

Organization of a Guild of Sap-feeding Insects: Equilibrium vs. Nonequilibrium Coexistence

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1 Introduction

The great majority of ecological literature assumes that communities are in equilibrium and that interspecific competition plays a primary role in their organization (e.g., Lotka 1931, Gause 1934, Slobodkin 1961, MacArthur and Wilson 1967, Schoener 1974, Hutchinson 1977). For insects, several hypotheses have been invoked when attempting to explain coexistence under equilibrium conditions. McClure and Price (1975) suggest that coexistence in a guild of sycamore-feeding leafhoppers may be partially explained by frequency-dependent competitive ability, since at high densities each species adversely affects its own fitness more than that of its competitors. However, by far the most common explanation for equilibrium existence is resource partitioning, whereby species reduce interspecific competition by exploiting different aspects of resources (e.g., Connell 1961, MacArthur 1972, Cody 1974, Schoener 1974, Harper 1977, Diamond 1978). As Strong points out in his contribution (Chapter 10), competition has been invoked primarily by ecologists working with vertebrates, plants or marine organisms rather than insects.

By contrast, Hutchinson (1953) suggested two situations where species may coexist without achieving a stable equilibrium. First, nonequilibrium coexistence can be attained by organisms with several generations per year, where changing environmental conditions shift species-dominance and prevent any one species from excluding the other. Secondly, Hutchinson (1953) as well as Skellam (1951) emphasize that a nonequilibrium community is possible if catastrophic events destroy existing habitats while new ones are simultaneously created. Under these circumstances, competitively weaker species (those that would be excluded under equilibrium conditions) may coexist because of their increased ability to disperse and colonize vacant sites. We would add to this category any species that by virtue of any particular life history trait(s) (dispersal or otherwise) is favored during catastrophe.

Recently, the notion of equilibrium and competition mediated communities has been challenged (see Dayton 1971, Caswell 1978). For instance, Connell (1978) provides evidence that tropical rain forests and coral reefs, though traditionally regarded

as highly ordered equilibrium communities, are actually seldom near equilibrium because of either frequent disturbances or more gradual climatic changes. Thus, intermediate levels of disturbance prevent the elimination of inferior competitors. The findings of Hubbell (1979) on the organization of tropical dry forests are also consistent with a nonequilibrium hypothesis.

There is considerable literature on niche differentiation in coexisting parasites of fish, leading one to the conclusions that competition is keen and species-packing tight in these communities (Holmes 1973, Hair and Holmes 1975, Price 1980 and many references therein). Yet, Kennedy (1977) concluded that many fish parasites exist in nonequilibrium conditions and that interspecific competition plays little role in regulating their populations.

Strong (1977a, 1977b; Chapter 10) has studied rolled-leaf hispine beetles that feed in the New World tropics on the leaves of the monocot, *Heliconia*. Food and space within rolled leaves were well in excess of the levels that would adversely affect the beetles, and interspecific competition was not shown to structure communities. Furthermore, the most recent and convincing hypothesis to account for the coexistence of eight species of leafhoppers on sycamore trees in Illinois invokes nonequilibrium conditions (McClure and Price 1976, Price 1980). In a recent volume on parasites (broadly defined as an organism living in or on another living organism—and including most conventional parasites and parasitoids as well as phytophagous organisms), Price (1980) concludes that there is little evidence to suggest that competition has been an organizing force in parasite communities, that nonequilibrium conditions often prevail, and that the partitioning of resources and subsequent specializations we see result from evolutionary constraints other than competition.

In this report we hope to elucidate some of the factors that are important in organizing phytophagous insect communities by examining a guild of sap-feeding insects (mostly leafhoppers and planthoppers) that feed on the intertidal marsh grass, *Spartina patens* Loes. Several characteristics of this system make it attractive for examining community processes. The grass is widespread and is a dominant component of salt marsh vegetation from New Hampshire to Florida. It often occurs in pure stands that exist as an archipelago of "islands" varying in size from several square meters to huge (> 10-ha) patches set in a "sea" of other marsh plants. The sap-feeding insects on *S. patens* are abundant, diverse (≈ 10 species) and for the most part host-specific. Also, several very different life history patterns are represented in the guild.

Here, we review evidence suggesting that the community of sap-feeders associated with *S. patens* is occasionally in equilibrium and is organized by competitive interactions. Then we provide additional evidence suggesting that the community is not in equilibrium at least during some years and that coexistence is achieved by the selective elimination of certain species during catastrophic events creating vacant sites for others to exploit.

2 Distribution, Structure, and Growth Dynamics of *Spartina patens*

North of North Carolina, in the mid-Atlantic and New England states, the high intertidal marsh association (mean high water level to ≈ 0.5 m above) is quite simple, where it is covered primarily by the grass, *Spartina patens* (Ait.) Muhl. (Miller and Egler 1950, Blum 1968, Redfield 1972). The high marsh is inundated only by the highest spring tides and storm tides. In this geographic area, variation in the elevational relief of the marsh surface results in an archipelago of usually pure *S. patens* patches ranging in size from just a few square meters to mammoth "islands" (> 3 ha) surrounded by another grass species, *Spartina alterniflora* Loes, that dominates the low intertidal marsh. In the Carolinas and south to Florida and along the Gulf Coast, *S. patens* occurs as a broken fringe of vegetation along the high marsh (Mobberley 1956, Adams 1963). Here, stands of grass can be pure, but rarely attain sizes greater than 1000 m². Also, in this portion of its range, plants tend to be a bit larger and more robust.

S. patens is a slender-culmed grass with narrow, convoluted blades (Mobberley 1956, Blum 1968). The living culms of *S. patens* grow and project through a thick (5-20-cm), dead horizon of prostrate culms and blades resulting from the previous year's growth. New culms, shaped like vertical awls, first protrude through the thatch in spring. As the season progresses, older leaf blades separate from newer, upright ones by bending at the sheath-blade junction. As subsequent blades fold back in this fashion, they make contact with the surface of the dead thatch. By summer, the dead thatch becomes overlaid with an entanglement of living leaf blades. Further prostration occurs in summer and fall, when the culms of *S. patens* fold over at a weak area in the stem, which coincides approximately with that portion of the stem that is included in and surrounded by the dead thatch (Blum 1968). Prostration usually occurs in a mosaic fashion, leaving behind small patches of somewhat erect culms. Flowering occurs during summer and early fall.

If the structure of *S. patens* is examined during summer, one finds an uppermost layer of living, partially prostrate grass overlying a dead horizon of dry culms from the previous year. Beneath this dry horizon is a layer of entangled moist culms and blades two and three years old. Between the moist layer of culms and the marsh surface is a horizon of decaying grass older than three years. Often, near the base of individual plants, the lower layer of thatch fails to contact the surface of the marsh because it is suspended by the dense crowns of the individual plants. Young tillers commonly protrude from the crown into the open space. Also, foraging voles (*Microtus*) create a labyrinth of tunnels underneath the thatch and appear to play an important role in maintaining this open space at certain locations. See Fig. 9-3 for a stylized representation of the grass system.

Maximum live biomass of *S. patens* occurs between mid-July and mid-August on mid-Atlantic state marshes, with no apparent relationship between grass patch size and either maximum live biomass or date of peak biomass (Fig. 9-1A). However, large patches of grass (those > 1001 m²) do possess significantly greater amounts of dead thatch than small (< 1000 m²) patches (*F*-test, *P* < 0.01) (Fig. 9-1B). The difference is particularly large early in the season in June prior to decay.

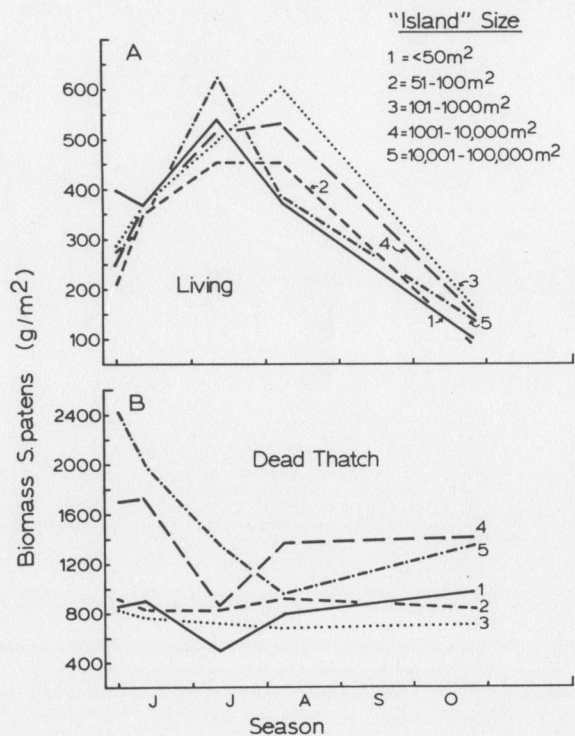


Figure 9-1. Seasonal changes in living biomass (A) and dead thatch (B) in 5 different "island" (stand) sizes of *S. patens* at Tuckerton, New Jersey, during 1978. Means are based on 3 samples in at least 3 "islands" for each size category except the largest (5) that consisted of only a single large island. For details on grass biomass sampling see Denno 1977.

We used percent crude protein (determined by standard macro-Kjeldahl analysis) as an index of grass quality. Percent crude protein was highest during May (12-14%), after which it dropped rapidly until mid-July, whereafter it remained continuously low (Fig. 9-2). Grass patches of all sizes showed this pattern, and there was no apparent relationship between patch size and quality.

3 Guild of Sap-feeders on *Spartina patens*

Although *S. patens* is fed upon by a number of functional feeding groups of insects (e.g., strip-feeders and stem borers), by far the most abundant and diverse herbivorous insects are sap-feeders in the suborder Auchenorrhyncha (leafhoppers and planthoppers) (Davis and Gray 1966, Denno 1976, 1977, 1980). Seven resident sap-feeding insects occur abundantly and develop on *S. patens* on New England and mid-Atlantic

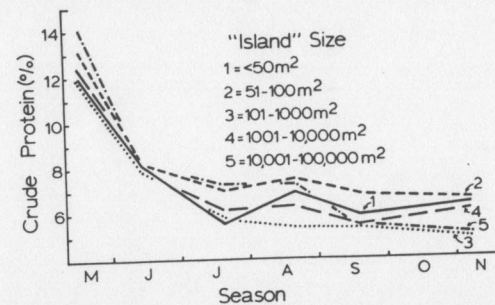


Figure 9-2. Seasonal changes in the quality (% crude protein) in 5 different "island" (stand) sizes of *S. patens* at Tuckerton, New Jersey, during 1979. Sampling scheme as in Fig. 9-1. The % crude protein in each sample was determined using the standard macro-Kjeldahl analysis (see Horwitz 1965).

state marshes south through Virginia. Of these, four are planthoppers (Delphacidae), *Delphacodes detecta* (Van Duzee), *Neomegamelanus dorsalis* (Metcalf), *Tumidagena minuta* McDermott, and *Megamelus lobatus* Beamer, and two are leafhoppers (Cicadellidae), *Amplicephalus simplex* (Van Duzee) and *Destria bisignata* (Sanders and DeLong). There is also the fulgoroid (Issidae), *Aphelonema simplex* (Uhler). The leafhopper, *Hecalus lineatus* (Uhler), occurs rarely on mid-Atlantic marshes, but is abundant only at the extreme northern end of the range of *S. patens* in New Hampshire.

Aphelonema decorata (Van Duzee) replaces *A. simplex* on *S. patens* in South Carolina south through Florida. *Tumidagena terminalis* (Metcalf) replaces *T. minuta* on North Carolina marshes, and is common on *S. patens* south through Florida. These congeneric pairs contain extremely similar taxa (both morphologically and ecologically) that may in fact represent the ends of step clines. *D. detecta*, *N. dorsalis*, *M. lobatus* and *D. bisignata* all range south through Florida. Several other sap-feeders are residents on *S. patens*, but because they are rare they are not included in this discussion (see Denno 1977).

4 Ecotope Differentiation in the Guild of Sap-feeders

In this section we review the resource-use patterns and body-size relationships of the common sap-feeders associated with *S. patens* on mid-Atlantic marshes. Resource partitioning was studied using one habitat factor (marsh elevation) and two niche factors (microhabitat distribution within the grass system and temporal utilization) (details on insect sampling are available in Denno 1980).

To determine the microhabitat distribution of the various sap-feeders, the grass system was divided into five rather distinct vertical zones (see the definition of zones in the stylized representation of the grass system at the top of Fig. 9-3): Zone 5 consisted of the seed heads and terminal blades of the upright living grass. Zone 4 comprised subterminal blades and stems of the living grass, and was like zone 5 except that most plant parts were shaded. Prostrate living culms and blades knocked over by winds

formed zone 3. A thatch layer of horizontal dead culms and blades through which passes the basal portion of ensheathed, vertical, living culms defined zone 2. Zone 1 consisted of the crowns and tillers of the grass beneath the thatch layer.

Four sap-feeders, *D. detecta*, *N. dorsalis*, *A. simplex*, and *Am. simplex* occurred primarily in the upper stratum (zones 3-5) of the grass system above the thatch layer (Fig. 9-3). A second group of three species, *T. minuta*, *M. lobatus* and *D. bisignata*, inhabited primarily the lower stratum of the grass, in and beneath the thatch layer (zones 1 and 2) (Fig. 9-4).

Sap-feeders of the upper stratum had very similar seasonal distributions (Fig. 9-5A-D). For *D. detecta*, *N. dorsalis* and *A. simplex*, populations began increasing in May, peaked in September, and then decreased rapidly. Only *Am. simplex* peaked earlier in the season during July. *T. minuta*, *M. lobatus* and *D. bisignata*, the lower-stratum residents, also showed very similar seasonal distributions, but as a group tended to peak

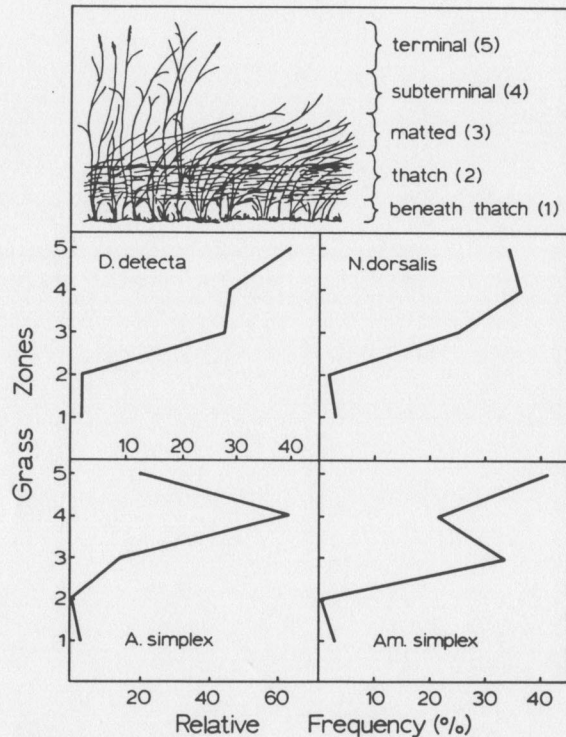


Figure 9-3. Microhabitat niche diversification of sap-feeders on *S. patens* at Tuckerton, New Jersey. Relative frequency of *D. detecta*, *N. dorsalis*, *A. simplex* and *Am. simplex* in terminal (5), subterminal (4), matted (3), thatch (2) and beneath thatch (1) zones of *S. patens* (see Denno 1980 for details on sampling).

about one month later than upper-stratum species (Fig. 9-5E-G). Populations increased in June, peaked during October or November and then declined rapidly. For details on the phenology of these species see Denno (1977, 1980) and Raupp and Denno (1979). The similarity in phenology of all of the sap-feeders is probably the result of selective pressures associated with peak biomass and quality of the grass (see Figs. 9-1A, 9-2) (Denno 1980).

Denno (1980) also determined the distribution of the sap-feeders along an elevational gradient in similar-sized patches of *S. patens* that occurred from approximately mean high water level (MHW) to 25 cm above. All sap-feeders but *N. dorsalis* were most abundant on patches of grass that occurred within 10 cm of MHW (Fig. 9-6). Only *N. dorsalis* predominated on, and was for the most part restricted to, patches at the upper end of the elevational range of the grass (Fig. 9-6).

Hutchinson (1959) measured the feeding apparatus of closely related species when they were sympatric and allopatric. He found that the ratio of the largest to the smallest dimension was $\cong 1.0$ when the species were allopatric, but where they co-occurred the species differed by a factor of 1.2-1.4. He tentatively concluded that a difference of about 1.2-1.4 was necessary for two congeners to coexist. Some work tends to support this conclusion. For example, Rosenzweig and Sterner (1970) and Brown (1975) suggested that coexistence in heteromyid rodent communities is permitted by body size (mass) differentials. Similarly, various sizes of sap-feeders may be able to negotiate the microhabitat in different ways, and oviposition, feeding and hiding sites that are available to a small species may not be to a larger one. Consequently, sap-feeders that differ in size may use resources differently and, thereby, reduce competition. We used

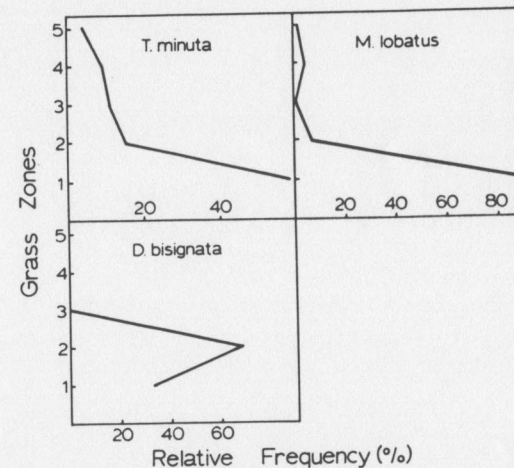


Figure 9-4. Microhabitat niche diversification of sap-feeders on *S. patens* at Tuckerton, New Jersey. Relative frequency of *T. minuta*, *M. lobatus* and *D. bisignata* in terminal (5), subterminal (4), matted (3), thatch (2) and beneath thatch (1) zones of *S. patens* (see Denno 1980 for details on sampling).

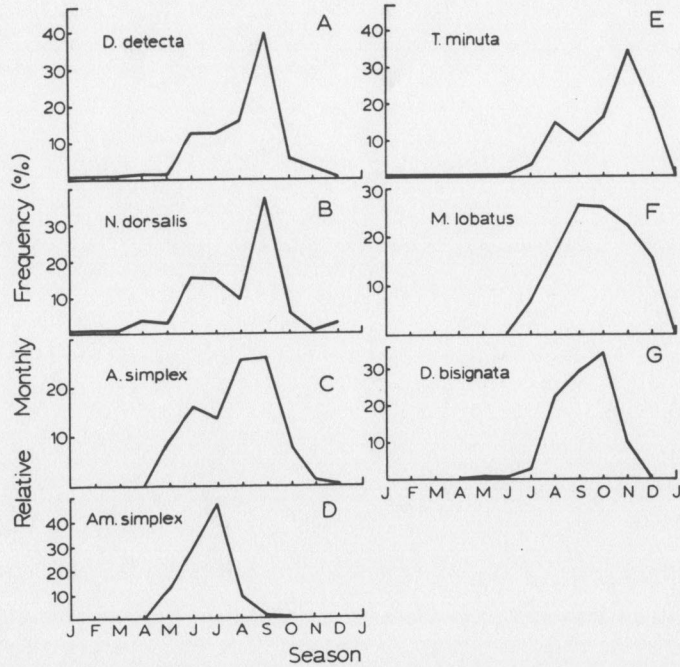


Figure 9-5. Seasonal niche diversification at Tuckerton, New Jersey. Relative monthly frequency of sap-feeders on *S. patens* (see Denno 1980 for details on sampling).

a body size ratio of 1.3 (midpoint of Hutchinson's 1.2-1.4 range) as a measure of the difference necessary to permit coexistence. Because stylets can be retracted through the beak and coiled within the head of these animals, beak length is not an appropriate measure of potentially important differences in the way sap-feeders use resources.

The mean dry adult body mass of the various *S. patens* sap-feeders ranged from 0.11 to 0.78 mg (Table 9-1). When the entire assemblage was considered as a unit, three species pairs (*M. lobatus* and *D. detecta*, *D. detecta* and *D. bisignata*, and *A. simplex* and *Am. simplex*) failed to differ in body weight by a factor of at least 1.3 (Ratio A of Table 9-1). However, when species were grouped by microhabitat into upper- and lower-zone residents (Ratios B and C, resp., of Table 9-1), only *A. simplex* and *Am. simplex* differed by a ratio (1.15) of less than 1.3.

Based on MacArthur's (1972) $d > \sqrt{\sigma_1^2 + \sigma_2^2}$ analysis that estimates the probability for competitive exclusion along resource dimensions (microhabitat, season and elevation), and Hutchinson's (1959) ratio of ≈ 1.3 as an indication of the amount of morphological (body size, in this case) difference necessary to permit coexistence, all species but two (*Am. simplex* and *A. simplex*) differ enough in the way they use *S. patens* to allow for co-occurrence (Fig. 9-7) (see Denno 1980). The sap-feeders segregate well into two subguilds (upper- and lower-strata species) along the microhabitat

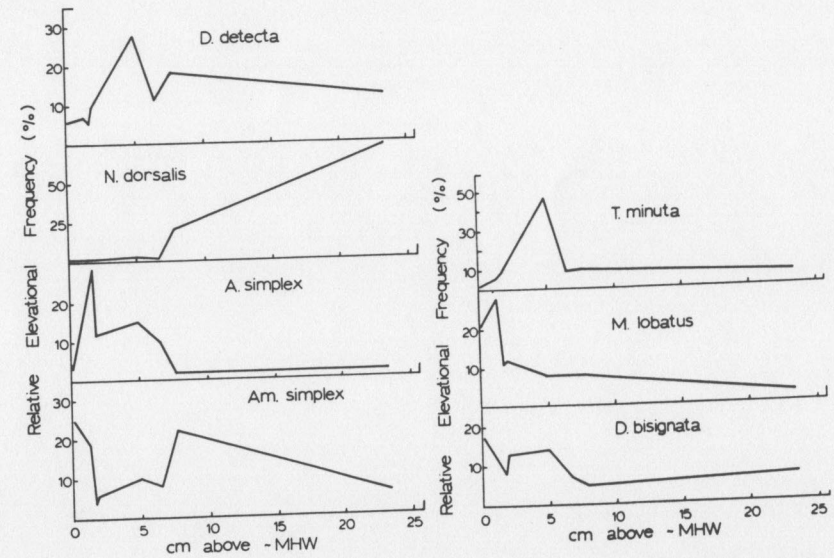


Figure 9-6. Elevational habitat diversification. Relative elevational frequency of *D. detecta*, *N. dorsalis*, *A. simplex*, *Am. simplex*, *T. minuta*, *M. lobatus* and *D. bisignata* on patches of *S. patens* along a gradient from \approx mean high water level (MHW) to 25 cm above at Tuckerton, New Jersey (see Denno 1980 for elevation determination and sampling).

Table 9-1. Adult dry body mass (mg) and body mass ratios^a (large species/small species) for the resident sap-feeders on *S. patens*

Species	Dry weight ($\bar{x} \pm \sigma$)	Ratio A	Ratio B	Ratio C
<i>N. dorsalis</i>	0.11 \pm 0.008	1.36	2.73	1.67
<i>T. minuta</i>	0.15 \pm 0.018	1.67		
<i>M. lobatus</i>	0.25 \pm 0.032	1.20	2.27	1.36
<i>D. detecta</i>	0.30 \pm 0.037	1.13		
<i>D. bisignata</i>	0.34 \pm 0.012	2.00	1.15	
<i>A. simplex</i>	0.68 \pm 0.036	1.15		
<i>Am. simplex</i>	0.78 \pm 0.044			

^aNOTE: Ratios between all species (A), upper-stratum species (B) and lower-stratum species (C).

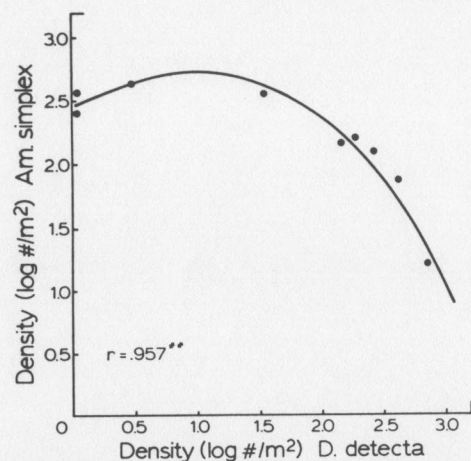


Figure 9-9. Relationship between the mean spring densities (May, June) of *Am. simplex* and *D. detecta* for a 6-year period (1974-1979) at Tuckerton, New Jersey. Two large (> 1000 m²) stands of *S. patens* were sampled each year except during 1974 (** $P < 0.01$).

5 Dispersal Abilities, Overwintering Styles and Oviposition Characteristics of Sap-feeders

Dispersal ability and other life history characteristics discussed below affect a species' ability to track resources in time and space, and ultimately reflect on the potential for achieving equilibrium in populations. Wing dimorphism is a common phenomenon in planthoppers (Delphacidae and Issidae) and some leafhoppers (Cicadellidae), and can be used to elucidate dispersal ability. There are short-winged, flightless individuals (brachypters) and individuals with fully developed wings (macropters) that fly. Because of their ability to escape deteriorating resources and colonize new ones (see Denno and Grissell 1979, Denno et al. 1980), macropters should be adaptive in unstable habitats where resources fluctuate greatly and better alternatives are available elsewhere. On the other hand, the brachypters of several species of planthoppers have been shown to have a higher fecundity and oviposit at an earlier age than macropters (Tsai et al. 1964, Kisimoto 1965, Nasu 1969, May 1971, Mochida 1973). As a result, the reproductive potential of brachypters is greater than for macropters. Also, because of their flightlessness, brachypters are more likely to remain on the immediate resource. For these reasons, brachypters can more effectively exploit persistent resources (Denno 1976, 1978, 1979, Denno and Grissell 1979, Denno et al. 1980), particularly those that occur in climatically harsh habitats, where it is adaptive to balance high mortality with increased fecundity. Consequently, by examining the proportion of wing forms in a population, the potential for colonization can be estimated for a species.

Wing form is mediated by an individual's response during the nymphal stage to various proximate environmental cues (e.g., host plant quality and crowding) that measure the probability of current resource deterioration (Kisimoto 1956, 1965, Mochida 1973, Denno 1976). When the fitness of an individual can be increased by moving from deteriorating to more favorable resources, selection has apparently favored a low threshold, at which a developmental switch responds to environmental cues resulting in the production of a long-winged individual. By contrast, where conditions are not better "elsewhere" than "here," selection favors a high-threshold response resulting in a short-winged animal (see Denno 1976, Denno and Grissell 1979, Denno et al. 1980).

Historically, salt marshes and most of their included vegetation types (see Denno and Grissell 1979, Denno et al. 1980 for one exception) have been considered persistent systems (Southwood 1962, Brinkhurst 1963, Johnson 1969), and brachypters are by far the most abundant wing-morph in planthopper populations (Denno 1976, 1978). The wing-morph frequencies of most of the planthoppers and leafhoppers in the *S. patens* guild of sap-feeders are consistent with this general pattern. Populations of all species but one, *Am. simplex*, are composed of at least 86% brachypters (Table 9-2). Consequently, the dispersal capabilities for most individuals of most species are greatly reduced. Only *Am. simplex* completely retains the ability to fly.

In New Jersey, the planthoppers *D. detecta* and *N. dorsalis* are trivoltine and overwinter as active nymphs on the marsh surface or in the dead thatch of *S. patens* (Denno 1977). Although they do gain some protection within the thatch during winter, they are still exposed to very cold temperatures, and even ice, in harsh seasons. *T. minuta* has an identical life history, except that it completes only two generations per year. *D. bisignata* and *M. lobatus* also complete two generations per year, but overwinter as eggs that are inserted deep into the culms or blades of the grass with a saw-like ovipositor (see Fig. 9-10). *Am. simplex* (Fig. 9-10) and *H. lineatus* also insert their eggs into the grass where they remain hidden during winter, but these two species are univoltine. Although *A. simplex* overwinters as eggs, it lacks the saw-like ovipositor possessed by the other species and is unable to insert its eggs (Fig. 9-10). Eggs remain exposed on the vegetation. With regard to overwintering styles, the sap-feeders on *S. patens* fit into two categories: There are species that overwinter either as exposed eggs or nymphs (*D. detecta*, *N. dorsalis*, *T. minuta* and *A. simplex*), and should be vulnerable to harsh winter conditions. *D. bisignata*, *Am. simplex*, *H. lineatus* and *M. lobatus* insert their eggs, and should be less susceptible to the rigors of winter. The overwintering styles and generational information of these sap-feeders are summarized in Table 9-3.

6 Density Patterns of Sap-feeders along a Size Gradient of *S. patens* Patches

Patchiness per se may promote nonequilibrium conditions. For instance, resource area has been shown to have major effects on immigration and extinction rates and subsequently on the density of individuals and number of species that are able to obtain in a particular patch (MacArthur and Wilson 1967, Simberloff 1969, 1976, Simberloff and Wilson 1969, 1970, Raupp and Denno 1979, Rey 1981). Raupp and Denno (1979) suggest that, in general, extinction rates of sap-feeders are higher on small compared to

Table 9-2. Flightlessness in populations of sap-feeders

Species	% Brachypters
<i>Am. simplex</i>	0
<i>D. detecta</i>	86
<i>N. dorsalis</i>	88
<i>M. lobatus</i>	97
<i>T. minuta</i>	> 99
<i>A. simplex</i>	> 99
<i>D. bisignata</i>	100 (♀)
<i>H. lineatus</i>	100

large "islands" of *S. patens* because mortality associated with tidal flooding is greater there. Distance of resource from source area has also been proposed to have an effect on immigration rate (MacArthur and Wilson 1967). However, Rey (1981), working with the community of insects (also dominated by sap-feeders) associated with *Spartina alterniflora* in Florida, was unable to find a statistically significant effect of isolation on "island" immigration rate. We have concentrated on area rather than distance effects in our study by sampling sap-feeders on ≈ 25 "islands" of *S. patens* ranging in size from $< 50 \text{ m}^2$ to patches $\approx 100,000 \text{ m}^2$. All "islands" sampled were located within 25 m of large ($> 1000 \text{ m}^2$) source "islands" that were included in a large archipelago of patches on a marsh in Tuckerton, New Jersey.

Differences in the life history characteristics (e.g., migration ability and overwintering style) of the *S. patens* sap-feeders probably influence each species' ability to colonize and remain on small compared to large patches of grass. Denno and Grissell (1979) and Denno et al. (1980) show that the brachypterous morph in dimorphic populations of planthoppers is virtually immobile and unable to move more than a few meters. By contrast, macropters are capable of long-distance flight, and are able to colonize distant, more favorable patches. Also Denno (1977), by defaunating large plots of *S. patens* and measuring recolonization, has shown that fully winged species like *Am. simplex* are excellent colonists. Thus, species that produce mostly flightless brachypters

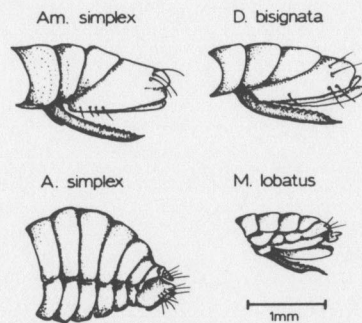


Figure 9-10. Abdomens of *Am. simplex*, *D. bisignata* and *M. lobatus* with saw-like ovipositors capable of inserting eggs into vegetation. *A. simplex* lacks a piercing ovipositor and is unable to embed its eggs.

Table 9-3. Generations and overwintering stages of sap-feeders

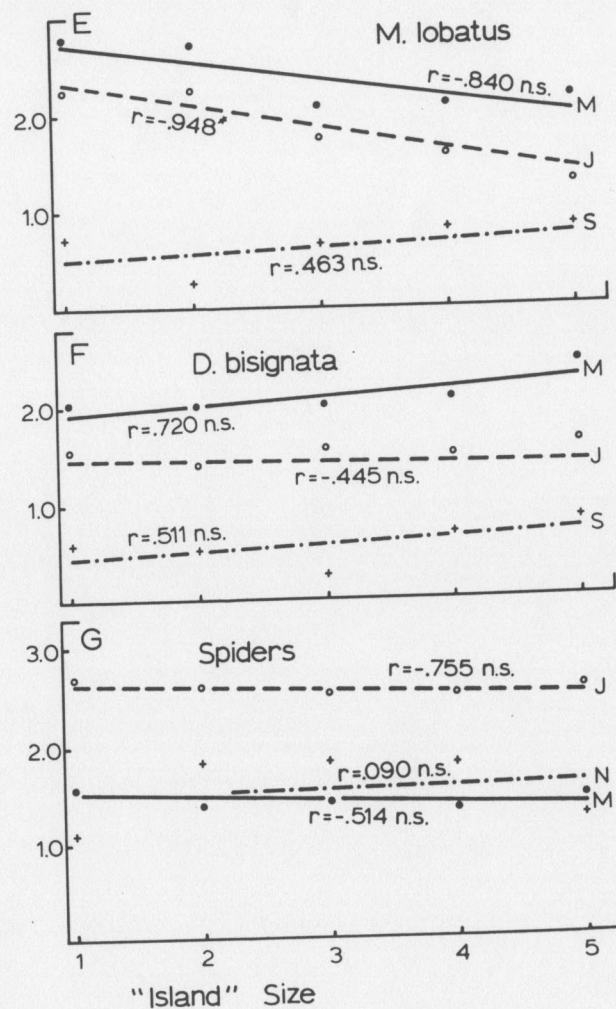
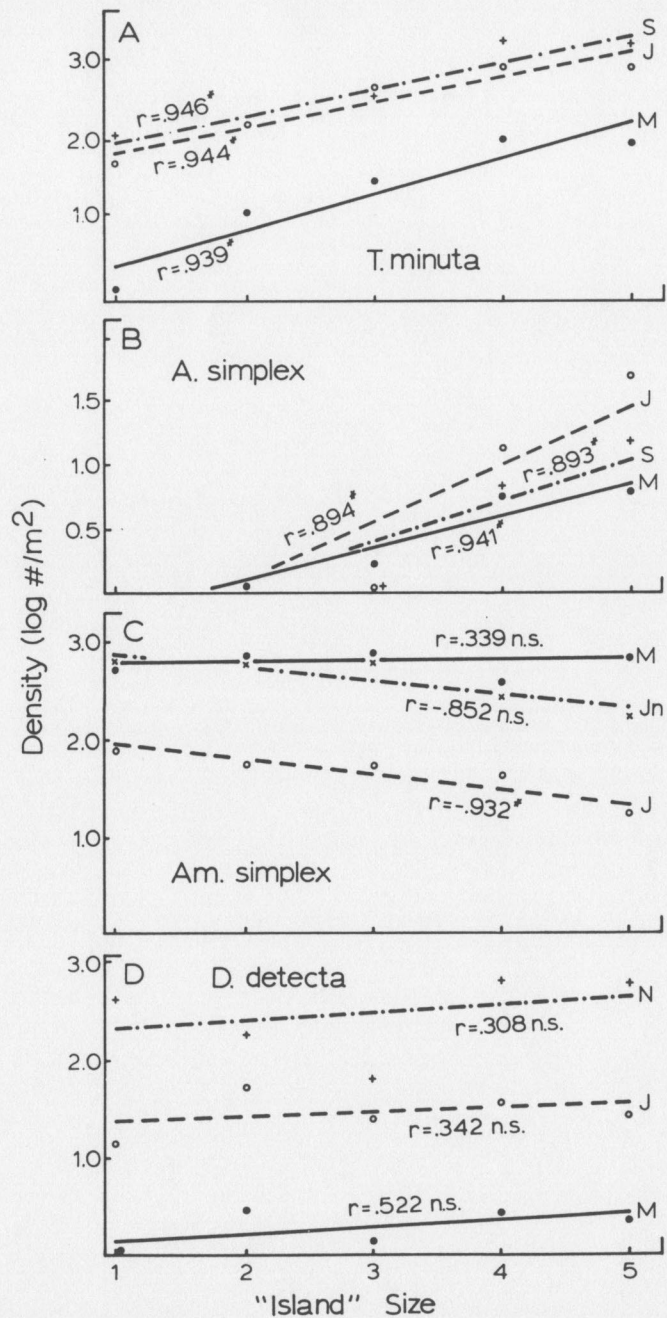
Species	#Gen/Yr	Overwintering Stage	Site and exposure of overwintering stage
<i>T. minuta</i>	2	nymph	marsh surface (exposed)
<i>D. detecta</i>	3	nymph	marsh surface (exposed)
<i>N. dorsalis</i>	3	nymph	marsh surface (exposed)
<i>A. simplex</i>	2	egg	on vegetation (exposed)
<i>D. bisignata</i>	2	egg	in vegetation (embedded)
<i>M. lobatus</i>	2	egg	in vegetation (embedded)
<i>Am. simplex</i>	1	egg	in vegetation (embedded)
<i>H. lineatus</i>	1	egg	in vegetation (embedded)

(see Table 9-2) should be poor colonists (have low immigration rates) and be under-represented on small, isolated "islands."

Overwintering style should also affect the ability of sap-feeders to remain on small islands. Species that overwinter as exposed eggs or nymphs should incur more winter mortality than those that overwinter as eggs embedded in vegetation (see Table 9-3). Extinction rates should be particularly high on small islands for exposed species, because there is less protective thatch there during the winter season (see Fig. 9-1B). Tallamy and Denno (1979) show that the overwintering success of sap-feeders with exposed stages (see *Tumidagena minuta*) is comparably low in plots of grass where the protective thatch has been removed.

Based on life history data, several predictions can be made concerning the success of sap-feeders on small as opposed to large patches of *S. patens*. Species with low immigration rates (those that are mostly brachypterous) and high extinction rates (in part those that overwinter in an exposed stage) should be least likely to maintain populations on small islands. Sap-feeders with these characteristics are *T. minuta* and *A. simplex*. Populations of both are composed of $> 99\%$ brachypters and both overwinter as exposed stages (see Tables 9-2 and 9-3). The responses of these two species are as predicted; both become increasingly more abundant as grass patch size increases (Fig. 9-11A and B). The differential effects of winter mortality on small "islands" are particularly evident for *T. minuta* (Fig. 9-11A). Population size was very small on small "islands" ($< 100 \text{ m}^2$) during May prior to reproduction. By September, population size had increased on small "islands," but remained small compared to that attained on large "islands." The fact that populations do build rapidly on small "islands" suggests either that reproductive increase is high for *T. minuta* or that colonization is occurring. The former is probably more likely because most adults are brachypterous, although nymphs may be dispersed to small "islands" during tidal inundation. Nymphs have a waxy substance on their cuticle that allows them to float on the water's surface. Nevertheless, high extinction rate during winter is probably the major factor dictating the poor success of *T. minuta* on small islands.

A. simplex showed the same trend of abundance along the island size gradient, but never occurred on the smallest islands of grass ($< 50 \text{ m}^2$) and achieved high densities only on the very largest of grass patches (Fig. 9-11B). Denno (1977) documents the poor colonizing ability of this sap-feeder. Thus, low immigration rate and high extinction rate during winter act in concert on small islands dictating its poor success there.



1 = <50m²
 2 = 51-100m²
 3 = 101-1000m²
 4 = 1001-10,000m²
 5 = 10,001-100,000m²

M = May
 Jn = June
 J = July
 S = September
 N = November

Figure 9-11. Relationship between the "island" (stand) size of *S. patens* and the densities of sap-feeders and spiders at several times during 1979 at Tuckerton, New Jersey. Means are based on 4 samples taken in 3 "islands" in each size category (largest size excepted) with a D-vac vacuum sampler. One sample consisted of 4 placements (30 sec each) of the sampler on the *S. patens* surface. Only one "island" in the 10,001-100,000 m² category occurred at the study area (** $P < 0.01$; * $P < 0.05$; n.s., not significant).

Species with the opposite combination of life history traits (e.g., high colonization ability coupled with reduced winter extinction rate) should have the best chance for success on small islands. The only species with this combination of traits, *Am. simplex*, was equally abundant on all sizes of *S. patens* patches during May and June and even showed a significant negative relationship between density and "island" size during July (Fig. 9-11C).

Species with good colonizing ability (10-20% macropters) and exposed overwintering stages like *D. detecta*, or species with poor colonizing ability (> 95% brachypters) and protected overwintering stages like *M. lobatus* and *D. bisignata*, were for the most part equally abundant on small and large "islands," but for different reasons (Fig. 9-11D, E and F). *D. detecta*, even though it was absent from small "islands" (< 50 m²) during May, achieved densities later in the season (November) similar to those in the larger island sizes (Fig. 9-11D). Winter mortality is great on small islands, but macropterous adults colonize these sites early in the season and subsequently reproduce (Denno et al., in prep.).

By contrast, *M. lobatus* (97% brachypterous) and *D. bisignata* (100% of females brachypterous) have poor colonizing ability, but withstand the rigors of winter very well in both small and large patches of grass because they embed their eggs. Compare May densities (populations composed of newly hatched nymphs at this time) of these species on large and small islands (Fig. 9-11E and F). Once they have colonized small islands, extinction rates for these species are apparently low. Colonization may be a rare event, but we emphasize that nymphs and adults of these species are able to drift on the tidewater's surface by virtue of their waxy integument. However, the mortality associated with drifting behavior must be great, particularly during storm and high spring tides, due to the inability of these insects to direct their course on the water's surface and greater susceptibility to density-independent mortality factors. It seems unlikely that selection would favor such precarious dispersal behavior over macroptery in adults if dispersal were an adaptive event in the life histories of *M. lobatus* and *D. bisignata*. Instead, we suggest that the life histories of these two species have been shaped to ensure intimate contact with immediate large patches of grass and that their occupation of small islands is the result of historical accident.

To ensure that the density responses of the various sap-feeders to grass-patch size did not constitute a reflection of predation, we also measured spider density along the *S. patens* "island" size gradient. Spiders, mostly in the family Lycosidae, are by far the most abundant predators in the *S. patens* marsh system (Denno 1977, Raupp and Denno 1979). Measured during May, July and November, there was no significant relationship between spider density and "island" size (Fig. 9-11G). Parasitoids of the eggs, nymphs and adults of these sap-feeders are not abundant in the mid-Atlantic states (Denno 1977). Therefore, it is unlikely that the responses of several of the sap-feeders to patch size are attributable to either predation or parasitism.

Lastly, we emphasize that the life histories of all but one sap-feeder, the fully winged leafhopper *Am. simplex*, have been adjusted in varying degrees to maintain contact with occupied patches of *S. patens*. The brachypterous adults and/or embedded eggs characteristic of most species are consistent with this hypothesis. At high densities, some planthoppers are able to alter their life history by virtue of a developmental switch and long-winged morphs are produced. This behavior can be adaptive only if

more favorable alternative sites are available. The argument can be made that small "islands" of *S. patens* are more favorable than large ones because certain species (potential competitors) are rare there (see Fig. 9-11A and B). However, small patches have less protective thatch than large patches and are probably less favorable, particularly for those species that overwinter as an exposed stage. Thus, small "islands" probably serve as predictable refuges for only *Am. simplex*. The presence of other sap-feeders on small patches is due probably to either accidental colonization by nymphs or dispersal among larger patches by adults. Consequently, nonequilibrium conditions are probably the rule rather than the exception on small patches. In the section that follows we show that large patches too can be even more favorable alternatives for colonization because they are sporadically free of potential competitors, yet unlike small "islands" have more protective thatch.

7 Equilibrium Status of the Sap-feeder Guild in Large Patches

A six-year assessment of sap-feeders on the same large patches (> 10 ha) of *S. patens* in New Jersey reveals drastic fluctuations in the populations of some species and not others. For instance, early-season (May, June) densities of *D. detecta* during 1978 and 1979 were excessively low compared to the previous four years, while *Am. simplex* failed to show this decline (Fig. 9-12). A more detailed analysis shows that sap-feeder species fit into one of two categories. There are three species, *D. detecta*, *T. minuta* and *A. simplex*, whose populations were drastically reduced following the winters of 1978-79, and particularly 1977-78 (Fig. 9-13A, B and C). Three other species, *Am. simplex*, *M. lobatus* and *D. bisignata*, did not show this pattern, and in fact their early-season densities were highest following the winter of 1977-78, when the densities of the other three species were most depressed (Fig. 9-13D, E and F). We anticipated

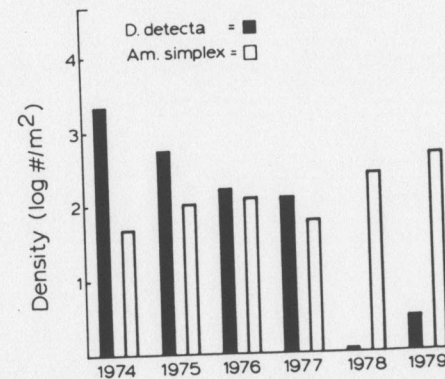


Figure 9-12. Mean spring densities (May-June) of *D. detecta* and *Am. simplex* in large stands (> 1000 m²) of *S. patens* at Tuckerton, New Jersey, 1974-1979.

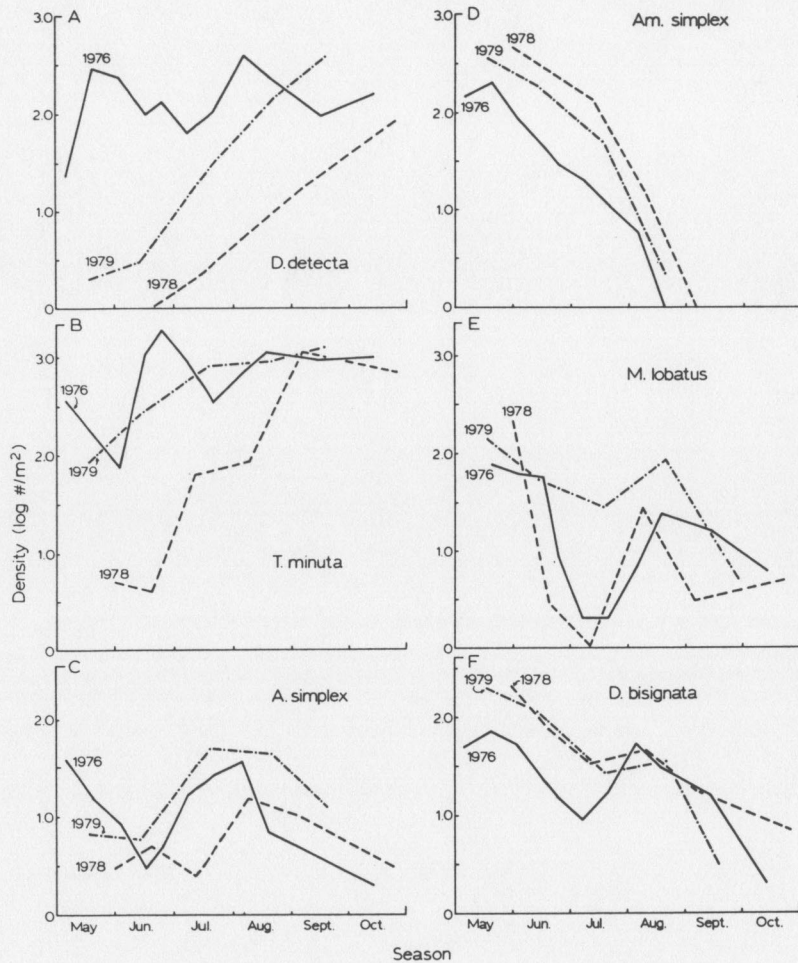


Figure 9-13. Seasonal densities of sap-feeders in a large stand ($> 10,000 \text{ m}^2$) of *S. patens* during 3 years at Tuckerton, New Jersey. Winters of 1977-78 and 1978-79 were severe compared to that of 1975-76. Insects were sampled with a D-vac vacuum as in Fig. 9-11.

that severe winters were selectively killing *D. detecta*, *T. minuta* and *A. simplex*, but not the remaining species.

The relationship between the severity of the previous winter (number of days the minimum daily temperature fell below 0°C) and the following early-season density (measured prior to reproduction) was negative and highly significant for these three species substantiating the winter-kill hypothesis (Fig. 9-14A, B and C). Regressions

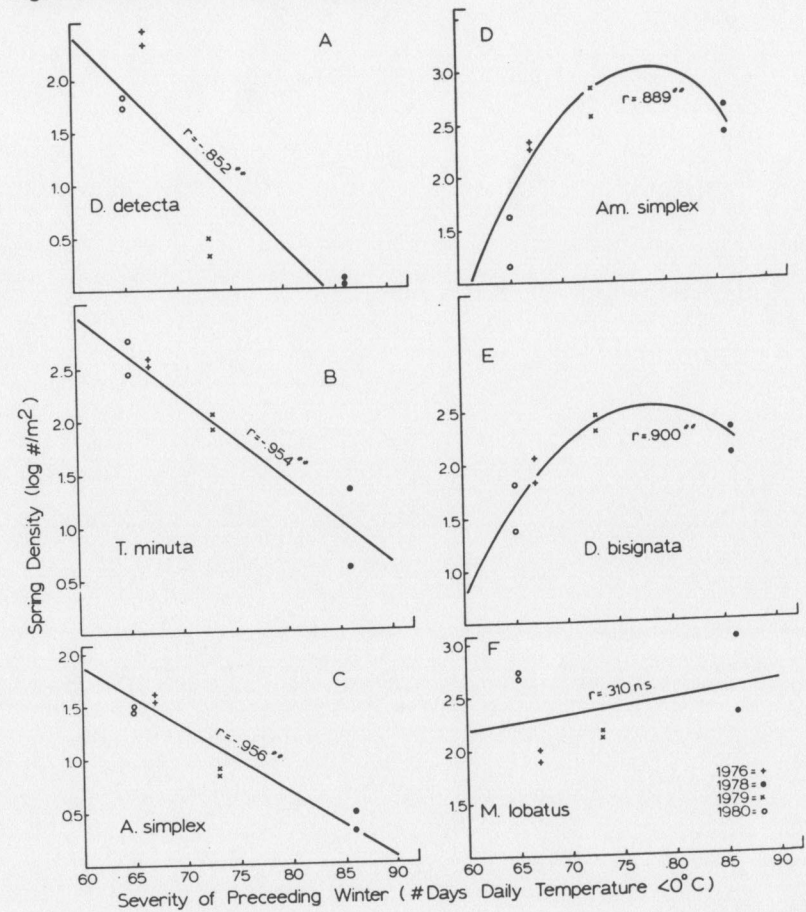


Figure 9-14. Relationship between the severity of the preceding winter (no. of days the daily temperature fell below 0°C from April 1 to October 31) and the following spring density of sap-feeders (May or June density prior to reproduction). Insect samples were taken with a D-vac vacuum as in Fig. 9-11 during a 4-year period (1976-1980) in 2 large stands ($> 10,000 \text{ m}^2$) of *S. patens* at Tuckerton, New Jersey.

using average daily temperature during the winter season and number of days the maximum daily temperature fell below 0°C as other measures of winter harshness (independent variables) produced the same results. There was no relationship between the severity of the previous winter and the spring density of *M. lobatus* (Fig. 9-14F). *Am. simplex* and *D. bisignata* showed a significant positive relationship between winter severity and spring density (Fig. 9-14D and E). The only explanation we have to offer for this result is that predators (spiders and the mirid egg predator, *Tytthus alboornatus*

Knight) may be more active during mild winters, resulting in higher mortality on those years.

It is not surprising that the species which were affected by winter-kill all overwinter as either exposed nymphs or eggs. Species not affected by severe winters all overwinter as embedded eggs in the vegetation. The result is a guild of sap-feeders, half of which can be brought to near local extinction following very harsh winters.

These data conjure up questions concerning the equilibrium status of the guild, the degree and frequency of resource limitation, and the reality of competition among the guild members. Following a severe winter (1978), certain species (see *T. minuta*, Fig. 9-13B) reach densities by the end of the season that compare with those after mild winters (e.g., 1976). Other species (*D. detecta* and *A. simplex*, Fig. 9-13A and C) fail to attain densities that they obtain during the season following a mild winter. Thus, certain species appear to be contained well below carrying capacity at a frequency proportional to the occurrence of severe winters. Consequently large patches of grass as well as small ones can be relatively empty in certain years, apparently allowing for the coexistence of competitively weaker species under nonequilibrium conditions.

8 The Fugitive Coexistence of *Amplicephalus simplex*

Based on our niche analysis, *Am. simplex* appears to occupy a rather precarious position in the guild of sap-feeders (see Fig. 9-7). It shares a niche very similar to that of *A. simplex* as well as *D. detecta*, and it appears to be negatively affected by the presence of these species (Fig. 9-8A and C). We do not think it is coincidental that, of the six sap-feeder species on the low marsh in the mid-Atlantic area, *Am. simplex* is the only one totally retaining its ability to fly. Flightlessness is a common life history feature in the remaining five species.

Vacant sites are frequently available on small "islands" of *S. patens*, offering a rather consistent refuge for *Am. simplex*, and *A. simplex* is always rare there (Fig. 9-11B). Also, relatively vacant sites are unpredictably created in large patches by the catastrophic reduction of its closest competitors during severe winters (see *D. detecta* and *A. simplex*, Fig. 9-14A and C). Our results are consistent with the hypothesis that *Am. simplex* retains its wings and hedges its bets by moving among patches of *S. patens* depositing some eggs in each. In New Jersey frequent disturbances apparently allow this species to coexist in the guild.

9 Latitudinal Distribution of Sap-feeders

One prediction emerging from the previous discussion is that, as the frequency of disturbance (winter-kill of competitors) decreases, so should the probability of *Am. simplex* coexisting in the guild. A latitudinal transect along the eastern seaboard of North America from Hampton Beach, New Hampshire, to Crescent Beach, Florida, confirms this prediction (Fig. 9-15). South of Virginia, *Am. simplex* does not occur on *S. patens* and becomes increasingly more abundant to the north (Fig. 9-16E). Also consistent

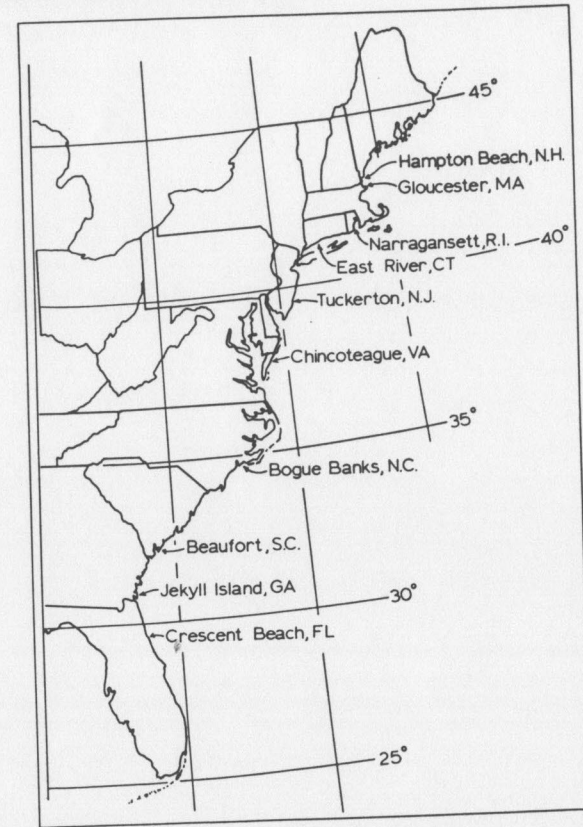


Figure 9-15. Locations of intertidal marshes along the eastern seaboard of North America sampled to determine latitudinal distributions of sap-feeders on *S. patens*.

with the argument is the fact that *D. detecta* and the *A. simplex-A. decorata* complex (species that share a niche very similar to *Am. simplex*) become increasingly more abundant on southern marshes (Fig. 9-16A and B).

Latitudinal species patterns appear to be mediated in part by life history type that is legislated by climate. For instance, univoltine species that embed their eggs in vegetation (*Am. simplex* and *H. lineatus*) occur only on northern marshes (Fig. 9-16E and F). It may be that univoltine sap-feeders are disadvantaged at southern latitudes because of long periods of exposure to competitors, egg predators and/or parasitoids coupled with infrequent bouts of reproduction. The positive relationship we found between the severity of the preceding winter and the following early-season density of *Am. simplex* is consistent with the argument that mortality is greater when there is potentially greater exposure to predators (Fig. 9-14D).

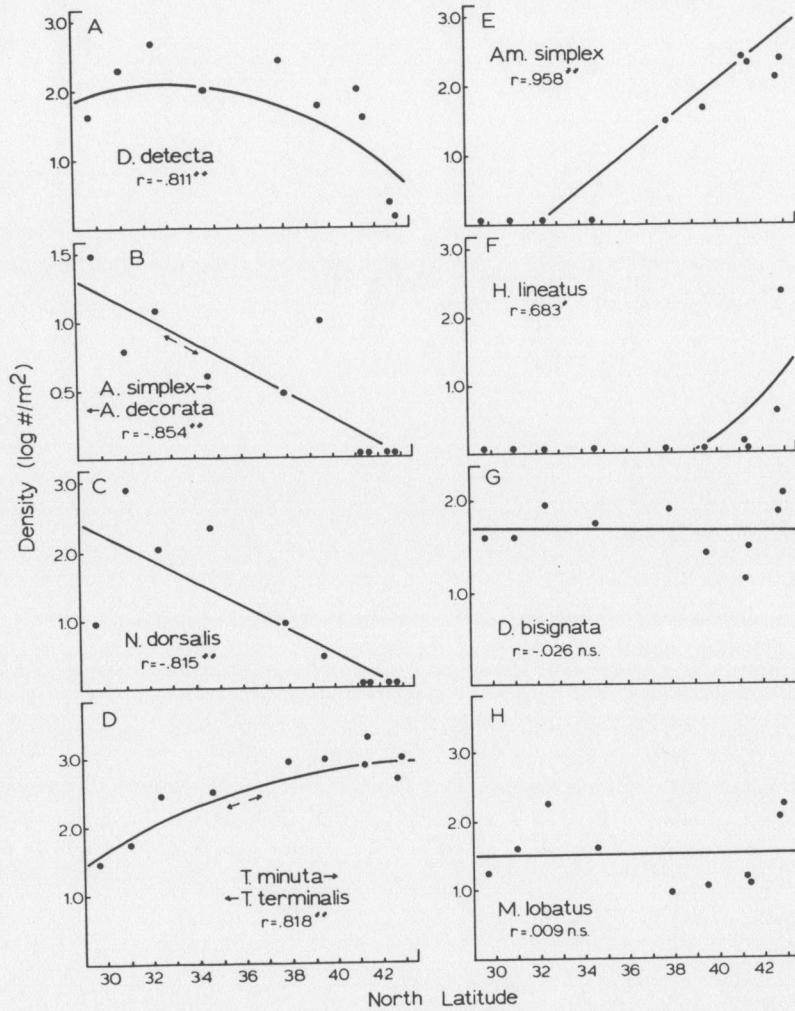


Figure 9-16. Relationship between density and latitude for sap-feeders on *S. patens*. Sample points correspond to the 10 locations from northern Florida to New Hampshire shown in Fig. 9-15. Points are means calculated from 6 samples taken in stands of *S. patens* at least 500 m² in area. One sample as in Fig. 9-11. Marshes to Chincoteague, Virginia south, were sampled during early June 1980. Tuckerton, New Jersey, and locations north were sampled during early July 1980 (** $P < 0.01$; * $P < 0.05$; n.s., not significant).

Southern marshes are dominated by multivoltine species that overwinter as either exposed eggs (*A. simplex*) or nymphs (*D. detecta* and *N. dorsalis*) (Fig. 9-16A, B and C). These species are apparently susceptible to cold temperatures and are selectively eliminated at northern latitudes (see Fig. 9-14A, B and C). However, farther to the south where winter temperatures are less severe, it may be adaptive to overwinter as nymphs that are able to begin feeding as soon as temperature permits in spring, when the quality of the grass is highest (see Fig. 9-2). Mittler (1958), van Emden (1966), Dixon (1969), Auclair (1976), Horsfield (1977), McClure (1977, 1979) and Mitsuhashi and Koyama (1977) have all shown that the fitness (fecundity, growth rate, survival and adult size) of sap-feeding insects is positively related to host plant quality (total nitrogen or amino nitrogen). The *T. minuta*-*T. terminalis* complex is also multivoltine and overwinters as nymphs in New Jersey, but is more abundant on northern marshes (Fig. 9-16D). There may be several reasons for this apparent exception. First, of the multivoltine species that overwinter as exposed stages, *T. minuta* is the only species that inhabits the lower stratum of the grass system (see Fig. 9-4); *D. detecta*, *N. dorsalis* and *A. simplex* all reside in the upper stratum (see Fig. 9-3). This may afford more protection, particularly during harsh winters. The fact that *T. minuta* was present on the marsh in June 1978 while *D. detecta* was not suggested that *T. minuta* is better able to survive severe winter temperatures (compare Fig. 9-13A with B). An alternative explanation for *T. minuta*'s success in the north may be a variable life history. While it overwinters as susceptible nymphs in New Jersey, it has the potential to overwinter as embedded eggs further to the north. *T. minuta* does have a saw-like ovipositor very much like that of *M. lobatus* (see Fig. 9-10). We would add, however, that *D. detecta* also have a saw-like ovipositor and thus the potential to vary its life history, but is rare or absent from the northernmost marshes (Fig. 9-16A). Thus, it seems likely that the association of *T. minuta* with the protective thatch of *S. patens* offers the most parsimonious explanation for its success on northern marshes.

Bivoltine species that overwinter as embedded eggs in New Jersey (*D. bisignata* and *M. lobatus*) were similarly abundant along the entire latitudinal gradient (Fig. 9-16G and H). It may be that these species vary their life history with latitude, overwintering as eggs to the north and reproducing continuously in the south. The presence of adults of these species during April, June, July and late October support this contention. If this is the case, the advantage of embedded eggs to the north and continuous reproduction to the south might explain the success of *D. bisignata* and *M. lobatus* on *S. patens* from Florida to New Hampshire. *D. bisignata* also shows depressed densities following mild winters in New Jersey, suggesting that it may incur increased mortality from egg predators there (Fig. 9-14E). This latter possibility underscores the importance of continuous reproduction to the south, unless there are other overriding constraints like those associated with host plant quality or quantity.

10 Summary and Conclusions

Population equilibrium exists when birth and death rates are equal, resulting in a net growth rate of zero (MacArthur and Wilson 1967, May 1973, Price 1980). More practically, equilibrium exists when population size fluctuates with a steady average variance around an average population size (May 1973, Price 1980). Price (1980) defines a population in a nonequilibrium state as one that does not fluctuate within

a typical probability range around an average population size. He also suggests that steady population growth following colonization, with subsequent rapid extinction, provides no indication of an equilibrium. The populations of several of the sap-feeders on *S. patens* fluctuate in ways that strongly violate the tenets of equilibrium theory and suggest nonequilibrium behavior. For instance, following the severe winter of 1977-78, populations of *A. simplex* and *T. minuta* were drastically reduced, and *D. detecta* was annihilated altogether from the study area in Tuckerton, New Jersey (Fig. 9-13A, B and C). Furthermore, we show that in general the overwintering success of these species is negatively related to the severity of the winter (Fig. 9-14A, B and C). Other species are unaffected by severe winters (Figs. 9-13 and 9-14D, E and F). Consequently, certain species can be selectively reduced or eliminated from the guild following a harsh winter and never attain the population size at the end of the season that they do following mild winters (e.g., Fig. 9-13A).

The overwintering success of a species is dictated in large part by the exposure of the overwintering stage. Species like *D. detecta* and *A. simplex* that overwinter as exposed nymphs and eggs respectively incur great mortality during severe winters compared to species like *Am. simplex*, which protect their eggs by inserting them into vegetation. Where winters are usually severe in northern New England, most species that overwinter in an exposed stage are either absent or extremely rare (Fig. 9-16A, B and C).

Southern marshes, where mild winters prevail, are characterized by multivoltine species that overwinter as exposed nymphs (*D. detecta*), exposed eggs (*A. simplex*) or embedded eggs (*D. bisignata*). Univoltine species like *Am. simplex* and *H. lineatus*, which are so common on northern marshes, are absent on southern marshes. We suggest that a high premium is placed on continuous reproduction and development in the south, where exposure of a single stage to competitors, predators and parasitoids is minimized.

In mid-Atlantic states (New Jersey), and probably in southern New England states as well, where the variance in winter harshness is great, we suggest that populations of *D. detecta* and *A. simplex* in particular are maintained below carrying capacity at a frequency equivalent to the occurrence of catastrophic winters. Consequently, populations of these species in both large and small patches are often in a state of nonequilibrium. Additionally, certain species of sap-feeders are consistently rare or absent on small patches, suggesting that they are inherently harsher and harder to track than large patches. Thus, the picture we paint is one of frequent nonequilibrium conditions in both space and time.

Despite our arguments in support of a nonequilibrium hypothesis, the guild of sap-feeders associated with *S. patens* appears to be organized in a way that is also consistent with a competition interpretation. There is a considerable amount of niche diversification, particularly along the microhabitat dimension, where species sort out into upper- and lower-strata residents. Also, among the upper-stratum species there are considerable negative density effects. At our major study site in New Jersey, a niche analysis suggests that the sap-feeder guild is overpacked where *Am. simplex*, *A. simplex* and *D. detecta* share very similar niches. Of these species and of the remainder as well, *Am. simplex* is the only one that has fully developed wings and can fly. We suggest that this species can coexist in the guild by colonizing empty sites created by

cold-winter elimination of its closest competitors, *A. simplex* and *D. detecta*. South of New Jersey, where cold-winter disturbance is rare and competitors persistent, *Am. simplex* is rare and drops out completely south of Virginia. To the north of New Jersey *Am. simplex* is abundant.

The structure of the subguild of species associated with the lower stratum of the grass remains unchanged from Florida to New Hampshire (*D. bisignata*, *M. lobatus* and the *T. minuta-T. terminalis* complex are similarly abundant along the entire latitudinal gradient). The buffering effects of the thatch coupled with overwintering style may be responsible for the constancy in structure of this subguild. There are several latitudinal replacements among upper-stratum species. *Am. simplex* and *H. lineatus* occur on New England marshes, but are absent on southern marshes, where *N. dorsalis* and the *A. simplex-A. decorata* complex are restricted. All of these species occur on mid-Atlantic state marshes, but *H. lineatus* and *N. dorsalis* are rare there (Table 9-4). We suggest that levels of disturbance (winter mortality) are intermediate on mid-Atlantic compared to southern and New England marshes, and that sap-feeder richness is highest there because the populations of potential competitors are often in a state of nonequilibrium.

We have tried to interpret our data according to both nonequilibrium and equilibrium hypotheses. To date, two features of our system impress us. First, density-independent mortality coupled with patch heterogeneity appear to play a major role in preventing the populations of certain species from often attaining equilibrium numbers and in shaping the life histories of those species. Second, if our data are correct in suggesting that equilibrium conditions are attained often enough to maintain niche diversification among the various sap-feeders, then competition must be intense during at least a portion of the time these conditions occur. Finally, the validity of a competition hypothesis will be elucidated only by laboratory experiments where the fitness of sap-feeders is evaluated in paired compared to pure cultures established at realistic field densities. Only then will we be able to assess the impact of species interactions in guilds of herbivorous insects.

Table 9-4. Richness of sap-feeders on New England, mid-Atlantic and southern marshes

Southern	Mid-Atlantic	New England	Stratum
<i>T. minuta-T. terminalis</i>	<i>T. minuta-T. terminalis</i>	<i>T. minuta-T. terminalis</i>	lower
<i>D. bisignata</i>	<i>D. bisignata</i>	<i>D. bisignata</i>	lower
<i>M. lobatus</i>	<i>M. lobatus</i>	<i>M. lobatus</i>	lower
<i>D. detecta</i>	<i>D. detecta</i>	<i>D. detecta</i> (rare)	upper
<i>A. simplex-A. decorata</i>	<i>A. simplex-A. decorata</i>		upper
<i>N. dorsalis</i>	<i>N. dorsalis</i> (rare)		upper
	<i>Am. simplex</i>	<i>Am. simplex</i>	upper
	<i>H. lineatus</i> (rare)	<i>H. lineatus</i>	upper
Species total	6	8	6

Acknowledgments. Barbara Denno processed the many samples for this study. Vera Krischik, Mark McClure, Peter Price, Don Strong and Tom Whitham made helpful comments on earlier drafts of this report. Jim Kramer (Systematic Entomology Laboratory, USDA) made the initial sap-feeder identifications. Susan Smith typed the several drafts of this report. To these people we are most grateful.

Scientific Article No. A2888, Contribution No. 5942 of the Maryland Agricultural Experiment Station, Department of Entomology. Figs. 9-3 to 9-8 were reproduced, with permission, from Denno (1980), Duke University Press, Durham, N.C., U.S.A.

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