Naturwissenschaften (2008) 95:233–239
DOI 10.1007/s00114-007-0322-3

ORIGINAL PAPER

Dietary and prey-capture adaptations by which *Zodarion germanicum*, an ant-eating spider (Araneae: Zodariidae), specialises on the Formicinae

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Received: 5 July 2007 / Revised: 26 September 2007 / Accepted: 20 October 2007 / Published online: 10 November 2007

Abstract There has been considerable recent interest in the biology of spiders that specialise on ants as prey, but previous studies have tended to envisage the level of adaptation as being to ants as a group. In this paper, we provide evidence that *Zodarion germanicum* is a spider that has dietary and venom adaptations by which it targets a particular subset of ants, the subfamily Formicinae. We reared spiders from first instar in the laboratory on three different diets: formicine ants only, myrmicine ants only and mixed (both formicine and myrmicine ants). Fitness-related life-history parameters were determined, and we found that the spiders on the formicine-only diet lived longer and grew at a faster rate. Lipid, carbon and nitrogen compositions of ants were analysed, but we found no evidence of formicines differing from myrmicines in macro-nutrient content. This suggests that effects on longevity and growth depended on more specific nutrients or on compounds the prey uses for defence. We investigated how efficient *Z. germanicum* was at paralysing different ants and our findings suggest that the spider's venom is especially effective against formicines. Taken together, our findings suggest that *Z. germanicum* has evolved specialisation at the level of targeting a particular ant subfamily, the Formicinae.

Keywords Ants · Formicidae · Spiders · Myrmecophagy · Prey specialisation

Introduction

Diet range is a central issue in many ecology studies. For predators, observational studies of natural prey can reveal realised trophic niches of study populations, and it is known that various extrinsic factors can influence a species' realised niche (Sih and Christensen 2001). Another approach to understanding a predator's prey range comes from optimal foraging and optimal diet theory. An optimal prey within a predator's fundamental niche is prey that provides the predator with highest fitness, with highest possible nutritional and energetic gain being the typical indicators adopted for highest fitness. However, a full understanding of specialisation requires that we investigate adaptations that are associated with prey searching and prey handling (Ferry-Graham et al. 2002). In particular, behavioural traits are often important determinants of how effective a predator is at capturing particular types of prey, and physiological traits are often important influences on a predator's ability to secure required nutrients. The traits that lead to an increased fitness on one prey might, however, be detrimental when deployed against other types of prey, this being a basic assumption based on the widely accepted adaptive trade-off concept in evolutionary biology (Futuyama and Moreno 1988).

Predators that feed on ants have been of particular interest. Although some predators may only enrich a more

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generalised diet by eating ants opportunistically (e.g. reptiles [Suarez et al. 2000], frogs [Duellman and Lizana 1994]), there are also predators that seem to be primarily, if not exclusively, predators of ants. Ant eating has been documented in mammals (AbenspergTraun and Steven 1997), birds (Kopij 2003), reptiles (Meyers and Herrel 2005), amphibians (Cardwell 1996) and invertebrates (see Hölldobler and Wilson 1990) but with data coming primarily from analysis of natural diet and from prey-choice experiments. In general, the fundamental niche of these species is only poorly understood, and details about how these predators might be adapted specifically to eating ants tends to be unclear. However, ants are potentially dangerous to many potential predators, and we might expect strong selection for the evolution of morphological (Naples 1999) or behavioural (Meyers and Herrel 2005) traits that increase capture efficiency and reduce foraging risk. Nutritional adaptations might also be important for predators that prey primarily on ants.

Ant-eating predators (or myrmecophages) are generally envisaged as feeding on ants in general. However, some ant-eaters have been observed to feed on only some genera or species of ants (e.g. Umeda et al. 1996, Castanho and Oliveira 1997), suggesting that they discriminate strongly between different subfamilies of ants. Yet, little is known whether the morphology, behaviour and metabolism of myrmecophages are ever adaptations specific to particular subfamilies of ants. *Zodarion germanicum* (C.L Koch) is a myrmecophagic spider for which specialisation to the level of ant subfamily has been suggested by previous research. In the field, although *Z. germanicum* has been reported to feed on a genus of myrmicine ants, *Tetramorium*, this spider's most common prey seems to be formicine ants from the genera *Camponotus*, *Lasius* and especially *Formica* (Pekár 2004).

In this paper, we investigate whether *Z. germanicum* has adaptations that make it especially effective at handling formicine ants and whether it has become nutritionally adapted to a diet of formicine ants. Because nutrient composition of prey has direct effect on the fitness of polyphagous predators (Mayntz and Toft 2001), we analysed macro-nutrient contents of prey ants.

Materials and methods

Nutritional specialisation experiment

We reared spider on three different diets: (1) a monotypic diet of formicine ants, *Lasius alienus* (Förster), (2) a monotypic diet of myrmicine ants, *Tetramorium caespitum* (Linnaeus), and (3) a mixed-ant diet of formicine (*L. alienus*) and myrmicine (*T. caespitum*) ants offered alternately. All ants were regularly collected in the field a day before feeding.

Three egg sacs of *Z. germanicum* were allowed to hatch in the laboratory. Three days after leaving egg sacs, spiderlings were randomly assigned to one of the three diet treatments (16 individuals per treatment). Spiderlings were housed singly in tubes (diameter 12 mm, length 60 mm) with a layer of plaster of Paris on the bottom. The tubes were plugged with a rubber-foam, and kept in a climate-controlled chamber. At 5-day intervals, we added a few drops of water to the plaster of Paris, and this provided sufficient humidity. We kept the spiders at 29±2°C (light/dark=16:8), corresponding to the surface temperature at their habitats.

We standardised feeding of spiderlings to either a single *Lasius* ant or to two individuals of *Tetramorium* ants. The rationale for the different numbers used was to compensate for the weight difference: *Lasius* ants (mass 1.06 mg, SE=0.03, $N=15$) and *Tetramorium* (0.57 mg, SE=0.02, $N=15$). The head of each ant was crushed with forceps before being introduced into a tube occupied by a spider. This was an essential preparation of the ants before using them as prey because preliminary work showed that in the confined space of the rearing tubes, intact ants often killed the spider. Preliminary experiments also revealed that freshly immobilised ants were as readily accepted as live ones (Pekár, unpublished). In the mixed-ants treatment, one *Lasius* or two *Tetramorium* were offered on alternate feeding days. Each prey item was removed the following day to avoid ill effects of having decaying prey items in the tube.

Using a Sartorius balance (precision, 0.001 mg), spiders were weighed at about 7-day intervals. Mortality and moulting were checked daily during 110 days of rearing. The experiment was terminated at the end of October because reliable numbers of ants were no longer available in the field because of the cold weather. None of the spiders reached adult stage (only sub-adult stage) by this time. At the end of the experiment, the width of each spider's prosoma (at the widest point) was measured under a stereomicroscope using an eyepiece micrometer.

Body contents of the formicine (*L. alienus*) and the myrmicine (*T. caespitum*) were analysed for total lipids, total elemental nitrogen and non-lipid elemental carbon. Five ants of each species were first dried to constant dry mass at 60°C under vacuum, and the dry mass was measured to the nearest gram (10^{-6}). Total lipid contents were then estimated as the difference in dry mass before and after going through two subsequent 24-h extractions in pure chloroform (AOAC 2006). After lipid extraction, ant elemental nitrogen and carbon were measured using a dry combustion analyser (Na2000). As the carbon contents were measured after lipid extraction, we assumed this non-lipid carbon was correlated with total carbohydrate contents of the ants. Crude protein content was calculated by multiplying elemental N by 6.25 (AOAC 2006).

Paralysis efficiency experiment

One day before the experiments started, 40 female *Z. germanicum* spiders were placed individually in Petri dishes (diameter 40 mm) with filter paper glued to the bottom and a thin layer of fluon on the sides. We used four ant species, selected among the species known from the field to be potential prey namely, *Lasius platythorax* Seifert (body size=4 mm), *Formica cunicularia* Latreille (6 mm; both Formicinae), *Myrmica sabuleti* Meinert (5 mm) and *T. caespitum* (3 mm) (both Myrmicinae). Ants (approximately 30 individuals) were collected in the field a few days before their use in the experiment. *L. platythorax* and *T. caespitum* (body length, 3–4 mm) were classified as small and *F. cunicularia* and *M. sabuleti* (5–6 mm) as large ants. For each ant species, there were ten trials, each individual spider being used only once. A single trial consisted of releasing an ant into a dish occupied by a spider. Spiders usually attacked the ant within 30 s. If the spider did not attack the ant within 10 min, the experiment was terminated. For each trial, we recorded the number of attacks and the paralysis latency (the time between first being attacked and the prey's complete immobilisation [evidence: an ant turned upside down and unable to raise itself; we turned it over with forceps]). After an attack, the spider waited away from the ant, but it usually returned a few minutes after the prey became completely quiescent.

Statistical analyses

Data were analysed using various methods within R (R Development Core Team 2006). Proportions of spiders fed on each feeding date were compared with a paired *t* test. The longitudinal data on absolute weight were analysed with linear mixed-effect models (LME) available from the nlme package (Pinheiro et al. 2006). To model the weight change (and compare slopes of treatment levels), the fixed component of the model included two variables, diet and time. The only random component was the time variable. This was to take account of the temporal pseudoreplications. The model was tested for the inclusion of autocorrelation (corCAR1) and variance (varPower) structures. Other data were analysed either with a linear model or generalised linear models (GLMs) with appropriate family and canonical link functions. For data on counts (number of attacks), Poisson family (GLM-p) was used. Underdispersion in the minimal model was adjusted by using the quasipoisson family. For continuous measurements (duration of instar, weight at moulting, size of prosoma, paralysis latency), the Gaussian family (analysis of variance [ANOVA]) was used. However, when the Gaussian model residuals did not meet criteria for variance homogeneity and normality, log transformation was applied on the data. Alternatively, GLM with Gamma errors (GLM-g) was used if the variance increased with the mean. For data on time to death, the survival regression (from survival package [Therneau and Lumley 2006]) with the Weibull family was used as the scale parameter (0.63) was significantly different from 1 (p=0.02). The adequacy of each model was checked based on the diagnostic plots. The minimal adequate model was achieved using the deletion of insignificant terms at α=0.05 based on the *F* or Chi-square test and posteriori simplification by lumping treatment levels. Comparison between treatment levels in the minimal model was done using 'treatment' contrasts (Crawley 2002).

Results

Nutritional specialisation experiment

How often spiders accepted and fed on *Lasius* was not significantly different from how often they accepted and fed on *Tetramorium* (paired *t* test, t_{26}=−1.3, p=0.2). Pooling data on each feeding date, 63% (N=16) of spiders fed on ants offered.

Survival of spiders was significantly affected by the diet (survival regression, χ^2_2=7.5, p=0.023, Fig. 1). Expected mean survival of spiders on the myrmicine diet was 95 days, which is significantly shorter than that for the other two diets (contrasts, p<0.037): 215 days for mixed-ant and 203 days for formicine diet. There was no significant

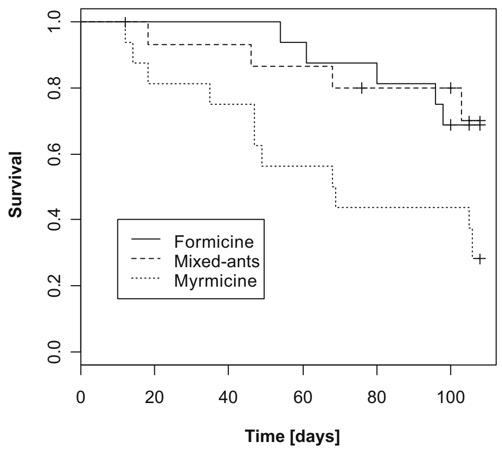

Fig. 1 Survival of spiders reared on three diets during 110 days of the experiment. Diet: formicine (*L. alienus*), myrmicine (*T. caespitum*) and mixed-ants (*L. alienus* and *T. caespitum*)

difference between the survival of spiders fed these two diets (contrast, $p=0.89$).

Developmental rates varied with diet, differences becoming apparent from the second instar, when 60% of spiders on the myrmicine diet and 83% of spiders on the mixed-ant and 87% of spiders on formicine diets moulted to the third instar. Of these, 54% of the spiders on the formicine and 25% of the spiders on the mixed-ant diet moulted to the fourth instar. No spider on the myrmicine diet moulted to the fourth instar. However, for the first instar, there was no significant difference between diet groups (ANOVA, $F_{3,\ 34}=1.5$, $p=0.23$, Table 1). Concerning the instar duration, a difference became apparent from the second instar onwards (ANOVA, $F_{2,\ 26}=5.1$, $p=0.013$). This instar lasted significantly longer for spiders fed on myrmicines than for those fed on formicines (contrasts, $p<0.03$, Table 1). For mixed-ant and formicine diets, the durations of the third instar were similar (ANOVA, $F_{1,\ 9}=1.1$, $p=0.3$).

Growth rate also differed significantly among groups (LME, $F_{2,\ 505}=9.7$, $p=0.0001$, Fig. 2). The greater increase in weight was for spiders fed on formicine ants (slope $b=0.018$). Those fed on mixed-ant diet increased less, but they were not significantly different from those fed on formicines ($b=0.0148$, contrast, $p=0.23$) and those that fed myrmicine ants increased significantly less than those on formicine ($b=0.0066$, contrast, $p<0.0001$). Spider weight after moulting (approximated by the nearest weight measuring) did not differ between ant diets at any instar (ANOVAs, $p>0.27$). The mean mass at the first moult was 0.746±0.03 (SE) mg, 1.266±0.064 mg at the second moult and 2.243±0.191 mg at the third moult. At the end of the experiment, the surviving spiders differed in prosoma width. The prosoma of spiders on the formicine diet was 0.85 mm wide (SE=0.03, $N=12$), on myrmicine 0.72 mm (SE=0.01, $N=10$) and on mixed-ants was 0.77 mm (SE=0.03, $N=7$). Spiders fed on the formicine diet were significantly larger than those fed on the myrmicine diet (ANOVA, $F_{2,\ 26}=3.8$, $p=0.034$). However, the differences between the mixed-ants diet and the myrmicine or the formicine diet was not significant (contrasts, $p>0.45$).

The relative contents of lipids, nitrogen and non-lipid carbon of the two ant species used in the diet experiment, *L. alienus* and *T. caespitum*, did not differ (ANOVAs, $F_{1,\ 8}<3.2$, $p>0.11$, Fig. 3).

Paralysis efficiency experiment

There was a significant interaction between ant subfamily and ant size (GLM-p, $F_{1,\ 36}=19$, $p=0.0001$, Fig. 4a). The number of attacks was similar (two to three attacks) for small formicine and small myrmicine ants (contrast, $p<0.76$), but for large myrmicine ants, it was 7.2 times larger than for large formicine ants (contrast, $p<0.0001$). Paralysis latency was significantly different between ant sub-families (GLM-g, $F_{1,\ 38}=140$, $p<0.0001$) and for size of ants (GLM-g, $F_{1,\ 37}=117$, $p<0.0001$, Fig. 4b). When ants were small, mean latency was 1.8 times longer for myrmicines than for formicines. When ants were large, the mean was 7.8 times longer for myrmicines than for formicines.

Discussion

On the whole, our two hypotheses are supported by our findings. *Z. germanicum*, a spider already known to feed on ants, appears to be adapted, in its dietary requirements and its venom characteristics, at a level narrower than the family Formicidae. In the dietary experiment, *Z. germanicum* clearly performed better on a pure diet of the formicine ant *Lasius* than on a pure diet of the myrmicine ant *Tetramorium*. This held for all measured parameters (survival, growth and development).

We were unable to measure time spent feeding on each prey, nor were we able to compare intake during feeding during each feeding event. Therefore, it remains unclear whether the effects we found are primarily a consequence of a nutritional variable or, instead, related primarily to consumption of insufficient quantity of nutrients or to the consumption of an unbalanced diet resulting from restricted feeding. However, the spiders gained less weight on *Tetramorium*, and this suggests that *Z. germanicum* fed on

Table 1 Mean (±SE) duration of instars (days) for *Z. germanicum* reared on three diets: formicine (*L. alienus*), myrmicinmae (*T. caespitum*) and mixed-ants (*L. alienus* and *T. caespitum*)

	Duration of instars (days)		
	1st	2nd	3rd
Formicine	32.03±4.41 ($N=15$)	37.92±4.27^{a} ($N=13$)	29.57±3.95 ($N=7$)
Myrmicine	37.80±4.71 ($N=10$)	53.17±5.98^{b} ($N=6$)	–
Mixed-ants	41.75±5.49 ($N=12$)	30.30±3.37^{a} ($N=10$)	37.02±5.91 ($N=4$)

Significant differences (contrast, $p<0.05$) between diet groups are assigned with a different superscript.

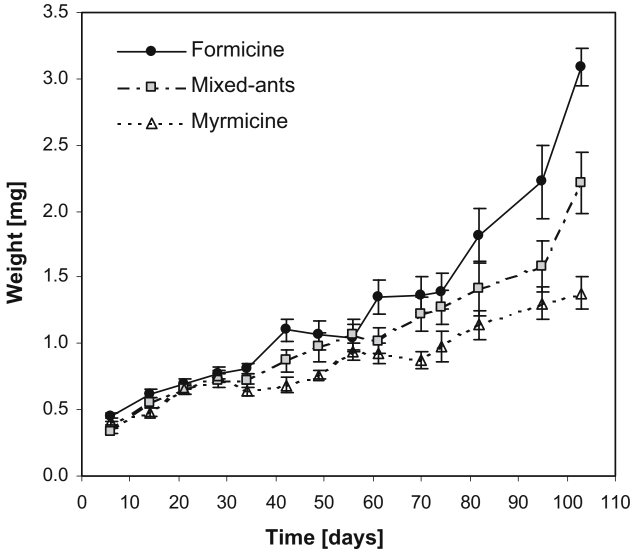

Fig. 2 Mean (±SE) of absolute weight of spiders on three diet types during 110 days of the experiment. Diet: formicine (*L. alienus*), myrmicine (*T. caespitum*) and mixed-ants (*L. alienus* and *T. caespitum*)

both ants for a shorter time or fed only on one and discarded the other *Tetramorium* ant and, therefore, gained less. Restricted feeding might be due to an acquired aversion to these ants. It is known from studies with spiders that are more polyphagous than *Z. germanicum* that prey of low quality may induce aversion (Toft and Wise 1999). Alternatively, short-term satiation may have caused cessation of the processing of the second *Tetramorium* ant. This suggests that our experiments could be envisaged as simulating a situation in which spiders hunt two different ant species at similar hunting rate.

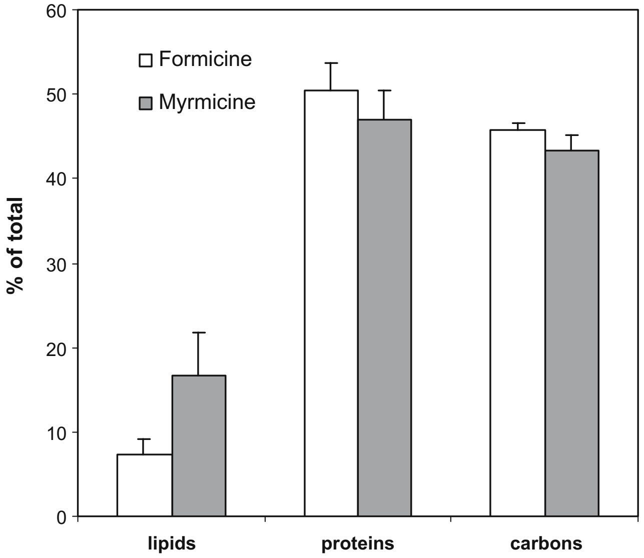

Fig. 3 Composition of lipids, proteins and carbon macronutrients as the percent of total body weight (mean±SE) in the two ant species (*L. alienus* and *T. caespitum*) belonging to different subfamilies

In our study, the growth rate of spiders on the mixed diet was intermediate between the growth rates of spiders on two pure ant diets. Yet, other studies have shown that polyphagous predators can benefit from dietary mixing (Toft 1999, Bilde and Toft 2000). Our findings suggest that a diet of formicine ants is simply superior to a diet of myrmicine ants, with mixed diet being intermediate because of the inclusion of some formicines. When restricted to feeding on myrmicines alone, the spider may have experienced intake of nutrients that were inferior to the nutrients that it could acquire from formicines. An alternative is that feeding efficiency alone accounted for the difference in performance. Perhaps, the nutrients were similar, but the spider could not extract these nutrients as effectively from myrmicines as from formicines. This would result in decreased calorie intake and thereby reduced growth. If the first hypothesis is true, then our results are in accordance with studies on other stenophagous predators, such as *Coccinella septempunctata* Linnaeus, an aphidophagous beetle (Hauge et al. 1998, Nielsen et al. 2002), and *Portia fimbriata* (Doleschall), an araneophagous salticid spider (Li and Jackson 1997). In both the beetle and the salticid spider, mixed diet was inferior to a pure diet of the preferred prey.

We expected that the content of flesh of the two ant species would vary strongly. Yet, our analysis of macronutrient compositions showed no significant differences in lipids, proteins and non-lipid carbon contained in the ants we used. Myrmicines generally have tougher cuticle than formicines. This suggests the two ants we used may differ in ratio of chitin to digestible tissues. Perhaps, this difference was larger when two *Tetramorium* ants were used. Whether this caused the differences in performance of spiders is unclear, but we observed higher mortality on pure myrmicine diet virtually from the very beginning of rearing, and this suggests that deficiency of some essential micronutrients in this ant was the primary cause of the difference. Further work is needed to determine whether there is some less easily detected difference between the ants in composition of amino acids, fatty acids, carbohydrates, sterols, vitamins or formic acid and whether these might be responsible for the observed differences in the spider's performance on the different diets.

In the second experiment, we found that *Z. germanicum*'s paralysis efficiency was better when the ants were formicines instead of myrmicines. At present, it is not clear whether this result is due to different susceptibility of ants to the venom of *Z. germanicum* or due to some morphological, behavioural or physiological characters inherent to ants. For example, the spider might have experienced more difficulty puncturing the thicker cuticle of myrmicine ants

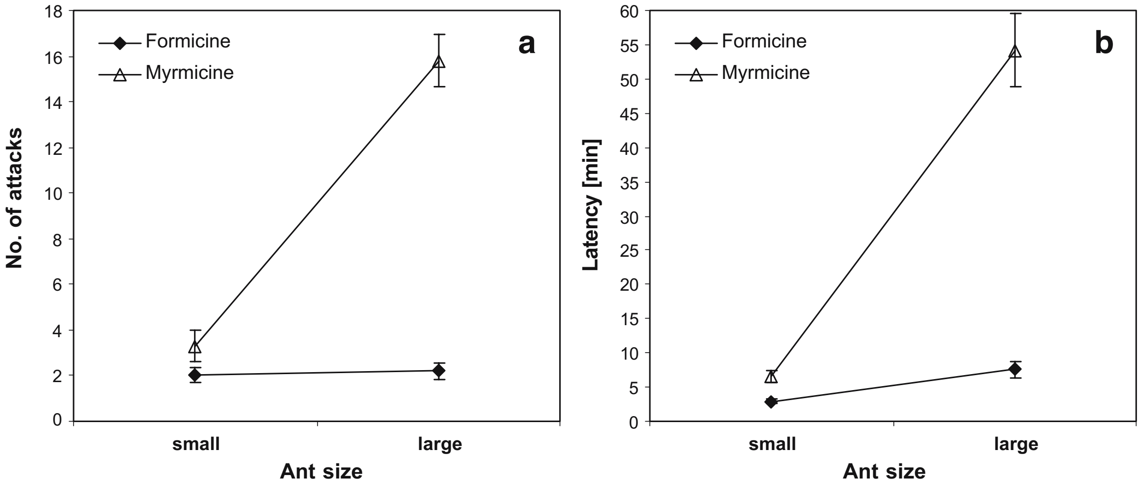

Fig. 4 Comparison of the mean (±SE) number of attacks (**a**) and the paralysis latency (**b**) for *Zodarion* spiders capturing ants of two size categories (small, large) from two ant subfamilies (formicine: *F. cunicularia*, *L. platythorax,* myrmicine: *M. sabuleti*, *T. caespitum*)

with its chelicerae. However, recent studies on the paralysis efficacy of other *Zodarion* species have revealed that some species are more efficient at subduing formicines (*Cataglyphis*, *Camponotus*, *Formica*) and others are more efficient at subduing myrmicine (*Aphaenogaster*, *Messor*; Pekár et al. 2005, Pekár 2005, unpublished). We found no morphological or behavioural differences between these *Zodarion* spiders that help explain the observed variation in paralysis latency, and this suggests that the venom of *Zodarion* spiders, like that of some other spiders (e.g. *Tetragnatha*; Binford 2001), have potency that is specific to particular kinds of prey. Nevertheless, further work is needed, especially work using a combination of biochemical and physiological methods. In particular, it would be useful to compare the chemical composition of the venom of *Zodarion* species that prey primarily on different ants, focusing on the efficacy of venom under standardised conditions.

In central Europe, where we studied *Z. germanicum*, the prevalent formicine genera are *Camponotus*, *Formica* and *Lasius*, and *Z. germanicum* has been seen feeding especially on large *Formica* ants (Pekár 2004). Spiderlings might not be able to capture these large ants, and we predict that they may feed especially on smaller formicine species, such as *Lasius* spp. However, we can not rule out the possibility of even narrower stenophagy, perhaps to the level of genus or species. Such species-specific stenophagy might be present in *Zodarion* species that feed on polymorphic ants, such as *Messor* (Myrmicinae). Consequently, there might have been two different pathways of myrmecophagy in *Zodarion* spiders: Species feeding on polymorphic ants evolved specialisation to the level of species, while those feeding on non-polymorphic ants evolved specialisation to the level of sub-family.

Although prey specificity below the family level appears to be very rare in spiders, there is evidence of this in *Evarcha culicivora* Wesolowska, a salticid spider that feeds indirectly on vertebrate blood by choosing blood-carrying mosquitoes as prey (Wesolowska and Jackson 2003, Jackson et al. 2005). *E. culicivora* has specific prey-capture behaviour for a particular mosquito genus, *Anopheles* (Nelson et al. 2005) and, in prey-choice situations, prefers *Anopheles* to other mosquito genera (Nelson and Jackson 2006).

Our results are in general agreement with expectations from the optimal diet theory (Sih and Christensen 2001). The capture of formicine ants (i.e. optimal prey) required fewer attacks (i.e. presumably less energy), which appears to be less costly because the shorter time before paralysis restricts the chances that ants will harm the spider, and the nutritional payoff from feeding on formicines appears to be greater than from feeding on myrmicines.

Altogether, we have evidence on prey specificity of *Z. germanicum* from four different approaches. Analysis of natural prey and laboratory prey-choice experiments from an earlier study (Pekár 2004) combined with the new findings from the present study has delimited the optimal prey. Obtaining extensive data from diet experiments is particularly difficult because these experiments are labour intensive and require considerable time. This difficulty is compounded by how we detected diet effects only after the second instar, which means only after 2 months of rearing. It is encouraging that our findings from experiments on paralysis efficacy were comparable to the findings from the diet experiment. This suggests that for *Zodarion* species, using analysis of natural diet combined with results from experiments on paralysis might, as a rule, be an effective predictor of dietary specificity on the same prey.

Acknowledgements We would like to thank D. Wanacker for help with weighing spiders, C. Haddad for correction of English and an anonymous reviewer for very constructive and helpful comments that largely improved the paper. SP was supported by a grant provided by the Carlsberg Foundation and the project no. MSM0021622416 provided by the Ministry of Education, Youth and Sports of the Czech Republic. MH was supported by the grant no. 524/05/4536 of the Czech Science Foundation. Experiments performed comply with the current laws of the Czech Republic.

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