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Contrasting patterns of macroptery in Roesel's bush cricket *Metrioptera roeselii* (Orthoptera, Ensifera)

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Abstract. We studied the wing dimorphism in Roesel's bush cricket populations. A total of 410 individuals (77 macropterous and 333 brachypterous) were sampled in seven sites. We found a high frequency (≤53%) of macropterous individuals in some meadows surrounded by forests. We measured the body weight, thorax weight, and abdomen weight in connection with macroptery vs brachyptery. We could find a positive correlation between macroptery and thorax weight. The abdomen weight of females showed high individual variation; thus the supposed trade-off between macroptery and lower fertility of females was not supported.

Key words: body weight, climate, frequencies, migration, wing dimorphism, wing musculature.

INTRODUCTION

Insects are known to react actively to recent climate change (e.g. Parmesan, 2006, 2007; Andrew, 2013). However, the climatic responsiveness of insects shows considerable interspecific differences as a consequence of their immense species richness, diversity of life histories, and manifold connections within ecosystems (reviewed by Andrew et al., 2013). Nevertheless, a number of general trends have been detected (Stange and Ayres, 2010):

(i) Warmer temperatures frequently amplify insect species' population dynamics through effects on survival, generation time, fecundity, and dispersal capacity.
(ii) Insect populations in mid- to high latitudes are expected to benefit from climate change through more rapid development and increased survival.
(iii) The physiological effects of climate warming on insect species can act both directly, e.g. by effects on the endocrine system, and indirectly through trophic interactions.

(iv) The effects of climate change can be enhanced by relatively short life cycles, high reproductive capacity, and high degree of mobility, thus the physiological responses to warming temperatures can produce considerable effects on population dynamics, including expansion.

Some insect species have already been used as targets of bioclimatic studies, for instance species characterized by wing dimorphism, which can be influenced by environmental factors. Wing dimorphism is well known in different orthopterans (e.g. Acrididae: *Chorthippus* spp.; Gryllidae: *Gryllus* spp.; Tettigoniidae: *Conocephalus*, *Platycleis*, *Metrioptera* spp.; *see* Harz, 1957; Uvarov, 1977; Harrison, 1980; Zera and Denno, 1997; Zera, 2005; Hochkirch and Damerau, 2009). Previous investigations have shown that climatic factors, especially temperature, can strongly influence the wing form either directly by hormonal changes or indirectly by the crowding effect (e.g. Zera et al., 1983; Zera and Denno, 1997; Zera and Zhao, 2003; Zera, 2005; Poniatowski and Fartmann, 2009), which can promote the colonization of new habitats and areas by macropterous individuals (Ingrisch and Köhler, 1998; Simmons and Thomas, 2004). In several cases, mostly since the 1980s, macropterous individuals were assumed to have been responsible for the range shifts (Simmons and Thomas, 2004; Gardiner, 2009; Hochkirch and Damerau, 2009).

As the bush cricket *Metrioptera roeselii* (Hagenbach, 1822) is characterized by wing dimorphism and a higher frequency of long-winged individuals in dry–hot environmental conditions, this orthopteran classifies as an ideal candidate for climate studies (Marshall and Haes, 1988; Gardiner, 2009). The expansion of this species has been observed for more than 20 years, mostly in Central and Northern Europe as well as in the British Isles (Wake, 1997; Hochkirch, 2001; Thomas et al., 2001; Simmons and Thomas, 2004; Gardiner, 2009; Preuss et al., 2011) but also in North America, where it was introduced (Vickery, 1965). Range expansion seems to be connected to changes in land use and to climate change (Thomas et al., 2001; Hochkirch and Damerau, 2009).

It was hypothesized that macropterous individuals exhibit higher mobility and dispersal range than brachypterous individuals. Thus, macropterous individuals can occupy new habitats and expand faster than brachypterous morphs (Zera and Denno, 1997). Previous experimental surveys, however, failed to show that movements of long-winged and short-winged individuals differ, but detected that males were significantly more mobile than females (Poniatowski and Fartmann, 2011).

Recent surveys have suggested that macroptery has physiologically mediated costs of dispersal as female macropters seem to have lower fecundity (Mole and Zera, 1993, 1994; Zera and Denno, 1997; Suzuki and Tanaka, 1998). For instance, in some cricket species (e.g. *Gryllus firmus*) the musculature of thorax was found to be significantly weaker in brachypterous individuals but the genitalia were more developed; thus a trade-off of these characters was suggested (Roff, 1986; Roff and Bradford, 1996). The spermatophore production also requires considerable investment for males (Wedell, 1992; Vahed and Gilbert, 1996), which also indicates a possible trade-off between macroptery and reproductive success. The costs of macroptery in males are less studied (Simmons and

Thomas, 2004), however. As the relationships between macroptery and climate change are not straightforward, especially in relation to transformed flight muscles and its possible trade-offs with reduced fertility, we aim to test the following hypotheses:

(i) We predict that consistent differences emerge between the body weights of macropterous and brachypterous individuals due to the different development of flight musculature.
(ii) In case the previous hypothesis is true, we predict that weight difference is related to thorax weight because flight muscles are more developed in macropterous individuals.
(iii) We predict that the costs of more developed flight muscles induce lower fertility in females; thus macropterous females are expected to have reduced abdomen weight.
(iv) We expect that the reduction in the abdomen weight of females is a consequence of the reduced egg production. If so, we also expect that the reduction of the abdomen weight is less expressed in males than in females.
(v) Finally, if a higher frequency of macroptery is connected to crowding within the population, we predict that higher frequency of macropterous individuals is connected to higher variations of body weight among the individuals, especially that of the thorax.

MATERIALS AND METHODS

Sampling

Sampling was carried out on six sites (i–vi) in the Aggtelek karst area (North Hungary) and on one site (vii) in the Bereg Lowland (West Ukraine, Transcarpathian region) between 15 and 27 July 2013. As all sites are characterized by dense tall grass–tall forb vegetation, sweep-netting (4 times 50 flaps) was usually combined with hand-picking and simultaneously executed by three or four persons. The sampling was usually carried out at the same time and during the same season (second half of July, between 10 and 12 h a.m.) and also under similar weather conditions (sunny weather with temperatures over 20 °C). Thus, the number of sampled individuals reflects the density of *Metrioptera roeselii* at the sampling sites. The numbers of sampled individuals (sexes and wing morphs) are shown in Table 1 together with geographical information on the sites.

Sites

(i) The *Kis-Gaja Ridge* site is located in a shallow depression (*dolina*) of a karstic plateau with semi-humid tall grasses (*Arrhenaterum elatius*, *Dactylis polygama*, *Brachypodium pinnatum*) rich in different Asteraceae (*Cirsium arvense*, *Centaurea* spp.) and Apiaceae (*Daucus carota*, *Pastinaca sativa*, *Seseli libanotis*) and scrubs (*Cornus sanguinea*, *Prunus spinosa*, *Rosa* spp.).

Table 1. Georeferences of the sampling sites and the number and frequency of macropterous and brachypterous individuals in the samples. Deviation from the summarized proportion of macropterous individuals in the whole sample (18.8%) was tested using the binominal test (* $p < 0.05$, ** $p < 0.01$)

Site	Height, m a.s.l.	Coordinates	Macropterous			Brachypterous			Total
			♂♂	♀♀	Sum	♂♂	♀♀	Sum	
Kis-Gaja ridge	275	48°29′N 20°32′E	4 (21%)	6 (32%)	10 (53%)**	4	5	9	19
Lófej Valley	301	48°30′N 20°32′E	8 (12%)	10 (15%)	18 (28%)*	21	26	47	65
Szelce Valley	355	48°30′N 20°36′E	1 (2%)	0 (0%)	1 (2%)**	28	23	51	52
Lókosár meadow	478	48°31′N 20°35′E	8 (12%)	6 (9%)	14 (21%)	28	24	52	66
Forest clearing S of Ménes Valley	496	48°32′N 20°33′E	13 (21%)	13 (21%)	26 (43%)**	16	19	35	61
Nagy-Nyilas meadow	516	48°31′N 20°33′E	0 (0%)	2 (5%)	2 (5%)*	20	15	35	37
Kis-Gejőc pasture	102	48°27′N 22°19′E	0 (0%)	6 (6%)	6 (6%)**	71	33	104	110
Total			34	43	77 (19%)	188	145	333	410

The site was earlier mowed and now is irregularly grazed by horses. The site is part of a larger plateau with scattered groups of oak (*Quercus petraea*), hornbeam (*Carpinus betulus*), and aspen (*Populus tremula*).

(ii) The *Lófej Valley* site is an irregularly grazed (by horses) semi-humid meadow in a forested valley (oak–hornbeam forest mixed with *Fraxinus excelsior* and *Acer pseudoplatanus*) crossed by a small brook of the lower karstic plateau. The vegetation is dominated by common species of hayfields such as *Arrhenaterum elatius*, *Dactylis polygama*, *Achillea millefolium*, *Daucus carota*, *Knautia arvensis*, *Leucanthemum vulgare*, and *Trifolium pratense*, and interspersed with patches of some weeds of pastures such as *Cirsium arvense*, *Agrimonia eupatoria*, etc.

(iii) The *Szelce Valley* site is an unmowed part of a largely mowed, desiccated marshy meadow characterized by *Cirsium palustre* and tall grasses (*Dactylis polygama*, *Calamagrostis arundinacea*) and sedges (*Carex* spp.). This habitat is part of a larger shallow karstic depression with abandoned arable land and partly abandoned, partly mowed hayfields.

(iv) The *Lókosár meadow* site extends to a shallow karstic depression with mosaics of short (*Festuca rupicola*, *Brachypodium pinnatum*) and tall grass (*Calamagrostis arundinacea*) vegetation, rich in lower (*Trifolium* spp., *Thymus* spp., *Hippocrepis comosa*, *Coronilla varia*, *Gentiana cruciata*, *Helianthemum ovatum*) and tall (*Cirsium pannonicum*, *Centaurea scabiosa*, *Seseli libanotis*, *Peucedanum cervaria*) forbs. The depression is completely surrounded by oak–hornbeam and spruce (*Picea abies*) forests.

(v) The *forest-clearing* site south of the *Ménes Valley* is a semi-dry meadow with patches of short (*Festuca rupicola*, *Brachypodium pinnatum*) and tall grass (*Arrhenaterum elatius*, *Bromus erectus*, *Calamagrostis arundinacea*) vegetation, rich in lower (*Dianthus pontederae*, *Thymus* spp., *Coronilla varia*, *Polygala maior*, *Gentiana cruciata*) and tall forbs (*Centaurea scabiosa*, *Peucedanum cervaria*) and scattered scrubs. The earlier mowed sward is surrounded by karstic oak–hornbeam and submontane beach forests.

(vi) The *Nagy-Nyilas meadow* site is a shallow karstic depression within a large meadow complex with mosaics of short (*Festuca rupicola*, *Brachypodium pinnatum*) and tall (*Bromus erectus*, *Arrhenaterum elatius*, *Calamagrostis arundinacea*, etc.) grasses, lower forbs (*Dianthus pontederae*, *Filipendula vulgaris*, *Leucanthemum vulgare*, etc.), and scattered groups of oak, hornbeam, wild *Sorbus*, and lime (*Tilia cordata*). The sampling was carried out in a relatively humid part of the meadow partly surrounded by light-penetrated karstic oak–hornbeam forests.

(vii) The *Kis-Gejőc pasture* site lies on the lowest part of the Ukranian section of the Bereg Lowland. It is mostly mowed every year and the dryer parts are grazed by cattle. The dominant grass species is *Alopecurus pratensis*, often mixed with *Calamagrostis epigeios*. The number of forb species is rather low; the dominant species are *Iris pseudacorus*, *Cirsium arvense*, and *Dipsacus laciniatus*. The large open, mostly humid grassland is partly surrounded by soft- and hardwood gallery forests, willow scrubs, and reeds.

Bush-cricket data

We collected 410 individuals (77 macropterous and 333 brachypterous, see details in Table 1) of *Metrioptera roeselii* from which we selected equal numbers (42–42) of macropterous and brachypterous individuals, with a nearly equal proportion of males (40) and females (44). The proportion of macropterous and brachypterous individuals was counted in all sampling sites (Table 1).

The specimens were desiccated for four hours at 80 °C in a desiccator. The following data were measured in both sexes and separately in macropterous and brachypterous individuals: dry body weight, thorax weight, and abdomen weight.

Statistical analysis

Binominal tests were used to analyse deviation of the proportion of macropterous individuals in the sites from the summarized proportion in the whole sample (18.8%, 77/410 individuals; see details in Table 1). The mean dry weight of the body (head + thorax + abdomen), thorax, and abdomen of the sexes and wing types (macropterous and brachypterous) were compared with two sample *t*-test. A comparison of macropters and brachypters was also performed by sexes. The Kolmogorov–Smirnov test for normality and the Levene test were used to test normality and the equality of variance assumptions of the *t*-test. Relationships between the ratio and weight of macropters were estimated using correlation analysis (Reiczigel et al., 2007). All statistical analyses were performed with SPSS 21.0 statistical software (Ketskeméty et al., 2011).

RESULTS

The proportion of macropterous and brachypterous individuals was rather different among sites. The deviation of the proportion of macropterous individuals in the sites from the summarized proportion in the whole sample was in all cases (except site (iv), Lókosár meadow) significant (* $p < 0.05$) or strongly significant (** $p < 0.01$) (Table 1).

The number of macropterous individuals was notably low in three extended and densely populated sites, independently from their geographical location and elevation (sites iii, vi, and vii), but we observed a fairly high frequency of macropterous individuals (10–53%) in the other four sites. Two of them are almost completely surrounded by forests and one of them was densely populated with the highest observed number (26 from 61 sampled specimens) of macropterous individuals. The proportion of macropterous females was in most sites higher than that of males.

We found significant differences between males and females both in total body weight and weight of the abdomen (*t*-test, $p < 0.05$). The weight of the thorax showed only a marginally significant difference ($0.1 > p > 0.05$). These results correspond to our expectations as females are generally larger and difference in the body weight is the consequence of the larger abdomen (Fig. 1).

The body weight of macropterous and brachypterous individuals was nearly equal but a significant difference was found in the weight of the thorax. The abdomen weight of macropterous and brachypterous individuals did not differ significantly. The thorax weight was significantly larger in macropterous individuals, both in males and females (Fig. 2), which is likely to be the consequence of the more developed thoracal musculature in macropters.

Considering the females and males separately, we observed that the thoracal weight of macropterous males was significantly higher than in brachypterous ones while the weight of the body and of the abdomen did not show significant differences on average, despite the apparent differences in extreme values (see: Figs 3 and 4). The body weight of macropterous individuals showed lower variance while some brachypterous individuals had extremely high abdomen weight values, possibly connected to more developed fat bodies and/or reproductive organs (Figs 3 and 4).

Macropterous females had a significantly larger ($p < 0.05$) thorax weight than brachypterous ones while the body and abdomen weight did not show significant differences between macropterous and brachypterous females. The variance of abdomen weight was smaller in macropterous females (Fig. 4).

As the next step, we calculated Pearson's correlation coefficients between the proportion of macropterous individuals and body weight. We found only a weak correlation in males ($r_{\text{body}} = -0.2604$, $p = 0.282$; $r_{\text{abdomen}} = -0.4027$, $p = 0.087$; $r_{\text{thorax}} = -0.0718$, $p = 0.770$) between the proportion of macropterous individuals

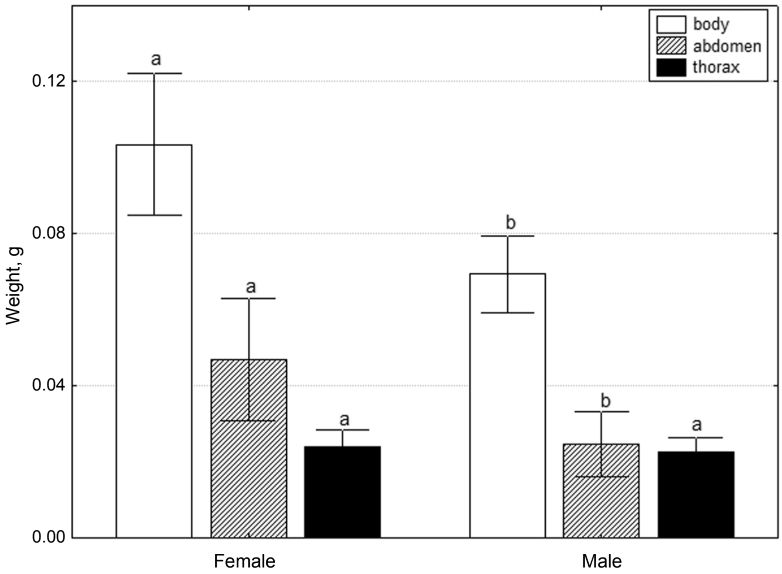

Fig. 1. Weight of the body, abdomen, and thorax of female (44) and male (40) Roesel's bush crickets. The lowercase letters refer to the results of the *t*-test ($p < 0.05$).

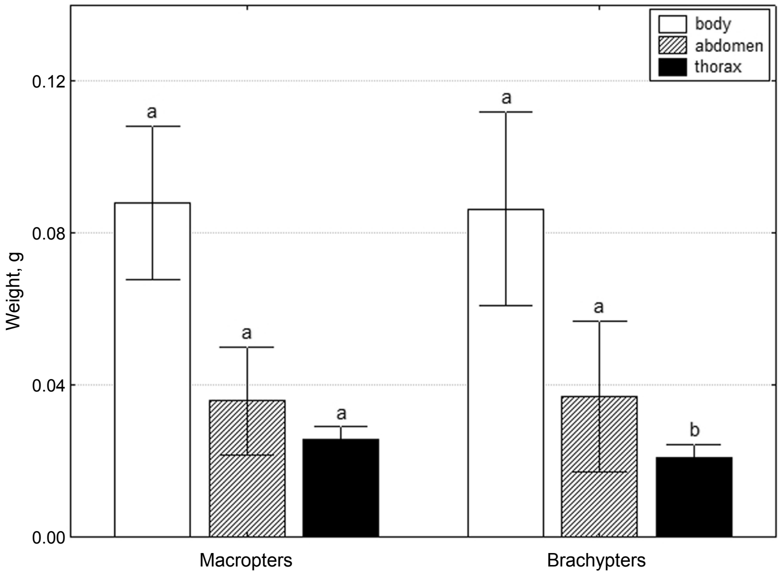

Fig. 2. Weight of the body, abdomen, and thorax of macropterous and brachypterous Roesel's bush cricket individuals. The lowercase letters refer to the results of the *t*-test ($p < 0.05$).

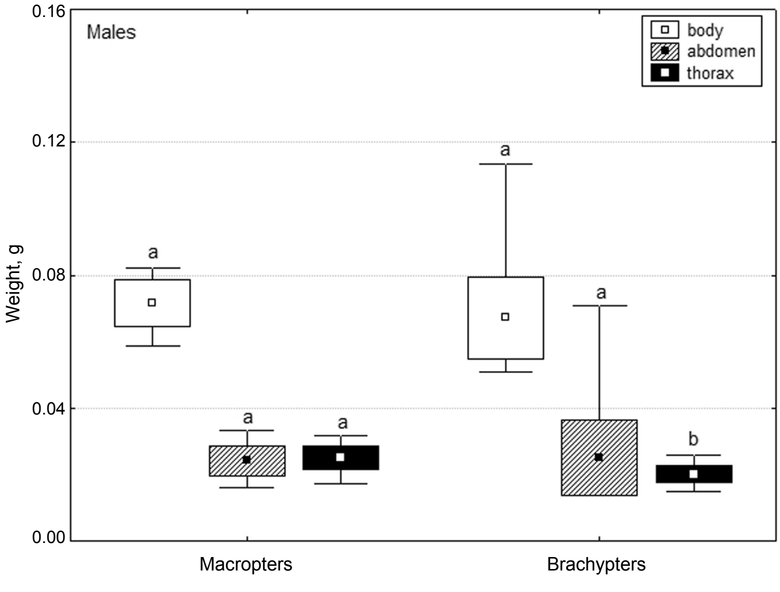

Fig. 3. Mean values and variance (mean/SD/min–max) of the body, abdomen, and thorax weight of macropterous and brachypterous male Roesel's bush crickets. The lowercase letters refer to the results of the *t*-test ($p < 0.05$).

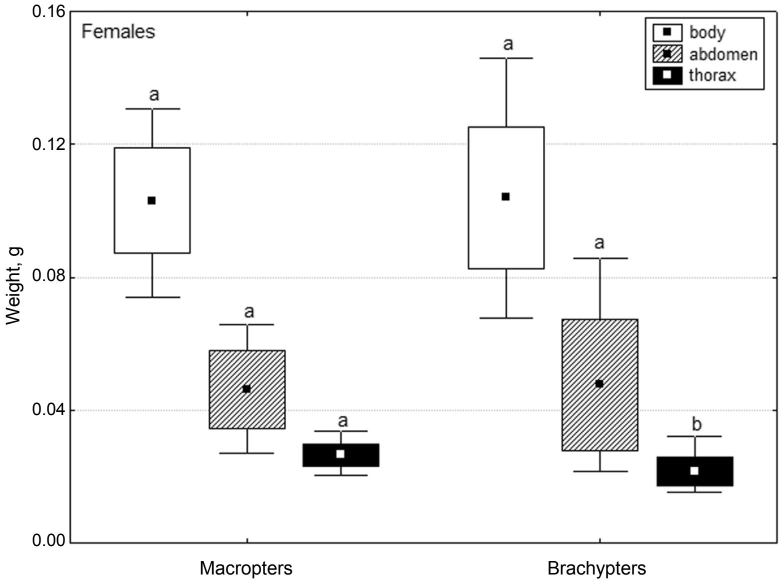

Fig. 4. Mean values and variance (mean/SD/min–max) of the body, abdomen, and thorax weight of macropterous and brachypterous female Roesel's bush crickets. The lowercase letters refer to the results of the *t*-test ($p < 0.05$).

and weight of the abdomen. In the case of body and thorax weight we could not find any significant correlation. Similarly, we found no significant correlation in females between the frequency of macropterous individuals and body, thorax, or abdomen weights ($r_{\text{body}} = -0.0907$, $p = 0.688$; $r_{\text{abdomen}} = -0.0942$, $p = 0.677$; $r_{\text{thorax}} = -0.3435$, $p = 0.118$).

DISCUSSION

We expected to find consistent differences between the body weights of macropterous and brachypterous individuals due to the different development of flight musculature. Unfortunately, this expectation was only partly fulfilled. We could not find significant differences in the total body weight although the females were consequently larger than the males. We only could find significant differences between the thoracal weight of macropterous and brachypterous individuals in both sexes. Furthermore, the variance of the body weight of the macropterous individuals was steadily lower and it was also connected with the larger weight of the thorax. These data support, however, our second prediction. This also implies that macropterous individuals can actively use the wings for dispersal (colonization of grassy patches surrounded by forests).

In a recent review (Bonte et al., 2012) it was suggested that energetic costs may arise in connection with the development of specific machinery associated with dispersal, i.e. for the construction of special dispersal organs and tissues (muscles, wings). Also, considering some other relevant publications (e.g. Zera and Denno, 1997; Suzuki and Tanaka, 1998), we predicted that the costs of more developed flight muscles could induce lower fertility in females. It was suggested that considering likely trade-offs between macroptery and reproduction success, the costs of the more developed flight musculature connected to the macroptery would result in the underdevelopment of reproductive organs (Zera and Denno, 1997; Zera, 2005; Zeng et al., 2010; Zeng and Zhu, 2012). In this connection, there are at least three different, partly contradicting possible outcomes mentioned in the literature. Firstly, the body weight of macropters is on average larger due to the increased mass of thoracal muscles but it does not generate any trade-off. Secondly, macroptery is not connected with the increase of body weight since flight muscles do not function actively, thus macropterous individuals are also pedestrian (as suggested by Poniatowski and Fartmann, 2011). Thirdly, the increased weight of flight musculature (i.e. thorax weight) is counterbalanced by the loss of the weight of the abdomen (i.e. less developed reproductive apparatus; for references see above).

From our alternative expectations we only could confirm that the thoracal weight and probably also the mass of thoracal muscles were increased in macropterous individuals. Conversely, we could not observe any significant decrease of abdominal weight but its variance was larger in brachypterous individuals (see Figs 3 and 4). Thus, we could not support the expected trade-off between macroptery and underdevelopment of reproductive organs.

We supposed that the reduction in the abdomen weight of females was a consequence of the reduced egg production. In this connection, we also expected that the reduction of the abdomen weight was less expressed in males than in females. Comparison of the weight of males and females – as females are on average larger than males – provided valuable data especially on the variation of the weight of the abdomen in females. The variance of the weight was larger in brachypterous individuals, but much more in females, which can be connected to the larger energy reserves (fat bodies) in the more sedentary females. This implies that our hypothesis (*iv*), according to which the reduction in the abdomen weight was less expressed in males than in females, was at least partially supported.

Several authors (Zera and Denno, 1997; Applebaum and Heifetz, 1999; Olvido et al., 2003; Zera, 2005; Zeng et al., 2010; Zeng and Zhu, 2012) suggest that the pressure connected with increasing density of individuals can result in hormonal changes inducing the development of macropterous individuals. Thus, our last expectation was that the higher frequency of macroptery was connected with the crowding within the population. In this respect we received highly contrasting data. In two extended, open sites (Szelce Valley, Nagy-Nyilas meadow) not surrounded by forested barriers, the proportion of macropterous individuals was rather low and macroptery was practically restricted to females, similarly to the large and fairly homogeneous tall-grass site in the Bereg Lowland. Since the density of the population was the highest in the Bereg Lowland site where the proportion of macropters was rather low, we cannot expect that population density could there positively influence the appearance of macroptery. In two sites, however, we found rather high proportions of macroptery (Kis-Gaja ridge: 53%; the forest clearing south of the Ménes Valley: 42%). The altitude and also the vegetation of these sites are very different. The sample from the Kis-Gaja population is relatively small (8 ♂♂ and 11 ♀♀), thus the high proportion of macropters may be simply accidental. The other site is a completely closed forest clearing which possibly has been colonized quite recently. We think that there the rather high proportion of macroptery was due to the spatial connectivity of numerous, less open or closed grassland patches of the surveyed grassland plateau harbouring for example a metapopulation network of other bush-cricket (*Pholidoptera transsylvanica*) and/or a grasshopper (*Arcyptera fusca*) species (Jordán et al., 2003; Benedek et al., 2011; Szanyi et al., 2014). This observation seems to coincide with the results of Wissmann et al. (2009) that the expansion of *M. roeselii* takes place by short-distance colonization rather than by accidental long-distance dispersal events.

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