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The effect of plant- and parasitoid-induced egg mortality on the interspecific distribution of an oligophagous herbivore

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Abstract Plant-mediated egg mortality varied greatly for the oligophagous leafhopper, *Carneiocephala floridana*, a common inhabitant of the salt marshes along Florida's Gulf coast. In the laboratory, survivorship from egg to first instar was generally greater on two herbaceous plants, *Borrichia frutescens* and *Salicornia virginica* (80 and 81% respectively) than it was on two grasses, *Distichlis spicata* and *Spartina alterniflora* (41 and 77% respectively). Although *C. floridana* laid significantly more eggs per clutch on *Sp. alterniflora* than on the two herbaceous species, this increase in egg number was offset by the higher mortality of eggs laid on this species. The greatest source of identifiable plant-mediated egg mortality was death due to desiccation of the leaf tissue surrounding the egg clutch. In addition, field experiments in which the four host species were infested with eggs of *C. floridana* at natural densities consistently yielded higher parasitism rates by two mymarid wasps on the grasses, regardless of the background plants. *C. floridana* switches host plants seasonally, using the grass species mainly during the winter months, when the herbaceous species experience a substantial dieback. The herbaceous species are nutritionally superior to the two grass species as a food source for *C. floridana*. *C. floridana* reared on the herbs produce larger, more fecund, adults than they do on the grasses (Rossi 1991). However, during cold winter snaps the grasses, while less "attractive", may provide the most abundant nutritional and ovipositional resources available to *C. floridana*. The results of this study indicate how variable rates of plant- and parasitoid-mediated egg mortality may work synergistically with the interspecific nutritional status of the plants to explain host switching for this insect.

Key words Leafhopper · Parasitoids · Egg mortality · Host-plant preference · Host switching

Introduction

An understanding of the factors shaping oviposition choices for phytophagous insects is essential to the development of a predictive theory of plant-insect interactions (Thompson 1988). According to optimal foraging theory, herbivores should choose to consume plants on which they can maximize their assimilation of nutrients per unit time (Rhoades 1979). However, field and laboratory experiments frequently do not support this prediction (Futuyma and Moreno 1988). Some of the paradoxes may be caused by plant-mediated sources of mortality that are unrelated to nutritional ecology (Barbosa 1988; Futuyma and Moreno 1988). For example, several recent studies have stressed the importance of tri-trophic (plant-herbivore-predator) interactions and especially the effect natural enemies can have on the patterns of host plant use by herbivores (Rotheray 1981; Price and Clancy 1986; Eller et al. 1988; Rossi et al. 1992).

A key facet of tri-trophic interactions may be the interplay of plant quality and natural enemies in determining egg survival. Death during the egg stage has been found to be a primary cause of mortality for several herbivorous insects (Kiritani et al. 1970; Sasaba and Kiritani 1972; Stiling 1980; Dempster 1983; Cook and Perfect 1989). Plant characteristics may influence egg survival either directly through leaf toughness and water content, or indirectly by influencing the third trophic level – specifically predators and parasitoids. Indeed, numerous studies suggest that the host plant plays an important, sometimes critical, role in herbivore-parasitoid interactions (Vinson 1976, 1981; Price et al. 1980; Barbosa 1988; Simms and Fritz 1990), often because volatile plant chemicals provide cues to searching parasitoids (Monteith 1960; Noldus and van Lenteren 1985; Naranjo and Stimac 1987; Vinson et al. 1987; Turlings et al. 1989).

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High egg mortality on a particular host plant species may provide a strong selective pressure for the herbivore to choose alternative hosts. As a result egg mortality may work synergistically with the nutritional quality of the plant to influence host choice, or it may act antagonistically if the host is nutritionally superior, but few progeny survive to exploit it. Few studies have investigated the effects of egg mortality and interpreted them along with information about the nutritional value of the host plant species.

Carneiocephala floridana is an oligophagous leafhopper that utilizes at least four main host plants for ovipositing and feeding in the salt marshes of Florida's Gulf coast (Rossi and Strong 1990; Rossi 1991). These plants, which are very different both structurally and taxonomically, can be placed into two general groups, herbs and grasses. *Borrchia frutescens* and *Salicornia virginica*, which are used during most of the year, are herbaceous species that are typically low-growing and found within the salt barrens of the marsh habitat. Conversely, the winter hosts, *Spartina alterniflora* and *Distichlis spicata*, are tall coarse grasses that are generally found above or below the salt barrens. From spring through fall, *C. floridana* is found primarily on the herbaceous species, but in the winter, when these plants typically experience a substantial dieback in north Florida, the leafhoppers switch to "poorer" quality (low nitrogen) grass species.

Both laboratory and field studies have suggested that *C. floridana* performance (from first instar to adult) is highest on the two herbaceous species and that the grasses should only be accepted into the leafhopper's diet when the herbs are unavailable (Rossi 1991). While patterns of host plant utilization by *C. floridana* are consistent with a nutritional hypothesis, the importance of interspecific plant-mediated egg mortality and parasitism are unknown for this species. Both herbaceous species are succulent compared to the grasses and host water content may be important to egg survival. In addition, eggs of *C. floridana* are attacked by two undescribed species of *Gonatocerus* (Hymenoptera: Mymaridae) or fairy flies (Rossi and Strong 1990), and the eggs may suffer different rates of parasitism on the four host species.

The first objective of this study was to assess the direct influence of host plant species on *C. floridana* egg mortality, focusing on interspecific differences in water content. Secondly, we tested whether host plant species influenced the parasitism rate of *C. floridana* by the mymarid wasps in natural populations and through experimental manipulation.

Methods

In January of 1991, female *C. floridana* were collected from mixed vegetation by sweep netting and brought back to the laboratory. They were placed in groups of three individuals per plant, which is within their natural range of density variation (Rossi 1991), and maintained on each of the four host species. At least 20 plants from each species were used in the experiment. The females

were contained on the plants using large acetate tubes, sealed at the top with organdy cloth, which completely enclosed each plant (for details see Rossi and Strong 1991).

After 24 h, the leafhoppers were removed and the number of eggs in each clutch was recorded. Clutches were identified with an indelible pen mark on the plant. The plants were watered to saturation and placed in a greenhouse under ambient lighting and temperature. The clutches were checked daily and any mortality among the eggs was recorded. When possible, the source of mortality was also noted. Easily identifiable sources of mortality included: deformed eggs, eggs or clutches that died because the leaf tissue surrounding them desiccated and contracted thus crushing the eggs, eggs that desiccated themselves while the surrounding tissue remained hydrated and subtle, and first-instar nymphs that died during eclosion because they could not squeeze through the original oviposition slit while emerging from the egg.

After approximately 18 days, when all the remaining viable eggs had eclosed, each plant was carefully dissected under a stereomicroscope and the number of empty skins (indicating successful emergence) and remaining dead eggs were recorded. Differences in clutch size were assessed using a one-way ANOVA. Comparisons among species means were subjected to a Tukey's HSD post-hoc test for separation of means when appropriate. Number of eggs surviving to eclosion on each host species was analyzed using a G-test.

Leaf water content was determined for all of the host species except *S. virginica* which lacks leaves completely (Duncan and Duncan 1987). For *S. virginica* water content was determined using stems. The ten most recently opened leaves (or stems) for each species were collected and weighed individually on an analytical balance. Leaves were dried in a vacuum oven at 65°C and -12 bars for 72 h, then reweighed, and the water content, expressed as a percent, was calculated as $[1 - (\text{dry mass}/\text{fresh mass})] \times 100$. A mean percent water content was calculated for each plant species and a linear regression was used to describe the relationship between egg mortality (excluding death intrinsically attributable to the leafhopper, i.e., deformed eggs) and water content.

To determine natural parasitism rates of *C. floridana* eggs, we haphazardly collected 40 stems of the four host species once a month from December 1988 through November 1989 from four sites around Oyster Bay, Florida. Egg clutches were dissected from the plants and placed in petri dishes on moist filter paper. Eggs were checked daily for signs of parasitism (parasitized eggs turn bright orange) and the proportion of parasitized eggs was recorded.

Experimentally, we tested the effect of host plant species on parasitism rate by placing potted plants, of approximately equal wet mass and infested with *C. floridana* eggs of a similar age and density, into "common gardens" in the field. As before, groups of three female *C. floridana* were maintained on individual plants using acetate cages. After 24 h, females were removed and the clutches were marked using small plastic bands. Individual plants contained one to three clutches of eggs which is within the natural range for *C. floridana* (personal observation). To account for the effect of habitat (background plants) on parasitism rate, we placed blocks of four plants (containing a single infested plant of each species obtained as above) at sites which consisted primarily of a single host plant species at Goose Creek, Florida. Two replicates (a block of four plants) were placed in each habitat and the position of the plant species within each block was randomly assigned. The pots were placed in shallow holes until the surface of the potting soil was even with the surrounding substrate. This experiment was repeated on four dates in February and March 1991 when *C. floridana* can be found on all four host species.

After 7 days the plants were returned to the laboratory and placed in an isolated room to prevent subsequent parasitism from greenhouse plants. After an additional 7 days, but before any insect emergence, the marked leaf clutches were dissected from each plant and the number of parasitized eggs and the total number of eggs were recorded. Several leaves died during each period, so data from all dates were pooled for statistical analyses. Thus, the number of parasitized and unparasitized eggs were summed for

Table 1 Host plant species and egg performance parameters for *Carneiocephala floridana*, expressed as percentages. Values are either means \pm SE or total percentage with sample sizes given in parentheses. Means followed by different letters within a column are significantly different at $\alpha=0.05$

Plant species	Plant type	% Water content	Clutch size (eggs/clutch)	% Non-parasitoid-mediated mortality	% Field parasitism	% Experimental parasitism ^a
<i>Borrhichia frutescens</i>	herbaceous	89 \pm 1a	3.7 \pm 0.2b	20 (96)	24 (38)	11.0 \pm 3.8b
<i>Salicornia virginica</i>	herbaceous	88 \pm 1a	3.6 \pm 0.2bc	19 (130)	17 (53)	14.3 \pm 6.8ab
<i>Distichlis spicata</i>	grass	53 \pm 2c	3.1 \pm 0.2c	59 (110)	18 (51)	44.9 \pm 10.9a
<i>Spartina alterniflora</i>	grass	70 \pm 1b	4.8 \pm 0.3a	23 (296)	33 (345)	38.3 \pm 4.3a

^a Means from eight pooled replicates

Table 2 Sources of *C. floridana* egg mortality, expressed as percentages, on four host plant species. Twenty plants of each species were inoculated with leafhopper eggs by confining females for 24 h and then plants were kept in the laboratory for 18 days as egg mortality was recorded (see text for details)

Plant species	Plant type	% Viable eggs	% Egg desiccated	% Leaf desiccated	% Deformed eggs	% Died emerging	% Unknown mortality	n
<i>B. frutescens</i>	herbaceous	80	5	9	3	3	0	96
<i>S. virginica</i>	herbaceous	81	6	0	8	5	0	130
<i>D. spicata</i>	grass	41	6	44	0 ^a	9	0	110
<i>Sp. alterniflora</i>	grass	77	8	6	3	5	1	296

^a Value is probably greater than 0%, but due to high desiccation rates no deformed eggs were identified

treatments across all dates. Parasitized eggs were assumed to have experienced the same rate of plant-mediated mortality as unparasitized eggs. Therefore, parasitized eggs that survived the experiment were assumed to represent an additional source of leafhopper mortality which is additive. For each plant species, parasitism rate was calculated by dividing the number of parasitized eggs by the total number of eggs. Proportions of eggs parasitized by *Gonatocerus* were arcsine-square-root transformed and analyzed by a two-way ANOVA with plant species (on which the eggs were located) and habitat (the predominant species in which the block of plants was located) as main effects. Comparisons among treatment means were subjected to a Tukey's HSD when appropriate. Because parasitism rate may be affected by egg density, we assessed density-dependence in parasitism rate using linear regression techniques on both the number of eggs per clutch and the number of eggs per plant for each host species.

Results

Host plant species had a highly significant effect on clutch size ($F=10.90$, $df=3,222$, $P<0.001$). Mean clutch size ranged from approximately 3 eggs/clutch on *D. spicata* to almost 5 eggs/clutch on *Sp. alterniflora* (Table 1). These results are similar to clutch sizes from field-collected plants (Rossi and Strong 1990; Rossi 1991; unpublished data). Moreover, plant species had a highly significant effect on non-parasitoid-mediated mortality ($G=59.39$, $df=3$, $P<0.001$). While this plant-mediated egg mortality was similar among *S. virginica*, *B. frutescens* and *Sp. alterniflora*, it was considerably higher for eggs laid on *D. spicata* (Table 1). Specifically, the high rate of plant-mediated mortality on *D. spicata* resulted when the leaf tissue surrounding the clutch desic-

cated; this factor alone accounted for 44% of the non-parasitoid-mediated egg mortality on this species (Table 2). While not significant, the relationship between egg mortality and percent water content suggested that host plant moisture was inversely related to egg survivorship ($r=-0.8717$, $P<0.09$; $n=4$, adjusted for small sample size).

Field levels of parasitism varied greatly among the four host plants and ranged from 17% on *S. virginica* to 33% on *Sp. alterniflora* over the period of a year (Table 1). The large number of eggs collected from *Sp. alterniflora* is due in part to the obvious nature of the eggs to human observers on this plant. In addition, the larger size of *Sp. alterniflora*, relative to the other species, also biased egg totals for this plant when values were calculated on a per stem basis. For instance, *Sp. alterniflora* commonly has stems that are >1 m in length and 1–1.5 cm in diameter, while *S. virginica* stems are typically around 10 cm in length and 2–5 mm in diameter (personal observation). Consequently, field levels of parasitism had to be determined by pooling the monthly collections for the entire year (owing to small sample sizes for all but *Sp. alterniflora*).

Levels of parasitism were significantly affected by the host species in the "common garden" experiment (Table 3). Egg mortality caused by parasitism ranged from 11% on *B. frutescens* to 45% on *D. spicata* (Table 1). Neither habitat (background plant species) nor the interaction between host species and habitat were significant (Table 3). None of the regressions between parasitism rate and egg number were significant at either the level of the clutch or the level of the plant for any of the host species.

Table 3 Analysis of variance of the proportion (arcsine-square-root transformed) of *C. floridana* eggs parasitized when located on four common host plant species in four habitats, composed primarily of only one of the four host plant species

Source	Sum of squares	df	Mean square	F-ratio	P-value
Species	1.168	3	0.389	4.808	0.014
Habitat	0.167	3	0.056	0.688	0.572
Speciesxhabitat	0.938	9	0.104	1.287	0.316
Error	1.295	15	0.081		

Table 4 Estimated survival of *C. floridana* eggs on four host plant species, based on average clutch size laid on each host species. Estimates were calculated using plant-mediated egg mortality and parasitoid-mediated mortality from field experiments (see text and Tables 1–2 for full details). Letters above columns are used to indicate how subsequent values in each were obtained

Plant species	Plant type	a Mean no. eggs/clutch	b Proportion of non- parasitoid-mediated mortality	c [a-(axb)] Expected no. surviving per/clutch	d Proportion of eggs parasitized	e [c-(cxd)] Expected survival of eggs/clutch
<i>B. frutescens</i>	herbaceous	3.7	0.20	3.0	0.110	2.7
<i>S. virginica</i>	herbaceous	3.6	0.49	1.6	0.449	0.88
<i>D. spicata</i>	grass	3.1	0.19	2.9	0.143	2.5
<i>Sp. alterniflora</i>	grass	4.8	0.23	3.7	0.383	2.3

Discussion

C. floridana feeds and oviposits primarily on the herbs, *B. frutescens* and *S. virginica*, during most of the year and switches to the grasses, *Sp. alterniflora* and *D. spicata*, during the winter (Rossi 1991). This pattern of host switching accords well with the seasonality and nutritional quality of *C. floridana*'s host plants (Rossi 1991). In this study, we found that other measures of leafhopper performance (i.e., egg survival), apparently unrelated to the nutritional status of the host species, also favor the observed temporal pattern of host use for this insect. *Carneiocephala floridana* experienced its highest levels of egg mortality, both developmentally and through parasitism, on the grasses. Although *C. floridana* is capable of laying the largest clutches on *S. alterniflora* because of its greater size, the potential gain to the female of producing a larger clutch is offset by the high parasitism those eggs are likely to incur (Table 4). Eggs of *C. floridana* fared poorest on *D. spicata*; in fact, our results suggest that less than one egg per clutch would be expected to survive the egg stage (Table 4). The high rate of egg mortality on *D. spicata* may be related to an interaction between ovipositional wounding and the plant's relatively low water content.

The parasitism rates obtained from field-collected eggs did not always correspond with the experimental data (Table 1). Both *S. virginica* and *Sp. alterniflora* showed similar rates of parasitism for field vs. experimental data, while *B. frutescens* and *D. spicata* differed by 13 and 27% respectively. This is not surprising because the monthly samples had to be pooled in order to provide a meaningful sample size. As a result seasonal variation in parasitism rate, which is common for many herbivorous insects (Stiling and Strong 1982; Stiling et

al. 1992), is lost and pooled field parasitism data must be viewed with caution. However, for *Sp. alterniflora*, the only species with an adequate sample size, during the winter months of December–March (covering the time of the experiment) the field parasitism rate was 35.6% ($n=317$), which is comparable to the experimentally determined rate of 38.3%. Performing field experiments such as ours, during the period when the leafhopper is found on all four hosts, is more meaningful because parasitoids should be searching for *C. floridana* on all four plant species. This should prevent parasitism rates from being biased on the low side for plant species that would not be included in the parasitoids' search image.

The ability of a parasitoid to locate hosts within a habitat is often more important than host suitability in limiting the rate of parasitism (reviewed by Nordlund 1987). The highly significant effect of plant species suggests that *Gonatocerus* either prefer, or are better at locating, *C. floridana* on the grasses than the herbaceous species. The high levels of parasitism among the grass species may have resulted from the location of the eggs relative to the surface of the plant. *C. floridana* lays its eggs parallel to the plant surface just below the epidermis on the grasses, and eggs are visually apparent (Rossi and Strong 1990). Conversely, eggs on *B. frutescens* and *S. virginica* are often perpendicular to the plant surface and, as a result, much less of each egg is visible to humans and, presumably, parasitoids. The lack of a background plant effect or an interaction, suggests that *Gonatocerus* are equally adept at locating eggs of *C. floridana* regardless of their location within the range of typical host plants of the leafhopper.

To understand the population dynamics of herbivorous insects, we must investigate three-trophic-level interactions (Price and Clancy 1986; Rossi et al. 1992). Yet interactions among the third trophic level, although often cited

as being very important in regulating their herbivorous hosts, are largely unknown (Nordlund 1987). This study demonstrated that the temporal and spatial switching of host plants by *C. floridana*, while consistent with the nutritional quality of the host species (Rossi 1991), could also be explained as the leafhopper seeks refuge (enemy-free-space) on particular host plant species (Atsatt 1981; Holt 1984; Lawton 1986). Our experimental results indicate that by ovipositing on the two herbaceous species when available, *C. floridana* should reduce both plant- and parasitoid-mediated mortality to its eggs. Selective pressures to reduce egg mortality and choose nutritionally superior plants appear to be working synergistically in this system. Together these factors suggest that *C. floridana* should utilize the grasses only when the *B. frutescens* and *S. virginica* are unavailable. This is exactly what is seen in nature, with *C. floridana* using the grasses largely only in the winter, after the herbaceous hosts have died back.

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