

## Fight or flight: agonistic interactions between females of *Acanthogonatus centralis* Goloboff 1995 (Araneae, Mygalomorphae)

Nelson FERRETTI<sup>1\*</sup>, Sofia COPPERI<sup>2</sup>, Gabriel POMPOZZI<sup>2</sup>

<sup>1</sup>Center for Parasitological Studies and Vectors, La Plata, Argentina

<sup>2</sup>Invertebrate Zoology Laboratory II, Department of Biology, Biochemistry and Pharmacy, National University of the South, Bahía Blanca, Argentina

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**Abstract:** Using a resident (R)–intruder (I) paradigm, 132 encounters between female *Acanthogonatus centralis* were investigated in order to study its intrasexual interactions and aggressiveness. We also examined the effect of presumed increased hunger levels on the incidence of killing and cannibalism. We selected 3 groups with different satiation levels: medium group (M), low group (L), and high group (H). Interactions took place in 79.54% of the trials. Aggression by lunges or bites was observed in 21.96% of encounters. Spiders made foreleg vibrations and touched the silk, which functioned as an aggression-attenuating mechanism. Other general behaviors observed include threat behavior and hug behavior. We found significant differences between charges and retreats in the following treatments: M(R)–M(I), L(R)–L(I), H(R)–H(I), and H(R)–M(I). During encounters we observed 9 cases of cannibalism between females. Interactions were predominantly nonaggressive, at least in the resident–intruder paradigm. Intraspecific predation was not a response to presumed increased hunger. Future approaches to agonistic behavior and cannibalism should include analyses of diet characteristics over longer periods and of experience in determining the outcome of encounters between adult females.

**Key words:** Mygalomorph spider, Nemesiidae, agonistic behavior, female–female interaction, Argentina

### 1. Introduction

Agonistic interactions between spiders take place in 2 basic scenarios: fighting between males to gain access to a female (Rovner, 1968; Dijkstra, 1969; Aspey, 1976, 1977; Austad, 1983; Suter and Keiley, 1984; Elias et al., 2008) and territorial conflicts (Buskirk, 1975; Ross, 1977; Riechert, 1978, 1979; Wise, 1983). Findings in game theory have shown that aggressive or agonistic encounters between conspecifics usually minimize and/or delay aggression, improving the individual fitness of the opponents (Maynard-Smith and Price, 1973; Maynard-Smith and Parker, 1976; Whitehouse, 1997). The tactic adopted is usually associated with differences in fighting ability and/or in rewards associated with winning. These characteristics determine an individual's probability of winning (Hodge, 1987). Game theory predicts that individuals involved in territorial conflicts will evaluate their own probability of winning and use a behavioral strategy suitable to their status (Parker, 1974; Hodge, 1987).

Nearly all studies of intraspecific encounters have focused on antagonistic interactions between males; however, female–female contests are also observed in some

taxa, for example in cichlids (Draud et al., 2004), whip spiders (Weygoldt, 1969, 2000; Fowler-Finn and Hebets, 2006), pied flycatchers (Dale and Slagsvold, 1995), and spiders (Nossek and Rovner, 1984; Hodge, 1987; Jackson and Whitehouse, 1989; Fernández-Montraveta and Ortega, 1990). Because males and females adopt different strategies to maximize reproductive success, selection has acted differentially on the sexes to result in different agonistic behaviors between males and females (Draud et al., 2004; Fowler-Finn and Hebets, 2006).

Additionally, the majority of studies of intrasexual contests have also centered on animals that rely primarily on vision, e.g., jumping spiders (Jackson and Whitehouse, 1989; Faber and Baylis, 1993; Taylor et al., 2001; Lim and Li, 2004). Under these systems, individuals begin displaying visually from a distance and only step forward for tactile displays and physical contact in extended contests (Davies and Halliday, 1978; Faber and Baylis, 1993; Neat et al., 1998). There are only a small number of studies on intraspecific encounters in nonvisual specialists (Paz, 1988; Jackson and Pollard, 1990; Pérez-Miles and Costa, 1992; Ferretti and Pérez-Miles, 2011), perhaps due

\* Correspondence: [nferretti@conicet.gov.ar](mailto:nferretti@conicet.gov.ar)

to difficulties related to studies in other sensory modalities or observer biases toward the importance of vision.

Mygalomorph spiders usually have life history characteristics that noticeably differ from those of other spiders. For example, they are habitat specialists and females and juveniles are sedentary (Main, 1978; Coyle and Icenogle, 1994). *Acanthogonatus centralis* Goloboff 1995 (Nemesiidae) is a mygalomorph spider that inhabits the hilly areas of central Argentina and constructs tunnel webs connected to a short burrow under stones. Ferretti et al. (2012) reported on the unusually high motility of adult males, females, and juveniles of this species in the field; thus the probability of encounter between females is highlighted.

In this study, we provided the first description of agonistic behavior in female *A. centralis*. Furthermore, a resident–intruder paradigm was used to examine interactions between female *A. centralis* in order to study its intrasexual aggressiveness. Finally, we examined the effect of presumed increased hunger levels on the incidence of killing and cannibalism.

## 2. Materials and methods

### 2.1. Specimens

Adult females of *Acanthogonatus centralis* were collected from Sierra de la Ventana (38°04'21.3"S, 62°03'02.6"W), Buenos Aires Province, Argentina, in 2010 and were housed individually in the laboratory in plastic petri dishes (90-mm diameter and 15-mm high), with soil as substratum and wet cotton wool. We used a 12-h light/dark cycle. The room temperature during breeding and experiments was 26.7 °C ± 1.52 °C. All individuals were housed in the laboratory for at least 1 year prior to experiments. All animals were fed 1 cockroach (*Blatella germanica*) of approximately 10 mm once a week for at least 2 months before experiments. Spiders were weighed 1 day before and after experiments with an Ohaus PA313 Explorer Precision balance (310 g, 0.001 g). Voucher specimens are deposited in the collection of the Laboratorio de

Zoología de Invertebrados II, Universidad Nacional del Sur, Argentina.

### 2.2. Experimental design

Three groups with 10 adult females per group were maintained prior to and during experiments. Each group was exposed to a different satiation degree: i) medium degree of satiation group (M), where each spider was fed 1 cockroach once a week 15 days prior and during the experimental period; ii) low degree of satiation group (L), where spiders were prohibited food 15 days prior and during the experimental period; and iii) high degree of satiation group (H), which spiders were fed 2 cockroaches per week 15 days prior to and during the experimental period. Total number of encounters (132) between females was examined using an intruder–resident paradigm. The different treatments were: M–M; L–L; H–H; M–H; H–M; M–L; L–M; H–L; L–H. Each individual was used as the resident and the intruder against 2 different females in each treatment. The average body length of females from the M group was 13.58 mm ± 2.09 SD, from the L group was 13.04 mm ± 2.15 SD, and from the H group was 14.64 mm ± 1.80 SD.

### 2.3. Experimental arena

All contests were run in a 2-chamber circular (9-cm diameter and 7-cm high each chamber) arena constructed of clear plastic connected to a plastic tube of 15-mm diameter and 4-cm length acting as a spider pathway. One spider designated as the resident and its petri dish were placed inside the left side of the arena along with its tunnel web (Figure 1). One hour after this, another spider, designated as the intruder, was introduced in the right side of the arena. At this point, both the resident and the intruder were allowed to encounter each other. All contests were videotaped using a Panasonic SDR-S7. The camera was positioned approximately 52 cm directly above the arena. Each encounter ended when a “losing” spider was identified (e.g., when either one of the opponents ran away from the rival or abandoned the interaction by moving backwards) or when cannibalism was observed.



Figure 1. Females *A. centralis* in their tunnel webs before experiments.

## 2.4. Data analysis

We conducted a Kruskal–Wallis test to compare differences in mean weights among groups. We used chi-square tests to compare frequencies of occurrences of each behavior between 2 samples. Aggressive behaviors included lunges or bites. Encounters without occurrence of these lunges or bites were defined as nonaggressive encounters. The predominance of these aggressive and nonaggressive encounters was tested using the chi-square test. All statistical analyses were performed using PAST version 1.89 (Hammer et al., 2001).

## 3. Results

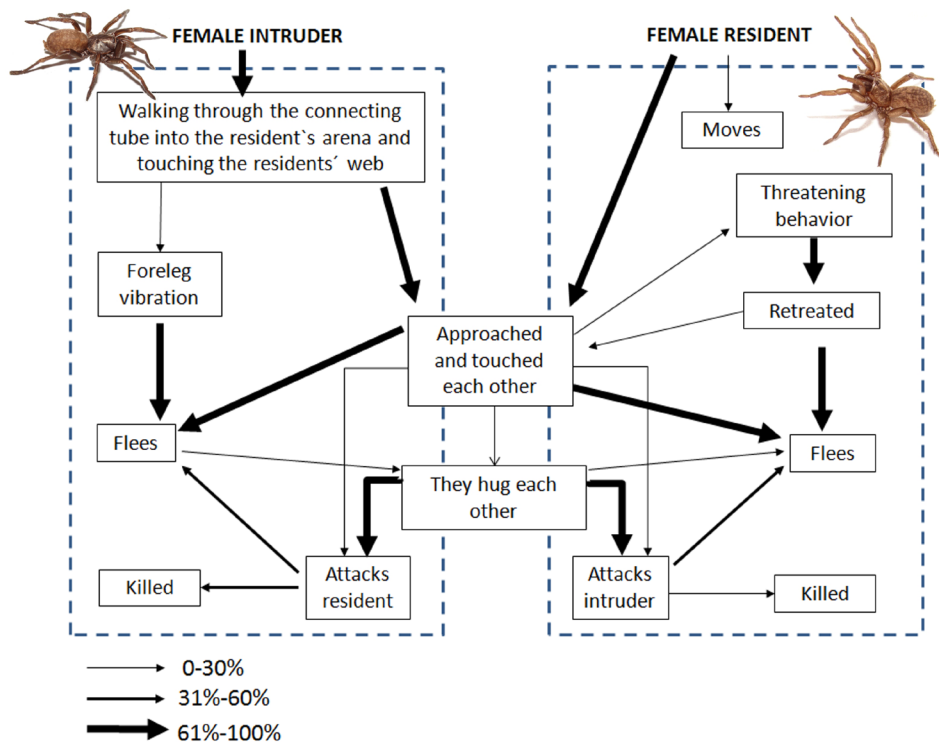
The spiders in the M group weighed  $0.25 \text{ g} \pm 0.05 \text{ SD}$  before encounters and  $0.30 \text{ g} \pm 0.06 \text{ SD}$  after experiments. Females in the L group weighed  $0.30 \text{ g} \pm 0.13 \text{ SD}$  before encounters and  $0.30 \text{ g} \pm 0.15 \text{ SD}$  after experiments. The spiders in the H group weighed  $0.33 \text{ g} \pm 0.08 \text{ SD}$  before encounters and  $0.38 \text{ g} \pm 0.12 \text{ SD}$  after experiments. We found significant differences in weights among the groups (Kruskal–Wallis,  $H = 6.93$ ,  $P < 0.05$ ,  $n = 30$ ). Weight variation during experiments was not significant in females from the L group; for example, 6 spiders lost between nearly 2.5% and 21% of their body weight, but some females gained about 1.2% to 3.5% of their body weight. In the M group, all spiders increased their body

weight, and females gained about 20% of their body weight (range = 8.5–27.1). Finally, in the H group, 1 female lost about 14% of her body weight, 4 females remained without significant changes in body weight, and 5 females gained approximately more than 30% of their body weight (range = 20.7–36.8).

### 3.1. General behaviors

Interactions took place in 105 of the trials (79.54%). When females of *A. centralis* engaged in encounters, a common pattern occurred (Figure 2). The general pattern began with the intruders walking through the connecting tube into the arena and touching the resident's web ( $n = 131$ ). In one instance, the resident moved first. After these first movements, in 7 cases, the intruders made foreleg vibrations, which include simultaneous vertical movements of the pair of legs whose tarsi touched the resident's silk, and in all cases intruder spiders retreated. The mean duration from the initial contact with the tunnel web to the resident female was  $89 \text{ s} \pm 137.22 \text{ SD}$ . After they made contact, some spiders made a threat behavior: gaping chelicerae with fangs extended and the carapace, palps, and the first 2 pair of legs raised (Figure 3a). Resident females made more threatening behavior than the intruder spiders ( $n = 105$ ,  $\chi^2 = 6$ ,  $P < 0.05$ ).

In most types of approaches involving contact between spiders, females of each pair approached and touched each



**Figure 2.** Flow diagram of the female–female interaction of *A. centralis* ( $n = 132$ ). Arrows indicate frequency.



**Figure 3.** a: Female *A. centralis* displaying threat behavior (fangs extended). b: Hug finished in cannibalism with female biting the female cephalothorax.

other with their forelegs. When the opponents reached the face-to-face position, they overlapped their forelegs, named “hug” behavior, and one spider of the pair either fled or lunged at its opponent. The mean duration of hug behavior was  $137.92 \text{ s} \pm 129.27 \text{ SD}$  ( $n = 14$ ). In this position, aggressive encounters involved physical injury, with chelicerae holding a part of the body of a spider and the fangs piercing the cuticle; in some cases cannibalism subsequently occurred (Figure 3b). On the other hand, after hug behavior, the intruder (in 12 encounters, 9.09%) or resident spider (in 16 cases, 12.12%) could abandon the interaction and flee. Nonaggressive encounters were preponderant (78.03%) ( $n = 103$ ,  $\chi^2 = 41.48$ ,  $P < 0.001$ ). Aggression (occurrence of lunges, bites, or cannibalism) took place in 29 encounters (21.96%).

### 3.2. Treatments

The frequencies of charges, retreats, hugs, and cannibalism between resident and intruder spiders during all treatments are shown in the Table. In M(R)–M(I) encounters, we observed more retreats by the resident spiders (Table) and one case of cannibalism from the intruder towards the

resident female. During L(R)–L(I) cases, resident females made more charges than the intruder females (Table). We observed 2 cases of cannibalism between female *A. centralis*: in the first, the intruder female bit the cephalothorax of the resident spider after hugging for about 150 s; in the second case, the resident lunged and bit the abdomen of the intruder female after 59 s of hugging. In H(R)–H(I) encounters, we found that resident spiders made more charges than intruders (Table). During H(R)–M(I) interactions, resident spiders made more charges than intruder females and consequently intruder spiders retreated more times than residents (Table). One case of cannibalism without previous hugging was registered, with the resident female biting the intruder’s cephalothorax. In M(R)–H(I), M(R)–L(I), L(R)–M(I), H(R)–L(I), and L(R)–H(I) encounters, we found no significant differences in occurrences of charges and retreats between resident and intruder females (Table). During the L(R)–H(I) treatment, 3 cases of cannibalism were observed, all of them after hugging. Resident females won in 2 cases, biting the intruder females, and 1 intruder spider won in 1 case over the resident.

**Table.** Frequencies of behaviors and results from the chi-square test between resident (R) and intruder (I) spiders in all treatments.

	M(R)–M(I)	L(R)–L(I)	H(R)–H(I)	M(R)–H(I)	H(R)–M(I)	M(R)–L(I)	L(R)–M(I)	H(R)–L(I)	L(R)–H(I)
Retreats	$\chi^2 = 13.5$ , $P < 0.001^*$	$\chi^2 = 3.66$ , $P = 0.05$	$\chi^2 = 0.02$ , $P = 0.86$	$\chi^2 = 1.81$ , $P = 0.17$	$\chi^2 = 4.73$ , $P < 0.05^*$	$\chi^2 = 1.2$ , $P = 0.27$	$\chi^2 = 0.09$ , $P = 0.76$	$\chi^2 = 0.4$ , $P = 0.52$	$\chi^2 = 0.39$ , $P = 0.53$
Frequencies	31 – 8	15 – 22	17 – 18	14 – 10	5 – 18	18 – 12	6 – 5	4 – 8	10 – 13
Charges	$\chi^2 = 2.66$ , $P = 0.10$	$\chi^2 = 6.44$ , $P < 0.05^*$	$\chi^2 = 6.42$ , $P < 0.05^*$	$\chi^2 = 1$ , $P = 0.31$	$\chi^2 = 4$ , $P < 0.05^*$	$\chi^2 = 1$ , $P = 0.31$	$\chi^2 = 3$ , $P = 0.08$	$\chi^2 = 1.6$ , $P = 0.2$	$\chi^2 = 2.66$ , $P = 0.1$
Frequencies	1 – 5	9 – 1	9 – 1	0 – 1	4 – 0	0 – 1	3 – 0	7 – 3	5 – 1
Frequencies of hugging	1	4	6	1	1	1	3	3	3
Cases of cannibalism	0 – 1	1 – 1	0 – 1	0 – 0	1 – 0	0 – 0	1 – 0	1 – 0	2 – 1

\* = Significant differences.



#### 4. Discussion

Observations of intruder leg beating behavior upon contact in a conspecific tunnel web suggest that some chemical cue may exist (Hodge, 1987; Jackson and Pollard, 1990). However, Vetter and Rust (2010) reported (based on silk with absence of a resident spider) that physical attributes of silk may be more important for selection of the refugia than the chemical aspects of the fresh silk. In our study, the intruder spider might have been more concerned with the live resident spider than the quality of the silk and its chemical cues; however, the chemical cues associated with silk threads that elicit a number of responses in mygalomorph spiders (mainly in males) have been widely reported (Costa and Pérez-Miles, 2002; Ferretti et al., 2013). The large number of retreats in response to leg beating performed by an opponent reflects the apparent effectiveness of leg beating in inhibiting closer approach (Nosseck and Rovner, 1984). The present study indicates that interactions between female *A. centralis* are predominantly nonaggressive, at least in the resident–intruder paradigm. When aggression (lunges, bites, or cannibalism) took place, it mostly occurred after the hug (one case of cannibalism was observed without previous hugging). However, in this species, the hug does not necessarily trigger aggression, since it also occurred in nonaggressive female–female encounters as was reported for other species (Stropa and Rinaldi, 2001; Stropa, 2007). Although few data are available for a tentative conclusion, the occasional occurrence of injury or death during a hug suggests that fighting behavior in female *A. centralis* is semiritualized (Nosseck and Rovner, 1984; Pérez-Miles and Costa, 1992; Ferretti and Pérez-Miles, 2011). Behaviors that restrain approach and/or attack by other females probably function as spacing mechanisms in the field, serving to maintain inter-individual distances and to reduce the possibility of being cannibalized.

The hug is possibly used by adult *A. centralis* females to evaluate fighting ability and/or the size of their opponents, allowing for a decision between fleeing and fighting (Turner and Huntingford, 1986; Stropa and Rinaldi, 2001) and probably functions primarily as a tactile display (Jackson and Pollard, 1990). If this is true, as stated by Stropa (2007): “the hug is an aggression-attenuating mechanism since it delays aggression and, as a consequence, improves individual fitness.” This portrayal could be expected when asymmetric animal contests occur (Maynard-Smith and Price, 1973; Maynard-Smith and Parker, 1976; Whitehouse, 1997).

As had been determined for other spiders (Jackson, 1980; Riechert, 1981; Nossek and Rovner, 1984), intraspecific predation was not a response to presumed

increased hunger, under the conditions we established in this mygalomorph spider. Moreover, we observed cases of cannibalism in 7 of the different 9 treatments analyzed in this study. All treatments with spiders in equal conditions of hunger showed cannibalism, and even spiders of the H–H group presented one case of cannibalism. Resident spiders cannibalized intruder females in 6 cases from the total of 10 cannibalisms. This could be in relation to a more aggressive behavior exhibited by resident spiders, as was proposed for a Dipluridae species (Paz, 1988) and other animals (Maynard-Smith, 1974; Hammerstein, 1981). However, not all encounters finished quickly in favor of the resident spider. Moreover, we found that in M–M treatments, the resident spiders retreated in more cases. In L–L and H–H treatments, the number of charges from resident spiders was significantly higher than intruders, and in H–M the residents made more charges and intruders retreated in many cases. Given that it is known that spiders are well-adapted and can resist to long periods of food deprivation (Anderson, 1974), a starving spider may not be any more likely than a satisfied spider to prey upon a similar size conspecific (Nosseck and Rovner, 1984). Furthermore, because of its possibly reduced fighting potential, it might even be less likely to attack. While most females in the different treatments were not observed engaging in cannibalism, several spiders cannibalized more than once each. Perhaps some individuals have an advantage over others due to higher levels of aggressivity (Fernández-Montraveta and Ortega, 1990). Dominance shown by an individual must depend on more than just hunger level differences (which we had controlled in our groupings) as was reported by Fernández-Montraveta and Ortega (1990).

Widespread field studies that explore aspects of natural history and behavior are necessary to represent a more decisive scenario about the selective forces acting on contests in *A. centralis*. Moreover, further investigation of the natural history of *A. centralis* would provide a good framework within which their semiritualized fighting behavior can be studied. Future approaches to agonistic behavior and cannibalism in spiders should include analyses of diet characteristics during a more extended period and of experience with fighting in determining the outcome of encounters between adult females.

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