

Interactions between a hunting spider and a web-builder: consequences of intraguild predation and cannibalism for prey suppression

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Abstract. 1. Antagonistic interactions among invertebrate predators such as intraguild predation and cannibalism have the potential to dampen top-down impacts on shared prey at lower trophic levels. Two abundant spider predators, the large wolf spider *Pardosa littoralis* and the small sheet-web builder *Grammonota trivitatta* co-occur on the salt marshes of eastern North America where they both attack planthoppers (*Prokelisia* spp.), the dominant herbivores on the marsh. Experiments both in the laboratory and field were used to assess the incidence of intraguild predation and cannibalism in these spiders and elucidate how such antagonistic interactions influence planthopper suppression.

2. Functional response experiments showed that with an increase in planthopper prey density, *Grammonota* captured more prey but not a higher proportion of that offered. *Pardosa* exhibited the same response when *Grammonota* were offered as intraguild prey. Both functional responses were type I over the range of prey densities offered.

3. *Grammonota* is moderately cannibalistic, and the presence of planthopper prey reduced the incidence of cannibalism.

4. Factorial experiments in the laboratory showed that *Pardosa* but not *Grammonota* reduced planthopper prey populations when prey density was low. By contrast, at high prey densities, both *Pardosa* and *Grammonota* had significant adverse effects on planthopper populations. Moreover, there was an interactive effect such that *Grammonota* reduced planthopper populations relatively more when *Pardosa* was absent than when it was present.

5. There was direct evidence for the intraguild predation of *Grammonota* by *Pardosa* such that fewer *Grammonota* survived in the presence of *Pardosa* than when it was absent. This result occurred whether planthopper prey were abundant or not.

6. Field releases of *Grammonota* in open plots resulted in significant but small decreases in the density of planthopper prey, both nymphs and adults.

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7. Enhancing densities of *Pardosa* in open plots resulted in *Grammonota* suppression. The intraguild predation of *Grammonota* at this enhanced *Pardosa* density, however, did not preclude *Pardosa* from significantly reducing planthopper populations.

8. Although there was evidence that *Grammonota* reduced planthopper populations and that the intraguild predation of *Grammonota* by *Pardosa* occurred, the strength of these interactions was relatively weak given the low consumption rate of planthoppers by *Grammonota* ($< 3 \text{ day}^{-1}$) and *Grammonota* by *Pardosa* ($\approx 2 \text{ day}^{-1}$). Thus, weak asymmetric intraguild predation among spiders on the marsh likely dampens but does not eliminate the ability of *Pardosa* to exert significant top-down control on planthopper populations.

Key words. Antagonistic predator–predator interaction, biological control, food-web dynamics, functional response, *Grammonota trivittata*, *Pardosa littoralis*, *Prokelisia* planthopper, salt marsh, *Spartina*, top-down control.

Introduction

Intraguild predation and cannibalism are antagonistic interactions that frequently occur among arthropod predators inhabiting both natural (Polis *et al.*, 1989; Finke & Denno, 2002, 2003a) and agricultural systems (Rosenheim *et al.*, 1993; Snyder & Ives, 2001). Notably, such aggressive interactions among predators can diminish top-down impacts on shared prey (Rosenheim *et al.*, 1995; Snyder & Ives, 2001; Finke & Denno, 2003a), alter food-web dynamics (Polis & Strong, 1996; Fagan, 1997; McCann *et al.*, 1998), influence ecosystem function (Ostrom *et al.*, 1997), and disrupt biological control (Rosenheim *et al.*, 1995; Hodge, 1999; Symondson *et al.*, 2002). Thus, it becomes essential to assess the occurrence of intraguild predation in arthropod-dominated communities and elucidate factors that alter its prevalence, strength, and potential consequences for prey.

The occurrence of intraguild predation including cannibalism is not a surprising feeding option given that arthropod predators are often prey limited (Hurd & Eisenberg, 1984; Polis & McCormick, 1986; Rosenheim *et al.*, 1993; Wise, 1993; Hodge, 1999; Marshall & Rypstra, 1999; Stamp, 2001) and nitrogen deprived (Denno & Fagan, 2003), factors that are known to adversely affect their growth and survival (Strohmeyer *et al.*, 1998; Toft, 1999; Mayntz & Toft, 2001). Within this context of food limitation, however, numerous factors are known to alter the frequency and intensity of intraguild predation. These factors include characteristics of the intraguild predator, the intraguild prey, and the habitat where they forage. For example, the voraciousness, foraging strategy (e.g. sit-and-wait vs. active forager), and diet breadth of the top predator can affect the risk of attack for intraguild prey (Wise, 1993; Döbel & Denno, 1994; Balfour *et al.*, 2003). Moreover, the abundance, size, behaviour, and nutritional content of intraguild prey (Uetz & Stratton, 1982; Polis, 1988; Lucas *et al.*, 1998; Marshall & Rypstra, 1999; Samu *et al.*, 1999;

Fagan *et al.*, 2002; Persons *et al.*, 2002; Denno & Fagan, 2003), as well as the structure of the habitat as it provides spatial refuges for intraguild prey (Finke & Denno, 2002; Langellotto, 2002; Langellotto & Denno, 2004) can all influence the frequency of intraguild predation. The presence of abundant herbivorous prey can also diminish intraguild predation as top predators switch their attack to herbivores (Elgar & Crespi, 1992; Lucas *et al.*, 1998; Hodge, 1999). Just how these factors integrate to influence intraguild predation and prey suppression in the field is poorly understood in most systems.

Spiders offer an ideal opportunity to study the consequences of antagonistic predator–predator interactions for prey suppression because they engage frequently in intraguild predation and cannibalism (Elgar & Crespi, 1992; Hodge, 1999; Wise & Chen, 1999; Finke & Denno, 2003a). However, many experimental studies of intraguild predation involving spiders have pitted a spider against other insect or vertebrate predators (e.g. Spiller & Schoener, 1988; Heong *et al.*, 1989; Hurd & Eisenberg, 1990; Moran & Hurd, 1994, 1997; Fagan, 1997; Fagan *et al.*, 1998; Finke & Denno, 2003a). Fewer studies, especially ones conducted in the field, have explored intraguild predation between co-occurring spider species and its consequences for shared prey (but see Spiller, 1984; Hodge & Marshall, 1996; Riechert & Lawrence, 1997; Marshall & Rypstra, 1999; Wise & Chen, 1999; Balfour *et al.*, 2003). This is somewhat surprising given the prevalence and diversity of spiders in most natural and managed habitats (Wise, 1993; Hodge, 1999; Sunderland, 1999; Symondson *et al.*, 2002; Denno *et al.*, 2002) and their broad diet range (Hodge, 1999; Balfour *et al.*, 2003). The result is a paucity of experimental research on spider–spider interactions, especially between hunters and web-builders, as they affect food-web dynamics (Hodge, 1999).

Using manipulative experiments in the laboratory and field, this study quantified the intensity of intraguild

predation between two abundant intertidal spiders, the hunting spider *Pardosa littoralis* (Araneae: Lycosidae) and the web-builder *Grammonota trivitatta* (Araneae: Linyphiidae), and measured its consequences for the suppression of shared planthopper prey (Hemiptera: Delphacidae: *Prokelisia*). There are several reasons to expect intense, but asymmetric, intraguild predation between these two spiders with extended consequences for their planthopper prey. First, *Pardosa* is a much larger spider (6 mm) than *Grammonota* (3 mm), and asymmetry in body size is known to promote intraguild predation and cannibalism (Polis, 1988; Samu *et al.*, 1999), with the larger species often being the intraguild predator (Lucas *et al.*, 1998; Marshall & Rypstra, 1999; Balfour *et al.*, 2003). Second, *Pardosa* is a voracious predator with a high daily consumption rate of prey including non-spider intraguild prey (Döbel & Denno, 1994; Finke & Denno, 2003a). Third, both spider species are extremely abundant increasing the probability for interspecific contact and thus intraguild predation (Denno *et al.*, 2002; Gratton & Denno, 2003). Fourth, *Grammonota* has a high nitrogen content ($12.0 \pm 0.1\%$), higher than that for herbivores ($9.2 \pm 0.3\%$) and other predators ($11.5 \pm 0.2\%$) in its habitats (Matsumura *et al.* in press). Notably, such discrepancies between the nitrogen content of potential herbivorous prey and intraguild prey such as *Grammonota* are thought to promote intraguild predation (Fagan *et al.*, 2002; Denno & Fagan, 2003). Last, *Pardosa* alone can suppress effectively planthopper populations in certain habitats, an effect that is greatly diminished in the presence of non-spider intraguild prey (Döbel & Denno, 1994; Finke & Denno, 2002, 2003a). Together these data suggest that intraguild predation between these two spider species is potentially intense, which might relax their collective effect on shared planthopper prey.

Alternatively, characteristics of *Grammonota* such as aggression and avoidance might diminish its risk of *Pardosa* attack, characteristics that are known to minimise intraguild predation and promote weak interactions among spider species (Uetz & Stratton, 1982; Marshall & Rypstra, 1999; Persons *et al.*, 2002; Balfour *et al.*, 2003). That the spider community at large can effectively reduce pest herbivores in several agricultural systems suggests that on average antagonistic interactions among spider species are insufficiently strong to substantially reduce top-down control on herbivores (Riechert & Lawrence, 1997; Hodge, 1999; Sunderland, 1999; Symondson *et al.*, 2002). Nonetheless, there is certainly variation in the strength of spider–spider interactions (Riechert & Lockley, 1984; Spiller, 1984; Marshall & Rypstra, 1999).

Thus, the specific objectives were to: (1) determine the inherent ability of *Grammonota* to suppress planthopper populations and assess the intensity of cannibalism such that it might dampen the potential impact of this spider on planthoppers, information that is already known for *Pardosa* (Döbel & Denno, 1994; Langellotto, 2002; Denno *et al.*, 2003), (2) determine the intensity of intraguild predation between *Pardosa* and *Grammonota*, and (3) measure the singular and interactive effects of these two spider spe-

cies on planthopper populations. Data generated here will be compared with published information on *Pardosa*'s interactions with other non-spider predators of planthoppers to assess characteristics of intraguild prey that promote or moderate intraguild predation and evaluate its broader impacts on planthopper populations in this system. Ultimately, this assessment will provide needed insight into the effects of spider–spider interactions on prey dynamics.

Materials and methods

Study site and system

Field experiments (spider manipulations) were conducted on an intertidal salt marsh in the Great Bay–Mullica River estuarine system in Tuckerton, New Jersey, U.S.A. ($39^{\circ}30.8'N$, $74^{\circ}19.0'W$). Within the intertidal zone, the dominant vegetation on this marsh is the perennial cordgrass *Spartina alterniflora*, which grows as expansive pure stands as well as in archipelagos of small *Spartina* islets surrounded by open water (Gallagher *et al.*, 1988; Denno *et al.*, 2002).

The most abundant herbivores on *Spartina* are the specialist planthoppers *Prokelisia dolus* and *Prokelisia marginata* (Hemiptera: Delphacidae), and densities of these phloem-feeders frequently exceed 1000 adults per m^2 and up to 100 000 nymphs per m^2 (Denno *et al.*, 2000, 2002). *Prokelisia* planthoppers are trivoltine on mid-Atlantic marshes, overwinter as nymphs, and eggs are deposited within the leaf blades of *Spartina* (Denno *et al.*, 1996). A variety of other much less abundant herbivores also occur including other planthoppers (Delphacidae), leafhoppers (Cicadellidae), plant bugs (Miridae), and long-horned grasshoppers (Tettigoniidae) (Denno, 1983).

A number of spider species serve as the major predators of planthoppers on mid-Atlantic salt marshes (Döbel *et al.*, 1990; Döbel & Denno, 1994). Of these, generalist wolf spiders (Araneae: Lycosidae), particularly *Pardosa littoralis* (5–6 mm), are the most abundant and voracious predators of the active stages of planthoppers (Döbel *et al.*, 1990; Denno *et al.*, 2002, 2003). *Pardosa* reaches a marsh-wide average of ≈ 300 individuals per m^2 in late summer and its per capita consumption rate of prey is high (70 planthoppers per 24 h) (Döbel *et al.*, 1990; Döbel & Denno, 1994). *Prokelisia* planthoppers comprise 61% of the total prey captured in the field by these polyphagous spiders (Döbel & Denno, 1994). Notably, *Pardosa* accumulates at very high densities in certain litter-rich habitats ($> 500 m^{-2}$) where it very effectively suppresses planthopper populations (Denno *et al.*, 2002, 2003; Gratton & Denno, 2003). *Pardosa* is also a voracious intraguild predator of other spiders and invertebrate predators on the marsh (Finke & Denno, 2002, 2003a), and it is moderately cannibalistic (Langellotto, 2002).

Of the several web-building spiders on the marsh, *Grammonota trivitatta* (Araneae: Linyphiidae) is by far the most abundant (500–1500 individuals per m^2 ; Denno *et al.*, 2002; Gratton & Denno, 2003). *Prokelisia* planthoppers have

been observed caught in the sheet-webs of this small (3 mm) spider, and *Grammonota* also falls prey to *Pardosa* wolf spiders (Denno *et al.*, 2002). However, little is currently known about the ability of this spider to suppress planthoppers and how intraguild predation and cannibalism might deter this possibility, a situation this study aims to rectify.

Risk of predation and intraguild predation assessed by functional response

To determine the risk of planthoppers to *Grammonota* predation and *Grammonota* to intraguild predation by *Pardosa*, two functional response experiments were conducted in the laboratory using plastic (cellulose butyrate) tube cages (30 cm high \times 7.5 cm in diameter) capped at the top with an organdy-mesh cover. Each cage enclosed three potted *Spartina* transplants (25 cm in height), a density designed to mimic culm densities in high-marsh *Spartina* habitats where spiders abound (Döbel *et al.*, 1990). For both experiments, a single adult predator (*Grammonota* or *Pardosa*) was exposed to one of five prey densities (5, 10, 15, 25, and 50 individuals per cage). For the *Grammonota*–planthopper experiment, second-instar nymphs (1.5 mm) of *Prokelisia dolus* were used as prey (10 replicates for each prey density treatment) and for the *Grammonota*–*Pardosa* trials, large *Grammonota* spiders (3 mm) were used as prey (three replicates). In both experiments, prey (planthoppers or *Grammonota*) were introduced 24 h in advance of predators to allow planthoppers to settle on preferred feeding sites and *Grammonota* to construct its web. Spiders and prey interacted for 12 days, after which the number of prey captured (also proportion) was determined by subtracting the number of remaining insects from the density of prey offered.

The relationship between prey density and the number of prey taken (functional response) was determined by fitting a polynomial logistic model (PROC CATMOD) on the proportion of prey eaten vs. density of prey offered (Juliano, 1993; SAS, 2003). Models tested included the intercept and linear, quadratic, and cubic density terms. Likelihood ratios were used to determine which function best described the relationship with nonsignificant, high-order terms removed sequentially. The shape of the functional response curve was determined by testing for a significant positive (type III), significant negative (type II), or nonsignificant (type I) linear coefficient in the best-fit model (Juliano, 1993).

Planthoppers and spiders used in this laboratory experiment and the two that follow were collected from the field site at Tuckerton. *Spartina* plants, planthoppers, and spiders were maintained in laboratory cultures at $24 \pm 1^\circ\text{C}$ prior to use in experiments (see Denno *et al.*, 2000 for details of *Spartina* culture and planthopper husbandry). Planthoppers were raised to second instars on caged *Spartina* plants and spiders were isolated and maintained in prey-free plastic cups (1 oz) containing a water-soaked cotton ball for

1 week prior to use in experiments. Spiders (both sexes) were selected randomly from cultures for use in experiments.

Cannibalism in Grammonota

Self-damping mechanisms such as cannibalism have been implicated in the reduced ability of spiders to limit prey populations (Wise, 1993; Riechert *et al.*, 1999). Thus, it was integral to this study to determine the frequency of cannibalism and how it might change in the presence of planthopper prey. The incidence of cannibalism in *Grammonota* was measured at different spider densities and in the presence and absence of planthopper prey in tube-cages. Using a full factorial design, four densities of *Grammonota* (1, 5, 20, and 40 spiders \approx 3 mm in length) were crossed with prey presence (20, second instars of *P. dolus*) or absence, and each treatment combination was replicated five times. A relatively constant density of prey was maintained by visual censusing twice on days 4 and 8 and replacing them if need be. Because *P. dolus* nymphs feed preferentially at the leaf-blade junction of basal *Spartina* leaves, they are relatively easy to locate and count, thus facilitating their accurate replacement. After 12 days of interaction, the number and proportion of *Grammonota* cannibalised was determined by census. The effects of spider density, prey presence, and their interaction on the number and proportion of spiders cannibalised were determined using ANOVA (SAS, 2003).

Laboratory assessment of intraguild predation and prey suppression

The intraguild predation of *Grammonota* by *Pardosa*, and the singular and interactive effects of the two spiders on the suppression of *P. dolus* were determined with two factorial experiments, one using a low density of planthopper prey (10 second-instar nymphs per tube cage) and the other a high prey density (40 nymphs per cage). For both experiments, a full 2×2 factorial design was used whereby two levels of *Pardosa* (1 or 0 per cage) were crossed with two densities of *Grammonota* (5 or 0 per cage), and each treatment combination was replicated five times. Predators and prey were allowed to interact for 20 days after which the number of remaining planthoppers, *Grammonota*, and *Pardosa* were censused. This experiment was allowed to run longer than the others to increase the chances of detecting a significant interactive effect of *Pardosa* and *Grammonota* on planthopper suppression, given the suspicion that the smaller *Grammonota* might have a relatively low consumption rate of prey compared to the larger *Pardosa*.

The effects of *Grammonota*, *Pardosa*, and their interaction on the number of remaining planthoppers were assessed using ANOVA (SAS, 2003). Intraguild predation was determined by comparing the density of *Grammonota* between treatments with and without *Pardosa* using *t*-tests (SAS, 2003).

Field assessment of *Grammonota* predation on planthopper populations

The effect of *Grammonota* on planthopper density was assessed with a release experiment in small open plots (1.5 m² plots containing ambient populations of planthoppers) on a *Spartina* meadow at the Tuckerton field site in 2000. On each of two dates (9 and 16 August), the standing population of *Grammonota* was augmented by adding 500 spiders to the centre of each of five plots and withheld from five others. The two treatments were randomly assigned to plots. These releases resulted in elevating *Grammonota* densities to a naturally occurring high (Denno *et al.*, 2002). Spiders (large immatures and adults) for this release were obtained by vacuuming neighbouring *Spartina* meadows with the D-vac suction sampler.

Populations of *Prokelisia* planthoppers and *Grammonota* (no. per m²) were assessed on four dates: 9 August (pre-treatment assessment), 16 August, 1 September, and 5 October using a D-vac suction sampler. One sample was taken in each plot on each of the four dates, and one sample consisted of one 30-s placement of the sampling head on the marsh surface such that a total of 0.1 m² of *Spartina* was vacuumed. Planthoppers and spiders were killed in an ethyl-acetate jar, transferred to 95% ethanol sample bottles, and returned to the laboratory where they were counted. The effect of *Grammonota* addition on planthopper density (adults and nymphs) and *Grammonota* density was assessed using repeated measures MANOVA with the last three post-treatment dates in the model (SAS, 2003). Density data were log-transformed prior to analysis to meet assumptions of normality and heteroscasticity.

Field assessment of intraguild predation

To test for the effects of intraguild predation by *Pardosa* on *Grammonota*, a *Pardosa* addition experiment was conducted on an archipelago of small, uncaged *Spartina* islets located in a flooded mud-flat area on the high marsh at the Tuckerton field site (see Denno *et al.*, 2000). Islets averaged 1.85 ± 0.13 m² in area, and were separated from each other by 1–3 m. Islets were used for this experiment rather than open plots in *Spartina* meadows because mobile wolf spiders are more likely to remain, and thus the spider addition treatment to persist, on islets surrounded by standing water (see Denno *et al.*, 2002).

Prior to adding spiders, all islets were defaunated three times (10, 16, and 25 June 1999) to remove ambient planthoppers and spiders. Using a D-vac suction sampler, each islet was vacuumed for 10 min, which achieved nearly complete defaunation (Denno *et al.*, 2000).

Following the final defaunation, *Grammonota*, planthoppers and other arthropods could freely colonise all islets. This procedure helps equalise initial arthropod densities among islets (Denno *et al.*, 2002). The *Pardosa* augmenta-

tion treatment was initiated on 30 June, and was applied on five subsequent dates (8, 15, 21, 28 July, and 3 August). On each date, *Pardosa* wolf spiders were applied at a rate of 100 large immatures per m² to those islets assigned to the spider treatment. In all, eight islets received spiders and eight others did not.

The effect of the spider treatment on the size of *Grammonota* and planthopper populations (no. per m²) was assessed nearly two months later on 17 August using a D-vac suction sampler (Denno *et al.*, 2000). Each islet was sampled once and one sample consisted of two 30-s placements of the D-vac sampling head on the marsh surface such that a total of 0.2 m² of *Spartina* was vacuumed. ANOVA was used to examine the effect of *Pardosa* addition on the densities (log-transformed no. per m²) of *Grammonota*, planthopper nymphs, and planthopper adults (SAS, 2003). MANOVA was used to determine the overall effect of *Pardosa* addition on planthopper populations with nymphs and adults entered as dependent variables (SAS, 2003).

Results

Risk of predation and intraguild predation assessed by functional response

There was a significant effect of density on the number of planthopper prey captured by *Grammonota* ($F_{4,40} = 94.69$, $P < 0.0001$), but not on the proportion of prey captured ($F_{4,40} = 0.43$, $P = 0.78$; Fig. 1a). At high prey densities, the daily capture rate of planthoppers was less than three planthoppers per day. With planthoppers as prey, *Grammonota* exhibited a type I functional response with a constant proportion of prey taken as planthopper density increased (linear coefficient not significantly different from zero; 0.0071 ± 0.0039 , $\chi^2_1 = 3.27$, $P = 0.07$).

Pardosa exhibited a significant functional response to *Grammonota* density with more intraguild prey killed at higher densities ($F_{4,12} = 14.08$, $P = 0.0002$), but the proportion of prey captured was not significantly different across densities ($F_{4,12} = 1.19$, $P = 0.36$; Fig. 1b). The daily predation rate of *Grammonota* was approximately two spiders per day at high prey densities. *Pardosa* exhibited a type I functional response with a constant proportion of prey taken as *Grammonota* density increased (linear coefficient not significantly different from zero; -0.0017 ± 0.0063 , $\chi^2_1 = 0.08$, $P = 0.78$).

Cannibalism in Grammonota

Grammonota showed clear evidence of cannibalism. With an increase in conspecific density, significantly more spiders were cannibalised ($F_{2,23} = 13.81$, $P = 0.0001$; Fig. 2a), but the proportion cannibalised of those offered did not differ across densities ($F_{2,23} = 0.92$, $P = 0.41$; Fig. 2b). The presence of planthopper prey resulted in a significant reduction in the proportion of spiders cannibalised ($F_{2,23} = 5.31$,

$P=0.03$; Fig. 2b), but not in the number cannibalised ($F_{2,23}=1.75$, $P=0.19$; Fig. 2a). There were no significant interactive effects of spider density and the presence of planthopper prey on either the number ($P=0.94$) or proportion of spiders cannibalised ($P=0.43$), although there was a non-significant trend for the incidence of cannibalism to decrease at low spider densities in the presence of planthoppers (Fig. 2b). No spiders died in the cannibalism control where single spiders were isolated.

Laboratory assessment of intraguild predation and prey suppression

At low prey densities (10 planthoppers per cage), *Pardosa* ($F_{1,14}=11.48$, $P=0.004$) but not *Grammonota* ($F_{1,14}=0.18$, $P=0.68$) significantly reduced planthopper populations and there was no interactive effect such that *Pardosa* suppressed planthoppers equally well whether *Grammonota* was present or not ($F_{1,14}=0.01$, $P=0.92$; Fig. 3a). In con-

trast, at high prey densities (40 planthoppers per cage), both *Pardosa* ($F_{1,16}=38.56$, $P<0.0001$) and *Grammonota* ($F_{1,16}=18.19$, $P=0.0006$) had significant adverse effects on planthopper populations and there was an interactive effect such that *Grammonota* reduced planthopper populations relatively more when *Pardosa* was absent than when it was present ($F_{1,16}=7.0$, $P=0.018$; Fig. 3b). There was also direct evidence for intraguild predation in this experiment. Significantly fewer *Grammonota* survived in the presence of *Pardosa* at both low ($t_6=4.43$, $P=0.004$) and high prey densities ($t_8=9.00$, $P<0.0001$; Fig. 3c,d respectively).

Field assessment of *Grammonota* predation on planthopper populations

Releasing *Grammonota* into open field plots resulted in a close to significant increase in spider populations ($F_{1,8}=3.89$, $P=0.08$; Fig. 4a). This trend is particularly evident on the first date following their release in mid-

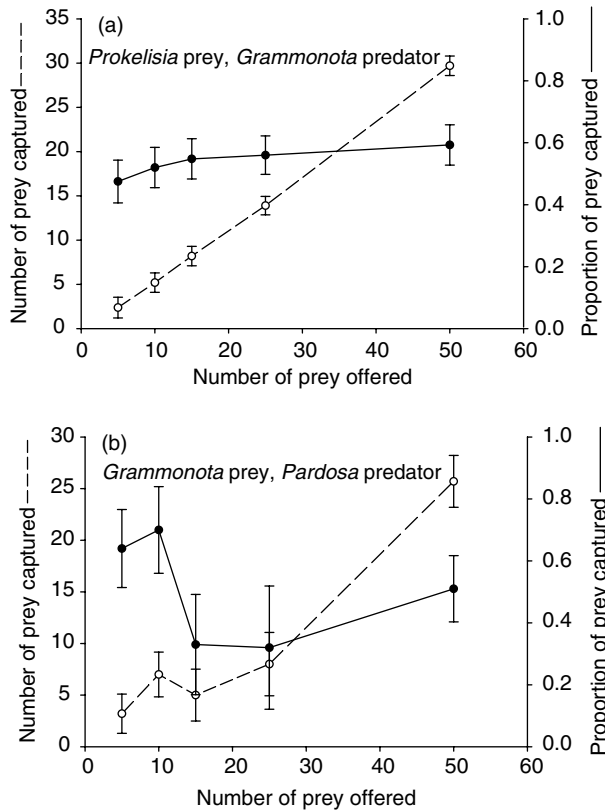


Fig. 1. Functional response of (a) the web-building spider *Grammonota trivittata* to increasing densities of the planthopper *Prokelisia dolus*, and (b) the wolf spider *Pardosa littoralis* to increasing densities of the intraguild prey *Grammonota trivittata*. Both the number (○) and proportion (●) of prey captured in a 12-day period are shown. Logistic regression showed that both predators exhibited a type I functional response across the range of prey densities offered. Means \pm SEM are shown.

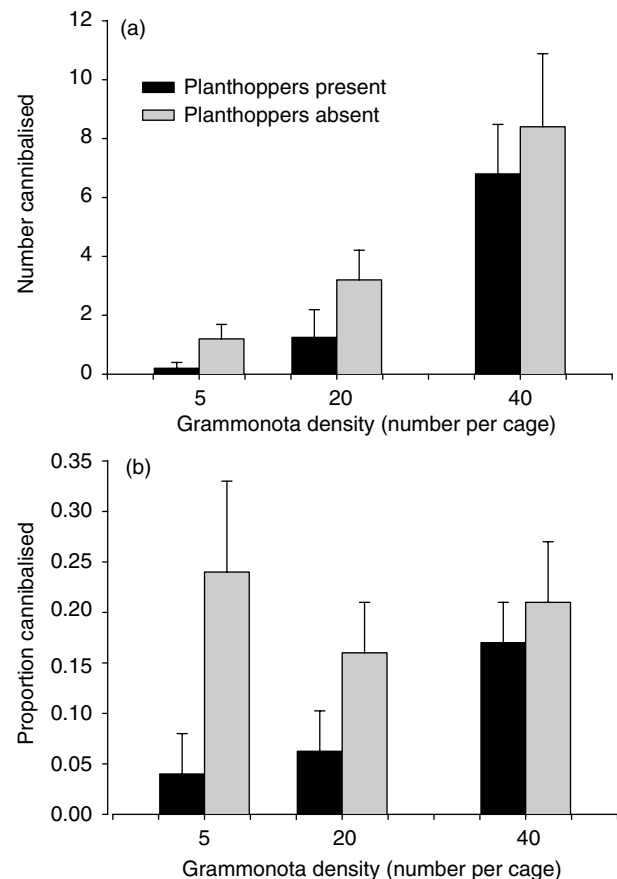


Fig. 2. Number (a) and proportion (b) of *Grammonota trivittata* cannibalised under conditions of increasing conspecific density and in the presence and absence of planthopper prey (*Prokelisia dolus*). Means \pm SEM are shown.

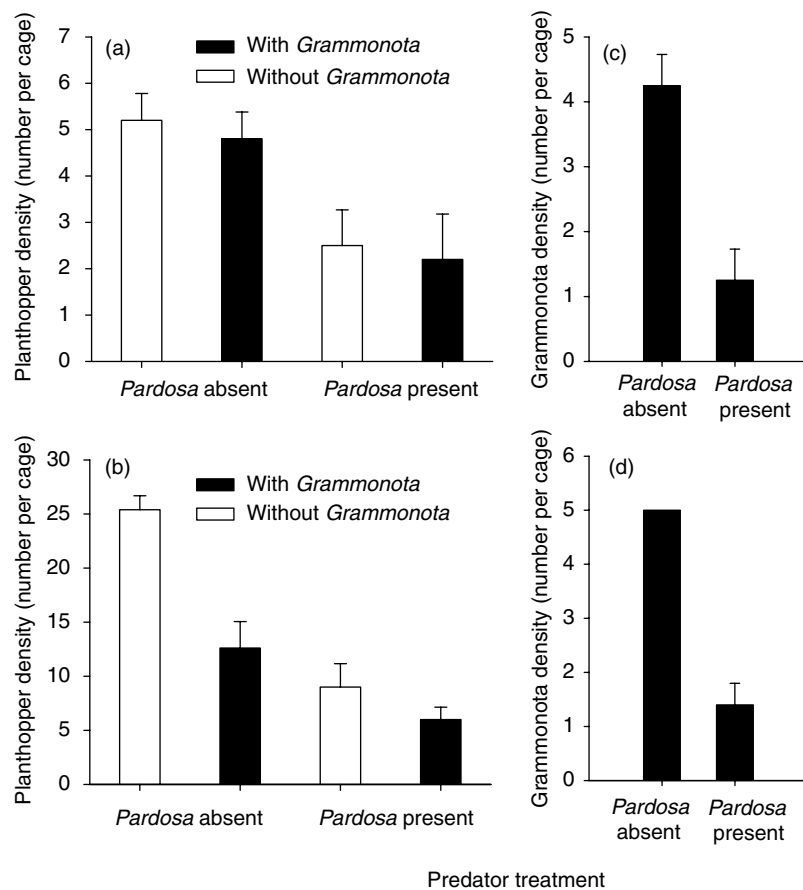


Fig. 3. Number of surviving planthoppers exposed to one of four factorial treatment combinations of predators (*Grammonota trivitatta* present or absent crossed with *Pardosa littoralis*) under (a) low-density prey conditions (10 planthoppers per cage) and (b) high prey densities (40 planthoppers per cage). Intraguild predation was assessed in the same experiment by examining the number of *Grammonota* remaining in the presence and absence of *Pardosa* under conditions of low (c) and high densities (d) of planthopper prey. Means \pm SEM are shown.

August when spider densities were elevated from 974 ± 104 in control plots to 1314 ± 98 spiders per m^2 in release plots. Enhancing *Grammonota* density by $\approx 35\%$ resulted in significant decreases in both the adults ($F_{1,8} = 7.09$, $P = 0.029$) and nymphs of *Prokelisia* planthoppers ($F_{1,8} = 7.90$, $P = 0.023$; Fig. 4b,c respectively). Treatment effects on planthoppers, however, were observed only during September for adults and October for nymphs as evidenced by a significant treatment by date interaction for both planthopper adults ($F_{1,8} = 8.49$, $P = 0.013$) and nymphs ($F_{1,8} = 5.0$, $P = 0.045$). Averaged across the three post-release dates, the *Grammonota* release resulted in a 26% and 8% decrease in the density of planthopper adults and nymphs respectively.

Field assessment of intraguild predation

By adding *Pardosa* to *Spartina* islets densities of this intraguild predator were significantly increased ($F_{1,16} = 19.34$, $P = 0.0004$; Fig. 5a). Moreover, *Grammonota* densities were significantly lower on islets where *Pardosa*

was released ($F_{1,16} = 6.71$, $P = 0.021$; Fig. 5b), strongly suggesting intraguild predation. Despite its adverse effects on *Grammonota*, *Pardosa* was able to reduce significantly populations of planthoppers. With planthopper adults and nymphs included as separate dependent variables, MANOVA found a significant overall reduction in planthopper populations on islets where *Pardosa* was released ($F_{2,15} = 4.49$, $P = 0.03$). Separate univariate analyses found a significant adverse effect of the *Pardosa* release on planthopper adults ($F_{1,16} = 5.82$, $P = 0.03$; Fig. 5c), but not nymphs ($F_{1,16} = 1.39$, $P = 0.26$; Fig. 5d).

Discussion

Both intraguild predation and cannibalism are widespread phenomena in arthropod-based communities (Polis *et al.*, 1989; Rosenheim *et al.*, 1993; Hodge, 1999; Finke & Denno, 2002). Such predator–predator interactions are thought to result in more reticulate food webs, diminished top-down control on herbivores, and the reduced probability for trophic cascades in general (Rosenheim *et al.*, 1995;

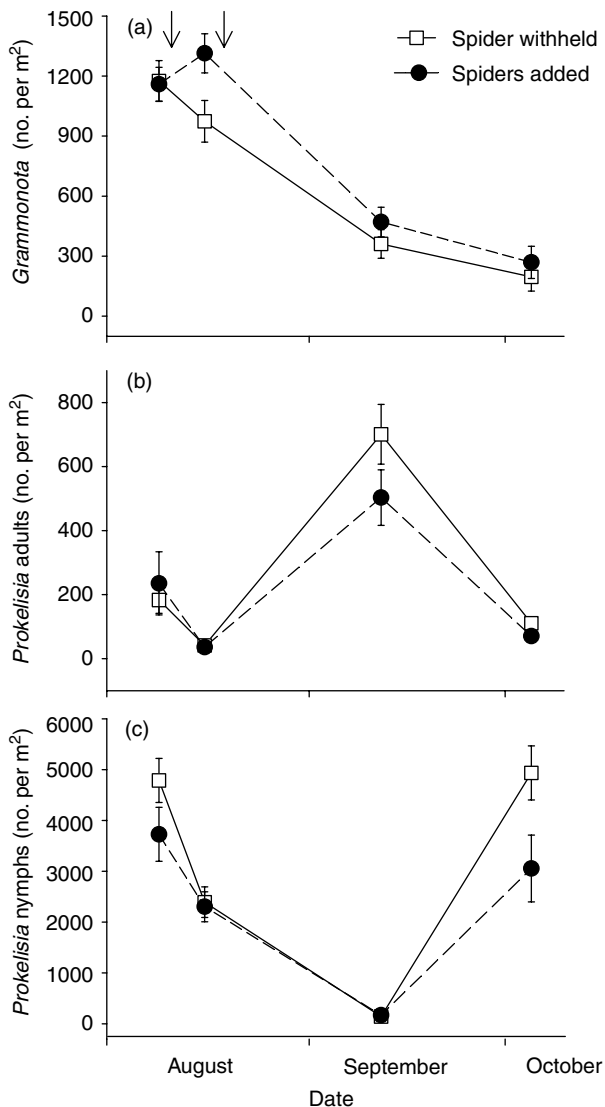


Fig. 4. Density of (a) *Grammonota trivittata*, (b) planthopper (*Prokelisia*) adults, and (c) planthopper nymphs following two field releases of the web-building spider *Grammonota* (arrows) in open plots on a salt marsh near Tuckerton, New Jersey, U.S.A. Spider releases had a significant but small suppressing effect on planthopper population density. Means \pm SEM are shown.

Polis & Strong, 1996; Fagan, 1997; Snyder & Ives, 2001; Finke & Denno, 2003a). However, the impact of such predator–predator interactions on trophic levels beneath depends on their frequency and strength (McCann *et al.*, 1998; Schmitz *et al.*, 2000; Halaj & Wise, 2001).

This study found evidence for weak antagonistic interactions between *Pardosa* and *Grammonota* with minor consequences of the interaction for shared planthopper prey. For example, planthopper density was reduced relatively more by *Grammonota* when *Pardosa* was absent than when it was present (Fig. 3b), a result attributable to intraguild predation (Fig. 3d). Despite the significant interactive effect of *Pardosa*

and *Grammonota* on planthopper density, the incidence of intraguild predation was low due to *Pardosa*'s low consumption rate of *Grammonota* (≈ 2 per day). Importantly, the densities of *Pardosa* (one per cage), *Grammonota* (five per cage), and planthopper nymphs (40 per cage) that were used to assess intraguild predation and its consequences for planthopper suppression in laboratory cages (0.005 m²) scale up to field densities of 200, 1000, and 8000 individuals per m² respectively. These densities are very representative of those found in the field (see Döbel *et al.*, 1990; Döbel & Denno, 1994; Denno *et al.*, 2002; Gratton & Denno, 2003), and thus the results of the laboratory experiment are likely to be indicative of the real-world strength and consequences of such interactions in the field.

Weak predatory interactions occurred between *Pardosa* and *Grammonota*, even though *Grammonota* is much smaller than *Pardosa* (Döbel & Denno, 1994) and is a very nutritious potential prey (12% nitrogen; Matsumura *et al.*, in press). Its low risk of intraguild predation may result in part from its behaviour. For example, *Grammonota* is a sit-and-wait predator that builds sheet webs near the marsh surface where it can detect both prey and approaching predators via web vibrations (Döbel *et al.*, 1990; Matsumura *et al.*, in press). Other spiders are known to use a variety of cues (vibrations, chemicals, and frass) to detect other spiders, avoid them, and ultimately reduce the probability of attack (Uetz & Stratton, 1982; Persons *et al.*, 2002). Araneophagic spiders aside (Li & Jackson, 1997), such avoidance mechanisms may promote weak interactions among some spider species (see Marshall & Rypstra, 1999; Persons *et al.*, 2002; Balfour *et al.*, 2003), especially between hunters and web-builders.

Moreover, interactions between *Grammonota* and planthoppers were relatively weak. This resulted from its low capture rate of planthoppers (three per day), even under high prey-density conditions (Figs 1a and 3a,b). That *Grammonota* was unable to suppress planthoppers when prey density was low (compare Fig. 3a with b) further diminishes the potential impact this spider might have on planthopper population growth (see Riechert *et al.*, 1999). Field releases of *Grammonota*, designed to achieve a naturally high spider density, also corroborated the mild impact of this spider on planthopper populations. For example, field plots augmented with *Grammonota* resulted in only a 26% and 8% reduction in the density of planthopper adults and nymphs respectively (Fig. 4b,c). *Grammonota*-related reductions in the density of planthopper nymphs in October (Fig. 4c) appear to stem from the adverse effect of the *Grammonota* augmentation on planthopper adults earlier in September (Fig. 4b). Overall, *Grammonota*'s relatively low impact on planthopper populations in the field may be further exacerbated by its feeding on alternative prey such as ephydrid and chloropid flies that abound on the marsh surface (Gratton & Denno, 2003). Thus, despite its abundance on the marsh, *Grammonota* appears to exert only weak adverse effects on planthopper prey. Contributing to its weak effect on planthoppers is a type I functional response and lack of evidence for density-dependent suppression (Fig. 1a).

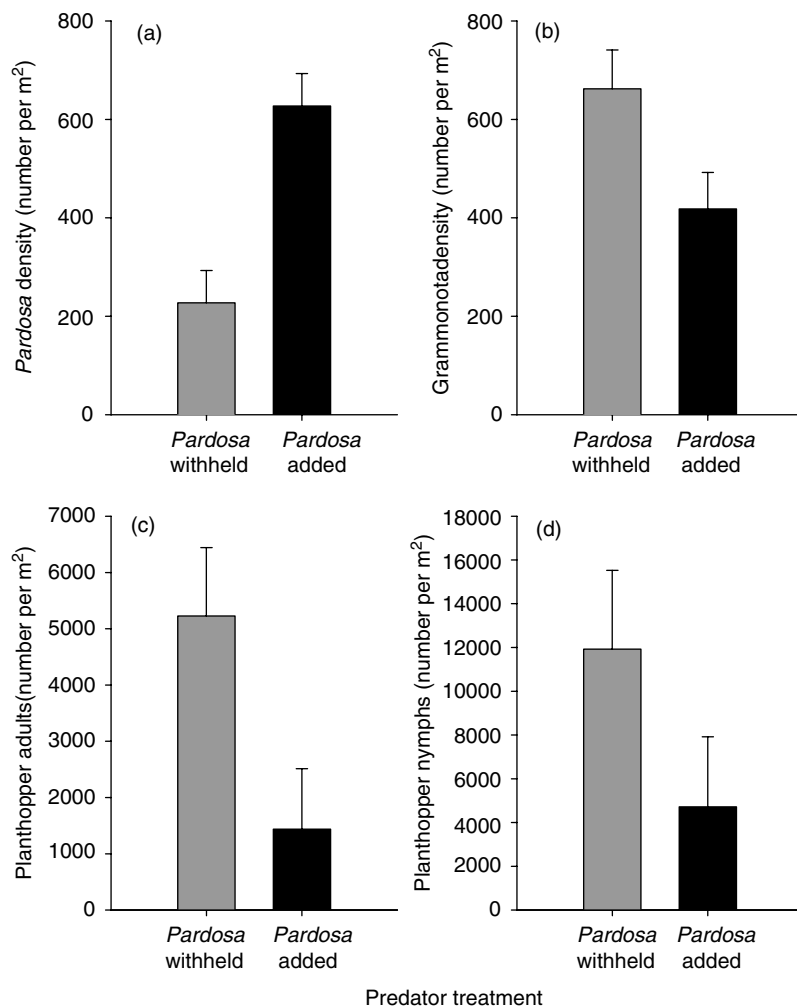


Fig. 5. Density of (a) *Pardosa littoralis*, (b) *Grammonota trivittata*, (c) planthopper (*Prokelisia*) adults, and (d) planthopper nymphs following the release of *Pardosa* on islets of *Spartina cordgrass* at Tuckerton, New Jersey, U.S.A. Despite significant reductions in *Grammonota* density from intraguild predation, the *Pardosa* release resulted in significantly lower densities of planthoppers. Means \pm SEM are shown.

Moderate levels of cannibalism in *Grammonota* ($\approx 20\%$; Fig. 2b) may further limit its ability to suppress planthopper populations. Such self-damping mechanisms have been implicated in the reduced ability of other spiders to limit prey populations (Wise, 1993; Riechert *et al.*, 1999). Cannibalism was diminished somewhat in the presence of planthopper prey, a result that occurred when spiders re-directed their attacks to planthoppers (Fig. 2). However, relaxed cannibalism under conditions of planthopper presence is not likely to substantially enhance its ability for prey suppression due to its inherently low capture rate and the tremendous intrinsic rate of population increase for *Prokelisia* planthoppers (Döbel & Denno, 1994). In contrast, cannibalism in *Pardosa* is not significantly diminished in the presence of planthopper prey (Döbel & Denno, 1994; Langellotto, 2002).

Thus, both the direct (via consumption) and indirect (via cannibalism and redirected *Pardosa* predation) effects of *Grammonota* on planthoppers are relatively weak as are

the direct effects of *Pardosa* on *Grammonota*. In the context of weak spider–spider interactions, it is not surprising that despite the intraguild predation of *Grammonota* in the field (Fig. 5b), *Pardosa* still was able to reduce planthopper populations substantially (Fig. 5c). Results of laboratory experiments also confirm the strong direct effects of *Pardosa* on planthopper populations at both low (Fig. 3a) and high prey densities (Fig. 3b). Previous work further corroborates that *Pardosa* alone can effectively suppress populations of planthoppers due in part to its high consumption rate (Döbel & Denno, 1994; Denno *et al.*, 2002, 2003).

Given the weak *Pardosa*–*Grammonota* interactions revealed by this study, it can be asked if *Pardosa*'s interactions with other invertebrate predators in the system are similarly weak with correspondingly mild consequences for planthoppers – in fact they are not. In particular, *Pardosa* is an effective intraguild predator of the heteropteran *Tytthus vagus*, which specialises on the eggs of *Prokelisia*

planthoppers (Finke & Denno, 2002). For instance, in the absence of *Pardosa*, *Tytthus* can annihilate planthopper populations from laboratory cages (Finke & Denno, 2002) and it can decimate populations in certain habitats in the field (Finke & Denno, 2003a). Notably, in the presence of *Pardosa*, *Tytthus* readily falls victim to *Pardosa*, and the effectiveness of these predators to collectively suppress planthoppers is diminished dramatically (Finke & Denno, 2003a), an effect that cascades down to influence plant productivity (Finke & Denno, 2003b). In this case, intraguild predation has such a strong relaxing effect on planthoppers that population growth is positive and similar to that in predator-free controls (Finke & Denno, 2003a). Thus, interactions among *Pardosa*, *Tytthus*, and their shared planthopper prey can be both strong and frequent.

One can ask why the difference in risk of *Pardosa* predation between *Grammonota* and *Tytthus*? Compared with the relatively sessile and aggressive *Grammonota*, *Tytthus* are active and defenceless foragers that scurry along leaves in search of planthopper eggs, and are thus much more susceptible to attack from movement-orienting wolf spiders (Finke & Denno, 2002). Moreover, *Grammonota* is larger (3 mm) on average than *Tytthus* (2 mm) and together with its aggressive behaviour may be more difficult for *Pardosa* to capture (Matsumura *et al.*, in press). Thus, differences in foraging style and body size likely explain the difference in risk of intraguild predation from *Pardosa* between *Grammonota* and *Tytthus*. Moreover, differences in foraging style between *Pardosa*, *Grammonota*, and *Tytthus* likely influence their attack rate and impact on planthopper populations. For example, active foragers such as *Pardosa* and *Tytthus* consume up to 70 and 25 planthoppers per day respectively (Döbel & Denno, 1994). *Grammonota*, a sit-and-wait forager that relies on the passive entrapment of prey in its sheet web, captures less than three planthoppers per day. Together, differences in consumption rate, foraging style, and aggression provide an explanation for why predator–predator interactions are weak between *Pardosa* and *Grammonota*, strong between *Pardosa* and *Tytthus*, and why the collective impact of these predator combinations on planthopper populations differs so greatly. Variation in the extent to which specific predator combinations are additive and exert top-down control of herbivores has been attributed to predator characteristics (size, aggression, mobility, and foraging style) in other systems as well (Rosenheim *et al.*, 1993; Lucas *et al.*, 1998).

It remains to be seen whether interactions such as intraguild predation between hunting and web-building species, like those studied here, are more often than not weak. Webs may allow their inhabitants to detect and avoid aggressive hunting spider species. The result may be diminished intraguild predation with additive effects on shared prey. Interactions between spiders, primarily hunting spiders, and other insect predators are frequently intense resulting in strong non-additive effects on shared prey (Heong *et al.*, 1989; Fagan, 1997; Finke & Denno, 2002, 2003a). For interactions between hunting spiders and other insect predators, large spider size and the vulnerability of intraguild

prey to attack appears to dictate the strength of the interaction. Similarly, there are many cases of strong interactions between insect predators that are also attributable to asymmetries in body size, aggression, or defence (Rosenheim *et al.*, 1993; Lucas *et al.*, 1998; Eubanks, 2001).

Strong predator–predator interactions are likely to relax the collective effect of the predator complex on insect herbivores and promote increased populations (Rosenheim *et al.*, 1993; Finke & Denno, 2002, 2003a). Weak predator–predator interactions (e.g. *Pardosa*–*Grammonota*) alone are unlikely to significantly diminish top-down control, but collectively they may be important in promoting food-web persistence and stability (Fagan, 1997; McCann *et al.*, 1998). As more is discovered about the role of intraguild predation in this system and others, it will be possible to better understand the strength of top-down forces in food webs and factors that buffer or enhance natural enemy effects on herbivores.

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