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

3

4 Eva Líznarová & Stano Pekár*

5 Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611

6 37, Brno, Czech Republic

7

8

9

10 * Corresponding author: E-mail address: pekar@sci.muni.cz (S. Pekár)

11

12

13

14

15

16

17

18

19

20

21

22 Running head: LÍZNAROVÁ & PEKÁR: TROPHIC NICHE OF *EURYOPIS EPISINOIDES*

23

24

25

Abstract — Field and laboratory observations of the feeding ecology (natural diet, prey acceptance, and predatory behavior) of *Euryopis episinoides* spiders were combined in this study to reveal their trophic niche and capture efficacy and to test the hypothesis that this species is a myrmecophagous specialist. Natural prey was investigated from individuals collected in southern Portugal and was found to contain only ants of several species. Prey acceptance experiment revealed that spiders accepted several prey types occasionally, but only ants, termites, and fruit flies were accepted with a high frequency. Prey capture behavior was similar for four tested prey types. Wrapping time, number of bites, and waiting time differed among prey types with longest wrapping time, highest number of bites and longest waiting time during capture of Myrmicinae ants. From our findings we conclude that *E. episinoides* is a myrmecophagous specialist possessing specialized adaptations that enable them to capture ants. Yet, they maintain the ability to capture alternative prey.

38

39

40

41

42

44

Spiders are among the most abundant predators in terrestrial ecosystems and diversified enormously in foraging habits (Cardoso et al. 2011). The majority of spider species seem to be euryphagous or oligophagous with a slightly restricted diet (Nentwig 1987) and only a few species are stenophagous, feeding on restricted prey types. Most spider species hunt preferably prey which is innocuous (Pekár et al. 2012), so the prey capture is not risky for them, but some spiders catch also 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 hunt dangerous prey frequently, evolved various adaptations to avoid being injured or even killed by such prey during prey capture (Pekár & Toft 2015).

Specifically, ants as dangerous prey are avoided by most of the euryphagous spiders (e.g. Huseynov et al. 2008). However, some spider species specialized on ant capture; indeed myrmecophagy is the most frequent type of stenophagy in spiders (Pekár et al. 2011a). 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* feed only on ants and reject other prey types (Pekár 2004, Allan et al. 1996; Pekár et al. 2005; Pekár et al. 2008).

Myrmecophagous spiders use specialized capture strategies to subdue ants (Cushing 2012; Jackson & Nelson 2012), which differ from the hunting strategy used for other prey. For example, myrmecophagous web-building spiders from the family Theridiidae use sticky silk when preying on ants (Nørgaard 1956; Nentwig 1987). Passing ant is stuck at the end of the trip line, which is equipped with highly adhesive gumdrops (Hölldobler 1970; MacKay 1982; Nyffeler et al. 1988). Web-building spiders situate their webs close to places with high ant occurrence. 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).

69   Cursorial myrmecophagous spiders may not use silk but venom for ant capture (Jackson &

70   Nelson 2012). Ant-eating spiders from the family Zodariidae or Salticidae typically employ

71   attack-and release strategy that minimize the time in the ant proximity (Pekár 2004; Li et al.

72   1999; Jackson & Li 2001; Huseynov 2008). Cursorial spiders occur near to ants as well and they

73   must be able to move among them safely. *Zodarion* spiders build igloo-like shelters from the

74   detritus under the rock that are situated in the close proximity to ant nests and serves them as a

75   safe place when they are not hunting (Jocqué 1991; Pekár & Král 2001). Both *Zodarion* spiders

76   and myrmecophagous crab spider of the species *Aphantochilus rogersi* O. P.-Cambridge use

77   paralyzed ant as a shield to protect themselves from attack by passing ants (Castanho & Oliveira

78   1997; Pekár & Král 2002).

79   In this study, we focused on the spider species *Euryopis episinoides* (Walckenaer) from the

80   family Theridiidae that occurs in the Mediterranean area and Asia (World Spider Catalog 2017).

81   Although most theridiid species are web-builders, spiders of the genus *Euryopis* do not build any

82   permanent web for prey capture (Carico 1978). However, they use silk during prey capture as

83   they throw silk over the prey from their spinnerets while running around it, in similar way as

84   spiders of the genus *Oecobius* (Glatz 1967) and *Hersilia* (Bristowe 1930). After the prey is

85   tangled in silk and cannot escape, they give one or more bites to paralyze it.

86   There has been more than 70 species of *Euryopis* described in the world (World Spider

87   Catalog 2017). Published data on their prey indicate that *Euryopis* spiders prey mostly on ants,

88   suggesting they are myrmecophagous. For example, Levi (1954) listed observations on several

89   *Euryopis* species preying on ants. Berland (1933) reported that *Euryopis episinoides* captured

90   *Crematogaster* ants. Carico (1978) observed individuals of all instars and both sexes of *Euryopis*

91   *funebris* (Hentz) wandering on the trunks, branches and leaves; adult females fed mainly on large

92   red carpenter ant *Camponotus castaneus* (Latreille), whereas immature spiders fed on variety of

4

93   other ant species corresponding to their body size. Gertsch (1979) observed female of *Euryopis*

94   *texana* Banks preying upon small ants. Porter & Eastmond (1982) frequently observed spiders of

95   *Euryopis coki* Levi closely associated with *Pogonomyrmex* ants. However, adult females and late

96   instars accepted also fruit flies in a laboratory (Porter & Eastmond 1982).

97   Here, we studied specifically natural diet, prey acceptance, prey capture behavior and capture

98   efficacy of *E. episinoides* spiders to reveal if this species is stenophagous and specialized on ants

99   as suspected.

100

101   METHODS

102   **Study species.—**We collected individuals of *Euryopis episinoides* spiders together with their

103   silken retreats made under stones in Lagoa do Santo André, Alentejo, Portugal. After transfer to

104   the laboratory in the Czech Republic, we kept living individuals singly in plastic tubes (diameter

105   5 mm, height 50 mm) with a layer of plaster of Paris at the bottom. The tubes were plugged with

106   rubber-foam and maintained under controlled conditions (26 °C, L: D = 16:8). The plaster of

107   Paris was moistened with a few drops of water at 4-day intervals.

108

109   **Natural prey analysis.—**Spiders' silken retreats contained prey remnants (carcasses). These

110   spiders usually place prey carcass after feeding on one spot, thus creating small bundles of prey

111   remnants. We collected seven prey bundles and placed them separately in plastic tubes with

112   ethanol. We took them to laboratory where we counted number of prey individuals in each prey

113   bundle and identified each prey individual to the species level. We identified collected ant

114   remnants to species level using Collingwood & Prince (1998).

115

Prey acceptance experiment.—In the prey acceptance experiment, we observed the spiders'

capture success with different prey types. We used 11 prey species from ten invertebrate orders

and only adult female spiders. We took fruit flies (*Drosophila melanogaster*, Diptera, mean body

length 2.0 mm), termites (workers of *Reticulitermes* sp., Isoptera, 3.5 mm), springtails (*Sinella*

curviseta Brook, Collembola, 4.0 mm), crickets (*Gryllus assimilis* (Fabricius), Orthoptera, 5.0

mm), and cockroaches (*Paratemnopteryx couloniana* (Saussure), Blattodea, 5.0 mm) from

laboratory reared cultures. We collected spiders (Thomisidae, Araneae, 3.5 mm), beetles

(Curculionidae, Coleoptera, 3.0 mm), bugs (Miridae, Heteroptera, 3.5 mm), ants (workers of

Messor sp., 7 mm, *Myrmica* sp., 5 mm, *Lasius* sp., 3 mm, Hymenoptera) and thrips

(Thysanoptera, 1.0 mm) from the field.

Before start of the experiment we placed spiders (*n*=45) individually in a Petri dish (diameter

40 mm). We used only adult female spiders. We left spiders in the Petri dish for one hour before

we released one living prey individual in each dish occupied by spider. We recorded whether the

spider attacked and captured the prey. If the spider did not attack the prey within 15 minutes, we

removed the prey from the dish and replaced with another prey type. 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 using 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 narrow niche (Novakowski et al.

2008).

Prey capture behavior.—In the prey capture behavior experiment, we observed predatory sequence with different prey types. We used only adult female spiders. As prey we used ants from the two ant subfamilies, Formicinae (*Lasius* spp., *n*=11) and Myrmicinae (*Messor* sp., *Myrmica* sp., *n*=14), termites (*Reticulitermes* sp., *n*=10), and fruit flies (*Drosophila melanogaster*, *n*=12) because these were frequently accepted in acceptance experiments. Before start of the experiment, we placed spiders individually in a Petri dish (diameter 40 mm). We left spiders in the Petri dish for one hour before we released one living prey individual in Petri dish occupied by spider. Following prey capture behavior was recorded on a videocamera (Canon Legria HF R56). These recording were then analysed and used to construct a kinematic diagram of prey capture behaviours.

We distinguished the following behavioural events: *encounter* - when the spider first encountered prey; *wrap* - the spider circled around the prey and wrapped it in silk; *bite* – the spider bit the prey; *wait* – the spider retreated from the prey and waited for a while at a distance; *attach* – the spider attached immobilised 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 behaviour that followed encounter and ended with a successful subduing (*feed*) were recorded to construct the flow diagrams with transition frequencies for selected prey types. The transition frequencies for the first step were estimated from the total number of individuals used with particular prey. The transition frequencies for all next steps were estimated from the number of individuals, which went through the previous step thus the sum of the transition frequencies leaving each step was 1.

From the predatory sequence for each prey species we estimated entropy index using the Shannon formula (Lehner 1998) to measure the stereotypy of hunting behaviour.

163   **Capture efficacy.**— During prey capture behavior experiment we also measured the time during

164   which the spiders wrapped the prey into the silk; number of bites; and waiting time (time between

165   bite and beginning of feeding).

166

167   **Data analyses.**—We performed all analyses with R (R Development Core Team 2010). The

168   probability of prey acceptance was compared using GLM with Binomial distribution. Wrapping

169   time and waiting time were compared among prey types using GLM with Gamma distribution

170   (GLM-g). Number of bites was compared among prey types using GLM with Poisson

171   distribution (GLM-p) (Pekár & Brabec 2016).

172

173   RESULTS

174   **Natural prey.**—Analysis of seven prey bundles collected from the retreat of *E. episinoides*

175   female spiders revealed in total 94 prey items. All individuals were ants, belonging to three

176   species (Table 1): the majority of the prey (94.6%, n=94) were *Tapinoma erraticum* Latreille

177   (Dolichoderinae, 3-4 mm), remaining individuals were *Messor marocanus* Santschi (6-8 mm,

178   Myrmicinae), and *Aphaenogaster senilis* Mayr (6-7 mm, Myrmicinae).

179

180   **Prey acceptance.**—The probability of prey acceptance in laboratory differed significantly among

181   11 used prey types (GLM-b, X^2_{309}=256.37, P<0.0001, Table 2). *Euryopis episinoides* spiders

182   accepted only termites, ants and fruit flies in more than 50% of the cases. Springtails, crickets and

183   bugs were accepted much less frequently (< 10%), and beetles, cockroaches, spiders, and thrips

184   were rejected. Levin's index (B_A) of fundamental trophic niche breadth was 0.38 indicating

185   narrow niche.

186

187 **Prey capture behavior.—**When on hunt, *Euryopis episinoides* spiders used a specific hunting

188 posture, with the first three pairs of legs placed on the ground and hind legs lifted up in the air

189 alongside its elevated abdomen. At the same time, they drew a short thread of silk from

190 spinnerets by repeated lifting of abdomen. Once prey walked close enough to the threads, the

191 spider started throwing silk from its spinnerets on it while circling around with abdomen pointing

192 at the prey (Fig. 1A). Usually the hunting sequence continued with the spider biting the prey (Fig.

193 1B) and wrapping it in more silk, then the spider waited for some time, until the prey become

194 motionless. Finally, the spider started to feed on the hunting spot or attached immobilized prey to

195 its spinnerets and carried it away (Video 1).

196 There were some differences in prey capture sequence among four prey types (Fig. 2). Ants,

197 both Formicinae and Myrmicinae, were always bitten at least once during prey capture sequence,

198 while termites and fruit flies were not often bitten and spiders started feeding immediately after

199 wrapping the prey.

200 The Shannon entropy index of behavioral sequences was 2.05 for Formicinae, 2.64 for

201 Myrmicinae, 2.22 for termites and 0.83 for fruit flies.

202

203 **Capture efficacy.—**Wrapping time differed among prey types (GLM-g, $F_{3,99}=34.2$, P<0.0001):

204 wrapping of Myrmicinae ants was much longer than other prey types (Fig. 3A). Number of bites

205 during prey capture also differed among used prey types (GLM-p, $\chi^2_3=20.4$, P<0.0001):

206 significantly more bites were used in capture of Myrmicinae ants than other prey types (Fig. 3B).

207 The waiting time differed among prey types too (GLM-g, $F_{3,\ 99}=14.3$, P<0.0001): the longest

208 waiting time was during capture of Myrmicinae ants and the shortest during capture of fruit flies

209 (Fig. 3C).

210

DISCUSSION

Analysis of natural prey revealed that realised 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 would be tempting to consider *E. episinoides* specialized myrmecophagous spiders. Yet, narrow diet may be observed in unspecialized predators if the habitat is dominated by a single prey type (Pekár et al. 2011a; Monzó et al. 2013). Indeed, *Euryopis* spiders seem to prefer microhabitats with high ant abundances.

Yet, acceptance experiments revealed that the fundamental trophic niche of *E. epsinoides* is wider than realized as it includes some other prey types than ants. Nevertheless, according to the Levin's index the fundamental trophic niche is still narrow. 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. movement pattern) and are therefore accepted. Fruit flies were captured as well by *E. episinoides* with quite high frequency; nevertheless, we believe that flies are seldom captured in nature because capture strategy of *E. episinoides* is designed for crawling insects (Carico 1978).

Results of realized and fundamental trophic niche indicate that *E. episinoides* spiders are myrmecophagous thus able to feed on ants. Yet, are they specialized in the capture of ants? A strict specialist *sensu* Pekár & Toft (2015) involves presence of a variety of adaptations that enhance efficiency in preferred prey utilization. Moreover, prey-specific adaptations will be found primarily when predators take exceptionally dangerous prey (Brodie & Brodie 1999), which applies to ants as a prey for most of the spiders (Huseynov et al. 2008). Hereafter, we will deal with traits, which might be specialized in ant capture.

234   Due to the restricted diet range, specialists have adapted to recognize a narrow range of prey

235   cues (Dukas & Kamil 2001). Predatory behavior of *E. episinoides* is driven by olfactory cues

236   deposited on the substrate and was found that they have innate olfactory preference to ants (Pekár

237   & Cardenas 2015). Such selective attention is beneficial as it may help the spider to prepare for

238   the use of a specific foraging strategy, may increase prey capture efficiency, and decrease the risk

239   when hunting dangerous ants. Chemical cues from their preferred prey are found to be important

240   in prey capture in other myrmecophagous and araneophagous salticids as these chemical cues

241   primed selective attention to visual cues of their prey (Clark et al. 2000; Jackson et al. 2002).

242   The ability to recognize prey type before initiation of the hunting sequence may be important

243   if predator uses versatile strategies tuned to the particular prey type (Jackson & Nelson 2012).

244   The hunting sequence when hunting various prey types may be distinctively different. For

245   example, in *Portia fimbriata* (Doleschall)*,* an araneophagous spider, uses three different hunting

246   tactics for catching other salticid depending on the prey species and context (Jackson 1992). Most

247   myrmecophagous salticids capture ants using ant-specific prey capture tactics but use other

248   tactics to take other prey (Jackson & Olphen 1991; Jackson & Li 2001). One myrmecophagous

249   salticid *Anasaitis canosa* (Walckenaer) even distinguish ant of different size and accordingly use

250   different hunting tactic (Edwards et al. 1974). Web–building spider *Araneus diadematus* Clerck

251   attacked muscid flies twitching in the web by first wrapping them in silk and biting them after,

252   whereas motionless flies were attacked first by biting and then by wrapping (Robinson &

253   Robinson 1976).

254   On the other hand, the hunting sequence used when hunting different prey may be overall

255   similar. Hunting of bigger or more dangerous prey usually requires more silk, or venom, and time

256   investment. Prey capture of *E. episinoides* when hunting four different prey types did not differ

257   much in sequence of behavior events. Only in trials with fruit flies or termites, the prey was only

258 wrapped into silk and not bitten. Probably the wrapping was efficient enough to immobilize the

259 prey and spider did not need to invest any venom. The lowest value of Shannon entropy index of

260 fruit fly hunting sequence indicate that this prey was hunted in the most stereotyped way, while

261 other prey types required more complex hunting behavior.

262 However, greater difference among prey types appeared when we looked into investment of

263 silk, venom and handling time. Wrapping and waiting time was longest and number of bites

264 highest during capture of Myrmicinae ants, which were the biggest prey used and thus were more

265 dangerous. On the contrary, capturing of smaller Formicinae (*Lasius*) ants required similar

266 investment of venom, silk and time as capture of innocuous fruit flies. The size of *Lasius* ants

267 was probably optimal for *E. episinoides* spiders as it was similar to body size of *Tapinoma*

268 *erraticum* Latreille ants that were the most abundant prey of *E. episinoides* in nature. Termites

269 were wrapped only for a short time bur their capture involved repeated bites and long waiting for

270 the paralysis, probably due to less efficient venom (Líznarová, unpublished data).

271 Even if the specialized predator is able to catch alternative prey, it may have negative effect on

272 its fitness. Our previous study (Líznarová & Pekár 2016) with *E. episinoides* revealed that fruit

273 flies do not provide suitable food source. Probably the presence of metabolic adaptations to ants

274 constrains the utilization of alternative prey. Their ability to capture and feed on alternative prey

275 is probably advantageous only for a short period of preferred prey scarcity.

276 Our results revealed that *E. episinoides* is stenophagous, capturing only ants. Further, we

277 found that *E. episinoides* was able to capture Formicinae ants with a similar efficiency as

278 innocuous alternative prey indicating that it is adapted to ant capture with adaptations such as

279 hunting strategy suitable for dangerous prey and efficient venom. Their capture strategy even

280 allows them to catch ants bigger then themselves, which is another indication of specialization.

281 However, presence of specialized adaptations may constrain the ability to feed efficiently on

282 alternative prey (Pekár 2005; Cárdenas et al. 2015). This is supported by finding that fitness of *E.*

283 *episinoides* reared on alternative prey was markedly decreased (Líznarová & Pekár 2016). All

284 these findings together indicate that *E. episinoides* spiders have specialized adaptations in ant

285 capture and thus we can consider them as myrmecohagous specialist.

286

287 **Acknowledgment**

290

291 **LITERATURE CITED**

292 Allan, R.A., M.A. Elgar & R.J. Capon. 1996. Exploitation of an ant chemical alarm signal by the

293   zodariid spider *Habronestes bradleyi* Walckenaer. Proceedings of the Royal Society of

294   London B: Biological Sciences 263(1366):69–73.

295 Allred, D.M. 1969. Spiders of the national reactor testing station. Great Basin Naturalist 29(2): 5.

296 Berland, L. 1933. Contribution a 1'etude de la biologie des arachnides . Archives de zoologie

297   experimentale et generale 76(1):1–23.

298 Brodie, E.D. III & E.D. Brodie, Jr. 1999. Predator–prey arms races. Asymmetrical selection on

299   predators and prey may be reduced when prey are dangerous. BioScience 49:557–568.

300 Cárdenas, M., P. Jiroš & S. Pekár. 2012. Selective olfactory attention of a specialised predator to

301   intraspecific chemical signals of its prey. Naturwissenschaften 99(8):597–605.

302 Cardoso, P., S. Pekár, R. Jocqué & J.A. Coddington. 2011. Global patterns of guild composition

303   and functional diversity of spiders. PLoS One 6(6): e21710.

304 Carico, J.E. 1978. Predatory behavior in *Euryopis funebris* (Hentz)(Araneae: Theridiidae) and the

305   evolutionary significance of web reduction. In Symposia of the Zoological Society of

306   London 42:51–58.

307 Castanho, L.M. & P.S. Oliveira. 1997. Biology and behaviour of the neotropical ant-mimicking

308   spider *Aphantochilus rogersi* (Araneae: Aphantochilidae): nesting, maternal care and

309   ontogeny of ant-hunting techniques. Journal of Zoology 242(4):643–650.

310 Clark, R.J., R.R. Jackson & B. Cutler. 2000. Chemical cues from ants influence predatory

311   behavior in *Habrocestum pulex*, an ant-eating jumping spider (Araneae, Salticidae). Journal

312   of Arachnology 28(3):309–318.

313 Collingwood, C.A. & A. Prince. 1998. A guide to ants of continental Portugal (Hymenoptera:

314   Formicidae). Boletim da Sociedade Portuguesa de Entomologia Suplemento 5:1–49.

315 Cushing, P.E. 2012. Spider-ant associations: an updated review of myrmecomorphy,

316   myrmecophily, and myrmecophagy in spiders. Psyche: A Journal of Entomology 2012:1–

317   23.

318 Dukas, R. & A.C. Kamil. 2001. Limited attention: the constraint underlying search image.

319   Behavioral Ecology 12(2):192–199.

320 Eberhard, W.G. 1991. *Chrosiotes tonala* (Araneidae:Theridiidae): a web-building spider

321   specializing on termites. Psyche: A Journal of Entomology 98:7–20.

322 Edwards, G.B., J.F. Carroll & W.H. Whitcomb. 1974. *Stoidis aurata* (Araneae: Salticidae), a

323   spider predator of ants. Florida entomologist 57(4):337–346.

324 García, L.F., M. Lacava & C. Viera. 2014. Diet composition and prey selectivity by the spider

325   *Oecobius concinnus* (Araneae: Oecobiidae) from Colombia. Journal of Arachnology

326   42(2):199–201.

327   Hölldobler, B. 1970. *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. Psyche: A

328   Journal of Entomology 77(2):202–208.

329   Hölldobler, B. & E.O. Wilson. 1990. The Ants. Harvard Belknap, Cambridge.

330   Hurlbert, S.H. 1978. The Measurement of Niche Overlap and Some Relatives. Ecology: 67–77.

331   Huseynov, E.F., R.R. Jackson & F.R. Cross. 2008. The meaning of predatory specialization as

332   illustrated by *Aelurillus m-nigrum*, an ant-eating jumping spider (Araneae: Salticidae) from

333   Azerbaijan. Behavioural Processes 77:389–399.

334   Jackson, R.R. 1992. Conditional strategies and interpopulation variation in the behaviour of

335   jumping spiders. New Zealand journal of zoology 19(3-4): 99–111.

336   Jackson, R.R., R.J. Clark & D.P. Harland. 2002. Behavioural and cognitive influences of

337   kairomones on an araneophagic jumping spider. Behaviour 139(6):749–775.

338   Jackson, R.R., & D. Li. 2001. Prey-capture techniques and prey preferences of *Zenodorus*

339   *durvillei*, *Z. metallescens* and *Z. orbiculatus*, tropical ant-eating jumping spiders (Araneae:

340   Saiticidae) from Australia. New Zealand Journal of Zoology 28(3):299–341.

341   Jackson, R.R., & X.J. Nelson. 2012. Specialized exploitation of ants (Hymenoptera: Formicidae)

342   by spiders (Araneae). Myrmecological News 17:33–49.

343   Jackson, R.R. & A.V. Olphen. 1991. Prey-capture techniques and prey preferences of *Corythalia*

344   *canosa* and *Pystira orbiculata*, ant-eating jumping spiders (Araneae, Salticidae). Journal of

345   Zoology 223(4):577–591.

346   Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the

347   American Museum of Natural History 201:1–160.

348   Lehner, P.N. 1998. Handbook of ethological methods. Cambridge University Press. Cambridge.

349 Levi, H.W. 1954. Spiders of the genus *Euryopis* from North and Central America (Araneae,

350   Theridiidae). American Museum novitates no. 1666.

351 Li, D. & R.R. Jackson. 1997. Influence of diet on survivorship and growth in *Portia fimbriata*, an

352   araneophagic jumping spider (Araneae: Salticidae). Canadian Journal of Zoology

353   75(10):1652–1658.

354 Li, D., R.R. Jackson & D.P. Harland. 1999. Prey-capture techniques and prey preferences of

355   *Aelurillus aeruginosus*, *A. cognatus*, and *A. kochi*, ant-eating jumping spiders (Araneae:

356   Salticidae) from Israel. Israel Journal of Zoology 45(3):341–359.

357 Líznarová, E., L. Sentenská, García, S. Pekár & C. Viera. 2013. Local trophic specialisation in a

358   cosmopolitan spider (Araneae). Zoology 116(1):20–26.

359 Líznarová, E. & S. Pekár. 2015. Trophic niche of *Oecobius maculatus* (Araneae: Oecobiidae):

360   evidence based on natural diet, prey capture success, and prey handling. Journal of

361   arachnology 43(2):188–193.

362 Líznarová, E. & S. Pekár. 2016. Metabolic specialisation on preferred prey and constraints in the

363   utilisation of alternative prey in an ant-eating spider. Zoology 119(5):464–470.

364 MacKay, W.P. 1982. The effect of predation of western widow spiders (Araneae: Theridiidae) on

365   harvester ants (Hymenoptera: Formicidae). Oecologia 53(3):406–411.

366 Monzó, C., M. Juan-Blasco, S. Pekár, Ó. Mollá, P. Castañera & A. Urbaneja. 2013. Pre-adaptive

367   shift of a native predator (Araneae, Zodariidae) to an abundant invasive ant species

368   (Hymenoptera, Formicidae). Biological invasions 15(1):89–100.

369 Nentwig, W. 1987. The prey of spiders. Pp. 249–263. In Ecophysiology of Spiders. (W. Nentwig,

370   ed.). Springer-Verlag, Berlin.

371 Novakowski, G. C., N. S.Hahn & R. Fugi. 2008. Diet seasonality and food overlap of the fish

372   assemblage in a pantanal pond. Neotropical Ichthyology 6(4):567-576.

373 Nørgaard, E. 1956. Environment and behaviour of *Theridion saxatile*. Oikos 7(2): 159–192.

374 Nyffeler M., D.A. Dean & W.L. Sterling. 1988. The southern black widow spider, *Latrodectus*

375 *mactans* (Araneae, Theridiidae), as a predator of the red imported fire ant, *Solenopsis invicta*

376 (Hymenoptera, Formicidae), in Texas cotton fields. Journal of Applied Entomology 106(1–

377 5):52–57.

378 Oliveira, P.S. & I. Sazima. 1984. The adaptive bases of ant-mimicry in a neotropical

379 aphantochilid spider (Araneae: Aphantochilidae). Biological Journal of the Linnean Society

380 22(2):145–155.

381 Pekár, S. 2004. Predatory behavior of two European ant-eating spiders (Araneae, Zodariidae).

382 Journal of Arachnology 32:31–41.

383 Pekár, S. 2005. Predatory characteristics of ant-eating *Zodarion* spiders (Araneae: Zodariidae):

384 potential biological control agents. Biological Control 34(2):196–203.

385 Pekár, S., T. Bilde & M. Martišová. 2011a. Intersexual trophic niche partitioning in an ant-eating

386 spider (Araneae: Zodariidae). PloS one 6(1):e14603.

387 Pekár, S. & M. Brabec. 2016. Modern analysis of biological data. Generalized linear models in R.

388 Masarykova univerzita.

389 Pekár, S. & M. Cárdenas. 2015. Innate prey preference overridden by familiarisation with

390 detrimental prey in a specialised myrmecophagous predator. The Science of Nature 102(1–

391 2):8.

392 Pekár, S., J.A. Coddington & T. Blackledge. 2012. Evolution of stenophagy in spiders (Araneae):

393 evidence based on the comparative analysis of spider diets. Evolution 66:776–806.

394 Pekár, S. & J. Král. 2001. A comparative study of the biology and karyotypes of two central

395 European zodariid spiders (Araneae, Zodariidae). Journal of Arachnology 29(3):345–353.

396   Pekár, S. & J. Král. 2002. Mimicry complex in two central European zodariid spiders (Araneae:

397   Zodariidae): how *Zodarion* deceives ants. Biological Journal of the Linnean Society

398   75(4):517–532.

399   Pekár, S., J. Král & Y. Lubin. 2005. Natural history and karyotype of some ant-eating zodariid

400   spiders (Araneae, Zodariidae) from Israel. Journal of Arachnology 33(1):50–62.

401   Pekár, S., J. Šobotník & Y. Lubin. 2011. Armoured spiderman: morphological and behavioural

402   adaptations of a specialised araneophagous predator (Araneae: Palpimanidae).

403   Naturwissenschaften 98(7):593–603.

404   Pekár, S. & S. Toft. 2009. Can ant-eating *Zodarion* spiders (Araneae: Zodariidae) develop on a

405   diet optimal for euryphagous arthropod predators?. Physiological Entomology 34(2):195–

406   201.

407   Pekár, S. & S. Toft. 2015. Trophic specialisation in a predatory group: the case of prey-

408   specialised spiders (Araneae). Biological Reviews 90:744–761.

409   Pekár, S., S. Toft, M. Hrušková & D. Mayntz. 2008. Dietary and prey-capture adaptations by

410   which *Zodarion germanicum*, an ant-eating spider (Araneae: Zodariidae), specialises on the

411   Formicinae. Naturwissenschaften 95(3):233–239.

412   Porter, S.D. & C.D. Jorgensen.1980. Recapture studies of the harvester ant, *Pogonomyrmex*

413   *owyheei* Cole, using a fluorescent marking technique. Ecological Entomology 5(3):263–

414   269.

415   R Development Core Team. 2010. R: A Language and environment for statistical computing.

416   Vienna: R Foundation for Statistical Computing. http://www.R-project.org.

417   Robinson, M.H. & B. Robinson. 1976. Discrimination between prey types: an innate component

418   of the predatory behaviour of araneid spiders. Ethology 41(3):266–276.

419   Stephens, D.W. & J.R. Krebs. 1986. Foraging theory. Princeton University Press. Princeton, 247

420   pp.

421   Thompson, J.N. 1994. The coevolutionary process. University of Chicago Press, Chicago.

422   Whitehouse, M.E.A. 1987. 'Spider Eat Spider': the predatory behavior of *Rhomphaea* sp. from

423   New Zealand. Journal of Arachnology 15:355–362.

424

425 Table 1: List of prey items found in seven bundles in the retreat of *Euryopis episinoides* females.

Prey species (number of individuals)
Tapinoma erraticum (13)
Messor marocanus (1), *Tapinoma erraticum* (15)
Aphaenogaster senilis (1), *Tapinoma erraticum* (15)
Aphaenogaster senilis (1), *Tapinoma erraticum* (11)
Messor marocanus (2), *Tapinoma erraticum* (25)
Tapinoma erraticum (9)
Tapinoma erraticum (1)

426

427

428

429

430

431

432

433

434

435

436

437

438

439

440

441

442

443   Table 2: Probability of acceptance of different prey types by *Euryopis episinoides* females.

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

444

445

446

447

448

449

450

451

452

453

454

455 Fig. 1. *Euryopis episinoides* spider attacking a *Messor* ant: A. Throwing silk from spinerrets. B.

456 Biting into base of antennae.

457 Fig. 2.: Kinematic diagrams of prey capture behaviour of *Euryopis episinoides* used against four

458 prey types with the relative frequencies of transitions. A. Formicinae ants ($n=11$), B. Myrmicinae

459 ants ($n=14$), C. termites ($n=10$), D. fruit flies ($n=10$). The transition frequencies between events

460 are also indicated by the width of the line.

461 Fig. 3: Comparison of the wrapping time (A), the number of bites (B), and the waiting time (C) of

462 *Euryopis episinoides* for four different prey types: fruit flies ($n=20$), Formicinae ants ($n=39$),

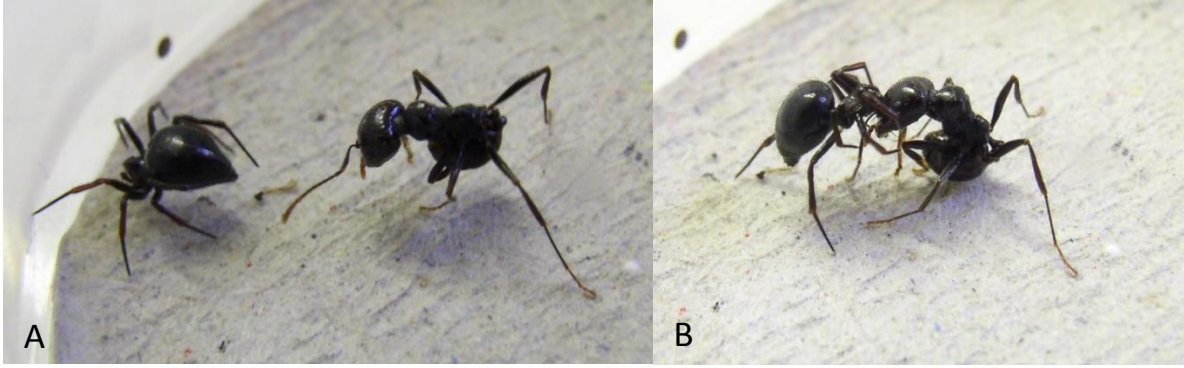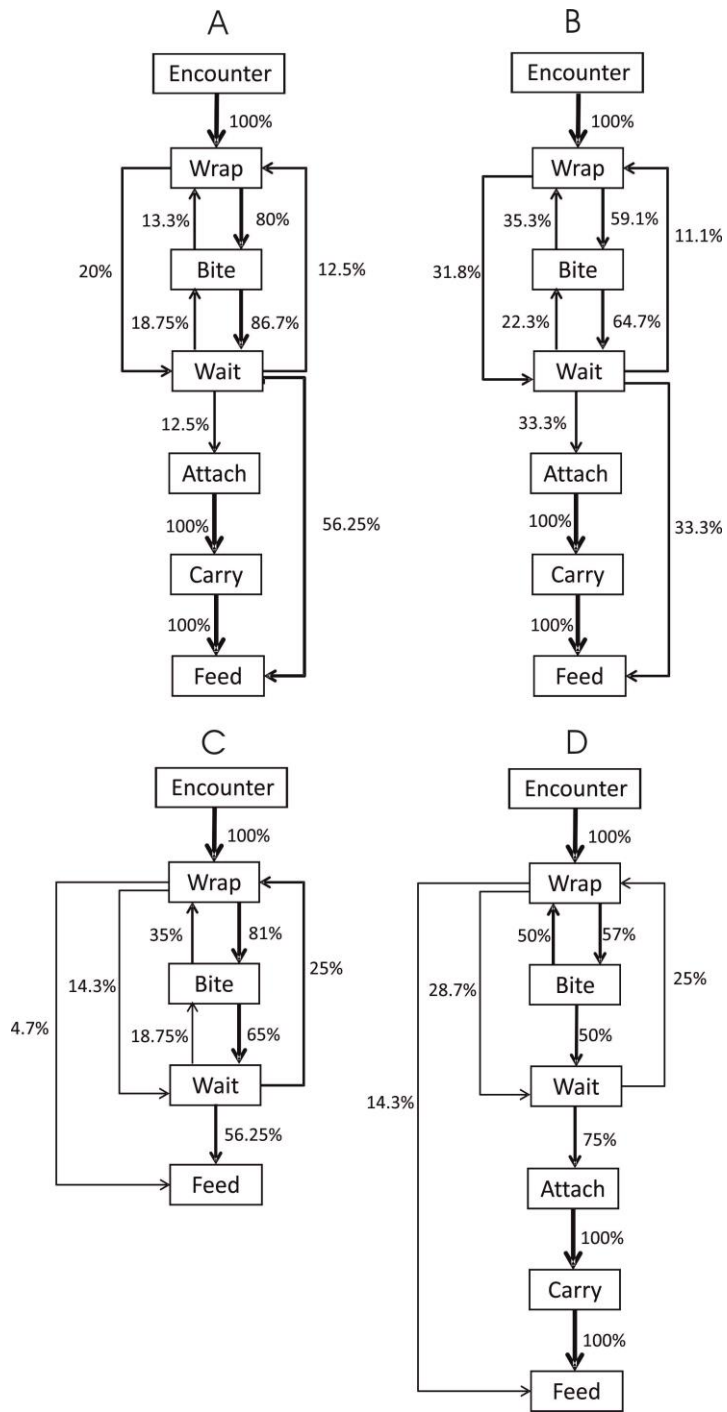463 Myrmicinae ants ($n=27$), and termites ($n=17$).

464

465

466

467

468

469

470

471

472

473   Fig. 1

A

Encounter
↓ 100%
Wrap
13.3% ↑ ↓ 80%
Bite
18.75% ↑ ↓ 86.7%
Wait
20% (left) 12.5% (right)
↓ 12.5%
Attach
↓ 100%
Carry
↓ 100%
Feed
56.25%

B

Encounter
↓ 100%
Wrap
35.3% ↑ ↓ 59.1% 11.1%
Bite
22.3% ↑ ↓ 64.7%
Wait
31.8% (left) 33.3% (right)
↓ 33.3%
Attach
↓ 100%
Carry
↓ 100%
Feed

C

Encounter
↓ 100%
Wrap
35% ↑ ↓ 81% 25%
Bite
18.75% ↑ ↓ 65%
14.3%
4.7%
Wait
↓ 56.25%
Feed

D

Encounter
↓ 100%
Wrap
50% ↑ ↓ 57% 25%
Bite
28.7%
↓ 50%
Wait
14.3%
↓ 75%
Attach
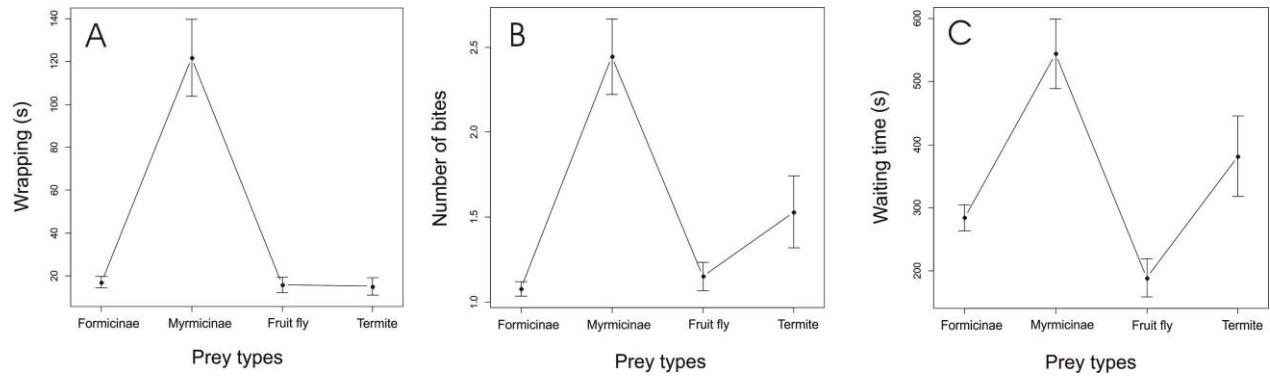↓ 100%
Carry
↓ 100%
Feed

474

475   Fig. 2

476

477

478   Fig. 3

479

480

481

482

483   Video 1. Capture and handling of *Messor* ant by *Euryopis episiniodes* female.