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Trophic niche of *Oecobius maculatus* (Araneae: Oecobiidae): evidence based on natural diet, prey capture success, and prey handling

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Abstract. Field and laboratory observations of the feeding ecology (natural diet, prey capture success, and prey handling) of *Oecobius maculatus* Simon 1870 were combined in this study to reveal the level of trophic specialization by this species. Natural prey were investigated on the Croatian island of Brac. Field observations revealed that although spiders captured prey belonging to five invertebrate orders, the most frequently captured prey were ants, which were also the most abundant available prey in the locality. In laboratory experiments, *O. maculatus* spiders accepted three other prey types with a higher probability than ants and were significantly more efficient at capturing and handling flies than ants. These results suggest that this species is a stenophagous generalist with a narrow prey range due to ecological circumstances.

Keywords: Ants, diet breadth, myrmecophagous, spider, trophic specialization

The degree of trophic specialization can be viewed in two contexts. The ecological context describes the diet breath of species in nature: euryphagous species have a wide diet range and stenophagous species have a narrow diet range (Pekár & Toft 2014). The second context focuses on evolutionary adaptations for feeding on a range of food: generalists are able to feed and perform on a wide diet range, while specialists exhibit enhanced handling and use of one or several food types, often associated with poorer performance on alternative food types (Pekár & Toft 2014). Specialists do well when a habitat is stable and the preferred food type is abundant; however, they are vulnerable to changes in their environment (Goldstein 2009).

Predators seem to be less frequently adapted to a narrow diet range than herbivores, parasites or parasitoids (Thompson 1994). Spiders are predators that capture several prey taxa throughout their lives, including a wide variety of invertebrate and vertebrate prey. The number of prey taxa accepted by spiders varies considerably among species. 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. The most frequent type of stenophagy in spiders is myrmecophagy or ant-eating (Pekár et al. 2011). This is probably because ants are highly abundant in many different terrestrial habitats (Hölldobler & Wilson 1990). However, ants often have slender bodies with limited usable body mass and can be dangerous because they are often predatory, have effective defense mechanisms, and are similar to spiders in size (Hölldobler & Wilson 1990).

Small predators, such as spiders, are often exposed to predation themselves when handling prey, so they tend to minimize handling time. Nevertheless, dangerous prey such as ants should be handled more carefully than innocuous prey due to the risk of harm by the prey (Lima & Dill 1990). Furthermore, besides time, spiders usually need to invest more silk and venom when dealing with dangerous prey (Nentwig & Heimer 1987; Malli et al. 1999). Thus, the handling of dangerous prey is energetically costly. Predators can take dangerous prey less often (Forbes 1989) or become specialized and decrease the handling time and energetic costs by increasing the effectiveness of their capture.

Most generalist spiders with no specialized adaptations for ant capture are not able to hunt ants without risk of harm, and thus they avoid ants as prey. However, a few spider species with specialized adaptations for ant capture are stenophagous specialists and feed primarily on ants. For example, members of the genus *Zodarion* Walckenaer 1826 (Zodariidae) use specialized adaptations to overcome ant defenses: they use a unique hunting strategy which involves quickly approaching and attacking an ant's appendage, after which they retreat to a safe distance (Pekár 2004, 2005). Their venom is potent on ants – a single bite suffices to paralyse an individual (Pekár et al. 2014). However, venom specialization carries trade-offs: in particular, it is not so effective on other prey types (Pekár 2004).

Another spider genus that has been considered to be a stenophagous ant-eating specialist is *Oecobius* Lucas 1846 (Oecobiidae). This assumption was based on anecdotal observation of the natural diet of *Oecobius navus* Blackwall 1859 (Glatz 1967; Voss et al. 2007). Exclusive ant-eating in this species was further supported by laboratory observations in which the spiders accepted no arthropods other than ants as prey (Glatz 1967). However, more recent evidence shows that *O. navus* is not strictly stenophagous. The natural diet of two populations of *O. navus* was studied (Líznarová et al. 2013). One population fed mostly on ants, whereas the other population fed primarily on flies and springtails. The most commonly captured prey in each locality corresponded closely to the most abundant potential prey (Líznarová et al. 2013), suggesting that *O. navus* is more likely a stenophagous generalist with its diet in different localities dependent on available prey. Similarly, Garcia et al. (2014) revealed that, in nature, *Oecobius concinnus* Simon 1893 captured mostly ants and dipterans.

We studied the natural diet, prey capture success, and prey handling of *Oecobius maculatus* Simon 1870. The predatory biology of this species has not been systematically investigated. In nature, this species was observed preying primarily on ants (Líznarová, personal observation). We tested whether this species possesses specialized adaptations for ant capture and, moreover, if this specialization carries some trade-offs, namely reduced proficiency at capturing an alternative prey. We combined field observations of its natural diet with laboratory experiments, investigating the spider's capture success for different prey types and its handling tactics with respect to ants and flies. We selected these two prey types because a previous study indicated that *Oecobius* spiders could feed predominantly either on ants or dipterans (Líznarová et al. 2013).

METHODS

Spiders of the genus *Oecobius* build tent-like webs (double sheet webs) that consist of two parallel sheets and several signal threads that run out into the vicinity (Hingston 1925). Spiders use the webs as retreats and most of the time sit hidden between the two sheets with their legs touching the signal threads. When the prey touches the thread, the spider quickly runs out of the web and starts to subdue the prey by circling around it and throwing silk over it. The subdued prey is then taken to the web retreat and consumed; prey remnants remain attached to the web.

We collected *Oecobius maculatus* spiders in the town of Sumartin (GPS: 43° 17′ 5″ N, 16° 52′ 19″ E) on the island of Brac (Croatia) from the stone walls around houses where they were especially abundant. The spider individuals collected ($n = 29$) were at different developmental stages. We placed each collected spider into a plastic tube together with silk from a web that contained prey remnants. *Oecobius* spiders do not chew their prey during feeding; thus, prey remnants are usually preserved in a good condition, enabling their identification. To obtain information about potential prey in the spiders' vicinity, we collected invertebrate individuals within 50 cm of spiders' webs using a pooter (aspirator) and placed them in vials with ethanol at the time of collection. The collection was performed on two days in September 2010 for two hours each day (one hour in the morning, one hour in the afternoon) by one person, amounting to 240 'person-minutes.'

We identified spiders using Nentwig et al. (2010) and Santos & Gonzaga (2003). We identified all prey, potential and actual (i.e. prey remnants found in webs), to the lowest taxonomic level allowed by the physical condition of the specimens. In most cases, we identified the prey specimens to order level. We split Diptera into Nematocera and Brachycera, and Hymenoptera into Formicidae and others. We identified ants collected as potential prey and ant remnants from the webs to species level using Collingwood & Prince (1998).

After transfer to the laboratory, we placed living spiders ($n = 24$, 10 adult females, 14 juveniles) in individual Petri dishes (30 mm diameter × 10 mm height) and left them for three days, during which they built normal webs. Before and during the trials, the spiders were kept at room temperature (approximately 22 °C) and under a natural 14L:10D photoperiod. We maintained moisture levels by adding a drop of water to the bottom of the dish. Seven days before the beginning of experiments, we fed the spiders with fruit flies until satiated to standardize their hunger level. After each trial we fed the spiders with fruit flies *ad libitum* and then left them for seven days without prey prior to the next trial.

In the first experiment, we observed the spiders' capture success for different prey types. We used prey from nine invertebrate orders, most of which occur on Brac. From laboratory-reared cultures, we took fruit flies (*Drosophila* sp., Diptera, mean body length 2.0 mm), termites (workers of *Reticulitermes* sp., Isoptera, 3.5 mm), springtails (*Sinella curviseta*, Collembola, 4.0 mm), crickets (*Acheta domestica*, Orthoptera, 5.0 mm), and beetles (*Oryzaephilus surinamensis*, Coleoptera, 3.0 mm). From the field, we collected spiders (*Zodarion* sp., Araneae, 3.0 mm), millipedes (Julidae, Diplopoda, 4.0 mm), ants (workers of *Lasius* sp., Hymenoptera, 3.0 mm), beetles (Curculionidae, Staphylinidae, Coleoptera, 3.0 mm), and aphids (Aphidinae, Hemiptera, 2.5 mm).

We placed one prey individual in each dish occupied by a spider ($n = 24$) on the opposite side of the dish to where the spider web was built. The webs were usually built on the base of the dish or in the angle between the base and wall; thus, opening the dish did not damage the web. In each trial, we recorded whether the spider captured and then consumed the prey. If the spider did not attack the prey within one hour, then we removed the prey from the dish. We used a randomised incomplete block design so that each prey type was used with at least ten spider individuals in a random order.

In the second experiment, we compared the handling of ants (*Lasius* sp.) and fruit flies (*Drosophila melanogaster*). We offered ants and flies to individual spiders successively in a random order. As before, we placed the prey in the dish occupied by the spider on the opposite side of the dish to where the spider web was built and observed the prey capture behaviour in detail. We recorded the duration of the handling time (the time that elapsed from the first contact with the prey to the start of consumption) using a stopwatch. We measured the following two components of the handling time separately: (1) the time required to wrap the prey and (2) the waiting time (when the spider waited at a safe distance from the prey after envenomation). We also recorded the number of bites delivered to the prey individual. There were 21 replications with ants and 24 with fruit flies.

We performed all analyses with R (R Development Core Team 2010). For both actual and potential prey, we estimated the niche breadth as the inverse of the Simpson index, because it is not affected by rare species that could appear accidentally in a sample (Levins 1968). We compared the proportions of prey types in the diet using Morisita's index, which is suitable when comparing samples of different size and diversity (Horn 1966). Using the Chi-square test, we compared the relative frequencies of prey found in the webs and the prey available on the walls. For each ant species, we measured the selectivity of attack according to the Savage selectivity index (W) (Manly et al. 2002). The results of the prey-capture success experiments and the results of the prey handling experiments were analysed using Generalised Estimating Equations (GEE), which is a linear method that can handle correlations resulting from repeated use of the same spider individuals. We used GEE for non-normally and log-normally distributed response variables (Pekár & Brabec 2012). To compare the acceptance of prey, GEE with binomial errors (GEE-b) were used because the response variable was composed of binary scores. To compare the handling time, wrapping time, and waiting time, GEE with Gamma errors (GEE-g) were used because the response variables were expected to have a Gamma distribution. We used GEE with Poisson errors (GEE-p) to compare the numbers of bites, because the response variable was expected to have a Poisson distribution.

Table 1.—Relative frequencies of prey taxa found in the webs (= actual prey) and around the webs (= potential prey) of *Oecobius maculatus* in the town of Sumartin on the island of Brac (Croatia).

Order	Actual	Potential
Diptera		
Nematocera	0.03	0.00
Hymenoptera		
Formicidae	0.87	0.91
Other	0.01	0.01
Hemiptera	0.01	0.01
Araneae	0.03	0.03
Acari	0.03	0.00
Isopoda	0.00	0.01
Psocoptera	0.00	0.01
Gastropoda	0.00	0.01
Total (*N*)	70	157

RESULTS

Natural prey analysis.—Representatives from five invertebrate orders were found in the webs (actual prey) of *O. maculatus* and representatives from six invertebrate orders were found in the vicinity of spiders' webs (potential prey) (Table 1). The most abundant prey in the webs were ants (89%) and ants were also the most frequent prey occurring around the spiders webs (91%). There were three ant species from two subfamilies found around spiders' webs: *Crematogaster scutellaris* (Olivier) (Myrmicinae), *Pheidole pallidula* (Nylander) (Myrmicinae), and *Lepisiota frauenfeldi* (Mayr) (Formicinae). The similarity between prey taxa composition found in the webs and that of the potential prey was 99.8% (Morisita's index) and did not differ significantly (Chi-square test: $\chi^2_9 = 0.01$, $P = 0.99$). The diversity of potential prey expressed by Simpson's reciprocal index was 1.27, indicating that one prey type was dominant in the sample. Selectivity was computed for each ant species (*i*) according to the Savage selectivity index (W_i); there was almost no selection in *C. scutellaris* ($W = 0.89$), positive selection in *P. pallidula* ($W = 5.99$), and negative selection in *L. frauenfeldi* ($W = 0.60$) (Fig. 1).

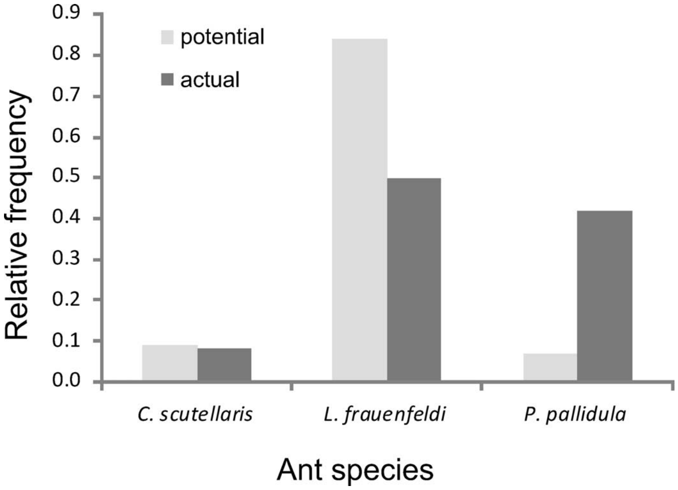

Figure 1.—Relative frequencies of ant species in the composition of potential and actual prey of the spider *Oecobius maculatus*.

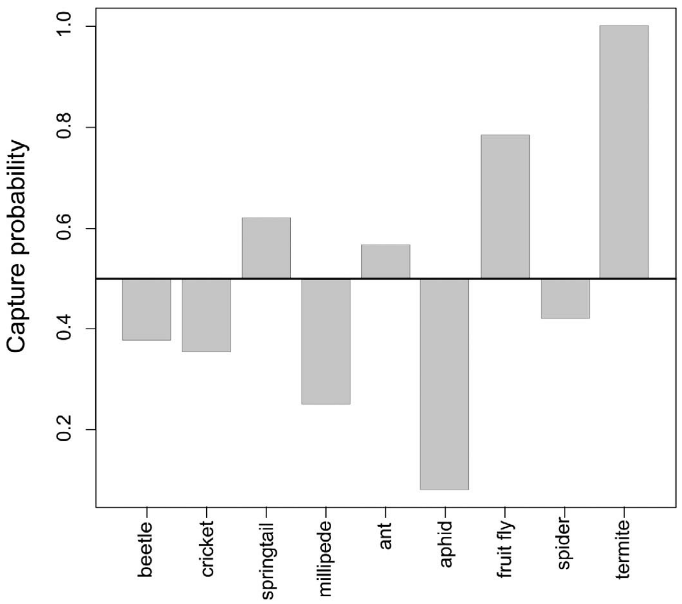

Figure 2.—Capture probability for nine different prey types compared to the average (thick horizontal line) prey capture probability (= 0.495) of the spider *Oecobius maculatus*.

Prey-capture success.—All of the offered prey types were captured by some (at least two) spider individuals. The capture success differed significantly among prey types (GEE-b, $\chi^2_1 = 21974$, $P = 0.001$). The only prey type that was captured with significantly less than the average probability of 49.5% was aphids (8%, $n = 24$, contrasts, $P = 0.007$). Millipedes (25%, $n = 12$), beetles (38%, $n = 21$), spiders (42%, $n = 19$), and crickets (42%, $n = 19$) were captured with less than average probability, but not significantly less ($P > 0.05$). In contrast, termites (100%, $n = 19$, contrasts, $P = 0.001$) and fruit flies (78%, $n = 23$, contrasts, $P = 0.039$) were captured with significantly higher than average probability. Springtails (62%, $n = 21$) and ants (57%, $n = 23$) were captured with only slightly higher than average probability (Fig. 2). All prey individuals that spiders captured were consumed, except beetles, where 62% ($n = 21$) of individuals were not killed following the spider's attack or were rejected by the spider after being subdued.

Prey handling.—The handling times for flies and for ants differed significantly (GEE-g: $\chi^2_1 = 3.33$, $P = 0.002$). Ants were handled for a significantly longer time than flies (Fig. 3). When the components of the handling process were compared separately, the wrapping time did not differ significantly between flies and ants (GEE-g: $\chi^2_1 = -0.9$, $P = 0.38$), but the number of bites used during the attack was significantly higher for ants (GEE-p: $\chi^2_1 = 2.3$, $P = 0.02$). Also, the waiting time for prey paralysis was significantly longer for ants than for flies (GEE-g: $\chi^2_1 = 2.4$, $P = 0.02$).

DISCUSSION

Natural prey analysis showed that *O. maculatus* spiders captured mainly ants at the study site. From such data alone, it would be tempting to claim that *O. maculatus* are stenophagous predators specialised on ants. A similarly

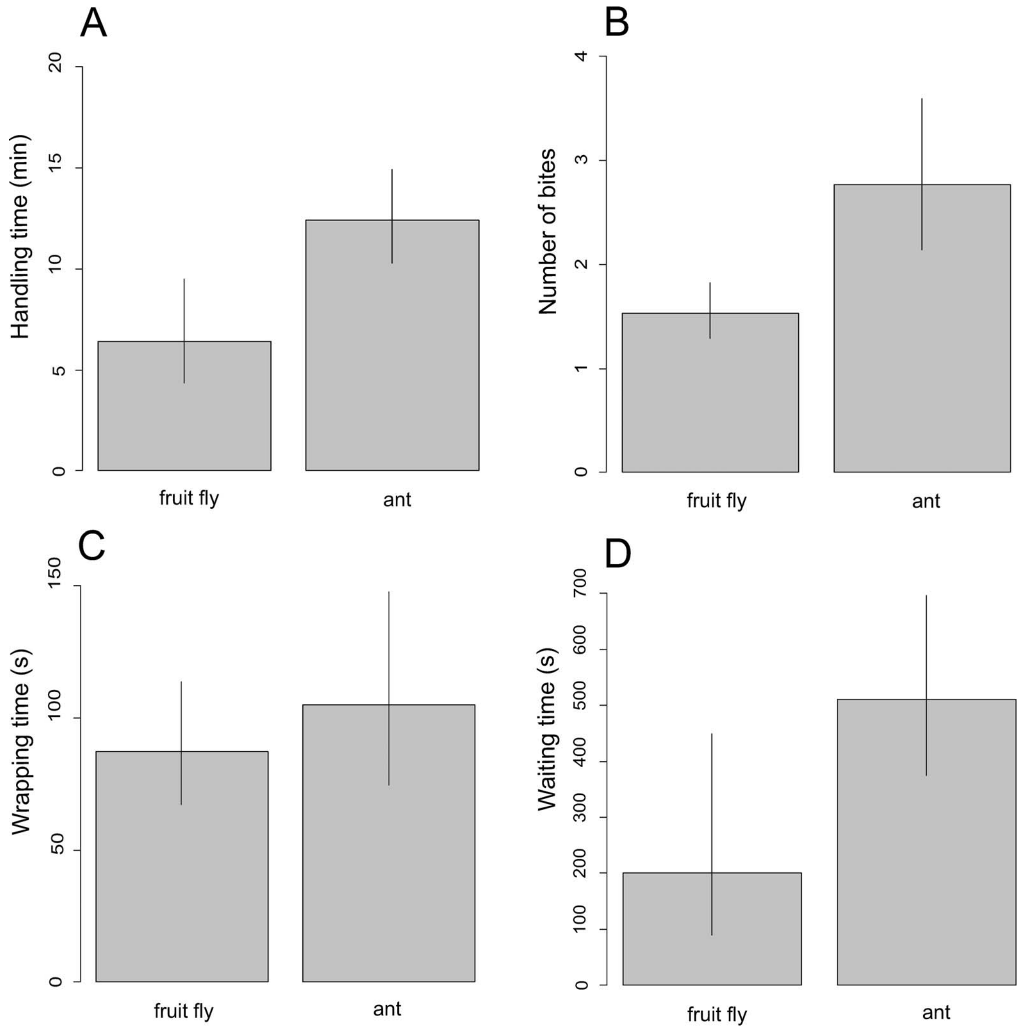

Figure 3.—Comparison of the total handling time (A), number of bites (B), wrapping time (C), and waiting time (D) of *Oecobius maculatus* for two different prey types, fruit flies ($n = 17$) and ants ($n = 13$). Bars are means; whiskers are 95% confidence intervals.

erroneous conclusion was made in the past with respect to *O. navus.* This species was formerly considered as a stenophagous specialist (Glatz 1967); however, recent laboratory experiments revealed that this species is able to successfully subdue a wide variety of prey, indicating that *O. navus* is only a stenophagous generalist (i.e., local trophic specialist) (Líznarová et al. 2013). This may also apply to many other *Oecobius* species.

It is assumed that foraging individuals should discriminate among prey types on the basis of their relative profitability (Reichert & Luczak 1982), usually expressed as a cost:benefit ratio (Krebs 1978). Commonly unprofitable prey types with higher costs than benefits for spiders are animals that are beyond the spiders' size range, are distasteful prey, and are predatory species that can attack the spider (Reichert & Luczak 1982). Our laboratory experiments showed that termites, fruit flies, and springtails were captured by *O. maculatus* spiders at a higher frequency than ants, suggesting that these prey types are actually more profitable for the studied spiders than ants. These prey types are most likely to be of optimal size, palatable, and non-dangerous. In contrast, many aphid species are distasteful or even noxious for spiders (e.g. Malcolm 1989; Toft 1995), which could be the reason why aphids were captured by *O. maculatus* spiders with the lowest frequency.

In addition, the foraging tactics of spiders may also differ when hunting different prey types—in this case, either innocuous or dangerous prey (O'Connell & Formanowicz 1998). *Oecobius maculatus* was able to discriminate between innocuous fruit flies and dangerous ants and to employ different hunting tactics. To subdue ants, it was necessary to use more bites, possibly to inject more venom. The waiting time was also longer for ants than for flies; possibly, the venom took longer to paralyze ants or the spiders were more vigilant when hunting dangerous prey and waited until the ants were completely paralyzed before feeding. By contrast, spiders were able to consume flies immediately after an attack without risk of harm. This is in line with the dangerous prey hypothesis, which states that predators may need more time to handle individuals exhibiting strong defensive behaviour compared to defenseless prey (Forbes 1989). In general, *Oecobius* spiders use the tactic that is efficient for hunting dangerous prey for all prey types. Since these spiders throw their silk from some distance and face away from their prey in a similar fashion as ant-eating *Euryopis* spiders (Carico 1978; Porter & Eastmond 1982), they are able to entangle the prey in silk before it can retaliate.

Specialists have often evolved morphological, metabolic, venomic, and behavioral traits used in prey capture and processing that are absent in generalists. These adaptations increase the efficiency of capture of the principal prey; however, they may constrain the spiders' ability to catch alternative prey. Despite that, there are also examples of polyspecialists, which are simultaneously specialized on more than one type of prey (e.g., Jackson & Blest 1982). Ant-eating *Zodarion* spiders use specialized predatory behavior (Pekár 2004) and selectively potent venom to subdue ants effectively (Pekár et al. 2014). We did not observe any of these adaptations in *O. maculatus*. Furthermore, it is not known whether *Oecobius* spiders are able to develop and grow on ants exclusively, as are *Zodarion* spiders (Pekár et al. 2010), and thus possess metabolic adaptations which enable them to balance the nutrient intake and extract all essential nutrients from just one prey type, or whether they require additional nutrients from other prey species.

In nature, *Oecobius maculatus* captured ants of three species. Yet, we observed some degree of selectivity in *O. maculatus* among these ant species. The spiders hunted *P. pallidula* more often than expected and *L. fraunfeldi* less than expected. This suggests some ability by *O. maculatus* to discriminate even between ant species and actively choose more profitable ones. *Pheidole* ants are primarily scavengers that occasionally hunt small insects (Detrain & Deneubourg 1997); therefore, they may be less aggressive, and thus less dangerous, than strictly predatory *Lepisiota* ants (Sekamatte et al. 2003). Alternatively, the selection could be passive, due to the spider's lower success rate at subduing *Lepisiota* ants.

The obtained data support the view that *O. maculatus* spiders are stenophagous generalists rather than stenophagous specialists, because we did not observe any specialized adaptations in capturing ants. Their hunting tactics are well adapted to a wide variety of prey types including ants and the successful capturing of ants does not result in trade-offs in capturing alternative prey types. Because *Oecobius* spiders captured a variety of insects in the laboratory, their sedentary foraging mode suggests selection for a preferred habitat rather than prey (Uetz et al. 1992), which is rather frequent in spiders (Reichert 1981). Because the *Oecobius* species studied were typically found near high ant aggregations (Glatz 1967; Voss et al. 2007; Líznarová et al. 2013; Garcia et al. 2014), their prey choice in nature is probably made indirectly by choosing spots with high ant densities.

Here, we show that in order to understand the trophic ecology of a predatory species completely, it is necessary to combine both field and laboratory approaches. Field observations of natural prey reveal what the predator actually eats, whereas laboratory experiments help to determine the level of trophic specialization of the studied species, e.g., by exploring the predator's likelihood of catching different prey types and the respective efficiencies with which they are caught.

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LITERATURE CITED

Carico, J. 1978. Predatory behavior in *Euryopis funebris* (Hentz) (Araneae: Theridiidae) and the evolutionary significance of web reduction. Symposia of the Zoological Society of London 42: 51–58.

Collingwood, C.A. & A. Prince. 1998. A guide to ants of continental Portugal (Hymenoptera: Formicidae). Sociedade Portuguesa de Entomologia, Suppl. 5:1–49.

Detrain, C. & J.L. Deneubourg. 1997. Scavenging by *Pheidole pallidula*: a key for understanding decision-making systems in ants. Animal Behaviour 53:537–547.

Forbes, L.S. 1989. Prey defences and predator handling behaviour: the dangerous prey hypothesis. Oikos 55:155–158.

García, L.F., M. Lacava & C. Viera. 2014. Diet composition and prey selectivity by the spider *Oecobius concinnus* (Araneae: Oecobiidae) from Colombia. Journal of Arachnology 42:199–201.

Glatz, L. 1967. Zur Biologie und Morphologie von *Oecobius annulipes* (Araneae: Oecobiidae). Zoomorphology 64:185–214.

Goldstein, N. 2009. Animal Hunting and Feeding. Infobase Publishing, New York.

Hingston, R.W.G. 1925. Nature at the Desert's Edge, Studies and Observations in the Bagdad Oasis. Witherby, London.

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

Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist 100:419–424.

Jackson, R.R. & A.D. Blest. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. Journal of Zoology 196:255–293.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators. Pp. 23–63. *In* Behavioural Ecology: An Evolutionary Approach. (J.R. Krebs, N.B. Davies, eds.). Blackwell Scientific Publications, Oxford.

Levins, R. 1968. Evolution in Changing Environments: Some Theoretical Explanations. Princeton University Press, Princeton.

Lima, S.L. & L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Líznarová, E., L. Sentenská, L.F. García, S. Pekár & C. Viera. 2013. Local trophic specialisation in a cosmopolitan spider (Araneae). Zoology 116:20–26.

Malcolm, S.B. 1989. Disruption of web structure and predatory behavior of a spider by plant-derived chemical defenses of an aposematic aphid. Journal of Chemical Ecology 15:1699–1716.

Malli, H., L. Kuhn-Nentwig, H. Imboden & W. Nentwig. 1999. Effects of size, motility and paralysation time of prey on the quantity of venom injected by the hunting spider *Cupiennius salei.* Journal of Experimental Biology 202:2083–2089.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald & W.P. Erickson. 2002. Resource Selection by Animals: Statistical Analysis and Design for Field Studies. Nordrecht, Kluwer.

Nentwig, W. 1987. The prey of spiders. Pp. 249–263. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Nentwig, W. & S. Heimer. 1987. Ecological aspects of spider webs. Pp. 211–225. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Nentwig, W., A. Hänggi, C. Kropf & T. Blick. 2010. Central European Spiders – Determination Key. Online at http://www.araneae.unibe.ch/

O'Connell, D.J. & D.R. Formanowicz, Jr. 1998. Differential handling of dangerous and non-dangerous prey by naive and experienced

Texas spotted whiptail lizards, *Cnemidophorus gularis*. Journal of Herpetology 32:75–79.

Pekár, S. 2004. Predatory behavior of two European ant-eating spiders (Araneae, Zodariidae). Journal of Arachnology 32:31–41.

Pekár, S. 2005. Predatory characteristics of ant-eating *Zodarion* spiders (Araneae: Zodariidae): potential biological control agents. Biological Control 34:196–203.

Pekár, S. & M. Brabec. 2012. Modern Analysis of Biological Data. 2. Linear Models with Correlation R. Masaryk University Press, Brno [in Czech].

Pekár, S. & S. Toft. 2014. Trophic specialisation in a predatory group: the case of prey specialised spiders (Araneae). Biological Reviews (in press).

Pekár, S., J. Šobotník & Y. Lubin. 2011. Armoured spiderman: morphological and behavioural adaptations of a specialised araneophagous predator (Araneae: Palpimanidae). Naturwissenschaften 98:593–603.

Pekár, S., D. Mayntz, T. Ribeiro & M.E. Herberstein. 2010. Specialist ant-eating spiders selectively feed on different body parts to balance nutrient intake. Animal Behaviour 79:1301–1306.

Pekár, S., O. Šedo, E. Líznarová, S. Korenko & Z. Zdráhal. 2014. David and Goliath: potent venom of an ant-eating spider (Araneae) enables capture of a giant prey. Naturwissenschaften 101:1–8.

Porter, S.D. & D.A. Eastmond. 1982. *Euryopis coki* (Theridiidae), a spider that preys on *Pogonomyrmex* ants. Journal of Arachnology 10:275–277.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reichert, S.E. 1981. The consequences of being territorial: spiders, a case study. American Naturalist 117:871–892.

Reichert, S.E. & J. Luczak. 1982. Spider foraging: behavioral responses to prey. Pp. 353–385. *In* Spider Communication: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, New Jersey.

Santos, A.J. & M.O. Gonzaga. 2003. On the spider genus *Oecobius* Lucas, 1846 in South America (Araneae, Oecobiidae). Journal of Natural History 37:239–252.

Sekamatte, B.M., M. Ogenga-Latigo & A. Russell-Smith. 2003. Effects of maize–legume intercrops on termite damage to maize, activity of predatory ants and maize yields in Uganda. Crop Protection 22:87–93.

Thompson, J.N. 1994. The Coevolutionary Process. University of Chicago Press, Chicago.

Toft, S. 1995. Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. Journal of Applied Ecology 32:552–560.

Uetz, G.W., J. Bischoff & J. Raver. 1992. Survivorship of wolf spiders (Lycosidae) reared on different diets. Journal of Arachnology 20:207–211.

Voss, S.C., B.Y. Main & I.R. Dadour. 2007. Habitat preferences of the urban wall spider *Oecobius navus* (Araneae, Oecobiidae). Australian Journal of Entomology 46:261–268.

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