2017

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Behavioral interactions between terrestrial salamanders and spiders: competition or intraguild predation?

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Several studies suggest that small terrestrial salamanders are important regulators of leaf litter arthropod communities, and likely contribute to ecosystem processes such as decomposition and nutrient cycling. Despite the recognition that salamanders have the potential to strongly affect ecosystem function through both direct and indirect pathways, little is known regarding the nature of interactions between small vertebrates and the large, predatory arthropods with which they share both microhabitat and prey. Our study was designed to explore interactions between Eastern Red-backed Salamanders, *Plethodon cinereus*, and spiders in the genus *Wadotes* in an eastern North American temperate forest ecosystem. We were particularly interested in teasing apart behaviors such as territoriality and intraguild predation in an attempt to determine specifically which interaction is most likely responsible for the observed negative relationship between salamander and spider abundance at our field site. Field data indicate that *P. cinereus* and large syntopic spiders exhibit negative spatial associations in the microhabitat beneath cover objects, a possible indication of interspecific territoriality. In our laboratory experiments, resident salamanders displayed agonistic postures similarly toward both intruding conspecifics and spiders, suggesting that salamanders may perceive large intruding spiders as competitors. Finally, we observed no injuries to individual *P. cinereus* or adult spiders even though occasional chases and bites by both were recorded during the behavioral trials. We found no evidence that adults or juveniles of *P. cinereus* were envenomated by adult *Wadotes* spp., and there were no instances of intraguild predation in this study. Multiple lines of evidence from this study, and others, suggest that the primary interaction between individuals of *P. cinereus* and large spiders is competitive in nature rather than predatory. We suggest that the cost associated with intraguild predation on salamanders with noxious skin secretions may preclude them from being preyed upon by spiders.

KEY WORDS: *Plethodon cinereus*, Agelenidae, *Wadotes* spp., spatial distribution, food webs.

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INTRODUCTION

Ecologists have, for decades, argued that the magnitude of salamander biomass (Burton & Likens 1975a) in forested ecosystems makes them likely top-down regulators of terrestrial detrital food webs (Burton & Likens 1975b; Hairston 1987; Walton 2005, 2013; Best & Welsh 2014), and that numerous ecosystem processes might be directly or indirectly affected by the presence of these amphibians (Davic & Welsh 2004). Recent estimates of the biomass of small terrestrial salamanders are higher than previously reported, suggesting that their occurrence in these ecosystems may be even more important than previously thought (Semlitsch et al. 2014). Numerous studies attempting to quantify the effects of terrestrial salamanders in their communities have found that, as predicted, salamanders can regulate invertebrate numbers (Wyman 1998; Walton 2005, 2013; Walton & Steckler 2005) which may, in turn, contribute to effects on leaf litter decomposition (Best & Welsh 2014) and nutrient cycling (Burton & Likens 1975b).

Despite the recognition that salamanders have the potential to strongly affect ecosystem function through both direct and indirect pathways, little is known regarding the nature of interactions between salamanders and larger predatory arthropods with which they share both microhabitat and prey. Studies aimed at uncovering the precise nature of these interactions are important because they can help ecologists to understand how salamanders regulate invertebrate abundance and to predict what role salamanders have in the functioning of healthy forest ecosystems. One possible interaction between terrestrial salamanders and ecologically similar forest floor invertebrates is via intraguild (IG) predation. The role of IG predation in food webs was popularized, in part, by Polis et al. (1989) and can be defined as the killing and consuming of species that are also potential competitors. IG predation is an important and widespread behavioral interaction (Arim & Marquet 2004) that has the potential to weaken trophic cascades (Holt & Polis 1997; Denno et al. 2004) and increase food web stability (McCann et al. 1998). For example, terrestrial salamanders are top predators in detrital webs of temperate forests and may stabilize or weaken indirect effects in their communities by decreasing the magnitude of strict predator/prey interactions. This occurs as they switch from foraging in the confined, simple space beneath cover to broadly foraging in the heterogeneous interstitial spaces within the leaf litter (Hickerson et al. 2012).

A recent predator removal study conducted in unenclosed field plots found that the consistent removal of individuals of *P. cinereus* resulted in significant increases in the densities of spiders relative to nonremoval plots (Fig. 1A; Hickerson et al. 2012). It is unclear whether the negative influence on spider abundance was the result of direct (e.g. IG predation by salamanders) or indirect effects (e.g. competition for shared prey) by salamanders. In the absence of specific diet data clearly explaining food web topology (e.g. spider gut contents), it is often assumed that IG predation occurs whenever guild members pass through developmental stages that place smaller individuals at a risk of predation from larger individuals of the competing species, or when one of the involved species is able to use venom to subdue IG prey. For example, large venomous spiders could easily prey upon small hatchlings of *P. cinereus* [snout-to-vent length (SVL) 11–14 mm; Anthony & Pfingsten 2013], yet it is unknown whether IG predation actually occurs. Understanding the mechanisms involved in dictating numerical responses seen in predator removal studies should further our general understanding of the role of competition and predation in shaping communities.

Individuals of *Plethodon cinereus* and ecologically similar spiders in the genus *Wadotes* (Aranae Agelenidae, formerly Amaurobiidae) are abundant and commonly
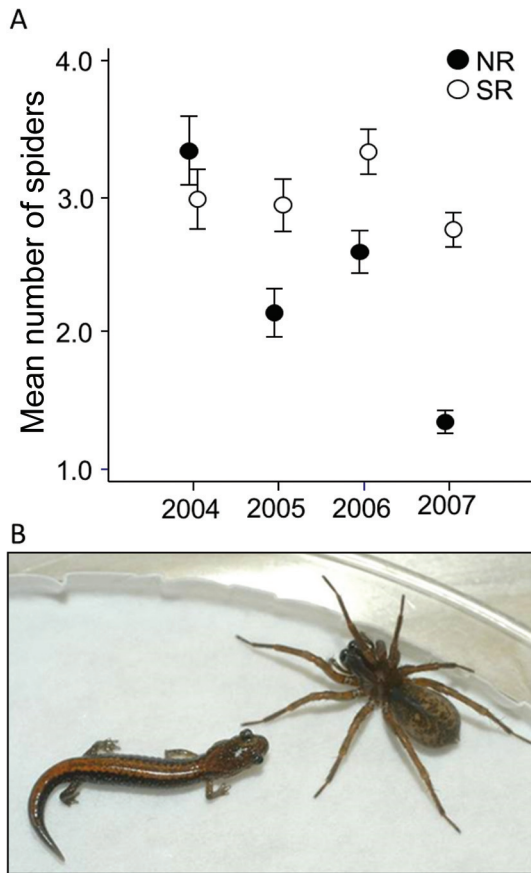
Fig. 1. — A: Mean number of spiders in nonremoval plots (NR, controls – black symbols) compared with salamander removal plots (SR, salamander removal – white symbols) over 4 years (2004–2007). Bars represent SE. B: A juvenile Eastern Red-backed Salamander, *Plethodon cinereus* (SVL = 14.99 mm) paired with a large adult spider, *Wadotes* spp. (total length = 11.05 mm) shown in a laboratory testing arena during our behavior trials.

found in the eastern temperate forests of North America (Bennett 1987; Petranka 1998; Varady-Szabo & Buddle 2006). *Plethodon cinereus* belongs to a group of lungless salamanders (Caudata Plethodontidae) and is therefore reliant on cutaneous respiration (reviewed in Gifford 2016). As a result, the microhabitat with which these salamanders, and their invertebrate prey, reside must be wet enough to prevent desiccation. *Plethodon cinereus* and spiders in the genus *Wadotes* are able to avoid desiccation while foraging because the thick dampened leaf litter substrate in temperate forest provides a humid microhabit (for spiders Bultman & Uetz 1982; for salamanders reviewed in Jaeger et al. 2016). During periods between precipitation events, individuals of *P. cinereus* are known to retreat beneath cover objects (rocks, logs and bark) as the leaf litter substrate dries (Jaeger 1980). Forest floor spiders may risk desiccation during dry periods and thus also utilize cover objects during those times (Foelix 1996).

Individuals of *P. cinereus* are generalist predators that feed on a variety of leaf litter inhabiting invertebrates. Although the diets of species in the genus *Wadotes* are not specifically known, the diets of *P. cinereus* have been studied extensively and *Wadotes* spp. at our field site likely share many prey taxa with *P. cinereus*. For example, Collembola, Acari, Diptera, Formicidae and Coleoptera are among the most commonly reported prey found in the gut contents of individuals of *P. cinereus* (reviewed in Anthony & Pfingsten 2013) and are also thought to be important prey taxa for many species of spiders (Nentwig 1983; Lawrence & Wise 2000; Agusti et al. 2003; Harwood et al. 2007). More specifically, spiders in the genus *Wadotes* apparently derive about 95% of their prey from the detrital food web and therefore share abundant prey such as Collembola with salamanders (Hladilek 2008).

Adults of *P. cinereus* are territorial and actively defend focal cover objects that retain moisture and invertebrate prey during dry periods (reviewed in Mathis et al. 1995; in Ohio Anthony & Pfingsten 2013). The defended space beneath cover objects is relatively homogenous, and it is within this confined area that salamanders likely interact with large spiders (Bennett 1987; Hickerson et al. 2012). For spiders in the genus *Wadotes*, territoriality is unknown, but females are known to aggressively defend egg sacs from potential predators (Bennett 1987). Previous work has shown that *P. cinereus* responds aggressively to carabid beetles (*Platynus tenuicollis*; Gall et al. 2003) and to centipedes (*Scolopocryptops sexspinosus*; Hickerson et al. 2004). Additionally, these salamanders are less likely to share cover with centipedes both in the field (Hickerson et al. 2004) and in laboratory mesocosms (Anthony et al. 2007).

The purpose of our study was to examine interactions between terrestrial salamanders (adults and juveniles of *P. cinereus*) and spiders (adult *Wadotes*) that potentially share both prey and microhabitat within temperate forests of eastern North America. Our work was conducted in two parts. First, we examined co-occurrence of salamanders and spiders beneath cover objects within their shared microhabitat. We predicted that if interference competition is an important force shaping the distribution on the forest floor, spiders and salamanders would be negatively associated and non-overlapping in their occupancy of cover objects. Second, we conducted a controlled laboratory experiment to examine whether interactions of both juvenile and adult salamanders paired with large adult spiders were predatory in nature. Based on the findings of Gall et al. (2003) and Hickerson et al. (2004), we predicted that salamanders would behave similarly toward spiders and conspecifics, displaying aggressive behavior toward both types of intruders. Furthermore, we predicted that large venomous spiders would readily prey on this small terrestrial salamander species, and that predation should be greatest on juvenile salamanders compared to adults.

METHODS

Co-occurrence under artificial cover objects (ACOs) in the field

In April 2004, we placed 144 ACOs on a north-facing forested hillside within the Cuyahoga Valley National Park (Ohio, USA; for details see Hickerson et al. 2012). We used ceramic floor tiles (30.5 × 30.5 cm) as ACOs and we assembled the cover objects in arrays of nine ACOs (*n* = 16 arrays). ACOs were separated by at least 1 m and were placed in direct contact with the soil substrate by removing the intervening leaf litter. We examined salamander and spider co-occurrence under cover objects in the field during seasons when salamander and spider abundances were high (spring and fall 2005, 2006). We sampled the 144 ACOs four times during each season (once every 2 weeks) and

recorded the number of adult spiders *Wadotes* spp. and adult (> 34 mm, SVL) and juvenile (< 22 mm, SVL) *Plethodon cinereus* under each ACO. We focused on adult salamanders because they are known to defend cover objects in territorial disputes (reviewed in Jaeger & Forester 1993; Mathis et al. 1995), and on juveniles because they are tolerated within adult territories (Jaeger et al. 1995) and may defend territories themselves (Ousterhout & Liebgold 2010). We used the total number of observations of each individual as a measure of cover object use. We predicted that total observations of spiders would correlate negatively with total juvenile and adult salamander observations if these organisms are negatively associating on the forest floor. This method overestimates the frequency of co-occurrence between taxa because an ACO occupied by a spider on one collecting date and by a salamander on another is considered a shared cover object in the analysis. This approach, therefore, makes finding a significant negative correlation more difficult. Bivariate correlations (two-tailed) of adult salamander/spider and juvenile salamander/spider were estimated within each season. We used Spearman's rank correlations because the data did not meet the assumptions of parametric statistics.

Behavioral responses of resident salamanders to intruders

We collected adult males of *Plethodon cinereus* (n = 25; mean SVL = 37.8 mm, SE = 0.41, median = 37.5 mm) and adult spiders (genus *Wadotes*; n = 25; mean total length = 11.0 mm, SE = 0.30, median = 11.1 mm) from a single forested locality adjacent to our field plots described above but on private land. Salamanders and spiders were collected August to September 2005 and were transported to the laboratory individually in plastic centrifuge tubes containing paper towels dampened with spring water. In the laboratory, and prior to behavioral trials, we housed salamanders and spiders individually under a natural photoperiod at 16.7 ± 1.1 °C on a moistened leaf litter substrate. Salamanders and spiders were fed wingless fruit flies (*Drosophila melanogaster*) ad libitum between trials, but they were denied food for 4 days prior to testing. Salamanders and spiders were weighed periodically throughout the study, and no individuals lost mass over the duration of the experiment. We minimized mass differences between paired animals by sorting them by mass and then randomly pairing within each of five mass classes.

In October and November 2005, we exposed each of our 25 resident male salamanders to three intruder treatments: (1) a control treatment consisting of a rolled paper towel of intermediate size between a salamander and a spider [this object served as a focal point from which to collect baseline levels of behavior and has been used in many laboratory behavior studies (reviewed in Jaeger et al. 2016)]; (2) a salamander intruder treatment in which a male salamander of similar size was introduced into the test arena; and (3) a spider intruder treatment in which a spider was introduced into the test arena. To avoid temporal bias in the data, equal numbers of each treatment were run on each testing day (Hurlbert 1984), and to avoid experimenter bias, only one of us (A.M. Figura) collected the behavioral data. The order in which resident salamanders were exposed to the three treatments was randomized. We used plastic Petri dishes (1.5 × 14 cm diameter) lined with moistened 15 cm diameter Ahlstroms qualitative filter paper (Ahlstrom Corporation, Mt Holly Springs, PA, USA) for our experimental arenas. Test salamanders were allowed to establish territorial residency in their arenas for 5 days prior to each intruder treatment (Mathis et al. 1995).

At the beginning of each behavioral trial, we placed an opaque acclimation dish over the resident salamander and then carefully placed an intruder into the arena under a separate opaque dish. After a 5 min acclimation period, the acclimation dishes were lifted and the trial was started immediately after it was apparent that the resident salamander was aware of the presence of the intruder (indicated by the salamander turning its head toward the intruder, or the intruder moving across the salamander's forward field of vision). In the control treatment the trial was initiated after the first movement by the salamander. The software package EVENT-PC (James C. Ha, University of Washington) was used to record the duration of salamander behaviors during each 15 min trial. We recorded the following behaviors (as defined in Jaeger 1984): look toward (LT), salamander turns its head in the direction of the intruder; move toward (MT), salamander approaches the intruder in a direct path that would result in contact if the movement were to continue; look away (LA) salamander turns its head away from the intruder; move away (MA), salamander increases the distance between itself and the intruder; and biting (BITE), closing

of the jaws around any part of the intruder's body and immediately releasing the grip. Biting was considered an aggressive behavior because spiders exceeded the gape size of resident salamanders and this behavior is used by territorial residents to expel intruders (Jaeger et al. 1982). We estimated aggressive responses of residents with an index using the aggressive behaviors MT and LT and the submissive behaviors MA and LA. The index (aggressive index, AI) is calculated as [(MT + LT) – (MA + LA)] (Mathis et al. 2000; Hickerson et al. 2004). We employed permutational MANOVA (using the adonis function in the R package vegan) to examine the effect of treatment on the AI and on bites delivered by residents to intruders. We stratified our data by resident number to maintain our paired design. We employed paired Wilcoxon tests with Monte Carlo permutation (n = 99999) to make post-hoc comparisons among the three treatments (PAST version 3).

Juvenile salamanders as intraguild prey of spiders

In October 2005, we collected 20 juvenile (mean SVL = 16.8 mm, SE = 0.90, median = 16.2 mm) *P. cinereus* from the field site described above. Juvenile salamanders were only slightly larger than hatchlings and were presumably small enough to be overpowered by adult *Wadotes*. In November 2005, we paired the salamanders with a subset of the same spiders (mean total length = 10.9 mm, SE = 0.46, median = 11.1 mm) used in the behavioral interaction experiment (Fig. 1B). We used the same simple test arenas described above to maximize the likelihood of predation by spiders, and we size-matched predators and presumptive prey so that the largest spiders were paired with the largest salamanders. Salamanders and spiders were placed under separate acclimation dishes simultaneously for 5 min. Once the dishes were lifted, we observed and recorded interactions (as described above) between the two species for 15 min after the movement by one of the interacting individuals.

RESULTS

Field sampling

Adult salamanders were observed more often than juveniles and spiders under ACOs (Table 1). Juvenile salamanders were negatively correlated with adult spiders in all seasons and adult salamanders were negatively correlated with adult spiders in all seasons except fall 2005 (Table 2). Estimates of co-occurrence ranged from 13 to 14.8% for adult salamanders/spiders and 3.9 to 11.5% for juvenile salamanders/adult spiders. These numbers include cases where spiders and salamanders used the same ACO on different sampling days within a season and, therefore, overestimates the actual co-occurrence of these guild members.

Table 1.

Numbers of spiders *Wadotes* spp. (adult agelenids) and salamanders (adults and juveniles of *Plethodon cinereus*) observed under ACOs during the four sampling seasons.

	2005		2006	
	Spring	Fall	Spring	Fall
Adult *Plethodon cinereus*	170	184	155	115
Juvenile *Plethodon cinereus*	23	43	7	20
Adult agelenid spiders	25	21	33	33

Table 2.

Spearman's rank correlations of spider and salamander abundance under ACOs. Estimates of co-occurrence (in parentheses) are presented as percent of occupied ACOs that were used by both species.

	Adult salamanders and adult spiders		Juvenile salamanders and adult spiders	
	Rho	P	Rho	P
Spring 2005	− 0.357 (13.0%)	0.001**	− 0.834 (11.5%)	< 0.0001**
Fall 2005	− 0.086 (13.5%)	0.414 NS	− 0.799 (4.8%)	< 0.0001**
Spring 2006	− 0.288 (13.4%)	0.005**	− 0.804 (3.9%)	< 0.0001**
Fall 2006	− 0.478 (14.8%)	< 0.0001**	− 0.826 (7.5%)	< 0.0001**

**Significant correlation at $P < 0.01$ (two-tailed).

Behavioral responses of resident salamanders to intruders

Treatment (control, salamander intruder, spider intruder) had a significant effect on the aggressive index and biting behavior of resident salamanders (for AI, $F_{(2,72)} = 3.65$, $P = 0.018$, Fig. 2A; for bites, $F_{(2,72)} = 4.26$, $P = 0.006$, Fig. 2B). When paired with conspecifics, salamanders exhibited increases in the aggressive behaviors "look toward" and "move toward", but they switched to biting as a tactic when interacting with spiders. Compared with control trials, resident salamanders responded with significant increases in aggression (estimated by AI) to conspecific ($z = 2.60$; $P = 0.004$) but not to spider intruders ($z = 1.22$; $P = 0.115$). Resident salamanders delivered significantly more bites to intruding spiders ($z = 2.75$; $P = 0.002$), but not to intruding salamanders ($z = 1.60$; $P = 0.124$). Biting by resident salamanders occurred in 36% of trials with spider intruders (mean 0.8 bites/trial), but only in 12% of trials with conspecific intruders (mean 0.6 bites/trial). Biting by resident salamanders did not result in visible injury to either species of intruder. Intruding spiders attempted to bite salamanders in 16% of trials (0.28 bites/trial), but we saw no evidence of envenomation from these attacks.

Juvenile salamanders as intraguild prey of spiders

We observed no cases of intraguild predation by spiders on juvenile salamanders. Spiders occasionally chased juvenile salamanders, and in 30% of trials they attempted to grasp the salamanders with their forelimbs, but no apparent cases of envenomation were observed. Juvenile salamanders did not bite spiders in any trials.

DISCUSSION

Our study was designed to explore interactions between the salamander, *Plethodon cinereus*, and spiders (*Wadotes* spp.) in a temperate forest system. We were particularly interested in teasing apart behaviors (territoriality and IG predation) responsible for the increase in spider numbers in salamander removal plots previously reported in Hickerson et al. (2012); Fig. 1A. We found that spiders and salamanders were negatively associated beneath cover objects on the forest floor, a result that corroborates that of Hickerson et al.
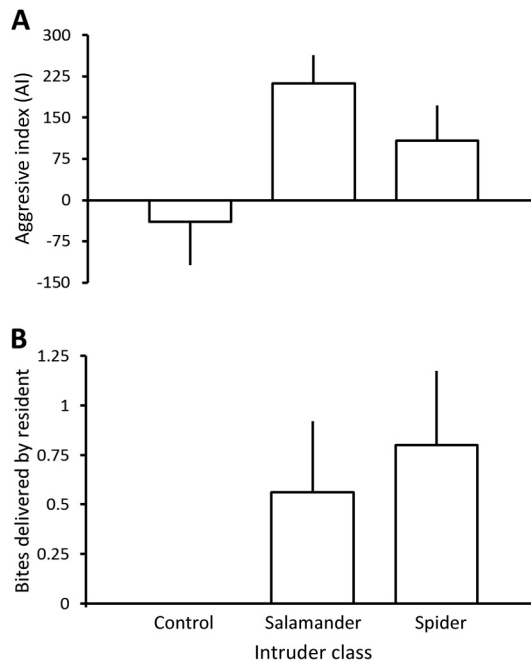
Fig. 2. — Mean responses of resident salamanders in control and live intruder treatments. Bars represent SE. A: The aggression index (AI) was calculated from the aggressive behaviors LT and MT, and the submissive behaviors LA and MA. Negative AI values are possible when submissive behaviors exceed aggressive behaviors displayed by an individual. B: Bites by resident salamanders to intruders. Salamanders significantly elevated their aggressive responses (AI and bites) to live versus control intruders.

(2012). Typically, negative spatial associations are indicative of either competition for space or result from differences in microhabitat use. We suggest that, in this case, the former is more likely. Previous work has provided multiple lines of evidence suggesting that individuals of *P. cinereus* interact with centipedes in a competitive context (Hickerson et al. 2004; Anthony et al. 2007) even though, like spiders (Foelix 1996), centipedes are venomous and should be able to consume small terrestrial salamanders (Lewis 1981). Although we did not measure all possible abiotic conditions beneath ACOs, the soil surface beneath cover occupied by salamanders and spiders did not differ in temperature (mean for salamander ACOs = 14.48 °C, n = 64; mean for spider ACOs = 13.07 °C, n = 32; $F_{(1,93)}$ = 0.348, P = 0.558), and we observed no differences in microhabitat under our ACOs. Additionally, resident *P. cinereus* in our experiments were similarly aggressive (as measured by mean number of bites and by our aggression index) toward both conspecific and spider intruders. These results, and those reported by Gall et al. (2003) and Hickerson et al. (2004), suggest that interspecific territorial defense by *P. cinereus* toward large predatory arthropods may be more common in nature than previously thought.

In laboratory encounters with adult carabid beetles (Gall et al. 2003) and adult centipedes (Hickerson et al. 2004; Anthony et al. 2007), no instances of IG predation by salamanders or by arthropod guild members were reported. This was true even when the arthropods were venomous and presumably able to capture and consume larger prey. Diet

studies on *P. cinereus* indicate that arthropod predators (e.g. spiders, adult beetles and centipedes) are only occasionally consumed by small terrestrial salamanders, and comprise a relatively small proportion of the diet (Jaeger 1990; Maglia 1996; Adams & Rohlf 2000; Anthony et al. 2008; Stuczka et al. 2016). Comprehensive data on the diet of *Wadotes* spiders is limited in the literature, but Collembola (Lawrence & Wise 2000; Agusti et al. 2003), Diptera (Nentwig 1983; Harwood et al. 2007), Formicidae, and Coleoptera (Nentwig 1983) have been reported as important prey groups for temperate forest floor spiders. Studies have also shown, using stable isotope analysis and feeding experiments, that retreat web spiders, in general, feed from both the detrital compartment (Collembola) and the grazing compartment (e.g. larvae) of forest food webs (reviewed in Hladilek 2008). Collembola are also a preferred prey group of *P. cinereus* (reviewed in Jaeger et al. 2016). These studies suggest that *Wadotes* spiders (1) may share prey taxa with *P. cinereus* and (2) may not engage in IG predation of salamanders.

Spiders are frequently food limited and are thought to commonly engage in many forms of cannibalism to gain energy during resource limitation (reviewed in Wise 2006). Other researchers have suggested that cannibalism (which some consider a form of IG predation) functions to remove intraspecific competitors; however, there is little evidence that this is a benefit of IG predation (Polis et al. 1989). During periods of food limitation the acquisition of high quality resources from cannibalism may outweigh the costs of injury or of contracting parasites (Wise 2006). However, an additional risk for spiders may be increased handling time associated with consuming a salamander with noxious skin secretions (Brodie et al. 1979). Such increases in handling time of alternative prey might be especially costly during periods when preferred prey are scarce. Therefore for spiders, cannibalism may be a more effective way to gain energy than IG predation on small salamanders.

Optimal foraging theory predicts that predators should be able to assess and rank the profitability of various prey types (Pyke 1984). If salamanders and spiders share prey resources, one strategy employed by both might be to invest in exploitative competition to gain access to high-quality prey. This strategy would require predators to recognize and prioritize high quality prey over other prey types. One way that predators might judge prey profitability is based on prey size (assuming equal nutritional quality otherwise). Jaeger and Barnard (1981) found that when presented with large and small flies individuals of *P. cinereus* preferentially fed on large flies relative to small ones. Evidence suggests that spiders that capture larger prey items grow to a larger size at sexual maturity, or reach maturity earlier, which has been shown to directly increase individual fitness (reviewed in Uetz 1992). Another important consideration for judging prey profitability is the rate at which prey are digested. Heavily armored prey may pass through the gut more slowly than soft-bodied, less chitinous prey resulting in poor assimilation efficiency (Bobka et al. 1981). Individuals of *P. cinereus* are thought to rank the profitability of prey based upon prior experience (Jaeger & Rubin 1982). These authors suggested that learning may be an important component to judging calorie, nutrient content, and digestion rates of different prey types. Although there is no information on the ability of *Wadotes* spp. to assess prey nutrient quality or content, there is evidence that some species of spiders [e.g. *Pardosa prativaga* (Lycosidae) and *Stegodyphus lineatus* (Eresidae)] have the ability to judge prey profitability. However, spiders with differing foraging modes (sit-and-wait vs. web building) do so in different ways (Mayntz et al. 2005). So if salamanders and spiders are able to assess the quality of their shared prey resources, they may be able to maximize their individual energy intake by engaging in competition for profitable

prey. For spiders, the cost of IG predation on salamanders may result in the use of suboptimal prey or in cannibalism as preferred strategies.

Multiple lines of evidence suggest that the interaction between *P. cinereus* and large spiders in the genus *Wadotes* may be competitive in nature rather than predatory. However, the complexity of the interaction is still largely unknown. For example, further studies on the predictors of contest theory in this system should examine the role of body size asymmetry of *P. cinereus* and *Wadotes* spp. through ontogeny, prior experience, food limitation (i.e. availability of alternative prey), and habitat heterogeneity in niche partitioning. Future studies should also examine the cost of reciprocal interference competition associated with population regulation of the two species (e.g. Paijmans & Wong 2017). More broadly, the use of contest theory as a framework for investigating interspecific interactions within communities should help researchers improve their understanding of the relative importance of specific interactions such as interference competition and IG predation in determining species coexistence.

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