NATURAL HISTORY AND KARYOTYPE OF SOME ANT-EATING ZODARIID SPIDERS (ARANEAE, ZODARIIDAE) FROM ISRAEL

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ABSTRACT.   Natural history, including phenology, circadian activity, mimicry, reproduction, prey specialization and karyotype was studied in the zodariid spiders *Trygettus sexoculatus*, *Zodarion cyrenaicum*, *Z. lutipes* and *Z. nitidum* (Zodariidae, Zodariinae) found in Israel. The spiders were active throughout the year, with maximum seasonal activity in the summer. Two distinct reproductive periods were found for *Z. cyrenaicum* and *Z. nitidum*, one in May and the other in November. Individuals of all species studied were observed hunting only in the morning. Three zodariid species were found to generally mimic ants: *Trygettus sexoculatus* mimicked tiny yellow-brown ants such as *Monomorium niloticum*, *Z. cyrenaicum* mimicked large black ants such as *Messor arenarius*, and *Z. lutipes* mimicked large yellow-brown ants such as *Camponotus fellah*. The zodariids observed were able to subdue various ant species, from the subfamilies Formicinae, Myrmicinae and Dolichoderinae. *Trygettus sexoculatus* appeared to specialize on *Monomorium* sp., *Z. lutipes* on *Camponotus* sp. and *Z. cyrenaicum* on *Messor* sp. ants, i.e., the same ant species they imitate. When bitten by zodariids, Formicinae and Dolichoderinae ants were paralyzed much more quickly than Myrmicinae. Female zodariid paralyzed ants faster than juveniles and males. Courtship and mating were observed only in *Z. lutipes* and were found to be similar to other *Zodarion* species. The mean fecundity for all three *Zodarion* species ranged from 38–45 eggs per egg sac, thus being higher than reported in central European species. Females of all three species guarded egg sacs inside of their retreats. Karyotypes of studied *Zodarion* spiders were similar to the karyotypes of other zodariid spiders in terms of the diploid number (26 in *Z. cyrenaicum* and 25 in both *Z. lutipes* and *Z. nitidum*), sex chromosome systems and morphology of chromosomes. Most of the data indicate that the *Zodarion* species of this study have a close affinity to a group of Western European *Zodarion* species.

Keywords: Myrmecophagy, specialization, mimicry, Formicidae, chromosomes

The family Zodariidae is a species rich group of spiders, which includes more than 570 species in six subfamilies with worldwide distribution, but is most abundant in the subtropical region (Platnick 2002). Zodariid spiders were neglected on a worldwide scale until recently, when Jocqué (1991) produced a generic revision. Very little information is reported on the natural history of zodariid spiders (e.g. Wiehle 1928; Harkness 1976; Cushing & Santangelo 2002).

In the Mediterranean region, representatives of two subfamilies and more than 110 species have been found. The majority of species belong to the most advanced subfamily, Zodariinae. The diversity of this subfamily seems to decline from west to east in the Mediterranean region. In the western and the central area, three genera and about 60 species of Zodariinae were found and in the eastern part five genera with only about 30 species. This may be explained, in part, by the lack of collecting in the eastern region. In fact, in the eastern Mediterranean only the zodariid spiders of Israel have been revised so far. Altogether 13 species of the genera *Palaestina*,

Ranops, *Trygettus* and *Zodarion* were reported from Israel (Levy 1992).

In spite of the lower number of species in the eastern Mediterranean, the zodariid fauna of Israel shows a remarkable diversity perhaps due to the fact that Israel is situated where two biogeographic regions, the Palearctic and the Ethiopian, meet. However, little is known of the natural history of these zodariid spiders. The purpose of this study was to gather data on the natural history and karyotypes of the four most abundant species, *Trygettus sexoculatus* (O.P.-Cambridge 1872), *Zodarion cyrenaicum* Denis 1935, *Zodarion lutipes* (O.P.-Cambridge 1872), and *Zodarion nitidum* (Audouin 1826) and to compare them to the European *Zodarion* species that have been studied (Couvreur 1990a; Pekár & Král 2001). This study contributes to the understanding of the adaptive radiation within Zodariinae and particularly within the genus *Zodarion*. Members of the subfamily Zodariinae are remarkable for their diet specialization on some social insects (ants and termites) and for the frequent occurrence of ant mimicry. Information on phenology, diet specialization and mimicry as well as the number and morphology of their chromosomes was compared with similar data reported for the European species (Pekár & Král 2001).

Trygettus sexoculatus, *Z. cyrenaicum*, and *Z. nitidum* are found in Israel and in North Africa; *Z. lutipes* occurs in Crete and north of Israel, in Lebanon and Turkey (Levy 1992). In Israel, *T. sexoculatus* occurs in the central and southern arid region. *Zodarion nitidum*, a desert spider, occurs mainly in the Negev desert. *Zodarion lutipes* was found only as far south as the north-western part of the Negev desert (desert edge). *Zodarion cyrenaicum* occurs in the northern part of the Negev desert. It is occasionally sympatric with *Z. nitidum* in the desert, while in the northern Negev it occurs syntopically with *Z. lutipes* (Fig. 1).

METHODS

Study areas.—Numerous specimens of *Z. cyrenaicum* and *Z. lutipes* were collected in the weedy margin of a melon field at the Bitronot-Be'eri Nature Reserve (about 40 km NW of Be'er Sheva, 31°26′N, 34°29′E). These two species, together with *T. sexoculatus*, were collected and observed also on an open slope of a semi-desert steppe character close
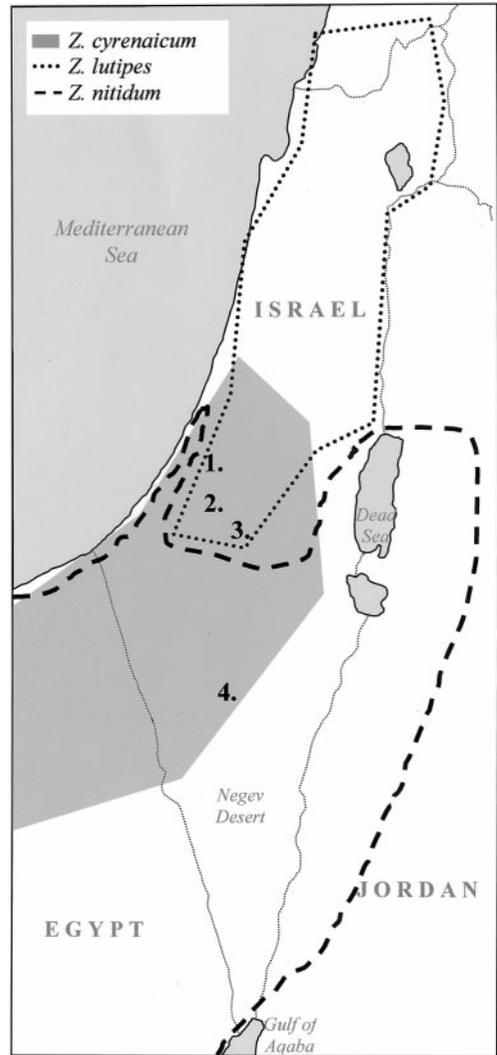

Figure 1.—The distribution of *Zodarion* species in Israel reported in this study. Sites mentioned in the text are indicated: 1. Be'eri Nature Reserve, 2. Fura Nature Reserve, 3. Lehavim, 4. Sede Boqer.

to Lehavim, at the northern edge of the Negev desert (about 10 km NE of Be'er Sheva, 31°22′N, 34°48′E). *Zodarion lutipes* was also found in Fura Reserve in semi-desert grassland habitat (about 20 km N of Be'er Sheva, 31°27′N, 34°45′E). *Zodarion nitidum* was very abundant in a large-scale spider diversity project of the Negev desert that began in the early 1990's (Pekár & Lubin 2003). However, in March & April 2001 a three-week intensive search for these spiders in the surroundings of Sede Boqer (Haluqim Ridge, 30°51′N

34°45′E) yielded only five specimens. Boeken et al. (2001) noted that a severe drought in 1999 followed by drought in 2000 caused a dramatic decline of plant density in the Negev. It is likely that these droughts considerably reduced the population density of *Zodarion* species.

Material and analyses.—Data used to extrapolate the seasonal activity and phenology of zodariids came from the large-scale project on the diversity of spiders of the Negev desert (Proszyński & Lubin 1994; Pekár & Lubin 2003). Spiders were sampled at 45 sites in the Negev between September 1990 and July 1993. The spiders were collected using pitfall traps that were opened for 3 consecutive days each month. No preservative was used in the traps (diameter and depth 10 cm) and the spiders were collected each morning. Immature *Zodarion* individuals were identified to species based on the color.

Circadian activity of spiders was observed in 2001 as the number of spiders found during 5 min in the vicinity of ant nests or along ant trails (in the case of *Messor* ants). As the sites in the northern Negev were not easily accessible, the activity of spiders was observed only during the day, between 0900 and 1900. At Sede Boqer, the activity of ants was observed for 24 hours on one day in the beginning of April. On that day the sunrise was at 0530 and the sunset at 1800. Activity of four ant species (the most frequent in the study sites), namely *Camponotus fellah* Dalla Torre 1893, *Cataglyphis albicans* (Roger 1859), *Messor arenarius* (Fabricius 1787) and *Monomorium niloticum* Emery 1881, was estimated every hour as the number of ants counted per 15 s at four nest entrances.

The behavior of the different species was investigated in the laboratory. Twenty-seven individuals of *Z. cyrenaicum*, 21 of *Z. lutipes*, 10 of *Z. nitidum* and four of *T. sexoculatus* were brought to the laboratory. Spiders were kept singly in glass tubes (60 x 15 mm) in a constant temperature 25 ± 2 °C and L:D = 14:10 and were fed twice a week with various ant species. To observe courtship and mating, adult males were introduced into tubes occupied by females. After mating the males were separated from the females. The number of egg sacs produced and the fecundity (total number of eggs) were recorded.

In the feeding experiments spiders were put singly to a Petri dish (diameter 40 mm, with a filter paper attached to the bottom) a day before the experiment started. Ten individuals of each *Zodarion* species and four specimens of *Trygettus* were used. Four ant species, namely *C. albicans* (Formicinae), *M. arenarius*, *M. niloticum* (Myrmicinae) and *Tapinoma simrothi* Krausse 1911 (Dolichoderinae), were offered to each individual of *Zodarion* species. Three ant species, *Pheidole pallidula* Nylander 1849, *M. niloticum* (Myrmicinae) and *T. simrothi* (Dolichoderinae), were offered to *T. sexoculatus*. The ants were offered to spiders randomly over a 4 day interval. All ants were weighed before the experiment. *Cataglyphis* and *Messor* ants were disabled by removing the distal parts of mandibles before the experiments. Other ant species were not disabled. An ant was released into a dish occupied by a spider; if the spider did not attack the ant within 15 min the experiment was terminated. Latency to the first attack, number of attacks and the paralysis latency (time to paralyze the ant) were observed for each trial. The latency to the first attack was estimated as the time from the first encounter between spider and ant to the first attack. The paralysis latency was estimated as the time between the first attack and complete immobilization, i.e. when an ant could not raise itself after being touched with forceps.

Data were analyzed using Generalized Linear Models (GLM) in Statistica (StatSoft 2001). The body mass of an ant was expected to have an effect on the number of attacks and on paralysis latency, therefore ant mass was first regressed (using linear regression) on these dependent variables. However, ant mass had no effect on the number of attacks and therefore could be ignored in the analyses. As the data followed a Poisson error structure, a log-linear analysis was used with three factors (see below). Over-dispersion was resolved by adjusting the scale parameter. The same method was used to analyze data on the latency to the first attack. The paralysis latency was affected by ant body mass, which was set as a covariate. The paralysis latency data were log transformed and further analyzed using ANCOVA. In all analyses the factors were (1) *Zodarion* species (*Z. cyrenaicum*, *Z. lutipes*, and *Z. nitidum*), (2) developmental stage or sex of spider (female, male, and juvenile) and (3) ant subfamily (Dolichoderinae, Formicinae

and Myrmicinae). Post-hoc comparisons were made using Tukey's HSD test.

For the karyological analyses three individuals of *Z. cyrenaicum* (locality Bitronot-Be'eri), five individuals of *Z. lutipes* (Lehavim), and 12 individuals (reared from two egg sacs) of *Z. nitidum* (Hatira), representing both sexes and various developmental stages, were used. However, only the testes of subadult males (two in *Z. cyrenaicum*, three both in *Z. lutipes* and *Z. nitidum*) gave interpretable chromosomal figures. The chromosome preparations were obtained by a modification of the spreading technique used by Traut (1976). The gonads were dissected from the abdomen in a hypotonic solution (0.075M KCl) and moved to fresh hypotonic solution so that the tissue was hypotonized for 10 min in total. This was followed by 10 min fixation in freshly prepared Carnoy fixative (ethanol: chloroform: glacial acetic acid 6:3:1) and 25 min fixation in a new Carnoy fixative. Afterwards, the tissue was placed in a drop of 60% acetic acid on a clean slide and quickly shredded as finely as possible with a pair of fine tungsten needles. The slide was quickly moved onto a warm histological plate (surface temperature of 40 °C) and the drop of dispersed tissue was allowed to evaporate while moving it constantly using a fine tungsten needle. Slides were air-dried at room temperature overnight and stained with 5% Giemsa solution in Sörensen phosphate buffer (pH = 6.8) for 25–30 min (Cokendolpher & Brown 1985).

Zodariid spiders were identified using Levy (1992) and ants were determined using an unpublished key of Kugler (1984). Voucher specimens of spiders and ants are deposited at the Department of Entomology of the Research Institute of Crop Production, Prague, the Czech Republic.

RESULTS

Phenology.—Pitfall-trap sampling at regular intervals allowed us to outline the seasonal activity and phenology of *Z. cyrenaicum* and *Z. nitidum*. Data for *Z. lutipes* and *T. sexoculatus* were insufficient to determine any pattern. *Zodarion cyrenaicum* and *Z. nitidum* were active during the whole year (Fig. 2). The maximum seasonal activity (between 27–44 % of the total annual activity) of both species was in the summer months, June (*Z. nitidum*) and July (*Z. cyrenaicum*). There was
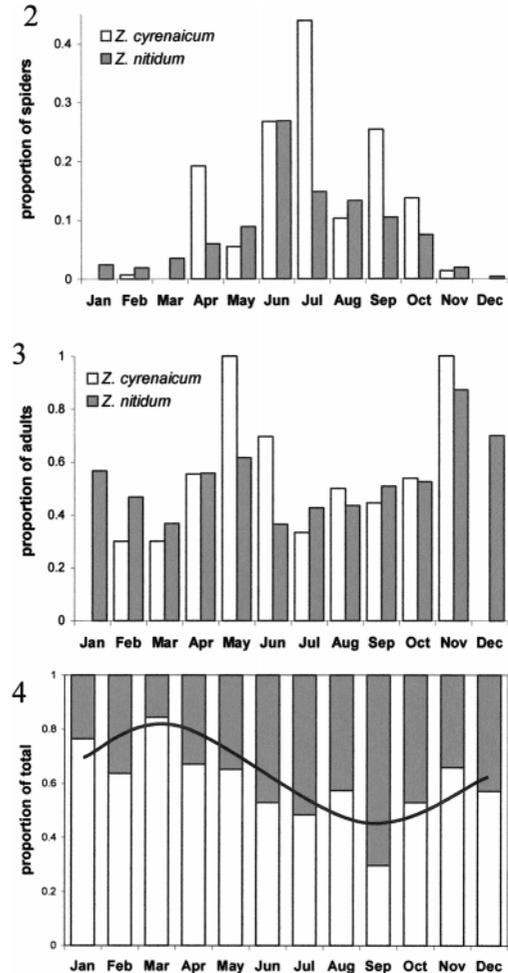
Figures 2–4.—Phenology of zodariid spiders collected in pitfall traps: data from three years (1991–3) combined. 2. Seasonal activity of *Z. cyrenaicum* and *Z. nitidum*, expressed as a monthly proportion. Total number of individuals: *Z. cyrenaicum* = 146, *Z. nitidum* = 2403. 3. Phenology of *Z. cyrenaicum* and *Z. nitidum* expressed as the proportion of adult spiders per month. 4. Monthly proportions of males (empty bars) and females (gray bars) of *Z. nitidum* with a polynomial curve.

minimal or no activity in the winter months, December (*Z. nitidum*) and January (*Z. cyrenaicum*). Adults of *Z. nitidum* were found throughout the year (Fig. 3), while no individuals of *Z. cyrenaicum* were trapped during the winter months. Both species had two reproductive peaks annually: spiders matured in spring (March) and autumn (November) and reproduced soon after. The proportion of males to females of *Z. nitidum* changed during
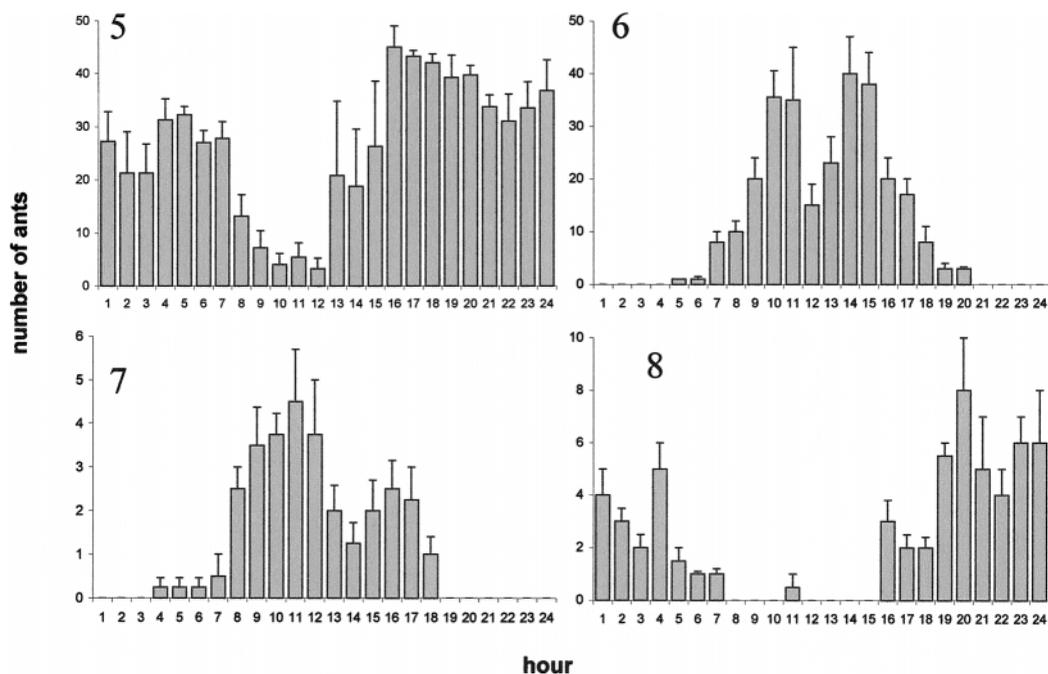
Figures 5–8.—Daily activity of ants expressed as number of ants recorded in 15 s: 5. *Messor arenarius*; 6. *Monomorium niloticum*; 7. *Cataglyphis albicans*; 8. *Camponotus fellah*. Bars represent mean + SE.

the year (Fig. 4). Whereas males dominated in spring (peak in March), females dominated in autumn (peak in September). In total the M/F ratio of individuals collected in pitfall traps was significantly skewed toward males 1/0.83 (binomial test, $P = 0.002$).

Activity.—*Zodarion* spiders were collected from igloo-shaped retreats underneath stones where they rest during the day. The retreats were made of sand pebbles or pieces of gastropod shells and were proportional to the size of the spider. In females the retreats were up to 2 cm in diameter. Individuals of *T. sexoculatus* were found under stones but never in a retreat. *Trygettus sexoculatus*, *Z. cyrenaicum* and *Z. lutipes* were active only in the morning, from 0900–1100, running among ants or hunting them. No *Z. nitidum* was observed at all during March–April 2001. In 2002, however, *Z. nitidum* was seen active in the morning hours (males and females) in the vicinity of nests of *M. arenarius* in sandy habitats. Activity of the four most abundant ant species, which are the prey of observed zodariid spiders, followed different patterns. *Messor* ants were active in the day as well as at night (Fig. 5), with a decline in activity between 0900

and 1400. *Monomorium* ants were active only during the day, from 0500–2000, with a decline at midday (Fig. 6). *Cataglyphis* ants were also active during the day only, from 0400–1800, with a slight decline between 1300 and 1400 (Fig. 7). *Camponotus* ants were active only from the afternoon (1600) and through the night until morning (0700; Fig. 8). The activity of ant species and of the spiders overlaps broadly.

Batesian mimicry.—Tentative ant models were found for three spider species. *Trygettus sexoculatus* imitates tiny yellowish-brown ants, especially *Monomorium niloticum*. Adult spiders are 2–2.5 mm in length, with yellowish prosoma and legs and the opisthosoma is dorsally dark brown with a glossy scutum (Fig. 9). Workers of *M. niloticum* are 3–3.5 mm in length with head, thorax, antennae and legs yellow to orange and the gaster dark brown. Adult spiders of *Z. cyrenaicum* mimic larger black ants, e.g. the small workers of *Messor arenarius*. The spiders are 3.5–8 mm in length with uniform blackish prosoma and opisthosoma. The legs are black, except for the coxae and patellae, which are pale (Fig. 10). Workers of *M. arenarius* are polymor-
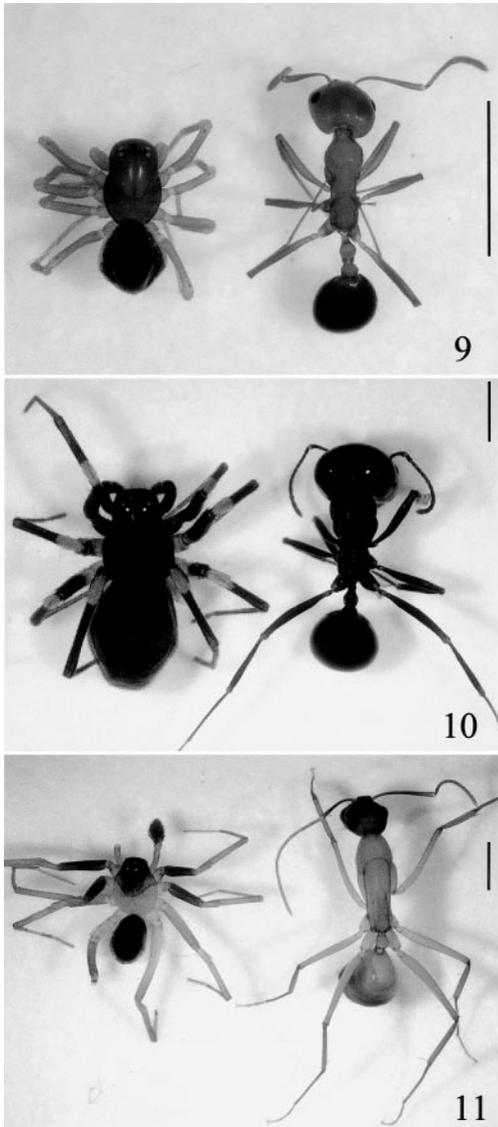
Figures 9–11.—Spider mimics and their ant models. 9. *Trygettus sexoculatus* (female) and *Monomorium niloticum*; 10. *Zodarion cyrenaicum* (female) and *Messor arenarius*; 11. *Zodarion lutipes* (male) and *Camponotus fellah* (freshly hatched individual with light gaster). Scale lines = 2 mm.

phic, 4–15 mm and are uniformly black. Adult individuals of *Z. lutipes* resemble larger yellowish-brown ants, notably small workers of *Camponotus fellah*. The spiders are 3.5–6.5 mm in length, the prosoma is yellow with a brown cephalic part and the opisthosoma is dark brown (Fig. 11). All leg segments are yellow except for the first and second femora,

which are brown. The model ants are 6–17 mm, with head and gaster dark brown while the thorax, antennae and legs are yellow to light brown. Individuals of *Z. nitidum* were observed with *M. arenarius* ants, which they do not appear to mimic closely.

Prey.—A few individuals were observed feeding on ants in the field. Four individuals of *Z. cyrenaicum* were observed feeding on *M. arenarius*, two individuals of *Z. lutipes* fed on *Messor semirufus* (André 1883) or *C. fellah* and three individuals of *T. sexoculatus* fed on *M. niloticum*. Feeding of *Z. nitidum* was not observed in the field. In laboratory experiments all *Zodarion* species were able to subdue larger ants of the genera *Cataglyphis* and *Messor*. Tiny ants were often ignored: only 24% ($n = 30$) of all *Zodarion* individuals attacked *M. niloticum* ants and 75% of *Z. cyrenaicum* and *Z. lutipes* ($n = 20$) attacked *T. simrothi* ants while no *Z. nitidum* attacked this ant. All *T. sexoculatus* ($n = 4$) attacked *M. niloticum* and *P. pallidula* but failed to catch *T. simrothi*. *Trygettus sexoculatus* always attacked ants only once while *Zodarion* spiders averaged two attacks per ant. There was no difference in the number of attacks on ants from different subfamilies, nor was there a difference between the *Zodarion* species. The latency to the first attack was significantly different for the three *Zodarion* species (GLM, $P = 0.002$). *Zodarion cyrenaicum* took almost four times longer to attack (119 s, SE = 46) than the other two species (30 s, SE = 5.1). There was also a difference between sexes and developmental stages (GLM, $P = 0.0001$). Males took about five times longer to attack (150 s, SE = 46) than females and juveniles (31.5 s, SE = 5.2). In *T. sexoculatus* the latency was on average 20 s (SE = 14.2). Myrmicinae ants attacked by *T. sexoculatus* were paralyzed on average after 3.1 min (SE = 0.34, $n = 6$) (Table 1). In *Zodarion* spiders the paralysis latency differed for developmental stages and species (Fig. 12). It was longest in males and shortest in females (GLM, $P = 0.003$). There was also a significant difference in paralysis latency between ant subfamilies (GLM, $P < 0.0001$). Myrmicinae ants were paralyzed on average after 64 min while Formicinae and Dolichoderinae after 17–19 min (Table 1). The three *Zodarion* species did not differ significantly in the paralysis latency for Myrmicinae. However, *Z. lutipes* paralyzed

Table 1.—Comparison of the number of attacks and the paralysis latency (min) on three ant subfamilies for three zodariid spiders. *Zodarion nitidum* did not attack dolichoderine ants, presumably because the spiders were large in comparison with the ants. *Trygettus sexoculatus* was not tested with formicine ants because the ants were too large for this species. All numbers are means ± SE.

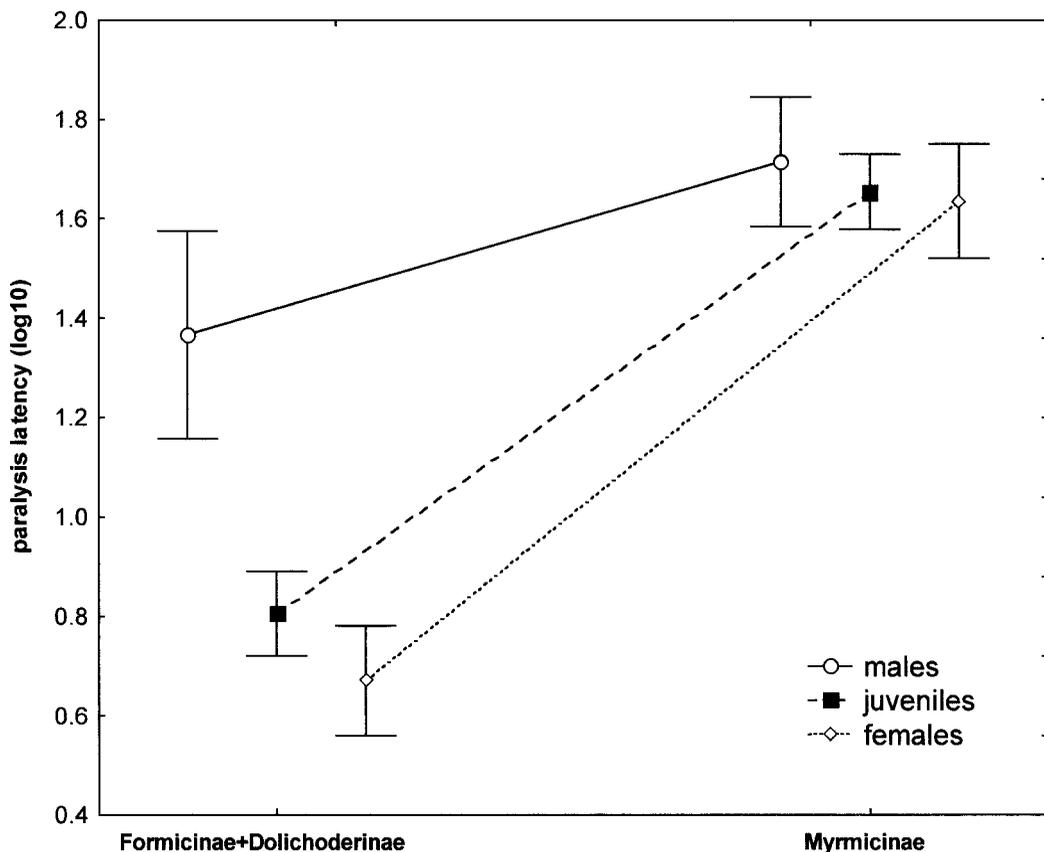| Spider	Ant subfamily	No. of attacks	Paralysis latency
T. sexoculatus	Myrmicinae	1.0 ± 0.0	3.6 ± 0.13
	Dolichoderinae	0	—
Z. cyrenaicum	Formicinae	1.9 ± 0.4	26.7 ± 11.7
	Myrmicinae	2.2 ± 0.4	56.5 ± 11.1
	Dolichoderinae	2.1 ± 0.3	28.1 ± 15.3
Z. lutipes	Formicinae	2.2 ± 0.4	6.7 ± 1.4
	Myrmicinae	1.8 ± 0.2	71.2 ± 15.8
	Dolichoderinae	2.0 ± 0.7	3.5 ± 1.1
Z. nitidum	Formicinae	3.0 ± 0.6	19.0 ± 5.6
	Myrmicinae	2.4 ± 0.5	65.6 ± 11.7

Figure 12.—Comparison of the mean (±SE) paralysis latency (min) for different *Zodarion* sexes and developmental stages (pooled for the three *Zodarion* species) and two ant subfamilies (Formicinae were pooled with Dolichoderinae).

Formicinae ants in a significantly shorter time than *Z. nitidum* and *Z. cyrenaicum* (Tukey HSD, $P = 0.0002$).

Enemies.—Of 73 collected specimens, only one subadult male of *Z. cyrenaicum*, collected from an igloo-shaped retreat in Lehavim, was found to have a larva of *Polysphincta* sp. (Hymenoptera, Ichneumonidae) attached to the anteriodorsal region of its abdomen. No other *Zodarion* spider in this study was found with a parasitoid wasp larvae and no other enemies were observed attacking *Zodarion*.

Reproduction.—Courtship was similar in all three *Zodarion* spiders. Males began to court after a brief contact with the female. The male slowly approached the female from the front with rapidly quivering forelegs, and touched her lightly. If the female was receptive she first responded by similar quivering of forelegs, then crouched and allowed the male to climb onto her and copulate. Copulation was observed only in *Z. lutipes*, lasting on average 1.58 min (SE = 0.5, $n = 5$). Males copulated from both sides inserting the appropriate palp, and interrupted several times. After each interruption males quivered the forelegs, otherwise the female would respond aggressively. In the other two *Zodarion* species only several attempted copulations (unsuccessful insertion of palpal organs) were observed, each lasting less than 10 s. Females of *Z. cyrenaicum* and *Z. lutipes* produced only one egg sac while females of *Z. nitidum* produced 1–3 egg sacs in captivity. Females of all species guarded the egg sac inside the retreat. A new egg sac was produced only after the previous one hatched. Mean fecundity in *Z. cyrenaicum* was 45 eggs/sac (SE = 7.5, $n = 5$), 39 eggs/sac (SE = 17.9, $n = 3$) in *Z. lutipes* and 38 eggs/sac (SE = 4.3, $n = 11$) in *Z. nitidum*. Spiderlings (pooled for all three *Zodarion* species, as there was no difference between species (ANOVA, $P = 0.22$)) hatched on average after 36.3 days (SE = 4.8, $n = 8$). No information on reproduction was obtained for *T. sexoculatus*.

Karyotype.—Both mitotic and meiotic phases were obtained from the testes of subadult males. The diploid chromosome numbers were as follows: *Z. cyrenaicum* 26 (Figs. 13, 15), *Z. lutipes* 25 (Figs. 16, 18), and *Z. nitidum* 25 (Figs. 19, 21). No individuals of *T. sexoculatus* were collected for karyological analysis. Karyotypes of all studied species were formed by acrocentric chromosomes exclusively. Chromosome pairs decrease gradually in size except for two shortest pairs in *Z. lutipes* (Fig. 18). Sex chromosome(s) of all species are among the longest chromosomes in the karyotype. Observation of sex chromosomes during meiotic division indicated an X_1X_20 sex chromosome system in *Z. cyrenaicum*. Sex chromosomes X_1 and X_2 were similar in size, the X_2 being somewhat shorter than X_1 (Fig. 14). *Zodarion lutipes* and *Z. nitidum* have an X0 sex chromosome system (Figs. 17, 20). The X chromosome of *Z. lutipes* and *Z. nitidum* exhibits positive heteropycnosis (greater condensation than autosomes) during the first meiotic division and interkinesis as well as in prophase II. Heteropycnosis of sex chromosomes in *Z. cyrenaicum* continues only to diplotene. However, weak heteropycnosis reappears also during interkinesis and prophase II. Sex chromosome(s) in males of all species lie on the periphery of meiotic figures until metaphase II.

DISCUSSION

Aspects of the biology of five species of the genus *Zodarion* have been reported (Couvreur 1990b; Harkness 1977; Pekár & Král 2001; Schneider 1971; Wiehle 1928), but only two central European species, *Z. germanicum* (C.L. Koch 1837) and *Z. rubidum* Simon 1914, have been studied in detail (Couvreur 1990b; Pekár & Král 2001). The latter authors found that these two species differ considerably from each other in their circadian activity, reproduction and karyotype.

The seasonal activity of the three *Zodarion* species studied here is similar to the central European species with greater activity in summer. Central European zodariid spiders are active from April to October. In the winter, between November and March, European species are inactive, obviously overwintering (Pekár & Král 2001) while the species studied in Israel have low activity levels throughout winter. Central European species are univoltine and stenochronous with one maturation period in June. Spiderlings hatch in July and reach adulthood the following year, 10–11 months after hatching (Couvreur 1990a; Pekár & Král 2001). Data on two species, *Z. cyrenaicum* and *Z. nitidum*, show that Israeli species are bivoltine and eurychronous, with two major maturation periods, one in spring and
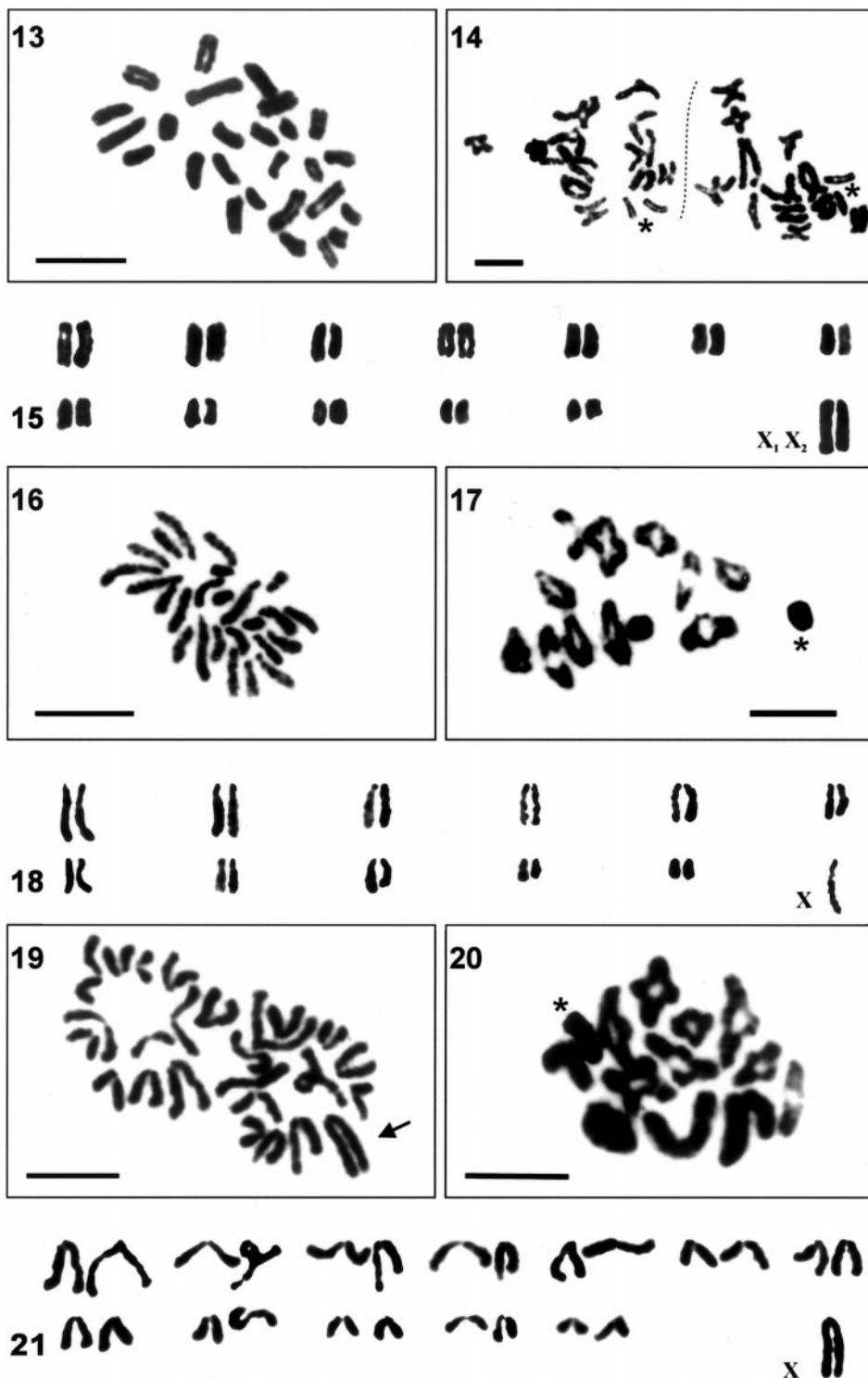
Figures 13–21.—Karyotype of *Zodarion* males. 13–15. *Zodarion cyrenaicum*. 13. Mitotic metaphase. 14. Diplotene. 15. Karyogram. 16–18. *Zodarion lutipes*. 16. Mitotic metaphase. 17. Diplotene. 18. Karyogram. 19–21. *Zodarion nitidum*. 19. Metaphase of the second meiotic division. Arrow identifies X chromosome that differs from autosomes by closely aligned chromatids. 20. Diplotene. 21. Karyogram. Karyo-

the other in autumn. Data collected by Levy (1992) and data from this study suggest that *T. sexoculatus* and *Z. lutipes* have a similar phenological pattern. The tendency to multivoltinism is known also for other Mediterranean arthropods (so called ''Mediterranean biotype''). For example, Bodenheimer (1943) found that populations of *Coccinella septempunctata* L. (Coleoptera) in Israel are bivoltine with one complete and one partial generation in spring and in autumn. Observations on the desert widow spider, *Latrodectus revivensis* Shulov 1948 (Theridiidae), indicate that this species has two peaks of maturation in Israel; a major one in spring and a minor one in autumn (Lubin et al. 1991). *Zodarion* species in Israel follow a similar pattern. It is not known how long it takes to complete one generation. Provided the development takes about six months there should be two non-overlapping generations in one year. If the development is about 10 months then there are two overlapping generations. For the spring generation it may be possible to mature in 6 months, i.e. by the end of summer, because ants are abundant and the temperature, controlling the rate of development, is sufficient. The autumn generation, however, might not be able to reach maturity by May as the temperature is rather low and ants are less active in winter. Thus it is assumed that the autumn generation is only partial, resulting in the eurychronous character of phenology.

Observations suggest that the zodariid spiders studied are mainly nocturnal (foraging in the morning and in the evening) like other Mediterranean species that have been studied. *Zodarion frenatum* Simon 1884 was found to have nocturnal activity, hunting ants mainly at dawn and dusk and searching for mates in the night (Harkness & Harkness 1992). The nocturnal activity may be due to excessive surface temperatures during the day, particularly in summer. Nocturnal activity may be an adaptation to avoid high densities of ants, which can be dangerous to hunting *Zodarion*. Current observations, however, do not support the latter hypothesis because many ants, for example *Messor*, are also active at night.

Similar to European *Zodarion* spiders, species in this study exhibited Batesian mimicry. Central European *Zodarion* spiders were found to be generalized mimics of ants (Pekár & Král 2002). They do not bear an exact resemblance to a specific model as do some corrinid spiders, for example *Myrmecium* (Hillyard 1997), but have a superficial resemblance to a group of similar ant species. Ant mimicry has been observed also in other species of the subfamily Zodariinae occurring in the Mediterranean region. Pierre (1959) suggested that *Zodariellum* (*Acanthinozodium*) *sahariense* Denis 1959 and *Zodarion bicoloripes* (Denis 1959) resemble *Messor aegyptiacus* (Emery 1878) in Algeria. In this study *Z. cyrenaicum* was found to resemble larger black (*Messor*) ants, *Z. lutipes* to resemble larger yellowish-brown (*Camponotus*) ants, and *Trygettus* to resemble tiny yellowish-brown (*Monomorium*) ants. The mimics are found in the same area as the models (Collingwood & Agosti 1996) and all these spiders closely associate with their models in order to feed on them. We failed to find a tentative model for *Z. nitidum*. It appears that males are better mimics than females, owing to the fact that females have larger abdomens. We suggest that more improved mimicry of males may be due to the different behavior of male and female *Zodarion* spiders. When running among ants, females are foraging and they retreat after capturing an ant, while males are patrolling for females and are therefore more visible to potential predators. This could select for closer mimicry in males, as it does for example in *Seothyra henscheli* Dippenaar-Schoeman 1991 (Eresidae), in which the males alone are ant mimics, while the sedentary females are not (Dippenaar-Schoeman 1991). *Messor* ants seem to be the most common ant model as many of these ants are polymorphic and can provide appropriate models for nearly all of the spiders' developmental stages.

Our results showed that *Zodarion* species are able to subdue several different ant species, as were European species of *Zodarion* (Harkness 1976; Pekár & Král 2001). Spiders ignored ants that were very small in compar-

←

grams were made from depicted metaphases. * identifies the sex chromosome(s) at diplotenes. Note the positive heteropycnosis of the sex chromosome. Scale lines = 10 μm.

ison with the spider. It is likely that the *Zodarion* spiders studied here can feed naturally on several ant species, as does *Z. frenatum* in Greece, which hunts both *Cataglyphis* and *Messor* ants (Harkness 1976). In general, all three *Zodarion* species possess more effective venom for paralyzing Formicinae and Dolichoderinae than for Myrmicinae ants. This is consistent with results of other studies. Harkness (1976) observed in the field that *Z. frenatum* paralyzed *Cataglyphis bicolor* (Fabricius 1793) (Formicinae) ants in 15 min. Wiehle (1928) noticed that it requires about two hours for *Z. elegans* (Simon 1873) to paralyze myrmicine ants, *Messor* sp. Couvreur (1990b) found in laboratory experiments that *Z. rubidum* paralyzed several species of formicine ants in about 6 min whereas large myrmicine ants were paralyzed in about 45 min. It is believed that such effective venom against formicine ants is an important adaptation. Formicinae, in contrast to Myrmicinae, are very fast and agile. They can easily harm or even kill the spider (Schneider 1971). The attacked ant becomes aggressive and seeks the attacker but immediately after the attack, the spider retreats and waits at a distance (Pekár 2004). If the venom were less effective, the attacked ant could harm the spider or the ant could move away from the attack site and be lost to the spider. Moreover, our results suggest a certain degree of specialization in particular species. *Zodarion lutipes* may be specialized on formicine ants as it had the shortest latency to paralysis among the species studied. This species hunts and imitates *Camponotus* ants, which are very large, requiring effective venom. Also *T. sexoculatus* and *Z. cyrenaicum* both hunt the same ant species that they imitate. The former species imitates and feeds on *Monomorium* ants and the latter hunts and mimics *Messor* ants. *Zodarion cyrenaicum* was the slowest to attack of all the species studied. The explanation may lie in its specialization on myrmicine ants, which are slow moving. This is supported by recent observation when juvenile individuals of this species were seen in the vicinity of *Crematogaster nigriceps* Emery ants (Myrmicinae) (Lubin, pers. obs.). *Zodarion nitidum* was observed hunting *M. arenarius* in the field, however, it does not seem to be specialized on this species (having a long paralysis latency). Observations on ant feeding in *T. sexoculatus*

support Jocqué's (1991) hypothesis that all genera of Zodariinae are either myrmecophagous or termitophagous. Females of all the species studied were better at paralyzing ants than were juveniles or males. Since it was not possible to observe how much venom was discharged at every bite, we do not know whether this difference is due to more efficient biting or to injecting more venom. The females, being larger might have more venom, however, experiments by Cushing & Santangelo (2002) showed that the size of the spider did not influence the paralysis efficiency.

Records of predators of zodariid spiders are rare (Pekár & Král 2002). Ferton (1896) described a sphecid wasp, *Psen* (*Miscophus*) *bonifaciensis* that parasitized *Zodarion elegans* and *Z. nigriceps* (Simon 1873). For the first time, an ichneumonid parasitoid attacking *Zodarion* was recorded. Since these are the only records of parasitoids, we believe that the frequency of parasitism in *Zodarion* is very low. Batesian mimicry, nocturnal activity and anachoresis, i.e. the habit of hiding in retreats (Pekár & Král 2002) may explain this low parasitism rate. *Polysphincta* wasps attack many different spider species, mainly web-building spiders (Araneidae, Dictynidae, Linyphiidae, Tetragnathidae and Theridiidae) but also hunting species living in the vegetation (Clubionidae) and occasionally epigeal species (Lycosidae) (Rollard 1984).

Courtship and copulation in *Z. lutipes* was identical to that observed in other *Zodarion* spiders (Pekár & Král 2001). Although *Zodarion* females are able to copulate repeatedly (Gerhard 1928), it seems that after a certain period, shortly before producing an egg sac, they do not copulate again. However, another copulation was recorded after the first egg sac had hatched. The copulation time of *Z. lutipes* was rather short, similar to that observed for *Z. rubidum* (Pekár & Král 2001). Females of *Z. cyrenaicum* and *Z. nitidum* copulated before they were brought to the laboratory as they refused to mate but produced egg sacs. Like in the central European species *Z. germanicum*, females guard the egg sac inside the retreat until hatching. Fecundity in all three species is higher than that found for the central European species, a likely consequence of a larger body size. Simpson (1995) found that fecundity (clutch size) is a function of the female body size in spiders and the data on *Zo-*

darion species from Israel fit his model for cursorial spiders very well.

The karyotypes of only three zodariid species, *Storena indica* Tikader & Patel 1975 (Datta & Chatterjee 1983), *Zodarion germanicum* and *Z. rubidum* (Pekár & Král 2001), have been described. Diploid chromosome numbers of males range from 22–29. Chromosome morphology of *S. indica* was not described. In the karyotype of the latter two species acrocentric chromosomes predominate. *Storena indica* and *Z. rubidum* employ a sex chromosome system X_1X_20 that is thought to be an ancestral condition in spiders (White 1973). A derived sex chromosome system X0 in *Z. germanicum*, with the acrocentric chromosome X, probably originated by tandem fusion of chromosomes X_1 and X_2. The karyotypes of the three *Zodarion* species from Israel are quite similar to each other, differing however by the length of some chromosome pairs and the type of sex chromosome system. These karyotypes are similar to karyotypes of other zodariid spiders in terms of the diploid number, sex chromosome system and morphology of chromosomes. The acrocentric sex chromosome X in the X0 system found in *Z. lutipes* and *Z. nitidum* might have originated independently from the one in *Z. germanicum*.

ACKNOWLEDGMENTS

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