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**Volume: 1 Issue: 4**  
**Month/Year: 01 1976 Pages: 257-266**

**Article Author: DENNO R F**  
**Article Title: ECOLOGICAL SIGNIFICANCE  
OF WING POLYMORPHISM IN  
FULGOROIDEA WHICH INHABIT TIDAL SALT  
MARSSES**

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# Ecological significance of wing polymorphism in Fulgoroidea which inhabit tidal salt marshes

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## Abstract

(1) The vegetation of New Jersey tidal salt marshes is composed primarily of two grasses, *Spartina patens*, which occupies a narrow elevational zone of high marsh and varies little in structure from site to site, and *Spartina alterniflora*, an intertidal species which occurs as two spacially separated growth forms (tall and short). Fulgoroids, polymorphic for wing length, inhabit these grasses.

(2) Populations of the common fulgoroid inhabiting short form *S. alterniflora* were composed of equal numbers of macropters and brachypters. Mesothoracic wings of brachypters were subequal in length to the abdomen allowing for short but inefficient flights compared to macropters.

(3) Fulgoroids residing in *S. patens* produced mostly brachypters having small meso- and vestigial metathoracic wings and were incapable of flight.

(4) Brachypter density of all fulgoroids was correlated with the seasonal increase in biomass of the host grass, while macropter density was not.

(5) Peak macropter density occurred shortly before maximum biomass of the host grass was attained.

(6) The production of macropterous forms was correlated with high levels of crowding incurred during nymphal stages.

(7) Spatial and temporal variation in the structure of the host grasses and habitat reliability are suggested as important factors dictating the wing-polymorphism strategies of fulgoroids.

## Introduction

Throughout much of the taxonomic and ecological literature dealing with the Fulgoroidea, reference

is made to the occurrence of wing polymorphism especially in the Delphacidae, Issidae and Dictyopharidae (e.g. Metcalf, 1923; Swezey, 1936; Osborn, 1938; DuBose, 1960). Most species produce two discrete alary morphs: flightless brachypterous forms, with abbreviated mesothoracic and vestigial metathoracic wings, and macropterous forms where both pairs of wings are fully developed allowing for flight and dispersal.

The frequency of a particular wing-morph in a population can be related to the advantage or disadvantage of flight. Southwood (1962) reasons that dispersal can be a wasteful process if large numbers of individuals migrate and fail to locate suitable food resources or habitats. The advantages of dispersal lie in the colonization of new resources or in the escape from resources that are deteriorating in quality or availability. Presumably, for these reasons, macropters should predominate in populations that are associated with resources which are patchy in time and/or space (Southwood, 1962; Brinkhurst, 1963).

A 'commitment' to brachyptery could allow energy and body-space that is devoted to wings and flight muscles to be allocated to other organ systems, where, for example, reproductive effort might be increased. Also, it would seem advantageous for a species to sacrifice or reduce dispersal ability only when its resources are certain (Johnson, 1969). Brown (1951) and Vepsäläinen (1973, 1974), respectively, found flightless forms of corixids and gerrids associated with large permanent bodies of water. Similarly, Lindroth (1949) concluded that stable or isolated habitats favoured the production of the flightless morph of dimorphic carabid beetles. Using polymorphic fulgoroids inhabiting salt marsh vegetation, I attempted to test the prediction that brachyptery would prevail where resources are reliable and continuous, while macroptery should be favoured where resources are patchy and uncertain.

### Host plants of fulgoroids

Salt marshes are extensive ecosystems which occur as a narrow strand of halophytic vegetation along much of the sheltered portions of the Atlantic seaboard of North America. The vegetation of these tidal salt marshes is dominated by two grasses, *Spartina alterniflora* Loos. (Salt Marsh Cordgrass, hereafter abbreviated SA) and *Spartina patens* (Ait.) Muhl. (Salt Meadow Cordgrass, hereafter abbreviated SP), which are fed upon by an array of fulgoroid species.

SP occupies a narrow elevational zone of well-drained marsh above mean high water level (MHW) where it can grow in extensive pure stands (Redfield, 1972). The culms of SP are narrow, cylindrical and permanently convolute (Anderson, 1974), growing and projecting through a dead horizon of matted fibrous culms from previous years' growth. The entanglement of living and dead culms is so dense that the marsh surface is rarely visible. As the season progresses and the spindly culms elongate, they eventually fall over to form a prostrate mat of living culms which overlies the accumulation of dead plants (Blum, 1968). Matting usually occurs in a mosaic fashion, leaving behind small 'islands' of wispy, erect plants.

SA, an intertidal species, occurs throughout most of the elevational range of SP, but also extends to levels far below ( $\sim 2$  m) MHW (Blum, 1968; Redfield, 1972). There are two distinct growth forms of SA. Near MHW, where the marsh is flat and poorly drained, SA grows as a short form (SAS) consisting of stiff rosettes of flat, divergent leaves, and attains a height of only 10–40 cm. Although the leaves of adjacent rosettes may overlap, reduced culm density combined with the lack of an extensive thatch allow for the exposure of the marsh surface. Along the depressed borders of natural tidal creeks which dissect the marsh, at elevations well below MHW, the culms of SA grow tall (SAT), commonly reaching a height of  $\sim 2$  m (Blum, 1968; Redfield, 1972). Squiers & Good (1974), working on a New Jersey salt marsh, reported that new shoots of both SAS and SAT first appeared in April, and by mid-May a sharp height delineation between the two forms was evident. Even though SA grows faster and taller along creeks, the absolute elevation at these sites is low and it is not until late May or June in New Jersey when SAT has reached a height to prevent plants from significant inundation. On most New Jersey salt marshes, there are extensive

areas of flat high marsh covered by SAS which abruptly intergrade, over the distance of a few metres, into SAT along the depressed margins of creeks.

For New Jersey salt marshes, the living, above-ground vegetation reaches maximum biomass in July or August for both forms of SA (Squiers & Good, 1974) and in July for SP (Busch, 1975). The living standing crop of both grasses remains high, although it may decline slightly, until late fall when seasonal effects accelerate the death of above-ground plant parts. The dead culms of SP are incorporated into the dense thatch where they decompose very slowly over the course of three or more years (Blum, 1968). The dead plants of SAS fall in place to form a loose layer of litter which decomposes during the following year. SAT, which grows on exposed creek banks, is sheared off by the combined action of winter winds, tides and ice and by spring little indigenous litter remains on SAT sites (Squiers & Good, 1974). Debris formed in this fashion accumulates in large mats which are carried about the high marsh by winds and tides.

Each species of *Spartina* presents to herbivorous insects a very different resource with respect to plant structure and dispersion. SP is characterized by a complex microstructure of dead thatch and living culms which remain green from April to November, but provides a rather uniform habitat, deviating little in growth form from one site to the next on the high marsh. SA, in contrast, can be divided into two patch-types (SAS and SAT) which differ structurally in space and behave differently in time. SAS grows at higher elevations on the marsh, where it is less subjected to tidal inundation and after dying in November or December remains in place throughout the winter as dead culms. SAT has a much larger standing crop during mid-summer than does SAS, but due to the relatively low elevation and exposed nature of the sites on which it grows, is an exploitative risk during spring when it is not tall enough to avoid significant tidal inundation. SAT is sheared off completely during winter, leaving exposed creek banks which afford little protection for overwintering insects.

### Study site and sampling methods

The study site was an extensive salt marsh in the Barnegat National Wildlife Refuge located  $\sim 3$  km east of Manahawkin, Ocean Co., New Jersey ( $39^{\circ}$ ,  $42'$  N lat.). Both SAS and SP occurred as a

mosaic of large ( $\geq 1$  ha), primarily pure stands. By measuring aerial photographs with a planimeter, the relative cover of SAS and SP was calculated at 52% and 48% respectively. SAT fringed the natural creeks, ditches and potholes on the marsh and represented a small percentage of the total grass cover.

Three widely separated sampling areas were established about 400 m apart on the marsh, each incorporating large expanses of both grasses. Using a 38 cm diam. sweep net, fulgoroids were sampled on twenty-eight dates at approximately 1 week intervals between March and December 1974. Each sample consisted of thirty sweeps taken while walking through pure stands of SP and SAS. On each date, five samples were taken from both grass species in each sampling area. Swept insects were killed in a large ethyl-acetate jar, transferred to 250 ml alcohol (95% ethanol) bottles and returned to the laboratory where they were sorted to species, instar, and wing-morph, and counted. All wing-morph density values were transformed to common logarithms prior to analysis of variance.

## Results

### Wing polymorphism in the resident fulgoroids

The only fulgoroid commonly occurring in SA was the extremely abundant and host-specific delphacid, *Prokelisia marginata* (Van Duzee). *P. marginata* produces both long-winged and short-winged forms, but the development of brachyptery was not extreme in this species (Fig. 1). Metathoracic wings of brachypters are reduced to small veinless flaps, while mesothoracic wings are subequal in length to the abdomen. Both the meso- and metathoracic wings of the macropter are fully developed and extend well beyond the end of the abdomen. Compared to macropters, brachypters are inefficient fliers, but they can fly or leap distances up to  $\sim 1$  m.

Several fulgoroid species occurred on SP. Two delphacids, *Delphacodes detecta* (Van Duzee) and *Tumidagena minuta* McDermott, and one issid, *Aphelonema simplex* Uhler, all dimorphic for wing length, were abundant. Unlike *P. marginata*, the degree of brachyptery found in SP-inhabiting fulgoroids is extreme and prevents flight (Fig. 1). Metathoracic wings are absent and mesothoracic wings have reduced veination and cover only the basal segments of the abdomen. Macropters have fully developed wings and can fly.

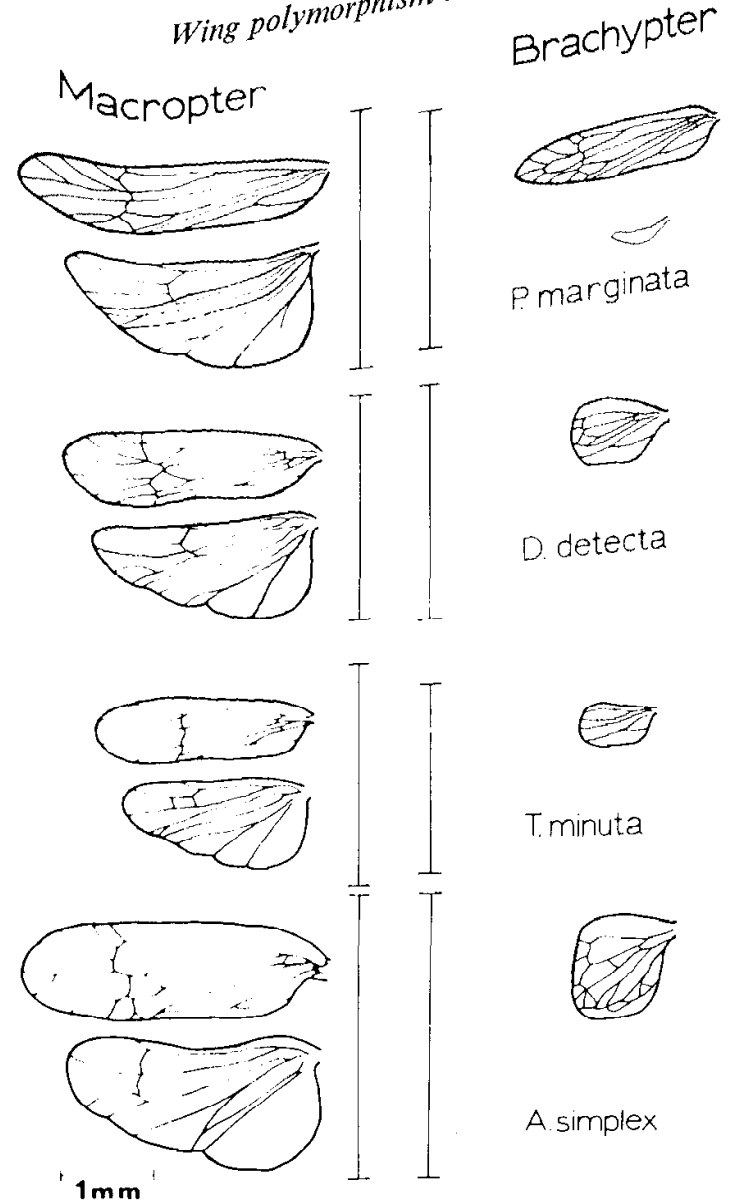


Fig. 1. Meso- and metathoracic wings of macropters and brachypters of salt marsh fulgoroids. Only mesothoracic wings are present on brachypters of *D. detecta*, *T. minuta* and *A. simplex*. Relative body lengths (vertex to tip of abdomen) of wing-morphs are pictured in the centre.

### Incidence of brachyptery

The relative seasonal densities of macropters and brachypters for *P. marginata* are pictured in Fig. 2A. Three rather synchronous peaks of macropter and brachypter density occurred, indicating that *P. marginata* is trivoltine. An analysis of variance, performed on wing-morph densities throughout the season, revealed no significant difference between macropter and brachypter density ( $F_{1, 24}$ ;  $P > 0.05$ ). Macropter density was greatest in generation during May, while brachypter density reached a maximum in July during the generation. Brachypters were the first to appear on the marsh in April and were more abundant than macropters at the close in late September and October.

Trends in the relative frequency, and to

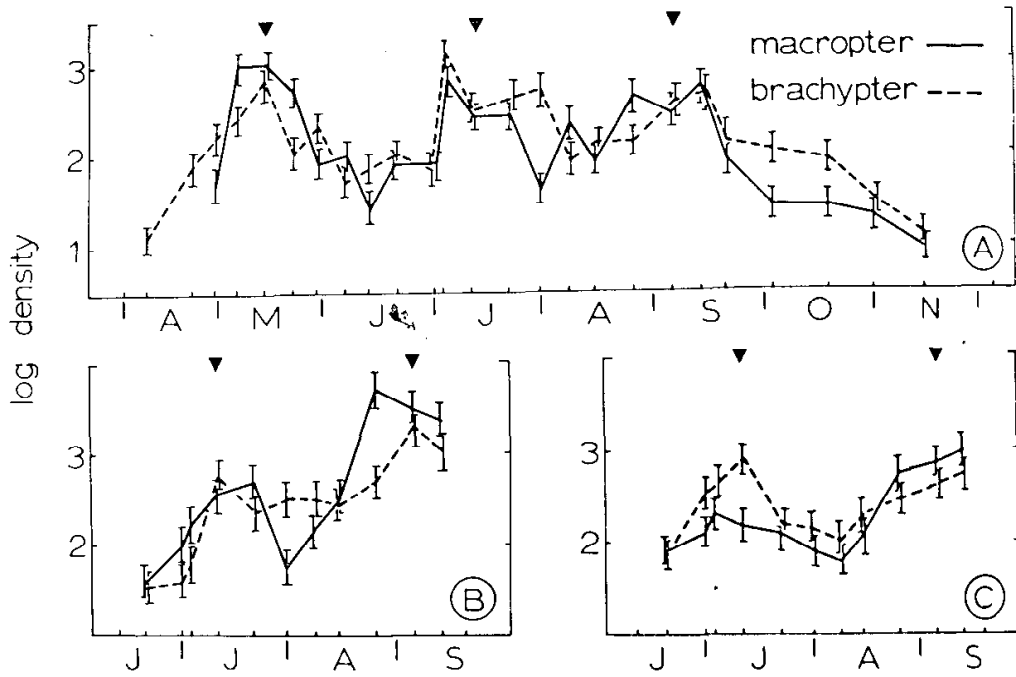


Fig. 2. Seasonal density (common log) trends of the macropters and brachypters of *P. marginata* sampled from three study areas (A, B, C) of short-form *S. alterniflora*. The interval surrounding means is the standard error. Triangles indicate generations.

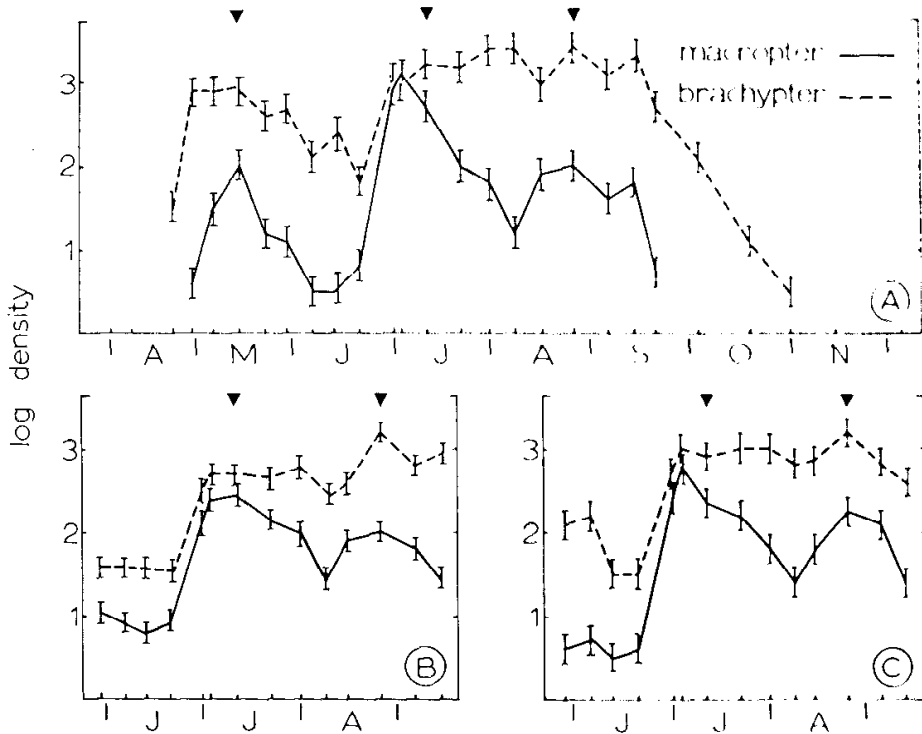


Fig. 3. Seasonal density (common log) trends of the macropters and brachypters of *D. detecta* sampled from three study areas (A, B, C) of *S. patens*. Statistical intervals surrounding means are Least Significant Intervals (LSI) calculated at the 5% significance level. Graphical non-overlap of LSIs indicates significant differences between means. Triangles indicate generations.

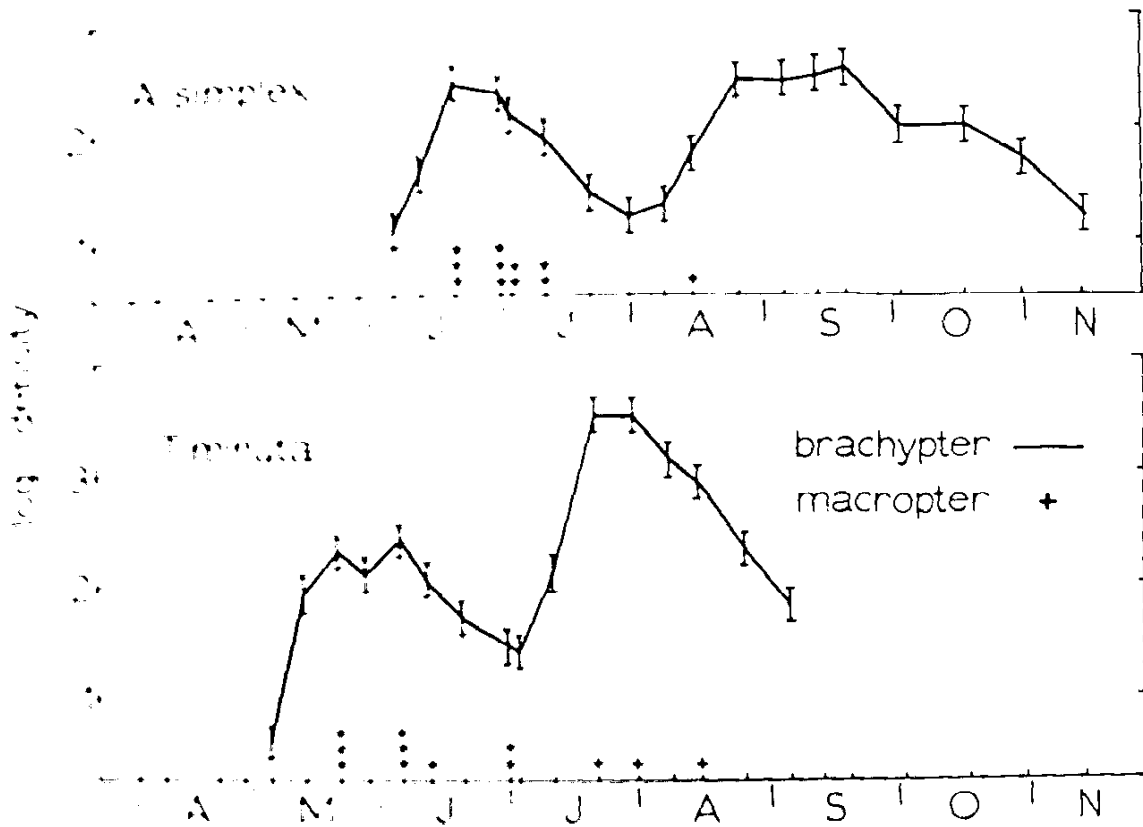


Fig. 4. Seasonal density trends of wing-polymorphs of *A. simplex* and *T. minuta* sampled from *S. patens*. Brachypters (common log density) were sampled from study area A and macropters (+ = one individual per five samples) were pooled from areas A, B and C. The interval surrounding means is the standard error.

ent the density, of wing-morphs of *P. marginata* were similar at the three sampling areas (Fig. 2). Again there was no significant difference between macropter and brachypter density in area B ( $F_{1,20} = 0.308$ ,  $P > 0.05$ ) or C ( $F_{1,10} = 1.177$ ,  $P > 0.05$ ) and the second and third generations are evidenced as peaks in wing-morph density during mid-July and early September. The large third generation of *P. marginata* found in area B during August and September is explained by an intrusion of SAT which supported high delphacid densities relative to SAS.

The seasonal density trends for the wing-morphs of *D. detecta*, a trivoltine species residing in SP, showed brachypter density to be significantly greater than that of macropters throughout most of the sampling season in areas A ( $F_{1,23} = 84.977$ ,  $P \leq 0.001$ ), B ( $F_{1,13} = 56.065$ ,  $P \leq 0.001$ ), and C ( $F_{1,13} = 87.002$ ,  $P \leq 0.001$ ) (Fig. 3). Brachypter density generally increased throughout the season and peaked during August or September. Macropters were most abundant in the second generation when their density did not differ significantly from that of brachypters, as indicated by overlapping Least Significant Intervals, calculated at the 5% significance level. Macropters were not produced either very early in

the season during April or at the end of the season in late September and October.

*T. minuta* and *A. simplex*, two other SP-inhabiting fulgoroids, produced many more brachypters than macropters and were bivoltine (Fig. 4). Peak macropter density for both species occurred in June or July, while brachypters were most abundant during the second generation in July or August. Brachypters were the first adults to mature in spring and the last adults found on the marsh prior to the onset of winter.

Table 1. Annual percentages of wing-polymorphs in populations of salt marsh fulgoroids

Species	Food resource	Macropter	Brachypter
<i>P. marginata</i>	<i>S. alterniflora</i>	50%	50%
<i>D. detecta</i>	<i>S. patens</i>	13%	87%
<i>T. minuta</i>	<i>S. patens</i>	<1%	>99%
<i>A. simplex</i>	<i>S. patens</i>	<1%	>99%

Table 1 summarizes the relative abundance of each wing-morph, expressed as a percentage of the annual total of adults, for each fulgoroid. SP-residing species produce mostly brachypters whereas in SAS, populations of *P. marginata* are composed of equal numbers of brachypters and macropters.

**Table 2.** Relationships of seasonal wing-morph density of salt marsh fulgoroids with the standing crop biomass of their host-grass

Species	Macropter	<i>n</i>	<i>r</i>	Brachypter	<i>n</i>	<i>r</i>
<i>P.marginata</i>	$y = 294.535 - 5.387x$	10	-0.134 <sup>(ns)</sup>	$y = 109.819 + 16.597x$	10	0.540 <sup>(ns)†</sup>
<i>D.detecta</i>	$y = 27.181 + 10.367x$	10	0.354 <sup>(ns)</sup>	$y = -76.800 + 85.699x$	10	0.900**
<i>T.minuta</i>	—	—	—	$y = -276.501 + 65.327x$	10	0.712*
<i>A.simplex</i>	—	—	—	$y = -12.512 + 7.738x$	12	0.667*

\*, \*\* Significance at 5% and 1% probability respectively; ns = not significant.

† *r* significant (0.665\*) when brachypter densities transformed to common logarithms prior to correlation.

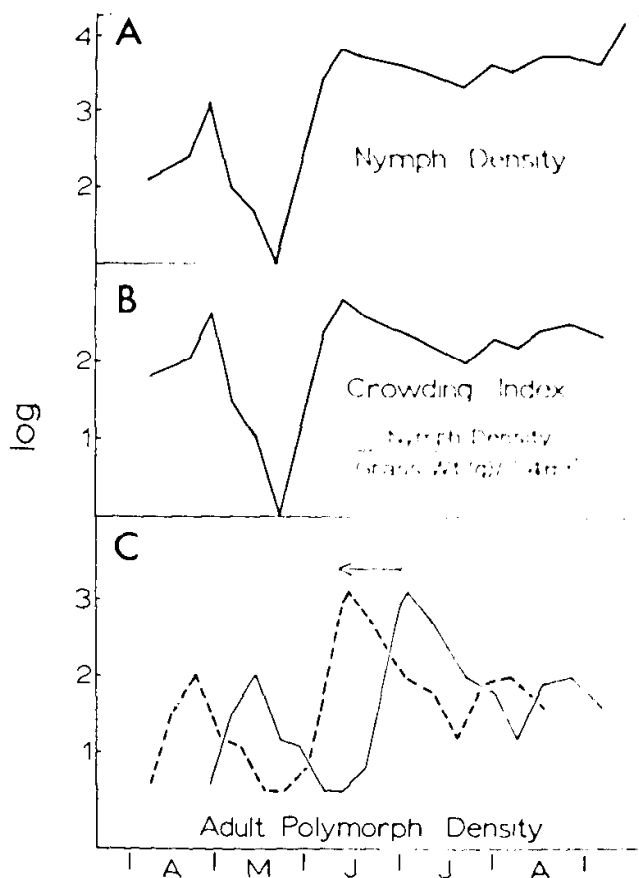
### Responses of wing-morphs to the biomass of standing grass

All SP-inhabiting fulgoroids responded by increasing the density of brachypters in their populations until August or September. Macropters, on the other hand, were produced most commonly during June or July. To investigate possible differences in the functional significance of each wing-morph, the following analyses were performed.

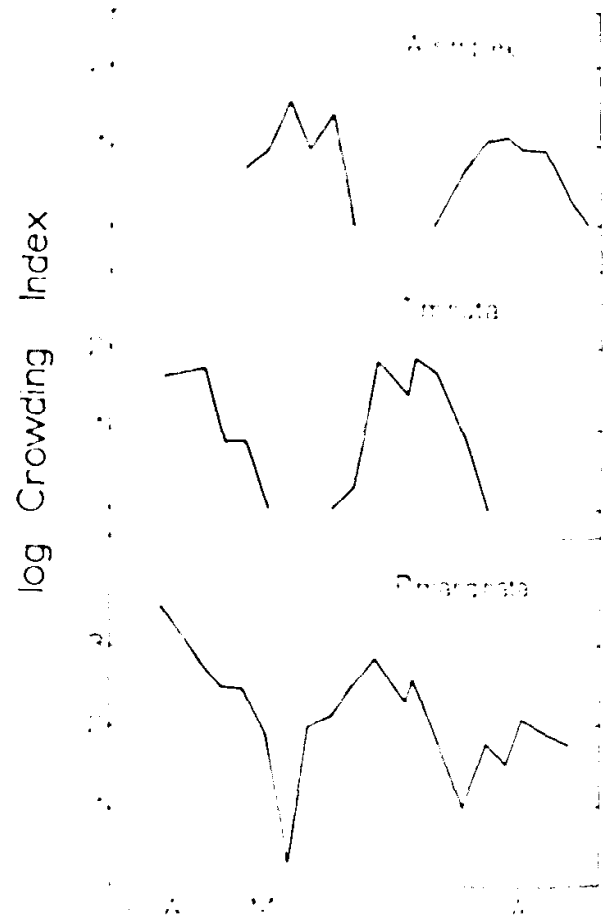
Five-date running averages of mean absolute macropter and brachypter density were calculated

for each species in order to smooth seasonal trends in wing-morph density and minimize generational fluctuations. Grass standing crop was sampled in the insect study plots during 1974 by Busch (1975). Pivotal wing-morph densities were then correlated with corresponding seasonal values of live host-grass standing crop biomass (g dry grass per 0.04 m<sup>2</sup>). Only those values between April and mid-September were considered in the analysis in order to avoid seasonal events which might selectively affect insect density.

Brachypter density of SP-inhabiting species was significantly correlated with living grass biomass



**Fig. 5.** Derivation of nymphal crowding index for correlation with wing-morph density. (A) Seasonal density (common log) trend for nymphs of *D.detecta*. (B) Seasonal pattern of nymphal crowding expressed as a ratio between nymph density and live standing crop biomass of *S.patens* (g dry wt per 0.04 m<sup>2</sup>). (C) Temporally adjusted seasonal trend of macropter densities used in a correlation with the above corresponding crowding index values.



**Fig. 6.** Seasonal patterns of nymphal crowding for *A.simplex* and *T.minuta* on *S.patens* and *P.marginata* on *S.alterniflora*, expressed as a ratio between nymph density and live standing crop biomass of host-grass (g dry wt per 0.04 m<sup>2</sup>).

Table 3. Relationships between seasonal wing-morph densities and indices of nymphal crowding

Species	Macropter	<i>n</i>	<i>r</i>	Brachypter	<i>n</i>	<i>r</i>
<i>P.marginata</i>	$y = -165.214 + 1.834x$	16	0.671**	$y = 326.175 + 0.419x$	16	0.152(ns)
<i>D.detecta</i>	$y = 125.210 + 0.400x$	17	0.767**	$y = 107.479 + 0.81x$	17	0.324(ns)

\*\* Significance at 1% probability. ns = not significant.

(Table 2). Absolute brachypter density values of *P.marginata* were not significantly correlated with the standing crop of SAS, however, the correlation of log-transformed brachypter density with grass biomass was significant. These data suggest that as host-grass biomass increases during the season there is a corresponding increase in brachypter abundance. The correlation of macropter density of *P.marginata* and *D.detecta* with host-grass standing crop was not significant. Macropters of *T.minuta* and *A.simplex* were rare, preventing meaningful correlation, but early seasonal fluxes in density (Fig. 4) would imply that macropterous forms of these and other species are not responding to the general increasing seasonal trend in resource biomass.

#### Crowding as a determinant of wing-morph

Crowding is a function of the amount of available resource relative to the density of exploiters. Crowding indices were calculated for each species by dividing mean nymphal density (Fig. 5A) by contemporaneous values of live host-grass standing crop (g dry grass per 0.04 m<sup>2</sup>). It is understood that grass biomass may be only an indication of those resources which are important to the various fulgoroids, and in no direct way represents available or suitable resources. Indices of nymphal crowding were plotted at intervals of about a week from April to September, generating a seasonal crowding trend for each species (Figs. 5B and 6). Nymphal crowding was most intense for *D.detecta* in the second generation during June. *A.simplex* was most crowded during the first generation and *T.minuta* was equally crowded during both generations. Of the three fulgoroids inhabiting SP, *D.detecta* experienced the most intense nymphal crowding, followed by *T.minuta*, and *A.simplex* was least crowded. There was a general seasonal decline in crowding for *P.marginata* after an initial peak during the first generation. Nymphal crowding was similarly intense for both *P.marginata* and *D.detecta*.

To determine the effect of crowding on wing-morph

production for *D.detecta* and *P.marginata*, the seasonal abundance curves for both brachypters and macropters were moved back in time approximately 3 weeks (peaks and valleys of adult and nymph density distributions were matched up) so that adults could be synchronized with an index of crowding which they experienced as nymphs (e.g. Fig. 5C). Linear correlation between crowding index values and adjusted macropter and brachypter density showed that macropter densities for both *P.marginata* and *D.detecta* correlated significantly with changes in crowding indices, while brachypter density did not (Table 3). These data suggest that crowding is an important determinant of wing-morph.

#### Discussion

One patch of resource rarely assures a continuous supply of requisites for the survival of exploiters. Suitable conditions for exploitation are affected by qualitative characteristics of the resource (e.g. nutrient and toxin modes and morphology) and the availability of the resource which is modified by the dispersion of the resource in time and space, resource size, competition from coexploiters, predation regimes, physical environmental factors and the like. Various combinations, intensities, and states of these modifying factors place resources along a risk-continuum from certain to uncertain. Organisms which exploit resources that lie at the uncertain end of the spectrum should pay a high premium for mobility in order to keep pace with changes in the location of optimum resources (Southwood, 1962; Johnson, 1969).

Relative to herbivorous insects, a stand of host-plants has components of certainty and uncertainty. It may be difficult for herbivorous insects to find and remain on isolated plants (Root, 1973, 1975) and one stand may provide only enough suitable resource for one generation of insects (Southwood, 1960). Plants with these characteristics dictate mobility in populations of their exploiters. On the other hand, if plants are long-lived relative to



generation time of herbivores and occur in concentrated patches, resource certainty increases, and it would seem energetically advantageous to relinquish mobility to some degree in exchange for the assurance of a resident population. However, while flight increases mobility, promoting more effective host-location, it will also decrease an insect's ability to remain on the host.

Herbivorous insects have evolved a number of solutions to the problem of finding and remaining on a host. Holometabolous herbivores may have bulky, sessile larvae that remain on the host-plant and active flying adults adept at locating larval food-plants. Hemimetabolous insects, where the food niche of immatures and adults is often similar, may produce one adult phenotype that is heavy enough to resist the forces of wind and water and yet is winged, maintaining its host-finding capability. The single phenotype strategy, depending on the characteristics of the host-plant, could suffer from the 'jack of all trades, master of none' dilemma. As the body size of winged insects gets small, they become more subject to physical forces which could remove them from their host. Berland (1935) reported that 'aerial plankton' (insects carried aloft by ascending air currents) was composed primarily of small, light, weak flying insects with a large surface to weight ratio. Assuming that it is indeed worthwhile to remain on a resource, another alternative is to develop a polymorphism where host 'finding' and 'remaining' functions are discretely partitioned between two phenotypes or morphs. This is apparently the strategy that has developed in some fulgoroids, aphids, mirids, lygaeids and other phytophagous insects.

The positive correlation of the brachypter density of salt marsh fulgoroids with the seasonal fluctuation in host-grass biomass supports the contention that brachypters serve to remain on and utilize the immediate resource. One commonality arises when seasonal macropter density patterns are examined for fulgoroids which inhabit both SP and SAS. Macropter density increases during the early part of the season, reaches a peak in either late spring or early summer and declines as the season progresses. Because the biomass of live grass remains high through summer and early fall, macropter density is poorly correlated with grass biomass for fulgoroids inhabiting SP and SA, implying that macropters afford a different advantage to the population than do brachypters. Peak macropter density occurs prior to the time when both SAT and SP reach maximum height and live standing biomass. These data suggest

that macropters function to locate previously unexploited resources. Colonization and subsequent resource utilization are maximized by dispersing when the grass biomass is increasing and about to peak and before resource quality deteriorates due to herbivore pressure or natural senescence.

Concerning aphids, Lees (1961) states that even though genes doubtless participate in the realization of polymorphic characters, genetic mechanisms are not known to play a role in controlling the choice of alternative polymorphic states. Raatikainen (1967), working with *Javesella* (= *Delphacodes*) *pellucida* (F.) and Kisimoto (1956a), studying *Sogata furcifera* (Horv.), *Delphacodes* (= *Laodelphax*) *striatella* (Fallen) and *Nilaparvata lugens* (Stål), concluded that wing-dimorphism in delphacids, like aphids, is not under genetic control, but is determined by environmental factors acting during the nymphal period. With aphids, environmental factors act through a hormonal messenger operating a developmental switch mechanism that in turn selects one of several alternative morphogenic pathways (Lees, 1961).

Johno (1963) showed that changes in temperature and photoperiod affect the proportion of brachypters in populations of *N.lugens*. Kisimoto (1956b) demonstrated that populations of *S.furcifera* and *N.lugens* produce mostly macropters when reared on deteriorating host plants. High levels of crowding incurred during the nymphal stages stimulated the production of macropterous or alate forms in populations of delphacids (Kisimoto, 1956a, b; Raatikainen, 1967) and aphids (Lees, 1961, 1966, 1967; Johnson, 1965). The correlation of macropter production in salt marsh delphacids with high levels of crowding during the nymphal stages suggests that crowding may be a generalized cue that triggers the production of macropters in a number of homopterans.

Even though a regime of environmental cues switches the production of macropters on or off, the switch threshold probably varies between different species and possibly between populations of the same species and is probably under genetic control. The fact that *P.marginata* produces many more macropters than does *D.detecta* under similar magnitudes of crowding and on fresh host-plants during the same season (photoperiod), suggests that switch thresholds differ between these two species. However, both *T.minuta* and *A.simplex* showed crowding indices and proportions of macropters of lesser magnitude than those of *D.detecta*. This could be interpreted to mean that switch thresholds

for these three fulgoroids are similar and crowding intensity alone is responsible for the observed differences in wing-morph ratio. The ultimate factors which dictate the exploitation strategy of fulgoroids are undoubtedly related to the nature of the host-plant. The evolution of a complex of response thresholds to proximate environmental cues that control wing-polymorphism has allowed these insects to solve the problems of finding and remaining on their host-plants.

Two very different 'adaptive syndromes' exist in fulgoroids which exploit congeneric species of salt marsh grasses. *P.marginata* produced approximately equal numbers of brachypters and macropters over the course of the year in stands of SAS. The brachypter of this species, while having smaller wings than the macropter, can make short flights. Populations of *D.detecta*, *T.minuta* and *A.simplex* in SP were composed primarily of flightless brachypters.

One possible explanation for the preponderance of macropterous individuals in SA is that increased tidal action, due to low marsh elevation and intensified by the lack of a protective thatch (present in SP), selects for mobile populations of delphacids. This may be true for populations of delphacids in SAT, but SAS occupies an elevational site just centimetres below extensive stands of SP, and, even though the washing action of tides is felt more in SAS habitats, it is unlikely that the tidal stress incurred there is much different from that found in SP. Although it may contribute, it does not seem reasonable to explain the nearly opposite wing-polymorphism syndromes of the respective fulgoroids solely on the basis of a difference in tidal influence between SP and SAS habitats.

SA exists as two dynamically different growth forms; SAT, which has a large standing crop biomass during summer and fall, but is ephemeral, and SAS which is much smaller than SAT, but is available for exploitation throughout much of the year, is subjected to fewer tidal inundations, is a safe overwintering site for nymphs, and is generally a more reliable resource. The optimum resource of *P.marginata* apparently shifts from SAS in the spring, to SAT during summer and then back to SAS in the late fall and winter (Denno, in preparation). Due to the expansiveness of SAS, the two grass forms can be separated by large distances (~100 m), which extend far beyond the effective dispersal range of brachypters. A large mobile component is apparently necessary for the delphacid population to track spatial oscillations in the resource optimum,

which best explains the strong 'commitment' to macroptery by *P.marginata*.

Conversely, on New Jersey salt marshes, SP is structurally a rather uniform grass and consequently has a spatially fixed resource optimum. Also, the presence of a protective thatch and the large stand size of this grass provide elements of resource certainty. Populations of the resident fulgoroids, *D.detecta*, *T.minuta* and *A.simplex*, respond by producing mostly sessile brachypters, which insures the efficient use of the immediate resource and prevents the waste of energy on dispersal. This was particularly true with *T.minuta* and *A.simplex*, where over 99% of the annual adult catch was composed of brachypterous individuals.

Differences in the degree of brachyptery between *P.marginata* and the SP-inhabiting fulgoroids may be attributable to structural characteristics of the host-grasses and accompanying tidal stress. The dense entanglement of living and dead culms of SP acts as an effective transportation network, allowing fulgoroids to walk from one living culm to another without contacting the marsh surface. Although fulgoroids in SP must contend with tidal fluctuations, tidal action is significantly buffered by the dense thatch in which insects may retreat during periods of inundation. Remaining on the host-grass, moving through it, and incurring the tidal fluctuations do not pose insurmountable problems for flightless brachypters.

Reduced interculm contact and the lack of a protective thatch in SAS, which intensifies the action of winds and tides, may explain why brachypters of *P.marginata* maintain restricted flight, which allows them to negotiate the structure of the SAS habitat, and still insures a resident population of adults.

#### Acknowledgments

I am indebted to B. D. Denno for the laborious task of processing samples, to J. P. Kramer (Systematic Entomology Laboratory, IIBII, ARS, USDA, USNM) for determining the various species of Fulgoroidea, to W. H. Swallow for his help with certain statistical aspects of the work, to D. F. Caccamise, E. E. Grissell, A. K. Rust and R. W. Rust for their critical reviews and to J. B. Bellanca for typing the manuscript. This study was supported in part by a grant from the N.J. State Mosquito Control Commission. This is a paper of the journal

series, New Jersey Agric. Exp. Sta., Cook College, Rutgers Univ., New Brunswick, N.J.

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Received 5 April 1976