

Cannibalism and density-dependent mortality in the wolf spider *Pardosa milvina* (Araneae: Lycosidae)

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Abstract: Cannibalism is an important regulating mechanism in many terrestrial and aquatic arthropod communities. Spider ecologists have suggested that cannibalism with wolf spiders (Araneae: Lycosidae) in the genera *Schizocosa* and *Pardosa* is common and can act in population regulation. This hypothesis was tested with the species *Pardosa milvina* (Hentz), a small wolf spider that shows high densities in disturbance-driven ecosystems, including agricultural fields, throughout eastern North America. Under laboratory conditions, cannibalism was more common between pairs of *P. milvina* with the greatest differences in both mass and size. Field studies, in which we stocked natural densities, 2× natural densities, and 4× natural densities of *P. milvina* in enclosures placed in soybean fields, revealed that survival was lowest when conspecific density was highest, and larger individuals prevailed under high-density conditions. Thus, cannibalism likely plays an important role in governing populations of *P. milvina*, and the generality about the prevalence and importance of cannibalism with wolf spiders is supported.

Résumé : Le cannibalisme est un mécanisme important de régulation chez plusieurs communautés d'arthropodes terrestres et aquatiques. Les spécialistes de l'écologie des araignées croient que le cannibalisme est commun chez les lycoses (Araneae : Lycosidae) des genres *Schizocosa* et *Pardosa* et qu'il peut servir à contrôler les populations. Nous avons éprouvé cette hypothèse chez *Pardosa milvina* (Hentz), une petite espèce de lycose qui atteint de fortes densités dans les écosystèmes sujets aux perturbations, dont les champs cultivés, dans l'est de l'Amérique du Nord. En laboratoire, le cannibalisme est plus commun chez les paires de *P. milvina* qui affichent les plus fortes différences de masse et de taille. En nature, nous avons introduit dans des enclos placés dans des champs de soja des populations de *P. milvina* à la densité naturelle, à 2× la densité naturelle et à 4× la densité naturelle : la survie est minimale lorsque le nombre d'araignées de même espèce est maximal et les plus grands individus dominant dans les conditions de forte densité. Le cannibalisme joue donc vraisemblablement un rôle significatif dans le contrôle des populations de *P. milvina*; nos résultats confirment que le cannibalisme est répandu et important chez les lycoses.

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Introduction

Predation between members of the same guild (intraguild predation) can have significant consequences for food-web and population dynamics (Polis et al. 1989). Cannibalism, as one form of intraguild predation, is a widespread, natural phenomenon that occurs in many taxa (Elgar and Crespi 1992). Cannibalism is particularly prevalent in aquatic and terrestrial arthropod communities, where it can act to regulate populations (e.g., Jormalainen and Shuster 1997; Benoit et al. 1998; Briggs et al. 2000). Spiders (Araneae) frequently exhibit cannibalism, but they have mostly been studied as prime examples of sexual cannibalism (e.g., Prenter et al. 1994; Spence et al. 1996). Nonsexual cannibalism, defined here as one spider consuming a conspecific, is also common

with spiders and may be an important limiting factor, particularly in the Lycosidae (wolf spiders) (e.g., Edgar 1970; Hallander 1970; Wagner and Wise 1996; Samu et al. 1999; Anthony 2003).

Because spiders are generally considered to be food limited (Wise 1993), cannibalism among wolf spiders is more frequent when prey resources are scarce (Wagner and Wise 1997; Samu et al. 1999). Consuming conspecifics both provides nutrients and, because it eliminates a conspecific, may reduce intraspecific competition (Polis 1981, 1988; Wagner and Wise 1997). In addition there is evidence that cannibalism can have population-level consequences in wolf spiders. Wagner and Wise (1996) found cannibalism to regulate densities of young *Schizocosa ocreata* (Hentz) in a beech-oak forest and, in research not initially designed to test for canni-

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balism, Orazi and Grigarick (1989) suggested that high densities of *Pardosa ramulosa* (McCook) in rice fields are in part regulated by cannibalism.

This evidence suggesting that cannibalism can regulate wolf spider populations must be evaluated with other species in different habitats, especially with species that may be important natural enemies of pest species occurring in economically important crops. Here, intraguild predation may potentially negate the positive effects of natural biological control from generalist predators such as spiders (Snyder and Wise 2001). Our research focused on the occurrence, causes, and consequences of cannibalism in *Pardosa milvina* (Hentz), a species occurring in field crops and other disturbance-driven habitats throughout eastern North America (Dondale and Redner 1990; Young and Edwards 1990; Marshall and Rypstra 1999). One study on cannibalism has been done with *P. milvina* (Anthony 2003), but this laboratory research focused on the effects of genetic relatedness on cannibalism of young spiderlings (i.e., juveniles emerging from the egg sac and subsequently from their mother's abdomen) by adults, rather than potential population-level consequences of cannibalism between non-spiderlings. Our objectives were to (i) confirm that *P. milvina* exhibits cannibalism under laboratory conditions, (ii) determine whether the frequency of cannibalism depends on size ratios of interacting individuals, and (iii) assess whether populations of *P. milvina* in soybean fields are regulated by cannibalism in enclosures stocked with increasing densities of conspecifics.

Materials and methods

Pardosa milvina used for this study were collected in agricultural fields located at Miami University's Ecology Research Center (ERC) (Butler County, Oxford, Ohio, U.S.A.). Recently dispersed juveniles (spiderlings) were not collected. Field-caught spiders were placed in plastic vials (2.9 cm diameter, 6 cm high) and held in chambers at 23 °C, 70% RH, and 12 h light : 12 h dark cycle. Spiders were given water and fed fruit flies (*Drosophila melanogaster*) or domestic crickets (*Acheta domesticus*) ad libitum.

Testing the size-dependent occurrence of cannibalism was done in the laboratory, using plastic arenas (33 cm × 18.4 cm × 10.8 cm) filled with about 2 cm of pine bark mulch. Prior to starting the experiment, spiders were weighed on a Mettler balance and their carapace width was measured using an ocular micrometer. Carapace width is a measure of overall spider size (Hagstrum 1971). To standardize hunger levels, spiders were fed one cricket 24 h before experimentation.

Pardosa milvina were paired at random to encompass a range of differences in carapace width and mass. Trials involved releasing one individual from each pair into the arena, followed immediately by the second. After 24 h, the arenas were searched to determine coexistence (both spiders present and uninjured) or cannibalism (one spider consumed). Trials in which one spider was injured but not consumed were excluded, since it was difficult to assess whether these interactions may influence future fitness and (or) foraging behavior. Fifty trials were conducted between June and October 1996. Logistic regression tested if the occurrence of cannibalism was significantly related to differences in mass and carapace width of the interacting pairs.

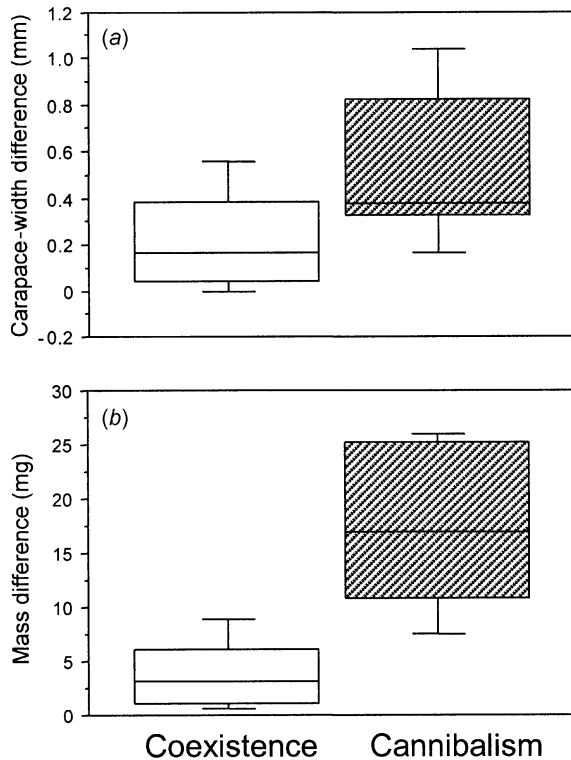
Testing population-level effects of cannibalism was done in the field. These experiments were completed in 1997 and 1998 in six 60 m × 70 m soybean fields at ERC. In each plot, three 1.5 m × 1.5 m enclosures were constructed from aluminum flashing (50 cm high, sunk 10 cm deep). The smooth surface of the aluminum flashing prevents spider immigration and emigration, as shown in a separate mark-recapture study (Buddle and Rypstra 2003). Ten to 12 soybean plants were contained by the aluminum flashing in each enclosure. Enclosures were filled with 9–12 cm of straw to ensure the habitat structure available to spiders was homogeneous across enclosures. We also added 50 g/m² of fruit fly medium (Formula 4–24, Carolina Biological Supply Company, Burlington, N.C., U.S.A.) about 2 weeks prior to experimentation to enhance potential prey (i.e., invertebrates, including Diptera and Collembola; see Chen and Wise (1997) and Marshall et al. (2000)). Although we did not quantify potential prey, based on past studies in the soybean system (Marshall et al. 2000), this process acts to increase and equalize prey in small habitat patches such as our enclosures. On 24 August 1997 and 21 August 1998, either 16, 32, or 64 female or immature *P. milvina* were stocked in enclosures (at a natural density (ND) of about 7.1 spiders/m² (Marshall and Rypstra 1999), 2× ND, and 4× ND). After 7 d, all enclosures were searched and *P. milvina* were counted. Ten individuals were randomly chosen from each enclosure and brought to the laboratory for measures of carapace width and abdomen width. Abdomen width was included to assess overall body condition and nutritional status (Jakob et al. 1996).

We modeled whether the proportion of *P. milvina* surviving per enclosure was a function of initial density by using logistic regression with a multistate categorical independent variable (i.e., density treatment) (Sokal and Rohlf 1995), including plot as a block effect. A random coefficients model (Littell et al. 1996) was used to examine the relationship between density, size (carapace width), and body condition while accounting for the variation between plots. Tests on body condition used abdomen width as the response variable and carapace width and initial density as covariates; thus, changes in abdomen width that would indicate nutritional status of individuals could be evaluated independently of overall spider size.

Results

Overall, the laboratory trials paired spiders that were about 2× different in mass (ratio of larger spider to smaller spider was 2.1 ± 0.19 (mean ± SE) and ranged from 1.02 to 9.15; 0.1–26 mg difference), and 1.2× different in carapace width (ratio of 1.2 ± 0.03 and ranged from 0 to 2.0; 0–1.042 mm difference). Cannibalism occurred in 5 trials pairing *P. milvina*, coexistence in 41 trials, and 4 trials were excluded owing to injury, but not death, of one spider. Cannibalism was more frequent with large differences in carapace width and mass between paired individuals (Fig. 1); these differences were significantly different as determined by logistic regression (carapace width, slope (±SE) = 3.68 ± 1.72 , $\chi^2 = 4.59$, df = 1, $P = 0.032$; mass, slope = 0.300 ± 0.11 , $\chi^2 = 7.88$, df = 1, $P = 0.005$). In all cases where cannibalism occurred, the larger spider preyed upon the smaller spider.

Fig. 1. Boxplots (95% confidence intervals, 25%–75% percentiles, median) showing coexistence ($n = 41$) and cannibalism ($n = 5$) between pairs of *Pardosa milvina* differing in carapace width (a) and mass (b).



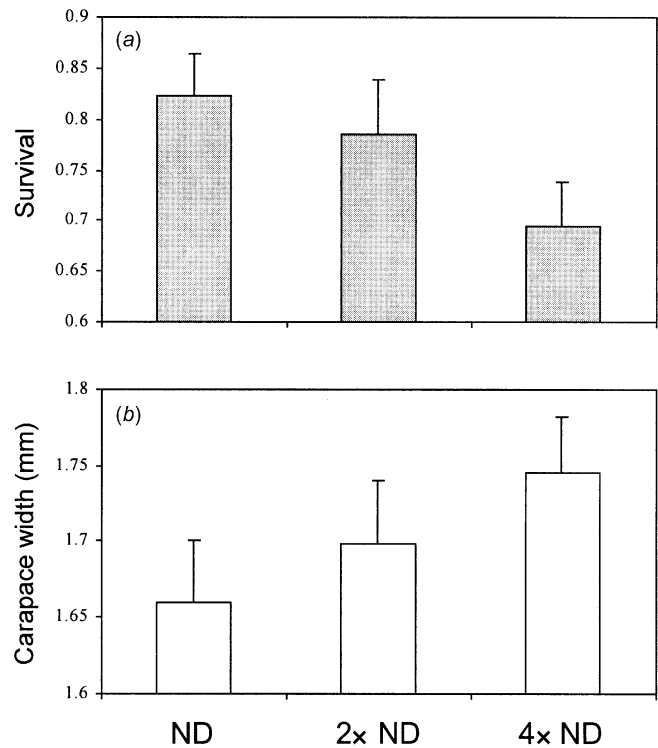
Under field conditions, *P. milvina* survival was significantly affected by initial density ($\chi^2 = 10.153$, $df = 2$, $P = 0.0062$). Although there was no significant difference in survival between ND and $2\times$ ND treatments ($\chi^2 = 0.556$, $df = 1$, $P = 0.455$), enclosures stocked with the highest ($4\times$ ND) densities of *P. milvina* had significantly lower survival than those stocked at $2\times$ ND ($\chi^2 = 5.52$, $df = 1$, $P = 0.0188$) and at ND ($\chi^2 = 6.21$, $df = 1$, $P = 0.0127$) (Fig. 2). The random coefficients model showed survivors in high-density treatments had the largest carapace width (Table 1, Fig. 2). The analysis of body condition showed that carapace width was a significant covariate (Table 1) and that overall body condition was not significantly different across density treatments (Table 1).

Discussion

Our results show cannibalism is potentially an important density-dependent mortality factor regulating populations of *P. milvina*. Under laboratory conditions, cannibalism is more common between individuals showing large differences in mass and size, and in enclosures placed in soybean fields, survival was lowest and larger individuals prevailed when *P. milvina* densities were increased.

In intraguild predation and cannibalism, larger individuals typically prey upon smaller individuals (see Polis (1988) and references therein). Our results are consistent with this pattern, and are supported by past research with wolf spiders (Samu et al. 1999; Anthony 2003) and other arachnids (e.g., scorpions, Polis 1980; Polis and McCormick 1987). Our overall rate of cannibalism in the laboratory (11%; 5 of 46

Fig. 2. Mean (\pm SE) survival (a) and carapace width (b) of *P. milvina* by experimental density treatment (natural density (ND) of 7.1 spider/m²). Survival measures are per plot ($n = 6$) and carapace-width measures are per individual spider ($n = 60$ (ND), 60 ($2\times$ ND), and 59 ($4\times$ ND)).



trials) was lower than reported elsewhere; previous studies with *Pardosa* spp. suggest cannibalism occurs between 15% and 26% of the time (Edgar 1970; Hallander 1970; Samu et al. 1999). Samu et al. (1999) report the largest cannibalism rate (26%, 29 of 110 trials) in laboratory trials with *Pardosa agrestis* (Westring). One reason for our lower cannibalism rate compared with Samu et al. (1999) may be because our mean in overall mass ratio between pairs of spiders was lower (a mean of 2.1 compared with a mean of 2.45 for Samu et al. (1999)). Since larger mass differences tend to result in a higher frequency of cannibalism, if we completed more trials with larger mass differences between *P. milvina* pairs we expect a higher percentage of cannibalistic interactions. Alternatively, our laboratory arenas were much larger and offered a more complex substrate (mulch) than the petri dishes used by Samu et al. (1999); more complexity and larger area may have led to our lower cannibalism rates. Together with research by Anthony (2003), who found cannibalism to occur between adult *P. milvina* and their spiderlings, it is clear that virtually all life stages of *P. milvina* are at risk of becoming prey to a conspecific.

Results from the laboratory suggest that if cannibalism is an important mortality factor under field conditions, we might expect larger *P. milvina* to prevail under more natural conditions. We found that this occurs along a gradient of increasing densities. Elevating the number of conspecifics in enclosures increases the frequency of intraspecific interactions at the same time that pressure on resources is higher (i.e., exploitation competition) and the probability of physically

Table 1. Results from linear mixed model relating carapace width and body condition of surviving *Pardosa milvina* to initial density stocked in field enclosures.

| | Estimate | SE | <i>T</i> | df* | <i>P</i> |
|-----------------------------|----------|--------|----------|------|----------|
| Carapace width | | | | | |
| Intercept | 0.4722 | 0.05 | 9.39 | 6.62 | <0.0001 |
| Density treatment | 0.0011 | 0.0005 | 1.97 | 6.74 | 0.0460 |
| Body condition [†] | | | | | |
| Intercept | -0.0211 | 0.0413 | -0.51 | 35.2 | 0.6115 |
| Carapace width (mm) | 0.9265 | 0.0644 | 14.38 | 149 | <0.0001 |
| Density treatment | -0.00008 | 0.0005 | -0.14 | 11.6 | 0.8874 |

Note: Parameter estimate, SE, *t* value, df, and *P* value are given for tests on fixed effects. Plots were included as a random effect (not shown).

*Degrees of freedom for *F* and *t* tests from the mixed models were obtained using a Satterthwaite approximation (Littell et al. 1996).

[†]ANCOVA with abdomen width as the response variable, carapace width and density as covariates; carapace width × density interaction was not significant ($F_{[1,43.2]} = 0.62$, $P = 0.437$), and therefore was removed from the final model.

encountering more conspecifics increases (i.e., interference competition). If encounter rates increase, and more spiders are present, the number of interactions between individuals differing in size will also increase. Thus, the probability of cannibalistic interactions increases and larger individuals become larger as they consume their conspecifics. The low survival under high densities in our field enclosures also implicates cannibalism as one of the main density-dependent mortality factors regulating *P. milvina* populations.

Wise and Wagner (1992) also report density-dependent survival of the wolf spider *S. ocreata*. In this work, however, increasing spider density resulted in lower growth rates, and together with effects on prey, Wise and Wagner (1992) suggest exploitative competition is occurring in their study system. The lower growth rates under high-density conditions may be a result of frequent interactions (interference, including possible cannibalism) between conspecifics (Wise and Wagner 1992). Our study suggests that under high-density conditions, where prey is presumably nonlimiting, interactions between individuals may result in higher cannibalistic events, with larger spiders surviving. The different results between our study and Wise and Wagner's (1992) research may have been due to the different life stage of spiders used in field trials; we use primarily larger immature, subadult, and adult spiders, whereas Wise and Wagner (1992) concentrated on young spiderlings. Since adult and immature spiders may behave and forage differently (Wise 1993), it is perhaps expected that results differ. Also, Wise and Wagner (1992) completed their work over an entire season, whereas our short-term experiment may not have allowed for all potential growth effects to be detected.

It is unlikely that starvation was a significant mortality factor in our enclosures, as *P. milvina* can withstand starvation for >14 d (S.E. Walker, personal observation; also see Walker et al. 1999), and we supplemented enclosures with prey-enhancing medium, which has consistently been shown to increase prey that is suitable for spiders (Chen and Wise 1997; Marshall et al. 2000). Furthermore, body condition did not vary across density treatments, which verifies that all spiders were of approximately the same nutritional state at the end of the experiment. Therefore, spiders in high-density treatments either consumed fewer prey and more con-

specifics or these individuals depleted prey faster than individuals in low-density treatments. Either way they ended up supplementing their diet with conspecifics, which implicates cannibalism as an important mechanism regulating *P. milvina* populations.

It is also possible that other natural enemies could have affected *P. milvina* in a density-dependent manner, especially since spider wasps (e.g., Hymenoptera: Pompilidae) and other flying predators and parasitoids had access to the study enclosures. Data on these interactions are generally lacking in the literature (Wise 1993), so it is difficult to speculate on whether these effects could indeed operate in a density-dependent fashion. Given the relatively short-term nature of our field experiment, however, it is doubtful such predators would be able to respond strongly, and we believe other natural enemies likely affected all enclosures in a similar fashion.

Wolf spiders are among the dominant ground-dwelling arthropods in numerous habitat types, and many species (particularly in the genus *Pardosa*) can rapidly colonize newly disturbed and early-successional habitats (e.g., Dondale and Redner 1990; Marshall and Rypstra 1999; Buddle et al. 2000; Marshall et al. 2000). The genus *Pardosa* is known to track habitat patches rich in prey and structure (Marshall et al. 2000), and can depress numbers of suitable prey such as Collembola (Wise and Wagner 1992; Buddle 2002). In our enclosures, where habitat and prey were presumably nonlimiting, their populations appear self-regulating. This study provides evidence to support the hypothesis that wolf spider survival is, at least in part, regulated by cannibalism (e.g., Wagner and Wise 1996), and ecological studies with generalist predators should consider cannibalism as a potential intraspecific regulating factor.

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