Observations on the natural history and ecology of the wolf spider *Hogna carolinensis* (Walckenaer) (Araneae, Lycosidae) in the northern Chihuahuan Desert

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Summary

Hogna carolinensis (Walckenaer) (Araneae: Lycosidae) is a large wolf spider found throughout the USA. This research was undertaken in order to study various aspects of the natural history and ecology of this species in the northern Chihuahuan Desert. The study site was located in Big Bend National Park (Brewster Co., Texas). Both males and females were strongly nocturnal in their diel periodicities during the summer months. No spiders were active at the surface from the beginning of November through February. Only 6% of the adults observed were associated with a burrow at this site. Seventeen percent were located on the surface away from any observable burrow, and 77% were found under rocks or surface debris (decaying vegetation), or within rock crevices. The mean home range for these spiders was $0.91 \pm 0.05 \text{ m}^2$ for males, and $1.34\pm0.02\ m^2$ for females. The burrows were distributed randomly in this area but at a uniform distance from plants. and no active burrows were found to have overlapping home ranges. Males and females fed on a variety of arthropod prey including beetles (25 and 22.7%), orthopterans (13.8 and 27.2%), sand cockroaches (5.5 and 9.1%) and spiders (13.5 and 0%), respectively. Clutch size (the number of eggs per egg sac) ranged from 89-103. Agonistic interactions between females consisted of foreleg contact followed in some cases by flight or escalation consisting of foreleg extension, cheliceral spreading, and attack. Possible agonistic interactions between males were not observed during the course of this study. The courtship behaviour of this spider is also discussed.

Introduction

Hogna carolinensis (Walckenaer) is found throughout the United States (Gertsch, 1979). It is one of the largest members of the genus *Hogna*, with adult males and females ranging in length from 18–20 mm and 22– 35 mm, respectively (Kaston, 1953). Like most lycosids, *H. carolinensis* feeds on a wide variety of arthropod prey and typically hunts at night, although it has also been observed moving about during daylight hours (Kaston, 1981). Juveniles and adults can be found wandering over the surface as well as beneath stones or in shallow burrows usually topped with turrets of silk, leaves, and grasses. Males generally live for only one year, but females may live for up to 3 years (Farley & Shear, 1973).

Most of the observations concerning the natural history and ecology of *H. carolinensis* have been conducted on animals from mesic habitats (Gertsch, 1979; Kaston, 1981). There is a paucity of information available on this lycosid from desert regions, which are characterised by harsh and more stressful conditions (Punzo, 1998, 2000). Shook (1978) reported on the burrowing activities, seasonal activities, and home range movements in a population of *H. carolinensis* (sub *Lycosa carolinensis*) from the Lower Sonoran Desert of Arizona. The present study provides, for the first time, data on the natural history and behavioural ecology of *H. carolinensis* from Big Bend National Park (Brewster Co., TX).

Material and methods

Big Bend National Park (BBNP) lies within the northern region of the Chihuahuan Desert in the Trans-Pecos region of west Texas. The climate in this region can range from semi-arid to arid (Wauer, 1980). Within the park, annual rainfall is typically between 16.8–31.4 cm, depending on location and altitude, with 60–80% occurring from May through October (Medellín-Leal, 1982). Mean monthly air temperatures can range from 5.5°C (January) to 32.8°C (July), with low and high air temperatures of 3.7 and 46.1°C, respectively, depending on elevation (U.S. Dept. of Interior, 2000).

There is a wide range of topographic diversity within BBNP, ranging from limestone deposits with internally draining basins, gypsum formations, and igneous rock, which provide a variety of substrates including mountain ridges, slopes, canyons, alluvial fans, fine-textured basins, gypsum flats, salt playas, silaceous and gypsum dunes, freshwater seeps, and springs (Maxwell *et al.*, 1967; Medellín-Leal, 1982). BBNP is bordered on the south-east and south-west by the Rio Grande River. The vegetative zones of BBNP have been described in detail by Tinkam (1948).

The study site was a circular plot with a radius of 0.8 km surrounding the entrance of Santa Eleña Canyon (29°11'N, 103°45'W) at an elevation of 857 m. The dominant vegetation consisted of creosote bush (*Larrea divaricata*), mesquite (*Prosopis glandulosa*), sage (*Franseria deltoidea*), sotol (*Dasylirion leiophyllum*), tarbrush (*Flourensia cernua*), prickly pear cactus (*Opuntia engelmannii*), and scattered clumps of grasses including chino gramma (*Bouteloua breviseta*) and fluffgrass (*Erioneuron pulchellum*). The soils at this site were predominantly a mixture of sand, gravel, and adobe.

Collections and observations occurred from May through October 1999. Hogna carolinensis occurs throughout this area. Adult females may construct burrows, and some were collected from or near the burrow entrance during evening hours. They were also collected manually on the surface of the ground using a black light in the same way that I collected other nocturnal arthropods from this site (Punzo, 2001), or by using pitfall traps as described by Punzo & Henderson (1999). Burrows containing spiders were marked for future reference and to ascertain site fidelity. The following data were recorded for each spider within 5 hr after collection: time (Central Standard Time) and location of capture, size, weight, and sex (for adults). Carapace width and length were used to determine size because these measurements are among the most reliable morphometric indices for age/size determinations (Dondale, 1961). Weights were measured using a portable Metler electronic analytical balance.

A total of 24 active burrows were located during this study. Other adult spiders were found on the surface of

the ground (without any observable burrow in the vicinity), under rocks or surface debris associated with decaying vegetation, or within rock crevices. Because immature spiders were observed infrequently (n=12), only data on adults were included in statistical analyses.

Soil and air temperatures were recorded with a Li-Cor Model 1400 digital thermometer, and a VSI Model 170 hygrometer was used to record relative humidity (Forestry Suppliers, Inc., Jackson, MS). Light intensity was measured using a Li-Cor Model 250 light meter equipped with a scale that displayed light intensity in lux and footcandles (10.76 lux=1 footcandle). Overhead sky light intensity was used because this is what a spider would have been exposed to when looking upward from a burrow entrance.

If a spider had a prey item in its chelicerae, the prey was removed and placed in 70% ethanol for subsequent identification and diet composition analyses. I also collected egg sacs from females that had them (n=24) and maintained them in ventilated plastic containers placed inside insulated cooler boxes ($1.0 \times 0.5 \times 0.5$ m) at 26 ± 2 °C and 68-72% relative humidity, until the spiderlings emerged, in order to determine clutch size and gestation period. Data on time of capture were used to determine diel and seasonal patterns of activity. I also recorded all observations stemming from those situations in which I observed interactions between adults, including agonistic interactions and mating activities.

Throughout the study, daily visits were made at 2-hr intervals throughout the day and night to each active burrow that had been located, numbered, and marked with a plastic tent peg (n=24). The distribution of plants and the topography of the ground around each burrow were recorded. At each burrow I marked the position of the spider relative to the burrow entrance. At the end of the study period I pooled and plotted weekly data on locations of spiders on 1-mm grid graph paper in order to represent the positions of spiders around their burrows. The outermost points of this distribution were connected by a straight line, thereby forming a polygon with the least area. The area of the polygon was used to represent the minimal home range of the spiders. I used a planimeter to determine the home range to the nearest 0.1 m^2 as described by Shook (1978).

Data were also collected on the width of the burrow entrance, height and composition of the turret, presence of tumulus debris, and the distance away and species of the plant nearest to the burrow. All observations near burrows at night were conducted using red light to minimise disturbance to spiders.

All statistical analyses followed procedures described by Sokal & Rohlf (1995).

Results and discussion

Daily and seasonal activity patterns

Data on the time of day, surface temperature, relative humidity, overhead light intensity, and minutes after sunset when spiders were observed at the entrance of representative burrows are shown in Table 1. Data for all burrows during summer months (21 June–10 September) showed that spiders were first observed at the burrow entrance between 21–109 min after sunset when surface temperatures ranged from 23.7–27.8 °C.

Date	Burrow number	Time	Temperature °C	Relative humidity (%)	Overhead light intensity (lux)	Minutes after sunset
5 May	1	1900	18.4	39.2	169	38
	4	1900	17.8	38.8	172	51
	1	2100	17.3	39.5	1	ND
	10	2100	17.1	40.1	0	52
	12	2100	16.9	39.1	0	67
	4	2300	17.1	38.3	0	ND
	7	2300	17.4	37.7	0	81
	2	0200	16.7	29.3	0	108
	9	0200	17.1	35.9	0	ND
	1	0400	16.4	36.1	0	ND
	4	0400	17.1	37.2	0	ND
	5	0600	16.6	38.2	6	ND
	12	0600	17.3	37.7	5	ND
20 May	1	1900	18.5	39.5	0	44
	4	1900	18.6	39.1	0	ND
	7	2100	21.3	26.6	7	81
	9	2100	22.1	27.3	7	59
20 I	10	0200	23.2	31.6	0	ND
20 June	2	2100	24.7	40.7	25	34
	5	2100	25.1	38.8	21	50
20 Jh.	2	0200	24.1	39.7	0	ND
20 July	1	1900	28.7	66.6	458	ND
	1	2100	27.7	64.2	45	44
	6	2100	26.6	66.4	50	63
	3	0200	25.8	64.6	43	ND
	8	0200	26.4	65.5	39	ND
20 August	1	2100	30.2	47.4	378	97
	3	2100	31.1	51.1	391	109
	8	2100	29.9	54.6	401	85
	1 12	0200 0200	28.5 29.2	51.7 48.3	0 0	ND ND
	5	0600	25.3	47.6	188	ND
10 Septembe	r 3	2100	29.4	49.9	298	63
	9	2100	28.7	52.3	311	78
	12	2100	30.1	46.6	307	54
	7	0200	28.8	47.5	0	ND
	11	0200	28.2	49.7	0	ND
	1	0600	24.4	44.7	173	ND
	5	0600	25.1	45.9	166	ND

Table 1: Data on representative burrows of *Hogna carolinensis* from the Chihuahuan Desert collected during 1999. Data include date, burrow number, time of day (Central Standard Time), surface temperature (°C), relative humidity (RH, %), overhead light intensity (lux), and time (min) after sunset at which a spider was observed at the burrow entrance. No spiders were observed on the surface or at the burrow entrance between 0350–1950 during the months of November through March at this site. ND=no spider detected at burrow entrance.

Maximum daily surface temperatures during the summer ranged from 49-62°C, depending on plant cover, and no spiders were observed at the surface during these periods. Because so few juveniles were observed during this study, only data on adults are described and used in statistical analyses. Surface activity was defined as any time a spider was observed on the ground surface away from or outside a burrow. These spiders were strongly nocturnal in their diel activity patterns at this time of the year, although some diurnal activity was observed during the early spring when surface temperatures were more moderate (21-31°C) (Table 2). A G-statistic showed no significant difference between the activity patterns of males and females (p > 0.50). From March through October most surface activity occurred between 2000-2400hr, and no spiders were observed at the surface from the beginning of November through February at this site. This is not surprising because wolf spiders are known to enter a state of torpor during winter months (Edgar, 1971; Marshall & Rypstra, 1999).

Twenty-four out of 96 adults (25%) observed at the surface were found to be associated with a burrow at this site. Thus, even in an area characterised by harsh desert conditions, most of these adult lycosids were not associated with a burrow when they were initially observed. This is in marked contrast to a population of *H. carolinensis* from Arizona where most of the adults were associated with burrows (Shook, 1978). In the present study, 72 adults (43 males; 29 females) were located on the surface of the ground without any observable burrow in the vicinity, and another 320 adults (148 males; 172 females) were found under rocks or surface debris associated with decaying vegetation, or within rock crevices, giving a total of 416 spiders.

Only 12 juveniles were found during this study, and all of them were located under rocks. It is difficult to explain why so few juveniles were encountered at this site. At a site near Guadalupe, Arizona, the percentage of juveniles collected ranged from 28% (June) to 91% (October) of the total number of spiders sampled (Shook, 1978). I have observed larger numbers of juveniles during the months of May (21%) and September (33%) at other sites in BBNP (unpubl. data).

Home range

Based on data collected from spiders associated with burrows, the mean home range for *H. carolinensis* at this site was $0.91 \text{ m}^2 \pm 0.05 \text{ SD}$ for males (n=4) and $1.34 \text{ m}^2 \pm 0.02$ for females (n=20) (t=0.82, p>0.5). Shook (1978) reported a mean home range of 0.8 m^2 (males) and 1.2 m^2 (females) for a population of *H. carolinensis* from the Sonoran Desert. Studies on home ranges for other species of wolf spiders have reported values ranging from $0.6-12.1 \text{ m}^2$ (Kuenzler, 1958; Chew, 1961; Nyffeler & Benz, 1988).

The contour of the home range was compared with topographical features and plant distribution, and no clear correlation was found. In some cases, home range boundaries were associated with a distinct change in topographical relief (e.g. when the home range

Time of day	Percent activity										
	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.			
0400-0559	0	0	5	2	7	4	0	0			
0600-0759	0	0	0	8	5	7	3	8			
0800-0959	0	4	5	0	0	0	0	5			
1000-1159	4	8	2	0	0	0	0	2			
1200-1359	6	2	0	0	0	0	0	2			
1400-1559	7	4	0	0	0	0	0	2			
1600-1759	9	14	0	4	0	0	3	8			
1800-1959	11	9	11	9	6	3	5	5			
2000-2159	38	32	25	35	43	52	37	24			
2200-2359	20	14	34	31	26	30	39	33			
2400-0159	5	9	12	4	8	4	8	3			
0200-0359	0	4	6	7	5	0	5	8			

Table 2: Diel periodicity during those months when Hogna carolin-
ensis was active on the surface. Data expressed as the
percentage of the total number of adult spiders (males and
females pooled) observed. No significant difference was
found between the activity patterns of males and females.
No surface activity was observed from November through
February. See text for details.

boundary came into contact with arroyos, stream beds, or clumps of grasses or bushes).

The statistical distribution of distances from the burrow entrances to the nearest plants (measured to the nearest 0.5 m) was compared to a Poisson distribution. The results showed that the burrows of H. carolinensis did not occur in a random pattern from plants (p < 0.05) but were uniformly distributed. However, when random points were chosen and the distance to the nearest spider burrow recorded, the sum of the ratio of these squared distances divided by the sample size yielded an index of distribution (A), as originally described by Holgate (1965). An A-value of 0.5 indicates random distribution; A>0.5 indicates clumped distribution. I obtained an A-value of 0.48 at this study site. Combining the results of the two tests suggests that these lycosid burrows were distributed randomly throughout this area, but at a uniform distance from plants.

It should also be pointed out that no active burrows were found to have overlapping home ranges. This may be the result of the cannibalistic tendencies of these spiders. Thus, the maximum wandering distance of spiders from their nearest neighbour was always less than the interspider burrow distance. This is in general agreement with the results reported for another population of *H. carolinensis* (Shook, 1978) and from another site within BBNP (Tuff Canyon) which is located about 10.9 km south-east of Santa Eleña Canyon (Punzo, unpubl. data).

Diet composition, hunting behaviour, and predators

Fifty-eight out of 416 spiders (13.9%) were found to have prey items in their chelicerae when first observed. The diet composition for these spiders is shown in Fig. 1. The results indicate that these spiders are generalist predators and feed on a variety of arthropod prey. For males, 52.3% of the prey items consisted of beetles, orthopterans, and spiders. Almost 50% of the prey items for females consisted of beetles and orthopterans. The 402

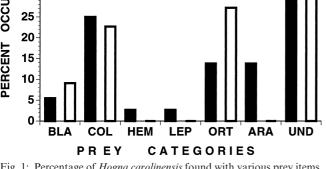


Fig. 1: Percentage of Hogna carolinensis found with various prey items in their chelicerae. Solid bars represent data for males (n=36), open bars for females (n=22). BLA (Blattaria: sand cockroaches); COL (Coleoptera); HEM (Hemiptera); LEP (Lepidoptera: caterpillars and adults); ORT (Orthoptera: grasshoppers, locusts, katydids); ARA (Arachnida: spiders); UND (prey items undetermined due to advanced stage of digestion).

majority of beetles captured were carabids. Although no females were observed feeding on other arachnids, spiders were found in the chelicerae of 13.5% of the males. None of the spiders at this site was found with vertebrate prey, although I have observed adult females of H. carolinensis feeding on juveniles of the Texas Banded Gecko (Coleonyx brevis) at other locations in BBNP (unpubl. data).

Most of the adult males and females associated with burrows awaited the approach of prey within the entrance of the burrow or within 2-8 cm of the burrow entrance. When a prey species moved within 1.5 cm of the burrow entrance, it was seized and carried into the burrow. Spiders outside the burrow seized prey and began feeding for 3-24 min before returning to the burrow. These spiders responded to strong ground vibrations (such as foot tapping) by retreating into the burrow. Spiders typically responded to ground vibrations caused by a tuning fork (256 Hz, placed within 1-3 cm of the spider) by orienting their bodies toward the vibration. Many web-building and cursorial wandering spiders are known to respond to vibrations in the detection of prey (Foelix, 1996; Punzo, 2000).

On one occasion, a column of numerous worker and soldier ants of the genus Pheidole was observed approaching burrow no. 13, located in a dry stream bed near a clump of grasses and several small rocks. An adult female wolf spider was located on the surface, 15 cm from the burrow entrance. Several ants made contact with the pedipalps of the spider at 1745hr. The spider immediately retreated into the burrow. The ant column made contact with the lip of the burrow at 1810hr and some workers began to enter the burrow at 1822hr. At 1835hr additional workers and soldiers began to enter the burrow. I returned at 0830hr the next morning and after excavating the burrow no spider was found. This suggests that some ants may evict spiders from their burrows or prey on wolf spiders. This may represent a significant potential source of mortality for desert lycosids since predatory ant species are well represented in desert regions (Cloudsley-Thompson, 1965; Punzo, 2000).

Other potential predators upon wolf spiders that occur in this area, and that have been reported to feed on large spiders in other desert regions, include large arthropods (Punzo, 1998, 2000) such as wasps, scorpions, solifugids, and theraphosid spiders, as well as road runners, coyotes, and several species of owls (Cloudsley-Thompson, 1991).

Agonistic interactions and mating activity

Observations were made on the agonistic interactions between females on nine occasions. Possible agonistic interactions between males were not observed during the course of this study. In cases where females were not associated with a burrow (n=2), they approached one another and then remained motionless for 6-22 s after their forelegs made contact, before running away. In some cases (n=4), when resident females sitting near their burrow entrance made foreleg contact with an intruding female, they exhibited palpal drumming, foreleg extension, and spreading of the chelicerae before the intruder ran off. In three other instances, the intruder was attacked and killed by the resident female.

I observed mating activity on four occasions during this study. In all cases, the male approached to within 3 cm of the palps of the female and began to rub the surface of the ground with his palps. This stage preceding male courtship display in lycosids has been referred to as chemo-exploration (Hebets et al., 1996). An initial anterior vertical extension of the first legs by the male immediately after contact with a female was reported by Farley & Shear (1973) for L. carolinensis from West Virginia. This was not observed in the males from BBNP. The chemo-exploration phase was followed by several bouts of palpal drumming (male rapidly lifts and lowers the palps) and palpal stridulation, interrupted by brief periods (4-12 s) of rest. This was followed by extended leg taps by the male, when the right or left foreleg was lifted, extended and lowered, resulting in a tapping on the substrate. The females remained motionless during these male activities. Leg-tapping was followed by push-up displays (male lowers his body to the substrate, displays palpal drumming and palpal stridulation, and then lifts the entire body up on the tips of his legs). No obvious vibration of the abdomen was observed as described by Farley & Shear (1973).

In response to push-ups by the male, the female approached the male, orienting her face toward his, and typically elevated legs I and II on one side of her body with a slight bend at the joint of the femur and patella; this has been referred to as "arching" (Stratton, 1985). In this pre-mounting position, the female is ready to engage in copulation with the male. During copulation the male inserted a palp several times on each side of the female, followed by haematodochal expansion. The female typically rotated her abdomen in a lateral fashion, which presumably facilitates contact between the male genital bulb and her epigynum (Hebets *et al.*, 1996). Following copulation, the males rapidly withdrew from the female and moved away.

Morphometric and reproductive parameters

For adult males, the carapace length and width ranged from 9.1–13.1 mm (mean 11.2 ± 0.11 SD) and 4.9–6.7 mm (5.5 ± 0.08), respectively; concomitant values were 9.9–15.4 mm (mean 13.4 ± 0.18) and 5.1–7.4 (6.7 ± 0.11) for females.

Thirty percent of all males observed on the surface were encountered during the month of June, whereas the highest percentage of females (37.7%) was encountered in July. Twenty-four females were observed carrying egg sacs between 21 June and 27 August. Females with young on their backs (n=13) were observed between 9 July and 16 October.

Because females were not marked, I do not know whether any females carried more than one egg sac at different times of the year at this site. However, Shook (1978) reported one female at his study site in Arizona that produced one egg sac on 25 July from which young emerged, and another on 24 August, although he was unable to determine if the second egg sac was fertile. The production of multiple broods has been reported for other species of lycosids (Gertsch, 1979; Kaston, 1981; Foelix, 1996).

Egg sacs ranged in weight from 0.78-1.11 g (mean 0.89 ± 0.02 g). The relationship between clutch size (number of eggs per egg sac) and carapace length is shown in Fig. 2. The clutch size ranged from 89–193 with a mean of 137.4 ± 28.8 SD. This is similar to those values reported for *H. carolinensis* from Arizona (mean 149; range 112–180) (Shook, 1978).

Some females with egg sacs, that were also associated with a burrow, were observed sitting at the entrance to the burrow with their abdomen and attached egg sac exposed to the night air and to sunlight during the day. This is consistent with observations on a number of lycosid species showing that females often "sun" their

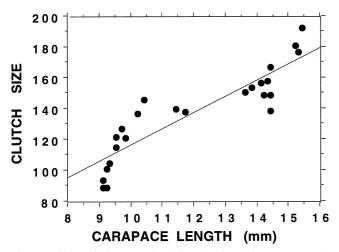


Fig. 2: Relationship between clutch size (number of eggs per egg sac) and carapace length (in mm) for adult females of *Hogna* carolinensis from the Chihuahuan Desert (n=24). Regression equation: y=11.847+10.497; r²=0.801.

eggs during the warmer parts of the day (Gertsch, 1979; Punzo & Ludwig, 2002), which presumably hastens development. It has also been suggested that the higher relative humidities (RH) typically associated with deeper burrow depths in desert regions (55–70% RH at a depth of 20-25 cm; Hadley, 1970; Punzo, 2000) are more conducive to the growth of fungi that may kill developing embryos (Shook, 1978). By the female's moving the egg sac to the burrow entrance, humidity is markedly decreased, which may thus increase fitness. The average burrow depth at this site was 27.8 ± 4.9 cm (*n*=11), with a range of 21-34 cm. The shape of the burrows varied from straight vertical tubes to vertical tunnels with numerous bends, most probably associated with soil penetrability and the presence of large rocks. The RH at the burrow entrance during the day (1000-1600hr) ranged from 16.2-23.8% during May and June, months usually devoid of rainfall. At depths of 22-30 cm, RH values increased up to 71% during the summer months. Thus, the microenvironment at the burrow entrance is markedly drier than that found deep within the burrow. At night, however, RH values could increase markedly (Table 1).

In summary, wolf spiders (Lycosidae) are a common representative of the arachnid fauna in desert regions of the USA. With respect to *H. carolinensis*, there is a strong tendency toward nocturnal diel periodicity, especially during summer months. Like many other lycosids, these spiders feed on a variety of arthropods. There appears to be some degree of geographical variation in seasonal activity patterns, clutch size, the size of the home range, and frequency of burrow construction. They are also territorial and engage in well-defined agonistic interactions with conspecifics that can, in some cases, culminate in fighting and death. The territorial behaviour of these spiders may to some degree account for the observation that home ranges did not overlap. Some aspects of courtship behaviour in H. carolinensis in the present study differed from those described by Farley & Shear (1973) for a population of conspecifics from West Virginia. Future studies should focus on growth rates, age and size at maturity, longevity, dispersal distance of spiderlings, survivorship as a function of age cohort, age class distribution, and the frequency with which these spiders produce multiple clutches. Data on some of these parameters could be used to construct accurate life tables for this species.

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