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Author(s): Robert F. Denno, George K. Roderick, Karen L. Olmstead and Hartmut G. Dobel

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DENSITY-RELATED MIGRATION IN PLANTHOPPERS (HOMOPTERA: DELPHACIDAE): THE ROLE OF HABITAT PERSISTENCE

ROBERT F. DENNO, GEORGE K. RODERICK, KAREN L. OLMSTEAD,
AND HARTMUT G. DÖBEL

Department of Entomology, University of Maryland, College Park, Maryland 20742

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Abstract.—We investigated the selective pressures associated with the possession of wings and migration in wing-dimorphic planthoppers (Homoptera: Delphacidae). Both migratory (macropterous) and flightless (brachypterous) forms occur. We found that levels of migration (% macroptery) in field populations decreased significantly as the persistence of their habitats increased. By using phylogenetically independent contrasts between congeners, we obtained the same result, which suggests that habitat persistence has influenced levels of migration independent of common ancestry. Also, there was a clear difference in the density–wing form response between species in temporary and persistent habitats. Macropterous forms were triggered at lower densities for species inhabiting temporary rather than persistent habitats. However, males of species in temporary habitats were macropterous at both low and high rearing densities; macroptery was positively density-dependent in the females of these species and in both sexes of species in persistent habitats. Our results suggest that habitat persistence influences the migratory capability of planthoppers in two ways: (1) by selecting for habitat escape, and (2) by dictating the availability of mates. In persistent habitats wings are less necessary for habitat escape and they are rarely required for mate location. As a consequence and because wings impose a reproductive penalty, flightlessness prevails. For species in temporary habitats, wings are favored in males to locate females at low colonizing densities and are favored in both sexes at high densities for reasons of habitat escape. We conclude that habitat persistence has played a major role in shaping patterns of migration in this group of sap-feeding herbivores.

Migration is essential to the success of insects that exploit temporary habitats; otherwise, local extinctions would lead to their demise (Southwood 1962, 1977; Dingle 1972, 1985; Solbreck 1978; Denno and Grissell 1979; Denno 1983, 1985; Roff 1986*a*, 1986*b*, 1986*c*). Even in persistent environments, dispersal characters such as wings may be retained at low frequencies if adults compete for limited sites (Hamilton and May 1977) or if winged individuals rarely fly (Fairbairn 1986, 1988; Roff 1986*a*, 1990). Migration can have a strong stabilizing influence on population fluctuations and the outcome of species interactions (Reddingius and den Boer 1970; Roff 1974*a*, 1974*b*, 1986*a*; Vance 1980; den Boer 1981; Kuno 1981; Hastings 1982), and it directly determines gene flow and the genetic structure of populations (Taylor et al. 1984; Slatkin 1985; Bull et al. 1987; Coyne and Miltstead 1987). Finally, migration is considered to be as important as reproductive components of fitness by those who study insect life-history strategies (Dingle 1972, 1974, 1985; Solbreck 1978; Denno and Dingle 1981; Denno et al. 1981; Denno 1983, 1985; Roff 1986*a*, 1986*b*; Taylor and Karban 1986; Roderick and Caldwell,

in press). Consequently, those factors that determine the frequency, timing, and success of migration events are generally important in population biology, and of particular interest in the management of highly mobile agricultural pests (Kisimoto 1979; Rabb and Kennedy 1979; Kenmore et al. 1984; Cook and Perfect 1985*a*, 1985*b*; Holt et al. 1987).

Here we investigate how habitat persistence has influenced the migration strategies of planthoppers (Homoptera: Delphacidae), a group of wing-dimorphic, phloem-feeding, herbivorous insects. Wing-dimorphic insects such as planthoppers are ideal organisms for investigating the advantages of wings and the evolution of migration because flightless and dispersive forms are so easily recognized. Brachypterous adults have reduced wings and cannot fly, whereas macropterous adults possess fully developed wings and can disperse long distances (Denno and Roderick 1990). Macropters of some planthopper species migrate from 600 to 1,000 km (Kisimoto 1976; Kuno 1979; Rosenberg and Magor 1983), but most dispersal occurs over shorter distances from 1 to 3 km (Raatikainen 1967; Denno and Grissell 1979; Denno et al. 1980; Perfect and Cook 1987; Riley et al. 1987; Roderick 1987). Even though the macropter is the only form able to fly and partake in the mass migrations observed for many species (Waloff 1973; Kisimoto 1976; Perfect and Cook 1982; Denno 1988; Denno and Roderick 1990), some macropterous individuals do not disperse (Padgham 1983). Macropterous planthoppers cannot histolyse their wing muscles (T. J. Perfect, personal communication) as can other wing-dimorphic insects (Dingle 1985; Roff 1986*a*) and, as a consequence of flightlessness, become "functional brachypters." Field populations of most delphacid planthoppers contain both wing forms, but the proportion of each can vary tremendously among different species (Denno 1976, 1978; Drosopoulos 1977; Denno et al. 1981, 1987), and even within the same species geographically (Raatikainen and Vasarainen 1976; Denno and Grissell 1979; Iwanaga et al. 1987; Roderick 1987; Iwanaga and Tojo 1988), seasonally (Waloff 1973; Cook and Perfect 1985*b*), and sexually (Kisimoto 1965; Denno et al. 1985; Roderick 1987; Denno, in press).

The advantage of flightlessness in female planthoppers is that brachypters are both more fecund and reproduce earlier in life compared to their long-winged counterparts (reviewed by Denno et al. 1989). Roff (1984) and Denno et al. (1989) argue that the reproductive delay and reduced fecundity observed in the macropterous form of many dimorphic insects support the hypothesis that flight capability is costly and that there are phenotypic trade-offs between flight and reproduction. The advantage of brachyptery in males is less clear. Flightless males in some thrips species secure mates more successfully than winged males (Crespi 1986), but flightlessness in male crickets does not confer a paternal advantage over macropters in female choice experiments (Roff and Fairbairn 1991). Delayed gonadal development in macropterous males has been observed only in bruchid beetles (Utida 1972), but this phenomenon has not been reported for planthoppers. In fact, Mochida (1973) found no difference in gonadal development time between the male wing forms of the planthopper *Javesella pellucida*. However, Ichikawa (1982) reports that brachypterous males of *Nilaparvata lugens* are more aggressive and outcompete macropterous males for females when both wing

forms of both sexes are present. Also, brachypterous males of *Prokelisia marginata* survive longer than macropters under laboratory conditions (Roderick 1987). Consequently, brachyptery appears to be advantageous in both sexes of planthoppers as long as conditions remain favorable for development and mates are locally available.

Wing form in planthoppers is determined by a developmental switch that responds to environmental cues (Ammar 1973; Mochida 1973; Mahmud 1980; Kisimoto 1981; Cook and Perfect 1985*b*; Roderick 1987, unpublished data; Denno and Roderick 1990; Roderick and Caldwell, in press). The sensitivity of the switch is heritable and under polygenic control (Ammar 1973; Kisimoto 1981; Iwanaga et al. 1987; see Roff 1986*a* for a review; Roderick 1987; Denno and Roderick 1990). For wing-dimorphic insects in general it is thought that the developmental switch is controlled by the level of a hormone (Lees 1966; Hales 1976; Hardie 1980; Nijhout and Wheeler 1982; Roff 1986*a*, 1986*b*; Zera and Tiebel 1989). Iwanaga and Tojo (1986) provide strong evidence for the involvement of juvenile hormone in the determination of wing form in the brown planthopper, *N. lugens*.

Various environmental cues such as crowding, host plant condition, temperature, and photoperiod are known to trigger the developmental switch and influence wing form (Kisimoto 1956*a*, 1956*b*, 1965; Johno 1963; Mochida 1973; Drosopoulos 1977; Denno et al. 1985; Iwanaga et al. 1985, 1987; Roderick 1987). Depending on the conditions it experiences as a nymph, an individual will molt into either a brachypter or macropter (Kisimoto 1965). Of all the environmental factors known to affect wing form in planthoppers, population density is clearly the most influential for most species (Johno 1963; Kisimoto 1965; Mori and Kiritani 1971; Takagi 1972; Fisk et al. 1981; Cook and Perfect 1985*b*; Denno et al. 1985; Iwanaga and Tojo 1986; Denno and Roderick 1990). In most species, the production of migratory forms (macropters) is density-dependent, is associated with crowded conditions, and is intensified by nutritionally inadequate host plants (Denno et al. 1985, 1986; Denno and Roderick 1990). However, there is extreme variation in the density-wing form response, and one objective of this report is to describe this variation and elucidate causal factors.

The threshold density that triggers the production of macropterous forms differs among species (Denno 1976, 1978; Drosopoulos 1977; Denno et al. 1987), among populations of the same species (Iwanaga et al. 1985, 1987; Iwanaga and Tojo 1988), and even between the sexes of the same species (Kisimoto 1965; Denno et al. 1985; Roderick 1987). For example, macroptery is density-dependent in the females of *N. lugens*, but males remain mostly macropterous even when raised at low densities in isolation (Kisimoto 1956*a*, 1956*b*, 1965). By contrast, macroptery is density-dependent and similar in both sexes of *Muellerianella fairmairei* (Drosopoulos 1977). Variation in the wing-form response suggests that the advantage of possessing wings varies with population density and differs between the sexes for some species.

The production of macropterous forms allows for escape from deteriorating local conditions and colonization of new habitats (Denno and Grissell 1979; Dyck et al. 1979; Cook and Perfect 1985*b*). However, wings also function in mate location (Ichikawa 1977; Denno and Roderick 1990), and therefore density-wing

form relationships probably reflect selective pressures associated with both mating success and migration to new habitats. Only males actively search for stationary females and locate them by using acoustical communication (Ichikawa 1976, 1977; Ichikawa and Ishii 1974; Ichikawa et al. 1975; Claridge 1983, 1985*a*, 1985*b*; de Vrijer 1984, 1986; Claridge et al. 1985*a*, 1985*b*; den Bieman 1987; Heady and Denno 1991). Furthermore, species in temporary habitats face extremely low density conditions following colonization and after one successive generation as well (Kuno 1979). Because the females of most planthopper species mature sexually and mate after long-distance migration and upon arrival in the new habitat (Kanervo et al. 1957; Raatikainen 1967; Kisimoto 1971, 1976; Ohkubo and Kisimoto 1971; Kuno 1979; Chen and Cheng 1980; Noda 1986; Denno, in press; O. Mochida, personal communication; but see Padgham et al. 1987), macroptery in males should facilitate locating virgin females. However, macroptery in females should be disadvantageous at low densities because of reduced fecundity and delayed reproduction (Denno et al. 1989). Thus, factors such as habitat persistence may influence the density-wing form response of the sexes differently because the male response is shaped by additional selective pressures associated with mate location.

Here we test the major hypothesis that habitat persistence determines levels of migration by influencing the availability of resources, including mates. Three predictions follow from this general hypothesis. (1) Generally, a negative relationship should exist between habitat persistence and levels of migration (% macroptery). In persistent habitats with long durational stability, selection should favor flightless forms as a result of their reproductive advantage. In temporary habitats, wings should facilitate the tracking of changing resources. (2) The density-wing form responses of the sexes should differ for species in temporary habitats, but not for taxa in persistent habitats. For species in temporary habitats (migratory species), most males should be macropterous regardless of population density because wings should be advantageous at both low and high densities for reasons concerning mate location and habitat escape. In temporary habitats, males simply cannot count on females being in the new habitat and must retain wings to move among patches in their search of mates. In contrast, macroptery should be density-dependent and triggered at a low threshold density in the females of these dispersive species. For species in persistent habitats (sedentary species), macroptery should be density-dependent in both sexes; males should not require wings to find mates at low densities because the probability of female presence is high, and neither sex should produce winged forms except at the very highest of densities (high threshold density). Less risky alternatives to migration such as diapause (Southwood 1977; Solbreck 1978) become possible in persistent habitats. (3) Last, macroptery (%) should increase in males compared to females as habitat persistence decreases because finding mates becomes more difficult.

We tested these predictions by analyzing dispersal (wing form) and habitat characteristics for 35 species of planthoppers in both temporary (e.g., agricultural crops) and persistent (e.g., most salt-marsh and freshwater marsh vegetation) habitats. To control for possible phylogenetic nonindependence, contrasts (replicated using five genera) were made in which dispersal characters were compared

between congeneric pairs of species, one congener an inhabitant of temporary habitats and the other an inhabitant of persistent habitats (see Felsenstein 1985, 1988; Burt 1989). Additionally, detailed density–wing form responses were examined for seven species, five inhabitants of temporary and two inhabitants of permanent habitats. New data were collected for *P. marginata* and *Prokelisia dolus*, two planthoppers that occur in the intertidal marshes of North America (see Denno et al. 1987). With the data provided in this report we attempt to determine the selective pressures associated with habitat persistence and their influence on the possession of wings and migration.

METHODS

Relationship between Habitat Persistence and Macroptery

Habitat persistence for a particular species depends on the relationship between the generation time of the organism (τ) and the length of time the habitat remains favorable for development (H ; Southwood 1962; Southwood et al. 1974). Persistent habitats are characterized by $H/\tau \gg 1$ and temporary habitats by $H/\tau \approx 1$ (Southwood 1962). We estimated habitat persistence for 35 species (41 populations) of planthoppers by multiplying habitat age (yr) by the maximum number of generations per habitat per year; thus, habitat persistence is expressed as the maximum number of generations attainable during the existence of the habitat. Data on habitat age were extracted from the geological, ecological, and agronomic literature, and information on the number of generations per year was taken from the ecological literature on planthoppers (see table 1).

For a few species of planthoppers, habitat persistence cannot be estimated by habitat age and generational information. Necessary resources may not persist, even though the habitat has existed for years. For example, if host plants deteriorate and nitrogen requirements are specific, some species of planthoppers (e.g., *Javesella pellucida* and *Toya propinqua*) must migrate repeatedly to find suitable host plants (see Raatikainen 1967; Prestidge 1982; Prestidge and McNeill 1982, 1983; Roderick 1987). Similarly, Atlantic and Pacific coast populations of *Prokelisia marginata* also undergo annual interhabitat migrations between persistent overwintering sites on the high marsh and temporary summer development sites on the low marsh (Denno and Grissell 1979; Denno 1983; Roderick 1987; Denno and Roderick 1990). For these species we have estimated habitat age conservatively at 1 yr because there is little evidence that these planthoppers survive in the same local patch (e.g., low marsh habitats for *P. marginata*) for more than a few generations (see Denno et al. 1987; Roderick 1987; table 1).

The relationship between habitat persistence and macroptery (%) in field populations for the 41 populations was determined by using Spearman's rank correlation (SAS 1985). Macroptery data were used only from studies that employed standard sampling techniques (suction samplers, sweep nets [e.g., all Denno and Roderick, and Waloff collections in table 1], or absolute counts [e.g., Kisimoto 1965]) in order to minimize the selective collection of wing forms or sexes. Data for females and males (% macroptery in table 1) were analyzed separately because

TABLE 1

MACROPTERY (%) IN THE MALES AND FEMALES OF PLANTHOPPERS IN FIELD POPULATIONS WITH HOST PLANT, HABITAT, AGE, AND GENERATIONAL DATA

SPECIES	MACROPTERY (%)		n	GENERATIONS (no./habitat/yr)	LOCATION	HOST PLANT	HABITAT	HABITAT AGE (yr)	SOURCES
	♂	♀							
<i>Criomorphus albomarginatus</i>	6*	6*	54	1	England	<i>Holcus</i> sp.	Acidic grassland	75	Waloff 1973; Waloff and Solomon 1973; [V. K. Brown, personal communication]
<i>Delphacodes detecta</i> †	12*	13*	1,869	3	USA(NJ)	<i>Spartina patens</i>	Salt marsh	2,000	Denno collection; Denno 1977; [Redfield 1972]
<i>D. penedetecta</i> †	3*	4*	1,887	3	USA(NJ)	<i>Spartina alterniflora</i>	Salt marsh	2,000	Denno collection; Denno 1977; [Redfield 1972]
<i>D. puella</i> †	74	56	58	3	USA(NJ)	<i>Festuca</i> sp.	Mowed lawn	1‡	Denno collection; [R. F. Denno, personal observation]
<i>D. shermani</i>	10	7	345	3§	USA(MD)	Unknown	Grassy meadow	...	Denno collection
<i>Dicranotropis hamata</i>	1*	2*	328	1	England	<i>Holcus</i> sp.	Acidic grassland	75	Waloff 1973; Waloff and Solomon 1973; [V. K. Brown, personal communication]
<i>Javesella pellucida</i> †	72*	56*	64	2	Netherlands	Polyphagous, grasses	New polder	1‡	Schultz and Meijer 1978; Waloff and Solomon 1973; [Prestidge 1982; Prestidge and McNeill 1982, 1983]
<i>J. pellucida</i> †	80*	72*	2,063	2	England	Polyphagous, grasses	Acidic grassland	1‡	Waloff 1973; Waloff and Solomon 1973; [Prestidge 1982; Prestidge and McNeill 1982, 1983]
<i>J. similima</i> †	0	0	21	1	Canada, Yukon	<i>Eriophorum</i>	Bog, water-course	12,000	Wilson collection; [Kitchie 1987]
<i>Kelisia flava</i>	0	0	34	3	USA(MD)	<i>Scirpus cyperinus</i>	Freshwater marsh	5,000	Denno collection; [Odum et al. 1984]
<i>Keyflana hasta</i>	0	0	22	3	USA(MD)	<i>Juncus roemerianus</i>	Salt marsh	2,000	Denno collection; [Redfield 1972]
<i>Laodelphax elegantulus</i> †	1*	1*	1,502	2	England	<i>Festuca rubra</i>	Acidic grassland	75	Waloff 1973; Waloff and Solomon 1973; [V. K. Brown, personal communication]
<i>L. striatellus</i> †	100§	34§	221	3	Japan	<i>Oryza sativa</i>	Rice paddy	1	Mitsuhashi and Koyama 1974; Tsai et al. 1964; [Kuno 1979]
<i>Megamelus davisi</i>	7	7	73	6	USA(FL)	<i>Nuphar luteum</i>	Freshwater lake	5,000	Denno collection; [Odum et al. 1984]

<i>M. lobatus</i>	3*	3*	224	3	USA(NJ)	<i>S. patens</i>	Salt marsh	2,000	Denno collection; Denno 1977; [Redfield 1972]
<i>M. nr lobatus</i>	1*	1*	469	3	USA(NJ)	<i>S. alterniflora</i>	Salt marsh	2,000	Denno collection; Denno 1977; [Redfield 1972]
<i>M. paleatus</i>	0	0	35	6	USA(FL)	<i>Pontederia cordata</i>	Freshwater lake	5,000	Denno collection; [Odum et al. 1984]
<i>M. trifidus</i>	0	0	20	6	USA(FL)	<i>J. roemerianus</i>	Salt marsh	3,000	Denno collection; [Nixon 1982]
<i>Muellerianella brevipennis</i>	1*	2*	512	2	Netherlands	<i>Deschampsia caespitosa</i>	Forest edge	12+	[Drosopoulos 1977]
<i>M. fairmairei</i>	8*	10*	6,266	2	Netherlands	<i>Holcus</i> sp.	Grassy field	12+	[Drosopoulos 1977]
<i>Mutrodelphax exiguus</i>	0*	0*	1,320	2	England	<i>F. rubra</i>	Acidic grassland	75	Waloff 1973; Waloff and Solomon 1973; [V. K. Brown, personal communication]
<i>Neomegamelanus dorsalis</i>	0	0	41	3	USA(FL)	<i>S. patens</i>	Salt marsh	2,000	Denno collection; Denno 1977; [Redfield 1972]
<i>N. penillanatus</i>	1	1	220	...	USA(FL)	<i>Spartina sparinae</i>	Sandy flat	...	Denno collection
<i>Nilaparvata lugens</i> †	89*	12*	934	3	Japan	<i>O. sativa</i>	Rice paddy	1	Kisimoto 1965; [Kuno 1979]
<i>N. lugens</i> †	69*	50*	245	3	Philippines	<i>O. sativa</i>	Rice paddy	1	Cook and Perfect 1982, 1985b; [Dyck et al. 1979]
<i>N. muiri</i> †	<10	<10	...	3	Japan	<i>Leersia oryzoides</i>	Wet meadow	>10	[Kisimoto 1981]; M. Claridge, personal communication
<i>Numata muiri</i>	20*	15*	621	6	Mauritius	<i>Saccharum officinarum</i>	Cane field	1	Williams 1957; Fennah 1969; [O. Sosa, personal communication]
<i>Paralburnia dalei</i>	0*	0*	1,078	2	England	<i>Agrostis tenuis</i>	Acidic grassland	75	Waloff 1973; Waloff and Solomon 1973; [V. K. Brown, personal communication]
<i>Peregrinus maidis</i>	67*	67*	...	3	USA(HI)	<i>Zea mays, sorghum</i>	Cornfield	1	Napompeh 1973; Fisk et al. 1981; [Fullaway 1918]
<i>Perkinsiella saccharicida</i>	91	16	191	6	Australia	<i>S. officinarum</i>	Cane field	1	Osborne 1969; Fennah 1969; [O. Sosa, personal communication]
<i>P. saccharicida</i>	94*	68*	1,249	6	Mauritius	<i>S. officinarum</i>	Cane field	1	Williams 1957; Fennah 1969; [O. Sosa, personal communication]
<i>Pissonotus piceus</i>	13*	7*	324	2	USA(MO)	<i>Polygonum</i>	Lake edge	104	Wilson collection; [S. Wilson, personal communication]
<i>P. quadripustulatus</i>	0	0	47	6	USA(FL)	<i>Borrchia frutescens</i>	Salt marsh	3,000	Denno collection; [Nixon 1982]
<i>Prokelisia crocea</i>	100*	98*	176	3	USA(MO)	<i>Spartina pectinata</i>	Prairie/roadside	...	Wilson collection; [S. Wilson, personal communication]
<i>P. dolus</i> †	30*	31*	1,521	3	USA(NJ)	<i>S. alterniflora</i>	Salt marsh	2,000	Denno collection; Denno et al. 1987; [Redfield 1972]
<i>P. dolus</i> †	0	4	228	6	Mexico	<i>S. alterniflora</i>	Mangrove	3,000	Denno collection; [Nixon 1982]

TABLE 1 (Continued)

SPECIES	MACROPTERY (%)			GENERATIONS (no./habitat/yr)	LOCATION	HOST PLANT	HABITAT	HABITAT AGE (yr)	SOURCES
	♂	♀	n						
<i>P. dolus</i> †	0	0	36	3	USA(CA)	<i>Spartina foliosa</i>	Salt marsh	110	Denno collection; [Zedler 1982]
<i>P. marginata</i> †	93*	69*	2,065	3	USA(NJ)	<i>S. alterniflora</i>	Salt marsh	1‡	Denno collection; Denno et al. 1987; [Denno and Gris-sell 1979]
<i>P. marginata</i> †	72*	50*	2,960	3	USA(CA)	<i>S. foliosa</i>	Salt marsh	1‡	Roderick collection; [Roder- ick 1987]
<i>Ribautodelphax angulosus</i>	0*	1*	209	2	England	<i>F. rubra</i>	Acidic grassland	75	Waloff 1973; Waloff and Sol- omon 1973; [V. K. Brown, personal communication]
<i>Sogatella furcifera</i>	100*	80*	144	3	Philippines	<i>O. sativa</i>	Rice paddy	1	Cook and Perfect 1982, 1985b; [Dyck et al. 1979]
<i>Togasodes orizicolus</i>	100	50§	...	3	Mexico	<i>O. sativa</i>	Rice field	1	Elias et al. 1962; [Everett 1969; King and Saunders 1984]
<i>Toya propinqua</i>	71*	65*	1,020	3	USA(CA)	<i>Distichlis spicata</i>	Salt marsh	1‡	Roderick collection; [Roder- ick 1987]
<i>T. propinqua</i>	15	17	44	...	USA(FL)	<i>D. spicata</i>	Salt marsh	...	Denno collection
<i>Tumidigena minuta</i>	1*	1*	2,759	2	USA(NJ)	<i>S. patens</i>	Salt marsh	2,000	Denno collection; Denno 1977; [Redfield 1972]

NOTE.—Sources enclosed in brackets include information on habitat age.

* Mean of several generations and/or yr.

† Species included in congeneric contrasts (see text).

‡ Indicates habitat age relative to planthopper tenure; evidence exists for annual interhabitat migration despite longer persistence of the habitat.

§ Laboratory data, but pattern confirmed by qualitative observations in the field.

|| Estimated from other sympatric species (see Denno et al. 1987).

we hypothesized that the wing form of males is influenced by other factors (mate finding) in addition to habitat persistence.

Wing-Form Response to Density: Interspecific Variation

We investigated interspecific variation in the density–wing form response for planthoppers occurring in temporary and persistent habitats in two ways. First, we surveyed the literature and found detailed density–wing form information for four planthopper species inhabiting temporary agricultural habitats (*J. pellucida* [Mochida 1973], *Laodelphax striatellus* [Kisimoto 1956a], *Nilaparvata lugens* [Kisimoto 1956a, 1965], and *Sogatella furcifera* [Kisimoto 1956a]) and one species occurring in more persistent grasslands (*Muellerianella fairmairei* [Drosopoulos 1977]). Second, we conducted experiments in the laboratory to determine the density–wing form patterns for *P. marginata*, a colonist of temporary salt-marsh habitats along the Atlantic coast of North America (Denno and Grissell 1979; Denno 1983, 1985; Denno et al. 1985, 1986, 1987), and *Prokelisia dolus*, an inhabitant of persistent habitats in the same geographic area (Denno et al. 1986, 1987).

The effect of nymphal crowding on the wing form of *P. marginata* and *P. dolus* was determined by raising nymphs in pure cultures at several different densities in the laboratory. Nymphs were caged over potted seedlings of *Spartina alterniflora* and raised to adults (see Denno et al. 1985, 1986 for details on *Spartina* culture and plastic tube-cage design). Different densities of nymphs were obtained by placing three females and three males (randomly selected) in each tube cage and allowing females to oviposit for varying periods of time. By allowing females to oviposit for 3, 7, and 14 d before removal, a spectrum of density conditions ranging from 1 to >100 nymphs/cage was achieved. This procedure is justified because, in *Prokelisia*, there is no tendency for early- or late-deposited eggs to molt into a particular wing form (G. K. Roderick, unpublished data). Eighteen replicates were set up at each of the three oviposition categories resulting in 54 cages for each species. All emerging nymphs were raised to adults and wing form was determined. Adult planthoppers for this experiment were field-collected at Tuckerton, Ocean County, New Jersey, on June 26, 1986. The relationship between planthopper density (no. individuals/cage) and macroptery (%) was determined for the sexes of both species using nonlinear least-squares regressions. Cumulative frequency distributions of macroptery (%) were compared between sexes and species by Kolmogorov-Smirnov two-sample tests (SAS 1985).

Wing-Form Response to Density: Intraspecific Variation

The density–wing form response was compared between Atlantic (New Jersey, where habitats are temporary) and Gulf coast (Florida, where habitats are persistent) populations of *P. marginata*. Along the Gulf coast, populations of *P. marginata* are composed on average of 10% macropters, a situation very different from the 80% macroptery observed along most of the Atlantic coast (Denno and Grissell 1979; McCoy and Rey 1981; Wilson 1982; Denno 1983, 1985; Strong and Stiling 1983).

Plants containing eggs from Cedar Key, Levy County, Florida, and Tuckerton,

New Jersey, were transplanted into pots on May 31 and July 20, 1987, respectively. First instar nymphs hatching from these eggs were used to establish three density treatments (3, 10, and 40 nymphs/tube-cage) on *Spartina* seedlings as before. Each treatment was replicated 15 times. Staggered plantings were used so that nymphs from the two populations were raised on plants of similar age. As adults emerged, their wing forms were determined. Caged seedlings from all experiments were maintained at $24^{\circ} \pm 2^{\circ}\text{C}$ in a 14L:10D cycle. Differences between the sexes and populations in wing-form response to density were evaluated by ANOVA (SAS 1985).

Because the eggs used in this experiment were taken from a largely macropterous population in New Jersey and a primarily brachypterous population in Florida, it could be argued that maternal wing form (a nonadditive genetic effect) contributes to any population difference in offspring wing form. However, for *J. pellucida* and *N. lugens* there is no clear relationship between the wing form of parents and offspring (Kisimoto 1965; Raatikainen 1967). Also, by using mid-parent/offspring regression, Roderick (1987) found no significant relationship between maternal and offspring wing form within a population of *P. marginata*.

Sexual Differences in Wing-Form Composition in the Field

From the literature we extracted wing-form information (% macroptery) for both sexes of 35 species (41 populations) of planthoppers (see table 1). The relationship between sexual bias in macroptery (macroptery [% + 1] in males/macroptery [% + 1] in females) and habitat persistence (maximum number of generations attainable) was evaluated by using Spearman's rank correlation.

Phylogenetic Independence

Related species might not be independent observations (see Harvey and Mace 1982; Felsenstein 1985; Burt 1989) because there exists the possibility that species share both habitat type and wing-morph composition as a result of common ancestry and not because natural selection acted similarly and independently on each species (anonymous reviewer). Phylogeny may thus confound the effect of habitat persistence on (1) levels of macroptery (%) and (2) any bias in macroptery toward males. To address this problem, a phylogeny can be used to identify which species contrasts are independent (Felsenstein 1985, 1988; Burt 1989; Wanntorp et al. 1990). However, a phylogeny for the Delphacidae is available only at the tribal level (Asche 1985) and most of the species we examined are in one tribe, the Delphacini. Alternatively, we followed a method suggested by Felsenstein (1985, 1988) and Burt (1989) that extracts "phylogenetically independent contrasts" from the Linnean classification. The method relies on comparisons between "pairs of nearest relatives" (Felsenstein 1988; Burt 1989). If "two duck species are sister species, and so are two goose species, the difference in phenotype between the two ducks should be statistically independent of the difference between the two geese. This is expected because the evolutionary events within the duck lineage are distinct from, and independent of, those in the goose lineage" (Felsenstein 1988, p. 456). To this end, we selected all available planthopper

genera that contained at least one species inhabiting a persistent habitat (≥ 20 complete generations possible) and at least one species inhabiting a temporary habitat (≤ 10 generations possible). We defined persistent and temporary habitats in this way (≥ 20 and ≤ 10 possible generations, respectively) because there is a gap in the data at this point and to avoid borderline cases (see table 1). Any difference in macroptery between members of each congeneric pair must have evolved independently of those in other such congeneric pairs except in the unlikely event that the genera are polyphyletic. Five genera met our criterion: *Delphacodes*, *Javesella*, *Laodelphax*, *Nilaparvata*, and *Prokelisia* (species used in congeneric contrasts are marked with a † in table 1). Because the genus *Delphacodes* contained two species in the persistent habitat category (see table 1), all possible combinations of *Delphacodes* species were contrasted resulting in two separate congeneric analyses. When data were available for more than one population of the same species in the same habitat persistence category (e.g., *P. dolus*), we averaged macroptery values across populations. Habitat means for overall levels of macroptery (arcsine-transformed %) and male bias in macroptery (macroptery [% + 1] in male/macroptery [% + 1] in female) were compared by using paired *t*-tests (SAS 1985). A significant effect of habitat on macroptery would be independent of phylogeny for the subset of species used in this analysis.

Further, phylogeny may contribute to the overall (all species in table 1 considered) relationship between habitat persistence and macroptery if the genera found within one habitat category were related. If there were a phylogenetic contribution to the overall relationship, one would expect the effect of habitat on macroptery in the total species analysis to differ from that seen when only contrasts between congeners were used. To test for such a phylogenetic contribution, we compared habitat means (temporary and persistent) for macroptery (%) and male bias in macroptery obtained from the congeneric contrasts (species with a † in table 1) with habitat means based on all remaining taxa among which no control for phylogeny was possible (species not marked with a † in table 1). A significant difference (*t*-tests) would suggest a measurable contribution of phylogeny to wing-form patterns of species in temporary and persistent habitats.

One genus that we analyzed contained two species for which all individuals sampled were brachypterous (*Megamelus paleatus* and *Megamelus trifidus*). As an anonymous reviewer pointed out, once wings are lost, regaining them may not be possible. Consequently, speciation events involving flightless taxa may result in flightless lineages regardless of habitat persistence. Thus, one might consider pooling monomorphically brachypterous congeners for any analysis of the effect of habitat on dispersal characters. In fact, macropters are known to occur for these *Megamelus* species (Beamer 1955) and for several other species that we report as entirely brachypterous (Waloff 1973; Denno 1978; R. F. Denno and G. K. Roderick, unpublished data; table 1); macropters are simply too rare to appear in most samples. There are few examples of unambiguous monomorphism in our data set, and for sampling reasons it is most parsimonious to interpret 0% macroptery as "near 0%." For this reason, we chose not to pool monomorphic congeners for analysis.

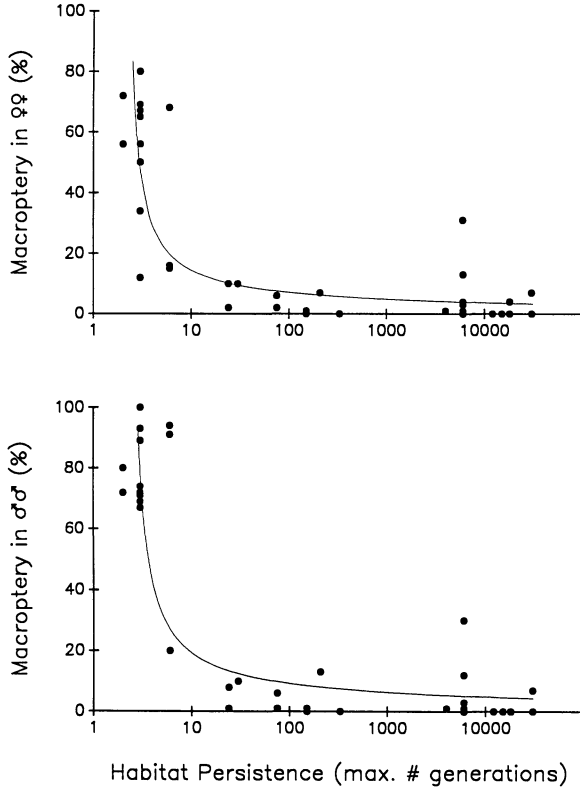


FIG. 1.—Relationship between macroptery (%) in the field and habitat persistence (the maximum number of generations attainable) for the females (*top*) and males (*bottom*) for 35 species (41 populations) of planthoppers. Habitat persistence was estimated by multiplying habitat age (yr) by the number of generations attainable per habitat per yr for each species. Some overlapping points occur (see table 1). Fitted curves are of the form $y = a + 1/(x^b + c)$, where y = macroptery (%); x = log habitat persistence; and for males $a = -5.450$, $b = 0.039$, $c = -0.960$; and for females $a = -4.812$, $b = 0.045$, $c = -0.948$.

RESULTS

Relationship between Habitat Persistence and Macroptery

There was a significant negative relationship between habitat persistence and macroptery (%) in both female ($r_s = -0.78$, $P < .001$) and male planthoppers ($r_s = -.79$, $P < .001$; fig. 1). The highest levels of macroptery (50% or greater in both sexes) were recorded for species inhabiting ephemeral agricultural crops (e.g., *Nilaparvata lugens*) or natural habitats (e.g., *Prokelisia marginata*) that persist in the field for less than 1 yr (see table 1). The lowest levels of macroptery ($\leq 1\%$ in both sexes) occurred in species associated with persistent habitats such as bogs (e.g., *Javesella simillima*), freshwater marshes (e.g., *Megamelus paleatus*), and salt marshes (e.g., *Tumidagena minuta*) that have existed in North America for 2,000–12,000 yr (see table 1). Nevertheless, levels of macroptery

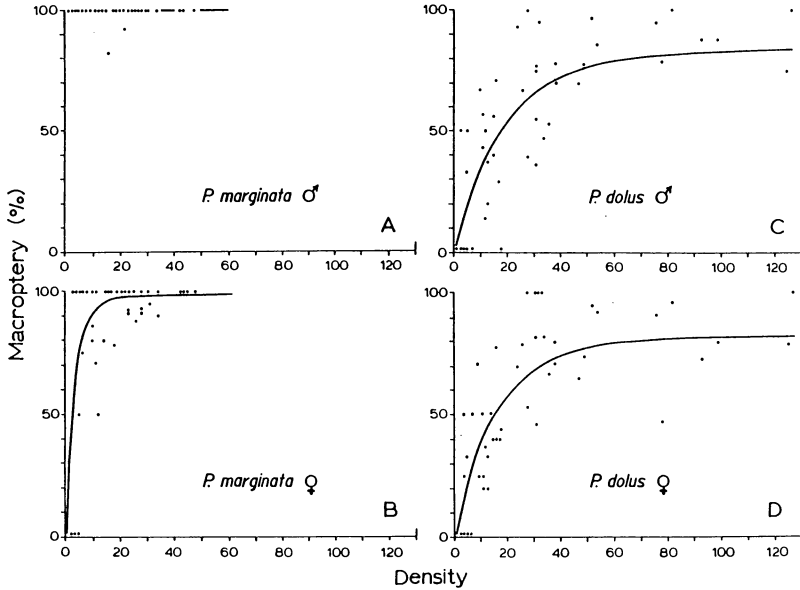


FIG. 2.—Wing-form responses (% macroptery) to rearing density (no. planthoppers/cage) of the males (A) and females (B) of *Prokelisia marginata* and the males (C) and females (D) of *Prokelisia dolus*. *Prokelisia marginata* exploits temporary habitats, whereas *P. dolus* occurs in persistent habitats in this Tuckerton, N.J., location.

were similarly very low ($\leq 3\%$ in both sexes) in several species (e.g., *Dicrano-tropis hamata*) inhabiting much less persistent (75 yr) acidic grasslands in England (see table 1). With an increase in habitat persistence there was an abrupt decrease in macroptery (%); habitats that provided the opportunity for at least 10 successive generations of planthoppers showed no higher levels of macroptery than habitats 1,000 times more persistent (fig. 1).

Wing-Form Response to Density: Interspecific Variation

Prokelisia marginata (from temporary habitats in N.J.) differed dramatically from *Prokelisia dolus* (from persistent habitats in N.J.) in its wing-form response to density. Most males of *P. marginata* emerged macropterous regardless of rearing density (fig. 2A), and the few brachypterous males that did emerge did so at an intermediate density of about 20 planthoppers per cage. Macroptery was density-dependent in the females of *P. marginata* (fig. 2B) and differed significantly from the male response ($n_1 = 54$, $n_2 = 54$; $D = 0.33$, $P < .01$). By contrast, macroptery was density-dependent in both the males (fig. 2C) and the females (fig. 2D) of *P. dolus*, and the responses did not differ significantly ($n_1 = 48$, $n_2 = 51$; $D = 0.07$, $P > .05$).

The threshold density that triggered the production of macropters was much lower for *P. marginata* than *P. dolus*, resulting in higher maximum levels of macroptery for *P. marginata*. For example, it took a density of only five planthoppers per cage to trigger 75% of *P. marginata* females to molt into macropters

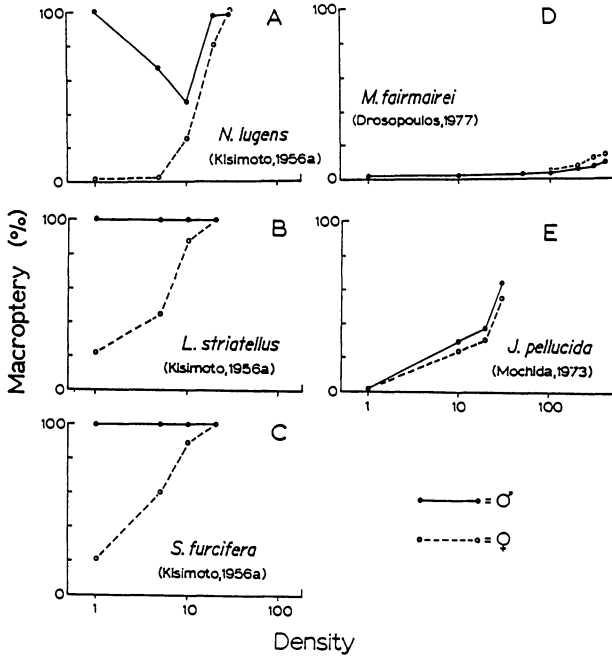


FIG. 3.—Wing-form responses (% macroptery) to rearing density (no. planthoppers/cage) of the males and females of *Nilaparvata lugens* (A), *Laodelphax striatellus* (B), *Sogatella furcifera* (C), *Muellerianella fairmairei* (D), and *Javesella pellucida* (E). All species are migratory and occur in temporary habitats except *M. fairmairei*, which resides in more persistent grasslands. Data from A–C, D, and E were extracted from Kisimoto (1956a), Drosopoulos (1977), and Mochida (1973), respectively.

(fig. 2B). For *P. dolus* females, 75% macroptery resulted at a density of 50 planthoppers per cage (fig. 2D). The wing-form responses of the females ($n_1 = 54$, $n_2 = 51$; $D = 0.64$, $P < .01$) and males ($n_1 = 54$, $n_2 = 48$; $D = 0.90$, $P < .01$) of *P. marginata* and *P. dolus* were highly significantly different. Thus, migratory forms are produced in *P. marginata* at a density about one order of magnitude lower than for *P. dolus*.

The density–wing form responses for three other migratory planthoppers that occur in temporary habitats, *N. lugens*, *Laodelphax striatellus*, and *Sogatella furcifera*, were similar to that for *P. marginata* and exhibited the following three characteristics (see fig. 3A,B,C). First, the wing-form responses of the sexes were very different. Males were usually macropterous across all rearing densities, even when raised in isolation, and macroptery was density-dependent in females. Second, if brachypterous males were produced, as was the case for *N. lugens* (fig. 3A), they appeared at intermediate levels of crowding. Third, the density threshold that triggered the macropterous form in females was low (between 20 and 30 planthoppers per cage resulted in 100% macroptery). Rearing conditions were the same for *N. lugens*, *L. striatellus*, and *S. furcifera* and very similar to ours for

Prokelisia, justifying interspecific comparisons of macroptery (%) across the density categories (see Kisimoto 1956a; Denno et al. 1985, 1986).

Muellerianella fairmairei, an inhabitant of more persistent habitats, exhibited a wing-form response similar to that for *P. dolus* (cf. fig. 3D with fig. 2C and D). Macroptery (%) was density-dependent and the response was the same for both sexes. Furthermore, the threshold density that triggered the production of migratory forms was very high. At a density of 400 planthoppers per cage, less than 20% macropterous forms were produced. Again, rearing conditions (planthoppers caged on a single seedling of host plant; see Drosopoulos 1977) were similar to ours and those of Kisimoto (1956a), allowing for rough comparisons among species.

Javesella pellucida appeared exceptional in that macroptery was density-dependent and the same in both sexes (Mochida 1973, fig. 3E), a wing-form response characteristic of *P. dolus* and *M. fairmairei*, two species in persistent habitats. However, results from another study (Ammar 1973) involving different lines of *J. pellucida* are consistent with the density-related pattern of macroptery characteristic of other species in temporary habitats. Most males from one line were macropterous (87%) regardless of rearing density and macroptery in females was density-dependent, increasing from 44% to 58% over the same range of densities (Ammar 1973). Like other species that occur in temporary habitats (cf. fig. 3E with fig. 3A–C), *J. pellucida* is migratory (Nuorteva 1962; Raatikainen 1967; Waloff 1973; Raatikainen and Vasarainen 1976) and produces macropterous forms at relatively low levels of crowding (Ammar 1973; Mochida 1973).

Wing-Form Response to Density: Intraspecific Variation

Perhaps the strongest evidence for a difference in wing-form response to density between planthoppers in ephemeral and persistent habitats comes from a comparison between two geographically separated populations of *P. marginata*. In the migratory New Jersey population that occurs in temporary habitats, males emerged macropterous across all rearing densities, but macroptery (%) was density-dependent in females (fig. 4A). The significant “density by sex” interaction term in ANOVA table 2A documents this difference in wing-form response between the sexes. By contrast, in the sedentary Florida population, macroptery (%) was density-dependent in both sexes (fig. 4B), and the responses were the same (there was not a significant density by sex or sex effect in the ANOVA; see table 2B).

A comparison of the two populations also reveals a difference in the threshold density whereby macropterous forms are produced. In the migratory New Jersey population, a rearing density of 10 nymphs per cage resulted in nearly 100% macroptery in both sexes. A rearing density of 10 triggered only 40% of adults to molt into macropters in the Florida population (cf. fig. 4A with 4B).

Sexual Differences in Wing-Form Composition in the Field

There was a significant negative relationship between the ratio of macroptery (% + 1) in males to macroptery (% + 1) in females and habitat persistence

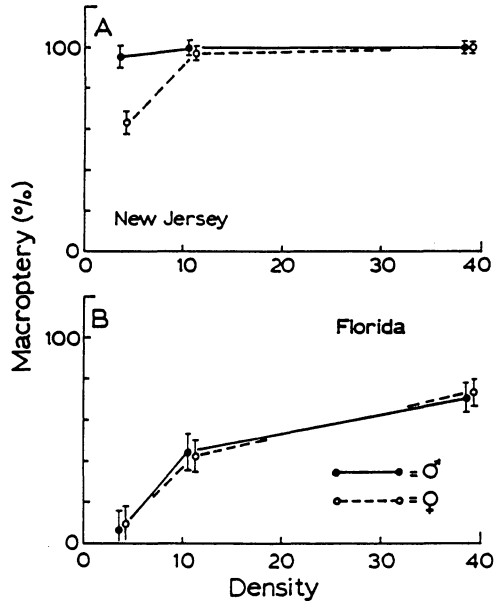


FIG. 4.—Wing-form responses (% macroptery) to rearing density (no. planthoppers/cage) of the males and females of *Prokelisia marginata* from a migratory population associated with temporary habitats in Tuckerton, N.J. (A) and from a sedentary population associated with persistent habitats at Cedar Key, Fla. (B). Means \pm 1 SE are plotted.

(maximum number of generations; $r_s = -0.60$, $P < .001$; fig. 5). On average, males were 2.5 times as macropterous as females of species inhabiting the most temporary habitats, while macroptery was similar between the sexes (ratio \approx 1.0) for species occurring in the most persistent habitats. These data suggest that males are more macropterous than females in field populations of species that occur in temporary habitats, but not in species that reside in persistent habitats.

Phylogenetic Independence

Macroptery was significantly greater for species (both sexes) inhabiting temporary habitats than for their congeners occurring in persistent habitats (table 3). Also, macroptery was significantly male biased for species in temporary habitats relative to their congeners in persistent habitats (table 3). These data suggest that patterns of macroptery in temporary and persistent habitats have evolved to a large extent independent of ancestry. Furthermore, habitat means for macroptery (%) and male bias in macroptery for the species used in congeneric contrasts did not differ from the overall means based on all species (less those used in congeneric contrasts). This result, coupled with the known evolutionary lability of the wing-form response to density among populations of conspecific planthoppers (Iwanaga et al. 1987; Roderick 1987; Denno and Roderick 1990), suggests that to a reasonable approximation, individual species can be regarded as evolutionarily independent indicators of selective influences on wing form.

TABLE 2

ANOVA FOR THE WING-FORM COMPOSITION (MACROPTERY, ARCSINE-TRANSFORMED %) OF *PROKELISIA MARGINATA* FROM A TEMPORARY HABITAT (TUCKERTON, N.J.) AND A PERSISTENT HABITAT (CEDAR KEY, FLA.) WHEN RAISED AT THREE DENSITIES (3, 10, 30 NYMPHS/CAGE) ON SEEDLINGS OF *SPARTINA ALTERNIFLORA*

Source	df	SS	F	P
A. Temporary habitat:				
Density	2	1.903	13.75	.0001
Sex	1	.768	34.44	.0001
Density × sex	2	.888	6.42	.0031
Replicate (cage)	55	3.808	3.10	.0001
Error	332	7.409		
B. Persistent habitat:				
Density	2	20.424	30.46	.0001
Sex	1	.007	.04	.8348
Density × sex	2	.036	.06	.9465
Replicate (cage)	60	20.114	1.95	.0001
Error	429	73.653		

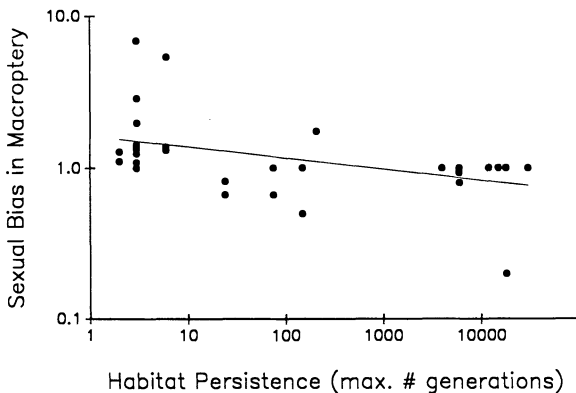


FIG. 5.—Relationship between sexual bias in macroptery (macroptery [% + 1] in males/macroptery [% + 1] in females) and habitat persistence (maximum number of possible generations) for 35 species (41 populations) of planthoppers ($r_s = -0.60$, $P < .001$). On average, males were 2.5 times as macropterous as females of species inhabiting the most temporary habitats, while macroptery was similar between the sexes (ratio ≈ 1.0) for species occurring in the most persistent habitats. Data are from the field and are plotted for all species and populations listed in table 1 for which habitat persistence information was available.

DISCUSSION

Habitat persistence has been identified as a critical factor in the evolution of migration and wing dimorphism in insects (Southwood 1962, 1977; Southwood et al. 1974; Jarvinen and Vepsäläinen 1976; Denno 1978, 1979; Harrison 1980; Brown 1986; Roff 1986*b*, 1990; Denno and Roderick 1990, 1991). However, quantitative data on the age of many insect habitats are often unavailable, making a rigorous assessment of the relationship between habitat persistence and levels of migration

TABLE 3

COMPARISON OF MACROPTERY (MEAN % \pm SE FOR MALES AND FEMALES) AND SEXUAL BIAS IN MACROPTERY (MACROPTERY [% + 1] IN MALE/MACROPTERY [% + 1] IN FEMALE) AMONG PLANTHOPPER SPECIES INHABITING TEMPORARY AND PERSISTENT HABITATS

	CONGENERIC CONTRAST	ALL OTHER SPECIES	<i>t</i> STATISTICS	
			<i>t</i>	<i>P</i>
Macroptery in males (%):				
Temporary	82.3 \pm 4.6	75.1 \pm 12.5	.17	NS
Persistent _(Dd)	6.4 \pm 2.5	2.3 \pm 0.8	1.82	NS
Persistent _(Dp)	4.6 \pm 2.1	2.3 \pm 0.8	1.32	NS
<i>t</i> Statistics	<i>t</i> _(Dd) = 6.84, <i>P</i> < .002			
	<i>t</i> _(Dp) = 7.89, <i>P</i> < .001			
Macroptery in females (%):				
Temporary	48.9 \pm 6.8	53.2 \pm 9.4	.33	NS
Persistent _(Dd)	6.9 \pm 2.7	2.2 \pm 0.7	1.93	NS
Persistent _(Dp)	5.1 \pm 2.3	2.2 \pm 0.7	1.45	NS
<i>t</i> Statistics	<i>t</i> _(Dd) = 5.25, <i>P</i> < .006			
	<i>t</i> _(Dp) = 5.59, <i>P</i> < .005			
Bias in macroptery:				
Temporary	1.85 \pm 0.35	1.47 \pm 0.20	1.00	NS
Persistent _(Dd)	.96 \pm 0.03	.97 \pm 0.06	.07	NS
Persistent _(Dp)	.93 \pm 0.04	.97 \pm 0.06	.29	NS
<i>t</i> Statistics	<i>t</i> _(Dd) = 2.67, <i>P</i> < .050			
	<i>t</i> _(Dp) = 2.81, <i>P</i> < .048			

NOTE.—Habitat means were calculated in two ways: (1) by using congeneric pairs of species from *Delphacodes*, *Javesella*, *Laodelphax*, *Nilaparvata*, and *Prokelisia*, one species of which occurred in each of the two habitat types ($n_{\text{temporary}} = 5$, $n_{\text{persistent}} = 5$; see species with † in table 1), and (2) by using all other species not contained in the five genera above ($n_{\text{temporary}} = 6$, $n_{\text{persistent}} = 18$). Habitat means based on congeners were compared by using paired *t*-tests (statistics in columns). Because two species of *Delphacodes* occurred in the persistent habitat category (*D. detecta* [Dd] and *D. penedetcta* [Dp]), the analysis was repeated using each *Delphacodes* species combination. Habitat means based on congeners were compared with those based on all other species by using *t*-tests (statistics at end of rows). Macroptery (%) data were arcsine-transformed prior to analysis.

difficult. We were able to obtain age data on the habitats of 35 species of planthoppers, and there was a highly significant negative relationship between habitat persistence and the level of migration (% macroptery in both sexes; fig. 1). Furthermore, by using replicated phylogenetically independent contrasts between congeners, we obtained the same result, thus suggesting that habitat persistence has influenced levels of migration independent of common ancestry. That migratory and sedentary populations of the same species occur (e.g., *Prokelisia marginata* [this article] and *Nilaparvata lugens* [Iwanaga et al. 1987]) casts further doubt on the constraining effects of phylogeny on dispersal characters in planthoppers.

In our data set, most of the very temporary habitats (those that persisted 1 yr or less) were agricultural crops (see table 1). One might question whether the high levels of macroptery in planthopper species associated with ephemeral crops are the result of long-term adaptation to the current host habitat, or whether evolution occurred on a different but similarly transient plant species followed

by a recent host shift. All evidence points to the former. Outbreaks of *N. lugens* on rice date back to 18 A.D. (Paik 1977), *Peregrinus maidis* was associated with corn during the collapse of the classic Mayan civilization in the sixteenth century (Brewbaker 1979), and *Perkinsiella saccharicida* was probably introduced to Mauritius along with sugar cane in the seventeenth century (Williams 1957). Coupled with a primarily monophagous feeding habit and the rarity of host shifting in the Delphacidae (Denno and Roderick 1990), these data suggest that most pest planthoppers have exploited their temporary agricultural habitats for centuries and that their wing-form patterns are the result of selection under this long-standing association.

Most agricultural crops are monocultures, and vegetation structure including stand purity can affect the abundance, diversity, and life histories of sap-feeding herbivorous insects (Denno and Roderick 1991). Consequently, patterns of dispersal in agricultural crops may differ from those in natural habitats. However, many of the naturally occurring host plants we surveyed (e.g., *Borrchia*, *Distichlis*, *Juncus*, *Nuphar*, *Pontedaria*, and three species of *Spartina*) also occur as extensive monocultures (Waisel 1972; Duncan 1974; Denno 1978; Denno and Roderick 1991) and have been identified as attractive systems for ecological study because the effects of mixed vegetation are minimal (Denno and Roderick 1991). For this reason, we doubt that stand purity and the effects of mixed vegetation are factors that have contributed to the differences we found in planthopper dispersal between temporary and persistent habitats.

In addition to overall levels of migration, habitat persistence also influences the wing-form response of planthoppers to crowding. Our results strongly suggest that the density–wing form responses of migratory species in ephemeral habitats differ from those of sedentary planthoppers in persistent habitats. Species and populations in persistent habitats are characterized by density-dependent macroptery in both sexes and much higher thresholds above which migratory forms are produced. Apparently, because mate location is less difficult and density–wing form responses of the sexes are the same for planthoppers in persistent habitats, we predicted and found similarity in the proportion of macropterous males and females in the field (see fig. 5). In contrast, species and populations in temporary habitats are characterized by sexual differences in their wing-form response to crowding. Males are usually macropterous regardless of rearing density, macroptery is positively density-dependent in females, and the threshold density for migrant production is low. The result is a high level of macroptery in males and brachyptery in females, which facilitates both mate location and increased reproduction for colonizing species experiencing very low densities in the field. Sexual biases in wing form occur in other insects as well. For example, among those orders of insects in which both winged and flightless species occur, the female is the most frequently flightless sex in nine orders (e.g., Psocoptera, Neuroptera, Lepidoptera, Hymenoptera, and Diptera), the male in only two orders (Plecoptera and Thysanoptera), and either sex in six orders (Roff 1990). Roff (1990) argues that among sexual species, flightlessness should be more frequent in females because eggs are more costly than sperm, and males should retain

wings to locate mates. Furthermore, Roff reports an association between flightlessness in males and female mobility; species in which the females are immobile have winged males.

We argue that the density–wing form responses of planthoppers (figs. 2, 3, and 4) reflect two density-related advantages of flight, namely, habitat escape and mate location. At high densities, the development, survival, and fecundity of planthoppers are adversely affected (Kisimoto 1965; Mochida 1973; Kenmore et al. 1984; Denno et al. 1986; Heong 1988; Denno and Roderick 1990, in press), as are the nutritional quality and survival of host plants (Sogawa and Cheng 1979; Kenmore 1980; Roderick 1987), and wings are advantageous because they facilitate escape. At high densities females disperse to more suitable oviposition sites (see Roff 1986*c*, 1990), and, since female planthoppers migrate before they mate (Kanervo et al. 1957; Raatikainen 1967; Kisimoto 1976; Noda 1986; Padgham et al. 1987), males must disperse as well as locate receptive females in new habitats (Roff 1986*c*).

The density-related increase in macroptery seen in the females of all planthoppers and the high proportion of macropterous males produced under crowded conditions (figs. 2, 3, and 4) are consistent with the argument that wings facilitate the escape from fitness-reducing conditions. However, maximum levels of macroptery (%) differ depending on the persistence of the habitat. For most migratory species in temporary habitats, macroptery reaches 100% (fig. 3*A,B,C*). For species in persistent habitats, macroptery plateaus well below 100% (fig. 2*C* and *D*) and may never exceed 25% even under extremely crowded conditions (fig. 3*D*). In persistent habitats, planthoppers may diapause or overwinter on site when host plants deteriorate (Denno et al. 1981). For species in very ephemeral habitats, migration becomes the only alternative when summer breeding sites are destroyed during winter (Raatikainen 1967; Southwood 1977; Solbreck 1978; Denno and Grissell 1979).

When population density is low, wings also facilitate mate location (Ichikawa 1977). However, features of the mating system in planthoppers explain why only males and not females of some species are macropterous at low population densities (figs. 2*A,B* and 3*A,B,C*). Even though both sexes of planthoppers emit substrate-transmitted sounds that function in mate location and recognition (Ichikawa and Ishii 1974; Ichikawa 1976, 1977; Claridge 1983, 1985*a*, 1985*b*; de Vrijer 1984, 1986; Claridge et al. 1985*a*, 1985*b*; den Bieman 1987; Heady and Denno 1991), only males actively search for females (Ichikawa and Ishii 1974; Ichikawa et al. 1975; Ichikawa 1976). Males and sexually mature, virgin females engage in acoustical exchanges. Although the males may be as far away as 1 m, they move closer to the females until copulation can take place (Ichikawa and Ishii 1974; Ichikawa et al. 1975; Ichikawa 1976; Claridge et al. 1985*b*; de Vrijer 1986). Given this mechanism of mate location, females do not require wings to acquire mates. Apparently because wings impose a reproductive penalty on female planthoppers (Denno et al. 1989), females remain flightless at low densities as long as conditions remain suitable for their development and for that of their offspring.

In males, wings appear to be more important for mate location in temporary than in persistent habitats. For species in temporary habitats, most males emerge

macropterous when raised at low densities (figs. 2A,B and 3A,B,C); in persistent habitats, most males are brachypterous even at very low densities (figs. 2C and 3D). We argue that because the probability is low of there being mates on site in temporary habitats (see Kuno 1979), males must fly among habitat patches to locate females (see Ichikawa 1977; R. Hunt, personal communication). In habitats with high persistence, the probability of there being a mate on site and within the range of a brachypter is higher. Consequently, only at very low densities will locating mates be difficult. Also, if habitats are persistent, but small, the accidental loss of winged individuals will select against flight (see Roff 1990).

The density-related advantages of flight associated with both mate location and escape from deteriorating conditions combine to influence the wing form of male and female planthoppers at different densities. Because females sit and call and do not play a mobile role in mate location, and because there is a reproductive cost associated with flight capability (Denno et al. 1989), their density-wing form response results primarily from the negative effects of crowding.

We argue that the male response is more complex and is influenced by the interacting advantages of flight for escape from poor conditions at high densities and for mate finding at low densities. For species in temporary habitats, males are macropterous at high and low densities, and if brachypterous males occur at all they do so at intermediate densities (figs. 2A and 3A), probably for reasons concerning their ability to outcompete macropterous males for mates (see Ichikawa 1982). For species inhabiting persistent habitats, the probability of habitat deterioration alone has played a more singular role in influencing the wing-form responses of males as it has for females.

The general density-wing form responses of planthoppers may be modified by several factors. First, the dimensionality of the habitat can have a profound influence on the evolution of flightlessness in insects (Denno 1978, 1979; Waloff 1983; Roff 1990; Denno and Roderick 1991). Wing-dimorphic planthoppers inhabit low-profile vegetation and arboreal species are exclusively monomorphic with well-developed wings (Kirkaldy 1906; Denno 1979; Waloff 1983; Denno and Roderick 1991). However, all of the species we investigated and most of the more than 1,800 species of delphacid planthoppers (O'Brien and Wilson 1985) feed on low-profile monocots (Denno and Roderick 1990).

Second, if female planthoppers were to mate before they migrated, rather than after, which is the usual case (see Kisimoto 1976; Noda 1986), then males would not necessarily have to follow winged females to new habitats to obtain mates (see Roff 1986c). Consequently, brachyptery in males would not be as disadvantageous at high densities.

Third, if planthoppers use environmental cues in addition to population density as measures of the probability for habitat deterioration, then density may not be a precise predictor of wing form. For example, some Philippine populations of *N. lugens* show weak responses to changes in nymphal density, while the physiological condition of the host plant greatly influences wing form (Saxena et al. 1981; Iwanaga et al. 1987). Also, brachyptery and diapause are associated with short photoperiod and cold temperatures in some populations of *Laodelphax striatellus* (Kisimoto 1958, 1969; Klein 1967). Nevertheless, density appears to be

the primary determinant of wing form in most planthopper species (see Denno and Roderick 1990).

For insects, wings serve a variety of functions such as mate location and the tracking of suitable habitats for feeding, development, and overwintering. For most species, it is very difficult to determine the role of specific factors in the evolution of dispersal characters. However, wing-dimorphic insects such as delphacid planthoppers with environmental wing-form determination offer the opportunity for a more specific investigation of the selective pressures associated with flight. For planthoppers, the need for wings to locate mates is inversely related to density, while the need for wings to escape deteriorating habitats is positively density-dependent. By examining wing-form responses to density among and within species we were able to isolate the selective factors associated with the advantages of wings. Our results with planthoppers show that overall levels of migration (% macroptery) as well as a bias toward macroptery in males are inversely related to habitat persistence. In persistent habitats where mates are apparently available even under low-density conditions, males of most species emerge brachypterous. Their counterparts in temporary habitats emerge macropterous at low densities and at times must fly great distances to locate females. Thus, for reasons concerning both the durational stability of the habitat and the reduced availability of mates, selection has favored high levels of migration in temporary habitats.

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