

THE RELATION BETWEEN HABITAT STABILITY AND
THE MIGRATORY TACTICS OF PLANTHOPPERS

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(HOMOPTERA: DELPHACIDAE)¹

Robert F. Denno²

ABSTRACT

Populations of many planthopper species contain 2 wing-forms. There are flighted, macropterous individuals with fully developed wings and flightless, brachypterous individuals with reduced meso- and vestigial metathoracic wings. The reproductive potential of brachypters is higher than that of macropters, but macropters have the unique ability to escape deteriorating vegetation and colonize new habitats. Thus, brachypters are adaptive in stable (persistent) habitats and macropters in unstable (ephemeral) ones. In low profile, essentially two-dimensional vegetation like grasslands, it is the proportion of stable to unstable habitats in a local area that ultimately dictates the wing-form composition of planthopper populations. However, as resources become three-dimensional (woodlands) the fitness of brachypters decreases because of their inability to relocate host plants if dislodged. Consequently, the planthoppers of three-dimensional vegetation should be mostly macropterous regardless of the stability of the resource.

INTRODUCTION

In a rather classic paper, Southwood (1962) suggests that high levels of migration should be associated with unstable habitats (temporary and/or unpredictable) so that organisms can keep pace with their changing resources. Alternatively, he suggests that reduced amounts of energy should be allocated to migration in stable habitats where resources are more persistent. Southwood et al. (1974) define the stability of a habitat as a relationship between the generation time of the exploiting organism (τ) and the length of time the habitat remains favorable for development (H). Therefore, where $\tau/H \ll 1$ habitats are stable, and where $\tau/H \sim 1$ habitats are unstable.

Some of the families of Auchenorrhyncha (Homoptera), especially the planthoppers (Delphacidae), provide an excellent opportunity to test some of the predictions concerning insect migration and habitat stability because

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²Department of Entomology, University of Maryland, College Park, MD 20742.

they exhibit wing-dimorphism. Populations of many planthoppers contain flighted, macropterous individuals with fully developed meso- and meta-thoracic wings, as well as flightless, brachypterous individuals with reduced meso- and vestigial metathoracic wings. Subsequently, by measuring the proportion of brachypters to macropters in populations, the migration tactics of different species or populations of the same species can be compared among habitats of varying stability.

PREDICTIONS CONCERNING HABITAT STABILITY AND THE WING-FORM COMPOSITION OF POPULATIONS

There are several important differences between brachypters and macropters. Tsai et al. (1964) and Nasu (1969) report that brachypters of *Laodelphax striatella* (Fallen) have a higher fecundity than macropters. May (1971)¹ finds the same trend with *Stenocranus minutus* (Fab.). Kisimoto (1965) and Mochida (1973) find that the preoviposition period of brachypters is shorter than that for the macropters of *Nilaparvata lugens* Stal and *Javesella pellucida* (Fab.) respectively. Thus, the reproductive potential of brachypters can be greater than that of macropters. Also, because of their flightlessness, brachypters are more likely to remain on the immediate resource.

Macropters are capable of long distance (> 600 km, see Kisimoto 1976) and interhabitat (Denno and Grissell 1979) flight. As a result, macropters are capable of escaping deteriorating resources and colonizing new ones. Brachypters and nymphs do not have this capability except over very short (< 5 m) distances (see Raatikainen 1967).

The optimum composition of wing-forms in populations of planthoppers in local habitats can be studied by using fitness sets (Levins 1961, 1962, 1964, 1968; Vepsäläinen 1974, 1978) (Fig. 1). The vegetation upon which planthoppers feed can be rather simplistically divided into 2 phases or states that form the coordinates of the fitness set. Thus, the vegetation in a local environment may be either suitable or not for planthopper development. Unsuitable vegetation may result from either natural or artificial destruction and deterioration. The fitnesses of individuals and populations are pictured in the coordinate system formed by the state of the vegetation in the 2 habitats. Fitness is at 0 at the origin and increases away from it. As long as the vegetation remains suitable for development, brachypters (B) should be more fit than macropters (M) because of their greater reproductive potential and ability to remain on the immediate stand of host plants (Fig. 1). However, as the vegetation deteriorates the fitness point of macropters moves up and to the right because of their ability to escape and colonize more suitable host plants in other habitats (Levin 1968; Vepsäläinen 1974, 1978). Because the 2 resource states

¹MAY, Y.Y. 1971. The biology and population ecology of *Stenocranus minutus* (Fab.) (Delphacidae, Hemiptera). Ph.D. Dissertation, University of London.

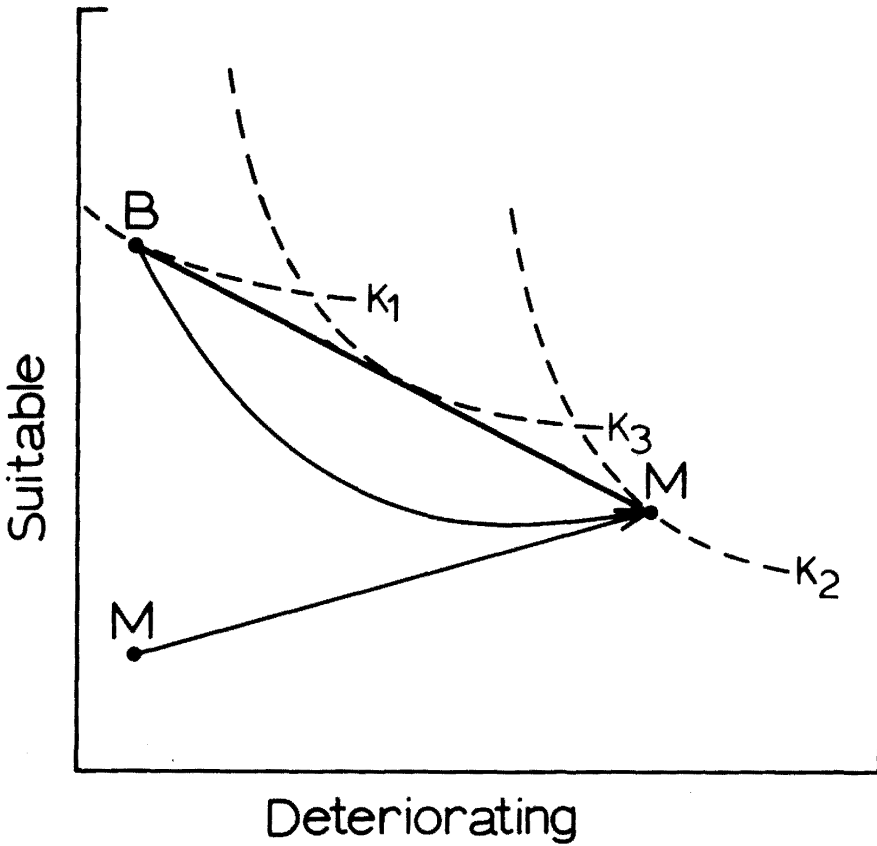


Fig. 1.--The fitness of brachypters (B) and macropters (M) in an environment composed of suitable and deteriorating patches of vegetation. On suitable vegetation, the fitness of brachypters is greater than macropters because of their increased reproductive potential and ability to remain on the immediate resource. On deteriorating vegetation the fitness point of macropters moves up and to the right because of their ability to escape and colonize new resources. The line BM (extended fitness set) describes the average fitness of a population consisting of various proportions of brachypters and macropters. The point of tangency of adaptive functions (K) with the extended fitness set (BM) defines the optimum wing-morph composition of a planthopper population in a particular environment having a certain proportion of suitable and deteriorating habitats. K_1 =where the probability of habitat deterioration is low, the optimum population structure is monomorphic brachyptery. K_2 =where the probability of habitat deterioration is high, the optimum population structure is monomorphic

macroptery. K_3 describes a "harlequin environment" containing both stable and unstable habitats. Here, wing-morphs should occur in proportion to the relative abundance of the habitat to which they are best adapted.

are so different, where a change in vegetation increases the fitness of one wing-form but drastically lowers the fitness of the other, the shape of the set is concave (Levins 1968). The shape of the fitness set merely describes the fitnesses available phenotypes (wing-morphs) in the population under the 2 contingencies, but it does not describe the optimum wing-morph composition of a particular population. To do this, the fitness set must be combined with adaptive functions (K) that measure the fitness of the whole population in the heterogeneous environment (Levins 1962, 1968).

In coarse-grained environments with temporal uncertainty, where the difference between environmental contingencies is large compared to the tolerance of individuals (wing-morphs), the adaptive function is hyperbola-like in shape (Levins 1961). Because selection acts to increase fitness, the available phenotype with the highest fitness of all those in the population will be selected. That phenotype is described by the point on the set tangent to the adaptive function. On a concave fitness set, however, the line BM (extended fitness set) does not define available phenotypes except at either end. The line (BM) does describe the average fitness of a population consisting of various proportions of brachypters (B) and macropters (M). The point of tangency of the adaptive function (K) with the extended fitness set (BM) defines the optimum population composition or mix of long- to short-winged morphs for a particular environment having a certain proportion of stable to unstable patches.

When all patches of vegetation in a local area are stable, the optimum population composition should be brachypterous monomorphism. This situation is pictured in Fig. 1 where the adaptive function K_1 predicts the structure of delphacid populations on vegetation when the probability of destruction or disturbance is low. On the other hand, populations exploiting vegetation where the risk of destruction is high should be composed of mostly macropters (K_2 of Fig. 1). K_3 (Fig. 1) describes the "harlequin environment" of Horn and MacArthur (1972) where there are both unstable and stable patches in a local area. Under these circumstances, wing-morphs should occur in proportion to the relative abundance of the habitat (stable or unstable) to which they are best adapted.

WING-FORM PATTERNS IN PLANTHOPPER POPULATIONS

To test the hypothesis that the brachypterous morph should predominate in environments composed of stable habitats (situation K_1 in Fig. 1), I sampled planthoppers from many different species of tidal and fresh water

marsh vegetation and scored the composition of wing-morphs in populations. Marshes have historically been considered as stable habitats because of the permanency of resources there (Southwood 1962, Brinkhurst 1963, Johnson 1969, Denno 1976). The mean percentage of brachyptera (pooled species and locations in populations of tidal and fresh water marsh planthoppers) was 95.7 ± 6.8 and 98.2 ± 3.5 respectively (Denno 1978).

According to the fitness model (situation K_2 in Fig. 1), the macropterous morph should be adaptive in unstable habitats that are frequently disturbed or destroyed. This prediction is supported by the fact that $70.7 \pm 25.8\%$ of the planthopper populations inhabiting agricultural crops, lawns, managed roadsides, and other unstable habitats with high temporal uncertainty are composed of macropterous forms (Denno 1978).

The most rigorous test of the effect of habitat stability on migration is to look at the wing-morph composition of one species that inhabits a "harlequin" resource with a wide distributional range over which the proportion of stable to unstable habitats changes (situation K_3 in Fig. 1). With this situation, wing-morphs should occur in proportion to the relative abundance of the habitat (stable or not) to which they are adapted. One planthopper, *Prokelisia marginata* (Van Duzee), fits these criteria.

Prokelisia marginata feeds and oviposits exclusively on the adaxial surfaces of the leaf blades of the intertidal perennial grass, *Spartina alterniflora* Loos. (Denno 1977, 1978; Denno and Grissell 1979). At more northerly locations, nymphs of this multivoltine species overwinter under a loose thatch of dead culms associated with the living grass or inside dead, rolled blades. In Florida adults occur and breeding takes place all year.

Spartina alterniflora occurs along the Atlantic Coast from Nova Scotia south to northern Florida and along the Gulf coast from Florida to Texas (Mobberley 1956, Duncan 1974). The plant structure of *S. alterniflora* changes dramatically with marsh elevation, and two growth forms (tall and short) occur at many Atlantic Coast localities (Miller and Egler 1950, Teal 1962, Adams 1963, Blum 1968, Redfield 1972, Squiers and Good 1974, Hatcher and Mann 1975). The vegetation along the banks of tidal creeks that run through the marsh is composed of robust plants with long leaves and stout culms reaching heights well over 2 m (Redfield 1972, Squiers and Good 1974). However, on the high marsh at approximately Mean High Water level where nitrogen is limiting (Valiela and Teal 1974), the plants occur as a dense bed of short rosettes that attain heights of only 10-40 cm (Blum 1968). Many of the salt marshes of the Atlantic Coast are characterized by large expanses of short-form on the high marsh which intergrade into a fringe of tall-form that borders the array of tidal creeks.

The short-form habitat on the high marsh provides food and oviposition sites during the growing season and contains thatch for overwintering. In

contrast, tall-form vegetation along the streambanks offers more food and oviposition space than short form during the growing season, but due to the action of winds, waves and ice, is knocked over and finally sheared off completely during winter, leaving exposed creek banks. Consequently, northern marshes usually contain 2 dynamically different habitats, one stable (short-form) providing requisites all year and the other unstable (tall-form) that is destroyed during winter, but provides more food and oviposition sites in summer (Denno and Grissell 1979). Thus, northern marshes conform to the "harlequin environment" of Horn and MacArthur (1972). Denno and Grissell (1979) have shown that brachypters of *P. marginata* remain in the stable short-form habitat, and macropters (78% of population) effectively colonize the tall-form vegetation in spring and escape it in fall prior to winter destruction. Fall migrators move to short-form habitats where they mix with brachypters, mate, and deposit eggs that hatch to overwintering nymphs.

In Florida (Gulf Coast) the structure of *S. alterniflora* is very uniform. There is very little difference in the height of streamside and high marsh vegetation and there is little destruction of streamside grass during winter. Subsequently, all evidence suggests that there is one rather stable patch (resources available year-round in both streamside and high marsh vegetation). Here, planthopper populations contain mostly brachypters (90%) that are equitably distributed over the marsh (Denno and Grissell 1979).

To determine the proportion of stable to unstable habitats at various locations, I used the coefficient of variation of grass stand height (CVSH) (see Denno and Grissell 1979). Where grass height is uniform and the habitat exists as a single stable patch (Florida Gulf Coast), the CVSH is low. However, where grass height is very tall along creeks and short on the high marsh comprising two habitats, one stable and the other not (many Atlantic Coast locations), the CVSH is high. Therefore, as the proportion of the unstable habitat (tall-form) increases, there should be a commensurate increase in the CVSH.

If it is the proportion of stable to unstable habitats in a local area that ultimately dictates the wing-morph composition of populations (situation K_3 in Fig. 1), then the CVSH should be positively correlated with the proportion of macropters in local populations. Indeed this is the case. There is a significant positive relationship ($r = +0.943$, $p < .01$) between the CVSH of *S. alterniflora* and the % macroptery in local populations of *P. marginata* (Fig. 2).

EXCEPTIONS

There are several reasons why some planthopper species may deviate from the predictions of the fitness set model. First, habitats may be stable ($r/H \ll 1$) and yet offer a spectrum of resources varying in quality. If some patches

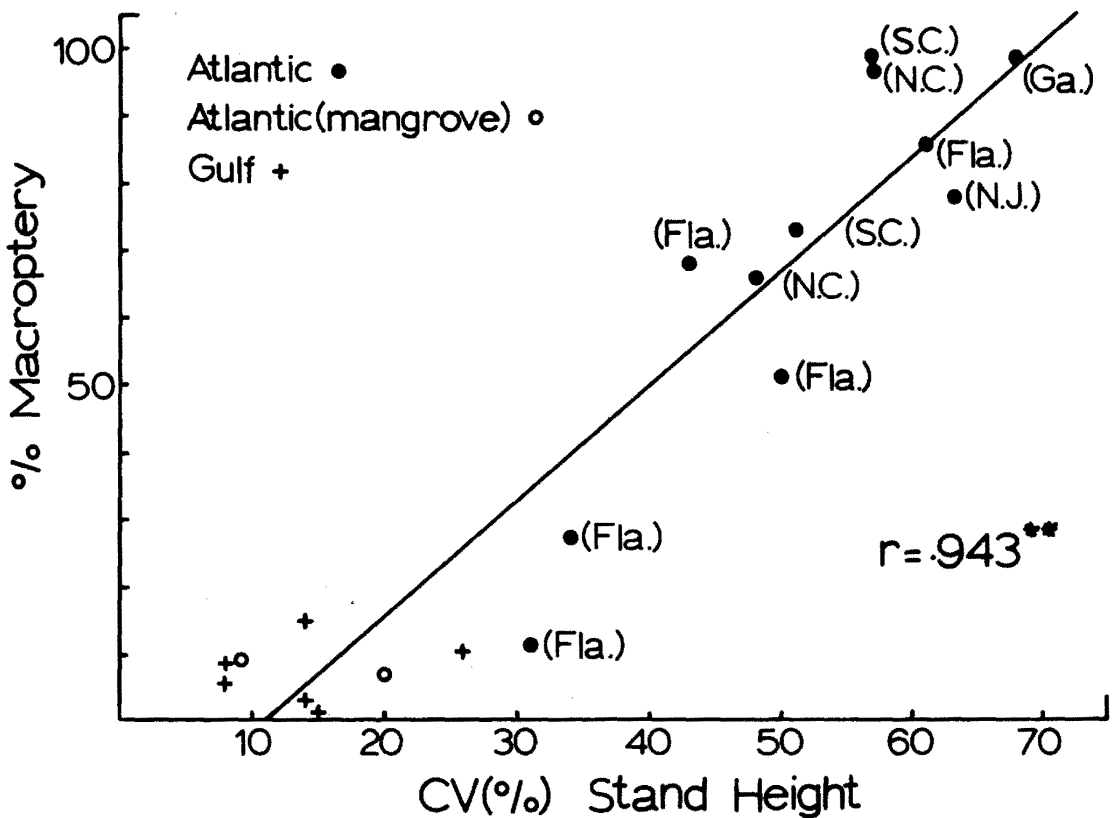


Fig. 2--Relationship between the coefficient of variation in stand height (CVSH) of *Spartina alterniflora* and % macroptery in local populations of *Prokelisia marginata* at various Atlantic and Gulf Coast localities. Locations with a high CVSH contain a higher proportion of unstable habitats than locations with a low CVSH.

are more suitable than others and the size of the patches is large (beyond the effective range of brachypters), then macropters would be adaptive because of their ability to track spatial and temporal oscillations in favorable patches. Consequently, low levels of macroptery may be found in stable habitats. This may explain why Florida (Gulf Coast) populations of *P. marginata* contain 10% macropters and yet occur in very stable habitats.

Also, the model I have presented here is based on planthoppers inhabiting grass and other low profile vegetation (essentially 2-dimensional systems). Planthoppers usually avoid predators by quickly leaping from their holds. In low profile dense vegetation, an escaping planthopper or dislodged one usually lands on or near a suitable host. However, if the host plant was a large tree and the planthopper brachypterous, it may be virtually impossible to relocate suitable resources. For a macropter, relocating the host would be much less energy demanding. Consequently, as resources become 3-dimensional populations of planthoppers should be composed mostly of macropterous individuals, regardless of the stability of the resource.

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