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Behavioral ecology of cave and epigean Phrynus longipes

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Behavioral ecology of cave and epigean *Phrynus longipes*

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in Biology

by

Kenneth James Chapin

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ABSTRACT OF THE DISSERTATION

Behavioral ecology of cave and epigean *Phrynus longipes*

by

Kenneth James Chapin

Doctor of Philosophy in Biology

University of California, Los Angeles, 2016

Professor Peter Nicholas Nonacs, Chair

Behavioral researchers using Amblypygi have noted the regularity at which species engage in agonistic interactions. Despite this, why agonistic interactions occur and how they are resolved is unknown. I conducted paired interactions of the amblypygid *Phrynus longipes* in Puerto Rico to understand the dynamics of agonistic interactions. Through a series of analyses, I found that agonistic interactions are territory contests common across the demographic range of the species. Further, I decoded the strategy that opponents use to negotiate contests, and used resource contests to explain the peculiar pattern of cannibalism that this species exhibits. I used these results to identify the variation in contests and other behavioral phenotypes across cave and surface populations. This research broadens theory of resource contest evolution and behavioral variation by investigating phenomena in a non-model study system.

The dissertation of Kenneth James Chapin is approved.

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Chapin KJ. 2014. Microhabitat and spatial complexity predict group size of the whip spider *Heterophrynus batesii* in Amazonian Ecuador. Journal of Tropical Ecology 30(2):173–177.

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CHAPTER 1: Behavioral ecology of amblypygids

Chapin KJ, Hebets EA. 2016. Behavioral ecology of Amblypygi. Journal of Arachnology 44:1–14. Reproduced with permission.

1.1 Abstract

Arachnologists have uncovered tantalizing details about amblypygid behavioral ecology—the study of the fitness consequences of their behavior. Thus, it is the aim of this review to position Amblypygi as a useful system in which to investigate the principles of animal behavioral ecology. We synthesize amblypygid habitat preference and navigation modalities; predator, prey, parasite, parasitoid, cannibal, and commensal interactions; resource contests and territoriality; mating systems and mate choice; parental investment and sociality; and genetics and genomics as they relate to behavioral ecology. We present ideas for future research in each of these areas and discuss future directions for Amblypygi behavioral ecology research as they relate to four areas of behavioral ecology: adaptation, evolutionary history, mechano-sensory control of behavior, and behavioral development. We conclude by identifying several avenues of Amblypygi behavioral ecology that we think have the highest potential for transformative discoveries.

Keywords: *Damon*, cannibalism, fitness, *Heterophrynus*, microhabitat preference, navigation, *Paraphrynus*, *Phrynus*, tailless whip scorpions, territoriality, whip spiders

1.2 Forward

> "Whip spiders are bizarre yet spectacular animals… Their appearance is so horrible that many of the local people are extremely afraid of them and consider them to be poisonous and dangerous. Even the first European scientists had similar views…. To me, however, these creatures do not appear horrible; rather they are extremely fascinating."
>
> – Peter Weygoldt (2000, p. 9)

Scientists have long been intrigued by the behavior of animals. Behavioral ecologists and animal behaviorists in particular are interested in the fitness consequences of behavior (Birkhead & Monaghan 2010); in how selection pressures ranging from an organism's abiotic environment to its inter- and intraspecific interactions ultimately shape morphology and behavior. The history of these fields shows that scientists are drawn toward the study of evolutionary paradoxes that animals reveal through their behavior. For example, classic questions in ethology and behavioral ecology include why eusocial insects forgo reproduction (Hamilton 1964), why some birds display such vibrant plumage (Fisher 1915; Zahavi 1975) or why male lions kill cubs (Parker 1979). We posit that amblypygids (Class Arachnida, Order Amblypygi) offer exceptional behavioral phenomena whose further study could contribute substantially to our understanding of animal behavior and its evolutionary relationships with morphology and sensory physiology.

The new century has seen the proliferation of tantalizing behavioral studies on amblypygids (Fig. 1.1), providing a solid foundation from which future work can build. For example, researchers have discovered that some amblypygid species exhibit initial levels of sociality (Rayor & Taylor 2006), individual-level recognition (Walsh & Rayor 2008), tactile learning (Santer & Hebets 2009a), and intraspecific behavioral divergence (Chapin 2015; Fig. 1.1). Further, research on the physiology, neuroanatomy, and sensory biology of Amblypygi (reviewed in Santer & Hebets 2011a) has opened the doors for investigations connecting proximate and ultimate mechanisms (sensu Tinbergen 1963), improving our understanding of the evolution of specialized sensory systems and associated behavior. The purpose of this review is to synthesize and outline the history of Amblypygi behavior research as a means of stimulating future work on these remarkable organisms. It is our view that Amblypygi are both fascinating organisms and excellent study systems for many questions in behavior, especially those addressing evolutionary relationships between sensory systems, neurophysiology, and complex behavior, as well as those focused on the role of the environment in behavioral divergence.

1.3 Introduction to the order

1.3.1 Diversity and evolutionary relationships

To date, within the arachnid order Amblypygi, there are approximately 151 extant named species divided among 17 genera and 4 families (Harvey 2002, 2003; Beccaloni 2009; ITIS 2015; Fig.

1.1). Amblypygi form a monophyletic group with Schizomida (short-tailed whip scorpions) and Thelyphonida (vinegaroons) called the Pedipalpi. These three orders together with Araneae form the clade Tetrapulmonata (Shultz 1990, 2007; Wheeler & Hayashi 2005; Regier et al. 2010). Fossil Amblypygi date to 312 mya, placing their divergence from Araneae prior to the Upper Carboniferous (Dunlop 1994, 2011; Dunlop & Martill 2002).

1.3.2 External morphology

Amblypygids have dorso-ventrally flattened bodies, orthognathous chelicerae, raptorial pedipalps, and a front pair of extremely elongate legs (Fig. 1.2). The front legs are not used for locomotion, but serve as specialized sensory structures adorned with thousands of sensory organs (reviewed in Santer & Hebets 2011a). All legs, including the antenniform first pair, autotomize at the patella-tibia joint using muscles specialized for this purpose. Similar to some spiders and contrary to all harvestmen (Gnaspini & Hara 2007), amblypygid limbs regenerate with ecdysis (Weygoldt 1984, 2000). Amblypygi have eight ocelli (except some troglomorphic forms) in three groups (two lateral, one medial) and all species are nocturnal (Beck & Pabst 1969; Beck 1972; Weygoldt 2000).

1.3.3 Sensory physiology and neuroanatomy

A recent in-depth review of amblypygid sensory physiology provides both an overview and specific details regarding the current understanding of amblypygid sensory physiology and how their unique sensory adaptations may be related to their natural history and behavior (Santer & Hebets 2011a). Briefly, distinct sensory organs on the legs of amblypygids can detect a variety of substrate-borne and airborne chemical and mechanical cues (Beck et al. 1974, 1977; Foelix et al. 1975; Foelix & Troyer1980; Hebets & Chapman 2000a; Santer & Hebets 2008, 2009a, b, 2011a, b) including near-field particle velocity (Robert & Hoy 2007; Santer & Hebets 2008, 2011b) and substrate texture (Santer & Hebets 2009a). Details of these sensory structures and their putative functions were reviewed in Santer & Hebets (2011a). Amblypygids also possess giant interneurons that connect receptor cells to the central ganglia allowing for an extremely fast pathway of information (Foelix & Troyer 1980; reviewed in Foelix & Hebets 2001, Spence & Hebets 2006). This pathway seems important for several context-specific roles in Amblypygi behavior (reviewed in Santer & Hebets 2011a).

The central ganglia of amblypygids also include the largest mushroom bodies of any arthropod, relative to their body size (Strausfeld et al. 1998). Mushroom bodies are higher brain centers located in the first brain segment of all arthropods and their common ancestors (Kenyon 1896; Strausfeld et al. 2006; Brown & Wolff 2012; Strausfeld 2012; Wolff et al. 2012). In insects, they are important in contextual information processing, learning, and memory (fruit flies: de Belle & Heisenberg 1994; Zars et al. 2000; Pascual & Preat 2001; Heisenberg 2003; honey bees: Erber et al. 1980, Menzel 2001; cockroaches: Mizunami et al. 1998). Compared to insects, lobes of amblypygid mushroom bodies are extraordinarily large and elaborately folded and are hypothesized to be associated with complex behavior such as multisensory integration during homing (Hebets et al. 2014a, b).

1.3.4 Reproductive physiology and life history

Males transfer sperm to females using a spermatophore that they attach to the substrate for females to pick up with sclerotized claspers (gonopods) on their genitalia (Weygoldt 2000). Oviposition occurs weeks to months later, after which females carry eggs inside an eggsac located on the ventral surface of their opisthosoma (Fig. 1.3c; Weygoldt 2000). Young hatch from eggs after about three months. Young molt, emerge from the eggsac, and move to the dorsal surface of the mother's opisthosoma (Fig. 1.3d) before molting again, after which they are free-living. The amblypygid lifespan is not well known, but larger species can live over 10 years in captivity (Weygoldt 2000). They are the only order of arachnid in which all species exhibit post-ultimate molts. Across the Arachnida, post-ultimate molts occur in only a few spider groups (Kraus & Kraus 1988; Coddington & Levi 1991; Vetter 2011), and usually only females continue to molt. They occur in tropical through temperate regions throughout the world, where they represent primary and secondary predators (Beccaloni 2009).

1.4 Environmental interactions

1.4.1 Microhabitat use and preference

Amblypygi are found throughout tropical and subtropical zones across all continents (Fig. 1.1). Species distributions are generally limited to latitudes where freezing temperatures are rare. Within this climate zone, amblypygids inhabit a variety of ecosystem types, from tropical wet forests to xeric deserts, caves, and island environments. Like many other organisms, amblypygids show preferences for specific microhabitats (Table 1). In common across studied Amblypygi is the occupation and defense of small areas around a single refuge. Refuges typically follow a shape suitable to accommodate the dorso-ventrally flattened amblypygid body form such as in cracks and crevices in cave walls (Chapin 2015) or in tropical tree buttresses (Hebets 2002; Dias & Machado 2006; Carvalho et al. 2012; Chapin 2014), under debris like rocks and logs (Fowler-Finn & Hebets 2006), in appropriated abandoned burrows (Weygoldt 2000), in bracts of bromeliads (Jocque & Giupponi 2012), or even in termite mounds (Carvalho et al. 2011). Refuges house individuals during daylight hours and provide shelter from predators.

Most research on Amblypygi habitat preference has been limited to species dwelling in and on tree trunks—a common microhabitat of forest amblypygids (Table 1). These species show preferences for large, buttressing trees with refuges in abandoned burrows under bark, under leaf litter piles, or in crevices created by decay or buttressing (Hebets 2002; Dias & Machado 2006; Carvalho et al. 2012; Chapin 2014, 2015). Thus, tree-dwelling species appear to rely on large, old growth trees for territory formation (Chapin 2014). As such, selective logging negatively impacts population sizes (Bloch & Weiss 2002). Intriguingly, seasonal variation in microhabitat preference appears to occur in some species, perhaps explained by prey abundance, competition, or ontogeny (Curtis & Bloch 2014)—a finding worthy of future research. Finally, recent research investigated behavioral variation across habitats. In *Phrynus longipes* (Pocock, 1894) of Puerto Rico, cave populations exhibit distinct, environment-specific variation in activity level, vigilance, hunting behaviors, and aggression relative to epigean (surface-dwelling) conspecifics (Chapin 2015). The selection pressures or behavioral plasticity that promote this variation are yet unknown.

While habitat preference is relatively well studied among some Amblypygi species (Table 1), the costs and benefits of habitat preferences remain unresolved. Preferred microhabitats should provide limiting resources like prey, predator defense, or access to mates. Indeed, some differences in site fidelity occur across sexes with females demonstrating higher site fidelity than males (Hebets 2002), but the reason for this is unclear. Laboratory or semi-natural experiments that manipulate the potential benefits afforded to microhabitat holders could reveal putative adaptive value of microhabitat preference. Further, the field research has been biased toward only a few genera and localities (Fig. 1.1), with a notable underrepresentation of old world ecosystems. Research on microhabitat preferences of additional amblypygid species across distinct ecosystems, combined with analyses of costs and benefits associated with microhabitat preferences, are needed to obtain a general understanding of the relationship between amblypygids and the ecosystems in which they occur.

1.4.2 Navigation

Given that studied amblypygid species tend to reside in refuges that they reliably occupy over various time frames (Hebets 2002; Dias & Machado 2006; Carvalho et al. 2012; Porto & Peixoto 2013; Chapin 2014, 2015; Curtis & Bloch 2014; Chapin & Hill-Lindsay 2015), it may not be surprising that residents are capable of finding their way back to these refuges—a phenomenon known as homing. The distances over which amblypygids have been shown to home, in combination with the complex habitats through which they travel (e.g., lowland tropical rainforests), make these feats quite impressive. Similar homing activities have been studied extensively in the wolf spider Lycosa tarantula (Linnaeus, 1758) (Ortega-Escobar 2002, 2011; Reyes-Alcubilla et al. 2009; Ortega-Escobar & Ruiz 2014) and the wandering desert spider Leucorchestris arenicola Lawrence, 1962 (Norgaard et al. 2003, 2007, 2008, 2012; Norgaard 2005). Like many of their arthropod relatives (e.g., ants, bees, crabs, etc.; reviewed in Cheng 2006, 2012), homing in L. tarantula involves path integration, or the constant updating of a homeward vector during an outward route (Ortega-Escobar 2002; Reyes-Alcubilla et al. 2009; Ortega-Escobar & Ruiz 2014); and in both L. tarantula and L. arenicola, nocturnal navigation appears to be based on vision (Ortega-Escobar 2002, 2011; Norgaard et al. 2007, 2008, 2012; Reyes-Alcubilla et al. 2009; Ortega-Escobar & Ruiz 2014). In contrast to their spider relatives, however, neither path integration nor vision appears necessary for amblypygid homing, though more work is needed to further explore the putative role of vision (Hebets et al. 2014a, b).

Physical displacement studies that moved individuals up to 10 m in a tropical rainforest understory found that amblypygids can return to their home refuge within three nights, many of them returning after only one (Beck & Görke 1974; Hebets et al. 2014a). Their successful homing in the face of physical displacement demonstrates that path integration is not critical for nightly homing. It is important to note, however, that path integration may nonetheless be important in establishing a working knowledge of an unfamiliar environment (e.g., during learning walks; Norgaard et al. 2012). In addition to successfully homing, radio telemetry experiments have demonstrated that the return paths of displaced amblypygids are often not direct—they include stopovers at additional refuges along the way (Hebets et al. 2014a). This observation is intriguing and suggests that amblypygids might possess a more general working knowledge of their local microhabitat (e.g., cognitive maps; Hebets et al. 2014a). Future work involving long-term tracking of individuals or long-term observations of amblypygids in a novel environment may shed light on the degree to which prior knowledge of an environment influences homing ability.

Though many nocturnal arthropods appear to exhibit visually-guided navigation behavior (Cheng 2006, 2012), olfaction has long been suggested as important in amblypygid navigation. Indeed, work by Beck & Görke (1974) suggested an olfactory mechanism in amblypygid homing. More recent field displacement studies using *Phrynus pseudoparvulus* Armas & Viquez, 2002 with occluded olfactory or visual capacities further support the role of olfaction and potentially vision in amblypygid homing. Sensory-occluded individuals were less successful in homing compared to sensory intact individuals (Hebets et al. 2014b). Importantly, the methods used to occlude olfactory capacities involved either clipping of the distal tip of the antenniform legs or physically covering the distal tip of the antenniform legs with nail polish. Both methods undoubtedly influence mechanosensory perception as well, making it impossible to rule out the importance of tactile information. Laboratory trials have also demonstrated that the amblypygid *Phrynus marginemaculatus* C.L. Koch, 1840 can learn tactile cues to navigate to a retreat (Santer

& Hebets 2009b) and this additional modality may also be important in amblypygid navigation. Future work should focus on determining the relative importance of distinct sensory information (e.g., olfactory, visual, tactile) and their probable interactions on amblypygid navigation.

The size of arthropod mushroom bodies has been hypothesized to reflect their spatial navigation strategies (Jacobs 2012), and amblypygids are well-known for their enlarged mushroom bodies (Strausfeld 1998). In the visually guided desert ant, Cataglyphis bicolor (Fabricius, 1793), researchers were able to demonstrate a remarkable increase in mushroom body size during the extremely short lifespan (ca. 6 days), and argued that the need for higher-level navigational requirements might drive their observed increase in neuropile volume (KuhnBuhlmann & Wehner 2006). Subsequent comparative work on the desert ant Cataglyphis fortis (Forel, 1902) and Melophorus bagoti Lubbock, 1883 further suggest that species-specific navigational capacities are influenced by environment-dependent characteristics such as habitat complexity (e.g., presence or absence of landmarks; Buehlmann et al. 2011). For example, C. fortis, which is found in a more featureless natural habitat than M. bagoti, tends to rely more on vector-based navigational strategies while M. bagoti can use landmark-guided navigation (Buehlmann et al. 2011). Research that focuses on diverse arthropod taxa, such as amblypygids, could greatly enhance our understanding of the links between such navigation strategies and selection pressures imposed by environmental complexity. Additionally, the demonstrated navigational capacities of amblypygids and their possible relationship with multisensory integration and enlarged mushroom bodies makes them another putative model system for a more general understanding of the neural mechanisms underlying complex navigation.

1.5 Interspecific interactions

1.5.1 Predators and prey

Amblypygids act as secondary and tertiary consumers of the ecosystems in which they occur. The amblypygid diet is varied and seemingly opportunistic, comprised mainly of primary consumer arthropods, especially Orthoptera and Blattodea (Table 2). Amblypygids have also been observed feeding on sphingid and noctuid moths, orb weaving spiders (Fig. 1.3b), the scorpion Centruroides gracilis (Latreille, 1804), Anolis lizards, hummingbirds, and crayfish captured from streams (Table 1.2). Interestingly, some species seem quite adept at aerial or aquatic prey capture (Hebets & Chapman 2000b; Hebets 2002; Ladle & Velander 2003). Individuals hunt prey using sit-and-wait tactics and are commonly seen with open pedipalps awaiting prey (Fig. 1.3a). Species inhabiting vertical environments (e.g., tree trunks, cave walls) are most often seen facing down (Weygoldt 2000; Hebets 2002; Chapin 2014), possibly for efficiency in prey capture (Fig. 1.3a), though this remains to be tested.

Amblypygids fall prey to large lizards and small mammals, including bats (Table 1.3). Field studies recorded lycosid spiders (Chapin 2011) and scorpions (Hebets 2002; Teruel & Toledo 2014) preying on amblypygids (Table 1.3). Thus, many Amblypygi species engage in symmetrical intraguild predation by preying on species that are both competitors for prey and potential predators (Polis et al. 1989; Holt & Polis 1997). Intraguild predation has structural effects on ecosystems in which it occurs, including the reduction of predators when prey of lower trophic levels are scarce (Polis & McCormick 1987). This highlights the potentially important role of amblypygids in the trophic structure of ecosystems in which they are abundant. Further, amblypygids engage in a special case of symmetric intraguild predation: cannibalism. Cannibalism rates vary across species, from being quite rare to up to 20% of interactions ending in cannibalism during laboratory trials (Weygoldt 2000; Pinto-da-Rocha et al. 2002; Torres-Contreras et al. 2015; Chapin & Hill-Lindsay 2015). It is unclear, however, how prevalent cannibalism is under natural conditions. Most cannibalism among amblypygids is size-structured or assumed so, such that ontogenetically asymmetric predation is the norm (Persson et al. 2004). Some amblypygid species, however, also cannibalize as a resolution to contests (Chapin 2015). In such cases, cannibalism is most likely to occur among size-matched contest opponents rather than size-asymmetric pairs.

Intraguild predation and cannibalism offer interesting avenues to understand the dynamic relationships within an ecosystem. In particular, how prey choice, including cannibalism, changes with individual condition might reveal the fitness costs that may disfavor cannibalism in times of plenty. Further, cannibalistic behavior under laboratory conditions is often a consequence or by-product of agonistic interactions. Thus, contests can impact the ecology of environments in which they occur. More aggressive populations should have higher rates of cannibalism due to the escalation of agonistic interactions. To date, most information on both predators and prey of amblypygids comes from opportunistic field observations, and more quantitative assessments of the role of amblypygids in ecosystem trophic structures are needed.

1.5.2 Parasites and parasitoids

New instances of amblypygid parasites and parasitoids continue to be documented as the number of field studies on these fascinating creatures increases (Fig. 1.4). For example, Armas & Trueba (2003) found a prostigmatan mite infesting *Phrynus kennidae* Armas & González, 2002. The mite was described as an ectoparasite on other arthropods as well, indicating that it is not host-specific. A mite of the genus Odontacarus Ewing, 1929 was similarly found parasitizing the amblypygid *Charinus brasilianus* Weygoldt, 1972 in southeastern Brazil (Gonçalves-Souza et al. 2014) and an unidentified *Brachyceran* fly has been documented to parasitize the abdominal lumen of adult *Heterophrynus batesii* (Jorya & Rojas 2013). Several P. marginemaculatus died from mite infestations under laboratory conditions (Rayor & Taylor 2006).

Parasitoids are also known to use Amblypygi as hosts. The parasitoid chloropid fly (Pseudogaurax sp.) parasitizes the eggsacs of *P. pseudoparvulus* and *Paraphrynus laevifrons* (Pocock, 1894) (Viquez & Armas 2009). It is believed that eggs are laid on the eggsacs of females and the fly larvae consume the Amblypygi eggs upon hatching. The larvae then pupate on the female's opisthosoma before emerging. Parasites and parasitoids of wild amblypygids are probably more common than reported due to the lack of field research on the order (Gonçalves-Souza et al. 2014). In fact, recent field work on *P. laevifrons* in Costa Rica has identified multiple parasitized females in close proximity (Fig. 1.4; Tyler Corey personal observation). Research into parasite- and parasitoid-host relationships does not yet exist in amblypygids, yet is surely a fruitful avenue for future research. Studies of host-specificity and parasite defense could highlight the role of amblypygids in their ecosystems.

The literature does not report any information on potential bacterial or fungal relationships among Amblypygi. Field observations of cave-dwelling *Phrynus longipes* in Puerto Rico, however, have noted a white substance covering the cuticle of some individuals (E.A. Hebets personal observation). While this substance was not identified, the possibility of fungus- or bacterial-amblypygid relationships remains a real possibility.

1.5.3 Commensalism

Amblypygids interestingly share the active burrows of several other animals, including birds, mammals, scorpions, ants, and termites (Weygoldt 2000; G. Machado personal communication). Termite mounds appear to provide both shelter and a food source for *Damon medius* (Herbst, 1797) (Weygoldt 2000), the blind *Paracharon caecus* Hansen, 1921, and *Heterophrynus longicornis* (Butler, 1873) (Carvalho et al. 2011). Amblypygids are also found in ant nests. *Charinus quinteroi* Weygoldt, 2002 and *Charinus platnicki* (Quintero, 1986) both associate with ant nests and both have reduced eyes (Weygoldt 2000). Of particular note is the neotropical species *Phrynus gervaisii* (Pocock, 1894), which was found to occupy nearly half of the nests of *Paraponera clavata* (Fabricius, 1775)—the particularly toxic bullet ant (Schmidt et al. 1984)—on Barro Colorado Island, Panama (LeClerc et al. 1987). Follow-up observations on *Phrynus pseudoparvulus* in Costa Rica, however, found the presence of amblypygids to be independent of the presence of *P. clavata* nests (E.A. Hebets unpublished data), suggesting that the presence of amblypygids in these nests might reflect opportunistic refuge use as opposed to any special relationship between amblypygids and ants. Regardless, numerous observations highlight the potential for amblypygids to share the homes of other animals and in these cases, amblypygids seem to be able to avoid the antipredator defenses of their host nests. The potential for interesting interspecific interactions, including undescribed commensalisms and mutualisms, exists between amblypygids and the hosts of shared nests. We see a combination of field and laboratory studies exploring first, refuge choice associated with animal burrows and second, the costs and benefits of this choice as particularly interesting areas for future study.

1.6 Intraspecific interactions

1.6.1 Contests and territoriality

Several lines of evidence suggest that territoriality is common throughout the order Amblypygi. Under laboratory conditions, amblypygids exhibit territory defense, such that territory holders are more likely to win contests than intruders (Chapin & Hill-Lindsay 2015). In the field, putative territories with resident Amblypygi removed are recolonized by smaller conspecifics (Porto & Peixoto 2013), indicating that large animals might exclude smaller would-be usurpers. Further, field observations have recorded site associations lasting for months with several species exhibiting high site fidelity (Beck & Görke 1974; Hebets 2002; Chapin 2011; Hebets et al. 2014a, b). Taken together, these findings show that territoriality occurs in at least some Amblypygi species.

Contests within select amblypygid species are well-described (Weygoldt 1969, 1974a, b, 1977a, b, 2000; Fowler-Finn & Hebets 2006; Santer & Hebets 2008; Chapin 2015). Interactions appear quite ritualized and stereotyped as they frequently follow a regular sequence of behaviors supposedly adapted for communication (e.g., Santer & Hebets 2008). For example, when presented with an opponent, individuals generally engage in a series of pedipalp and antenniform leg movements that may escalate to physical aggression in a regular sequence (Santer & Hebets 2008). Injuries during contests range from nonexistent (Weygolt 1977a; Fowler-Finn & Hebets 2006; Santer & Hebets 2008) to frequent death and cannibalism (Chapin 2015). While specifics of agonistic interactions vary across species, most species studied to date include vibrations and fencing with antenniform legs in addition to pedipalp movements in agonistic displays (Weygoldt 2000; Santer & Hebets 2008; Chapin 2015). Detailed work combining high speed videography and electrophysiology demonstrated that amblypygids communicate with air particle displacement (near-field sound), detected by opponent trichobothria (Santer & Hebets 2008, 2011b). Amblypygids were the first arthropod where filiform hairs were confirmed to function in communication (Santer & Hebets 2008, 2011b), demonstrating their potential for novel contributions to animal communication more broadly.

Contest outcome is predicted by proxies for contestant resource holding potential (RHP), or the absolute fighting ability of animals (Parker 1974). Laboratory trials show that size, body condition, antenniform leg movement, and body raising predict RHP and contest outcome (Fowler-Finn & Hebets 2006; Santer & Hebets 2008; Chapin & Hill-Lindsay 2015). Further, males of many species have elongated pedipalps as compared to females (Weygoldt 2000; Chapin 2011, 2014), which might play a role in territory contests. Available data to date suggest a predominant role of mechano-sensory stimuli (i.e., generated from probing and antenniform leg vibrations; Santer & Hebets 2008) in agonistic interactions while the roles of vision or olfaction remain less clear (Santer & Hebets 2011a). That being said, olfaction may be important for territory recognition (Chapin & Hill-Lindsay 2015).

Territorial behavior typically reflects the need to defend a valuable resource (Briffa & Hardy 2013), but the exact resource and its putative value have not been directly identified in amblypygids. Individuals most likely benefit from territorial behavior by securing retreats used for predator defense, which might be particularly valuable for females during maternal care. How territoriality might differ across sexes is unclear; both sexes engage in territory contests (Chapin 2015), but some research suggests that females show higher site fidelity than males (Hebets 2002). Further, females of at least one species, *P. marginemaculatus*, are less likely to escalate to more risky behaviors than males in laboratory conditions (FowlerFinn & Hebets 2006).

1.6.2 Mating systems and mate choice

Reproductive behavior is the best studied area of amblypygid biology, but all observations published to date have been conducted in the laboratory (Alexander 1962a, b; Klingel 1963; Weygoldt 1969, 1970, 1972, 1974a, b, 1977a, b, 1995, 1996, 1997, 1999a, b, 2002, 2003, 2005, 2006, 2007; Weygoldt & Hoffmann 1995; Peretti 2002; Weygoldt et al. 2010). Survivorship beyond reproduction provides no fitness benefits in most arthropods because they have no post-ultimate molt and often only reproduce one or a few times before death (Triplehorn & Johnson 2005; Beccaloni 2009). Amblypygids, however, spend most of their lives as adults and post-ultimate ecdysis probably increases adult survivorship by providing opportunities for injury recovery, limb regeneration, parasite shedding, and even sperm rejection. Furthermore, growth seems indeterminate (Chapin 2011)—a rare trait among arachnids. This may result in older individuals having both increased fecundity and greater resource holding potential, allowing for higher reproduction and more mating opportunities. This effect may be promoted by the sexual dimorphisms found in most species, which become more pronounced as they age (Chapin 2011).

Amblypygids mate by indirect sperm transfer via a sclerotized spermatophore. Courtship lasts from one to eight hours and the pre-copulative ritual involves a varied repertoire of behavior (Weygoldt 2000). This includes male antenniform leg vibrations, jerking motions, petting with special bristles involved in antenniform leg cleaning, extending pedipalps, angling pedipalps at the trochanter, and stroking the female's distal pedipalp with the male's chelicerae. Behavior and timing are thought to be species specific, and might play a role in interspecies copulation avoidance (Weygoldt 2000). That being said, spermatophore and gonopod morphology are probably greater barriers to interspecies copulation than behavior, as is thought to be the case with other arachnid groups (Eberhard 1985; Huber 2002). Spermatophore deposition takes about five minutes in observed species. The female collects spermatozoa by lifting the genital operculum and grasping with gonopods, which are articulating sclerotized structures for taking spermatozoa packets (Weygoldt 2000). In laboratory settings, the pair mates multiple times, sometimes over several weeks (Weygoldt 2000).

Mating systems have not been explicitly studied in any species of amblypygid. Across the order, polygyny (males mating with multiple females) is expected because females invest in egg guarding by carrying eggsacs attached to the ventral abdomen and young on their dorsum, thereby freeing males to mate with other females but precluding females from mating again until offspring are free-living. It could be the case, however, that females mate multiply before producing egg clutches. As mentioned previously, females offered a single male in laboratory conditions often mate multiply (Weygoldt 2000). In natural conditions, however, this may be realized as multiple mating with separate males. Alternatively, males may mate guard and mate multiply to ensure clutch-wide paternity. Weygoldt (2000) proposed that multiple mating episodes might stimulate reproductive physiology, ensure fertilization, ensure paternity, overcome possible genetic defects occurring as sperm ages, or enable sperm competition. Other researchers have suggested that female defense polygyny (sensu Emlen & Oring 1977) seems likely (Weygoldt 2000). Monogamy via parental care is suspected in at least one amblypygid species (*H. longicornis*; Weygoldt 1977a), however, mate guarding might be a better explanation for male presence. Lastly, parthenogenesis likely occurs in at least four species of Amblypygi, as evidenced by female-only populations or captive reproduction by virgin females (Armas 2000, 2005; Weygoldt 2005, 2007; Seiter & Wolff 2014). Given the relatively small number of observations on species-specific reproductive behavior, we lack a comprehensive overview of amblypygid mating system diversity and thus have an incomplete understanding of the selection pressures that might lead to variable mating systems.

1.6.3 Parental investment and sociality

Amblypygi have altricial development and substantial parental investment. Following sperm acquisition and gestation, female amblypygids lay a clutch of eggs that adhere to their ventral opisthosoma where embryos develop externally before emerging. Offspring emerge from the eggsac and climb to the opisthosoma dorsum, after which they molt and are thereafter free-living. Amblypygid clutch sizes range from about 10 to 90 eggs depending on the species, of which only a portion will hatch into free-living offspring (Gray & Robinson 1986; Weygoldt 2000; K.J. Chapin personal observation). Survivorship has not been tracked in any naturally-occurring amblypygid populations, but the greatest mortality is likely experienced early in life. That being said, cannibalism is more common among adults than juveniles, at least in some species (Chapin & Hill-Lindsay 2015; see Predators and prey).

Social behavior beyond maternal care is suggested to exist for a few species (Weygoldt 1977a; Rayor & Taylor 2006; Chapin 2011). For example, field observations suggest that *Heterophynus longicornis* occur in family groups of a mated pair and their offspring (Weygoldt 1977a) with observed juveniles as old as the fourth or fifth instar. Adults of this species were almost never found singly or in larger groups, but it remains unclear whether or not groups were of related animals (Weygoldt 1977a). Later research on *H. longicornis* found that multiple individuals are sometimes found in association, but the benefits that group living might afford remain unknown (Dias & Machado 2006; Carvalho et al. 2012). Similarly, laboratory observations found that immature *Phrynus marginemaculatus* from Florida and *Damon diadema* (Simon, 1876) from Kenya and Tanzania associated with each other and their mothers for as long as a year in captivity (Rayor & Taylor 2006), but field observations of these phenomena remain undocumented. Research on group-living *Heterophrynus batesii* (Butler, 1873) in Ecuador found that groups occurred on larger, more complex trees with more leaf litter when compared to the same microhabitat variables of random trees in the environment (Chapin 2011, 2014). It is clear that increased resources allow for larger groups. Given that the co-occurrence of individuals in this species is related to microhabitat characteristics, it remains unknown whether aggregations result from resource abundance, an emergent benefit provided by group living, or both.

The observations of group living and the suggestion of potential sociality in amblypygids continues to intrigue biologists, and sociality is certainly not unknown among their close relatives (Shivashankar 1994; Machado 2002; Rayor & Taylor 2006; Lubin & Bilde 2007; Del-Claro & Tizo-Pederso 2009). It remains important, however, to explore the costs and benefits of group living beyond increased access to resources. While one might imagine several ways in which group living might be beneficial to amblypygids (e.g., foraging, defense, or reproduction), these possibilities must be directly assessed in the field. For example, amblypygid groups may benefit from predator defense or offspring food sharing, or grouping may be important for a mating system like harems (i.e., mate guarding multiple females). Nonetheless, the possibility of individual recognition, potentially quite long life spans, and monogamy in at least one amblypygid species (proposed as an essential starting point for sociality; Hughes et al. 2008; Boomsma 2009; Boomsma et al. 2011; but see Nonacs 2011) certainly establishes a plausible foundation for some level of sociality among amblypygids.

1.6.4 Genetics and genomics

Genetic research on amblypygids is largely limited to universal markers typically used for phylogenetics (Table 4). Masta (2008) and Fahrein et al. (2009) sequenced Amblypygi mitochondrial genomes and more recently, approximately 2 million basepairs of nuclear DNA were sequenced for *H. batesii* (K.J. Chapin unpublished data). Additionally, the chromosomes of two species have been mapped with cytogenetic techniques. *Heterophrynus longicornis* and *D. medius* have 2n 5 66 and 70 chromosomes with homomorphic sex chromosomes (Vitková et al. 2005; PaulaNeto et al. 2013). Most recently, Amblypygi have been instrumental in understanding the biogeography of Caribbean islands (Esposito et al. 2015). Research on *Phrynus sp.* from Puerto Rico and surrounding islands revealed exceptional levels of endemism at island, geologic region, and cave scales, thereby presenting a multilevel model for phylogeography (Esposito et al. 2015). How behavioral variation might be both impacted by, or contribute to, genetic isolation has yet to be investigated.

1.7 Conclusion & future directions

Researchers have documented fascinating behavioral phenomena across several Amblypygi species. These findings, coupled with the unique neurophysiology and life histories of amblypygids, have opened several avenues for future research. Indeed, our current knowledge raises many unanswered questions. For example, much remains to be explored in regards to amblypygid relationships with their abiotic and biotic environment. While we recognize that site fidelity, homing, and agonistic contests are indicative of territoriality, resource defense has not been tested. Which resources promote the evolution of territoriality in amblypygids? How does territorial behavior interact with the mating systems and potential sociality of amblypygids? Similarly, how does the spatial distribution of resources, including potential mates, influence navigational demands and how might this select for increased navigational capacities?

A handful of field studies have enabled glimpses into potentially interesting predatory behavior, but how specialized are amblypygids as predators? Some species are known to have the capacity to breathe underwater (Hebets & Chapman 2000b) and others have been observed feeding on aquatic prey (Ladle & Velander 2003). Do amblypygids have special adaptations that allow them to forage underwater? Similarly, amblypygids can catch moths in flight. Does their giant interneuron system underlie this incredible capacity, and what role do trichobothria play? Further, how important are food resources in determining spatial distributions and carrying capacities?

We know very little about major survival challenges of amblypygids in the wild. What are their main predators? Do they have special adaptations or behavior associated with predator avoidance? Leg autotomy is common across amblypygid species as a strategy to avoid predation. How does autotomy affect other areas of life history, like mating success or territoriality? How often does cannibalism occur and is it a major selective agent? Recent field observations suggest that parasitoids of amblypygids may be much more common than previously appreciated. Are these parasitoids specialists of amblypygids, and how has parasite selection pressure affected amblypygid behavioral ecology?

Intraspecific interactions also offer opportunities for valuable additions to behavior research. While the reproduction of select amblypygid species has been studied in the laboratory, few field studies exist on intersexual interactions or variation across species. We know nothing about the level of mate preference that either males or females might exhibit. Males produce large, sometimes quite complex, spermatophores with refractory periods that may last several days. This pattern hints at male mate choice, which could make amblypygids an important research system contributing knowledge to this relatively understudied phenomenon (relative to female mate choice). We know nothing of whether females or males might mate multiply in the field—with either the same or different mates. Given that amblypygids continue to molt throughout their lives, can females molt as a means to dispose of unwanted sperm? If so, cryptic female mate choice could be a driver of sexual selection. Further, behavioral variation between juvenile and adult male and female behavioral repertoires remains unstudied. Despite this, juveniles experience different predators and prey, including cannibalism risks, which might have important effects on behavioral evolution. Understanding when in development male and female behaviors diverge may elucidate important mating system details across Amblypygi species.

Social behavior among amblypygids remains a fruitful avenue for research. Preliminary studies, combined with field observations, raise the distinct possibility that at least some amblypygid species exhibit basic levels of sociality via both fraternal and egalitarian pathways (Weygoldt 1977; Rayor & Taylor 2006; sensu Bourke 2011; Chapin 2014). If so, amblypygids could provide an excellent system for studying the initial transition from a solitary to social life history and the costs and benefits thereof. This is especially true given the aggressive and sometimes cannibalistic inclinations of the ancestors of putative social species.

Amblypygid learning abilities are remarkable (Santer & Hebets 2009a, 2011a) but poorly understood. The functional value of learning in nature and the full repertoire of learning abilities across amblypygid species remain unknown. The unique combination of Amblypygi sensory modalities and learning and memory abilities would make amblypygids a great addition to the diversity of learning research across animals.

While much amblypygid research has been driven by curiosity regarding their unusual morphology and neurophysiology, much remains to be done to link these with amblypygid behavior. Santer and Hebets (2011a) provide an excellent starting point for understanding the relationship between amblypygid neurophysiology and behavior but major questions remain unanswered. We still know little about the function of amblypygid giant interneurons or enlarged mushroom bodies, yet future work connecting this neuroanatomy to complex behavior will provide fundamental insights into neural mechanisms underlying behavior. Following from this proximate view of behavior, little is known about development in amblypygids.

Finally, amblypygid species are often discussed en masse and variation across species is poorly understood. Understanding behavioral variation across species and populations under different suites of selection pressures will allow for a broader understanding of amblypygid behavior and evolution (Chapin 2015). The continued combination of field research around the globe (Fig. 1.1) with semi-natural or laboratory manipulative experiments will be the best approach for increasing our understanding of these incredible animals.

Amblypygi research has been tantalizingly suggestive of Amblypygi exceptionalism and has built the requisite foundation for behavioral ecology research. Amblypygids have remarkable neuroanatomy and sensory biology; curious conspecific interactions ranging from cannibalism and territoriality to extended parental care and sociality; and a litany of community interactions that make them an important component of the ecosystems in which they occur. It is our hope that amblypygids and their researchers continue to contribute to our understanding of how ecologies shape the evolution of behavior and become seated at the leading edge of behavioral research.

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1.9 Table & Figures

Table 1.1. Amblypygi microhabitat preference studies. While informative, current research is limited to New World tropical and subtropical forests.

Species	**Habitat**	**Microhabitat**	**Study**
Heterophrynus batesi	Wet tropical forest	Large, complex, and buttressing trees	Chapin 2014
Phrynus longipes	Wet subtropical forest	Large trees, variation in tree species with season	Curtis & Bloch 2014
H. longicornis	Wet tropical forest	Trees with burrows at bases, not tree size	Porto & Peixoto 2013
H. longicornis	Wet tropical forest	Areas with large trees and termite nests	Carvalho et al. 2012
H. longicornis	Wet tropical forest	Large trees with burrows at base	Dias & Machado 2006
P. longipes	Wet subtropical forest	Lower density in disturbed forests	Bloch & Weiss 2002
P. pseudoparvulus	Wet tropical forest	Large trees with high moss cover	Hebets 2002

Table 1.2. Known prey of amblypygids delineated by vertebrate and invertebrate taxa.

Prey	**Predator**	**Citation**
Harvestmen (Opiliones)	*Phrynus pseudoparvulus*	Hebets 2002
Scorpion (*Centruroides gracilis*)	*Paraphrynus cubensis*	Forcelledo & Armas 2014
Spiders (Araneae)	*P. pseudoparvulus*	Hebets 2002
Giant golden orb-weaver spider (Nephilidae)	*Heterophrynus batesii*	Chapin 2011a
Crickets and katydids (Orthoptera)	*H. batesii*, *P. pseudoparvulus*	Hebets 2002, Chapin 2011a
Cockroaches (Blattodea)	*Phrynus longipes, P. pseudoparvulus*	Hebets 2002, Chapin 2015
Moth (Lepidoptera)	*P. longipes*	Hebets 2002
Sphingid moth (Sphingidae)	*H. batesii*, *P. pseudoparvulus*	Beck & Görke 1974
Freshwater prawn (*Macrobrachium* sp.)	*Heterophrynus cheiracanthus*	Ladle & Velander 2003
Millipedes (Myriapoda)	*P. pseudoparvulus*	Hebets 2002
Antillean crested hummingbird (*Orthorhyncus cristatus*)	*P. longipes*	Owen & Cokendolpher 2006
Anoline lizards (*Anolis* sp.)	*P. longipes*	Reagan 1996
Goldenscale anole (*Anolis nitens chrysolepis*)	*Heterophrynus longicornis*	Kok 1998

Table 1.3. Known predators of amblypygids delineated by vertebrate and invertebrate taxa.

Predator	**Prey**	**Citation**
Lycosid spider (Araneae: Lycosidae)	*Heterophrynus batesii*	Chapin 2011a
Alayotityus sierramaestrae (Scorpionida: Buthidae)	*Phrynus damonidaensis*	Armas et al. 2013
Rhopalurus junceus (Scorpionida: Buthidae)	*Phrynus pinarensis*	Teruel & Toledo 2014
Centruriodes edwardsii (Scorpionida: Buthidae)	*Phrynus whitei*	Armas 1995
Phrynus longipes (Amblypygi: Phrynidae)	*Phrynus hispaniolae*	Armas & Ramírez 1989
White-throated round-eared bat (*Lophostoma silvicolum*)	Amblypygi sp.	Reid 1997
Common coqui frog (*Eleutherodactylus coqui*)	*P. longipes*	Stewart & Woolbright 1996
Bronze coqui frog (*Eleutherodactylus richmondi*)	*Phrynus longipes*	Stewart & Woolbright 1996
Cuban solenodon (*Solenodon cubanus*)	*Paraphrynus robustus*	Armas 1987
Asian water monitor (*Varanus salvator*)	*Stygophrynus dammermani*	Dammerman 1948

Table 1.4. Amblypygi genomic and transcriptomic studies.

Loci	Citations
nDNA	
28S	Wheeler & Hayashi 1998; Giribet et al.2000; Prendini et al. 2005; Mallatt & Giribet 2006; Pepato et al. 2010; Arabi et al. 2012; Esposito et al. 2015
Actin 5S	Vink et al. 2008
EF-1α, EF-2, Pol II	Regier & Shultz 2001
H3	Prendini et al. 2005; Esposito et al. 2015
mtDNA	
12S, 16S	Prendini et al. 2005; Esposito et al. 2015
18S	Wheeler & Hayashi 1998; Giribet et al.2000; Prendini et al. 2005; Mallatt & Giribet 2006; Pepato et al. 2010; Arabi et al. 2012
CO1	Prendini et al. 2005; Arabi et al. 2012; Esposito et al. 2015
ATP6, ATP8, COX1, COX2, COX3, ND2	Hassanin et al. 2005
mtDNA genome	Fahrein et al. 2009; Masta 2008
mRNA	
56 mRNA sequences	Regier et al. 2010
reduced representation transcriptome	Borner et al. 2014
HcA-HcG	Rehm et al. 2012

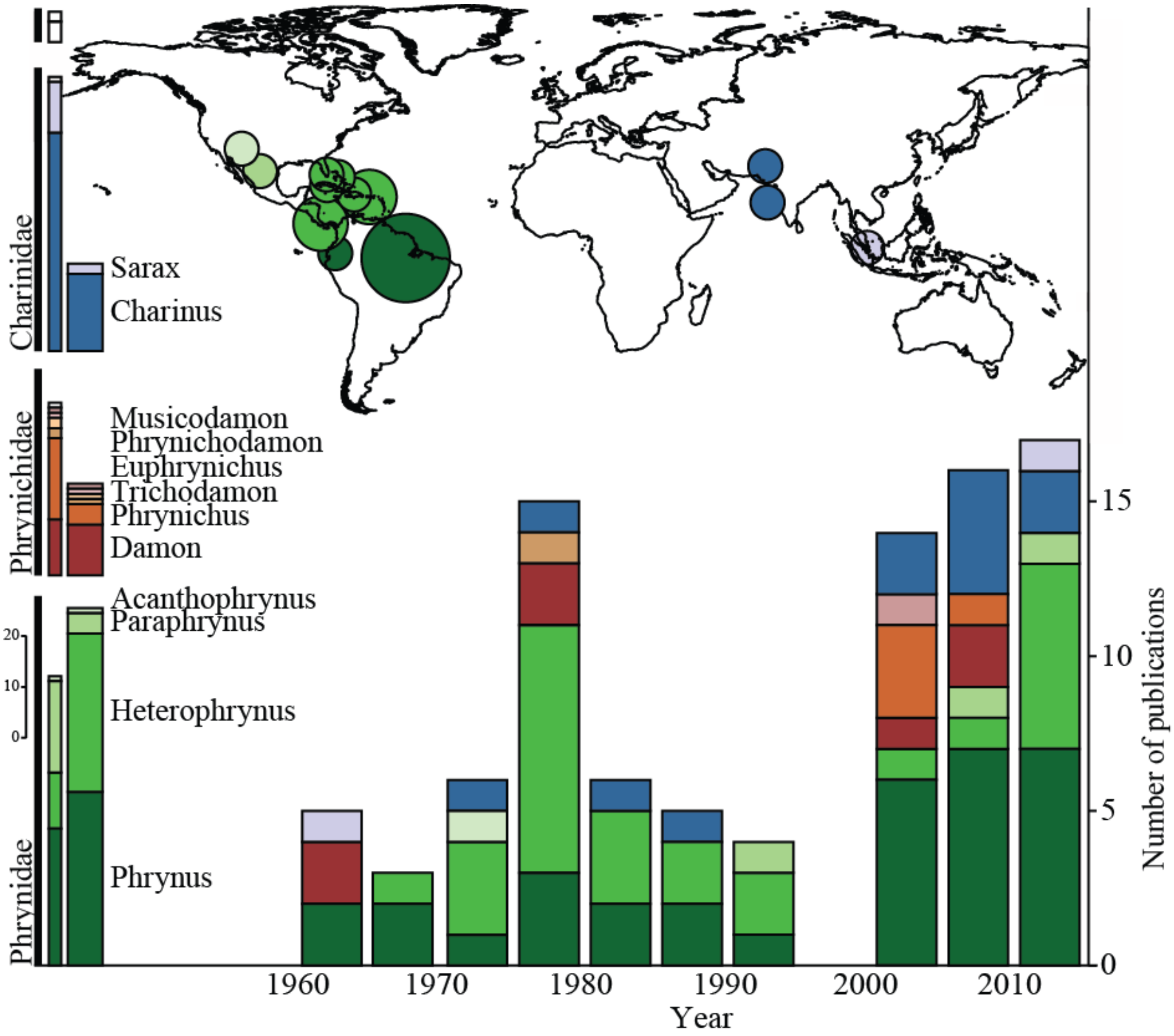

Figure 1.1. Summary of behavioral ecology-related research using Amblypygi species as study organisms. Left bars: species richness (thin bars) compared to publication richness (thick bars) by genus. Right bars: Number of publications per half decade by genus. Map: Location of field studies. Circle color and size indicate genus studied and number of publications.

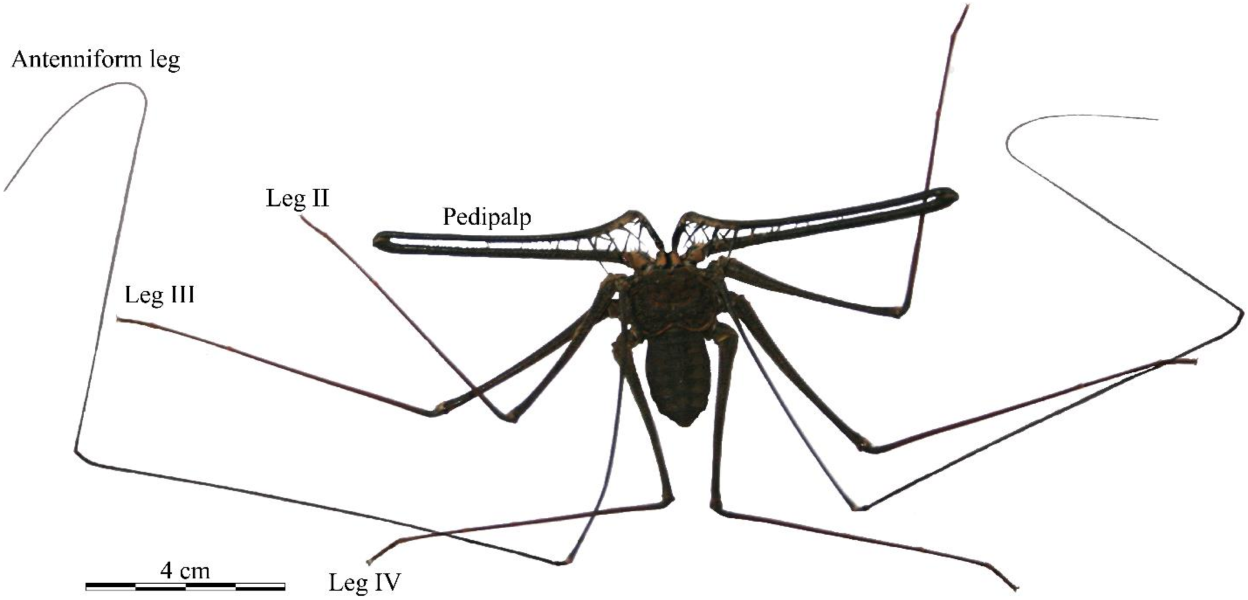

Figure 1.2. Image of *Heterophrynus batesii*, indicating main appendages. Antenniform legs are used for sensing the environment and communication, not walking. The pedipalps act as the main prey capture appendages. The main body is divided into two segments: The anterior prosoma and posterior opisthosoma. Amblypygi do not produce silk or venom. In this species, pedipalp length is longer in males (shown). Photograph by K.J. Chapin.

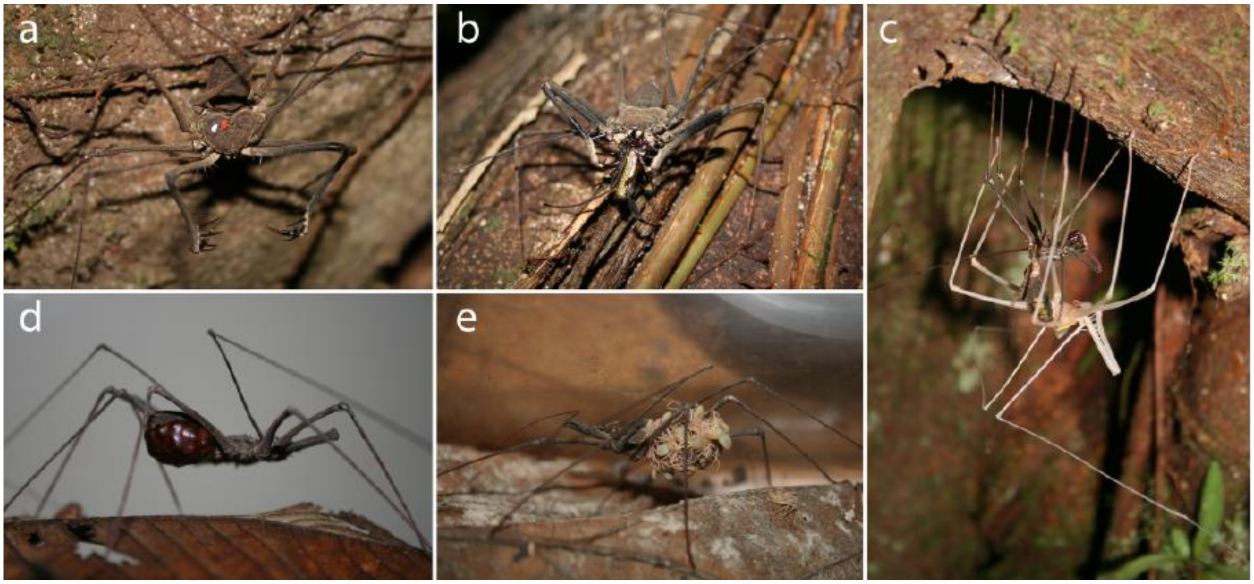

Figure 1.3. Photographs of the natural history of the amblypygid *Heterophrynus batesii* in Amazonian Ecuador, (a) awaiting prey (b) feeding on a *Nephila sp.* spider, (c) engaging in ecdysis, (d) carrying an eggsac, and (e) carrying offspring. Photographs by K.J. Chapin.

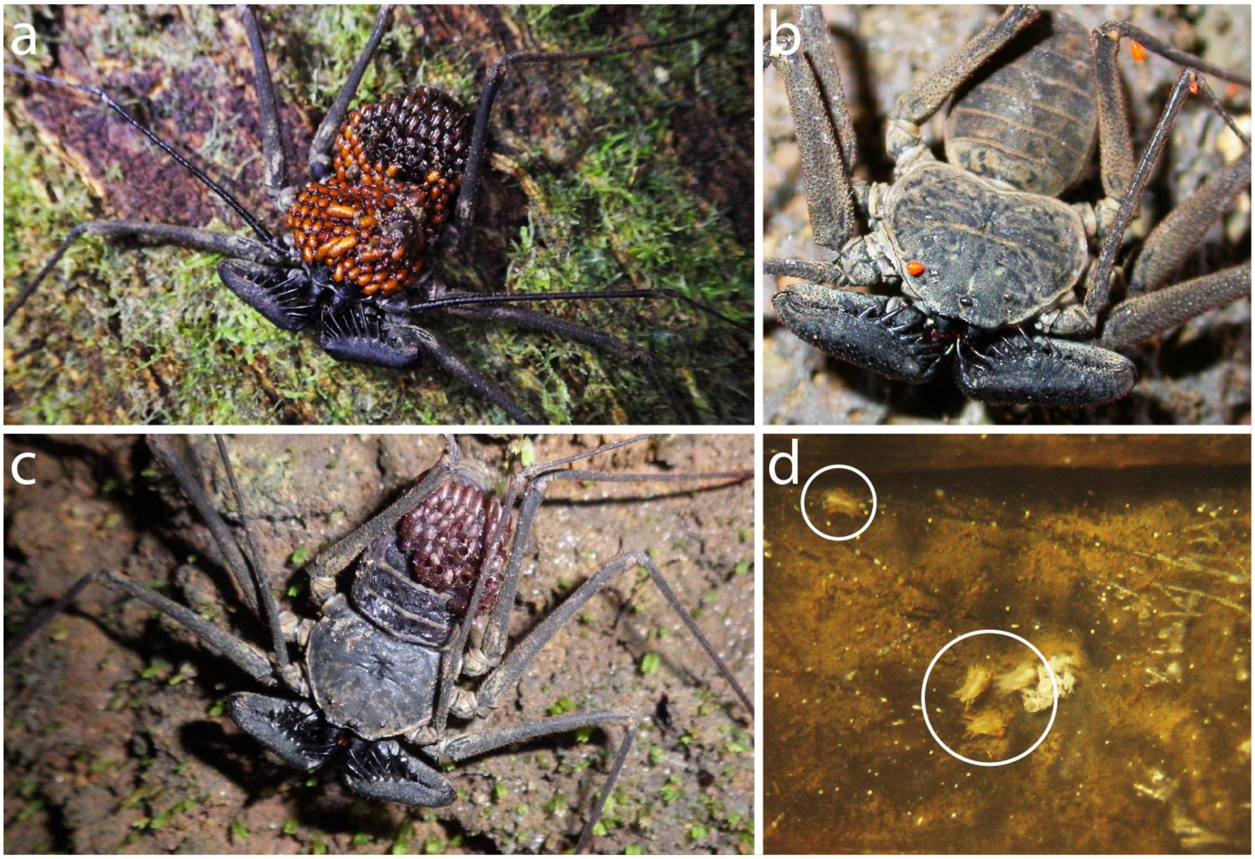

Figure 1.4. Ectoparasites of some Amblypygi species. (a, c) The amblypygid *Paraphrynus laevifrons* in Costa Rica with parasitoid eggs. The parasitoid species is yet to be identified. Photo by Tyler Corey. (b) Amblypygi sp. with mites. Photo by Glauco Machado. (d) Microscopy image of the ventral opisthosoma of *Phrynus longipes* with mites in association with intersclerite membranes (top circle) and spiracles (bottom circle). Photo by K.J. Chapin.

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CHAPTER 2: Cave-epigean behavioral variation of the whip spider *Phrynus longipes* (Arachnida: Amblypygi) evidenced by activity, vigilance, and aggression

Chapin KJ. 2015. Cave-epigean behavioral variation of the whip spider *Phrynus longipes* (Arachnida: Amblypygi) evidenced by activity, vigilance, and aggression. Journal of Arachnology. 43:214–219.

2.1 Abstract

Caves are peculiar ecosystems; they are most often small, isolated habitats that lack the energy sunlight provides. Cave-adapted species, isolated from epigean selection pressures, have been discovered with aphotic adaptations like blindness, depigmentation, and enhanced extra-optic sensory systems. This evolutionary process, however, only occurs in a fraction of cave ecosystems. Many cave species, especially those in tropical latitudes, occur with epigean conspecifics with ongoing gene flow and epigean migration. This includes populations of the amblypygid *Phrynus longipes*, which occur in both epigean and cave environments. I hypothesized that cave and epigean populations exhibit behavioral variation to meet the selection pressures of their respective environments. I conducted open arena and interaction behavioural assays to test for behavioral variation between populations. Assays revealed that cave and epigean amblypygids exhibited environment-specific behavioral variation. Cave animals were more vigilant and engaged in hunting behaviors more, but were less active in general, relative to epigean conspecifics. Comparative modeling indicated that aggressive behaviors during agonistic interactions were the best predictors of environment. Indeed, epigean interactions escalated to physical aggression sooner and included longer weaponry displays than cave conspecifics. Trial design allowed for measurements of territorial behavior, which evidenced that residency effects were more profound in epigean than cave conspecifics. The high density of amblypygids in the cave population may have resulted in more tolerant, less aggressive behaviors relative to epigean conspecifics. Thus, these findings fit the ecological and demographic conditions of each environment.

Keywords: aggression, agonistic, personality, populations, Puerto Rico, speleology, territory

2.2 Introduction

Our understanding of adaptation to cave environments is dominated by the morphological consequences of aphotic conditions, including eye reduction or loss, depigmentation, and advanced extra-optic sensory systems (Culver & Pipan 2009). Caves, of course, are not only of note for their darkness; cave ecosystems are rare and fragile (Elliott 2005), with constituents seeded from, and nourished by, the surface environment. Cave-living species were once thought of as the result of regressive evolution or relaxed selection (Barr 1968; Romero 2009). We now understand caves as unique ecosystems with their own selective pressures and important connections with the surrounding surface environment (Krajick 2001). Despite this, the relationship of cave populations with epigean (surface-dwelling) conspecifics has rarely been investigated (Culver & Pipan 2009).

Darkness is the ubiquitous feature of the ecosystems, but darkness has farther-reaching effects than just promoting the evolution of extra-optic sensory systems. Darkness means that cave systems lack the energy source of nearly all other ecosystems: the sun. Instead, trophic levels begin with an influx of energy from animals that forage in epigean environments but defecate in caves, usually bats or birds (Culver & Pipan 2009). The number of trophic levels and population sizes at each are determined by this initial energy influx, which can vary widely depending on the population size of the energy transport species. Additionally, cave species richness is often small, following species-area theory (Arrhenius 1921; Christman & Culver 2001). This results in simplified ecosystems (at least among macroorganisms), which can support large populations of relatively few species (Culver & Pipan 2009; Culver & Sket 2000).

The stark contrast between the cave and epigean environments suggests that cave animals should adapt behaviorally to a subterranean life history. Indeed, many of the most studied caves are found to house hypogean (cave-dwelling) endemics (Culver & Sket 2000). Caves populations at tropical latitudes, however, are much less studied but are likely to have epigean conspecifics; glaciation did not extirpate epigean populations, as is the hypothesized case for temperate caves (Neimiller et al. 2008). Thus, many tropical cave communities include the same species as epigean environments, but with greatly different selection pressure that potentially promote behavioral variation.

Behavioural phenotypes, being highly labile, are often the first to change in a new environment (Blomberg et al. 2003; Mayr 1963). For example, animals that colonize new habitat (Duckworth 2006) or occur along an altitudinal gradient (Leticia Avilés et al. 2007) exhibit behavioral variation across habitats, the presumed consequence of which are behavioral trade-offs suited for one environment but not the other. In this scenario, natural selection for either cave-adapted behavioral phenotypes or behavioral plasticity could result in distinct behavioral variation between cave and epigean populations. Indeed, tropical cave systems may house cryptic species only diagnosable by behavioral variation or genetic analyses. Alternatively, tropical cave systems with migration between cave and epigean environments may support metapopulations with limited, but measurable, behavioral variation.

In the karst Puerto Rican caves of this study, arachnids make up the majority of predators in high energy caves, with amblypygids (Arachnida: Amblypygi) being the large majority. Amblypgyi is a pantropical order of some 160 nocturnal, and oftentimes cannibalistic, predators outfitted with extremely elongate front legs used to sense their environment and raptorial, claw-like pedipalps used for ambush prey capture (i.e., “sit-and-wait” predation) and defensive weaponry (Weygoldt 2000). Amblypygids have gained attention for their exceptional neurobiology and sensory systems (Strausfeld 1998; Hebets & Chapman 2000; Foelix & Hebets 2001; Santer & Hebets 2008, 2011). More recent research has made advances in connecting these proximate studies with ultimate, field-based research (Bloch & Weiss 2002; Hebets 2002; Chapin 2011, 2014; Carvalho et al. 2012; Porto & Peixoto 2013). The amblypygid *Phrynus longipes* (Pocock 1894) appears to reach extreme population densities in high-energy Puerto Rican caves. This observation, while anecdotal, is surprising, given the solitary, aggressive, and cannibalistic nature of the species. Thus, I hypothesized that cave animals may have adapted more tolerant behaviors to meet the high conspecific density of the cave environment. Cannibalism may be a greater threat to cave amblypygi, while interspecific predators are likely more important for surface conspecifics. Indeed, patterns of reduced aggression in cave animals have been shown in disparate taxa (Burchards et al. 1985; Parzefall 2001). Thus, I hypothesize that cave populations of *P. longipes* have exhibit distinctly different behaviors characterized by tolerance and reduced aggression.

2.3 Methods

2.3.1 Study site

Assistants and I collected cave and epigean *P. longipes* by hand from Cueva de los Culebrones and the surrounding forest at Mata de Plátano Natural Reserve (MPNR) in the karst belt of Puerto Rico (generally located at 18.414°, −66.726°) in September 2012. Cueva de los Culebrones is a hot subtropical cave with an enormous and diverse bat population estimated at 300,000 individuals across six species (Rodríguez-Durán 1996; Puente-Rolón & Bird-Picó 2004). The cave houses a simple environment, with bat guano supplying initial energy instead of sunlight. Cockroaches dominate as the primary consumer macroinvertebrate, and serve as the main prey item for *Phrynus longipes*, which are the dominant predators. Amblypygids are commonly found in a myriad of cracks and crevices in the cave wall. Data loggers placed in and outside the cave recorded $\bar{x}$ ± sd temperatures of 26.68°C ± 0.43 (range: 25.56 – 28.89°C) within the cave and 24.57°C ± 1.92 (21.11 – 30.56°C) in the epigean environment. Relative humidity was recorded at 99.36% ± 1.33 (91.50 – 100%) in the cave and 93.23% ± 3.44 (74.50 – 96.50%) on the surface. Temperature and humidity within the cave increased linearly an estimated 0.06°C per meter into the cave ($ß = 0.06$, Adjusted $R^2_{11} = 0.96$, $P > 0.0001$). The amblypygid population terminated at the beginning of a dead zone; a portion of the cave with low oxygen beginning at ca. 120 m from the cave entrance. The cave continues several hundred meters, but amblypygids were never found beyond this point. I assume this is due to the low oxygen levels in this area of the cave. The cave entrance was generally steep and muddy, but amblypygids could certainly move between cave and epigean environments via large connected rock outcroppings on either side of the main entrance.

2.3.2 Population density estimate

I conducted mark-recapture surveys to estimate cave population density in September 2012 from ca. 2000 to 0400 h along 5 cave sections by capturing all observed *P. longipes* and marking them with paint on the prosoma dorsum. Animals were recaptured the following night and the proportion of marked and unmarked captures were used in population estimates. The short latency between marking and recapture surveys allowed for Chapman-Peterson estimates, which assume closed populations (i.e., no birth, death, migration, or mark loss). Population estimates for the surface were also conducted in this manner, but individuals were too uncommon and dispersed in the forest to meet the assumptions of population estimate statistics, so minimum number known alive was calculated instead.

2.3.3 Behavioural trials

I tested cave and epigean individuals for behavioural variation via two successive behavioural assays. First, a 10 min open arena assay assessed activity level, vigilance, and sit-and-wait responses when exposed to a novel environment. Next a 45 min agonism assay assessed latency to physical aggressive and weaponry displays of paired individuals. Open arena assays were scored using three groups of behaviors developed from direct observation of *P. longipes* and published ethograms of other Amblypygi species (Walsh & Rayor 2008; Fowler-Finn & Hebets 2006): sit-and-wait, vigilance, and activity. Behaviors were pooled by function, which coincided with the morphology involved in the behavioral action. The sit-and-wait category included grooming and prey-waiting behavior using mainly the pedipalps. Both of these behaviors only occur when animals are not exploring their environment or threatened. Grooming is achieved via specialized combing structures on the pedipalps that clear the antenniform and walking legs of debris (Weygoldt 2000). Since amblypygids are sit-and-wait predators, they often sit for hours with pedipalps extended awaiting prey (Weygoldt 2000). Thus, these behaviors are indicative of a calm, or at-rest state (Weygoldt 2000). The vigilance category included tactile and olfactory exploration with the antenniform legs. These behaviors are conducted to identify changes to their immediate environment. Amblypygids rely primarily on olfactory and tactile cues via the antenniform legs to gain information from their environment (Weygoldt 2000, Fowler-Finn & Hebets 2006, Santer & Hebets 2009). Thus, scanning and making contact with antenniform legs were measured to record vigilant behaviors. Lastly, the activity category included walking, running, and climbing using the walking legs. These behaviors are consistent with exploring the environment, and represent the activity level of individuals.

Behaviors recorded during agonistic interactions included the duration and latency (from the beginning of the interaction) of pedipalp displays, touching with the antenniform legs, flicking, fencing, and physical contact (see Fowler-Finn & Hebets 2008 for a description of these behaviors). My focus was to measure the latency to escalate agonistic interactions and the dwuration of displays. Agonism opponents were collected from their respective environments and randomly paired. Thus, I assumed that individuals were naïve of opponents.

Animals were housed individually in plastic terraria with paper used for walking and hiding for 24 h prior to trials. All trials were conducted in the laboratory of MPNR after dark, in 85–95% rh and 23–27°C from 2000–0400 h. The behavioural arena was a 70 × 30 cm × 33 cm glass enclosure divided equally by removable acrylic sheets and with a paper substrate. After the 10 min open arena assay, the acrylic divider was lifted and animals were able to interact for the 45 min interaction assay. Arenas were washed with 70% isopropyl between trials (sensu Fowler-Finn & Hebets 2006). Trials were conducted in total darkness under 920 nm peak wavelength infrared LED lights using an infrared digital camera recording 640 × 480 p at 30 fps. Behaviours were recorded to the nearest frame.

2.3.4 Statistical analyses

A nonmetric multidimensional scalar (NMDS) ordination using binomial deviance dissimilarity (a likelihood based version of the improved Bray-Curtis measure; Millar & Anderson 2004) was used to test if cave and epigean amblypygids exhibit distinct behaviours in open arena assays. I compared these data in an analysis of similarity (ANOSIM) to test if cave and epigean individuals exhibited distinct behavioral repertoires. I tested interaction assays for behavioral variation using a multimodel comparative approach with logistic regressions. I randomly selected one of the two opponents from each trail to be included in the analysis to avoid pseudoreplication. I chose predictor variables that lacked collinearity and represented the diversity of behavioral displays that occurred during agonistic interactions. These included total pedipalp display time, latency to physical aggression, and flicking with location (cave or epigean) as the response variable ($n = 42$). I then compared this global model to more parsimonious iterations using Akaike's Information Criterion corrected for small sample size (AICc) and Akaike Weights (w_i). Reviews of this information-theoretic, multimodel statistical approach can be found in Richards (2005) and Symonds & Moussalli (2010). The initial open arena assay caused a territorial residency effect in subsequent interactions (own data). Thus, I tested the effect of residency between cave and epigean populations with Wilcoxon tests. Lastly, I compared aggression levels in subsequent interactions with $\chi2$ tests. I conducted all statistics using R 3.0.1.

2.4 Results

2.4.1 Population density

The cave-wide population estimate was 335 ± 1541 (Chapman-Peterson estimate ± 95% CI) individuals in a 2 × 123.5 m area of cave wall or a density of ca. 2 individuals m-2. Densities increased with cave depth (Table 2.1). The minimum number known alive (MNKA) for the cave transect was 237 individuals (1.40 m-2). The survey area was searched in five sections, with a two-person search time of less than 1 h per section. Comparatively, only 25 surface individuals were found during a two-person search over 12 nights lasting ca. 4 hours each night. I never found surface animals in spatial association. Thus, the cave population was extremely dense relative to epigean populations.

2.4.2 Behavioral trials

The NMDS of open arena assay behaviours produced a low stress statistic of 0.06 with two dimensions, suggesting a good fit. An Analysis of Similarity (ANOSIM) indicated that cave (n = 70) and epigean (n = 20) individual behaviours are distinct (R = 0.14, P = 0.010, 10,000 permutations). Cave animals exhibited more vigilant and sit-and-wait behaviors, while epigean conspecifics had higher activity levels (Fig. 2.1).

Comparative analyses of logistic regressions of agonistic interactions found that native environment (cave or epigean) was best predicted by latency to physical aggression and duration of pedipalp displays (w_i = 0.487; Table 2.2). Models without pedipalp displays were only slightly worse at predicting native environment, while a model without aggression suffered substantially, with an AICc close to that of a null model (ΔAICc = 8.15).

Cave territory residents were 20% more likely to win territorial contests than cave intruders. Epigean residents, however, were 400% more likely to win than epigean intruders. Furthermore, epigean interactions escalated to physical aggression sooner ($\bar{x}$ ± SE: 3.24 s ± 1.79) than cave conspecifics (23.24 s ± 4.91; $W = 733$, $P = 0.044$). Epigean animals were not more likely to initiate agonistic interactions prior to physical contact (21.05% of trials) relative to cave conspecifics (9.84%; $\chi^2_1 = 1.66$, $P = 0.197$). Similarly, I failed to detect a difference between the latency for cave and epigean animals to escalate to physical aggression in subsequent interactions (17% vs. 36%; $\chi^2_1 = 1.94$, $P = 0.164$).

2.5 Discussion

Cave and epigean individuals exhibited distinct behavioral variation; cave animals were tolerant and vigilant while epigean conspecifics were exploratory and aggressive. Additionally, cave agonistic interactions led to physical attack sooner and individuals displayed weaponry longer than cave conspecifics. The most important parameter for predicting native environment was physical aggression (Table 2.2). Epigean amblypygids escalated to physical aggression sooner than cave conspecifics, which was also the most important parameter for predicting native environment.

These results support the hypothesis that the high conspecific density of caves promoted conspecific tolerance. Conspecific density affects aggression levels in several other groups of Animalia as well. For example, rodents (Davis 1958; Sachser 1986), birds (Craig 1979), grasshoppers (Simpson et al. 1999), and cats (Benson et al. 2006) all show increased tolerance with density. For cave *P. longipes,* the high conspecific density of caves and resultant higher frequency of aggressive interactions may select for tolerance or less costly interactions. Indeed, agonistic interactions in *Phrynus longipes* are costly both energetically and due to the risk of injury. Amblypygids may engage in less aggressive ways of negotiating agonistic interactions if they occur too frequently.

Alternatively, other mechanisms may have promoted the observed behavioral variation. For example, losing a territory in the forest likely comes at a great cost since suitable spaces are scarce (Chapin 2014, Bloch C. & L. Weiss. 2002, Hebets 2002). Comparatively, the cave presents a higher density of suitable spaces to establish territories, which might make them less valuable; contest losers are likely to attain an alternate territory, though perhaps of less value. This is indirectly supported by the result that residency had a greater effect on contest outcome for forest interactions.

Interaction assays failed to show that forest animals were more likely to initiate agonistic interactions prior to physical contact than cave conspecifics. This could be because olfaction or other non-contact sensory cues are more important for forest animals than caves. These avenues of communication are important for amblypygids (Foelix & Hebets 2001; Hebets 2002; Walsh & Rayor 2008, Hebets et al. 2014), but their usefulness may be compromised in the cave environment. Airborne olfactory cues might also be less useful in high-density cave populations where the environment may be oversaturated with conspecific chemical cues. Future research could elucidate differences in how cave and epigean amblypygids gather external information.

The cave population size is exceptionally large, and is certainly the largest estimated to date (Carvalho et al. 2012; Bloch & Weiss 2002). The estimate had a wide CI but is still conservative considering the elusive nature of the animals and the complex network of cracks and crevices within the cave wall in which they live. Considering that large adult *P. longipes* have an antenniform leg span of 45–50 cm (pers. obs.) and that individuals are not evenly dispersed, the surface area density estimate indicates that most, if not all, individuals were within contact distance of another individual. This is confirmed by our observations in the field. Amblypygids are clearly impacted by increased interaction rates with conspecifics relative to forest conspecifics, which rarely come into contact. This, combined with low predator abundance in caves, likely makes cannibalism the most important factor for survivorship for cave amblypygids. Increased cannibalism risk presents selection pressure for agonism avoidance, less aggressive encounters, or other tolerant behaviours.

Phrynus longipes exhibit environment-specific behavioral variation. Cave animals exhibited more tolerant behaviors relative to epigean conspecifics that were more aggressive and active. These adaptations seem to correlate with population density—a hypothesis that can be tested by extending this research across multiple cave systems. Indeed, environment-specific behavioural variation has the potential to elucidate the mechanisms for the development and maintenance of behavioural variation within species. Understanding phenotypic variation of cave-adapted animals with epigean conspecifics is a new avenue of biospeleology that can inform management plans for cave conservation.

2.6 Acknowledgements

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2.7 Tables & Figures

Table 2.1. Mark-recapture population estimates (Chapman-Peterson estimate ± 95% confidence interval), minimum number known alive (MNKA), and individual per area estimates for five sections of the cave wall 0–2 m from the cave floor. Overall, there are estimated to be ca. 2 whip spiders m^{-2}.

	Section 1	Section 2	Section 3	Section 4	Section 5	Overall
Section depth	43.6	50.7	60.8	74.1	84.5	84.5
MNKA	36	28	31	62	53	237
MNKA m^{-2}	0.41	1.97	1.53	2.33	1.12	1.40
Estimate	56 ± 107	42 ± 73	39 ± 66	90 ± 221	63 ± 121	335 ± 1541
Estimate m^{-2}	0.64	2.95	1.93	3.38	3.03	1.98

Table 2.2. Logistic regression with total pedipalp display time, latency to physical aggression, and flicking during agonism assays as predictor variables and location (cave or epigean) as the response variable (*n* = 42).

model	k	AICc	ΔAICc	wi
aggression + display + flick	4	45.94	2.41	0.146
aggression + display	3	43.53	0.00	0.487
aggression + flick	3	46.88	3.35	0.091
display + flick	3	51.68	8.15	0.008
aggression	2	45.07	1.54	0.226
display	2	49.79	6.27	0.021
flick	2	52.49	8.96	0.006
intercept	1	50.40	6.88	0.016

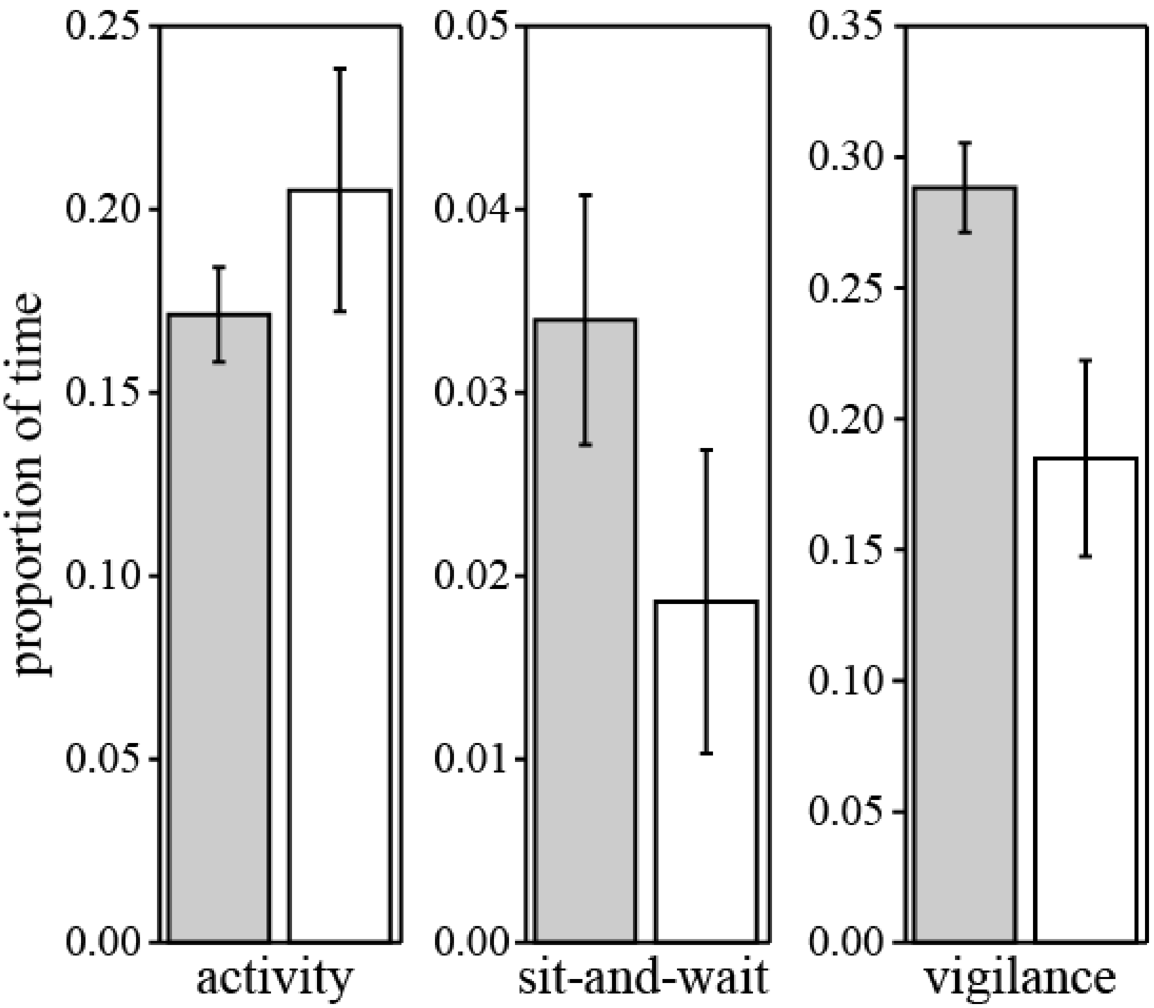

Figure 2.1. Boxplot of the proportion of time cave (grey) and epigean (white) animals spent enacting behaviors within three groups. Activity behaviors including walking, running, and climbing walls are measures of activity level and exploration. Sit-and-wait behaviors, including grooming and opening the pedipalps to await prey, are indicative of being at rest. Lastly, vigilance behaviors included scanning the environment and investigating points in the arena with the antenniform legs. Bars represent mean proportions spent enacting each behavioral group and lines represent standard error of the mean.

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CHAPTER 3: Territoriality evidenced by asymmetric intruder-holder motivation in an amblypygid

Chapin KJ, Hill-Lindsay S. 2015. Territoriality evidenced by asymmetric intruder-holder motivation in an amblypygid. Behavioural Processes 122:110–115. Reproduced with permission.

3.1 Abstract

Territoriality has an extensive and thorough history of research, but has been difficult to impossible to test empirically in most species. We offer a method for testing for territoriality by measuring the motivation of territory intruders to win contests in controlled trials. We demonstrated this approach by staging paired trials of the Amblypygi *Phrynus longipes* (Chelicerata: Arachnida). Amblypygids engaged in agonistic interactions after the opportunity to establish a putative territory on one side of an arena. We found that intruders of putative territories had lower motivation to win contests, thus evidencing territoriality. Physical components of individuals (i.e. energy stores) increased the probability of winning the contest for holders but not intruders, thereby providing insight into the differing decision rules opponents use in territory contests. We discuss why alternative hypotheses, including loser-initiator covariation and home field bourgeois advantage, fail empirical tests. We demonstrated that analyzing animal motivation in territorial contests is tractable even for animals where territories are inconspicuous and cues are outside the normal perceptions of researchers.

Keywords: Agonism, Asymmetric resource value, Contest, Motivation, Resource holding potential, Whip spider

3.2 Introduction

Territoriality occurs when animals defend spatially-associated resources against competing individuals (Marshall 1996; Riechert 1978). Territories are formed to defend food, mates, or refuges, often when they are limiting resources and patchily distributed (Maher & Lott et al. 2000). Animals communicate territory boundaries with signals, including those olfactory, auditory, vibrational, or visual (Pryke et al. 2001; Radford 2003; Bowen et al. 2008). Territory signaling acts to reduce incidences of actual encounters by signaling individual resource holding potential(RHP), or the absolute fighting ability of an animal (Parker 1974).The effect of territory ownership communicated by territory signals is measurable during agonistic contests—territory intruders are more likely to lose agonistic interactions than holders (Kemp & Wiklund 2004; Bergman et al. 2007; Jennions & Backwell 2008; Sacchi et al. 2009).

A hallmark of territoriality is that, all else being equal, territory intruders value the territory less than territory holders (Maynard Smith 1974; Maynard Smith & Parker 1976). This is most commonly because there are costs for holders to attain a new territory and familiarity with a territory increases its value (Briffa & Hardy 2013; Kokko 2013). This effect is measured as variation in RHP. For example, Green hairstreak butterflies (*Chrysozephyruss maragdinus*) intruding on an already established territory holder have lower RHP and are less likely to win contests than intruders (Takeuchi 2006). RHP includes both motivation to win a contest (mRHP) and physical metrics like weaponry and body condition (pRHP). Thus, intruders should have a lower mRHP and be less likely to win territory contests than holders.

In a territory contest, mRHP (the component of RHP caused by motivation to win a contest), but not pRHP (the component of RHP caused by body size, weaponry, and energy stores), changes if an individual is the intruder or holder of a territory. This change in motivation is sometimes termed a residency effect (Kemp & Wiklund 2004). If pRHP is accounted for, then the remaining difference in RHP between contestants is due to mRHP; an effect caused by territorial behavior. Thus, individual *A* has recognized the territory of *B* if, $\mathrm{RHPA}–\mathrm{pRHP}_A < \mathrm{RHP}_B – \mathrm{pRHP}_B$, or $\mathrm{mRHP}_A < \mathrm{mRHP}_B$. That being said, mRHP and pRHP can interact to produce non-intuitive contest outcomes (Härdling & Kokko 2005; Parker & Rubenstein 1981). For example, large individuals might have lower mRHP because there is little cost for high pRHP individuals to acquire new territories (Kemp 2006). In this sense, mRHP is less important because total pRHP is much higher than the population average. Thus, mRHP × pRHP interactions must be considered in interpreting territory effects.

Territoriality has been documented across most animal groups (Baker 1983; Colwell 2000; Maher & Lott 2000; Reichert & Gerhardt 2011) but often via abductive reasoning or anecdotal observation of territorial defense instead of empirical, experimental testing (Börger et al. 2008). Evidencing territoriality in animals has ranged from difficult to impossible because territorial behaviors remain inconspicuous and outside the regular perceptive abilities of researchers (Adams 2001; Maher & Lott 2000; Powell 2000). Such is the case for species of the arachnid order Amblypygi. Amblypygids exhibit site fidelity (Chapin 2014; Hebets 2002) and agonistic interactions that follow stereotyped escalation (Fowler-Finn & Hebets 2006; Weygoldt

2000). While these observations point to territorial resource defense, territoriality has not been tested in any amblypygid species (Chapin & Hebets 2016). This is no doubt in part due to their extraordinary sensory systems, communication modalities, and life histories, all of which seem alien to human researchers. Thus, we developed an empirical approach for testing territoriality in Amblypygi that is broadly applicable across taxa regardless of sensory modality and relies on established con-test theory instead of abductive reasoning. In particular, we test for territory recognition evidenced by lowered motivational resource holding potential (RHP) of intruders informed by territorial cues.

We used the Amblypygi *Phrynus longipes* as a case study for our empirical approach to test for territoriality. Amblypygids are large, nocturnal, pantropical, predatory, and cannibalistic sister taxon of spiders (Giribet et al. 2002; Weygoldt 2000; Wheeler & Hayashi 1998). Amblypygids navigate with two elongate, antenniform front legs replete with sensory organs (Video 1–3; Santer & Hebets 2008, 2009a). They employ olfactory (Hebets & Chapman 2000), tactile (Santer & Hebets 2009a, b), and air movement signals (Santer & Hebets 2011).

Amblypygids engage in aggressive but highly ritualized and stereotyped agonistic interactions when confronted with an opponent (Video 1–3; Weygoldt 2000; Fowler-Finn & Hebets 2006; Santer & Hebets 2008) and seem likely candidates for territorial behavior (Weygoldt 2000; Chapin 2015). Contest outcomes for related species can be predicted by body size and agonistic dis-plays (Fowler-Finn & Hebets 2006). Several species exhibit site fidelity, homing, and habitat preference (Chapin 2011, 2014, 2015; Chapin & Hebets 2016; Hebets 2002; Hebets et al. 2014), all of which are associated with territoriality in other animals. Additionally, their life history hints at the need for a spatial resource worth defending: Amblypygids spend daylight hours in retreats to protect from daytime desiccation and predation. At night, they emerge and remain motionless to ambush prey (Weygoldt 2000). Field research has shown that suitable retreats with available prey are oftentimes a limiting resource for amblypygids (Chapin 2014).Although amblypygid agonism has been well studied relative to other areas of their biology, the function of agonistic interactions is unresolved and territoriality has not been tested (Weygoldt 2000; Fowler-Finn & Hebets 2006). Interpreting amblypygid interactions is challenging because they employ sensory modalities far different from those of humans. In particular, near-field communication (Santer & Hebets 2008, 2009a) and complex olfaction (Hebets & Chapman 2000) are used for intraspecific communication in the order. Thus, we tested amblypygid motivation to evidence for territoriality instead of more standard methods that would require measurements of territory signaling (Naguib 2005), resources (Adams 2001), or movement patterns (Atwood & Weeks 2003).

We staged paired agonistic interactions of *P. longipes* to test for territoriality using the motivational and physical components of RHP. *P. longipes* agonistic displays involve tapping and vibrating with long antenniform legs and displaying and attacking with raptorial pedipalps (Video 1–3). These two agonistic “weapons” likely have distinct functions during interactions. Thus, we recorded weapon size in addition to contest outcome, residency, and body condition of the putative territory holders against intruders. We used scaled mass index (SMI) as a proxy for body condition of *P. longipes*. SMI is a superior estimate of body condition relative to mass-weight ratios or residuals because it accounts for the varying relationship of body mass and weight at different values of mass (Peig & Green 2009). This measure incorporates energy stores given overall size, which are important for territorial contests (Marden & Rollins 1994; Martínez-Lendech et al. 2007; Peixoto & Benson 2008). Overall body size alone can be a weak predictor of contest outcome in territorial disputes, especially for arthropods (Kemp & Wiklund

2001; Peixoto & Benson 2008). We designed a statistical model that included pRHP, mRHP, and their interaction and used an information-theoretic multimodel comparative approach to ascertain our prediction: *P. longipes* is territorial if putative territory holders and intruders exhibited asymmetric mRHP.

3.3 Methods

3.3.1 Study animals

In August 2012, we caught and measured *P. longipes,* held them individually for 24 h and then staged paired behavioral trials before their release. We collected animals between 1000–0400 h in August2012 from Cueva de los Culebrones at Mata de Plátano Field Station, Puerto Rico generally located at 18.414°, −66.726°. Cueva de los Culebrones is replete with cracks and crevices used by amblypygids as retreats. As with most other amblypygids species, cave individuals were repeatedly found at the same retreat for weeks, and individuals would return to their same retreat after use in behavioral trials. For each animal, we recorded several morphological measurements as proxies for pRHP. We measured body size using maximum prosoma width and weaponry sizes as pedipalp femur length and antenniform femur length. Measurements were recorded using digital calipers to the nearest0.01 ± 0.03 mm. Additionally, we measured weight with a gram scale to the nearest 0.01 g. A summary of morphological measures is presented in Table 3.1. Following Peig and Green (2009), we calculated SMI = M_i ×

$(M_x/W_i)^b$, where M_i and $\mathrm{W_i}$ are the total mass and maximum carapace width of individual i, W_x is the mean W of individuals, and b is the slope of an ordinary least squares log-log regression of M and W. We found that sexing by external structures was unreliable and instead sexed individuals by lifting the genital operculum after anesthetization via carbon dioxide gas. We recorded measurements at least 24 h before behavioral trials except for sexing via anesthesia, which we conducted after trials. Animals were housed separately in deli containers prior to trials for that 24 h period. We returned individuals to their capture site after experimentation. Animals that did not survive trails (due to occasional cannibalism) were preserved for further research.

3.3.2 Behavioral trials

Behavioral trials ($n = 48$) were conducted in 75 × 30 × 30 h cm glass arenas divided into two equal parts with a removable acrylic sheet (Video 1–3). We designed the arena to be large enough for individuals to move outside the antenniform leg-scanning zone (33.77 ± 9.25 cm dia.) of trial partners but small enough to encourage interactions. The arena floor was lined with unbleached paper to provide traction for movement. *P. longipes* cannot walk on glass, so animals were restricted to movement on the arena floor. We replaced paper and cleaned enclosures with isopropyl between trials. Territory recognition likely occurs via olfactory cues of opponents (Chapin & Hebets 2016). Other research found that olfactory cues are used in individual-level recognition, and amblypygids have the physiology to detect a variety of compounds (Hebets & Chapman 2000; Walsh & Rayor 2008). Increased mRHP can occur just moments after territory acquisition (Bergman et al. 2007) and many territorial animals will engage in territory defense, even when relocated to laboratory conditions or otherwise unfamiliar areas (Fowler-Finn & Hebets 2006; Tanner & Adler 2009). Thus, we implemented an initial 10 min solitary period for animals to acclimate and potentially from territory cues after which we removed the divider to permit individuals to interact for 45 min. Since our analysis focused on the reaction of intruders, we were not concerned with the time territory holders needed to establish a territory. Instead, the reaction of intruders when faced with putative territory cues were of interest. We randomly selected captured individuals for inclusion in trials. Thus, contestant pairs included all size and sex combinations.

Behavioral trials were video recorded in darkness and at night under 940 nm peak wavelength infrared LED lights and a modified CCD camera with infrared bypass filter removed and fixed focus lens recording 640 × 480 p at 30 fps (Video 1–3). For each trial, we randomly chose one amblypygid to serve as the focal individual. We recorded whether this individual was the interaction initiator (i.e., oriented and began agonistic behaviors first), since contest initiation could interact with the contest outcome. Additionally, we recorded which side of the arena the focal individual was on at the start of the interaction; focal individuals were considered holders if the interaction started on their side of the arena, or intruders if not. Lastly, we recorded if the focal individual won or lost the contest by if it or its opponent ended the interaction by fleeing (i.e. orienting away from opponents or moving away from interactions). All behavioral data were recorded from video recordings of trials by one author (SLH) blind to project data to avoid inter-observer error and reduce bias.

3.3.3 Analyses

We included physical and motivational components of RHP, sex, and their interactions in a binomial generalized linear model to determine which, if any, predicted contest outcome. We used scaled mass index to represent pRHP. Antenniform leg length, pedipalp femur length, carapace width, and weight all correlated with SMI (Fig. 3.1), and were thus not included in model comparisons. We used residency (intruder or holder) as a measure of mRHP, and predicted that holders are more motivated than intruders. Thus, all else controlled, we predict that putative holders should win more often due to higher mRHP. Since RHP components can have inter-active effects, we included interaction terms of predictor variables. Furthermore, we included sex as a predictive factor to account for potential differences in territoriality between the sexes. We com-pared the global model to more parsimonious versions via Akaike's Information Criterion corrected for small sample sizes (AICc) and Akaike weights (w_i). We tested parameters of the best model using Wald z-tests. We tested if males or females, and if intruders or holders, were more likely to win contests via χ^2 tests. Since contest initiators and holders could confound contest outcome, we tested if contests initiators were more likely to win contests using a χ^2 test.

3.4 Results

Agonistic interactions occurred in all trials (*n* = 48) and followed a series of stereotyped, ritualized displays similar to other species (Video 1–3; Fowler-Finn & Hebets 2006). Mean interaction time was 1.58 ± 0.30 min, and ranged from nearly instantaneous (i.e., immediately retreating after initial orientation) to up to 16.33 min. Multimodel comparisons indicated that the best model predicting contest outcome included SMI (pRHP), residency (mRHP), and their interaction (Table 3.2). Models with sex, without residency, or without SMI were worse at predicting contest outcome. Thus, both physical and motivational components of RHP affected con-test outcome and intruders changed their behavior in response to the territory cues of holders. We confirmed this with post-hoc inference tests of best model parameters (Table 3.3). We plotted model estimates to illustrate interaction of SMI and residency (Fig. 3.2). High SMI improved the probability of winning contests for holders ($b = 3.81$) but not for intruders (b = −0.06). Furthermore, residency (i.e., mRHP) increased the probability of winning contests among individuals with greater body condition.

Territory recognition is confirmed inferentially by a χ^2 test indicating that contests were 67% more likely to be won than lost by the holder ($\chi^2_2 = 7.26$, $P = 0.007$; $n = 88$ individuals). Contest winners had larger body size, weight, weaponry size, and SMI than losers (Fig. 3.3). We failed to detect if one sex was more likely to win con-tests than the other ($\chi^2_1 = 0.19$, $P = 0.667$) which is in agreement with the unimportance of sex as a predictive variable in multimode comparisons (Table 3.2).

We tested if these results were due to effects other than asymmetric mRHP, thereby discrediting the finding that the species is territorial. Since holders and intruders are assigned by where the interaction occurs (i.e., either in one or the other’s side of the arena), the case could be made that individuals that initiate interactions are more likely to both be intruders and lose contests (i.e., that the intruder-loser relationship is confounded by which individual initiates contests). We tested this by assigning an individual of each trial as the interaction initiator. We found that opponents that initiated the interaction were no more likely to win or lose than opponents that did not ($\chi^2_3 = 5.19$, $P = 0.16$) and were no more or less likely to be holders than intruders ($\chi^2_3 = 0.17$, $P = 0.98$).

3.5 Discussion

We found that *P. longipes* is territorial because contesting individuals displayed asymmetric mRHP, which interacted with pRHP. Intruders showed lower mRHP when in the presence of territory cues, indicating that intruders recognized the territory of their opponent and were less motivated to win the contest than holders. This held regardless of which individual initiated the contest. Put simply, individuals fought weaker when among the territory cues of another. Our research provides proof-of-concept results that intruder motivation is a measure of territoriality that can apply to animals with unobvious territorial behavior.

The mRHP × pRHP interaction indicated that high pRHP improved the probability of winning for holders but not intruders. This result provides a glimpse into the different contest strategies in which holders and intruders engage. We posit that intruders always fight maximally against any holders regardless of pRHP, while holders hedge their bets in light of their own energy stores. Thus, holders enact a bourgeois-like, resource quality-dependent strategy when engaging in contests (Maynard Smith & Parker 1976). This makes sense if, in the wild, territory holders have variable food stores while vagrants without territories fast until a new territory is acquired. Indeed, it is likely that a characteristic of high-quality territories is proximity to food resources (Chapin 2014). In keeping with this, holders with poor body condition may interpret their territory as equally poor, and therefore may not value it as much as holders with high body condition. Thus, amblypygids may use their own body condition as an indicator of territory quality. This corroborates to the lack of slope for intruders, which of course would not use their own body condition as a predictor of an opponent's territory quality. Thus, an intruder's probability of winning contests is unlinked with their body condition. The pRHP × mRHP interaction indicated that holders should be more willing to give up territories if their body condition is poor, indicating poor territory quality.

An alternative explanation for increased holder mRHP is that familiarity with the space increases motivation (Kokko 2013). A classic example is the home advantage in human sports competitions, where teams or individuals playing in familiar spaces (e.g., their home court) are more likely to win than rivals (Pollard 2008). We argue that this is not the case with our study; we posit that gaining information about their side of the arena provides little advantage to holders, as there are no distinct physical features across arena sides. While it is unlikely that this effect influenced our study, territory holders in nature could benefit from this information. For example, holders may make better use of the spatial structures of their territory when engaging in agonistic interactions. Staging contests in structurally complex arenas may elucidate the effect this has on contest outcome.

Another alternative explanation is that the probability of individuals losing contests co-varies with some other variable, such as which individual initiates the interaction. If initiating is correlated with a lower probability of winning contests, then an intruder-loser holder-winner pattern might explain our results. We tested for this pattern and failed to detect a difference in the probability of contest initiators winning contests. We found that the observed pattern of territoriality and contest outcome was not explained by a correlation between losers and initiators. Animals that are more active were not more likely to be the intruder. Instead, contestants alter their mRHP based on their role (intruder or holder) in the interaction (Maynard Smith & Parker 1976).

Territory effects have not been tested in any other Amblypygi species, but site fidelity seems pervasive throughout the order(Chapin & Hebets 2016). Field research on three other Amblypygi species showed that individuals return to their capture site upon relocation and were found in the same location for repeated nights (Hebets 2002; Hebets et al. 2014; Porto & Peixoto 2013; Weygoldt 1977). High quality territories likely attract mates, provide protection from predators and daytime desiccation, and are adjacent to the best foraging areas (Bloch & Weiss 2002; Carvalho et al. 2012).

Olfaction is likely the primary mechanism for territory recognition in Amblypygi. Both physiological and ecological research on amblypygids has shown that olfaction plays an important role in amblypygid navigation (Hebets & Chapman 2000). Indeed, olfactory cues were the only alteration to the arena available to opponents, and there exists no evidence of amblypygids altering their territory. Tactile perception is also important for amblypygids, but the arena did not offer tactile cues that would identify a territory (Hebets et al. 2014; Santer & Hebets 2009b). Furthermore, at least one species of amblypygid has the ability to recognize individuals by olfactory cues (Walsh & Rayor 2008). Given this, it seems likely that the short establishment period of our study is sufficient for individuals to engage in territorial defense; individuals in areas with olfactory cues of themselves behave like territory holders, while those among stranger olfactory cues behave like intruders. Holder behavior alone is not sufficient to explain the asymmetry in mRHP, because individuals often moved around the entire arena before engaging in contests. Indeed, our results show that holders that leave their putative territory and return to find an intruder are still more likely to win contests.

Territoriality has been hard to measure and test (Powell 2000).One common measure of territoriality is to estimate to what extent home ranges are non-overlapping (Genovesi et al. 1997; Powellet al. 1996). This indirect method is limited to species with clear home ranges and that are amenable to long term, high resolution tracking. Another intuitive, but obviously challenging to execute, method is identifying territoriality by quantifying the costs and benefits of territorial behavior (Adams 2001). Less common are field studies that manipulate home range spacing to test for residency. For example, spiders placed in artificial burrows close to territory holders were more likely to abandon their burrows (Moya-Laraño et al. 2002). This protocol is unfortunately intractable for most species and introduces asymmetry in resource quality. Our protocol does not require consideration of resource quality, or even the identity of the resource. Instead, we test the reaction of intruders to cues of a territory regardless if there is one, or if there is any reason to form one. Territoriality is evidenced by the response of intruders. This, however, should not imply that the type or value of the defended resource is unimportant. Species with conditional territoriality, in particular, require an understanding of resource value to replicate territoriality in the laboratory or examine animals in nature already in territorial behavioral states. Territory formation can depend on phenology, ontogeny, sex, phenotype, and resource abundance (Apio et al. 2007; Bibby & Green 1980a, b; Johansson & Jonzén 2012; Messier 1985; Pröhl 2005; Sinervo & Lively 1996). An advantage of our assay is that, by repeated trials, it can identify the territorial season, sex, age, and environmental conditions for a species or population. For example, we showed here that *P. longipes* territoriality is not sex or ontogeny-dependent—individuals responded to territory cues regardless of the sex or size of opponents.

We demonstrate an empirical approach to testing for territoriality by measuring motivation in putative intruders. mRHP evidenced territoriality. This method can address the challenge of testing for territoriality in species with less conspicuous territorial behaviors. Testing for territoriality via intruder mRHP can enable contest and territoriality research on a wider variety of taxa and conditions, thereby enabling further investigations into the diversity and functioning of territorial behaviors across Animalia.

3.6 Acknowledgements

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3.7 Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2015.11.014.

3.8 Tables & Figures

Table 3.1. The $\bar{x}$ ± SD and range of morphological measurements of *Phrynus longipes* considered for inclusion in models predicting the outcome of putatively territorial contests.

measure	**range**	$\bar{x}$ **± SD**
maximum antenniform leg length (mm)	63.03 – 236.93	161.94 ± 40.05
maximum pedipalp femur length (mm)	3.08 – 18.82	10.94 ± 3.34
carapace width (mm)	6.36 – 19.04	13.77 ± 2.89
weight (g)	0.10 – 5.18	2.15 ± 1.24
scaled mass index	0.16 – 1.52	1.01 ± 0.04

Table 3.2. Comparison of binomial generalized linear models predicting contest outcome in *Phrynus longipes*. The best model included the physical (scaled mass index; SMI) and motivational (residency) components of resource holding potential and their interaction. AICc is Akaike's information criterion corrected for small sample sizes; *k* is the number of model parameters (intercept included); ΔAICc is the difference in AICc of the i^{th} model and the lowest-scoring model; and w_i is the Akaike weight representing the conditional probabilities for each model.

model	**AICc**	***k***	**ΔAICc**	w_i
SMI × residency × sex	114.65	12	12.52	< 0.01
SMI × residency	102.13	4	0.00	0.51
SMI + residency	104.94	3	2.80	0.13
SMI	103.89	2	1.76	0.21
residency	106.98	2	4.85	0.05
intercept-only	105.37	1	3.24	0.10

Table 3.3. Model estimates and Wald tests for a binomial generalized linear model predicting contest outcome in *Phrynus longipes*. mRHP (residency), pRHP (scaled mass index; SMI) and their interaction are included in the model. Results indicate a significant interaction of SMI and residency.

parameter	**estimate ± se**	***z***	***P***
SMI	−0.06 ± 1.08	0.054	0.957
residency	−3.34 ± 1.94	1.73	0.084
SMI × residency	3.87 ± 1.86	2.08	0.038

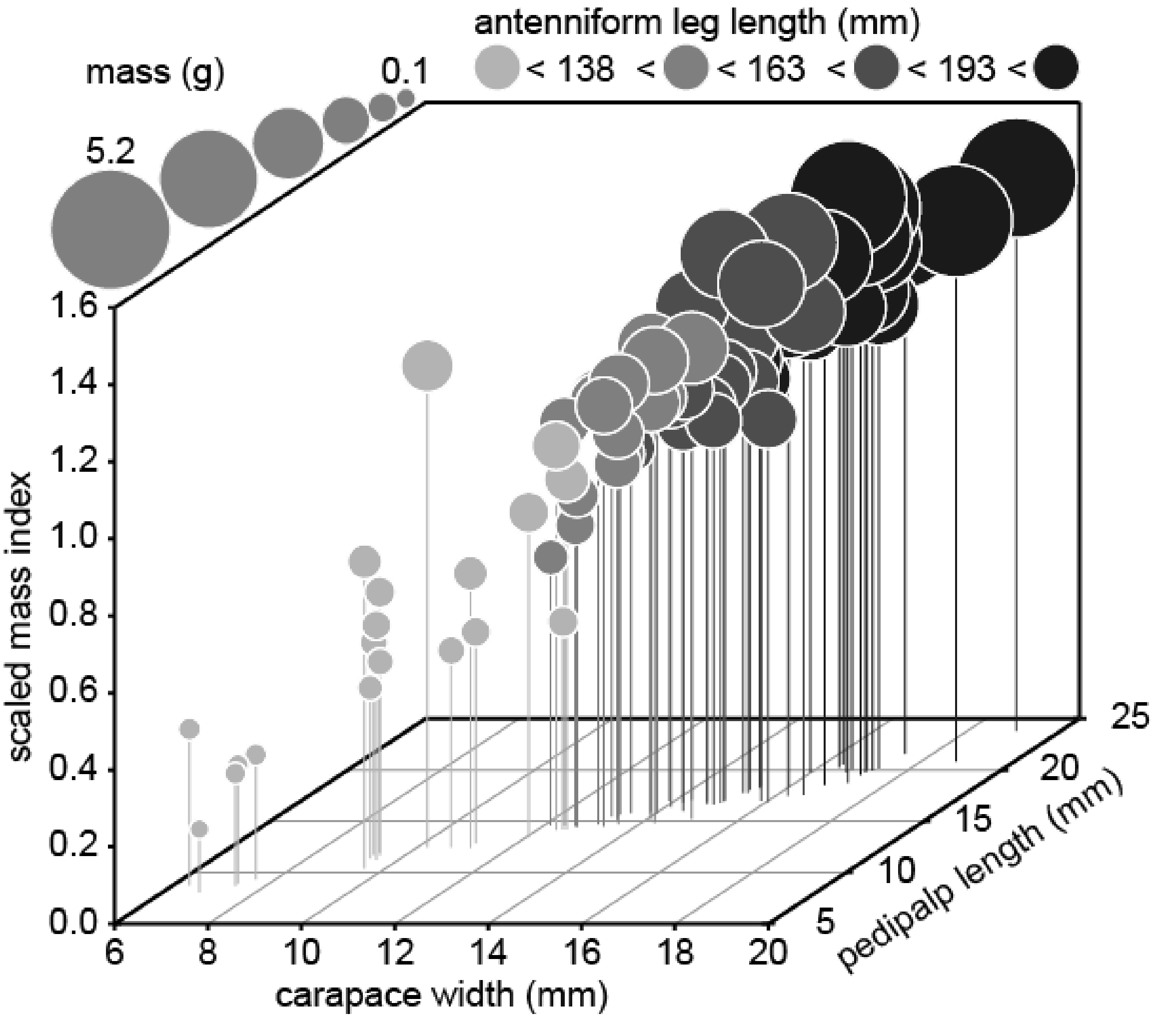

Figure 3.1. Three-dimensional scatterplot illustrating collinearity of physical resource holding potential proxies for *Phrynus longipes*. Measures include scaled mass index, maximum carapace width (mm), and maximum pedipalp femur length (mm). Circle sizes represent antenniform leg length (mm) and circle color represents mass (g). A multivariate regression of all variables is strongly correlated (Adj. $r^2 = 0.88$, $F_{4,70} = 135.7$, $P > 0.0001$).

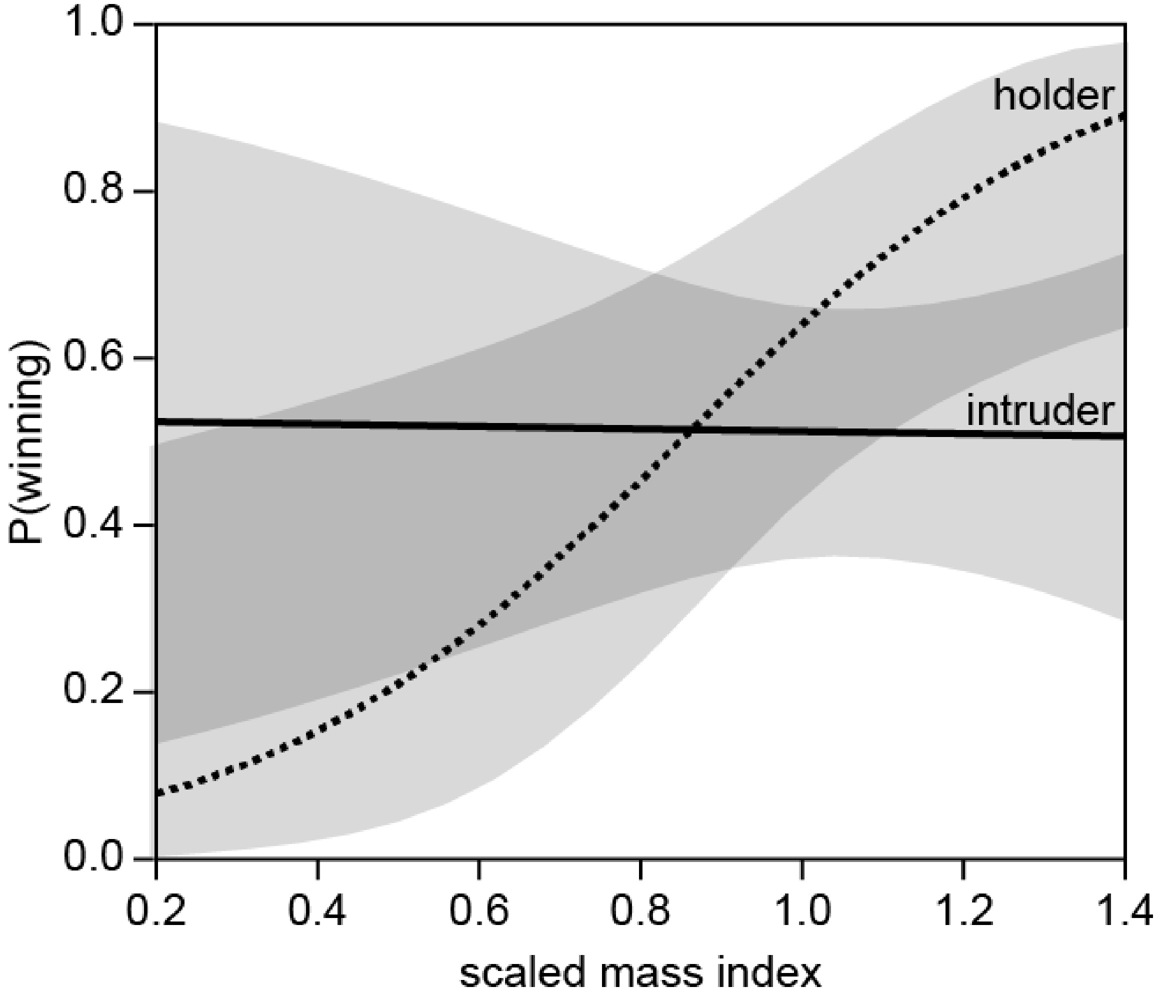

Figure 3.2. Interaction plot of a binomial generalized linear model of residency (a measure of motivational resource holding potential; *b* = −0.06) and scaled mass index (a measure of physical resource holding potential; *b* = 3.81) predicting contest outcome for *Phrynus longipes* agonistic interactions. The dotted line represents putative territory holders and the solid represents intruders. Shaded areas indicate 95% confidence intervals.

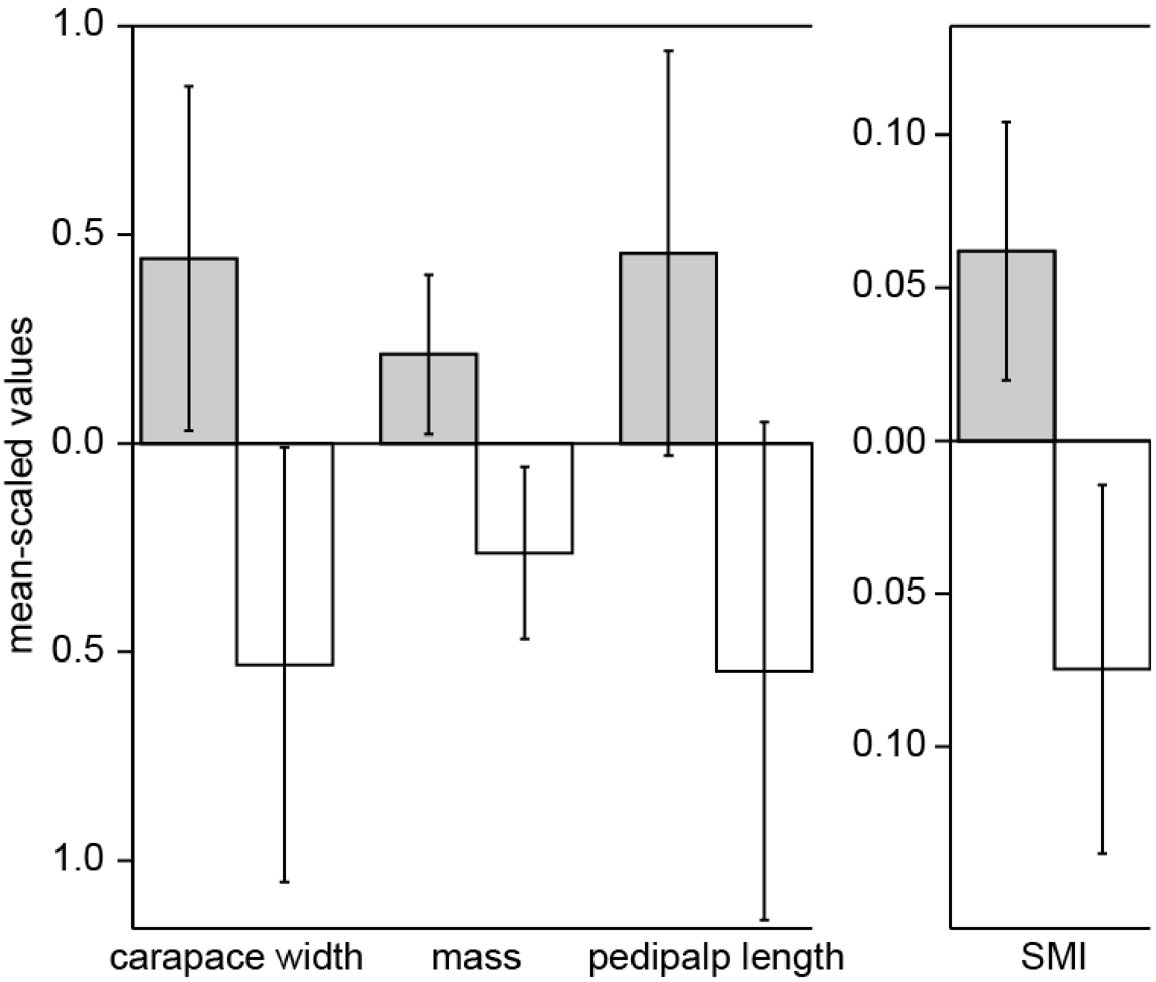

Figure 3.3. Bar plot of mean-centered carapace width (mm), weight (g), scaled mass index, and pedipalp femur length (mm) of contest winners (grey bars) and losers (white bars). Lines indicate standard error of the mean.

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CHAPTER 4: Cannibalism among rivals: atypical symmetric cannibalism caused by territoriality in the amblypygid *Phrynus longipes*

4.1 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 consequence or byproduct of territory contests. We staged paired interactions and recorded behavioral data 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 most similar in armament, but most dissimilar in body mass. This suggests a discrepancy between phenotypes evolved to communicate resource holding potential (which benefit individuals if dishonest), and the more honest signal of actual body mass, which is a better estimate of true resource holding potential. Further, it shows that symmetric cannibalism in *Phrynus longipes* can be explained by an interaction between agonism and conspecific predatory behavior.

Keywords: Arachnida, resource holding potential, resource contests, size-structured, speleology

4.2 Introduction

Cannibalism can shape both the demography of populations and phenotypes of individuals (Polis 1981). Cannibalism may stabilize the amplitude of population size variation (Claessen 2004) by reducing intraspecific competition and providing an alternative food source when resources are limited (Landahl & Hansen 1975; van den Bosch et al. 1988; Deikmann 2003). This controls population size and structure, thereby stabilizing populations under stress (Costantino et al. 1997). Asymmetric cannibalism (sometimes termed size-structured cannibalism), in which larger individuals prey on smaller conspecifics, has received the majority of attention by biologists (Polis 1981; Gurtin & Levine 1982; Claessen, et al. 2004). A recent review found that, out 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 (Polis 1981; Kohlmeier & Ebenhoh 1995). Polis (1981) asserted that, while reversals of traditional size structure may occur, there exists no theoretical or otherwise explanatory framework for why such a paradigm would occur (Rose 1976; Polis 1980). The paucity of literature in this area is not altogether surprising inasmuch as cannibalism has only recently been considered important in understanding population and ecological dynamics (Deikmann, et. al 1986; Huston et al. 1988; Kohlmeier & Ebenhoh 1995; Dong & DeAngelis 1998). While research on asymmetric cannibalism has described how cannibalism occurs under many conditions, the literature does not address the mechanism by which symmetric cannibalism occurs.

The cannibalistic amblypygid *P. longipes* appears to show no preference for smaller conspecific prey, though data are limited (Chapin 2015, Chapin & Hebets 2016, Torres-Contreras et al. 2015). *P. longipes* is a species of Amblypygid; an order of cannibalistic, nocturnal, and territorial Arachnids (Chapin & Hebets 2016). Amblypygi are outfitted with elongate forelegs used to sense the environment and communicate with conspecifics and spiny pedipalps used capture prey and communicate threat displays (Spence et al., 2005; Weygoldt 2000; Chapin & Hebets 2016). When a conspecific enters an individual's territory, a set of ritualized agonistic interactions begins that can end in cannibalism (Chapin 2015, Chapin & Hill-Lindsay 2016, 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 was *Phrynus barbadensis* in Colombia cannibalizing a recently-molted conspecific (Torres-Contereras et al. 2015). It seems that symmetric cannibalism occurs in *P. longiepes* as a consequence of territorial contests, and thus presents an opportunity to expand on our understanding of cannibalism. We aimed to address the following questions using the amblypygid *Phrynus longipes*: (1) What morphological features best predict cannibalism during territorial contests? (2) Are those features the same that predict if the contest will escalate to physical aggression? (3) If not, how do cannibalism and resource contests interact?

Agonistic interactions between pairs of *P. longipes* escalate in a predictable pattern, similar to other amblypygid species (Fowler-Finn & Hebets 2006; Chapin 2015, Chapin & Hebets 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 escalate in injury or cannibalism if an opponent does not retreat

(Chapin & Hill-Lindsay 2015; Chapin & Hebets 2016). Contests escalate according to the relative resource holding potentials (RHP), or absolute fighting abilities, of opponents (Parker 1974; Chapin & Hill-Lindsay 2016). RHP is usually estimated by proxies such as body size, body mass, or armament size (Koskimäki et al. 2003). Game theory models for animal contests predict that individuals with more similar RHP are more likely to escalate interactions to more aggressive and risky states (Barlow 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, are 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 et al. 2007). Therefore, armament measures may not give an accurate estimate of fighting ability. Measures of body size or mass, however, may provide more honest indicators of RHP (Morris et al. 1995; Bath et al. 2015; Theis et al. 2015).

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.

4.3 Methods

In August 2012 and 2014**,** we collected *P. longipes* between 1000–0400 h from forests and caves in Arecibo, Puerto Rico generally located at 18.414°, −66.726°. We measured the mass of each individual with a gram scale to the nearest 0.01 g, body size by measuring maximum prosoma width, and measured pedipalp femur length with digital calipers to the nearest 0.01 ± 0.03 mm. We housed animals separately for 24 hours in deli containers (14 cm tall, 11.5 cm top dia, 9 cm base dia) lined with butcher paper prior to trials. We returned surviving individuals to their capture site after experimentation.

Behavioral trials (*n* = 48) were conducted sensu Chapin (2015). Briefly, arenas were made from 75 × 30 × 30 h 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 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 to observations of natural interactions (Weygoldt 2000, Chapin & Hebets 2016). 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 lights with a modified CCD 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. Individuals were only used in one trial.

We employed a multimodel comparative approach to test if body size, body mass, armament size, or an interaction of those measures best predicted escalation to physical aggression and cannibalism (Burnham, et al. 2011, Richards, et al. 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). 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 *t* tests.

4.4 Results

Multimodel comparisons found that escalation was best predicted by armament size, while cannibalism was best predicted by the interaction of armament size and mass (Table 4.1). 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 4.2; Fig. 4.1). This effect is exacerbated among pairs that both escalated and cannibalized (Fig. 4.2). Individuals were more likely to cannibalize if the agonistic interaction escalated (16.5% of 34 trials) than if they did not (11.8% of 164 trials). Of those pairs that did escalate, the individuals that cannibalized were larger (15.57 ± 0.43 vs. 11.06 ± 0.55; $t_{55} = 6.46$, $P < 0.001$) and of greater mass (2.85 ± 0.17 vs. 1.00 ± 0.13; $t_{54} = 8.58$, $P < 0.001$) than individuals that did not cannibalize (Table 4.2; Fig. 4.3). Cannibalism was occasionally seen in the wild while collecting animals, indicating that this behavior occurs outside of our experimental conditions (Fig. 4.4).

4.5 Discussion

Weapon size symmetry predicted escalation and body mass asymmetry predicted cannibalism in pairs that escalated. This illustrates that the unusual pattern of symmetric cannibalism found in *P. longipes* can be explained by a two-stage interaction with resource contests. 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. Occasionally, cannibalism occurred without escalation, but these instances were rare and only minimally affected the general pattern of our findings. The first stage is consistent with game theory models predicting a negative relationship between contest escalation and the difference in RHP among opponents (Barlow 1986; Arnott & Elwood 2009). The second stage is consistent with models of asymmetric cannibalism, which predict that larger individuals should consume smaller conspecifics (Classen 2004). When interactions escalated such that cannibalism could occur, the individual with lower body mass fell prey to the larger opponent.

The variables that best predicted escalation and cannibalism match our understanding of behavior ritualization and dishonest signaling. Pedipalps, which advertise RHP, were the best predictor of escalation, although pedipalp size did not predict cannibalism (Table 4.1). Displays are open to both higher error and dishonest signaling than measures of body mass (van Staaden et al. 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 4.1, Fig. 4.2). 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; Maynard Smith 1974; Parker and Thompson 1980), where information error decreases as the contest escalates (Maynard Smith 1974: Enquest et al. 1990).

Contests between *P. longipes* may resolve themselves in two ways; an individual retreats or is 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 agonism begin (Cullen 1966; Chapin 2015). We found that RHP-symmetric opponents are more likely to escalate an agonistic interaction. This is consistent with ecological models of intraspecific contests (Kemp & Wiklund 2001; Arnott & Elwood 2009). 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 analyses and modeling are needed to examine the relationship between conspecific density, resource availability, and symmetric cannibalism in this species. This study models cannibalism as it occurs under laboratory settings, but symmetric cannibalism has been observed in the field (Fig. 4.4). That said, there is little known about the specific circumstances under which symmetric cannibalism may occur in natural populations. In many species where asymmetric cannibalism has been documented, cannibalism occurs only under specific conditions (Rose 1976; Lannoo and Bachmann 1984; Deikmann 2003). For example, in the salamander *Ambystoma t. tigrinum*, cannibalism only occurs when larvae are at high densities (Lannoo & Bachmann 1984). This mechanism may serve to stabilize populations that exceed the limitations of available resources. In populations of certain arthropods, cannibalism may allow a population to persist under conditions in which no other food sources are available (van den Bosch and Gabriel 1997). Ecologists have modeled how size structured cannibalism occurs and what role, if any, it plays in the stabilization of populations (Claessen et al. 2004). Other models of asymmetric cannibalism build in the generational impacts of older individuals eating their smaller younger conspecifics (Polis 1988, 1981; Claesen et al. 2003, 2004). But we caution against applying traditional population models of asymmetric cannibalism to *P. longipes* and other animals that might exhibit symmetric cannibalism.

Cannibalism plays an important role in the structure of populations and the behavior of individuals. Traditional models of cannibalism focus on larger, older, and stronger individuals consuming their smaller, younger, weaker counterparts. We find that *P. longipes* is more likely to cannibalize RHP-similar opponents. Individuals with similar armament sizes are more likely to escalate interactions. Once interactions escalated, individuals with better body mass were most likely to cannibalize opponents. Better body mass indicates more energy stores which provide an advantage when engaged in lethal contests. Thus, 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. Although we do not yet understand the significance of RHP-symmetric cannibalism, there is great potential for this research on this phenomenon to expand our understanding of population dynamics and the evolution of behavior.

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4.7 Tables & Figures

Table 4.1. Multimodel comparisons of logistic regressions of the difference of size, mass, and armament between opponents in paired trials predicting cannibalism and escalation. Size was estimated by maximum carapace width, mass was estimated by total body weight, and armament was estimated by pedipalp femur length. 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 ($n = 198$).

		Cannibalism			**Escalation**		
Models	***k***	**AICc**	**ΔAICc**	w_i	**AICc**	**ΔAICc**	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	0.00	0.078
armament	1	170.42	6.57	0.013	173.06	2.32	**0.248**
intercept only	0	169.44	5.59	0.011	182.47	11.72	0.001

Table 4.2. Estimates of the best-fitting logistic regression predicting cannibalism or escalation. The best model predicting cannibalism included the proportional difference in body mass, armament, and their interaction, while the best model predicting escalation included only the proportional difference in armament.

Parameter	**Estimate ± SE**	***z***	***P***
predicting cannibalism			
mass	1.91 ± 0.77	2.489	0.013
armament	3.84 ± 2.22	1.73	0.083
mass × armament	−3.15 ± 1.20	2.62	0.009
predicting escalation			
armament	−2.03 ± 0.66	3.06	0.002

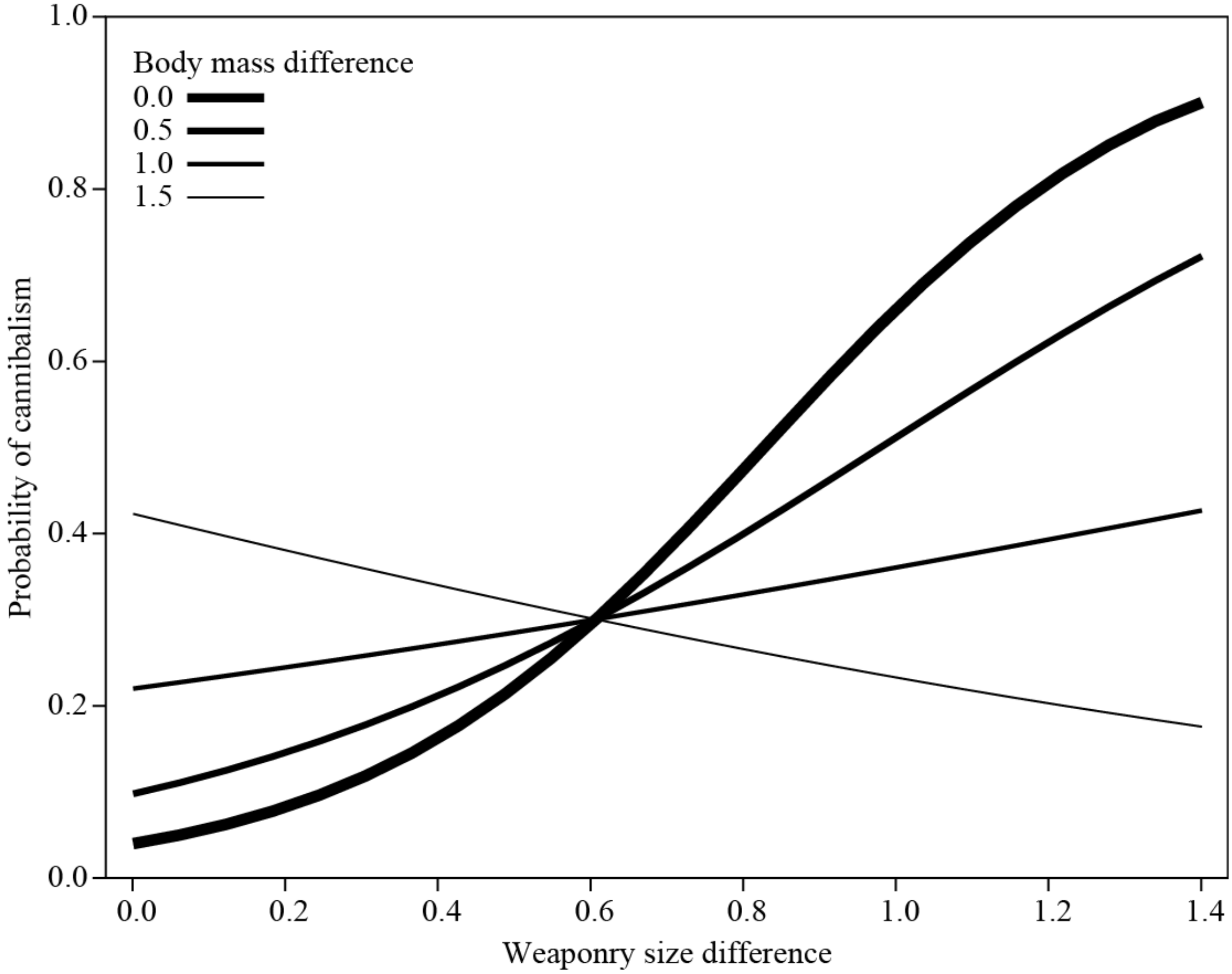

Figure 4.1. Interaction plot of a logistic regression of the interaction of body mass and armament size predicting cannibalism (estimate ± SE: −3.15 ± 1.20, z = 2.62, P = 0.009). Line thickness indicates one of four body mass values.

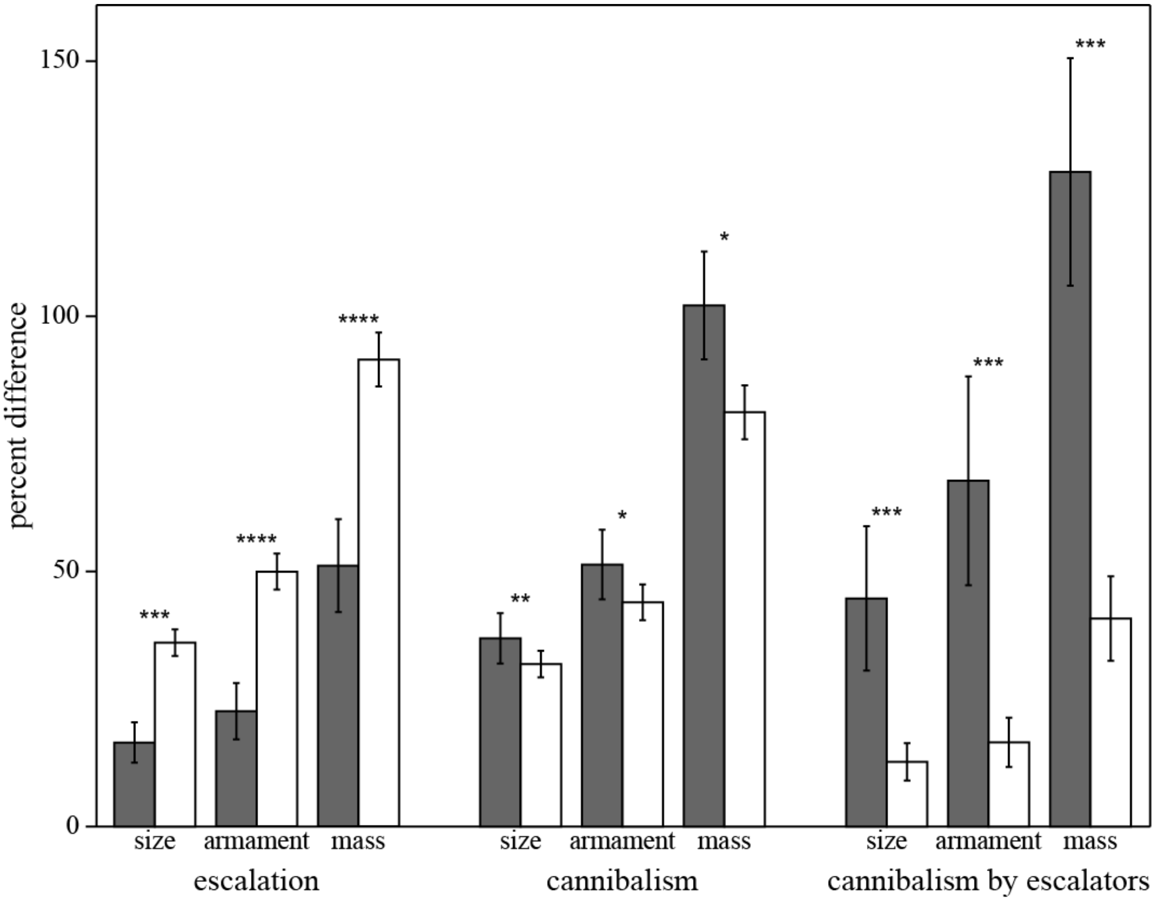

Figure 4.2. Mean percent difference in body mass, size, armament, and scaled mass index (SMI) for trials that did (grey bars) or did not (white bars) a) progress to escalated agonism b) ended in cannibalism and c) progress to escalated agonism and ended in cannibalism (*n* = 198). Whiskers indicate standard error of the mean. Number of asterisks indicate *P* < 0.1, 0.05, 0.01, or 0.001 for Wilcoxon tests.

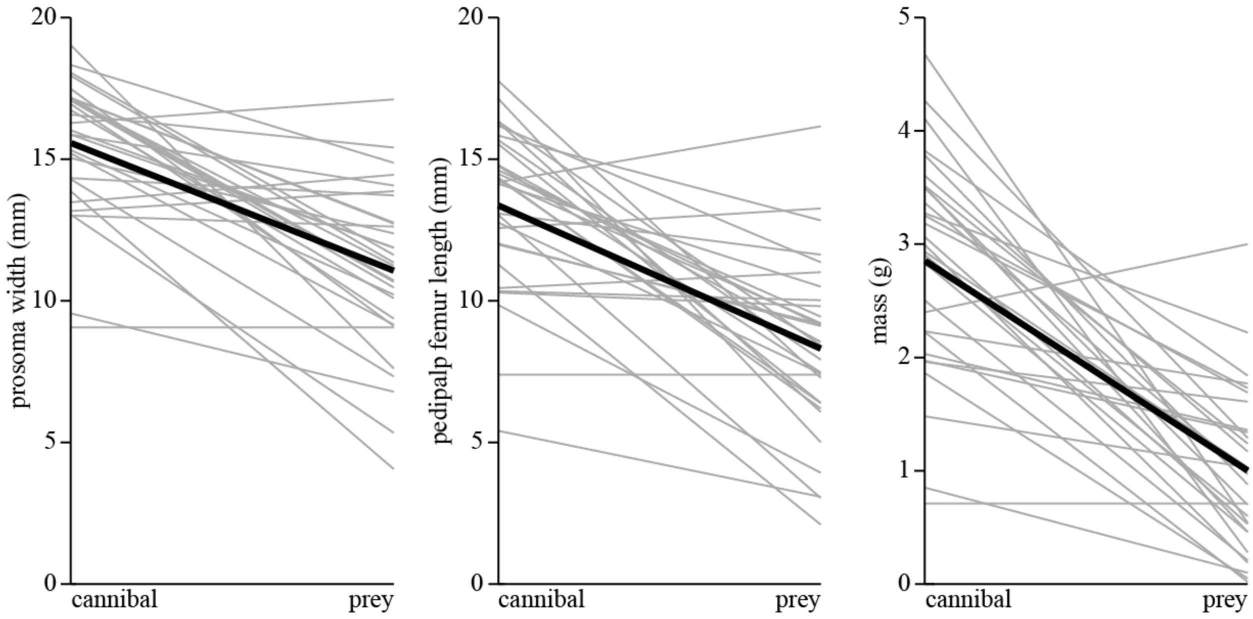

Figure 4.3. Comparison of carapace width (mm), pedipalp femur length (mm), and mass (g) of *Phrynus longipes* pairs that either cannibalized or were prey to cannibals in paired trials. Grey lines represent one pair that ended in cannibalism. Thick black line represents the mean. Cannibals were larger, more massive, and had a higher scaled mass index than conspecific prey ($t_{55} = 6.46$, $P < 0.001$; $t_{54} = 8.58$, $P < 0.001$; $t_{57} = 6.50$, $P < 0.001$).

Figure 4.4. Photograph of symmetric cannibalism of *Phrynus longipes* in nature.

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CHAPTER 5: When tradeoffs break down: increased parental investment in offspring number but not quality in an amblypygid

5.1 Abstract

Natural selection predicts that organisms should maximize reproductive fitness by exhibiting a tradeoff between the quality and quantity of offspring. We tested this prediction in the amblypygid *Phrynus longipes*—a long-lived, iteroparitous arachnid with indeterminate growth, post-ultimate molts, and parental care. We measured the size of gravid females and the mass and number of eggs in their clutches. Egg count, but not mass, was predicted by female size, indicating that this species does not exhibit the offspring quality-quantity tradeoff. We posit that *P. longipes* eggs are already larger than optimum, likely due to physiological constraints on ontogeny. This study is the first of its kind in any amblypygid species, and adds to the diversity of life histories across Animalia.

Keywords: Amblypygi, Arachnida, clutch**,** egg, parental investment, reproductive tradeoff

5.2 Introduction

Natural selection predicts that organisms should maximize reproductive fitness by exhibiting a tradeoff between the quality and quantity of offspring (Lack 1947, 1954; Smith & Fretwell 1974; Hendriks & Mulder 2008). This was expressed by Lack's solution, which predicted that intermediate clutch sizes should procure the highest parental reproductive fitness (Lack 1954). Lack's solution served as the foundation for the Smith & Fretwell (1974) model which predicted optimal parental investment as the tangent of a curve the relationship between offspring investment and survivorship. Indeed, this fitness-optimizing tradeoff occurs in many species (Pianka 1970; Montague et al. 1981; Kaufman & Kaufman, 1987; Berrigan 1991; King, 1993; Guisande et al. 1996; Fox et al. 1997; Hendriks & Mulder 2008), where parents strive to achieve an optimum between producing few, high quality offspring, or many low quality offspring. Species optima are complicated by parent-offspring conflict, parent life history, and physiological constraints (Parker & Begon 1986; Olsson & Shrine 1997). Further, individuals may deviate from optima if resource availability changes and as parents age (Charlesworth 1980; Pianka & Parker 1975; Charlesword 1980). Individuals may invest more per offspring as they reach senescence and future reproduction becomes less certain. This is often described as decreased residual reproductive value (Pianka & Parker 1975).

Species of the order Amblypygi (Arachnida) have a unique combination of life history traits making them aptly suited for intraspecific parental investment trade-off research. Unlike nearly all other arthropods, amblypygids have indeterminate growth and molt after sexual maturity (Weygoldt 2000; Chapin & Hebets 2016). Thus, amblypygid initial egg size is unlikely to determine final adult size (Smith 1997). Amblypygids are long-lived (perhaps 7–10 years), iteroparous, produce 10–90 eggs per clutch, and engage in parental care (Chapin & Hebets 2016).

There is no clear intuition regarding the potential for amblypygids to deviate from the quality-quantity tradeoff. Amblypygids might be likely to exhibit the tradeoff because they produce eggs together in an eggsac, which should emphasize energetic constraints on offspring number and mass (Fig. 5.1a; Parker & Begon 1986). The quantity-quality tradeoff is more obvious in oviparous species, which, unlike viviparous species, allocate a discrete amount of resources to offspring upon or soon after fertilization (Ford & Seigel 1989; King 1993). Further, animals with high parental investment tend to not exhibit the tradeoff. This is because offspring number is limited by postzygotic invest (Boyce & Perrins 1987; Oksanen et al. 2001; but see Walker et al. 2008). Amblypygids exhibit low parental care relative to traditional quality-quantity tradeoff study organisms, but high parental care relative to most arthropods (Fig. 5.1; Chapin & Hebets 2016). Females carry the eggsac on the ventral prosoma. After hatching, young emerge and climb onto the back of the female where they molt before becoming free-living (Weygoldt 2000; Chapin & Hebets 2016). Organisms with more complex life histories and iteroparity are less likely to exhibit a trade-off (Fox & Czesak 2000). Further, the closely related Araneae tend to not show the trade-off, but scorpions do (Killebrew & Ford 1985; Marshall & Gittleman 1994, Brown et al. 2003, Skow & Jakob 2003), and the phenomenon is common among other arthropod groups (Berrigan 1991; Fox & Czesak 2000). The goal of this experiment is to determine if individuals of amblypygid *Phrynus longipes* deviate from the egg size-number trade-off to better understand the parental investment variation across arthropods.

5.3 Methods

We collected twenty-four gravid *Phrynus longipes* from Cueva Matos generally located at 18.38, −66.68 (decimal degrees) in Arecibo, Puerto Rico in August 2014. We measured the maximum prosoma width of each female using digital calipers to the nearest 0.1 mm ± 0.1. The prosoma shows allometric growth throughout the life of amblypygids, and correlates well with body mass (Chapin 2011; Chapin & Hebets 2016). We stored specimens in 95% ethanol and shipped them to our laboratory at UCLA for further analysis. We recorded the total number of eggs per female, and binned eggs into one of 5 developmental stages (Table 5.2) based on development of the germinal bands, legs, and eyes. We recorded dry mass of ten randomly selected eggs from each clutch. Selected eggs were placed in microcentrifuge tubes and dried in a drying oven at 60℃ for 120 h before being weighed with a microbalance scale to the nearest 1 μg ± 1μg (Orion Cahn C-33). We used the mean of the 10 weights to estimate egg mass for each clutch.

We compared generalized linear models (GLM) of egg mass and count predicting female size using Akaike's information criterion corrected for small sample size (AICc) and Akiake's weights (w_i; Burnham et al. 2011; Symonds & Mousalli 2011). We used linear regressions to examine the relationship between mean egg mass, total egg count, developmental stage, and female size.

5.4 Results

Amblypygids had a clutch size of 67 ± 3.3 eggs ($\bar{x} \pm s$; range: 29–94; $n = 24$ clutches). Overall eggs mass was 4.01 ± 0.12 µg (Range: 3.10–5.21) and the prosoma width of females was 15.80 ± 0.36 mm (range: 12.3–18.9). The best GLM predicting female size included only egg count, not mass (Table 5.1; estimate ± s = 0.071 ± 0.018, $t_{23} = 3.94$, $P < 0.001$). Larger females laid more eggs per clutch (adjusted $r^2 = 0.435$, $F_{1, 21} = 17.96$, $P < 0.001$; Fig. 5.2) and larger clutches were composed of larger eggs (adjusted $r^2 = 0.193$, $F_{1, 21} = 6.265$, $P = 0.021$; Fig. 5.2) but female prosoma size failed to predict egg mass (adjusted $r^2 = 0.012$, $F_{1, 21} = 1.268$, $P = 0.273$; Fig. 5.2). Eggs became smaller as eggs advance in developmental stage ($\beta = -0.21$, Adj. $R^2 = 0.30$, $F_{1, 20}=9.938$, $P= 0.005$; Fig. 5.3).

5.5 Discussion

Our research showed that *P. longipes* does not show a quality-quantity tradeoff, but instead exhibit an optimum offspring size (Fig. 5.2). This is in agreement with the Smith-Fretwell (1974) model for optimal parental investment. Larger females had a greater reproductive output but not lower quality offspring. Females with greater reproductive output invest more resources into producing more eggs rather than investing more into each egg. This generally aligns with Araneae (Marshall & Gittleman 1994).

Egg quantity and mass increase with female size in other species (Tejedo 1992). This is often due to females investing beyond predicted optima when resources are high and stable

(Simons 2006). Conversely, unpredictable resources can promote increased an increased number of offspring at the sacrifice of quality (Lalonde & Roitberg 1989). The environment of *P. longipes* examined in this study is very stable and houses extremely high resource abundance, but similarly high conspecific density (Chapin 2015; Chapin & Hill-Lindsay 2016). Thus, it could be the case that meeting these results are specific to high resource cave populations, and that epigean conspecifics exhibit a trade-off. Future research should also examine the distribution of egg sizes across females, and quantify the relationship between egg mass and survivorship and reproductive fitness.

5.6 Acknowledgements

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5.7 Table & Figures

Table 5.1. Multimodel comparisons of generalized linear models predicting female carapace width ($n = 24$). The full model includes egg count, egg mass, and their interaction as predictor variables. Egg count, but not mass, best predicted female size.

model	**AICc**	***k***	**ΔAICc**	w_i
count × mass	93.00	4	0.00	0.08
count + mass	91.12	3	−1.88	0.21
count	88.72	2	−4.28	0.70
mass	99.84	2	6.84	0.00
intercept only	99.15	1	6.15	0.00

Table 5.2. Stages of egg development used to categorize eggs of *Phrynus longipes*.

Stage	Description
1	Eggs undeveloped cell mass
2	Germinal band and grooves where leg development will occur are present
3	Legs developed and general outline of individual legs visible
4	Egg takes on contours of embryo, eyes may or may not be present
5	Eyes formed and body segmentation present

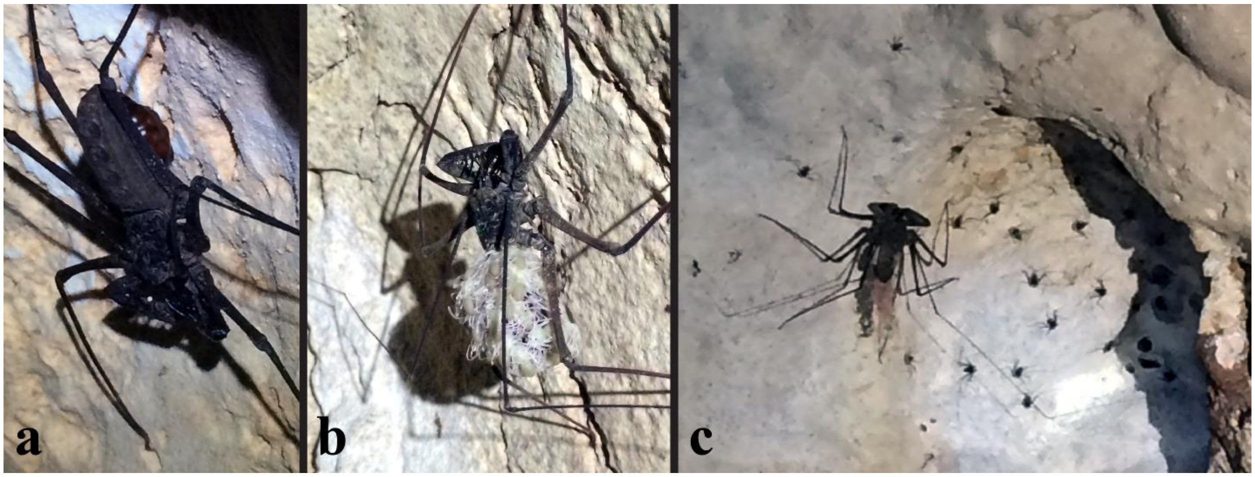

Figure 5.1. Female *Phrynus longipes* with young. (a) An eggsac attached to the ventral opisthosoma; (b) newly-hatched young cling to their mother’s back; (c) free-living young near their mother.

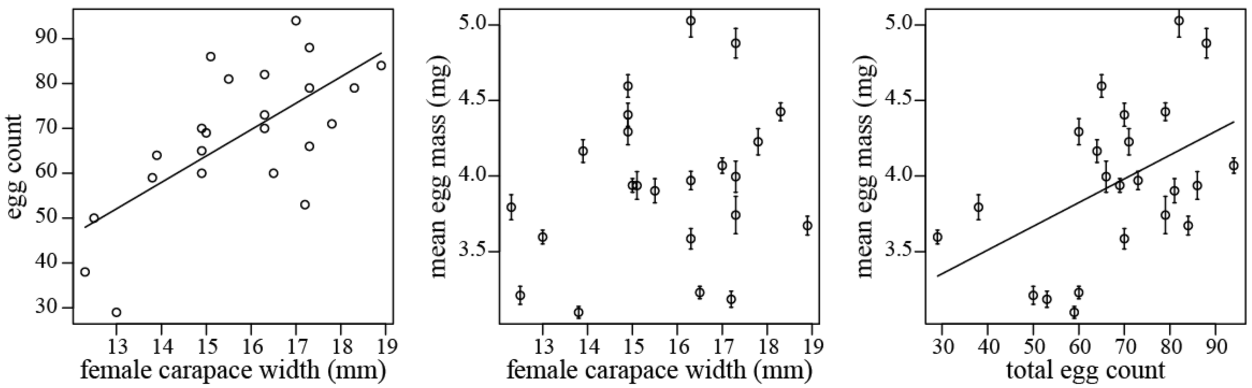

Figure 5.2. Plots of egg clutch and female measurements for *Phrynus longipes*. Left to right; Total egg count per clutch predicted by female carapace width (adjusted $r^2 = 0.44$, $F_{1,21} = 17.96$, $P < 0.001$); mean egg mass predicted by female carapace width (adjusted $r^2 = 0.01$, $F_{1,21} = 1.27$ $P = 0.273$); mean egg mass predicted by total egg count (adjusted $r^2 = 0.19$, $F_{1,21} = 6.27$, $P = 0.021$).

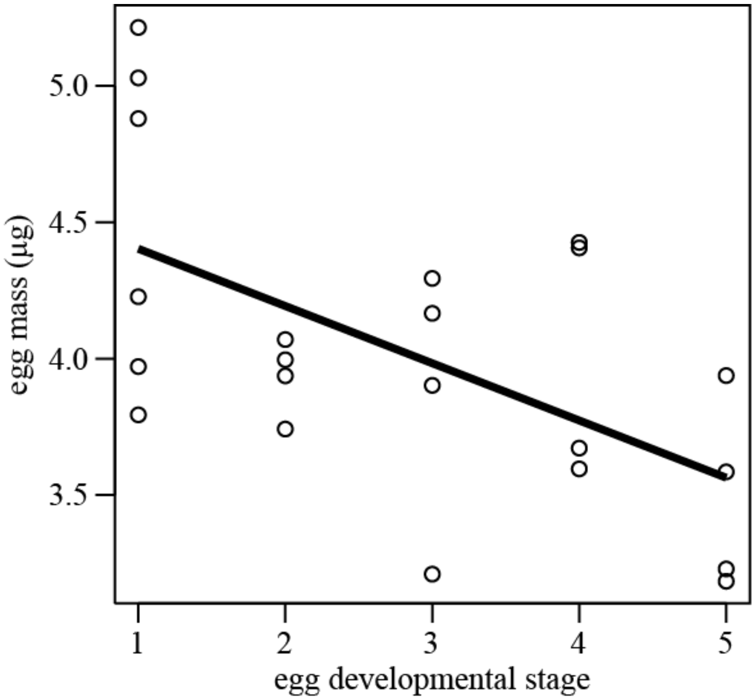

Figure 5.3. *Phrynus longipes* egg mass predicted by developmental stage. ($\beta = -0.21$, Adj. $R^2 = 0.30$, $F_{1,\,20} = 9.938$, $P = 0.005$).

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CHAPTER 6: Assessment strategy of the whip spider *Phrynus longipes* during territory disputes.

6.1 Abstract

Animal resource contests were largely thought of as communicative interactions where paired opponents gain information about each other to decide contest outcomes. Recent real-world tests of game theoretic contests models, however, suggest that some species resolve resource disputes without assessing the fighting ability of opponents. Amblypygids are eminently suited for testing this because their agonistic interactions include displays that may function to advertise fighting ability but they share ancestry with taxa that resolve contests without this information. I staged paired interactions of amblypygids and tested if they used self-assessment or mutual assessment strategies to make contest decisions. I established that prosoma width was the best predictor of contest outcome, and used it as a proxy for resource holding potential. Loser, but not winner, body condition (a proxy for resource holding potential) predicted contest duration, thus evidencing self-assessment decision-making.

Keywords: agonistic interaction, animal contest, Arachnida, contest assessment, resource holding potential, self-assessment, territoriality, whip spider

6.2 Introduction

Resource contests were thought of as interactions between opponents where the individuals make contest decisions by assessing their and their opponents' strength (Parker, 1974; Parker & Rubenstein 1981; Enquist & Leimar 1987; Enquist et al. 1990; Briffa & Hardy 2013). This was in part because agonistic interactions often involve ritualized, stereotyped behaviors (Huxley 1966). Recent research, however, has questioned the ubiquity of opponent assessment in animal contests (Taylor & Elwood 2003; Arnott & Elwood 2009; Elwood & Arnott 2012; Kokko 2013). Instead, animals may use only information about their own fighting ability—not that of their opponent—to determine when to give up a contest (Taylor & Elwood 2003). A lack of opponent assessment can seem counterintuitive when agonistic interactions include complex behaviors. I tested between assessment strategies using an animal with ritualized contest displays (Weygoldt 2000; Fowler-Finn & Hebets 2006; Chapin 2014, 2015; Santer & Hebets 2011), but with an evolutionary history that suggests they would not assess opponents (Wheeler & Hayashi 1998; Giribet et al. 2002): the Amblypygi.

Strategies that use only an individual's own information, and not that of the opponent, are termed self-determined persistence strategies (Arnott & Elwood 2009; Taylor & Elwood 2003). This can be imagined as follows: individuals might have a maximum display duration based on their own resource holding potential (RHP), or absolute fighting ability (Parker 1974), after which they check for opponent presence. Individuals give up if an opponent continues to display or win if their opponent has already given up. In this thought-example, individuals need not determine opponent RHP—only opponent presence. Self-assessment and a mix of self and mutual assessment strategies have been identified in diverse taxa (amphipods, Prenter et al.

2006; honeybees, Dietemann et al. 2008; house crickets, Briffa 2007; jumping spiders, Elias et al. 2008; shore crabs, Smallegange et al. 2007). In contrast, mutual assessment strategies incorporate estimates of an individual's own RHP and also that of its opponent (Taylor & Elwood 2003). In mutual assessment, individuals gain information about the RHP of opponents via displays. Thus, opponents can recognize and respond to relatively high-RHP opponents by fleeing earlier than would be expected if using a self-assessment strategy. Self-assessment strategies include war of attrition without assessment (Mesterton-Gibbons 1996) and energetic war of attrition game-theoretic models (Payne & Pagel 1996, 1997), while mutual assessment strategies include sequential assessment (Enquist et al. 1990) and asymmetric war of attrition models (Parker & Rubenstein 1981). Apparently mutual assessment interactions cannot be assumed as such without empirically determining the decision rules used to negotiate contests.

Assessment strategies can be discerned via statistical modeling (Arnott & Elwood 2009). Namely, multiple regressions of winner and loser RHP predicting contest duration can evidence self- or mutual assessment (e.g., Stuart-Fox 2006; Smallegange et al. 2007; Dietemann et al. 2008). A negative correlation between winner RHP and contest duration is consistent with mutual assessment, where information about winner RHP is used by the loser to determine contest duration. If, however, winner RHP does not or only slightly correlates with contest duration, then disputes are settled by the loser giving up regardless of winner RHP, thereby evidencing a self-assessment strategy. A correlation of the RHP difference between contestants and contest duration was thought to be diagnostic of mutual assessment. I tested between assessment strategies via multimodel comparisons (Burnham et al. 2011; Symonds & Moussalli 2011).

I tested between self-determined persistence and mutual assessment in the amblypygid *Phrynus longipes*. Amblypygids regularly engage in stereotyped agonistic territory disputes that involve several ritualized behaviours when put in contact (Fowler-Finn & Hebets 2006; Chapin 2015). Species of the order use complex signaling to communicate with conspecifics (Fowler-Finn & Hebets 2006, Chapin & Hebets 2016), with obvious utility in agonistic interactions. Amblypygids also have very large mushroom bodies, which may be involved in learning and memory (Strausfeld et al. 1998). However, recent advances in agonistic contest research has made clear that assessment strategies cannot be assumed using anecdotal observations of interactions (Arnott & Elwood 2009). Indeed, self-assessment or a mix of self-assessment and other strategies occur in other arachnid species (Whitehouse 1996; Bridge et al. 2000; Taylor et al. 2001; Carvalho et al. 2004Elias et al. 2008; Keil & Watson 2010; Constant 2011; Kasumovic et al. 2011; Elwood & Prenter 2013; McGinley 2015). Thus, I designed a study to understand the assessment strategies employed by the amblypygid *Phrynus longipes*.

6.3 Methods

I staged interaction assays of randomly paired *P. longipes* including all size and sex combinations and looked for correlates of contestant RHP with contest duration and outcome. Individuals of a variety of sizes and sexes interact under natural conditions and all hold territories (Chapin & Hill-Lindsay 2016). I collected *Phrynus longipes* at Mata de Plátano Field Station, Puerto Rico (18.414°, −66.726°) in August and September 2012. Animals were collected nightly and used in trials the following night. I measured maximum prosoma width and pedipalp femur length to the nearest 0.01 mm using digital calipers (accuracy: ± 0.03 mm; Neiko 01407A) and total mass to the nearest 0.01 g with a gram scale (± 0.01; American Weigh AWS-100-BLK). Sex was identified after trials by lifting the genital operculum of individuals asphyxiated with carbon dioxide gas. Individuals were kept separately in plastic deli containers (ca. 11 × 14 cm) lined with butcher paper for 24 hours prior to trials. Behavioural trials (n = 48 paired trials) were conducted the night after collection and measurement in 70 × 30 cm glass arenas lined with butcher paper. Individuals were placed in opposite ends of the arena and allowed a 10 min acclimation period, after which a divider was lifted and animals were allowed to interact for 45 min. Pairs always initiated interactions upon recognizing the presence of conspecifics. This acclimation period also introduces territory effects, which introduce experimental error, but should not alter the general findings of this research (Chapin & Hill-Lindsay 2016). I recorded the duration of the first interaction, which started when animals initiated contact or oriented toward each other and ended when one retreated. Butcher paper was replaced and enclosures were cleaned with 70% isopropyl between trials. Since amblypygids are nocturnal, interactions were video recorded at night in darkness with an infrared camera (a modified Logitech C270) at 30 fps. Infrared LED lights (920 nm peak wavelength) illuminated the arena.

I tested which measure of several potential proxies for RHP best predicted contest duration using linear regressions. These included the absolute difference between opponent prosoma width, body weight, pedipalp femur length, and scaled-mass index—a measure of body condition following Peig and Green (2009). The best measure of RHP was used in subsequent analyses.

Some research shows that contest escalation is an important predictor in assessment strategy test (Elias et al. 2008). Thus, we used both contest duration and escalation to physical aggression as measures of contest escalation. Further, sex could have an effect on these predictors, so I used multimodel comparisons to test if opponent sex affected contest duration

I used a linear regression that included winner RHP, loser RHP, and their interaction predicting contest duration to test between contest assessment strategies. Further, I used a logistic regression of the same independent variables predicting escalation to physical aggression. I compared model versions to the global model with Akaike Information Criterion corrected for small sample sizes (AICc) and Akaike weights (w_i; Burnham et al. 2011; Symonds & Moussalli 2011). All statistical analyses were conducted in R version 3.0.1 (R Core Team 2013).

6.4 Results

6.4.1 The agonistic interaction

Agonistic interactions followed a stereotyped sequence of behaviours. Typical interactions started with opponents orienting towards each other while displaying open pedipalps, which often remained open in a display posture for the duration of the contest. Individuals proceeded by exploring and probing the opponent with antenniform legs. One or both individuals usually engaged in flicking behaviour, which included quick movements of the antenniform legs (*sensu* Fowler-Finn & Hebets 2006). Many interactions terminated after flicking, but some advanced to aggressive physical contact where individuals hit or grabbed each other with pedipalps. Most interactions that escalated to physical contact ended after only one bout of aggressive behaviours, but some continued on and switched between bouts of flicking and physical aggression.

6.4.2 Opponent assessment

The best proxy of RHP was prosoma width (Table 6.1) and was used in subsequent analyses that required a RHP proxy. We included both contest duration and escalation to physical aggression as measures of contest escalation. Both mature and juvenile males and females were included in random contest pairings. Cursory observations of agonistic interactions did not indicate any difference between female-female, female-male, and male-male contests. Nevertheless, to understand any effect sex might have on contest, we compared linear regression models with and without sex as predictors of contest outcome. The sex of very young animals cannot be determined by physical examination, so only individuals with sexually dimorphic genitalia were included in analyses ($n = 35$). Models without sex were the best predictors of contest duration, suggesting that opponent sex is unimportant in determining the contest duration (Table 6.2).

Comparative modeling indicated that models that only included loser RHP predicted both contest duration and escalation better than winner RHP or winner RHP × loser RHP interaction (Table 6.3, 6.4). Loser RHP had a significant positive relationship with both contest duration ($b = 0.06 \pm 0.03$, $t = 2.34$, $P = 0.02$) and escalation (0.33 ± 0.14, $t = 2.37$, $P = 0.018$). A mutual assessment strategy would have been supported if winner RHP was an important predictor of contest duration, given the increase in model complexity. Linear regressions of winner and loser RHP predicting contest duration corroborate these results by indicating that loser RHP ($b = 0.06$

$\pm$ 0.03, $r^2 = 0.108$, $F_{1,36} = 5.50$, $P = 0.025$), but not winner RHP ($b = 0.03 \pm 0.03$, $r^2 = 0.003$, $F_{1,39} = 0.85$, $P = 0.363$), predicted contest duration (Fig. 1). The regression of contest duration and opponent RHP difference was negatively correlated (RHP difference: -4.45 ± 1.48; adjusted $r^2 = 0.11$, $P = 0.007$; Fig. 2). Body condition, pedipalp femur length, mass, and prosoma width autocorrelated (Linear regression adjusted $r^2 = 0.9699$, $F_{3,71} = 795.4$, $P > 0.0001$).

6.5 Discussion

Comparative modeling indicated that *P. longipes* use self-determined persistence to resolve resource contests despite observations of activities that have the appearance of mutual assessment. A model using only loser RHP predicted contest duration better than models including winner RHP or their interaction. Multimodel comparisons showed a lack of predictive value for winner RHP or RHP winner × RHP loser interaction, further supporting a self-assessment strategy.

Self-determined persistence in *P. longipes* is counterintuitive for several reasons. Ritualized behaviors are usually communicative, but self-determined persistence does not require contestant information transfer to occur (Briffa 2008). Amblypygids may be communicating information other than RHP or for reasons other than contest assessment. For example, sex, sexual maturity, or species identity could be signaled; information potentially divorced from territory disputes. Additionally, animals must continually check that the opponent is engaging in the interaction and associated displays, which may also act to prevent cheating (e.g., by engaging in less energetic displays or temporarily ceasing to interact). While self-determined persistence may explain the decision rules that amblypygids follow during contests, information transfer still occurs before and after interactions in the form of conspecific recognition and recognizing contest outcome. Further, contest, especially between RHP-matched pairs, end by escalation to physical aggression. Self-determined persistence should not include physical contact, which would convey information about RHP (Egge et al. 2011). This represents a breakdown of self-determined persistence, and might indicate a second stage of assessment using mutual assessment.

It is important to note that assessment strategies are not mutually exclusive. The decision to engage in one of a set of assessment strategies can be context-dependent. For example, the jumping spider *Phidippus clarus* primarily uses self-assessment, but also mutual assessment to make contest decisions (Elias et al. 2008). Similarly, agonistic interactions in a killifish (*Kryptolebias marmoratus*) can be delineated into stages where distinctly different assessment strategies are employed (Hsu et al. 2007). In the most basic sense, animals must at least recognize and orient relative to contestants; some sort of assessment is required for interactions to initiate at all. A third category of assessment strategies, the cumulative-assessment strategy, includes information of the individual’s own RHP and information gained by the injury or energetic costs inflicted by the opponent. While often treated as a subcategory of self-assessment strategies (Arnott & Elwood 2009), it shares with mutual assessment the exchange of information from one opponent to the other; via displays in one case, and physical cost in the other. For the purposes of the present analyses, I treated cumulative assessment models as a type of mutual assessment

The neurobiology of amblypygids suggests that they may have evolved exceptional learning and memory abilities (Strausfeld et al. 1998; Santer & Hebets 2011), which may enable individual-level discrimination (Walsh & Rayor 2008) and presumably contest outcome memory. The self-assessment model of animal contests is presumed to be the least cognitively demanding (Elwood & Arnott 2012; Fawcett & Mowles 2013; Elwood & Arnott 2013). Instead, learning and memory may be important for spatial navigation instead of conspecific interactions (Hebets et al. 2014a, b; Wiegmann et al. 2016).

The adaptive value of one assessment strategy over another is unresolved. Animals employing self-determined persistence might compare their RHP to an estimated population RHP. This would allow the relationship between RHP and contest duration to be affected by population demography. Strategies might be impacted by the ease at which opponents can assess one another, either due to environmental or physiological constraints (Elwood & Arnott 2012; Fawcett & Mowles 2013).

Both males and females performed agonistic interactions when confronted with either sex. This is contrary to anecdotal accounts reporting that male-female interactions were never agonistic (Weygoldt 2000) or that sexes showed agonistic differences in other species (Fowler-Finn & Hebets 2006). It is possible that male-female interactions begin as agonistic contests and progress to courtship, but this was not observed during trials. Instead, it seems likely that both males and females engage in resource contests, which suggests that territories may only secondarily serve in mate choice, and instead be important for sex-neutral resource requirements like food or shelter.

Contests between RHP symmetric contestants lasted much longer and escalated to aggressive physical contact more often than RHP asymmetric contestants. This is an expected among contesting opponents, and escalation to injurious physical contact is expected when the RHP of the combatants are similar (Parker 1974). Escalation was much more common for *P.*

longipes in our study than *Phrynus marginemaculatus* (Fowler-Finn & Hebets 2006), which engaged in fencing more often than *P. longipes*. This suggests that *P. marginemaculatus* may have evolved less risky behaviours than *P. longipes*. Future comparative research of resource contests across Amblypygi species is a fruitful area of research to understand the evolution and diversity of contests. This experiment showed that the amblypygid *Phrynus longipes* uses self-assessment strategies to make contest decisions.

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6.7 Table & Figures

Table 6.1. Linear regressions of several potential proxies for resource holding potential (RHP) for the whip spider *Phrynus longipes*. All measures are $\log_{10}$+1 transformed. Prosoma width best predicted contest duration, and was used as the proxy for RHP.

Measurement	$\beta \pm s$	**Adj.** r^2	F	P
Prosoma width	−1.67 ± 0.50	0.209	11.04	0.002
Total mass	−0.46 ± 0.19	0.111	5.61	0.023
Scaled mass index	−0.48 ± 0.21	0.104	5.29	0.027
Pedipalp femur length	−0.18 ± 0.07	0.135	6.94	0.012

Table 6.2. Mutlimodel comparisons of linear regressions predicting $\log_{10}$+1 transformed contest duration by the resource holding potential (RHP) and sex or winning and losing contestants. Models were compared with Akiake's information criterion corrected for small sample sizes (AICc) and Akaike weights (w_i). Models without sex are the best predictors of contest outcome.

model	**AICc**	***k***	**ΔAICc**	w_i
winner RHP × loser RHP × winner sex × loser sex	79.27	15	28.85	0.000
winner RHP × loser RHP + winner sex + loser sex	54.49	5	4.07	0.062
winner RHP × loser RHP	50.42	3	0.00	0.474
winner RHP + loser RHP + winner sex + loser sex	54.99	4	4.57	0.048
winner RHP + loser RHP	52.14	2	1.715	0.201
Intercept only	52.00	0	1.58	0.215

Table 6.3. Multimodel comparisons of linear regression models predicting $\log_{10}$+1 transformed contest duration or escalation to physical aggression by the RHP (body size) of the winner, loser, and their interaction for *Phrynus longipes* (*n* = 42). The loser-only model predicts contest duration better than the other models, indicating that loser RHP determined contest duration. This indicates that amblypygid territory contests fit the self-assessment model, where individuals do not assess opponents in making contest decisions.

Parameter	**AICc**	***k***	**ΔAICc**	w_i
winner × loser	54.76	3	1.162	0.289
winner + loser	55.74	2	2.14	0.177
loser	53.60	1	0.00	0.516
winner	62.37	1	8.77	0.006
intercept only	61.15	0	7.55	0.012

Table 6.4. Multimodel comparisons of logistic regressions models predicting escalation to physical aggression by the RHP (body size) of the winner, loser, and their interaction for *Phrynus longipes* (*n* = 42). The loser-only model predicts contest duration better than the other models, indicating that loser RHP determined contest duration. This indicates that amblypygid territory contests fit the self-assessment model, where individuals do not assess opponents in making contest decisions.

Parameter	**AICc**	***k***	**ΔAICc**	w_i
winner × loser	50.17	3	2.89	0.136
winner + loser	48.70	2	1.43	0.28
loser	47.27	1	0.00	0.577
winner	58.57	1	11.30	0.002
intercept only	57.62	0	10.35	0.003

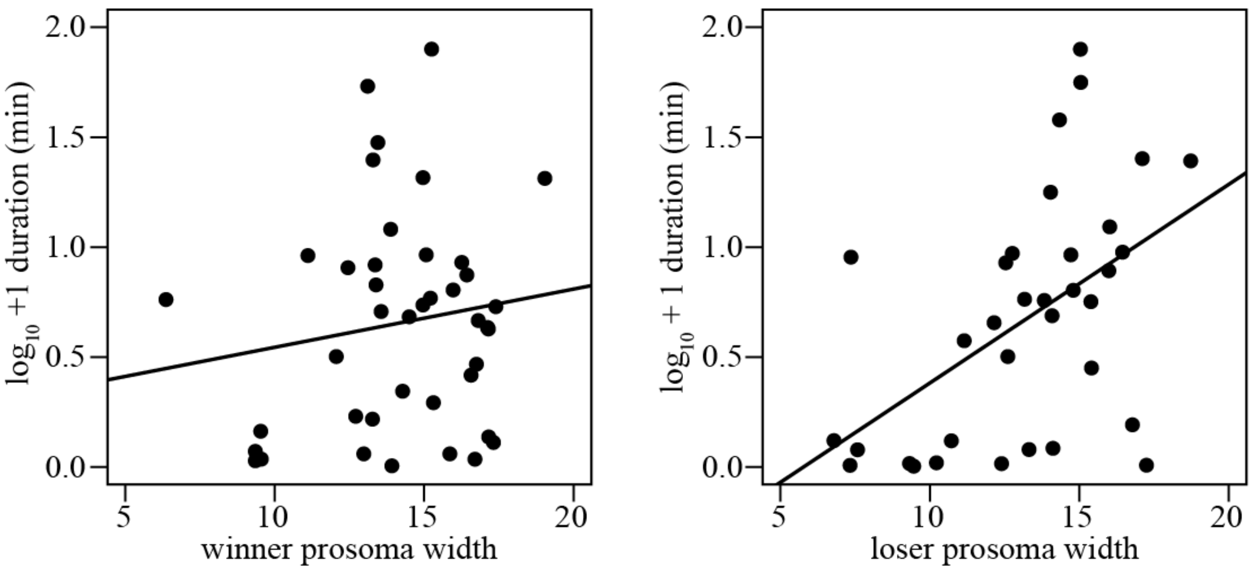

Figure 6.1. Linear regressions predicting contest duration by winner or loser resource holding potential (RHP; body size). Y-axis is natural $\log_{10}$ scale. Loser ($r^2 = 0.233$, $F_{1,32} = 11.04$, $P = 0.002$) but not winner ($r^2 = -0.003$, $F_{1,32} = 0.847$, $P = 0.363$) RHP predicted contest duration.

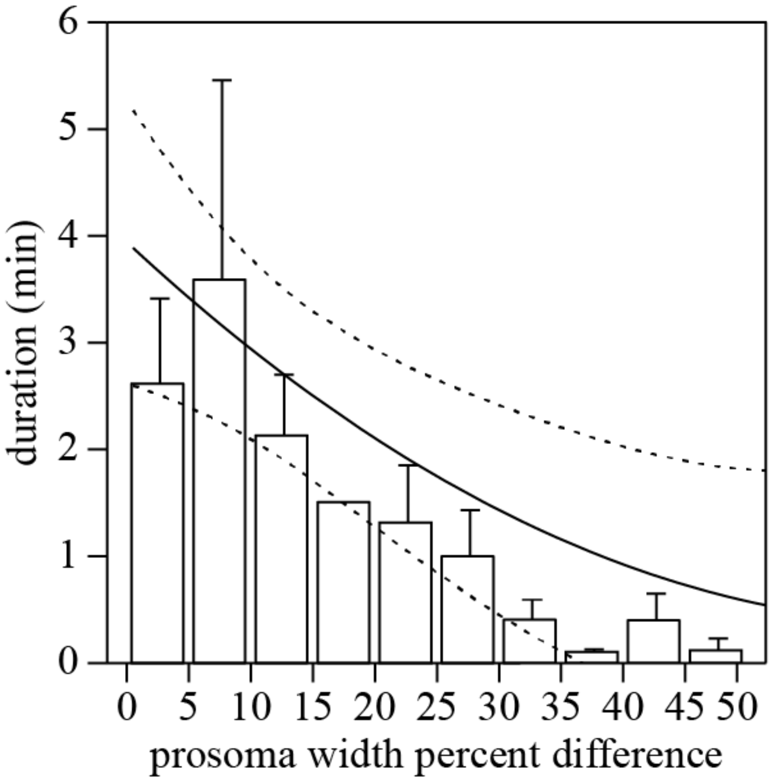

Figure 6.2. Mean ± SEM of *Phrynus longipes* interaction time of contests delineated by body size asymmetry (RHP percent difference) at 5% intervals; and a quadratic regression of RHP percent difference predicting contest duration (solid line; $\bar{\boldsymbol{R}}^2 = 0.11$, $F_{2,71} = 5.33$, $P = 0.007$). The dashed lines represent the 95% confidence interval.

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