

Invasive plant architecture alters trophic interactions by changing predator abundance and behavior

Dean E. Pearson

Received: 26 June 2008 / Accepted: 14 November 2008 / Published online: 10 December 2008
© Springer-Verlag 2008

Abstract As primary producers, plants are known to influence higher trophic interactions by initiating food chains. However, as architects, plants may bypass consumers to directly affect predators with important but underappreciated trophic ramifications. Invasion of western North American grasslands by the perennial forb, spotted knapweed (*Centaurea maculosa*), has fundamentally altered the architecture of native grassland vegetation. Here, I use long-term monitoring, observational studies, and field experiments to document how changes in vegetation architecture have affected native web spider populations and predation rates. Native spiders that use vegetation as web substrates were collectively 38 times more abundant in *C. maculosa*-invaded grasslands than in uninvaded grasslands. This increase in spider abundance was accompanied by a large shift in web spider community structure, driven primarily by the strong response of *Dictyna* spiders to *C. maculosa* invasion. *Dictyna* densities were 46–74 times higher in *C. maculosa*-invaded than native grasslands, a pattern that persisted over 6 years of monitoring. *C. maculosa* also altered *Dictyna* web building behavior and foraging success. *Dictyna* webs on *C. maculosa* were 2.9–4.0 times larger and generated 2.0–2.3 times higher total prey captures than webs on *Achillea millefolium*, their

primary native substrate. *Dictyna* webs on *C. maculosa* also captured 4.2 times more large prey items, which are crucial for reproduction. As a result, *Dictyna* were nearly twice as likely to reproduce on *C. maculosa* substrates compared to native substrates. The overall outcome of *C. maculosa* invasion and its transformative effects on vegetation architecture on *Dictyna* density and web building behavior were to increase *Dictyna* predation on invertebrate prey ≥ 89 fold. These results indicate that invasive plants that change the architecture of native vegetation can substantially impact native food webs via nontraditional plant $\rightarrow$ predator $\rightarrow$ consumer linkages.

Keywords Biological invasions · Community assembly · Preadaptation · Predator–prey interactions · Trait-mediated indirect interactions

Introduction

Food webs have been conceptualized as linear, density-driven, bottom-up versus top-down chains of interactions. Either plants supply resources that fuel higher trophic structure from the bottom-up, or strong predator–consumer interactions cascade downward to structure communities from above (Hairston et al. 1960; Oksanen et al. 1981; Hunter and Price 1992). Although it has long been appreciated that these simple interaction chains are caricatures of more complex trophic structure (Polis and Strong 1996), the varied ways that indirect effects travel through food webs has only recently come to light. For example, in the Aleutian Islands, exotic foxes indirectly transform subarctic grasslands to tundra, not by suppressing herbivores, but by disrupting nutrient subsidies (Croll et al. 2005), and in old field systems, spiders affect plant composition and

Communicated by Sven Bacher.

D. E. Pearson (✉)
Rocky Mountain Research Station, USDA Forest Service,
800 E. Beckwith Ave., Missoula, MT 59801, USA
e-mail: dpearson@fs.fed.us

D. E. Pearson
Division of Biological Sciences, University of Montana,
Missoula, MT 59812, USA

ecosystem properties more by altering the behavior than the density of their prey (Schmitz 2006).

Just as predators can influence food webs via novel pathways, so too can plants. Typically, plants are viewed as producing the energy that travels upwards through food webs, thereby affecting higher trophic levels only as food resources. However, plants are not only primary producers—they are architects. Plants create three-dimensional structures that define the physical landscape for predators and prey. Although it is well established that plants provide habitats that affect animal abundance and diversity (Crooks 2002; Langelotto and Denno 2004), few studies have examined how plant architecture alters predator–prey interactions (e.g., Denno et al. 2002). Furthermore, despite increasing recognition that predator-driven indirect effects can be mediated by changes in both prey behavior and density (Werner and Peacor 2003; Schmitz et al. 2004; Pressier et al. 2005), the potential for plant architecture to influence indirect interactions through their direct effects on predator behavior and density remains unstudied. Yet such interactions may have broad ramifications for trophic dynamics, particularly following anthropogenic habitat changes and exotic plant invasions (e.g., Tylianakis et al. 2007).

Biological invasions represent massive natural experiments offering potentially significant insights for understanding the roles of trophic interactions in community assembly. Although extensive research shows that exotic plant invasions can radically alter native plant communities (Mack et al. 2000; Levine et al. 2003) and exotic predators can severely impact native prey (Blackburn et al. 2004), little is known about how exotic plants affect predator–prey interactions and trophic outcomes (Levine et al. 2003). One underappreciated means by which exotic plants may alter trophic interactions is by changing vegetation architecture. In many western North American grasslands, forbs offer the primary source of three-dimensional structural diversity. However, these plants are predominantly herbaceous and ephemeral, often disappearing by the end of the growing season. Western grasslands are currently being overrun by Eurasian forbs like spotted knapweed (*Centaurea maculosa*) (Sheley et al. 1998), which produce flowering stems that are larger, more structurally complex and rigid, and far more persistent than those of most natives. As a result, exotic plant invasions are transforming vegetation architecture over vast regions, with important implications for predator–prey interactions.

In western Montana in the United States, *Dictyna coloradensis* and *Dictyna major* occur as small, uncommon native spiders that build persistent, irregular webs in the upper one-third of the vegetation. *Dictyna* spp. appear to be limited by their requirement for the more rigid, complex architecture offered by the flowering stalks of certain

relatively uncommon native forbs. Thus, the invasion of these structurally depauperate grasslands by exotic forbs that are larger, more structurally complex and more persistent than most native forbs may have important ramifications for these native spiders and their prey. In this paper, I use data from long-term monitoring, field observations, and field experiments to examine how a functionally unique exotic plant architecture alters native web spider abundance and foraging behavior, and to determine how these plant-induced changes in predator abundance and behavior may affect predation rates and indirect interactions.

Materials and methods

Study system

This research was conducted in semi-arid low elevation grasslands in western Montana. These grasslands are dominated by the bunchgrasses *Psuedoroegneria spicata* and *Festuca scabrella*, and by forbs such as silky lupine (*Lupinus sericeus*), arrowleaf balsamroot (*Balsamorhiza sagittata*), and yarrow (*Achillea millefolium*). Native forbs generally flower in May and June, senesce in July, and their flowering stalks fall and rapidly decompose around September. Additionally, their flowering stems are generally not very large or complex. Due to their minimalist structure and low persistence, they offer poor substrates for web building spiders. An exception is *A. millefolium*, which produces more rigid and persistent flowering stems than most natives. Although *A. millefolium* stems are small and sparse, they often support spider webs the following spring. Within these grasslands, *Centaurea maculosa* is a particularly potent invader that can reach high densities and usurp native plant communities (Ortega and Pearson 2005). These plants occur as rosettes early in the growing season, but bolt and produce upright flowering stalks in May and June. *C. maculosa* flowering stalks are larger, more complex, and more rigid than most native forbs and tend to persist to the next growing season when they are readily used by native spiders.

The dominant web building spiders in these grasslands are *D. major* and *D. coloradensis*. These are small (carapace length ≤ 1 mm), univoltine spiders that overwinter in plant litter during their 4th and 5th instars (Wheeler et al. 1990). *Dictyna* emerge from April to May and seek out dried, upright flower stalks from the previous year's growth as scaffolding on which to construct webs. Spiderlings develop into adults, breed, and begin laying eggs by mid-to-late June. Young spiders begin to disperse in July. Both adult and young spiders travel by ballooning from plant to plant at the vegetation surface about 0.5 m above the

ground. *Dictyna* construct irregular webs that are built up over time, but do not reconstruct webs daily like some orb weavers (Jackson 1978). These spiders retain prey items in their webs and drag all but the largest consumed prey to a lair in a crotch of the plant. Consumed prey items can generally be counted and identified to order. Since both *Dictyna* species are ecologically similar (Jackson 1978) and cannot be distinguished in the field (J. Slowik, Denver Museum of Nature and Science, Denver, CO, personal communication), I treat them here as a species complex (referred to as “*Dictyna*”).

Spider and prey abundance in native and *C. maculosa*-dominated sites

I assessed spider density by counting active spider webs (webs containing a live spider). Each active web represents one spider, except during breeding when a male and female briefly cohabit the web. In conjunction with another *C. maculosa* study (see Pearson and Callaway 2006), I monitored *Dictyna* densities from 2001 to 2006 during late summer by counting active webs within 0.5 m² quadrats embedded in 1 ha grids scattered across west-central Montana. Sampling effort ranged from 100 quadrats on each of 21 grids in 2001 to 35 quadrats on each of four grids in 2006. Sampling effort was reduced to conform to another study. The number of grid cells was decreased from all cells to a stratified random subsample of cells to focus sampling effort, and the number of grids sampled was reduced due to experimental mowing of *C. maculosa* and herbicide applications for weed management. Reductions in sampling effort did not bias the current study. Each quadrat was designated as native or *C. maculosa*-invaded based on presence or absence of *C. maculosa* flowering stems.

To more thoroughly quantify effects of *C. maculosa* invasion on web spiders, I evaluated web spider abundance in 2006 on 10–20 pairs of belt transects (1 × 10 m) at three of the long-term monitoring locations (Blackfoot, Flathead, and Missoula valleys). Transects were paired such that one transect was placed within an uninvaded native grassland patch and one was placed within a similar adjacent *C. maculosa*-invaded patch. Transects were parallel and averaged 9.4 m apart (± 7.1 SD). I sampled spider populations twice: first at the beginning of June when overwintered spiders had reached maturity and were beginning to lay eggs, and again in mid-July when young spiderlings were dispersing and establishing webs. At the first location, during the first sampling period, I sampled 20 transect pairs; after this ten transect pairs were sampled at each location each sampling period, since this effort appeared sufficient (sample size was 80 transects in June and 60 in July). I counted all active webs on vegetation

along each transect and assigned webs either to *Dictyna* spp or other web spiders. Other web spiders were comprised primarily of the orb weaver *Aculepeira packardii* with additional taxa being uncommon-to-rare. I also determined the proportion of active *Dictyna* webs containing egg sacs and estimated the relative abundance of spider prey in the two habitats by placing one 7.6 × 12.7 cm sticky card at each end of each belt transect. Sticky cards were placed near the vegetation surface approximately 0.5 m above the ground. Cards were sprayed on both sides with Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) to make them sticky and set out for 7 days before collecting and quantifying captures.

Individual spider and substrate-level effects

I quantified native (*A. millefolium*) versus exotic (*C. maculosa*) substrate effects on web size to determine how changes in plant architecture due to invasion affected *Dictyna* web building behavior, per capita prey capture rates, and clutch sizes. *A. millefolium* was the most commonly used native substrate (>50% of all native substrates) and supported larger webs than other native plants. Thus, *A. millefolium* was representative of native substrates proportionally, but likely overestimated web size and capture rates relative to other natives.

I established substrate pairs near each set of belt transects by locating the nearest *A. millefolium* plant with an active *Dictyna* web and then finding an adjacent *C. maculosa* plant with an active web ($n = 30$ substrate pairs). Pairing minimized the distance between substrates to control for microsite conditions and prey communities (mean distance between substrates = 4.7 m $\pm$ 10.2 SD). For each web on the substrate pairs and belt transects, I measured substrate width (widest point horizontal to the ground), substrate height (ground to top), web width (greatest width horizontal to the ground), web length (greatest vertical distance from bottom to top of web), web height above ground (distance from ground to bottom of web), and counted whole prey items within each web. Web area was calculated from web length and width based on the geometry of a triangle (Jackson 1978). I also counted egg sacs in each web and collected a sub-sample of egg sacs to rear young spiderlings in the laboratory to determine the number of spiderlings emerging per egg sac. Eggs sacs were kept at approximately 24°C in Petri dishes with tissue paper covers for ventilation and checked daily for emerging spiderlings.

To experimentally determine effects of plant substrate on spider density and behavior, I introduced *Dictyna* spiders that had never experienced *C. maculosa* onto randomly selected, paired *C. maculosa* and *A. millefolium* stems placed in native grasslands. This experiment

controlled for microsite conditions, *C. maculosa*-induced effects on invertebrates and vegetation communities, and spider body size. It also allowed me to evaluate whether web building behavior associated with *C. maculosa* architecture might be recently evolved or pre-adapted.

In June 2006, I collected a random sample of dead stems (prior year's growth) of *A. millefolium* and *C. maculosa* from the belt transect survey locations. Stems were randomly assigned to *C. maculosa*/*A. millefolium* pairs and placed in the ground 1 m apart at ten stations spaced 10 m apart. I replicated this arrangement at three locations within a native (uninvaded) *F. scabrella*-dominated grassland (average distance between locations was $0.66 \text{ km} \pm 0.22 \text{ SD}$; average distance to nearest *C. maculosa* infestation was $1.72 \text{ km} \pm 0.35 \text{ SD}$). Before *C. maculosa* stems were set out, the contents of the seedheads were extracted to remove biocontrol agents that could be captured in webs and to prevent introducing exotic seeds into native grasslands. Removal of seedhead contents does not affect *C. maculosa* structure for web building. In early July, I collected *Dictyna* from a native *F. scabrella* grassland at Elk Creek, an isolated mountain valley near Augusta Montana located $>70 \text{ km}$ and across the Continental Divide from the nearest major *C. maculosa* invasion front. This site was chosen to ensure that spiders had no direct contact with *C. maculosa* and minimal chance of a genetic linkage to *Dictyna* potentially adapted to *C. maculosa*. I randomly introduced these *Dictyna* (spiders were adult females because adult males do not build webs and assignment was random relative to body size) onto the *C. maculosa* and *A. millefolium* stems, measured the resulting webs (as described above), and determined prey capture rates for 5–7 days. I counted new prey items in each web each day to calculate daily capture rates, and estimated the size of each prey item to the nearest millimeter.

Analyses

For belt transects, I examined spider densities/ m^2 (*Dictyna* spp. vs other spiders) by habitat (*C. maculosa*-invaded vs native) using MANOVA in PROC GLM (SAS Institute 1999). I used general linear models in PROC MIXED to compare *Dictyna* density/ m^2 by habitat and sampling period (June vs July) by incorporating habitat as a fixed factor, sampling location and transect location as random blocking factors, and sampling period as a repeated measure. Similarly, I compared the mean number of prey items per sticky card, treating habitat as a fixed factor and location and transect as random factors. A chi-square goodness-of-fit test was used to test for differences in the proportion of spiders producing egg sacs between habitats. For field observations of substrates, I compared the number of prey

items, egg sacs, and emerging spiderlings per web by substrates using PROC MIXED, treating substrate (*C. maculosa* or *A. millefolium*) as a fixed factor and sampling location and substrate location (transects where pairings occurred) as random blocking factors. To determine how substrate affected prey captures, I conducted a covariate analysis of the effect of web area and web height from the ground on prey captures treating web height and web area as fixed factors and using Type III sums of squares (SAS Institute 1999). For substrate experiments, I examined how substrate affected web area and daily total capture rates by treating substrate as a fixed factor and the location and substrate pair as random blocking factors. Large prey were not normally distributed, so I used Multiresponse Permutation Procedures for block designs (MRBP; Mielke et al. 2001) to analyze daily capture rates of large prey with location and substrate pair as random blocking factors. Prey $\geq 6 \text{ mm}$ were deemed large based on breaks in prey size distributions. I used a test of ratios of random variables (Manly et al. 1993) to compare the ratios of the differences in capture success (*C. maculosa* capture rate/*A. millefolium* capture rate) between the observational and experimental data sets.

Results

Spider and prey abundance in native and *C. maculosa*-dominated sites

Dictyna spp ($F_{1,141} = 32.25$, $P < 0.01$) and other spiders ($F_{1,141} = 44.07$, $P < 0.01$) that used vegetation as web substrates were more abundant on *C. maculosa*-invaded transects compared with closely paired native transects (Fig. 1a). *Dictyna* spiders responded to *C. maculosa* invasion substantially more than other web spiders, resulting in a considerable shift in relative abundance of web spider taxa (Fig. 1a). In early June 2006, *Dictyna* spiders were 45.5 times more abundant within *C. maculosa*-invaded patches than in nearby native-dominated grasslands ($F_{1,84}^{\text{habitat}} = 37.13$, $P < 0.01$; Fig. 1b). From June to July, *Dictyna* abundance increased due to dispersal and establishment of young spiders ($F_{1,83}^{\text{sampling period}} = 5.79$, $P = 0.02$), and this increase was greater in the presence of *C. maculosa* ($F_{1,84}^{\text{habitat} \times \text{sampling period}} = 4.30$, $P = 0.04$). This resulted in *Dictyna* densities 73.7 times higher within *C. maculosa*-invaded grasslands versus native grasslands (Fig. 1b). Six years of monitoring indicated that *Dictyna* were consistently more abundant on *C. maculosa*-invaded quadrats (mean density = $0.605 \pm \text{SE } 0.03$ spiders/ m^2) versus uninvaded quadrats (mean density = 0.019 ± 0.01 spiders/ m^2), despite annual fluctuations (Fig. 2). Because *Dictyna* were not detected in many years on native

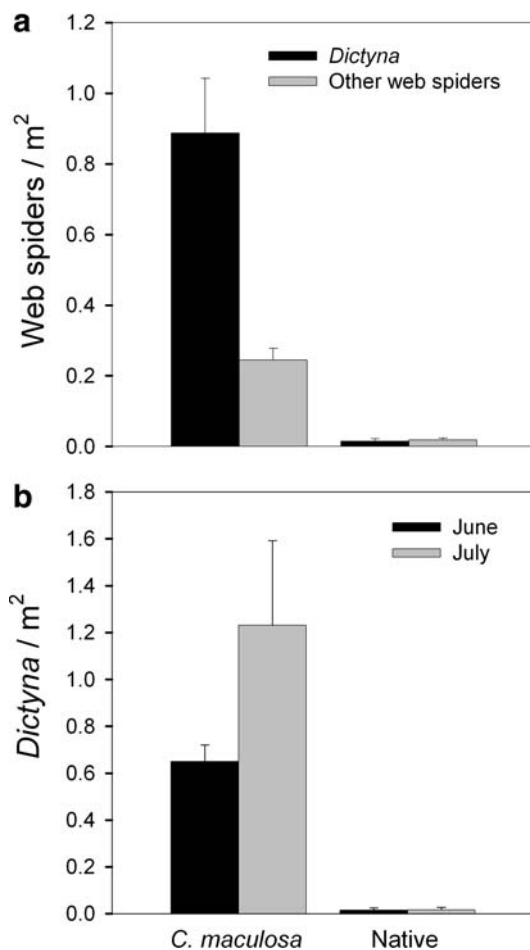


Fig. 1 Densities of web spiders on paired *Centaurea maculosa*-invaded and native (uninvaded) belt transects sampled in western Montana in 2006. **a** Comparison of overall densities of *Dictyna* spiders and other web spiders between habitats. **b** Comparison of *Dictyna* densities from June (when adult spiders begin to lay eggs) to July (when spiderlings have begun to disperse) between habitats. Means $\pm$ 1 SE

quadrats, these data are presented only as long-term trends (no analyses were conducted). In addition to reaching higher densities, the proportion of *Dictyna*-producing egg sacs was substantially higher on *C. maculosa*-invaded compared to native transects (18.2% vs 10.5% of spiders produced egg sacs, respectively; $\chi^2 = 5.36$, $df = 1$, $P = 0.021$). Prey densities were slightly lower on *C. maculosa*-invaded ($\bar{x} = 23.0 \pm 8.03$ SE) versus native ($\bar{x} = 25.5 \pm 8.03$) transects, but the difference was not significant ($F_{1,28} = 2.04$, $P = 0.16$). The greater spider abundance in *C. maculosa*-invaded habitat appeared to be due to the greater abundance of suitable web substrate. *Centaurea maculosa* was 51.9 times more abundant than *A. millefolium* on the invaded transects, and 96% of active *Dictyna* webs and 100% of other spider webs on invaded transects were located on *C. maculosa* stems.

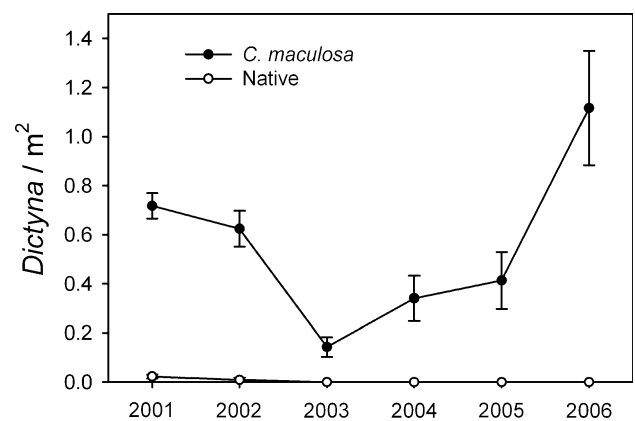


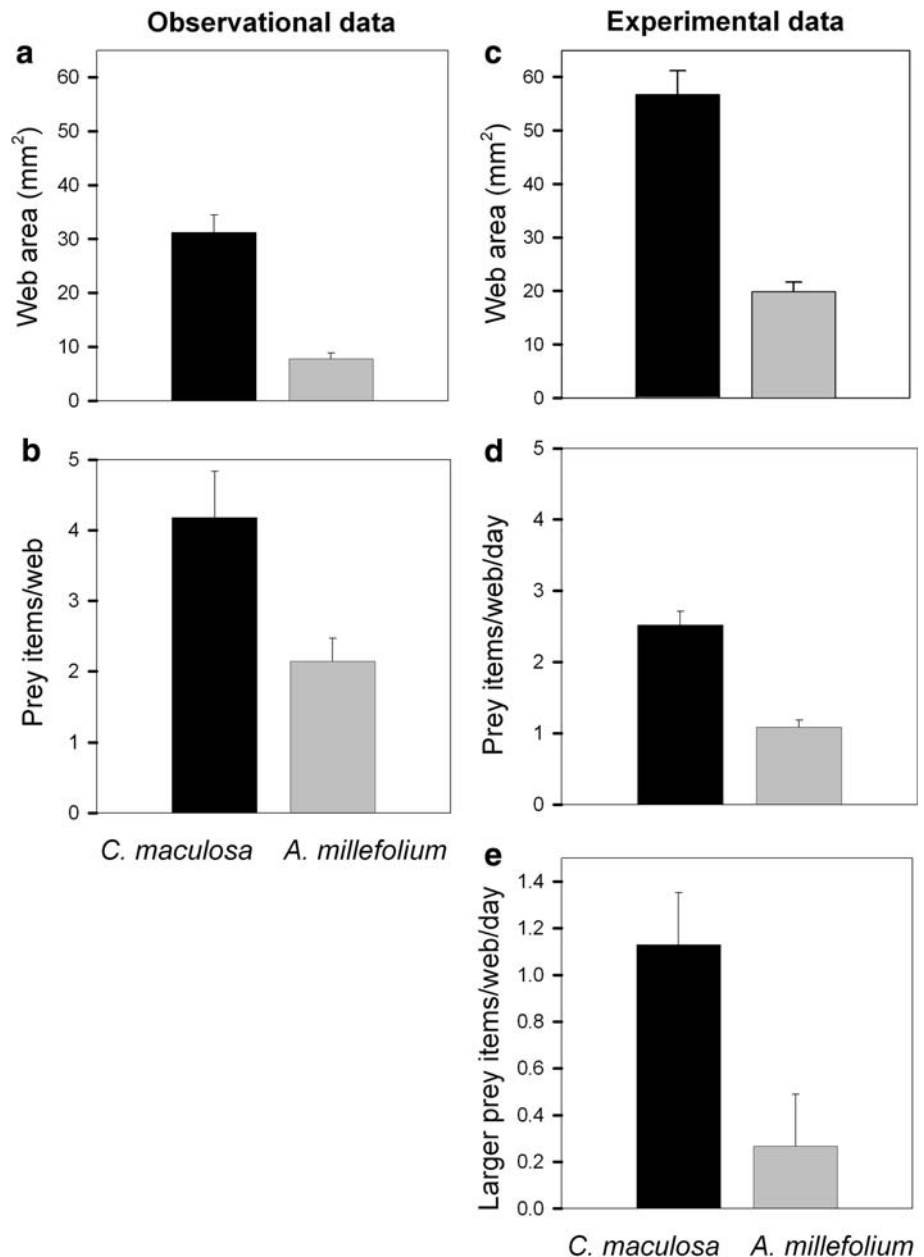
Fig. 2 Long-term trends in *Dictyna* density on *C. maculosa*-invaded and native quadrats sampled each fall from 2001 to 2006 on 1 ha grids scattered across western Montana. Means $\pm$ 1 SE

Individual spider and substrate-level effects

Examination of adjacent, naturally established *C. maculosa* and *A. millefolium* web substrates indicated *Dictyna* webs were on average 4.0 times larger on *C. maculosa* plants ($F_{1,54} = 48.77$, $P < 0.01$; Fig. 3a). Additionally, webs on *C. maculosa* contained 2.0 times more prey than webs on *A. millefolium* ($F_{1,52} = 8.03$, $P < 0.01$; Fig. 3b), despite the close proximity of paired substrates. Although, *Dictyna* readily consume the exotic flies *Urophora affinis* and *Urophora quadrifaciata* (both introduced for *C. maculosa* biological control; Story et al. 1995), differences in prey captures are not explained by the consumption of *C. maculosa* biological control agents, which made up only 8% of all prey captures and were found in both *A. millefolium* and *C. maculosa* webs. Because *C. maculosa* plants are larger than *A. millefolium* plants, webs in *C. maculosa* plants were 1.4 times higher above the ground than those in *A. millefolium* ($F_{1,52} = 8.03$, $P < 0.01$), suggesting that web height could explain differences in capture rates between substrates. However, covariate analysis indicated capture rates were unrelated to web height above ground ($F_{1,50} = 0.29$, $P = 0.59$) but were strongly related to web area ($F_{1,52} = 19.37$, $P < 0.01$).

These outcomes were not restricted to *C. maculosa* and *A. millefolium*. Of 725 *Dictyna* webs identified on belt transects in both habitats, 78% of webs not on *C. maculosa* were on four other exotic forbs. Moreover, these exotic forb substrates were similarly larger ($F_{1,723} = 8.77$, $P < 0.01$) and favored larger webs ($F_{1,723} = 6.73$, $P = 0.01$) than the native substrates used by *Dictyna* (Fig. 4), suggesting that plant architecture is driving the observed response of web spiders and *C. maculosa* is only one of numerous exotic forbs increasing web spider substrate. Despite larger webs and greater prey captures in *C. maculosa* webs, the number of egg sacs found in *Dictyna* webs ($\bar{x} = 0.61 \pm 0.27$ SE for

Fig. 3 Comparisons of *Dictyna* web size and prey captures between paired exotic *C. maculosa* and native *Achillea millefolium* substrates naturally established near belt transects (**a**, **b**) or experimentally set out in the field to control for extraneous factors (**c**–**e**). Prey captures were the total number of prey found in each observational web (**b**) or daily capture rates in experimental webs (**d**). Large prey captures are reported only for experimental webs where prey size was measured (**e**). Large prey are ≥ 6 mm. Means ± 1 SE



A. millefolium and $\bar{x} = 0.75 \pm 0.27$ for *C. maculosa*; $F_{1,27} = 0.46$, $P = 0.50$), and the number of spiderlings emerging from egg sacs ($\bar{x} = 19.9 \pm 6.7$ SE for *A. millefolium* and $\bar{x} = 25.7 \pm 7.7$ for *C. maculosa*; $F_{1,10} = 0.35$, $P = 0.57$) did not differ significantly between *C. maculosa* and *A. millefolium* substrates.

Experimentally introducing spiders onto paired *C. maculosa* and *A. millefolium* stems randomly placed within native grasslands confirmed correlative field observations. Web area was 2.9 times greater ($F_{1,29} = 50.99$, $P < 0.01$) and total capture rates were 2.3 times higher ($F_{1,29} = 61.58$, $P < 0.01$) on *C. maculosa* than on *A. millefolium* substrates (Fig. 3c,d). Additionally, spiders captured 4.2 times more of the larger prey items that are crucial for reproduction when

on *C. maculosa* compared to *A. millefolium* (MRBP = -8.23 , $P < 0.01$; Fig. 3e). The proportional increase in per capita prey capture rates between webs located in *A. millefolium* compared with *C. maculosa* did not differ between field observations and experiments that controlled for differences in web density (1.95-fold vs 2.34-fold increase in capture rates on *C. maculosa* from field observations and field experiments, respectively; $t = -1.54$, $P = 0.13$).

Discussion

Centaurea maculosa invasion into semi-arid grasslands of western North America illustrates that plants, through their

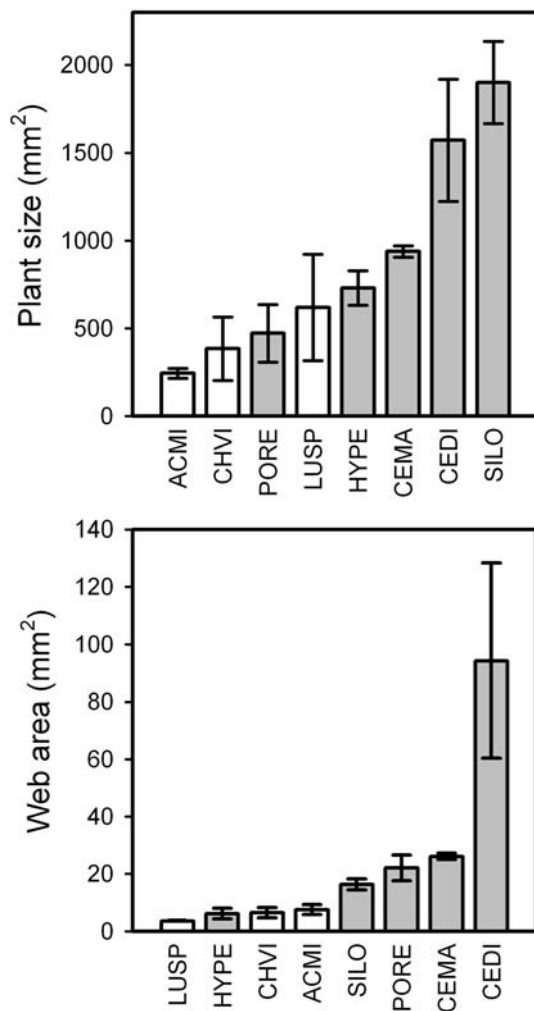


Fig. 4 Average plant and web size for eight substrates used by *Dictyna* spiders. ACMI *Achillea millefolium*, CHVI *Chrysopsis villosa*, PORE *Potentilla recta*, LUSP *Lupinus* spp., HYPE *Hypericum perforatum*, CEMA *Centaurea maculosa*, CEDI *Centaurea diffusa*, SILO *Sisymbrium loeselii*. White bars Native forbs, gray bars exotic forbs. Means $\pm$ 1 SE

architecture, can directly alter predator densities and behaviors in ways that substantially influence predator community structure, predator–prey interactions, and the potential impacts predators have on prey populations. Spiders that used vegetation as web substrates were collectively 38 times more abundant on *C. maculosa*-invaded transects than on native transects (Fig. 1a). Although all web spiders responded positively to *C. maculosa* invasion, *Dictyna* spp. appeared most affected, increasing 46–74 fold. This differential response among spider taxa resulted in a substantial shift in web spider community structure in invaded habitats. Moreover, *Dictyna* densities were elevated in *C. maculosa*-invaded grasslands for all 6 years monitored, so these effects appeared chronic. Since prey densities were similar on *C. maculosa*-invaded and uninvaded transects, differences

in spider densities could not be attributed to differences in prey abundance. The fact that 96% of *Dictyna* webs and 100% of webs of other spiders on the invaded transects were located on *C. maculosa* plants suggests that spider densities increased due to the increase in favorable substrate afforded by *C. maculosa*. Notably, after *C. maculosa*, the most common web substrates for *Dictyna* were other exotic forbs (Fig. 4a). These exotic forbs represented a diversity of plant families, including Asteraceae, Rosaceae, Brassicaceae, and Clusiaceae, suggesting different plant chemistries, pollinator communities, herbivore guilds, etc. However, these plants generally shared the architectural attributes of being larger and having more open and rigid flowering stalks than the native forbs, suggesting the novel architecture of these exotic forbs provides favorable substrates for native web building spiders.

In addition to the density response, *Dictyna* responded behaviorally to the architectural changes associated with invasion by *C. maculosa* and other exotic forbs by constructing larger webs than they did on native forbs (Fig. 4b). Field observations indicated that *Dictyna* spiders built 4.0 times larger webs on *C. maculosa* than on *A. millefolium*, their primary native substrate (Fig. 3). This increase in web size translated into a 2-fold increase in total prey captures in the *C. maculosa* webs. These observational results were corroborated by field experiments that controlled for potential differences between invaded and non-invaded sites in prey assemblages, vegetation communities, microsite conditions, and spider size. In these experiments, spiders built 2.9 times larger webs on *C. maculosa* stems than on *A. millefolium* stems that were paired and placed in native grasslands. Moreover, *Dictyna* webs on *C. maculosa* generated 2.3 times higher prey captures than on *A. millefolium*. This experiment also established that larger prey classes, which are crucial for spider survival and reproduction (Venner and Casas 2005), were captured over four times more frequently in the larger *C. maculosa* webs.

The increase in *Dictyna* web size on *C. maculosa* substrates appeared to be a behavioral response by individual spiders to increase foraging success. Individual spiders can modify web attributes as a behavioral response to variation in predation threats, prey availability, microclimatic conditions, and changing resource demands (Higgins 1990, 1992; Henschel and Lubin 1992; Heiling 1999; Venner et al. 2003). Thus, although changes in web size generally reflect foraging effort (Sherman 1994, 1999; Watanabe 2001; Venner and Casas 2005), *Dictyna* web size could differ among substrates for other reasons. In this study, predators appeared unimportant for *Dictyna*. The only known predators of these small spiders are wasp egg parasites (Wheeler and McCaffrey 1989), but parasitism was extremely low (wasps emerged from 4% of incubated egg

sacs). Prey availability did not differ in the observational studies, and prey communities and microclimate were controlled for in the field experiment by placing substrates 50 cm apart in a random arrangement relative to wind, solar inputs, and vegetation. It is possible that, even after controlling for microsite conditions and prey abundance in the field experiments, prey availability could differ between substrates at a very fine scale if prey associated with *C. maculosa* more than *A. millefolium* substrates. However, this seems unlikely given that substrates were dead stems from the previous year that were not actively growing, did not flower, were similar in color, and had likely leached potential chemical attractants through weathering. Additionally, insects introduced for *C. maculosa* biological control were excluded by removing the seedhead contents from *C. maculosa* stems, where some biocontrol insects overwinter, and by conducting the experiments in native grasslands away from *C. maculosa* infestations. As a result, only one of 472 prey items (0.2%) in experimental webs was a *C. maculosa* biocontrol insect (only 8% of prey items in observational webs were *C. maculosa* biocontrol insects). Thus, differences in web size were not likely due to differences in prey densities, predation risk, or microclimate. Rather, the increase in *Dictyna* web size on *C. maculosa* appeared to be a behavioral response by *Dictyna* to improve their foraging success and increase their chances of reproducing (Venner and Casas 2005)—a behavior made possible by exotic plant architecture.

Spiders are commonly food limited, and increased prey captures can increase spider fecundity and survival (Wise 1979; Sherman 1994; Adams 2000; Kreiter and Wise 2001; Venner and Casas 2005). The average number of egg sacs produced per spider and the average number of spiderlings emerging from egg sacs tended to be greater on *C. maculosa* substrates, but these differences were not statistically significant. Although spiders commonly increase clutch size in response to increased food (Wise 1975, 1979; Kreiter and Wise 2001), food addition did not alter clutch size in *D. volucris* (Blackledge and Wenzel 2001). It is possible that clutch size is fixed in these small spiders and increased food resources simply determine whether *Dictyna* can survive to maturity and produce offspring (Venner and Casas 2005). The probability of *Dictyna* reproducing increased substantially for spiders on *C. maculosa*. Nearly twice as many spiders produced clutches on *C. maculosa* (18.2%) versus *A. millefolium* (10.5%). Given the larger web size on *C. maculosa* and the resulting four-fold increase in larger prey items captured (Fig. 3e), these results support recent conclusions that large prey are critical for spiders to reproduce, and spiders construct larger webs to increase chances of capturing rare but crucial large prey (Venner and Casas 2005). Thus, *C. maculosa* may

increase *Dictyna* fitness relative to native substrates, in part, by allowing spiders to execute more effective hunting strategies, i.e., construct larger webs that increase their chances of capturing bigger prey and reproducing.

In substrate-dependent species like web spiders, increasing reproductive output will not affect population densities if the species is substrate-limited (i.e., if propagule output already exceeds substrate availability; Poulsen et al. 2007). In western Montana grasslands, web spiders appeared to be substrate-limited prior to *C. maculosa* invasion. On native transects, *Dictyna* densities did not increase following spiderling dispersal. In contrast, *Dictyna* densities doubled following spiderling dispersal on *C. maculosa*-invaded transects (Fig. 1b). Given the close proximity of *C. maculosa*-invaded and native transect pairs, dispersing spiderlings had comparable access to both habitats (transect length of 10 m exceeded the mean distance between transect pairs of 9.4 m). Therefore, the difference in the relative change in spider densities between the two habitats following dispersal must have been due primarily to differences in offspring establishment resulting from greater substrate availability on *C. maculosa* transects (*C. maculosa* was 52 times more abundant than *A. millefolium*). Thus, *C. maculosa* appeared to increase offspring survival by alleviating substrate limitations. Because *C. maculosa* also increased reproductive outputs, it is unclear exactly how increased reproduction versus decreased substrate limitation contributed to the total increase in *Dictyna* density. However, increasing reproductive outputs without relieving substrate limitation probably would have little effect on density.

Field experiments revealed that *Dictyna* spiders readily constructed larger webs on the more favorable but unfamiliar exotic substrate, even when spiders had not previously experienced *C. maculosa*. Experimental spiders also came from an isolated population with low likelihood of genetic exchange with *Dictyna* populations potentially adapted to *C. maculosa*. These results suggest that *Dictyna*'s dramatic success following *C. maculosa* invasion may be due to their ability to employ a preadapted trait (sensu Gould and Vrba 1982), web building for prey capture, to increase their fitness under new conditions. Preadaptation is sometimes casually invoked to explain invader success, but seldom tested (Mondor and Addicott 2007). Though not conclusive, my results suggest that preadaptation could play an important role in invasion ecology that warrants further study.

The direct effects of *C. maculosa* architecture on *Dictyna* density and behavior have potentially significant ramifications for *Dictyna* prey through indirect interactions. Field estimates indicated capture rates of *Dictyna* prey increased approximately 89 times from 0.03 prey captures/m² in native habitats to 2.71 prey captures/m² in

C. maculosa-invaded habitats. Notably, elevated predation rates may not always translate into changes in abundance of a prey species if mortality is compensatory. Although I estimated *Dictyna* prey densities on belt transects and found no difference in prey abundance, these data were indicative only of relative abundances of prey between habitats and not of *Dictyna* impact on prey because transects were established close together to control for prey differences and the vagile prey could readily move between transect pairs. Nonetheless, such dramatic increases in predation are likely to impact some prey populations in at least some years and could create strong selective pressures for predator avoidance within prey populations.

The data also suggest that indirect effects of *C. maculosa* architecture on *Dictyna* prey would transmit most strongly through density-mediated indirect interactions (DMII) versus behavioral pathways or trait-mediated indirect interactions (TMII) (Abrams et al. 1996). In *C. maculosa*-invaded habitats, prey capture rates increased 45 times due to increases in *Dictyna* web densities (the density effect) and 1.95 times due to higher per capita capture rates from larger webs (the trait effect). Hence, DMIIs appeared 23 times stronger than TMIIs. Because estimates of predation rates from field data did not experimentally isolate the independent contributions of TMIIs and DMIIs, potential interactions between TMIIs and DMIIs could confound these estimates (Werner and Peacor 2003; Griffin and Thaler 2006). However, independent estimates of trait effects from the field experiment (*C. maculosa*/*A. millefolium* per capita capture rates = 2.34), which controlled for density effects, did not differ significantly from estimates of trait effects from field observations (*C. maculosa*/*A. millefolium* per capita capture rates = 1.95), where web density varied naturally. Thus, there was no evidence for TMII $\times$ DMII interactions sufficient to change qualitative conclusions from the field estimates. Although additional experimental work is needed to more rigorously test this hypothesis, these results suggest that DMIIs may be substantially stronger than TMIIs under certain conditions. In contrast to the current study, which examined a nontraditional plant $\rightarrow$ predator $\rightarrow$ consumer pathway, studies indicating TMIIs are stronger than DMIIs have focused on traditional top-down predator $\rightarrow$ consumer $\rightarrow$ producer pathways (Werner and Peacor 2003; Schmitz et al. 2004; Pressier et al. 2005). These results suggest that the relative influence of TMIIs versus DMIIs on the net outcomes of indirect interactions may vary as a function of the trophic pathways examined.

This study of *C. maculosa* invasion into western North American grasslands offers several insights for invasion biology and community ecology. First, not all native species are negatively impacted by invaders; some greatly benefit. This research expands prior understandings (White

et al. 2006) with a detailed case study that documents both novel and conventional mechanisms by which an exotic plant can increase the abundance and fitness of native predators. At the community level, I show that entire guilds of species such as web building spiders can be positively affected by invasion, but that differential species-specific responses to invasion can cause their relative abundances, and hence community structure, to shift substantially. Such initial responses to invasions may substantively influence future community composition and structure. Positive direct effects of invaders on native species can lead to negative indirect effects on other natives. Although I document predation rates rather than population-level impacts of native spiders on their prey, the data illustrate how predator populations elevated by invasion may impact native prey. Additionally, such striking increases in predation rates could intensify selective pressures on prey populations even when species compensate at the population level. More generally, architecture is revealed as an important plant attribute that can directly affect not only predator density but also predatory behavior and foraging success, with important implications for indirect interactions. The finding that DMIIs may be stronger than TMIIs in this plant $\rightarrow$ predator $\rightarrow$ consumer pathway, suggests that trophic linkages may affect the relative importance of TMIIs and DMIIs. This research illustrates how investigations of biological invasions as natural experiments can generate novel hypotheses and lay the groundwork for future experiments that advance general understandings in ecology.

Acknowledgments I thank R. Fletcher, R. Callaway, T. Martin, J. Maron, Y. Ortega, L. Ruggiero, M. Schwartz, and anonymous reviewers for helpful comments. R. King advised on statistical analysis. Spiders were identified by P. Cushing and J. Slowik, Denver Museum of Nature and Science, Denver, CO. C. Crowder, R. Jensen, S. Sears, and J. Smith assisted in data collection. This work was funded by the National Science Foundation (DEB-0236061) and Bitterroot Ecosystem Management Research Project, USDA Forest Service. This research was conducted in compliance with United States laws.

References

- Abrams P, Menge BA, Mittelbach GG, Spiller D, Yodzis P (1996) The role of indirect effects in food webs. In: Polis GA, Winemiller KO (eds) Food webs: integration of patterns and dynamics. Chapman and Hall, New York, pp 371–395
- Adams MR (2000) Choosing hunting sites: web site preferences of the orb weaver spider, *Neoscona crucifera*, relative to light cues. *J Insect Behav* 13:299–305
- Blackburn TM, Casey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinctions and mammalian introductions on oceanic islands. *Science* 305:1955–1958
- Blackledge TA, Wenzel JW (2001) State-determinate foraging decisions and web architecture in the spider *Dictyna volucris* (Araneae Dictynidae). *Ethol Ecol Evol* 13:105–113

- Croll DA, Maron JL, Estes JA, Danner EM, Byrd GV (2005) Introduced predators transform subarctic islands from grassland to tundra. *Science* 307:1959–1961
- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166
- Denno RF, Gratton C, Peterson MA, Langellotto GA, Finke DL, Huberty AF (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83:1443–1458
- Gould SJ, Vrba ES (1982) Exaptation; a missing term in the science of form. *Paleobiology* 8:4–15
- Griffin CAM, Thaler JS (2006) Insect predators affect plant resistance via density- and trait-mediated interactions. *Ecol Lett* 9:333–346
- Hairton NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425
- Henschel JR, Lubin YD (1992) Environmental factors affecting the web and activity of a psammophilous spider in the Namib Desert. *J Arid Environ* 22:137–189
- Heiling AM (1999) Why do nocturnal orb-web spiders (Araneidae) search for light? *Behav Ecol Sociobiol* 46:43–49
- Higgins LE (1990) Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes* (Araneae: Araneidae). *J Insect Behav* 3:773–783
- Higgins LE (1992) Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae: Tetragnathidae). *J Insect Behav* 5:635–655
- Hunter MD, Price JS (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732
- Jackson RR (1978) Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae): I, social organization and web characteristics. *Rev Arachnol* 1:133–164
- Kreiter NA, Wise DH (2001) Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia* 127:417–424
- Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139:1–10
- Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc* 270:775–781
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Manly B, McDonald L, Thomas D (1993) Resource selection by animals. Chapman and Hall, London
- Mielke PW Jr, Kenneth BJ (2001) Permutation methods: a distance function approach. Springer, New York
- Mondor EB, Addicott JF (2007) Do exaptations facilitate mutualistic associations between invasive and native species. *Biol Invasions* 9:623–628
- Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118:240–262
- Ortega YK, Pearson DE (2005) Strong versus weak invaders of natural plant communities: distinguishing invasibility from impact. *Ecol Appl* 15:651–661
- Pasquet A, Leborgne R, Lubin Y (1999) Previous foraging success influences web building in the spider *Stegodyphus lineatus* (Eresidae). *Behav Ecol* 10:115–121
- Pearson DE, Callaway RM (2006) Biological control agents elevate hantavirus by subsidizing mice. *Ecol Lett* 9:442–449
- Polis GA, Strong DR (1996) Food web complexity and community dynamics. *Am Nat* 147:813–846
- Poulsen JR, Osenberg CW, Clark CJ, Levey DJ, Bolker BM (2007) Plants as reef fish: fitting the functional form of seedling recruitment. *Am Nat* 170:168–183
- Pressier EL, Blonick DL, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509
- SAS Institute (1999) SAS/STAT user's guide, version 8. SAS Institute Inc., Cary, NC
- Schmitz OJ (2006) Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology* 87:1432–1437
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect effects. *Ecol Lett* 7:153–163
- Sheley RL, Jacobs JS, Carpinelli MF (1998) Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Technol* 12:353–362
- Sherman PM (1994) The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive success. *Anim Behav* 48:19–34
- Story JM, Boggs KW, Good WR, White LJ, Nowierski RM (1995) Cause and extent of predation on *Urophora* spp. larvae (Diptera: Tephritidae) in spotted knapweed capitula. *Environ Entomol* 24:1467–1472
- Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445:202–205
- Venner S, Bel-Venner MC, Pasquet A, Leborgne R (2003) Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zygiella x-notata*. *Naturwissenschaften* 90:269–272
- Venner S, Casas J (2005) Spider web designed for rare but life-saving catches. *Proc R Soc Lond* 272:1587–1592
- Watanabe T (2001) Effects of web design on the prey capture efficiency of the Uloborid spider *Ooctonoba sybotides* under abundant and limited prey conditions. *Zool Sci* 18:585–590
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100
- White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. *Divers Distrib* 12:443–455
- Wheeler GS, McCaffrey JP, Johnson JB (1990) Developmental biology of *Dictyna* spp. (Araneae: Dictynidae) in the laboratory and field. *Am Midl Nat* 123:124–134
- Wheeler GS, McCaffrey JP (1989) Egg predation by *Catolaccus* prob. n. sp. (Hymenoptera, Pteromalidae) on the spider, *Dictyna coloradensis* (Dictynidae). *J Arachnol* 17:371–373
- Wise DH (1975) Food limitation of the spider *Linyphia marginata*: experimental field studies. *Ecology* 56:637–646
- Wise DH (1979) Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving spider species (Araneae: Araneidae). *Oecologia* 41:289–300