

Dispersal capability in a habitat specialist bush cricket: the role of population density and habitat moisture

DOMINIK PONIATOWSKI and THOMAS FARTMANN Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Münster, Germany

Abstract. 1. In fragmented landscapes many insect species depend on a regular exchange of individuals between subpopulations to ensure the persistence of the population. Thus, the ability to disperse is of particular relevance.

2. However, in some insect species mobility is not a fixed trait. Hence, knowing the causes of phenotypic plasticity is of great importance when evaluating whether a species is able to survive in fragmented landscapes or not.

3. A multi-year field study was conducted to identify possible causes of macroptery in the wing-dimorphic habitat specialist *Metrioptera brachyptera* L. and to quantify its dispersal capability (% macropters). Therefore, 746 individuals of the species were caught on 135 plots. Additionally, environmental variables that possibly induce the development of macropters (population density and habitat moisture) were recorded.

4. Dispersal capability of *M. brachyptera* was very low. Less than 3% were long-winged. The statistical analysis revealed that the proportion of long-winged *M. brachyptera* was strongly correlated with high bush-cricket densities and not with habitat moisture.

5. The low dispersal capability of *M. brachyptera* leads to the conclusion that individual exchange between isolated populations is limited or even impossible. Habitat specialists, like *M. brachyptera*, may thus be unable to respond to rapid changes in the availability of suitable habitats by dispersing, and hence may be especially dependent on habitat management activities that promote the long-term stability of existing habitat patches.

Key words. Abundance, crowding, fragmentation, macroptery, *Metrioptera brachyptera*, *Metrioptera roeselii*, Orthoptera, wing dimorphism.

Introduction

Land-use change is believed to be the main driver of terrestrial biodiversity loss (Sala *et al.*, 2000). Intensification, abandonment, and afforestation of semi-natural grassland habitats have resulted in the decline of many specialised insect species (van Swaay, 2002; WallisDeVries *et al.*, 2002; Krauss *et al.*, 2010). One major problem of this process is not only habitat loss, but also an increase in the degree of habitat fragmentation (Tschamtker *et al.*, 2002; Fahrig, 2003; Ewers & Didham, 2006), because many insect species depend on regular exchange of individuals between subpopulations to ensure the persistence of the population (Hanski, 1998; Casula, 2006;

Polus *et al.*, 2007). Thus, the ability to disperse is of particular relevance in fragmented landscapes (Thomas, 2000; Diekötter *et al.*, 2005; Wang *et al.*, 2011).

In insects, mobility may not be a fixed trait. For example, long-winged individuals regularly occur in some predominantly short-winged species. This phenomenon is known as macroptery or wing dimorphism and has been observed in many groups of insects (Harrison, 1980; Roff, 1986; Zera & Denno, 1997). Even though long-winged individuals have reduced fecundity, they are fertile (Ando & Hartley, 1982; Ritchie *et al.*, 1987) and in contrast to their short-winged conspecifics are excellent dispersers (Gardiner, 2009; Poniatowski & Fartmann, 2011a). Thus, they are able to react to environmental changes such as global warming (Hochkirch & Damerau, 2009) and habitat disturbance (Roff, 1994; Denno *et al.*, 2001) more rapidly than the regular forms. However, the ecological relevance of these long-winged individuals depends on their frequency in nature, which to a large extent varies from

Correspondence: Dominik Poniatowski, Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Robert-Koch-Straße 28, 48149 Münster, Germany. E-mail: poni@uni-muenster.de

population to population (Simmons & Thomas, 2004; Gardiner, 2009; Poniowski & Fartmann, 2011b). It is believed that such variation is influenced by environmental factors (e.g. temperature, photoperiod, population density) and/or genetic effects (Harrison, 1980; Zera & Denno, 1997).

Within the Orthoptera, research on the causes of macroptery has mainly focused on laboratory experiments on Gryllidae (e.g. Walker, 1987; Masaki & Shimizu, 1995; Olvido *et al.*, 2003; reviewed by Harrison, 1980). However, knowledge on how species react in nature is scarce. Only a few field observations are available indicating that climatic factors are major determinants of macroptery. Ramme (1931) and Ebner (1950), for example, found long-winged individuals only in moist habitats, which they attributed to a high sensitivity to unfavourable microclimatic conditions (cool and moist). However, a recently conducted field study demonstrated that wing dimorphism is density-induced (Poniowski & Fartmann, 2011b). At first glance these factors seem to be mutually exclusive. A cool and moist microclimate usually results in high mortality and thus low population densities (Ingrisch & Köhler, 1998).

These contradictory findings illustrate the need for extensive field studies to reveal the causes of macroptery in nature. This is the only way to develop reliable predictions regarding to what extent wing-dimorphic species can persist in fragmented landscapes. Focusing on species with high habitat specificity is of particular importance, because these species often live in highly isolated populations and are thus greatly affected by fragmentation (Eichel & Fartmann, 2008; Bauerfeind *et al.*, 2009; Brückmann *et al.*, 2010). One of these species is the bush cricket *Metrioptera brachyptera* L., which is typical of threatened habitats such as heathlands and semi-dry calcareous grasslands (Marshall & Haes, 1988; Kleukers *et al.*, 2004; Poniowski & Fartmann, 2008, 2010). In contrast to its sibling species *Metrioptera roeselii* Hagenbach, which is regularly long-winged (Simmons & Thomas, 2004; Gardiner, 2009; Poniowski & Fartmann, 2011b), the long-winged form of *M. brachyptera* is very rare. In the Netherlands for example, only three macropterous individuals of *M. brachyptera* have been found to date (Kleukers *et al.*, 2004). It is not yet known why the long-winged form of *M. brachyptera* is so extraordinarily rare.

The aim of this study was to identify possible causes of macroptery in the habitat specialist *M. brachyptera* and to quantify the proportion of long-winged individuals, which functions as a reliable index of dispersal capability (cf. Denno *et al.*, 2001; Matsumura & Suzuki, 2003). Specifically, the following questions were addressed: (i) Is macroptery in *M. brachyptera* positively correlated with population density, as would be expected if it is induced at high densities, or with habitat moisture as previously postulated? And (ii), is the long-winged form of *M. brachyptera* really rare?

Materials and methods

Model system

The bog bush cricket *Metrioptera brachyptera* (Orthoptera: Tettigoniidae) is a medium-sized bush cricket, 11–21 mm long



Fig. 1. Macropterous *Metrioptera brachyptera* female (Diemeltal, 12 August 2005).

and usually flightless (Marshall & Haes, 1988). Individuals capable of flight (macropterous form, Fig. 1) are very rare (cf. Kleukers *et al.*, 2004; Simmons & Thomas, 2004). *Metrioptera brachyptera* shows high habitat specificity (Schouten *et al.*, 2007), i.e. the species inhabits only a few habitat types such as heath, stands of *Molinia caerulea* (L.) Moench, and semi-dry calcareous grasslands (Marshall & Haes, 1988; Kleukers *et al.*, 2004; Poniowski & Fartmann, 2008, 2010). As in most bush-cricket species, densities of *M. brachyptera* are generally low and vary between 0.1 and 3.8 individuals/10 m² (Ingrisch & Köhler, 1998).

Study areas

The study areas are located in north-west and central Germany (Fig. 2) and harbour many *M. brachyptera* populations. Münsterland (1) is close to the Dutch–German border (52°08'N, 7°20'E) and is dominated by intensive agricultural land use. Only a few small remnants of the formerly widespread heath and raised bogs remain. Diemeltal (2) is situated on the border between North Rhine-Westphalia and Hesse (51°28'N, 9°08'E). The majority of the region consists of limestone, which supports semi-dry grassland. It represents the largest area of calcareous grassland in the northern half of Germany. The headwaters of the Diemel (3) belong to the montane zone and are located southwest of Diemeltal (51°15'N, 8°34'E), i.e. on the border between North Rhine-Westphalia and Hesse. The area is dominated by *Picea abies* forests. Only some of the highest peaks are covered by upland heath, which are remnants of the historical landscape. Medebacher Bucht (4) is a hilly depression east of the Rothaargebirge mountain range in southern Westphalia on the border with Hesse (51°10'N, 8°40'E). The land-use intensity is relatively low due to the shallow soils in this area. Hence, patches of traditionally used acidic grassland and *Cytisus scoparius* shrubland regularly occur. The same holds true for species-rich wet grassland, which can be found adjacent to small rivers.

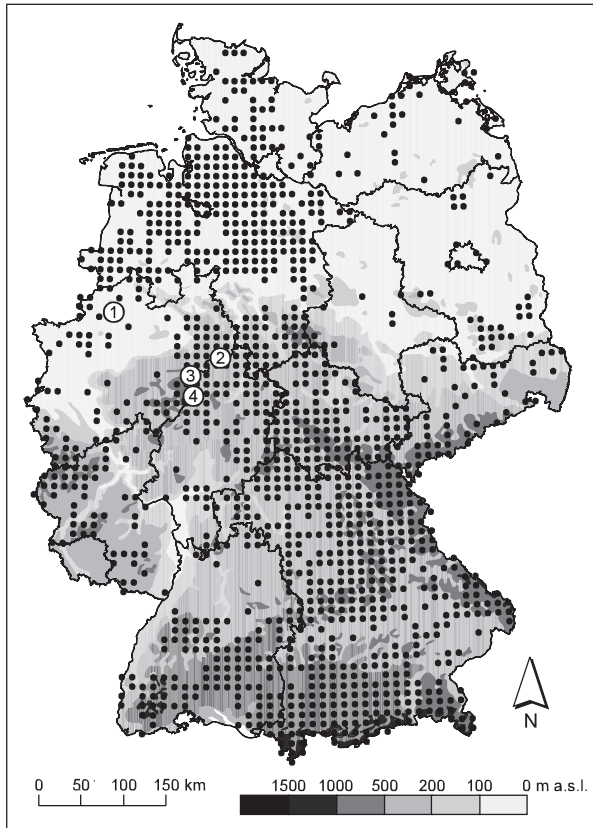


Fig. 2. Grid map distribution of *Metrioptera brachyptera* in Germany (small black dots, modified data from S. Maas, unpublished) and location of the four study areas (white circles: 1, Münsterland; 2, Diemeltal; 3, Headwaters of the Diemel; 4, Medebacher Bucht).

Study plots and environmental variables

From 2004 to 2010, 135 plots on which *M. brachyptera* were present were studied. These study plots were selected randomly using aerial photographs of each study area in order to reflect the range of environmental variation (cf. Poniatowski & Fartmann, 2011b). Each plot was sampled once during the study period. To avoid edge effects each plot covered at least 500 m² and was characterised by a homogeneous vegetation structure in terms of vegetation height, density, and cover (Poniatowski & Fartmann, 2008). The following environmental parameters were recorded for the multivariate analysis (see below), based on the possibility that they may induce the development of macropters: population density (e.g. Higaki & Ando, 2003; Poniatowski & Fartmann, 2009, 2011b) and habitat moisture (e.g. Ramme, 1931; Clark, 1942; Ebner, 1950). Habitat moisture was classified according to two categories: 1 (semi-dry) – upland heath (vegetation dominated by *Calluna vulgaris* (L.) Hull) and calcareous grasslands, and 2 (moist) – lowland wet heath (vegetation with *Erica tetralix* L.) and stands of *Molinia caerulea*. All these habitats are very rare or are even threatened habitat types. Thus, they represent habitat islands in an intensively used agricultural landscape (Poniatowski & Fartmann, 2010).

Bush-cricket sampling

Bush-cricket sampling took place from the beginning of July to mid-August. Densities were recorded using a box quadrat (Ingrisch & Köhler, 1998; Gardiner *et al.*, 2005), which, according to Gardiner and Hill (2006), is the best sampling method for assessing bush-cricket abundance. The box quadrat was 2 m² (1.41 × 1.41 m) with white gauze covered sides of 0.8 m in height. It was randomly dropped over the vegetation at 20 different points per plot; i.e. in total an area of 40 m² was studied in each plot. All surveys were conducted under favourable weather conditions (>15 °C and sunny) between 10.00 and 16.00 hours (cf. Poniatowski & Fartmann, 2010).

To compare the population densities of *M. brachyptera* with those of its sibling species *M. roeselii*, field data from studies carried out between 2002 and 2010 were used (D. Poniatowski & T. Fartmann, 2011b; unpublished). *Metrioptera roeselii* abundance was also recorded using the box quadrat sampling method mentioned above.

Definition of macropterous individuals

Adult bush crickets were classified as long-winged (macropterous) if their wing length clearly exceeded that of the short-winged (brachypterous) form (Poniatowski & Fartmann, 2009), i.e. if they reached the end of the abdomen or even overlapped the hind knees (Ramme, 1951). The wing status of older nymphs was measured using a calliper gauge (0.1 mm accuracy) according to the key published by Ingrisch (1977).

Statistical analyses

As density data did not fit the model assumptions of the *t*-test (i.e. no normal distribution, Kolmogorov–Smirnov test), the Mann–Whitney *U*-test was used to compare two independent samples (i.e. comparison of population densities).

To evaluate whether population density and/or habitat moisture correlates with macroptery rates (proportion data) a binomial generalised linear mixed-effects model (GLMM: *lmer*, Bates *et al.*, 2008) with a two-vector response variable was conducted (for details see Crawley, 2007) using R-2.9.0 (R Development Core Team, 2009). The variables *study year* and *study area* were included as random factors and the significance of the predictor variables was assessed using likelihood ratio tests (Type III test).

All analyses were performed using R-2.9.0 (R Development Core Team, 2009) and SPSS 11.5 statistical packages. SigmaPlot 11.0 was used for graphical analyses.

Results

During the study period, 746 individuals of *M. brachyptera* were caught on 135 plots. Dispersal capability (% macropters) was very low with 2.9% ($N_{\text{individuals}} = 22$) of the total. Macropters originated exclusively from calcareous grasslands ($N_{\text{plots}} = 12$). *Metrioptera brachyptera* was significantly more

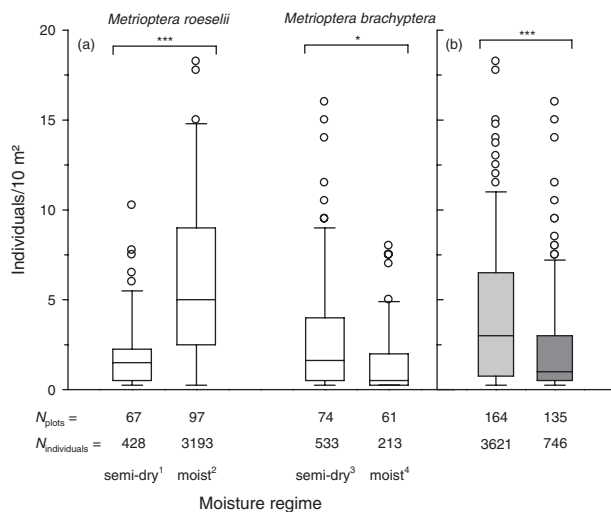


Fig. 3. Population densities of *Metrioptera roeselii* and *M. brachyptera*. Box plots show 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boundary of the box), median (line), and outliers (open circles). Mann–Whitney *U*-test for significance ($\alpha = 0.05$): * $P < 0.05$, *** $P < 0.001$. (a) For two different moisture regimes (semi-dry and moist): 1, calcareous grassland and semi-dry mesophilous grassland; 2, mesic and wet mesophilous grassland; 3, upland heath and calcareous grassland; 4, lowland wet heath and stands of *Molinia caerulea*. For *M. roeselii* (moist moisture regime) some outliers are not shown (23.5, 28.5, 2×38.5 , 46, and 48 individuals/10 m²). (b) In total. *Metrioptera roeselii* (grey), *M. brachyptera* (dark grey). For *M. roeselii* some outliers are not shown (23.5, 28.5, 2×38.5 , 46, and 48 individuals/10 m²).

abundant in these semi-dry habitats than in moist habitats (Fig. 3a). In contrast, *M. roeselii* was three times more abundant in moist than in semi-dry habitats (comparison of medians) (Fig. 3a). Moreover, the population densities of *M. roeselii* were significantly higher than those of *M. brachyptera* (Fig. 3b): abundance ranged from 0.25 to 48 individuals/10 m² (median: 3 individuals/10 m²) for *M. roeselii* and from 0.25 to 16 individuals/10 m² (median: 1 individual/10 m²) for *M. brachyptera* (Fig. 3b).

Comparison of plots with and without macropterous individuals of *M. brachyptera* showed that the bush-cricket densities varied significantly (Mann–Whitney, $U = 27.5$, $P < 0.001$; Fig. 4). The density of *M. brachyptera* populations containing macropters was 9.5 times higher than that of purely short-winged (brachypterous) populations (comparison of medians). With regard to the influence of the environmental variables ‘population density’ and ‘habitat moisture’, the GLMM revealed that the proportion of *M. brachyptera* macropters was only correlated with bush-cricket densities. High abundances are correlated with high macroptery rates [Pseudo R^2 (McFadden) = 0.37, Table 1].

Discussion

Although long-wing individuals of *M. brachyptera* are very rare, the results of this study support the idea that macroptery

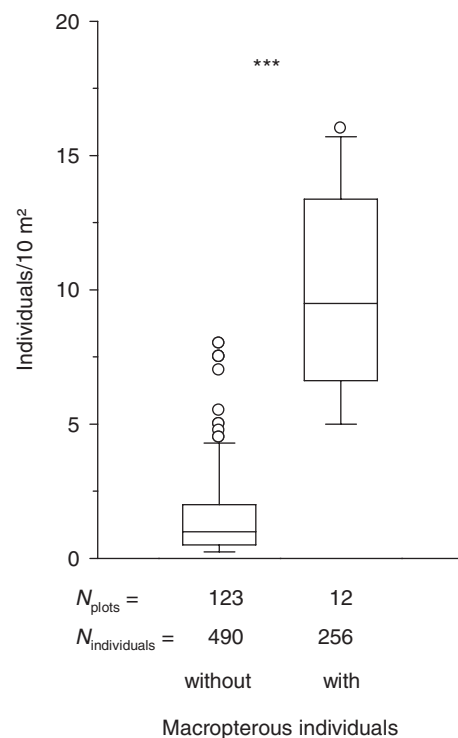


Fig. 4. Populations of *Metrioptera brachyptera* without and with macropterous individuals. Mann–Whitney *U* test for significance ($\alpha = 0.05$): *** $P < 0.001$ (see also Fig. 3).

Table 1. GLMM statistics: relationship between macroptery rates (proportional response variable) and the environmental variable ‘population density’ (predictor variable).

Variable	Estimate	SE	Z	P
Population density (individuals/10 m ²)	—	—	—	<0.0001*
High	0.23132	0.02055	11.26	<0.0001

Pseudo R^2 (McFadden) = 0.37, $N_{plots} = 135$.

The variable ‘habitat moisture’ was excluded from the final model by stepwise backward selection ($P > 0.05$).

* P -value of the likelihood ratio tests.

is density dependent in this low-density species. Long-winged individuals were only observed in high-density populations. No evidence was found that a cool and moist microclimate acts as a trigger of wing dimorphism, as previously assumed (e.g. Ramme, 1931; Clark, 1942; Ebner, 1950). This is in line with the findings of Sanger and Helfert (1975) and Poniatowski and Fartmann (2009, 2011b), who linked macroptery in the sibling species *M. roeselii* to density stress (crowding) and not microclimatic conditions. The link between habitat moisture and macroptery, as discussed by Ramme (1931) and Ebner (1950), might be the result of species-specific habitat preferences: the authors found long-winged individuals of *M. roeselii* exclusively in moist habitats with a high sward. However, *M. roeselii* is typical of moist habitats (Ingrisch, 1982; Poniatowski &

Fartmann, 2005) and can thus easily reach high population densities in this type of habitat (Fig. 3a). In contrast, all macropterous individuals of *M. brachyptera* were observed in semi-dry habitats, in which they were significantly more abundant than in moist habitats (Fig. 3a). However, this does not imply that long-winged *M. brachyptera* can only be found in semi-dry calcareous grasslands. In conditions that favour high population densities, macropterous individuals can also be observed in moist habitats (Galunder *et al.*, 1991). Hence habitat moisture and the interlinked microclimate have at best indirect effects on the occurrence of macropters, as – beside habitat structure and land use (Poniatowski & Fartmann, 2010) – they affect population density (Gardiner & Dover, 2008). Consequently, crowding effects due to high population densities seem to be the main drivers of macroptery, even in low-density bush-cricket species.

The hypothesis of density-dependent macroptery is supported by the laboratory study of Poniatowski and Fartmann (2009): under high rearing densities, significantly more individuals of *M. brachyptera* became long-winged than if reared individually. Density-induced wing dimorphism is not only a bush-cricket-specific phenomenon (Ando & Hartley, 1982; Higaki & Ando, 2003; Poniatowski & Fartmann, 2009), but has also been observed in Gryllidae (Olvido *et al.*, 2003), Gomphocerinae (Köhler, 2002; Behrens & Fartmann, 2004), and other insect groups (Denno *et al.*, 2001; Sasaki *et al.*, 2002; Matsumura & Suzuki, 2003).

However, why is the long-winged form of *M. brachyptera* so extraordinarily rare in nature compared to that of its sibling species *M. roeselii*? The main reason could be that sites with high densities of *M. brachyptera* are rare (Fig. 3), which means that the likelihood of density stress is much higher in *M. roeselii* than in *M. brachyptera* (Poniatowski & Fartmann, 2009). This is in line with the results of other studies, showing that the density of *M. brachyptera* populations is generally low, varying between 0.1 and 3.8 individuals/10 m² ($N_{\text{studies}} = 5$), while *M. roeselii* populations can reach values between 0.7 and 11 individuals/10 m² ($N_{\text{studies}} = 5$) (reviewed by Ingrisch & Köhler, 1998).

Conclusion

According to Roff and Fairbairn (2007), dispersal may be a risky strategy, especially for species that inhabit very isolated habitat patches (Ahlroth *et al.*, 2010), such as *M. brachyptera* (Poniatowski & Fartmann, 2010). With increasing isolation, the probability of failing to find a suitable habitat increases, which presumably results in a decrease in the survival rate of dispersing individuals (Harrison, 1980). Consequently, species living in isolation either evolve a low or a high dispersal capability (Travis & Dytham, 1999; van Dyck & Matthysen, 1999). The first assumption is probably true for *M. brachyptera*. Although distinctly more long-winged individuals than previously reported were found, only 22 out of 746 examined individuals were long-winged. However, such adaptation probably involves some risks, because individual exchange, and thus gene exchanges between isolated populations, in species

with highly reduced wing dimorphism (low dispersal capability) seems to be limited or impossible. Habitat specialists, like *M. brachyptera*, may thus be unable to respond to rapid changes in the availability of suitable habitats by dispersing, and hence may be especially dependent on habitat management activities that promote the long-term stability of existing habitat patches (cf. Baur *et al.*, 2005; Poniatowski & Fartmann, 2010).

Acknowledgements

We are extremely grateful to Fabian Borchard, Annika Brinkert, Jan Distel, Patrick Dolle, Florian Hackmann, Thomas Hermann, Annemarie Krieger, Simon Leib, Claudia Reks, Phillip Remke, Sören Schweineberg, Alexander Terstegge, Claudia Tillmann, Frederike Velbert, Martin Vogel, and Joschka Walk (all from Münster) for their help during the field work in 2010. Moreover, we would like to thank Martin Behrens (Kirchlinteln), Stefanie Heinze (Bonn), Alexander Salz (Münster), and Stephan Maas (Saarlouis) for providing data. Aline Meyer (Münster) and two anonymous reviewers provided valuable comments on an earlier version of the manuscript. The Akademie für ökologische Landesforschung e.V. partly funded this study.

References

- Ahlroth, P., Alatalo, R.V. & Suhonen, J. (2010) Reduced dispersal propensity in the wingless waterstrider *Aquarius najas* in a highly fragmented landscape. *Oecologia*, **162**, 323–330.
- Ando, Y. & Hartley, J.C. (1982) Occurrence and biology of a long-winged form of *Conocephalus discolor*. *Entomologia Experimentalis et Applicata*, **32**, 238–241.
- Bates, D., Maechler, M. & Dai, B. (2008) *lme4: Linear mixed-effects models using Eigen and S4 classes*. R package version 0.999375-28 [WWW document]. URL <http://lme4.r-forge.r-project.org/> [accessed on 20 April 2011].
- Bauerfeind, S., Theisen, A. & Fischer, K. (2009) Patch occupancy in the endangered butterfly *Lycaena helle* in a fragmented landscape: effects of habitat quality, patch size and isolation. *Journal of Insect Conservation*, **13**, 271–277.
- Baur, B., Coray, A., Minoretti, N. & Zschokke, S. (2005) Dispersal of the endangered flightless beetle *Dorcadion fuliginator* (Coleoptera: Cerambycidae) in spatially realistic landscapes. *Biological Conservation*, **124**, 49–61.
- Behrens, M. & Fartmann, T. (2004) Sind hohe Populationsdichten die Ursache der Makropterie beim Gemeinen Grashüpfer (*Chorthippus parallelus*; Caelifera: Acrididae)? *Articulata*, **19**, 91–102.
- Brückmann, S.V., Krauss, J. & Steffan-Dewenter, I. (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology*, **47**, 799–809.
- Casula, P. (2006) Evaluating hypotheses about dispersal in a vulnerable butterfly. *Ecological Research*, **21**, 263–270.
- Clark, E.J. (1942) Occurrence of *Chorthippus parallelus* (Zett.) f. *macroptera* (Orth., Acrididae) in Britain. *The Entomologist's Monthly Magazine*, **78**, 161–166.
- Crawley, M.J. (2007) *The R Book*. Wiley, Chichester, U.K.
- Denno, R.F., Hawthorne, D.J., Thorne, B.L. & Gratton, C. (2001) Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure. *Ecological Entomology*, **26**, 25–36.

- Diekötter, T., Csencsics, D., Rothenbühler, C., Billeter, R. & Edwards, P.J. (2005) Movement and dispersal patterns in the bush cricket *Pholidoptera griseoaptera*: the role of developmental stage and sex. *Ecological Entomology*, **30**, 419–427.
- van Dyck, H. & Matthysen, E. (1999) Habitat fragmentation and insect flight: a changing 'design' in a changing landscape? *Trends in Ecology & Evolution*, **14**, 172–174.
- Ebner, R. (1950) Ueber Macropterie bei *Metrioptera* (Orthoptera). *EOS Sonderband*, 267–274.
- Eichel, S. & Fartmann, T. (2008) Management of calcareous grasslands for Nickerl's fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation, and patch area. *Journal of Insect Conservation*, **12**, 677–688.
- Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.
- Galunder, R., Nicke, H. & Stevens, M. (1991) Bericht über die Exkursion anlässlich der Sommertagung des Naturhistorischen Vereins der Rheinlande und Westfalens in Engelskirchen (Oberbergisches Land) am 11. und 12.8.1990. *Decheniana*, **144**, 163–170.
- Gardiner, T. (2009) Macropterism of Roesel's bushcricket *Metrioptera roeselii* in relation to climate change and landscape structure in eastern England. *Journal of Orthoptera Research*, **12**, 95–102.
- Gardiner, T. & Dover, J. (2008) Is microclimate important for Orthoptera in open landscapes? *Journal of Insect Conservation*, **12**, 705–709.
- Gardiner, T. & Hill, J. (2006) A comparison of three sampling techniques used to estimate population density and assemblage diversity of Orthoptera. *Journal of Orthoptera Research*, **15**, 45–51.
- Gardiner, T., Hill, J. & Chesmore, D. (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. *Journal of Insect Conservation*, **9**, 151–173.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Harrison, R.G. (1980) Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics*, **11**, 95–118.
- Higaki, M. & Ando, Y. (2003) Effects of crowding and photoperiod on wing morph and egg production in *Eobiana engelhardti subtropica* (Orthoptera: Tettigoniidae). *Applied Entomology and Zoology*, **38**, 321–325.
- Hochkirch, A. & Damerau, M. (2009) Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. *Biological Journal of the Linnean Society*, **97**, 118–127.
- Ingrisch, S. (1977) Beitrag zur Kenntnis der Larvenstadien Mitteleuropäischer Laubheuschrecken (Orthoptera: Tettigoniidae). *Zeitschrift für Angewandte Zoologie (N.F.)*, **64**, 459–501.
- Ingrisch, S. (1982) Orthopterengesellschaften in Hessen. *Hessische Faunistische Briefe*, **2**, 38–46.
- Ingrisch, S. & Köhler, G. (1998) *Die Heuschrecken Mitteleuropas*. Westarp Wissenschaften, Magdeburg, Germany.
- Kleukers, R.M.J.C., van Nieukerken, E.J., Odé, B., Willemsse, L.P.M. & van Wingerden, W.K.R.E. (2004) *De sprinkhanen en krekels van Nederland (Orthoptera)*, *Nederlandse Fauna 1*. Nationaal Natuurhistorisch Museum, KNNV Uitgeverij & EIS-Nederland, Leiden, the Netherlands.
- Köhler, G. (2002) Experimente und Erhebungen zur Flügeligkeit beim Gemeinen Grashüpfer, *Chorthippus parallelus* (Zetterstedt) (Caelifera: Acrididae) – ein Beitrag zur Interpretation von Makropterie. *Articulata*, **17**, 1–19.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M. *et al.* (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597–605.
- Marshall, J.A. & Haes, E.C.M. (1988) *Grasshoppers and Allied Insects of Great Britain and Ireland*. Harley, Colchester, U.K.
- Masaki, S. & Shimizu, T. (1995) Variability in wing form of crickets. *Researches on Population Ecology*, **37**, 119–128.
- Matsumura, M. & Suzuki, Y. (2003) Direct and feeding-induced interactions between two rice planthoppers, *Sogatella furcifera* and *Nilaparvata lugens*: effects on dispersal capability and performance. *Ecological Entomology*, **28**, 174–182.
- Olvido, A.E., Elvington, E.S. & Mousseau, T.A. (2003) Relative effects of climate and crowding on wing polymorphism in the southern ground cricket, *Allonemobius socius* (Orthoptera: Gryllidae). *Florida Entomologist*, **86**, 158–164.
- Polus, E., Vandewoestijne, S., Choutt, J. & Baguette, M. (2007) Tracking the effect of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. *Biodiversity and Conservation*, **16**, 3423–3436.
- Poniatowski, D. & Fartmann, T. (2005) Die Ökologie von Roesels Beißschrecke (*Metrioptera roeselii*) im Feuchtgrünland der Medebacher Bucht (Südwestfalen). *Articulata*, **20**, 85–111.
- Poniatowski, D. & Fartmann, T. (2008) The classification of insect communities: lessons from orthopteran assemblages of semi-dry calcareous grasslands in central Germany. *European Journal of Entomology*, **105**, 659–671.
- Poniatowski, D. & Fartmann, T. (2009) Experimental evidence for density-determined wing dimorphism in two bush-cricket (Ensifera: Tettigoniidae). *European Journal of Entomology*, **106**, 599–605.
- Poniatowski, D. & Fartmann, T. (2010) What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? *Journal of Insect Conservation*, **14**, 637–645.
- Poniatowski, D. & Fartmann, T. (2011a) Does wing dimorphism affect mobility in *Metrioptera roeselii*? *European Journal of Entomology*, **108**, 409–415.
- Poniatowski, D. & Fartmann, T. (2011b) Weather-driven changes in population density determine wing dimorphism in a bush-cricket species. *Agriculture, Ecosystems and Environment*. DOI: 10.1016/j.agee.2010.10.006.
- Ramme, W. (1931) Verlust oder Herabsetzung der Fruchtbarkeit bei macropteren Individuen sonst brachypterer Orthopterenarten. *Biologisches Zentralblatt*, **51**, 533–540.
- Ramme, W. (1951) Zur Systematik, Faunistik und Biologie der Orthopteren von Südost-Europa und Vorderasien. *Mitteilungen des Zoologischen Museums Berlin*, **27**, 1–432.
- R Development Core Team (2009) *R: a language and environment for statistical computing* [WWW document]. URL <http://www.R-project.org> [accessed on 20 April 2011].
- Ritchie, M.G., Butlin, R.K. & Hewitt, G.M. (1987) Causation, fitness effects and morphology of macropterism in *Chorthippus parallelus* (Orthoptera: Acrididae). *Ecological Entomology*, **12**, 209–218.
- Roff, D.A. (1986) The evolution of wing dimorphism in insects. *Evolution*, **40**, 1009–1020.
- Roff, D.A. (1994) Habitat persistence and the evolution of wing dimorphism in insects. *American Naturalist*, **144**, 772–798.
- Roff, D.A. & Fairbairn, D.J. (2007) The evolution and genetics of migration in insects. *BioScience*, **57**, 155–164.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000) Biodiversity – global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Sänger, K. & Helfert, B. (1975) Spontanes Auftreten holopterer Formen von *Tessellana vittata* und *Metrioptera roeseli* (Orthoptera: Tettigoniidae) in Laborzuchten. *Anzeiger der Österreichischen Akademie der Wissenschaften (Mathematisch-Naturwissenschaftliche Klasse)*, **11**, 192–194.
- Sasaki, R., Nakasugi, F. & Fujisaki, K. (2002) Environmental factors determining wing form in the lygaeid bug, *Dimorphopterus*

- japonicus* (Heteroptera: Lygaeidae). *Applied Entomology and Zoology*, **37**, 329–333.
- Schouten, M.A., Verweij, P.A., Barendregt, A., Kleukers, R.J.M. & de Ruiter, P.C. (2007) Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life–history traits. *Journal of Biogeography*, **34**, 1938–1946.
- Simmons, A.D. & Thomas, C.D. (2004) Changes in dispersal during species' range expansions. *American Naturalist*, **164**, 378–395.
- van Swaay, C.A.M. (2002) The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, **104**, 315–318.
- Thomas, C.D. (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London Series B*, **267**, 139–145.
- Travis, J.M.J. & Dytham, C. (1999) Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London Series B*, **266**, 723–728.
- Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research*, **17**, 229–239.
- Walker, T.J. (1987) Wing dimorphism in *Gryllus rubens* (Orthoptera, Gryllidae). *Annals of the Entomological Society of America*, **80**, 547–560.
- WallisDeVries, M.F., Poschlod, P. & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, **104**, 265–273.
- Wang, R., Ovaskainen, O., Cao, Y., Chen, H., Zhou, Y., Xu, C. *et al.* (2011) Dispersal in the Glanville fritillary butterfly in fragmented versus continuous landscapes: comparison between three methods. *Ecological Entomology*, **36**, 251–260.
- Zera, A.J. & Denno, R.F. (1997) Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology*, **42**, 207–230.

Accepted 30 August 2011

First published online 27 October 2011