. Spiders are among the most taxonomically diversified orders of predators, but data on the trophic niche of most species are still unknown. Here, we investigated the fundamental trophic niche of two species of jumping spiders, *Cyrba algerina* (Lucas, 1846) and *Heliophanus termitophagus* Wesołowska & Haddad, 2002, for which data on their realized trophic niche suggest trophic specialization (feeding on other spiders or termites, respectively). We investigated their fundamental trophic niche by means of acceptance experiments. Both species accepted a broader spectrum of prey under laboratory conditions than in the field, suggesting they are euryphagous specialists.

Keywords: Araneophagy, diet breadth, prey acceptance, specialization, termitophagy

https://doi.org/10.1636/JoA-S-20-060

Spiders are a highly diversified order of predators that feed on various prey and utilize different hunting strategies (Cardoso et al. 2011). However, trophic interactions have only been described in a fraction of the total spider diversity (Pekár et al. 2012), which is still increasing as new species are being described at an exponential rate annually (World Spider Catalog 2020). Although a little information on a species' biology may accompany its description, or scientific studies focused on different phenomena may have been published, such information is mostly anecdotal. Detailed observations, ideally both in the field and in the laboratory, need to be performed to provide more reliable information about a species' biology and diet.

The diet of a given species is typically evaluated by measuring the breadth of its trophic niche. Two types of trophic niche can be distinguished – fundamental and realized (Hutchinson 1957). The fundamental trophic niche comprises two dimensions represented by prey type and prey size, whereas the realized trophic niche is further determined by prey availability at the locality investigated (Pekár et al. 2017). Investigation of the fundamental trophic niche can be performed in the laboratory with a reasonable number of spider individuals collected in the field, whereas the realized trophic niche can only be inferred from field data – either from direct observations of predatory events or by means of gut content analysis (Pekár et al. 2017).

Based on the breadth of their diet, stenophagous species with narrow trophic niche and euryphagous species with a broad niche can be distinguished. Additionally, predators can be defined as either specialists or generalists, depending on the adaptations they utilize to handle prey (Pekár & Toft 2015). Most spiders are considered euryphagous and generalists, hunting a wide variety of prey indiscriminately; species with restricted diets are less common, although more stenophagous species may be discovered with increasing research effort into their diet (Pekár et al. 2012). The level of prey specialization cannot be assessed solely from the breadth of the realized trophic niche, as even spiders with narrow niches may be utilizing generalized adaptations to handle a prey (Líznarová & Pekár 2015). The level of specialization can be confirmed by means of laboratory experiments only, as specialists usually have a narrower fundamental trophic niche, due to the possession of specialized adaptations (morphological, behavioral, or physiological) that do not allow them to capture alternative prey.

Here, we investigated the fundamental trophic niche of two presumed prey-specialists from the family Salticidae that preferentially prey on their respective focal prey in nature. *Cyrba algerina* (Lucas, 1846) (Fig. 1a) is a jumping spider with a broad distribution from the Canary Islands to Central Asia (World Spider Catalog 2020), preferring other spiders as prey in nature and in laboratory prey-preference tests as well (Guseinov et al. 2004). *Heliophanus termitophagus* Wesołowska & Haddad, 2002 (Fig. 1b) is an endemic South African jumping spider associated with *Trinervitermes trinervoides* (Sjostedt, 1911) termite mounds and often feeding on termites in nature (Wesołowska & Haddad 2002). Current evidence, based on the realized niche and some laboratory experiments, therefore, suggests that these spiders are prey specialists.

We collected 33 individuals of *C. algerina* spiders (prosoma size 1.76 ± 0.29 mm) in Mértola, Portugal, in July 2015, and 23 individuals of *H. termitophagus* spiders (prosoma size 2.04 ± 0.17 mm) were collected in Bloemfontein, South Africa, in January 2016. Spiders were brought into the lab and kept in vials with moisturized gypsum on the bottom at a constant temperature (22 °C) and under a 16:8 LD regime.

To investigate their fundamental trophic niche, acceptance trials were performed. Trials with 20–30 individuals of each spider species were performed for each of the ten prey types (Table 1). Various arthropod orders were used to cover a broad spectrum of potential prey. Prey species/genera were chosen based on their availability in our rearing facility and the surroundings of the university campus. Spider individuals were placed singly into Petri dishes (diameter 5cm) and the trial began after at least 1 hour of acclimation. One of the selected prey types was offered to each individual spider in a random order. If the prey was not attacked within 1 hour, it was replaced with a different prey type. The trial ended when a spider killed and consumed prey. The data were excluded if the spider did not accept any prey types during a trial, to rule out cases where the spider was satiated or preparing to molt. Trials were repeated in approximately one-week intervals. The breath of the trophic niche was then calculated using the standardized Levins' index (B_A) (Hurlbert 1978). The index is standardized on a scale from zero to one; values closer to zero indicate a narrow niche, while values closer to unity indicate a broad niche.

Statistical analyses were performed in R (R Core Team 2019). The difference in rates of acceptance of prey types was analyzed using

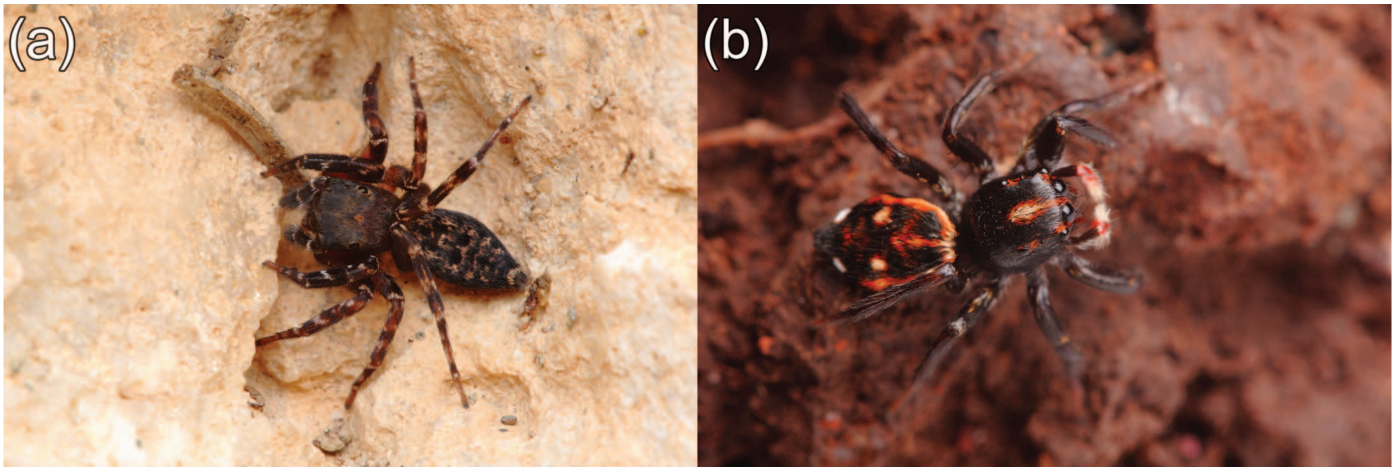

Figure 1.—*Cyrba algerina* (a) and *Heliophanus termitophagus* (b). Photos by O. Michálek.

Generalized Estimating Equations (GEE) from the geepack package (Halekoh et al. 2006). We used a GEE model with a binomial distribution and a logit link, due to the occurrence of repeated measurements on the same spider individuals (Pekár & Brabec 2018). Prey acceptance represented a response variable and prey type was an explanatory variable. We used an AR1 (the first-order autoregression model) correlation matrix to account for temporal replications, as the selected prey types were offered to the same individuals one by one in a randomized order. The acceptance rate of each prey type was also compared to the average acceptance rate, using a binomial test. The difference in acceptance of distinctively sized prey was analyzed separately using GEE, with prey size categories as an explanatory variable. Prey size was classified into four distinct categories – tiny, small, medium, and large (Table 1), as the exact size was not measured for each prey individual.

Cyrba algerina accepted seven out of the ten prey types offered (Fig. 2a). The average prey acceptance rate was 42.4%. It did not accept woodlice, beetles, and ants. The other seven prey types were accepted at significantly different rates (GEE, $\chi^2_7 = 26.1$, $P < 0.001$). Spiders were generally accepted at only slightly higher, not statistically significant, rate than the average (acceptance 55%; Binomial test, $P = 0.08$), but the acceptance rate differed between representative prey of two broad spider guilds: cursorial spiders were accepted at a higher rate (Zodariidae, acceptance 73%; Binomial test, $P = 0.004$) than web-building spiders, which were accepted at slightly less than the average rate only (Theridiidae, acceptance 38%; Binomial test, $P = 0.8$). Besides spiders, *C. algerina* also accepted springtails at high rates (acceptance 96%; Binomial test, $P < 0.0001$) and other insects (Blattodea, Isoptera, Ensifera, Lepidoptera, Diptera) at intermediate rates (acceptance 45–60%; Binomial tests, $P > 0.05$). The breadth of its trophic niche was on the border between intermediate and slightly wide ($B_A = 0.61$). *Cyrba algerina* accepted distinctively sized prey at significantly different rates (GEE, $\chi^2_3 = 36.5$, $P < 0.0001$), as it subdued either tiny or large prey at higher rates than small and medium prey (Fig. 2b).

Heliophanus termitophagus accepted seven out of the ten prey types offered (Fig. 2a). The average prey acceptance rate was 55.5%. Woodlice, beetles, and ants were not accepted. The other seven prey types were accepted at significantly different rates (GEE, $\chi^2_6 = 23.3$, $P < 0.001$). Springtails, termites, and fruit flies were accepted at very high rates (acceptance 90–96%; Binomial tests, $P < 0.001$). Spiders and caterpillars were accepted at rates slightly above average (acceptance 76–86%; Binomial tests, $P < 0.01$). Cockroaches and crickets were accepted at intermediate rates (acceptance 55–57%; Binomial tests, $P = 1.0$). The breadth of its trophic niche was also on the border between intermediate and slightly wide ($B_A = 0.64$). *Heliophanus termitophagus* accepted distinctively sized prey at significantly different rates (GEE, $\chi^2_3 = 62.5$, $P < 0.0001$). Similar to *C. algerina*, *H. termitophagus* subdued either tiny or large prey at higher rates than small and medium-sized prey (Fig. 2b).

Strictly specialized predators are not able to hunt alternative prey, due to extreme adaptations (e.g., behavioral or metabolic) for

Table 1.—List of prey types used in acceptance experiments, their body size, and the number of offered prey.

Order/Family	Species	Prey size		N	
		Length (mm)	Category	*C. algerina*	*H. termitophagus*
Isopoda/Armadillidiidae	*Porcellio scaber* Latreille, 1804; *Armadillidium vulgare* Latreille, 1804	4.62±1.10	Medium	25	21
Araneae/Zodariidae, Theridiidae	gen. et sp. indet.	2.05±0.28	Tiny	22	21
Collembola/Entomobryidae	*Sinella curviseta* Brook, 1882	1.50±0.00	Tiny	25	21
Dictyoptera/Blattellidae	*Symploce pallens* (Stephens, 1835)	3.77±0.98	Medium	23	22
Isoptera/Rhinotermitidae	*Reticulitermes* sp., *Termes* sp., or *Trinervitermes* sp.	3.00±0.00	Small	22	21
Ensifera/Gryllidae	*Acheta domestica* (Linnaeus, 1758)	4.03±0.53	Medium	22	21
Lepidoptera/Pyralidae	*Ephestia kuehniella* Zeller, 1879; caterpillars	6.57±1.67	Large	19	21
Hymenoptera/Formicidae	*Lasius* sp.	3.53±0.12	Small	21	20
Diptera/Drosophilidae	*Drosophila melanogaster* Meigen, 1830; *Drosophila hydei* Sturtevant, 1921	2.00±0.32	Tiny	26	23
Coleoptera/Chrysomelidae	*Callosobruchus maculatus* (Fabricius, 1775)	2.92±0.34	Small	21	21

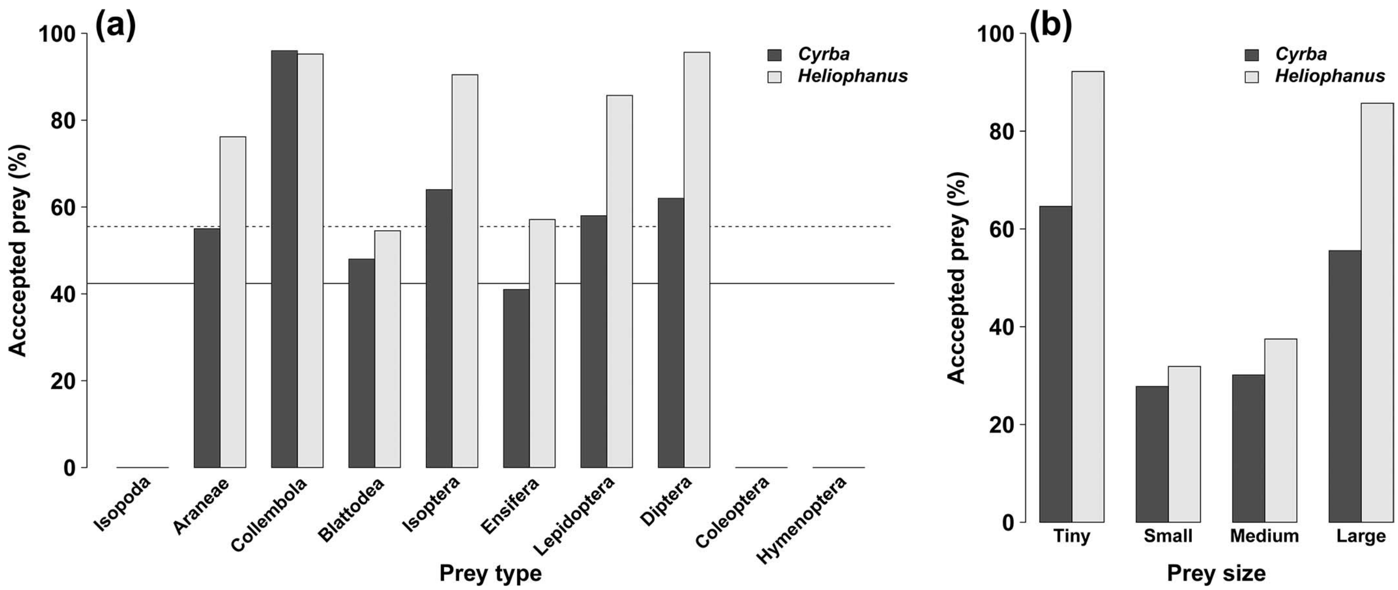

Figure 2.—(a) Comparison of the relative frequencies (in percentages) with which *Cyrba algerina* and *Heliophanus termitophagus* accepted ten prey types in the laboratory. The full and dashed horizontal lines show the overall mean of prey acceptance for *C. algerina* and *H. termitophagus*, respectively. (b) Comparison of the relative frequencies (in percentages) with which *C. algerina* and *H. termitophagus* accepted prey of four size categories.

capturing their focal prey (Pekár & Toft 2015). Less extremely specialized predators (euryphagous specialists *sensu* Pekár & Toft 2015) are, however, able to capture and consume prey other than their focal taxon as well. Therefore, their fundamental trophic niche is wider, although the realized trophic niche is often narrower (Pekár & Haddad 2011). A similar situation is also observed in stenophagous generalists, which have a narrower realized trophic niche due to, e.g., ecological constraints, but generalized prey-capture adaptations (Líznarová & Pekár 2015).

A comparison of the encounter rate and prey selection of different prey types in the field can help to distinguish between specialists and stenophagous generalists. If in a microhabitat the spiders are almost exclusively confronted with a single type of prey which they capture, it would indicate stenophagous generalists. If they encounter many types of prey but show strong selectivity towards one type, they would be classified as specialists. However, more experiments would be still needed to reveal prey-specific adaptations. For example, metabolic adaptations can be tested via long-term feeding experiments (e.g., Pekár & Toft 2009). Detailed observations on predatory strategies would be necessary to look for behavioral adaptations (i.e. specific hunting strategies for different prey) (e.g., Michálek et al. 2017). We did not perform such thorough experiments here.

Data from previous studies suggest that *C. algerina* is a euryphagous specialist, as it utilized prey-specific capture behavior and chose mainly spiders as prey in a prey-preference test over three types of insects (Diptera, Homoptera, Lepidoptera) (Guseinov et al. 2004). The same study reported that 56% of all field prey records were represented by spider prey, while none of the other arthropod orders (including Collembola, Diptera, Homoptera, Lepidoptera, Opiliones, Acari, Pseudoscorpiones, Heteroptera, and Hymenoptera) accounted for more than one-tenth of the prey records (Guseinov et al. 2004). However, in our experiment, *C. algerina* accepted a broad range of prey types at high frequencies. We also observed that *C. algerina* accepted cursorial spiders at a far higher rate than web-building spiders. Indeed, some araneophagous spiders specialize on spider prey from a particular guild (Harland & Jackson 2000). Interestingly, in a former study (Guseinov et al. 2004), *C. algerina* preferentially chose web-building *Oecobius* spiders over other predominantly cursorial spiders. We used a population from Portugal, while *C. algerina* from Guseinov et al. (2004) came from Azerbaijan. Perhaps these two distinct populations specialize on different spider guilds (Jackson et al. 1998), although this hypothesis requires further experiments.

Similar to *C. algerina*, *H. termitophagus* feed mostly on one prey taxon in the field – in this case, termites – and use a different strategy to hunt termites than other insects (Wesołowska & Haddad 2002). However, behavioral versatility has also been observed in other jumping spiders commonly considered as generalists (e.g., Bear & Hasson 1997; Bartos 2013). *Heliophanus termitophagus* was supposed to be a termitophagous specialist (Wesołowska & Haddad 2002), but the level of specialization was not tested in detail. Although field observations revealed *H. termitophagus* fed mainly on termites, attacks on other prey, including springtails, mites, and small flies, were also observed (Wesołowska & Haddad 2002). The broader spectrum of accepted prey was confirmed by our laboratory experiments. The broad fundamental but narrow realized trophic niche suggests that *H. termitophagus* is a euryphagous specialist, utilizing a specific prey capture strategy to capture termites, an adaptive strategy also encountered in the myrmecophagous salticid *Mexcala elegans* Peckham & Peckham, 1903 (Pekár & Haddad 2011).

Alternatively, *H. termitophagus* might be a stenophagous generalist with a flexible prey capture repertoire that utilizes the most abundant co-occurring prey (Líznarová & Pekár 2015). Other jumping spiders of the genus *Heliophanus* seem to be rather generalized predators (Haddad et al. 2004; Huseynov 2006), although they are not as closely associated with one abundant prey type as *H. termitophagus*. Experiments on paralysis latency have shown *H. termitophagus* does not paralyze termites quicker than other prey (Pekár et al. 2018). It, therefore, probably does not possess venomic adaptations to subdue termites. Specialists tend to feed on their focal prey for a longer period than generalists, as they are metabolically fine-tuned to utilize their focal prey to maximize nutrient gain (Michálek et al. 2017; García et al. 2018). In our experiments, *H. termitophagus* preyed on medium-sized prey like cockroaches and crickets for a longer period, but termites were consumed for a similar time as other smaller prey (Michálek, pers. obs.). This indicates that *H. termitophagus* might not be metabolically adapted to utilize termite prey only.

Most predators usually subdue prey smaller than themselves, as larger prey is harder to handle or it could be even dangerous for a predator (Griffiths 1980; Mukherjee & Heithaus 2013). However, specialized predators can capture even large prey because they possess specialized adaptations (Michálek et al. 2017). In our study, both *C. algerina* and *H. termitophagus* captured either tiny prey or large prey in the lab. Prey size was not independent of prey type, as most of the prey types used differ inherently in their size. Both spider species subdued bigger and more agile cockroaches and crickets at intermediate frequencies only, although they preyed on larger but less mobile caterpillars at higher rates. Such a bimodal distribution in prey size choice can be explained by a preference for more easily handled prey types, rather than the importance of particular prey size.

To conclude, *C. algerina* and *H. termitophagus* are not strict stenophagous specialists (*sensu* Pekár & Toft 2015). Consistent with previous studies, *C. algerina* can be classified as a spider-eating euryphagous specialist. More experiments would be needed to reveal the presence of specific or generalized prey-capture adaptations in *H. termitophagus*, and characterize the nature of its association with termite prey.

ACKNOWLEDGMENTS

The research was supported by the Czech Science Foundation (project no. GA15-14762S). Ondřej Michálek was supported by Masaryk University (project no. MUNI/A/1484/2014). Charles Haddad was supported by the National Research Foundation of South Africa (grant no. 95569). South African spiders were sampled under permit no. 01/25209 from the Free State Department of Economic Development, Tourism and Environmental Affairs.

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Manuscript received 7 August 2020, revised 21 September 2020.