

**THE  
ECOLOGY AND  
MANAGEMENT  
OF WETLANDS**

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Volume 1:  
Ecology of Wetlands

**Edited by  
D. D. Hook  
and  
Others**

## THE ECOLOGY AND MANAGEMENT OF WETLANDS

### Volume 1: ECOLOGY OF WETLANDS

This two-volume work presents selected papers from a symposium on wetlands organised by the International Society of Anaerobiosis, held in June 1986 in Charleston, South Carolina. Contributors are international authorities from all over the world, but principally the USA and Europe.

Volume one covers the general ecology of wetlands. Principal subject areas addressed include how plants are adapted to waterlogged soils, plant-animal interactions, soils and geology of wetlands, hydrology and estuarine ecosystems. Volume two covers more applied topics such as agricultural use, restoration and regulation, use for forestry, fisheries and wildlife, the development of wetlands for agriculture and evaluation methods. The volumes represent a definitive statement of the current subject and almost everyone that works with wetlands will find topics of interest in each volume. More specifically, ecologists, botanists and soil scientists as well as workers in forestry, fisheries and wildlife management will find much of value in these volumes.

Edited by Donal D. Hook, Clemson University, South Carolina, and others

# THE ECOLOGY AND MANAGEMENT OF WETLANDS

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## Volume 1: Ecology of Wetlands

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## Chapter Forty-four

### HERBIVORE POPULATION DYNAMICS IN INTERTIDAL MARSHLANDS: THE ROLE OF HOST PLANT NUTRITION

Robert F. Denno

#### INTRODUCTION

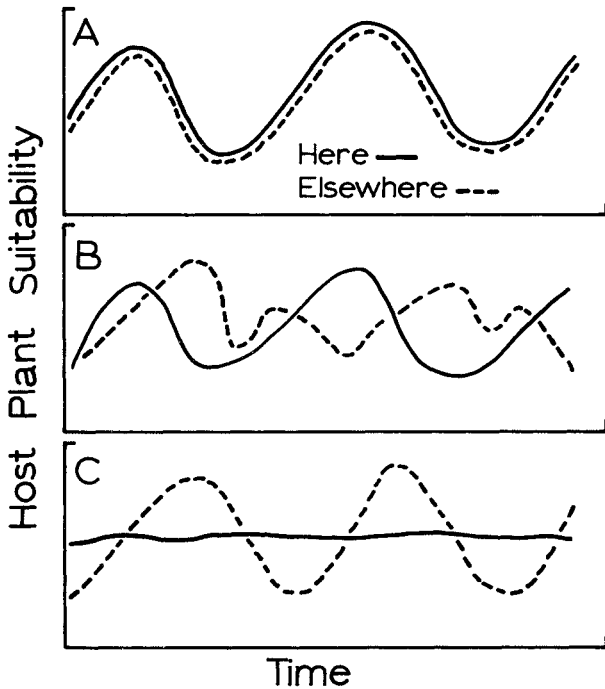
Several researchers in population dynamics have attempted to predict when insects will migrate based on changes in habitat quality. Several very general models have been proposed (Southwood, 1962, 1977; Solbreck, 1978; Denno and Grissell, 1979). Solbreck's (1978) model discusses an environment containing an archipelago of habitat patches variable in time and space and an insect which may respond with either immediate reproduction, migration, or diapause (Figure 44.1). For an insect to develop the appropriate strategy, it needs information concerning environmental variability in both spatial and temporal dimensions. Consequently, information is needed about the future quality of the immediate resource here, as well as the future quality of alternative patches elsewhere. Selection will make the appropriate life history decision.

For example (Figure 44.1A), if changes in the quality of resource patches here and elsewhere mimic each other, then diapause rather than migration should be favored when resources are unsuitable. Why move if you can't improve your situation? However, if changes in resource abundance (quality) here and elsewhere are not in phase, migration should be adaptive because as conditions deteriorate here they are improving elsewhere (Figure 44.1B). Also, migration should be favored if conditions are always suitable here, but oscillate between better and worse elsewhere. The opportunity to colonize a seasonally proliferating resource describes this situation (Figure 44.1C). These models are generally logical, but if we are ever able to predict the conditions that lead to migration, we must know the specific components of habitat favorableness as they vary within and between habitats.

This chapter focuses on temporal and spatial variation in several habitat factors, particularly host plant nutrition, and its contribution to the population dynamics and migration behavior of a single herbivorous insect. The herbivore is a planthopper (*Prokelisia marginata*, Homoptera: Delphacidae) that inhabits the intertidal marshes of the Atlantic and Gulf Coasts where it occurs on its only host plant, the grass, *Spartina alterniflora*. My objectives include (1) demonstrating differences in the distribution and abundance of this planthopper in its various *Spartina* habitats and (2) trying to understand how factors like host plant quality con-

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Figure 44.1: Predicted life-history responses of herbivorous insects to spatial and temporal changes in the favorableness of resources in patches here (—) and elsewhere (---). (A) Where changes in the favorableness of patches here and elsewhere are similar, better alternatives are not available, and diapause rather than migration should be favored when the quality of all patches is low. (B) In contrast, if the favorableness of patches elsewhere improves while the current patch deteriorates, migration should be favored. (C) If resources are permanently available in one habitat here yet fluctuate seasonally elsewhere, migrations to and from the temporary habitat can occur.



Source: From Solbreck (1978)

tribute to the performance, population dynamics, and migration behavior of Prokelisia.

### STUDY ORGANISMS

Prokelisia marginata is the most abundant herbivore in Atlantic marshes where it feeds in the phloem cells of its host grass,

Spartina alterniflora (Denno and Grissell, 1979; Denno, Douglass and Jacobs, 1986). Using saw-like ovipositors, females insert their eggs between the ridges on the upper blade-surfaces of the grass. Eggs hatch and nymphs feed on the leaf blades passing through five instars or stages. In the mid-Atlantic states of the USA, there are three generations a year and nymphs overwinter by nestling into the thatch of the grass (Denno and Grissell, 1979; Tallamy and Denno, 1979).

Like most planthoppers, populations of Prokelisia are composed of two discrete wing-forms, thus facilitating the study of migration (Denno, 1976). There are macropterous individuals with fully developed wings, and brachypterous individuals with reduced wings that cannot fly. Macropters are capable of long distance flight and consequently are able to escape from unfavorable host plants and colonize new ones (Denno, 1983). Because of their flightlessness, brachypters can move only short distances up to several meters and are unable to track large-scale changes in the abundance and quality of their hosts (Denno, Raupp, Tallamy and Reichelderfer, 1980). However, brachypters have a reproductive advantage because they reproduce earlier and lay more eggs (Denno and McCloud, in press). Thus, as long as conditions remain favorable, brachypters have an advantage.

For planthoppers in general, wing-form is not inherited by any simple genetic rule and is polygenic in the few species studied (Kisimoto, 1956, 1965; Raatikainen, 1967; Roff, in press). However, there is a strong environmental component to wing-form determination. Individuals have the capability of molting into either a brachypter or a macropter. Various environmental cues trigger a developmental switch that determines wing-form. Crowding, host plant nutrition and temperature are three cues that influence wing-form in Prokelisia (Denno, Douglass and Jacobs, 1985).

The host plant of Prokelisia, Spartina alterniflora dominates the vegetation of many Atlantic coast marshes in North America where it grows predominantly below MHW level often in large pure stands (Denno, 1983). On Atlantic Coast marshes Spartina alterniflora occurs as two dynamically different growth forms in two fairly discrete habitats (Denno and Grissell, 1979). Along the depressed borders of tidal creeks and on bay edges, tall-form plants grow. Here, plants may reach 2 m in height. On the high flat marsh near MHW level, short-form grows where plants reach only 10-40 cm in height.

Short-form plants sprout in spring, die in fall, but remain standing through winter and have associated with them a thatch where nymphs overwinter. By contrast, tall-form plants obtain very large biomass in early summer, die back in fall, but due to the action of winds, waves, and ice are knocked over and finally sheared off completely during winter leaving exposed creek banks unsuitable as overwintering sites for Prokelisia. Thus, the Spartina system consists of two major habitat types, short-form grass on the high marsh that is persistent year round, and tall-form grass that is temporarily available during summer and fall for exploitation by planthoppers.

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### PLANTHOPPER POPULATION DYNAMICS

Nymphs of Prokelisia overwinter on the high marsh and begin molting to adults in spring (Figure 44.2A). Because of the low elevation of the streamside habitat, short plants are often inundated during early spring. As a consequence, the offspring of first generation adults develop mostly on the high marsh. It is not until early summer (Figure 44.2B) that streamside Spartina grows tall enough for exploitation by planthoppers. During late spring and early summer, macropters migrate from the high marsh and colonize streamside vegetation where they oviposit. Some adults (both macropters and brachypters) remain on the high marsh and reproduce. During summer (Figure 44.2C), eggs hatch on streamside vegetation where huge populations of developing nymphs can occur. Much smaller populations of nymphs occur on the high marsh during summer. During fall (Figure 44.2D), nymphs on streamside vegetation molt mostly as macropters that migrate, colonize high marsh vegetation, and oviposit along with resident adults. These eggs hatch into the overwintering generation of nymphs and the cycle begins again (see Denno and McCloud, 1985 for details).

### RESULTS AND DISCUSSION

In the sections that follow, I focus on an investigation of what factors are responsible for driving the population dynamics of Prokelisia. To do so I have divided the remainder of this report into three parts. First I investigate in the laboratory how two factors, host plant nutrition and crowding, affect the fitness of Prokelisia. Second, I review how these two factors influence the production of migrants. Last, I extend my laboratory findings to the field to explain the underlying mechanisms involved in the interhabitat migrations of Prokelisia as well as the consequences of these movements.

#### Planthopper Performance

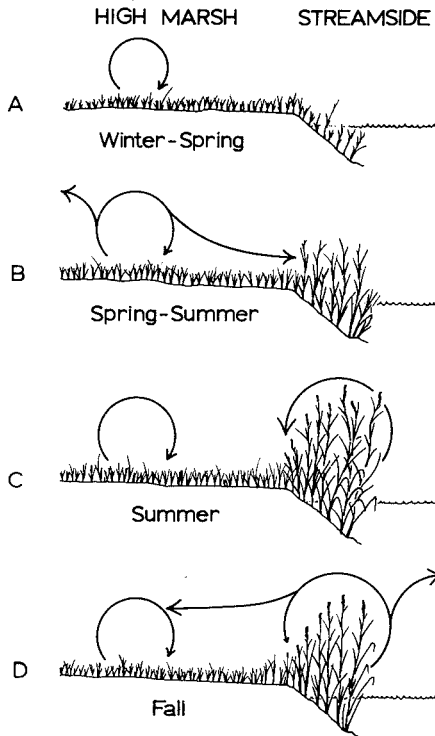
The effects of host plant nutrition and crowding on the fitness of Prokelisia were examined by setting up a 2 x 5 factorial experiment in the greenhouse. By fertilizing some Spartina seedlings heavily and others lightly I was able to establish two nutritional categories of hosts that represent the extremes available in the field. On average, heavily fertilized plants contained 65 mg/g soluble protein, whereas lightly fertilized plants contained only 15 mg/g.

Five densities of newly hatched first instar nymphs were caged on the two nutritional categories of plants. The five densities were 1, 5, 10, 25 and 50 nymphs/tube cage. To correct for differences in plant size, these densities were ultimately expressed as load values (no. of nymphs/g of Spartina). Nymphs were allowed to feed, and the size of eclosing adults and their development time were measured.

Nymphal crowding had a profound effect on the development time to adult. Increasing the level of crowding from 2 to 75



Figure 44.2: Population dynamics and interhabitat migration in *Prokelisia marginata*. (A) Nymphs overwinter on the high marsh and begin eclosing to adults in spring. Because of the low elevation of the streamside habitat, plants remain inundated during early spring. As a consequence, the offspring of first-generation adults develop mostly on the high marsh. (B) It is not until early summer that streamside *Spartina* grows tall enough for exploitation by plant-hoppers. During late spring and early summer, macropters migrate from the high marsh and colonize streamside vegetation, where they oviposit. Some adults (both macropters and brachypters) remain on the high marsh and reproduce. (C) During summer, eggs hatch on streamside vegetation, where huge populations of developing nymphs occur. Smaller populations of developing nymphs occur on the high marsh. (D) Nymphs on streamside vegetation eclose mostly as macropters in fall; these macropters migrate, colonize high-marsh vegetation, and oviposit along with resident adults. These eggs hatch into the overwintering generation of nymphs. (See Denno and Grissell, 1979 for greater detail).



Source: From Denno and McCloud (1985)

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nymphs/g Spartina extended development time by more than ten days. The effect was general on all sexes and wing-forms (Denno et al., 1986). Interestingly, there was no effect of host plant nutrition on development time for any of the sexes and wing-forms (Denno et al., 1986).

However, host plant nutrition had a major effect on the body size of Prokelisia. The body length of both sexes increased when they were raised on nutritionally superior hosts compared to less nutritious ones, but females showed a proportionally greater increase. When raised on more nutritious seedlings of Spartina, the body length of females increased 7 per cent. We may ask what the fitness ramifications of large body size are. For Prokelisia, there is a significant positive relationship between average daily fecundity and body length (Denno and McCloud, 1985). Using this relationship and the body size data from the greenhouse experiment, a 25 per cent increase in daily fecundity should be realized by females feeding on the more nutritious grass (Denno and McCloud, 1985).

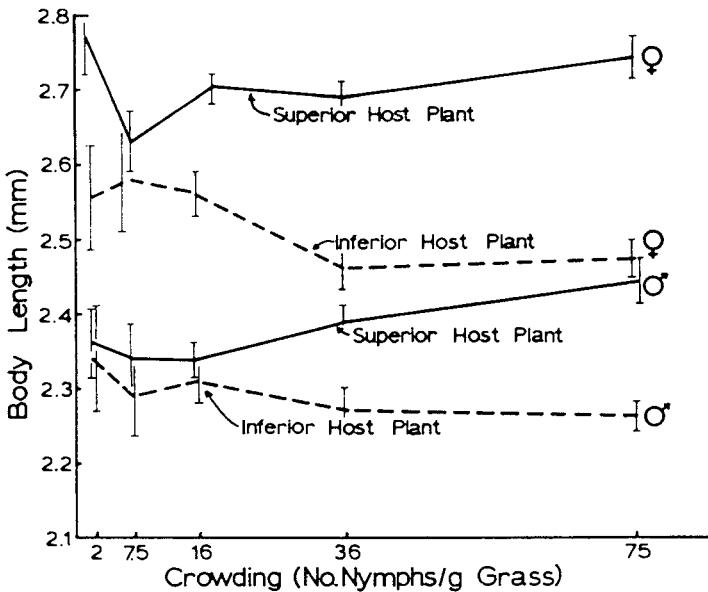
Perhaps the most interesting effect of the treatments on the body length of Prokelisia was a significant interaction between crowding and host plant nutrition (Denno et al., 1986). Crowding had a greater reducing effect on body length if hoppers were raised on marginal quality seedlings compared to nutritionally superior ones (Figure 44.3). Note that the body size decreases with crowding (= load) on inferior hosts (dashed lines) while it remains the same or increases slightly on superior hosts (solid lines). We can conclude that body size-mediated fecundity in Prokelisia is increased by feeding on nutritious host plants, that crowding reduces fitness by extending development time, and that superior host nutrition in part moderates the negative effects of crowding.

### Production of Migratory Forms

To look at the effect of crowding and host nutrition on wing-form, I return to the results of the greenhouse experiment where five densities of nymphs were raised on both heavily and lightly fertilized seedlings of Spartina (see Denno and McCloud, 1985). The wing-form responses of males and females to crowding and host quality are different. On lightly fertilized grass (Figure 44.4A) proportionally more females molt to macropters as density increases. This is not the case with males where macroptery is high at low densities as well. At very low densities perhaps macroptery is favored in males to facilitate locating females by flight. On heavily fertilized hosts (Figure 44.4B) macroptery is suppressed at high densities for both males and females. However, at low densities males remain long-winged despite high host nutritional quality.

Thus, the production of migratory forms is density-dependent in females, and superior host nutrition dampens the migration response that otherwise occurs in both sexes at high densities on poor quality hosts.

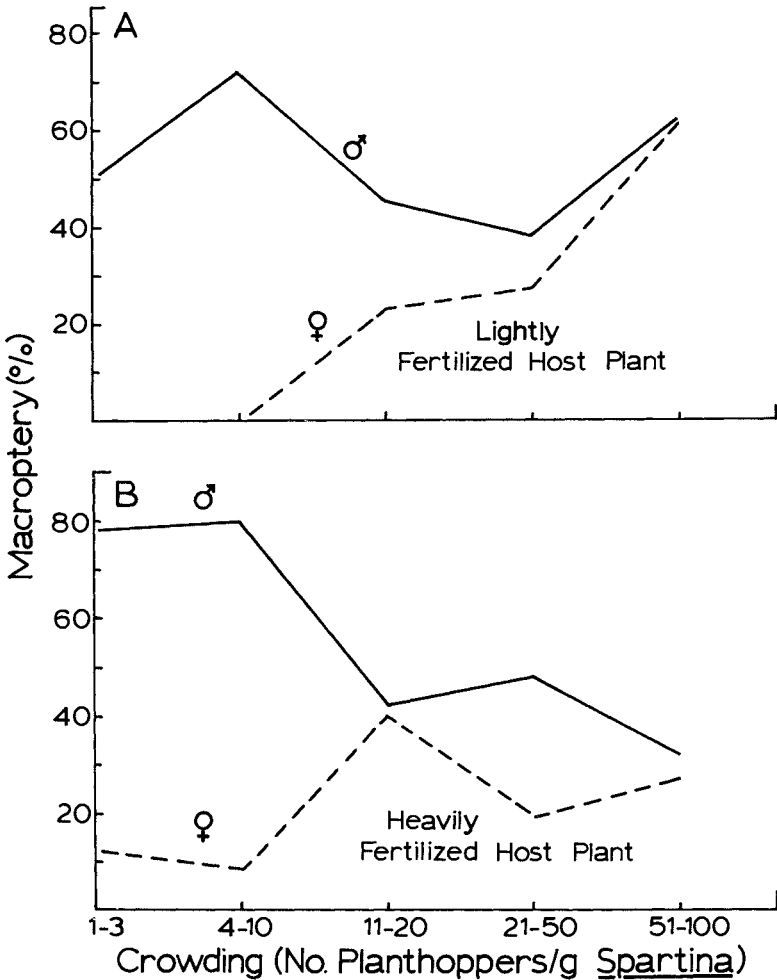
Figure 44.3: Relationship between planthopper load (level of crowding incurred during the nymphal stage) and the adult body length of male and female *Prokelisia marginata* raised on heavily and lightly fertilized seedlings of *Spartina alterniflora*. Because the effects of plant nutrition and sex and their interaction on body length were significant (ANOVA), separate regressions for body length and crowding are plotted for all combinations of sex and plant nutrition. The significant interaction between crowding and host plant nutrition (ANOVA) is illustrated by the divergence in body length ( $\bar{y}$ , in mm) of planthoppers raised on nutritionally superior and inferior host plants as crowding ( $\bar{x}$ , number of nymphs per gram *Spartina* dry mass) increases. For females on superior hosts:  $\bar{y} = 2.72 - 0.0011\bar{x}$ ,  $n = 26$  cages,  $R^2 = 0.014$ . For females on inferior hosts:  $\bar{y} = 2.56 - 0.0013\bar{x}$ ,  $n = 22$  cages,  $R^2 = 0.086$ . For males on superior hosts:  $\bar{y} = 2.37 + 0.00005\bar{x}$ ,  $n = 30$  cages,  $R^2 = 0.0001$ . For males on inferior hosts:  $\bar{y} = 2.31 - 0.0005\bar{x}$ ,  $n = 23$  cages,  $R^2 = 0.031$ . Data are means  $\pm 1$  SE.



Source: From Denno et al. (1986)

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Figure 44.4: Relationship between the level of crowding incurred during the nymphal stage and per cent macroptery in eclosing males and females of *Prokelisia marginata* raised on lightly fertilized (A) and heavily fertilized (B) seedlings of *Spartina alterniflora*. The soluble protein content of heavily fertilized seedlings ( $\bar{X} \pm SD$ ) was  $61.5 \pm 7.4$  mg/g and of lightly fertilized seedlings  $15.5 \pm 4.3$  mg/g. For males on lightly fertilized hosts,  $r = 0.179$ ,  $n = 24$  cages,  $P = 0.4015$ ; for females on lightly fertilized hosts,  $r = 0.738$ ,  $n = 22$  cages,  $P = 0.0001$ ; for males on heavily fertilized hosts,  $r = -0.268$ ,  $n = 30$  cages,  $P = 0.1523$ ; for females on heavily fertilized hosts,  $r = 0.124$ ,  $n = 26$  cages,  $P = 0.5449$



Source: From Denno et al. (1985)

### Crowding and Host Nutrition in the Field

In this last section of this chapter I extend these laboratory findings on host plant nutrition and crowding to the field in order to understand the underlying mechanisms driving the interhabitat migrations of Prokelisia. Movements between habitats must necessarily be associated with the fitness benefits in the respective patches. Knowing that crowding and host nutrition can affect the fitness of Prokelisia I would like to compare these two factors between the two major habitats of this planthopper - the high marsh and streamside habitats. First let us concentrate on the high marsh habitat. A common pattern on the high marsh is for planthopper density to increase exponentially throughout the season. By mid-summer there can be over 1,000 planthoppers/m<sup>2</sup>. Furthermore, following a high in May, the nutritional quality of Spartina (measured as soluble protein) decreases rapidly (Denno et al., 1985). We may now ask what the consequences are for planthoppers that remain in the high marsh habitat during July when conditions can be crowded on poor quality hosts.

We find that the body length of female Prokelisia is shortest (2.74 mm) during the summer in the high marsh habitat. By migrating to the streamside habitat in early June, Prokelisia is able to realize a much larger body size (2.95 mm) (Denno et al., in preparation). During July and August when nymphs are developing, the soluble protein content of the streamside vegetation is 36 mg/g. This compares with only 21 mg/g for Spartina on the high marsh. This nutritional difference is also confirmed by the fact that the total free amino acid content is always higher in streamside vegetation (Denno et al., in preparation).

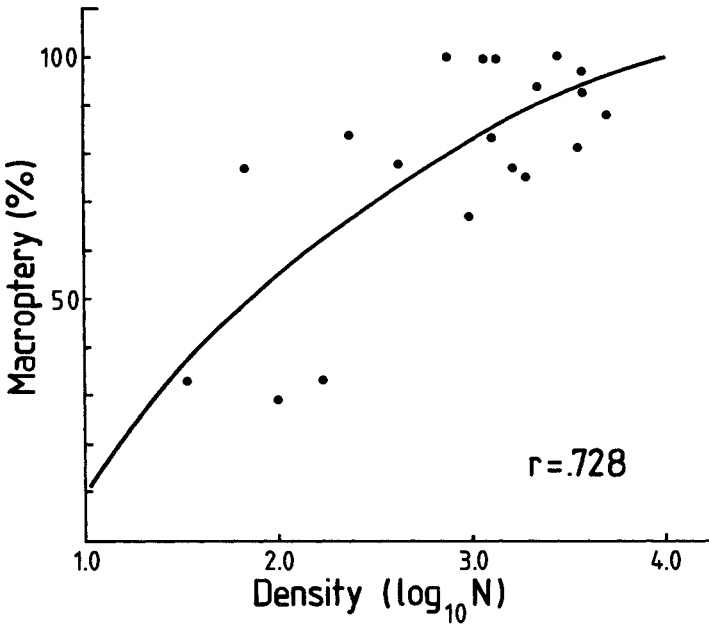
The absolute difference in body size between high marsh and streamside Prokelisia cannot be attributed to temperature because the leaf blade temperature of Spartina is virtually the same between high marsh and streamside habitats at the same time on any given day (Denno et al., in preparation). Both field and experimental data strongly implicate host nutrition as the factor primarily responsible for the larger body size and fecundity of hoppers in streamside vegetation.

Now I confirm by laboratory findings and show that changes in the density of planthoppers and the nutritional quality of Spartina both contribute to wing-form determination in field populations of Prokelisia. To test the effects of density on wing-form in the field, I took seasonal samples and correlated the percentage macroptery in adult female Prokelisia with the density or level of crowding they experienced as nymphs 4 weeks before. There is a positive curvilinear relationship between density and the proportion of macropters as predicted (Figure 44.5).

Results of the greenhouse experiment showed that density-dependent macroptery was dampened on superior quality hosts. To manipulate host plant quality in the field, I fertilized large (100 m<sup>2</sup>) plots of Spartina on the high marsh. Fertilization resulted in a significant increase in the soluble protein content of Spartina culms throughout the season. By August, fertilized plants contained 43 mg/g soluble protein and non-fertilized plants contained only 25 mg/g soluble protein. I also followed changes in the frequency of macroptery in adult females in both control and fertilized plots.

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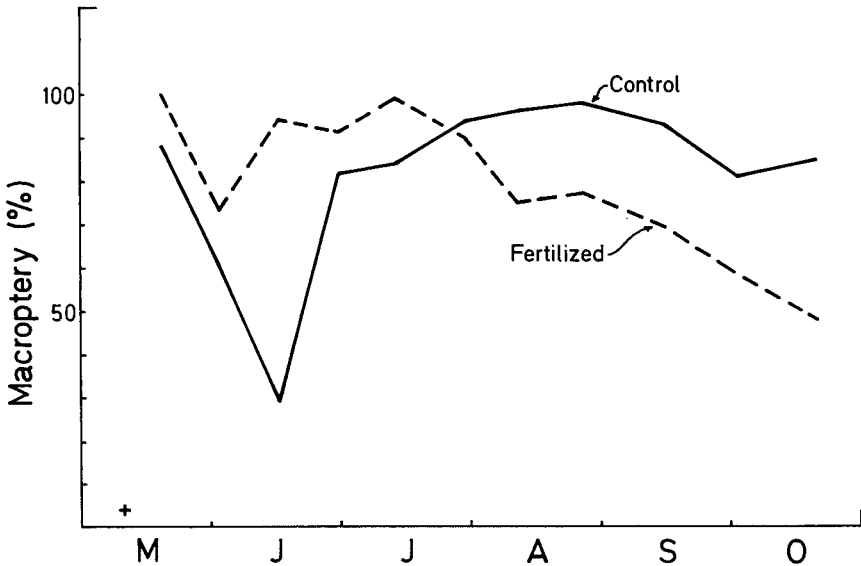
Figure 44.5: Relationship between % macroptery in adult females of *Prokelisia marginata* and the population density they experienced as developing nymphs. A greater percentage of females molt to potential migrants at high densities. The relationship was generated from data collected at Tuckerton, New Jersey



The frequency of macroptery was higher in the fertilized compared to the control plots through July (Figure 44.6). Independent experiments show that this early season pattern resulted from higher rates of colonization by macropters in the fertilized plots (Denno, 1983). However, after July, the frequency of macroptery in females was significantly less in the fertilized treatment. This late season pattern was the result of an absolute increase in the density of brachypters in the fertilized *Spartina* (Denno et al., in preparation). These data provide strong field conformation of my laboratory findings that superior host nutrition can dampen the migration response in *Prokelisia*.

In conclusion, I contend that it is the unique seasonal opportunity to exploit a more nutritious resource that has provided conditions favoring the evolution of migration. The process is mediated by environmental cues like crowding and host plant nutrition that trigger a developmental switch to determine the migratory fate of individuals. Wing-dimorphism is maintained in *Prokelisia* because brachypters have a reproductive advantage in localized persistent patches of *Spartina* on the high marsh. In

Figure 44.6: Percentage macroptery in populations of *Prokelisia marginata* in fertilized and non-fertilized plots of *Spartina alterniflora* on the high marsh at Tuckerton, New Jersey. Elevated levels of macroptery in fertilized plots during June and July are the result of immigrating macropters. Lower levels of macroptery in fertilized plots during the fall are the result of absolute increases in the brachypterous form. Superior host plant quality dampens the migration response.



these local patches associated with mud pannes, we feel that the proximate nutritional quality of *Spartina* may be unusually high due to stress-induced increases in the concentration of free amino acids (Denno *et al.*, in preparation).

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