

## PREDATORY BEHAVIOR OF TWO EUROPEAN ANT-EATING SPIDERS (ARANEAE, ZODARIIDAE)

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**ABSTRACT.** Prey specialization and the predatory behavior of two European ant-eating zodariid spiders, *Zodarion germanicum* and *Zodarion rubidum*, were studied in detail. The spiders were offered 12 ant species and seven other insects (termites, beetles, aphids, silverfish, flies, crickets and grasshoppers). Study spiders turned out to be ant specialists as they were able to subdue many ant species but ignored all other insects, except termites, which they attacked but rarely subdued. The best capture success was obtained with medium-sized ants (e.g. *Lasius* and *Formica*). The predatory behavior of the zodariid spiders involves an attacking and a handling phase separated by a period of waiting at a safe distance. The attacking phase consisted of a very rapid lunge from the rear, followed by a bite on the most extended ant leg. After an attack, the spider retreated to a safe distance, perhaps an indication that natural selection has favored such caution in the presence of an aggressive prey. The spider waited until the ant ceased moving. Such predatory behavior, which limits contact with the predator and prey, is clearly an effective means of handling a dangerous prey.

**Keywords:** Ant predation, myrmecophagy, prey specialization, predatory specialization

Although there is limited information on the diet of many spider species, it is believed that most of the 37,000 species known in the world (Platnick 2002) are generalists, able to subdue and consume a rather wide variety of prey types (Nentwig 1987). A few spiders are specialists such as the araneophagous mimitids (Jackson & Whitehouse 1986) and some genera of salticid spiders (Jackson & Hallas 1986), both of which feed predominantly on web-building spiders. Other spiders, such as the araneid spiders of the genus *Mastophora*, feed exclusively on noctuid moths and psychodid flies (Yeargan & Quate 1997). Yet other spiders are termitophagous, like ammoxenids (Dippenaar-Schoeman et al. 1996) or some theridiids (Eberhard 1991). But most of the specialized spiders are ant-eaters; perhaps a consequence of ants being numerous in the habitats of many spiders. Some of the better known ant-eating spiders are in the families Salticidae (Jackson & Pollard 1996), Theridiidae (Porter & Eastmond 1982), Dinopidae (Austin & Blest 1979), Gnaphosidae (Heller 1974) and Zodariidae (Simon 1864).

Albeit ants provide a rich source of nour-

ishment, they are dangerous prey. Ants recognize each other and become aggressive towards an intruder. They can bite, sting and mount a communal attack and they are so numerous that it is difficult to avoid encountering them (Hölldobler & Wilson 1990). Any ant-eating predator must adopt a foraging tactic which will overcome the ant's defensive system. Some spiders, e.g. a theridiid *Theridion*, capture ants using silk threads. This spider builds a web above ground with several sticky threads hanging down. The ant sticks to the threads and only after it becomes entangled in the web does the spider approach and bite it (Nørgaard 1956). Similarly, *Dinopis* uses a small snare to throw over foraging ants (Austin & Blest 1979) while hanging on a thread above the colony of ants. A gnaphosid spider, *Callilepis*, approaches solitary ants rapidly and bites them on the antennae. In a short time the ant is immobilized and taken away by the spider (Heller 1974). Some salticid spiders, for example *Chrysilla*, *Natta* and *Siler*, stalk solitary ants from behind (Jackson & Van Olphen 1992) dropping down from the foliage on a thread when another ant approaches. Species of the genus *Zodarion* catch ants on the ground (Fig. 1) using a very rapid attack. After the attack, *Zodarion* retreats and waits at a distance until the ant is

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Figure 1.—Male *Zodarion germanicum* carrying a captured ant in the vicinity of *Formica cinerea* nest.

paralyzed (Harkness 1976, 1977). Such a rapid attack raised the question about how zodariid spiders subdue ants. Jocqué & Billen (1987) hypothesized that ants are paralyzed by means of an insecticidal compound released from the femoral organ of these spiders. However, recent investigations of Couvreur (1990) and Cushing & Santangelo (2002) on the foraging of *Zodarion rubidum* Simon 1914 supported an earlier observation of Harkness (1977) that the ants are killed instead by venom injected via the spiders' fangs. This conclusion is also supported by the peculiar morphology of zodariid chelicerae, which are medially fused. Such fusion, according to Wunderlich (1980), enables the short and stout fang to penetrate the strong ant cuticle.

Except for the unpublished study of Couvreur (1989), we have no information on prey preference in *Zodarion*. My first objective in this study was to investigate the degree of prey specialization in two species of Zodariidae that occur in Slovakia: *Zodarion germanicum* (C.L. Koch 1837) and *Z. rubidum*. The second objective was to study the predatory behavior in detail. All previous observations on this behavior come from field studies (Simon 1864; Wiehle 1928; Harkness 1976). As the spiders are quite small and the attack is very quick, the field observations gave a rather superficial description of the predatory behavior. I have therefore used laboratory studies to examine the details of the predatory behavior.

## METHODS

**Prey preference experiments.**—In order to investigate the degree of specialization in the two spider species, I combined field observations with laboratory investigations. The field sites were a mining dump in Nováky (Slovakia) for *Z. rubidum* and a steep outcrop in Opatovce nad Nitrou (Slovakia) for *Z. germanicum*. Field observations were made between 1600 h and 1800 h when the spiders are most active (Pekár & Král 2001). The study sites were visited for three days each month between May and August 1997. During each visit, the frequency of spiders running among or catching various ant species nesting in the ground was recorded. There were 5 and 8 ant species found in the study sites (see Table 1). In total, there were 17 and 21 nests in Nováky and Opatovce nad Nitrou, respectively, visited each time. Each nest was checked for presence of spiders at every visit but it was included in the analysis only once in order to avoid repeated measures. An observation at one nest took about 15 min.

To study the degree of specialization more completely, I performed laboratory experiments. For both spider species, 10 each of first instar, adult male and adult female specimens were used. Each specimen was kept singly in a glass tube (17 mm x 60 mm, with soil substrate) at room temperature ( $20 \pm 2^\circ\text{C}$ ) under natural photoperiod (L:D ~ 14:10). The substrate was moistened with a drop of water at 3-day intervals. The spiders were not fed for the five days before the experiment. During this time the majority of spiders constructed an igloo-shaped retreat. Shortly before the experiment, the spiders were pushed out of their retreats using a fine brush. Each spider was offered one individual of each of the following ant species: *Camponotus ligniperda* (Latreille), *Formica cinerea* Mayr, *Formica cunicularia* Latreille, *Formica truncorum* Fabricius, *Lasius flavus* (Fabricius), *Lasius platythorax* Seifert, *Monomorium faraonis* (Linnaeus), *Myrmica sabuleti* Meinert, *Plagiolepis vindobonensis* Lomnicki, *Solenopsis fugax* (Latreille), *Tapinoma erraticum* (Latreille) and *Tetramorium caespitum* (Linnaeus). Most of these species occur at the study sites. Some other species were added in order to represent a wide range of the ant body lengths. Ants were offered to spiders intermixed in a

Table 1.—Relative frequency of successful capture ( $n = 10$ ) of various ant species observed for juveniles (the first instar), males and females of *Zodarion germanicum* and *Zodarion rubidum*. Ant subfamily (ASF): F = Formicinae, D = Dolichoderinae, M = Myrmicinae. <sup>a</sup>identifies species occurring in Nováky, <sup>b</sup>identifies species occurring in Opatovce nad Nitrou. Spider body sizes are means calculated from 5 individuals. Prey body size is the range of sizes measured on 10 individuals.

ASF	Species Spider body length (mm) →	Body length (mm)	<i>Z. germanicum</i>			<i>Z. rubidum</i>		
			Juv.	♂	♀	Juv.	♂	♀
			2.6	3.8	5.2	1.9	3.1	4.2
Tiny ant species								
		↓						
M	<i>Solenopsis fugax</i> <sup>b</sup>	1.8–2.1	1.0	0	0	1.0	0	0
F	<i>Plagiolepis vindobonensis</i> <sup>b</sup>	2.1–2.3	1.0	0	0	1.0	0	0
M	<i>Monomorium faraonis</i>	2.2–2.3	0.8	0.4	0.6	0.7	0.9	0.9
Medium sized ant species								
M	<i>Tetramorium caespitum</i> <sup>a,b</sup>	2.8–3.3	0.7	1.0	1.0	0.6	0.9	1.0
D	<i>Tapinoma erraticum</i> <sup>b</sup>	3.0–3.3		0.9	1.0		1.0	0.9
F	<i>Lasius flavus</i> <sup>a</sup>	3.2–3.6	0.8	0.9	1.0	0.6	0.8	0.9
F	<i>Lasius platythorax</i> <sup>b</sup>	3.3–3.9		1.0	0.9		0.8	0.9
M	<i>Myrmica sabuleti</i> <sup>a</sup>	4.7–4.9		0.2	0.4		0.1	0.3
Large ant species								
F	<i>Formica cinerea</i> <sup>b</sup>	5.9–6.3		0.6	0.8		0.8	0.9
F	<i>Formica cunicularia</i> <sup>a</sup>	6.2–6.8		0.8	0.9		0.3	0.5
F	<i>Formica truncorum</i> [small form] <sup>b</sup>	4.9–5.2		1.0	1.0		0.7	0.8
F	<i>Formica truncorum</i> [large form] <sup>b</sup>	7.7–8.0		0.1	0.2		0	0.1
F	<i>Camponotus ligniperda</i> <sup>b</sup>	7.3–8.0		0.3	0.4		0.1	0.1

random order once every 5 days. An ant was released into a tube occupied by a spider and the spider's attack and capture success were recorded. The tests lasted at most 60 min. If the spider did not capture the ant or the ant bit the spider, the ant was immediately taken out of the tube. Ants killed a few spiders. Each killed spider was replaced by other specimen. Juvenile spiders were offered only small ant species.

In another experiment, each specimen of *Z. germanicum* used in the previous experiment

was offered one specimen of each of the alternative prey: an aphid (*Aphis fabae*), a beetle (*Tribolium confusum*), a cricket (*Acheta domestica*), a fly (*Drosophila melanogaster*), a grasshopper (*Locusta migratoria*), a silverfish (*Atelura formicaria*) and a termite (*Reticulitermes flavipes*). The prey was offered to spiders in a random order once every 2 days. The experiment was carried out using similar procedures and under similar conditions as the one with ants. The total body size of the spiders and the prey (Table 1 & 2) was estimated

Table 2.—Relative frequency of successful capture ( $n = 10$ ) of various alternative invertebrates observed for juveniles (the first instar), males and females of *Zodarion germanicum*. Insect orders: A = Caelifera, C = Coleoptera, D = Diptera, E = Ensifera, I = Isoptera, S = Sternorrhyncha, T = Thysanura.

Order	Species	Size [mm]	Juv.	♂	♀
E	<i>Acheta domestica</i>	3.7	0	0	0
D	<i>Drosophila melanogaster</i>	2.9	0	0	0
A	<i>Locusta migratoria</i>	6.9	0	0	0
I	<i>Reticulitermes flavipes</i>	3.8	0.1	0.1	0.2
S	<i>Aphis fabae</i>	3.4	0	0	0
C	<i>Tribolium confusum</i>	3.2	0	0	0
T	<i>Atelura formicaria</i>	4.1	0	0	0

under a stereoscopic microscope as a mean number from 5 dead individuals.

The differences in capture success of the tested ant species were compared between the sexes and between *Zodarion* species using log-linear analysis of binary data within generalized linear models as the data followed a binomial distribution. In order to identify the most optimal ant species for the two *Zodarion* species, a regression model was fit to the obtained data. Because the relationship between the spider success and the ant body length turned out to have an unimodal character, polynomial (parabola:  $y = a + bx + cx^2$ ) regression was used. Parameters obtained from the parabola were used to calculate the optima (the ant size that gives maximum capture success) and their standard deviations (see Jongman et al. 1995 for more details). The differences between the optima of the two *Zodarion* species were compared using a t-test.

**Predatory behavior experiments.**—In order to investigate the details of the predatory behavior, I conducted laboratory observations. Ten third-instar juvenile spiders of *Z. rubidum*, kept singly in a Petri dish (40 mm, with filter paper attached to the bottom moistened at 3-day intervals) were used. Experiments were performed at room temperature ( $20 \pm 2^\circ\text{C}$ ) and under natural photoperiod (L:D ~ 14:10). To each spider, one ant worker of each *M. faraonis*, *T. caespitum* and *L. flavus* was offered once every 3 days. Latency to the first attack, frequency of attacks on ant appendages, paralysis time (time from the first attack until ant became motionless), and the timing of attacks were recorded. Pearson correlation was used to study the relationship between frequency of bites of each ant appendage and the length of the appendage. The length of appendages was estimated from an image taken by a digital camera rather than by direct measurement because ants stretch out their appendages differently when moving.

Foraging behavior was recorded on a video-recorder (Sony SLV-E 1000 with 25 fps) using a CCD color camera (SONY DXC-LS1P) attached to a stereoscopic microscope (Nikon SMZ-U). Some sequences were then digitized using a frame-grabber and slowly replayed so that events of prey capture could be recorded. Events were analyzed as first order Markov chains using the UNCERT program (Hailman & Hailman 1993) in order to show that the

transitions between events are dependent on one another at some level of probability greater than chance (Lehner 1996). A homogeneity (chi-square) test was used to compare observed frequencies of transitions with the expected ones. Standard errors (SE) are used to show variance of means throughout the paper.

Voucher specimens of spiders and ants are deposited at the Research Institute of Crop Production, Department of Entomology, Prague, Czech Republic.

## RESULTS

**Prey preference.**—In the field, subadult and adult specimens of *Z. germanicum* were often seen feeding on or running among *F. cinerea*, followed by *T. caespitum*, *C. ligniperda*, *F. truncorum*, and *L. platythorax* (Fig. 2). Subadult and adult specimens of *Z. rubidum* were seen feeding most frequently on *T. caespitum* and *L. platythorax* (Fig. 2). Early instars of this species fed on small workers of *T. caespitum*. None of the spider species were seen to catch prey other than ants. In the laboratory experiments, the first instar of both species readily attacked and subdued tiny ant species and some of the medium-sized ants (Table 1). Adult spiders did not attack tiny ants but easily seized all medium sized ants except for workers of *M. sabuleti*, which the spiders attacked but seldom subdued. Some of the large ants (*F. cinerea*, *F. cunicularia* and the small form of *F. truncorum*) were successfully subdued while others (*C. ligniperda* and the large form of *F. truncorum*) were seldom captured by either *Zodarion* species. The two largest ant species often bit legs of the spiders (in 56% of trials,  $n = 80$ ) and in 3 trials (4%) even killed them.

Males of both species attacked and subdued on average (pooled for all ant species) slightly fewer ants than females but this difference was not significant (log-linear analysis:  $\chi^2_2 = 1.2$ , NS). Neither was there a difference between the capture success of the two zodariid species (males and females combined) (log-linear analysis:  $\chi^2_1 = 0.9$ , NS). The relationship between the size of ants and the capture success for both *Zodarion* species (pooled for both sexes), disregarding data on *M. sabuleti* (due to low capture success) was modeled using a parabola (Fig. 3). It is apparent from the response curves that the optimal size of ants for *Z. germanicum* is very similar (optimum

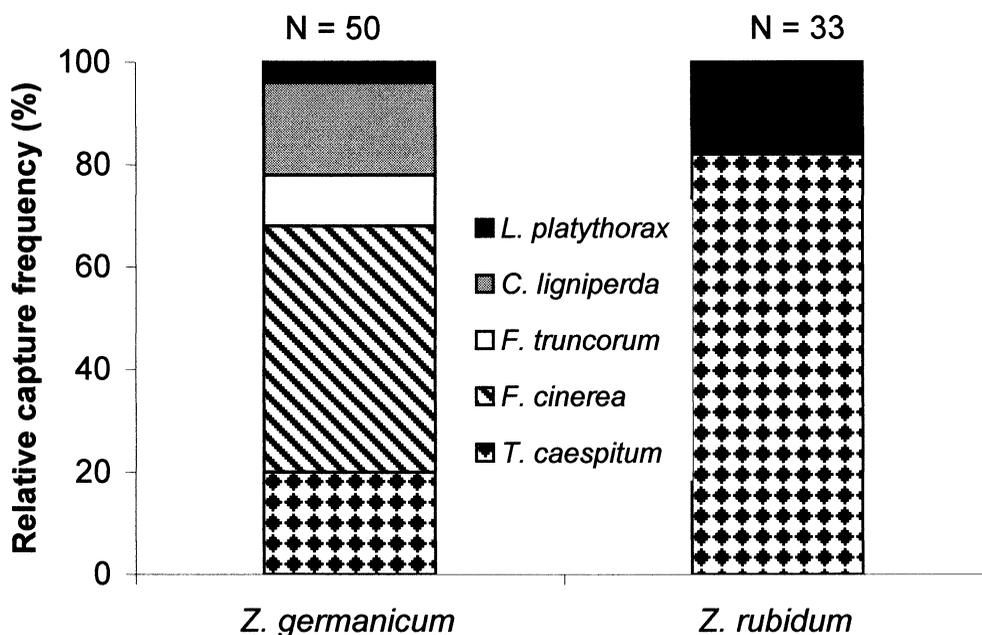


Figure 2.—Relative frequency of ant species captured by subadult and adult specimens of *Zodarion germanicum* and *Zodarion rubidum* observed in the study sites.

= 4.9, SD = 2.1) to that for *Z. rubidum* (optimum = 4.6, SD = 2.3) (t-test:  $t = 0.29$ , NS). These values correspond to the size of the small form of *F. truncorum*. The optimal prey is thus equal or smaller in size than adult individuals of *Z. germanicum*, but it is larger than adult individuals of *Z. rubidum*. Of the other insects offered to the spiders, only termites were attacked but rarely subdued by *Zodarion* spiders. No other invertebrate was attacked or subdued (Table 2).

**Predatory behavior.**—During the attacking phase (Fig. 4), spiders moved slowly while waving the first pair of legs. I recognized five events (I—V) that took place during the attack. After orientation toward an ant, the spider quickly approached (I) it with half-raised forelegs (Fig. 5). As the spider got closer, it first lightly touched (II) the ant's body with the tarsi of the forelegs (Fig. 6); occasionally the spider touched (III) the ant using the tips of the palpal tarsi. Afterwards the spider grabbed hold of a leg by its palps, bit (IV) the leg (Fig. 7), and retreated (V). The sequence of recognized events (Fig. 8) did not occur by chance (Chi-square test:  $\chi^2_{29} = 536$ ,  $P < 0.001$ ). The entire attack sequence, from approaching to retreating, lasted only  $0.17 \pm 0.01$  seconds.

Detailed analysis of the behavior showed that after the first encounter with an ant, the spider often stopped and positioned itself with legs fully outstretched. The spider oriented toward an ant which passed at a distance less than 1.6 mm ( $n = 30$ ) from the tip of its tarsi. When an ant passed by, the spider stalked it and approached it (Fig. 4). Latency to the first attack was similar for all three ant species (*M. faraonis*, *T. caespitum* and *L. flavus*) being on average 70 s. Spiders attacked rapidly by biting any of the ant's appendages. There were many more attacks (pooled for all three ant species) from a side or rear (77%,  $n = 102$ ) than on the head of ants (23%). Bites were most often applied to the longest appendages, with bite frequency and appendage length being positively correlated (Pearson correlation:  $r = 0.81$ ,  $P = 0.04$ ). Thus the most frequently bitten leg was the longest, one of the hind legs (Fig. 9). Ants were repeatedly bitten until immobile. There were on average 3.4 attacks made on the study ant species. Most of the attacks (62%,  $n = 102$ ) occurred within the first 3 min and only 4% occurred after 10 min. The frequency of attacks tended to decrease steadily with time as the ant slowed down.

Immediately after being bitten the ant be-

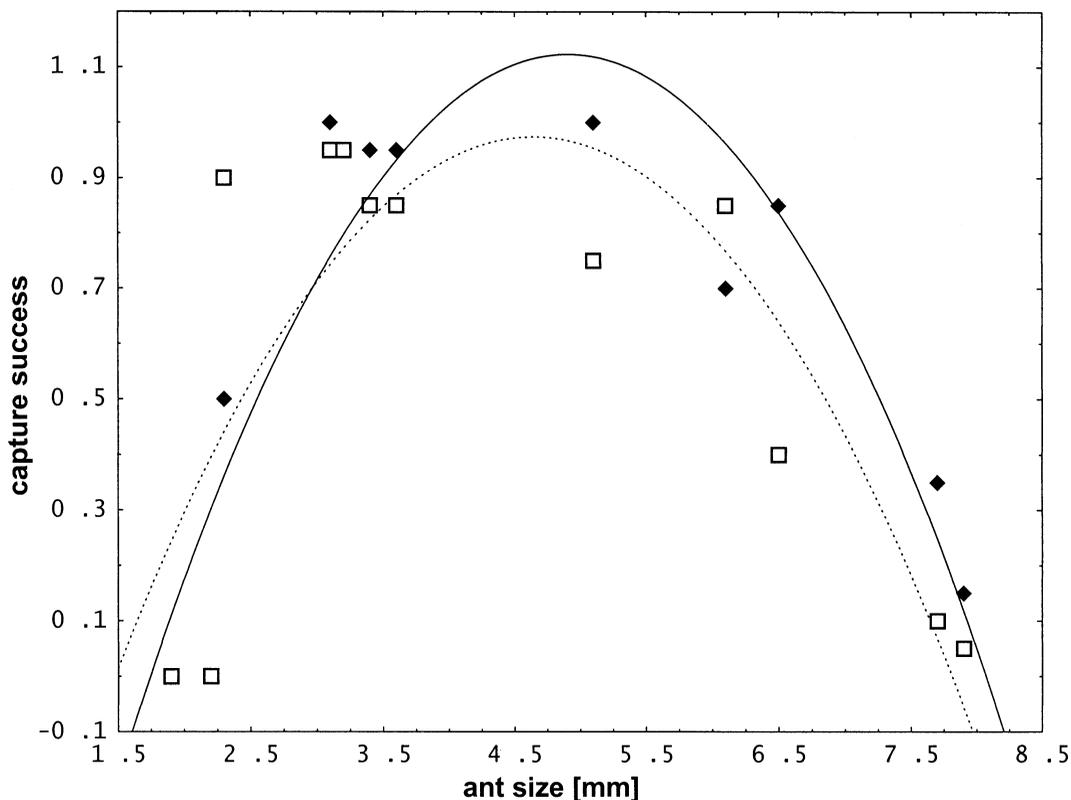


Figure 3.—Parabolic model describing relationship between the capture success of adult spiders of *Zodarion germanicum* (◆) and *Zodarion rubidum* (□) and the size of ants (ordered by size): *M. faraonis*, *T. caespitum*, *T. erraticum*, *L. flavus*, *L. platythorax*, *F. cinerea*, *F. cunicularia*, *F. truncorum*, and *C. ligniperda*. The coefficient of determination ( $R^2$ ) is 0.91 and 0.81 for *Zodarion germanicum* and *Zodarion rubidum*, respectively.

came excited (open mandibles), moved around and made attacks to the surrounding area. The stabbed leg was visually cramped and the velocity of the ant gradually decreased: it began to stumble, its gaster twisted and finally the whole body was overcome by paralysis. Ants (*T. caespitum*) that had been stabbed only once were immobile  $3:35 \pm 0.4$  min after the stab.

The handling phase was separated from the attacking phase by a period of waiting. After the last attack the spider waited 2–29 min crouched in a corner of the dish. Then it began to search for the immobilized prey. The spider moved slowly with raised forelegs and palps lightly tapping the substrate, then stopped at a distance of  $3.2 \pm 0.1$  mm from the ant, and probed with forelegs waving dorso-ventrally (Fig. 10). It then stretched one foreleg forward and gently touched the prey (Fig. 11). If the

prey was quiescent the spider would carefully palpate it (Fig. 12), grab hold of the ant's thorax and carry it away to feed up on. If the prey was still moving, the spider would run away. Sometimes (46%,  $n = 30$ ) the spider grabbed a still wriggling ant. During feeding, the spiders moved the ant corpse around and gradually sucked up various body parts, starting with the thorax, legs, head and abdomen. Feeding took on average 2.5 hours ( $n = 30$ ) but varied considerably (1–7 hours). The remains of the ant were discarded as an empty shell.

## DISCUSSION

Unlike ant-eating salticids which are also able to capture other insects (Jackson & Van Olphen 1991), zodariid spiders turned out to be more specialized in their diet. The two species of *Zodarion* were found to feed on ant

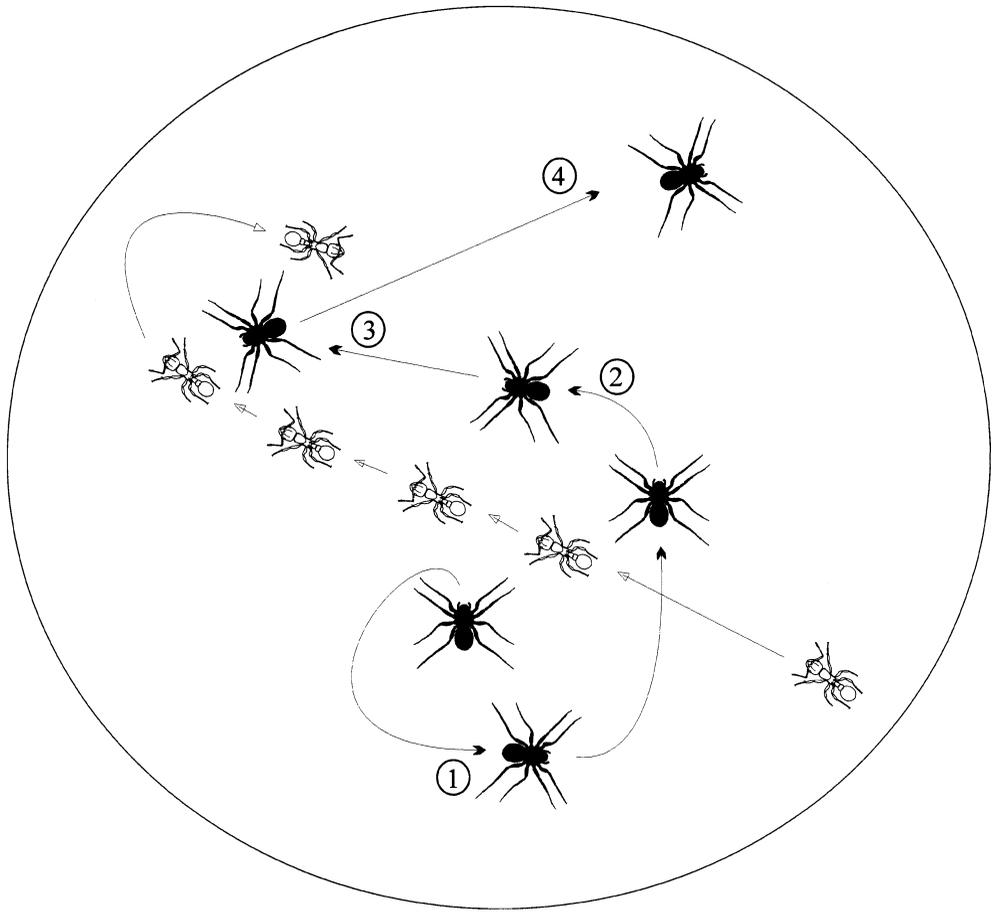


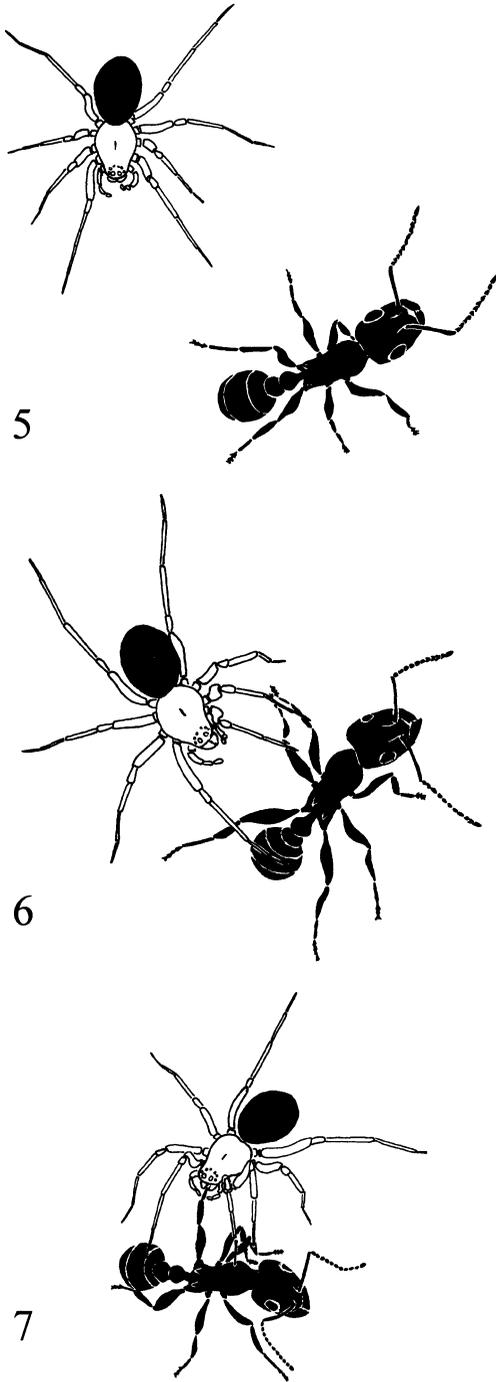
Figure 4.—Sample attack path of *Zodarion rubidum* (black) pursuing the ant (white). 1 = spider orients toward the ant; 2 = spider stalks the ant; 3 = spider attacks the ant from the rear; 4 = spider retreats.

species of different sizes and belonging to different subfamilies. With the exception of termites, they ignored other insects offered. Although the spiders attacked termites, they seldom killed them. Similar results on the prey preference of *Z. rubidum* were obtained by Couvreur (1989). These results suggest that the two study species of *Zodarion* are strict ant specialists.

Couvreur (1990) observed that only females of *Z. rubidum* capture ants. In my experiments, males captured ants as well, although less frequently than females. The ability to subdue ants for both zodariid species in both sexes was found to be dependent to some extent on the size of prey. The best success of adults was obtained with medium sized ants which are about the same size as the tested spiders. The two species showed

similar abilities in the capture of the ant species. The tiny ant species were usually not attacked by adult spiders. It appears to me that these ants did not produce a signal, either visual (being too tiny), vibratory (being too light) or olfactory (producing an alarm pheromone that is not detected by spiders), that would elicit attack by *Zodarion*. However, the lack of response can also be explained applying the optimal foraging hypothesis (Riechert & Luczak 1982). Tiny ant species might be considered unprofitable for study *Zodarion* species: greater energy would be spent attacking and subduing them than gained by their consumption.

The red ants (*M. sabuleti*) were seldom subdued by either species of spiders. Unlike in tiny ant species, *M. sabuleti* was attacked by spiders but the attack did not lead to immo-



Figures 5–7.—The attacking phase. Illustrative example of *Zodarion rubidum* capturing the ant (*T. caespitum*). Taken from a video analysis (time frame in parentheses). 6. Spider approaches ant from the rear with raised forelegs (0.00 s); 7. Spider taps the ant's gaster (0.13 s); 8. Spider bites ant's tibia of the third leg (0.19 s).

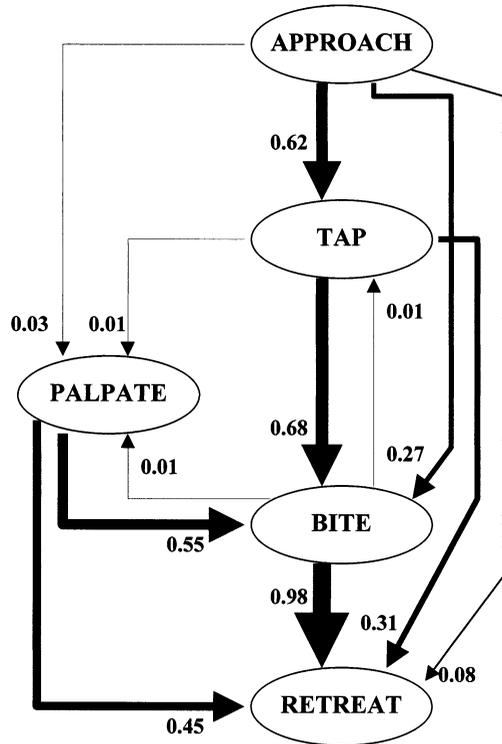


Figure 8.—Flow diagram of the events (pooled for the three ant species) of the attacking phase with probability frequencies ( $n = 102$ ). After retreating spiders either continued attacking (starting with approach) or waited and continued handling phase.

bilization. I assume that the spiders were not able to penetrate the heavy, sclerotized cuticle of this ant species. Alternatively, the venom of the two spider species might not be effective in immobilizing this ant. The ability to subdue large ants, like *F. truncorum*, was very low in tube trials because the ants often bit the spiders' legs. In the field, the ability is greater because the spider has more room to hide from the excited ant (pers. observ.). Lower capture success might be also due to more agile behavior of larger ant species. Formicinae ants are generally moving fast so the chances of *Zodarion* to attack it might decrease.

The capture of ants is risky. At the study sites I found 47% ( $n = 30$ ) of *Zodarion* spiders missing at least a part of one leg presumably as a result of an ant's attack. That ants are very dangerous prey for *Zodarion* as can be seen from the analysis of the spider's predatory behavior. First, the behavior is com-

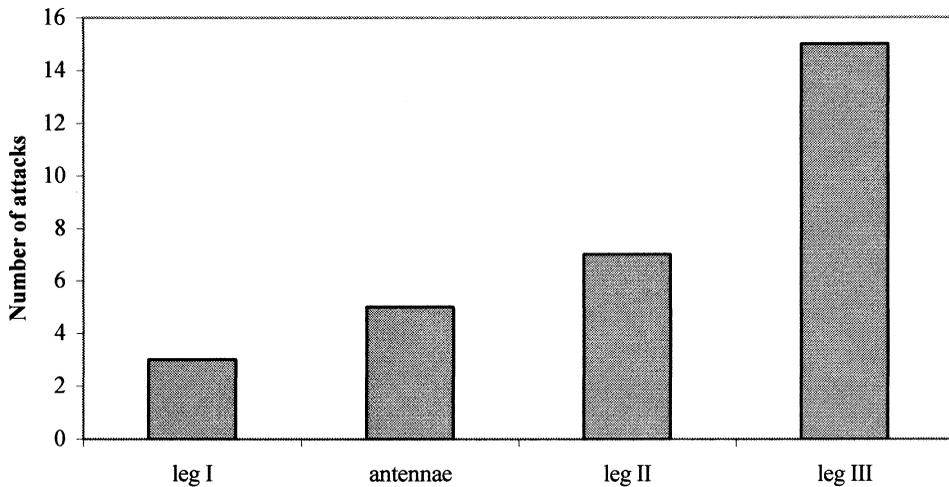


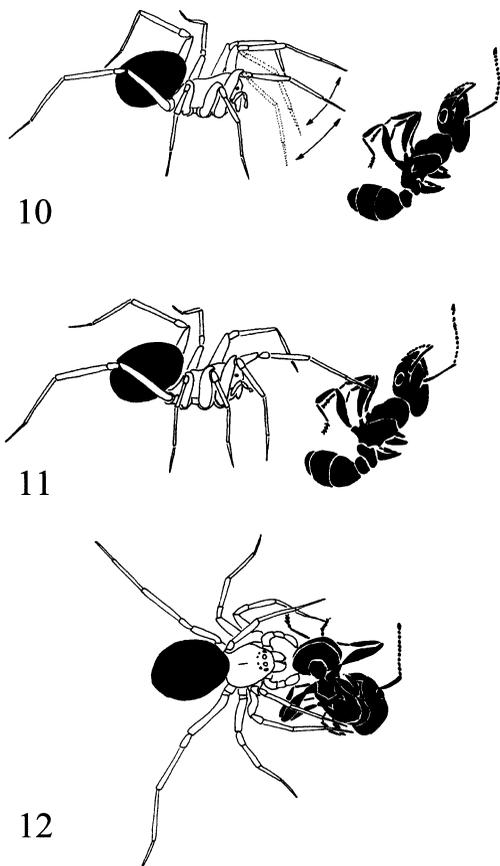
Figure 9.—Relationship between the frequency of the attacks and the length of each ant appendage (pooled for the three ant species). Appendages are ordered by visual size: leg I, antennae, leg II, leg III.

posed of two phases, separated by a period of waiting at a safe distance. As the bitten ant becomes aggressive, spiders are at risk. Indeed, attacked ants often tried to attack the spider which generally fled. Second, the spider generally attacked very quickly by a surprise attack from the rear. Third, the spider bit the most extended appendage. All these acts compose a predatory strategy that enables the spider to stay away from the ant. Finally, the spider handled the ant only when it was immobilized. Such predatory behavior is likely to be an adaptation to the capture of a dangerous prey.

This predatory tactic corresponds well to that adopted by other ant-eating zodariid spiders, namely *Z. elegans* (Simon 1873) and *Z. frenatum* Simon 1884 (Harkness 1976, 1977; Wiehle 1928). A similar tactic, i.e. the attack from the rear followed by a retreat, has also been reported for some ant-eating salticids (Jackson & Van Olphen 1992; Jackson et al. 1998). Such a tactic is obviously a very effective means of overcoming the ant's defenses. Other ant-eating salticid spiders, however, attack ants head-on (Jackson & Van Olphen 1991). So does *Callilepis nocturna* Linnaeus 1758 (Heller 1974), which bites the ant's antennae. This may accelerate the paralysis (since the antennae are close to the ant's brain) and may enable this spider to grab hold of an ant's body within about a minute after the seizure, whereas *Zodarion* has to wait much longer.

There might be a trade-off between the two foraging tactics, attacking head-on and from the rear. The former tactic is obviously more risky as the spider exposes its body close to an ant's mandibles, but enables the spider to take hold of the prey shortly after the attack. The latter tactic is safer (the spider runs away from the excited ant), but the ant can be collected by another predator (or ant nestmates) in the meantime. I suggest that robust and non ant-mimicking spiders, such as *Callilepis*, use the head-on tactic. Slender ant-mimicking spiders, such as the zodariids that are protected from visually hunting predators by mimicry (Pekár & Král 2002) use the rear tactic.

The diet specialization appears to be apomorphic for zodariid spiders. Although very little information is available for the more than 50 genera of zodariid spiders described so far (Jocqué 1991) some common traits are apparent. Primitive representatives of Zodariidae appear to be polyphagous. *Lutica*, from the subfamily Lachesaninae, feeds on various invertebrates and captures prey in a similar fashion to that of *Atypus* (Ramirez 1995). More derived representatives show some specialization. For example, the Namibian zodariid spider *Psammoduon deserticola* (Simon 1910), a member of the subfamily Cydrelineae, feeds mainly on tenebrionid beetles, which are located while diving through the sand but will also prey on syrphid larvae and Thysanoptera (Rössl & Henschel 1999). Finally the most derived representatives seem to be strictly spe-



Figures 10–12.—The handling phase. Illustrative example of *Zodarion rubidum* handling the ants. Taken from a video analysis. 11. Spider approaches and begins to probe (forelegs waved); 12. Spider taps the ant's leg; 13. Spider palpates ant's head.

cialized. South African species of the genus *Diores* feeds on termites which are ambushed on their mounds during the night (Jocqué & Dippenaar-Schoeman 1992). *Acanthozodium* in North Africa (Pierre 1959) and *Zodarion* in Europe were observed to feed on ants. However, more investigation into the diet of other representatives of zodariid spiders should be carried out in order to support this hypothesis.

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