

Competition as a factor underlying the abundance of an uncommon phytophagous insect, the salt-marsh planthopper *Delphacodes penedetecta*

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Abstract. 1. Recent reviews of experimental studies provide compelling evidence that competition should be retained as a potential factor influencing the success of phytophagous insects. In this context, the objective of the study was to determine the role of interspecific and intraspecific competition, both contemporaneous and plant mediated (feeding-induced resistance), in limiting the population density of a consistently rare insect in a guild of abundant potential competitors.

2. Competitive interactions were assessed experimentally between two phloem-feeding planthoppers, the abundant *Prokelisia dolus* and the rare *Delphacodes penedetecta* (Hemiptera: Delphacidae). Both species are monophagous on the cordgrass *Spartina alterniflora* and overlap broadly in their use of habitats in the intertidal salt marshes along the Atlantic coast of North America.

3. The two planthoppers partition their cordgrass host plant, with *D. penedetecta* feeding more on the basal stems (particularly females) and *P. dolus* occurring most often on the canopy leaves. Notably, there was no evidence for niche shifting in *D. penedetecta* because its distribution on the plant did not change in the presence or absence of *P. dolus*.

4. Interspecific interactions with *P. dolus* had very little effect on the performance (development time and body size) and survival of *D. penedetecta*, a result demonstrated in both the laboratory and field. This result occurred both in contemporaneous interactions and on plants fed on previously by *P. dolus*. Only the males of *D. penedetecta* experienced weak competitive effects from *P. dolus*, as evidenced by reduced body size and slightly protracted development.

5. By contrast, there were strong adverse effects of intraspecific crowding (both from contemporaneous interactions and on plants fed on previously by conspecifics), whereby the survival, development time, and body size of *D. penedetecta* were affected very adversely.

6. These results suggest that interspecific competition is a weak force influencing the abundance of *D. penedetecta* in the field. Rather, strong intraspecific competition, a high requirement for plant nitrogen, and intrinsically low lifetime fecundity combine to explain the rarity of *D. penedetecta*.

Key words. Bottom-up control, community structure, induced resistance, inter-specific competition, intraspecific competition, rare species.

Introduction

Phytophagous insect communities are typically dominated by a few species that are associated with an assemblage of less common and rare herbivore species (Dixon, 1998;

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Novotný & Basset, 2000; Stiling, 2002). Understanding the factors that determine such patterns of herbivore abundance and dictate community structure has been a central theme in ecology (Hairston *et al.*, 1960; Strong *et al.*, 1984; Karban, 1989; Hunter & Price, 1992; Damman, 1993; Denno *et al.*, 2002). Historically, there has been heated debate over the relative importance of competition, host-plant resources (bottom-up factors), and natural enemies (top-down forces) in structuring herbivore communities (Hairston *et al.*, 1960; Price *et al.*, 1980; Hunter & Price, 1992; Denno *et al.*, 1995, 2002).

Interspecific competition in particular has experienced a chequered history with regard to views on its frequency, strength, and general role in influencing community structure (Hairston *et al.*, 1960; Lawton & Strong, 1981; Strong *et al.*, 1984; Damman, 1993; Denno *et al.*, 1995). Recent reviews of experimental studies, however, have shown that interspecific competition can be an important force in affecting the performance and population dynamics of herbivorous insects, and that its effects are often mediated through feeding-induced changes in plant nutrition or allelochemistry (Damman, 1993; Denno *et al.*, 1995). Another finding of recent reviews is that interspecific competition occurs more frequently between sap-feeding species such as planthoppers, aphids, and scale insects than between mandibulate folivores like lepidopterans and beetles, a finding that has been reported previously (Lawton & Strong, 1981; Karban, 1986; Denno & Roderick, 1992). Nonetheless, not all herbivorous insects are affected by interactions with other species, and for those that are, the effects of competition are frequently asymmetric, with one species incurring most of the adverse consequences (Lawton & Hassell, 1981; Strong *et al.*, 1984; Karban, 1989; Denno *et al.*, 1995, 2000).

The traditional approach to most competition studies has been to select two abundant herbivores from a community, manipulate their densities, then measure reciprocal fitness effects or changes in their distribution (Damman, 1993; Denno *et al.*, 1995). The expectation is competitive displacement, niche shifting, or an adverse effect on performance or density (Karbon, 1989; McClure, 1990; Settle & Wilson, 1990). For this study, an alternative approach was employed, whereby it was hypothesised that the density of a rare species in a community results from competitive interactions with an abundant potential competitor. This hypothesis was tested using two planthoppers (Hemiptera: Delphacidae) that co-occur in the intertidal salt marshes along the Atlantic coast of North America where they feed exclusively on the cordgrass *Spartina alterniflora* Loisel (Denno, 1977). *Prokelisia dolus* Wilson is extremely abundant and *Delphacodes penedetecta* Beamer is much less common (Denno, 1977; Denno *et al.*, 2000). This pair of phloem feeders was selected for study because: (1) *P. dolus* is competitively superior to other abundant planthopper species on the marsh (Denno & Roderick, 1992; Denno *et al.*, 2000), (2) *P. dolus* induces reductions in plant nitrogen and thus has the potential to influence potential competitors both contemporaneously and at later times in the season via induced plant resistance (Bacheller & Romeo, 1992;

Olmstead *et al.*, 1997; Denno *et al.*, 2000), (3) *D. penedetecta* is very sensitive to changes in host-plant nutrition and populations increase greatly when plant nitrogen is altered (Denno *et al.*, in press), and (4) *D. penedetecta* is relatively unaffected by natural enemies (both invertebrate predators and parasitoids) (Döbel & Denno, 1994; Ferrenberg, 2002; Denno *et al.*, in press). Thus, the potential exists for *D. penedetecta* to be affected adversely by its abundant associate *P. dolus*.

Using laboratory and field experiments, competition as a force explaining the rarity of certain species in sap-feeder-dominated communities was assessed. The objectives were: (1) to investigate niche shifting by comparing the within-plant distributions of *D. penedetecta* in the presence and absence of *P. dolus*, (2) to determine the effects of contemporaneous competition (interspecific and intraspecific) by raising *D. penedetecta* in pure and mixed cultures with *P. dolus* at different densities and assessing its survivorship and performance (development time and body size), and (3) to assess plant-mediated competitive effects (interspecific and intraspecific) by raising *D. penedetecta* on plants fed on previously by either conspecifics or cohorts of *P. dolus* then measuring its performance. By examining interspecific interactions between these two planthoppers, insight was provided into factors that underlie the rarity of certain species in communities of phytophagous insects.

Methods

Study site and system

Field experiments were conducted on an expansive intertidal salt marsh in the Great Bay–Mullica River estuarine system near Tuckerton, New Jersey, U.S.A. (39°30'N, 74°19'W). The marsh is characterised by extensive meadows of short-form *Spartina alterniflora* growing at higher elevations in the intertidal zone. Occasional mud flats and flooded potholes are nested within the meadows on the high marsh. A serpentine array of tidal creeks penetrates the marsh, and at this lower elevation creek banks are lined with a fringe of tall-form *Spartina* (Denno *et al.*, 2000).

The dominant herbivores in the *Spartina* marshes along the Atlantic coast are host-specific, phloem-feeding planthoppers (*Prokelisia dolus* and *P. marginata* Van Duzee), the adult densities of which frequently exceed 1000 individuals/m² (Denno, 1977; Denno *et al.*, 2000). *Prokelisia dolus* is restricted to high-marsh habitats where it co-occurs in *Spartina* meadows with the much less common planthopper *Delphacodes penedetecta* (often <100 adults/m²) (Denno, 1977; Denno *et al.*, 1996). *Delphacodes penedetecta* and *P. dolus* are positively associated across high-marsh habitats, a pattern that probably results from corresponding responses to changes in host plant nitrogen (Denno *et al.*, 2002; Ferrenberg, 2002). Both *P. dolus* and *D. penedetecta* are trivoltine with synchronised generations throughout the growing season (Denno, 1977), and are wing-dimorphic as adults with populations comprised mostly

(>85%) of flightless brachypters (Denno *et al.*, 1991). The lifetime fecundity of *D. penedetecta* (≈ 50 offspring) is about half that of *P. dolus* (≈ 100 offspring) (Denno *et al.*, 1989; Ferrenberg, 2002). Thus, due to their co-occurrence and immobility, there is ample opportunity for these two planthoppers to compete.

Prokelisia dolus was selected for study because it is by far the superior competitor in interactions with its abundant congener *P. marginata* (Denno & Roderick, 1992; Denno *et al.*, 2000). Previous feeding by *P. dolus* has an adverse effect on the survival and performance of *P. marginata* that feeds on the same plant in the subsequent generation (Denno *et al.*, 2000). The mechanism underlying this plant-mediated competitive effect is feeding-induced reductions in amino nitrogen (Bacheller & Romeo, 1992; Olmstead *et al.*, 1997). *Prokelisia marginata* exhibits reduced performance on nitrogen-poor plants (Cook & Denno, 1994), and *P. dolus* is far less sensitive to changes in plant nitrogen than *P. marginata*, which may explain why *P. dolus* suffers less under high-density conditions (Denno *et al.*, 2000). By contrast, *D. penedetecta* is affected far more by changes in plant quality than is *P. dolus* (Denno *et al.*, in press), and thus may suffer from interspecific crowding with *P. dolus*.

There is also a striking difference in the impact of natural enemies on these two planthoppers. *Delphacodes penedetecta* is far less susceptible than *P. dolus* to predation by wolf spiders (Lycosidae), the dominant predators of planthoppers on the marsh (Döbel & Denno, 1994). Moreover, invertebrate predation accounts for only 7% of the total population variation in *D. penedetecta* whereas it explains 49% of the variance in *P. dolus* (Denno *et al.*, in press). Neither *D. penedetecta* nor *P. dolus* is parasitised heavily (<6%) by the predominant parasitoids of planthoppers on the marsh, *Elenchus koebelei* Pierce (Strepsiptera: Elenchidae) and *Haplogonotopus americanus* Perkins (Hymenoptera: Dryinidae) (Denno, 1983; Ferrenberg, 2002). Thus, all evidence suggests that natural enemies play a minimal role in affecting the abundance of *D. penedetecta*.

Within-plant distribution of planthoppers and niche shifting

To determine patterns of spatial overlap for *D. penedetecta* and *P. dolus* and to test for niche shifting, the distribution of *D. penedetecta* was determined in the presence and absence of *P. dolus* on caged *Spartina* seedlings (three culms, 25 cm in height per cage). Tube cages were stocked with one of three planthopper treatments and each was replicated 10 times. Treatments were a pure culture of three *D. penedetecta* (either one male and two females or the reverse), a pure culture of 10 *P. dolus* (five males and five females), or a mixed culture of three *D. penedetecta* and 10 *P. dolus* (sex ratios as in pure cultures). These densities were chosen to represent density conditions in the field. Cages were established on 14 July 2000 and the location of each planthopper was scored 2 days later in one of three plant-height categories: basal stem (0–5 cm), mid-plant (6–10 cm), and canopy (>10 cm). Chi-square tests were used to compare the within-plant

distributions of the sexes of *D. penedetecta* and the within-plant distribution of *D. penedetecta* in the presence and absence of *P. dolus* (SAS Institute, 2000).

Laboratory cages used to cover potted *Spartina* seedlings in this experiment and all laboratory experiments that follow were constructed of clear plastic cellulose butyrate tubing and were 30 cm long and 7.5 cm in diameter. Each cage contained four ports (5.5 cm diameter) covered with organdy gauze and was capped with a screened top for easy access. Tube cages were placed over potted seedlings and pots were arranged randomly in plastic trays that were maintained in three incubators at 22 °C on a LD 14:10 h cycle. Nymphs used in this laboratory experiment and those that follow were taken from laboratory cultures that were established from field-collected planthoppers taken from the experimental site.

Contemporaneous effects of intraspecific and interspecific crowding on the performance of D. penedetecta

Interactions in the laboratory. To determine the effects of intraspecific competition and interspecific interactions with *P. dolus* on the survival and performance of *D. penedetecta*, this planthopper was raised at three densities in pure and mixed cultures (with *P. dolus*) in the laboratory. Density treatments were established by aspirating first instars into tube cages (21 July 2000) containing three *Spartina* seedlings and allowing nymphs to develop to adults, at which time their survivorship, development time to adult (days), and body length (indexed by metathoracic tibia length in mm) of *D. penedetecta* were determined. Because *D. penedetecta* is so rare compared with *P. dolus* in the field, the reciprocal effects of *D. penedetecta* on *P. dolus* were not assessed.

Intraspecific effects were evaluated by raising *D. penedetecta* in pure culture on *Spartina* seedlings at three densities (three, 11, and 40 total individuals per cage). Interspecific effects were assessed by comparing the response of three individuals of *D. penedetecta* reared in pure culture with the response of three individuals of *D. penedetecta* reared in the presence of eight and 37 individuals of *P. dolus* at combined densities of 11 and 40. Each treatment combination was replicated 15 times. For both this experiment and the field assessment that follows, the effects of density (intraspecific or interspecific) and sex on development time, body size, and survival (sexes pooled) were assessed by ANOVA, and pre-planned comparisons among means (within intraspecific and interspecific density treatments) were made using Tukey–Kramer Honest Significant Difference tests (SAS Institute, 2000; see Denno & Roderick, 1992).

Interactions in the field. Effects of intraspecific competition and interspecific competition with *P. dolus* on the performance of *D. penedetecta* were assessed in field cages placed over short-form *Spartina* on the high marsh at the experimental site. Field cages (30 cm tall \times 10 cm diameter) were constructed of cylindrical PVC drainpipe with two

rectangular, organdy-covered side ports (10 × 20 cm) and an organdy top for air circulation. On 3 July 2000, cages were pushed into the marsh surface so that they housed 20 living *Spartina* culms. All cages were defaunated on 3, 5, and 11 July using a D-Vac suction sampler. Cages were set randomly in a grid and were separated by 1 m.

Intraspecific effects were tested in *D. penedetecta* by stocking field cages with either low (10) or high (60) densities of first-instar nymphs on 3 August 2000. Interspecific effects of *P. dolus* on *D. penedetecta* were assessed by stocking field cages with either 10 nymphs of *D. penedetecta* (no-competition control) or with a mix of *D. penedetecta* nymphs (10) and *P. dolus* nymphs (50) for a combined density of 60 planthoppers per cage. Treatment cages (14 replicates per treatment) were established on 3 August 2000 and were removed from the field on 14 August 2000 just prior to adult eclosion. On removal, each cage containing the soil core of *Spartina* plants with planthoppers was returned to the laboratory and maintained in plastic trays. Field cages were inspected every 2 days until all individuals either eclosed or died. All eclosing adults were collected every 2 days and their survivorship (sexes pooled), development time (days to adult for each sex), and body size (metathoracic tibia length for both sexes) were determined.

Effects of previous feeding (intraspecific and interspecific) on the performance of D. penedetecta

Plant-mediated interactions in the laboratory. To test for plant-mediated interactions between *P. dolus* and *D. penedetecta*, *Spartina* seedlings were exposed to one of three treatment combinations designed to explore the consequences of previous feeding, both by conspecifics and heterospecifics, on the subsequent performance of *D. penedetecta*. Two competition (previous-feeding) treatments, intraspecific and interspecific, were established on 26 July 2001, by caging 40 first instars of either *D. penedetecta* or *P. dolus* on plants and raising them to adults, after which they were removed. The 1-month duration of the two previous-feeding treatments was designed to simulate one generation of *Spartina* exposure to planthoppers.

Shortly after removal of the previous feeding generation of planthoppers, cohorts of 10 first-instar nymphs of *D. penedetecta* were caged on the previously fed-on *Spartina* plants (23 August 2001). All eclosing adults were collected every 2 days and their survivorship (per cent survival from first instar to adult), development time (days to adult for both sexes), and body size (metathoracic tibia length for both sexes) were determined.

A third *no-competition* control treatment (no previous feeding) was also established, whereby plants remained planthopper free during the time that previous feeding generations were on their respective *Spartina* plants. After this period, 10 first-instar nymphs of *D. penedetecta* were caged on these plants (23 August 2001) and allowed to eclose, at which time their survivorship, development time,

and body size were determined. Each treatment combination was replicated 15 times. For both this experiment and the field test that follows, the effect of the competition treatments on the survivorship, development time, and body length of *D. penedetecta* was analysed using ANOVA, and pre-planned comparisons among means were made using Tukey–Kramer Honest Significant Difference tests (SAS Institute, 2000).

Plant-mediated interactions in the field. The impact of previous feeding by *P. penedetecta* (intraspecific effect) and *P. dolus* (interspecific effect) on the performance of *D. penedetecta* was assessed in small PVC field cages (same field-cage design as above) at the experimental site on 20 June 2001. Cages were pressed into the marsh surface on the high marsh such that 20 living culms of *Spartina* were enclosed. Cages were arranged in a grid pattern and were assigned randomly to one of the three competition treatments (no competition, intraspecific or interspecific competition), each replicated 10 times. To establish the two previous-feeding treatments, 400 first-instar nymphs of either *D. penedetecta* or *P. dolus* were aspirated into cages on 24 July 2001. The no-competition control was established by caging plants without planthoppers and allowing them to age for the same period of time that the competition treatment plants were exposed to planthoppers. After ≈1 month (one planthopper generation), all planthoppers used to establish previous-feeding treatments were removed from the cages using a D-Vac suction sampler.

Shortly after removing the initial generation of planthoppers, all field cages were stocked on 25 August 2001 with a focal cohort of 40 first-instar *D. penedetecta* nymphs. Just prior to adult eclosion of the focal cohort, all cages containing the core of *Spartina* with planthoppers were removed from the field (9 September 2001) and returned to the laboratory. Cages were checked every 2 days for the number of emerging adults until all individuals either eclosed or died. All eclosing adults were collected every 2 days and their survivorship (sexes pooled), development time (days to adult for each sex), and body size (metathoracic tibia length for both sexes) were determined. The caged *S. alterniflora* cores were maintained in water-filled plastic trays kept under 1000 W sodium vapour broad-spectrum growth lights on a LD 14:10 h cycle.

Results

Within-plant distribution of planthoppers and niche shifting

There was a significant difference in the spatial distribution of the sexes of *D. penedetecta* within a *Spartina* plant ($\chi^2 = 20.00$, $P < 0.001$; Fig. 1). Most females (≈80%) occurred on the basal stems of *Spartina* in the crown, with only ≈20% located higher in the mid-plant zone. By contrast, males were distributed more equitably on the plant with ≈33% located in each plant stratum (basal stem, mid-plant zone, and canopy). The within-plant

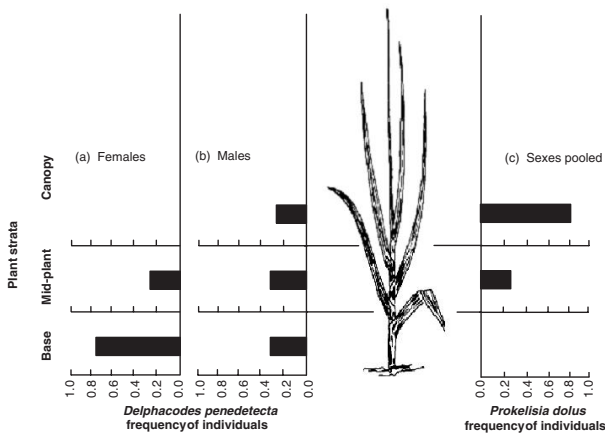


Fig. 1. Resource partitioning in *Delphacodes penedectata* and *Prokelisia dolus*. The frequency of individuals of *D. penedectata* (a) females, (b) males, and (c) *P. dolus* (sexes pooled) observed feeding on three strata of *Spartina alterniflora* (canopy, mid-plant, and base) over a 4-day period.

distribution of *D. penedectata* (sexes pooled) also differed from that of *P. dolus*, with *D. penedectata* occurring most frequently on the basal stems and *P. dolus* residing mostly ($\approx 80\%$) in the canopy of the plant ($\chi^2 = 132.14$, $P < 0.001$; Fig. 1). These distributions suggest that the two plant-hoppers partition the host-plant resource.

There was, however, no evidence for niche shifting by *D. penedectata* in the presence of *P. dolus*. For example, the within-plant distribution of *D. penedectata* females was the same in pure culture as it was when raised in mixed culture with *P. dolus* ($\chi^2 = 0.19$, $P = \text{NS}$); females remained mostly on the basal stems regardless of the presence of *P. dolus*. Similarly, the within-plant distribution of *D. penedectata* males did not change in the presence of *P. dolus* ($\chi^2 = 0.001$, $P = \text{NS}$).

Contemporaneous effects of intraspecific and interspecific crowding on the performance of *D. penedectata*

Interactions in the laboratory. There were strong adverse effects of intraspecific crowding on the development time, body size, and survivorship of *D. penedectata* (Fig. 2). At high intraspecific densities, development time was extended for *D. penedectata* (density effect, $F_{2,57} = 7.59$, $P = 0.001$), a result that was similar for both females and males (density \times sex interaction, $F_{2,579} = 1.39$, $P = 0.25$; Fig. 2a,b). There was also a significant effect of sex on development time and body size, with males developing to adults slightly faster than females (sex effect, $F_{1,579} = 18.59$, $P < 0.001$). Intraspecific crowding also resulted in significant reductions in body size (metathoracic tibia length) (density effect, $F_{2,57} = 10.01$, $P < 0.001$) for both females and males (density \times sex interaction, $F_{2,579} = 0.42$, $P = \text{NS}$; Fig. 2c,d). The survivorship of *D. penedectata* was also affected

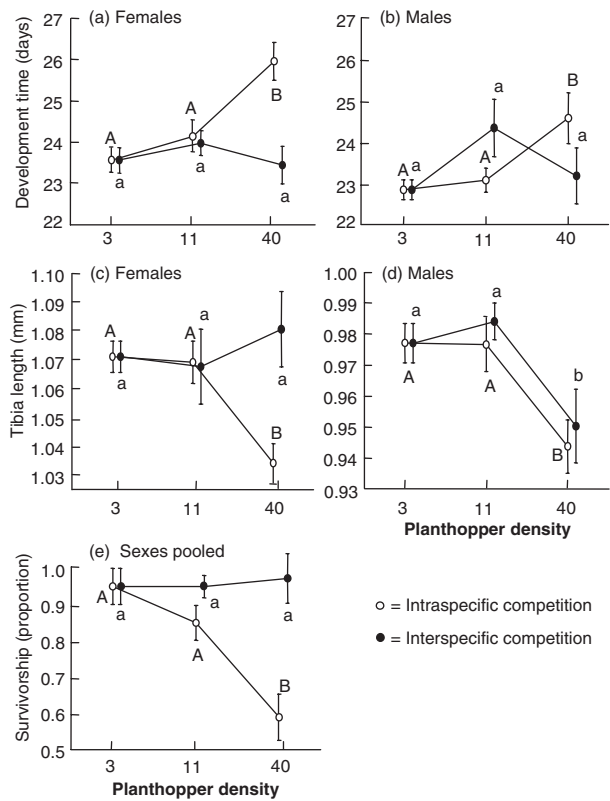


Fig. 2. Effect of intraspecific crowding and interspecific crowding with *Prokelisia dolus* on the development time (days from first instar to adult) for (a) females and (b) males, tibia length (index of adult body size) for (c) females and (d) males, and (e) survivorship (from first instar to adult, sexes pooled) of *Delphacodes penedectata* in laboratory cages. Means (± 1 SE) with different letters (upper case for intraspecific, lower case for interspecific) are significantly different (ANOVA followed by Tukey–Kramer Honest Significant Difference multiple comparisons, $P < 0.05$). Lines are inserted to indicate trends among treatments.

negatively under conditions of high intraspecific crowding, where it dropped from 96% in the low-density treatment to 59% at the highest density (density effect, $F_{2,57} = 20.25$, $P < 0.001$; Fig. 2e).

In contrast to the widespread effects of intraspecific crowding on *D. penedectata*, interspecific crowding with *P. dolus* had no overall effect on the development time, body size, or survival of *D. penedectata* (respective density effects, $F_{2,57} = 0.07$, $P = \text{NS}$; $F_{2,57} = 0.107$, $P = \text{NS}$; $F_{2,57} = 0.03$, $P = \text{NS}$; Fig. 2a–e). Only the body size (tibia length) of male *D. penedectata* was affected adversely by interspecific crowding with *P. dolus* (density \times sex interaction, $F_{2,152} = 4.25$, $P < 0.05$), an effect that was as strong as the intraspecific effect (Fig. 2d). Thus, under density conditions that mimicked those occurring naturally in the field (Denno *et al.*, 2000), evidence suggests that interspecific interactions with the abundant *P. dolus* have only weak effects on the males of *D. penedectata*.

Interactions in the field. Intraspecific crowding resulted in significant negative effects on the development time, body size, and survival of *D. penedectea* in field cages (Fig. 3). Although there were no main effects of intraspecific crowding on development time ($F_{1,34} = 1.82$, $P = \text{NS}$) or body size ($F_{1,34} = 2.53$, $P = \text{NS}$), it did affect the sexes differently; the development time of females but not males was extended under high-density conditions (sex \times density interaction, $F_{1,269} = 7.43$, $P = 0.01$; Fig. 3a,b). There was also a significant effect of conspecific crowding on the body size of females only (sex \times density interaction, $F_{1,269} = 5.76$, $P < 0.05$; Fig. 3c,d). Survival dropped significantly from 50% under low-density conditions to 28% in cages with high densities of conspecifics (density effect, $F_{1,34} = 10.74$, $P < 0.01$; Fig. 3e).

Crowding with *P. dolus* had no detectable effect on the survival, development time, or body size of *D. penedectea* (respective density effects: $F_{1,34} = 1.40$, $P = \text{NS}$; $F_{1,34} = 2.03$, $P = \text{NS}$; $F_{1,34} = 0.09$, $P = \text{NS}$; Fig. 3a–e). These results

corroborate laboratory findings that *D. penedectea* suffers large decreases in performance and survival under conditions of intraspecific crowding but that interspecific competitive effects imposed by *P. dolus* are weak at best.

Effects of previous feeding (intraspecific and interspecific) on the performance of D. penedectea

Plant-mediated interactions in the laboratory. Prior feeding on *S. alterniflora* had significant adverse effects on the development time of *D. penedectea* ($F_{2,41} = 8.54$, $P = 0.001$), but neither body size ($F_{1,41} = 1.27$, $P = \text{NS}$) nor survival ($F_{1,41} = 1.23$, $P = \text{NS}$) were affected significantly (Fig. 4a–e). Prior feeding by conspecifics delayed the development of both sexes of *D. penedectea* (Fig. 4a,b). When *Spartina* plants were subjected to prior feeding by *P. dolus*,

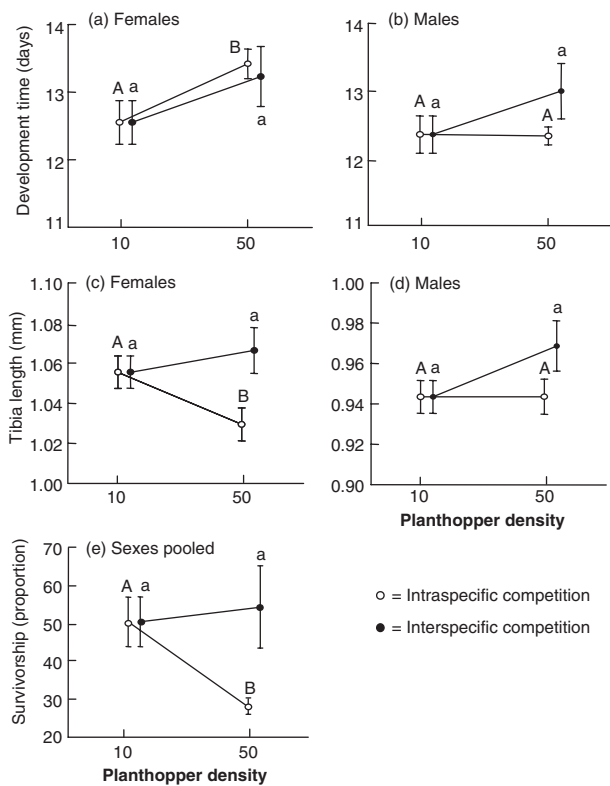


Fig. 3. Effect of intraspecific crowding and interspecific crowding with *Prokelisia dolus* on the development time (days from first instar to adult) for (a) females and (b) males, tibia length (index of adult body size) for (c) females and (d) males, and (e) survivorship (from first instar to adult, sexes pooled) of *Delphacodes penedectea* in field cages on a salt marsh in New Jersey, U.S.A. Means (± 1 SE) with different letters (upper case for intraspecific, lower case for interspecific) are significantly different (ANOVA followed by Tukey–Kramer Honest Significant Difference multiple comparisons, $P < 0.05$). Lines are inserted to indicate trends among treatments.

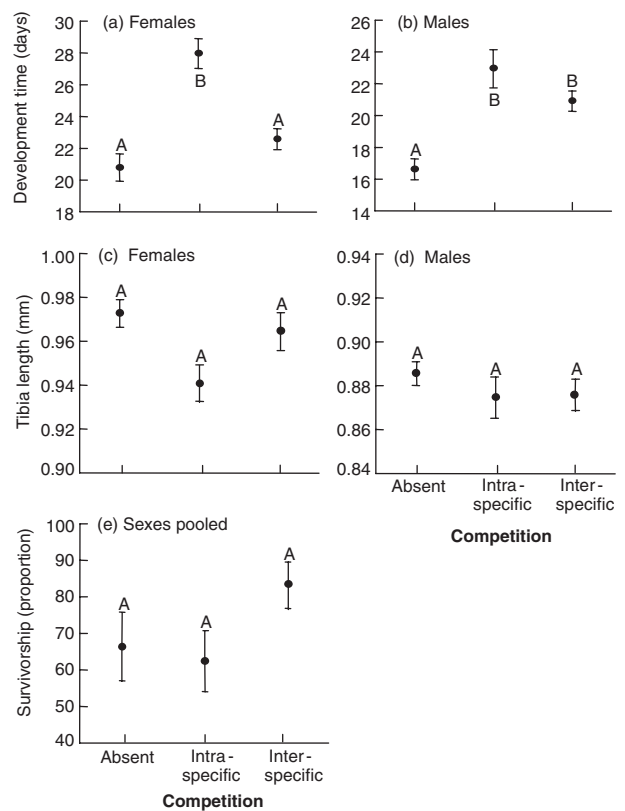


Fig. 4. Development time (days from first instar to adult) for (a) females and (b) males, tibia length (index of adult body size) for (c) females and (d) males, and (e) survivorship (from first instar to adult, sexes pooled) of *Delphacodes penedectea* subjected to one of three competition treatments in the laboratory: no previous feeding (competition absent), previous feeding by conspecifics (intraspecific competition), or previous feeding by *Prokelisia dolus* (interspecific competition). Means (± 1 SE) with different letters are significantly different (ANOVA followed by Tukey–Kramer Honest Significant Difference multiple comparisons, $P < 0.05$).

only the development time of male *D. penedetector* was extended significantly (Fig. 4b).

Plant-mediated interactions in the field. Previous feeding, either by conspecifics or heterospecifics, had no significant effect on the development time ($F_{2,27} = 1.10$, $P = \text{NS}$), body size ($F_{2,27} = 1.61$, $P = \text{NS}$), or survival ($F_{2,27} = 0.48$, $P = \text{NS}$) of *D. penedetector*.

Discussion

Interspecific competition with the abundant planthopper *Prokelisia dolus* appears to play very little role in explaining the rarity of *Delphacodes penedetector* in the field. Laboratory and field experiments examining potential contemporaneous and plant-mediated (consequences of previous feeding) interactions confirmed the minimal impact of interspecific competition on *D. penedetector*. Only the males of *D. penedetector* suffered from interactions with *P. dolus*, whereby either body size was reduced (Fig. 2d) or development time was extended (Fig. 3b).

Notably, it is the males of *D. penedetector*, not the females, that share similar microhabitats on *Spartina* plants with *P. dolus* (Fig. 1). Males of *D. penedetector* occur more frequently in the canopy of *Spartina* where *P. dolus* resides, probably for reasons of mate searching (Langellotto & Denno, 2001). On the other hand, females that experience no adverse effects from interactions with *P. dolus*, feed on the basal stems of *Spartina* well away from most individuals of *P. dolus*. This pattern suggests that resource partitioning may play a role in diminishing competitive effects between these two planthopper species, however neither sex of *D. penedetector* showed any evidence of niche shifting in the presence of *P. dolus*. Although resource partitioning may play some part in reducing interactions between *D. penedetector* and *P. dolus*, spatial segregation on the host plant by many sap-feeding insects does not appear to preclude interspecific competition (Denno *et al.*, 1995). For example, strong interspecific competitive effects are felt between pairs of aphids and adelgids even though they feed on different parts of the plant (Addicott, 1978; McClure, 1989; Moran & Whitham, 1990). Such cases of interspecific competition are thought to result from the sharing of a common phloem resource, because even foliar-feeding and root-feeding sap-feeders can compete intensively (Moran & Whitham, 1990). Sharing of a common phloem resource also appears to mediate competitive interactions between sap-feeders that result from feeding-induced changes in plant nutrition in the previous generation (Denno *et al.*, 2000). Nonetheless, even though *D. penedetector* and *P. dolus* are phloem feeders, resource partitioning appears to contribute to reduced competition between these two planthoppers. Thus, there appears to be no general paradigm in sap-feeding insects concerning the role of resource partitioning in influencing interspecific interactions.

The scarcity of *D. penedetector* in the field appears to result not from interspecific interactions with the common herbivores in the system but from strong intraspecific

competition. *Delphacodes penedetector* suffers adverse effects on survival, development time, and body size, both as a result of contemporaneous interactions with conspecifics (Figs 2 and 3a,c,e) and also from conspecifics that feed on the same plants in the previous generation (Fig. 4a,b), although the latter was not evident from the field experiment, perhaps because plants with highly developed root systems are more resistant to induced changes in plant nutrition (Denno *et al.*, 2002). The reductions in female body size resulting from competition (Figs 3a and 4a) should affect fecundity directly as well, because the two traits are related positively in most planthoppers (Denno *et al.*, 1994). Importantly, *D. penedetector* suffers the effects of intraspecific crowding at quite low densities (three individuals per stem; Fig. 3), densities that are representative of those that can occur for this species in the field (Denno, 1977; Denno *et al.*, in press).

Intraspecific effects are probably mediated by the host plant and result from the local depletion of plant nitrogen due to excessive feeding, an effect shown for *P. dolus* and other planthopper species (Bacheller & Romeo, 1992; Denno *et al.*, 1994; Olmstead *et al.*, 1997). If this were the case, however, the effect on the plant must be very local (restricted to basal stems) because *P. dolus* feeding higher on the plant largely on leaves has little effect on *D. penedetector*. This plant-quality argument is consistent with the apparent importance of plant nitrogen for the performance of *D. penedetector*. For instance, the abundance of *D. penedetector* is correlated positively with plant nitrogen across habitats in the field (Ferrenberg, 2002), and its populations increase when nitrogen-poor *Spartina* is fertilised (Denno *et al.*, in press). Alternatively, conspecifics may interfere physically with each other's feeding, resulting in decreased performance, a phenomenon known to occur in aphids (Whitham, 1979).

This study corroborates the general trend that intraspecific effects are often stronger than interspecific effects for many sap-feeding insects (Denno *et al.*, 1995). For *Eupteryx* leafhoppers on nettles, strong intraspecific effects diminished the potential negative impact of interspecific interactions (Stiling, 1980). Similar effects also occurred between *Eurythronera* leafhoppers on sycamore trees (McClure & Price, 1975) but both studies noted that intraspecific interactions did not preclude interspecific competition. For these studies, however, intraspecific competition prevented interspecific effects from becoming either frequent or strong. *Prokelisia dolus*, one of the most abundant herbivores on *Spartina*, is very insensitive to crowding, either intraspecific crowding or interspecific competition from its common congener (Denno & Roderick, 1992; Denno *et al.*, 2000). Despite the weak density effects limiting populations of *P. dolus*, however, *D. penedetector* is affected little by interspecific interactions with this very abundant herbivore. Thus, intense intraspecific competition in *P. dolus* is probably not pre-empting interspecific effects on *D. penedetector*.

No single force is responsible for structuring the sap-feeder dominated community of herbivores on *Spartina*,

and interspecific competition certainly does not have wide-spread effects on all species. The strength of bottom-up, lateral (competition), and top-down impacts varies tremendously across species. For example, the most important extrinsic factors influencing populations of *D. penedetecta* are intraspecific competition (this study) and plant nutrition (N content), and neither parasitoids nor predators have much effect (Döbel & Denno, 1994; Denno *et al.*, in press). For *P. dolus*, natural enemies and plant nutrition are the important drivers of population dynamics, and interspecific competition with its abundant congener *P. marginata* is inconsequential (Denno & Roderick, 1992; Denno *et al.*, 2000, in press). By contrast, *P. marginata* is affected very adversely by competitive interactions with *P. dolus* (Denno & Roderick, 1992; Denno *et al.*, 2000), and both plant nutrition and natural enemies have important population consequences as well (Denno *et al.*, in press). If one factor is to be singled out as broadly important, albeit to varying degrees, it would have to be plant nutrition. Populations of all sap-feeders in the community are affected by changing plant nutrition, and bottom-up factors in general (vegetation structure and nutrition) dictate the strength of interactions with natural enemies (Denno *et al.*, 2002, in press). Moreover, elevated plant nitrogen tends to moderate density effects in this community of sap-feeders, thus mediating competitive interactions as well (Denno *et al.*, 1994). Although plant nutrition surfaces as the most central factor influencing community-wide dynamics, the impact of competition and natural enemies varies tremendously among the planthoppers and leafhoppers in this assemblage, a pattern that has been documented in other communities of phytophagous insects (Karban, 1989).

Unravelling the factors that structure communities of phytophagous insects is proving complex, and the singular paradigms of interspecific competition and natural enemies are being challenged as more in-depth assessments of herbivore communities emerge. For *D. penedetecta*, a rare herbivore in the *Spartina* community, neither interspecific competition nor natural enemies are important factors dictating its abundance. Rather, intraspecific competition, plant nutrition, and an inherent fecundity limitation appear to constrain its population size. This finding is consistent with a paradigm of bottom-up control whereby host-plant resources are limiting and dominate impacts on phytophagous insect populations (Hunter & Price, 1992).

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