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Trophic strategy of ant-eating *Mexcala elegans* (Araneae: Salticidae): looking for evidence of evolution of prey-specialization

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Abstract. We investigated the trophic strategy of *Mexcala elegans* Peckham & Peckham 1903, an ant-eating salticid spider from South Africa, in order to gain baseline information concerning the evolution of prey specialization. We studied its natural prey, prey acceptance, and choice using a variety of prey species. In its natural habitat, the spider captured only ants, mainly its mimetic model *Camponotus cinctellus*, indicating that the species is a stenophagous ant-eater. However, in the laboratory, *M. elegans* captured 12 different invertebrate taxa with efficiency similar to the capture of ants, suggesting that it is euryphagous. For the capture of ants but not for other prey, it used a specialized prey-capture behavior. In prey-choice experiments, the spiders did not prefer ants to flies. We found no evidence for neural and behavioral constraints related to identification and handling of prey. Our results suggest that *M. elegans* is a euryphagous specialist using a specialized ant-eating capture strategy in which prey specialization has evolved as a byproduct of risk aversion ("enemy-free space" hypothesis).

Keywords: Prey, hunting behavior, myrmecophagy, mimicry, evolution

Stenophagy, the utilization of a narrow prey range, may be a product of an innate response due to evolutionary transitions and fitness trade-offs or a proximate response due to specific environmental conditions; i.e., dominance of a certain prey species. In the former case, such species are stenophagous specialists because they are not able to catch and utilize alternative prey. In the latter case, such predators are stenophagous generalists since they possess versatile adaptations allowing them to capture and process a variety of prey in environments with diverse prey (Sherry 1990).

Evolution of stenophagous specialists has been explained by a number of hypotheses (particularly in herbivores). The enemy-free space hypothesis postulates that stenophagy has evolved as a byproduct of using host/prey as a refuge or defense (Brower 1958). The neural constraints hypothesis (Jermy et al. 1990) suggests an inability to recognize cues from other than preferred prey. The physiological trade-off hypothesis (Singer 2001) is relevant when the predator is constrained in utilization of other than its preferred food. And, the optimal-foraging hypothesis (Singer 2008) predicts lower efficacy in the capture of alternative prey.

Revealing the trophic strategy of a species requires multiple approaches. Analysis of natural prey alone cannot provide complete evidence for a trophic strategy. Such data need to be supplemented by extensive laboratory prey acceptance and choice experiments. This is because the natural prey analysis reveals only the realized trophic niche that measures actual diet use and results from the effect of both intrinsic and extrinsic variables. In contrast, laboratory experiments can reveal the fundamental trophic niche that is determined by intrinsic variables only (Bolnick et al. 2003). Furthermore, trade-offs (behavioral, morphological, or physiological) that constrain prey utilization in stenophagous specialists can only be determined experimentally. The gathered evidence can then be used to draw conclusions on the trophic strategy.

Spiders have been found to be mainly euryphagous (Nentwig 1987), but there are quite a few cases of stenophagous species. Evidence for stenophagy is mainly anecdotal. The most frequent type of stenophagy observed is myrmecophagy; spiders in several families (e.g., Zodariidae, Gnaphosidae, Theridiidae) demonstrate specialization in ant predation (Heller 1976; Carico 1978; Pekár 2004). While the majority of salticid spiders rarely feeds on ants (e.g., Nentwig 1986; Guseinov 2004), some tropical species are myrmecophagous (Cutler 1980; Wing 1983; Jackson & Van Olphen 1992; Li et al. 1999; Allan & Elgar 2001; Jackson & Li 2001). These myrmecophagous species use a specialized tactic to capture ants (e.g., Jackson & Van Olphen 1992; Jackson & Li 2001). However, no salticid species is known to prey exclusively on ants.

We investigated the prey capture behavior of a salticid spider *Mexcala elegans* Peckham & Peckham 1903 in South Africa. *Mexcala elegans* appears to be an inaccurate Batesian mimic of a few ground-living ant species. It is a distinctively polymorphic spider, with three color variations: 1) a metallic silver-gray body with black triangular abdominal marking in late instar immature and adult specimens, resembling silver-gray ground-dwelling ants (Fig. 1A), presumably *Camponotus cinctellus* that are common on the ground surface and low foliage in northeastern South Africa; 2) a metallic silver-gray body adorned by two pairs of large yellow abdominal spots (Fig. 1B) in adult specimens resembling large ground-dwelling wingless female mutillid wasps; and 3) a metallic blue prosoma and bright metallic green abdomen in early instar immatures, possibly inaccurate ant mimics.

Other species of the genus *Mexcala* feed on their ant models (Curtis 1988). Therefore, we predicted that *M. elegans* also hunts its model ants, thus supporting the enemy-free space hypothesis. In order to reveal any trade-offs, neural or behavioral, that would lead to support alternative evolutionary hypotheses, we performed both field and laboratory

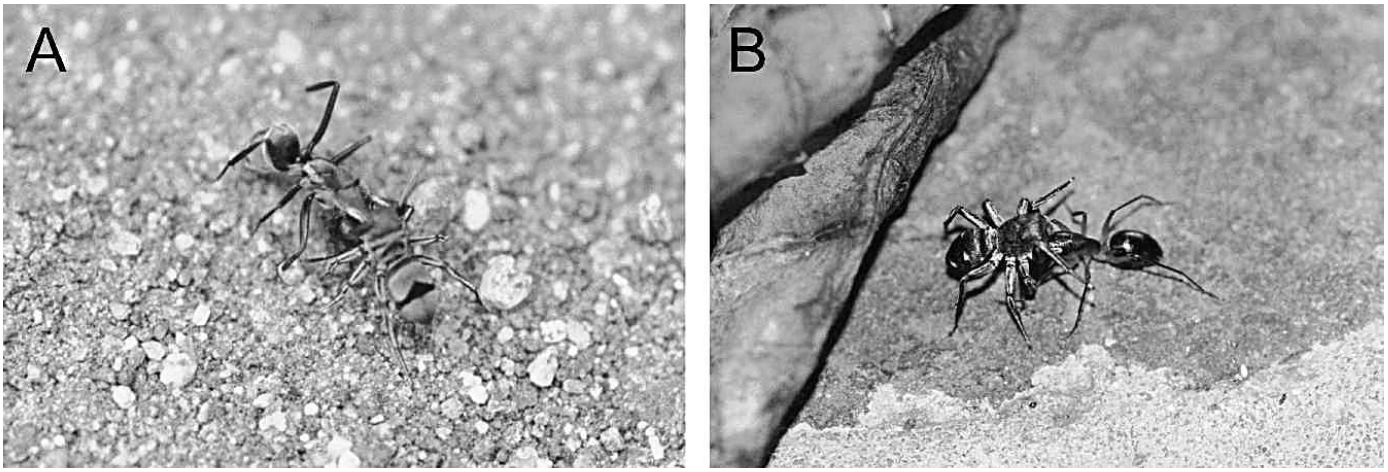

Figure 1.—*Mexcala elegans* capturing ants in the field. A. Female of the gray color variation capturing *Camponotus cinctellus*; B. Female of the spotted variation capturing *Camponotus* sp. 2.

surveys. After examining natural prey capture in the field, we tested the ability of this species to catch and eat alternative prey in the laboratory, and also whether it prefers ants to alternative prey.

METHODS

Field survey.—We investigated the natural prey of *M. elegans* during field trips to Ndumo Game Reserve, South Africa in June–July and November–December 2004–2009 (11 trips in total) that formed part of a larger arachnid biodiversity survey in the reserve. We collected 64 *M. elegans* spiders in a variety of habitats: *Acacia nigrescens* woodland (1.6% of total), *A. xanthophloea* forest (7.8%), broadleaf woodland (25%), floodplains (25%), *Ficus sycomorus* forest (3.1%), and subtropical bush (37.5%). Individual spiders were followed for up to 10 minutes to see whether they would capture ants and to note the prey capture behavior and interactions with different ant species. If they had a prey in their chelicerae, the spiders were collected and preserved in ethanol and brought to laboratory where their sex and the prey was identified to species level. We measured the size of adult males ($n = 15$) and females ($n = 15$) and 15 ant workers of each species captured in the field using an ocular micrometer within a binocular stereomicroscope.

Laboratory experiments.—For intensive studies of prey capture and prey choice, we brought 15 live juvenile *M. elegans* (body size 3.5–5.3mm) collected at Ndumo Game Reserve to the home laboratory. We housed spiders individually in Petri dishes (diam. 4.5 cm) with a filter paper attached to the bottom. A small piece of cotton moistened at 2-day intervals served as a water resource. Using these spiders, we performed two different experiments.

In the acceptance experiment, we used a complete repeated measures design, offering each spider ($n = 15$) each of 17 potential prey species in random order (Table 2). The prey were not native to the spider, as the experiments were performed in Europe, but we used only prey from orders that also occur in South Africa. The relative body size of the prey (1.6–8.0 mm) to spider body length (3.3–5.3 mm) was 0.3–2.4. We observed each trial continuously. If spiders did not respond to a prey item within 15 min, we stopped the trial and 12 h later initiated a new trial with a different prey. If a prey was accepted, we initiated the next trial 24 h later. For each trial, we recorded whether the prey was attacked and subsequently consumed. In trials with ant or termite prey, we also recorded the latency to attack (i.e., time between the spider orientation toward the prey and the attack) and the latency to paralysis (i.e., time between the attack and grabbing the prey in the chelicerae).

In the prey-choice experiment, performed after the acceptance experiment with a paired design, we released two non-native prey items of similar size (relative prey/spider size: 0.4–1) at the same time into the dish occupied by a spider. Spiders ($n = 15$) were starved for two days prior to each trial. We used an ant, *Tetramorium caespitum* (Myrmicinae), and a fly, *Drosophila melanogaster* (Drosophilidae), or two ant species, *T. caespitum* and *Lasius niger* (Formicinae). These two alternative treatments were repeated for each individual on a random basis. In these paired trials, we recorded which of the two prey insects was attacked and which one was consumed. At least one of the prey insects was attacked and consumed in each trial. All experiments were performed between 09:00 and 16:00 h.

Data analysis.—We analyzed data using various methods within R (R Core Development Team 2009). For the field data, we used ANOVA to compare prey size among immature, adult male and adult female spiders. Because there were repeated measures of the same individuals in both experiments, we used Generalized Estimating Equations (GEE) as an alternative to Generalized Linear Models. This method allows implementation of an association (correlation) structure that corrects for too small standard errors of parameter estimates and inferences favoring acceptance of the alternative hypothesis (Hardin & Hilbe 2003). We used GEE with binomial error structure (GEE-b) to compare capture frequency of the prey acceptance experiment, since the response variables were relative frequencies. We used GEE with Gamma errors and log link (GEE-g) to compare latencies among selected prey species, as the response variable was time, and variance was expected to increase with the mean. We used a proportion test to compare the frequency of attack and consumption separately for selected prey species. We analyzed the prey-choice experiments data with the McNemar test due to paired trials.

Table 1.—Natural prey of juvenile, male, and female *Mexcala elegans* specimens determined during field observations in Ndumo Game Reserve from 2004 to 2009. The size is an average total body length of workers attacked by spiders.

Ants		Spider predators			
Subfamily/species	Size [mm]	Juveniles	Males	Females	Total
Formicinae					
Anoplolepis custodiens (Smith)	5.9	0	1	4	5
Camponotus cinctellus (Gerstäcker)	7.2	6	12	6	24
Camponotus sp. 2 (*maculatus* group)	8.6	2	3	3	8
Polyrhachis sp.	8.6	0	4	5	9
Myrmicinae					
Crematogaster sp.	3.5	2	0	1	3
Myrmicaria natalensis (Smith)	6.3	0	1	3	4
Tetramorium quadrispinosum Emery	3.5	3	0	0	3
Ponerinae					
Pachycondyla tarsata (Fabricius)	16.5	0	0	4	4
Streblognathus peetersi Robertson	11.6	0	0	2	2
Pseudomyrmicinae					
Tetraponera ambigua (Emery)	6.8	2	0	0	2
Total		15	21	28	64

RESULTS

Field survey.—In the field, *M. elegans* captured and consumed ten species of ants from four subfamilies (Table 1). We observed no prey other than ants being captured. Among ants, the most frequent prey was *Camponotus cinctellus*. Adult male (body size 5.3–8.3 mm) and female (6.1–8.9 mm, Fig. 1) *M. elegans* captured significantly larger ant species (*Camponotus*, *Polyrhachis*, *Anoplolepis* and *Myrmicaria*) than the juveniles, which generally preyed on smaller ants such as *Crematogaster*, *Tetramorium,* and *Tetraponera* (ANOVA, $F_{2,60} = 4.5$, $P = 0.013$, Fig. 2).

Laboratory experiments.—Although the prey acceptance experiment showed that the spiders were capable of attacking diverse prey, and the prey choice experiment showed no preference between prey types, the spiders did respond differently to varying prey types. In the acceptance experiment, spiders responded differently to the 17 potential prey species. The frequency of attacks differed among the 17 prey species (GEE-b, $X^2_{16} = 194$, $P < 0.0001$). Spiders did not attack crickets, beetles, *Theridion* spiders, or woodlice and springtails and beetle larvae were only attacked by half of the spiders. Other prey species such as ants, *Pardosa* spiders, termites, flies, and moths were always attacked (Table 2). Although spiders consumed the majority of prey species they attacked, they were less likely to consume *Tribolium* larvae and *Pardosa* spiders (Proportion tests, $X^2_1 > 5.5$, $P < 0.02$). Spiders attacked prey that were on average 1.03 of their body length ($Q_{25} = 0.64$, $Q_{75} = 2.2$, $n = 255$). In the choice experiments, spiders attacked and consumed ants as frequently as flies (McNemar tests, $X^2_1 = 0$, $P = 1$ $n = 15$). Similarly, spiders attacked and consumed *Lasius* ants as frequently as *Tetramorium* ants (McNemar tests, $X^2_1 > 0.4$, P > 0.5).

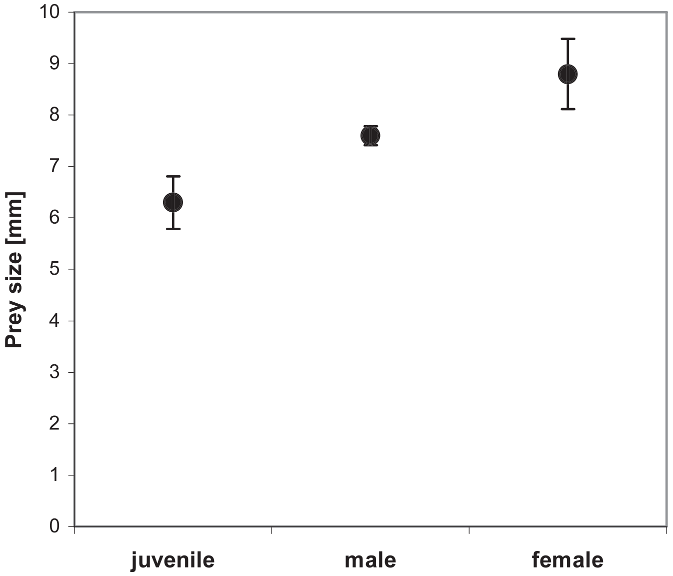

Figure 2.—Comparison of the prey size (mean ± SE) captured by juveniles, males and females in the field.

Mexcala elegans used different predatory behavior to catch different prey taxa. Although spiders ignored woodlice and beetles, they stalked aphids, crickets, bugs, and *Theridion* spiders but did not attack them. Spiders grabbed small springtails, leafhoppers, moths, and flies with their forelegs and moved them to their chelicerae. In contrast, they repeatedly attacked termites head-on, and then grabbed hold of the insect's thorax. To catch ants, the spider approached from the rear, maintaining a distance of three to four body lengths from an ant, all the while moving the front legs and abdomen up and down. The spider attacked quickly from behind, biting the ant on the abdomen. The spider then retreated and followed its ailing prey with raised forelegs (Fig. 3A), maintaining a distance of about two body lengths. Once the ant slowed down, the spider grabbed the ant's antenna with its chelicerae (Fig. 3B), and after a minute, it moved its hold to the thorax.

Among the four ant and one termite species used in the trials, the spiders showed significantly different latency in their attacks (GEE-g, $X^2_4 = 9.6$, $P = 0.047$, Fig. 4A). Spiders attacked *Lasius* and *Messor* ants with a significantly shorter latency than *Formica* ants (contrasts, $P < 0.02$). There was also a significantly different paralysis latency among these prey ants (GEE-g, $X^2_4 = 49.4$, $P < 0.0001$, Fig. 4B). Large *Formica* and *Messor* ants had a significantly longer latency to paralysis than small *Lasius* and *Tetramorium* ants (contrasts, $P < 0.03$). Termites of the same size as small ants were paralyzed more quickly than all ant species (contrasts, P < 0.0001).

Table 2.—List of prey used in laboratory experiment. The size of prey is an average total body length. $n = 15$ trials for each species. Percentage of consumed is of those that were attacked.

Order/species	Size [mm]	% Attacked	% Consumed
Araneae			
Theridion sp.	3.0	0	0
Pardosa sp.	2.5	100	10
Isopoda			
Porcellio scaber Latreille	3.5	0	0
Collembola			
Sinella curviseta Brook	1.6	45.5	100
Isoptera			
Reticulitermes sp.	4.7	100	100
Ensifera			
Acheta domesticus (Linnaeus)	3.5	0	0
Heteroptera			
Lygus pratensis (Linnaeus)	6.0	0	0
Sternorhyncha			
Aphis fabae Scopoli	1.7	9.1	0
Auchenorhyncha			
Eupteryx sp.	3.5	81.8	100
Lepidoptera			
Plodia interpunctella (Hubner)	6.5	81.8	100
Hymenoptera			
Formica pratensis Retzius	6.3	100	100
Lasius niger (Linnaeus)	3.5	100	100
Messor muticus (Nylander)	6.0	91.7	100
Tetramorium caespitum (Linnaeus)	3.5	91.7	100
Coleoptera			
Phylotreta sp. imago	3.3	0	0
Tribolium castaneum (Herbst) larva	8.0	50	0
Diptera			
Drosophila melanogaster Meigen	2.0	100	100

DISCUSSION

We found a contrasting trophic strategy in *M. elegans*. Our field observations suggest a stenophagous habit, but laboratory experiments conversely indicate a euryphagous habit. In the field, *M. elegans* captured only ants. This is consistent with observations of two other species of this genus, *M. namibica* Wesołowska 2009 and *M. rufa* Peckham & Peckham 1902 from Namibia, that feed on *Camponotus fulvopilosus* (Curtis 1988). In the laboratory, however, *M. elegans* caught a wide variety of prey. So, the fundamental trophic niche includes a wide assortment of prey, whereas the realized niche includes only ants.

Mexcala elegans recognized and captured prey other than ants as efficiently, or even more efficiently, than ants. Thus neural and behavioral trade-offs resulting in an inability to recognize cues from other prey and to catch non-ant prey were not present. This is in contrast to stenophagous ant-eaters of the genus *Zodarion*, for example, which are unable to subdue prey other than ants (Pekár 2004; Pekár & Toft 2009). Yet *M. elegans* used completely different behavior to catch ants than other prey, so this species has clearly evolved a specialized capture strategy that seems to be very effective and safe for ant capture, as we have not witnessed a single successful reversed attack by an ant toward the spiders in laboratory experiments (0%, $n = 60$, pooled across the acceptance trials with ants).

Mexcala elegans used a ‘bite-and-release’ tactic to catch ants. This specific tactic is also used by other ant-eating salticids, namely *Naphrys pulex* (Hentz 1846), *Aelurillus muganicus* Dunin 1984, and *Tutelina similis* (Banks 1895) (Wing 1983; Li et al. 1996; Huseynov et al. 2005). This special tactic includes a short leap with a quick bite, followed by release and retreat. Interestingly, a similar tactic is used by other non-salticid, ant-eating spiders, such as gnaphosids, zodariids, and thomisids (Heller 1976; Lubin 1983; Oliveira & Sazima 1985; Pekár 2004). In all cases, the spiders usually attack either head-on; i.e., bites between head and thorax (Edwards et al. 1974), or from the rear; i.e., on the abdomen or legs (Jackson & Van Olphen 1992; Jackson et al. 1998), both tactics making it impossible for the ant to defend itself.

As the most frequent natural prey of *M. elegans* were *Camponotus* ants (subfamily Formicinae), we expected that

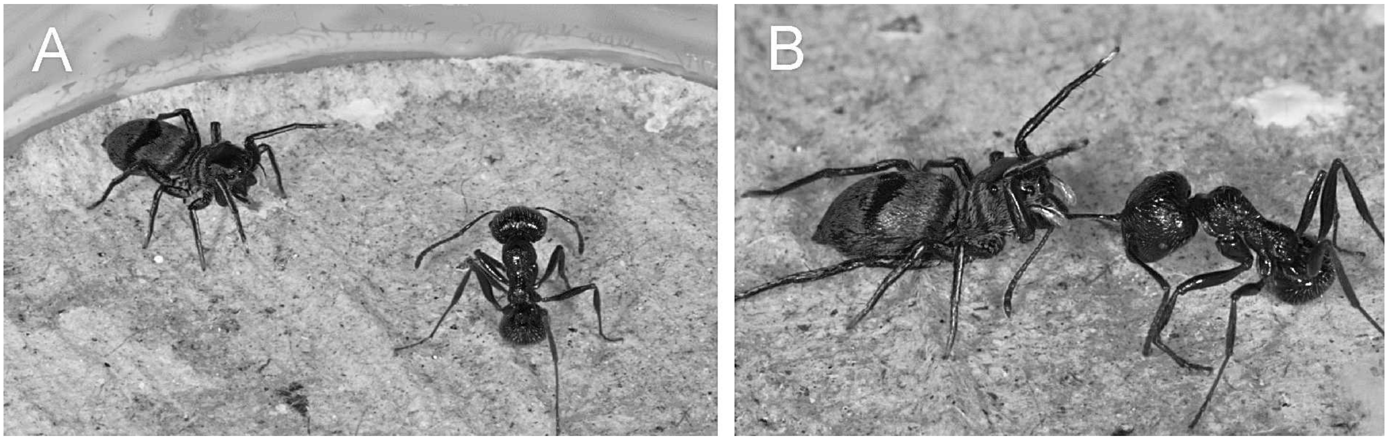

Figure 3.—Predatory behavior of *M. elegans* when capturing ants. A. Spider stalks attacked ant with raised forelegs. B. Spider grabs antennae of ant in chelicerae.

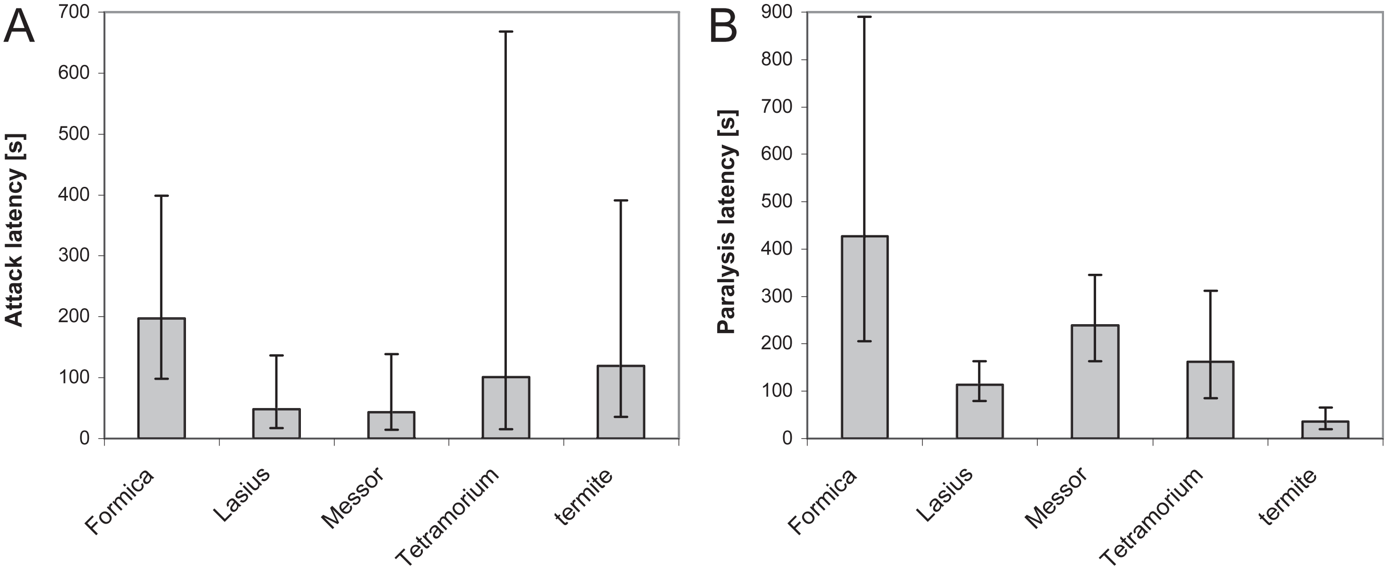

Figure 4.—Comparison of the attack latency (A) and paralysis latency (B) for four ant (*Formica*, *Lasius*, *Messor*, *Tetramorium*) and one termite species. Bars indicate means, whiskers indicate 95% confidence intervals of each mean.

related ants (*Formica* and *Lasius*) would be attacked and paralyzed more quickly than others. The spiders attacked four ant species used in the acceptance trials at significantly different latencies. Slow-moving species (*Messor* and *Lasius*) were attacked more rapidly than fast-moving *Formica*. Larger ant species had longer paralysis latencies than small ant species, regardless of their taxonomic relatedness, suggesting that the venom of *M. elegans* is not specific for certain subfamilies of ants, as was found in ant-eating *Zodarion* (Pekár et al. 2008).

In the field, *Mexcala elegans* frequently captures ants with a greater body length than itself; the largest, *Pachycondyla tarsata*, is double the spider's body length. Similarly, in laboratory experiments, the spiders captured prey up to twice their own length, consistent with observations of other myrmecophagous spiders that catch prey much larger than themselves (e.g., Soyer 1943; Pekár 2004).

Absence of neural and behavioral trade-offs does not preclude the presence of physiological trade-offs. We have not studied the effect of prey type on fitness aspects such as survival or reproduction. Thus we cannot exclude the possibility that *M. elegans* has evolved a physiological trade-off in their utilization of alternative prey. However, in another ant-eating salticid, *Siler cupreus* (Simon 1889), Miyashita (1991) did not find evidence for either behavioral or physiological trade-offs, as the spider was able to catch alternative prey and suffered high mortality when reared on a pure ant diet. Therefore, we expect that physiological trade-offs may not have evolved in *M. elegans*, either. If our predictions are correct, then the evolution of stenophagy in *M. elegans* cannot be explained by the physiological trade-off hypothesis.

Mexcala elegans, like *M. rufa* and *M. namibica*, not only imitates ants but also feeds on the model species (Curtis 1988). It is therefore likely a Batesian mimic. This spider associates closely with its ant models, which are abundant in a variety of habitats. Myrmecomorphy, combined with spatial association with ants, may provide *M. elegans* with higher protection from enemies. Thus it appears to favor the enemy-free space hypothesis.

We conclude that the evidence gained on the trophic strategy of *M. elegans* suggests that it is a euryphagous specialist, because it has the versatility to catch a variety of prey but uses a specialized prey capture tactic on ants. Observed stenophagy in the field has presumably resulted as a byproduct of adaptive dynamics related to risk aversion (avoiding of enemies).

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