

Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure

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Abstract. 1. The effects of habitat isolation, persistence, and host-plant structure on the incidence of dispersal capability (per cent macroptery) in populations of the delphacid planthopper *Toya venilia* were examined throughout the British Virgin Islands. The host plant of this delphacid is salt grass *Sporobolus virginicus*, which grows either in undisturbed habitats (large expanses on intertidal salt flats and around the margins of salt ponds, or small patches of sparse vegetation on sand dunes along the shore), or in less persistent, disturbed habitats (managed lawns).

2. Both sexes of *T. venilia* were significantly more macropterous in disturbed habitats (77.1% in males, 12.5% in females) than in more persistent, undisturbed habitats (19.2% in males, <1% in females).

3. Males exhibited significantly higher levels of macroptery ($26.9 \pm 7.6\%$) than did females ($2.0 \pm 1.7\%$), and per cent macroptery was positively density dependent for both sexes in field populations.

4. There was no evidence that the low incidence of female macroptery in a subset of island populations inhabiting natural habitats ($1.7 \pm 1.2\%$) was attributable to the effects of isolation on oceanic islands. The incidence of macroptery in British Virgin Island populations of *T. venilia* was not different from that observed in mainland delphacid species existing in habitats of similar duration.

5. Rather, the persistence of most salt grass habitats throughout the British Virgin Islands best explains the evolution of flight reduction in females of this island-inhabiting delphacid.

6. Males were significantly more macropterous in populations occupying dune vegetation ($37.6 \pm 9.8\%$) than in populations occupying salt flat–pond margin habitats ($7.6 \pm 5.6\%$). By contrast, females exhibited low levels of macroptery in both dune (0%) and salt flat–pond margin (<1%) habitats. Variation in salt-grass structure probably underlies this habitat-related difference in macroptery because flight-capable males of planthoppers are better able to locate females in the sparse-structured grass growing on dunes. This habitat-related difference in male macroptery accounted for the generally higher level of macroptery observed in males than in females throughout the islands.

7. The importance of habitat persistence and structure in explaining the incidence of dispersal capability in *T. venilia* is probably indicative of the key role these two factors play in shaping the dispersal strategies of many insects.

Key words. Delphacid planthopper, dispersal, flightlessness, habitat isolation, habitat persistence, habitat structure, host plant architecture, life history evolution, *Sporobolus virginicus*, *Toya venilia*, wing polymorphism.

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Introduction

With the evolution of flight in insects came an increased ability to track changing resources, negotiate structurally complex habitats, locate mates, and escape predators (Southwood, 1962; Roff & Fairbairn, 1991; Wagner & Liebherr, 1992; Denno, 1994a; Denno *et al.* 1996, in press). Moreover, associated with the appearance of flight capability was the tremendous diversification of the class Insecta (Wagner & Liebherr, 1992). As a consequence of the association between flight capability and the increased radiation and success of the insects, reasons underlying the secondary loss of wings or flight capability, which has occurred repeatedly throughout the Insecta (Roff, 1990; Wagner & Liebherr, 1992), are not immediately apparent.

One of the keys to understanding the evolution of flight reduction in insects lies in elucidating the costs associated with building and maintaining wings and flight muscles, and in demonstrating how such costs are levelled against other life-history traits (Roff, 1986; Denno *et al.*, 1989; Zera & Denno, 1997). Most often, the diversity of costs associated with flight capability are imposed on reproduction (Roff, 1984; Srygley & Chai, 1990; Marden & Chai, 1991; Roff & Fairbairn, 1991; Zera & Denno, 1997). Such reproductive penalties are revealed most easily by comparing the reproductive success of the volant and flightless wing forms of wing-dimorphic insects (Roff, 1986; Denno *et al.*, 1989, in press; Roff & Fairbairn, 1991; Langellotto *et al.*, 2000). In general, flightless females have higher fecundity, reproduce at an earlier age, and produce larger progeny than their flight-capable counterparts (Solbreck, 1986; Roff & Fairbairn, 1991; Denno, 1994b; Zera & Denno, 1997). Similarly, flightless males can acquire matings more successfully and sire more offspring than macropterous males (Novotný, 1995; Langellotto *et al.*, 2000). Indeed, such wing-form comparisons provide widespread evidence for an antagonistic trade-off between flight capability and reproductive success across a wide variety of insect taxa including crickets, planthoppers, aphids, thrips, true bugs, and beetles (Utida, 1972; Roff, 1984; Zera, 1984; Solbreck, 1986; Crespi, 1988; Denno *et al.*, 1989; Dixon, 1998; Langellotto *et al.*, 2000).

Although flightless forms clearly have an inherent reproductive advantage, they are extremely sedentary and are unable to effectively exploit ephemeral habitats, track spatial changes in food availability, manoeuvre efficiently in heterogeneous habitats, or locate widely scattered mates (Waloff, 1983; Roff, 1990; Denno *et al.*, 1991, 1996, in press; Langellotto, 1997; Langellotto *et al.*, 2000). Thus, the dispersal strategy that evolves in a particular species will reflect a balance between the advantage of increased reproductive success resulting from flight loss and the need for wings to track resources (Roff, 1990; Zera & Denno, 1997).

Among the selective forces considered central in shaping the evolution of insect dispersal strategies are habitat isolation, persistence, and structure (Southwood, 1962, 1977; Roff, 1990; Denno *et al.*, 1991, in press; Wagner & Liebherr, 1992; Travis & Dytham, 1999). In general, theory predicts reductions in flight capability for species exploiting habitats that are very

isolated, persistent, or dense and low-profile in structure (Southwood, 1962; Roff, 1990; Langellotto, 1997; Denno *et al.*, in press). In particular, habitat isolation has been a longstanding but controversial explanation for the evolution of flightlessness in insect taxa inhabiting oceanic islands (Darwin, 1876; Roff, 1990). The argument asserts that the constant loss of emigrants from oceanic islands should select against flight capability (see Roff, 1990), however the spatial scale at which habitat isolation selects against dispersal has been a subject of considerable debate (Roff, 1990; Wagner & Liebherr, 1992; Denno *et al.*, in press). Notably, recent modelling efforts have shown that the propensity to disperse generally declines with increased habitat fragmentation, but that the predicted outcome depends on patterns of habitat availability and persistence (Travis & Dytham, 1999).

Isolation, and other habitat-related hypotheses for the evolution of flightlessness in insects, have proved difficult to test empirically, however, primarily because of the difficulty of assessing the dispersal ability of the inhabitants (Denno *et al.*, 1991, 1996, in press). Wing-dimorphic insects such as delphacid planthoppers (Hemiptera: Delphacidae) are ideal for investigating the effects of habitat factors on dispersal because migratory adults (macropters with fully developed wings) and flightless adults (brachypters with reduced wings) are so easily recognised (Denno *et al.*, 1991). Moreover, the proportion of macropters in a population can be used as a reliable index of the incidence of potential dispersal (Denno *et al.* 1991, in press). Testing the habitat isolation--flightlessness hypothesis has been challenging as well because comparisons of the incidence of dispersal between island and mainland populations are frequently confounded by other factors such as habitat persistence and structure (Roff, 1990; Denno *et al.*, in press).

Using British Virgin Island populations of the wing-dimorphic delphacid *Toya venilia* (Fennah), the objectives of the work reported here were threefold. First, the incidence of dispersal (per cent macroptery) was compared between populations of *T. venilia* inhabiting undisturbed (relatively persistent) and disturbed habitats throughout the British Virgin Islands, with the expectation of higher levels of macroptery in disturbed habitats. Second, to test the hypothesis that flight reduction is more prevalent on oceanic islands, the incidence of macroptery in island populations of *T. venilia* was compared with known levels of macroptery in mainland populations of other grass-inhabiting delphacid species. For this analysis, possible differences in habitat persistence were controlled by comparing the incidence of dispersal capability between taxa inhabiting habitats of similar age. Last, the incidence of macroptery was compared between populations of *T. venilia* inhabiting two structurally different and habitat-associated growth forms of its host grass *Sporobolus virginicus* (L.) (dense stands on salt flats and sparse stands on beach dunes). Because vegetation structure (dense vs. sparse) is known to influence the ability of male planthoppers to locate mates (Denno, 1994b; Langellotto, 1997; Denno *et al.*, in press), its contribution to habitat-related variation in the incidence of dispersal capability in *T. venilia* populations was examined. Ultimately, this information was used to assess the relative

contribution of habitat isolation, persistence, and vegetation structure to the dispersal strategy of this oceanic island-inhabiting planthopper.

Methods

Study organisms

Toya venilia is Caribbean in distribution, having been recorded from the British Virgin Islands, Puerto Rico, and Montserrat (Fennah, 1959). This delphacid is multivoltine and monophagous on the perennial salt grass *Sporobolus virginicus*. Like most delphacids, *T. venilia* is wing dimorphic with both macropters and brachypters occurring in most populations. Wing form in planthoppers is determined by a developmental switch that responds to environmental cues (Denno, 1994b). The sensitivity of the switch, however, is heritable and under polygenic control (Iwanaga & Tojo, 1986; Denno, 1994b; Zera & Denno, 1997). Of all the proximate cues known to affect wing form in planthoppers, population density is by far the most influential (Denno & Roderick, 1990). For most delphacids, the production of the macropterous wing form is density-dependent (Denno *et al.*, 1985; Denno, 1994b), however the threshold density that triggers the production of macropterous forms can differ among species, among populations of the same species, and even between the sexes of the same species (Kisimoto, 1965; Denno *et al.*, 1991). Thus, macroptery may or may not be correlated between the sexes of a species (Denno *et al.*, 1991; Denno, 1994a). Moreover, patterns of density-dependent macroptery in the sexes, be they the same or different, can be maintained under common environmental conditions, suggesting an underlying genetic basis (Denno *et al.*, 1991).

Besides allowing for habitat escape and the colonisation of new habitats (Southwood, 1962, 1977), wings also function in mate location (Ichikawa, 1977; Hunt & Nault, 1991; Langellotto, 1997). In planthoppers, only males search actively for stationary females (Ichikawa, 1977; Claridge & de Vrijer, 1994; Langellotto *et al.*, 2000) and acoustic communication is essential for locating mates (Claridge, 1985; Denno *et al.*, 1991; Heady & Denno, 1991; Heady, 1993). Both males and females communicate through substrate-transmitted vibrations, whereby calls are produced by vibrating their abdomens (Claridge, 1985). Vibrations are transferred to the host plant through the legs or mouth parts (Claridge, 1985). Planthoppers sitting on the same host plant or on adjacent plants in physical contact can sense each other's calls from as far away as 1 m (Ichikawa & Ishii, 1974), however planthoppers resting on neighbouring but slightly separated plants do not detect each other's presence (Ichikawa & Ishii, 1974). Sexually mature males and virgin females call spontaneously on their food plants. After sensing each other, they begin to alternate calls in a duetting fashion (Ichikawa & Ishii, 1974; Claridge, 1985; Heady & Denno, 1991). During duetting, males move toward stationary females and, after locating a female, courtship ensues, followed by mating (Ichikawa & Ishii, 1974; Heady & Denno, 1991).

Given their substrate-borne system of mate location, it is not surprising that vegetation structure has a major impact on the ability of the male wing forms of planthoppers to locate mates. When host plants are isolated and do not come into contact, flight is essential for mate location because only macropterous males can fly among plants, locate females effectively, and acquire matings (Langellotto, 1997). Macropterous males also locate females much more effectively than brachypters under low female-density conditions (Langellotto, 1997). In contrast, in contiguous vegetation, brachypterous males obtain most matings, apparently due in part to their inherent ability to displace rival macropters aggressively during courtship (Langellotto *et al.*, 2000).

The host plant of *T. venilia* is salt grass *S. virginicus*, a perennial that grows in several different habitat types throughout the Caribbean, including most of the vegetated British Virgin Islands (Chase, 1971; Acevedo-Rodriguez, 1996; Table 1). Salt grass grows on intertidal salt flats and around the margins of salt ponds, where it often occurs in dense, expansive, pure stands, frequently in association with mangroves. It also occurs as small patches on the dunes of sandy beaches and the bases of cliffs along the shore. In this beach-dune habitat, the structure of the grass stand is sparse, with culms growing further apart than those occurring on tidal flats. *Sporobolus virginicus* is also grown in managed, suburban habitats where it is encouraged by home owners as a lawn grass in low-lying areas. Although frequently disturbed by mowing, the dense structure of the grass in lawns is more like that of grass growing on salt flats than dunes. Such structural variation in grass form may influence the dispersal strategy of the resident *T. venilia*, particularly the males.

Study sites

The British Virgin Islands lie 100 km east of Puerto Rico and comprise more than 50 small islands and islets between 18°18' and 18°46'N, and 64°15' and 64°52'W (Fig. 1). Among the largest islands are Tortola (64 km²), Anegada (34 km²), Virgin Gorda (21.5 km²), and Jost van Dyke (9 km²). Other islands (e.g. Guana, Beef, Great Camanoe) measure <5 km², and others yet (e.g. Necker, Great Dog, and Salt) are very small (<1 km²).

All 11 islands visited supported at least one population of salt grass (Table 1). Although vast expanses of salt grass occurred on the intertidal flats of some islands (e.g. Anegada, Beef, and Virgin Gorda), and wide swaths (5–20 m) surrounded salt ponds on others (e.g. Guana, Great Camanoe, and Tortola), only single small patches occurred on the upper beach and dunes of other islands (e.g. Great Dog and Great Thatch). On some islands such as Guana, salt-pond and dune populations of salt grass co-occurred, but in this case they grew on either side of a central ridge (266 m) and were separated by 500 m. Moreover, these were the only two stands of salt grass on Guana. With the exception of the expansive salt flats on Beef Island (Airport and Trellis Bay area) and Anegada (Flamingo Pond area), salt grass populations were generally small and isolated.

Table 1. Habitats, density, and macroptery of populations of the planthopper *Toya venilia* on salt grass *Sporobolus virginicus* throughout the British Virgin Islands. The location (island and sample site) and date of samples are shown as is the sample size (total number of planthoppers taken at each site) and number of samples (sweeps or D-vac placements) per site. Populations are sorted by habitat, either salt flat/salt pond, beach/dune, or disturbed.

Island, sample site, date	Habitat (area, m ²)	Density (number per)		Macroptery (%)			Sample size total (male, female)	Sample no. and type
		20 sweeps	m ²	Males	Females	Overall		
Salt-flat and salt-pond populations								
Anegada, Flamingo Pond, 19/10/97	Salt flat (5000+)	–	–	75	0	50	6 (4, 2)	D-vac
Beef, Bridge, 16/10/96	Salt flat (500)	3.0	2.8	0	0	0	15 (3, 12)	2, 50 sweep
Beef, Airport, 16/10/96	Salt flat (3000)	3.6	3.4	0	0	0	27 (6, 21)	3, 50 sweep
Beef, Airport, 22/10/98	Salt flat (3000)	28.7	26.7	0	0	0	86 (42, 44)	3, 20 sweep
Beef, E Trellis Bay, 17/10/98	Salt flat (3000)	59.7	55.5	2	0	1	179 (93, 86)	3, 20 sweep
Great Camanoe, Lee Bay, 17/10/96	Pond edge (800)	74.0	68.8	14	7	7	185 (35, 150)	1, 50 sweep
Great Camanoe, Lee Bay, 14/10/98	Pond edge (800)	55.3	51.5	3	0	1	166 (38, 128)	3, 20 sweep
Guana, Salt Pond, 15/10/96	Pond edge (2000)	40.4	37.6	8	1	2	202 (38, 164)	5, 20 sweep
Guana, Salt Pond, 14/10/98	Pond edge (2000)	22.2	20.7	4	0	1	111 (24, 87)	5, 20 sweep
Guana, Salt Pond, 23/10/98	Pond edge (2000)	–	17.5	0	0	0	66 (32, 34)	3, 40 D-vac
Guana, Salt Pond, 23/10/98	Pond edge (2000)	18.8	17.5	3	0	1	94 (26, 68)	5, 20 sweep
Jost Van Dyke, S side 18/10/98	Pond edge (600)	11.0	10.2	0	0	0	22 (9, 13)	2, 20 sweep
Salt, N Side, 15/10/98	Pond edge (200)	–	–	–	–	–	2 (nymphs)	D-vac
Tortola, Belmont Pond, 23/10/98	Pond edge (150)	–	5.8	0	0	0	22 (9, 13)	3, 40 D-vac
Tortola, Josiah Bay, 16/10/98	Salt flat (300)	–	–	0	0	0	40 (9, 31)	D-vac
Virgin Gorda, Biras, 23/10/97	Salt flat (2000)	–	–	46	0	40	15 (13, 8)	D-vac
Beach and dune populations								
Beef, W Trellis Bay, 17/10/98	Beach/dune (60)	19.7	18.3	27	0	8	59 (18, 41)	3, 20 sweep
Great Dog, S Side, 15/10/98	Beach/dune (50)	–	14.2	10	0	7	15 (10, 5)	1, 40 D-vac
Great Thatch, N Side, 18/10/98	Beach/dune (30)	–	30.2	46	0	32	19 (13, 6)	1, 20 D-vac
Guana, North Beach, 21/10/98	Beach/bank (25)	–	32.5	69	0	44	57 (36, 21)	2, 40 D-vac
Necker, N Side, 24/10/97	Beach/dune (75)	–	–	48	0	30	43 (25, 18)	D-vac
Necker, N Side, 19/10/98	Beach/dune (75)	12.6	11.8	9	0	3	38 (11, 27)	3, 20 sweep
Disturbed habitat populations								
Anegada, Settlement, 20/10/97	Lawn (300)	–	–	78	25	62	13 (9, 4)	D-vac
Virgin Gorda, Pond Bay, 22/10/97	Cattle pond (300)	–	–	76	0	49	39 (25, 14)	D-vac

Incidence of dispersal capability in planthopper populations inhabiting undisturbed and disturbed habitats throughout the British Virgin Islands

The incidence of dispersal capability in populations of *T. venilia* (per cent macroptery in both sexes) was compared between undisturbed (relatively persistent) and disturbed (relatively temporary) habitats throughout the British Virgin Islands over the course of a 3-year period (1996–1998). For this comparison, stands of salt grass growing on salt flats, along the margins of salt ponds, and on the upper reaches of beaches and dunes showed no signs of disturbance and were considered relatively persistent habitats for *T. venilia* (Table 1). By contrast, managed lawns and cattle-trampled and browsed stands of salt grass surrounding some salt ponds were regarded as disturbed habitats (Table 1). Using a combination of D-vac and sweep-net sampling, 18 populations (16 undisturbed and two disturbed) were assessed in disjunct stands of salt grass on 11 islands: Anegada (The Settlement and Flamingo Pond), Beef (Bridge, Airport, West Trellis Bay, and East Trellis Bay), Great Camanoe (Lee Bay), Great Dog (South Side), Great Thatch (North Side), Guana (Salt Pond and North Beach), Jost

van Dyke (Great Harbor), Necker (North Side), Salt (North Side), Tortola (Belmont Pond and Josiah Bay), and Virgin Gorda (Biras Creek and Pond Bay).

For this assessment, planthoppers were sampled in 1996 using a sweep-net (38 cm diameter) and in 1997 and 1998 using a portable D-vac (1 HP Echo, model PB210E, Gempler's, Mount Horeb, Wisconsin). Extraction of most planthoppers from the dense stands of salt grass required a prolonged period of vacuuming with this portable D-vac in 1997. To achieve more time-efficient extraction of planthoppers in 1998, the conventional sampling head of this D-vac (0.093 m²) was constricted to 0.031 m² by fitting the sampler with a smaller cylindrical plastic head (40 cm long, 20 cm diameter). One sample with this modified D-vac consisted of either 20 or 40 placements of the D-vac head on the vegetation, depending on the size of the grass stand. Each sample with the sweep net consisted of 20 or 50 sweeps to and fro while walking through the stand. The number and size of samples at each site and the date on which they were taken are shown in Table 1. Given the slow extraction of planthoppers in 1997, a consistent number of samples was not taken. Rather, the vegetation was vacuumed at each location for ≈ 30 min.

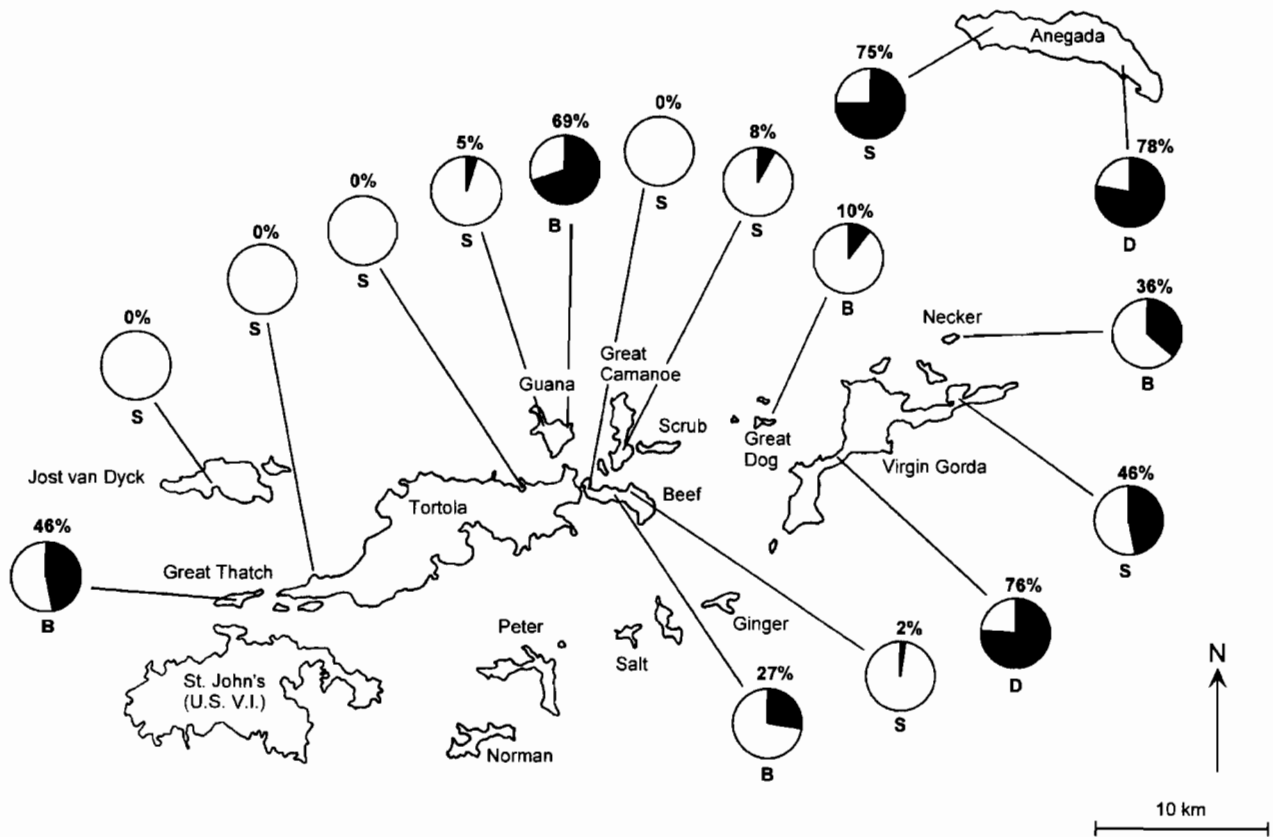


Fig. 1. Incidence of dispersal (% macroptery in males) in populations of the planthopper *Toya venilia* inhabiting salt flat-pond edge habitats (S), beach-dune habitats (B), and disturbed habitats (D) throughout the British Virgin Islands. The black portion of each pie diagram reflects the percentage of macropters in each population.

Planthopper samples were bottled in 95% ethanol and returned to the laboratory where the incidence of macroptery (%) in both sexes of *T. venilia* was determined for each population.

The incidence of macroptery (%) in males and females of *T. venilia* was compared between persistent and disturbed habitats using *t*-tests on angular-transformed data (SAS, 1990). For these analyses, only one value of macroptery (%) was used for each population, and if a population was sampled several times, macroptery was averaged across dates to generate this value. Populations from which fewer than five individuals of either sex were sampled were not included in the analysis.

Incidence of dispersal capability in island and mainland taxa: habitat isolation vs. persistence

To test whether flightlessness was more prevalent on oceanic islands, the incidence of macroptery in British Virgin Island populations of *T. venilia* was compared with published levels of macroptery for mainland-inhabiting delphacids (extracted from Denno *et al.*, 1991). Because habitat persistence has a strong influence on the dispersal strategies of planthoppers (Denno, 1994a; Denno *et al.*, 1991,

1996, in press), it was essential to make the island and mainland comparison between taxa occupying similarly persistent habitats. Thus, it was necessary to quantify habitat persistence roughly for several *T. venilia* populations.

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 favourable for development (*H*) (Southwood, 1962; Southwood *et al.*, 1974). Persistent habitats are characterised by $H/\tau \approx 1$ and temporary habitats by $H/\tau \approx 1$ (Southwood, 1962). Habitat persistence was quantified for three populations of *T. venilia* (Guana, Salt Pond; Beef, East Trellis Bay; Great Camanoe, Lee Bay) by multiplying habitat age (years) by the maximum number of generations/habitat/year; thus, habitat persistence was expressed as the maximum number of generations attainable during the existence of the habitat (see Denno *et al.*, 1991).

Minimum estimates of habitat age were obtained by questioning senior residents of the islands, in particular Oscar Chalwell from Guana/Tortola, who placed minimum estimates of the salt grass habitats sampled on Guana, Beef, and Great Camanoe at 64, 60, and 60 years respectively. Estimates of the annual number of generations for these populations of *T. venilia* were predicted from an existing model established explicitly for planthoppers: *number of*

annual generations = $10.12 - 0.157(^{\circ}N)$ (from Denno, 1994b). By substituting the latitudes of Guana (18°29'N), Beef (18°26'N), and Great Camanoe (18°28'N) into this equation, the number of annual generations for the three populations of *T. venilia* was estimated at 7.2. Thus, habitat persistence (maximum number of generations attainable) was estimated at 460, 432, and 432 generations respectively for the Guana, Beef, and Great Camanoe populations.

The mean incidence of macroptery (%) in these three populations of *T. venilia* was then compared with the mean level of macroptery in mainland taxa of delphacids in three ways. First, the observed incidence of macroptery in these three British Virgin Island populations was compared with expected levels of macroptery predicted by a model describing the relationship between habitat persistence and macroptery for mainland delphacid species: $\text{macroptery (\%)} = -5.450 + 1/(\text{habitat persistence}^{0.045} - 0.095)$ (from Denno *et al.*, 1991). Expected macroptery for the British Virgin Island populations was obtained by substituting habitat persistence values for the three British Virgin Island populations into the mainland-derived model. Observed and expected levels of macroptery were compared using a paired *t*-test on angular-transformed data (SAS, 1990). Due to small sample size ($n=3$), a power analysis was performed where $\text{power} = 1 - \beta$, the probability of committing a Type II error (Zar, 1996).

Second, the observed level of macroptery in the three British Virgin Island populations of *T. venilia* was compared with that for six species of mainland delphacids [*Laodelphax elegantulus* (Boheman), *Muirodelphax exiguus* (Boheman), *Paraliburniella dalei* (Scott), *Pissonotus piceus* (Van Duzee), *Prokelisia dolus* Wilson, and *Ribautodelphax angulosus* (Ribaut)] existing in similarly persistent grassland habitats (150–350 generations) (extracted from Denno *et al.*, 1991). For this and the following analysis, the incidence of macroptery (%) in British Virgin Island and mainland taxa was compared using a *t*-test on angular-transformed data.

Third, macroptery in British Virgin Island populations of *T. venilia* was compared with that observed in populations of seven mainland species [*Delphacodes detecta* (Van Duzee), *D. penedetector* Beamer, *Neomegamelanus dorsalis* (Metcalf), *N. penelautus* (McDermott), *Prokelisia dolus* Wilson, *P. marginata* Van Duzee, and *Toya propinqua* (Fieber)] occupying the same low-profile habitat type (grasses growing on marshes and dunes) along the Gulf of Mexico shore (extracted from Denno, 1978; Denno *et al.*, 1991). For this analysis, no estimates of habitat persistence were required, although the habitats of all the delphacids were generally very persistent (>500 years; see Denno *et al.*, 1991).

For these three analyses, the incidence of macroptery in British Virgin Island populations should be less than that for mainland taxa if oceanic isolation was an important contributor to the evolution of flightlessness in delphacids. Thus, one-tailed tests were used to assess significance (SAS, 1990). Moreover, for all three analyses, the assessment of macroptery was limited to the female sex because the dispersal strategies of female planthoppers are not compromised by possible flight constraints associated with mate location, as is the case for males (Denno, 1994a; Denno *et al.*, 1991, in press).

Habitat structure and the incidence of macroptery in planthopper populations

The stand area (m²) of salt grass growing on salt flats, around pond margins, and on beach dunes was estimated visually or by pacing at each of the 18 locations visited (Table 1). Stand area was compared between the salt flat–pond edge habitat and the beach-dune habitat using a *t*-test. The structure of salt grass (culm density, culm length, and above-ground biomass) was determined by clip-quadrat sampling for stands growing in the two major habitat types (salt flats–pond edges vs. dunes) on three islands (Beef, Guana, and Necker) (Denno *et al.*, 1985). Five samples were taken in each habitat type on the three islands during 19–23 October 1998. Each sample consisted of the removal of all above-ground grass within a 0.047-m² wire frame. Subsequently, culm density (number per m²), culm length (cm), and wet weight biomass (g per m²) were determined. Because island effects were minimal (ANOVA), *t*-tests were used to compare culm density, culm length, and grass biomass between the two habitat types. For these analyses, the five habitat samples were averaged within each island resulting in a sample size of three for each habitat type.

The influence of habitat structure on the dispersal capability of both sexes of *T. venilia* was examined by comparing the incidence of macroptery between populations occurring in the two habitat types (sparse stands of salt grass occurring on dunes and dense stands growing on salt flats or around salt pond margins). For each sex, the incidence of macroptery (%) in the two habitat types was compared using a *t*-test on angular-transformed data. Similarly, a *t*-test on angular-transformed data was used to compare macroptery (%) between the sexes within each habitat. Sites at which <10 individuals were collected were excluded from the analysis. The expectation was that higher levels of macroptery would be found in males inhabiting the dunes than in males inhabiting the salt flats because flight is likely to be essential for mate location in the sparsely structured habitat. Habitat-related variation in salt grass structure was not envisioned to influence macroptery in females because they do not search actively for mates. Because macroptery is density dependent in most planthoppers (Denno *et al.*, 1994), the slopes of the relationship between macroptery in both sexes (angular-transformed) and population density in the two habitats (dune and salt flat) were tested to see whether they differed from zero (*t*-test on the regression coefficients). To test further for habitat effects on the incidence of macroptery, the slopes of the relationship between macroptery (%) and population density (number per m²) were compared between the two habitat types using ANCOVA with density as the covariate (SAS, 1990). This analysis was run separately for each sex.

Estimates of population density were necessary for the above approaches. D-vac sampling during 1998 allowed for the association of variation in the incidence of macroptery (%) in *T. venilia* with absolute population size (number per m²). Sweep-net sampling, however, provided only a relative density estimate. To convert sweep-net counts to absolute density data, side-by-side, replicated D-vac (3, 40 placement) and sweep-net

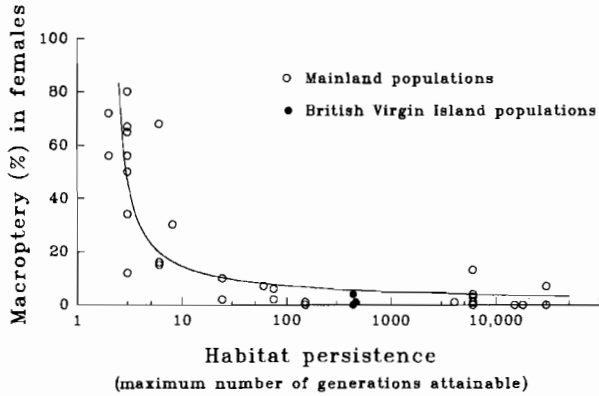


Fig. 3. Relationship between macroptery (%) and habitat persistence (the maximum number of generations attainable) for the females of 41 field populations (35 species) of mainland-inhabiting species of delphacid planthoppers (○) (data from Denno *et al.*, 1991) and three British Virgin Islands populations (Beef, Guana, and Great Camanoe) of the delphacid *Toya venilia* (●). The observed levels of macroptery in island populations of *T. venilia* were not significantly different from those expected using the mainland model [$\text{macroptery} (\%) = -5.450 + 1/(\text{habitat persistence}^{0.045} - 0.095)$; paired *t*-test, NS] (model adapted from Denno *et al.*, 1991). Thus, with habitat persistence controlled, the incidence of dispersal in field populations was the same for British Virgin Island and mainland taxa of planthoppers.

$t = -2.35$, NS; Fig. 3). Had the error associated with the full regression model been taken into account in the analysis (Fig. 3), however, the one-tailed *P*-value (0.072) would most certainly have been larger. Moreover, given an average difference of 3.85% macroptery between expected (mainland) and observed (island) data, a power analysis on arcsin-transformed data revealed that the likelihood of detecting a difference between the two samples, if indeed it existed, was 43%. Thus, the hint of a difference in macroptery between British Virgin Island and mainland populations does not even verge on significance.

Second, the average incidence of macroptery in British Virgin Island populations of *T. venilia* ($1.7 \pm 1.2\%$) did not differ from that for six species of mainland delphacids ($1.4 \pm 1.1\%$) existing in similarly persistent grassland habitats ($t = 0.16$, NS). Third, macroptery in British Virgin Island populations of *T. venilia* ($1.7 \pm 1.2\%$) did not differ from that observed in populations of seven mainland species of delphacids occupying the same type of low-profile grassland habitats (marshes and dunes) along the shore of the Gulf of Mexico ($3.4 \pm 1.8\%$) ($t = -0.59$, NS).

Together, these data suggest that with habitat persistence controlled, habitat isolation at the scale of oceanic islands contributes little to explaining the dispersal strategy of *T. venilia* in the British Virgin Islands. Be it an island or mainland population, habitat persistence appears to be the most crucial factor shaping the dispersal strategy of female delphacid planthoppers (Fig. 3).

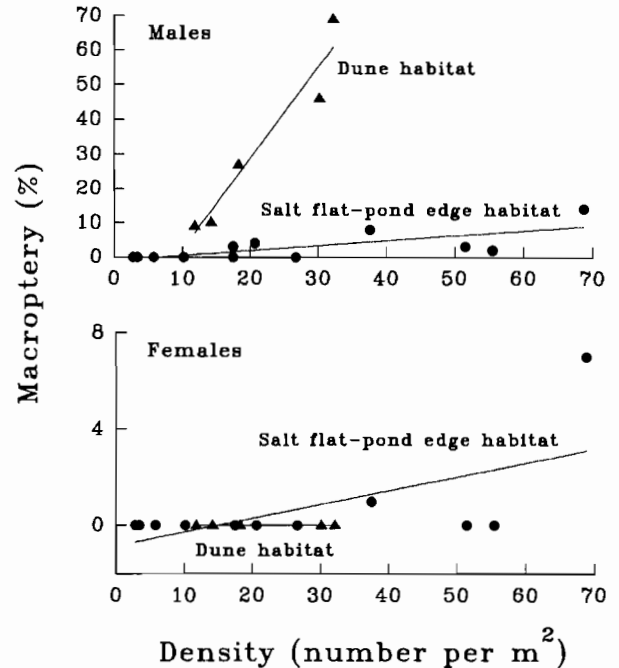


Fig. 4. Relationship between the incidence of macroptery (%) in males and females of the planthopper *Toya venilia* and population density (number per m^2) in two salt-grass habitats (dense stands of *Sporobolus virginicus* growing on salt flats or along edges of salt ponds and sparse stands inhabiting beach dunes) in the British Virgin Islands. For males, macroptery was significantly density dependent in both habitats, but the slopes of the relationship differed (ANCOVA, $F = 96.5$, $P < 0.001$). Macroptery was significantly density dependent for females inhabiting the salt flat-pond edge habitat [$\text{macroptery} = -0.85 + 0.57(\text{density})$, $R^2 = 0.39$, $P < 0.05$], but density-dependent macroptery was not detected for females occurring in the dune habitat.

Habitat structure and the incidence of macroptery in planthopper populations

On average, stands of salt grass were significantly smaller on dunes ($48 \pm 9 \text{ m}^2$, mean \pm SEM, $n = 5$) than on salt flats and around the margin of salt ponds ($1595 \pm 471 \text{ m}^2$, $n = 11$) ($t = 2.52$, $P < 0.05$). Moreover, culms of salt grass grew significantly denser ($3753 \pm 352 \text{ culms m}^{-2}$ vs. 2232 ± 364) and longer ($49 \pm 2 \text{ cm}$ vs. 33 ± 3) on salt flats than on dunes ($t_{\text{culm density}} = 3.0$, $P < 0.01$; $t_{\text{culm length}} = 4.77$, $P < 0.001$). Also, the above-ground biomass (wet weight) of salt grass was significantly greater for salt flat ($2755 \pm 221 \text{ g m}^{-2}$) than for dune ($761 \pm 228 \text{ g m}^{-2}$) vegetation ($t = 6.28$, $P < 0.001$).

Males of *T. venilia* were significantly more macropterous in populations occupying dune vegetation ($37.6 \pm 9.8\%$) than in populations occurring in stands of salt grass growing on intertidal flats and around salt ponds ($7.6 \pm 5.6\%$) ($t = 3.28$, $P < 0.01$). This habitat-related difference in male macroptery accounted for most of the disparity in macroptery between the sexes of *T. venilia* throughout the British Virgin Islands

(compare Figs 1 and 2). Moreover, there was a significant positive relationship between macroptery in males (%) and population density in both dune [macroptery = $-24.12 + 2.64(\text{density})$, $R^2 = 0.93$, $P < 0.01$] and salt-flat [macroptery = $-0.94 + 0.14(\text{density})$, $R^2 = 0.54$, $P < 0.01$] habitats (Fig. 4). The slope of the relationship between macroptery and density was significantly steeper for males in dune-inhabiting populations than for males occupying salt flats (ANCOVA, $F = 96.5$, $P < 0.001$), however, further indicating a habitat effect on dispersal capability.

In contrast, there was no difference between the incidence of macroptery in female planthoppers in dune (0%) and salt-flat ($0.6 \pm 0.5\%$) populations ($t = 1.11$, NS) (Fig. 2). Also, the incidence of macroptery in female ($0.6 \pm 0.5\%$) and male ($7.6 \pm 5.6\%$) planthoppers did not differ in the salt-flat habitat ($t = 1.45$, NS). In the dune habitat, however, males were significantly more macropterous ($37.6 \pm 9.8\%$) than females ($0\% \pm 0$) ($t = 5.95$, $P < 0.01$). Thus, habitat structure appears to have a selective influence on the dispersal strategy only of male planthoppers. Macroptery was significantly density dependent for females inhabiting the salt flat-pond edge habitat [macroptery = $-0.85 + 0.57(\text{density})$, $R^2 = 0.39$, $P < 0.05$; Fig. 4], a slope that did not differ from that for males in this habitat (ANCOVA, $F = 3.24$, NS). Density-dependent macroptery was not detected for females occurring in the dune habitat (0% macroptery at all densities), probably because the high densities that occurred occasionally in salt flat habitats (> 35 planthoppers per m^2) were never observed in dune vegetation (Fig. 4).

Discussion

Both sexes of *T. venilia* exhibit elevated macroptery in disturbed habitats (managed lawns) and reduced flight capability in natural, more persistent habitats (salt flats, salt ponds, and dunes) throughout the British Virgin Islands, a pattern that has been reported for many insects including other delphacid species (Roff, 1990; Denno *et al.*, 1991; Novotný, 1994). Dispersal capability is apparently retained to track the frequent changes in resource quality and abundance that occur in disturbed and temporary habitats (Southwood, 1977; Denno *et al.*, 1991, 1996). Although the incidence of macroptery in populations of *T. venilia* is generally low in undisturbed habitats ($< 30\%$ on average), the dispersal strategies of males and females are clearly different (Figs 1 and 2). Males exhibit higher levels of macroptery ($26.9 \pm 7.6\%$) than do females ($2.0 \pm 1.7\%$) but this difference in dispersal ability is habitat dependent, with males significantly more macropterous than females in dune habitats (37.6 vs. 0%) but not in salt flat-pond edge habitats (7.6 vs. 0.6%). For both sexes, the occurrence of the macropterous form in field populations is positively density dependent (Fig. 4). Thus, fluctuations in population density in the field, coupled with density-dependent macroptery, probably explain much of the within-habitat variation in the incidence of dispersal (Figs 1 and 2). The mechanism underlying the disparity in macroptery between the sexes of *T. venilia* is probably a genetically based difference in the

induction of macroptery under crowded conditions, a well documented occurrence for other species of delphacids (Kisimoto, 1965; Denno *et al.*, 1991, 1994).

The selective forces underlying the discrepant dispersal strategies of the sexes of this planthopper probably involve several habitat-related factors. Of the major habitat-associated factors thought to influence the dispersal strategies of insects, namely persistence, structure, and isolation (Roff, 1990; Denno *et al.*, 1991, 1996, in press), only habitat persistence and structure showed an effect on island populations of *T. venilia*. There was little evidence that the low incidence of dispersal in several island populations ($1.7 \pm 1.2\%$ in females) was attributable to the effects of isolation on oceanic islands (Fig. 2). Three analyses revealed that the low level of macroptery in several British Virgin Island populations of *T. venilia* was no different from that observed in mainland delphacid species existing in habitats of similar duration. Rather, the persistence of the natural salt grass habitats throughout the British Virgin Islands probably best explains the evolution of flight reduction in this island-inhabiting delphacid (Fig. 3). That flight capability is retained under certain conditions on oceanic islands is evidenced by the high incidence of macroptery (25%) in females of *T. venilia* exploiting the disturbed lawn habitats on Anegada (Fig. 2).

It might be argued that the assessments of habitat age, and thus persistence for salt grass habitats in the British Virgin Islands (~ 450 possible planthopper generations), are underestimated. This is probably the case. Nonetheless, two lines of evidence suggest that brachyptery increases very rapidly in populations of wing-dimorphic planthoppers given the appropriate circumstances. First, with an increase in habitat persistence, dispersal capability (% macroptery) in field populations declines sharply, suggesting that when the demand for flight is relaxed, flight capability diminishes rapidly (Denno *et al.*, 1991; Fig. 3). Planthoppers existing in habitats lasting only 30 generations are nearly as brachypterous ($> 90\%$) as species occupying habitats a thousand times more persistent. Second, macropterous and brachypterous lines of the planthopper *Nilaparvata lugens* Stål can be established after only 30 generations of selection in the laboratory on an initial population consisting of an equal mix of both wing forms (Marooka & Tojo, 1992). Thus, both field data on habitat persistence (Denno *et al.*, 1991, 1996) and selection experiments in the laboratory (Marooka *et al.*, 1988; Marooka & Tojo, 1992) suggest that dispersal characters respond very rapidly to selection over the course of ecological time. Therefore, the habitats of *T. venilia*, even though possibly underestimated in age, have probably persisted long enough for the dispersal strategy of this planthopper to stabilise. The reduction in dispersal capability of planthoppers in persistent habitats is probably attributable to the reproductive advantage of brachypterous adults (Denno *et al.*, 1989; Zera & Denno, 1997; Langellotto *et al.*, 2000).

Other studies have also shown that habitat persistence rather than oceanic isolation underlies the dispersal strategy of other planthopper species and insects. For example, the incidence of macroptery in Hawaiian island delphacids is low ($1.26 \pm 0.25\%$), not different from the mainland average

($1.50 \pm 1.15\%$) (Denno *et al.*, in press), and very similar to the level observed in British Virgin Island populations of *T. venilia* ($1.7 \pm 1.2\%$). Notably, habitat persistence and dimensionality were controlled in the Hawaiian island-mainland comparison, whereby the incidence of macroptery was compared only between taxa inhabiting persistent, low-profile vegetation. Similarly, in an extensive analysis of the effects of habitat isolation on the dispersal strategies of a wide diversity of insect taxa (Orthoptera, Hemiptera, Thysanoptera, Psocoptera, Neuroptera, Coleoptera, and Diptera), Roff (1990) showed that oceanic islands do not have higher-than-expected incidences of flightlessness than mainland faunas.

Habitat isolation may contribute to reduced dispersal capability via migrant loss only in the very smallest of habitat patches (Roff, 1990). The highly fragmented yet persistent salt marshes in southern California may provide an example where isolation contributes to the evolution of flightlessness in delphacids. In these habitats, dispersal is virtually absent in populations of *Prokelisia dolus* ($0.16 \pm 0.36\%$ macroptery; Denno *et al.*, 1996), a level below that (5–8%) predicted by habitat persistence alone (see Denno *et al.*, 1991). By contrast, males of *T. venilia* were much more macropterous ($32.2 \pm 11.4\%$) in the small, isolated patches of salt grass on dunes than they were in the large expanses of salt grass associated with salt flats ($5.7 \pm 3.3\%$). Although this pattern is attributed here to the constraints associated with mate finding, it illustrates that flight capability can be retained when necessary even in the smallest and most isolated habitats. Therefore, it is argued that at the scale of oceanic islands, and perhaps also at much smaller spatial scales, isolation *per se* plays little role in the dispersal strategies of planthoppers.

Habitat type (dune vs. salt flat-pond edge vegetation) influenced the incidence of macroptery in *T. venilia*, but only in the male sex (Fig. 4). Macroptery in males was almost five times higher in dune habitats (38%) than in salt flat and salt pond vegetation (8%). Higher levels of macroptery in male planthoppers than in females are symptomatic of the difficulties associated with mate location, because only the male sex searches actively for mates (Denno *et al.*, 1991, in press; Claridge & de Vrijer, 1994; Denno, 1994a; Langellotto, 1997). Variation in salt-grass structure, coupled with a generally low population density (25 ± 5 adults per m^2 ; Table 1), probably underlies this habitat-related difference in macroptery in males of *T. venilia*. The sparse structure of dune vegetation apparently favours the retention of wings because macropters are better able to negotiate such habitats and locate calling females, an effect that has been shown for other delphacid species (Langellotto, 1997). Brachypterous males neither sense nor locate calling females efficiently in heterogeneous vegetation. The situation is reversed in contiguous vegetation, such as the dense stands of salt grass on intertidal flats, a situation where brachypterous males of other planthopper species have been shown to be more successful in locating males and outcompeting macropters for access to them (Langellotto, 1997).

Macroptery was density dependent in the males of *T. venilia*, but the slope of the relationship was significantly steeper in populations occupying dune vegetation than in salt-flat/pond-

margin vegetation, further corroborating the effect of habitat type on the incidence of dispersal capability (Fig. 4). A difference in the slope of this relationship is consistent with the view that there is a genetic difference between dune and salt flat-inhabiting populations of *T. venilia*, whereby the density that triggers the production of macropters in males differs between the two populations (Denno *et al.*, 1991, 1996). An independent assessment using amplified fragment-length polymorphism markers also found a significant genetic difference between the dune and salt-pond populations of *T. venilia* on Guana Island (D. J. Hawthorne, unpublished). This is a remarkable finding considering that these two disjunct populations are separated by only 500 m, albeit by an upland ridge. Other marsh-inhabiting planthopper species with similarly low incidences of macroptery (<20%) show no evidence for the genetic subdivision of populations at such a small spatial scale, although their habitats are relatively contiguous (Peterson & Denno, 1997, 1998). Apparently, the homogenising effects of gene flow between these two populations on Guana Island are offset by the strength of habitat-related differences in selection for the enhancement of flight capability in one habitat and its reduction in the other. The strength of the opposing forces, however, may be less than it appears because gene flow between populations of *T. venilia* depends not only on the fraction of macropters in the population but also on the flight capability of the individuals. One study with Gerrids suggests that the flight capability of the macropterous morph decreases as the proportion of macropters declines in the population (Fairbairn & Desranleau, 1987). Thus, for a planthopper species that averages <30% macroptery, males may be relatively weak flyers, simply flitting around within the habitat in search of females, a behaviour that may diminish frequent gene flow between disjunct populations.

It has been argued that isolation may promote macroptery because only winged adults can colonise small, isolated, and extinction-prone patches (see Travis & Dytham, 1999). If this were the case for the dune-inhabiting populations of *T. venilia*, elevated levels of macroptery would be expected in both sexes in such habitats because planthoppers mate only after they have dispersed to new habitats (reviewed by Denno & Roderick, 1990). In the 3 years of sampling dune vegetation, not one macropterous female was found, even though macropterous males were relatively abundant (Table 1). Moreover, on Guana Island, the extensive Salt Pond population would be the closest source of colonists for the dune-inhabiting population on North Beach. Yet, it is these two populations that show evidence for genetic divergence. Macropterous males in the dune population are more genetically related to their brachypterous counterparts in the dune population than they are to brachypters in the salt-pond population (D. J. Hawthorne, unpublished). Together, these data do not suggest that macroptery in dune populations results from selective colonisation by macropters. Rather, within-habitat selective pressures associated with mate finding appear to be a more parsimonious explanation for elevated macroptery in males.

The lability of dispersal characters in delphacid planthoppers, coupled with their wing-dimorphism, allows the teasing apart of the selective effects of habitat persistence and

structure that interact to shape the dispersal strategies of insects. For planthoppers exploiting low-profile host plants, there is an inverse relationship between habitat persistence and dispersal capability (% macroptery), with volant species predominating in temporary habitats and flightless taxa occurring primarily in long-lived habitats (Denno *et al.*, 1991). Habitat dimensionality and macroptery are related positively, with flight reduction evident in species exploiting low-profile vegetation, and wing retention characteristic of arboreal species (Denno, 1994b). Habitat persistence and dimensionality interact such that flight is retained in species exploiting arboreal habitats, even though habitats are persistent (Denno *et al.*, in press). Thus, the effect of habitat persistence on the incidence of flight capability is realised only for species occupying low-profile habitats such as *T. venilia*.

In addition to the three-dimensional nature of the habitat, finer-scale differences in habitat structure also affect the dispersal strategies of planthoppers, particularly for males. It is argued here that the difference in the structure of salt grass between dune and salt-flat habitats influences the searching efficiency of the male wing forms of *T. venilia*, and hence their mating success. Macropterous males of other delphacids are far more effective at locating females in sparse vegetation and under low-density conditions than are brachypters (Langellotto, 1997). The enhanced incidence of macroptery in males of *T. venilia* occupying sparsely vegetated dune habitats probably also reflects the advantage of flight in mate location.

Historically, coastal strand, marsh, and dune communities have been targeted as habitats where isolation may promote the evolution of flightlessness in insects (see Roff, 1990; Wagner & Lieberr, 1992). Recent studies in these same habitats have played a pivotal role in both challenging the significance of isolation and in demonstrating the importance of habitat persistence and structure in the evolution of insect dispersal strategies (Denno *et al.*, 1991, 1996, in press).

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