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Comparison of Female Reproductive Effort and Male Mating Success between Macropterous and Brachypterous Forms of the Small Brown Planthopper, *Laodelphax striatellus* (Homoptera: Delphacidae)¹

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The reproductive traits of female adults of the small brown planthopper, *Laodelphax striatellus* were compared between brachypterous and macropterous forms under 25°C and 16L–8D conditions. The reproductive rate and the reproductive effort of brachypterous females were higher than that of macropterous females. Brachypterous females appeared to allocate more energy to reproduction than macropterous females. The mating success of males was assessed in terms of the eye color of nymphs, sired by either of the males in competition between the two forms. The mating success of males did not differ between the winged forms at 17°C or 25°C. Thus, the fitness advantage of wing reduction in males was not clear.

Key words: *Laodelphax striatellus*, brachypter, macropter, reproductive effort, mating success

INTRODUCTION

The small brown planthopper, *Laodelphax striatellus*, has two wing forms: macroptery and brachyptery. Various environmental factors such as population density, temperature and nutritional conditions of host plants during the nymphal period (KISIMOTO, 1959) and genetic factors (MAHMUD, 1980; MORI and NAKASUJI, 1990) influence the determination of wing forms. The sexes respond to different environmental factors when producing brachypters. The incidence of brachypters is high among females, given low population density, whereas males are influenced by shorter days (KISIMOTO, 1956 a).

So far, the relative fitness between wing morphs and the phenotypic trade-off associated with wing reduction has been demonstrated in females (ROFF and FAIRBAIRN, 1991, 1994). In general, females with reduced wings begin reproduction earlier and have greater fecundity than fully winged females (ROFF and FAIRBAIRN, 1994). On the other hand, possible fitness advantages to wing reduction in males have received little

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attention (ROFF and FAIRBAIRN, 1991). In this paper, we compared the reproductive ability of females and the mating success of males between the wing forms in *L. striatellus*.

MATERIALS AND METHODS

Insects used. A wild strain and a mutant red-eyed strain of *L. striatellus* were maintained on rice seedlings (var. Akebono) under 25°C and 16L-8D conditions as stock cultures. There is no difference in ecological and physiological traits between the two strains, and inheritance of red eye color follows Mendelian simple recessive gene theory (ISHII, 1966).

Eight of the first instar nymphs, obtained from the stock cultures within 24 h after hatching, were caged in a glass tube (2 cm dia. and 17 cm ht.) with six rice seedlings, and reared at 25°C and 16L-8D or 25°C and 12L-12D until adult eclosion. Glass tubes and rice seedlings were renewed every seven days. The emerged adults were used for the experiments. For nymphs reared under the conditions of 25°C and 16L-8D, the nymphal period was examined.

Reproductive ability of females. The wild strain reared at 25°C and 16L-8D was used in this experiment. A brachypterous or macropterous female was paired with a macropterous male within 24 h after adult eclosion. Each pair was kept in a glass tube with three rice seedlings. Fifteen replications were prepared for each pair.

Rice seedlings were dissected every day to determine whether eggs were laid. The laid eggs were counted every two days during the life span of females. Dead males were replaced by new ones of a similar age. Head and pronotum widths were measured after the death of each female.

The length (L) and breadth (B) of three eggs from each pair were measured every two days under a stereomicroscope and the egg volume (V) was calculated by the formula, $V=L \cdot (B/2)^2 \cdot \pi$, assuming egg shape is columnar.

Male mating success. All insects used in this experiment were reared at 25°C and 12L-12D. Four males or females with the same wing form were introduced into a glass tube with three rice seedlings within 24 h after adult eclosion. The adults were reared for six days, because both sexes reach sexual maturity within this period (KATAYAMA, 1975).

Two males of different wing forms and one female were introduced into a glass tube with three rice seedlings. They were reared at 25°C or 17°C and 16L-8D. In each triplet, the female and one of the two males were obtained from the red-eye strain. This design allowed us to determine the paternity exactly, since all red-eyed offspring were sired by the red-eyed male and all normal-eyed offspring by the wild male. The glass tube and rice seedlings were renewed every two days. The rice seedlings were kept for 14 days at 25°C. The number of hatchlings and their eye color were examined. For unhatched eggs, the presence of eye spots was used to distinguish between fertilized and unfertilized eggs. If at least one member of the triplet died within two days after being established, or no fertilized eggs were laid, the data were excluded from the analysis.

RESULTS

Comparison of reproductive ability of females between the wing forms

The preoviposition period of brachypters (2.23 ± 0.12 d, mean \pm S.E.) was significantly shorter than that of macropters (3.50 ± 0.32 d) ($p < 0.05$, MANN-WHITNEY'S *U*-test). The total number of eggs laid was compared between brachypterous and macropterous females (Table 1). The egg volume was calculated and the reproductive effort was estimated by multiplying the egg volume by the number of eggs laid (Table 1). The total fecundity and egg volume were significantly larger in brachypters than in macropters ($p < 0.05$ and $p < 0.01$, respectively, MANN-WHITNEY'S *U*-test). The reproductive effort was also significantly larger in brachypters than in macropters ($p < 0.05$, MANN-WHITNEY'S *U*-test), and daily changes of the reproductive effort were shown in Fig. 1.

Various demographic parameters of the females were compared for the macropterous and brachypterous forms (Table 2). The intrinsic rate of natural increase (r_m) was calculated by the iterative method described by BIRCH (1948). A 1:1 sex ratio was assumed and the nymphal mortality rate was assumed to be 0%. The mean

Table 1. Comparison of reproductive characteristics of female adults between the two wing forms

Wing form	Total fecundity (Mean \pm S.E.)	Egg volume (mm ³) (Mean \pm S.E.)	Reproductive effort ^a (mm ³) (Mean \pm S.E.)	Ratio of reproductive effort (B ^b /M ^c)
Brachypter	434.4 \pm 58.0	0.0129 \pm 0.0001	7.05 \pm 0.92	1.78
Macropter	259.2 \pm 37.5	0.0115 \pm 0.0002	3.96 \pm 0.64	

^a Reproductive effort = Σ (Egg volume \times No. of eggs/day).

^b B: Brachypter.

^c M: Macropter.

*: $p < 0.05$, **: $p < 0.01$ (MANN-WHITNEY'S *U*-test).

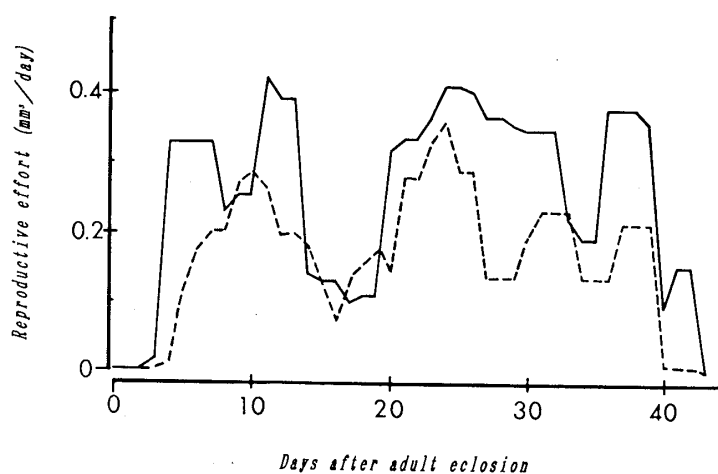


Fig. 1. Daily changes of the reproductive effort of brachypters (solid line) and macropters (dotted line). The value of the daily reproductive effort is the product of daily fecundity and mean volume of eggs laid on each day.

Table 2. Comparison of demographic parameters between the wing forms

Wing form	Net reproductive rate (R_0)	Intrinsic rate of natural increase per day ^a (r_m)	Mean generation time (days) (T)
Brachypter	579.1	0.252	25.235
Macropter	255.1	0.224	24.764

^a Intrinsic rate of natural increase was calculated using the formula; $\sum e^{-r_m \cdot l_x} \cdot m_x = 1$.

Table 3. Effects of competition between brachypterous and macropterous males in terms of the proportion of fertilized eggs laid by a female which mated with either male

Temperature	Female \times male	Wing form of males	No. of mated males ^e	Proportion of fertilized eggs (Mean \pm S.E.) ^f	
25°C	Br ^a \times (Br + MR) ^b	B ^c	5	0.935 \pm 0.020	
		M ^d	8	0.909 \pm 0.035	
	Br \times (BR + Mr)	B	8	0.893 \pm 0.020	
		M	7	0.959 \pm 0.017	
	Mr \times (Br + MR)	B	6	0.915 \pm 0.071	
		M	8	0.983 \pm 0.013	
	17°C	Mr \times (BR + Mr)	B	9	0.942 \pm 0.025
			M	8	0.934 \pm 0.016
Br \times (Br + MR)		B	4	0.587 \pm 0.090	
		M	5	0.871 \pm 0.054	
Br \times (BR + Mr)	B	11	0.765 \pm 0.053		
	M	4	0.744 \pm 0.090		

^a r: Red eye type.

^b R: Wild type.

^c B: Brachypter.

^d M: Macropter.

^e All cases are not significantly different between the male wing forms (sign test).

^f All cases are not significantly different between the male wing forms (MANN-WHITNEY's *U*-test).

duration of nymphal periods of macropters and brachypters were 14.2 and 13.1 days, respectively.

All demographic parameters of brachypters tended to be larger than those of macropters, particularly in R_0 . The mean widths of head and pronotum of females were 0.683 mm and 0.795 mm in macropters, and 0.687 mm and 0.794 mm in brachypters, respectively. Those measurements were not significantly different between the wing forms ($p > 0.05$, MANN-WHITNEY's *U*-test). Furthermore, egg volume did not significantly correlate with female body size.

Comparison of male mating success between the wing forms

The number of males which could mate with females was not significantly different in any combination of sexes and the total number of mated males was not different between the male wing forms ($p > 0.05$, sign test). Furthermore, the proportion of fertilized eggs was not significantly different between the male wing forms ($p > 0.05$, MANN-WHITNEY'S *U*-test) (Table 3). The proportion of fertilized eggs at 17°C tended to be lower than that at 25°C, although there was no significant difference between them ($p > 0.05$, KRUSKAL-WALLIS analysis).

DISCUSSION

In many wing-polymorphic insects, winged and wing-reduced morphs differ in various life history traits, including the development period of immature stages, body size and longevity of adults and egg production pattern (ROFF, 1984; ZERA, 1984). Faster developmental rate, higher fecundity and earlier age of first reproduction are almost always associated with wing-reduced morphs (ZERA, 1984). There is a trade-off between flight capability and reproduction (ROFF and FAIRBAIRN, 1994).

In this experiment, the nymphal period of the brachypterous form of *L. striatellus* females was shown to be shorter than that of the macropterous one, and the total fecundity of brachypterous females was greater than that of macropterous ones (Table 1). Therefore, the net reproductive rate and the intrinsic rate of natural increase were larger in brachypterous females than in macropterous ones (Table 2). These results apparently confirm the female fitness advantage to wing reduction in *L. striatellus*. Generally speaking, larger body size of females correlates with higher fecundity (ROFF and FAIRBAIRN, 1991). However, the female body size of *L. striatellus* was not different between wing forms, and did not influence total fecundity.

The volume of eggs laid by brachypterous *L. striatellus* females was larger than that of macropterous ones (Table 1). Therefore, the amount of energy which is allocated to reproduction should be expressed more exactly by the reproductive effort than by fecundity. The reproductive effort of brachypterous females was much greater than that of macropterous ones (Table 1). This indicates that brachypterous females allocate more energy to reproduction than macropterous ones. An obvious peak in daily reproductive effort of macropterous females was observed about 15 days after adult eclosion in a lygaeid bug, *Horvathiolus gibbicollis* (SOLBRECK, 1986). This was evidently related to wing muscle histolysis taking place during the early oviposition period. However, there was no apparent peak in daily reproductive effort in *L. striatellus* (Fig. 1).

In order to compare the male mating success between the wing forms, two temperature conditions, 17°C and 25°C, were used. The former corresponds to the temperature condition in the early spring when adults from the overwintering generation emerge. The incidence of brachypterous males is relatively high in this season (KISIMOTO, 1956 a). Under both temperature conditions, the number of males mated and the proportion of fertilized eggs did not differ between male wing forms, although the proportion of fertilized eggs was lower at 17°C than at 25°C (Table 4). In the brown planthopper, *Nilaparvata lugens*, the nymphal period of brachypterous males is somewhat shorter than that of macropterous ones (KISIMOTO, 1956 b), and the former can copulate within two days after emergence (TAKEDA, 1974). In *L. striatellus*, macropterous males reach sexual maturity within one day of adult eclosion (ICHIKAWA, 1979).

Furthermore, we observed that most males of both wing forms copulated with sexually mature females within one day after adult eclosion (unpublished data). There may be no difference between the pre-mating periods of males of each wing form.

Brachypterous males of *N. lugens* might be more aggressive than macropterous ones when they communicate continuously with other males (ICHIKAWA, 1982). UTIDA (1972) noted that in flying males of a bruchid beetle, *Callosobruchus maculatus*, the testes were not developed at eclosion, while those of flightless males were well-developed. In a thrips, *Hoplothrips pedicularius*, wingless males have longer forelegs than winged ones. Forelegs are used in agonistic encounters between males (CRESPI, 1986). Flightless males of another thrips, *H. karnyi*, copulate more than winged ones (CRESPI, 1988). Brachypterous males of the oriental chinch bug, *Cavelerius saccharivorus*, mature earlier than macropterous ones (FUJISAKI, 1992). These studies indicate that the advantage of wing reduction in males is to divert their energies from the flight apparatus, such as wing muscle, to the development of testes or weapons used in fighting for females.

In the case of *L. striatellus*, females change their wing forms in response to population density, whereas males do so in response to day length. Shorter days of early spring, when the overwintering generation emerges, would be unsuitable for producing macropters. This indicates that the appearance of brachypterous males at this time may be a simple result of seasonality. Genetic similarities between the sexes may also explain wing reduction in males, because the evolution of wing dimorphism in males will be influenced by the genetic correlation of the trait between the sexes (ROFF and FAIRBAIRN, 1994). However, there is a possibility that the wing reduction of males in the early spring has some ecological significance, specific to this season. Further studies are necessary to clarify the adaptive significance of wing reduction in *L. striatellus* males.

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