Feeding habits of the blackwidow spider *Latrodectus lilianae* (Araneae: Theridiidae) in an arid zone of south-east Spain

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Abstract

The diet of the blackwidow spider *Latrodectus lilianae* (Araneae: Theridiidae) was studied in an arid shrub-steppe of south-eastern Spain during 1990–93. For the first 3 years, prey mummies attached to spider webs were collected once the spiders' activity period was finished, at the end of September. In the fourth year, webs were marked and checked bi-weekly from April to September during the activity period of the blackwidow spider. We identified 2106 prey items from 164 webs. Most prey were Tenebrionidae and Oniscidae, which together represented from 65.4% to 82.0% in frequency and from 78.6% to 92.0% in biomass of all prey. An analysis of selectivity comparing prey availability from prey collected in pitfalls and those collected in the webs showed that spiders preferred Tenebrionidae and Oniscidae. However, an analysis of prey size reflects also that spiders mostly selected prey ranging from 12.5 to 22.5 mm long, suggesting that prey size, rather than taxon, determines prey capture. Other predatory arthropods, as well as five small lizards, were found as prey of the blackwidow spider. This suggests that the blackwidow spider may play an essential role in regulating the food web and trophic structure in this community by preying on other species that potentially compete with or prey upon blackwidow spiders.

Key words: blackwidow spider, *Latrodectus lilianae*, diet analysis, intraguild predation, vertebrate predation by arthropods, south-east Spain

INTRODUCTION

Predators are an important component of communities and are particularly common in habitats with low productivity, such as deserts. For instance, Seely & Louw (1980) found that carnivores represented 69% of the animal biomass in the Namib Desert dunes. Predatory arthropods play a key role in the structure of food webs in arid systems (Louw & Seely, 1982; Polis, 1991*a*,*b*,*c*; Polis & Yamashita, 1991), and are involved in a variety of direct and indirect interactions, including cannibalism and intraguild predation (Polis & McCormick, 1986; Polis, 1988). By combining the high importance of usual interactions with the occurrence of unusual ones, interspecific interactions are crucial as forces structuring the community and producing complex food webs in arid systems (Polis, 1991*a*). Diet studies are a critical first step to understand the complex relationships in a food web (Cohen *et al.*, 1993). Nevertheless, this role might be much more important when intraguild predation is involved, since the direct effects produced by predatory arthropods on herbivore–

detritivore populations may combine (by adding, subtracting, or compensating) with that of other predators.

Spiders are among the most common and best-studied predators in arthropod communities from arid habitats (Wise, 1984; Polis & McCormick, 1986; Polis & Yamashita, 1991). Several features characterize the role of spiders as predators, and give particular interest to their study. First, spiders differ from other predators in that they are not size limited, capturing prey with webs, which allow them to capture larger prey than similar (or larger) sized predators with which they share arid habitats, for instance lizards. Second, spiders are venomous, a factor which also helps them to prey on other predators and large-bodied prey (Polis & McCormick, 1986). Third, they can store prey in their webs, which again allows an increased profit from captures that might show a scattered distribution in time. These features represent important advantages in periods of food shortage, which is frequent in these harsh environments. Despite this apparent good fit of spiders to arid habitats, the general opinion is that they play a relatively minor role in food webs, since spiders usually cannot regulate the populations of their prey (Seely, 1985; Belovsky & Slade, 1993).

In this study, we investigated the feeding habits of the

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blackwidow spider *Latrodectus lilianae* (Melic, 2000) (Araneae, Theridiidae) in an arid region of south-east Spain. Prey remains are kept in the spider's web, which facilitates the assessment of diet composition. The diet of the blackwidow spider was compared with availability of potential prey to determine whether spiders prefer particular prey. This allowed us to explore the factors that influence prey capture, and to investigate the potential impact of blackwidow spiders on their prey.

METHODS

Natural history of *Latrodectus lilianae*

The blackwidow spider *L. lilianae* inhabits arid regions of south-east Spain. In the Guadix-Baza Basin, adult females (≈ 20 mm total body length) build their webs on low shrubs. The web consists of an inverted cone-shaped retreat (hereafter 'nest') and a platform of permanent, non-adhesive silk threads. The nest is usually located in a low shrub, 20–40 cm above ground. The platform of threads hangs downwards and is attached to the ground or the nearby vegetation. From this platform, the spider suspends highly adhesive hunting threads; these threads are spun at sunset and removed at sunrise. During nocturnal hunting, the spider waits at the centre of the platform, and when a prey is snared, it injects the prey with venom and then carries the body to the nest for feeding. The prey mummy is usually placed at the outer edge of the nest, but some mummies are discarded on the ground, at the farthest end of the silk (see Konigswald, Lubin & Ward (1990) and Lubin, Ellner & Kotzman (1993) for a detailed description of similar structures in other *Latrodectus* species, and Melic (2000) for *L. lilianae*).

In the Guadix-Baza Basin, spiders are active from April to September. Males are very small, and are found in the webs of females during the breeding period. Females produce egg sacs, which are placed inside the nests, between May and July. Spiderlings disperse during summer, and build small webs among the grass and weeds, where they feed mainly on ants (J. A. Hódar, pers. obs.). Many adults (and probably many spiderlings) die during July and August, the hottest and driest period of summer. The main predator of adult spiders in the area is the hoopoe *Upupa epops*, a bird that uses its long bill to open the upper end of the cone. Some spiders that survive the summer, hibernate by sealing the nest as a coccoon, but little is known about the overwintering strategies of adults and spiderlings.

Study area

The study was conducted at Barranco del Espartal (Baza, Granada, south-east Spain), a rambla (seasonal watercourse in a typical badlands landscape) with a substrate of silt with gypsum sediments. Although the annual average temperature is 14.4 °C, winters are very cold and summers are hot, with soil temperature ≥ 60 °C in summer (Castillo-Requena, 1989; Sánchez-Piñero & Gómez, 1995). Annual rainfall is *c.* 300 mm, but little remains in the soil, as potential evapotranspiration is 3 times the annual precipitation (Sierra *et al.*, 1990). A detailed description of the study area can be found elsewhere (see Sánchez-Piñero & Gómez, 1995; Hódar, Campos & Rosales, 1996). Spiders were studied on a 0.4-ha plot dominated by bare ground with some scattered shrubs of *Hammada articulata*, *Salsola vermiculata*, *Artemisia herba-alba* and *A. barrelieri*, all below 40 cm in average height.

Diet analysis

Abandoned blackwidow nests were collected at the end of September in 1990, 1991 and 1992, although the sampling was not exhaustive, so that, in these years the number of webs analysed was not related with the spider density. In 1993, all webs present on the plot were marked in April, at the beginning of the spiders activity period. Moreover, all the new webs which appeared during the study period were also marked. Prey remains in the marked webs were collected at the end of September, when the spiders abandoned their webs. Fortnightly censuses were established to monitor prey catches (by recording prey remains both in the web and on the nearby ground), as well as the abandonment of marked webs and the building of new ones. However, since spiders were not individually marked, it was impossible to detail if new webs that appeared during the study belonged to spiders which had abandoned already-marked webs (see Lubin, *et al.* (1993) for a detailed analysis of this phenomenon).

The difference in prey captures between 2 consecutive censuses was recognized as captures in this fortnight. At the end of the activity period, the web was collected and dissected in the laboratory. Prey were identified taxonomically (usually to species level) and measured (mm, total length) with a digital calliper. Prey biomass (mg, dry weight) was estimated using length–weight regression equations (Hódar, 1996). When only incomplete remains of a prey were found, both prey size and biomass were estimated using length–length and length–weight regression equations (Hódar, 1997).

Diet composition was computed separately for each year, and also monthly for 1993. The percentage of numeric frequency (percentage of items belonging to a prey class with respect to the total number of prey items) and biomass (percentage of biomass belonging to a prey class with respect to the total biomass of all prey items; Rosenberg & Cooper, 1990) were calculated.

Selectivity analysis

To assess whether spiders selected particular prey, prey availability was estimated in 1993 using 36 pitfall traps

(6.4 cm diameter), which were open for 48 h in each 2-week period between April and September. Pitfalls were collected every sunrise and sunset to distinguish diurnal and nocturnal prey. Capture rates in pitfall traps are strongly affected by arthropod activity and mobility, and therefore provide biased estimates of arthropod availability (but see Parmenter, MacMahon & Anderson, 1989; Cooper & Whitmore, 1990; Andersen, 1991). However, pitfalls were considered an adequate sampling of prey availability for black-widow spiders, since these spiders capture only active, ground-dwelling prey (Southwood, 1978; Cooper & Whitmore, 1990). Nevertheless, in order to achieve a better adjustment with diet data (Hutto, 1990; Wolda 1990), only nocturnal captures were used, and all arthropods with body length ≤ 2 mm (e.g. Acarina or Collembola) were ignored, because these small taxa are not captured by blackwidow spiders (Wolda, 1990). Also, to calculate selectivity indexes, a frequency of 1 prey/month was arbitrarily assigned to prey that were found in the diet but not in pitfalls (5 out of 42 cases). Selectivity was quantified using the W_i Savage's index, and significance of selection evaluated by χ^2 test (Manly, McDonald & Thomas, 1993), with *a posteriori* correction of significance by sequential Bonferroni procedure (Rice, 1989).

Lizard censuses

An interesting feature of the diet of *L. lilianae* was the capture of lizards by the spider. In order to assess the density and activity of lizards in the study site, a 975-m transect was marked, crossing the rambla. In 1993, lizard censuses were carried out bi-weekly between May and September. Censuses were conducted 6 times/day, every 2 h between sunrise and sunset. In each census, the species, the distance to the transect, and the snout–vent length (SVL) of each lizard observed was recorded. Accuracy in body-size estimates was checked whenever possible by direct capture of lizards. Nocturnal censuses for geckos resulted in few records.

Statistical analysis

Comparisons of diet composition between years (1990, 1991, 1992, 1993) or between months (in 1993) were made using *G* tests, whereas prey sizes were compared between years or between months with Kruskal–Wallis tests. Correlations between frequency of different prey groups in the diet and in pitfall traps was made by means of Spearman rank correlation. Non-parametric tests were applied because of the heteroscedasticity (Levene test) and non-normal distribution (Shapiro–Wilk test) of prey sizes (Zar, 1996). Whenever a test was performed more than once with the same model, a sequential Bonferroni adjustment (Rice, 1989) was made to correct probability values. Throughout the text, mean values are given as ± 1 SE.

RESULTS

General traits of the diet

An overview of the results obtained in the 4 years of study is shown in Table 1. The number of webs analysed and identified prey ranged between 14 and 202 in 1991 to 113 and 1267 in 1993, respectively. These differences are not surprising considering the higher sampling effort in 1993 with respect to the previous years. Diet composition differed significantly between years ($G = 184.8$, d.f. $= 18$, $P < 0.0001$, *G* test), but two taxa were always common, both in numeric frequency and in biomass: Tenebrionidae (especially *Pimelia* spp. and *Morica hybrida*) and woodlice (Oniscidae, *Oniscus asellus*), which together represented 65.4–82.0% in frequency and 78.6–92.0% in biomass. Predatory arthropods as scorpions *Buthus occitanus*, solpugids *Glubia dorsalis* and large Araneae (e.g. *Lycosa tarentula-fasciventris, Pachylomerus aedificatorius* and *Nemesia* sp.) were commonly captured, and one instance of cannibalism was also recorded.

In 1993, the number of active webs per month varied from 20 (September) to 59 (July), yielding estimated densities of 50–145 webs/ha for 1993 (assuming a uniform distribution of spider webs). The monthly comparisons of diet composition in 1993 (Table 2) showed a similar pattern to that found for the whole 4 years: there were significant differences in taxonomic composition of diet between months ($G = 106.4$, d.f. $= 20$, $P < 0.0001$, *G* test), but again Tenebrionidae and Oniscidae dominated in terms of numeric frequency (67.7–88.0%) and biomass (72–91.9%).

Capture rate of webs was highest in 1992 (20.5 ± 2.3 prey/web), and minimum in 1991 (8.5 ± 1.5, Table 1). Within 1993, the month with the highest capture rate was August (6.6 ± 0.8 prey/web), and the lowest April (2.5 ± 0.2; Table 2).

Prey sizes

The size of prey captured by *L. lilianae* ranged from the 3.7 mm length of a worker ant (*Messor bouvieri*, Formicidae) to the 50 mm length of a beetle (*Berberomeloe majalis*, Meloidae). Mean prey size differed among years ($Z = 133.85$, d.f. $= 3$, $P < 0.0001$, Kruskal–Wallis test), and the average prey size in webs varied from 14.7 ± 0.2 mm in 1992 to 17.1 ± 0.1 mm in 1993 (Table 1). In 1993, mean prey size varied significantly among months ($Z = 128.30$, d.f. $= 5$, $P < 0.0001$, Kruskal–Wallis test), ranging from 16.3 ± 0.4 mm in April to 17.5 ± 0.2 mm in August (Table 2).

Selectivity analysis

The single group showing a consistent positive and significant selection was Tenebrionidae, while Oniscidae and Arachnida were positively selected in July. In

Table 1. Taxonomic composition of the diet of the blackwidow spider *Latrodectus lilianae* at Barranco del Espartal during the 4 years of study. % N, numerical frequency; % B, biomass. Number of prey per web and mean prey length are expressed ± 1 SE

	1990		1991		1992		1993	
Groups	% N	% B	% N	% B	% N	% B	% N	% B
Araneae	8.9	12.0	8.7	10.0	2.0	1.3	5.6	3.7
Other Arachnida	2.5	1.7	5.5	6.2	1.8	1.1	3.1	4.1
Oniscidae	32.2	15.0	18.1	6.5	9.8	5.0	24.7	11.4
Tenebrionidae	38.6	63.6	47.2	72.2	69.1	86.9	57.3	74.0
Sepidium bidentatum Sol.	10.9	9.8	3.9	2.8	34.2	28.7	0.9	0.6
Pimelia spp.	15.8	27.7	17.3	23.1	19.1	30.2	31.9	38.5
Morica hybrida Charp.	2.0	4.8	14.2	27.6	6.7	13.1	10.5	16.8
Other	9.9	21.4	11.8	18.7	9.1	14.9	14.0	18.2
Other Coleoptera	9.4	5.9	5.5	2.4	8.4	4.3	6.3	4.5
Formicidae	2.0	0.1	8.7	0.6	5.8	0.4	0.2	0.1
Other Arthropoda	6.4	1.8	6.3	2.2	3.1	0.9	2.5	1.0
Reptiles	–	–	–	–	–	–	0.3	1.2
No. of webs	14		15		22		113	
No. of prey	202		187		450		1267	
No. of prey/web	14.4 ± 2.7		8.5 ± 1.5		20.5 ± 2.3		11.2 ± 0.6	
Mean prey length (mm)	16.1 ± 0.3		16.1 ± 0.5		14.7 ± 0.2		17.1 ± 0.1	

Table 2. Monthly taxonomic composition of the diet of the blackwidow spider *Latrodectus lilianae* at Barranco del Espartal in 1993. % N, numerical frequency; % B, biomass. Number of prey per web and mean prey length are expressed ± 1 SE

Months	April		May		June		July		August		Sept.	
Groups	% N	% B	% N	% B	% N	% B	% N	% B	% N	% B	% N	% B
Araneae	4.3	2.2	1.7	0.8	6.5	3.5	7.5	6.5	5.0	3.0	8.3	7.9
Other Arachnida	–	–	1.7	1.1	4.0	5.0	5.4	7.8	1.8	2.5	4.2	8.7
Oniscidae	13.7	4.4	10.9	4.0	21.0	9.6	31.6	15.7	31.5	14.7	28.1	16.6
Tenebrionidae imago	70.1	87.5	77.1	85.6	57.7	72.8	48.0	63.6	55.5	76.2	39.6	55.4
Scaurus spp.	–	–	3.4	2.6	4.4	3.8	4.4	4.3	3.3	2.9	5.2	6.3
Sepidium bidentatum	3.4	2.3	3.4	1.9	0.4	0.2	0.3	0.2	–	–	–	–
Pimelia spp.	38.5	44.8	53.1	58.3	31.5	36.8	27.6	36.0	25.8	30.3	20.8	30.1
Alphasida clementei	17.9	27.6	8.6	13.1	3.2	4.8	1.0	1.7	0.6	1.0	–	–
Morica hybrida	4.3	6.5	3.4	4.9	14.1	22.0	9.5	16.6	16.3	25.6	4.2	6.7
Others	6.0	6.3	5.1	4.8	4.0	5.1	5.1	4.7	9.5	16.5	9.4	12.3
Other Coleoptera	8.5	4.0	6.9	3.9	8.5	8.2	4.1	4.1	2.7	1.5	15.6	9.0
Formicidae	–	–	–	–	0.4	0.1	–	–	0.3	0.1	1.0	0.2
Other Arthropoda	3.4	1.9	0.6	0.1	2.0	0.9	3.1	0.9	3.0	1.3	3.1	2.2
Lacertidae	–	–	1.1	4.6	–	–	0.3	1.5	0.3	0.7	–	–
No. of webs	47		57		57		59		50		20	
No. of prey	117		175		248		301		330		96	
No. of prey/web/month	2.5 ± 0.2		3.1 ± 0.3		4.4 ± 0.3		5.1 ± 0.4		6.6 ± 0.8		4.8 ± 1.3	
Mean prey length (mm)	16.3 ± 0.4		16.7 ± 0.3		17.3 ± 0.3		17.3 ± 0.2		17.5 ± 0.2		16.4 ± 0.4	

contrast, Formicidae was consistently rejected throughout the study period (Fig. 1). On the other hand, the selectivity analysis by prey-size classes showed a clear selection for prey of intermediate sizes, which were positively selected throughout the 6 months of study (Fig. 2).

Predation upon vertebrates

In 1993 the capture of three small lizards and one gecko in the study plot was recorded (representing a 0.3% of the total spider captures this year; Table 1), as well as another lizard captured in a web outside the study plot. In May 1993, skeletal remains of two Spanish sand-racers (*Psammodromus hispanicus*, ≈ 38 and 40 mm SVL) were found firmly attached to the capture platform web. Due to the position of these prey, it was clear that the spider humped and attached the lizards to the web but, for some reason, the bodies were not carried to the nest. In the mummies, ants (*Tetramorium* sp. or *Crematogaster auberti*) were feeding on the last edible remains. In July 1993, a fresh carcass of a Moorish gecko *Tarentola mauritanica* (≈ 38 mm SVL) was found abandoned near the web on the ground, being eaten by ants. Also, in August 1993, a fresh carcass of a neonate fringed-toed lizard *Acanthodactylus erythrurus* (≈ 32 mm SVL) was found abandoned on the ground, near the web, again with ants scavenging on the lizard remains.
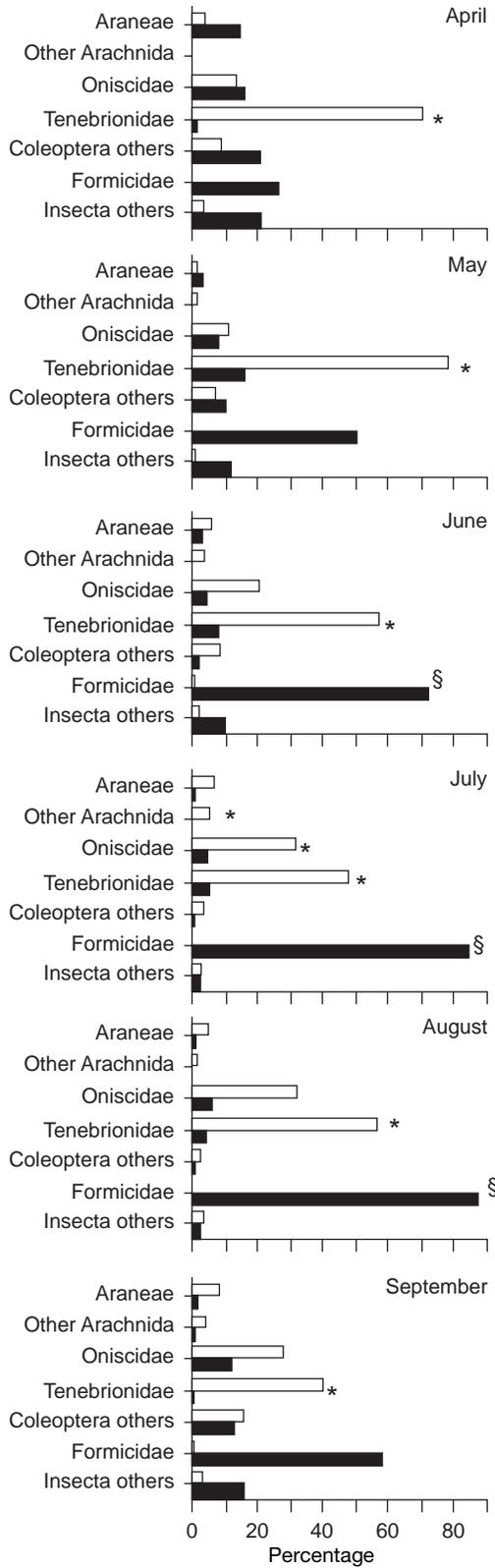
Fig. 1. Monthly selectivity for the different prey types found in the diet of the blackwidow spider *Latrodectus lilianae* in 1993. For each taxon: upper row (white), prey captured; lower row (black), potential prey availability. *, Significant positive selection, § significant rejection (*P* < 0.05, χ^2 test after Bonferroni correction).
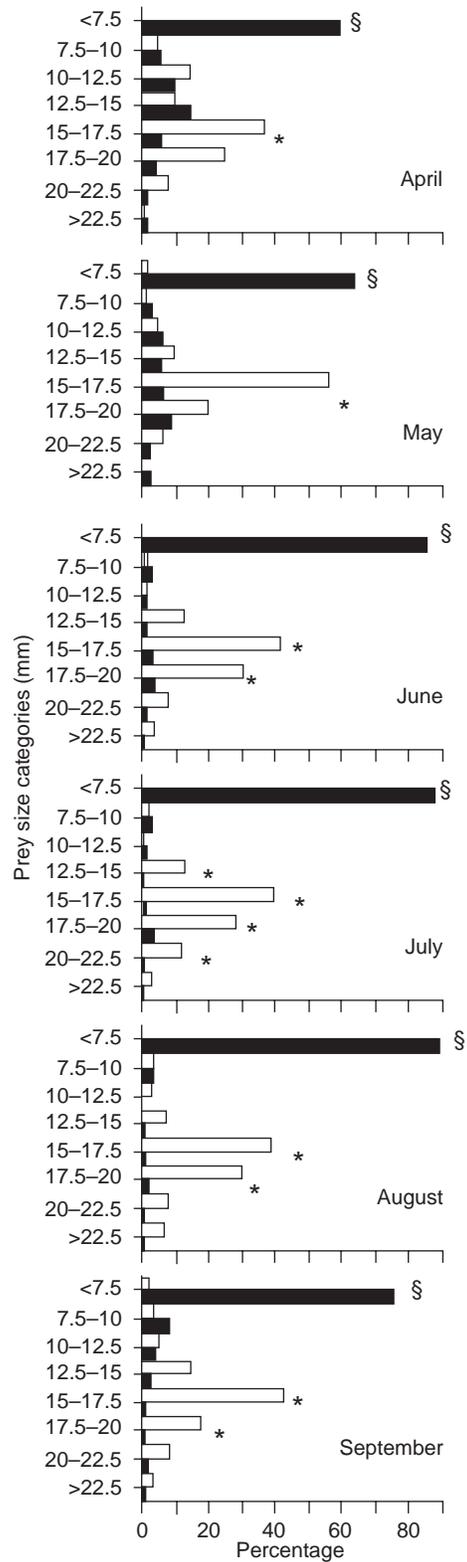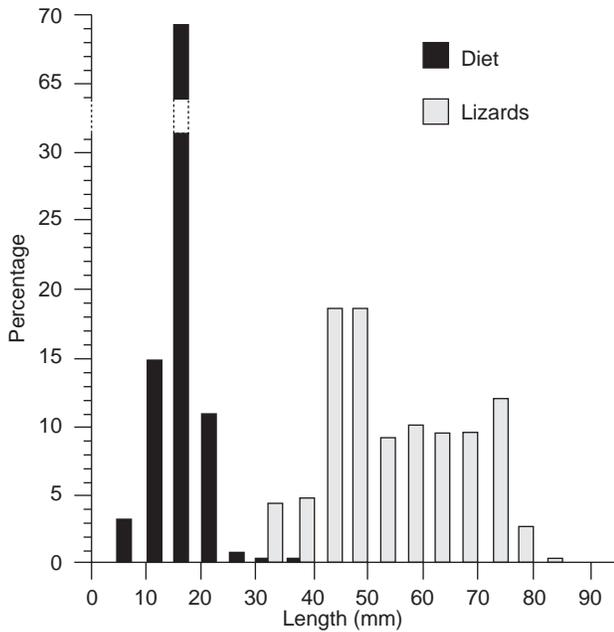
Fig. 2. Monthly selectivity for the different prey size categories found in the diet of the blackwidow spider *Latrodectus lilianae* in 1993. For each size category: upper row (white), prey captured; lower row (black), potential prey availability. *, Significant positive selection; §, significant rejection (*P* < 0.05, χ^2 test after Bonferroni correction).

Fig. 4. Mean size (snout–vent length, SVL) of active lizards at different times of the day at Barranco del Espartal in 1993.

Fig. 3. Frequency distribution (%) of *Latrodectus lilianae* prey size and lizard size (snout–vent length, SVL) at Barranco del Espartal in 1993. Note that there is little overlap between both frequency distributions.

The record registered outside the study plot was an Algerian sand-racer *Psammodromus algirus* (≈ 45 mm SVL). The prey was located still alive, captured by the hunting threads, early in the morning, but was not removed by the spider on this day. The following day, the lizard, now dead, was attached to the inner part of the nest, and the spider was feeding on it. On the third day, no remains of the lizard were found in either the web or on the ground nearby.

A total of 378 lizards was censused during the study period in 1993, with variable density between months and hours of the day. Since only four captures were recorded in the webs, it was not possible to establish any comparison between the two parameters. Most lizards were too large to be preyed upon by the spider, so there was little overlap between the size distributions of spider prey and lizards present in the study site (Fig. 3). Furthermore, it is interesting to note the size of active lizards in relation to the time of day (Fig. 4). Although no lizards except the Moorish gecko are strictly nocturnal, some temporal overlap may occur near sunrise or sunset, when active lizards are smaller in size than those present at midday (Fig. 4). Thus, these lizards may be vulnerable to blackwidow spiders.

DISCUSSION

Features of the diet

An effective venom and strong adhesive web allow blackwidow spiders to prey on animals larger than themselves (McCormick & Polis, 1982; Polis & McCor-
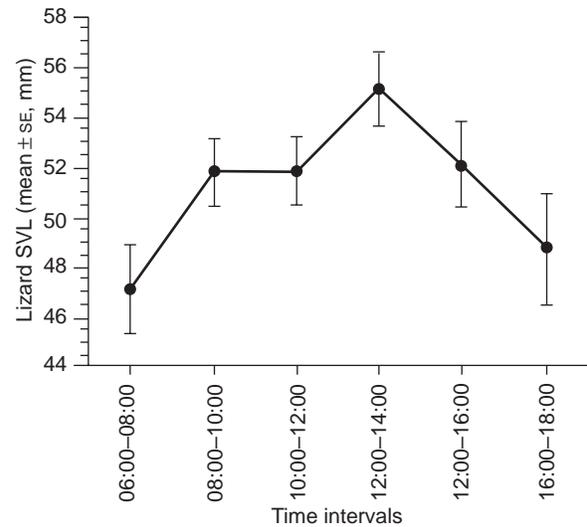
mick, 1986; Polis, 1988). Although both tenebrionid beetles and oniscid woodlice seemed to be significantly selected, and ants rejected, the selectivity analysis considering size classes suggests that size, rather than taxa, is the most important factor determining which animals are captured by the blackwidow spider. This seems obvious since the blackwidow spider does not actively select its prey: it has to wait for them to become snared by the hunting threads of the web. While a relatively small animal is able to walk through the threads without breaking the attachment of the hunting threads off the ground, an animal too large may destroy them, in both cases without being snared by the hunting threads. Therefore, most of the captures correspond to intermediate sizes (12.5–22.5 mm long; see Figs 2 & 3). Since both tenebrionid beetles and woodlice are usually in this size range, they are also selected when a taxonomic analysis of prey selection is performed.

As a consequence of the passive hunting device, the prey captured by the blackwidow spider (and, in turn, its diet) reflect changes in availability (McReynolds & Polis, 1987). While spring species, such as *Sepidium bidentatum*, *Elongasida rectipennis* and *Alphasida clementei* (Tenebrionidae), were caught only in the first months of the study, typically summer species such as *Morica hybrida* (Tenebrionidae) or *Oniscus asellus* (Oniscidae) have maximum capture in August. The beetles *Pimelia* spp. show a strong peak in May due to *P. monticola*, while most of the individuals caught during summer belong to *P. integra*. Similarly, most scorpions and solpugids were caught in the hottest months (Table 2). As summer advances, more groups of intermediate size are selected. This fact coincides with a higher capture rate and a maximum in beetle populations; however, the highest capture rate was obtained in August, a month in which beetle populations at the site show a sharp decline (Sánchez-Piñero & Gómez, 1995). This is a general pattern in other species living at

the Barranco del Espartal: for instance, the ocellated lizard *Lacerta lepida* shows a maximum consumption of tenebrionid beetles in August when it eats almost exclusively *Morica hybrida* (Hódar *et al.*, 1996).

Predation upon vertebrates

Even though spiders are nocturnal and lizards diurnal (except for the Moorish gecko), there is enough overlap in the activity periods of both *L. lilianae* and the lizards to allow some captures. Moreover, the smaller lizards are preferentially active close to dawn and sunset (Fig. 4), because their smaller body size enhances a better thermo-regulation at low solar heat intensities, and prevents activity in the hottest middle hours of the day. In fact, at midday in July and August, even large lizards like *Lacerta lepida* are not active or are sheltered in the shade of shrubs (Busack & Visnaw, 1989; Hódar *et al.*, 1996). Avoidance of cannibalism by larger lizards (J. A. Hódar, pers. obs.) may also be related with the circadian segrega-tion of activity depending on size (Polis, 1988). Consequently, the lizards active during the short periods that overlap with *L. lilianae* activity are small and, thus, can be captured by the hunting threads of the webs.

However, predation of blackwidow spiders on lizards might be more frequent than found. As stated above, the spider preferentially feeds protected inside its nest, but once it has eaten the prey, the carcass is placed on the outer side of the nest or, sometimes, is thrown away to the ground near the web. It seems that the spider selects which prey are attached to the nest and which ones are thrown away. No lizard was found in the nest, and from the five lizards captured by the spider that we were able to recognize, two of them were bone remains placed in the hunting platform not the nest; the remains of two other lizards were already on the ground; and the fifth disappeared in just 2 days without leaving any recognizable remains. These observations suggest that lizards are always thrown away from the web. Presum-ably, fresh lizard remains are easily located by ants, which can kleptoparasitize the spider web. Ants are sometimes able to reach the nest directly from shrubs and walk on the less sticky parts of the web (J. A. Hódar, pers. obs.). Consequently, prey that are attrac-tive to ants on the web (or the nest) may not be convenient for the spider, resulting in their quick rejec-tion after a short feeding time. This does not occur with most arthropod carcasses because they are dry once the spider has fed, and they do not attract ants. Therefore, our observations indicate that the number of lizards captured by *L. lilianae* may be higher than the number recorded throughout the study, but they were not found because of the periodicity of checking of the webs (once every 15 days). Although adequate for arthropod prey, this approach underestimates lizard captures in which the remains are quickly removed from the web and scavenged by ants. A more intense system of checking (every 2–3 days) would be necessary to prevent this possible source of error.

Role of the blackwidow spider as predator

The blackwidow spider plays a pre-eminent role as predator among the ground-dwelling arthropods at Barranco del Espartal, since no arthropod is free of predation by *L. lilianae*, unless too small to be caught in the trap. This place in the trophic structure of the community has two important consequences. First, the main prey are subjected to high rates of predation, at least in the zones in which the blackwidow spider is more abundant. At maximum density in July, there is an active web per 70 m^2 (145 webs/ha), and the web capture rate in this month is 5.1 ± 0.4 prey/web. This allows us to estimate that blackwidow spiders consume *c.* 24 arthropods/ha/night. The average beetle density on the ground per night is *c.* 349 ± 90 individuals/ha (Sánchez-Piñero, 1994; Sánchez-Piñero & Gómez, 1995). This suggests that, at least in the zones more densely popu-lated by spiders, prey would be depleted in only 15 days, assuming that all arthropods are active every night, which indicates the high predation rates caused by the spiders. However, we know that not all arthropods are active every night, but we do not know the proportion of animals in the population active in a single night. Polis *et al.* (1998) indicate that, in the Namib Desert, 4–5 days of continuous trapping are necessary to capture all the tenebrionid beetles in exclosures, which suggests that a minimum of 20–25% of beetles are active every night. In addition, our study plot shows a high density of spiders, while in other zones with more vegetation cover, higher vegetation, or which are more hilly, spider densities are much lower. This would allow a continuous recolonization of patches with high spider densities from those areas subjected to lower predation rates. Thus, these high predation spots would act as sink areas for arthropod populations.

Second, other predators of similar size and presum-ably similar diet to the blackwidow spider are also caught with certain frequency. Scorpions, solpugids, and large spiders (*Lycosa tarentula-fasciventris, Nemesia* sp., *Pachylomerus aedificatorius*) appeared in the diet, as also did spider-hunter wasps (*Batozonellus* sp.) and wolf flies (Asilidae). Intraguild predation often occurs in age/size structured populations of generalist predators (Polis, 1988): it is common that a species may eat a competitor that is at a younger stage of development and, consequently, is smaller. Juvenile blackwidow spiders are probably captured by a variety of other spiders and diverse invertebrate and vertebrate preda-tors, but they become relatively free of them once they are installed in the definitive web. Then, below the threshold limit imposed by the hunting threads of the web, prey size seems to be relatively unimportant: the blackwidow spider is able to capture scorpions 25 mm in prosoma length or wolf spiders 27 mm in total length, which are rather large prey. However, the advantage of eating potential competitors implies some risks: the blackwidow spider may itself be killed by the prey, and in fact this does sometimes occur. For instance, we recorded a dead blackwidow spider on the ground

below its hunting web, on which a dying wolf spider had been captured and partially covered with silk.

In conclusion, diet and selectivity analysis show three main features of the prey of the blackwidow spider: the prey are almost exclusively ground-dwelling animals, preferentially with nocturnal activity (coinciding with the spider activity), and of a size of 12.5–20 mm. This kind of prey is quite well exemplified by flightless tenebrionid beetles and woodlice, the staple food for the blackwidow spider. Another important factor is that some of the prey are also predators, potential competitors or even direct predators of *L. lilianae*. This is a well-known feature of predatory arthropods in other arid regions (e.g. Seely & Louw, 1980; Polis & McCormick, 1986; Polis & Yamashita, 1991), and suggests that blackwidow spiders may play an essential role in regulating the food web and trophic structure of the harsh environments which they inhabit.

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