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# Decreased mating propensity of macropterous morph in a flightless wing-polymorphic insect, *Pyrrhocoris apterus* (Heteroptera)

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**Abstract.** The effect of wing length (brachyptery and macroptery) on mating activity was investigated in adult males and females of a flightless wing-polymorphic insect, *Pyrrhocoris apterus* (L.). Mating activity of the brachypterous and macropterous adult bugs was assessed according to 14 different parameters. The competition tests revealed higher numbers of copulations and greater duration of mating activity in brachypterous than in macropterous males. Brachypterous males are between two to four times more successful in competition for females than their macropterous counterparts, depending on the wing morph and physiological status of the females. Decreased mating success of macropterous males is associated with the smaller size of their accessory glands. Lowered competitive ability for mates is a likely penalty associated with macroptery. Receptivity tests showed the highest tendency to mate in reproductive brachypterous females, lower in macropterous females and the least in diapausing brachypterous females. This is the first report of decreased mating propensity of macropterous morphs in insects with non-functional wing polymorphism. The association of lowered mating success with the higher dispersal activity of the macropterous morph in this bug and a trade-off between the ability to reproduce and to disperse in the flightless wing-polymorphic insects is discussed.

## INTRODUCTION

Alary polymorphism in insects is widely viewed as a visible manifestation of polymorphism for dispersal ability and has been intensively studied by behavioural ecologists, evolutionary biologists and physiologists for decades (Johnson, 1969; Kennedy, 1975; Harrison, 1980; Roff & Fairbairn, 1991; Rankin & Burchsted, 1992; Dingle, 1996; Zera & Denno, 1997). Insect wing polymorphism is one of the life history trade-off models because wing morph-related differences in dispersal and reproductive traits are often great. The trade-off between reproduction and dispersal has been only documented for flight-capable wing-polymorphic insects (Dingle, 1996; Zera & Denno, 1997). Whether the trade-off between reproduction and dispersal also occur in flightless wing-polymorphic insects is unknown. While the relationship between dispersal ability and reproduction in females of many flying wing-polymorphic species has been well documented, that in males is less well understood (Zera & Denno, 1997). The cost of reproduction is believed to be generally much lower in males than in females (Trivers, 1972) and the factors that influence the evolution of flightlessness in males are poorly understood and may differ from those influencing females (Holtmeier & Zera, 1993). Nonetheless, it was found that brachypterous males of some flying wing-polymorphic insects, such as water strider, bruchid beetle, ching bug, planthopper, and thrips, reproduce at an earlier age and/or mate more frequently than their macropterous counterparts (Utida, 1972; Crespi, 1988; Fujisaki, 1992; Kaitala & Dingle, 1993; Novotný, 1995; Langellotto et al., 2000). Despite the fact that some species have evolved flightlessness and their macropters are non-flying (Roff & Fairbairn, 1991) there is no evidence of mating disadvantage of the macropterous morph in insects with non-functional wing polymorphism, i.e. in species where all macropterous specimens are flightless.

*Pyrrhocoris apterus*, as a typical representative of the pterygomorphic insects which have evolved flightlessness (Honěk, 1995; Socha & Zemek, 2000a), appears to be a suitable model species for this kind of the study. It is a common palaearctic heteropteran with a core distribution in Mediterranean and eastern and central Asia producing two distinct wing morphs; long-winged (macropterous) and short-winged (brachypterous) (Socha, 1993). Developmental trajectories leading to either macropterous or brachypterous morph are genetically determined but environment-dependent. Macropterism of *P. apterus* is controlled by a recessive allele whose penetrance depends largely on photoperiod and temperature (Honěk, 1976, 1986). Despite the fact that all macropterous specimens of the bug are flightless (Socha & Zemek, 2000a) they differ from brachypters in various physiological and behavioural parameters, e.g. the length of pre-oviposition period (Honěk, 1985; Socha & Šula, 1996), the amount of hexameric storage protein in the haemolymph (Šula et al., 1995; Socha & Šula, 1996), feeding and digestive enzyme activities, the level of glycogen and lipids in the fat body (Socha et al., 1997, 1998), adipokinetic response (Socha & Kodrík, 1999) and walking activity (Socha & Zemek, 2000b). We also found that an increase in the speed of locomotion of macropters is positively correlated with a more intensive mobilization of lipids by adipokinetic hormone (Maxová et al., 2002) and a higher content of adipokinetic hormone in the CNS (Kodrík et al., 2003). All these data indicate that the two wing morphs of *P. apterus* differ in their life history strategies. This hypothesis is in accordance with our recent finding that macropters of this bug maintain a greater dispersal ability than brachypters despite the loss of flight capability (Socha & Zemek, 2003). It indicates the that flightless macropterous morph of *P. apterus* is still associated with dispersal and a trade-off between the ability to disperse and the ability to reproduce might also occur in insects with non-functional wing polymorphism.

The aim of the present study was therefore to reveal (1) whether the specimens of macropterous and brachypterous morphs of *P. apterus* are characterized by differential mating success and (2) whether a hypothesised decreased mating success in macropterous morph occurs in both sexes or only in males or females. The study was expected to demonstrate for the first time the occurrence of a decreased mating propensity in the macropterous morph in insects with non-functional wing polymorphism.

## MATERIAL AND METHODS

### Experimental animals

The stock cultures of *Pyrrhocoris apterus*, producing the adults of brachypterous and macropterous morphs (Socha et al., 1997, 1998), originated from a wild population collected at České Budějovice, Czech Republic (49°N). Larvae and adults were kept in 0.5 l glass jars in a mass culture (approximately 40 specimens per jar) and supplied with linden seeds and water in glass tubes plugged with cellulose wool. The food and water were replenished twice a week. It was found that macropterous females of *P. apterus* enter a non-reproductive state when reared under long-day (18L : 6D) photoperiod (Honěk, 1985). Long-day macropterous females with non-diapause type of reproductive arrest differ from short-day (12L : 12D) brachypterous females with diapause type of reproductive arrest by the length of pre-oviposition period and the content of hexameric storage protein in the haemolymph (Socha & Šula, 1996). Mating performance of macropterous (M) females with a non-diapause type of reproductive arrest was compared with that of reproductive brachypterous (B-R) and non-reproductive diapausing brachypterous (B-D) females. Thus, M and B-R bugs were maintained under a long-day (18L : 6D) photoperiod at constant temperature 26 ± 1°C, while B-D bugs were kept according to Hodek (1968) under short-day (12L : 12D) photoperiod and at the same temperature. Freshly ecdysed adults were removed from the culture, separated according to wing morph, physiological status and sex, placed in small glass jars (0.25 l) in groups of 10–15 specimens and maintained under the same photoperiodic regimen in which they developed.

### Competition and receptivity tests

Each of the competition and receptivity tests included thirty-two individual experimental trials which were carried out in small Petri dishes (6 cm in diameter). In each of the experimental trials one test animal was placed into a small Petri dish in the middle of the central compartment, and two test animals of opposite sexes placed into the opposite distal compartments. In order to avoid potential chemical cues from one experiment affecting the next, each experimental trial was performed in a new clean Petri dish. Each of competition or receptivity tests consisted of one 30 min observation period. Each of the competition tests included three bugs: two 10-day-old males (B-R and M) and one female from one of three possible combinations (5-day-old B-R female; 10-day-old M female; 10-day-old B-D female). The selected age of B-R females appeared as optimal due to their greatest attractiveness and receptivity and considerable synchrony of their reproductive states (time of the beginning of the 1st ovarian cycle); 10-day-old B-R females were not included into the tests due to greater variability in the phase of their reproductive states (i.e. different lengths of the period between the 1st and 2nd ovarian cycle). As B-R females are reproductively active, irrespective of whether they are 5 or 10 days old, the comparison of mating performance of 10-day-old non-reproductive M and B-D females with either 5 or 10 days old reproductive B-R females amounts like being compared with like. 10-day-old B-R and M males were used in the tests because the former are known to reach the peak of their mating activity (Žďárek, 1970). The following three combinations of competition tests were performed: (1) B-R vs. M males × B-R female, (2) B-R vs. M males × M female, and (3) B-R vs. M males × B-D female. In receptivity tests, two females from one of the three following experimental variants (B-R vs. M; M vs. B-D; B-R vs. B-D) were placed into a small Petri dish together with one male (B-R or M). Experiments where the alternative was ruled out, i.e. tests including different combinations of single pairs (1 male and 1 female of the same or different wing morph in one Petri dish) showed that data from the competitive tests resulted from male competition and not from female choice (Socha, unpubl. data). The age of males and females tested in the receptivity tests was the same as that used in the competition tests. The following six combinations were tested: (1) B-R male × B-R vs. M females, (2) B-R male × M vs. B-D females, (3) B-R male × B-R vs. B-D females, (4) M male × B-R vs. M females, (5) M male × M vs. B-D females, and (6) M male × B-R vs. B-D females. Experiments where the alternative was excluded, i.e. tests including different combinations of single pairs (1 male and 1 female of the same or different wing morph in one Petri dish) (Socha & Zemek, unpubl. data) showed that the outcome of the preference tests is not due to competition between females. All the tests only included virgin adults and each of tested animals was used only once. It must be noted that contrary to the reproductive B-R females, where the receptivity tests encompass both receptivity and attractiveness, the tendency of M and B-D females to mate measured in the receptivity tests encompasses receptivity only because they are not sexually attractive. The competition and receptivity tests did not involve diapausing males because their reproduction was completely inhibited and they did not mate. Null matings observed in some experimental trials were found to be caused by female resistance to mating.

Mating success of M and B-R males, as well as the tendency to mate in tested females (M, B-R or B-D), were determined for each of the experimental trials. The following 14 parameters of mating activity were recorded: (1) the percentage of mated males or females, (2) time of the 1st unsuccessful courtship (i.e. an attempt to mate not completed by copulation), (3) time of the 1st successful courtship (i.e. an attempt to mate completed by copulation), (4) time of the last courtship, (5) time of the 1st copulation, (6) duration of 1st unsuccessful courtship, (7) duration of 1st successful courtship, (8) duration of 1st copulation, (9) number of all unsuccessful courtships, (10) number of all copulations (is identical with number of all successful courtships), (11) duration of all unsuccessful courtships, (12) duration of all successful courtships, (13) duration of all copulations and (14) duration of mating activity (expressed as a sum of the values obtained for criteria 11,12 and 13). The start of courtship and copulation is defined as from the first appearance of these behaviours from the beginning of the test. The commencement of courtship was distinguished by the initiation of pre-genital engagement followed by the genital and antennal stimulation of the female. The onset of copulation was characterized by a genital connection (coupling). Details of the main phases of mating behaviour of *P. apterus* were described by Žďárek (1970). Durations and time periods are expressed in seconds and values obtained for each parameter averaged.

### Statistical analysis

Statistics were computed using PRISM (GraphPad Software, San Diego, CA, USA). The percentages of copulating pairs (parameter No. 1) were compared using the 95% confidence intervals (Glass & Hopkins, 1996) and the significance of wing morph-related differences in the percentage of mating was calculated using the chi-square test. The obtained values for other measured parameters of mating activity (Nos. 2–14) were compared by t-test.

## RESULTS

### Mating percentage (parameter No. 1)

The relationship between male mating success and wing morph is presented in Fig. 1. Analysis of the mating percentage values revealed significant wing morph-related differences ($P \leq 0.01$) in all three variants of competition tests. B-R males were two times more successful in competition for females than M males of the same age (Fig. 1A) and when the competition trial included M or B-D female the B-R males were three (Fig. 2B) to four fold (Fig. 1C) more successful than M males.

The six variants of receptivity tests are presented in Fig. 2. Differences in the tendency of tested females to mate as well as in mating success of males of two wing morphs were observed. When B-R males were given a choice between B-R and M females they mated significantly ($P \leq 0.05$) less frequently with macropterous (34.4%) than with brachypterous (59.4%) females (Fig. 2A). M males showed still greater preference ($P \leq 0.001$) for B-R females (71.9%) over M females (9.4%) (Fig. 2D). These results demonstrate a reduced tendency to mate in M than B-R females and a lowered mating vigour of M males when compared with B-R males. Significant differences between the mating efforts of B-R ($P \leq 0.001$) and M ($P \leq 0.05$) males in favour of B-R males were still more obvious when they were given a choice between B-R and B-D females (Figs 2C and 2F). In contrast to B-R males, which mated with M and B-D females in a ratio 59.4 : 12.5%, the M males mated with these females in a ratio 31.25 : 9.4% in favour of M females. As shown in Fig. 2E, there was a significantly decreased receptivity ($P \leq 0.05$) of B-D females when compared with that of M females with a reproductive arrest of non-diapause type. Nevertheless, the B-R males had high mating vigour so that mating frequencies of B-R males with M vs. B-D females did not differ ($P \leq 1.0$) and reached a ratio of 43.8% M : 40.6% B-D females (Fig. 2B).

### Other criteria of mating activity (parameters Nos. 2 – 14)

Significant differences in the average number of all copulations ($P < 0.05$) in three variants of competition tests and in five variants of receptivity tests were observed (Table 1). B-R males copulated more frequently than M males irrespective of the wing morph and the physiological status of the tested females. This accords with the greater mating success of B-R males over M males shown in Fig. 2. Analysis of the number of all copulations revealed that the receptivity of B-D females differed significantly from that of both M and B-R females. A significant difference between the numbers of copulations of M and B-D females was demonstrated only when they mated with M males ($P < 0.05$). However, no significant differences between the number of copulations of M and B-D females were recorded when they were tested with B-R males ($P < 0.05$). These results indicate that the inhibition of reproduction in M females is weaker than in B-D females but that this difference can be overcome by B-R males which have a higher mating vigour than M males of the same age. Duration of mating activity was usually longer in B-R males than in M males (Table 1). Significant wing morph-related differences ($P < 0.05$) between B-R females and both the M and B-D females were found only when tested with M males. When the females were tested with B-R males the significant differences in duration of mating activity were recorded only between B-R and B-D females; no difference in this parameter was observed between M and B-D females.

No wing morph-related differences were found in the time of the onset of 1st unsuccessful and 1st successful courtships with the exception of one trial combination

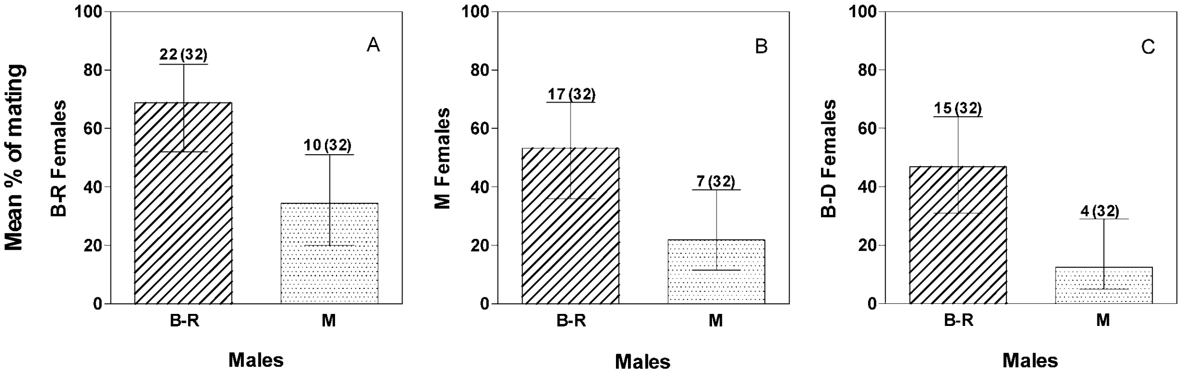

Fig. 1. *P. apterus* copulations (%) in competition tests. Abbreviations: M – macropterous; B-R – reproductive brachypterous; B-D – diapausing brachypterous; (*N*) – number of experimental trials. Vertical lines indicate the 95% confidence intervals (Glass & Hopkins, 1996).

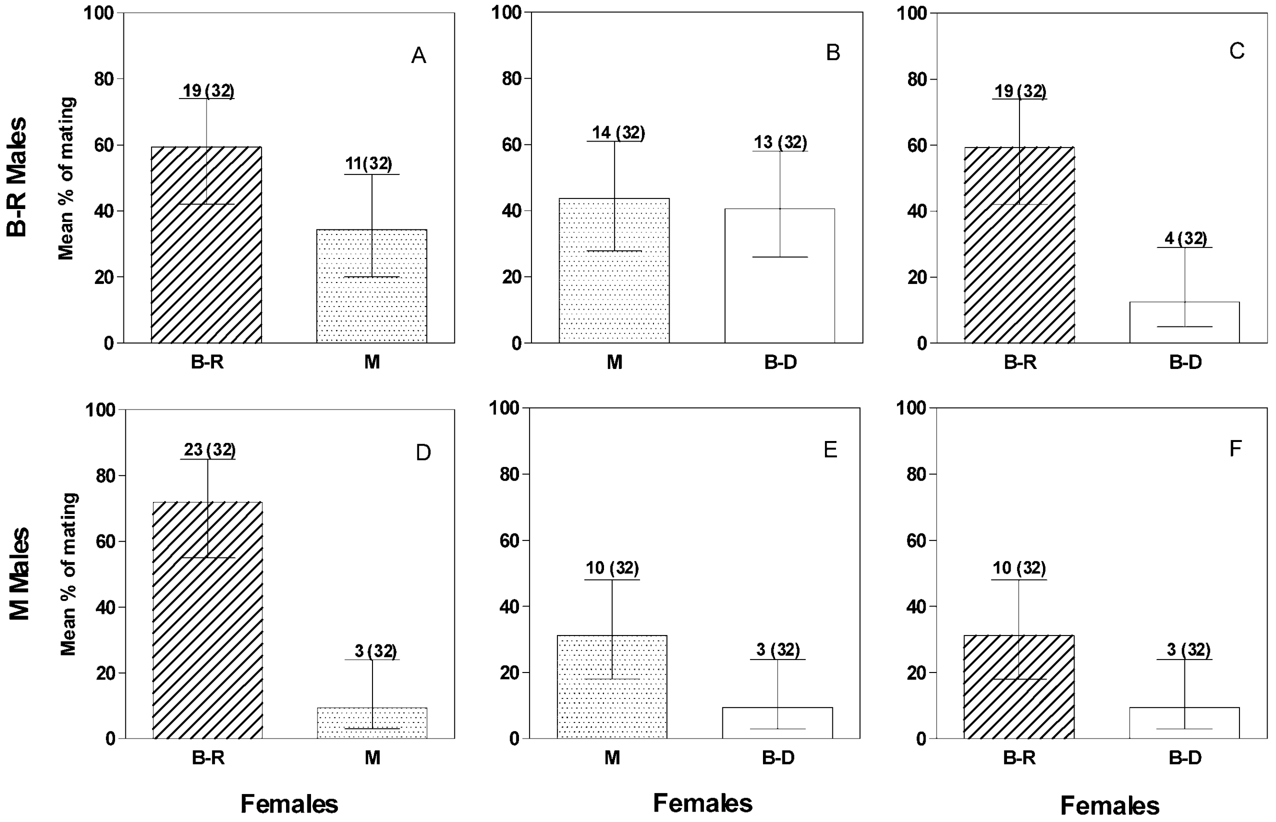

Fig. 2. *P. apterus* copulations (%) in receptivity tests. Abbreviations: M – macropterous; B-R – reproductive brachypterous; B-D – diapausing brachypterous; (*N*) – number of experimental trials. Vertical lines indicate the 95% confidence intervals (Glass & Hopkins, 1996).

(M male × B-R vs. M females). Similarly, no significant wing morph-related differences could be observed in times of the start of the last courtship, start of 1st copulation, number of all unsuccessful courtships, duration of 1st and of all copulations and in durations of 1st unsuccessful and 1st successful courtships with the exception of one competition (B-R vs. M males × B-D female) and one receptivity (B-R male × M vs. B-D females) test. Duration of the 1st unsuccessful courtship was significantly ($P < 0.05$) shorter when B-D females were courted by M males (97.29 ± 172.0 s, $N = 21$) than when by B-R males (353.9 ± 481.1 s, $N = 21$). Duration of the 1st successful courtship was significantly shorter ($P < 0.05$) when B-R males courted M females (63.25 ± 35.24, $N = 12$) and longer when they courted B-D females (96.45 ± 41.09, $N = 11$) which indicates that receptivity of B-D females is lower than that of M females.

Significant wing morph-related differences in durations of all unsuccessful or successful courtships occurred in only two variants of the receptivity tests (B-R male × M vs. B-D females; M male × M vs. B-D females) and one variant of competition test (B-R male × M vs. B-D females). Duration of all unsuccessful courtships was significantly ($P < 0.05$) shorter when B-R males were courting M females (172.4 ± 210.1 s, $N = 8$) and longer when they were courting B-D females (412.5 ± 414.5 s, $N = 13$). Similar significant relations ($P < 0.05$) were also recorded when M males were courting M females (89.85 ± 82.43 s, $N = 26$) and B-D females (250.6 ± 285.7 s, $N = 27$).

## DISCUSSION

### Wing morph-related differences in mating activity and their origin

The present results demonstrated an almost four fold greater competitive capability of B-R males for females over their M counterparts and significantly higher mating activity and receptivity of B-R females in comparison to M females. Despite the fact that ovary growth is inhibited in the pre-vitellogenic stage in both the M (Socha & Šula, 1996) and B-D (Hodek, 1968) females, our present results indicate that inhibition of reproduction is more intensive in the latter. Thus, the pattern of inhibition of reproduction in M females differs from that reported for B-D females by Žďárek (1970). The less intensive inhibition of reproduction of long-day M females than in short-day B-D females is also demonstrated by a shorter pre-oviposition period (19 days in M; > 3 months in B-D) (Socha & Šula, 1996).

The mating advantage of B-R males is probably due to their higher mating vigour which is associated with a shorter larval development period (Honěk, 1987) and earlier sexual maturation. Large males of *P. apterus* have been observed to copulate significantly more often than small males when the female was large but not when the

TABLE 1. Summary of the copulations and duration of mating activity.

| Trial combination (Males × Females) | Analysed criteria Mean ± S.D. ($N$) | | $t$-test ($P < 0.05$) and non-parametric test |
|---|---|---|---|
| | Number of all copulations* | | |
| B-R vs. M × M | 0.53 ± 0.51 (32) | 0.22 ± 0.42 (32) | s, $t$ = 2.685, df = 62 |
| B-R vs. M × B-R | 0.69 ± 0.54 (32) | 0.38 ± 0.49 (32) | s, $t$ = 2.432, df = 62 |
| B-R vs. M × B-D | 0.47 ± 0.57 (32) | 0.13 ± 0.34 (32) | s, $t$ = 2.950, df = 62 |
| B-R × B-R vs. M | 0.66 ± 0.60 (32) | 0.34 ± 0.48 (32) | s, $t$ = 2.292, df = 62 |
| B-R × M vs. B-D | 0.44 ± 0.67 (32) | 0.41 ± 0.61 (32) | ns, $t$ = 0.195, df = 62 |
| B-R × B-R vs. B-D | 0.59 ± 0.50 (32) | 0.13 ± 0.34 (32) | s, $t$ = 4.408, df = 62 |
| M × B-R vs. M | 0.78 ± 0.61 (32) | 0.09 ± 0.30 (32) | s, $t$ = 5.749, df = 62 |
| M × M vs. B-D | 0.31 ± 0.47 (32) | 0.09 ± 0.30 (32) | s, $t$ = 2.224, df = 62 |
| M × B-R vs. B-D | 0.31 ± 0.47 (32) | 0.09 ± 0.30 (32) | s, $t$ = 2.224, df = 62 |
| | Duration of mating activity (sec) | | |
| B-R vs. M × M | 854.1 ± 797.5 (32) | 339.8 ± 606.8 (32) | s, $t$ = 2.903, df = 62 |
| B-R vs. M × B-R | 1102 ± 777.4 (32) | 534.3 ± 774.6 (32) | s, $t$ = 2.928, df = 62 |
| B-R vs. M × B-D | 917.0 ± 689.7 (32) | 366.7 ± 547.3 (32) | s, $t$ = 3.536, df = 62 |
| B-R × B-R vs. M | 1425 ± 541.1 (21) | 1107 ± 792.2 (19) | ns, $t$ = 1.967, df = 38 |
| B-R × M vs. B-D | 617.4 ± 740.5 (32) | 709.5 ± 750.3 (32) | ns, $t$ = 0.494, df = 62 |
| B-R × B-R vs. B-D | 865.1 ± 782.0 (32) | 255.4 ± 522.9 (32) | s, $t$ = 3.667, df = 62 |
| M × B-R vs. M | 1054 ± 726.0 (32) | 219.5 ± 476.5 (32) | s, $t$ = 5.435, df = 62 |
| M × M vs. B-D | 340.5 ± 539.3 (32) | 248.5 ± 339.9 (32) | ns, $t$ = 0.817, df = 62 |
| M × B-R vs. B-D | 321.3 ± 560.1 (32) | 65.97 ± 299.8 (32) | s, $t$ = 2.273. df = 62 |

Abbreviations and definitions: M – macropterous; B-R – reproductive brachypterous; B-D – diapausing brachypterous; $N$ – number of bugs; S.D. – standard deviation; ns – non-significant; s – significant. * Number of all copulations (parameter 10) is identical with the number of all successful courtships.

female was small (Honěk, 2003). However, in the present study we found that M males of *P. apterus* mate less frequently than B-R males despite the fact that their average body size is greater and the range of its variation smaller than in B-R males (Honěk, 1995). Since there is no difference in winter survival, and post-hibernation mating is not assortative (Honěk, 1976), the lowered sexual efficiency and fitness of M males might be one of the reasons why the proportion of macropters in temperate wild populations of this bug is so low, typically between 0–14%. The inhibition of reproductive activity and establishment of a second generation which would be prevented by the approaching end of the season (Honěk, 1985) and a higher dispersal of macropterous morph (Socha & Zemek, 2003) are perhaps the main causes of the persistence of a low level of macropterism in wild populations of *P. apterus.* It must be noted that differences in apparent mating success need not always directly translate into reproductive success. Further work on this topic and an additional proof of translation of apparent mating rate into differences in fecundity of females might resolve the question of whether a trade-off between dispersal and reproduction occurs in non-flying wing-polymorphic insects.

Decreased mating success of M males is most probably associated with the smaller size of their accessory glands due to partial fasting and a decrease in the activity of their endocrine glands corpora allata (CA). The hypothesis is supported by two findings: (1) there is a large amount of food in the midgut of B-R males but very little in M males (Socha et al., 2001) and (2) the size of the accessory glands of the 10-day-old M males is significantly ($P = 0.0042$, $t = 3.280$, df = 18, $N = 10$) smaller (1625 µm) than that of their brachypterous counterparts (1883 µm) (Socha R., unpubl. data). Moreover, this suggestion also accords with the most recent finding that males of *Drosophila melanogaster* with larger accessory glands have a greater frequency of mating than males with smaller accessory glands (Bangham et al., 2002). Lowered CA activity in partially fasting *P. apterus* M males probably prolongs imaginal maturation of their accessory glands. It is known that size, function and adult maturation of accessory glands in many insects depends on the presence of juvenile hormone secreted from the CA (Chen, 1984; Happ, 1992). The tendency to mate in long-day M females was also found to be very low, almost as low as in B-D females. It is probable that the CA of spontaneously fasting M females and males is temporarily inhibited via nervous connections from the brain, as in artificially food-deprived B-R females (Hodková, 1982).

### Benefits of lowered mating activity of macropterous females

The non-diapause reproductive arrest with a weaker CA inhibition in long-day M females of *P. apterus* probably plays an important role in the dispersal and reproductive strategies, since their CA can be fully activated by favourable environmental conditions more rapidly than

CA in B-D females. The relatively flexible CA regulation in long-day M females, coupled with their higher walking and dispersal activity (Socha & Zemek, 2000b, 2003), is most probably responsible for the spread of the macropterous genotype into new habitats. It is known that patterns of gene flow are strongly influenced by the reproductive and dispersal strategies of animals (Olivieri et al., 1995; Paradis, 1998). Contrary to the B-R females, the lower tendency to mate and enhanced dispersal capability of M females allow them to easily leave their natal sites and to disperse to new areas. Provided that *P. apterus* also has a pre-diapause fertilization, then fertilization of M females before the dispersal movement and emigration might be an adaptive mechanism to occupy sites they otherwise could not and to lay fertilized eggs whether or not a male is present. An active role of macropterous females in maintenance of non-functional macropterism in this bug is supposed to produce observable differences in the long-term displacement of this wing morph in an ecological context. We showed that the macropterous morph of this representative species of insects with a non-functional wing-polymorphism maintains its dispersive function although lacking flight capability and disperses by walking only (Socha & Zemek, 2003). Since the higher dispersal by walking in macropterous females of *P. apterus* is associated with an inhibition of ovarian development and lowered mating success (present results), I suggest the term "oogenesis-walking" syndrome for this intermediate evolutionary stage between the "oogenesis-flight" syndrome in flying wing-polymorphic insects and an absence of any of these syndromes in brachypterous insects.

In summary, the present results showed significant wing morph-related differences in mating activity of both males and females of *P. apterus* and for the first time demonstrate a decreased mating propensity of the macropterous morph in wing-polymorphic insects with a flightless macropterous morph. The association of the mating disadvantage of the macropterous morph with the higher dispersal capability of this morph than in the brachypterous morph (Socha & Zemek, 2003) indicates that a trade-off between the ability to disperse and the ability to reproduce might occur also in insects with non-functional wing-polymorphism.

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