

SHORT COMMUNICATION

Capture efficiency of an ant-eating spider, *Zodariellum asiaticum* (Araneae: Zodariidae), from Kazakhstan

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Abstract. *Zodariellum asiaticum* (Tyschchenko 1970) is an ant-eating spider from Central Asia. Using five syntopically occurring ant species, namely *Cataglyphis aenescens*, *Formica cunicularia* (both Formicinae), *Messor aralocaspius*, *Tetramorium caespitum* (both Myrmicinae), and *Tapinoma erraticum* (Dolichoderinae) in a laboratory study of prey-capture behavior, I evaluated capture frequency, attack latency, number of attacks, and paralysis latency. Although spiders captured all five ant species, capture efficiency varied when spiders were tested with the different ant species, being highest when the spiders were tested with *F. cunicularia*. I concluded that small juvenile *Z. asiaticum* probably adapt to feed primarily on species of small dolichoderine and myrmicine ants and that large juvenile and the adult *Z. asiaticum* adapt to feed primarily on large formicine ants.

Keywords: Stenophagy, specialization, myrmecophagy, prey-capture behavior

Spiders are well known for being euryphagous predators, (i.e., consuming a wide variety of prey), but many have an aversion to ants. This makes any group of spiders that routinely eat ants ("myrmecophagy") especially interesting. Myrmecophagic spiders are of further significance because they often seem to adopt ant-specific prey-capture behavior, and they may actively choose ants in preference to other prey (e.g., Huseynov et al. 2008). There is particular interest in spider species that might be exclusively myrmecophagic.

Although myrmecophagy may be a rare phenomenon in spiders as a whole, examples are found in an assortment of spider families, including the Gnaphosidae, Oecobiidae, Salticidae, Theridiidae, Thomisidae, and Zodariidae (Glatz 1967; Heller 1976; Porter & Eastmond 1982; Jocqué 1991; Castanho & Oliveira 1997; Jackson et al. 1998). Species that appear to be exclusively myrmecophagic include a theridiid *Dipoena* and a thomisid *Aphantochilus* (Umeda et al. 1996; Castanho & Oliveira 1997). However, regardless of whether a species is exclusively or partially myrmecophagic, arachnologists have tended to envision myrmecophagic spiders as preying on ants in general rather than as having become adapted to particular kinds of ants. Yet there is evidence that at least some of the myrmecophagic spiders show a preference for certain genera or even species of ants within the family Formicidae as a whole. Researchers need to gather more information about myrmecophagic spiders so that we can determine how important the targeting of particular ant taxa is for these predators. "Targeting" includes a variety of adaptations by which a spider might specialize on particular kinds of ants, including adaptation related to morphology, physiology, and behavior.

The myrmecophagic spiders I investigated are from the family Zodariidae, one of the most diversified families of spiders (Platnick 2009). The family Zodariidae is known for including a number of myrmecophagic species (Jocqué 1991), but the natural history of the great majority of these species is still poorly known. Available evidence suggests the species in four of the genera in the subfamily Zodariinae, namely *Diores*, *Trygetus*, *Zodariellum*, and *Zodarion*, are exclusively myrmecophagous (Marikovskiy & Tyschchenko 1970; Pekár et al. 2005; Haddad & Dippenaar-Schoeman 2006). However, evidence that the predator distinguishes prey below the level of family (Formicidae) has come from only one of these genera, namely *Zodarion* (Pekár 2005; Pekár et al. 2008).

Here I consider a species from the genus *Zodariellum*. The species in this genus are morphologically uniform (Marusik & Koponen 2001), meaning that distinctive interspecific differences are evident only in the details of sexual organ shape, not in structures such as the spider's chelicerae that function directly in predation. This suggests that, for finding evidence of adaptation to specific types of ants, we should investigate behavioral and predatory-related physiological traits.

In this study, I focus on some traits related primarily to behavior. Ant-eating spiders typically capture ants using a 'bite-and-release' tactic (e.g., Jackson & van Olphen 1992; Cushing & Santangelo 2002). One probable advantage of this mode of attack is that it enables the predator to avoid being injured or killed when ants counter-attack. Using this mode of attack, species from the genus *Zodarion* can subdue a number of different kinds of ants, but apparently the spider's efficiency in capturing different kinds of ants varies considerably. Evidence that efficiency varies comes from data on paralysis latency (i.e., the time elapsing between when the ant is attacked and when it becomes immobile) and the frequency of attacks before the prey is eaten (e.g., Pekár 2005). These are the parts of the predatory sequence to which I paid particular attention in this study of *Zodariellum*.

Worldwide, there are 22 species in the genus *Zodariellum*, about 10 of which appear to be endemic to Central Asia (Platnick 2009). There are published anecdotal prey records for two species, *Z. asiaticum* Tyschchenko 1970 and *Z. sahariense* Denis 1959, feeding on ants (Pierre 1959; Marikovskiy & Tyschchenko 1970). Marikovskiy reported that the ant on which *Z. asiaticum* preys is primarily *Formica cunicularia* Latreille, but predation was also observed on *Tetramorium caespitum* (Linnaeus), *Messor aralocaspius* Ruzsky, and *Cataglyphis aenescens* (Nylander) (Marikovskiy & Tyschchenko 1970; Marikovskiy 1979).

Zodariellum asiaticum, the species I investigated, occurs in southeastern Kazakhstan. The specimens I used (eight female and seven subadult individuals; body lengths 3.5–4.5 mm) were collected in April on the sandy slopes of a semi-desert habitat along the Ili River, near the city of Kapchagay (43°56'93.4N, 77°03'56.7E). Spiders were identified using Marikovskiy & Tyschchenko (1970) and Marusik & Koponen (2001) and kept in glass tubes (diameter 10 mm, length 60 mm) with moistened substrate (plaster of Paris). All spider specimens are deposited in the collection of arachnids of the Department of Botany and Zoology, Masaryk University, Brno.

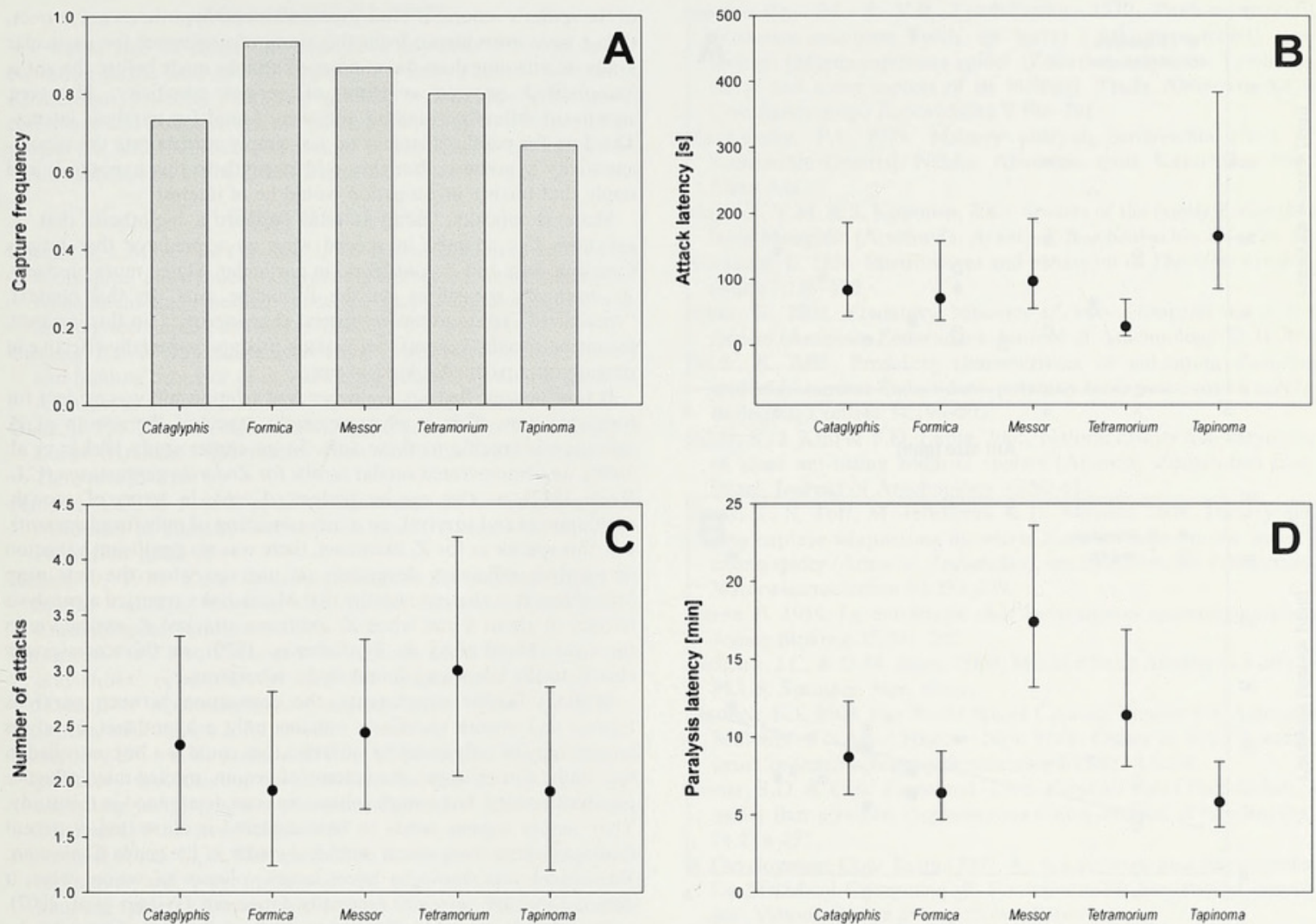


Figure 1.—Comparison of four predatory traits of *Z. asiaticum* for five ant species (from three ant subfamilies). A. Mean capture frequency. B. Mean latency to the first attack. C. Mean number of attacks. D. Mean latency to complete paralysis. Whiskers are 95% confidence intervals for means.

The ant fauna occurring syntopically with *Z. asiaticum* was surveyed at the same sites (ants identified using Marikovsky 1979). Five ant species were used in the experiments: *Cataglyphis aenescens* (body length 4.5–8 mm) and *Formica cunicularia* (4–6 mm) (both Formicinae), *Messor aralocaspius* (4.5–8 mm) and *Tetramorium caespitum* (3–3.5 mm) (both Myrmicinae), and *Tapinoma erraticum* (Latreille) (3.5–4 mm) (Dolichoderinae). We collected ants used as prey in the field a few hours before we used them in the experiment.

I chose one of the ant species (*Messor*) to serve as the standard for initial feeding (i.e., after being collected, the spiders were fed with a single individual of *Messor* the next day). Three days later, each spider was offered successively, in random order, a single ant from each of the five species. I tested each spider with each ant species only once.

There was a 2-day interval between successive trials. A single trial consisted of releasing an ant into a dish occupied by a spider (diameter 40 mm; filter paper glued to the bottom; thin layer of fluon on the sides). Each spider had been in the Petri dish for one day before the trial began. Spiders usually attacked within 30 s. If the spider did not attack the ant within 10 min, I terminated the trial. These aborted trials were classified as rejection of prey. For each trial, I recorded attack latency (i.e., the time between when the spider oriented itself toward the ant and the first attack), number of successive attacks, and paralysis latency (i.e., the time between the first attack and the prey becoming completely immobilized).

Data were analyzed using Linear Mixed-Effects Models (LME) from the NLME-package within the R-environment (R Development

Core Team 2007). I chose this method because observations were not independent (i.e., there was repeated use of the spider individuals) and LME is designed for taking into account repeated measurements (Pinheiro & Bates 2000). Both latencies appeared to come from asymmetrical (skewed to the right) distributions. Therefore, I applied logarithmic transformation, after which the data distribution approximated the normal distribution. I expected that the size of ant prey might affect the number of attacks and the paralysis latency. Therefore, I used prey size as a covariate when analyzing the data. Frequency of capture was compared using the Cochran Q test.

Predatory sequences in encounters between *Z. asiaticum* and ants were similar to predatory sequences in encounters between species of *Zodarion* and ants (e.g., Pekár 2004). *Z. asiaticum* approached ants quickly from behind and attacked, usually by contacting the ant's dorsal thorax or leg, releasing the ant, and then continuing to attack several more times or waiting until the ant became paralyzed.

Spiders attacked all five ant species, the most frequently attacked species being *F. cunicularia* and the least frequently attacked being *T. erraticum* (Fig. 1A). However, differences in frequency of attacking ant species were not statistically significant (Cochran Q test, $Q_4 = 4.8$, $P = 0.31$). Differences in latency of making the first attack were also non-significant across ant species (LME, $F_{4,42} = 1.9$, $P = 0.13$, Fig. 1B) and for number of attacks (LME, $F_{4,42} = 0.7$, $P = 0.6$, Fig. 1C). When number of attacks were considered in relation to ant size, differences in the data were not significantly different (i.e., number of attacks is independent of ant size) (LME, $F_{1,42} = 0.07$, $P = 0.79$).

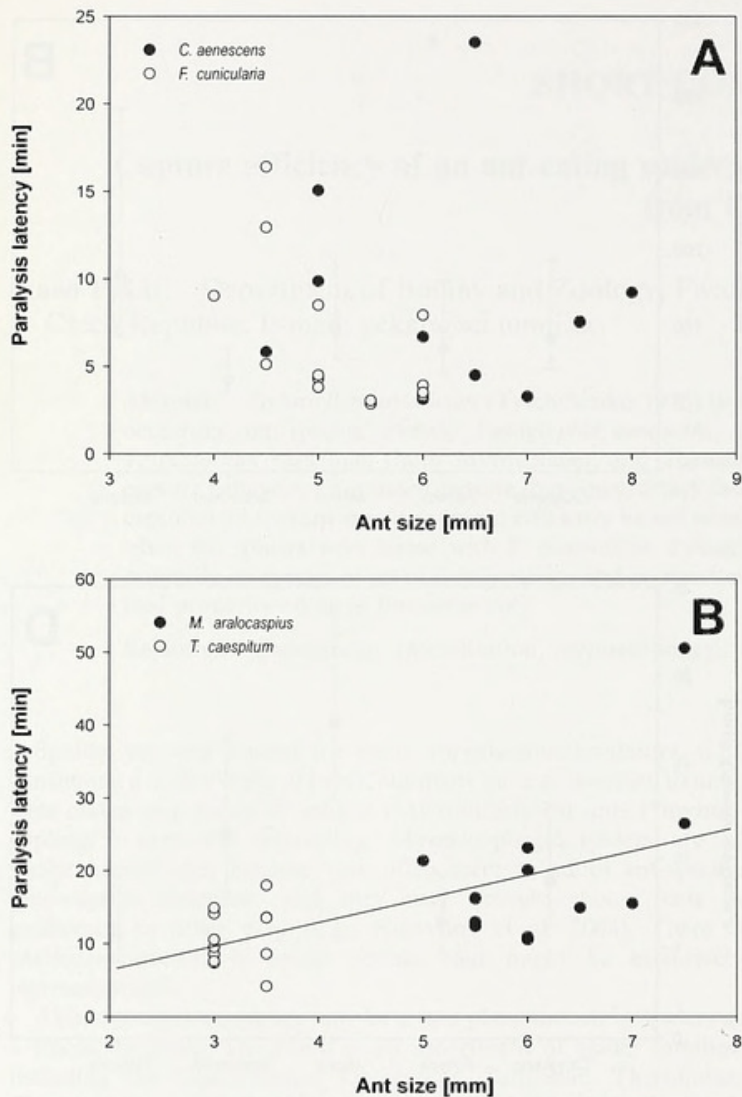


Figure 2.—Relationship between paralysis latency and the size of ants for two formicine (A) and two myrmicine (B) ant species. Linear model ($y = -0.78 + 3.33x$) is shown for myrmicine.

However, there were significant differences between ant species for paralysis latency (LME, $F_{4,42} = 10.8$, $P < 0.0001$, Fig. 1D), latency for *Messor* being about three times as long as latencies for *Cataglyphis*, *Formica* and *Tapinoma*. Latency for *Tetramorium* was similar to latency for *Messor* (Fig. 1D). For formicine ants (*Cataglyphis* and *Formica*), there were no significant differences in paralysis latency when considered whether latency depended on ant size (LME, $F_{1,23} = 0.14$, $P = 0.72$, Fig. 2A). For myrmicine ants (*Messor* and *Tetramorium*), on the other hand, latency for large ants was significantly longer than for small ants (LME, $F_{1,24} = 13.4$, $P = 0.001$, Fig. 2B).

I found that *Z. asiaticum* captured each of the five ant species used in this study, suggesting that this spider may have some general adaptations that enable it to be effective at capturing ants in general. Yet there are some critical differences indicating that this predator distinguishes ants below the level of family and has acquired adaptations by which it can be particularly effective as a predator of certain kinds of ants. Preference is a motivational trait that drives a predator's prey-choice behavior (Huseynov et al. 2008), and it seems likely that my data on capture frequency and attack latency are especially closely linked to the preferences of *Z. asiaticum*. I might predict that a predator will be more likely to attack and quicker to attack prey it prefers. However, my hypothesis is that paralysis latency and the numbers of attacks made by *Z. asiaticum* on different ant species are determined to a large extent by biochemical specificity

of the spider's venom. If these predictions and hypotheses are correct, then I have no evidence from this study of preference for particular kinds of ants, nor does the number of attacks made before the ant is immobilized provide evidence of venom specificity. However, significant differences among ants were found for paralysis latency. The data for paralysis latency do not simply corroborate the venom-specificity hypothesis, but they add strength to this hypothesis and imply that further investigation would be of interest.

More specifically, paralysis data support a hypothesis that *Z. asiaticum* has adapted in special ways as a predator that targets formicine ants and *F. cunicularia* in particular. Stated more precisely, *Z. asiaticum* specializes on the formicine ants. In this context, "specialized" refers to having special characteristics (in this instance, formicine-specific venom) that make a predator especially effective at preying on a particular kind of prey.

It is of interest that no size-dependent relationship was evident for formicine ants. This is what we might expect if the venom of *Z. asiaticum* is specific to these ants. In an earlier study (Pekár et al. 2008), we demonstrated similar results for *Zodarion germanicum* (C.L. Koch 1837), as this species performed best, in terms of growth, development and survival, on a diet consisting of only formicine ants. For this species as for *Z. asiaticum*, there was no significant variation in paralysis efficiency dependent on ant size when the ants were formicines. It is also noteworthy that Marikovsky reported a paralysis latency of about 4 min when *Z. asiaticum* attacked *F. cunicularia* in the field (Marikovsky & Tyschchenko 1970), as this corresponds closely to the latencies I found in the laboratory.

Without further experiments, the connection between paralysis latency and venom specificity remains only a hypothesis. Paralysis latency may be influenced by variables that could not be controlled in this study. For example, the volume of venom injected may influence paralysis latency, but venom volume was not determined in this study. That venom volume needs to be considered is illustrated by recent findings from a study on an unrelated spider of the genus *Cupiennius*. This spider was shown to inject larger volumes of venom when it detected that the prey was especially dangerous (Wigger et al. 2002).

For the genus *Zodarion*, two distinct groups appear to be identifiable in the context of prey specificity. First, there are species that may normally exploit a single ant species. More specifically, there appear to be species that exploit solely ants from the genus *Messor*. Being polymorphic, ants of this genus may be feasible prey for exploitation by *Zodarion* throughout the spider's life cycle, as there would always be available, regardless of the developmental stage to which an individual of *Zodarion* might belong, a suitable size morph of this ant species (Pekár, unpublished). The other group consists of *Zodarion* species whose adults tend to prey most often on monomorphic ant species. I hypothesize that these *Zodarion* species, specifically the smaller juveniles, prey primarily on ant species that are smaller than the species on which the adults prey. This implies that the spiders adapt to the ants they target as they progress through their life cycles. Often the stage-specific switch may be from smaller to larger ant species belonging to the same ant subfamily (Pekár et al. 2008).

Field data suggest that *Z. asiaticum* frequently exploits ant species from different subfamilies. For *Z. asiaticum*, there may be a developmental adaptation in the ants primarily targeted, with small juveniles feeding on small dolichoderine ants such as *Tapinoma* and on small myrmicine ants such as *Tetramorium*, and with large juveniles and adults feeding primarily on large formicines such as *F. cunicularia*. On one occasion, I found a juvenile of *Z. asiaticum* feeding on *Tapinoma* in the field, which helps to support this hypothesis. If this hypothesis is corroborated, then it will be of interest to investigate the venom specificity of the early juvenile stages of *Z. asiaticum* to determine whether small juveniles have venom that is specific not to formicines, but instead to dolichoderines or myrmicines or both.

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