

Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*

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Abstract

Cannibalism can have important demographic and ecological effects on populations. Typically, cannibalism is size-structured, where larger individuals eat smaller conspecifics. Initial cursory observations of the whip spider, *Phrynus longipes*, however, suggested that cannibalism might not be size-structured in this species, perhaps because cannibalism is often a by-product of territory contests. We staged paired interactions and recorded latency to escalate to physical aggression or cannibalize to understand the dynamics of cannibalism and resource contests. We employed a multimodel comparative approach to tease apart the contest characteristics that best predicted cannibalism during behavioral trials between *P. longipes* opponents. We found that, while armament size symmetry predicted escalation of contests, cannibalism was best predicted by body mass asymmetry. Further, cannibalism was most likely to occur among individuals similar in armament, but dissimilar in body mass. This suggests a discrepancy between phenotypes that may have evolved to communicate resource holding potential (e.g., armaments which benefit individuals if dishonest), and body mass as a cue of resource holding potential.

KEYWORDS

Arachnida, resource contests, resource holding potential, size-structured, speleology, whip spider

1 | INTRODUCTION

Cannibalism can shape both the demography of populations and phenotypes of individuals (Polis, 1981). Asymmetric cannibalism (sometimes termed size-structured cannibalism), in which larger individuals prey on smaller conspecifics, is the norm (Claessen, de Roos, & Persson, 2004; Gurtin & Levine, 1982; Polis, 1981). This is likely because the energetic cost of handling larger prey is greater than that required of small prey (Park, Jeong, & Park, 2005). Asymmetric cannibalism may also stabilize the amplitude of population size variation (Claessen et al., 2004) by reducing intraspecific competition and providing an alternative food source when resources are limited (van den Bosch, de Roos, & Gabriel, 1988; Diekmann, Gyllenberg, & Metz, 2003; Landahl & Hansen, 1975). One review found that, of 30 papers with population models that included cannibalism, all focused on asymmetric cannibalism (Claessen et al., 2004).

Symmetric cannibalism, where individuals prey on conspecifics more similar to their own size, has received little attention (Kohlmeier & Ebenhoh, 1995; Polis, 1981). Polis (1981) asserted that, while reversals of traditional size structure may occur, there is yet no theoretical or otherwise explanatory framework for why such a paradigm would occur (Polis, 1980; Rose & Armentrout, 1976). The paucity of literature in this area is not altogether surprising inasmuch as cannibalism has only recently been considered an important part of understanding population dynamics and that symmetric cannibalism is apparently very rare (Diekmann, Nisbet, Gurney, & van den Bosch, 1986; Dong & DeAngelis, 1998; Huston, DeAngelis, & Wilfred, 1988; Kohlmeier & Ebenhoh, 1995).

Phrynus longipes (Arachnida: Amblypygi: Phrynidae) is a species of amblypygid—an order of cannibalistic, nocturnal, and territorial arachnid (Chapin & Hebets, 2016). Agonistic interactions between pairs of *P. longipes* escalate in a predictable pattern, similar to other amblypygid

species (Chapin, 2015; Chapin & Hebets, 2016; Fowler-Finn & Hebets, 2006). Amblypygi are outfitted with elongate forelegs replete with sensory receptors (Santer & Hebets, 2011; Weygoldt, 2000). These antenniform legs are used to sense the environment and communicate with conspecifics (Chapin & Hill-Lindsay, 2016; Chapin & Hebets, 2016; Spence & Hebets, 2005). Amblypygids are also equipped with spiny pedipalps used to capture prey and communicate threat displays (Weygoldt, 2000).

We predicted that *P. longipes* showed no preference for cannibalizing smaller conspecific prey because cannibalism in this species is a result of territorial competitions that escalate to agonism (Chapin, 2015; Chapin & Hebets, 2016; Torres-Contreras, de Armas, & Alvarez-Garcia, 2015). When a conspecific enters an individual's territory, a set of ritualized agonistic interactions begin that can end in cannibalism (Chapin, 2015; Chapin & Hebets, 2016; Chapin & Hill-Lindsay, 2016). Opponents orient to each other and present displays by opening large, often sexually dimorphic, pedipalps. If contests are not decided by displays, opponents escalate to physical contact, which may end in injury or cannibalism if an opponent does not retreat (Chapin, 2015; Chapin & Hebets, 2016). Behavioral assays investigating territorial behavior in *P. longipes* found that, when territorial agonism ended in cannibalism, it was often among similarly sized individuals (Chapin & Hill-Lindsay, 2016). The only other report of cannibalism in any amblypygid was *Phrynos barbadensis* in Colombia cannibalizing a recently molted conspecific (Torres-Contreras et al., 2015). This is not to imply that cannibalism is rare among Amblypygi, only that it is rarely documented and poorly understood.

In general, territorial contests escalate according to the relative resource holding potentials (RHP), or absolute fighting abilities, of opponents (Chapin & Hill-Lindsay, 2016; Parker, 1974). Resource holding potential is usually estimated by proxies such as body size, body mass, or armament size (Koskimäki, Rantala, Taskinen, Tynkkynen, & Suhonen, 2004). Game theory models for animal contests predict that individuals with more similar RHP are more likely to escalate interactions to aggressive and risky states (Barlow, Rogers, & Fraley, 1986). A variety of measures are used to estimate RHP, including body size, mass, and armament used during interactions. Armament used in agonistic displays, however, is subject to selection for exaggeration and dishonest signaling (Dawkins & Guilford, 1991). For example, male crayfish (*Cherax dispar*) preferentially allocate energy to claw growth instead of strength when claw size is used as an indicator of performance in agonistic contests (Wilson, Angilletta, James, Navas, & Seebacher, 2007). Therefore, armament measures may not give an accurate estimate of fighting ability. Measures of body size or mass, however, generally provide more honest indicators of RHP (Bath, Wigby, Vincent, Tobias, & Seddon, 2015; Morris, Gass, & Ryan, 1995; Theis, Bosia, Roth, Salzburger, & Egger, 2015).

We hypothesized that cannibalism occurs in *P. longipes* as a consequence of territorial contests and aggression and as such presents an opportunity to expand on our understanding of cannibalism. We aimed to address the following questions using the amblypygid *P. longipes*: (i) What morphological features best predict cannibalism during territorial contests? (ii) Do those features also predict if the contest

will escalate to physical aggression? (iii) If not, how do those features differ and do they interact?

We analyzed data collected from behavioral interactions between *P. longipes* pairs to investigate what measures best predict cannibalism and escalation to physical aggression in *P. longipes* territory contests. We observed interactions in a controlled environment and recorded behavioral and morphological data. We compared RHP measures of opponents to understand cannibalism during resource contests in staged trials.

2 | METHODS

In August 2012 and 2014, we collected *P. longipes* between 1000 and 0400 hr from forests and caves in Arecibo, Puerto Rico, generally located at 18.414°, -66.726°. Cannibalism was occasionally seen in the wild while collecting animals, indicating that this behavior occurs outside of our experimental conditions (Figure 1). We measured the mass of each individual with a gram scale to the nearest 0.01 g, maximum prosoma width as an estimate of body size and pedipalp femur length as a measure of armament with digital calipers to the nearest 0.01 ± 0.03 mm. We housed animals separately for 24 hr in black polypropylene deli containers (14 cm tall, 11.5 cm top dia, 9 cm base dia) lined with butcher paper substrate prior to trials. We returned surviving individuals to their capture site after experimentation.

Behavioral trials ($n = 48$) were conducted sensu Chapin (2015). Arenas were made from 75 × 30 × 30 hr cm glass aquaria divided into two equal parts with a removable acrylic sheet. The arena floor was lined with unbleached paper to provide traction for movement. Individuals were restricted to movement on the arena floor (*P. longipes* cannot climb glass). We randomly selected individuals



FIGURE 1 Photograph of symmetric cannibalism of *Phrynos longipes* in a cave near Arecibo, Puerto Rico

to engage in paired interactions. Thus, contestant pairs included a variety of size and sex combinations. Once individuals were placed in the arena, we implemented a 10-min acclimation period before removing the divider to permit interactions for 45 min. Amblypygids reliably engage in agonistic interactions similar to these under natural conditions, and animals behaved typically compared to observations of natural interactions (Chapin & Hebets, 2016; Weygoldt, 2000). We replaced paper and cleaned enclosures with 70% isopropyl alcohol between trials.

Behavioral trials were video-recorded in darkness and at night under 940 nm peak wavelength infrared LED (light emitting diode) lights with a modified CCD (charge coupled device) camera with its infrared bypass filter removed and fixed focus lens recording 640 × 480 p at 30 fps. We recorded if individuals escalated to physical aggression or cannibalized during the 45-min trial. Aggression was identified by individuals engaging in physical contact with pedipalps or chelicerae, while cannibalism was identified by one opponent killing and beginning to consume the other. Individuals were only used in one trial, and researchers were blind to animal identity for all measures.

We compared logistic regressions to test whether the difference in body size, body mass, armament size between opponents or an interaction of those measures best predicted escalation to physical aggression and cannibalism (Burnham, Anderson, & Huyvaert, 2011; Richards, Whittingham, & Stephens, 2011; Symonds & Moussalli, 2011). Armament size was measured using pedipalp femur length. We compared this global model and simpler versions using Akaike's information criterion corrected for small sample sizes (AICc) and Akaike's weights (w_i ; see Wagenmakers & Farrell, 2004). Akaike's weights can be thought of as the estimated probability that a given model is the best relative to all models considered. We compared body size, body mass, and armament size between interactions that

did or did not escalate to physical aggression or end in cannibalism using Wilcoxon and Student's t -tests, depending on data normality. Lastly, we tested whether sex impacted the proportion of individuals that escalated or cannibalized with a chi-square test.

3 | RESULTS

Escalation was best predicted by armament size, while cannibalism was best predicted by the interaction of armament size and mass (Table 1; $n = 48$ paired trials). Interestingly, the direction of these relationships reverse; interactions were more likely to escalate among size-symmetric pairs, but more likely to end in cannibalism for size-asymmetric pairs (Table 2; Figure 2). This effect is exacerbated among pairs that both escalated and cannibalized (Figure 3). Individuals were more likely to cannibalize if the agonistic interaction escalated (16.5% of 34 escalated trials) than if they did not (11.8% of 164 non-escalated trials). Of those pairs that did escalate, the individuals that cannibalized were larger (15.57 ± 0.43 mm vs. 11.06 ± 0.55 mm; $t_{55} = 6.46$, $p < .001$) and of greater mass (2.85 ± 0.17 g vs. 1.00 ± 0.13 g; $t_{54} = 8.58$, $p < .001$) than individuals that did not cannibalize (Table 2; Figure 4). Lastly, we did not detect a difference in the proportion of males and females escalating or cannibalizing (escalation $\chi^2_1 = 0.033$, $p = .855$; cannibalism $\chi^2_1 = 0.013$, $p = .910$).

4 | DISCUSSION

Weapon size symmetry predicted escalation and body mass asymmetry predicted cannibalism in pairs that escalated during interactions.

TABLE 1 Multimodel comparisons of logistic regressions of the difference of size, mass, and armament between opponents in paired trials predicting cannibalism and escalation

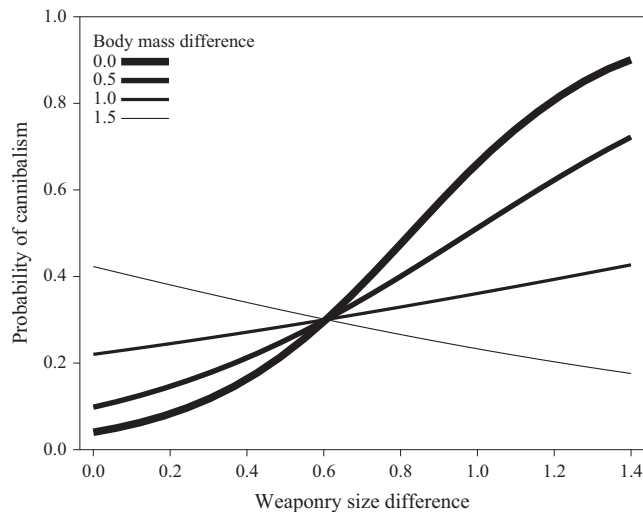
| Models | Cannibalism | | | | Escalation | | |
|------------------------|-------------|--------|---------------|--------------|------------|---------------|--------------|
| | k | AICc | Δ AICc | w_i | AICc | Δ AICc | w_i |
| Size × mass × armament | 7 | 171.38 | 7.54 | 0.008 | 180.22 | 9.47 | 0.002 |
| Size × mass | 3 | 164.20 | 0.35 | 0.303 | 174.06 | 3.32 | 0.047 |
| Size × armament | 3 | 165.47 | 1.63 | 0.160 | 172.79 | 2.04 | 0.089 |
| Mass × armament | 3 | 163.85 | 0.00 | 0.361 | 172.30 | 1.56 | 0.114 |
| Size + mass + armament | 3 | 170.03 | 6.18 | 0.016 | 174.75 | 4.01 | 0.034 |
| Size + mass | 2 | 168.18 | 4.33 | 0.041 | 173.73 | 2.98 | 0.056 |
| Size + armament | 2 | 172.40 | 8.556 | 0.005 | 172.73 | 1.99 | 0.092 |
| Mass + armament | 2 | 168.69 | 4.86 | 0.032 | 172.71 | 1.96 | 0.093 |
| Size | 1 | 170.86 | 7.02 | 0.011 | 171.81 | 1.06 | 0.146 |
| Mass | 1 | 168.98 | 5.13 | 0.028 | 170.74 | 2.32 | 0.078 |
| Armament | 1 | 170.42 | 6.57 | 0.013 | 173.06 | 0.00 | 0.248 |
| Intercept only | 0 | 169.44 | 5.59 | 0.011 | 182.47 | 11.72 | 0.001 |

Size was estimated by maximum carapace width (mm), mass was estimated by total body weight (g), and armament was estimated by pedipalp femur length (mm). The model that included an interaction of mass and armament was the best predictor of cannibalism. A model that included only the difference in armament was the best predictor of escalation, followed by the interaction of mass and armament (indicated in bold; $n = 198$).

TABLE 2 Estimates of the best-fitting logistic regression predicting cannibalism or escalation

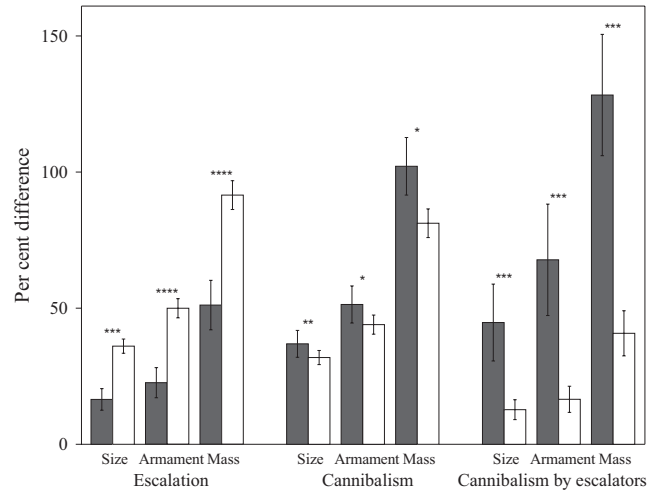
| Parameter | Estimate ± SE | z | p |
|------------------------|---------------|-------|------|
| Predicting cannibalism | | | |
| Mass | 1.91 ± 0.77 | 2.489 | .013 |
| Armament | 3.84 ± 2.22 | 1.73 | .083 |
| Mass × armament | -3.15 ± 1.20 | 2.62 | .009 |
| Predicting escalation | | | |
| Armament | -2.03 ± 0.66 | 3.06 | .002 |

The best model predicting cannibalism included the proportional difference in body mass (mm), armament (mm), and their interaction, while the best model predicting escalation included only the proportional difference in armament.

**FIGURE 2** Interaction plot of a logistic regression of the interaction of body mass and armament size predicting cannibalism (estimate ± SE: -3.15 ± 1.20 , $z = 2.62$, $p = .009$). Line thickness indicates one of four body mass values

This illustrates that the unusual pattern of symmetric cannibalism found in *P. longipes* can be explained by a two-stage interaction. In the first stage, size symmetry in armament drives the interaction to greater levels of escalation. In the second stage, already escalated interactions are driven to cannibalism by asymmetry in body mass. Although animals behaved as expected in the wild, the study was conducted under laboratory conditions; this type of cannibalism may be less common in natural populations. The first stage is consistent with game theory models predicting a negative relationship between contest escalation and the difference in RHP among opponents (Arnott & Elwood, 2009; Barlow et al., 1986). The second stage is consistent with models of asymmetric cannibalism, which predict that larger individuals should consume smaller conspecifics (Claessen et al., 2004). When interactions escalated such that cannibalism could occur, the individual with smaller body mass fell prey to the larger opponent.

Pedipalps, which advertise RHP, were the best predictor of escalation, although pedipalp size did not predict cannibalism (Table 1). Displays are open to both higher error and dishonest signaling than

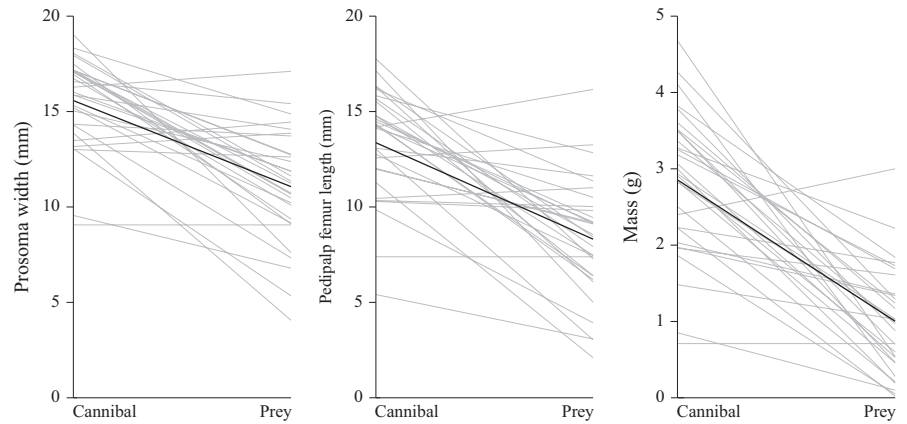
**FIGURE 3** Mean per cent difference in body mass, size, armament, and scaled mass index (SMI) for trials that did (gray bars) or did not (white bars), progress to escalated agonism, ended in cannibalism and, progress to escalated agonism and ended in cannibalism ($n = 198$). Whiskers indicate standard error of the mean. Number of asterisks indicates $p < .1$, $.05$, $.01$, or $.001$ for Wilcoxon tests

measures of body mass (van Staaden, Searcy, & Hanlon, 2011). Thus, while armament used in display was the best predictor of contest escalation, it was a poor predictor of cannibalism. Instead, cannibalism was best predicted by an interaction of mass and armament or, to a lesser extent, mass and size—models which both include estimates of individual body mass or fat stores (Table 1, Figure 3). These measures more closely estimate the actual RHP of opponents compared to display armament. This too matches some game theory models (e.g., war of attrition, sequential assessment; Smith, 1974; Parker & Thompson, 1980), where information error decreases as the contest escalates (Smith, 1974; Enquist, Leimar, Ljungberg, Mallner & Segerdahl, 1990).

Contests between *P. longipes* are resolved by either an individual retreating or being eaten. Such contests have very high risk. Thus, it would benefit individuals to assess rather than engage their opponents. Opponents will proceed with a series of ritualized displays, and only after a predictable progression does aggression begin (Chapin, 2015; Cullen, 1966). We found that RHP-symmetric opponents are more likely to escalate an agonistic interaction. This is consistent with ecological models of intraspecific contests (Arnott & Elwood, 2009; Kemp & Wiklund, 2001). If agonism proceeds to a level of aggression high enough to allow the winner to kill the loser, the body of the loser presents a feeding opportunity (Crump, 1983). The combination of escalation to lethal aggression and opportunistic predation, both phenomena observed in *P. longipes*, are consistent with our findings (Chapin, 2015). Further, we find no differences in the rate of escalation of cannibalism between sexes. This is likely because the contested resource (a territory, see Chapin & Hill-Lindsay, 2016) is valuable to both sexes.

This study models cannibalism as it occurs under laboratory settings, but symmetric cannibalism has been observed in the field (Figure 1). That said, there is little known about the specific circumstances

FIGURE 4 Comparison of carapace width (mm), pedipalp femur length (mm), and mass (g) of *Phrynus longipes* pairs that either cannibalized or were prey to cannibals in paired trials. Gray lines represent one pair that ended in cannibalism. Thick black line represents the mean. Cannibals were larger, more massive, and had a higher scaled mass index than conspecific prey ($t_{55} = 6.46, p < .001$; $t_{54} = 8.58, p < .001$; $t_{57} = 6.50, p < .001$)



under which symmetric cannibalism may occur in natural populations. Ecologists have modeled how size-structured cannibalism occurs and what role, if any, it plays in the stabilization of populations (Claessen et al., 2004). We caution against applying traditional population models of asymmetric cannibalism to *P. longipes* and other animals that might exhibit symmetric cannibalism. Symmetric cannibalism in this species is caused by an interaction of cannibalistic behavior with territory contests. This has interesting implications for the ecological role that cannibalism plays in this population. While it intuitively seems that symmetric cannibalism can have population-level effects, the population dynamics of species that exhibit this phenomenon remain unstudied. This is not to say that RHP similar cannibalism has no important impact; we assert only that it is poorly understood but structurally dissimilar to traditional cannibalism models. We are just beginning to understand the importance of RHP-symmetric cannibalism. Research on this phenomenon will expand our understanding of population dynamics and the evolution of both contest and cannibalism behavior.

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