

FORAGING STRATEGIES OF *ERIOPHORA EDAX* (ARANEAE, ARANEIDAE): A NOCTURNAL ORB-WEAVING SPIDER

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ABSTRACT. Studies on the ecology of orb spiders have focused on diurnal spiders, especially field studies. Nocturnal spiders, however, face different conditions due to the type of prey found at night. A field study was conducted to observe the activity of adult females of *Eriophora edax* in their natural environment, and to analyze their predation efficiency and web retention properties. Most of the spiders were observed around sunset, which suggests that *E. edax* tends to build webs in the early evening. In order to evaluate the predation efficiency of *E. edax* we compared its behavior and web retention properties with the behavior of a diurnal orb-weaving spider, *Verrucosa arenata*. Two prey types, a diurnal Hymenoptera and a nocturnal Lepidoptera, were selected and presented to the spiders, to record approach time and prey capture time. The results showed that *E. edax* spent more time to capture Hymenoptera than to capture Lepidoptera. During the experiments of web prey retention time, Hymenoptera consistently showed greater tumbling than Lepidoptera, but the total retention time was the same for both prey types. Our results showed that *E. edax* forages strictly at night and, in terms of prey capture and web retention, was more efficient when preying on Lepidoptera.

Keywords: *Eriophora edax*, web-building spider, nocturnal activity, prey selection.

Web-building spiders present a unique case of “sit-and-wait” predation (Heiling 1999), so they are not expected to exhibit prey specialization (Uetz 1990). However, recent studies have shown that many web-building spiders exhibit considerable dietary specialization (Riechert & Luczak 1982; Stowe 1986; Nentwig 1987). For example, *Tetragnatha montana* Simon 1874, an orb weaver found in Eastern Europe, feeds mainly on mosquitoes (Dabrowska-Port & Luczak 1968; Dabrowska-Port et al. 1968; Luczak 1980). Habitat choice and activity pattern of the species are closely tied to the occurrence and activity of the preferred prey (Uetz 1990).

It has been suggested that nocturnal web-building, particularly in the tropics, is an adaptation to avoid the visibility of webs in daytime (Rypstra 1979, 1982). The optical properties of some orb webs tend to reduce its visibility, especially in low-light and varying

background conditions (Craig et al. 1985; Craig 1986). Several species of orb weaving spiders ingest their previous web and replace it with a new one (Breed et al. 1964; Eberhard 1971; Carico 1986). The renewal of the web is critical, because a web’s ability to capture food decreases over time as a result of contact with prey and non-prey items that destroy both threads and glue (Chacon & Eberhard 1980).

In a study on the predatory capacity of four sympatric species of web-building spiders that inhabit coffee plantations in Southern Mexico, Hénaut et al. (2001) found that the consumption of prey was related to the predatory strategy of each spider species. For example, *Gasteracantha canciiformis* (Linnaeus 1785), a diurnal orb weaving spider, built a new web every morning and prey storage was never observed. In contrast, *Cyclosa caroli* (Hentz 1850), another diurnal orb web spider, built a “permanent” web (only renewed when damaged) and stored prey on a stablimentum,

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which may explain the very low incidence of immediate prey consumption observed in this species (Hénaut et al. 2001). However, a census of the prey captured by *C. caroli* and *G. canciformis* showed that both species have a marked positive electivity for Diptera and Hymenoptera (Ibarra-Nuñez et al. 2001).

There are numerous reports concerning predation by web-building spiders (Heiling 1999; Hénaut et al. 2001; Ibarra-Nuñez et al. 2001) although the vast majority involves diurnal species. In contrast, the present study investigated the foraging activity of a nocturnal orb web spider, *Eriophora edax* (Blackwell 1896 (Araneidae)). This Pan-american species with a body length ranging from 12–16 mm (Levi 1970) was selected due to its nocturnal activity and its abundance. The web of *E. edax* is vertical, and the spider stays at the hub of the web with its head facing down.

The study was divided in two parts. First, we examined *in situ* the activity and the prey captured by adult females of *E. edax*. Second, we compared the prey capture behavior of *E. edax* with the prey capture behavior of a diurnal orb weaving spider.

METHODS

Study site.—The study was conducted in July and August 2002 in a coffee plantation at the agricultural experimental station “Rosario Izapa” of the INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias), situated at 400 m above sea level in the state of Chiapas, southern Mexico (14° 58' N, 92° 09' W). The climate is tropical, warm and humid. Heavy rainfall (3000 mm per month) occurs from May–October. During the course of the study, temperature fell to approximately 23 °C at night, and rose to about 33 °C during the day. The relative humidity was around 85%, day and night.

Spider activity.—We observed the spiders' activity for three nights without rain (when spiders are active and observers can stay the entire night in the field). Observations were done from 1800 to 0700. At this time of the year sunset occurred between 1900 and 1930 and sunrise between 0630 and 0700. We walked hourly along a 200 m transect (using a chronometer to check the time), to check for *E. edax* spiders and their webs. It took from 30–45 min to record all the spiders of a transect. Flashlights with dark red plastic cover

facilitated observation while neither attracting insect prey, nor disturbing the spiders' natural photoperiod (Herberstein & Elgar 1994; Heiling 1999).

On each transect walk we recorded the spiders present in the bush with or without a web and the absence of individuals previously recorded. We marked spiders' positions individually with a numbered piece of white plastic located on the nearest twig. Spider activities were recorded as: building the web, catching a prey (when a spider was wrapping a prey with silk), and eating a prey (when a spider was actually biting a prey or was handling it in its chelicerae).

All voucher specimens are deposited in the Collection of the Laboratory of Arthropod Ecoethology (Laboratorio de Ecoetología de Artrópodos) in Ecosur, Tapachula, Mexico.

Spiders' prey.—Prey items captured in the webs were visually identified to the level of order. These prey items were not removed from the webs. Prey identification to lower levels, although desirable, would have resulted in substantial disturbance of the webs. We compared the hourly numbers of each order of prey captured by *E. edax* web with a Chi-square test (SPSS 10.00 for Windows).

Predation efficiency and web retention properties.—In order to evaluate the predation efficiency and the web retention properties of *E. edax*, we conducted two field experiments during the same months but on different nights than the activity observations. We selected *Verrucosa arenata* (Walckenaer, 1841) (body length: 8–15 mm) as a model of diurnal orb weaving spiders. Like *E. edax*, it is an araneid, builds its web every day, and dismantles it at the end of its daily activity period. However, it is as strictly diurnal as *E. edax* is nocturnal. Finally, *V. arenata* is present in the same habitats as *E. edax*. Two experimental prey types were selected, because they are abundant in the coffee plantation (Ibarra-Nuñez 1990). Adults of the moth *Sitotroga cerealella* (Olivier 1819) (Lepidoptera, Gelechiidae) were selected as representatives of a nocturnal prey, while the stingless bee *Scaptotrigona mexicana* Guérin (Hymenoptera, Apidae) was chosen as an example of a diurnal prey. Prey specimens were obtained from laboratory cultures. For both prey types, field experiments were performed during three days for *V. arenata* and during three nights

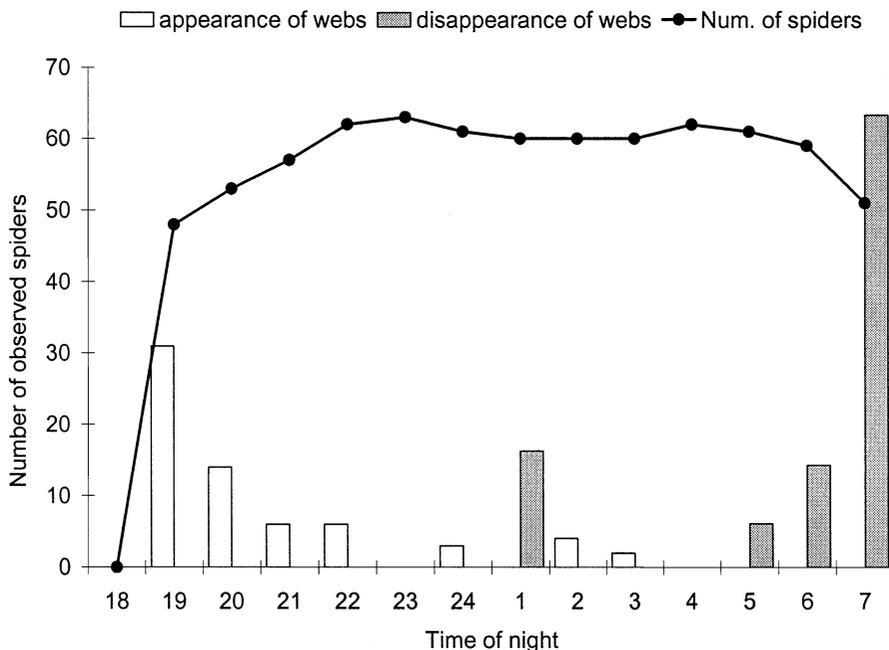


Figure 1.—Number of *Eriophora edax* individuals with or without a web (number of spiders), appearance of webs and disappearance of webs in the study site during a 12 hour observation period. Sunset occurred between 1900 hrs and 1930 hrs; sunrise between 0630 hrs and 0700 hrs.

for *E. edax*. For each type of prey and for each spider species, 20 individuals were tested for the predation and web retention studies. For each prey type, observations were made in the same 24 hour period for both spider species.

For the predation efficiency experiments, webs were selected based on the following criteria: no signs of remains of prey, spider was an adult female located at the center of the web. Each prey item was gently blown into the web with the aid of an inverted aspirator from a distance of 10 cm. All prey were alive and visually undamaged before and after introduction into the web.

Once the prey made contact with the web, the behavior of the spider was registered in terms of approach and prey capture (measured in seconds). The prey capture event started at the moment the spider bit the prey, continued with its manipulation and finished when the spider took it to the center of the web. Observations were conducted for a 5 min period, which was enough for recording the complete capture event. We compared the predation efficiency of both spider species with both types of prey with an ANOVA (Statistica 6.0).

For the web retention experiments, webs

were selected based on the same criteria as above. Spiders were carefully removed from their web, and prey items were blown the same way as mentioned before. Once the prey made contact with the web, a small piece of paper was set at the impact point to measure the distance the prey tumbled. The prey was observed for a 5 min period, after which the tumbling distance was measured in centimeters. If the prey remained on the web for more than 5 min, a second tumbling distance of the same prey was measured after 30 min. Once the experiment ended, the spider was returned to its web. The data obtained from both observation periods (5 min and 30 min) were contrasted for spider and prey types (nocturnal vs. diurnal) with an ANOVA (Statistica 6.0).

RESULTS

Spider activity.—*E. edax* was not observed before 1900. Most of the spiders appeared on coffee bushes or were building their webs between 1900–1930, around sunset time ($n = 48$ of a total of 74 spiders observed for the three nights). Around 68% of the spiders were present between 1900 and 2000, and we

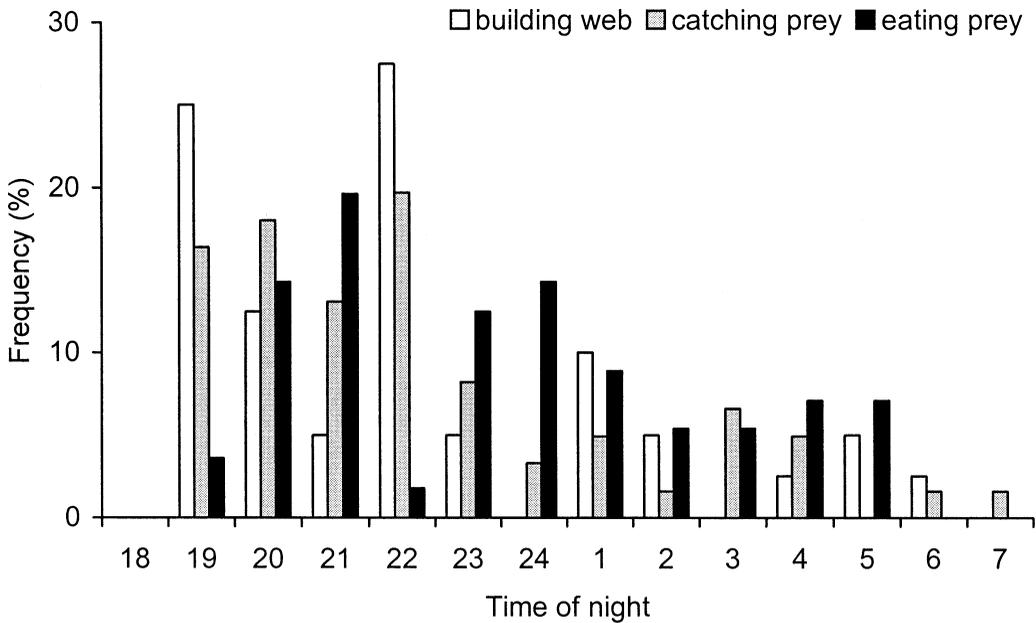


Figure 2.—Frequency of web building, prey catching and prey eating by *Eriophora edax* in a coffee plantation during the 12 hrs observation period. Sunset occurred between 1900 hrs and 1930 hrs; sunrise between 0630 hrs and 0700 hrs.

observed no spider after 0700, when the sun rose (Fig. 1).

Although spiders were able to build their web all night, this activity was more intense between 1900 and 2200. Other smaller peaks of this activity occurred around 0100 and 0500. *E. edax* requires less than one hour to build its web, as the web was completed between two subsequent data recordings, and most often the spiders had already caught a prey when its web was observed for the first time (Fig. 2).

Catching prey was most intense at the beginning of the night, between 1900 and 2300. Then the catching activity decreased through the night, although this activity increased again slightly between 0300 and 0400 just after the second peak of building (Fig. 2).

Spiders began to eat prey at 1900, but this activity peaked at 2100, right after the peak of catching activity. Other smaller peaks of eating activity occurred at 0000, and between 0400 and 0500. We also observed that spiders stopped eating before sunrise (0700), even if they had caught a prey (Fig. 2).

E. edax is more active at the beginning of the night than at the end of the night (Fig. 2).

Of the 74 spiders observed during the three nights, 55.4% caught only one prey, 9.5% caught two prey and 35.1% did not capture any prey.

Spiders' prey.—The main prey items caught by *E. edax* ($n = 55$) were Lepidoptera (67.7%), Coleoptera (21.5%), Diptera (9.2%), and Hymenoptera (1.5%). Minor taxa included Orthoptera and Hemiptera (< 0.1%). The number of prey items of different insect orders differed statistically ($\chi^2 = 150.7$, d.f. = 8, $P = 0.001$). Lepidoptera were mostly caught at the beginning of the night (1900–2100) with a second, smaller peak of capture between 0300 and 0400. Coleoptera were caught by the spiders between 1900 and 2200.

Predation efficiency and web retention properties.—The time spent to reach and capture a prey as well as the tumbling of the prey into the webs varied according to the spider species (Table 1). *E. edax* spent less time to reach Lepidopterans but more time to capture Hymenopterans than *V. arenata* and the tumbling is more important with the web of *E. edax* (Table 1). However, the comparison between prey show that the time spent to reach

Table 1.—Time (in seconds \pm SE) of each spider species (*Eriophora edax* and *Verrucosa arenata*) to reach and to capture the offered prey (Lepidoptera and Hymenoptera), as well as each prey's tumbling distance (in cm) in the web after 5 min and after 30 min of observation. ***, $P < 0.001$; *, $P < 0.05$; ns, Not significant $P > 0.05$, ANOVA.

		<i>E. edax</i>	<i>V. arenata</i>	Comparison
Time to reach prey (sec)	Lep.	3.3 \pm 0.7	46.3 \pm 18.3	*
	Hym.	12.8 \pm 8.6	17.2 \pm 7.5	ns
Prey capture time (sec)	Lep.	18.1 \pm 1.9	20.6 \pm 5.2	ns
	Hym.	71.3 \pm 7.5	20.7 \pm 2.6	***
Tumbling after 5 min (cm)	Lep.	1.1 \pm 0.8	1.9 \pm 1	ns
	Hym.	5.2 \pm 1.02	4.8 \pm 1.3	ns
Tumbling after 30 min (cm)	Lep.	8.6 \pm 1.2	0.8 \pm 0.4	***
	Hym.	8.5 \pm 1.2	5.8 \pm 1.6	ns

a prey was not significantly different between the two prey types ($F_{1,38} = 2$; $P = 0.16$).

We also found significant differences in the prey capture time between the two spider species. *E. edax* spent more time to capture Hymenoptera than to capture Lepidoptera ($F_{1,38} = 46$; $P = 0.000$). On the other hand, the time *V. arenata* spent to capture both Hymenoptera and Lepidoptera did not differ significantly ($F_{1,38} = 0.000$; $P = 0.9$).

Prey tumbled differently according their type (diurnal or nocturnal), and to the spider species to which the web belonged, for both observation periods (5 min and 30 min). During the 5 min observation period, Hymenoptera tumbled a longer distance than Lepidoptera in *E. edax* and it tended to be the same in *V. arenata* webs (*E. edax*: $F_{1,38} = 10$; $P = 0.002$; *V. arenata*: $F_{1,38} = 3.2$; $P = 0.08$). During the 30 min observation period Hymenoptera tumbled a longer distance than Lepidoptera in *V. arenata* but the tumbling was not different in *E. edax* (*E. edax*: $F_{1,38} = 0.005$; $P = 0.9$; *V. arenata*: $F_{1,38} = 15.6$; $P = 0.000$).

During the 5 min observation period, both *E. edax* and *V. arenata* webs retained 100% of the blown prey. After 30 min, *E. edax* web retained 95% of the Lepidoptera and 90% of the Hymenoptera, and *V. arenata* webs retained 80% of Lepidoptera and 50% of Hymenoptera ($\chi^2 = 0.5$, d.f. = 1, $P = 0.5$).

DISCUSSION

Our results confirm that *Eriophora edax* forages strictly at night, spins a new web every night and dismantles it at dawn. Most spiders started to build their web just after sunset, and all spiders had disappeared at sunrise. Even if *E. edax* caught prey during the 12 h

observation period, it seems to have a strategy to "build, catch and eat" in a short period of time. Most prey is caught and eaten within a two hour period after the web is built. In comparison with other orb-weaving spiders (Hénaud et al. 2001) this spider captures a low number of prey (generally just one per night) and never makes prey caches. We did not observe *E. edax* relocate its web after capture and consumption of a prey. Thus, whether new arrivals during the night are new spiders or spiders building a second web in a new place, remains to be tested.

Capture rates were higher at the beginning of the night, probably due to the level of prey activity at this time (unpubl. data). As other *Eriophora* species, *E. edax* preyed mainly on Lepidoptera. For example, Herberstein & Elgar (1994) found that *E. transmarina* (Keyserling 1865) captured mostly Lepidoptera, which were also more abundant at night.

Another evidence of the strategy of *E. edax* to maximize capture time is that most spiders waited on their web almost all night, even when they had already caught some prey. Also, spiders did not dismantle their web until just before dawn, even if they had not caught or eaten a prey.

Although *E. edax*'s main prey was Lepidoptera it did vary its diet by eating other orders of insects, such as Coleoptera, Diptera, Hymenoptera, Orthoptera and Hemiptera. Nyffeler (1999) found that overall fewer than 10 arthropod orders (Diptera, Homoptera, Hymenoptera, Heteroptera, Collembola, Coleoptera, Lepidoptera, and Araneae) make up the bulk of the prey of common agroecosystem spiders. Dietary mixing seems to be advanta-

geous by optimizing a balanced nutrient composition needed for survival and reproduction (Greenstone 1979; Uetz et al. 1992; Toft 1995). However, in comparison with the diurnal spider *E. edax* is more efficient at reaching and capturing the moth than the bee, and its web offers a better prey retention for Lepidoptera than *V. arenata*'s web. The predatory behavior of the nocturnal spider seems to be more specialized towards moths, though the results on web retention might be influenced by differences in web properties caused by the difference in temperature between day and night (around 10 °C).

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