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**Foraging modality and plasticity in foraging traits determine the
strength of competitive interactions among carnivorous plants,
spiders, and toads**

Running headline: Competition among sundews, spiders, and toads

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Summary

1. Foraging modalities (e.g., passive, sit-and-wait, active) and traits are plastic in some species, but the extent to which this plasticity affects interspecific competition remains unclear.
2. Using a long-term laboratory mesocosm experiment, we quantified competition strength and the plasticity of foraging traits in a guild of generalist predators of arthropods with a range of foraging modalities.
3. Each mesocosm contained eight passively foraging pink sundews, and we employed an experimental design where treatments were the presence or absence of a sit-and-wait foraging spider and actively foraging toad crossed with five levels of prey abundance. We hypothesized that actively foraging toads would outcompete the other species at low prey abundance, but that spiders and sundews would exhibit plasticity in foraging traits to compensate for strong competition when prey were limited.
4. Results generally supported our hypotheses. Toads had a greater effect on sundews at low prey abundances, and toad presence caused spiders to locate webs higher above the ground. Additionally, the closer large spider webs were to the ground, the greater the trichome densities produced by sundews. Also, spider webs were larger with than without toads and as sundew numbers increased, and these effects were more prominent as resources became limited. Finally, spiders negatively affected toad growth only at low prey abundance.
5. These findings highlight the long-term importance of foraging modality and plasticity of foraging traits in determining the strength of competition within and across taxonomic kingdoms. Future research should assess whether plasticity in foraging traits helps to

maintain coexistence within this guild and whether foraging modality can be used as a trait to reliably predict the strength of competitive interactions.

Key-words *Anaxyrus quercicus*; *Drosera capillaris*; interspecific competition; kleptoparasitism; *Sosippus floridanus*

Introduction

Understanding how diversity in functional traits affects the distribution of species and ecosystem functions has been a major focus of ecological research in recent years (Bolker *et al.* 2003; Werner & Peacor 2003; McGill *et al.* 2006). For instance, predator functional diversity (in terms of foraging modality) has been shown to have cascading effects throughout food webs (Finke & Denno 2004; Lazzaro *et al.* 2009; Schmitz 2009; Steffan & Snyder 2010). However, few studies have empirically examined interspecific interactions among multiple predators with varied foraging modalities (Eklov & VanKooten 2001; Carey & Wahl 2010), even though determining the strength and outcome of these interactions between predators could have important implications for theory in community ecology (Wilson *et al.* 1999; Abrams 2010; Lee, Miller & Inouye 2011).

For example, theory suggests that predators with active foraging modalities should encounter prey at a higher rate than more passively foraging predators (e.g., sit-and-wait), and as a result they might be superior competitors, particularly when prey abundance or movement directionality is low (Werner & Anholt 1993; Scharf *et al.* 2006). Conversely, when prey abundance is high or if prey exhibit high directionality in movement, encounter rates are likely to be more similar between passive and active foragers and consequently

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active foraging might be less advantageous (Scharf *et al.* 2006). Additionally, the presence of competitors can cause species to shift their utilization of habitat (Werner & Hall 1977; Nakano, Fausch & Kitano 1999; Harwood & Obrycki 2005), or adjust their investment in the expression of foraging traits (Relyea 2002; Relyea 2004). Such plasticity in foraging traits could enable competing species with different foraging modalities to coexist and therefore help to maintain predator diversity and any resulting community- or ecosystem-level outcomes of this diversity, such as top-down control of herbivore and parasite populations (Cardinale *et al.* 2003; Duffy *et al.* 2007; Rohr *et al.* 2015).

Here we quantify competitive interactions within a functionally diverse, syntopic guild of three generalist predators of arthropods: pink sundews (*Drosera capillaris*), which are passive foragers using sticky mucilage produced from leaf trichomes to capture prey; funnel-web-building wolf spiders (*Sosippus floridanus*), which are sit-and-wait foragers and rarely wander far from their webs in search of prey; and oak toads (*Anaxyrus quercicus*), which are active foragers hunting prey. All three of these relatively small, similarly sized species (pink sundews: mean leaf rosette diameter ~3.5 cm, *S. floridanus*: mean total length ~2 cm, and oak toads: mean total length ~2.5 cm) are common throughout much of the southeastern coastal plain of the United States and can be highly abundant in mesic habitats in Florida (Hamilton Jr. 1955; Brady 1972; Punzo 1995; Schnell 2002; Greenberg & Tanner 2005; Punzo & Haines 2006; Jennings *et al.* 2010; Jennings, Edwards & Rohr 2012). Evidence suggests that all three species predominantly feed on ants, collembolans, beetles, and spiders (Punzo 1995; Punzo & Haines 2006; Jennings *et al.* 2010). Furthermore, field research has already indicated high dietary overlap and likely competition between *S. floridanus* and pink sundews (Jennings *et al.* 2010). Given the apparent overlap in habitat and diet, plasticity in foraging traits could affect the outcome of competition among these three species.

Our objective was to determine the importance of foraging modality and plasticity of foraging traits for the strength of competitive interactions. More specifically, we examined: 1) how toad, spider, and prey abundance affect sundews and their leaf traits, 2) how toad, sundew, and prey abundance affect spider web traits, and 3) how spider, sundew, and prey abundance affect toad growth. Sundews do not rely on predation to provide all of their nutrition (compared with spiders and toads), but the addition of prey is known to increase seed production and vegetative propagation in some species (Thum 1988). Consequently, we predicted that sundews would be negatively affected by competitors because they cannot relocate to areas of high prey abundance. However, changes in prey and nutrient availability also have been shown to induce trait responses in other carnivorous plants, such as altering the number of trapping structures (Ellison & Gotelli 2002), amount of mucilage produced (Thoren *et al.* 2003), and size of leaves (Schulze & Schulze 1990). For this reason, we also predicted that sundews would decrease leaf area but increase trichome densities on leaves when prey abundance was low to increase their chances of catching prey. Spiders are capable of adjusting their web size and location in response to prey availability (Sherman 1994; Harwood, Sunderland & Symondson 2001; Harwood, Sunderland & Symondson 2003), and thus we predicted that spiders would shift their webs closer to the ground and increase web size as competition increases or prey abundance decreases. As the most active foragers and therefore potentially superior competitors, we predicted that toad growth would only be influenced by prey abundance and not the other two species. Additionally, consistent with theory (Werner & Anholt 1993), we predicted that toads would have the strongest adverse effect on competitors when prey were limiting.

Material and methods

EXPERIMENTAL DESIGN

We conducted a mesocosm experiment for one year in the laboratory, enabling us to examine the long-term effects of competition. Mesocosms consisted of terraria (33 x 20 x 13 cm) filled to a depth of 2.5 cm with a mixture of 1/3 peat moss and 2/3 silica-based sand, with each terrarium containing eight equally spaced pink sundews (mean leaf rosette diameter \pm SE = 3.10 ± 0.04 cm) transplanted from the field. We used a 2 x 2 x 5 design (spider presence/absence crossed with toad presence/absence crossed with 12, 16, 20, 24, or 28 commercially obtained pinhead [nymphs ~2 mm total length] house crickets [*Acheta domesticus*] added twice per week), with four replicates of each treatment combination (a total of 80 terraria). All terraria were covered with window screening to prevent animals from escaping, and then Plexiglas to maintain humidity (Plexiglas alone did not provide a sufficient balance between airflow and containment of animals). Light fixtures above terraria were equipped with full spectrum bulbs, and light regimes were varied by season (9 L : 15 D November-February, to 14 L : 10 D March-October). Temperature remained at ~23°C for the duration of the experiment. We added 100 ml of deionized water three times per week to ensure that moist conditions were maintained in the terraria. At the start of the experiment, terraria selected for toad and/or spider treatments received one individual of the appropriate species, and all animals were able to move throughout their particular terrarium. Thus, densities for each species in the mesocosms (sundews = 121/m², toads = 15/m², spiders = 15/m²) were within or as close as possible logistically to densities found in the field (sundews max. = 148/m², toads max. = 2/m², spiders max. = 16/m²) (Greenberg & Tanner 2005, DEJ unpublished data). We used immature oak toads (mean initial toad mass \pm 1 SE = 0.79 ± 0.04

g) and spiders because of the long-term duration of the experiment, and any toads or spiders that died were replaced with similar sized individuals (2 toads and 7 spiders died).

DATA COLLECTION

We collected data on several performance measures and traits of each species. Counts of living sundews (including any produced through vegetative propagation), number of leaves, leaf traits (trichome density and trapping area), and measurements of sundew diameter (cm) were conducted at the beginning and end of the experiment. To measure leaf traits, one randomly selected leaf from each sundew in a terrarium was removed and photographed. We then quantified the number of trichomes per leaf and trapping area (area of the leaf with trichomes) using ImageJ software (Schneider, Rasband & Elicieri 2012). Total trapping area was then estimated by multiplying the mean trapping area per leaf by the mean number of leaves per sundew per terrarium. We quantified spider web height (cm) and area (cm²) at the end of the experiment. Web area was calculated using ImageJ software (Schneider, Rasband & Elicieri 2012) after photographing webs. Toads were weighed (g) at the beginning and end of the experiment, and growth was calculated as a proportion of the initial mass of an individual. We also gathered baseline data on prey consumption. Terraria received crickets in a randomized order each week, and immediately after releasing crickets, we monitored any spider and/or toad for two minutes to record any predation events. Twenty-four hours after cricket releases, we counted the number of crickets captured on all sundew leaves.

STATISTICAL ANALYSES

All statistical analyses were conducted using R 3.1.1 (R Core Team 2014). We examined the effects of competitors and prey abundance on each of the three species using generalized linear models with appropriate error distributions. To test for effects on toad growth, web area and web height, and differences in trichome density and total trapping area (from the beginning to the end of the experiment), we used a Gaussian error distribution, and for sundew counts we used a Poisson error distribution ('glm' function, 'stats' package).

Significance was assessed with log-likelihood ratio tests and type II sums of squares. Initially we tested for all biologically relevant two-, three-, and four-way interactions in each model, but interactions with $P > 0.1$ were dropped from the final models. For prey consumption, data were square root transformed and we tested for the effects of competitor presence/absence using analysis of variance. Finally, to visualize regression results, we used the 'visreg' function in the 'visreg' package (Breheny & Burchett 2013) of R.

Results

EFFECTS ON SUNDEWS

Across all treatments, there was an increase in total sundew trapping area per terrarium from the beginning (mean \pm 1 SE = 89.88 ± 9.18 cm²) to the end (mean \pm 1 SE = 156.04 ± 16.87 cm²) of the experiment, and the number of sundews per terrarium at the end of the experiment (inclusive of original and newly germinated/propagated plants) ranged from 1-24 (mean \pm 1 SE = 10.03 ± 0.58). Sundews captured nearly five times more prey ($F = 42.39$, d.f. = 1, 78, $P < 0.001$) when toads were absent (mean total number of crickets captured by sundews per terraria = 23.15 ± 3.18) than present (4.80 ± 1.13). In fact, relative to the

absence of a toad, the presence of a toad essentially negated the benefit of the food gradient for sundews and reduced the number of sundews and total trapping area per terrarium at the end of the experiment (toad x prey interactions: number of sundews: $P = 0.014$, trapping area: $P = 0.028$; Fig. 1a, Table 1, Appendix A).

We also found that sundew numbers and sundew trapping area were negatively associated with web height, but the strength of this effect was dependent on web size (web area x web height interactions: number of sundews: $P = 0.033$, sundew trapping area: $P = 0.030$; Fig. 1b, Table 1, Appendix A). When webs were small and thus only weakly competitive with sundews, sundew trapping area (and sundew numbers) was generally independent of web height (Fig. 1b, Appendix A). However, when webs were large and thus posed a substantial competitive threat, the closer the webs were to the ground where the sundews grew, the less sundew trapping area (and total sundews) there was at the end of the experiment (Fig. 1b, Appendix A).

In addition to effects on sundew densities, there were also effects of the treatments on sundew traits. We measured leaf traits on a total of 1,442 sundews and counted 115,338 trichomes. Mean trichome density was higher at the end (mean \pm 1 SE = 133.97 ± 7.99 trichomes/cm²) than at the beginning (mean \pm 1 SE = 85.54 ± 1.87 trichomes/cm²) of the experiment. As a reminder, our hypothesis was that trichome densities would be negatively associated with prey abundance and should increase with competition from spiders and toads. Our findings generally supported these hypotheses. When toads were absent (Fig. 2a), trichome density was more negatively associated with prey abundance when webs were close to the ground (i.e., high spider competition) than when webs were located higher above the ground. When toads were present (Fig. 2b), trichome density was generally higher than when they were absent, but trichome densities were negatively associated with prey abundance at all web heights (toad x web height x prey: $P = 0.025$, Table 1).

EFFECTS ON SPIDERS

Spiders appeared to adjust the height and size of their webs in response to competitors and prey abundance. Webs were located more than two times higher above the ground when toads were present (mean \pm 1 SE = 6.00 \pm 0.61 cm) than when they were absent (mean \pm 1 SE = 2.70 \pm 0.60 cm). Spiders also captured significantly more prey ($F = 7.13$, d.f. = 1, 38, $P = 0.011$) when toads were absent (mean total crickets captured per spider \pm 1 SE = 21.70 \pm 3.29) than when toads were present (11.60 \pm 1.70). Further, when toads were present, web height was positively associated with prey abundance, but without toads there was a negative relationship between web height and prey (toad x prey: $P = 0.045$; Fig. 3, Table 2).

There was a significant three-way interaction between sundew trapping area, toad presence, and prey abundance on spider web area (total trapping area x toad x prey: $P = 0.023$; Fig. 2b,c, Table 2). When total sundew trapping area was low, web area exhibited only a weak negative association with prey abundance. In contrast, when total sundew trapping area was high, web area was strongly negatively associated with prey abundance. In both cases, the relationship between web area, trapping area, and prey was stronger when toads were present (Fig. 4a) than when they were absent (Fig. 4b).

EFFECTS ON TOADS

Toad growth was negatively associated with web area (web area: $P = 0.003$; Fig. 5a, Table 3) and positively associated with prey abundance (prey: $P < 0.001$; Fig. 5b, Table 3), although the mean total number of crickets we observed being captured per toad was similar ($F = 0.48$, d.f. = 1, 38, $P = 0.494$) whether spiders were present (mean \pm 1 SE = 110.10 \pm 7.10) or absent (mean \pm 1 SE = 116.50 \pm 6.48). We did not detect any significant effect of sundew densities

or trapping area on toad growth (Table 3). While relatively rare overall, on 97 occasions we observed toads consuming live crickets that had become trapped by sundews and were struggling in mucilage. Assuming that these crickets would otherwise have been consumed by sundews, this would have amounted to 8% of the total number of crickets captured by the plants.

Discussion

Results from our long-term experiment demonstrate that foraging modality and plasticity in foraging traits can be important determinants of the strength and outcome of competitive interactions (Fig. 6). Sundew numbers, total trapping area, and trichome density were all affected by competitors and prey abundance. For sundew numbers, toads had a negative effect, but the effect of spiders was mediated by the interaction between the height and size of their webs (though with generally more sundews as webs increased in size). Small webs did not appear to have much of a competitive effect on sundews regardless of where they were, but large webs closer to the ground where the sundews reside were more detrimental to sundews than large webs higher above the ground. Interspecific competition has been implicated as a potential cause of changes in total trapping area of sundews (Jennings *et al.* 2010), and thus it was not surprising to observe other leaf trait changes, such as increases in trichome density, associated with competition. In other plants, trichome production is also plastic. For instance, when trichomes are thought to serve a defensive function, herbivory can induce an increase in their densities (Holeski 2007; Bjorkman, Dalin & Ahrne 2008).

Spiders generally increased web area in response to reduced availability of prey caused by competition with toads or sundews, a behaviour consistent with findings from other studies (Sherman 1994). Additionally, toads caused *S. floridanus* to elevate the height

of their webs, consistent with this species locating webs anywhere from on the ground to above the ground among shrubs and cacti in the field (Punzo & Haines 2006). Previous work has indicated that spiders relocate or modify their webs to avoid competition or possibly predation (Harwood & Obrycki 2005; Manicom *et al.* 2008; Jennings *et al.* 2010), and web relocation is energetically costly for spiders that produce complex webs, such as sheet- and funnel-webs (Tanaka 1989). In this system, we believe that competition (exploitation or interference) rather than intraguild predation (i.e., toads, spiders, and sundews competing and depredating one another) was the driver of web location behaviour. Spiders might choose to locate webs higher above the ground to avoid interference competition with toads and to prevent these energetically costly webs from being damaged by their competitors. Although it is possible that under field conditions intraguild predation between these three species occurs, we did not observe it in the mesocosms and believe it to be relatively rare for several reasons. For example, field surveys indicate that spiders of any species are rarely captured by pink sundews, and those individuals that are caught are generally very small in size (Jennings *et al.* 2010). Additionally, *S. floridanus* spiders display maternal care, with spiderlings staying with their mother in the web for up to five months (Brach 1976; Punzo & Haines 2006). By the time these spiders leave their maternal webs, they are generally >1 cm in length (Punzo & Haines 2006) and likely too large to be caught in most sundews. At this size, they might also deter small oak toads from considering them as prey.

Oak toads were the strongest competitors, with just one individual influencing both sundews and spiders. As predicted, prey abundance was the main factor affecting oak toad growth; although at low prey abundance, spiders also caused a significant negative effect on toads. The competitive superiority of oak toads could partly be explained by our observations of them stealing crickets caught in sundew leaves, and this behaviour might partially explain why, contrary to our hypothesis, they still exerted a strong negative effect on sundew

numbers even at high prey abundance. Kleptoparasitic behaviour has been seen in a number of carnivorous plant-animal interactions (Zamora 1990; Zamora & Gomez 1996; Anderson & Midgley 2002). This kleptoparasitism between toads and sundews provides another example of the often surprising and complex interactions between carnivorous plants and animals (Clarke *et al.* 2009; Moon *et al.* 2010; Grafe *et al.* 2011). Although we showed that the actively foraging oak toads were superior competitors to the more passively foraging spiders and sundews, active foragers expend more energy in pursuit of food and their activity could increase their risk of predation. Thus, in the field, where space and predation pressures are greater than in our mesocosms, interaction strengths among oak toads, spiders, and sundews could be different.

We endeavoured to recreate a natural system using the mesocosms, but obviously there are some limitations with this type of experimental design. For example, the densities of oak toads used were higher than any that have been documented in the field (though to our knowledge very few data exist on the densities of this particular species in nature), and this could have been responsible in part for the strong effects of toads that were observed.

Additionally, although crickets comprise part of the diets of all three species (Punzo 1995; Punzo & Haines 2006; Jennings *et al.* 2010), clearly in natural habitats there is a much more diverse prey assemblage which could help to mitigate the intensity of competition.

Consequently, any future work in this system using mesocosms should increase prey diversity to determine if the outcomes of competition remain the same. Lastly, it is possible that certain soil characteristics (e.g., depth, composition, and drainage) could have affected the condition of the sundews in some cases. For instance, given the duration of the experiment, it is likely that toad defecation in the mesocosms increased the variability of nitrogen and phosphorous in the soil and provided additional nutrients for some sundews that could partly offset any resources lost from not catching prey directly. These limitations are all

important considerations when interpreting our findings, and improvements in the design of the mesocosms could be made for future work, but the trends in the results nonetheless appear to be robust.

In conclusion, our results further highlight the importance of considering functional diversity and plasticity in traits when examining species interactions and other community- and ecosystem-level patterns and processes. Predator functional diversity has previously been shown to have effects on trophic interactions that propagate through food webs (Schmitz 2007; Lazzaro *et al.* 2009; Schmitz 2009; Rohr *et al.* 2015), and it seems plausible that the results we observed could have similar effects. For example, if spiders relocate their webs higher above the ground in response to exploitative or interference competition with oak toads, then the prey assemblage caught in their webs would likely be considerably different than webs on the ground (Brown 1981; Knop, Zund & Sanders 2014). Capturing a greater diversity of arthropod prey (including many herbivorous insects) could have broader community-level effects, such as facilitating an increase in plant diversity, and plasticity in foraging traits could help to mediate coexistence among this guild (Kobler *et al.* 2009). However, further studies in this system are needed to test these hypotheses and improve our understanding of the population dynamics for species in these increasingly threatened taxa (Skerratt *et al.* 2007; Rohr *et al.* 2008; Jennings & Rohr 2011; Jennings, Congelosi & Rohr 2012; Rohr & Palmer 2013).

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Data Accessibility

Data available from the Dryad Digital Repository: doi:10.5061/dryad.m23g6 (Jennings *et al.* 2016).

References

- Abrams, P.A. (2010) Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology*, **24**, 7-17.
- Anderson, B. & Midgley, J.J. (2002) It takes two to tango but three is a tangle: mutualists and cheaters on the carnivorous plant *Roridula*. *Oecologia*, **132**, 369-373.
- Bjorkman, C., Dalin, P. & Ahrne, K. (2008) Leaf trichome responses to herbivory in willows: induction, relaxation and costs. *New Phytologist*, **179**, 176-184.
- Bolker, B., Holyoak, M., Krivan, V., Rowe, L. & Schmitz, O. (2003) Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology*, **84**, 1101-1114.
- Brach, V. (1976) Subsocial behavior in the funnel-web wolf spider *Sosippus floridanus* (Araneae: Lycosidae). *Florida Entomologist*, **59**, 225-229.
- Brady, A.R. (1972) Geographic variation and speciation in the *Sosippus floridanus* species group (Araneae: Lycosidae). *Psyche*, **79**, 27-48.
- Breheny, P. & Burchett, W. (2013) Visualizing regression models using visreg. Available online at: <http://myweb.uiowa.edu/pbreheny/publications/visreg.pdf>

Brown, K.M. (1981) Foraging ecology and niche partitioning in orb-weaving spiders.

Oecologia, **50**, 380-385.

Cardinale, B.J., Harvey, C.T., Gross, K. & Ives, A.R. (2003) Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, **6**, 857-865.

Carey, M.P. & Wahl, D.H. (2010) Interactions of multiple predators with different foraging modes in an aquatic food web. *Oecologia*, **162**, 443-452.

Clarke, C.M., Bauer, U., Lee, C.C., Tuen, A.A., Rembold, K. & Moran, J.A. (2009) Tree shrew lavatories: a novel nitrogen sequestration strategy in a tropical pitcher plant. *Biology Letters*, **5**, 632-635.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thebault, E. & Loreau, M. (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, **10**, 522-538.

Eklov, P. & VanKooten, T. (2001) Facilitation among piscivorous predators: effects of prey habitat use. *Ecology*, **82**, 2486-2494.

Ellison, A.M. & Gotelli, N.J. (2002) Nitrogen availability alters the expression of carnivory in the northern pitcher plant, *Sarracenia purpurea*. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 4409-4412.

Finke, D.L. & Denno, R.F. (2004) Predator diversity dampens trophic cascades. *Nature*, **429**, 407-410.

Grafe, T.U., Schoner, C.R., Kerth, G., Junaidi, A. & Schoner, M.G. (2011) A novel resource-service mutualism between bats and pitcher plants. *Biology Letters*, **7**, 436-439.

Greenberg, C.H. & Tanner, G.W. (2005) Spatial and temporal ecology of oak toads (*Bufo quercicus*) on a Florida landscape. *Herpetologica*, **61**, 422-434.

Hamilton Jr., W.J. (1955) Notes on the ecology of the oak toad in Florida. *Herpetologica*, **11**, 205-210.

Harwood, J.D. & Obrycki, J.J. (2005) Web-construction behavior of linyphiid spiders (Araneae, Linyphiidae): competition and co-existence within a generalist predator guild. *Journal of Insect Behavior*, **18**, 593-607.

Harwood, J.D., Sunderland, K.D. & Symondson, W.O.C. (2001) Living where the food is: web location by linyphiid spiders in relation to prey availability in winter wheat. *Journal of Applied Ecology*, **38**, 88-99.

Harwood, J.D., Sunderland, K.D. & Symondson, W.O.C. (2003) Web-location by linyphiid spiders: prey-specific aggregation and foraging strategies. *Journal of Animal Ecology*, **72**, 745-756.

Holeski, L.M. (2007) Within and between generation phenotypic plasticity in trichome density of *Mimulus guttatus*. *Journal of Evolutionary Biology*, **20**, 2092-2100.

Jennings, D.E., Congelosi, A.M. & Rohr, J.R. (2012) Insecticides reduce survival and the expression of traits associated with carnivory of carnivorous plants. *Ecotoxicology*, **21**, 569-575.

Jennings, D.E., Edwards, G.B. & Rohr, J.R. (2012) Associations among ground-surface spiders (Araneae) and other arthropods in mesic flatwoods. *Florida Entomologist*, **95**, 290-296.

Jennings, D.E., Krupa, J.J., Raffel, T.R. & Rohr, J.R. (2010) Evidence for competition between carnivorous plants and spiders. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 3001-3008.

Jennings, D.E., Krupa, J.J. & Rohr, J.R. (2016) Data from: Foraging modality and plasticity in foraging traits determine the strength of competitive interactions among

carnivorous plants, spiders, and toads. *Dryad Digital Repository*,
<http://doi:10.5061/dryad.m23g6>.

Jennings, D.E. & Rohr, J.R. (2011) A review of the conservation threats to carnivorous plants. *Biological Conservation*, **144**, 1356-1363.

Knop, E., Zund, J. & Sanders, D. (2014) Interactive prey and predator diversity effects drive consumption rates. *Oikos*, **123**, 1244-1249.

Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. (2009) Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia*, **161**, 837-847.

Lazzaro, X., Lacroix, G., Gauzens, B., Gignoux, J. & Legendre, S. (2009) Predator foraging behaviour drives food-web topological structure. *Journal of Animal Ecology*, **78**, 1307-1317.

Lee, C.T., Miller, T.E.X. & Inouye, B.D. (2011) Consumer effects on the vital rates of their resource can determine the outcome of competition between consumers. *American Naturalist*, **178**, 452-463.

Manicom, C., Schwarzkopf, L., Alford, R.A. & Schoener, T.W. (2008) Self-made shelters protect spiders from predation. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 14903-14907.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178-185.

Moon, D.C., Rossi, A.M., Depaz, J., McKelvey, L., Elias, S., Wheeler, E. & Moon, J. (2010) Ants provide nutritional and defensive benefits to the carnivorous plant *Sarracenia minor*. *Oecologia*, **164**, 185-192.

Nakano, S., Fausch, K.D. & Kitano, S. (1999) Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *Journal of Animal Ecology*, **68**, 1079-1092.

Punzo, F. (1995) An analysis of feeding in the oak toad, *Bufo quercicus* (Holbrook), (Anura: Bufonidae). *Florida Scientist*, **58**, 16-20.

Punzo, F. & Haines, L. (2006) Body size, duration of embryonic development, growth-rate, mother-offspring interaction, and diet in *Sosippus floridanus* Simon (Araneae: Lycosidae). *Bulletin of the British Arachnological Society*, **13**, 365-371.

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at: <http://www.r-project.org>

Relyea, R.A. (2002) Competitor-induced plasticity in tadpoles: consequences, cues, and connections to predator-induced plasticity. *Ecological Monographs*, **72**, 523-540.

Relyea, R.A. (2004) Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. *Ecology*, **85**, 172-179.

Rohr, J.R., Civitello, D.J., Crumrine, P.W., Halstead, N.T., Miller, A.D., Schotthoefer, A.M., Stenoien, C., Johnson, L.B. & Beasley, V.R. (2015) Predator diversity, intraguild predation, and indirect effects drive parasite transmission. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 3008-3013.

Rohr, J.R. & Palmer, B.D. (2013) Climate change, multiple stressors, and the decline of ectotherms. *Conservation Biology*, **27**, 741-751.

Rohr, J.R., Raffel, T.R., Romansic, J.M., McCallum, H. & Hudson, P.J. (2008) Evaluating the links between climate, disease spread, and amphibian declines. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17436-17441.

- Scharf, I., Nulman, E., Ovadia, O. & Bouskila, A. (2006) Efficiency evaluation of two competing foraging modes under different conditions. *American Naturalist*, **168**, 350-357.
- Schmitz, O.J. (2007) Predator diversity and trophic interactions. *Ecology*, **88**, 2415-2426.
- Schmitz, O.J. (2009) Effects of predator functional diversity on grassland ecosystem function. *Ecology*, **90**, 2339-2345.
- Schneider, C.A., Rasband, W.S. & Elicieri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671-675.
- Schnell, D.E. (2002) *Carnivorous Plants of the United States and Canada*, 2nd edition. Timber Press, Portland, OR.
- Sherman, P.M. (1994) The orb-web: an energetic and behavioral estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour*, **48**, 19-34.
- Schulze, W. & Schulze, E.-D. (1990) Insect capture and growth of the insectivorous *Drosera rotundifolia* L. *Oecologia*, **82**, 427-429.
- Skerratt, L.F., Berger, L., Speare, R., Cashins, S., McDonald, K.R., Phillott, A.D., Hines, H.B. & Kenyon, N. (2007) Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *Ecohealth*, **4**, 125-134.
- Steffan, S.A. & Snyder, W.E. (2010) Cascading diversity effects transmitted exclusively by behavioral interactions. *Ecology*, **91**, 2242-2252.
- Tanaka, K. (1989) Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. *Oecologia*, **81**, 459-464.
- Thoren, L.M., Tuomi, J., Kamarainen, T. & Laine, K. (2003) Resource availability affects investment in carnivory in *Drosera rotundifolia*. *New Phytologist*, **159**, 507-511.

- Thum, M. (1988) The significance of carnivory for the fitness of *Drosera* in its natural habitat. 1. The reactions of *Drosera intermedia* and *D. rotundifolia* to supplementary feeding. *Oecologia*, **75**, 472-480.
- Werner, E.E. & Anholt, B.R. (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist*, **142**, 242-272.
- Werner, E.E. & Hall, D.J. (1977) Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology*, **58**, 869-876.
- Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083-1100.
- Wilson, W.G., Osenberg, C.W., Schmitt, R.J. & Nisbet, R.M. (1999) Complementary foraging behaviors allow coexistence of two consumers. *Ecology*, **80**, 2358-2372.
- Zamora, R. (1990) Observational and experimental study of a carnivorous plant-ant kleptobiotic interaction. *Oikos*, **59**, 368-372.
- Zamora, R. & Gomez, J.M. (1996) Carnivorous plant-slug interaction: a trip from herbivory to kleptoparasitism. *Journal of Animal Ecology*, **65**, 154-160.

Table 1. Results from generalized linear models testing effects of toad presence/absence, spider web area and height, and prey abundance, on sundew number (Poisson error distribution), sundew trichome density, and sundew total trapping area (Gaussian error distributions). Interactions with $P > 0.1$ were dropped from final models (while respecting marginality). Shown are likelihood ratio χ^2 values with P values in parentheses, and all d.f. = 1.

Effect	Response		
	Sundew number	Trichome density	Total trapping area
Toad (presence/absence)	16.18 (< 0.001)	0.19 (0.664)	0.24 (0.625)
Web area	0.53 (0.465)	2.03 (0.154)	4.46 (0.035)
Web height	< 0.01 (0.991)	0.07 (0.792)	0.19 (0.662)
Prey abundance	3.06 (0.080)	2.05 (0.152)	1.11 (0.292)
Toad x web height	2.78 (0.096)	0.21 (0.649)	-
Toad x prey	6.07 (0.014)	0.13 (0.717)	4.81 (0.028)
Web area x web height	4.57 (0.033)	-	4.71 (0.030)
Web height x prey	-	0.13 (0.715)	-
Toad x web height x prey	-	5.02 (0.025)	-

Table 2. Results from generalized linear models testing effects of sundew total trapping area, toad presence/absence, and prey abundance on spider web height, and spider web area (Gaussian error distributions). Interactions with $P > 0.1$ were dropped from final models (while respecting marginality). Shown are likelihood ratio χ^2 values with P values in parentheses, and all d.f. = 1.

Effect	Response	
	Web height	Web area
Total sundew trapping area	0.74 (0.390)	4.92 (0.027)
Toad (presence/absence)	16.71 (< 0.001)	4.59 (0.032)
Prey abundance	0.21 (0.647)	24.25 (< 0.001)
Trapping area x toad	-	2.86 (0.091)
Trapping area x prey	-	1.45 (0.229)
Toad x prey	4.01 (0.045)	0.30 (0.587)
Trapping area x toad x prey	-	5.16 (0.023)

Table 3. Results from generalized linear model

testing effects of spider web area, sundew total

trapping area, and prey abundance on toad growth

(Gaussian error distribution). Interactions with $P >$

0.1 were dropped from final models (while

respecting marginality). Shown are likelihood ratio

χ^2 values with P values in parentheses, and all d.f.

= 1.

Effect	Response
	Toad growth
Web area	9.00 (0.003)
Web height	0.82 (0.365)
Total sundew trapping area	3.66 (0.056)
Prey abundance	31.96 (< 0.001)

Figure legends

Figure 1. Effects of toads, spiders, and prey abundance, on the number of sundews. Grey circles/lines indicate absence of toads (a), and black circles/lines indicate presence of toads (a) or spiders (b).

Figure 2. Effects of toads, spiders, and prey abundance on the difference in sundew trichome density (quantified at the beginning and end of the experiment). Three-way interaction plots show the interaction between web height and prey abundance (cross-sections represent 10th,

50th, and 90th quantiles) on the difference in sundew trichome density, in the absence (a) and presence (b) of toads (toad x web height x prey: $P = 0.025$).

Figure 3. Effect of toads on spider web height. Box plot shows median (horizontal line within box) and interquartile range (box), and whiskers extend to the lower and upper outermost data points.

Figure 4. Effects of toads, prey abundance, and sundews on spider web area. Three-way interaction plots show the interaction between prey and sundew trapping area (cross-sections represent 10th, 50th, and 90th quantiles) on spider web area, in the absence (a) and presence (b) of toads (total trapping area x toad x prey: $P = 0.023$).

Figure 5. Effects of spiders (a), and prey abundance (b), on toad growth. Grey circles/lines indicate absence of spiders (b), and black circles/lines indicate presence of spiders (a,b). Dashed line represents the overall fit for the main effect of prey.

Figure 6. Qualitative, heuristic representation of interactions among a guild of generalist arthropod predators at low (a) and high (b) levels of prey abundance. Arrows indicate direction and relative magnitude of effects (solid arrows represent positive effects and dashed arrows represent negative effects, and thickness is proportional to magnitude of effect). Clockwise from the top: pink sundew (*Drosera capillaris*), funnel-web-building wolf spider (*Sosippus floridanus*), and oak toad (*Anaxyrus quercicus*). Note how the arrows are, in general, much thicker when prey are limited compared with when they are abundant, indicating stronger effects of competitors. Photo credits: Christopher V. Anderson (Brown University) and David E. Jennings (University of Maryland).



