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ORIGINAL ARTICLE

Prey of selected epigeic velvet spiders (Araneae: Eresidae)

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Abstract. The natural prey of spiders has been studied in only a few species, which limits our understanding of their role in ecosystems. Eresid spiders often have a hidden lifestyle; thus, their ecology is still poorly understood. Here we investigated the natural prey of four species of ground-dwelling eresid spiders from Israel – *Adonea fimbriata*, *Dorceus fastuosus*, *Eresus* sp., and *Loureedia annulipes* – and one (*Eresus kollari*) from Central Europe. In the last species, we studied the prey in more detail: we compared the natural with the potential prey and investigated prey acceptance using six prey types (Blattodea, Coleoptera, Hemiptera, Hymenoptera, Isopoda, and Orthoptera) under semi-field conditions. The natural prey was studied by analysing the exoskeleton remains of prey found in the webs. We found that the prey composition in the webs differed significantly among species, though two insect groups, beetles and ants, dominated in all eresid species. Among beetles, tenebrionids were the most frequent in eresid species from Israel, while carabids dominated in *E. kollari*. Beside these beetles, weevils were frequent prey in all examined species. The index of the trophic niche breadth was narrow in all examined species, indicating trophic specialisation; however, feeding trials revealed that *E. kollari* accepted a wide variety of prey types, showing that it is a generalist opportunistic predator. All eresid species studied here appear to be stenophagous generalists, capturing mainly beetles and ants.

INTRODUCTION

Spiders are true predators, capturing mainly arthropods (Nentwig, 1987). The natural prey of spiders has been studied so far only in less than 5% of species (Pekár et al., 2012); thus, our knowledge of their diet is still very limited. A great majority of spider species seem to be euryphagous generalists, i.e. adapted to capture and consume a variety of prey types (Pekár & Toft, 2015). Generalists often reject well-defended prey types, such as ants or millipedes (von Drees, 1952; Edwards & Jackson, 1994; Jackson & Olphen, 1991; Shear, 2015). Yet, some generalists can be stenophagous (or local specialists), i.e. capturing only a limited number of prey types due to restricted prey occurrence, interspecific competition, or prey preference (Pekár et al., 2017).

Generalist spiders have evolved a broad variety of prey capture strategies (Cardoso et al., 2011) to catch an array of prey. These include the construction of two- or three-dimensional webs with viscid or cribellate silk to restrain prey movement. The prey composition of spiders that use cribellate silk differs between epigeic species and those building aerial webs. Webs on the ground capture epigeic arthropods, such as ants, orthopterans, woodlice, diplopods, and cockroaches (Heidger, 1988; Almeida-Silva et al., 2009; Líznarová & Pekár, 2015; Tsai & Pekár, 2019; Da Ponte et al., 2020). By contrast, aerial webs capture flying insects, namely dipterans, lepidopterans, and to a lesser extent orthopterans (Henderson & Elgar, 1999; Guseinov, 2002; Lopardo et al., 2004). Beetles are captured by both epigeic and aerial cribellate webs (Majer et al., 2013) as they often possess spines that become entangled in the cribellate silk (Opell, 2002).

Eresid spiders are ubiquitous inhabitants of arid environments (Henschel, 1997), as most of the nine genera can be found in this type of ecosystem (Miller et al., 2012). They build three-dimensional webs with cribellate silk either on the ground or in the crowns of trees and shrubs. Aerial webs are produced by *Stegodyphus*, while epigeic webs are

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produced by the other eight genera (Miller et al., 2012). The epigeic webs differ in their construction. *Dorceus* spp. and *Eresus* spp. dig vertically oriented burrows, which are braided with silk (Norgaard, 1941; Miller et al., 2012). *Dresserus* spp. and *Paradonea* spp. build silken burrows under stones or shrubs. *Adonea* spp. do not dig burrows but hide under a stone, from where they deploy strands of cribellate silk. *Seothyra* spp. dig a horizontal chamber with a vertical burrow in a sandy substrate, which is covered by a cribellate silk-lined mat (Lubin & Henschel, 1990). *Gandanameno* spp. build silken tubes in crevices under stones or under tree bark (Miller et al., 2012).

Of more than 100 species of eresids (World Spider Catalog, 2024), the natural prey of only a few species have been studied thus far. These include species of *Eresus* and *Stegodyphus* (Jacson, 1973; Ward, 1986; Crouch & Lubin, 2000; Miller et al., 2012; Majer et al., 2013; Henriques et al., 2018). Species of *Eresus* mainly feed on beetles, followed by orthopterans and hemipterans (Bristowe, 1958; Ergashev, 1979; Brehm & König, 1992; Walter, 1999; Zarcos & Piñero, 2016). Species of *Seothyra* and *Gandanameno* often hunt ants (Nørgaard, 1941; Arvidsson et al., 2020). Some authors suggest that *Seothyra* is specialised on ants (Henschel & Lubin, 1997). *Stegodyphus* species catch mainly flying insects, such as beetles (families Carabidae, Curculionidae, Elateridae), hemipterans (families Cicadellidae, Fulgoridae, Membracidae, Pentatomidae), hymenopterans (mainly family Apidae), and dipterans (Ward, 1986; Crouch & Lubin, 2000).

The aim of our study was to investigate the natural prey of epigeic eresid spiders whose diet has not yet been studied. We focused on four genera, *Adonea*, *Dorceus*, *Eresus*, and *Loureedia*, occurring in Israel. The natural prey was obtained by analysing web contents collected at several sites. This provided information on the breadth of the realised trophic niche of each species. To find the level of trophic specialisation, we analysed both the fundamental and realised trophic niches in one species from Central Europe, *Eresus kollari*, and then applied these findings to the trophic specialisation of species from Israel.

MATERIAL AND METHODS

Webs of four species of eresid spiders, namely *Adonea fimbriata* (Simon, 1873) (adult body size 12–25 mm), *Dorceus fastuosus* (C.L. Koch, 1846) (5–10 mm), *Loureedia annulipes* (Lucas, 1857) (8–20 mm), and *Eresus* sp., were collected in Israel, from the Negev desert and from adjacent sites north of the desert, specifically at Arad (31.2441019°N, 35.2182325°E), Beer Sheva (31.2081744°N, 34.7918472°E), En Avdat (30.8438028°N, 34.7775778°E, Halukim 1 (30.8533822°N, 34.7636517°E), Halukim 2 (30.8531861°N, 34.7648461°E), Hatira 1 (30.8702544°N, 34.8247631°E), Hatira 2 (30.8702581°N, 34.8373550°E), Lehavim (31.3560536°N, 34.8180256°E), Mashabbim (31.0060261°N, 34.7405417°E), Mashash (31.0769661°N, 34.8521969°E), Nizzana (30.8783764°N, 34.4245561°E), Ofakim (31.3029911°N, 34.5880636°E), Sde Boker 1 (30.8560433°N, 34.7868386°E), Sde Boker 2 (30.8646889°N, 34.7752461°E), Wadi Hazaz (30.8918061N, 34.8510839E), and Tel Arad (31.2805011°N, 35.1225869°E) between 2004 and 2009 (Fig. 1). In total, 239 webs were collected.

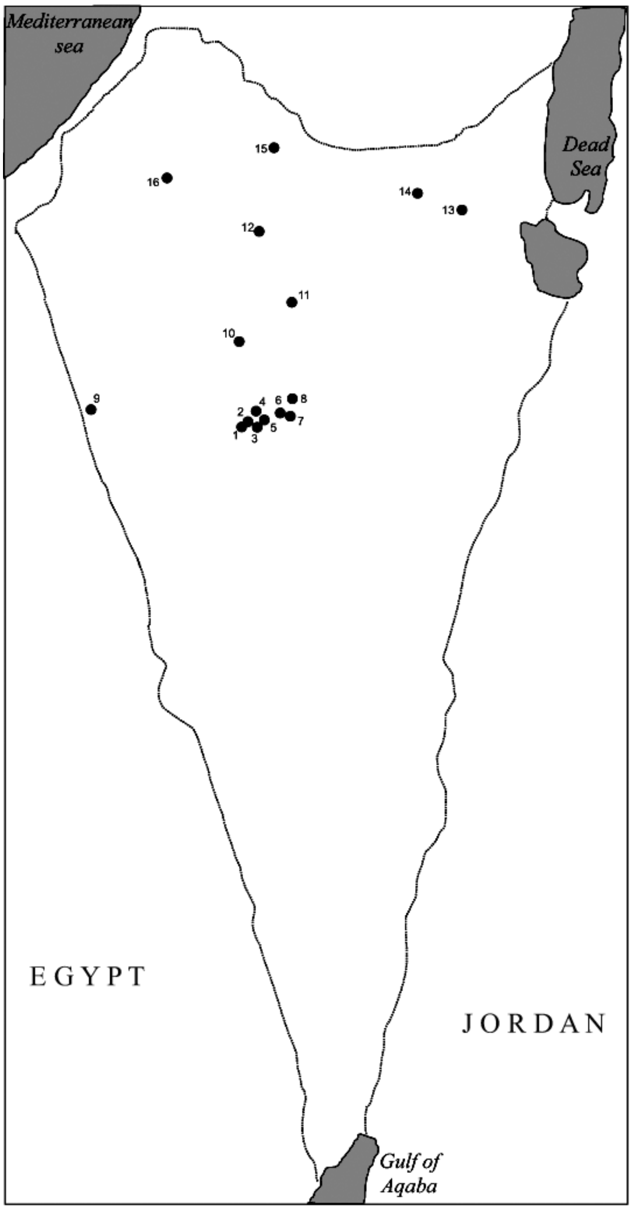

Fig. 1. Map of 16 sites in Israel where nests of eresid spiders were collected. 1 – Halukim 1, 2 – Halukim 2, 3 – En Avdat, 4 – Sde Boker 1, 5 – Sde Boker 2, 6 – Hatira 1, 7 – Hatira 28 – Wadi Hazaz, 9 – Nizzana, 10 – Mashabbim, 11 – Mashash, 12 – Beer Sheva, 13 – Arad, 14 – Tel Arad, 15 – Lehavim, 16 – Ofakim.

Identification of the eresid species was performed either using live or dead specimens or exuviae found in the webs. Some webs (22%) could not be identified to genus/species because they did not contain specimens or exuviae that would allow the identification of species (Table 1).

In addition, specimens of *E. kollari* (Rossi, 1846) (7–13 mm), together with their webs, were collected at a site close to Senorady, the Czech Republic (49.133677°N, 16.246595°E) during June and July 2021.

Natural prey

The natural prey of the spiders was investigated using the exoskeleton remains of prey caught in the webs. In total, 273 webs were examined: 55 webs of *Adonea* sp., 39 webs of *Dorceus* sp., 78 webs of *Eresus* sp., 15 webs of *Loureedia* sp., and 52 webs of unknown eresid species. The remaining 34 webs belonged to *Eresus kollari*. Webs were placed in plastic test tubes and dissolved in a 5% solution of sodium hypochlorite. Webs were torn apart to allow the penetration of sodium hypochlorite between the threads to improve the breakdown of the silk. The suspension with exoskeleton remains was filtered through a fine sieve and the remnants were sorted and stored in 75% ethanol in test tubes. Exoskeleton remains of all prey were identified to the lowest taxonomic level possible. Beetles were identified using Hůrka (1996, 2005); Lillig & Pavlíček (2022); iNaturalist (iNaturalist.com); collections of tenebrionid beetles, which were collected in Israel; and comparative material which was trapped in pitfall traps or hand-collected at the same collection sites as above. The number of prey specimens was estimated by the number of heads, scuta, or elytrae found in the webs.

Potential prey

In the case of *E. kollari*, we investigated the potential prey as well as the prey collected in nature. We installed five pitfall traps on the site where this species occurs (Senorady). Each pitfall trap consisted of a 200 ml plastic cup, buried singly in the ground up to the rim. Cups were filled to 1/3 of their volume with a 50% solution of ethylene glycol plus four drops of detergent to reduce the water surface tension. A plastic roof (diameter 10 cm) was placed above each cup to prevent rain from flooding the trap. Pitfall traps were installed near places with a high occurrence of *E. kollari* and emptied in three-week intervals from the middle of July to the end of August 2021. In total, three collections were made. Trapped invertebrates were placed in 70% ethanol, sorted, and identified to the lowest taxonomic level possible. Identification was performed using a LEICA EZ5 stereomicroscope. Beetles were identified to genus/species using Hůrka (1996, 2005). Other groups were identified only to an order.

Prey acceptance

Sixteen juveniles (late instars) of *E. kollari* were kept under semi-field conditions. Specimens were placed singly in plastic cups (volume 500 ml, height 15 cm, bottom diameter 5.6 cm, upper diameter 9.5 cm) with a substrate (soil, wooden sticks, and stems) filling two thirds of the cup. The bottoms of the cups were punctured and placed on a shallow tray filled with water. The cups were covered with a mesh and placed outside under the pergola roof, sheltered from rain and sun. The spiders dug a burrow which was later lined with silk (within about 24 h). They finished the rough web construction in a further day.

As prey, we used the following arthropods belonging to different orders: *Tenebrio molitor* (Linnaeus, 1758) (Coleoptera, N = 54), *Blaptica dubia* (Serville, 1839) (Blattodea, N = 81), *Acheta domesticus* (Linnaeus, 1758) (Orthoptera, N = 16), *Formica rufa* (Linnaeus, 1761) (Hymenoptera, N = 7), Miridae (Heteroptera, N = 7), and *Oniscus asellus* (Linnaeus, 1758) (Isopoda, N = 16), which were selected on the basis of their abundance on the site of *E. kollari* occurrence. A prey specimen was released into the cup using tweezers and the predatory behaviour of *E. kollari* was observed for at least 5 min. A prey was offered to each spider once a week. If the spider did not capture the offered prey, it was replaced by a *Tenebrio* beetle. Therefore, some prey types were offered to each spider only once, while others were offered repeatedly. We recorded whether the spider captured the prey.

Statistical analyses

For each species, we estimated the breadth of the trophic niche using Levin's formula (Hurlbert, 1978). The index takes values from 0 to 1, where values < 0.4 indicate a narrow niche (stenophagous species) and values > 0.6 indicate a wide niche (euryphagous species) (Novakowski et al., 2008).

Detrended correspondence analysis (DCA) ("vegan" package, Oksanen et al., 2022) was used to compare prey composition

Table 1. List of actual prey of eresid spiders (*A. fimbriata*, *D. fastuosus*, *Eresus* sp., and *L. annulipes*) from Israel organised by order (capital letters), suborder, and family. Numbers are relative frequencies (percentage). Unknown stands for unidentified eresid species.

Taxon	*Adonea*	*Dorceus*	*Eresus*	*Loureedia*	unknown
ACARIFORMES	–	0.16	–	–	–
ARANEAE	0.07	0.08	–	–	0.17
Dysderidae	0.07	–	–	–	0.08
Salticidae	–	–	–	–	0.08
ISOPODA	0.52	0.08	2.68	2.17	0.74
ORTHOPTERA	0.46	–	0.24	–	0.5
Acrididae	0.07	–	0.24	–	0.5
Tettigoniidae	0.39	–	–	–	–
HEMIPTERA	0.20	0.16	0.47	–	0.17
Pentatomidae	0.07	–	0.24	–	0.17
Ventocoris sp.	0.07	–	0.24	–	0.17
COLEOPTERA	35.32	78.85	45.16	62.17	52.81
larvae	0.13	–	0.24	–	0.25
Buprestidae	0.13	0.08	0.16	0.43	–
Acmaeoderella sp.	0.07	–	–	–	–
Carabidae	0.72	1.70	1.34	2.17	3.88
Graphipterus serrator	–	0.24	–	–	–
Chrysomelidae	–	0.57	–	1.30	0.08
Entomoscelis sacra	–	0.57	–	1.30	0.08
Coccinellidae	–	–	0.55	–	–
Coccinella septempunctata	–	–	0.55	–	–
Curculionidae	3.14	2.19	8.26	9.13	5.78
Brachycerus sp.	0.46	0.24	1.1	–	0.33
Entomoderus sp.	–	–	–	0.43	0.17
Larinus sp.	–	0.32	–	–	0.33
Lixus sp.	0.07	0.08	–	–	–
Ocladius sp.	–	–	0.08	–	–
Otiorhynchus sp.	–	–	0.16	–	–
Dermestidae	0.39	–	0.16	0.87	–
Elateridae	0.07	–	0	–	–
Cardiophorus sp.	0.07	–	0	–	–
Endomychidae	0.07	0.16	0.08	–	0.08
Meloidae	–	–	0.16	–	–
Meloe/Trichomeloe sp.	–	–	0.16	–	–
Scarabaeidae	–	–	–	–	0.08
Staphylinidae	–	–	0.16	–	0.08
Tenebrionidae	26.68	68.72	22.42	40.87	36.22
Adelostoma sulcatum	1.11	0.24	1.1	5.65	0.58
Adesmia sp.	0.26	0.49	0.47	1.30	0.33
Adesmia cancellata	0.13	–	–	–	–
Adesmia metallica	0.13	0.73	0.24	1.74	0.41
Akis sp.	0.26	–	0.31	–	0.17
Amnodeis sp.	4.51	–	0.94	0.43	0.66
Apentanodes arabicus edomitus	1.57	12.64	0.24	7.83	6.85
Blaps sp.	–	0.08	0.08	–	–
Blaps nitens laportei	0.78	0.16	0.16	2.17	0.83
Dendarus sp.	0.59	0.08	0.55	0.43	0.08
Erodius sp.	1.64	1.05	0.08	–	0.5
Erodius hebraicus/gibbus	1.50	13,70	0.16	0.43	4.62
Erodius kneuckeri	0.33	13.61	–	5.22	4.13
Erodius puncticollis sinaiticus	–	1.46	–	–	0.08
Machlopsis crenatocostata	0.07	1.22	0.31	0.87	0.99
Mesostena sp.	0.07	1.46	0.47	–	0.66
Oxycara sp.	0.46	3.48	0.87	–	0.25
Pimelia sp.	0.72	1.22	1.02	1.3	1.73
Pimelia arabica edomita	0.39	0.73	0.08	–	0.74
Pimelia bajula	0.07	0.65	0.16	–	1.07
Prochoma sp.	0.52	0.73	0.08	–	0.33
Pterolasia squalida	0.78	9.24	1.1	7.83	5.53
Sclerum sp.	0.07	–	0.16	0.43	–
Sepidium sp.	2.88	0.32	1.42	0.43	1.16
Tentyria sp.	6.34	3.73	7.24	3.04	5.78
Thraustocolus leptoderus	0.07	0.08	–	–	–
Trachyderma sp.	0.26	0.08	0.63	–	0.25
Zophosis sp.	1.31	0.41	4.64	1.3	0.99
Zophosis bicarinata	0.07	0.65	–	–	–
Zophosis pharaonis pharaonis	0.07	0.08	–	–	–
Helopini	–	–	0.08	–	–
Stenosini	–	–	–	0.43	0.08
DIPTERA	–	0.16	–	–	–
HYMENOPTERA	62.67	17.67	51.46	35.65	45.29
Formicidae	62.22	17.67	51.46	35.65	44.80
No. of webs	55	39	78	15	52
No. of specimens	1529	1234	1271	230	1212

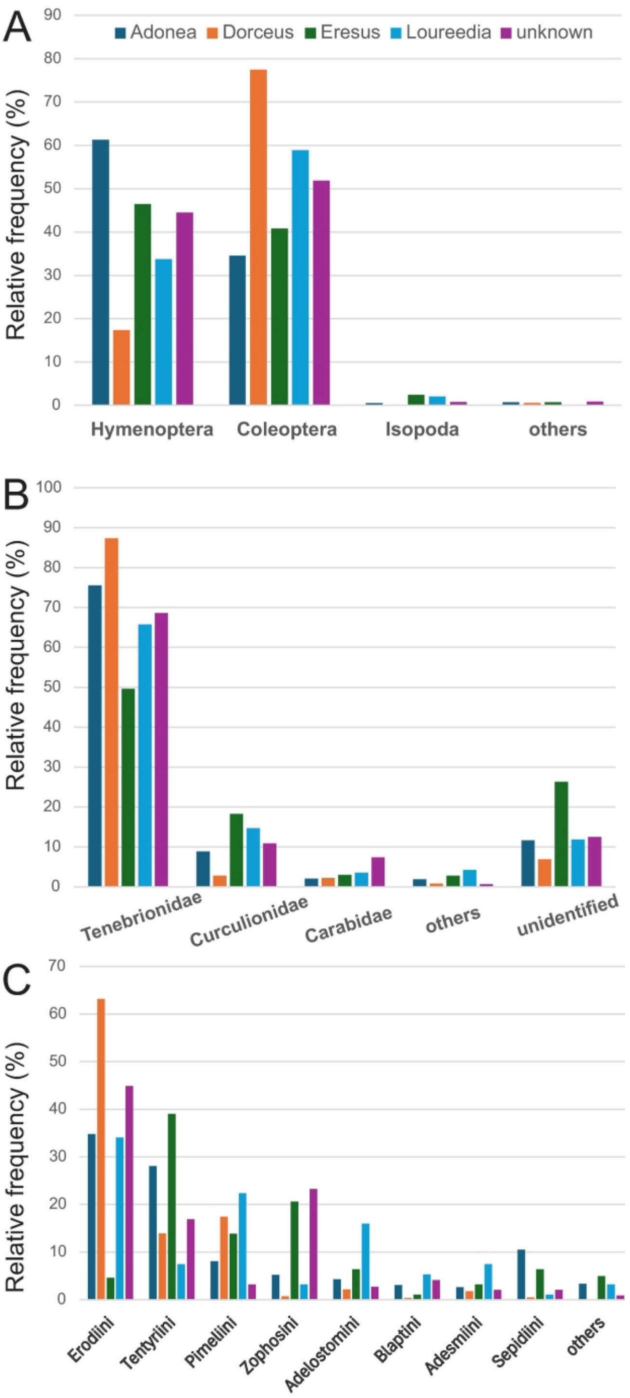

Fig. 2. Relative frequencies of prey found in the webs of eresid spiders from Israel. Unknown stands for unidentified eresid species. A – Relative frequency of prey orders. Others include Acari, Araneae, Diptera, Hemiptera, and Orthoptera. B – Relative frequency of beetle families. Others include: Buprestidae, Chrysomelidae, Coccinellidae, Dermestidae, Elateridae, Endomychidae, Meloidae, Scarabeidae, Staphylinidae. C – Relative frequency of Tenebrionidae tribes. Others include: Akidini, Dendarini, Helopini, Opatrini, and Stenosini.

among the four species from Israel. The relative frequencies of prey per species were used.

Generalised linear models (Pekár & Brabec, 2016) with a binomial error structure (GLM-b), were used to compare: (1) the relative frequencies of prey types (at order level) among the four Israeli species, using totals per species; (2) the relative frequencies of prey (at order level) of *E. kollari* found in the webs and those captured by pitfall traps using totals from all traps and trapping dates; (3) the relative frequencies of prey captured by *E. kollari* in prey-acceptance trials, omitting repeated trials with the same prey and the same individual.

RESULTS

Prey of *Adonea*, *Dorceus*, *Eresus*, and *Loureedia*

The most frequent prey found in the webs of all four eresid species from Israel were beetles and ants, followed by orthopterans and woodlice (Fig. 2A, Table 1). Other groups, namely Araneae, Diptera, and Isopoda, were rare. There were significant differences in the relative frequencies of the prey types among the four eresid species (GLM-b: $\chi^2_{21} = 1381$, $P < 0.0001$). Ordination analysis (DCA) revealed specific differences in prey composition among eresid species (Fig. 3): the prey compositions of *Eresus* and *Adonea* were more similar to each other than to those of *Dorceus* and *Loureedia*.

In the webs of *A. fimbriata*, hymenopterans were the most frequent prey, of which more than 99% were ants (Fig. 2A, Table 1). Among beetles, the most frequent were the families Tenebrionidae, followed by Curculionidae and Carabidae (Fig. 2B). Among tenebrionids, the most frequent tribes were Erodiini, followed by Tentyrini and Sepidiini (Fig. 2C). The breadth of the trophic niche at the prey order level was 0.16, indicating a narrow niche.

In the webs of *D. fastuosus*, most remnants belonged to beetles (Fig. 2A, Table 1), mostly Tenebrionidae, followed by Curculionidae and Carabidae (Fig. 2B). Among tenebrionids, the most frequent tribes were Erodiini, followed by Pimeliini (Fig. 2C). The index of the trophic niche breadth at the prey order level was 0.09, indicating a very narrow niche.

In the webs of *Eresus* sp., both ants and beetles predominated, followed by isopods (Fig. 2A, Table 1). The beetles were represented by the families Tenebrionidae and Curculionidae, which were the most frequent, followed by the family Carabidae (Fig. 2B). Among tenebrionids, there were mainly the tribes Tentyriini and Zophosini (Fig. 2C). The breadth of the trophic niche at the prey order level was 0.28, indicating a broader niche breadth compared to those of *A. fimbriata* and *D. fastuosus*.

In the webs of *L. annulipes*, the highest frequency of prey belonged to beetles (Fig. 2A, Table 1), mainly Tenebrionidae, followed by Curculionidae and Carabidae (Fig. 2B). Among tenebrionids, there were mainly remnants of the tribes Erodiini, Pimeliini, and Adelostomini (Fig. 2C). The breadth of the trophic niche at the prey order level was 0.47, indicating a wide trophic niche.

In the webs of unidentified eresid spiders, the most abundant prey were beetles, followed by ants (Fig. 2A, Table 1).

Prey of *E. kollari*

Representatives of seven arthropod orders were found in the webs of *E. kollari* (Fig. 4, Table 2). Ants and beetles formed the main part of the diet. All hymenopterans were ants, particularly *Camponotus* spp. Beetles were represented by the families Carabidae, Curculionidae, Tenebrionidae, and Coccinellidae. The index of trophic niche

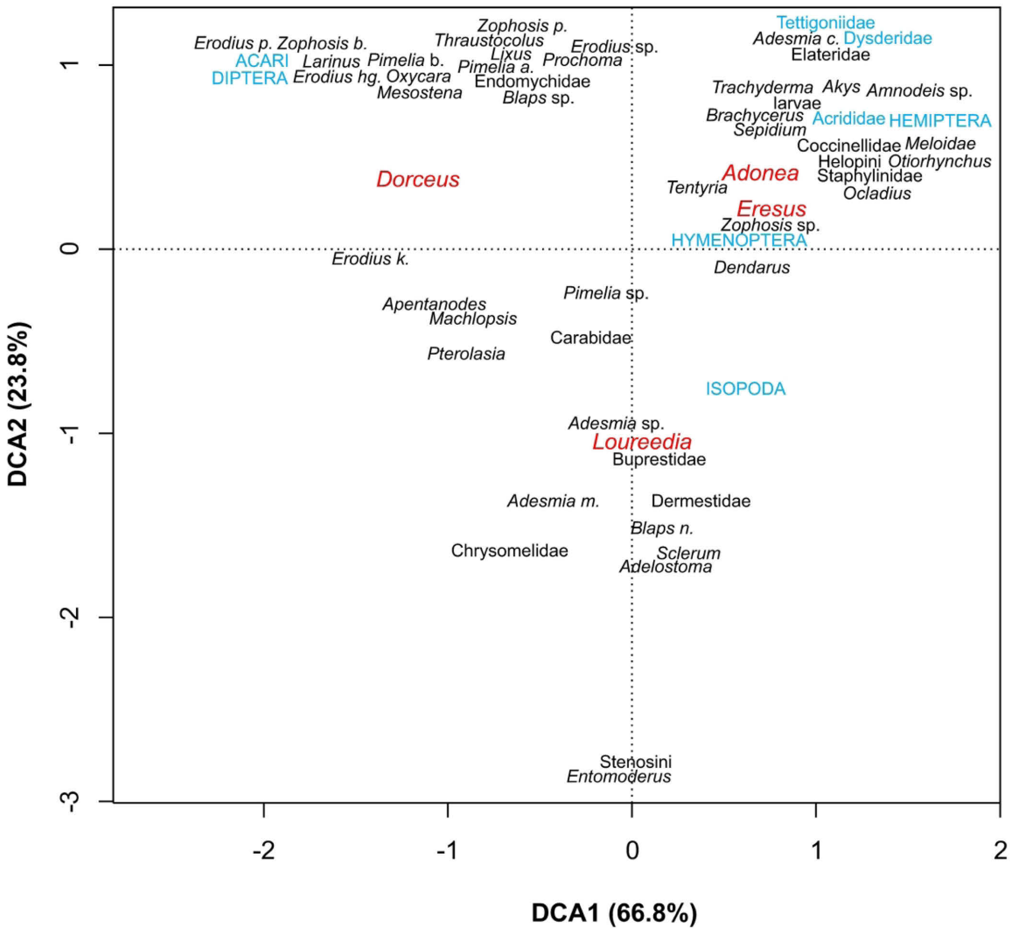

Fig. 3. Ordination (DCA) plot of the prey composition of four eresid genera (red) from Israel. The prey taxa are represented as orders (capital letters), families and tribes (normal font) or species (italics). Species names are abbreviated to one or two letters if more than one species of the same genus was found (for full names, see Table 1). Families and tribes are specified if more than one species per order was found. Species are specified if more than one species per family was found. Beetle taxa are in black, non-beetle taxa are in blue. Percentage of explained variance along first two axes is shown in parentheses.

breadth at the prey order level was 0.20, indicating a narrow trophic niche.

The potential prey was dominated by hymenopterans, mainly ants (*Camponotus* spp. and *Lasius* spp.), followed by spiders (mainly the families Lycosidae and Gnaphosidae), dipterans, orthopterans, and beetles (Table 2). The latter order was represented by several families with the highest number of Carabidae (tribes Harpalini and Trechini), Geotrupidae, and Curculionidae. The relative frequencies of potential prey orders were thus significantly

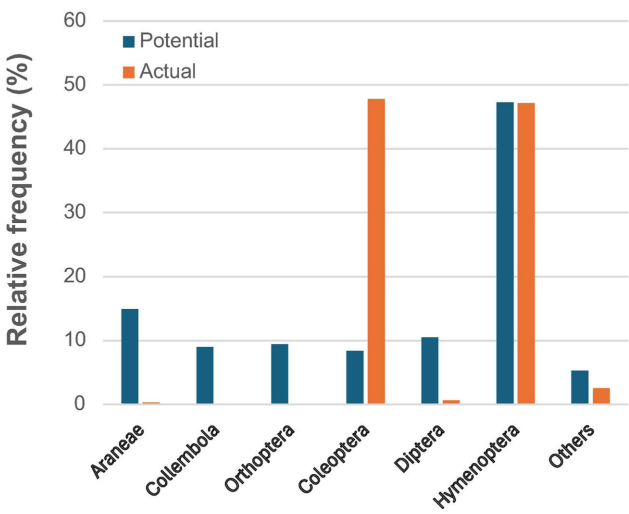

Fig. 4. Comparison of the relative frequencies of invertebrates trapped into pitfall traps and the actual prey of *E. kollari*. Others include Acari, Blattodea, Lithobiomorpha, Lepidoptera, Isopoda and Hemiptera, each representing less than 2%.

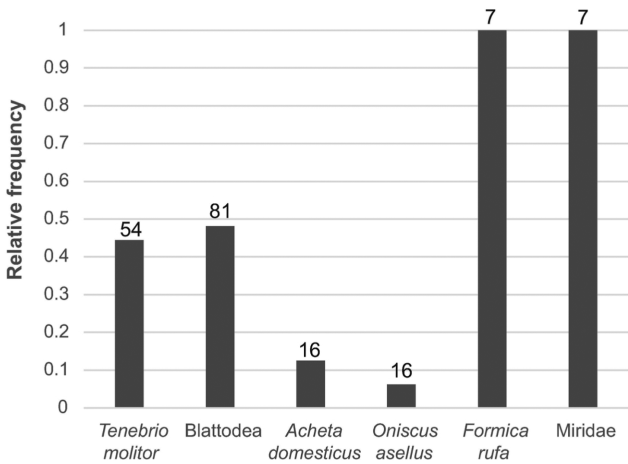

Fig. 5. Comparison of the relative frequencies of prey captured by juveniles of *E. kollari*. The number of prey items presented to *E. kollari* is above the bars.

Table 2. List of potential and actual prey of *E. kollari* organised by order (capital letters), suborder, and family. Numbers are relative frequencies (percentage). Potential prey was captured by pitfall traps on three dates. Actual prey was obtained by web content analysis of prey remnants (34 webs).

Taxon	Potential prey			Actual prey
	16/7/2021	6/8/2021	27/8/2021	
ACARIFORMES	0.27	0.22	3.47	–
Trombidiidae	0.27	0.22	–	–
ARANEAE	15.01	13.85	15.90	0.32
Amaurobiidae	0.27	–	–	–
Dysderidae	0.54	–	–	–
Eresidae	–	–	0.58	–
Gnaphosidae	2.41	4.18	7.80	–
Linyphiidae	–	0.22	–	–
Lycosidae	11.26	8.35	6.94	0.32
Philodromidae	0.27	0.44	0.29	–
Salticidae	–	0.22	0.29	–
Thomisidae	0.27	0.44	–	–
JULIDA	4.29	1.32	0.87	1.59
Julidae	3.75	1.32	0.87	1.59
Polydesmidae	0.54	–	–	–
Polydesmus sp.	0.54	–	–	–
LITHOBIOMORPHA	–	0.22	0.29	–
ISOPODA	1.07	0.66	0.58	1.59
Porcellionidae	1.07	0.66	0.58	1.59
COLLEMBOLA	–	–	8.96	–
BLATTODEA	–	0.44	0.58	–
ORTHOPTERA	4.29	9.67	14.16	–
Ensifera	0.54	2.20	4.62	–
Caelifera	3.75	7.47	9.54	–
HEMIPTERA	2.14	2.20	0.29	0.96
Heteroptera	–	1.98	0.29	–
Aphrophoridae	–	0.22	–	–
Philaneus sp.	–	0.22	–	–
COLEOPTERA	4.56	7.47	13.01	47.77
Tenebrionidae (total)	0.27	–	–	0.64
Crypticus sp.	0.27	–	–	–
Carabidae (total)	2.42	3.3	–	37.26
larvae	0.54	0.44	0.87	–
Trechini	0.27	0.22	–	–
Harpalini	1.61	2.42	2.89	–
Zabrini	–	0.22	0.29	–
Scarabaeidae (total)	0.27	–	0.29	–
Onthophagus sp.	–	–	0.29	–
Staphylinidae	1.61	1.54	3.18	–
Sylphidae	–	–	0.29	–
Nicrophorus sp.	–	–	0.29	–
Curculionidae (total)	–	–	0.29	9.55
Liparus glabrirostris	–	–	0.29	–
Mycetophagidae	–	0.22	–	–
Geotrupidae (total)	–	2.42	4.91	–
Trypocopris vernalis	–	2.20	4.91	–
Coccinellidae	–	–	–	0.32
DIPTERA	5.63	5.71	20.23	0.64
Nematocera	0.54	0.22	2.02	0.32
Brachycera	5.09	5.49	18.21	0.32
HYMENOPTERA	62.74	57.36	21.68	47.13
Formicidae	62.74	56.70	19.08	47.13
LEPIDOPTERA	–	0.88	–	–
No. of specimens	373	455	346	314

different from those of natural prey (GLM-b: $\chi^2_{13} = 723.8$, $P < 0.0001$, Fig. 4).

In prey acceptance experiments, we observed that as soon as the prey touched the silk, the spider ran towards it and bit one of its legs. After biting, the spider pulled the prey into the burrow. All attacked prey were consumed. Once the individual was consumed, the whole exoskeleton was thrown out of the burrow. The acceptance of prey was significantly different among six prey taxa (GLM-b: $\chi^2_5 = 42.6$, $P < 0.0001$, Fig. 5): ants and mirid bugs were captured with 100% frequency, beetles and cockroaches with about 50% frequency, and crickets and isopods with a low frequency (less than 15%).

DISCUSSION

We found that at the order level, the prey composition of all five eresid species was similar, mainly represented by ants and beetles, however, there were differences at lower taxonomic levels. While the most frequent beetle prey of Israeli species were tenebrionids, *E. kollari* primarily consumed carabids. This difference is related to the different habitats in which these eresids occur. *Eresus kollari* occurs in steppe-like habitats (Řezáč et al., 2008) where carabid beetles (mainly the tribe Harpalini) are common. In the desert habitats of Israel, detritivorous tenebrionid beetles are more abundant than Carabidae (Ahearn, 1971; Zachariassen et al., 1987; Ayal & Merkl, 1994). In the webs of Israeli species, the largest number of tenebrionids belonged to representatives of the tribes Erodiini and Tentyriini. This shows that prey availability on sites in Central and Northern Europe is different from those in Southern Europe and Israel.

The abundances of individual tribes of tenebrionid beetles could be influenced mainly by the microhabitat in which the burrows of eresid spiders were located (the microhabitat of the eresid burrows was not recorded). The most preferred habitat by tenebrionids is the wadi, where their diversity is high (Ayal & Merkl, 1994). In addition, larger species of these beetles (*Pimelia* spp., *Trachyderma* spp.) use wadi vegetation as a shelter from predators (Krasnov & Shenbrot, 1996). Species of *Adesmia*, *Tentyria*, and *Sepidium* prefer wadis with especially clay-like soil, while species of *Erodius*, *Zophosis*, *Mesostena*, and *Dendarus* prefer habitats with unconsolidated sand (Ayal & Merkl, 1994).

The prey composition of the four eresid species from Israel differed at the order level. *Adonea fimbriata* most frequently captured ants, whereas *D. fastuosus* and *L. annulipes* mainly captured tenebrionid beetles. In the case of *Eresus* sp., representatives of ants and beetles were captured with a similar frequency. The species *A. fimbriata* and *Eresus* sp. co-occurred at the study sites and their prey composition was similar even at lower taxonomic levels.

The breadth of the trophic niche was rather narrow ($B_A < 0.40$) for three out of the four species from Israel. *Dorceus fastuosus* had the narrowest trophic niche among Israeli species, as it captured mainly beetles. In *A. fimbriata*, the breadth of the trophic niche was also narrow due to the presence of a relatively high number of ants. The trophic niche of *Eresus* sp. was also narrow, as this species consumed mainly beetles and ants, but its breadth was the widest in comparison with *A. fimbriata* and *D. fastuosus*. *Loureedia annulipes* showed the widest trophic niche, as this species consumed representatives from three orders (Coleoptera, Hymenoptera, and Isopoda). The breadth of the niche of *E. kollari* was similar to that of three Israeli species (*A. fimbriata*, *D. fastuosus*, and *Eresus* sp.); the prey composition at the order level was similar as well.

Prey capture by web-building spiders is a result of the interaction between web trapability and spider capture behaviour. The cribellate web of eresid spiders is selective to some extent, a consequence of the differential stickiness of cribellate silk for different insects. Cribellate threads are most sticky for smooth surfaces and surfaces with large setae (Opell, 1994). Smooth surfaces are held effectively by silk threads due to van der Waals forces or capillary action, while long setae, hooks or claws can easily become entangled between cribellate fibres (Opell, 1994; Hawthorn & Opell, 2002, 2003). Cribellate threads are not very effective in adhering to surfaces with short setae or surfaces with detachable scales, which are typical for wings of moths or butterflies (Opell, 1994). Darkling beetles possess various morphological adaptations for hot environments, which may make it difficult for them to escape from cribellate silk. Specifically, species of *Adesmia* are equipped with long stilt-like legs, which increase the distance between the body and hot sand; species of *Erodius* have the first pair of legs with protuberances which are used for digging (Lillig & Pavlíček, 2022).

Curculionidae represented the second most frequent family of beetles in the webs of eresids from both Israel and Czechia. It appears that these weevil beetles became stuck in the cribellate webs because the web was attached to the plants on which they were feeding (Arnett et al., 2002; Liu et al., 2014). Furthermore, due to their clumsiness and the many hooks on the tarsi of their legs, they may have become entangled and therefore an easy prey for spiders (Arnett et al., 2002).

In terms of prey size, all eresid species studied here appeared to catch a wide variety of prey sizes. Although we did not measure the prey size explicitly because it was not possible for the majority of prey items, it was clear that some prey such as ants were relatively small prey (compared to the body of adult eresids) and that some beetles (the genera *Pimelia*, *Blaps,* and *Trachyderma*) were comparatively very big. Apparently, eresid spiders can overcome even very large prey (Nørgaard, 1941). This was especially true in *L. annulipes*, whose webs included very large beetles such as Pimeliini and Blaptini. Such ability may be explained by potent venom and a robust body shape, which can generate more power to pull large prey into the web, as well as by the action of cribellate silk.

Observations of prey capture in *E. kollari* showed that it directed its attacks mainly at the legs of prey, thus reducing the risk of contact with prey mandibles as the prey often tried to escape or attack the spider. In particular, attacking body extremities may reduce the risk of counterattack in the case of dangerous prey (ants, carabid beetles) (Pekár & Toft, 2015). After biting, *Eresus* pulled the prey into cribellate silk to entangle it more. Then, the spider pulled it into its burrow, holding the leg of the prey in its chelicerae, so that the head of the prey always faced the entrance.

The breadth of trophic niche resulting from web content analysis is affected by several factors. Not all entrapped prey is consumed (e.g., Nentwig, 1982). For example, in the prey acceptance trials, we observed that cockroaches buried themselves under the burrow where they could become entrapped by silk but not consumed by the spider. In addition, some prey types do not possess strong sclerotisation of their exoskeleton (e.g., Isoptera, Thysanura), so they decompose more quickly than skeletal remnants with a thicker chitin layer, and their frequency is then underestimated in the analysis. In the case of webs of unidentified Israeli eresids, some prey items could have been trapped after the spider abandoned the web or after the spider's death.

Prey composition in the webs of *E. kollari* differed from prey availability. We expected a higher frequency of epigeic spiders (especially lycosid spiders), isopods and julid millipedes in the webs than the actual capture, because they were abundant at the site of *E. kollari*. In pitfall traps, there was also a high frequency of dipterans (Brachycera), probably because these individuals were attracted by the smell of the preservation medium and dead invertebrates.

The composition of natural prey of *E. kollari* is consistent with former studies of the genus *Eresus* (e.g., Walter, 1999; Zarcos & Piñero, 2016), which found that the majority of prey were beetles, especially from the families Carabidae and Curculionidae. The prey composition of *Eresus* spiders has previously been studied in different parts of its distribution: in Spanish arid ecosystems, *Eresus* sp. mainly captured beetles (Tenebrionidae, Carabidae, and Curculionidae, in order of decreasing frequency), ants (*Messor* spp.), and hemipterans (Zarcos & Piñero, 2016); in Danish heath habitats, the main component of the *Eresus sandaliatus* (Martini & Goeze, 1778) diet was beetles from the families Byrrhidae, Carabidae, Curculionidae, Elateridae, Geotrupidae, and Scarabaeidae (Jensen-Haarup, 1904; Norgaard, 1941); in the British Isles, *E. sandaliatus* predominantly consumed beetles and grasshoppers (Bristowe, 1958); in the Uzbek steppes, the highest proportion of the *Eresus* sp. diet was represented by orthopterans, ants, and beetles from the families Carabidae, Meloidae, Scarabaeidae, and Tenebrionidae (Ergashev, 1979); in Germany, the most common prey of *Eresus* sp. were ants and carabid and byrrhid beetles (Brehm & König, 1992); in southwest Switzerland, the diet of *Eresus* sp. was composed mainly of beetles (Carabidae, Curculionidae, Elateridae, and Scarabaeidae) and ants (mostly *Camponotus* sp., *Formica* sp., *Lasius* sp., *Myrmica* sp.). All this shows that *Eresus* spiders catch a variety of prey, but beetles and ants are the most frequent. Within Coleoptera, there are differences among the studied populations that obviously reflect prey availability.

The narrow breadth of the trophic niche of all studied species could suggest trophic specialisation. However, a natural diet represents a realised trophic niche, which is always narrower than the fundamental niche. It is essential to know the fundamental niche to reveal whether and to what extent prey specialisation occurs. We did not study this in the Israeli spiders but in *E. kollari.* It turned out that *E. kollari* also has a narrow realised niche similar to that of the Israeli species, but its fundamental niche is wide, as revealed by the prey acceptance trials. *Eresus kollari* captured a variety of prey types and did not reject any of the seven prey types offered, including dangerous or well-defended prey, such as *F. rufa* and *T. molitor*, which are frequently rejected by other species of spiders (Nentwig, 1987; Michálek et al., 2019). A lower acceptance rate for woodlice was probably because this prey often quickly burrowed itself under the spider's web, thus avoiding contact with the silk threads. These results jointly indicate that not only *E. kollari* but also the Israeli species are adapted to catch various prey.

We conclude that all five eresid species examined here capture mainly beetles and ants, similar to other eresid genera (Lubin & Henschel, 1990; Henschel & Lubin, 1997; Polis et al., 1998; Miller et al., 2012; Henriques et al., 2018; Arvidsson et al., 2020). All these eresid species are thus stenophagous generalists (sensu Pekár & Toft, 2015) or local prey specialists.

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