COLLECTIVE PREY CAPTURE AND FEEDING BEHAVIOURS OF ANELOSIMUS JABAQUARA LEVI 1956 (ARANEAE: THERIDIIDAE)

by

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Summary

In this study we report on the predatory behaviour of Anelosimus jabaquara considering the frequency of bites in each prey body part during the immobilization phase, the proportion of the consumption time expended in each of these parts and the relative participation on capture and feeding processes by spiders of different body sizes. Generally, few individuals actively take part in prey immobilization events, biting mostly on fly’s legs (body segments which promote vibrations strong enough to attract spiders, but not to dissuade attacks). However, many spiders usually take part in the consumption of this medium size prey item. During the consumption phase appendages were rarely used, probably due to the higher nutritional value and biomass availability of central body segments (thorax, abdomen and head). Non-aggressive contests over displaced prey body parts were frequently seen during collective feeding in natural colonies, but not in small artificial groups in laboratory.

Keywords: Anelosimus, sociality, prey capture, food distribution.

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Introduction

Social spider species are able to use a wide range of prey types and sizes by cooperating in prey capture (Pasquet & Krafft, 1992; Rypstra & Tirey, 1991; Ward, 1986). The relatively large webs and joint action of several individuals assure a high capture efficiency over large prey items, which could not be immobilized by just one or a few spiders (Nentwig, 1985; Rypstra, 1990).

Collective prey capture and consumption, however, may result in an asymmetric distribution of prey biomass among colony members (Vollrath & Rohde-Arndt, 1983). In Stegodyphus mimosarum (Eresidae), for example, spiders which take part in the capture (‘catchers’) could feed longer and choose better prey body parts compared to those that approach only when the prey has already been subdued (‘intruders’). In Anelosimus eximius, the frequency of behaviours associated with prey capture, web maintenance and parental care varies as a function of spider weight and nutritional state (Ebert, 1998). Most of the web maintenance and searching for small prey items are conducted by small females. Larger insects are generally captured by spiders with intermediate sizes. The heaviest females usually do not participate in the capture process, but gain favourable access to food during collective feeding and obtain the largest proportion of the available biomass (Ebert, 1998; Rypstra, 1993). These females sometimes push smaller individuals away, and remove parts or the totality of prey to retreats, where they can consume them alone (Christenson, 1984). In that way, only some females ingest enough food for egg production (Vollrath & Rohde-Arndt, 1983; Vollrath, 1986).

In several social species, some individuals use the foraging investment of others to obtain limited resources (Barnard & Sibly, 1981; Ranta et al., 1996; Vickery et al., 1991). In social spiders, this scrounging could contribute to the maintenance of large colony sizes (Rypstra, 1993) and ensure that, even during periods of resource scarcity, at least some females will be able to produce eggs (Vollrath, 1986).

Although there is evidence that large individuals in A. eximius colonies can outcompete smaller ones and that contests involving prey parts and feeding positions are frequent during collective consumption (Vollrath & Rohde-Arndt, 1983), other factors could also be important in the maintenance and especially in the establishment of spider size asymmetry within colonies. Some individuals may extract or metabolize food more efficiently than others (Rypstra, 1993), or arrive faster at the consumption site (avoiding the
exploitation of an already unprofitable resource patch) (Willey & Jackson, 1993). Nevertheless, the relative importance of competitive interactions for food distribution, within spider cooperative groups, has only started to be evaluated, and *Anelosimus eximius* remains as the only really well studied species of this genus.

*Anelosimus jabaquara* is a subsocial spider species, from Southeast Brazil, which forms colonies composed of few to hundreds of individuals. Marques (1991) and Marques et al. (1998) investigated for the first time the social structure of this species and briefly described its hunting behaviour. They recorded that large females often attacked prey before the arrival of the smaller spiders and that females with different body sizes usually bite distinct prey body parts of varying nutritional value during consumption. These observations could indicate the existence of dominance hierarchies in *A. jabaquara*.

Gonzaga & Vasconcellos-Neto (2001) showed that the size of female *A. jabaquara* prior to the dispersal phase is an important factor determining emigration decisions and fecundity parameters. In this paper we examined the cooperative prey capture and feeding behaviours of *A. jabaquara* females in an attempt to investigate possible differences in food acquisition, the relation between attack and consumption and agonistic interactions among colony members. Based on Marques et al. (1998) observations, we expected large females to take part in the prey immobilization phase and assuming the most profitable positions (over prey’s thorax and abdomen) during the consumption, displacing smaller individuals to the appendages. Thus, we test whether spider size and participation in the initial efforts in prey capture may be important factors involved in biomass acquisition.

**Material and methods**

We studied a population of *A. jabaquara* located in the Serra do Japi, a protected subtropical humid forest which lies in the municipal district of Jundiaí (23° 11' S, 46° 52' W), state of São Paulo, Brazil.

Sixty three immature individuals were removed from a large colony, in May 1998. According to Marques et al. (1998) after May (reaching the 4th developmental stage) immature spiders are already capable of prey capture and, as female death occurs approximately at this time, predatory behaviour becomes essential to food acquisition. These spiders were classified into three weight classes: the first class was composed of individuals weighing between 0.4 mg and 0.8 mg (19 spiders), the second between 1.0 mg and 1.1 mg (25 spiders), and the last by individuals with more than 1.4 mg (19 spiders). We used these individuals to establish
three groups, each one composed of 3 small, 4 medium and 3 large spiders, selected by random sample. After this, spiders were individually marked with colored dots of enamel paint (Testors Co., Rockford, USA) and released in plastic cylindrical cages (300 ml), containing twisted wire and some dry leaves to supply web attachment and retreats. The same cages were previously used to keep adults in the laboratory and had already some web threads attached.

Behavioural observations were done, after 3 days for spider habituation to captivity, always between 18:00 and 20:00. Each group received one fly (Anastrepha sp., Thephritidae) every other day for 8 days. After prey introduction we recorded, for one hour, the number of spiders capturing and feeding upon it, the prey body segments attacked during prey immobilization (while the fly was still struggling) and consumption (after the end of prey movements), and the duration of each bite. The interval between each prey introduction and the limited time available to feeding were established to prevent spiders satiation. We used a tape recorder to allow continuous records.

The expected frequency of bites in each prey’s body segment was estimated by measuring the relative area available to be bitten in the head, thorax, legs, wings and abdomen of a fly. For this, each body segment was separated from the others and maintained for 24 hours in a solution of sodium hydroxide to dissolve the internal tissues. After this procedure, the exoskeleton of each segment was carefully divided in small planar segments that were drawn using a camera lucida. The drawings were digitalized and analyzed in the computer program ‘Area Measure’ Version 1.01 (Copyright 1995-1998 Hongu Akinori). To calculate the expected values, the total number of bites were multiplied by the proportional area of each segment in relation to total body area.

We compared the feeding time on the fly’s central body parts (head, thorax and abdomen), among spiders in different size classes, using one-way Anova. Each individual’s total feeding time was considered as a replicate. After this, we compared the proportion of consumption in head, thorax and abdomen among small, medium and large spiders performing Kruskal-Wallis tests.

We also made field observations of predatory behaviour in natural colonies. We registered 15 prey capture events, in September 1997, introducing one fly per previously identified and marked colony and recording all the capture and feeding behavioural sequences. We registered the number of spiders attracted during the first 2 minutes after prey introduction (considering as attracted every spider that moved toward the vibration source), the maximum number of spiders biting during prey immobilization and the maximum number of spiders feeding after the end of prey movements.

Results

Once entangled in the web’s threads, flies start a sequence of intermittent wing movements, until a few moments after receiving the initial bites. During this period the flies also move their legs vigorously, often touching other threads and promoting a strong vibration. The mean time between prey introduction and the end of its movements was 233.1 ± 176.3 seconds ($N = 12$) and the mean number of spiders taking part in the capture process was 4.45 ± 1.97 individuals ($N = 12$).
We observed 25 bites in the four prey immobilization records from group one, 37 from group two and 54 from group three, in a total of 116 bites. As the distribution of bite frequencies in body segments was significantly different from the expected in all groups (\( \chi^2 = 38.640, \text{df} = 4, p < 0.001 \) for group 1; \( \chi^2 = 10.580, \text{df} = 4, p < 0.05 \) for group 2; and \( \chi^2 = 29.379, \text{df} = 4, p < 0.001 \) for group 3), we used a heterogeneity chi-square analysis for replicated goodness of fit tests (\( \chi^2 = 10.602, \text{df} = 8, p > 0.10 \)) and calculated the total chi-square (\( \chi^2 = 67.999, \text{df} = 4, p < 0.001 \)) according to Zar (1996). The observed frequency of bites in the head, wings and abdomen seems to be similar to the expected frequency based on the available surface of these body parts. On the other hand, legs were bitten in a much higher frequency and thoraxes were rarely used (Fig. 1).

Analysing the consumption phase, the pattern seems to be inverse. The chi-square goodness of fit on the pooled data (\( \chi^2 = 2710.102, \text{df} = 4, p < 0.001 \)) regarding the consumption time of each body part shows that, once again, the observed distribution differs from the expected. In this case, however, appendages were rarely bitten (Fig. 2). Spiders of all weight classes spent a similar total consumption time over fly’s central body parts (\( F = 0.877, \text{df} = 25, p = 0.428 \)) (Fig. 3). There was no difference among spider size classes in the proportion of the time biting each one of the central body segments (\( H = 2.032, N = 28, p = 0.362 \) for head, \( H = 0.792, \)
Fig. 2. Proportion of time biting each prey body part during the consumption phase (after the end of prey movements).

Fig. 3. Mean total consuming time spent by spiders from each weight category in central body parts (head, thorax and abdomen) and in appendages (legs and wings).

\[ N = 28, \, p = 0.673 \] for abdomen, and \[ H = 0.385, \, N = 28, \, p = 0.825 \] for thorax.

The mean number of individuals feeding was \[ 7.50 \pm 1.98 \] (\[ N = 12 \]) in laboratory experiments. In all trials, some individuals that didn’t participate in prey capture fed upon the captured prey (‘intruders’), but almost all spiders were directly involved in at least one prey capture event. Four spiders (1 small and 3 medium) always behaved as ‘intruders’. In natural
Fig. 4. Relation between the time each spider spent biting during immobilization and consumption phases (where each is expressed as a percent of total duration of each phase). We considered the immobilization phase as the time between the first spider movement towards the prey and its immobilization, and the consumption phase as the time interval between prey immobilization and the end of observations (one hour after prey introduction).

colonies, many spiders were generally attracted when flies struggled against the web threads, but few of them contributed to prey immobilization biting or depositing silk around the prey. The mean number of individuals attracted until 2 minutes after prey introduction was $10.87 \pm 9.66$ ($N = 15$), biting during immobilization phase was $3.04 \pm 1.64$ ($N = 15$) and consuming was $13.21 \pm 9.35$ ($N = 15$). This latter value was statistically higher than the laboratory data ($t = 2.164$, df = 25, $p < 0.05$).

The spider’s initial weight did not appear to affect time spent consuming prey ($r^2 = 0.07$, $p > 0.05$, $N = 25$) in laboratory experiments. We did not observe agonistic interactions during prey consumption, but the displacement of individuals and conflicts involving removed prey body parts were observed many times in the field.

We found a positive, but weak, correlation between the proportion of time spent feeding and that invested in bites during the immobilization period (Pearson correlation, $r = 0.518$, $p < 0.01$, $N = 28$) (Fig. 4). Spiders which feed for a longer time, however, did not have a higher weight increase ($r^2 = 0.08$, $p > 0.05$, $N = 25$).

**Discussion**

The frequency of bites in each prey body part during prey immobilization is different from the results for *A. eximius*, especially in relation to bites in
the head and wings (see Souza, 1995). In *A. eximius*, wings were almost totally ignored and heads were bitten very often. In *A. jabaquara*, these segments were bitten according to the expected frequency by chance. Those differences could be due to variations in behavioural characteristics of flies used in each experiment (many unidentified species of flies in the case of *A. eximius* and only *Anastrepha* sp. for *A. jabaquara*).

Although bites in the head could increase the efficiency in subduing the prey, as suggested by Souza (1995), the recruitment of individuals to the capture site occurs mostly by the transmission of vibrations provoked by fly’s legs and, especially, wings movements. In this way, we expected that the number of bites in the legs and wings would be higher than in the central body parts if spiders used only the vibration source to guide them towards the bite position. The high intensity of wing flapping, however, could constitute a barrier to the correct positioning of the spiders and to the fixing of their fangs. So, it appears that, in *A. jabaquara*, spiders perceive the vibration and try to bite its source, being generally better succeeded on the legs.

Different prey types and body sizes will probably produce distinct vibration patterns (see McMahon & Bonner, 1986; Suter, 1978), attracting a larger or smaller number of individuals depending on vibration intensity and frequency (Riechert & Luczak, 1982). Capture of other prey types, such as crickets or wasps, could also include a higher risk of injury associated with some dangerous structures, such as the posterior legs and stings respectively (Souza, 1995). These parts could be therefore avoided or immobilized using silk threads prior to first bites. Thus, our results are restricted to the prey type we have tested.

Although they mainly bite appendages while subduing prey, spiders avoid these segments during prey consumption, using more profitable feeding sites. Thorax and abdomen, which probably contain the highest proportion of proteins and lipids, were mostly used. According to Ward & Enders (1985) the head may also be an important feeding site, containing resources more valuable than suggested by its weight, explaining why spiders spent so much time biting it. One should to consider that the time required to extract the same amount of food from each segment could also be different. The thorax appears to be the first body part from which spiders could feed, while the head requires a much higher investment for food extraction (Ward & Enders, 1985).
As observed for *Anelosimus eximius* (Souza, 1995), *A. studiosus* (Furey, 1998) and *Stegodyphus mimosarum* (Ward & Enders, 1985), the presence of medium or large prey items on *Anelosimus jabaquara* webs attracted ‘intruders’ — spiders that do not contribute to prey immobilization biting or entangling, but stay nearby and usually feed after the end of prey movements. According to Souza *et al.* (in prep.) this behaviour prevents the prey from escaping, and the interception of an insect that is almost escaping from the initial catchers, by these spiders, could be considered analogous to the ricochet effect ascribed to many colonial species (see Uetz, 1989).

The participation in prey capture may provoke risks of injury while the trapped insect is still struggling and, certainly, wastes of energy. Both effects are avoided or minimised by ‘intruders’, which feed only upon already subdued insects. However, at least in laboratory experiments, *A. jabaquara* individuals that arrived first and take part in capture (named ‘catchers’ or ‘producers’) seem to stay in contact with the prey body for a longer time. The same relation was also found for *Stegodyphus sarasinorum* groups (Willey & Jackson, 1993), but not for *A. eximius*. In this latter species, competitive interactions and the transport of prey body parts to retreats could be more important for obtaining food than participation during the attack (Vollrath & Rohde-Arndt, 1983).

However, it is still not possible to be sure if the ‘catchers’ advantage in time permanence relative to intruders also occurs in natural colonies, considering possible differences in the nutritional and motivational states of spiders in both conditions and, especially, in foraging group size and frequency of contests. Moreover, although significant, the correlation between time spent biting and feeding in our study was weak ($r = 0.518$) and we consider that the investment in prey capture could be one, but certainly not the only and perhaps not the more important factor influencing the consumption time.

It is important to note that the strategies of ‘intruders’ and ‘catchers’ were not fixed among individuals, except for 4 spiders (3 from group 1 and 1 from group 2) that always arrived after prey immobilization. We believe that these exceptions are due to the small number of prey introductions in each experimental group. Larger spiders did not avoid the involvement in prey capture, as was ascribed to large *A. eximius* females (Ebert, 1998; Vasconcellos-Neto *et al.*, 1995), which suggests that the stratification of the colony into high-ranking and low-ranking individuals in *A. jabaquara*, if
occurs, does not involve a behavioural task specialization concerning capture process.

We did not observe aggressive interactions during collective feeding and, as in other social spider species (see Vollrath & Rohde-Arndt, 1983), competition seems to occur through push-and-pull conflicts involving prey body parts and spider displacements from feeding positions, not through direct acts of aggression. In laboratory experiments even if all the spiders were feeding at the same time, they could find available sites to bite and conflicts were rare. Size differences among individuals does not seem to be an important variable determining feeding priorities in such situations. In natural colonies, however, when a greater number of individuals are participating in collective consumption, body size and/or weight could be more important to determine each spider’s success in biomass acquisition. It’s also important to consider that possible differences in the nutritional condition of spiders, in field and in laboratory, could have influence in the frequency and intensity of agonistic conflicts.

The lack of a relation between time spent feeding and gain in weight could be due to differences in the metabolism and/or food extraction ability of each individual, and also to the energetic expenses of those spiders which were involved in prey immobilization. These spiders, that usually fed for a longer time, may also have contributed a higher volume of digestive enzymes, spending part of the consumption time digesting tissues into resources available to be ingested (also by others). The total protein content in the digestive fluids released during feeding could amount to as much as 3.5% of a spider’s total body protein (Riechert & Harp, 1986). Thus, spiders which use other individuals’ investment in prey digestion can avoid a great expenditure and ingest an additional protein supply.

References


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