Journal of Insect Behavior, Vol. 18, No. 5, September 2005 (© 2005)
DOI: 10.1007/s10905-005-7013-8

Web-Construction Behavior of Linyphiid Spiders (Araneae, Linyphiidae): Competition and Co-Existence Within a Generalist Predator Guild

James D. Harwood[1,2] and John J. Obrycki[1]

Accepted December 17, 2004; revised March 15, 2005

---

*The web-construction behavior of three species of linyphiid spider (*Erigone autumnalis, Meioneta unimaculata *and* Bathyphantes pallida*) was studied in the laboratory to examine competition and co-existence within predator guilds. Competitive interactions between spiders potentially reduce their role in biological control. We tested the hypothesis that at high densities, intraguild competition for web-sites would occur but spatial separation of microhabitat would reduce interguild competition, thus allowing co-existence. High mortality and reduced web-size were observed at high* B. pallida *densities but Linyphiinae co-existed with Erigoninae which constructed webs at different strata. Competitive exclusion by larger individuals occurred between species whose microhabitat niche overlapped. The biocontrol potential of spider or arthropod predator guilds could ultimately be enhanced by maximizing the diversity of species whose niche axes vary.*

KEY WORDS: competition; displacement; web-location; intraguild predation; biological control; generalist predators.

INTRODUCTION

Spiders represent one of the most abundant components of the predatory arthropod fauna within terrestrial ecosystems throughout the world (Turnbull, 1973; Thompson, 1984; Wise, 1993). Their effectiveness at

---

[1] Department of Entomology, University of Kentucky, S-225 Agricultural Science Center North, Lexington, KY 40546-0091.
[2] To whom correspondence should be addressed. E-mail: James.Harwood@uky.edu.

0892-7553/05/0900-0593/0 © 2005 Springer Science+Business Media, Inc.

restricting pest populations, both alone and as part of the natural enemy complex, has been demonstrated many times (Riechert and Lockley, 1984; Sunderland *et al.*, 1997; Sunderland, 1999). Not only do web-building species exert control of pests through direct predation (pests constitute a significant proportion of their diet—Greenstone, 1999), but also through the low escape frequency of aphids from their webs (Carter *et al.*, 1982). It is the non-random web-location strategy of cereal spiders to areas where the density and biomass of prey (including pests) are high (Harwood *et al.*, 2001, 2003) and the frequency with which certain pests (such as aphids) fall from the crop (Sunderland *et al.*, 1986; Winder *et al.*, 1994; Losey and Denno, 1998) that enables these predators to exert significant control without directly feeding on the prey.

Generalist predators, such as spiders, have the advantage over specialist natural enemies in that they may engage in a sit-and-wait strategy (Murdoch *et al.*, 1985; Chang and Kareiva, 1999) and impact on pests once they arrive, by surviving on alternative, and often nutritious (Marcussen *et al.*, 1999; Bilde *et al.*, 2000), non-pest prey. Agustí *et al.* (2003) demonstrated the extent to which spiders preyed on Collembola in the field, which could maximize population growth and improve levels of biological control. The enhancement of predators through conservation biological control enables such predators to maintain favorable predator:pest ratios (Edwards *et al.*, 1979; Settle *et al.*, 1996), thereby reducing, or delaying, the exponential growth of pests until the arrival of specialist natural enemies. Although predator density can often be enhanced by within-crop habitat diversification (Samu *et al.*, 1999; Sunderland and Samu, 2000), this does not necessarily translate into improved biological control, due to competition, predator–predator interference and intraguild predation between natural enemies (Rosenheim *et al.*, 1993, 1995; Obrycki *et al.*, 1998; Snyder and Wise, 1999; Dinter, 2002; Snyder and Ives, 2003). Therefore, if populations of predators that compete for the same resource are enhanced such that a resource becomes limiting, negative interactions are likely to prevent the expected increase in pest suppression. It has also been demonstrated that alternative prey can reduce levels of direct predation on pests by linyphiid spiders in the field (Harwood *et al.*, 2004) and by lycosids in the laboratory (Madsen *et al.*, 2004). However, if natural enemy populations vary spatially and do not compete for the same resource, negative fitness consequences are unlikely, and the impacts of the predators on pests should be additive and synergistic, yielding significant levels of biological control (Losey and Denno, 1999; Dinter, 2002; Snyder *et al.*, 2004).

Within European agroecosystems, the Linyphiidae frequently account for >90% of the spider fauna (Nyffeler and Sunderland, 2003).

Despite their lower relative abundance in North America, where spider communities tend to be more diverse (Greenstone, 2001), their high rates of predation on aphids (Sunderland *et al.*, 1987; Harwood *et al.*, 2004) still implicate them as valuable biocontrol agents, especially early in the season. However, linyphiids are highly competitive in constructing web-sites (Samu *et al.*, 1996), non-randomly locating to areas of high prey density (Harwood *et al.*, 2001, 2003). Due to this competition, different species often build their webs at different strata (Sunderland *et al.*, 1986; Alderweireldt, 1994a) and compete for different prey resources (Harwood *et al.*, 2003), thereby reducing the likelihood of competitive interactions and intraguild predation. Thus, whilst increasing the density of conspecific natural enemies could reduce biological control due to competition (Agarwala *et al.*, 2003; Gnanvossou *et al.*, 2003), increasing diversity within a predator guild may not result in competitive interactions. Ultimately, the enhanced diversity could improve biological control due to co-existence at different strata; aerial web-building Linyphiinae would intercept and consume large numbers of falling aphids and the Erigoninae would feed on prey that initially evade capture (Harwood *et al.*, 2004). This additive effect would be further enhanced by ground-active spiders such as *Pachygnatha degeeri* Sundevall (Araneae: Tetragnathidae) which feed on aphids on the ground (Harwood *et al.*, 2005).

We tested the hypothesis that different subfamilies of linyphiid will construct webs at different microhabitat strata such that Erigoninae would build small webs on or close to the ground and the Linyphiinae would build larger webs higher up in the canopy. Furthermore, at increased conspecific densities, we would expect negative predator–predator interference resulting in increased mortality through intraguild predation and where space for web-sites was limiting, web-size would be reduced. In the Erigoninae, such interactions would be unlikely as these individuals tend to build small webs (Sunderland *et al.*, 1986; Alderweireldt, 1994a) close to the ground. In experimental arenas with different species of spider, we hypothesized that those individuals locating at different strata would co-exist and web-parameters be unaffected, ultimately improving the biocontrol potential of a diverse spider population.

MATERIALS AND METHODS

Study Organisms

Spiders belonging to the family Linyphiidae were collected from alfalfa, *Medicago sativa* L., fields at the University of Kentucky Spindletop

Farm. Female *Erigone autumnalis* Emerton (subfamily Erigoninae), *Bathyphantes pallida* (Banks) (subfamily Linyphiinae) and *Meioneta unimaculata* Banks (subfamily Linyphiinae) were collected individually by hand-held aspirator and transferred into clean triple-vented Petri dishes (diameter 5.5 cm). These three species are abundant in alfalfa (Culin and Yeargan, 1983a,b) and temporally overlap in seasonal occurrence (Culin, 1981). All dishes contained a Plaster of Paris and charcoal base to ensure high humidity and were maintained at 21°C ± SE 1°C on a 16:8 light:dark cycle. Spiders were provided with an *ad libitum* supply of prey (*Drosophila melanogaster* Meigen (Diptera: Drosophilidae) and mixed Collembola (Isotomidae, Entomobryidae, Sminthuridae and Poduridae)) for approximately 2 weeks prior to the experiment. Only females were used since they readily build webs (Sunderland *et al.*, 1986; Alderweireldt, 1994a), tend to be less active (Alderweireldt, 1994b) and, in terms of biological control, feed more extensively on pests in the field (Harwood *et al.*, 2004).

Experimental Arenas

All experiments were conducted in Perspex containers (150 mm height, 130 mm diameter) containing 40 mm of Miracle-Gro® Potting Mix (Miracle-Gro, Marysville, OH) planted with winter wheat (var. Clark) at a mean stand density of 40 stems per arena ($\sim$300 stems m^{-2}). The arenas were located within growth chambers under conditions described earlier. The high plant density ensured web-attachment sites were not a limiting factor during web-construction.

Measurement of Web-Construction Behavior and Data Analysis

Spiders were weighed and randomly assigned to one of nine treatments (Table I) which were designed to measure characteristics of web-construction under no competition (Treatments 1–3), web-construction under intraspecific competition (Treatments 4–6), and web-construction under interspecific competition (Treatments 7–9). Treatments were replicated 10 times and added to each arena was one spider (no competition), five individuals of the same species (intraspecific competition) or three individuals belonging to two different species (interspecific competition). Prior to the experiment, 20 *D. melanogaster* and ~100 mixed Collembola were added to each arena, and on a daily basis an *ad libitum* supply of prey (~20 *D. melanogaster* and 20 mixed Collembola) were added to all arenas. On no occasion were all Diptera or Collembola depleted from any arena.

Table I. Treatments in Which Spiders were Randomly Assigned to Measure Web-Construction Characteristics Under Varying Levels of Inter- and Intraspecific Competition

Treatment (code)	Spiders added to arenas
1 (Ea)	*Erigone autumnalis* ($n = 1$)
2 (Mu)	*Meioneta unimaculata* ($n = 1$)
3 (Bp)	*Bathyphantes pallida* ($n = 1$)
4 (Ea Comp)	*Erigone autumnalis* ($n = 5$)
5 (Mu Comp)	*Meioneta unimaculata* ($n = 5$)
6 (Bp Comp)	*Bathyphantes pallida* ($n = 5$)
7 (Ea + Mu)	*Erigone autumnalis* ($n = 3$) and *Meioneta unimaculata* ($n = 3$)
8 (Ea + Bp)	*Erigone autumnalis* ($n = 3$) and *Bathyphantes pallida* ($n = 3$)
9 (Mu + Bp)	*Meioneta unimaculata* ($n = 3$) and *Bathyphantes pallida* ($n = 3$)

Note. Each treatment was replicated 10 times, *n*: number of spiders added to each arena. Treatment codes are used to describe data presented in Figs. 1–3.

After 120 h, spiders were collected, mortality recorded and sheet webs were located using a fine atomizer spray. Only webs that contained spiders were categorized as web-sites, since some spiders leave their webs in active pursuit of prey (Alderweireldt, 1994a) or abandon these sites (Samu *et al.*, 1996) if they are perceived to provide insufficient prey. The height and area of webs were recorded. Web-size was determined by measuring the two longest dimensions and assuming them to be rectangular. This technique was employed by Sunderland *et al.* (1986) and produced comparable results to those obtained by Alderweireldt (1994a) who measured web-attachment sites and determined the area by digitizing the contours of the web.

In order to stabilize variances, data were log $(x + 1)$-transformed (spider weight, web-height and web-size) or arcsine-transformed (mortality rates) prior to analysis by one-way ANOVA, incorporating all treatments for which each spider was subjected. Data collected from Treatments 4–9 were calculated as means per arena prior to analysis. On occasions where the assumptions of ANOVA could not be met, analyses were made using a non-parametric Mann–Whitney *U*-test. All results are presented as means ± SE.

RESULTS

Web-Characteristics of Linyphiid Spiders Under No Competition

At the start of the experiments, there were no significant differences in mean weight of *E. autumnalis* ($F_{3,36} = 0.52$, $P = 0.671$), *M. unimaculata* ($F_{3,36} = 1.62$, $P = 0.201$) or *B. pallida* ($F_{3,36} = 0.40$, $P = 0.751$) among treatments.

Within single-species arenas, the erigonid spider *Erigone autumnalis*, constructed webs significantly closer to the ground (mean height = 0.13 ± 0.04 cm) than either of the Linyphiinae ($F_{2,26} = 140.88$, $P < 0.001$) (Fig. 1). LSD from ANOVA indicated that the two linyphiine species did not differ in height (mean height, *M. unimaculata* = 3.71 ± 0.25 cm; *B. pallida* = 3.96 ± 0.25 cm). However, web-size of all three species varied significantly; *B. pallida* (53.97 ± 8.37 cm^2) > *M. unimaculata* (23.93 ± 7.25 cm^2) > *E. autumnalis* (5.20 ± 0.49 cm^2) ($F_{2,26} = 30.40$, $P < 0.001$) (Fig. 2).

Web-Characteristics of *Erigone autumnalis*

The erigonid spider *E. autumnalis*, which constructed small webs close to the ground (Figs. 1a and 2a), showed no significant difference in height ($F_{3,36} = 0.44$, $P = 0.727$) or area ($F_{3,36} = 2.08$, $P = 0.120$) in any treatments with elevated conspecific and/or heterospecific competition (Figs. 1a and 2a). In microcosms containing an increased density of *E. autumnalis*, even if all five individuals constructed their webs in the same horizontal plane, only 20% of available space would have been occupied.

Web-Characteristics of *Meioneta unimaculata*

The Linyphiinae spider *M. unimaculata*, which constructed webs at a similar height to *B. pallida* under no competition but intermediate in size between this species and *E. autumnalis*, showed no reduction in web-size at increased levels of competition ($F_{3,35} = 0.28$, $P = 0.842$) (Fig. 2b). However, LSD from ANOVA indicated that although web-height did not vary in the presence of *E. autumnalis* or high levels of intraspecific competition, they were significantly lower in the presence of *B. pallida* ($F_{3,35} = 12.93$, $P < 0.001$) (Fig. 1b). Web-height of *M. unimaculata*, a smaller (Kaston, 1981) and lighter ($F_{1,78} = 113.11$, $P < 0.001$) spider compared to *B. pallida*, was vertically displaced 38% lower and they were competitively excluded from their natural web-location.

Web-Characteristics of *Bathyphantes pallida*

Web-size of *B. pallida*, a species which constructs large webs that intercept prey falling from above, varied significantly among treatments ($F_{3,36} = 4.67$, $P = 0.007$) (Fig. 2c). LSD from ANOVA indicated a highly significant 50% reduction in web-size at increased intraspecific competition

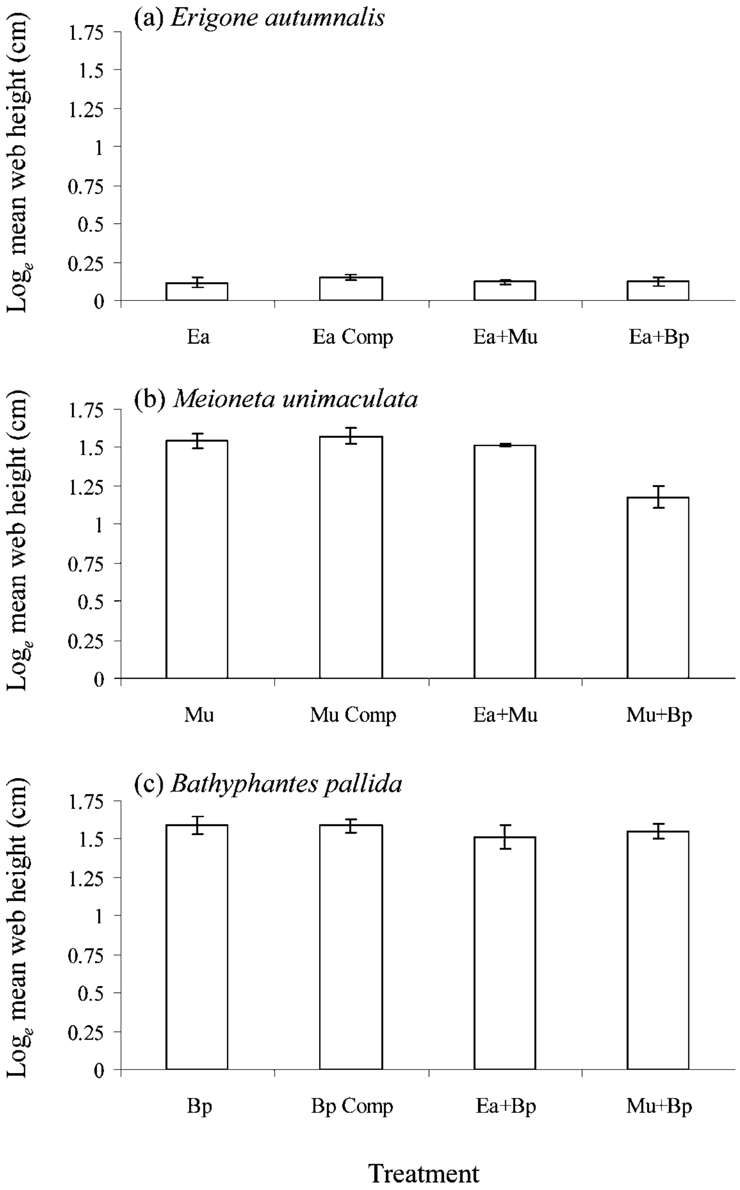
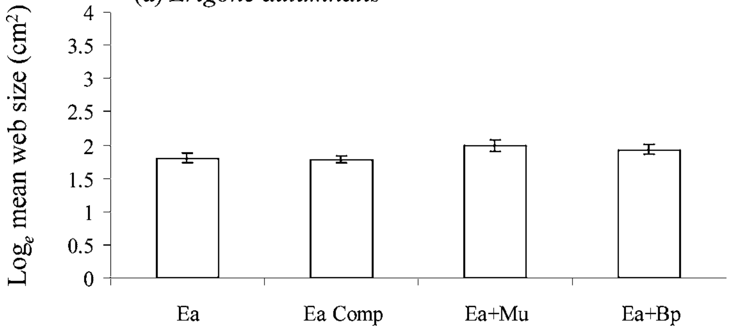
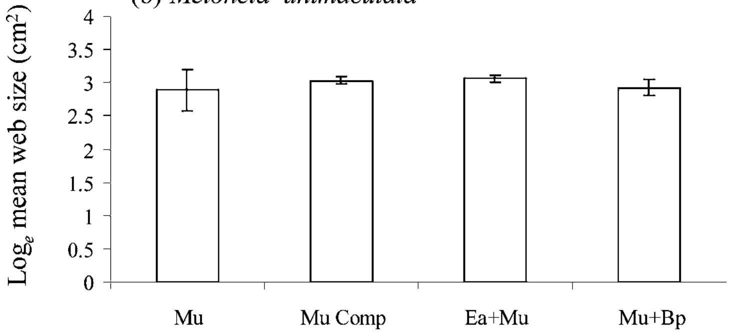


Fig. 1. Mean height of webs constructed by (a) *Erigone autumnalis*, (b) *Meioneta unimaculata* and (c) *Bathyphantes pallida*. Data are presented as means ± SE for spiders experiencing no competition (Ea, Mu, Bp), intraspecific competition (Ea Comp, Mu Comp, Bp Comp) and interspecific competition (Ea + Mu, Ea + Bp, Mu + Bp). Codes are described in Table I.

(a) *Erigone autumnalis*



(b) *Meioneta unimaculata*



(c) *Bathyphantes pallida*

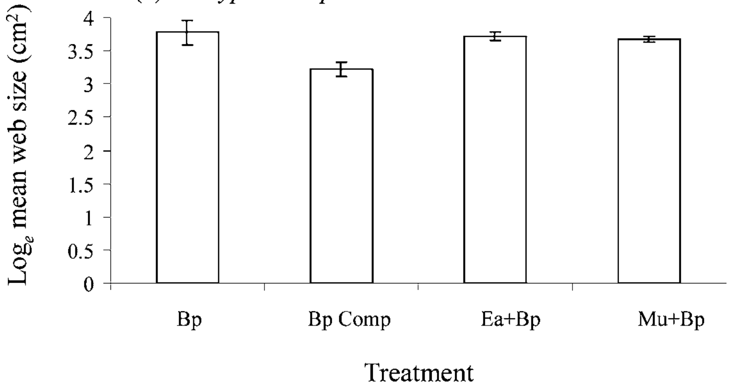


Fig. 2. Mean area of webs constructed by (a) *Erigone autumnalis*, (b) *Meioneta unimaculata* and (c) *Bathyphantes pallida*. Data are presented as means ± SE for spiders experiencing no competition (Ea, Mu, Bp), intraspecific competition (Ea Comp, Mu Comp, Bp Comp) and interspecific competition (Ea + Mu, Ea + Bp, Mu + Bp). Codes are described in Table I.

(Treatment 3) but not under lower levels of interspecific competition where other species of spider were also present (Treatments 8 and 9). It appeared that *B. pallida* was highly susceptible to web-size reduction at increased population densities when area was a limiting factor. The arena would have provided just 49% of required space if *B. pallida* were to build webs in a horizontal plane. The behavior of these Linyphiinae spiders appeared fixed in terms of selecting web-height which did not vary between treatments even though insufficient area was available ($F_{3,36} = 0.35$, $P = 0.791$) (Fig. 1c).

Rates of Mortality

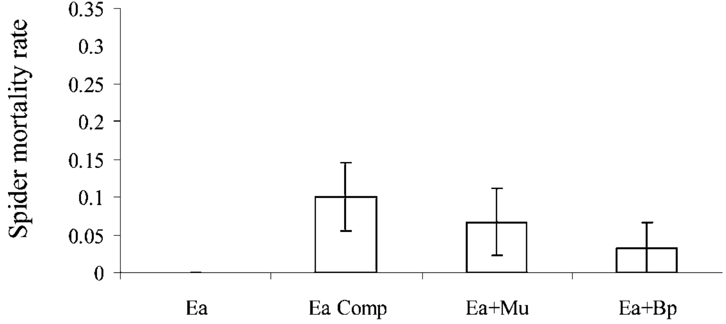
Under no competition, spider survival over the experimental period was extremely high—only one *M. unimaculata* died. However, at high population densities, the mean percentage mortality of *E. autumnalis* was significantly lower than that of *M. unimaculata* and *B. pallida* ($F_{2,27} = 4.00$, $P = 0.030$) (Fig. 3). LSD from ANOVA indicated no significant difference in mortality between the two Linyphiinae.

Interestingly, under reduced intraspecific competition but higher interspecific competition ($n = 3$ spiders compared to $n = 5$ spiders per arena—Treatments 7–9 compared to Treatments 4–6, respectively), there was no significant difference in mortality of *E. autumnalis* (Treatment 7: Mann–Whitney $U = 97.0$, $P = 0.571$; Treatment 8: $U = 91.0$, $P = 0.308$) or *B. pallida* (Treatment 8: $U = 89.0$, $P = 0.241$; Treatment 9: $U = 83.0$, $P = 0.104$). However, *M. unimaculata* experienced significantly reduced mortality in the presence of both *E. autumnalis* ($U = 71.0$, $P = 0.011$) and *B. pallida* ($U = 76.5$, $P = 0.034$) compared to high intraspecific competition arenas (Fig. 3).

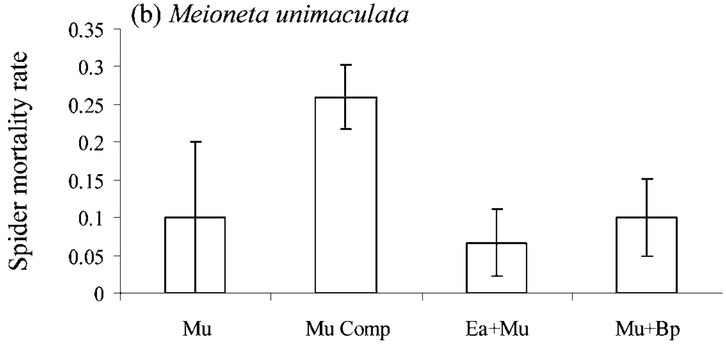
DISCUSSION

Implicating a guild of generalist predators as biocontrol agents cannot be based solely on the extent to which those individuals feed on pests in the field, but must account for competitive interactions which can negatively (or positively) affect their feeding habits. Linyphiid spiders, which feed on aphids in the field (Sunderland *et al.*, 1987; Harwood *et al.*, 2004) are also highly competitive for web-sites (Samu *et al.*, 1996), potentially leading to a reduced consumption of prey due to increased time spent defending good quality web-sites. The web-location behavior of three species reported here, one Erigoninae and two Linyphiinae, supports the hypothesis that whilst an enhanced density could increase competitive interactions between spiders

(a) *Erigone autumnalis*



(b) *Meioneta unimaculata*



(c) *Bathyphantes pallida*

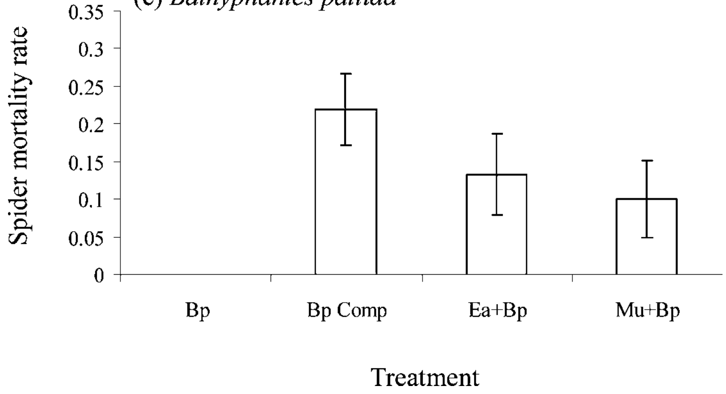


Fig. 3. Proportion (±SE) of (a) *Erigone autumnalis*, (b) *Meioneta unimaculata* and (c) *Bathyphantes pallida* experiencing mortality in arenas where spiders were subjected to no competition (Ea, Mu, Bp), intraspecific competition (Ea Comp, Mu Comp, Bp Comp) and interspecific competition (Ea+Mu, Ea+Bp, Mu + Bp). Codes are described in Table I.

within the same subfamily, increased diversity could support co-existence within a structurally diverse habitat.

Harwood *et al.* (2003) found that linyphiid spiders located non-randomly to areas where prey most likely to be captured by their individual hunting strategies would be located, such that Erigoninae, which leave webs in active pursuit of prey, were found in areas of high Collembola abundance, and Linyphiinae were found in areas where aerial prey (Diptera and Aphididae) were in greater abundance. The hypothesis that these two subfamilies would locate to strata where their prey are most likely to be captured was supported—Erigoninae constructed relatively small webs close to the ground whilst both Linyphiinae, which tend to be more dependent on their web to catch prey (Alderweireldt, 1994a), constructed larger webs higher in the canopy. Although webs of *M. unimaculata* were smaller than webs of *B. pallida*, possibly as a result of differences in body size, both Linyphiinae located to similar heights (in contrast to European species where *Meioneta rurestris* (C. L. Koch) webs were significantly lower than those of *Bathyphantes gracilis* (Blackwall)—Sunderland *et al.* (1986)). This could lead to high levels of competition at high densities. The Erigoninae, however, built webs close to the ground and competition with the Linyphiinae was unlikely. The height and area of *Erigone* and *Bathyphantes* webs were remarkably similar to those reported in European species (Sunderland *et al.*, 1986; Alderweireldt, 1994a) suggesting similar resource requirements across continents (or web-building constraints due to similar body sizes).

At increased densities where intraspecific competition for web-sites occurred, high mortality was observed in all species, although this was most evident in the Linyphiinae, whose larger webs put them at greatest likelihood of encountering other spiders constructing (or locating to) web-sites. *M. unimaculata* did not change web-size between treatments even though at very high conspecific densities (Treatment 2), webs would have covered 90% of available space, accounting for the increased mortality. This contrasts with *E. autumnalis*, where the horizontal area of the arena ($\sim$130 cm^2) provided sufficient space in which high densities of erigonid spiders co-existed. Even when all five spiders constructed webs in the same horizontal plane, total web-area would account for 20% of available space. Intraguild predation, which ultimately reduces a predator's efficiency in biological control (Hodge, 1999), was clearly occurring at high spider densities, even in the presence of suitable attachment sites and an abundance of prey. Interestingly, Dinter (2002) reported a lack of evidence for intraguild predation between the erigonid spiders *Erigone atra* (Blackwall) and *Oedothorax apicatus* (Blackwall) and lacewing larvae *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) in the presence of alternative prey, possibly because the Erigoninae are less competitive for web-sites and hunt for prey away from this central location. It appears that the Linyphiinae were competing not for prey resources or sites to attach their webs, but a horizontal area at a fixed height in which they would expect their large webs to catch significant quantities of prey.

Cannibalism can regulate certain spider populations (Wagner and Wise, 1996), but such a reduction would only be likely if the area in which predators are restricted is insufficient for hunting or web-site construction, as demonstrated here. The high levels of spider–spider interactions at web-sites in the field (Harwood *et al.*, 2001) implies that competitive interactions could occur in agroecosystems which, despite having lower densities than those used in the laboratory arenas (Nyffeler and Sunderland, 2003), may lead to cannibalism and population depletion. The Erigoninae had relatively low mortality at high population densities, since area was not a limiting factor and competitive interactions were only likely during hunting periods away from the web. Only *B. pallida* web-sizes were affected at higher population densities where horizontal area was insufficient, thereby forcing increased competition and mortality. This study provides little evidence that conspecifics avoid interactions with one another at high densities, as reported for parasitoids (Castelo *et al.*, 2003), despite the superabundance of prey and availability of attachment sites. Should web-size reduction occur in the field, where prey availability tends to be sub-optimal (Bilde and Toft, 1998; Harwood *et al.*, 2001, 2003), the fecundity and survival of *B. pallida* could decline significantly given that such spiders are unlikely to move away from the site in active pursuit of prey (Alderweireldt, 1994a). Therefore, the prey captured, per unit area, would be reduced and reproductive output decline, thus affecting their biocontrol potential due to increased mortality, reduced fecundity and increased emigration from the field which is important to the spiders ability to recolonize habitats (Weyman *et al.*, 2002; Thomas *et al.*, 2003).

Although high densities of individual species can occur in arable crops, most notably in Europe (Nyffeler and Sunderland, 2003), spider communities in North America can be extremely diverse (Greenstone, 2001); hence, the most likely interactions occur with other species of spider. In the presence of the small web-building *E. autumnalis*, web-characteristics of both Linyphiinae were unaffected due to web-construction at different microhabitat strata. The two subfamilies were clearly co-existing, experiencing low mortality, and utilizing different resources. The arenas in which *M. unimaculata* and *B. pallida* were located, however, demonstrated that at high densities of species which compete for the same resource (in this case spiders are competing for area in which to construct their web), the smaller *M. unimaculata* were competitively displaced downwards by the larger

B. pallida. Despite the smaller and possibly less-competitive spider being driven from its chosen microhabitat, such behavior may not result in depression of biocontrol activity since they will exploit prey resources at a different microhabitat. At high densities, these spiders clearly co-exist but the competitive displacement of *M. unimaculata* could have long-term fitness implications if prey availability at sub-optimal microhabitats is reduced.

ACKNOWLEDGMENTS

Support for this research was provided by the Kentucky Agricultural Experiment Station State Project KY099004. This is publication number 04-08-101 of the University of Kentucky Agricultural Experiment Station.

REFERENCES

Agarwala, B. K., Bardhanroy, P., Yasuda, H., and Takizawa, T. (2003). Effects of conspecific and heterospecific competitors on feeding and oviposition of a predatory ladybird: A laboratory study. *Entomol. Exp. Appl.* **106:** 219–226.

Agustí, N., Shayler, S. P., Harwood, J. D., Vaughan, I. P., Sunderland, K. D., and Symondson, W. O. C. (2003). Collembola as alternative prey sustaining spiders in arable systems: Prey detection within predators using molecular methods. *Mol. Ecol.* **12:** 3467–3476.

Alderweireldt, M. (1994a). Prey selection and prey capture strategies of linyphiid spiders in high-input agricultural fields. *Bull. Br. Arachnol. Soc.* **9:** 300–308.

Alderweireldt, M. (1994b). Day/night activity rhythms of spiders occurring in crop-rotated fields. *Eur. J. Soil Biol.* **30:** 55–61.

Bilde, T., and Toft, S. (1998). Quantifying food limitation of arthropod predators in the field. *Oecologia* **115:** 54–58.

Bilde, T., Axelsen, J. A., and Toft, S. (2000). The value of Collembola from agricultural soils as food for a generalist predator. *J. Appl. Ecol.* **37:** 672–683.

Carter, N., Gardner, S., Fraser, A. M., and Adams, T. H. L. (1982). The role of natural enemies on cereal aphid populations. Proceedings of the Entomology Group of the Association of Applied Biologists—Natural Enemies and Insect Population Dynamics. *Ann. Appl. Biol.* **101:** 190–195.

Castelo, M. K., Corley, J. C., and Desouhaut, E. (2003). Conspecific avoidance during foraging in *Venturia canescens* (Hymenoptera: Ichneumonidae): The roles of host presence and conspecific densities. *J. Insect Behav.* **16:** 307–318.

Chang, G. C., and Kareiva, P. (1999). The case for indigenous generalists in biological control. In Hawkins, B. A., and Cornell, H. C. (eds.), *Theoretical Approaches to Biological Control*, Cambridge University Press, Cambridge, pp. 103–115.

Culin, J. D. (1981). *The development, structure, and persistence of spider communities in alfalfa and soybean ecosystems*, Ph.D. Thesis, University of Kentucky.

Culin, J. D., and Yeargan, K. V. (1983a). Comparative study of spider communities in alfalfa and soybean ecosystems—Foliage-dwelling spiders. *Ann. Entomol. Soc. Am.* **76:** 825–831.

Culin, J. D., and Yeargan, K. V. (1983b). Comparative study of spider communities in alfalfa and soybean ecosystems—Ground-surface spiders. *Ann. Entomol. Soc. Am.* **76:** 832–838.

Dinter, A. (2002). Microcosm studies on intraguild predation between female erigonid spiders and lacewing larvae and influence of single versus multiple predators on cereal aphids. *J. Appl. Entomol.* **126:** 249–257.

Edwards, C. A., Sunderland, K. D., and George, K. S. (1979). Studies on polyphagous predators of cereal aphids. *J. Appl. Ecol.* **16:** 811–823.

Gnanvossou, D., Hanna, R., and Dicke, M. (2003). Infochemical-mediated intraguild interactions among three predator mites on cassava plants. *Oecologia* **135:** 84–90.

Greenstone, M. H. (1999). Spider predation: How and why we study it. *J. Arachnol.* **27:** 333–342.

Greenstone, M. H. (2001). Spiders in wheat: First quantitative data for North America. *Biocontrol* **46:** 439–454.

Harwood, J. D., Sunderland, K. D., and Symondson, W. O. C. (2001). Living where the food is: Web location by linyphiid spiders in relation to prey availability in winter wheat. *J. Appl. Ecol.* **38:** 88–99.

Harwood, J. D., Sunderland, K. D., and Symondson, W. O. C. (2003). Web-location by linyphiid spiders: Prey-specific aggregation and foraging strategies. *J. Anim. Ecol.* **72:** 745–756.

Harwood, J. D., Sunderland, K. D., and Symondson, W. O. C. (2004). Prey selection by linyphiid spiders: Molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. *Mol. Ecol.* **13:** 3549–3560.

Harwood, J. D., Sunderland, K. D., and Symondson, W. O. C. (2005). Monoclonal antibodies reveal the potential of the tetragnathid spider *Pachygnatha degeeri* (Araneae: Tetragnathidae) as an aphid predator. *Bull. Entomol. Res.* **95:** 161–168.

Hodge, M. A. (1999). The implications of intraguild predation for the role of spiders in biological control. *J. Arachnol.* **27:** 351–362.

Kaston, B. J. (1981). Spiders of Connecticut. *State Geol. Nat. Hist. Surv. Connecticut* **70:** 1020.

Losey, J. E., and Denno, R. F. (1998). The escape response of pea pahids to foliar-foraging predators: Factors affecting dropping behaviour. *Ecol. Entomol.* **23:** 53–61.

Losey, J. E., and Denno, R. F. (1999). Positive predator–predator interactions: Enhanced predation effects and synergistic suppression of aphid populations. *Ecology* **79:** 2143–2152.

Madsen, M., Terkildsen, S., and Toft, S. (2004). Microcosm studies on control of aphids by generalist arthropod predators: Effects of alternative prey. *BioControl* **49:** 483–504.

Marcussen, B. M., Axelsen, J. A., and Toft, S. (1999). The value of two Collembola as food for a cereal spider. *Entomol. Exp. Appl.* **92:** 29–36.

Murdoch, W. W., Chesson, J., and Chesson, P. L. (1985). Biological control in theory and practice. *Am. Nat.* **125:** 344–366.

Nyffeler, M., and Sunderland, K. D. (2003). Composition, abundance and pest control potential of spider communities in agroecosystems: A comparison of European and US studies. *Agric. Ecosyst. Environ.* **95:** 579–612.

Obrycki, J. J., Giles, K. L., and Ormond, A. M. (1998). Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia* **117:** 279–285.

Riechert, S. E., and Lockley, T. (1984). Spiders as biocontrol agents. *Annu. Rev. Entomol.* **29:** 299–320.

Rosenheim, J. A., Wilhoit, L. R., and Armer, C. A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* **96:** 439–449.

Rosenheim, J. A., Kaya, H. K., Ehler, L. E., Maroid, J. J., and Jaffee, B. A. (1995). Intraguild predation among biological control agents: Theory and evidence. *Biol. Control* **5:** 303–335.

Samu, F., Sunderland, K. D., and Szinetàr, C. (1999). Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: A review. *J. Arachnol.* **27:** 325–332.

Samu, F., Sunderland, K. D., Topping, C. J., and Fenlon, J. S. (1996). A spider population in flux: Selection and abandonment of artificial web-sites and the importance of interspecific interactions in *Lepthyphantes tenuis* (Araneae: Linyphiidae) in wheat. *Oecologia* **106:** 228–239.

Settle, W. H., Ariawan, H., Astuti, E. T., Cahyana, W., Hakim, A. L., Hindayana, D., Lestari, A. S., and Sartanto, P. (1996). Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* **77:** 1975–1988.

Snyder, W. E., and Ives, A. R. (2003). Interactions between specialist and generalist natural enemies: Parasitoids, predators, and pea aphid biocontrol. *Ecology* **84:** 91–107.

Snyder, W. E., and Wise, D. H. (1999). Predator interference and the establishment of genreralist predator populations for biocontrol. *Biol. Control* **15:** 283–292.

Snyder, W. E., Ballard, S. N., Yang, S., Clevenger, G. M., Miller, T. D., Ahn, J. J., Hatten, T. D., and Berryman, A. A. (2004). Complimentary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoid *Aphelinus asychis* on greenhouse roses. *Biol. Control* **30:** 229–235.

Sunderland, K. D. (1999). Mechanisms underlying the effects of spiders on pest populations. *J. Arachnol.* **27:** 308–316.

Sunderland, K. D., and Samu, F. (2000). Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders, with reference to spatial scale: A review. *Entomol. Exp. Appl.* **95:** 1–13.

Sunderland, K. D., Axelsen, J. A., Dromph, K., Freier, B., Hemptinne, J. L., Holst, N. H., Mols, P. J. M., Petersen, M. K., Powell, W., Ruggle, P., Triltsch, H., and Winder, L. (1997). Pest control by a community of natural enemies. *Acta Jutl.* **72:** 271–326.

Sunderland, K. D., Crook, N. E., Stacey, D. L., and Fuller, B. J. (1987). A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *J. Appl. Ecol.* **24:** 907–933.

Sunderland, K. D., Fraser, A. M., and Dixon, A. F. G. (1986). Distribution of linyphiid spiders in relation to capture of prey in cereal fields. *Pedobiologia* **29:** 367–375.

Thomas, C. F. G., Brain, P., and Jepson, P. C. (2003). Aerial activity of linyphiid spiders: Modeling dispersal distances from meteorology and behaviour. *J. Appl. Ecol.* **40:** 912–927.

Thompson, J. N. (1984). Insect diversity and the trophic structure of communities. In Huffaker, C. B., and Rabb, R. L. (eds.), *Ecological Entomology*, Wiley, New York, pp. 591–606.

Turnbull, A. L. (1973). Ecology of the true spiders (Araneomorphae). *Annu. Rev. Entomol.* **18:** 305–348.

Wagner, J. D., and Wise, D. H. (1996). Cannibalism regulated densities of young wolf spiders: Evidence from field and laboratory experiments. *Ecology* **77:** 639–652.

Weyman, G. S., Sunderland, K. D., and Jepson, P. C. (2002). A review of the evolution and mechanisms of ballooning by spiders in arable farmland. *Ethol. Ecol. Evol.* **14:** 307–326.

Winder, L., Hirst, D. J., Carter, N., Wratten, S. D., and Sopp, P. I. (1994). Estimating predation on the grain aphid *Sitobion avenae* by polyphagous predators. *J. Appl. Ecol.* **31:** 1–12.

Wise, D. H. (1993). *Spiders in Ecological Webs*, Cambridge University Press, Cambridge.