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# Evidence for competition between carnivorous plants and spiders

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Several studies have demonstrated that competition between disparate taxa can be important in determining community structure, yet surprisingly, to our knowledge, no quantitative studies have been conducted on competition between carnivorous plants and animals. To examine potential competition between these taxa, we studied dietary and microhabitat overlap between pink sundews (*Drosera capillaris*) and wolf spiders (Lycosidae) in the field, and conducted a laboratory experiment examining the effects of wolf spiders on sundew fitness. In the field, we found that sundews and spiders had a high dietary overlap with each other and with the available arthropod prey. Associations between sundews and spiders depended on spatial scale: both sundews and spiders were found more frequently in quadrats with more abundant prey, but within quadrats, spiders constructed larger webs and located them further away from sundews as the total sundew trapping area increased, presumably to reduce competition. Spiders also constructed larger webs when fewer prey were available. In the laboratory, our experiment revealed that spiders can significantly reduce sundew fitness. Our findings suggest that members of the plant and animal kingdoms can and do compete.

**Keywords:** competition; *Drosera capillaris*; Lycosidae; plant–animal interactions

## 1. INTRODUCTION

Competition is a fundamental ecological process in determining the structure of communities. Historically, competition was assumed to be strongest between closely related taxa, an idea dating back to Darwin (1859) and persisting into the recent past (Connell 1983; Schoener 1983; Gurevitch *et al.* 1992). For example, out of 112 interspecific competition studies in terrestrial and freshwater ecosystems reviewed in Schoener (1983) and Gurevitch *et al.* (1992), the vast majority of those involving animals were conducted on closely related taxa, while only one study focused on species from different kingdoms (figure 1). Nonetheless, competition between disparate taxa is frequently found to be strong when examined (Brown & Davidson 1977; Schoener & Spiller 1987; Morin *et al.* 1988; Mokany & Shine 2003). These findings suggest that ecologists might be missing important competitive interactions among distantly related species, or those that have few morphological similarities.

To the best of our knowledge, no previous studies have quantified competitive interactions between the plant and animal kingdoms, although carnivorous plants and animals seem likely to compete for arthropod prey. Sundews (Droseraceae: *Drosera*) are carnivorous plants that catch prey using sticky mucilage secreted from glands on the tips of modified trichomes found on their leaves, and research suggests that they are generalist arthropod predators (Van Achterberg 1973; Thum 1986; Porch 1989; Verbeek & Boasson 1993). Spiders are

candidate animal competitors with carnivorous plants because they are abundant, have considerable spatial overlap with carnivorous plants and are often generalist arthropod predators that can reduce arthropod populations (Riechert & Bishop 1990; Buddle 2002; Wise 2004).

We conducted a field census to quantify the dietary and microhabitat overlap of pink sundews (*Drosera capillaris*) and funnel-web-building wolf spiders (Lycosidae: *Sosippus floridanus*) and the plasticity of their phenotypic traits in the presence and absence of one another—all of which are potentially indicative of competition (Schoener 1983; Goldberg & Barton 1992; Agrawal 2001; Callaway *et al.* 2003). Additionally, we conducted a laboratory experiment to determine whether wandering wolf spiders (Lycosidae: *Rabidosa rabida*) could negatively impact growth and fitness of sundews by depleting the availability of a common prey.

*Drosera capillaris* is a small perennial carnivorous plant commonly found in mesic habitats throughout the south-eastern USA. This species forms basal leaf rosettes with an average diameter of 3.5 cm, reaching up to 7 cm (Schnell 2002). *Sosippus floridanus* is found in webs on or close to the ground in scrub and mesic habitats throughout Florida and southern Georgia (Brady 1972; Muma 1973; Punzo & Haines 2006), while *R. rabida* inhabits grasslands and open woodlands in the central and eastern USA (Brady & McKinley 1994). Both species mature at approximately 2 cm in length (Brady 1972; Brady & McKinley 1994; Punzo & Haines 2006) and along with various other spiders are consistently found on and around sundews (D. Jennings 2008, unpublished data).

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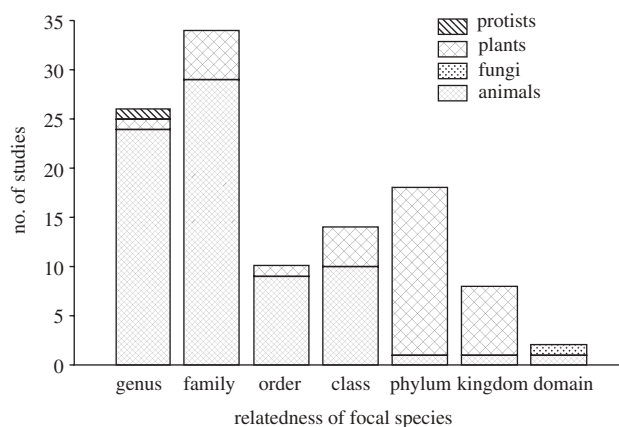


Figure 1. The relatedness of focal animal, fungal, plant and protist species from terrestrial and freshwater interspecific competition studies considered by Schoener (1983) and Gurevitch *et al.* (1992). Each level of classification indicates that all focal species from the study in question were within that classification (e.g. if two species were from different orders but within the same class, the study would be recorded under 'Class'). We used the lowest level of classification possible for all interactions, and we did not double-count classifications for any studies.

We hypothesized that sundews and spiders compete for arthropod prey, generating the following six predictions: (i) because both sundews and spiders use relatively opportunistic and passive prey capture mechanisms, they will be generalist arthropod predators with considerable dietary overlap; (ii) on a large spatial scale, sundews and spiders will be positively associated with each other, because both will be more abundant where prey resources are abundant, but (iii) on a small spatial scale, spiders will avoid building webs near sundews to avoid using the same prey resources. To compensate for competition for prey resources, (iv) spider web area will be positively correlated with sundew trapping area, and (v) sundew trichome density will be positively correlated with spider density. Finally, (vi) sundew fitness will be lower in the presence of spiders.

## 2. MATERIAL AND METHODS

### (a) *Censusing procedure*

This research was conducted at Brooker Creek Headwaters Nature Preserve (BCH) in Odessa, Florida (28°08.32' N, 82°33.32' W), and the University of South Florida Ecological Research Area (ERA) in Tampa, Florida (28°04.24' N, 82°23.44' W). Two 20 m transects (30 m apart at BCH and 200 m apart at the ERA) were surveyed at each study site, and 0.5 × 0.5 m quadrats were censused every 2 m along the transects. These transects were surveyed approximately once every two weeks between 1 July and 10 September 2008 at BCH, and between 22 September and 10 November 2008 at the ERA, for a total of 16 transect surveys and 160 quadrat censuses. All censuses were conducted between 07.00 and 11.00 h. Within each quadrat, the following data were recorded: number of sundews, leaves per sundew, *S. floridanus* webs, web area and prey per web. If applicable, we also recorded distance from webs to the nearest sundew. One leaf was also removed from up to 10 randomly selected sundews per quadrat for subsequent analysis in the laboratory.

### (b) *Dietary selectivity and overlap*

To sample arthropod availability, we used 4 × 4 cm sticky traps with no attractants (Olson Products, Medina, OH, USA). These were set approximately 0.5 cm off the ground, the height at which sundew leaves and *S. floridanus* webs are typically found in these locations (D. Jennings 2008, unpublished data). For each quadrat, one sticky trap was placed at least 15 cm away from sundews and webs, and when present, one sticky trap was placed adjacent to a randomly selected sundew and/or a web, and thus there were up to three sticky traps per quadrat. Traps were left out for 24 h. Arthropods caught were identified to the order level or below, and measured to the nearest 0.1 mm. We then estimated arthropod biomass using the general formula derived by Rogers *et al.* (1976):

$$W = 0.0305L^{2.62},$$

where  $W$  represents the mass in milligrams and  $L$  represents the length in millimetres.

Sundew leaves were examined under a dissecting microscope to record prey items. Prey items were identified to order level or below and measured to the nearest 0.1 mm. To reduce the likelihood of damaging or losing prey items through destructive web sampling, we recorded the number, size and order of prey caught in webs or chelicerae in the field using a ×16 hand lens. The hand lens, however, did not provide adequate magnification to detect many smaller arthropods, such as Collembolans. To adjust for this, we examined 24 randomly selected sticky traps from the quadrat censuses and identified and measured arthropods on them using both the ×16 hand lens and the dissecting scope and adjusted the spider diet for these missed prey items. In no case did including these missed prey items change the results, so we present only those results that included these prey items.

### (c) *Phenotypic plasticity in leaf and web traits*

After being examined for prey, sundew leaves were photographed under a dissecting microscope to count the number of trichomes per leaf and to calculate individual leaf capture area. All webs were photographed with a 30 cm ruler, and leaf capture area and web area were calculated using SIGMA SCAN PRO 4 (SPSS Inc., Chicago, IL, USA). For each quadrat, total trapping area was estimated by multiplying the mean capture area per leaf by the mean number of leaves per sundew by the total number of sundews.

### (d) *Statistical analyses for field census*

To determine whether sundews and spiders track arthropod prey in the environment, we used the generalized linear model to evaluate whether spider abundance (Poisson error and log link) and sundew presence or absence (binomial error and logit link) could be predicted by arthropod biomass in quadrats (cubed-root transformed). If variation in arthropod biomass is high at large spatial scales (among quadrats) but low at small spatial scales (within quadrats), we would expect the two species to co-occur at large spatial scales in order to track prey biomass, but to avoid one another at small spatial scales. To evaluate the level of variation in arthropod biomass within versus among quadrats, we compared the among-quadrat variation in arthropod biomass with the biomass variation among the three types of sticky traps (next to web or sundew, away from both) within quadrats using variance partitioning (Gotelli & Ellison 2004). To assess whether sundews or spiders were depressing local

arthropod resources, we conducted a one-way ANOVA, blocking by quadrat, to compare arthropod biomass among traps directly next to sundews, directly next to webs and away from both. Data were log-transformed when necessary to meet the assumption of the parametric analyses.

Both co-occurrence and dietary overlap were analysed using  $\chi^2$ -tests. Additionally, we analysed co-occurrence, and dietary overlap and selectivity, using EcoSIM (Gotelli & Entsminger 2001). To test for sundew and spider co-occurrence, we calculated a *C*-score (Stone & Roberts 1990) from observed data (presence/absence of each species within each quadrat) and compared it with *C*-scores obtained from 5000 randomly generated matrices (i.e. a Monte Carlo permutation test). Dietary overlap was estimated using Pianka's (1973) index (PI), which generates a value between 0 (complete segregation) and 1 (complete overlap). We used the 'RA3' algorithm, which retains the niche breadth of each species but randomizes the resource states that are actually used, and also incorporated our arthropod availability data into the resource-state matrix. The observed overlap was then compared with the indices from 1000 randomly generated matrices to test for the probability that it would have been generated by chance alone.

We were also interested in how sundew trapping area, arthropod biomass and other webs influenced the distance that spiders constructed their webs from the nearest sundew. However, measuring the distance of webs to the nearest sundew within a quadrat has clear limitations regarding the inferences that can be made from the results. For example, as the density and/or size of sundews per quadrat increases, the observed distance of webs will ultimately decrease because more of the space within the quadrat will be occupied by sundews. Therefore, we calculated the expected distance of a spider web from the nearest sundew at a given sundew density using a simulated null model in the statistical software R 2.8.1, available at [www.r-project.org](http://www.r-project.org) (R Development Core Team 2008). For a given number of sundews, positions of sundews and a single spider web were randomly assigned within a simulated 50 × 50 cm plot. Radii of sundews and of the spider web were selected from normal distributions, with means and standard deviations calculated from the observed dataset (sundews: mean = 0.94 cm, s.d. = 0.54 cm; spider webs: mean = 2.76 cm, s.d. = 1.15 cm). The distance from the edge of each spider web to the edge of the nearest sundew (0 if they overlapped) was then calculated, and this was repeated 10 000 times for each number of sundews to obtain an average (expected) distance at that sundew density.

We used path analysis to evaluate the effects of sundew trapping area, arthropod biomass (mean of sticky traps) and other webs on mean web area and the observed minus expected distance of webs from sundews. We chose to use path analysis because it allowed us to evaluate both the indirect and direct effects that each variable has on the focal response variable. All variables were log-transformed except for the observed minus expected web distance, and we used a least-trimmed squares regression approach and estimated regression coefficients using maximum-likelihood estimation (Gotelli & Ellison 2004). The significance of each path was evaluated by comparing the  $\chi^2$ -value of the full model with that of the model excluding the given path. Given that sundews are stationary, we assumed that they could depress local arthropod biomass and be influenced by local arthropod biomass (bidirectional path) and affect

spider traits. Conversely, given that spiders are mobile and thus more transient than sundews, we assumed that spider webs would not affect the traits of sundews or arthropod biomass at the scale of the quadrat. Path analyses were conducted using the SEPATH module of STATISTICA 8.0 (StatSoft Inc., Tulsa, OK, USA).

#### (e) *Laboratory experiment*

In 2004, immature sundews in winter dormancy and *R. rabida* nymphs were collected from a bog in Liberty County, Florida (30°02.32' N, 85°00.11' W), and transported to the University of Kentucky. In the laboratory, 40 glass terraria (21 l) with glass tops were filled with soil from the Florida bog to a depth of 3 cm, and six young sundews (approximately 1 cm diameter with two to eight leaves) were planted in each terrarium. Eight shelves (spatial blocks) each held five terraria, and four florescent bulbs were positioned 5 cm above each terrarium to provide a range of light wavelengths. We simulated winter dormancy with a photoperiod of 9 L : 15 D and temperatures of 15°C from 5 January to 1 February 2004 and again from 1 November 2004 to 1 February 2005. During all other times, a photoperiod of 14 L : 10 D and temperatures of 24°C were maintained (until 1 November 2005).

The 40 terraria were divided into five treatments (spider present + high food; spider present + low food; spider absent + high food; spider absent + low food; spider absent + no food) with eight replicates per treatment. Low- and high-food terraria received six and 24 pinhead crickets (2 mm in length) twice per week, respectively. By 1 June 2004, one large (12 mm body length) spider nymph, without stored sperm, was added to each of the 16 terraria with spiders. On 1 October, we stopped supplying crickets and removed the spiders. For each sundew, on five occasions from September 2004 to June 2005, we counted the number of leaves, flower stalks, flowers per stalk and seeds. We included seed production from the 2005 growing season as sundew reproduction can be influenced by the previous growing season (Thum 1989; Krafft & Handel 1993).

#### (f) *Statistical analyses for laboratory experiment*

Because we lacked a complete factorial design (spider + no food treatment was not possible), statistical analyses involved a two-step, hierarchical approach. We first tested for an effect of spider and a spider × food interaction by ignoring the no spider + no food treatment. This created a complete 2 × 2 factorial design. The second step was to test for the effect of food level (a continuous predictor) by using the three food treatments and controlling for the effect of spiders. Analyses for both steps involved the use of the general linear model. We first tested for multivariate effects using number of flowers, stalks and seeds as the responses, and if significant, we then evaluated the univariate effects. These were repeated-measures analyses, where the repeated-measures variables were the five dates when data were collected.

### 3. RESULTS

#### (a) *Field census*

For all analyses, the effect of site did not interact with any factors and was non-significant when arthropod biomass was included as a covariate in the statistical model because the sites differed in arthropod biomass. Consequently, we excluded site from the statistical models in favour of arthropod biomass, which accounted for more variation.

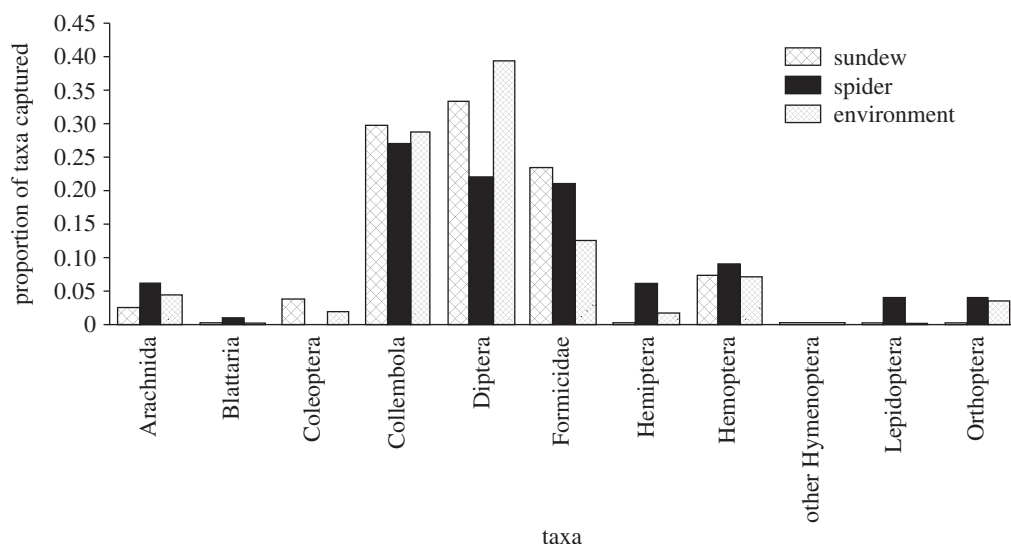


Figure 2. The relative proportions of arthropods caught by *D. capillaris*, *S. floridanus* and from the environment (sticky traps).

### (b) Dietary selectivity and overlap: prediction i

A total of 565 arthropods were quantified from 294 sticky traps, and there were no significant differences in their biomass among traps adjacent to sundews, adjacent to *S. floridanus* webs or located at least 15 cm from both ( $F_{2,88} = 1.12$ ,  $p = 0.331$ ). Dietary analyses of sundews and *S. floridanus* were calculated from 665 leaves and 45 webs. Eighty-one prey items were located on sundew leaves (mean = 1.4 mm, range = 0.1–3.6 mm, s.d. = 0.7 mm) and 54 prey were identified on *S. floridanus* webs. We were able to record prey size for only 33 *S. floridanus* prey items (mean = 3.13 mm, range = 1.1–8.7 mm, s.d. = 1.9 mm) because the remaining prey had been partly consumed or damaged.

The results generally supported our first prediction, that both sundews and spiders would be generalist arthropod predators with considerable dietary overlap. Orders Diptera and Collembola, and family Formicidae, were the most frequently captured taxa by both sundews (33.3, 29.6 and 23.5%, respectively) and *S. floridanus* (22.1, 26.5 and 20.6%, respectively; figure 2). When estimating dietary selectivity, we included only arthropods captured on sticky traps within the size range of prey that the sundews (0.1–3.6 mm) and *S. floridanus* catch (less than 16 mm in size because spiders generally eat prey 50–80% smaller than themselves; Nentwig 1987). The overlap of arthropods available in the environment and arthropods captured by sundews (0.93 PI) and *S. floridanus* (0.92 PI) was greater than expected by chance ( $p = 0.005$  and  $p = 0.030$ , respectively). As predicted, sundews and *S. floridanus* diets exhibited significant overlap ( $\chi^2_5 = 6.99$ ,  $p = 0.22$ ; 0.76 PI,  $p = 0.033$ ) within the prey size range of 0.1–3.6 mm, which included 100 and 79 per cent of the sundew and spider prey, respectively.

### (c) Spatial associations on a large spatial scale: prediction ii

The results supported our second prediction, that on a large spatial scale, sundews and spiders would be positively associated with each other because both would be where prey were abundant. At the level of the quadrat, co-occurrence of sundews and *S. floridanus* was highly

significant ( $\chi^2_1 = 10.78$ ,  $p < 0.001$ ). Specifically, in 28 of the 35 quadrats in which *S. floridanus* was present, sundews were also present. The *C*-score obtained from the observed data was significantly different from the mean *C*-score obtained from the simulated indices (standardized effect size =  $-2.95$ ,  $p < 0.001$ ), indicating that these species significantly co-occurred.

As predicted, sundews and *S. floridanus* significantly tracked arthropod biomass because plots with more arthropods were more likely to have sundews (model deviance = 1.29, coefficient = 1.400, s.e. = 0.490,  $\text{Wald}_{1,158} = 8.17$ ,  $p = 0.004$ ) and *S. floridanus* (model deviance = 0.89, coefficient = 0.850, s.e. = 0.411,  $\text{Wald}_{1,158} = 4.28$ ,  $p = 0.039$ ). This probably accounts for the positive covariance of these two species among quadrats. In fact, variation among quadrats accounted for 27 per cent of the variation in arthropod biomass, whereas variation within a quadrat among the three sticky traps accounted for only 2 per cent of the variation in arthropod biomass. These results indicate considerable arthropod heterogeneity among quadrats, but a relatively homogeneous distribution of arthropods within quadrats. This analysis could be conducted only on plots with sundews and spiders because they were the only plots with three sticky traps. If we could have conducted the variance partitioning analyses on plots with and without sundews or *S. floridanus*, we would have seen even greater among-quadrat variation in arthropod biomass.

### (d) Spatial associations on a small spatial scale: prediction iii

The results supported our third prediction, that on a small spatial scale, spiders would avoid building webs near sundews to reduce using the same prey resources. Within each quadrat, *S. floridanus* located their webs further away from sundews as the total sundew trapping area increased, representing a deviation from the expected distance values obtained from the null model (figure 3a). Mean arthropod biomass per sticky trap, and the presence of other webs within the quadrat, did not significantly affect the distance that *S. floridanus* located their webs from sundews (figure 3a).

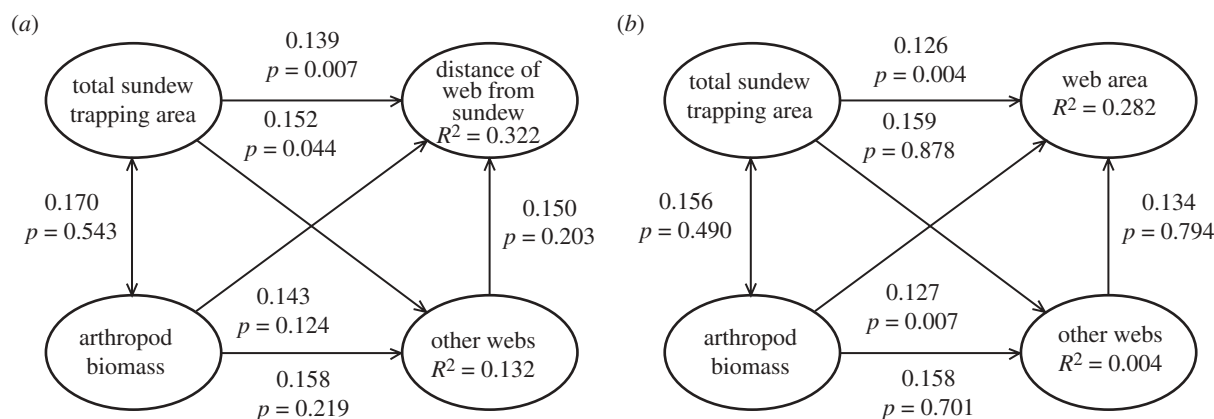


Figure 3. Path analysis models using (a) distance of web to nearest sundew and (b) web area, as the response variable. None of the indirect effects were significant for the models and therefore they are not displayed. Shown are standardized coefficients, probability values for each path and  $R^2$  values for each submodel.

#### (e) Phenotypic plasticity in web traits: prediction iv

Web area was positively correlated with total sundew trapping area (figure 3b), consistent with competition and in support of our fourth prediction. *Sosippus floridanus* webs had a mean area of 28 cm<sup>2</sup> (range = 3.7–98.6 cm<sup>2</sup>, s.d. = 23 cm<sup>2</sup>), and web area was negatively correlated with mean arthropod biomass on sticky traps (figure 3b). However, there was no significant association between web area and the presence of other webs (figure 3b).

#### (f) Phenotypic plasticity in sundew traits: prediction v

We found no support for our fifth prediction, that sundew trichome density would be positively associated with spider density or traits (all  $p > 0.05$ ), probably because spiders are transient and do not live near a given sundew long enough to induce phenotypic changes. In addition, arthropod biomass on sticky traps was not associated significantly with the mean number of leaves per sundew ( $\beta = -0.017$ , s.e. = 0.075,  $F_{1,85} = 0.05$ ,  $p = 0.823$ ), mean number of trichomes per individual leaf ( $\beta = 0.081$ , s.e. = 0.063,  $F_{1,84} = 1.68$ ,  $p = 0.199$ ) or mean trichome density per sundew leaf ( $\beta = -0.025$ , s.e. = 0.055,  $F_{1,83} = 0.020$ ,  $p = 0.653$ ). Mean number of trichomes per individual sundew leaf was 68.7 (range = 14–143, s.d. = 24.7), and mean trichome density per sundew leaf was 139.2 cm<sup>-2</sup> (range = 21.8–1300 cm<sup>-2</sup>, s.d. = 147.8 cm<sup>-2</sup>).

#### (g) Laboratory experiment: prediction vi

Our laboratory results supported our sixth prediction, that spider presence would reduce sundew fitness. *Rabidosia rabida* had an adverse multivariate effect on sundew fitness (Wilk's  $F_{3,27} = 4.14$ ,  $p = 0.015$ ) that was independent of food level (spider  $\times$  food: Wilk's  $F_{3,27} = 0.53$ ,  $p = 0.668$ ; figure 4a). *Rabidosia rabida* reduced the production of flower stalks ( $F_{1,29} = 13.10$ ,  $p = 0.001$ ), flowers ( $F_{1,29} = 7.87$ ,  $p = 0.009$ ) and seeds ( $F_{1,29} = 4.18$ ,  $p = 0.049$ ; figure 4a). Cricket additions had a significant, positive multivariate effect on sundew fitness (Wilk's  $F_{3,35} = 6.01$ ,  $p = 0.002$ ; figure 4b), increasing flower stalks ( $F_{1,37} = 11.81$ ,  $p = 0.001$ ), flowers ( $F_{1,37} = 18.94$ ,  $p < 0.001$ ) and seeds ( $F_{1,37} = 8.51$ ,  $p = 0.006$ ; figure 4b).

## 4. DISCUSSION

The results from our field census indicate that both sundews and *S. floridanus* are generalist predators, consuming arthropods in proportion to their availability in the environment, consistent with previous qualitative findings (Porch 1989; Punzo & Haines 2006). More importantly, for the question of whether these species compete, the diets of these two species had a high overlap, which might lead to competition for shared prey.

The high dietary overlap between sundews and *S. floridanus* might be explained by the passive trapping mechanisms used by each species and the similar heights at which the sundew leaves and webs are set above the ground. Some pitcher plants release certain chemicals that are thought to attract prey (Moran 1996; Di Giusto *et al.* 2008), and it has been implied that the red pigmentation common to many carnivorous plants might increase rates of prey capture (Schaefer & Ruxton 2008). In the present study, sundews did not appear to attract any arthropod taxa in particular because the diet matched the arthropod prey in the environment, and generalist diets appear to be common among carnivorous plants (Ellison & Gotelli 2009). However, the results could change with a higher taxonomic resolution of prey.

The spatial associations between sundews and *S. floridanus* were largely dependent on scale. At a large spatial scale (i.e. among quadrats), there was a positive correlation between the two species, yet at a smaller spatial scale (i.e. within each quadrat), there was a negative correlation between them. Sundews are sessile predators that are likely to have more specific abiotic requirements (particularly light and water) than the relatively mobile *S. floridanus*, and thus the patterns at small spatial scales are perhaps best explained by assuming spiders respond to sundews and not vice versa. At the scale of the entire transects, *S. floridanus* were predicted to preferentially select areas of high prey abundance, a behaviour that has been demonstrated in a number of other spider taxa (Sunderland *et al.* 1986; Harwood *et al.* 2001). However, at the smaller scale of each individual quadrat, *S. floridanus* were predicted to locate their webs further away from sundews to reduce competition for shared prey resources. In support of these predictions, the variance partitioning results suggested that positive spatial covariance between sundews and *S. floridanus* on

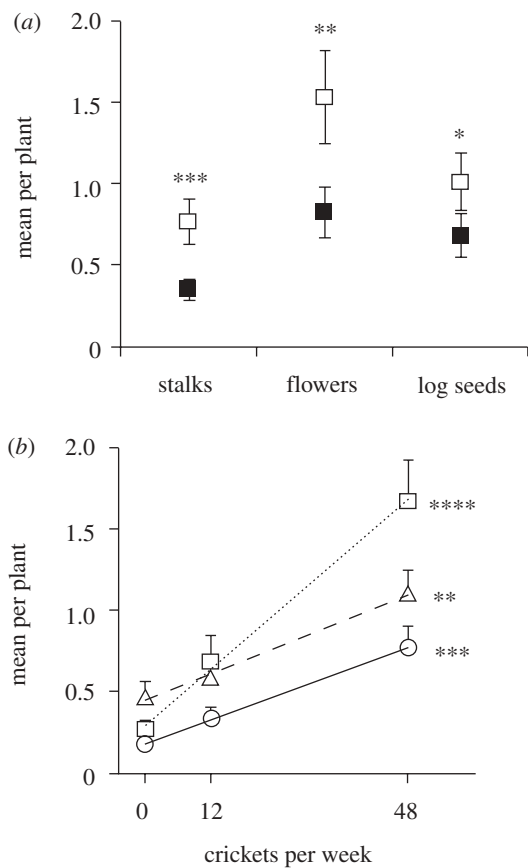


Figure 4. (a) Effects of spider (presence or absence) and (b) food level (0, 12 or 48 crickets per week) on the number of stalks, flowers and seeds produced per sundew. There was no interaction between the spider and food treatments, so only main effects are shown. In (b), we provide best-fit lines, and asterisks represent the significance of the relationship between the food level (continuous predictor) and the response variable. Shown are means and standard errors;  $n = 8$ . \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.005$ , \*\*\*\* $p < 0.001$ . (a) Open boxes, spider absent; filled boxes, spider present. (b) Open circles, stalks; open squares, flowers; open triangles, log seeds.

a large spatial scale (among quadrats) was driven by the two species being found where there was a high prey biomass, whereas the two species had negative spatial covariance within quadrats, probably owing to niche partitioning in light of the relatively homogeneous distribution of prey at this smaller scale.

Our observation that *S. floridanus* increased web area in response to a putative competitor contrasts with a previous finding that spiders reduced the area of webs they constructed when there were higher densities of conspecific competitors, presumably because of interference competition (Harwood & Obrycki 2005). Interference competition is unlikely to occur between *S. floridanus* and sundews, and we found no evidence that small *S. floridanus* were consumed by the carnivorous plants. Therefore, in the absence of interference competition with sundews, *S. floridanus* near sundews might invest more resources into web construction to mitigate the effects of exploitative competition with sundews. Spiders have also been shown to increase web area in response to reduced prey abundance (Sherman 1994), suggesting that prey resources were limited in the field.

Some carnivorous plants, such as pitcher plants (Ellison & Gotelli 2002), bladderworts (Englund & Harms 2003) and different species of sundew (Thorén *et al.* 2003), have been found to reduce their investment in carnivory (e.g. produce fewer traps) in response to increased nutrient levels. Hence, it was surprising that trichome density per leaf area was not negatively associated with the arthropod biomass from sticky traps. Further, there was no evidence that *S. floridanus* affected phenotypic traits of sundews at the scales studied, possibly because *S. floridanus* are transient in comparison to sundews and are therefore unlikely to remain close to a focal sundew on a small spatial scale. Additionally, effects on phenotypic traits might not have been detected if competition for prey was intense at a large spatial scale (i.e. among quadrats). Under such conditions, all of the sundews we observed might have been responding to competitive interactions of similar strength, and therefore no difference between them would have been detected. Although the spatial scale of our survey seemed too small to detect any detrimental effects of *S. floridanus* on sundews, our laboratory experiment supported the hypothesis that spiders adversely affect the fitness of sundews. Specifically, the presence of *R. rabida* in terraria resulted in a reduced number of flower stalks, flowers, and seeds produced by the sundews. Furthermore, as food levels increased, sundews produced more seeds, and grew more leaves. Sundews are known to invest nutrients obtained from prey into reproductive structures (Krafft & Handel 1993; Hanslin & Karlsson 1996) and *R. rabida* were observed consuming many of the crickets offered during feedings. Thus, it appears that *R. rabida* reduced arthropod prey causing the decrease in sundew fitness.

## 5. CONCLUSIONS

Our field census found a high dietary overlap between these two predatory species, and in the presence of greater total sundew trapping area, *S. floridanus* located their webs further away from sundews and increased the area of their webs. Additionally, our laboratory experiment demonstrated that *R. rabida* can negatively affect sundew fitness by depriving them of nutrients normally obtained from prey. All of this evidence is consistent with competition between the plant and animal kingdoms, but more work will be necessary to fully understand the implications of these findings. For example, we predict that competitive interactions between sundews and spiders will also reduce spider fitness, and that any competitive effects on sundew and spider traits and fitness will be stronger at lower arthropod prey densities. Future work should test these predictions using field experiments with manipulations of sundew, spider and arthropod prey densities. Quantifying the shapes of sundew and spider functional responses as a function of resource availability, and determining the fitness consequences of different traits and competitive interactions, will then allow generation of parameters for predictive population- and community-level models.

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