

# Weather-driven changes in population density determine wing dimorphism in a bush-cricket species

Dominik Poniatowski, Thomas Fartmann\*

Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Robert-Koch-Straße 26, 48149 Münster, Germany

## ARTICLE INFO

### Article history:

Received 21 December 2009  
Received in revised form 1 October 2010  
Accepted 7 October 2010  
Available online 10 November 2010

### Keywords:

Abundance  
Crowding  
Macroptery  
Mesoclimate  
Orthoptera  
Temperature

## ABSTRACT

Long-winged (macropterous) individuals that are capable of flight in predominantly short-winged (flightless) species can considerably affect population dynamics and range expansion. Understanding the triggers that determine macroptery is crucial for understanding whether the dispersal ability of species allows them to shift their distributions through fragmented landscapes or in response to climate change. From 2002 to 2009, we studied population densities and wing dimorphism (macroptery) of *Metroptera roeselii*, on 62 plots in central Germany. In the first step, we used a generalized linear mixed-effects model to assess the variables that influence macroptery. Macroptery rates are strongly positively correlated with bush-cricket abundance and not with vegetation structure and habitat moisture. Populations with macropters had significantly higher densities than those without. In the second step, we analysed the relationship between population densities and several mesoclimate/weather parameters. Densities were positively correlated with warm and dry weather conditions during hatching time in April, and previous year weather is less important than present year weather. In the light of the ongoing range expansion of *M. roeselii* in large parts of Europe, our results support the hypothesis that at high latitudes macroptery and range expansion are indirectly caused by weather-driven changes in population densities.

© 2010 Elsevier B.V. All rights reserved.

## 1. Introduction

Species range shifts to higher latitudes or altitudes due to climate change have been reported for several taxonomic groups (Walther et al., 2002; Parmesan, 2006). Among arthropods highly mobile taxa, such as Odonata, in particular have shown a strong response (Hickling et al., 2005). However, for many less mobile groups considerable range shifts have also been observed (Parmesan et al., 1999; Battisti et al., 2005; Gobbi et al., 2006). This is also true for Orthoptera, although to a lesser extent (Hickling et al., 2006). The majority of central European orthopterans are flightless and have low dispersal ability (Reinhardt et al., 2005). Hence, the ability to react to climate change should be low. However, since the 1980s – the beginning of the strong global temperature increase (IPCC, 2007) – some short-winged (brachypterous) species have been able to expand their range rapidly (Thomas et al., 2001; Simmons and Thomas, 2004; Gardiner, 2009; Wissmann et al., 2009). In those cases, long-winged (macropterous) individuals of the predominantly short-winged (flightless) species are assumed to have been responsible for range shifts (Simmons and Thomas, 2004; Gardiner, 2009; Hochkirch and Damerou, 2009). Macropters are potentially

capable of flight and, therefore, more mobile than their short-winged relatives (Chapman et al., 1978; Higaki and Ando, 2003). Consequently, Vickery (1965) characterised macropters as a dispersal phase.

Understanding the drivers that determine wing dimorphism (macroptery) is crucial for making predictions for population dynamics and range expansions (Gardiner, 2009). In Orthoptera, wing length is believed to reflect a trade-off between mobility and fecundity (Zera and Denno, 1997). Nevertheless, long-winged individuals are usually fertile (cf. Sanger and Helfert, 1975; Ritchie et al., 1987) and, therefore, able to establish new populations. Although the phenomenon of macroptery has been known since the early 1900s (Karny, 1913; Puschignig, 1914; Burr, 1936), its causes are still being discussed (Harrison, 1980; Zera and Denno, 1997). At first, climatic factors had been assumed as major determinants of macroptery. Ramme (1931) and Ebner (1950), for example, found macropters only in moist habitats with a high sward. Later on, evidence was growing that macroptery is density-induced (Ando and Hartley, 1982; Higaki and Ando, 2003). However, besides environmental factors, there is also the theory that wing dimorphism results from a variation in genotype or from a combination of both genetic and environmental effects (Harrison, 1980; Zera and Denno, 1997). Simmons and Thomas (2004), for instance, found distinct differences in frequencies of dispersive, long-winged (macropterous) individuals at the range margin of the species compared with longer-established populations in the range core. They explained

\* Corresponding author. Tel.: +49 251 8331967; fax: +49 251 8338338.  
E-mail address: [fartmann@uni-muenster.de](mailto:fartmann@uni-muenster.de) (T. Fartmann).

wing dimorphism by genetic differences and not by phenotypic plasticity.

Our aim was to explain which factors determine macroptery in predominantly flightless orthopterans. For this purpose a multi-year field study was conducted to test, if population density, habitat moisture and/or vegetation structure influence macroptery rates. Moreover, we analysed the effect of several mesoclimate/weather parameters on population densities. We suppose that the rapid range expansion of some wing-dimorphic insects in the last 20–30 years are caused by weather-driven changes in population density leading to high numbers of mobile macropters.

## 2. Materials and methods

### 2.1. Study organism

As study organism we choose *Metrioptera roeselii* (Hagenbach, 1822) (Orthoptera: Tettigoniidae), a medium-sized bush-cricket, 13–26 mm in total length (Marshall and Haes, 1988), which is currently expanding its range northwards in large parts of Europe (Kleuker et al., 2004; Gardiner, 2009; Wissmann et al., 2009). It is often used for research, such as genetic analyses (Hochkirch and Damerau, 2009; Holzhauer et al., 2009), range expansion studies (Simmons and Thomas, 2004; Gardiner, 2009; Wissmann et al., 2009), laboratory experiments (Sänger and Helfert, 1975; Poniatowski and Fartmann, 2009), and mobility studies (Kindvall et al., 1998; Berggren et al., 2002). Thus, it represents an ideal model organism. *M. roeselii* is an omnivorous habitat generalist occurring in a wide variety of different habitats (e.g. different types of grassland, fallow land and roadside verges) (Marshall and Haes, 1988). The species is wing-dimorphic, but the short-winged (brachypterous) morph dominates. However, long-winged *M. roeselii* occur regularly, particularly in recent years (Simmons and Thomas, 2004; Gardiner, 2009) and can be found even in great distance to the next population (Hochkirch and Damerau, 2009).

### 2.2. Study areas

Both study areas are located in central Germany (Fig. 1) and harbour many *M. roeselii* populations. The Diemelstal 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 maintains semi-dry grassland. It represents the largest area of calcareous grassland in the northern half of Germany (Fartmann, 2006). The Medebacher Bucht is a hilly depression east of the Rothaargebirge mountain range in southern Westphalia on the border to Hesse (51°10'N/8°40'E). Due to the shallow soils, the land-use intensity is relatively low. Hence, patches of traditionally used acidic grassland and broom shrubland regularly occur. The same holds true for species-rich wet grassland, which can be found adjacent to small rivers.

### 2.3. Study sites and environmental variables

From 2002 to 2009, we studied 62 plots with presence of the species. Study plots were selected randomly using aerial photographs for each region of the study areas in order to reflect the total environmental differences. During the whole study period each plot was sampled once. To avoid edge effects each plot had a size of at least 500 m<sup>2</sup> and was characterised by a homogenous vegetation structure in terms of vegetation height, density and cover (Poniatowski and Fartmann, 2008a). For the first multivariate analysis (see Section 2.6) several environmental parameters were recorded, which possibly induce the development of macropters – such as vegetation structure, habitat moisture (e.g. Ramme, 1931; Ebner, 1950) and population density (e.g. Higaki and Ando, 2003;

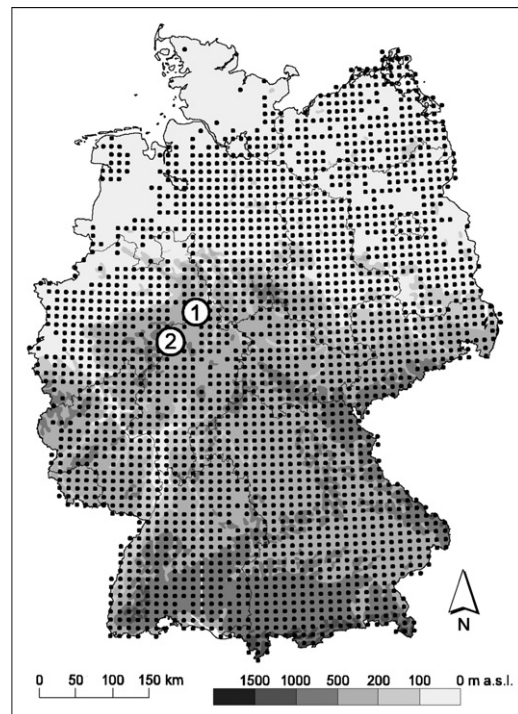


Fig. 1. Current records of *Metrioptera roeselii* in Germany (small black dots, modified data from Maas unpubl.) and location of the two study areas (white circles: 1 – Diemelstal, 2 – Medebacher Bucht).

Poniatowski and Fartmann, 2009) (Table 1: Model 1). Furthermore, we ascertained for each plot aspect, slope, latitude and altitude to analyse the relationship between mesoclimate and population densities (Table 1: Model 2). Weather data were obtained by the German weather service (Deutscher Wetterdienst) in a 1 km × 1 km grid-based resolution for each month and year. Analysis of weather parameters was conducted for hatching time of the nymphs in April, because nymphs are rather sensitive to unfavourable – cool/moist – weather conditions and the effect of weather on bush-cricket densities is probably highest during this developmental stage. However, there is also the assumption that previous year weather conditions determine abundances of *M. roeselii* in the following year (Gardiner, 2009). That is why we examined the impact of temperature and precipitation during the nymphal period of the parental generation (April–July) on population densities as well (Table 1: Model 2).

### 2.4. Bush-cricket sampling

Bush-cricket sampling took place from the beginning of July to mid-August. Densities were recorded with a box quadrat (Ingrisch and Köhler, 1998; Gardiner et al., 2005), which, according to Gardiner and Hill (2006), is the best sampling method to assess bush-cricket abundance. The box quadrat had an area of 2 m<sup>2</sup> (1.41 m × 1.41 m) with white gauze covered sides of 0.8 m height. It was randomly dropped over the vegetation at 10 different points per plot; i.e., in total an area of 20 m<sup>2</sup> was studied on each plot. All surveys were conducted under favourable weather conditions (>15 °C and sunny) between 10:00 and 16:00 (cf. Berggren et al., 2002; Poniatowski and Fartmann, 2010).

### 2.5. Definition of macropterous individuals

A bush-cricket was classified as long-winged (macropterous) if wing length clearly exceeded the measure of a brachypterous

**Table 1**  
Overview of parameters used in generalized linear mixed-effects model (GLMM).

Parameter	Factor levels
Model 1: macroptery rates vs. environmental parameters (binomial GLMM)	
<i>Response variable</i>	
Macroptery	Metric <sup>a</sup>
<i>Predictor variables</i>	
Abundance (individuals/10 m <sup>2</sup> )	Metric
Habitat-moisture regime	2 <sup>b</sup>
Total vegetation cover (%)	Metric
Vegetation height (cm)	Metric
Model 2: bush-cricket densities vs. mesoclimate/weather (Poisson GLMM)	
<i>Response variable</i>	
Abundance (individuals/10 m <sup>2</sup> )	Metric
<i>Predictor variables</i>	
Altitude	Metric
Heat load <sup>c</sup>	Metric
Mean temperature and precipitation during nymphal period of the parental generation (previous year weather conditions: April–July) <sup>d</sup>	Metric
Weather during hatching time of the nymphs in April <sup>d,e</sup>	Metric
<i>Random effects</i>	
Year	5 <sup>f</sup>
Study area	2 <sup>g</sup>

<sup>a</sup> Proportion data (two-vector response variable, for more information see Section 2.6).

<sup>b</sup> Two categories: 1 – semi-dry = semi-dry calcareous grassland ( $N_{\text{plots}} = 7$ ) and semi-dry to mesic grassland ( $N_{\text{plots}} = 14$ ); 2 – moist = mesic to wet grassland ( $N_{\text{plots}} = 41$ ).

<sup>c</sup> Conversion of aspect, slope and latitude by heat load index according to McCune and Keon (2002).

<sup>d</sup> Weather data are provided by the German weather service (Deutscher Wetterdienst) (1 km × 1 km grid-based resolution).

<sup>e</sup> Due to collinearity the variable mean temperature and precipitation during hatching time of the nymphs in April were summarized by PCA to one factor (for more information see Section 2.6).

<sup>f</sup> 2002, 2004, 2005, 2007, 2009.

<sup>g</sup> See Fig. 1.

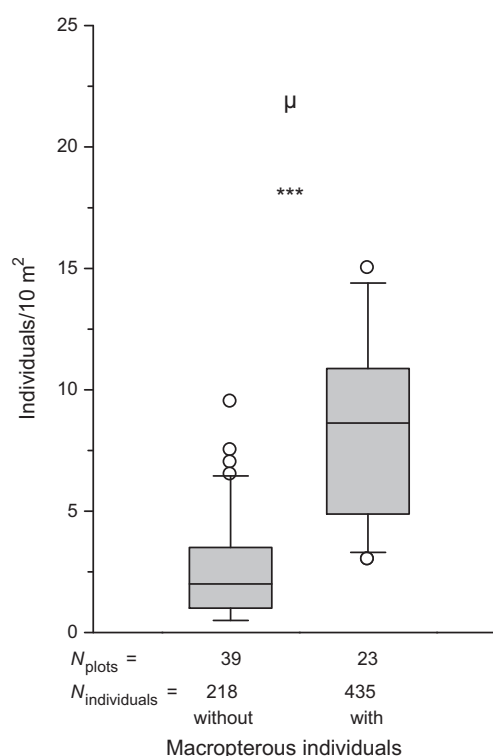
morph (Poniatowski and Fartmann, 2009), i.e. if they reached the end of the abdomen or even overlapped the hind knees (Ramme, 1951). The wing status of older nymphs was measured with a calliper gauge (0.1 mm accuracy) using the key by Ingrisch (1977).

## 2.6. Statistical analyses

As our density data did not fit the model assumptions of *t* test (i.e. no normal distribution, Kolmogorov–Smirnov-Test), we used the Mann–Whitney *U* test (MWU) for the comparisons of two independent samples (i.e., the comparison of populations with and without macropterous individuals).

Intercorrelations of predictor variables were examined prior to multivariate analysis (see below) by applying a Pearson's correlation matrix that included all metric predictor variables. Collinearity between predictor variables was generally low, with a Pearson correlation coefficient (*r*) of <0.5 for all pairs except mean temperature and mean precipitation during hatching time of the nymphs (Pearson  $r = -0.818$ ,  $P < 0.001$ ). To avoid problems associated with multicollinearity a principal component analysis (PCA) was conducted to create a summarizing factor (cf. McCreadie et al., 2004; Stefanescu et al., 2004), hereafter called weather during hatching time of the nymphs. The new variable represents an independent principal component with an eigenvalue of 1.8. It explained 90.8% of total variance in the data set and was positively correlated with temperature during hatching time of the nymphs (Pearson  $r = 0.953$ ,  $P < 0.001$ ) and negatively with precipitation during hatching time of the nymphs (Pearson  $r = -0.953$ ,  $P < 0.001$ ); i.e., the summarizing factor represents a clear gradient from warm/dry weather (positive values) to cool/moist weather (negative values).

To evaluate which parameters affect the macroptery rates (proportion data) a binomial generalized linear mixed-effects model



**Fig. 2.** Populations of *Metrioptera roeselii* without and with macropterous individuals. Box plots show 10th and 90th percentile (whiskers), 25th and 75th percentile (boundary of the box), median (line), and outliers (open dots). One outlier (46 individuals/10 m<sup>2</sup>) is not shown (category: with macropterous individuals). Mann–Whitney *U* test for significance ( $\alpha = 0.05$ ): \*\*\* $P < 0.001$ .

(GLMM: lmer, Bates et al., 2008) with a two-vector response variable using R-2.9.0 (R Development Core Team, 2009) was conducted (for details see Crawley, 2007) (Table 1: Model 1). In a second step, we analysed the relationships between bush-cricket density and several mesoclimate/weather parameters with a Poisson GLMM (Table 1: Model 2). For both GLMMs, the variables year and area were set up as random factors (Table 1). Non-significant predictors were excluded from the final model by stepwise backward-selection. The level of significance was set to 0.01 (cf. Crawley, 2002) and the significance of the predictor variables were assessed with 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. For graphical analyses, we used SigmaPlot 11.0.

## 3. Results

During the study period *M. roeselii* was caught on 62 plots with 653 individuals. 10% of them were macropterous (mean<sub>per plot</sub> =  $4.5 \pm 8.5$  SD; maximum value = 35%).

The comparison of plots with and without macropterous individuals showed that the bush-cricket densities differed significantly (MWU,  $U = 76.5$ ,  $P < 0.001$ ; Fig. 2). In populations with macropterous *M. roeselii* the densities were about 4 times as high as in purely short-winged populations (comparison of medians).

Concerning the influence of environmental variables the binomial GLMM revealed that the proportion of *M. roeselii* macropters was only correlated with high bush-cricket densities (Pseudo  $R^2$  [Nagelkerke's] = 0.58, Table 2). The other predictor variables had no significant effect.

We used Poisson GLMM to analyse the relationship between bush-cricket densities and several mesoclimate/weather param-

**Table 2**

Statistics of GLMM (binomial): relationship between macroptery rates (proportional response variable) and several environmental parameters (predictor variables) (Table 1: Model 1). Non-significant predictors were excluded from the final model by stepwise backward-selection ( $P > 0.01$ ).

Variable	Estimate	SE	Z	P
Abundance (individuals/10 m <sup>2</sup> )				<0.0001
High	0.1433	0.0187	7.650	<0.0001

Pseudo  $R^2$  [Nagelkerke's] = 0.58,  $N_{\text{plots}} = 62$ .

eters. The final model shows that abundances were positively correlated with warm and dry weather conditions during hatching time of the nymphs (Pseudo  $R^2$  [Nagelkerke's] = 0.17, Table 3); all other variables were excluded from the final model. However, when predictor variables were analysed separately, temperature during nymphal period of the parental generation had an effect on bush-cricket densities as well (GLMM: Estimate = 0.5024; SE = 0.1802; Z = 2.788;  $P < 0.01$ ; Pseudo  $R^2$  [Nagelkerke's] = 0.14).

#### 4. Discussion

Our results show that in *M. roeselii*, macroptery rates are strongly positively correlated with abundance and not with vegetation structure and habitat moisture. It is, therefore, reasonable to suggest that the development of long-winged individuals is determined by density stress (crowding), as has been shown for locusts (Uvarov, 1966). The hypothesis that macroptery in *M. roeselii* is induced by high habitat moisture (Ramme, 1931; Ebner, 1950) seems to be a result of its habitat preferences. *M. roeselii* is a typical species of wet grassland that can reach high population densities in this habitat type (Poniatowski and Fartmann, 2005).

However, our observations of a density-induced macroptery do not match the field and laboratory findings of Simmons and Thomas (2004), who did not find an influence of density on the development of macropters in *M. roeselii*. A reason for this might be that Simmons and Thomas (2004) conducted their field survey late in the season (mid-July to mid-October), when some of the dispersive macropters might already have left their source populations (cf. Hochkirch and Damerau, 2009). Moreover, the densities assessed in September or October might not reflect the abundances during the nymphal period due to loss of individuals through dismigration, death or predation. Why Simmons and Thomas (2004) did not find a correlation between abundance and occurrence of macropters in their laboratory study remains unanswered. However, other laboratory experiments (Sänger and Helfert, 1975; Poniatowski and Fartmann, 2009) support our findings, revealing a density-induced macroptery in *M. roeselii*. Similar results have also been reported for other bush-cricket species (Ando and Hartley, 1982; Sängler, 1984; Higaki and Ando, 2003), including the sibling species *Metrioptera brachyptera* (Poniatowski and Fartmann, 2009). High densities are thought to cause an excess of tactile and possibly visual stimuli affecting the endocrine control which induces the development of long wings (Uvarov, 1966; Zera and Denno, 1997; Zera, 2004).

**Table 3**

Statistics of GLMM (Poisson): relationship between bush-cricket density (response variable) and several mesoclimate/weather parameters (predictor variables) (Table 1: Model 2). Non-significant predictors were excluded from the final model by stepwise backward-selection ( $P > 0.01$ ).

Variable	Estimate	SE	Z	P
Weather during hatching time of the nymphs in April				<0.01
Warm/dry	0.6373	0.1636	3.895	<0.0001

Pseudo  $R^2$  [Nagelkerke's] = 0.17,  $N_{\text{plots}} = 62$ .

The causes of high population densities are often very complex (Joern and Gaines, 1990; Ingrisch and Köhler, 1998). As for Orthoptera in general, in bush-cricket land use and interrelated with this habitat structure plays an important role (Poniatowski and Fartmann, 2010). In addition, climatic factors strongly affect abundance (Gardiner and Dover, 2008). In the case of *M. roeselii*, favourable weather conditions during the hatching period in April in particular are essential for a successful development, as young nymphs are very sensitive to environmental conditions. Hence, favourable (warm/dry) weather conditions during the early nymphal period lead to high population densities that result due to crowding (see above) in a high proportion of macropters in summer. A striking example for this phenomenon was the year 2007. The April 2007 was extraordinarily warm in Western and Central Europe (Müller-Westermeier et al., 2008) and accordingly macropter proportions of more than 20% could be observed in several regions (Benton, 2008; Gardiner, 2008; Poniatowski and Fartmann, 2008b). But why are there observations of macropters in years with a wet and cool spring/summer? One reason might be favourable weather conditions during the previous year that have promoted high densities in the following year (Gardiner, 2009). However, the influence of the previous year seems to be less important than the conditions during the early nymphal period. Otherwise the proportion of macropters in the year following the European heat wave in 2003 should have been very high. However, this was not the case. The spring 2004 had a more or less averaged weather (Müller-Westermeier and Riecke, 2005) and at most 2% of all individuals in summer 2004 were long-winged (Gardiner, 2006; Wissmann et al., 2009).

#### 5. Conclusions

Although *M. roeselii* is predominantly short-winged and flightless, since the 1980s – hence in accordance with the strong temperature increase (IPCC, 2007) – a rapid northward expansion has been observed (Kleukers et al., 2004; Simmons and Thomas, 2004; Gardiner, 2009; Wissmann et al., 2009). As the driving force for this development long-winged individuals have been assumed (Simmons and Thomas, 2004; Gardiner, 2009; Hochkirch and Damerau, 2009). Until the end of the 1970s macropters were rarely observed (Gardiner, 2009) and higher proportions of long-winged individuals have been an exception (Burr, 1936). By now macropters occur significantly more frequent (Gardiner, 2009) and populations with more than 20% of macropters are not any longer a rarity (Benton, 2008; Gardiner, 2008; Poniatowski and Fartmann, 2008b; this study).

Based on the results of our study and in accordance with Gardiner (2009) we conclude that the rapid northward range expansion of *M. roeselii* is indirectly driven by climate change: favourable (warm/dry) weather conditions lead to high densities at high latitudes (cf. Bale et al., 2002) and in turn result in many macropters, thus potential dispersers. Even though not all long-winged individuals are capable of flight, it can be assumed that at least some have a high dispersal potential (Hochkirch and Damerau, 2009). Besides the occurrence of dispersers, the landscape structure and landscape permeability may play an important role for dispersal (cf. Berggren et al., 2002). In East England *M. roeselii* was strongly promoted by the introduction of set-aside and agri-environment schemes (e.g. grass field margins) (Gardiner, 2009).

#### Acknowledgements

We would like to thank Martin Behrens, Stefanie Heinze, Alexander Salz (Münster) and Stephan Maas (Saarlouis) for providing data. We are very grateful to Axel Hochkirch (University of Trier), Robert

J. Wilson (University of Exeter), Tim Gardiner (Rivenhall, Witham), the editors and two anonymous reviewers for helpful comments on an earlier version of the manuscript. Moreover, we would like to thank Jan Thiele (University of Münster) for help with R. The Akademie für ökologische Landesforschung e.V. partly funded this study.

## References

- Ando, Y., Hartley, J.C., 1982. Occurrence and biology of a long-winged form of *concephalus discolor*. Ent. Exp. Appl. 32, 238–241.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biol. 8, 1–16.
- Bates, D., Maechler, M., Dai, B., 2008. lme4: Linear mixed-effects models using Eigen and Eigen++. R package version 0.999375-28. <http://lme4.r-forge-project.org>.
- Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A., Larsson, S., 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol. Appl. 15, 2084–2096.
- Benton, T., 2008. Grasshoppers, bush-crickets and their allies: an up-date for NE Essex. In: Nature in North-East Essex. Colchester Natural History Society, Colchester.
- Berggren, Å., Birath, B., Kindvall, O., 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeselii*). Conserv. Biol. 16, 1562–1569.
- Burr, M., 1936. British Grasshoppers and their Allies: A Stimulus to their Study. Janson, London.
- Chapman, R.F., Cook, A.G., Mitchell, G.A., Page, W.W., 1978. Wing dimorphism and flight in *Zonocerus variegatus* (L.) (Orthoptera: Pyrgomorphidae). Bull. Ent. Res. 68, 229–242.
- Crawley, M.J., 2002. Statistical Computing: An Introduction to Data Analysis using S-Plus. Wiley, Chichester.
- Crawley, M.J., 2007. The R Book. Wiley, Chichester.
- Ebner, R., 1950. Ueber Macropterie bei *Metrioptera* (Orthoptera). EOS Sonderband, 267–274.
- Fartmann, T., 2006. Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany. Ann. Zool. Fenn. 43, 335–347.
- Gardiner, T., 2006. The impact of grassland management on Orthoptera populations in the UK. Ph.D. Thesis. University of Essex, Colchester, UK. Unpublished.
- Gardiner, T., 2008. Orthoptera and allied insects of Essex 2007. Essex Nat. (N.S.) 25, 72–75.
- Gardiner, T., 2009. Macropterism of Roesel's bushcricket *Metrioptera roeselii* in relation to climate change and landscape structure in Eastern England. J. Orthoptera Res. 12, 95–102.
- Gardiner, T., Dover, J., 2008. Is microclimate important for Orthoptera in open landscapes? J. Insect Conserv. 12, 705–709.
- Gardiner, T., Hill, J., 2006. A comparison of three sampling techniques used to estimate population density and assemblage diversity of Orthoptera. J. Orthoptera Res. 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. J. Insect Conserv. 9, 151–173.
- Gobbi, M., Fontaneto, D., de Bernardi, F., 2006. Influence of climate changes on animal communities in space and time: the case of spider assemblages along an alpine glacier foreland. Global Change Biol. 12, 1985–1992.
- Harrison, R.G., 1980. Dispersal polymorphisms in insects. Annu. Rev. Ecol. Syst. 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). Appl. Entomol. Zool. 38, 321–325.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biol. 12, 450–455.
- Hickling, R., Roy, D.B., Hill, J.K., Thomas, C.D., 2005. A northward shift of range margins in British Odonata. Global Change Biol. 11, 502–506.
- Hochkirch, A., Damerau, M., 2009. Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. Biol. J. Linn. Soc. 97, 118–127.
- Holzhauser, S.I.J., Wolff, K., Wolters, V., 2009. Changes in land use and habitat availability affect the population genetic structure of *Metrioptera roeselii* (Orthoptera: Tettigoniidae). J. Insect Conserv. 13, 543–552.
- Ingrisch, S., 1977. Beitrag zur Kenntnis der Larvenstadien mitteleuropäischer Laubheuschrecken (Orthoptera: Tettigoniidae). Z. Angew. Zool., NF 64, 459–501.
- Ingrisch, S., Köhler, G., 1998. Die Heuschrecken Mitteleuropas. Westarp Wissenschaften, Magdeburg, Germany.
- IPCC, 2007. Climate Change 2007: The Physical Science Basis. Cambridge Univ. Press, Cambridge.
- Joern, A., Gaines, S.B., 1990. Population dynamics and regulation in grasshoppers. In: Chapman, R.F., Joern, A. (Eds.), Biology of Grasshoppers. Wiley, New York, pp. 415–482.
- Karny, H., 1913. Über die Reduktion der Flugorgane bei den Orthopteren. Ein Beitrag zu Dollois Irreversibilitätsgesetz. Zool. Jahrb. (Physiologie) 33, 27–40.
- Kindvall, O., Vessby, K., Berggren, Å., Hartman, G., 1998. Individual mobility prevents an allee effect in sparse populations of the bush cricket *Metrioptera roeselii*: an experimental study. Oikos 81, 449–457.
- Kleukers, R.M.J.C., van Nieuwerkerken, E.J., Odé, B., Willemsse, L.P.M., van Wingerden, W.K.R.E., 2004. De sprinkhanen en krekels van Nederland (Orthoptera). In: Nederlandse Fauna 1, 2nd ed. Nationaal Natuurhistorisch Museum, KNNV Uitgeverij & EIS-Nederland, Leiden.
- Marshall, J.A., Haes, E.C.M., 1988. Grasshoppers and Allied Insects of Great Britain and Ireland. Harley, Colchester.
- McCreddie, J.W., Hamada, N., Grillet, M.E., 2004. Spatial-temporal distribution of preimaginal blackflies in Neotropical streams. Hydrobiologia 513, 183–196.
- McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13, 603–606.
- Müller-Westermeier, G., Lefebvre, C., Nitsche, H., Riecke, W., Zimmermann, K., 2008. Die Witterung in Deutschland. In: Deutscher Wetterdienst (DWD) (Ed.), Klimastatusbericht 2007, pp. 25–49.
- Müller-Westermeier, G., Riecke, W., 2005. Die Witterung in Deutschland 2004. In: Deutscher Wetterdienst (DWD) (Ed.), Klimastatusbericht 2004, pp. 93–100.
- Parnesan, C., 2006. Ecological and evolutionary responses to recent climate change. Ann. Rev. Ecol. Evol. Syst. 37, 637–669.
- Parnesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tamaru, T., Tennent, W.J., Thomas, J.A., Warren, M., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399, 579–583.
- 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., 2008a. The classification of insect communities: lessons from orthopteran assemblages of semi-dry calcareous grasslands in central Germany. Eur. J. Entomol. 105, 659–671.
- Poniatowski, D., Fartmann, T., 2008b. Massenvorkommen makropterer Roesels Beißschrecken (*Metrioptera roeselii*) im Sommer 2007. Articulata 23, 53–56.
- Poniatowski, D., Fartmann, T., 2009. Experimental evidence for density-determined wing dimorphism in two bush-crickets (Ensifera: Tettigoniidae). Eur. J. Entomol. 106, 599–605.
- Poniatowski, D., Fartmann, T., 2010. What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? J. Insect Conserv., doi:10.1007/s10841-010-9293-3.
- Puschig, R., 1914. Bemerkungen zur Arbeit H. Karnys: Über die Reduktion der Flugorgane bei Orthopteren. Zool. Jahrb. (Zoologie) 34, 515–542.
- Ramme, W., 1931. Verlust oder Herabsetzung der Fruchtbarkeit bei macropteren Individuen sonst brachypterer Orthopterenarten. Biol. Zbl. 51, 533–540.
- Ramme, W., 1951. Zur Systematik, Faunistik und Biologie der Orthopteren von Südost-Europa und Vorderasien. Mitt. Zool. Mus. Berlin 27, 1–432.
- R Development Core Team, 2009. R: a language and environment for statistical computing. <http://www.R-project.org>.
- Reinhardt, K., Köhler, G., Maas, S., Detzel, P., 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography 28, 593–602.
- Ritchie, M.G., Butlin, R.K., Hewitt, G.M., 1987. Causation, fitness effects and morphology of macropterism in *Chorthippus parallelus* (Orthoptera: Acrididae). Ecol. Entomol. 12, 209–218.
- Sänger, K., 1984. Die Populationsdichte als Ursache makropterer Ökomorphosen von *Tessellana vittata* (Charp.) (Orthoptera, Tettigoniidae). Zool. Anz. Jena 213, 68–76.
- Sänger, K., Helfert, B., 1975. Spontanes Auftreten holopterer Formen von *Tessellana vittata* und *Metrioptera roeseli* (Orthoptera: Tettigoniidae) in Laborzuchten. Anz. öst. Akad. Wiss. (Math.-Nat. Kl.), 192–194.
- Simmons, A.D., Thomas, C.D., 2004. Changes in dispersal during species' range expansions. Am. Nat. 164, 378–395.
- Stefanescu, C., Herrando, S., Páramo, F., 2004. Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. J. Biogeogr. 31, 905–915.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., Conradt, L., 2001. Ecological and evolutionary processes at expanding range margins. Nature 411, 577–581.
- Uvarov, B.P., 1966. Grasshoppers and Locusts. A Handbook of General Acridology, vol. 1. Cambridge University Press, Cambridge.
- Vickery, V.R., 1965. Factors governing the distribution and dispersal of the recently introduced grasshopper, *Metrioptera roeselii* (Hgb.) (Orthoptera: Ensifera). Ann. Entomol. Soc. Quebec 10, 165–171.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.
- Wissmann, J., Schielzeth, H., Fartmann, T., 2009. Landscape-scale expansion of Roesel's bush-cricket *Metrioptera roeselii* (Orthoptera: Tettigoniidae) at the north-western range limit in Central Europe. Ent. Gen. 31, 317–326.
- Zera, A.J., 2004. The endocrine regulation of wing polymorphism in insects: state of the art, recent surprises, and future directions. Integr. Comp. Biol. 43, 607–616.
- Zera, A.J., Denno, R.F., 1997. Physiology and ecology of dispersal polymorphism in insects. Annu. Rev. Entomol. 42, 207–230.