

A TRADE-OFF BETWEEN FLIGHT CAPABILITY AND REPRODUCTION IN MALES OF A WING-DIMORPHIC INSECT

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Abstract. The widespread occurrence of dispersal polymorphisms among insects is consistent with the hypothesis that fitness costs are associated with flight capability. Although trade-offs between flight capability and reproduction are well documented in the females of many wing-polymorphic insect species, the relationship between dispersal capability and reproductive success in males is poorly established. Here we examine the potential cost of flight capability in males of the salt-marsh-inhabiting planthopper *Prokelisia dolus* (Hemiptera: Delphacidae). This species exhibits a dispersal polymorphism with both flightless adults (brachypters) and migratory adults (macropters) occurring in populations.

In a competitive setting in the laboratory, brachypterous males exhibited a threefold mating advantage over macropterous males; they obtained 77% of the matings with brachypterous females. This mating advantage resulted, in part, from brachypterous males aggressively displacing rival macropters during courtship. There was also a nonsignificant tendency for brachypterous males to arrive before macropterous males to court a calling female. Neither female rejection behavior nor male body size appeared to contribute to the mating advantage of brachypterous males. When macropterous females were contested, the mating advantage of the male wing forms changed and macropterous males obtained the majority of matings. Thus, there was evidence for assortative mating based on wing form.

When placed with ten brachypterous females, brachypterous males sired twice as many offspring as did macropterous males. This advantage was due to brachypters siring more offspring per female and not from inseminating more females; hence differences in sperm load between the male wing forms are implicated in the siring advantage of brachypters. There was, however, no tendency for brachypterous males to survive longer than their macropterous counterparts; thus, differences in longevity did not contribute to enhanced siring ability. Overall, these results provide support for a trade-off between dispersal capability and reproductive success in males.

Key words: dispersal; flightlessness; mate location; planthopper; *Prokelisia dolus*; siring capability of male wing forms; trade-off between flight capability and reproduction; wing polymorphism.

INTRODUCTION

Dispersal polymorphism is widespread among insects (Harrison 1980, Roff 1986, Fairbairn and Desranleau 1987, Denno et al. 1991, Zera and Denno 1997). In some insects, such as planthoppers and aphids, the dimorphism is extreme and involves fully winged individuals capable of long-distance flight (macropters or alates) and flightless morphs without wings (apteres) or with reduced wings (brachypters) (Dixon 1985, Denno 1994). Because the hind wing is vestigial on brachypters, their dispersal capability is severely limited. In other polymorphic insects, flightless morphs result from wing muscle histolysis even though fully developed wings remain (Borden and Slater 1969, Dingle 1985).

The mere occurrence of flight polymorphisms suggests that fitness costs are associated with the ability

to fly (Roff 1984, Denno et al. 1991). The energy used to construct wings and flight muscles is simply not available for reproductive investment (Zera and Denno 1997). Generally, the literature provides support for such a trade-off in females. When raised on the same resource, macropterous females have lower fecundity than flightless females in crickets (Tanaka 1976, Roff 1984), aphids (Dixon 1972, Wratten 1977, Walters and Dixon 1983), planthoppers (Kisimoto 1965, Denno et al. 1989, Denno 1994), water striders (Anderson 1973, Zera 1984), corixids (Young 1965), and pea weevils (Utida 1972). Also, reproduction is delayed in the migratory forms of many female insects (Roff 1986, Zera and Denno 1997). Other costs associated with the possession of wings include delayed development, increased mortality, decreased mating success, or reduced egg size (Roff 1984, 1986, Solbreck 1986).

Although correlations between wing form and components of fitness in females have been well studied and have contributed toward the general understanding of the evolution, maintenance, and population conse-

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quences of variation in dispersal (Denno et al. 1991, 1996, Roff and Fairbairn 1991, Wagner and Liebherr 1992, Zera and Denno 1997), the relationship between wing form and components of fitness in males has been almost completely neglected (Denno 1994, Ott 1994).

The paucity of information on the relationship between wing form and components of fitness in males is an important omission from the study of dispersal polymorphisms in insects (Denno and Roderick 1990, Zera and Denno 1997). Verification of the ecological and evolutionary basis for dispersal polymorphisms requires that fitness differences be documented between the wing forms of both sexes. Although the frequency of wing reduction in males may be an artifact of a genetic correlation between the sexes (Roff and Fairbairn 1991), it is more likely that dispersal polymorphism in males reflects differential selection between the wing forms (Denno et al. 1991, Ott 1994).

Few published studies have explored the possible trade-off between dispersal capability and reproductive success in males, and those that have provide conflicting evidence for the existence of fitness costs associated with macroptery (Zera and Denno 1997). A limited number of studies involving planthoppers and other wing-dimorphic insects have demonstrated a fitness advantage in brachypterous males. Compared to the macropterous males of planthoppers, brachypters can be more aggressive in male–male interactions (Ichikawa 1982), develop quicker (Novotný 1995), acquire matings more successfully (Novotný 1995), and live longer as adults (Roderick 1987). Similarly, for other insects, such as water striders, bruchid beetles, chinch bugs, and thrips, brachypterous males reproduce at an earlier age (Utida 1972, Fujisaki 1992) and/or mate more frequently than their macropterous counterparts (Crespi 1988, Fujisaki 1992, Kaitala and Dingle 1993). In one cricket species, brachypterous males are more likely to attract females and spend more time calling than macropterous males (Crnokrak and Roff 1995). Importantly, sexual selection favors apterous males in several natural populations of a water strider species (Fairbairn and Preziosi 1996).

In contrast, other studies of male planthoppers have failed to detect wing-form differences in gonadal development (Mochida 1973), survival (Kisimoto 1965, Denno et al. 1989), or reproductive success (Mishiro et al. 1994). Two studies of male crickets have also failed to find consistent differences between wing forms in mating success and certain components of reproductive success (Roff and Fairbairn 1991, Holtmeier and Zera 1993). Thus, evidence for a trade-off between dispersal capability and reproductive success in male insects is mixed. However, variation in the conditions under which insects were raised to assess fitness differences between wing forms may have contributed to the conflicting evidence of a trade-off (Denno 1994, Zera and Denno 1997). Moreover, because the costs of reproduction are generally much lower in

males than in females (Trivers 1972), it may be more difficult to detect any reproductive penalties selectively imposed on macropterous males (Ott 1994, Zera and Denno 1997).

Although the advantage of wings in males is clear for reasons of habitat escape (Denno et al. 1991, 1996) and mate location (Roff 1990, Denno et al. 1991, Denno 1994, Langellotto 1997), the advantage of flightlessness in males remains poorly investigated. The key to understanding dispersal polymorphism in males is to identify costs associated with flight capability and to determine the conditions under which flightlessness and macroptery are advantageous (Denno 1994, Ott 1994, Zera and Denno 1997).

We selected the wing-dimorphic planthopper *Prokelisia dolus* Wilson (Hemiptera: Delphacidae) to determine if there are reproductive costs associated with the presence of wings in males that can give rise to fitness differences analogous to those observed in females (see Denno et al. 1989). Specifically, we assessed whether intrinsic differences exist between the male wing forms of *P. dolus* in (1) survivorship, (2) ability to locate and secure mates, (3) ability to acquire multiple matings, and (4) ability to sire offspring from multiple females. Based on existing evidence for a trade-off between dispersal and reproduction in females (Denno et al. 1989), we hypothesized that brachypterous males will outperform macropterous males on all of these counts. The results of these studies provide the basis for determining if fitness costs are associated with wing form in males, and will begin to elucidate the evolution of wing polymorphism from a more general perspective.

METHODS

Study organism

Prokelisia dolus is an abundant sap-feeding insect (densities up to 1,000 adults/m²) on the intertidal marshes along the Atlantic and Gulf Coasts of the United States, where it feeds in the phloem of its only host plant, the perennial cordgrass, *Spartina alterniflora* (Denno et al. 1987, 1994, 1996). This planthopper occurs predominantly in meadow habitats on the high marsh where it undergoes multiple generations annually (Denno et al. 1987, 1996). Populations of *P. dolus* are composed of both volant macropters and flightless brachypters (see Plate 1). On average, 65–92% of the adults are brachypterous in Atlantic Coast populations, a wing form composition which reflects the persistence of their habitats (Denno et al. 1996).

Wing form in planthoppers is determined by a developmental switch which responds to environmental cues (Denno and Roderick 1990, Denno et al. 1991). The sensitivity of the switch is heritable and under polygenic control (Denno and Roderick 1990, Denno et al. 1991, Denno 1994). Various environmental cues such as crowding and host plant condition trigger the



PLATE 1. Winged adults (flight-capable macropters and flightless brachypters) and nymphs of *Prokelisia* planthoppers on the cordgrass host plant, *Spartina alternifolia*. Brachypterous males (upper right) acquire more matings and sire more offspring than macropterous males (middle). Thus, flight capability appears to impose a reproductive penalty on male fitness. Photograph by Hartmut Döbel.

developmental switch and influence wing form (Kisimoto 1965, Denno et al. 1985, Denno 1994). Of all the environmental factors known to affect wing form in planthoppers, population density is clearly the most influential for most species (Denno and Roderick 1990, Denno et al. 1991, 1996). In *P. dolus*, the production of migratory forms (macropters) is density dependent and is associated with crowded conditions (Denno et al. 1991, 1994, 1996).

Males of *P. dolus* can mate multiply, but females usually mate once during adult life unless the male from the previous mating was sperm depleted (Heady 1993). Once mated, females of *P. dolus* are no longer receptive to courting males (Heady and Denno 1991). For *P. dolus*, female receptivity is inhibited by a substance in male ejaculate (Heady 1993). Mate location is achieved by acoustic communication whereby both sexes communicate through substrate-transmitted vibrations (Heady and Denno 1991). Calls are produced as duets between males and females with only the male

moving toward the stationary female (Heady and Denno 1991). Females may exhibit rejection behavior during courtship, but such behaviors are not attributable to differences in call structure between the two wing forms (Heady and Denno 1991). Female macropters mature later in life and begin calling at an older age than female brachypters. By contrast, males of both wing forms become reproductively mature soon after eclosion and begin calling almost immediately (Heady and Denno 1991).

For *P. dolus*, brachypterous females live longer, reproduce earlier, and are over twice as fecund as macropterous females (Denno et al. 1989). Furthermore, there is accumulating evidence that stress (e.g., poor nutrition and extended diapause) exacerbates the differences in fitness between brachypters and macropters with brachypters owning an even greater advantage in realized fecundity (Denno et al. 1989, Denno 1994, Zera and Denno 1997).

Comparative survivorship of male wing forms

To test the hypothesis that brachypterous males survive longer than macropterous males, two experiments were conducted. In the first experiment, males of both wing forms were maintained as adults on whole, potted, fertilized *Spartina* plants on which individuals were free to select their preferred feeding site (axil of subterminal blade) on the plant. In the second experiment, males of both wing forms were confined to preferred (axil of subterminal blade) or non-preferred feeding sites (middle of basal blade in the fourth leaf position) on the same plant, and their survival measured. These feeding sites were chosen because previous studies have shown that the mean crude protein content of *Spartina* leaves decreases from 9.4% at the apex to 6.0% at the base of the plant (Denno et al. 1980). Thus, this second experiment provided the opportunity to compare the survival of the two wing forms under ideal and stressed nutritional conditions. For both experiments, comparative survivorship of male wing forms was assessed in a growth chamber under controlled laboratory conditions (22°C, 14:10 light : dark cycle).

To assess survivorship when males of each wing form were free to choose preferred feeding sites, single pairs of newly eclosed virgin males (one macropter and one brachypter) were enclosed in a plastic tube cage (30.5 cm long × 3.8 cm diameter) which enclosed two culms of a potted *Spartina alterniflora* plant (see Denno et al. 1985). Potted plants were arranged in plastic tubs (48 × 26 × 13 cm) filled with 2–3 cm of water, and tubs were rotated in the incubator at each census.

The survivorship of 27 replicate pairs of male wing forms was visually assessed at two-day intervals until 100% mortality was observed. Survivorship curves were constructed for both wing forms by calculating the proportion of the initial cohort surviving to each census date. Differences in survivorship (*d*) between

wing forms were assessed using a Mann-Whitney *U* test (SAS 1990).

To test the effect of wing form and feeding-site quality on survivorship, pairs of newly emerged male wing forms were isolated in small plastic tube cages (5.5 cm long \times 1 cm diameter) each of which surrounded one preferred and one nonpreferred feeding site on a potted *Spartina* plant. Thus, one plant carried two cages each of which contained one male of each wing form. In all, 24 replicates were established on each of the two feeding-site treatments. Survivorship was assessed by visual inspection at two-day intervals until 100% mortality was observed. The effects of wing form, feeding site, and plant (block) on survival (days) were assessed using ANOVA (SAS 1990).

For both experiments, brachypterous and macropterous adults were obtained by raising cohorts of nymphs under low-density (20–40 nymphs/cage) and moderate-density conditions (40–80 nymphs/cage) respectively on fertilized seedlings of *Spartina*. The moderate-density condition promotes the production of macropters yet without any obvious adverse effects on plant quality (Denno et al. 1985, Denno and Roderick 1992). We have no evidence that this density difference in rearing conditions results in differential mortality between male wing forms, because the survival of female wing forms remains unaffected by density except under very crowded rearing conditions (Denno and Roderick 1992).

Comparative mating success of male wing forms

We examined the effect of wing form on several components of male mating success in a rival setting. Single pairs of two-day-old virgin males (one brachypter and one macropter) were isolated with a four-day-old, sexually mature (see Heady and Denno 1991), virgin brachypterous female so that the male which successfully acquired the mating could be observed. Two-day-old males were selected for this experiment because both wing forms of *P. dolus* are reproductively mature at this age and they continue to produce attraction calls for 10 d thereafter (see Heady and Denno 1991). Thirty replicate triads were established. Similarly, pairs of both male wing forms were also isolated with a six-day-old virgin macropterous female (18 replicate triads).

All triads were aspirated into small mating cages containing a single *Spartina* leaf. Cages consisted of the cut end of a 5.5 cm plastic Pasteur pipet inserted into the bottom of a 5 cm long segment of a plastic test tube (1 cm diameter). The top of the cage was capped with a foam rubber plug. Mating cages were suspended in a wooden rack above water-filled cups (78.8 mL) so that the basal end of the *Spartina* blade was submerged in water. Virgin females were placed on the top of the leaf, and both males were released together at the bottom of the leaf equidistant from the female. This release arrangement was chosen to mimic

a common mating scenario on a preferred feeding site, whereby virgin females position themselves atop the leaf blade and males approach from below (G. A. Langellotto, *unpublished data*). Females that did not exhibit calling behavior (rapid vibration of the abdomen) after 10 min were replaced with another female. During the experiment, all cages were maintained on a laboratory bench with a GE Miser Spot light (100 W; General Electric Company, Schenectady, New York) suspended 1.3 m above the setup. Temperature during all replicates of the experiment ranged from 24–27°C.

To elucidate possible mechanisms underlying variation in mating success, the following parameters were recorded for each replicate: (1) wing form of the male that acquired the mating, (2) morph which arrived first to court the female, (3) time to locate female (min), (4) body size (post-experiment live mass in mg), (5) male–male aggression (visual displays of aggression included wing-flitting, bending the abdomen directly towards the rival male, and physically pushing the rival male), (6) male displacement (pushing the rival wing form aside during courtship), and (7) female rejection behavior (walking or jumping away during attempted courtship). In addition, mating duration (min), a parameter which may influence siring capability, was measured for the successful rival wing form.

Categorical data analysis of counts was used to test if the observed frequency of males of each wing form that (1) acquired the mating, (2) arrived first to court the female, (3) expressed aggression toward the rival male, (4) displaced the rival male, and (5) was rejected at least once by the female (a rejected male may ultimately mate), differed from an equal expectation (CATMOD procedure, SAS 1990). ANOVA was used to test the effect of male wing form on (1) time to arrive at female, (2) body size, and (3) mating duration (SAS 1990). ANOVA was also used to assess differences in body size between males that were successful and unsuccessful in securing matings and a Wilcoxon Signed Rank Test was used to determine if the larger male in the pair was more likely to mate. In all cases, data were analyzed separately for males caged with brachypterous and macropterous females.

In a companion treatment, the mating duration of males of both wing forms was assessed under nonrival conditions using the identical small-cage setup. For this treatment, single brachypterous and macropterous males were isolated with a brachypterous female and their mating durations (min) were determined. In all, 32 and 19 replicates were established for brachypterous and macropterous males, respectively. Mating duration of the two wing forms in this nonrival setting was compared to mating duration in a rival setting using ANOVA with male wing form and rival setting (present vs. absent) in the model. Treatment means were compared using Sidak's adjustment for multiple comparisons (SAS 1990).

Comparative siring capability of male wing forms

The comparative siring ability of the male wing forms of *P. dolus* was determined with a mating experiment in the laboratory. The ability of virgin males (both wing forms) to sire offspring from multiple matings was tested by placing a single two-day-old male with a group of 10 brachypterous females (four-day-old) for eight hours in a plastic tube cage (30.5 cm long \times 7.6 cm diameter) containing two *Spartina* culms. After the mating period, all 10 females were removed and individually isolated on *Spartina* plants enclosed in plastic tube cages, and allowed to oviposit. The number of offspring sired was determined from the respective fecundity of each female (see Denno et al. 1989). Ten replicates were established for each male wing form.

For each replicate, the following measures of reproductive success were determined: (1) the total number of offspring sired (combined fecundities of the 10 females), (2) the number of females producing offspring (maximum of ten), and (3) the average number of offspring per female of those which deposited fertile eggs. ANOVA was used to test the effect of male wing form on each of these three measures of reproductive success.

Data from this experiment were also used to test indirectly the hypothesis that sperm load (number of sperm transferred during mating) is greater and that sperm depletion is less in brachypterous males compared to macropterous ones. ANCOVA was used to examine the relationship between the number of offspring sired per female and the number of females mated with by a male (indexed as number of females producing some offspring; covariate) for the two wing forms. If sperm load is greater for brachypters than macropters, then there should be a significant effect of wing form on the number of offspring sired per female. If sperm is depleted more rapidly in macropters than brachypters, then the slope of the relationship between the mean number of offspring sired per female and the number of females mated with should differ from zero and be steeper for macropters than brachypters. A significant interaction between wing form and the number of females producing offspring on the mean number of offspring sired per female would be consistent with greater sperm depletion in the macropter. Regression analysis was used to test if slopes for this relationship were different from zero (SAS 1990).

The virginity of males and females used in experiments was ensured by determining the sex of fifth instar nymphs (ovipositors and male genital capsules can be seen through the nymphal integument prior to adult eclosion) and establishing single-sex colonies of nymphs prior to their adult molt (Langellotto 1997). Newly-eclosed virgins were removed from the colonies on a daily basis, placed in a uniform-age cohort of

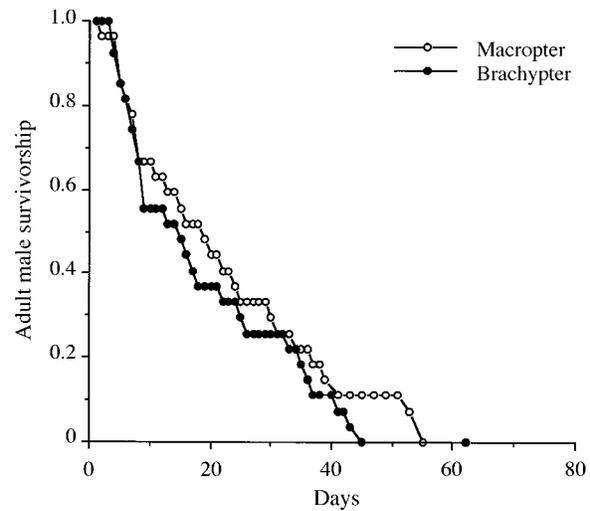


FIG. 1. Survivorship schedules of brachypterous and macropterous males of *Prokelisia dolus* assessed on caged plants of *Spartina* on which males were free to select optimal feeding sites. There was no significant difference in survivorship between the two male wing forms (Wilcoxon test, $Z = 0.572$, $P = 0.56$).

males or females and allowed to mature before they were used in experiments.

For all experiments, laboratory cultures of *P. dolus* were initiated with gravid females collected from meadows of short-form *Spartina alterniflora* at Elliott Island, Dorchester County, Maryland. Cultures of *P. dolus* were maintained in the laboratory on caged plants of *Spartina* (see Denno et al. 1989). The *Spartina* seedlings used in the experiments (20–25 cm in height) were potted in sand (6.5 cm diameter pots) and maintained in plastic-lined flats (1.0 \times 0.7 m) filled half-way with water so that sand was continuously wet yet seedlings were never inundated. Flats received applications of a 3:1 mixture of ammonium nitrate (N:P:K, 34:0:0) and phosphoric acid (0:46:0). Seven grams of fertilizer were applied once every two weeks to each flat and all seedlings were maintained in the greenhouse. These culture conditions result in plants which roughly represent the most nutritious alternative available in the field (Denno et al. 1985).

RESULTS

Comparative survivorship of male wing forms

When free to choose preferred feeding sites on the plant, there was no significant difference in survivorship between the two male wing forms ($U = 398$, $P = 0.56$; Fig. 1). On average, adult brachypterous males and macropterous males lived 17.5 ± 2.6 (mean \pm 1 SE) and 20.9 ± 3.1 d, respectively. When planthoppers were confined to preferred and nonpreferred feeding sites there was no effect of wing form on survivorship, with brachypters and macropters surviving 11.9 ± 1.4 and 12.1 ± 1.5 d, respectively ($F_{1,95} = 0.01$, $P = 0.91$).

TABLE 1. Comparison of components of mating success of the male wing forms (one brachypter and one macropter) of *Prokelisia dolus* when caged together with either: (a) a single brachypterous female or (b) a single macropterous female.

Parameter	Brachypterous male		Macropterous male		χ^2	P
	Proportion	n	Proportion	n		
a) Tests with brachypterous female						
Acquiring mating	0.77	30	0.23	30	5.59	0.02
First arrival to female	0.57	28	0.43	28	0.39	0.53
Displaced by a rival male	0.05	22	0.32	22	4.14	0.04
Initiating aggressive encounters	0.30	30	0.33	30	0.08	0.78
Rejected by female	0.04	28	0.18	17	2.14	0.14
b) Tests with macropterous female						
Acquiring mating	0.39	18	0.61	18	0.59	0.44
First arrival to female	0.44	18	0.56	18	0.15	0.70
Displaced by a rival male	NO†		NO†		N/A‡	N/A‡
Initiating aggressive encounters	0.28	18	0.44	18	1.07	0.30
Rejected by female	NO†		NO†		N/A‡	N/A‡

† NO = not observed. There were no observed instances in which a male displaced a rival wing form from beside a receptive female. There were no cases of male rejection by a macropterous female.

‡ N/A indicates that the χ^2 test is not applicable.

Males of both wing forms, however, did survive better on the preferred feeding site (16.2 ± 1.7 d) compared to the nonpreferred site (7.8 ± 0.9 d) ($F_{1,95} = 23.58$, $P = 0.0001$). Survival was also higher on some plants compared to others ($F_{23,95} = 1.92$, $P = 0.02$). Overall survival of males was probably higher in the free choice experiment (Fig. 1) because males were allowed to move from one preferred feeding site to another as the current one became nutrient depleted. Confining males to a particular site removes this behavioral option and saddles them with the consequences of feeding-induced reductions in plant quality (Olmstead et al. 1997).

Comparative mating success of male wing forms

Overall, brachypterous males were much more successful than macropterous males in acquiring matings with a brachypterous female when placed in a one on one competitive situation with a rival male ($\chi^2 = 5.59$; $P = 0.02$). In this confined setting, brachypterous males obtained 77% of the matings with brachypterous females (Table 1a).

This mating advantage was not explained by the earlier arrival of the brachypterous male to court the female. There was neither a significant difference in the

proportion of brachypterous (0.57) and macropterous males (0.43) which arrived first to court the female (Table 1a), nor was there a difference in their mean time of arrival at the female (Table 2a).

The mating advantage of the brachypterous male may be due in part to its ability to displace macropterous males which are attempting to mate. The proportion of macropterous males displaced by brachypterous males was significantly higher (0.32) than the reverse situation of macropters pushing brachypters aside (0.5) (Table 1a). However, displacement occurred in only 8 of the 22 paired approaches (36%). Displacement success was not attributable to either the initiator of male-male aggression or body size. For example, the proportion of brachypterous males which initiated an aggressive encounter with the rival macropter was not different (0.30) from the proportion of aggressive interactions initiated by macropterous males (0.33) (Table 1a). Also, there was no significant difference between the body mass of brachypterous (0.49 ± 0.02 mg) and macropterous males (0.54 ± 0.02 mg) used in the experiment (Table 2a). Furthermore, there was no difference in body mass between males which successfully acquired the mating (0.50 ± 0.02 mg) and

TABLE 2. Comparison of components of mating success of the male wing forms (one brachypter and one macropter) of *Prokelisia dolus* when caged together with either: (a) a single brachypterous female or (b) a single macropterous female.

Parameter	Brachypterous male		Macropterous male		Source of variation	df	MS	F	P
	Mean \pm 1 SE	n	Mean \pm 1 SE	n					
a) Brachypterous female									
Time to arrival (min)	6.54 \pm 1.36	20	8.71 \pm 1.76	6	wing form	1, 24	24.90	0.69	0.41
Body mass (mg)	0.49 \pm 0.02	26	0.54 \pm 0.02	26	wing form	1, 50	0.00	3.17	0.08
Mating duration (min)	6.00 \pm 0.25	19	5.17 \pm 0.40	6	wing form	1, 23	3.17	2.71	0.11
b) Macropterous female									
Time to arrival (min)	12.00 \pm 3.33	9	13.86 \pm 3.42	7	wing form	1, 14	13.58	0.15	0.70
Body mass (mg)	0.487 \pm 0.022	18	0.533 \pm 0.024	18	wing form	1, 34	0.000	2.02	0.17
Mating duration (min)	5.71 \pm 0.29	7	6.00 \pm 0.30	11	wing form	1, 16	0.349	0.42	0.53

those which failed to do so (0.53 ± 0.02 mg) independent of wing form ($F = 1.28$; $P = 0.264$). Moreover, the larger male in the pair was not more likely to mate with the female, again independent of wing form ($T_S = -45.5$, $P = 0.20$). Also, females rejected similar proportions of brachypterous (0.04) and macropterous males (0.18) by walking away from the courting male (Table 1a).

In the presence of a rival male, there was no difference in the mating duration of brachypterous (6.00 ± 0.25 min) and macropterous males (5.17 ± 0.40 min) ($F_{1,72} = 2.71$, $P = 0.11$; Table 2a). However, in the absence of a rival male, the mating duration of macropters was longer (8.16 ± 0.95 min) than that for brachypters (5.97 ± 0.31 min). This pattern is evidenced by an analysis which found a significant effect of rival male presence ($F_{1,72} = 4.88$; $P = 0.030$) and a significant rival by male wing form interaction on mating duration ($F_{1,72} = 5.09$; $P = 0.027$).

The above results were based solely on male wing-form responses to brachypterous females. When females were macropterous, the mating advantage of the male wing forms changed whereby brachypters and macropters obtained 39% and 61% of the matings respectively. Although these two proportions did not differ from an equal expectation (Table 1b), they did differ significantly from the 77% and 23% mating success of brachypterous and macropterous males respectively when the female was brachypterous ($\chi^2 = 6.41$; $P = 0.01$). Thus, there was evidence for assortative mating related to wing form.

Once again, no significant difference was found between the male wing forms in the proportion which arrived first to court the macropterous female (Table 1b), the average time of arrival at the female (Table 2b), or the proportion of males initiating an aggressive interaction with the rival male (Table 1a). No displacement behavior was observed between rival males, and no macropterous female exhibited rejection behavior toward any male. Moreover, there was no difference in the body mass of brachypterous males and macropterous males used in this experiment (Table 2b). Also, the larger male in the pair was no more likely to mate than the smaller male ($T_S = -23.5$, $P = 0.27$). Last, in the presence of a rival, there was no difference in the mating duration of brachypterous males and macropterous males (Table 2b).

Comparative siring capability of male wing forms

When caged with 10 virgin brachypterous females, brachypterous males sired significantly more offspring (295 ± 43) than macropterous males (142 ± 41) ($F_{1,16} = 6.62$, $P = 0.02$; Fig. 2a). However, the number of females in the group which produced offspring did not differ between the male wing forms ($F_{1,16} = 0.40$, $P = 0.53$; Fig. 2b). On average, brachypterous males inseminated 5.4 ± 0.7 females, whereas macropterous males inseminated 4.9 ± 0.5 females. There was a sig-

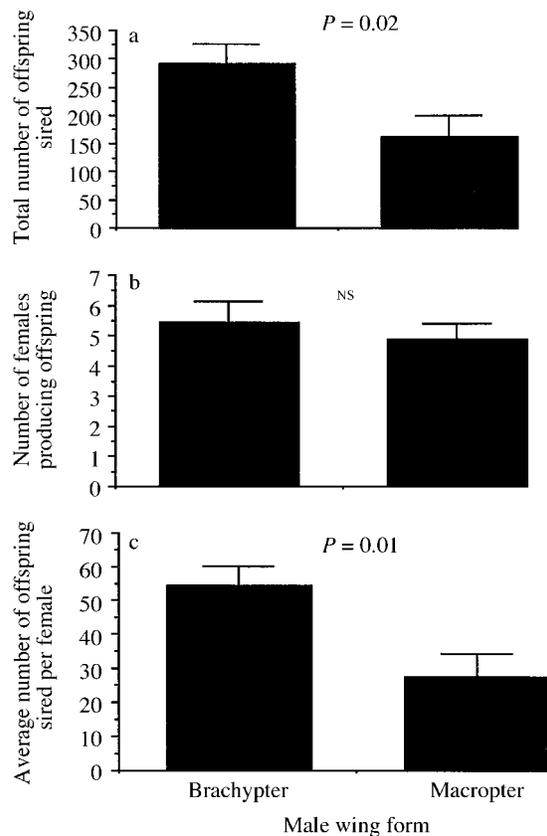


FIG. 2. (a) Total number of offspring sired, (b) number of females producing offspring, and (c) average number of offspring sired per female, by brachypterous and macropterous males of *Prokelisia dolus* when each was caged individually with 10 brachypterous females for an 8-h period. Significant (P) and nonsignificant differences (NS) are noted above each wing-form comparison (ANOVA).

nificant effect of wing form on the number of offspring sired per female ($F_{1,16} = 8.92$, $P = 0.01$; Fig. 2c). Brachypterous males sired 54.4 ± 5.8 offspring per female whereas macropterous male sired only 27.4 ± 7.0 offspring per female.

There was no indication of sperm depletion for either wing form, as evidenced by the lack of relationship between the number of females a male mated with and the mean number of offspring sired per female by brachypterous ($Y_{\text{Brachypter}} = 123.3 - 11.5X$, $R^2 = 0.28$, $P = 0.12$) or macropterous males ($Y_{\text{Macropter}} = 37.2 - 0.529X$, $R^2 = 0.0013$, $P = 0.92$). In addition, no significant interactive effect was found between male wing form and the number of females with whom males mated on the mean number of offspring sired ($F_{1,16} = 1.68$, $P = 0.21$). This result further supports the notion that sperm depletion does not occur when males mate repeatedly. There was, however, a significant main effect of male wing form on the mean number of offspring sired ($F_{1,17} = 4.58$, $P = 0.047$).

DISCUSSION

Although a trade-off between dispersal capability and reproductive success has been well documented in the females of many wing-dimorphic insects, the relationship between wing form and fitness remains poorly investigated for males (Denno 1994, Ott 1994, Zera and Denno 1997). Even though a few studies of planthoppers and other wing-dimorphic insects have shown a fitness advantage to brachyptery in males (Fujisaki 1992, Kaitala and Dingle 1993, Crnokrak and Roff 1995, Novotný 1995, Fairbairn and Preziosi 1996), others have failed to detect a significant difference in some component of reproductive success between male wing forms (Roff and Fairbairn 1991, Holtmeier and Zera 1993, Mishiro et al. 1994).

This study found substantial support for an inherent trade-off between flight capability and reproductive success in males of the wing-dimorphic planthopper, *P. dolus*. In a confined setting in which both male wing forms were present with a brachypterous female, brachypterous males acquired many more matings (77%) than macropterous males. Furthermore, brachypters sired more than twice as many offspring as macropterous males (Fig. 2a). For this assessment of siring capability, males were provided simultaneous access to several virgin brachypterous females, a situation which occurs frequently in the habitats of this common and aggregative planthopper (Denno and Roderick 1992, Cook and Denno 1994, Denno 1994).

Elucidating the mechanisms that underlie the siring advantage for brachypters of *P. dolus*, however, proved to be elusive and complicated. Costs associated with flight capability may impose asymmetries between male wing forms in their: (1) ability to detect and locate calling females, (2) aggressiveness during male-male interactions, (3) choice by females, or (4) sperm load and mating duration. Thus, the two wing forms may not acquire matings or sire offspring with equal frequency. The literature on planthopper mating systems suggests that some or all of these factors may play a role. First, both sexes of planthoppers communicate acoustically through substrate-borne vibrations, and males use female "calls" to locate potential mates (Claridge 1985, Heady and Denno 1991). Although the call structures of the male wing forms of *P. dolus* do not differ (Heady and Denno 1991), male wing forms may differ in their ability to detect a calling female. Thus, brachypterous males may sense and thereafter locate females more efficiently, at least at a small spatial scale. Second, male planthoppers exhibit aggressive behavior toward other males either by producing unique calls in their presence or by physically contacting them as they search for or court females (Ichikawa 1982). Consequently, brachypterous males may preempt macropters during courtship and thereby acquire more matings. Third, females of *P. dolus* exhibit rejection behaviors such as kicking and walking away

when some males court or attempt to mate (Heady and Denno 1991, Heady 1993). Last, females may employ "cryptic choice" in the sense that even though a male is accepted as a partner in copulation, he may be rejected as father of the female's offspring via mechanisms under her control (Eberhard 1994). Consequently, females may selectively choose brachypters over macropters if they court simultaneously, or females may use more of their sperm during copulation. Furthermore, differences in sperm load (number transferred during copulation) between brachypterous and macropterous males may contribute to the siring advantage of the brachypter, but this possibility has not been explored for any planthopper species.

To investigate the mechanisms which might underlie the mating and siring advantage of brachypterous males, we compared several characteristics between the male wing forms of *P. dolus* in a rival setting. The marked mating advantage of brachypterous males could not be explained by their ability to arrive before rival macropters at calling females. There was, however, a non-significant tendency in this direction (Table 2a). More meaningful, perhaps, was the significant difference in displacement behavior between the wing forms; brachypterous males displaced courting macropters much more frequently than the reverse case in which a macropter pushed a brachypter aside during a mating attempt (Table 1a). Furthermore, there was a nonsignificant tendency for brachypterous females to reject macropters more than brachypters either by kicking them away or by simply walking away herself. Because male size can influence both the outcome of male-male interactions as well as female choice in insects (McCauley and Wade 1978, Gwynne 1984, Crespi 1988, Fairbairn and Preziosi 1996), brachypterous males may have owned a mating advantage due to greater body mass. However, there was no significant difference in live body mass between the brachypterous and macropterous males used in the experiment (Table 1a). Moreover, males acquiring matings were not larger than those which failed to mate. Thus, the mating advantage of brachypterous males appears in part to result from a combination of the aggressive displacement of rival macropters and perhaps the selective rejection of macropterous males by females.

If wing forms mate assortatively, then the mating success of a particular male wing form may depend on the wing form of the calling female (Ott 1994). Consequently, the superior ability of brachypterous males to secure matings may change in the presence of macropterous females. For the planthopper *Nilaparvata lugens*, both male wing forms preferred to mate with brachypterous females (Takeda 1974), the more fecund wing form (Denno et al. 1989). Our data for *P. dolus*, however, suggest otherwise. There was a significant tendency for like wing forms to mate with each other; brachypterous males secured 77% of the matings with brachypterous females and macropterous males ob-

tained 61% of the matings in the presence of a macropterous female. However, the mating advantage of macropterous males with macropterous females could not be explained by arrival time at the female, male aggression, male displacement, male body size, or female rejection behavior. It may be that morphological similarity between the sexes facilitates copulation and promotes male mating success, but the mechanism remains enigmatic when macropterous females are involved. Determining the siring capability of male wing forms with macropterous females was beyond the scope of this study. Nevertheless, it should be pointed out that brachypters of both sexes are the most frequent morph in most habitats of *P. dolus* on mid-Atlantic marshes (65–92%) and that virgin macropters selectively encounter one another most often in newly colonized habitats or under low-density conditions (Denno et al. 1996). Thus, rivalry between both male wing forms and brachypterous females is the most frequent case. Noteworthy in this context is our finding that the mating duration of the macropterous male is significantly decreased in the presence of a rival brachypter, a result which does not occur for brachypterous males. Given that mating duration is roughly related to sperm load and the future propensity for the female to mate again (Heady 1993), male–male rivalry may selectively decrease the mating success of macropterous males.

The difference we observed in the siring capability of brachypterous and macropterous males (Fig. 2a) provides convincing evidence for the existence of intrinsic costs associated with flight capability in males. The overall siring advantage resulted not from the brachypter's ability to inseminate significantly more females than macropterous males (Fig. 2b), but instead from the brachypter's ability to sire more offspring per female (Fig. 2c). A possible explanation for the brachypter's siring advantage may result from a larger sperm load, more efficient sperm delivery during copulation, or cryptic female choice. Support for greater sperm volume in brachypterous than macropterous males stems from the experiment where single males were exposed to ten virgin females followed by a measurement of their fecundity. Brachypterous males sired more offspring per female than macropters when the number of females each inseminated was the same, suggesting that brachypterous males deliver a greater volume of sperm to females than macropters. There was, however, no evidence of sperm depletion for either wing form because the number of offspring sired per female did not decline with an increase in the number of inseminated females. However, sperm depletion does occur in males of *P. dolus* when they mate with a series of females within a very short time period (1 h) (Heady 1993). The duration of our experiment was much longer (8 h) and perhaps reduced the probability for sperm depletion.

Dispersal capability (macroptery) in *P. dolus* apparently does not impose a cost on male survivorship.

Survivorship schedules for both wing forms of *P. dolus* are remarkably similar when males are free to select preferred feeding sites on their *Spartina* host plant (Fig. 1). Thus, no siring advantage should accrue as a result of differential longevity between the male wing forms. Similarly, a general survey of experimental studies involving planthoppers found no consistent difference in adult survivorship between female wing forms (Denno et al. 1989). The exceptions, however, were consistent with the notion of a trade-off between dispersal and reproduction in that brachypters tended to outlive macropters (May 1975, Roderick 1987, Denno et al. 1989, Denno 1994).

Because fitness differences between the wing forms of female planthoppers are maximized under stressed conditions (Kisimoto 1965, Denno 1994), and because plant nutrition is strongly implicated in the reduced survival of sap-feeding insects (McNeill and Southwood 1978, Cook and Denno 1994), we examined the survival of the two male wing forms on preferred (nitrogen-rich) and nonpreferred (nitrogen-poor) feeding sites. However, we found that wing form had no effect on male survival, although survivorship for both wing forms was higher on the preferred feeding site. Thus, there does not appear to be any plant-quality-induced difference in survivorship of the male wing forms of *P. dolus* that might selectively influence siring capability.

Our results strongly suggest that intrinsic costs are associated with flight capability in the males of *P. dolus*. Brachypterous males exhibited a better than three to one advantage over macropterous males in securing matings with brachypterous females. Moreover, brachypterous males sired more than twice as many offspring as did macropterous males. Although differences in sperm load between the male wing forms are implicated, the mechanism underlying the siring advantage of brachypters remains unclear. Mechanism aside, there is considerable support for the existence of a trade-off between reproductive success and flight capability in males of *P. dolus*. As long as females are abundant and brachypterous, such that males do not have to fly to locate mates, brachyptery in males should be favored due to the inherent siring advantage associated with flightlessness. However, several situations in the field will likely shift the mating advantage to macropterous males. If mates are rare, and males must fly among plants to locate females, then macropters should incur dramatically enhanced mating success whereas that for brachypters should plummet (Denno et al. 1991). Also, under conditions of local patch deterioration, only virgin macropters of both sexes emigrate to colonize new habitats (Denno et al. 1991, Denno 1994). Under these conditions in new habitats, only macropterous males will be available to locate females and sire offspring. Thus, the reproductive cost associated with flight capability coupled with variation in habitat persistence and mate availability should act in concert to maintain

wing dimorphism in the males of this phytophagous insect.

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