



Retention, capture and consumption of experimental prey by orb-web weaving spiders in coffee plantations of Southern Mexico

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Abstract

This study focuses on the predatory capacity of four sympatric species of web-building spiders that inhabit coffee plantations in Southern Mexico: *Gasteracantha cancriformis*, *Cyclosa caroli*, and the morphologically similar species pair *Leucauge mariana* and *L. venusta* which were considered as one species group. The retention capabilities of the webs of these species and the incidence of prey capture and consumption were measured using eight types of insect prey belonging to the orders Coleoptera (1 species), Hymenoptera (3), Diptera (2) Lepidoptera (1) and Homoptera (1). The different characteristics of each prey such as body weight, body size, defensive behaviour, etc., were recorded. The incidence of prey retention, capture and consumption were significantly higher in *G. cancriformis* than in any of the other species. The lowest rates of retention, capture and consumption were observed in *C. caroli*, while *L. mariana/venusta* were intermediate in their predatory capabilities. Significant negative correlations between prey size and percent consumption were detected in *L. mariana/venusta* and in *G. cancriformis*; in both cases, large prey were less likely to be immediately consumed than small prey items. The results can be interpreted in the light of the morphological characteristics of the spiders. *G. cancriformis* possesses long legs and a carapace and appeared to have few difficulties to manipulate all types of prey. In contrast, *C. caroli* showed lesser abilities to manipulate and subdue aggressive prey items, perhaps due to the short leg length and unprotected body of this species. The consumption of prey items may be related to the predatory strategy of each spider. *G. cancriformis* constructs a new web every morning and prey storage was never observed. The absence of prey storage behaviour could explain why this species consumes prey soon after capture. In contrast, *C. caroli* constructs a permanent web and stores captured prey on a stabilimentum that may explain the very low incidence of immediate consumption of prey observed in this species.

Introduction

The spider's web is traditionally viewed as a passive net used to trap prey that happen to fly into the structure (Buskirk, 1975; Higgins, 1987). Eberhard (1990) suggested that in reality the web may have three functions: (i) interception of the prey in flight, defined as contact with the web that results in a change in the angle or velocity of insect flight, (ii) stopping the prey, which requires absorption of the prey's momentum without web breakage, and (iii) prey retention, in which the prey adheres or becomes entangled during

a period in which the spider must arrive to subdue the victim.

Prey interception, the first step in prey selection, will be affected by web location (open or sheltered sites, etc.) web orientation (vertical or horizontal structures) and web size (Eberhard, 1986). Clearly there is a relationship between the design of the web and its ability to resist prey impact such that certain prey may be selectively intercepted while others may be sufficiently strong or fast moving to break through the web and avoid the risk of predation (Eberhard, 1986; Chacon & Eberhard, 1980; Craig, 1987).

Once intercepted, the spider has the retention period available in which to consolidate the capture. The vibrations produced by the struggling prey item allow the spider to exercise another level of prey selection; to avoid the risk of injury or death, spiders may avoid subduing unusually large or fierce prey (Robinson & Robinson, 1981; Riechert & Harp 1987; Wise, 1993). For acceptable prey items, the success of the capture will depend on the speed of the spider's reaction and the nature of the spider's attack. Once subdued, the prey may be consumed immediately or may be removed from the web and stored for later consumption (Uetz, 1990).

Certain prey groups may possess the means of defence against the web or the attack of the spider. For example, strong fliers, such as Lepidoptera, Diptera and alate Hymenoptera may be able to struggle free of the web after the initial impact, such that the average retention times for these prey groups may often be relatively short (Hoffmaster & Hays, 1977). Other types of prey such as Orthoptera, Homoptera and certain Coleoptera can defend themselves from the spider's attack by kicking, biting or stinging in the case of some Hymenoptera.

Olive (1980) asserted the spider's morphology is highly influential in prey capture and may have an important role as a means of defence against aggressive prey; *Araneus trifolium* (Hentz, 1847), a species with short legs and well developed fangs was able to capture prey types with rapid escape behaviours (Diptera and Lepidoptera). In contrast, *Argiope trifasciatus* (Forsk., 1775), a species having long legs and small fangs was more adept at capturing potentially hazardous but relatively slow moving prey insects (Orthoptera, Homoptera and Hymenoptera) that gradually became entangled in the web structure. The functional morphology of the predator may therefore directly affect the type of insect predated.

In this study we examined the web retention properties and the attack behaviour of different species of spider found in coffee plantations in Southern Mexico. The observations were performed under semi-natural conditions using a selection of eight possible prey and three types of orb-web building spiders that were common in the coffee plantations of Chiapas, Mexico.

Materials and methods

The field site was a coffee plantation in the grounds of the agricultural experimental station, Rosario Izapa,

situated at 400 m above sea level in the state of Chiapas, Southern Mexico, approximately 15 km from the town of Tapachula and 1 km from the border with Guatemala. The climate is tropical; warm and humid with a typical daily temperature range 35 °C maximum and 23 °C minimum, and a relative humidity of approximately 85%. Heavy rainfall occurs during the months of May to October (approximately 300 mm month⁻¹) causing a marked reduction in spider activity in the field, but outside this period, rainfall is virtually nil and webs are common.

Webs and spiders. The spiders selected for this study were *Gasteracantha cancriformis* (L.) (Araneidae), *Cyclosa caroli* (Hentz) (Araneidae), *Leucauge mariana* (Keyserling) and *Leucauge venusta* (Walckenaer) (Tetragnathidae). Females of *L. mariana* and *L. venusta* cannot be differentiated visually. Because both species are known to be present in the study area (Ibarra-Núñez, 1990), they are hereafter referred to as one species group.

Each species differed in the morphological characteristics of the body (Levi, 1977, 1978, 1980) and the web constructed by each spider (Ibarra-Núñez & Lachaud, 1998). Fully grown *G. cancriformis* individuals have an overall body length of 7.2 mm (measured from the chelicerae [fangs] to the tip of the abdomen), the length of the first leg is 7.3 mm. This species has a well-developed, large and thick, six-spined carapace 3.2 mm in length. The web is oval and regular, vertical or nearly vertical with a mean diameter of 25 cm. *C. caroli* has an overall body length of 6 mm, the first leg is 4.4 mm long. The web of this species is vertical, oval and regular with a mean diameter of 7.4 cm. This web contains a stabilimentum that runs from the centre to the upper and lower parts of the web; the stabilimentum contains the remains of consumed prey, various other types of debris, and the reserves of captured, but not yet eaten prey items. *L. mariana/venusta* has an overall body length of 5.9 mm and the first leg is 22.2 mm. The web of this species pair is oval, regular, horizontal or almost horizontal and approximately 20 cm in diameter.

Prey types. Prey were selected as being representative of the type of prey abundant in the coffee-plantation habitat (Ibarra-Núñez, 1990) and available in sufficient numbers for the experimental observations. Adult Diptera, *Drosophila* sp. and *Anopheles albimanus* (Wiedemann) were obtained from labora-

tory cultures, as was the scolytid (Coleoptera) coffee berry borer, *Hypotenemus hampei* Ferrari, and the lepidopteran grain pest *Sitotroga cerealella* (Oliver). The Hymenoptera were represented by two species of ants: *Solenopsis geminata* (Fabricius) and *Crematogaster* sp. (Lund) collected from the field and a bethylid parasitoid of the coffee berry borer, *Cephalonomia stephanoderis* (Waterson), obtained from a laboratory culture. A mixture of species of cicadellids (Homoptera) was collected in the field, measured and grouped according to size and weight. Each type of prey differed in its overall body size, weight and methods of defence against predation (Table 1).

Body size was determined by measuring the distance from the extreme anterior point of the head to the hindmost part of the abdomen for 20 individuals of each prey group using a binocular microscope with a graduated eyepiece to an accuracy of ± 0.02 mm. The live body weights of 20 individual insects of each prey group were measured to an accuracy of 0.1 mg, using a precision electronic balance (Sartorius Basic model BA 110S). Very light insects had to be weighed in groups: in the case of *C. stephanoderis*, 10 groups each comprising 10 insects were weighed and in the case of *A. albimanus* and *H. hampei*, 10 groups of 5 insects per group were weighed.

Field observations. Field observations were performed in the dry season from September to March when spiders are common in the coffee plantations of the region. Observations occurred three times per week between 09:00 am and 12:00 noon. Webs were selected based on the following criteria: the webs had no signs of the remains of prey (except in the case of the stabilimentum of *C. caroli*) and the spider should be an adult female sited at the centre of the web awaiting the arrival of prey. Each prey item was gently blown into the web with the aid of an aspirator from a distance of 10 cm. All prey were living and visually undamaged before and after introduction into the web.

When web retention properties were being determined, rather than the stopping capabilities of the web, only the prey that touched the web were considered, and not those that passed between or broke through the threads of the web. The incidence of stopping in these cases was 100%, and the prey-related differences we observed were due to the retentive properties of the webs.

Once the prey made contact with the web, the web retention capacity and the behaviour of the spider were observed in terms of four aspects of the preda-

tion process: prey retention time, prey capture by the spider, immediate consumption of the prey or rejection of the prey by the spider. A retention event was recorded if the prey remained entangled in the web for a period of 20 sec. A capture event was recorded if the spider made contact with the prey wrapping it and or transporting it to another part of the web during the 10-min period following prey impact. Immediate consumption of prey was recorded if the spider was observed to feed upon the prey item within 10 min of prey capture. Other possible outcomes were storage of captured prey or ejection from the web.

For each species of spider, 10 individuals were studied and were each offered 10 prey items, giving a total of 100 observations for each prey-spider combination. In the case of ant prey, only 50 individuals were offered of each ant species, this being sufficient to obtain a clear result. The incidence of retention, capture, and immediate consumption of each prey type were individually compared for each spider species by χ^2 -test. Mean prey weight and size data were used to test for correlations between these parameters and the arcsine transformed percent retention, capture and consumption of prey items.

Results

Web retention. The frequency of retention of the webs of each spider species was highest in *G. cancriformis* with between 81% and 100% retention that did not differ significantly with prey type ($\chi^2=3.1$, d.f.=7, $P=0.8$). Webs of the other spiders studied showed high retention capabilities for the majority of prey although retention of Cicadellidae and *Drosophila* sp. was significantly reduced in comparison of other prey types, in webs of both *L. mariana/venusta* ($\chi^2=40.4$, d.f.=7, $P<0.001$) with a contribution of 74.3% of the χ^2 value for *Drosophila* sp. and *C. caroli* ($\chi^2=43.6$, d.f.=7, $P<0.001$) with a contribution of 38.6% of the χ^2 value for *Drosophila* sp. and 28.8% for Cicadellidae (Figure 1A). Compared to the other spider webs, retention of Cicadellidae and *Drosophila* flies was significantly greater in *G. cancriformis* webs ($\chi^2=18.8$, d.f.=2, $P<0.001$ for Cicadellidae; $\chi^2=25.3$, d.f.=2, $P<0.001$ for drosophilids). No correlations were detected between web-retention and prey size or weight or the ratio of weight/size for any of the spider species tested.

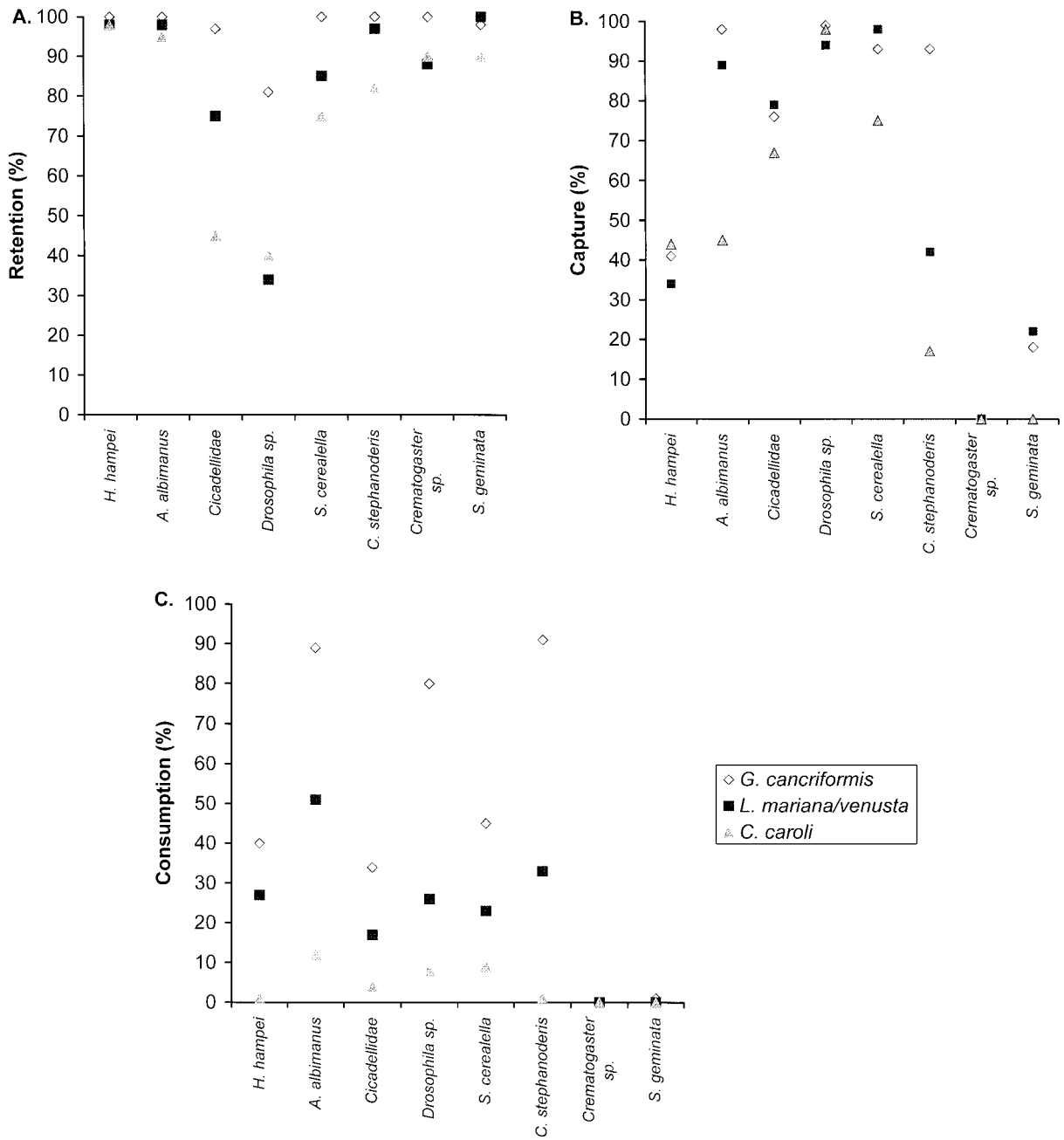


Figure 1. Incidence of (A) web retention, (B) prey capture and (C) immediate prey consumption by 3 spider groups offered six different types of prey. All figures are percentages based on 100 observations for each spider-prey combination except ant species for which 50 observations were made.

Table 1. Mean weight, mean size, and defence and flight characteristics for the eight types of prey used in the present study. In each case, the defence characteristics of prey have been considered to play an anti-predation role by the authors cited in the table

Type of prey (Order)	Weight (mg) (± SE)	Size (mm) (± SE)	Ratio (mg mm ⁻¹)	Defence mechanism	Flight characteristics	References
<i>Drosophila</i> sp. (Dipt.)	0.6 ± 0.05	2.68 ± 0.05	0.22	none	strong	Olive (1980), Uetz (1990)
<i>Anopheles albimanus</i> (Dipt.)	0.16 ± 0.003	4.53 ± 0.03	0.03	none	slow	Olive (1980)
<i>Sitotroga cerealella</i> (Lep.)	0.88 ± 0.06	6.51 ± 0.09	0.13	none	strong	Uetz (1990)
<i>Hypotenemus hampei</i> (Col.)	0.35 ± 0.004	1.71 ± 0.01	0.2	thick integument	weak	Olive (1980)
<i>Solenopsis geminata</i> (Hym.)	0.96 ± 0.04	3.76 ± 0.08	0.25	stinging	non-alate	Hölldobler & Wilson (1990)
<i>Crematogaster</i> sp. (Hym.)	2.1 ± 0.07	4.95 ± 0.06	0.42	chemical defence	non-alate	Hölldobler & Wilson (1990)
<i>Cephalonomia stephanoderis</i> (Hym.)	0.07 ± 0.001	1.79 ± 0.05	0.03	chemical defence	weak	Olive (1980), Kuwahara (1984)
Cicadellidae (Hom.)	3.5 ± 0.2	5.46 ± 0.17	0.64	kicking	strong jumpers	Olive (1980)

Prey capture behaviour. The percent prey capture was high for all prey types with the exception of the two ant species which were particularly low and which were excluded from the statistical analysis (Figure 1B). The capture efficiency was highest for *G. cancriformis* with 75-100% capture for all prey types except *H. hampei* with a 41% capture frequency that contributed 71% of the χ^2 value ($\chi^2=27.7$, d.f.=5, $P<0.001$). *L. mariana/venusta* showed a high percent capture for all prey except *H. hampei* (38.9% of the χ^2 value) and *C. stephanoderis* (24.5% of the χ^2 value) with a capture frequency of 34-42% ($\chi^2=54.2$, d.f.=5, $P<0.001$). *C. caroli* showed a high percent catch of *Drosophila* sp. representing 40.5% of the χ^2 value, an intermediate percent catch for *S. cerealella* and Cicadellidae (~70%) and less than 50% for the other prey, with the exception of a very low capture of *C. stephanoderis* (40.2% of the χ^2 value) ($\chi^2=24.3$, d.f.=5, $P<0.001$).

For all spider species, the scolytid *H. hampei*, had consistently low mean rates of capture (~40%) compared to the other prey tested, whereas the drosophilids suffered an extremely high mean incidence of capture (Figure 1B). No correlations were detected between the percent prey capture and prey size or weight or the ratio of weight/size.

For the majority of non-captured insects, no contact was observed between spider and prey. However, when prey contact with the web was not followed immediately by capture, it was often observed that the spider attempted to free an entangled insect that it may have been unable to consume or capture. Such web-cleaning behaviour was observed on 89 occasions in *L. mariana/venusta*, 52 of which involved *H. hampei*. Web-cleaning was significantly less common in *G. cancriformis* ($n=29$) and *C. caroli* ($n=12$) ($\chi^2=26.05$, d.f.=2, $P<0.001$).

Consumption of prey. Ant prey were not consumed by any spider in this study and are therefore excluded from the following analyses. For *G. cancriformis*, the consumption of prey differed according to prey type ($\chi^2=54.5$, d.f.=5, $P<0.001$). The percent immediate consumption of *A. albimanus*, *C. stephanoderis* and the drosophilids was higher (80-92%) than observed for *S. cerealella*, *H. hampei* and the cicadellids (34-40%) (Figure 1C). A very different pattern of prey consumption was observed in *C. caroli* which immediately consumed no more than 12% of the captured prey of whatever type. *L. mariana/venusta* was intermediate with a high incidence of consumption of *A. albimanus* (representing 66.8% of the χ^2 value) over other prey types ($\chi^2=23.4$, d.f.=5, $P<0.001$).

Significant negative correlations between prey size and percent consumption were detected in *G. cancriformis* ($F=18.5$, d.f.=1,4, $P=0.01$) (Figure 2A) and in *L. mariana/venusta* ($F=50.6$, d.f.=1,4, $P=0.002$) (Figure 2B). In both cases, large prey were less likely to be immediately consumed than small prey items.

Discussion

There are many reports concerning predation by web-spinning spiders, although the vast majority of these involve analysis of prey collected from spider webs and to a large degree, such data are dependent on the relative abundance of different prey types at or immediately prior to the moment of collection (Wise & Barata, 1983). In contrast, the present study investigated the retention capacity of webs spun by 3 sympatric groups of spiders in the natural habitat of a coffee plantation. The behavioural components of predation, prey capture and consumption were also observed.

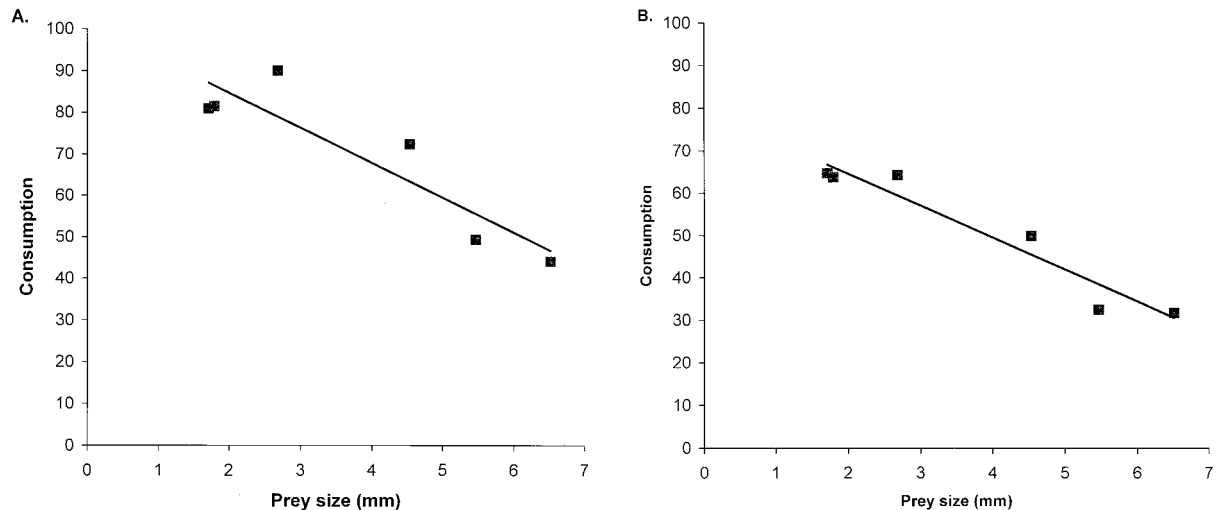


Figure 2. Correlation between prey weight and percentage immediate consumption for (A) *G. cancriformis* ($y = -8.4355x + 101.58$; adjusted $R^2 = 0.78$) and (B) *L. mariana/venusta* ($y = -7.5432x + 79.683$; adjusted $R^2 = 0.91$). Data are shown as arcsine transformed values. Ant prey were not consumed (data not shown).

Prey retention will clearly depend upon the strength and structure of the web, a species-specific characteristic that may reflect different strategies of prey selection by each group of spiders. We were unable to detect any correlation, however, between retention and the size or weight of prey for any of the spiders studied. Drosophilid flies and cicadellids, being strong fliers and jumpers respectively, were more able to escape from the webs than other prey types, as indicated by the lower incidence of retention of these insects. Therefore, it may be that morphological or behavioural characteristics are more important for insect escape than size or weight. The web of *G. cancriformis* showed the highest retention capacity for 7 of the 8 experimental prey types and also showed the highest incidence of retention of drosophilids and cicadellids indicating that it may be an intrinsically stronger structure than the webs of the other spider species. Web retention is also obviously correlated with the stickiness of the web and it is possible that the web of *G. cancriformis* owes its greater retention properties to a high degree of stickiness, although we have no data to support this idea.

Prey defence characteristics play an important role in the probability of prey capture (Olive, 1980). The capture behaviour shown by spiders may be interpreted in terms of a tradeoff between the risk of injury or death and the nutritional gains associated with the capture of a larger prey item. The risks taken by each spider appear to vary depending on species because

the morphology of the spider also clearly influences the type of prey that can be captured; heavily protected species may be able to attempt capture of larger and potentially more dangerous prey. In this respect, *G. cancriformis* with its well developed carapace and long legs, showed a high incidence of capture towards all types of prey except the ant species and the scolytid *H. hampei* which seemed to be a low value prey item for all spider species.

No data were collected on the abundance of natural prey items during the study period. The prey used in our study were selected for the diversity of morphological characteristics and defensive capabilities, but also represent common species, or are similar to common species (e.g., *S. cerealella* representative of small lepidopteran spp.) found in the coffee plantations of the region (Ibarra-Nuñez et al., 1996). Nentwig (1980) reported that the natural prevalence of prey capture was related to spider morphology and behaviour, and the body size, flight velocity and defensive characteristics of the prey. These observations are very similar to the results we obtained in semi-natural conditions wherein selected prey were fired at webs using an aspirator.

The position and structure of the web also influence prey catch characteristics (Rypstra, 1982). Prey capture may also be dependent upon the permanency of the web structure. *G. cancriformis* inhabits open spaces (Ibarra-Nuñez & Lachaud, 1998) and constructs a new web every morning (Y. Henaut, unpubl.). It is therefore not possible to maintain a reserve of cap-

tured prey items on the web that may explain the high incidence of immediate consumption of prey by this species. In contrast, *C. caroli* constructs a more permanent web that can last for several days in sheltered sites among the branches and foliage of the coffee bushes (Ibarra-Núñez & Lachaud, 1998). This species has short legs and lacks a protective carapace and may experience greater difficulty in subduing strong and potentially dangerous prey. *C. caroli* stores captured prey on a stabilimentum that probably represents an important food reserve during periods of low prey capture. This may explain the very low incidence of immediate consumption of prey observed in *C. caroli*.

The species pair *L. mariana/venusta* appears to be intermediate between the other spiders studied. The web is constructed in semi-open sites; the web is not rebuilt each morning but this spider engages in regular cleaning and repair activities (Y. Henaut, unpubl.). The spider lacks a carapace but has long legs that enable prey capture at a distance that minimizes the risk of injury.

All webs showed high retention of the two species of ants used in the study, but in general, spiders avoided capture and never consumed ant prey. The long-legged *G. cancriformis* and *L. mariana/venusta* were able to capture a small percentage of *S. geminata* individuals but no such behaviour was observed towards the *Crematogaster* sp. possibly because of the potent formic acid defence system of this ant. The ants used here were not alate, and the procedure of blowing ants at the web may appear strange. In the field however, it is not uncommon to see ants falling onto webs followed by a spider attack and winged ant sexuals are commonly found in the webs of the spiders considered in our study (J.P. Lachaud & G. Ibarra-Núñez, unpubl.) but because of their powerful defences, such potential prey are rarely consumed.

At first sight, it appears that *G. cancriformis* would be competitively superior to the other spider species. It is probable however, that the different microhabitats of the webs of these species are highly influential in determining the number and type of prey caught and possibly differences in the diurnal activity patterns of the different spider species (Uetz et al., 1978; Olive, 1980; Wise & Barata, 1983). The true degree of interspecific competition among sympatric web-weaving spiders remains difficult to resolve due to the diversity of physical, behavioural and ecological factors that influence competition.

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