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Deer herbivory reduces web-building spider abundance by simplifying forest vegetation structure

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Indirect effects are a common feature of ecological systems, arising when one species affects interactions among two or more other species. We examined how browsing by white-tailed deer (*Odocoileus virginianus*) affected the abundance and composition of a web-building spider guild through their effects on the structure of the ground and shrub layers of northern hardwood forests. We examined paired plots consisting of deer-free and control plots in Pennsylvania and Wisconsin. We recorded the abundance of seven types of webs, each corresponding to a family of web-building spiders. We quantified vegetation structure and habitat suitability for the spiders by computing a web scaffold availability index (WSAI) at 0.5 m and 1.0 m above the ground. At Wisconsin sites, we recorded prey availability. Spider webs were twice as abundant in deer-free plots compared to control plots, while WSAI was 7-12 times greater in deer-free plots. Prey availability was also higher in deer-free plots. With the exception of funnel web-builders, all spider web types were significantly more abundant in deer-free plots. Both deer exclusion and the geographic region of plots were significant predictors of spider community structure. In closed canopy forests with high browsing pressure, the low density of tree saplings and shrubs provides few locations for web-building spiders to anchor webs. Recruitment of these spiders may become coupled with forest disturbance events that increase tree and shrub recruitment. By modifying habitat structure, deer indirectly modify arthropod food web interactions. As deer populations have increased in eastern North America over the past several decades, the effects of deer on web-building spiders may be widespread throughout the region.

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Deer herbivory reduces web-building spider abundance by simplifying forest vegetation structure

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ABSTRACT

Indirect effects are a common feature of ecological systems, arising when one species affects interactions among two or more other species. We examined how browsing by white-tailed deer (*Odocoileus virginianus*) affected the abundance and composition of a web-building spider guild through their effects on the structure of the ground and shrub layers of northern hardwood forests. We examined paired plots consisting of deer-free and control plots in Pennsylvania and Wisconsin. We recorded the abundance of seven types of webs, each corresponding to a family of web-building spiders. We quantified vegetation structure and habitat suitability for the spiders by computing a web scaffold availability index (WSAI) at 0.5 m and 1.0 m above the ground. At Wisconsin sites, we recorded prey availability. Spider webs were twice as abundant in deer-free plots compared to control plots, while WSAI was 7-12 times greater in deer-free plots. Prey availability was also higher in deer-free plots. With the exception of funnel web-builders, all spider web types were significantly more abundant in deer-free plots. Both deer exclusion and the geographic region of plots were significant predictors of spider community structure. In closed canopy forests with high browsing pressure, the low density of tree saplings and shrubs provides few locations for web-building spiders to anchor webs. Recruitment of these spiders may become coupled with forest disturbance events that increase tree and shrub recruitment. By modifying habitat structure, deer indirectly modify arthropod food web interactions. As deer populations have increased in eastern North America over the past several decades, the effects of deer on web-building spiders may be widespread throughout the region.

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INTRODUCTION

Indirect effects—direct interaction of two species that affect a third species (Wooten 1994)—often arise due to the actions of dominant species, keystone species, or ecosystem engineers (Jones et al. 1994; Pringle 2008). Menge (1995) reported that indirect interactions account for ~40% of the change in the abundance and percent cover of species after experimental manipulations of rocky intertidal food webs. These indirect effects occurred coincident with or shortly after direct effects are observed (Menge 1997). Despite their importance, indirect effects can be difficult to detect, particularly in short-term studies (Hamilton 2000). Moreover, indirect effects can be conflated with direct effects and therefore overlooked entirely (Wooten 1994). Here, we examine the indirect effects of a large mammalian generalist herbivore on the structure of a web-building spider guild.

White-tailed deer (*Odocoileus virginianus*, hereafter deer) in North America have increased in abundance in recent decades throughout temperate zone (Crête 1999; Ripple et al. 2010; Bressette et al. 2012). In the early 20th century, deer were rare or absent from most of the United States (Leopold et al. 1947). Now, deer abundance presents several management problems in much of the United States (Warren 1997; Côté et al. 2004) including much of Wisconsin and Pennsylvania. Through selective feeding, deer directly affect forest communities by altering species composition and vegetation structure (Côté et al. 2004; Takatsuki 2009). These direct effects have the potential to indirectly alter the abundance of co-occurring animal species (Rooney 2001; Rooney and Waller 2003; Sakai et al. 2012). For example, through resource competition, deer can negatively affect the abundance of small granivorous mammals. McShea (2000) observed that in years of low food (acorn) abundance, deer reduced the abundance of two common species of rodent by 50%. Similarly elk (*Cervus elaphus*) reduced vegetation cover, thereby causing a decline in the abundance of woodrats, voles, and two species of mice (Parsons et al. 2013). Additionally, deer herbivory can alter resource quality for other herbivores by altering plant species composition, or increasing secondary metabolites of particular species (Vourc'h et al. 2001; Nuttle et al. 2011). A reduction in vegetation cover and vertical complexity alters habitat for birds and other flying species (Rooney 2001). The removal of deer can lead to an increase of vertical structure and ground cover. In studies where deer are removed, ground and shrub-nesting birds increase in abundance (McShea and Rappole 2000; Holt et al. 2011).

The indirect effect of deer on arthropods may be particularly strong because many arthropod species are direct competitors with deer for vegetation as food but also depend on this vegetation for habitat (Stewart 2001). Indeed, deer browsing reduces the three dimensional structure of the ground and shrub layers of forest habitats (Habek and Schultz 2015). This vegetation structure is important for web-building spiders, which use woody and herbaceous surfaces as anchoring points for their webs and these anchoring points serve as a limiting resource for web-builders (Rypstra 1983; Uetz 1991; Gómez et al. 2016). Miyashita et al. (2004) report that the abundance and richness of web-building spiders increased in areas without deer browsing. They attributed this to an increase in vegetation cover, or more specifically, physical structures for anchoring webs. In a follow-up study, Takada et al. (2008) found that web-building spiders were more vulnerable than non-web builders to deer browsing.

In this study, we determined whether deer affected assemblages of web-building spiders. We examined web-building spider assemblages with and without deer, using a paired exclosure-control design in two regions of the northern hardwoods forest of the U.S.—the Allegheny

Plateau of Pennsylvania and the Northern Highlands of Wisconsin—separated by approximately 1000 km. We surveyed webs and vegetation to determine the degree to which deer alter the abundance and composition of a web-building spider guild.

MATERIALS AND METHODS

Field Methods

We surveyed ten paired exclosure-control study plots located in the north-central and northeastern United States. Four paired plots were located in the Northern Highlands region of northern Wisconsin in Vilas County (46°9’ N, 89°51’ W) on a 2500 ha property owned by Dairymen’s Inc (Rooney 2009). This site supported high densities of deer throughout most of the 20th century, greatly altering plant community composition (Rooney 2009; Begley-Miller et al. 2014). In 1990, four deer exclosures were constructed in a 5 ha, old-growth hemlock-hardwood stand (predominantly *Tsuga canadensis*, *Acer saccharum*, and *Betula alleghaniensis*). Exclosures are 1.8m tall, constructed of wire mesh, and range in size from 169 m^2 to 720 m^2. Each exclosure has an adjacent control plot of the same area, but with ambient browsing pressure. The exclosures are separated from one another by a mean distance of 195 ± 15 m (Rooney 2009). The remaining six paired plots were located in the Allegheny Plateau region, in north-central Pennsylvania in Elk County (41°25’ N, 78°50’ W). In the early 2000s, the Pennsylvania Game Commission constructed and maintained an array of six deer exclosures in State Gamelands 44 and 28 across a 200 km^2 area. This forest is part of the Hemlock-Northern Hardwood Association (Whitney 1990), and is composed of second and third growth forests (predominantly *Acer rubrum*, *Prunus serotina*, and *Acer saccharum*). For a more detailed description of the region, see Horsley et al. (2003) and Chips et al. (2015). All exclosures were approximately 2.25 m tall, range in size from 500 m^2 to 900 m^2, and have an adjacent control plot in a randomly selected location within 20 m of the edge of each fence.

We surveyed our plots for spider webs, and classified spider webs according to their structure (Fig. 1). Spider families can often be identified by the types of webs they build. We did not always identify the spider that created the web because they were not always present. However, we identify the putative family of spider that created each type of web we tallied (Bradley 2013). We classified webs as: vertical orb web (Araneidae), horizontal orb web (Tetragnathidae), cobweb or tangleweb (Theridiidae), meshweb (Dictynidae), funnel web (Agelenidae), sheet web (Linyphiidae), and reduced orb web (Uloboridae).

In the Northern Highlands region, we sampled spider webs in each paired exclosure and control plot for five days each month in June, July, and August 2013. Each sampling day, we divided each control and each exclosure plot into a 2 x 2 grid of four equal sections. For each section, we randomly assigned a sampling distance (at least 1 m distance to next section) and angle (0-90^o) using a random number generator. At the random point, we established a cylindrical sampling area with a 0.5 m radius and a 2 m height. We used a spray mist bottle to fill the entire area with water. This increased the visibility of all webs.

In the Allegheny Plateau region, we sampled spider webs in each exclosure and control plot once in mid-July and once again mid-August of 2012 using a stratified random approach. We sampled a 20 m x 20 m area within each plot and divided each area into four 10 m x 10 m sections. Within each section, we assigned Cartesian coordinates using a random number generator to determine the sample location, a new location was generated for each sampling date. At each location, quantified spider webs using the protocol described above. We identified all

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spiders to family based on web architecture and indicated whether or not an individual was found in the web.

To quantify vegetation structure and estimate habitat suitability for web-building spiders, we used the Web Scaffold Availability Index (WSAI) developed by Miyashita et al. (2004). In natural environments, vegetation provides most of the supports for webs (Uetz 1991). The WSAI quantifies the structural complexity of vegetation. At the center of the same random point used to sample spiders, we rotated a 1 m stick at 0.5 m and 1 m above the ground. We recorded the number of times each web anchoring structure (branch, twig, leaf, etc.) touched the stick. The total number of recorded anchoring points at 0.5 m and 1.0 m are recorded as the WSAI 0.5 m and WSAI 1.0 m (Miyashita et al. 2004).

At the Northern Highlands site only, we also examined prey availability to web-building spiders using sticky traps. The traps were constructed using 23 x 33 cm sheets of clear plastic coated with Tangle Trap Sticky Coating Aerosol (Tanglefoot Company, Grand Rapids, Michigan). Traps were attached to 1 m high wooden poles. We deployed one sticky trap in each of the established sections within the 2 x 2 grid using the same randomization method outlined above. We set up the traps 24 hours before the first sampling day, and they were deployed for 5 days each month. We then removed each sticky trap, covered them with clear plastic wrap, and placed them on ice. In the lab, we counted all insects captured, and measured the total body length.

Statistical Methods

We examined the effect of deer on habitat suitability for web-building spiders by comparing WSAI values at 0.5 m and 1.0 m above the forest floor inside and outside of exclosures. Because our sampling intensity was greater in the Northern Highlands, we divided the abundance of spider webs by 7.5 to standardize on effort (15 days/2 days). We first used two-way nested ANOVAs to determine if study site location (Northern Highlands or Allegheny Plateau), the deer exclusion treatment, or the 4 replicate subsamples per plot were significant sources of variation in explaining (a) WSAI at 0.5 m and (b) WSAI at 1.0 m. For both WSAI heights, only the deer exclusion treatment was a significant source of variation. We therefore pooled our subsamples into a single value for each plot. We then used an independent two-sample t-test to examine differences in WSAI between exclosure and control plots. We conducted two tests, one for WSAI at 0.5 m, and one test for WSAI at 1.0 m. WSAI values were natural log transformed prior to analysis to improve normality.

We next examined the relationship between WSAI and spider web abundance using multiple regression. We constructed a preliminary model using WSAI at 0.5 m, and WSAI at 1.0 m as independent variables, and spider web abundance as the dependent variable. We performed stepwise regression with backwards elimination, and used the Bayesian Information Criterion (BIC) to choose the most parsimonious model.

To determine the effects deer exclusion on the abundance of spiders, we tallied the number of spider webs of each type (Fig. 1) in each exclosure and each paired control plot. We then computed the log response ratio L for the abundance of each web type where $L = \ln (N_{\text{no deer}}/N_{\text{deer}})$. When $N_{\text{no deer}} = N_{\text{deer}}$, $L = 0$. Negative values of L indicate more spider webs where deer are present, while positive values indicate more webs were deer are excluded. A 95% confidence interval was calculated for each spider web type L to determine if it differed from zero.

We combined results from all webs to examine the used techniques developed for meta-analysis. Data from each web type were combined to create a mean effect size, following the procedures outlined in Hedges et al. (1999). To account for among-web type variation in effect sizes, we combined effect sizes from each web type to calculate the mean effect size, or overall effect. The effect size of each spider web type was first weighted by their inverse sampling variance plus a constant, q. The computation of q is derived from homogeneity analysis and represents variability across population effects (Hedges et al. 1999). To determine if the mean effect size differed from zero, we constructed 95% confidence intervals. We considered the effects of deer on spider web abundance to be statistically significant if 95% confidence intervals did not include zero.

We counted the number of prey items captured on each sticky trap at our Northern Highlands site, and computed the mean number of prey items per plot. We also measured the length of each prey item to obtain a mean prey size. We calculated log response ratios of prey abundance and size, and computed 95% confidence intervals using the same procedure as above.

To examine the differences in spider assemblages between exclosures and controls, we created a web type x plot matrix with 7 web type abundance and 20 control-exclosure plots and performed an ordination. We used PRIMER 6 (Clarke and Gorley 2006) to create a dissimilarity matrix using Bray-Curtis distances. Abundance data were square root transformed prior to the creation of the dissimilarity matrix. This had the effect of down-weighting the most abundant web types. We used NMDS to project the ecological distances among plots, based on 100 random starting configurations and applied a stopping rule when Kruskal stress reached 0.005. We used two-way Analysis of Similarity (ANOSIM) based on 5000 permutations to test for significant differences in spider composition due to deer browsing (exclosure and control plots), and geographic location (Northern Highlands and Allegheny Plateau plots).

RESULTS

In plots without deer, web-building spiders had more structures upon which to anchor their webs. Web-scaffold availability 0.5 m above the forest floor was over seven times greater in plots without deer, and over twelve times greater 1.0 m above the ground (Fig. 2). Web-scaffold availability did not differ significantly between Northern Highlands and Allegheny Plateau plots at 0.5 m (df = 18; t = 0.38; P = 0.70), or 1.0 m (df = 18; t = 0.97; P = 0.34). The most parsimonious model predicting the abundance of spider webs had a single predictor variable: WSAI at 1.0 m (Fig. 3). The WSAI at 0.5 m was not a significant predictor of spider web abundance when the WSAI at 1.0 is taken into account (n = 20; $r^2 = 0.10$; P = 0.17).

We tallied 1567 spider webs (Table 1). There were about half as many spider webs in plots with deer compared to plots without deer (54.8 ± 6.0 vs. 101.9 ± 10.5; n = 10; paired t = 5.16; P < 0.001). In the Northern Highlands region, total prey availability was significantly higher in plots with deer (886.8 ± 160.8 SE) compared to plots without deer (330.0 ± 53.8 SE; effect size = -0.98 ± 0.13; 95%CI = -1.48, -0.65). Mean prey size did not differ between plots without deer (2.80 ± 0.16 mm SE) and plots with deer (2.61 ± 0.10 mm SE; effect size = 0.08 ± 0.04; 95%CI = -0.11, 0.25). We did not estimate prey availability in the Allegheny Plateau region.

Analysis of response ratios revealed that, with the exception of funnel web-builders, all spider web types were significantly more abundant in plots without deer (Fig. 1, 4). Vertical and

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horizontal orb weavers accounted for the largest responses. Both of these groups were nearly three times more abundant in plots without deer. When response ratios were combined for all web types, spider webs were clearly more abundant in deer-free plots (Fig. 4).

NMDS produced a 3-dimensional solution (Kruskal stress = 0.07). While NMDS ordination did not appear to reveal strong differences in the structure of web-building spider guilds between plots with and without deer (Fig. 5), differences were statistically significant (ANOSIM R = 0.37; P = 0.004). There were also significant differences in web-building spider guild composition between the Northern Highlands and Allegheny Plateau regions (ANOSIM R = 0.46; P = 0.002).

DISCUSSION

In both the Allegheny Plateau and Northern Highlands regions, web-building spiders differed in abundance and composition between areas with and without deer. With deer excluded, plots have about seven times the number of anchoring points for webs, and twice as many web-building spiders. Nearly all web structure types increased in abundance when deer were excluded; only funnel weavers were not strongly affected. Prey availability was higher in plots with deer, where the abundance of spiders was much lower. Miyashita et al. (2004) did not find a relationship between prey abundance and deer exclusion. This probably reflects a difference in sampling intensity. Our prey sticky traps were 7.5 times larger and deployed nearly 4 times longer. Our findings suggest that deer, not prey availability, account for differences in web-building spider assemblages between plots with and without deer. When deer are present, web-building spider abundance appears limited by vegetation structure and the availability of locations to anchor webs (Rypstra 1983; Miyashita et al. 2004; Takada et al. 2008). In the absence of deer, anchoring locations are abundant. Therefore, web-building spider abundance will often be limited by prey availability (Rypstra 1983; Wise 1993).

The configuration of sample plots in NMDS space (Fig. 5) suggests modest effects of deer on community structure, despite statistical significance. The absence of strong clustering of sample plots into those with and without deer probably reflects the effects of deer on nearly all web structures (Fig. 4). In plots with deer, the decline in spider web abundance is more or less evenly spread across all web types. As a result, community structure remains little changed as a more or less random loss of individual webs as the capacity of the habitat to support web-building spiders that rely on complex vegetation structure decline. Only the small, dense webs of funnel-weavers were unaffected. Funnel weavers tend to construct their webs at ground level, so these spiders are the least likely to be affected by changes in vegetation architecture.

The same configuration of sample plots in NMDS space indicates regional effects on community structure as well, and greater multivariate dispersion among plots. Pairwise distances among exclosure-control plot replicates in the Allegheny Plateau region were much greater than in the Northern Highlands. The reduced multivariate dispersion among Northern Highlands plots is probably due to species sorting of species drawn from the same local species pool, whereas the more broadly-distributed Allegheny Plateau plots reflects species sorting of species drawn from a local species pool, each of which was nested within a regional species pool (Leibold et al. 2004).

Other researchers report that the abundance and/or richness of web-building spiders increased in forest areas where deer are experimentally excluded (Miyashita et al. 2004; Suominen and Danell 2006; Takada et al. 2008). Under the closed forest canopies of our study region, the density of shrubs and tree saplings is often low, owing to low light levels, recalcitrant understory layers that inhibit woody plant growth, and feeding by deer (Horsley et al. 2003; Sage et al. 2003; Royo and Carson 2006). Hence there are few opportunities for web-building spiders to anchor their webs. Recruitment of web-building spiders might therefore become increasingly disturbance-dependent because large canopy disturbances increase the abundance and density of woody vegetation in the understory. These episodic disturbances could provide key web building substrates lacking in intact forest in areas where deer are abundant. While episodic recruitment is a common feature of marine systems and disturbance-dependent plant populations, it is possible that the widespread overabundance of deer have created conditions in which terrestrial predatory arthropods may develop this same recruitment pattern.

In their review of the effects of deer on ecosystems, Rooney and Waller (2003) differentiated between indirect effects due to modified food web interactions, and indirect effects arising form habitat modification. In this study, we can attribute changes in the distribution and abundance of web-building spiders to habitat modification. This is not simply cause and effect. Reductions in the density of spider webs probably contributed to the rise in arthropod prey we observed. In other words, habitat modification can lead to modified food web interactions. The distinction between habitat modification and modified food web interactions should not be viewed as a strict dichotomy. The linkages from deer to vegetation are trophic; deer reduce the density of saplings that provide web anchoring points (Begley-Miller et al. 2014). This structural change altered the abundance of web-building spiders at the third or fourth trophic level (depending on prey), which may have increased the abundance of arthropod prey at the second or third trophic level. Nuttle et al. (2011) introduced the concept of a trophic ricochet to describe a top-down effect that altered plant communities, but did not terminate at the lowest trophic level. Instead, it was transformed to a bottom-up effect that persisted for several decades. In this study,

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we observe different type of trophic ricochet: a top-down effect of deer on vegetation structure that indirectly affected organisms at multiple trophic levels. Deer directly reduced habitat quality and indirectly reduced the abundance of predators, albeit arthropod predators that do not feed on deer, which in turn apparently resulted in an increase in arthropod prey. Trophic ricochets may be a widespread response when dominant species, keystone species, or ecosystem engineers modify the habitats.

CONCLUSION

Deer browsing has profound implications for web-building spiders in the forest understory layer. Of the families of spiders we studied, only the funnel web-builders appeared unaffected. Deer greatly modified habitat structure, reducing opportunities for spiders to anchor webs. This reduced the density of spider webs, and in turn led to a 2.7-fold increase in spider prey abundance. Thus, deer herbivory indirectly altered arthropod predator-prey interactions throughout the forest understory. These changes are probably not unique to our study sites, but instead reflect changes throughout both the Allegheny Plateau and Northern Highland regions. Deer populations have increased in both regions since the 1970s (Ripple et al. 2010). The effect sizes we observed in our study are perhaps larger than occur throughout the region, because exclosures create the artificial condition of vegetation development in the absence of deer. However, we do not know if web-building spider abundance responds to thresholds in deer abundance, or whether such responses are linear. Studies that take advantage of natural gradients in deer abundance might provide better estimates of contemporary effect sizes, although such correlative studies have their own issues.

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Table 1. Web type, putative family (based on Bradley 2013), number of individual webs identified in Exclosure (deer free) and Control (browsed) plots, and web types encountered in 10 plots.

Web Type	Family	Exclosure	Control
Vertical orb weavers	Aranaeidae	133	45
Horizontal orb weavers	Tetragnathidae	131	48
Tangle web weavers	Theridiidae	190	97
Mesh weavers	Dictynidae	77	30
Sheet weavers	Linyphiidae	345	187
Funnel weavers	Agelenidae	122	136
Reduced orb or line weavers	Uloboridae	21	5

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FIGURE LEGEND

Fig. 1. Web structures (a) funnel web (Agelenidae), (b) sheet web (Linyphiidae), (c) mesh web (Dictynidae), (d) reduced orb web (Uloboridae) (e) vertical orb web (Aranaeidae), (f) tangle web (Theridiidae), (g) horizontal orb web (Tetragnathidae). Line drawings by E.J. Roberson.

Fig. 2. Web scaffold availability index (WSAI) in control and exclosure plots 0.5 m ($df = 18$; $t = 5.58$; $P < 0.001$) and 1.0 m ($df = 18$; $t = 7.37$; $P < 0.001$) above the ground. Horizontal lines indicate mean values. WSAI was natural log transformed prior to statistical analysis.

Fig. 3. The abundance of spider webs as a function of web scaffold availability index (WSAI) at 1.0 m ($df = 1, 18$; $F = 9.07$; $r^2 = 0.335$; $P = 0.008$).

Fig. 4. Log response ratio (ratios of number of webs in exclosure plots compared to paired control plots) and 95% confidence intervals for all web types. From top to bottom: vertical orb, horizontal orb, tangle web, mesh web, sheet web, funnel web, reduced orb web, all webs combined (thick bar). Positive values indicate greater web density in the absence of deer. Confidence intervals that intercept zero indicate no significant difference ($p > 0.05$).

Fig. 5. NMDS ordination of the abundance of web structures found in control (open) and exclosure (solid) plots in the Allegheny Plateau (AP) and Northern Highlands (NH) region. Only the first two dimensions of a 3-dimensional solution are shown.

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Fig 1

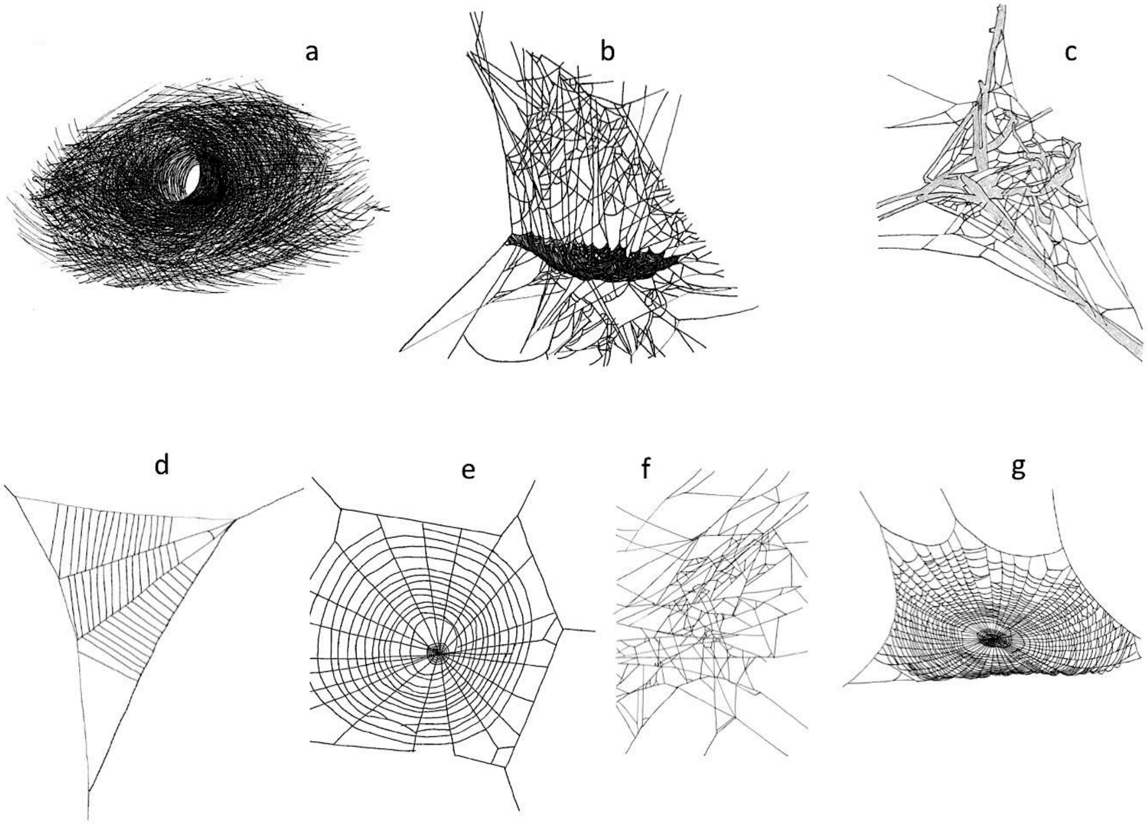

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Fig 2

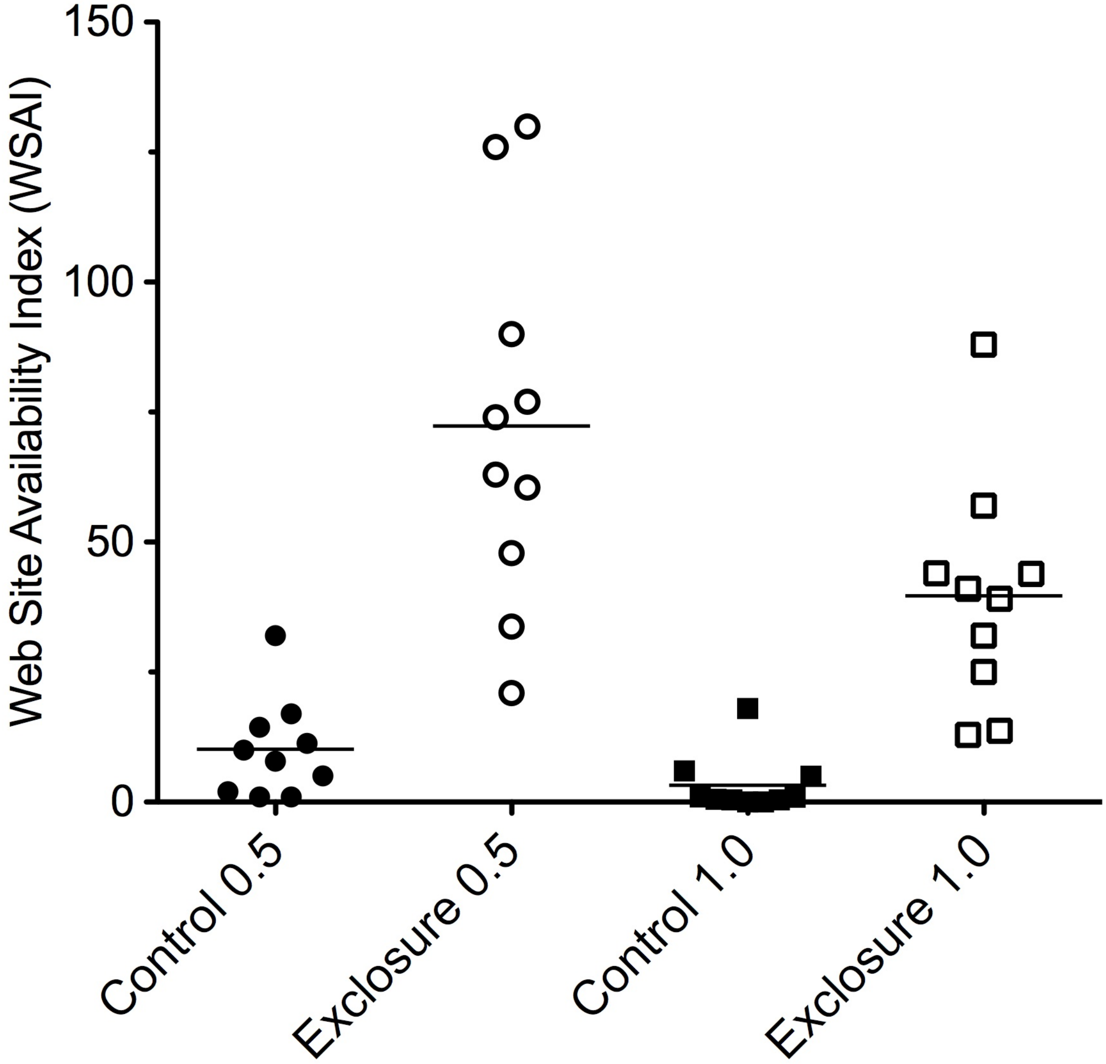

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Fig 3

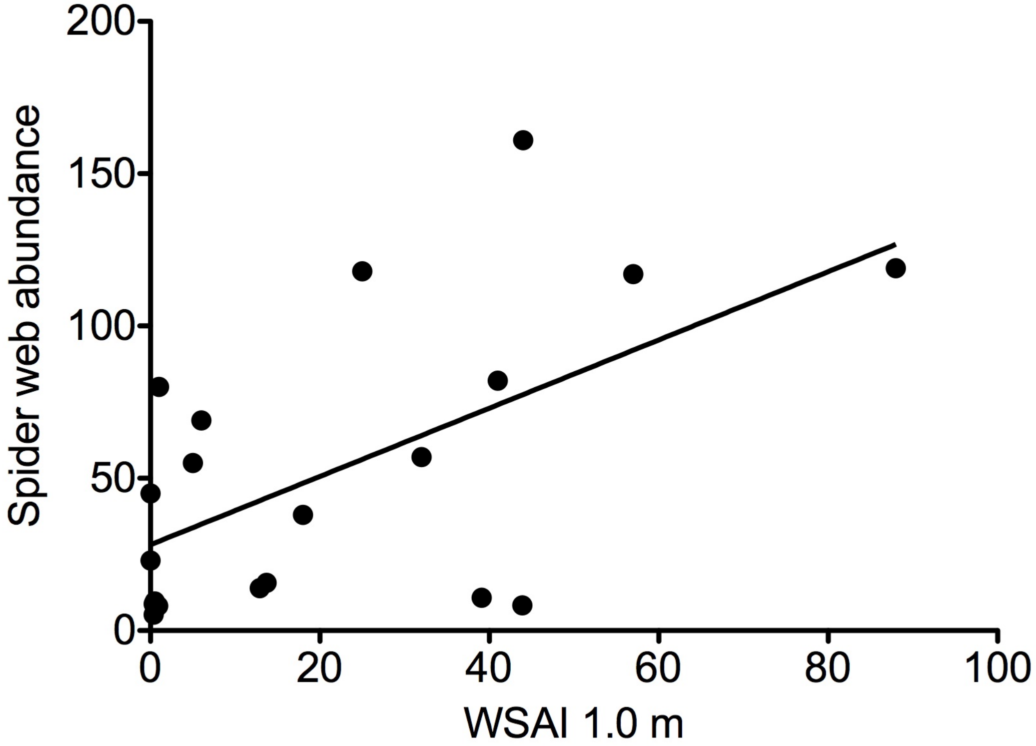


Fig 4

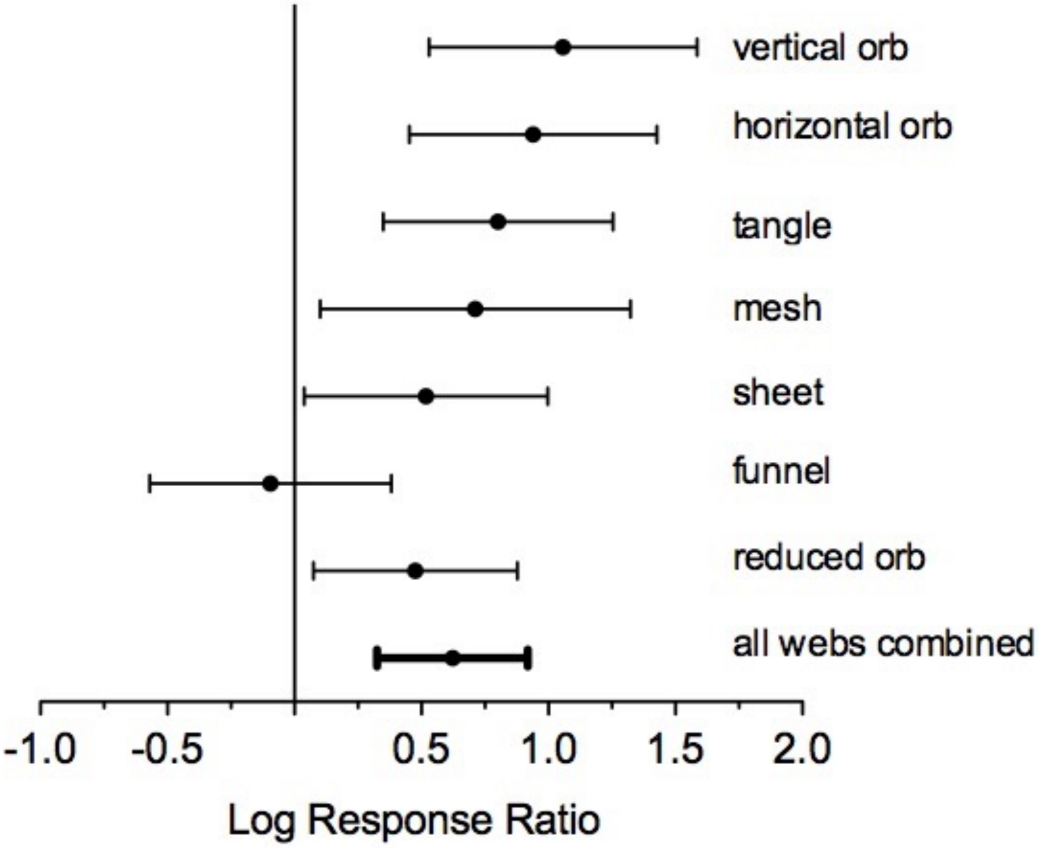
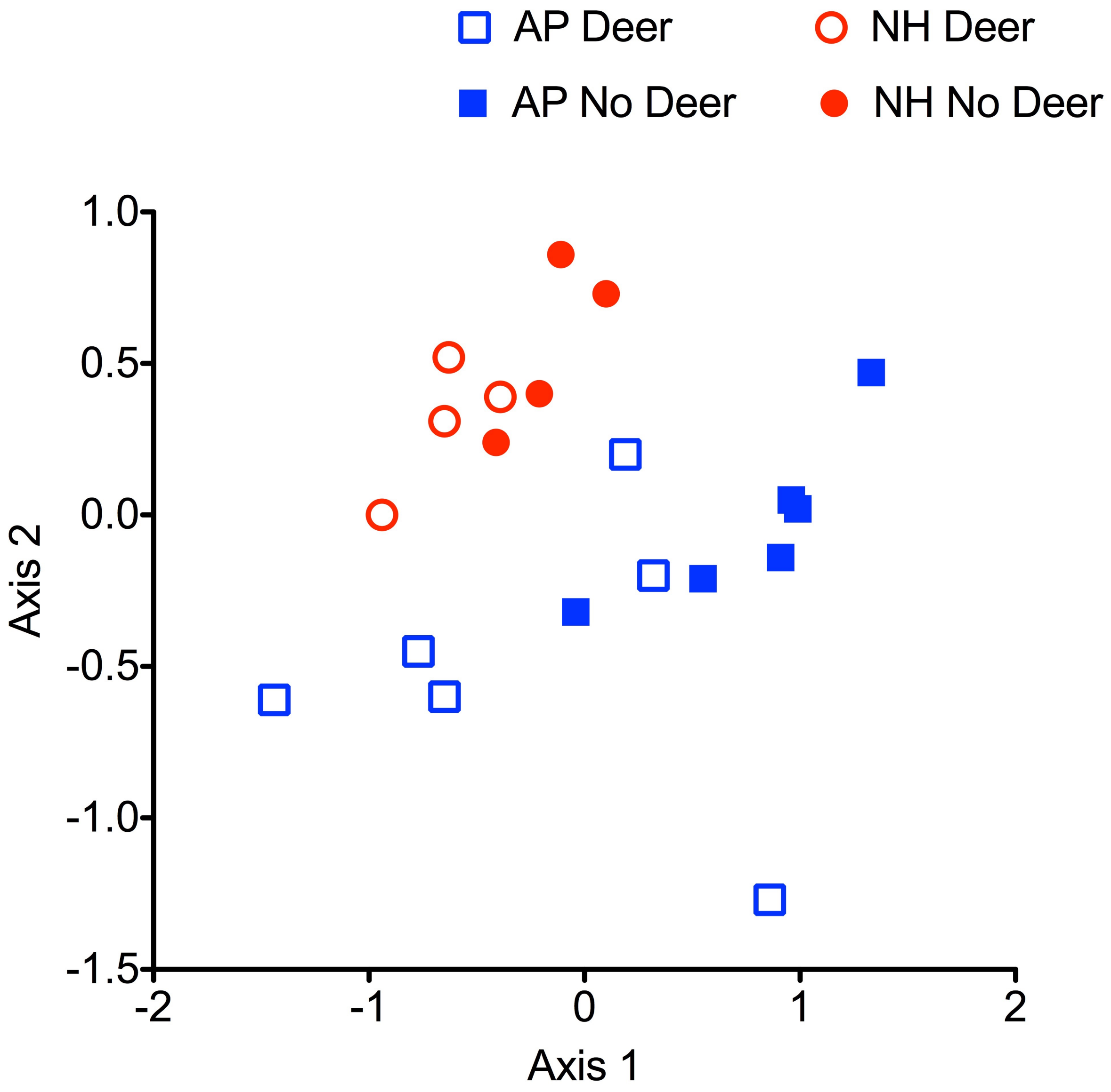

vertical orb
horizontal orb
tangle
mesh
sheet
funnel
reduced orb
all webs combined
-1.0
-0.5
0.5
1.0
1.5
2.0
Log Response Ratio

Fig 5



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