

# Ontogenetic shifts in competitive interactions and intra-guild predation between two wolf spider species

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**Abstract.** 1. The wolf spiders (Araneae: Lycosidae) *Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz co-occur in soybean fields of south-west Ohio, U.S.A. As adults, *Hogna* is the larger species and has the competitive advantage in most interactions; due to differing phenologies, however, their size-classes frequently overlap and as such there is potential for shifts in competitive ability and intra-guild predation. The hypothesis that competitive interactions and intra-guild predation will favour *Pardosa* when *Pardosa* is similar-sized, or has a size advantage over *Hogna*, was tested in laboratory and field experiments.

2. Studies in laboratory arenas, pairing similar-sized individuals of these species and *Hogna* spiderlings with larger spiders of both species, revealed that intra-guild predation seldom occurs with similar-sized *Hogna* and *Pardosa*, however *Pardosa* will consume small *Hogna* individuals in laboratory arenas.

3. Field experiments involved stocking high densities (50 m<sup>-2</sup>) of *Pardosa* and *Hogna* in enclosures placed in soybean fields. In experiments with spiders of similar size, no interspecific effects were uncovered, but an intraspecific effect was found for *Pardosa* as its survival and weight gain were lower in the presence of more conspecifics. Large *Hogna* or *Pardosa* had no effect on the survival or weight gain of *Hogna* spiderlings.

4. Although *Hogna* is a better competitor as an adult, it has no advantage over *Pardosa* when their size-classes overlap, and *Pardosa* effects on *Hogna* may be inconsequential under field conditions. Therefore, the co-existence of these species is fostered by the fact that there are few negative interspecific interactions during their ontogeny.

**Key words.** Density effects, intraspecific competition, Lycosidae, soybean fields, species co-existence.

## Introduction

Interactions among co-existing predators of the same guild are complicated, as competition and intra-guild predation can act simultaneously (Polis *et al.*, 1989). These interactions are confounded further by ontogenetic shifts in resource or habitat use (Werner & Gilliam, 1984; Wissinger, 1992). Changes or even reversals in competitive ability during development may have significant consequences for future populations, as documented for a variety of taxa including fish, salamanders, mantids, spiders, and scorpions (Spiller, 1984; Polis & McCormick, 1987; Walls, 1990; Osenberg *et al.*, 1992; Bergman & Greenberg, 1994; Snyder & Hurd, 1995).

Spiders (Araneae) are generalist predators with high resource overlap (Wise, 1993; Nyffeler *et al.*, 1994), and

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thus represent an ideal taxon for studying how intra-guild predation and competition vary with ontogeny. Intra-guild predation has been documented as an important feature structuring communities that contain spiders (e.g. Polis & McCormick, 1986; Wise, 1993; Hodge & Marshall, 1996; Halaj *et al.*, 1997; Wise & Chen, 1999). There are relatively few examples where competition plays a key role in governing spider populations, but most of the early work was conducted with web-building spiders (Wise, 1993). The few studies conducted with hunting or cursorial spiders suggest that they compete for resources (Wise & Wagner, 1992) or space (reviewed by Marshall & Rypstra, 1999a), but certainly not in all circumstances (Buddle, 2002).

Ontogenetic shifts in competitive ability and/or intra-guild predation have seldom been studied in spider communities. This is surprising because such data will help to uncover how spider assemblages are structured, which is of significant value given the importance of spiders in terrestrial food webs (Moulder & Reichle, 1972; Riechert & Bishop, 1990; Wise, 1993; Mason *et al.*, 1997; Lawrence & Wise, 2000). Spiller's (1984) research with two web-building spider species showed that competitive ability is mediated by body size, with the larger species out-competing the smaller species, but that the competitive advantage is reversed later in the season when the poorer competitor is larger due to asynchronous phenologies (Spiller, 1984).

The work reported here focused on how intra-guild predation and competition vary during certain stages in the ontogeny of two wolf spider species (Lycosidae): *Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz (henceforth *Hogna* and *Pardosa*). These are the dominant spider species inhabiting the ground-layer of agricultural fields in south-west Ohio, U.S.A. (Marshall & Rypstra, 1999b) and elsewhere (Young & Edwards, 1990). Adult *Hogna* typically weigh >300 mg and have densities below  $1\text{ m}^{-2}$  whereas adult *Pardosa* are 20–40 mg and can attain densities above  $5\text{ m}^{-2}$  (Marshall & Rypstra, 1999b). Due largely to the size discrepancy, adult and later instar *Hogna* are the superior competitors (Marshall & Rypstra, 1999a; Marshall *et al.*, 2000) and will readily consume *Pardosa* (Persons *et al.*, 2001), however this size advantage may be negligible or even reversed at other times in *Hogna* ontogeny as size-classes of these species frequently overlap in natural populations (i.e. first- to third- or fourth-instar *Hogna* and sub-adult to adult *Pardosa*) due to asynchronous and differing life cycles (Marshall & Rypstra, 1999b). The hypothesis is that when *Pardosa* and *Hogna* are similar-sized or when *Pardosa* has a size advantage, competitive interactions and intra-guild predation will favour *Pardosa*, or at least will be negligible compared with the interactions between large *Hogna* and *Pardosa*.

In a laboratory experiment, the propensity of late-instar or adult *Pardosa* to prey on *Hogna* in similar or smaller size-classes was quantified. The frequency of aggressive interactions would indicate the likelihood that there could be a reversal of intra-guild roles in a more natural setting. In field enclosures, survival and foraging success of late-instar or adult *Pardosa* on their own and with *Hogna*

in similar or smaller size-classes were quantified. These experiments provided a more realistic measure of the role of *Pardosa* as an intra-guild predator on *Hogna*. In addition, any competitive effects within or between the two species in these life stages, as revealed through differential access to food resources, could be compared.

## Materials and methods

### Study organisms

*Pardosa* and *Hogna* occur in disturbance-driven ecosystems (e.g. littoral zones, agro-ecosystems) throughout eastern North America (Kaston, 1981; Dondale & Redner, 1990; Young & Edwards, 1990; Marshall & Rypstra, 1999b). These species are sympatric in the agricultural fields at Miami University's Ecology Research Center (south-west Ohio, U.S.A., 39°22'N, 80°43'W). *Pardosa* are smaller, may reach higher densities, and are more active foragers than *Hogna* (Dondale & Redner, 1990; Marshall & Rypstra, 1999b; Walker *et al.*, 1999). Research has established that *Hogna* is the superior competitor, although it is limited by its ability to colonise agricultural fields (Marshall *et al.*, 2000). *Pardosa* is the superior coloniser, and is able to track prey abundance and preferred habitat patches rapidly (Marshall *et al.*, 2000). Each species detects chemical cues left behind by the other (i.e. silk and faeces) and uses information in those cues to change its behaviour. Large *Hogna* use cues to find and prey on *Pardosa* (Persons & Rypstra, 2000) and small *Pardosa* change their behaviour in the presence of cues from *Hogna* to reduce the likelihood of predation (Persons *et al.*, 2001). These findings suggest that intra-guild predation has been an important selective force shaping interactions among adults.

*Pardosa* used for experimentation were collected from agricultural fields at the Ecology Research Center. Individuals were housed in plastic vials (2.9 cm diameter, 6 cm height) and were given water and fed fruit flies *Drosophila melanogaster* or domestic crickets *Acheata domestica* at least once a week. *Hogna* specimens were obtained primarily from laboratory-reared populations. *Hogna* were housed in plastic cups (6 cm diameter, 3.5 cm height) with a 1-cm layer of moist peat moss on the bottom and fed primarily crickets (twice a week). All spiders were maintained at 23 °C and 70% RH under a LD 12:12 h cycle prior to experimentation.

### Laboratory experiment: relative likelihood of intra-guild predation

To standardise hunger levels, spiders were fed one cricket 24 h before the start of the experiments. On the day of the experiment, spiders were weighed to the nearest 0.1 mg on a Mettler AE balance (Mettler Instrument Corporation, Hightstown, New Jersey.). Experiments were conducted in plastic arenas, measuring  $33.0 \times 18.4 \times 10.8$  cm, filled with  $\approx 2$  cm of pine bark chip substrate. Arenas were misted with

water before each experimental run to ensure that animals were not water-stressed. Arenas were maintained under a LD 12:12 h cycle at 23 °C and 70% RH.

The first experimental treatment involved pairing *Pardosa* with similar-sized *Hogna*. The mean ( $\pm$ SE) per cent weight difference between the species was  $1.02 \pm 0.55\%$  ( $n=27$ ) (maximum difference of 12.8%). Each pair was placed in an arena within 10 s of each other, then the arena was closed and left undisturbed. After 24 h, the arenas were searched thoroughly for spiders. The outcome of the interaction between each pair was classified as either aggressive (injury or death of one individual) or non-aggressive (both spiders, alive and uninjured). Twenty-seven pairs were tested between July 1997 and April 1998.

To test whether *Pardosa* will prey on smaller *Hogna*, a second experiment paired adult female or penultimate *Pardosa* with *Hogna* spiderlings. *Hogna* were on average  $73.4 \pm 2.34\%$  ( $n=40$ ) the weight of *Pardosa* (range: 37.8–91.2%). Forty trials were completed between September and November 1997.

Fisher's two-tailed Exact Test (Sokal & Rohlf, 1995) was used to analyse the resulting  $2 \times 2$  contingency table (spider size pairing and aggressive vs. non-aggressive outcome). The null hypothesis was that the proportion of aggressive interactions between *Pardosa* and *Hogna* of similar size was the same as the proportion of aggressive interactions between *Pardosa* paired with *Hogna* spiderlings.

#### Field experiments: study area and enclosure design

Field experiments were conducted at the Ecology Research Center, in four soybean fields (each measuring  $60 \times 70$  m) selected randomly from an array of 12. Fields were separated by  $>15$  m grass border. Soybean fields were selected for study as they have a well understood spider fauna (Young & Edwards, 1990; Rypstra & Carter, 1995; Marshall & Rypstra, 1999b), are a dominant agro-ecosystem in south-west Ohio, are structurally simple, which facilitates insights into ecological processes (Wissinger, 1997; Marshall & Rypstra, 1999a), and naturally contain relatively high densities of *Hogna* and *Pardosa* (Marshall & Rypstra, 1999b).

In spring 1997, three  $0.20 \text{ m}^2$  circular enclosures were positioned randomly between rows of soybeans in each study field. Enclosures were constructed from aluminium flashing, and were sunk  $\approx 8$  cm into the ground. About 42 cm projected above ground, and the top edge was deflected inward to form an 8-cm overhang to prevent spider immigration and emigration. The top was left open so that potential prey (e.g. flying insects) could move freely into enclosures. The vegetation and ground debris were removed from inside the enclosures before the experiments began, and water was poured inside to set the enclosure firmly into the soil and to level out the soil. Five centimetres of straw were spread over the soil to provide structural heterogeneity and to moderate temperature and moisture

extremes. Before the experiment began, a visual search was conducted to remove other spiders from the enclosures.

#### Field protocols: testing for inter- and intra-specific interactions

*Hogna* and *Pardosa* used in field experiments were fed one cricket 24 h before the experiments began, and spiders were weighed to the nearest 0.1 mg about 10 h before being placed in field enclosures. Individuals that were large enough were marked with a small dot of non-toxic paint in order to differentiate spiders that were placed in enclosures from accidental immigrants.

The first field experiment was designed to test for inter- and intra-specific interactions between *Pardosa* and *Hogna* of similar size. Densities were elevated to  $50 \text{ m}^{-2}$  by adding the following combinations of spiders to the field enclosures: (1) 10 *Pardosa* (average weight, experiment-wide,  $10.78 \pm 0.58$  mg,  $n=80$ ), (2) 10 *Hogna* ( $24.70 \pm 0.62$  mg,  $n=80$ ), (3) five *Pardosa* ( $16.65 \pm 0.72$  mg,  $n=40$ ) with five *Hogna* ( $16.49 \pm 0.54$  mg,  $n=40$ ). Treatments were applied randomly within each field (four replicates each, 12 enclosures total). Establishing treatments involved introducing spiders into the enclosures at approximately 19.00 hours. After 5 days, the enclosures were searched thoroughly between 09.00 and 12.30 hours. The surviving spiders were counted, brought to the laboratory, and weighed.

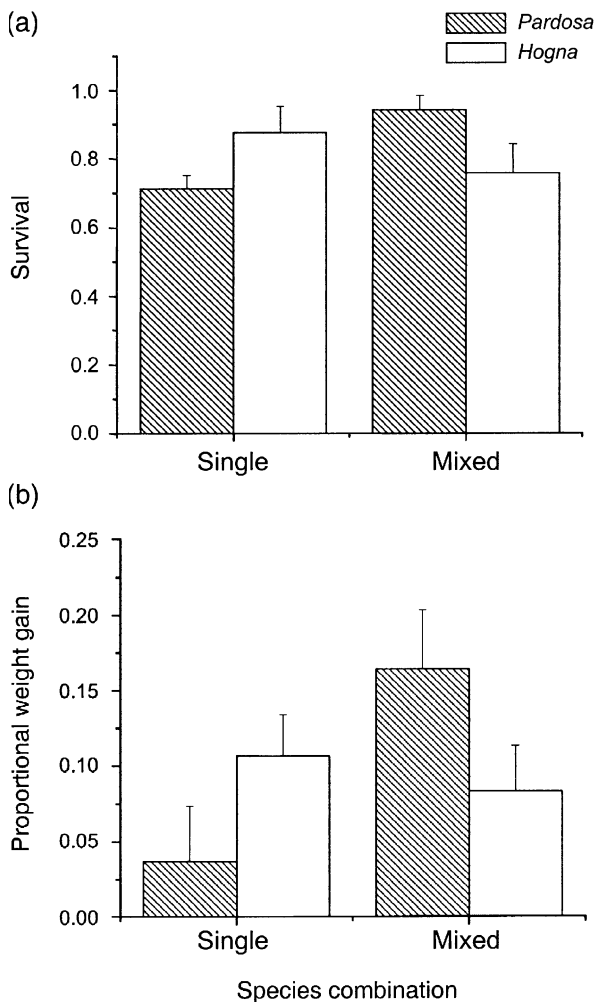
The experiment was run twice: between 10 and 15 July 1997 (early time period) and between 14 and 19 August 1997 (late time period). Between trials, the enclosures were washed and moved to different locations within the fields, and new spiders were used for the second trial.

The second field experiment tested the effect of large *Pardosa* and *Hogna* on *Hogna* spiderlings. The three treatments were (1) add 10 *Hogna* spiderlings, (2) add two large *Pardosa* and eight *Hogna* spiderlings, (3) add two *Pardosa*-sized *Hogna* and eight *Hogna* spiderlings. *Hogna* were considered to be similar in size to *Pardosa* if they weighed between 20 and 40 mg. Treatments were assigned randomly to one enclosure per field. The early trial was conducted between 2 and 7 August 1997, the late trial was conducted between 3 and 8 September 1997.

In order to determine the symmetry in the interactions between similar-sized *Hogna* and *Pardosa*, data for each species were analysed separately. Experiments with *Hogna* spiderlings were designed to determine the effects of large spiders, so only data for spiderlings were analysed. Dependent variables in the analyses were species survival on a per enclosure basis [(number found at the end of the trial)/(number initially placed in the enclosure)], and proportional weight gain per species per enclosure [(weights at the end of the trial) – (weights at the beginning of the trial)]/(weights at the beginning of the trial). Only spiders added to enclosures (i.e. identified by paint marks) were used in analyses (except for treatments with *Hogna* spiderlings as these were not marked). Data were proportional, and were therefore arcsin transformed prior

to analysis ( $x' = \arcsin \sqrt{x}$ ) (Sokal & Rohlf, 1995). The Kolmogorov–Smirnov test was used to test for normality and Levene's test was used for evaluating homogeneity of variances.

One-factor randomised block ANOVAs were used to test the effect of species combination on survival and weight gain. The species combination factor had two levels for the first field experiment (single species and mixed species, tested for *Pardosa* and *Hogna* separately) and three levels for the second experiment (spiderlings alone, spiderlings with *Pardosa*, spiderlings with *Hogna*). Date (early versus late) was used a block factor because the two trials were considered independent (i.e. enclosures moved to new locations and new specimens used), and the date  $\times$  species combination interaction was included in the model. The Bonferroni Multiple Comparison test was used for *post-hoc* comparisons of means for the second experiment (Sokal & Rohlf, 1995).



**Fig. 1.** (a) Mean ( $\pm$ SE) survival and (b) proportional weight gain of *Pardosa* and *Hogna* per experimental field enclosure in single ( $n=8$ ) and mixed-species ( $n=7$ ) treatments containing similar-sized spiders.

## Results

### Laboratory experiment

Evidence of an aggressive interaction was noted in 10 of 40 trials pairing *Pardosa* with *Hogna* spiderlings. In eight of these incidents, *Pardosa* consumed *Hogna*, and in two trials *Hogna* were injured but not killed. In only one instance out of 27 trials did a *Pardosa* consume a *Hogna* in its size-class. Fisher's Exact Test revealed that aggressive interactions were significantly more common between *Pardosa* and *Hogna* spiderlings than between similar-sized pairs of these species ( $P < 0.05$ ).

### Field experiments

In mixed-species enclosures with similar-sized spiders, *Pardosa* survival and proportional weight gain were significantly higher than in *Pardosa*-only enclosures (survival:  $F_{1,11} = 17.27$ ,  $P < 0.01$ ; weight gain:  $F_{1,11} = 5.45$ ,  $P < 0.05$ ; Fig. 1). The mean value of per cent weight gain was actually 4.4 times greater in enclosures containing *Hogna* (Fig. 1b). In contrast, species combination had no effect on *Hogna* survival or proportional weight gain (both  $P = \text{NS}$ ; Fig. 1). Interaction terms and the effect of date were not significant for either species (all  $P = \text{NS}$ ).

*Hogna* spiderlings were unaffected by date and species combination (all  $P = \text{NS}$ ), and there were no significant interactions between date and species combination on *Hogna* spiderling survival and weight gain (both  $P = \text{NS}$ ). The presence of other spiderlings, larger *Pardosa*, and *Pardosa*-sized *Hogna* did not influence the survival or weight gain of *Hogna* spiderlings.

## Discussion

### Intra-guild predation and interspecific interactions

*Pardosa* has little impact on *Hogna* when these species are similar in size or when *Pardosa* has a distinct size advantage. When size-classes overlapped closely, *Hogna* had no effect on *Pardosa* in terms of either intra-guild predation in the laboratory experiment or *Pardosa* survival and weight gain under field conditions. At this ontogenetic stage, *Hogna* has no advantage over *Pardosa*. The hypothesis that interspecific interactions in these experiments would favour *Pardosa* was not supported, but the lack of effects of *Hogna* on *Pardosa* during these life-stages illustrates that *Hogna* no longer has the competitive advantage. The lack of interactions between similar-sized spiders has been noted in terms of interspecific competition (Buddle, 2002), and Samu *et al.* (1999) showed that cannibalism in *Pardosa agrestis* (Westring) decreases when size ratios are similar. The risks of associating with a similar-sized predator are high (Elgar & Crespi, 1992), so similar-sized *Hogna* and *Pardosa* may simply avoid direct interactions.

Polis (1988) suggested that a greater asymmetry in size leads to an increase in cannibalism and intra-guild predation.

tion; the outcome of both can be interpreted as a form of interference competition. There are examples of research with wolf spiders that support this prediction (Schaeffer, 1975; Moeur, 1977; Marshall & Rypstra, 1999a). The size-classes of *Hogna* and *Pardosa* vary throughout the season, resulting in complex size-structured populations. The frequency of competition and intra-guild predation is known to vary throughout the ontogeny of the players in such communities (Spiller, 1984; Polis, 1988; Snyder & Hurd, 1995). When *Pardosa* were larger than *Hogna*, they consumed *Hogna* spiderlings 25% of the time in a laboratory setting. The identity of the intra-guild predator is therefore reversed in relation to the ontogeny of these species. Results from the second field experiment, which was conducted under more realistic conditions, however, suggest that intra-guild predation by *Pardosa* has little effect on the survival or weight gain of *Hogna* spiderlings.

The discrepancy between laboratory and field results in the levels of predation is perhaps not surprising as the laboratory environment was structurally simple compared with the straw habitat in field enclosures. On the other hand, enclosure densities were relatively high so the frequency of encounter should have been higher than that which might occur naturally. It may be that the complexity of the straw environment enhanced survival for long enough for spiders to deposit sufficient amounts of the chemical cues that they use to detect one another (Persons & Rypstra, 2000; Persons *et al.*, 2001). Those cues, largely absent in the short-term experiments conducted in simple laboratory containers, may be the mechanisms by which interactions between these species in natural situations are minimised.

#### Intraspecific interactions

The first field experiment showed that *Hogna* survival and weight gain did not differ in treatments containing *Pardosa*, yet *Pardosa* survival and weight gain were significantly higher in mixed-species enclosures. This suggests that the lower densities of *Pardosa* in the mixed-species enclosures (i.e. five per enclosure) are the factor causing higher *Pardosa* survival and weight gain compared with enclosures containing 10 *Pardosa*. Therefore, some form of intraspecific competition is playing a role in *Pardosa* populations at this scale. Ten *Pardosa* per enclosure, or 50 m<sup>-2</sup>, is a 10-fold increase above natural densities, and may have led to a rapid depletion of resources (exploitation competition) and/or high rates of cannibalism (interference competition). Without knowledge about changes in resources or the exact causes of *Pardosa* mortality, however, it is difficult to assign the type of intraspecific competition to this system. With the exception of research by Wise and Wagner (1992), this work represents one of the few examples of intraspecific competition playing a key role in ground-dwelling spider populations.

Marshall and Rypstra (1999a) showed that *Hogna* densities were limited in soybean fields and suggested that intraspecific competition might be the causal mechanism, however the field enclosure experiments revealed that *Hogna* survival

and weight gain did not differ by the species combination treatment. The low natural densities of *Hogna* may simply be a reflection of life-history traits [i.e. low colonisation ability and relatively sedentary habits compared with *Pardosa* (Dondale & Redner, 1990; Walker *et al.*, 1999; Marshall *et al.*, 2000)] rather than intraspecific interactions.

#### Summary

A good understanding of the interactions between *Hogna* and *Pardosa* has been gained for a wide range of *Hogna* size-classes and penultimate or adult *Pardosa*: (1) *Hogna* > *Pardosa* (Marshall & Rypstra, 1999a; Marshall *et al.*, 2000): *Hogna* has the competitive advantage and is the intra-guild predator; (2) *Hogna* = *Pardosa* (this study): interspecific interactions are negligible; and (3) *Hogna* < *Pardosa* (this study): *Hogna* can become the intra-guild prey but this interaction appears inconsequential in the field.

Marshall *et al.* (2000) proposed that the co-existence of *Hogna* and *Pardosa* is achieved through a trade-off in competitive ability and colonisation ability, as predicted by Nee and May (1992) and Tilman (1994). Results from the present research allow greater insight into some of mechanisms governing this co-existence. If *Hogna* were not limited by its colonisation ability, *Pardosa* would have little chance of survival given the asymmetric intra-guild predation and its anti-predator behaviour to large *Hogna*, and because *Pardosa* does not affect *Hogna* when *Hogna* are small. *Hogna* is probably limited by colonisation ability, however, as suggested by the results of manipulative experiments (Marshall *et al.*, 2000) and by its naturally low densities in soybean fields (Marshall & Rypstra, 1999b). Furthermore, there is no evidence to suggest that intraspecific interactions govern *Hogna* populations: once it has arrived in a suitable habitat, it will stay without interfering with its conspecifics, even under extreme high-density conditions. Although *Pardosa* is able to colonise soybean fields rapidly (Marshall *et al.*, 2000), at the scale of the present experiment, it is limited intraspecifically as reflected by lower survival and poor weight gain in high-density enclosures. Thus, species interactions, or lack thereof during certain ontogenetic stages, provide clues about how *Hogna* and *Pardosa* co-exist in soybean fields.

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