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The web of the acacia orb-spider *Eustala illicita* (Araneae: Araneidae) with notes on its natural history

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Abstract. A great number of spiders build orb-webs and although the overall structure is the result of fixed behavioral patterns, much small-scale inter- and intraspecific variation is nonetheless evident. Thus in order to fully understand the orb-web and web-building behavior in these spiders, we need to study substantial samples of many different species of orb-weavers. However, to date only a few species have been rigorously studied both in the field and in the laboratory. Here, we investigate the ecology, behavior and orb-web of the neotropical spider *Eustala illicita* (O. Pickard-Cambridge 1889) and suggest it as suitable for further studies based on 1) the ease at which it can be located in abundant numbers in the field, 2) its willingness to build webs in the laboratory, 3) the plasticity of its behavior, and 4) its interesting ecology in the form of interactions with the swollen-thorn acacias and their ant mutualists. Here, we introduce its natural history and then provide a detailed description of orb-webs built in the field and in the laboratory, which we compare to other orb-spiders.

Keywords: Orb-web, tropical spider, swollen-thorn acacias, web parameters

Spider webs provide accurate information on the evolution, plasticity and development of behavior, since they are in effect physical remains of behavior that is 'frozen in time' (Vollrath & Selden 2007). Although the web serves other functions such as a substrate for communication via web-borne vibrations (Landolfa & Barth 1996; Watanabe 2000), and as protection from predators (Chou et al. 2005), the main function of the spider web is to intercept and retain prey (Eberhard 1986; Blackledge & Eliason 2007). Thus web-building behavior is in effect a foraging behavior that is performed hours or days before actual prey capture (Higgins & Buskirk 1992).

Orb-webs are particularly good models for the study of behavior, since they are complex, while simultaneously being highly ordered with a two-dimensional structure that makes them readily quantifiable and thus suitable for both field and laboratory studies (Zschokke & Herberstein 2005). The orb-web evolved more than 120 million years ago together with the spider's predominant prey, holometabolous insects (Peñalver et al. 2006). It is still a highly successful foraging strategy, which can be found in more than 4,000 species from 7 families (Platnick 2009). Orb-spiders modify their behavior, expressed in their web design, in response to a wide range of internal and external factors, including spider size and age (Mayer 1952), nutritional state (Crews & Opell 2006), silk supply (Eberhard 1988), recent prey experiences (Venner et al. 2000), climatic factors (Vollrath et al. 1997) and the spatial layout of the web-building site (Vollrath et al. 1997; Harmer & Herberstein 2009).

The stereotyped web-building behavior is expressed even when the spiders are missing one or several legs (Vollrath 1987), exposed to drugs and pesticides (Samu & Vollrath 1992; Hesselberg & Vollrath, 2004), or in the absence of gravity (Witt et al. 1977). It is therefore not surprising that many aspects of behavior, ecology, structural and material properties of the orb-web have been and still are the focus of numerous studies. However, it is surprising that only a relatively limited number of species has been the subject of both field and laboratory studies (Zschokke & Herberstein 2005). Some of the most studied spiders include the palearctic *Uloborus walckenaerius* (Latreille 1806), the large *Nephila clavipes* (Linnaeus 1767) from tropical and subtropical America, the neotropical *Argiope argentata* (Fabricius 1775), the cosmopolitan *Argiope trifasciata* (Forsskål 1775), the Australian *Argiope keyserlingi* (Karsch 1878), the holarctic *Zygiella x-notata* (Clerck 1757) and finally the most studied orb-weaver of them all, the holarctic *Araneus diadematus* (Clerck 1757) (Eberhard 1982; Zschokke & Vollrath 1995; Kuntner et al. 2008).

The limited number of species used can partly be ascribed to the fact that many orb-weavers do not build webs reliably in the laboratory (Zschokke & Herberstein 2005; T. Hesselberg unpubl. observ.), but is probably also the consequence of some conservatism in species choice among arachnologists. In order to fully understand web-building in orb-spiders, it is, however, important to analyse the diversity that we observe in nature more closely in the laboratory. Here, we suggest the araneid *Eustala illicita* (O. Pickard-Cambridge 1889) as a suitable neotropical spider for studies on orb-webs and web-building behavior based on the ease with which it can be located in abundant numbers in the dry tropical forest, its interesting ecology and its willingness to build webs in the laboratory. In this paper we give a general overview of its natural history and a detailed description of its web.

METHODS

Natural history.—*E. illicita* is a relatively large orb-weaver (Fig. 1). The adult female is 6–9 mm in length (7.7 ± 0.6 mm, mean ± SD, n = 24) and weighs 25–70 mg (36.4 ± 12.3 mg, mean ± SD n = 24). The abdomen is slightly elongated with a yellow/green or gray striped pattern on the ventral side and a brighter yellow and black pattern on the dorsal side. The male is slightly smaller with a shorter and narrower abdomen (Chickering 1955). It is found from Mexico to Panama (Platnick 2009). All observations on the natural history presented in this paper occurred in Parque Natural Metropolitano (9°N, 80°W), a lowland tropical dry forest at the Pacific

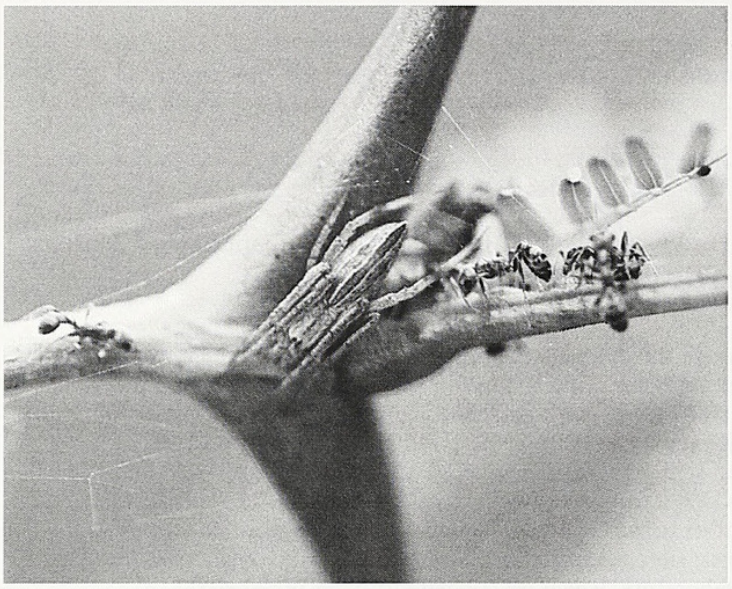

Figure 1.—Adult female *Eustala illicita* sitting on thorn of *Acacia collinsii*. Aggressive *Pseudomyrmex spinocola* ants can be seen patrolling close to the spider.

coast of Panama. We found that most *Acacia collinsii* trees contained numerous *E. illicita* individuals, whereas other trees seemed devoid of this species. On two mornings in June 2009, we counted, after spraying the trees with water from a plant mister, the number of *E. illicita* webs present in 18 randomly selected acacia trees and in another 18 similar sized and structured trees in the same area (we surveyed a different part of the forest on the second day, in order not to include the same trees twice). We furthermore compared the density of individual spiders per acacia tree between the dry season (December–April) and the rainy season (May–November) from seven visits to the forest in March and April 2009 and from a further seven visits in May and June 2009. Finally, we observed that spiders in the field resting away from the web seemed to show a high degree of behavioral plasticity as to what leg they used to maintain contact with the hub of the web via the signal thread. However, we decided to quantify the degree of behavioral plasticity in the laboratory, since it proved difficult to obtain reliable field data on this, as small disturbances to trees and branches caused the spiders to move and shift leg position. Spiders were treated similarly to the laboratory study (methods given below), and on days when they had built a web and were positioned away from the hub, we recorded the leg used to contact the signal thread. Since individual spiders showed a high variability from day to day in which leg they used, each spider was recorded between one and five times on consecutive days.

Webs in the field.—All measured webs were built by adult females on *A. collinsii* with resident *Pseudomyrmex spinicola* ants along trails. All sampled webs were below 2 m from the ground (141 ± 52 cm, mean ± SD, n = 18). For each web we measured the following parameters (Fig. 2A): 1) vertical diameter of the capture spiral (d_v), 2) horizontal diameter of the capture spiral (d_h), 3) location of the hub center from the top of the web (upper vertical radius, r_u) and 4) the vertical diameter of the hub and the free zone (H). Finally, we measured the total length of all the anchor threads that connected the web with the vegetation for a subset of the adult webs and for some early and late juvenile webs.

Webs in the laboratory.—Adult female spiders were collected throughout the year and maintained in the laboratory (23–26 ° C, 45–60% relative humidity, natural 12:12 h day/night cycle) following Zschokke and Herberstein (2005). We waited at least 5 days for the spiders to acclimate to the frames, since our prior observations indicated that some *E. illicita* spiders delay building in the laboratory (E. Triana & T. Hesselberg unpublished). We allowed each spider to build webs in a 29 × 29 × 5 cm frame made of clear Perspex. The frames were stacked like books on a shelf with thin Vaseline smeared sheets between them. They were sprayed with water from a plant mister every day. Each day a spider built a web, it was given one to two fruit flies before the web was cut using a cordless soldering iron leaving an intact radius in the north and south quadrant, thereby collapsing the web into a single vertical thread, which was left in the frame for the spider to ingest.

When a spider had built webs on two consecutive nights and at least three in total, the last web was placed in a custom-made black box with 8W fluorescent light from the side and 14W from below and photographed with a digital D60 SLR Nikon camera. The following parameters were extracted from the digital photographs using ImageJ (v1.41, National Institutes of Health, USA) (Fig. 2A): 1) Vertical diameter of the capture spiral (d_v), 2) horizontal diameter of the capture spiral (d_h), 3) location of the hub center from the top of the web (upper vertical radius, r_u), 4) the vertical diameter of the hub and the free zone (H), 5) area and 6) number of spiral turns of the hub (*E. illicita* removes the center of the hub, so the number of spirals counted here is only what are left outside of the removed center), 7) number of radii near the periphery of the capture spiral and 8) number of turns of the capture spiral (N) counted along a north, south, west and eastern radius (Nr, Sr, Wr and Er), where east is defined as the side with the signal thread (Fig. 2A) or arbitrarily in webs without a free sector.

Data analysis.—The following parameters were calculated from the measured values of the webs: 1) Capture spiral area was calculated from the Ellipse – Hub equation, $A_{cap} = (d_v/2)(d_h/2)\pi - (H/2)^2\pi$ (Herberstein & Tso 2000). The area of the free sector was not removed from the capture spiral area, but measurements from the laboratory webs show that this area constitutes less than 3% of the total capture spiral area (2.7% ± 1.8%, mean ± SD, n = 24). 2) The area of the hub and the free zone had a circular shape and was calculated from $A_{h+fz} = (H/2)^2\pi$. 3) Asymmetry in the web between the upper and lower part was calculated from $(r_u - r_l)/(r_u + r_l)$, where r_l is the lower radius found from $r_l = d_v - r_u$. The equation gives a value from −1 to 1, where 0 indicates a perfectly symmetric web. 4) The shape of the web was calculated from $(d_h - d_v)/(d_h + d_v)$, which again gives a value from −1 to 1, where 0 indicates a perfectly round web. 5) Average mesh size was calculated from the mesh size (distance from the inner to the outer spiral turn/ N−1) along the north, south, east and western radii (Fig 2A). Comparisons between field and laboratory webs were made with the two-tailed Welsch's T-test for independent samples with unequal variances, while we compared the ratio of anchor thread lengths to web diameter with a non-parametric Friedman ANOVA. The significance level was set at P = 0.05.

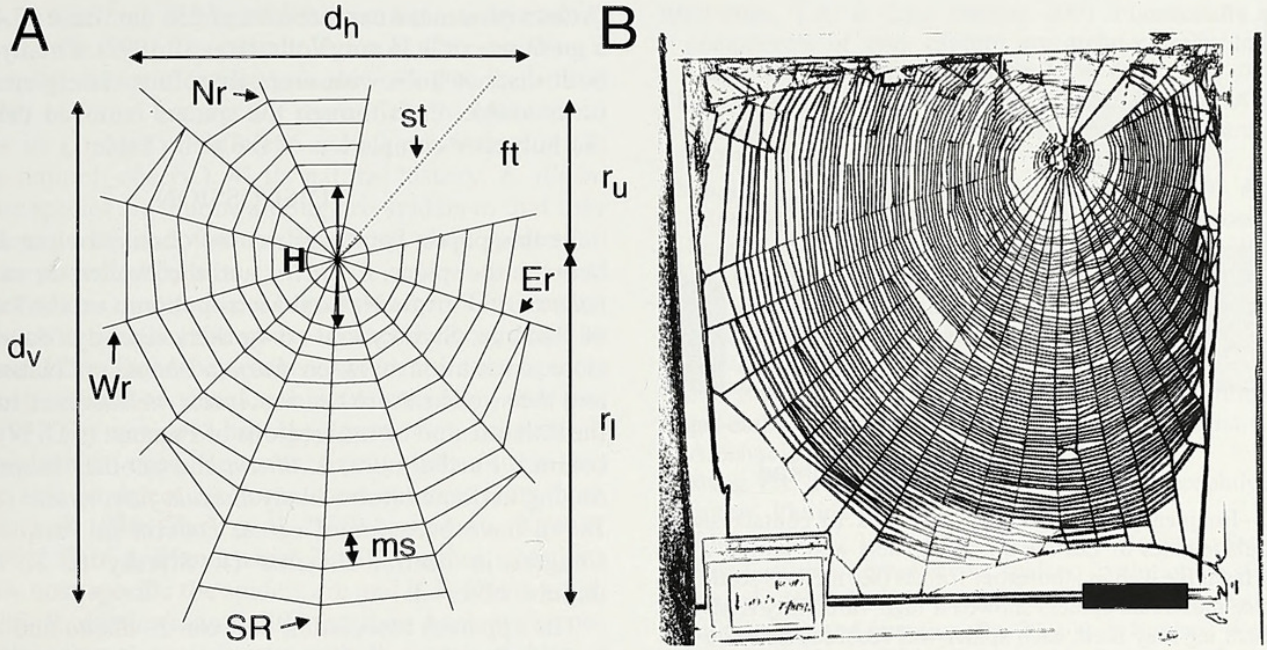

Figure 2.—Orb-web of *Eustala illicita*. A. Schematic drawing of a typical web showing the free sector (ft); signal thread (st); diameter of the hub and free zone (H); north (Nr), west (Wr), south (Sr) and east (Er) radius; mesh size (ms); upper (r_u) and lower (r_l) vertical capture spiral radius and vertical (d_v) and horizontal (d_h) capture spiral diameter. B. Photograph of an orb-web built in 29 × 29 × 5 cm frame. The photograph was inverted, sharpened and given higher contrast before the edge detect function was applied. All modifications were carried out with Corel Photo-Paint (V. 12, Corel Corporation 2003). Black bar in the lower right corner = 5 cm.

RESULTS

Natural history.—We found a close association between the spider and the swollen-thorn acacia, *Acacia collinsii*, in Parque Natural Metropolitano. We counted a mean of 6.2 ± 3.9 (mean ± SD) spiders per acacia, whereas only 0.2 ± 0.5 (mean ± SD) spiders were found per neighboring non-acacia tree (Mann-Whitney test: $U = 383.5$, $P < 0.001$). All of the four spiders in non-acacia trees were juveniles and were found on trees within a few meters of an acacia tree. However, during other visits some adults were observed on dead vegetation along a road in a different part of the forest. During the day, *E. illicita* often sat close to a bull-horn-shaped thorn of the acacia, where ants nested (Fig. 1). Resident *Pseudomyrmex* ants are extremely aggressive and usually attack all intruders, except for a few insects that have evolved mechanisms to avoid getting attacked (Janzen 1966). At present we do not know how the spider avoids attack by the ants (J.D. Styrsky, pers. comm.).

The spiders appeared to be active primarily at night, when they could be found in the hub of the webs in both the field and in the laboratory. Web-building in the laboratory usually occurred either just after dusk or shortly before dawn (T. Hesselberg, pers. observ.). During the rainy season most adult spiders also kept their webs up during the day (95% of adults observed, $n = 21$, vs. 31% of adults observed, $n = 13$, with webs during the dry season). Spiders with webs rested either on acacia branches and stems (28%, $n = 32$) or more usually on the thorns of the acacia (72%, $n = 32$) and maintained contact with a signal thread connected to the hub of the web. Spiders in the laboratory varied widely in terms of the leg used to grab the signal thread, except for the small third pair of legs, which was never used (Fig. 3). However, the other three pairs of legs were not used equally frequently. The spiders predominantly used the second pair of legs (48%, $n = 60$) to maintain contact with the web, while the front pair of legs was used less frequently (18%, $n = 60$) than the last pair (22%, $n = 60$) (Fig. 3). The signal thread sometimes ended in a V-shape and two legs held the signal line (12%, $n = 60$). In general, when one leg was used, the right leg was used significantly more often than the left (64% vs. 36%, $n = 60$, chi-square test: $\chi^2 = 4.25$, $P = 0.039$). However, this could be an artifact caused by the direction of light on the frames, which we did not control.

The web.—A total of 34 spiders was placed in frames, and 24 were photographed. The other spiders either died early or did not build webs regularly. The recorded spiders had an average web-building frequency of 80.7% ± 21.7% ($n = 24$) during the 5–10 days they were kept in the frames, which compares favorably with daily laboratory web-building frequencies of 80–90% for *A. diadematus* (Hesselberg & Vollrath 2004), 50–70% for *A. keyserlingi* (Herberstein et al. 2000; Walter et al. 2008) and 30–50% for *Z. x-notata* (Pasquet et al. 1994).

The webs of *E. illicita* showed three major deviations from the standard orb-web: 1) the upper part of the web was much reduced resulting in highly asymmetrical webs, 2) the webs had short anchor threads with no distinct frame towards the substrate, and 3) the web had a free sector (Fig. 2B). The short anchor threads were not only an artifact from laboratory frames, but were also observed in juvenile and adult webs in the field, where the ratio of the entire length of all anchor threads to the average diameter (vertical and horizontal) of the capture spiral was 1.9 ± 0.8 ($n = 32$). This is significantly lower than the ratio in juvenile and adult webs of two other sympatric neotropical orb-spiders; *Cyclosa caroli* (4.7 ± 1.5, $n = 16$) and *Nephila clavipes* (5.5 ± 1.8, $n = 30$, Friedman ANOVA $F_{(16,2)} = 24.1$, $P < 0.001$) (T. Hesselberg unpublished). The free sector was most often, but not always, found in an upper corner. Some adult females built webs without a free sector (4 out of 18 field webs, 4 out of 24 laboratory webs), and instead

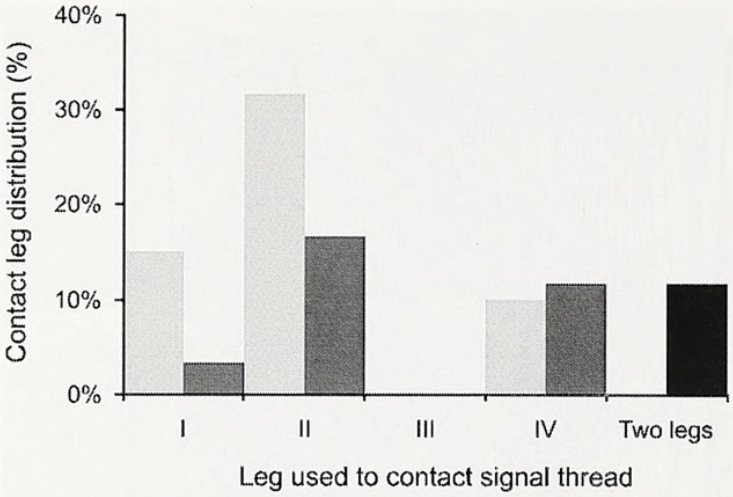

Figure 3.—Frequency distribution of leg used to contact signal thread in adult females of *Eustala illicita*. Spiders were scored when resting away from the web in laboratory frames (see method section in the text). Since individual spiders showed a high variability from day to day in which leg they used, each spider was recorded between one and five times on consecutive days. Data come from 60 observations of 24 individuals. Legs numbered from anterior to posterior end of the animal with front pair of legs labelled I. Light gray columns show right legs and darker gray columns show left legs. Signal thread sometimes ended in V-shape resulting in two different legs being in contact with it (black column).

they usually had either a signal thread that ran out of the web plane (in the field) or they had no signal thread and were found in the hub of the web (in the laboratory). The incorporation of a free sector in most webs allows comparisons to the spider, *Z. x-notata*, which also includes a free sector in the majority of its web (Venner et al. 2000).

Webs built in the laboratory were similar to webs built in nature. Natural webs and laboratory webs were almost equal in size, both in capture area and in the area of the hub and the free zone (Table 1). Laboratory webs, however, were significantly rounder and less symmetrical than natural webs (Table 1). This was probably due to adaptation to the frames provided to the spiders in the laboratory. The number of radii and the mesh size in laboratory webs of *E. illicita* were comparable to similar sized laboratory webs of *A. diadematus* (webs with a mean capture area of 236 cm^2 have 33.4 radii and a mesh size of 0.24 cm: Vollrath et al. 1997). Finally, *E. illicita* built distinct hubs with more than four closely spaced spiral turns visible, even though the spiders removed the center of the hub after completion of the web (Table 1).

Table 1.—Characteristics of adult female webs of *Eustala illicita* from the field and laboratory. All measurements given as means ± SD. Pairwise comparisons evaluated by applying two-tailed Welch's t-test for independent samples with unequal variance.

	Field webs	Laboratory webs	*t*	*p*
Sample size	18	24		
Number of radii	-	32.0 ± 7.0		
Capture area (cm^2)	300 ± 184	262 ± 69	0.95	0.348
Area of hub+free zone (cm^2)	58 ± 30	58 ± 25	0.08	0.940
Area of hub (cm^2)	-	4.7 ± 1.2		
Hub spiral turns	-	4.5 ± 1.2		
Asymmetry	−0.40 ± 0.18	−0.51 ± 0.11	2.16	0.041
Shape	−0.13 ± 0.10	−0.06 ± 0.07	2.75	0.028
Mesh size (cm)	-	0.27 ± 0.06		

DISCUSSION

In this paper, we described the observed close association between the spider, *E. illicita*, and the swollen-thorn acacia, *A. collinsii*, in Parque Natural Metropolitano on the Pacific coast of Panama. Styrsky and co-workers recently found a similar close association between *Eustala oblonga* (Chickering 1955) and the swollen-thorn acacia, *Acacia melanoceras*, in forests of the Atlantic and central regions of Panama (J.D. Styrsky pers. comm.). Furthermore, *E. illicita* and another *Eustala* with an oblong abdomen [most likely *Eustala fuscovittata* (Keyserling 1864)] have been found on *A. collinsii* in Parque Nacional Chagres in central Panama (J. Styrsky & T. Hesselberg unpubl. observ.).

The apparent association between *E. illicita* and *E. oblonga* and swollen-thorn acacias in Panama is the first reported case of such a high degree of plant specificity in an orb-weaving spider, but a few similar spider-plant interactions are known from other spider families, including Ctenidae (Barth et al. 1988), Desidae (Whitney 2004), Oxyopidae (Romero et al. 2008), Salticidae (Romero 2006), Theraphosidae (Santos et al. 2002) and Theridiidae (Gastreich 1999). However, what makes the interactions between the swollen-thorn acacias and *Eustala* spiders particularly interesting is that the trees are obligate mutualists with *Pseudomyrmex* ants (e. g. *A. melanoceras* with *P. satanicus* and *A. collinsii* with *P. spinicola*). The ants defend the plant against herbivores and encroaching plants in return for sugar, Beltian bodies and nest-space (Janzen 1966). The *Eustala* spiders might, therefore, be found in association with the two acacia species because of the protection conferred by their highly aggressive ant mutualists. A similar preference occurs in some bird species that predominantly make nests in the acacia trees, because the aggressive *Pseudomyrmex* ants prevent larger vertebrates, such as snakes and lizards from entering the acacia (Janzen 1969). However, *E. illicita*, as reported in this paper, readily builds webs in the laboratory and preliminary surveys suggest that the association with acacia trees is not obligatory, since numerous adults, both *E. illicita* and *E. oblonga*, were observed in dead vegetation along roads in Parque Natural Metropolitano at the Pacific coast and in Parque Soberania in central Panama (J. Styrsky & T. Hesselberg unpubl. observ.). Thus it is possible that the spiders employ an opportunistic strategy and inhabit dead vegetation when no suitable acacia trees can be located.

E. illicita is a promising neotropical spider for future studies on orb-webs and web-building behavior for the following reasons: 1) It is locally abundant and easy to locate in nature. The swollen-thorn acacias, and thus the spiders, are generally easy to find in the rainforest since the ants remove all other vegetation in their vicinity. However, we currently have no information on *E. illicita*'s abundance or relation to swollen-thorn acacias in the rest of Central America. 2) It builds regular orb-webs in the laboratory. *E. illicita* builds webs with a daily frequency of 80% and does not seem to be overtly disturbed by the drier and colder conditions found in the

laboratory. 3) The high degree of behavioral plasticity that *E. illicita* shows with regard to contact legs and while building a web. Especially, the location and presence of a free sector and the flexibility of frame and anchor thread lengths enable it to build webs in a range of different spatial environments (T. Hesselberg unpubl. observ.). 4) Its natural history. *E. illicita* and its sister species are unique among orb-spiders in that they occur predominantly on a few closely related plant species, all of which are protected by ants.

The observations reported here raise a number of interesting questions such as whether the spider locates the host plant by using chemical cues from the acacias or from the ants. Spiders are known to respond to visual and tactile cues from ants (see Cushing 1997 for review), but they were not believed to respond to chemical cues. However, recent studies show that spiders are able to detect air-borne chemical cues from both ants (Allen et al. 1996; Clark et al. 2000) and plants (Krell & Krämer 1998; Patt & Pfannenstiel 2008). Further questions include how host-specific the spiders are and if *E. illicita* on *A. collinsii* with *P. spinocola* ants differ in their host preference from *E. oblonga* on *A. melanoceras* with *P. satanicus*. Also, if these spiders are found in other swollen-thorn acacia – ant systems, such as for example in the *A. cornigera* – *P. ferruginea* system found from Mexico to Costa Rica (Janzen 1966). At present it is also not known whether the spiders use behavioral mechanisms or chemical mimicry to avoid attack by the aggressive ants. Some myrmecophilic spiders employ cuticular hydrocarbons to camouflage their presence (Allen et al. 2002). Answers to some of these questions are currently being pursued in our laboratory and in the working group of John Styrsky (J.D. Styrsky pers. comm.), but it is our hope that this paper will convince other arachnologists to pursue research on these fascinating spiders.

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