

## Experimental evidence for density-determined wing dimorphism in two bush-crickets (Ensifera: Tettigoniidae)

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**Key words.** Crowding, density, dispersal, macroptery, *Metrioptera brachyptera*, *Metrioptera roeselii*, Tettigoniidae, Orthoptera, phenotypic plasticity

**Abstract.** Macroptery is common in many species of Orthoptera, but the causes are still discussed. Besides the assumption that macroptery is genetically determined, there is evidence that wing dimorphism is induced by environmental factors, particularly population density. However, most of the research is on pest species. In contrast, knowledge of wing dimorphism in species that occur at low population densities is still poor. Our study aims to test how density actually affects macroptery. As model organisms we chose two bush-cricket species of the genus *Metrioptera* (Ensifera: Tettigoniidae): While long-winged *M. roeselii* (Hagenbach, 1822) occur regularly, macropterous *M. brachyptera* (Linnaeus, 1761) are rare and are never observed outside their mating habitat. Nymphs of populations from the range core of both species (340 individuals each) were reared in groups of three and six individuals per 500 cm<sup>3</sup> box, and individually. Our analyses revealed that development of macropters was mainly affected by the initial rearing densities. Compared with those reared individually the number of macropters was significantly higher among individuals reared at medium and high densities. The percentage of macropterous individuals was about twice as high in *M. brachyptera* as in *M. roeselii*, and the development of macropters significantly differed between the two species. These findings lead to the conclusion that macropterism is mainly influenced by density stress in both bush-crickets. Genetically determined wing dimorphism is unlikely, otherwise the observed high numbers of long-winged individuals of *M. brachyptera*, which are very rare under natural conditions, would never have developed in the laboratory. Macropterous *M. brachyptera* may rarely be found in the field, but we argue that this is due to low natural densities and, accordingly, to rare exposure to density stress.

### INTRODUCTION

Wing dimorphism is a widespread phenomenon in many insect groups; i.e. in addition to the predominant short-winged morph, frequently long-winged (macropterous) individuals occur (Harrison, 1980; Zera & Denno, 1997). Even though these macropters show reduced fecundity, they are fertile (Ritchie et al., 1987) and much more mobile than the regular forms (Chapman et al., 1978; Higaki & Ando, 2003). Macropterous individuals are thus likely to have high ecological relevance, for example, the rapid range expansions in recent decades (Thomas et al., 2001; Simmons & Thomas, 2004; Hochkirch & Damerau, 2009) or escape from disturbed habitats (Denno et al., 1996, 2001).

Although wing dimorphism has been known since the 1910s (Karny, 1913; Puschig, 1914), the causes are still being discussed: One theory is that macroptery is genetically induced (Harrison, 1980; Zera & Denno, 1997). Simmons & Thomas (2004) for example found much more macropters at the margins than at the core of a species range, which they attributed to an evolutionary adaptation. However, other authors contend that wing dimorphism might be influenced by environmental factors, particularly density (Harrison, 1980; Zera & Denno, 1997; Ingrisch & Köhler, 1998). Within Orthoptera, research on the causes of macroptery has mainly

focussed on Gryllidae (e.g. Masaki & Shimizu, 1995; Olvido et al., 2003; Endo, 2006) and phase dimorphism in locusts (e.g. Uvarov, 1966; Tanaka et al., 1993; Bouaïchi & Simpson, 2003). In contrast, studies on low-density species, like bush-crickets, with a partially different life cycle are rare (e.g. Sängner, 1984; Higaki & Ando, 2003).

The bush-cricket genus *Metrioptera* (Ensifera: Tettigoniidae) represents an ideal model system for studying wing dimorphism as it consists of several species that exhibit macroptery (e.g. Marshall & Haes, 1988; Fartmann, 1997; Thomas et al., 2001). For our experiments we used two related bush-cricket species (*M. roeselii* and *M. brachyptera*) that vary in their habitat requirements and their propensity to produce long-winged individuals in nature: While macropterous individuals of the habitat specialist *M. brachyptera* are rare and are never observed outside the mating habitat (Schouten et al., 2007), long-winged individuals of the habitat generalist *M. roeselii* occur regularly (e.g. Thomas et al., 2001; Simmons & Thomas, 2004; Poniatowski & Fartmann, 2008b).

Here, we test if and how density affects wing dimorphism in two related bush-cricket species. In addition, we want to explain why long-winged *M. roeselii* occur regularly in nature, whereas observations of macropterous *M. brachyptera* remain quite rare. If macropterism is induced by genetic factors, as suggested by Simmons & Thomas (2004), one would expect very few or no mac-

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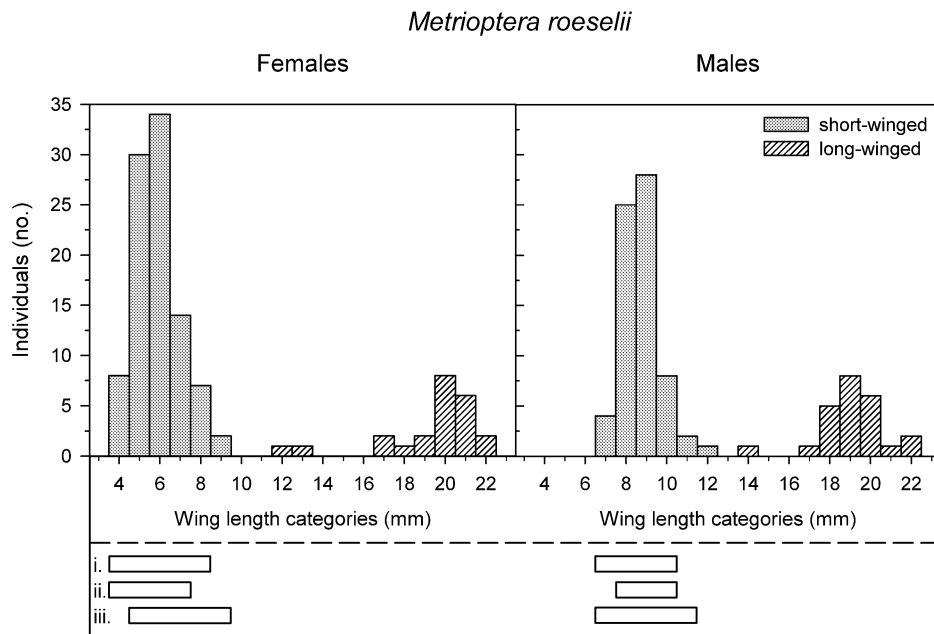


Fig. 1. *Metrioptera roeselii*: Wing length categories of the short-winged and long-winged individuals reared in the laboratory. As a reference the fore-wing range of field measured individuals is shown (boxes): i. Marshall & Haes (1988), ii. Harz (1969) and iii. own data (females:  $x_m = 6.8 \text{ mm} \pm 0.2 \text{ SE}$ ,  $n_{\text{individuals}} = 30$ ; males:  $x_m = 9.4 \text{ mm} \pm 0.1 \text{ SE}$ ,  $n_{\text{individuals}} = 49$ ).

ropterous *M. brachyptera* when reared at different densities.

## MATERIAL AND METHODS

### Model system

For this study we used a habitat generalist *Metrioptera roeselii* (Hagenbach, 1822) and a habitat specialist *M. brachyptera* (Linnaeus, 1761). *M. roeselii* is a widespread species in agricultural landscapes colonising a variety of different habitats (e.g. grasslands, fallow land and road verges) (Marshall & Haes,

1988; Kleukers et al., 1997; Poniatowski & Fartmann, 2005). Occurrence of *M. brachyptera* is mostly restricted to heathland and semi-dry calcareous grassland (Marshall & Haes, 1988; Poniatowski & Fartmann, 2007, 2008a). *M. roeselii* is currently expanding its range in large parts of Europe, while *M. brachyptera* has a more stable range margin (Simmons & Thomas 2004). The short-winged (brachypterous) morph of both species is flightless.

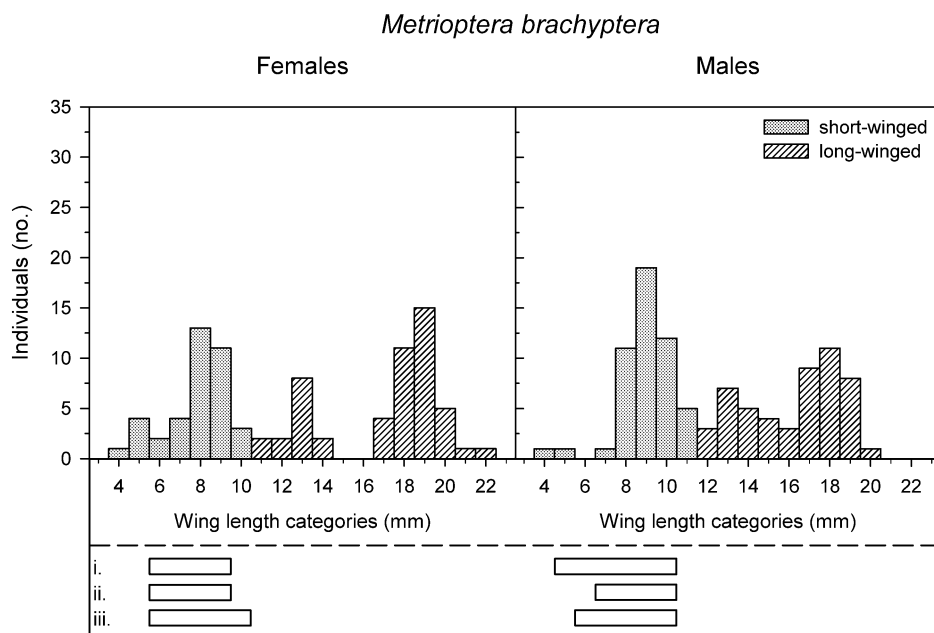


Fig. 2. *Metrioptera brachyptera*: Wing length categories of the short-winged and long-winged individuals reared in the laboratory. As a reference the fore-wing range of field measured individuals is shown (boxes): i. Marshall & Haes (1988), ii. Harz (1969) and iii. own data (females:  $x_m = 8.1 \text{ mm} \pm 0.1 \text{ SE}$ ,  $n_{\text{individuals}} = 59$ ; males:  $x_m = 8.7 \text{ mm} \pm 0.1 \text{ SE}$ ,  $n_{\text{individuals}} = 60$ ).

TABLE 1. Overview of the variables used in GLMM.

| Response variable   | Factor levels  |
|---------------------|----------------|
| Macroptery          | 2 <sup>1</sup> |
| Predictor variables |                |
| Fixed effects       |                |
| Density             | 3 <sup>2</sup> |
| Species             | 2 <sup>3</sup> |
| Sex                 | 2 <sup>4</sup> |
| Random effects      |                |
| Survival rate       | 6 <sup>5</sup> |
| Site                | 6 <sup>6</sup> |

<sup>1</sup> short-winged = 0, long-winged = 1 (definition see material and methods, as well as Fig. 1 and 2)

<sup>2</sup> low = 1 individual, medium = 3 individuals, high = 6 individuals

<sup>3</sup> *Metrioptera roeselii* = Mr, *Metrioptera brachyptera* = Mb

<sup>4</sup> Male = m, Female = f

<sup>5</sup> 17% = 1, 33% = 2, 50% = 3, 67% = 4, 83% = 5, 100% = 6

<sup>6</sup> Nymphs were collected from different sites (see also material and methods).

### Experimental design

Nymphs of *Metrioptera roeselii* and *M. brachyptera* (each  $n_{\text{individuals}} = 340$ ) were collected in the field between 9 and 22 May, 2008. Collection of nymphs took place in central Germany (Diemeltal, 51°28'N, 9°08'E; Medebacher Bucht, 51°10'N, 8°40'E) from populations at the core of the species range (distance of at least 100 km to the range margin) of both species (*M. roeselii*:  $n_{\text{sites}} = 4$ ; *M. brachyptera*:  $n_{\text{sites}} = 3$ ). Following Simmons & Thomas (2004) only first- and second-instar nymphs were collected, because macroptery may be induced during early nymphal stages (Köhler, 2002). These nymphs were reared to the adult stage under a 14L : 10D photoperiod at 25°C (SD = 2°C) (Higaki & Ando, 2003) in transparent plastic boxes (500 cm<sup>3</sup>) covered with dark nylon gauze. Humidity was kept at 45% (SD = 8%) because at higher humidities a high percentage of the nymphs fail to develop (Ingrisch, 1978). Nymphs of both species were reared in groups of three ( $n_{\text{boxes}} = 40$ ) or six ( $n_{\text{boxes}} = 30$ ) individuals per box. Moreover, forty nymphs of both species were kept individually as a reference (control). Box position was randomised. Preliminary studies showed that for successful rearing a mixed diet of plants and insects is necessary (Poniatowski & Fartmann, unpubl. data). Therefore, nymphs were fed ad libitum with fresh grass, blossoms and seeds as well

as cricket food (JBL TerraCrick) to provide vitamins, proteins and minerals. Water was supplied by spraying the boxes every day and offering pieces of fresh cucumber (replaced every second day) (cf. Helfert & Sängner, 1975).

At maturity, fore-wing length of each individual was measured using a calliper gauge (0.1 mm accuracy). As a reference, short-winged (brachypterous) individuals of both species were also measured in the field (*M. roeselii*:  $n_{\text{individuals}} = 79$ ,  $n_{\text{sites}} = 4$ ; *M. brachyptera*:  $n_{\text{individuals}} = 119$ ,  $n_{\text{sites}} = 6$ ). A bush-cricket was classified as long-winged (macropterous) whenever wing length clearly exceeded the usual measure (Figs 1 and 2), i.e. if they reached the end of the abdomen or overlapped the hind knees (Ramme, 1951).

### Statistical analyses

As our data did not fit the assumption of a t-test (i.e., a normal distribution; Kolmogorov-Smirnov test), a Mann-Whitney U-test was used to compare two independent samples. Differences between more than two continuous variables were analysed using Kruskal-Wallis H-test (incl. Mann-Whitney U-test with Bonferroni correction). Differences in frequencies of macropterous individuals and survival rate were compared for the three rearing densities using  $\chi^2$ -test. Where observed values were 0, 1 was added to each of the three classes (Leyer & Wesche, 2007) to allow  $\chi^2$ -test. Frequencies of survival rate per box were correlated with initial density per box using Spearman's rank correlations (test of significance: two-tailed). All statistical tests were done using SPSS 11.5 statistical package.

To evaluate which parameters affect the development of macroptery a binomial generalized linear mixed-effects model (GLMM: lmer, Bates et al., 2008) using R-2.9.0 (R-development-core-team 2009) was used (Table 1). The significance of the predictor variables and interactions were assessed using likelihood ratio tests (Type III test). Non-significant predictors were excluded from the final model.

### RESULTS

The survival rate differed significantly among the three rearing groups (Table 2). In both species, the survival rate was strongly negatively correlated with initial rearing density (*M. roeselii*: Spearman's correlation,  $r_s = -0.735$ ,  $n = 110$ ,  $P < 0.001$ ; *M. brachyptera*: Spearman's correlation,  $r_s = -0.696$ ,  $n = 110$ ,  $P < 0.001$ ).

There were also significant differences between the rearing densities concerning the percentage of macropters

TABLE 2. The effect of rearing density on the survival and frequency of macropterous individuals in a) *Metrioptera roeselii* and b) *Metrioptera brachyptera*.  $\chi^2$ -test (survival) for *M. roeselii*:  $\chi^2 = 8.533$ , d.f. = 2,  $P < 0.05$ , and *M. brachyptera*:  $\chi^2 = 12.765$ , d.f. = 2,  $P < 0.01$ ;  $\chi^2$ -test (frequency of macropterous individuals) for *M. roeselii*:  $\chi^2 = 13.372$ , d.f. = 2,  $P = 0.001$ , and *M. brachyptera*:  $\chi^2 = 16.708$ , d.f. = 2,  $P < 0.001$ .

| a) <i>Metrioptera roeselii</i>    |                           |       |                   |                          |                   |
|-----------------------------------|---------------------------|-------|-------------------|--------------------------|-------------------|
| Initial density <sup>1</sup>      | Sample size (individuals) |       | Survival          | Macropterous individuals |                   |
|                                   | Initial                   | Final | Mean (%) $\pm$ SE | n                        | Mean (%) $\pm$ SE |
| 1                                 | 40                        | 39    | 98 $\pm$ 3        | 0                        | 0 $\pm$ 0         |
| 3                                 | 120                       | 83    | 69 $\pm$ 4        | 30                       | 35 $\pm$ 5        |
| 6                                 | 180                       | 102   | 57 $\pm$ 3        | 22                       | 20 $\pm$ 4        |
| b) <i>Metrioptera brachyptera</i> |                           |       |                   |                          |                   |
| Initial density <sup>1</sup>      | Sample size (individuals) |       | Survival          | Macropterous individuals |                   |
|                                   | Initial                   | Final | Mean (%) $\pm$ SE | n                        | Mean (%) $\pm$ SE |
| 1                                 | 40                        | 36    | 90 $\pm$ 5        | 3                        | 8 $\pm$ 5         |
| 3                                 | 120                       | 82    | 68 $\pm$ 3        | 53                       | 62 $\pm$ 7        |
| 6                                 | 180                       | 84    | 47 $\pm$ 3        | 52                       | 61 $\pm$ 5        |

<sup>1</sup> = per 500 cm<sup>3</sup> box

TABLE 3. Statistics of GLMM [Pseudo  $R^2$  (Nagelkerke's) = 0.29;  $n_{\text{individuals}} = 400$ ]: Relationship between macroptery (response variable) and "density" as well as "species" (predictor variables). "Sex" was not a significant predictor. For more information see Table 1.

| Variable                    | Estimate | SE     | Z      | P        |
|-----------------------------|----------|--------|--------|----------|
| Density                     |          |        |        | < 0.0001 |
| Medium rearing density      | 3.5378   | 0.6244 | 5.666  | < 0.0001 |
| High rearing density        | 2.9408   | 0.6217 | 4.730  | < 0.0001 |
| Species                     |          |        |        | < 0.0001 |
| <i>Metrioptera roeselii</i> | -1.5834  | 0.2401 | -6.594 | < 0.0001 |

(Table 2). The GLMM showed that the development of macropters can be explained by medium and high initial rearing densities (Table 3). However, the percentage of macropters did not increase with increase in rearing density (Table 2). The percentage of macropterous individuals was about twice as high in *M. brachyptera* as in *M. roeselii* (Table 2), and the probability of macroptery differed significantly between the two species (Table 3). The median of wing length was highest at medium densities, although there was no significant difference between medium (3 individuals/500 cm<sup>3</sup>) and high (6 individuals/500 cm<sup>3</sup>) densities (Figs 3 and 4). Individually-reared *M. brachyptera* had significantly longer wings than field-grown individuals (Fig. 4), while those of *M. roeselii* did not differ (Fig. 3).

## DISCUSSION

Our laboratory findings show that the macroptery of both bush-crickets (*M. roeselii* and *M. brachyptera*) is

determined by density stress. Sanger & Helfert (1975) obtained similar results for *M. roeselii*: 21% of all individuals became long-winged when reared at high densities, irrespective of the climatic regime (temperature and humidity). Other laboratory studies on bush-crickets also support the hypothesis of macroptery being density-induced (Ando & Hartley, 1982; Sanger, 1984; Higaki & Ando, 2003).

Since temperature and humidity were the same at all rearing densities, these environmental parameters can be excluded as a driver of macropterism, otherwise there should have been high percentages of macropters among the individually-reared bush-crickets. Taking this into account, pheromones as main triggers of macropterism can also be excluded since all boxes were covered with nylon gauze allowing gas exchange between the boxes with different rearing densities. In contrast, tactile and possibly visual stimuli seem to be important. An excess of these stimuli due to crowding triggers the release of endo-

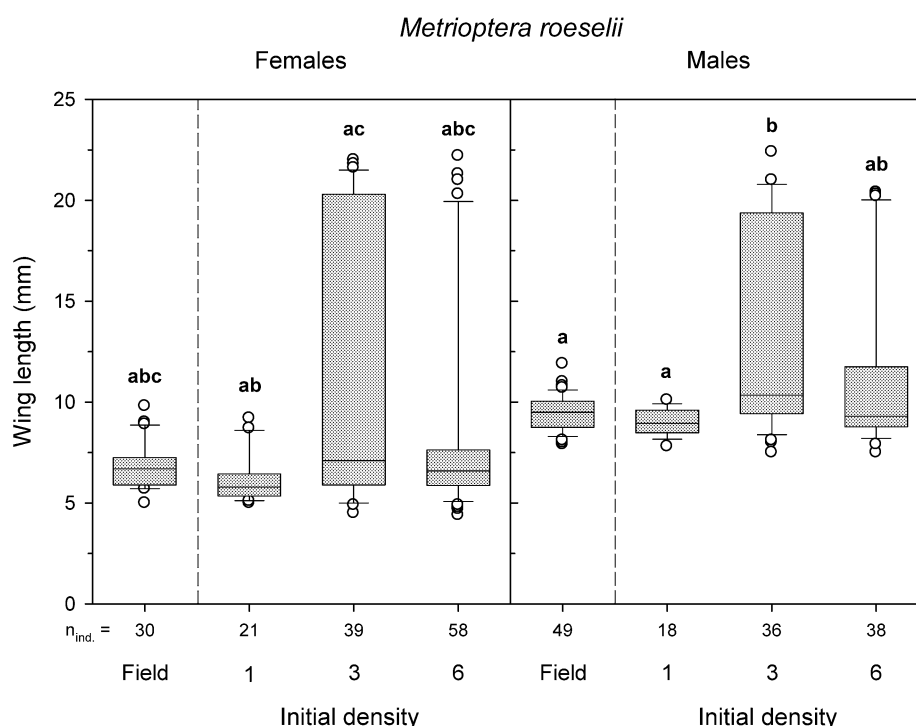


Fig. 3. *Metrioptera roeselii*: Wing length of short-winged individuals from the field and individuals reared at different densities in the laboratory (initial density: 1, 3 or 6 per 500 cm<sup>3</sup> box). Kruskal-Wallis H-test for females:  $\chi^2 = 10.842$ , d.f. = 3,  $P < 0.05$  and males:  $\chi^2 = 16.841$ , d.f. = 3,  $P = 0.001$ . Box plots show 10<sup>th</sup> and 90<sup>th</sup> percentile (whiskers), 25<sup>th</sup> and 75<sup>th</sup> percentile (boundary of the box), median (line) and outliers (open dots). Box plots capped with different letters indicate significant differences at  $P < 0.05$  (Mann-Whitney U-test with Bonferroni correction, level for significance:  $\alpha = 0.0083$ ). Ind. = individuals.

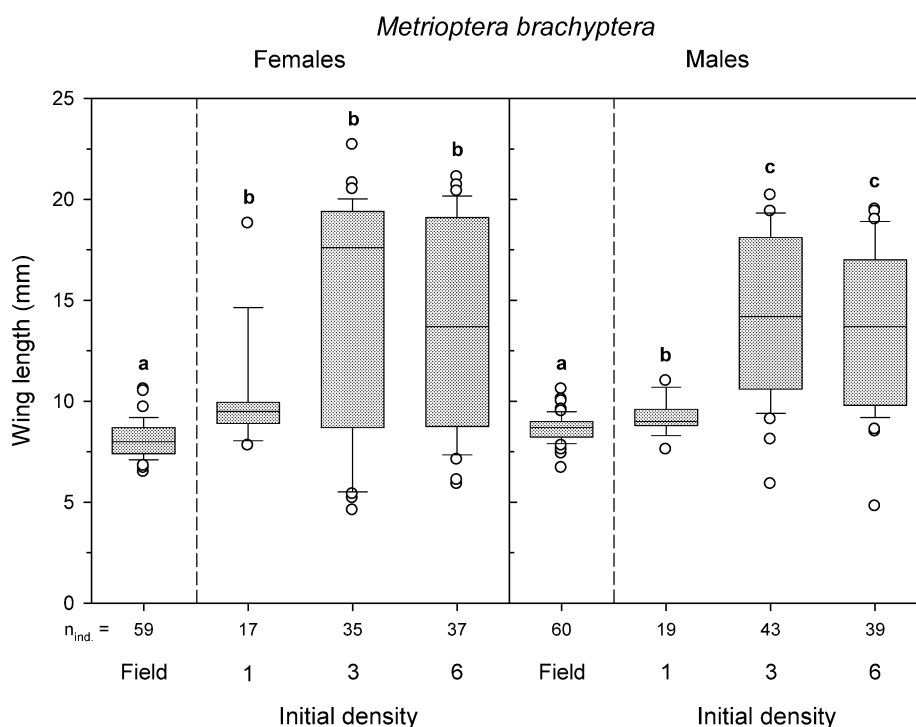


Fig. 4. *Metrioptera brachyptera*: Wing length of short-winged individuals from the field and individuals reared at different densities in the laboratory (initial density: 1, 3 or 6 per 500 cm<sup>3</sup> box). Kruskal-Wallis H-test for females:  $\chi^2 = 49.064$ , d.f. = 3,  $P < 0.001$ , and for males:  $\chi^2 = 89.747$ , d.f. = 3,  $P < 0.001$  (For further explanations see Fig. 3).

crines that induce the development of long wings (Zera & Denno, 1997; Zera, 2004). However, not all individuals reared under medium and high densities become macropters. There are two likely reasons for that: (i) There is a strong degree of individual variation in the affinity to become macropterous (genetic disposition) or (ii) the heterogeneity within the boxes leads to an uneven encounter rate among the individuals, which means that there is variation in the stimulation individuals received (cf. Harrison, 1980). However, phenotypic plasticity does not only differ intra-specifically but also inter-specifically. In *M. brachyptera* far more individuals developed into the long-winged form than in *M. roeselii*. *M. brachyptera* seems to be more sensitive to density stress. Hence, even some individually-reared individuals became long-winged and wings in general were longer than those of field-grown individuals. Probably this was a consequence of increased tactile stimuli due to disturbance during daily feeding of the bush-crickets and cleaning of the boxes. It might be argued that the good food quality promoted body and wing growth. However, this is unlikely as wing length did not differ between individually-reared *M. roeselii* and individuals in the field.

Besides population density habitat disturbance may have an influence on the percentage of macropters. Zera & Denno (1997) view macropterism amongst others as an evolutionary adaptation to disturbance: Whereas in disturbed habitats significantly more macropterous, highly mobile, individuals occur, in more persistent, undisturbed habitats short-winged individuals with a high fecundity dominate (e.g. Denno et al., 1996, 2001). These observations made on planthoppers seem to be transferable, at

first glance, to the two bush-crickets studied. *M. roeselii* is a species that is often long-winged (Simmons & Thomas, 2004; Poniatowski & Fartmann, 2008b) and colonises disturbed habitats like grassland and roadside verges (Marshall & Haes, 1988; Kleukers et al., 1997). *M. brachyptera* is a typical species of habitats with little or no land use (e.g. *Molinia caerulea*-dominated vegetation and abandoned calcareous grassland) (Poniatowski & Fartmann, 2008a; pers. observ.). Macropters are quite rare in the field (Marshall & Haes, 1988; Kleukers et al., 1997). Accordingly, we were surprised that the percentage of macropters in our experiment was higher in *M. brachyptera* than in *M. roeselii*. A possible explanation might be the different densities of the species in nature. According to Ingrisch & Köhler (1998), population densities of *M. brachyptera* vary between 0.1 and 3.8 adults/10 m<sup>2</sup> ( $n_{\text{studies}} = 5$ ), which is very low compared to *M. roeselii* (0.7–11 adults/10 m<sup>2</sup>;  $n_{\text{studies}} = 5$ ). Consequently, *M. brachyptera* is seldom exposed to density stress in its natural habitats.

In contrast to our results, Simmons & Thomas (2004) did not find any effect of density on the development of macropters. They regarded genetically induced macroptery as more likely than density-induced wing dimorphism. According to Simmons & Thomas (2004), in species with expanding ranges like *M. roeselii*, the development of macropters should occur more frequently at the edges of its range than in established populations at the core of the range, because of differences in the selective advantage of dispersal. Consequently, species with static range margins like *M. brachyptera* are considered low-dispersal specialists (Simmons & Thomas, 2004). Taking

this into account, one would expect no or very low numbers of long-winged individuals of *M. brachyptera* in our experiment. However, we observed the exact opposite: under medium and high densities more than 60% of all individuals became macropterous. The percentage of macropterous *M. brachyptera* was even significantly higher than in *M. roeselii*. A density stress-induced macroptery is thus more likely than genetically determined wing dimorphism in bush-crickets. Maybe there is a combination of both, as is the case in many insect species (Zera & Denno, 1997), with a dominance of density effects.

**ACKNOWLEDGEMENTS.** We are very grateful to A. Meyer (Münster) and three anonymous reviewers for valuable comments on an earlier version of the manuscript. Moreover, we would like to thank J. Thiele (University of Münster) for help. The Akademie für ökologische Landesforschung e. V. partly funded this study.

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Received March 5, 2009; revised and accepted May 18, 2009