The Influence of Patch Size on a Guild of Sap-feeding Insects that Inhabit the Salt Marsh Grass *Spartina patens*[1]

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ABSTRACT

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A guild of 12 sap-feeding Homoptera and Hemiptera, mostly leafhoppers and planthoppers, was sampled on large and small patches of the salt marsh grass *Spartina patens*. Several species maintained consistently larger densities (individuals per kg of live grass) in large (~20 ha) compared to small (~1 ha) patches and the herbivore load (total individuals per kg of live grass) was also greater in large patches. The number of resident sap-feeder species supported by large and small patches was the same. Small patches supported lower densities of sap-feeders because immigration rates were probably lower and removal rates higher there.

Insects often use resources that are discontinuous in time and space. The discontinuities result in a mosaic of resources varying in quality and quantity (Wiens 1976). For small organisms like insects the problem of finding and remaining on appropriate resources may be formidable, especially if resources are isolated and/or temporary.

MacArthur and Wilson (1967) theorized that the area of oceanic islands and their distance from source areas modified immigration and extinction rates that ultimately determined the number of established species. Experimental studies by Simberloff and Wilson (1969, 1970) and Simberloff (1974) supported these predictions. Janzen (1968, 1973) extended island biogeographic theory to include host plants as islands. Southwood (1960), Yarwood (1962), Opler (1974), Strong (1974 a,b,c, 1977) and Strong et al. (1977) found that the distributional area of host plants was positively correlated with the diversity of associated insects. Seifert (1975) found a similar relationship between the area of *Heliconia* stands and insect diversity.

By planting collards in large patches and in single rows interspersed within meadow vegetation, Tahvaninen and Root (1972) and Root (1973) demonstrated that less diverse assemblages and greater loads of herbivorous insects were associated with the large concentrated stands. Lower diversities were explained by the increased dominance of a few species. Root (1973, 1975) suggested that the increased number of herbivores, particularly specialists, was due to the ease with which those insects found and remained on larger patches. Collards planted in mixed vegetation had a more diverse (equitable) herbivore fauna because the dispersion of the host plant provided an associational resistance or spatial escape preventing the dominance of specialists. Root (1975), Feeny (1975), and Futuyma (1976) suggested that associational resistance was an inherent property of diverse vegetational systems, such as early successional communities, and might be a common mechanism by which plants avoid herbivory.

Two grasses, *Spartina alterniflora* Lois. and *Spartina patens* (Ait.) Muhl. (hereafter abbreviated SA and SP respectively), dominate the vegetation of Atlantic Coastal marshes, where they occur as a mosiac of rather pure patches (Blum 1968, Redfield 1972). Most of the herbivorous insects associated with these grasses are host specific (Davis and Gray 1966, Denno 1977). Suitable patches of host plants are thereby intermixed with unsuitable vegetation. Due to the rather large number of specialized herbivores and the variety of patch configurations of SP, the system provides an ideal opportunity to study the effects of patch size on insect community structure.

In this report we test the effect of stand size on the richness of the sap-feeder guild, mostly planthoppers and leafhoppers, and on the abundance (herbivore load) of individual guild members. If SP patches behave as ecological islands, then large patches should be utilized by a richer fauna of herbivores than small patches (MacArthur and Wilson 1967, Seifert 1975). Furthermore, if the effects of resource concentration operate, then the abundance of some specialists should be greater in large compared to small stands of host plants (Root 1973, 1975).

Host Plant Dispersion and Structure

SP and SA are distributed along an elevational gradient. SP occurs at higher elevations from approximately mean high water (mhw) to ~0.5 m above mhw, in a zone that is occasionally flooded by high tides (Blum 1968). SA is an intertidal grass that is regularly inundated and occupies a broader elevational range from mhw to ~2 m below mhw (Blum 1968, Redfield 1972). Variations in the elevational relief of the marsh surface result in a mosiac of interspersed patches (usually pure stands) of both grasses.

SP has a complex structure composed of several strata. An upright or partially prostrate living fraction forms annually as new shoots grow upward from the rhizomes present at the marsh surface. By autumn, these shoots have fallen over and joined a horizontal layer of thatch composed of dead culms and blades from the previous 2–3 seasons. This well ventilated stratum remains dry except during high flood tides. Beneath the thatch is a moist layer of decomposing grass fragments and other inorganic debris older than 3 yr (Blum 1968).

Study Site and Methods

A series of 4 SP study patches was selected in the extensive marshland bordering the Barnegat Bay, Ocean

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Co., New Jersey between 39°, 42′ and 39°,33′ N. Lat. To reduce variability due to location, all patches were chosen within the continuous grassland strand that forms the western boundary of the bay. Two large patches were located near Mayetta and Manahawkin (~20 and ~14 ha, respectively) and were separated by ~5 km. Two small patches (~3 and ~1 ha), separated by ~1 km, were chosen on the marsh at Tuckerton ~13 km south of Mayetta. Areas of the 4 patches were measured from aerial photographs using a planimeter.

To minimize isolation effects (see Simberloff 1974, Simberloff and Wilson 1969, 1970), the 4 patches were located within 100 m of, but were clearly separated from, other large source areas.

Using a D-Vac suction sampler (Model 1-A) with a 0.093-m^2 (= 1 ft^2) orifice, insects were sampled on 11 dates from May through Oct. 1976. On each date and in each patch 6 samples were taken. Each sample consisted of five 30-sec placements of the suction orifice on the marsh surface such that a total of 0.464 m^2 of grass was vacuumed. Arthropods were killed in an ethyl-acetate jar, transferred to 100 ml of 95% ethyl-alcohol and returned to the laboratory where they were sorted to species and counted. Samples were taken only on clear days within 3 h of noon when the grass was dry. To correct for possible diurnal activity patterns of insects, the order in which patches were sampled was purposefully changed throughout the course of the study.

Although equal areas of grass were sampled in each patch, the possibility remained that grass productivity differed between patches. To correct for possible biomass effects, the standing crop biomass for each of the 4 patches was measured. Ten random grass samples 0.047 m^2 [recommended by Wiegert (1962) as optimal quadrat size for sampling grass vegetation] were taken in each patch in late July, at the time when standing crop biomass reached a maximum (Squiers and Good 1974, Busch 1975). The grass was separated into living and dead components, dried at 100° C for 24 h, and weighed. Live weight biomass differed significantly between patches ($P<0.001$, F-test) with small patches supporting more grass than large ones. No significant differences in the biomass of dead grass were found between sites. Once live grass biomass was determined, the densities of all sap-feeders were expressed as individuals per kg (of live grass). This parameter was then used to test the effects of patch size on species density.

To compare the structure of the sap-feeding guild between large and small patches, we used total herbivore density and species richness. Total herbivore density was the sum of all sap-feeders present in a sample and was expressed as individuals per kg (of live grass). Herbivore richness (S) was the number of species belonging to the sap-feeding guild present in each sample.

All data were analyzed using analysis of variance for repeated measures to determine if densities or guild parameters differed significantly between large and small patches. Prior to the analysis of variance, densities of herbivores and predators were transformed using the common logarithm to reduce heteroscedasticity.

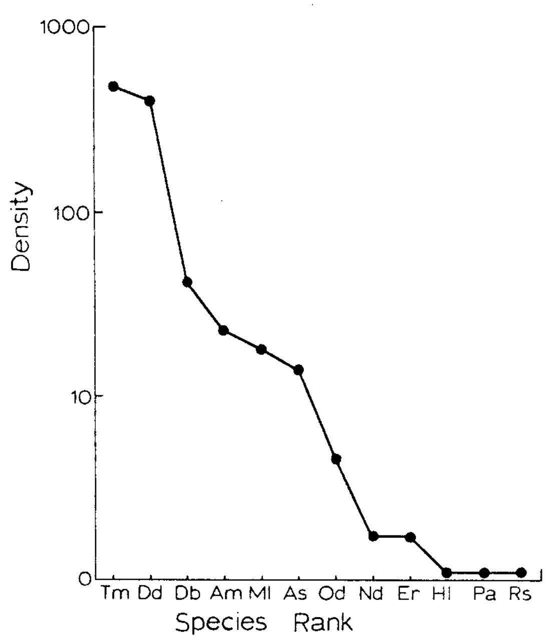

FIG. 1.—Mean density (individuals/kg live grass) over 6-mo sample period for each sap-feeder species ranked in order of decreasing abundance. Tm = *Tumidagena minuta*, Dd = *Delphacodes detecta*, Db = *Destria bisignata*, Am = *Amplicephalus simplex*, Ml = *Megamelus lobatus*, As = *Aphelonema simplex*, Od = *Odonaspis sp.*, Nd = *Neomegamelanus dorsalis*, Er = *Eriococcus n. sp.*, Hl = *Hecalus lineatus*, Pa = *Paraphlepsius sp.*, Rs = *Rhytidolomia saucia*.

Results

Influence of Patch Size on Sap-Feeder Density and Richness

Twelve species of sap-feeding Heteroptera were collected from SP (Fig. 1). The 2 most abundant species throughout the sampling season were 2 planthoppers (Delphacidae), *Tumidagena minuta* McDermott and *Delphacodes detecta* (Van Duzee). The mean density per sample of these species over a 6-mo period (seasonal mean density) was more than 400/kg of live grass. Four subdominant species had densities between 50 and 12/kg. Ranked in order of decreasing density, they were *Destria bisignata* (Sanders and DeLong) and *Amplicephalus simplex* (Van Duzee), (Cicadellidae), *Megamelus lobatus* Beamer (Delphacidae), and *Aphelonema simplex* (Uhler) (Issidae). Three species, *Odonaspis sp.* nr. *litoralis* Ferris (Diaspididae), *Neomegamelanus dorsalis* (Metcalf) (Delphacidae), and *Eriococcus n. sp.* (Eriococcidae), occurred infrequently or at consistently low densities (<5/kg) throughout the season. *Hecalus lineatus* (Uhler), *Paraphlepsius sp.* (Cicadellidae), and one sap-feeding stink bug, *Rhytidolomia saucia* (Say) (Pentatomidae) were collected very rarely and were not included in the forthcoming analysis of herbivore densities.

Of the 9 sap-feeders commonly sampled, mean densities of *D. detecta*, *D. bisignata*, *Amplicephalus simplex*, *M. lobatus*, and *Aphelonema simplex* were significantly greater in large compared to small patches of SP on 1 or more of the the 11 sample dates ($P<0.05$, F-test) (Fig. 2). The remaining 4 sap feeders, *T. minuta*,

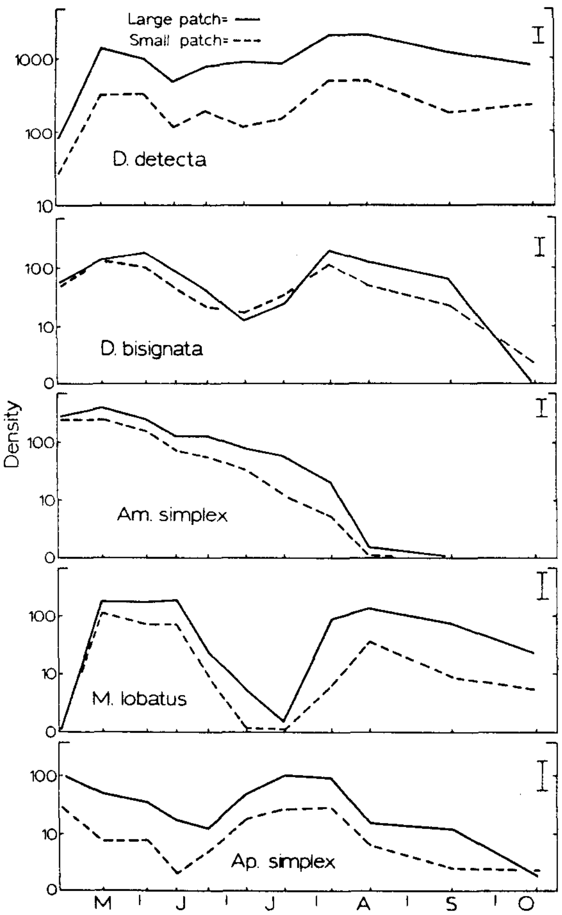

FIG. 2.—Comparisons of sap-feeder densities (individuals/kg of live grass) between large and small SP patches over a 6-mo study period (May–Oct.). The statistical interval in the upper right corner of each graph is a least significant difference (LSD) calculated at the 0.05 confidence level. Means differing by this interval or more are significantly different for patch comparisons made on the same date.

N. dorsalis, Odonaspis sp., and *Eriococcus n. sp.* were equally abundant on large and small patches between sample dates and over the entire sample period ($P > 0.1$, F-test) (Fig. 3). Total sap-feeder density was significantly greater on large rather than small patches ($P < 0.1$, F-test) (Fig. 4).

No significant differences in sap-feeder richness were found between large and small patches ($P > 0.1$, F-test). However, richness decreased at all sites at season's end (Fig. 4). The absence of the homopterans *Amplicephalus simplex* and *Aphelonema simplex,* which both overwinter as eggs, from a number of late season samples contributed to this decline.

Influence of Patch Size on Predator Density

Predaceous spiders, primarily lycosids and mirid bugs in the genus *Tytthus* were abundant in SP. Spider densities were not significantly different between large and small patches ($P > 0.1$, F-test) (Fig. 5); however, between many sample dates densities of *Tytthus sp.* were

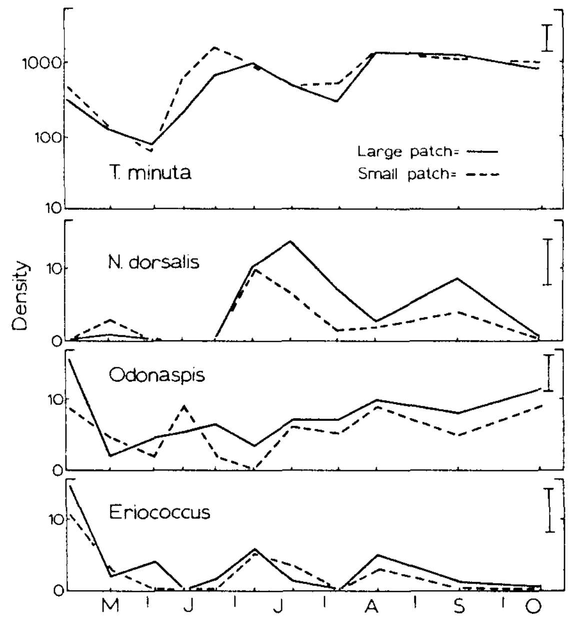

FIG. 3.—Comparisons of sap-feeder densities (individuals/kg live grass) between large and small SP patches over a 6-mo study period (May–Oct.). LSD as in Fig. 2.

significantly greater on small patches ($P < 0.05$, F-test) (Fig. 5).

Discussion

Root (1975) predicts that concentrated resources (those that grow in large, dense and/or pure patches) should support greater densities of specialized herbivores because the likelihood of locating and remaining on concentrated resources is greater. The studies of most herbivorous insects on collards by Tahvanainen and Root (1972), Root (1973), and Cromartie (1975) and of *O. fasciatus* on milkweed by Ralph (1977) support this hypothesis. Data presented here clearly indicate that 5 of the 9 sap-feeders, *D. detecta, D. bisignata, Amplicephalus simplex, M. lobatus,* and *Aphelonema simplex,* attain greater densities in large SP patches. These results

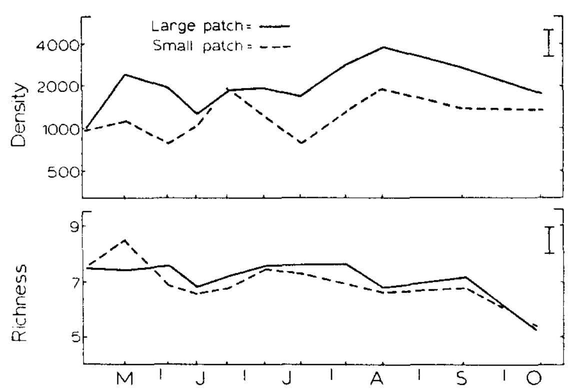

FIG. 4.—Comparisons of total sap-feeder density (individuals/kg of live grass) and sap-feeder richness between large and small SP patches over a 6-mo study period (May–Oct.). LSD as in Fig. 2.

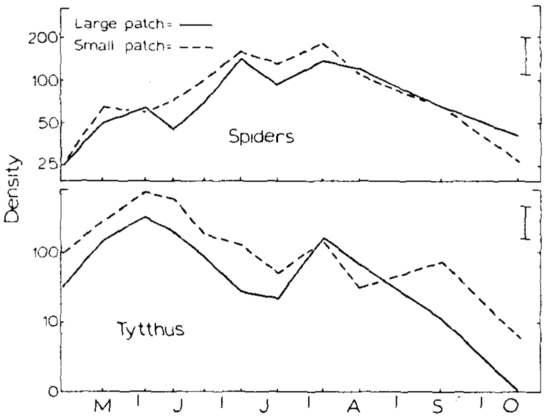

FIG. 5.—Comparisons of spider and mirid (*Tytthus*) predator densities (individuals/m^2) between large and small SP patches over a 6-mo study period (May–Oct.). LSD as in Fig. 2.

generally agree with the predictions of the resource concentration hypothesis. However, there are some inherent differences between seasonally transitory plants like collards and milkweeds and the SP grass system. Both collards and milkweeds senesce at the end of the season and many resident insects must move to overwintering sites elsewhere. Consequently these plants must be colonized annually. This is not the case with SP. The dense thatch associated with SP provides in situ overwintering sites for the sap-feeders (Denno 1977) thereby eliminating the need to search for food resources the following spring. Under these circumstances, where resources are persistent and all requisites are provided within the current habitat, Southwood (1962) predicts that insects should allocate little energy to flight. This hypothesis is in large part substantiated by the guild of sap-feeders inhabiting SP. All of the fulgoroids (Delphacidae and Issidae) as well as the leafhoppers except for *Amplicephalus simplex* on SP are either monomorphically brachypterous (flightless) or exhibit wing-dimorphism and produce mostly (>85%) brachypterous adults (Denno 1976, 1978). Subsequently, adults of the SP sap-feeders should be poor colonists. This contrasts with the studies of Moreton (1945) and Caldwell (1974) who respectively demonstrate the good colonizing abilities of *Phyllotreta* on collards and *Oncopeltus* on milkweed. Thus, the factors that enhance the ability of some sap-feeders to occur more abundantly on large compared to small patches of SP probably differ in several ways from collard and milkweed systems.

MacArthur and Wilson (1967) hypothesize that the equilibrium number of species on oceanic islands is a function of immigration and extinction rates of species and these rates vary depending on the area of islands and their distance from the mainland. Viewing the very largest patches of SP on the salt marsh as source areas (mainland), the remainder of various sized patches can be considered islands. Distance from source being equal, MacArthur and Wilson (1967) suggest that small islands should house fewer species because immigration rates are low and extinction rates high.

Because the populations of most SP sap-feeders are composed of flightless brachypters, the colonization potential (immigration rate) of these species should be low. Consequently it should be difficult for brachypterous adults to move between even the closest of patches. However, because of their flightlessness, the adults of these species have an increased ability to remain on their host plant. Therefore, the removal rate of brachypterous adults should be less than fully winged adults (macropters), particularly on small patches where the chance of winged adults actively moving from the patch or being dislodged is great.

The response of *Amplicephalus simplex* supports this hypothesis. This univoltine leafhopper is the only resident sap-feeder with fully winged adults and is probably a good colonizer. During the early season (May to mid-June), when only nymphs were present, densities on large and small patches remained similar. However, later in the season (mid-June to Sept.) when most nymphs have molted to adults, small patches contain fewer *Amplicephalus simplex* compared to large patches. We suggest that this reduction was due to the greater removal rate of winged leafhopper adults in small SP patches.

Cameron (1976), after studying the effect of periodic, regular tidal inundations on salt marsh insect communities, concluded that species richness and community structure did not change as a result of these inundations. However, when unusually high spring or storm tides submerge the entire SP marsh, resident insects may be washed out of patches by wave action. Due to changes in the ratio of surface area to perimeter, the chance of being washed out of a large patch should be less than that of a small one. Once dislodged, the insect is confronted with the problem of relocating its host plant. This must be a formidable task for both nymphs and adults of small Homoptera with reduced dispersal abilities. The loss of individuals due to tidal action is especially likely for vulnerable species such as *D. detecta, Amplicephalus simplex, Aphelonema simplex,* and *N. dorsalis* that inhabit the upper strata of SP (Denno, unpublished data). Three of these 4 upper strata inhabitants responded strongly to changes in patch size. Thus, as patch size decreases, removal rate should increase. Coupled with the low colonization potential of most adult sap-feeders, the high removal rates of nymphs should result in reduced populations on intermediate sized islands and fewer resident species on very small, isolated islands. Over the portion of the island size spectrum we examined (1–20 ha), our results support this progression. As island size decreases from one ha (the smallest island studied) to very small (10 m^2) we suggest that poorer dispersers will drop out of the herbivore assemblage until only the most mobile species remain.

Before accepting our proposition that reduced densities on small islands are the result of increased removal rates due to tidal effects and not some other factor, several points need examination. Predation might differentially influence the densities of herbivores on patches of different size. Spiders are generalized predators and probably feed on the active stages of the sap-feeders. However, our data suggest that spiders are equally abundant in large and small patches. Mirid bugs in the genus *Tytthus* are known egg predators of Homoptera (Swezey 1936). Greater densities of these predators occurred in small patches throughout much of the study period. However, mirids occur primarily beneath the thatch layer where they rarely encounter the upper strata residents that responded so strongly to patch size. Also, the number of adult parasites (mostly Hymenoptera and Strepsiptera) captured was small and did not appear to differ between large and small SP patches. For these reasons we dismiss predation and parasitism as causes of reduced sap-feeder densities in small patches.

Also, increased plant structural diversity has been shown to allow more species to coexist and change the density relationships of species in a given habitat (MacArthur and MacArthur 1961, Murdoch et al. 1972, Denno 1977). Although some variation was observed in the biomass of living SP among patches, no differences in litter biomass were found. We have no evidence to suggest that the plant structural diversity between large and small patches of SP differed in any apparent way.

Lastly, on the basis of these arguments, we suggest that factors associated with tidal flooding inflict the severest mortality on sap-feeder populations in SP and that the magnitude of this stress increases as grass patches become smaller. Thus, removal rates are higher on small compared to large patches resulting in reduced populations there.

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