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The behavioral ecology of amblypygids

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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

TABLE OF CONTENTS

1. Forward	1
2. Introduction to the order	2
2.1 Diversity and evolutionary relationships.	2
2.2 External morphology.	2
2.3 Sensory physiology and neuroanatomy.	2
2.4 Reproductive physiology and life history	2
3. Environmental interactions	2
3.1 Microhabitat use and preference	2
3.2 Navigation.	4
4. Interspecific interactions	5
4.1 Predators and prey	5
4.2 Parasites and parasitoids	6
4.3 Commensalism	7
5. Intraspecific interactions	7
5.1 Contests and territoriality.	7
5.2 Mating systems and mate choice.	8
5.3 Parental investment and sociality	8
5.4 Genetics and genomics	9
6. Conclusion & future directions	9

1. 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), 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). 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.

2. INTRODUCTION TO THE ORDER

2.1 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). 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).

2.2 External morphology.—Amblypygids have dorso-ventrally flattened bodies, orthognathous chelicerae, raptorial pedipalps, and a front pair of extremely elongate legs (Fig. 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).

2.3 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 & Troyer

1980; 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).

2.4 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. 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. 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).

3. ENVIRONMENTAL INTERACTIONS

3.1 Microhabitat use and preference.—Amblypygi are found throughout tropical and subtropical zones across all continents (Fig. 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 &

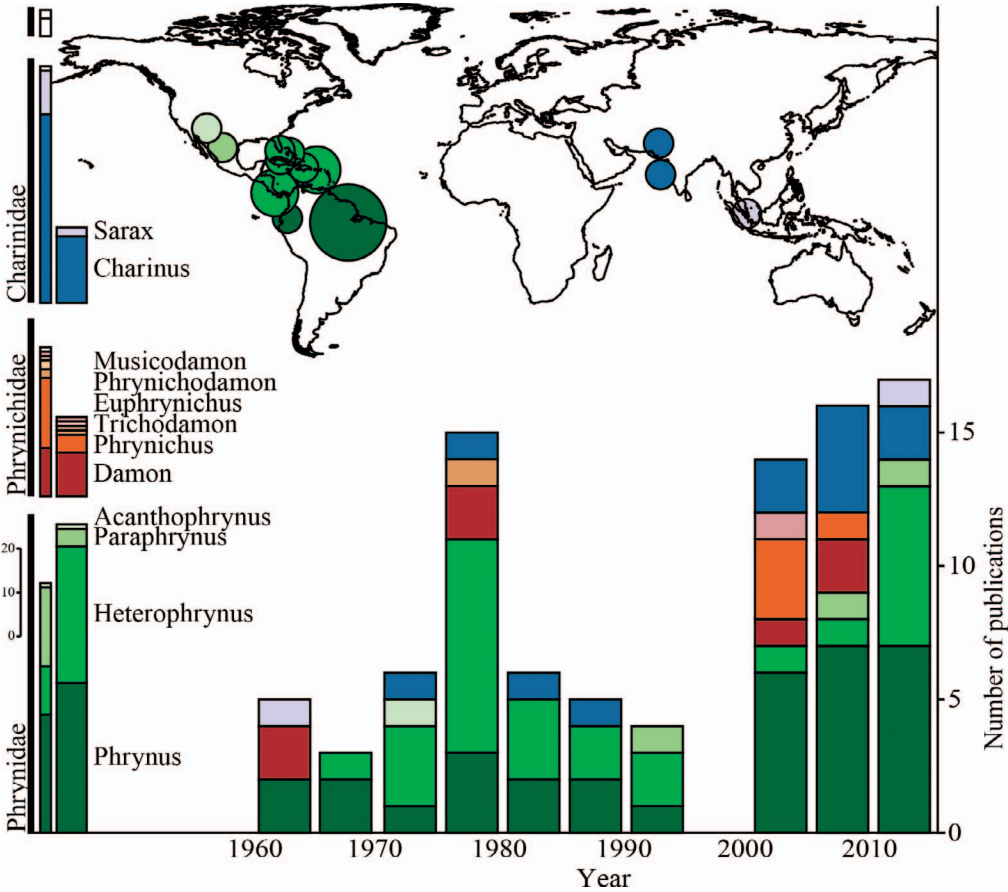


Figure 1.—Summary of behavioral ecology-related research using Amblypygi species as study organisms. Left bars: species richness (thin bars) compared to publication richness (thick bars) by genus. Right bars: Number of publications per half decade by genus. Map: Location of field studies. Circle color and size indicate genus studied and number of publications.

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

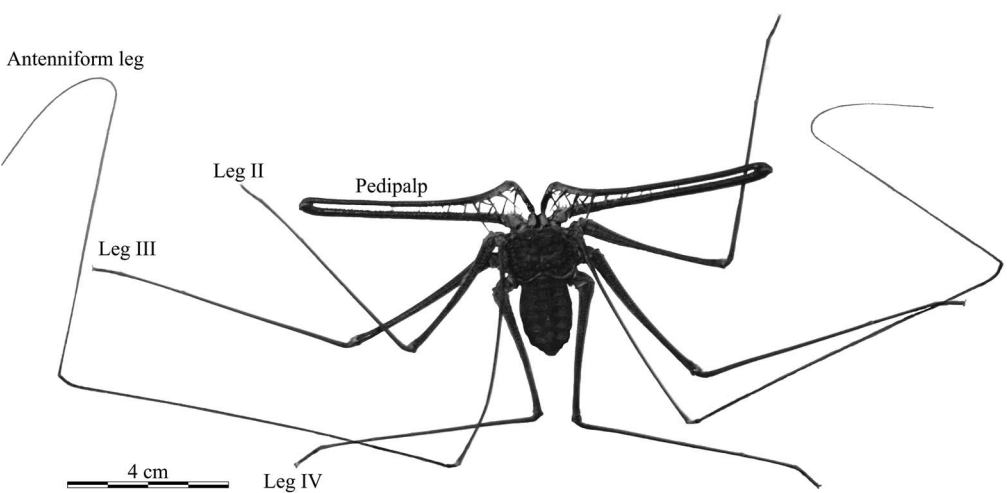


Figure 2.—Image of *Heterophrynus batesii*, indicating main appendages. Antenniform legs are used for sensing the environment and communication, not walking. The pedipalps act as the main prey capture appendages. The main body is divided into two segments: The anterior prosoma and posterior opisthosoma. Amblypygi do not produce silk or venom. In this species, pedipalp length is longer in males (shown). Photograph by K.J. Chapin.

Table 1.—Amblypygi microhabitat preference studies. While informative, current research is limited to New World tropical and subtropical forests.

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

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 epigeal (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), 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.

3.2 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

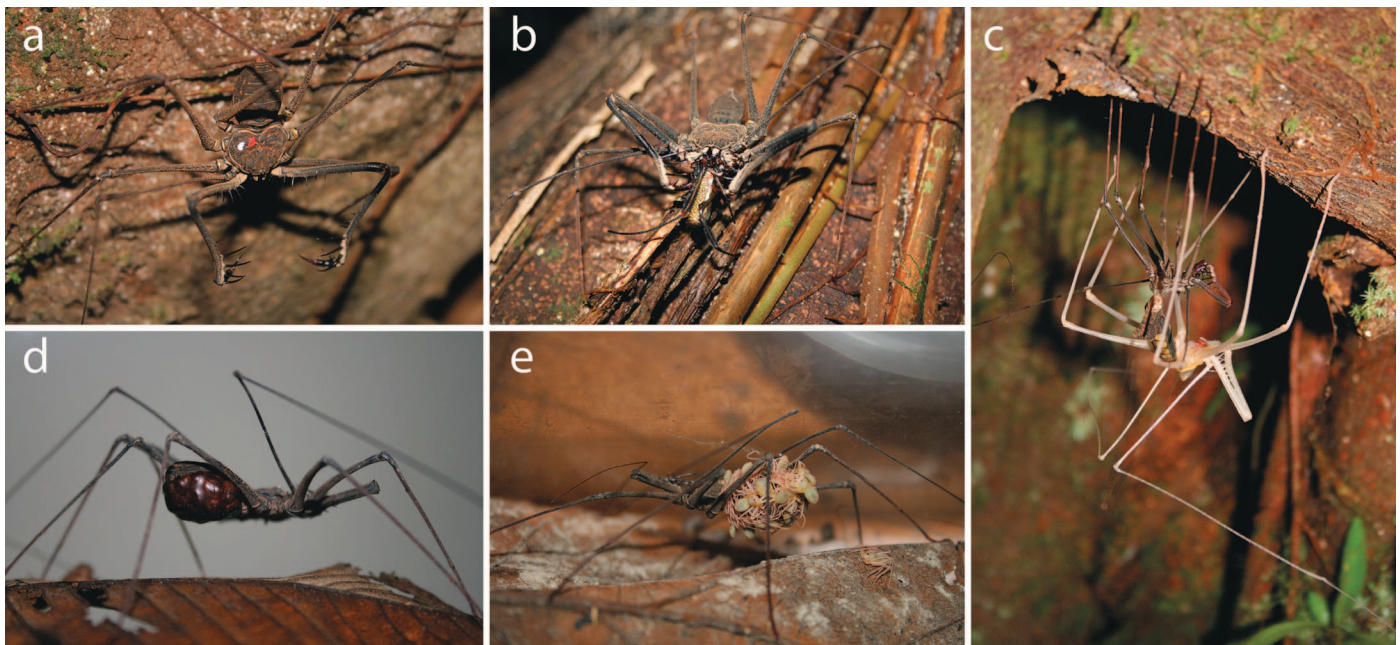


Figure 3.—Photographs of the natural history of the amblypygid *Heterophrynus batesii* in Amazonian Ecuador, (a) awaiting prey (b) feeding on a *Nephila* sp. spider, (c) engaging in ecdysis, (d) carrying an eggsack, and (e) carrying offspring. Photographs by K.J. Chapin.

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 *Phrynos 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 *Phrynos 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 (Kuhn-Buhlmann & 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.

4. INTERSPECIFIC INTERACTIONS

4.1 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. 3b), the scorpion *Centruroides gracilis* (Latreille, 1804), *Anolis* lizards, hummingbirds, and crayfish captured from streams (Table 2). Interestingly, some species seem quite adept at aerial or aquatic prey capture (Hebets & Chapman 2000b; Hebets 2002; Ladle & Velandier 2003). Individuals hunt prey using sit-and-wait tactics and are commonly seen with open pedipalps awaiting prey (Fig. 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. 3a), though this remains to be tested.

Amblypygids fall prey to large lizards and small mammals, including bats (Table 3). Field studies recorded lycosid spiders (Chapin 2011) and scorpions (Hebets 2002; Teruel & Toledo 2014) preying on amblypygids (Table 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;

Table 2.—Known prey of amblypygids delineated by vertebrate and invertebrate taxa.

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

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.

4.2 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. 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 brasiliensis* 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. 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.

Table 3.—Known predators of amblypygids delineated by vertebrate and invertebrate taxa.

Predator	Prey	Citation
Invertebrates		
Lycosid spider (Araneae: Lycosidae)	<i>Heterophrynus batesii</i>	Chapin 2011
<i>Alayotitius sierramaestrae</i> Armas, 1973 (Scorpionida: Buthidae)	<i>Phrynus damonidaensis</i>	Armas et al. 2013
<i>Rhopalurus junceus</i> (Herbst, 1800) (Scorpionida: Buthidae)	<i>Phrynus pinarensis</i>	Teruel & Toledo 2014
<i>Centruroides edwardsii</i> (Gervais, 1843) (Scorpionida: Buthidae)	<i>Phrynus whitei</i>	Armas 1995
<i>Phrynus longipes</i> (Amblypygi: Phrynidae)	<i>Phrynus hispaniolae</i>	Armas & Ramírez 1989
Vertebrates		
White-throated round-eared bat (<i>Lophostoma silvicolium</i>)	Amblypygi sp.	Reid 1997
Common coqui frog (<i>Eleutherodactylus coqui</i>)	<i>P. longipes</i>	Stewart & Woolbright 1996
Bronze coqui frog (<i>Eleutherodactylus richmondi</i>)	<i>Phrynus longipes</i>	Stewart & Woolbright 1996
Cuban solenodon (<i>Solenodon cubanus</i>)	<i>Paraphrynus robustus</i>	Armas 1987
Asian water monitor (<i>Varanus salvator</i>)	<i>Stygophrynus dammermani</i>	Dammerman 1948

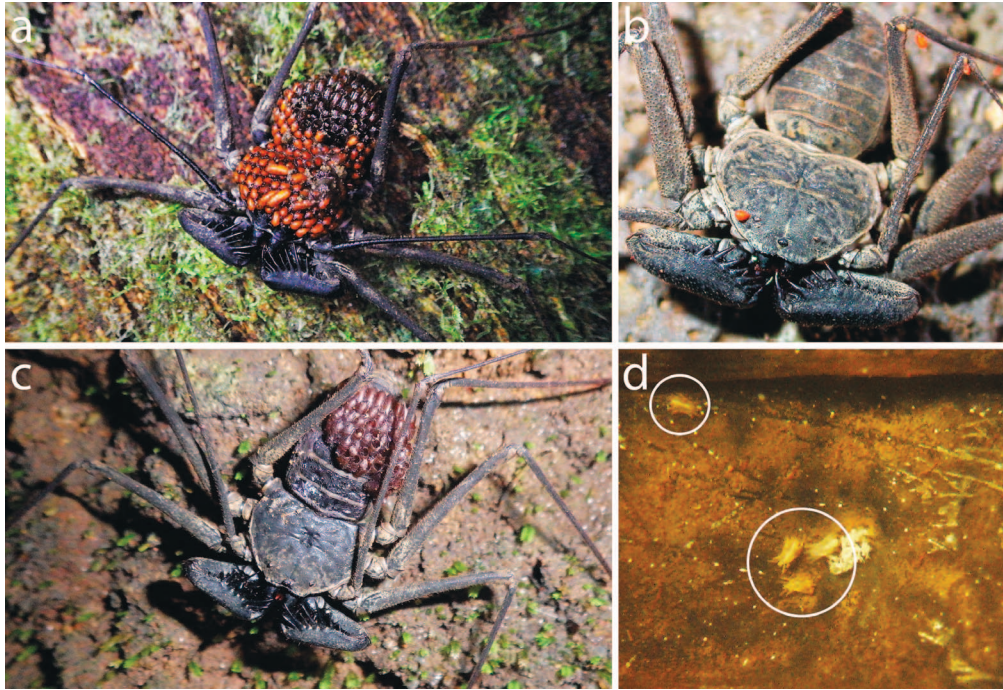


Figure 4.—Ectoparasites of some Amblypygi species. (a, c) The amblypygid *Paraphrynus laevisfrons* in Costa Rica with parasitoid eggs. The parasitoid species is yet to be identified. Photo by Tyler Corey. (b) Amblypygi sp. with mites. Photo by Glaucio Machado. (d) Microscopy image of the ventral opisthosoma of *Phrynus longipes* with mites in association with intersclerite membranes (top circle) and spiracles (bottom circle). Photo by K.J. Chapin.

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.

4.3 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 quintero* 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.

5. INTRASPECIFIC INTERACTIONS

5.1 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 (Weygoldt 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 (Fowler-Finn & Hebets 2006).

5.2 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.

5.3 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

Table 4.—Amblypygi genomic and transcriptomic studies.

Loci	Citations
nDNA	
28S	Wheeler & Hayashi 1998; Giribet & Ribera 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-1 α , EF-2, Pol II	Regier & Shultz, unpublished data
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 & Ribera 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	Fahreïn 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

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 4.1 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 *Heterophrynus 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 *Phrynos 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.

5.4 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 $2n = 66$ and 70 chromosomes with homomorphic sex chromosomes (Vitková et al. 2005; Paula-Neto et al. 2013). Most recently, Amblypygi have been instrumental in understanding the biogeography of Caribbean islands (Esposito et al. 2015). Research on *Phrynos* 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.

6. 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) 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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