

The role of macropters during range expansion of a wing-dimorphic insect species

Dominik Poniatowski · Stefanie Heinze · Thomas Fartmann

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Abstract Marked changes in distribution in consequence of global warming have been observed not only for highly mobile insect taxa, which are capable of flight, but also for wing-dimorphic species with predominantly short-winged individuals. In the special case of wing-dimorphic species, it is likely that the rarer long-winged (macropterous) morph plays an important role in the dispersal process, but little is known about how and to what extent it is involved. The aim of our study was to provide more information on the mechanisms behind dispersal processes in wing-dimorphic insects at expanding range margins. As solitary individuals are believed to play an important role in the range expansion of wing-dimorphic species (potential dispersers), we recorded the number of long-winged and short-winged solitary males at the local range margin of our model organism *Metrioptera roeselii* (Orthoptera: Tettigoniidae) in NW Germany. To investigate differences in dispersal capability (% macropters) between populations with different colonisation histories, we studied 43 populations of *M. roeselii*. Our results show that about 2/3 of the solitary males were long-winged and these long-winged individuals were significantly more frequent in recently colonised areas. Moreover, *M. roeselii* had a significantly higher dispersal capability (% macropters) in high-density populations and in recently established populations at the expanding range margin compared to populations characterised by medium- or long-term establishment nearer to the range core. Our study is the first that quantifies the importance of macropters for the recent range expansion of a wing-dimorphic species and it provides for the first time detailed insights into the complex dispersal processes that take place at the expanding range margin. It is likely that density stress and a changed genetic predisposition to become macropterous, and thus a combination of both ecological and evolutionary effects, leads to a high percentage of macropters in recently colonised areas.

Keywords Assortative mating · Climate change · Evolutionary change · Orthoptera · Range shift · Wing dimorphism

D. Poniatowski (✉) · S. Heinze · T. Fartmann
Department of Community Ecology, Institute of Landscape Ecology, University of Muenster,
Robert-Koch-Str. 28, 48149 Muenster, Germany
e-mail: poni@uni-muenster.de

Introduction

The consequences of global warming on species are highly diverse (Thomas et al. 2001; Parmesan and Yohe 2003; Davies et al. 2006). Remarkable examples are range shifts to higher latitudes and/or altitudes (Parmesan 2006; Wilson et al. 2007), which may lead to rigorous changes in the composition of biotic communities (McCarty 2001; Walther 2010). Among insects, especially the highly mobile Odonata exhibited strong responses due to rising temperatures (Hickling et al. 2005). However, for some taxa with lower dispersal capability, such as most butterflies, northward range shifts have been recorded (Parmesan et al. 1999; Hill et al. 2002). This is also true for Orthoptera (Hickling et al. 2006). In addition to species with passive dispersal strategies (Fartmann 2004), species with generally high flight capability (Kleukers et al. 1996; Kočárek et al. 2008) or a well-developed wing dimorphism are involved (Simmons and Thomas 2004; Hochkirch and Damerau 2009).

Here we focus on the latter dispersal type. Wing dimorphism (macroptery) means that, in addition to the predominant short-winged (brachypterous) morph, long-winged (macropterous) individuals occasionally occur (Harrison 1980; Zera and Denno 1997). Even though these long-winged individuals have a reduced fecundity, they are fertile (Ando and Hartley 1982; Ritchie et al. 1987) and, in contrast to their short-winged conspecifics, they are capable of flight (Higaki and Ando 2003; Smith 2007). Consequently, macropters can be important for the dispersal of individuals from a population (Simmons and Thomas 2004; Gardiner 2009; Hochkirch and Damerau 2009).

The ecological relevance of macropterous individuals depends not only on their capability to fly, but also on their frequency (Poniatowski and Fartmann 2011c). Gardiner (2009) observed a significant increase in the sightings of macropterous bush crickets since 1980. Poniatowski and Fartmann (2011b) attributed this to rising temperatures in spring due to global warming, as favourable (warm/dry) weather conditions promote high population densities at high latitudes that in turn lead to a greater proportion of macropters as a consequence of density stress. However, in addition to the theory of a density-induced macroptery (Higaki and Ando 2003; Poniatowski and Fartmann 2009, 2011c), there is also evidence that wing dimorphism is a result of genotypic variation or a combination of both genetic and environmental effects (Harrison 1980; Zera and Denno 1997).

Whereas the causes of wing dimorphism have been studied in detail, studies considering the relevance of macropters to dispersal processes are lacking. Until now, the role of long-winged individuals during recent range expansions of wing-dimorphic species has been largely unknown (Poniatowski and Fartmann 2011a). Wissmann et al. (2009) highlighted short-distance colonisation by brachypters and attributed little to the relevance of macropters to range expansion due to their rarity. In contrast, other studies illustrated the great dispersal potential of macropters: According to Hochkirch and Damerau (2009) the European heat wave in 2003 induced a strong and long-distance immigration of macropterous bush crickets into a previously unoccupied area in Lower Saxony, Germany. Moreover, recently established populations at the range margin in Great Britain have shown a higher proportion of macropterous bush crickets compared with longer-established populations at the range core (Simmons and Thomas 2004).

Here we analyse the role of long-winged individuals during recent range expansion of the wing-dimorphic bush cricket *Metrioptera roeselii* (Hagenbach, 1822) (Orthoptera: Tettigoniidae) at its north-western range margin in Germany. The clear association between macroptery and dispersal in *M. roeselii* (Simmons and Thomas 2004; Gardiner 2009; Hochkirch and Damerau 2009) allowed us to use the proportion of long-winged

individuals as a reliable index of dispersal capability (cf. Denno et al. 2001; Matsumura and Suzuki 2003; Poniatoski and Fartmann 2011c). *M. roeselii* is an ideal model organism for studying dispersal strategies because dispersing males are easy to detect, regardless of their wing morph, due to their noisy song (Hochkirch and Damerau 2009).

The aim of our study was to provide more information on the mechanisms behind dispersal processes in wing-dimorphic insects at expanding range margins. From an ecological point of view, this contributes to specifying the role of individuals capable of flight of a predominantly flightless species and estimates the general adaptability of wing-dimorphic insects during periods in which the environment is changing. The study focuses on the following research questions: (1) Is the wing-dimorphic species *M. roeselii* expanding its range any further? And if so, are the macropters the driving force of the recent range expansion or do we undervalue the dispersal potential of brachypters? (2) Is the dispersal capability (% macropters) affected by colonisation history (different population ages); i.e., is there evidence for evolutionary changes in dispersal?

Materials and methods

Study organism

As a study organism, we chose *Metriopectera roeselii* (Hagenbach, 1822) (Orthoptera: Tettigoniidae), a medium-sized bush cricket, 13–26 mm in total length, which is common in large parts of European agricultural landscapes (Marshall and Haes 1988). As an omnivorous generalist, *M. roeselii* colonises a wide variety of habitats (e.g., different types of grassland and fallow land) (Marshall and Haes 1988; Kleukers et al. 2004). The species is frequent along linear structures such as road or field margins, which may serve as dispersal corridors (Berggren et al. 2001, 2002; Wissmann et al. 2009). As in most bush-cricket species, densities of *M. roeselii* are generally low and vary between 0.7 and 11 individuals per 10 m² (Ingrisch and Köhler 1998). However, extraordinary favourable weather conditions in spring may lead to higher population densities of up to 46 individuals per 10 m² (Poniatoski and Fartmann 2011b). Since the 1980s, *M. roeselii* is expanding its range northwards in Europe (e.g., Kleukers et al. 2004; Simmons and Thomas 2004; Gardiner 2009; Hochkirch and Damerau 2009), and it has been assumed that long-winged (macropterous) individuals of this predominantly short-winged (brachypterous) species are responsible for this expansion (Simmons and Thomas 2004; Gardiner 2009; Hochkirch and Damerau 2009; Poniatoski and Fartmann 2011b).

Study areas

The main study area is located in NW Germany (51°57'N, 7°37'E), at the edge of the regional range limit of *M. roeselii* (Wissmann et al. 2009). It represents the municipal area of Münster, which covers a total area of about 300 km² (maximum north–south extension: 24 km, and maximum east–west extension: 21 km). Except at the urban core, Münster is dominated by an intensively used agricultural landscape, including improved grassland and arable land. The other study area, Medebacher Bucht (51°11'N, 8°42'E), is located about 120 km away from the regional range limit of *M. roeselii* in Münster and functions as a reference for populations of *M. roeselii* that established a long time ago (see subsection below: “Colonisation history and dispersal capability”). The Medebacher Bucht is a hilly depression east of the Rothaargebirge mountain range in southern Westphalia at the border

to Hesse and is characterised by a patchwork of different nutrient-poor habitats (Poniatowski and Fartmann 2011b).

Grid-based survey

Former surveys

The first Orthoptera surveys in the 1940s and 1950s failed to record *M. roeselii* in Münster (Röber 1951). Since the 1990s, three grid-based surveys covering the whole municipal area of Münster were conducted: (1) In 1990 and 1991, Passlick (1992) conducted a complete survey of all Orthoptera (including *M. roeselii*) based on a 2×2 km grid (referred to here as survey 1991). (2) Between 1992 and 1996, all species of Orthoptera were surveyed again based on a 1×1 km grid (Tumbrinck and Passlick 1997; referred to here as survey 1996) and (3) in 2004, the distribution was exclusively mapped for *M. roeselii* based on a 1×1 km grid (Wissmann et al. 2009).

Recent survey

To document the current distribution of *M. roeselii* in Münster, we conducted a grid-based survey from 17th June to 9th September 2009, based on the same 1×1 km grid used by Tumbrinck and Passlick (1997) and Wissmann et al. (2009). We registered the bush cricket while examining transects along roads and tracks because road and field margins are important habitats of *M. roeselii* and may function as dispersal corridors (Marshall and Haes 1988; Berggren et al. 2001, 2002). Furthermore, we analysed aerial photographs to identify all potential planar habitats of *M. roeselii*, such as fallow land and grassland. Because the study concentrated on the noisy species-specific male stridulation, we performed all field work during warm and sunny days ($>18^\circ\text{C}$) without precipitation and between 10 am and 4 pm, when almost every male stridulates. The survey was supported by an ultrasound detector (Berggren et al. 2001; Poniatowski and Fartmann 2010) to detect stridulating males at distances of up to fifty meters away from the recorder. As in 2004, we visited every grid cell for a maximum of 3 h if no individual had been previously found. Grid cells with no sighting of males were checked a second time after about 2 weeks.

As solitary individuals are believed to play an important role in range expansion of wing-dimorphic species (potential dispersers), we recorded the number of long-winged and short-winged solitary stridulating males for every grid cell. Stridulating males were defined as solitary when they were separated from the nearest population by more than 300 m, and if no other individuals were found despite careful search for conspecifics in the surrounding area.

Colonisation history and dispersal capability

To investigate differences in dispersal capability (% macropters) (cf. Denno et al. 2001; Matsumura and Suzuki 2003; Poniatowski and Fartmann 2011c) between populations with different colonisation histories, we studied 43 populations of *M. roeselii*. Only populations with high abundances were chosen as these are more likely to produce macropters (Higaki and Ando 2003; Poniatowski and Fartmann 2009, 2011b, c).

Based on former grid-based surveys, we determined the maximum number of years since colonisation ('maximum years since colonisation') for the populations in Münster.

Table 1 Colonisation history and sampling design for 43 plots with populations of *M. roeselii* in 2009

Colonisation history	Long-term established	Medium-term established	Short-term established
Sample sites	15	12	16
Distance to range margin (km)	~ 120	~ 15	0
Years since colonisation	>20	13–19 ^a	1–12
Date population recorded	Before 1990	1990–1996	2004, 2009
Reference (colonisation history)	Biologische Station Hochsauerlandkreis	Passlick (1992); Tumbrinck and Passlick (1997)	Wissmann et al. (2009), 'own survey in 2009'
Study area	Medebach (51°11'N, 8°42'E)	Münster (51°51'N, 7°36'E)	Münster (52°01'N, 7°36'E)

Groups are distinguished by different times since colonisation

^a Partly older because colonisation data before 1990 are not available for Münster

We classified populations first recorded in 2004 or 2009 as 'short-term established' (Table 1). Therefore, the age of these populations was at most 12 years because the survey in 1996 failed to record *M. roeselii* in these grids (from 1997 to 2009 = 12 years). Most likely they were much younger. We classified populations that have been established in Münster for a longer time period (before 1997 or 1992; Passlick 1992; Tumbrinck and Passlick 1997) as 'medium-term established' (Table 1). Furthermore, we sampled 'long-term established' populations around Medebach (51°11'N, 8°42'E, North Rhine-Westphalia, Germany) as a reference: This area has most likely been populated by *M. roeselii* before the recent period of climate warming (i.e. >50 years), and there is no evidence for a recent range expansion in that area (Biologische Station Hochsauerlandkreis, personal communication).

Samples were taken between 13th July and 9th August in 2009 when adults were present. For each population, we examined dispersal capability (% macropters) and population density (individuals/10 m²). We recorded *M. roeselii* using a box quadrat (Ingrisch and Köhler 1998; Gardiner et al. 2005; Poniatowski and Fartmann 2010), which, according to Gardiner and Hill (2006), is the best sampling method to assess bush-cricket abundances. The box quadrat had an area of 2 m² (1.41 m × 1.41 m) with white gauze-covered sides of 0.8 m height. It was randomly placed at 20 different points per plot (surveyed area per plot = 40 m²).

Statistical analysis

Grid-based survey

We analysed the relationship between the 'proportion of solitary macropters' (response variable) and 'years since colonisation' (four age classes, see Fig. 2) (predictor variable), with a binomial generalised linear model (GLM) in R-2.9.2 (R Development Core Team 2009) as described by Crawley (2007). A quasi-binomial error structure was used to counteract over-dispersion. The statistical significance of the model was calculated using analysis of deviance (Zuur et al. 2009).

Colonisation history and dispersal capability

As the population density data did not fit the model assumptions of ANOVA (i.e., no normal distribution, Kolmogorov–Smirnov-Test), we used the Kruskal–Wallis H test for comparisons of more than two independent samples. To evaluate which parameters affect the dispersal capability (% macropters), we conducted a generalised linear mixed-effects model (GLMM: *lmer*, Bates et al. 2008) with a two-vector response variable employing R-2.9.2 (R Development Core Team 2009) (for details see Crawley 2007). We used ‘population density’ and ‘colonisation history’ as predictor variables. ‘Habitat characteristic’ (planar or linear) was included as a random effect in order to consider the influence of habitat disturbance (cf. Denno et al. 1996, 2001), as linear structures often underlie a higher management intensity than planar grassland habitats colonised by *M. roeselii*. We assessed the significance of the predictor variables and interactions using likelihood ratio tests (Type III test).

Results

Grid-based survey

Range expansion

Since the first survey of *M. roeselii* in 1991, a rapid range expansion has been observed for the study area (Fig. 1). While the distribution was still sparse in 1991, *M. roeselii* has shifted its range distinctly northwards by 1996 and 2004. In 2009, almost the whole municipal area of Münster had been colonised, except the outermost north and the urban core.

Distribution of solitary males

In total, we found 188 solitary males of *M. roeselii*. Of these, 128 (68%) males were long-winged occurring in 59 grid cells (Fig. 2a). Approximately 75% of these grid cells have been populated for at most 4 years, which corresponds to about half of the recently colonised grids. In contrast, 60 (32%) of the found individuals were short-winged (within 41 grid cells; Fig. 2b), and about half of these grids have been colonised for at most 4 years. This represents something more than a fifth (21%) of all newly colonised grid cells. The GLM revealed that the proportion of solitary, long-winged individuals was correlated with the variable ‘years since colonisation’ (Analysis of deviance: $F = 2.726$; $df = 3, 79$; $P < 0.05$, Pseudo R^2 [Nagelkerke’s] = 0.12); i.e. solitary, long-winged individuals were significantly more frequent in recently-colonised grid cells than they were in cells with well-established populations.

Colonisation history and dispersal capability

Population density was high in all sampled populations and did not differ among the three groups (Fig. 3a; Kruskal–Wallis H test: $\chi^2 = 1.46$, $P = 0.482$, $N_{\text{plots}} = 43$). GLMM analysis showed that dispersal capability (% macropters) increased significantly with population density (Table 2). Dispersal capability also varied significantly among populations with different colonisation histories, with the most recently established populations

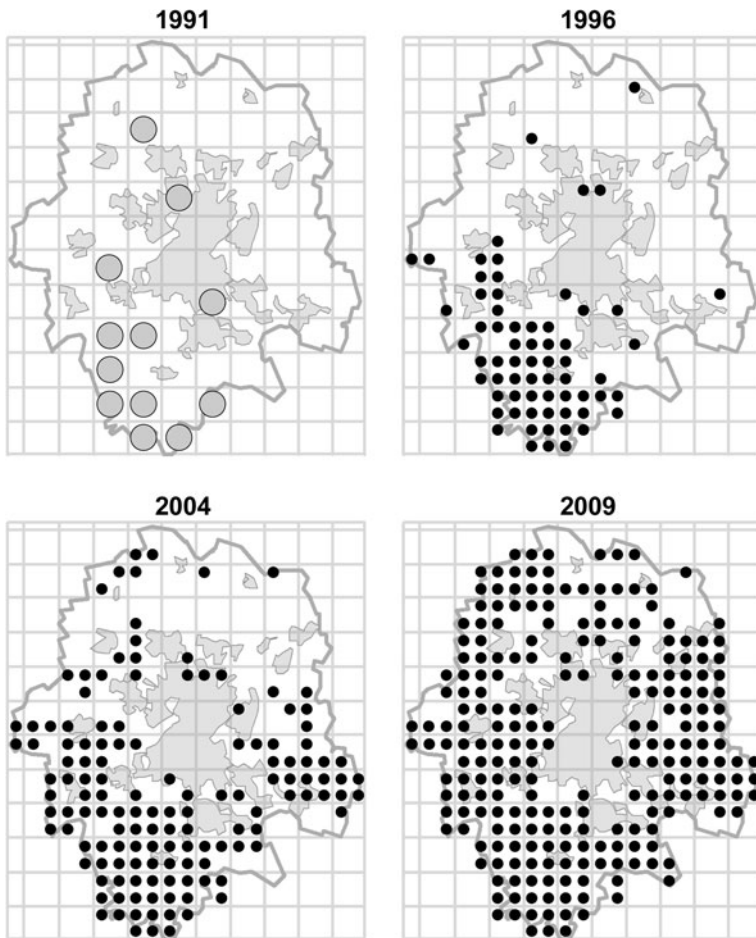


Fig. 1 Range expansion of *Metrioptera roeselii* at its north-western range margin in Münster (NW Germany) from 1991 to 2009. Large grey dots represent records in 1991 based on a 2×2 km grid (Passlick 1992) and small black dots represent records in 1996, 2004 and 2009 based on a 1×1 km grid (Tumbrinck and Passlick 1997; Wissmann et al. 2009; this study). Light grey = urban areas. Maximum north–south extension of the study area is 24 km, and maximum east–west extension is 21 km

having relatively more macropters than either medium-term or long-term established populations (Fig. 3b).

Discussion

In 2009, 19 years since *M. roeselii* was first documented in Münster (=north-western range limit in Germany) (Passlick 1992), it has colonised suitable habitats scattered across the entire municipal area (maximum north–south extension = 24 km; Fig. 1). We documented conspicuous dispersal patterns at the recently expanding range margin for *M. roeselii*: (1) More solitary long-winged males were found in recently populated areas (Fig. 2).

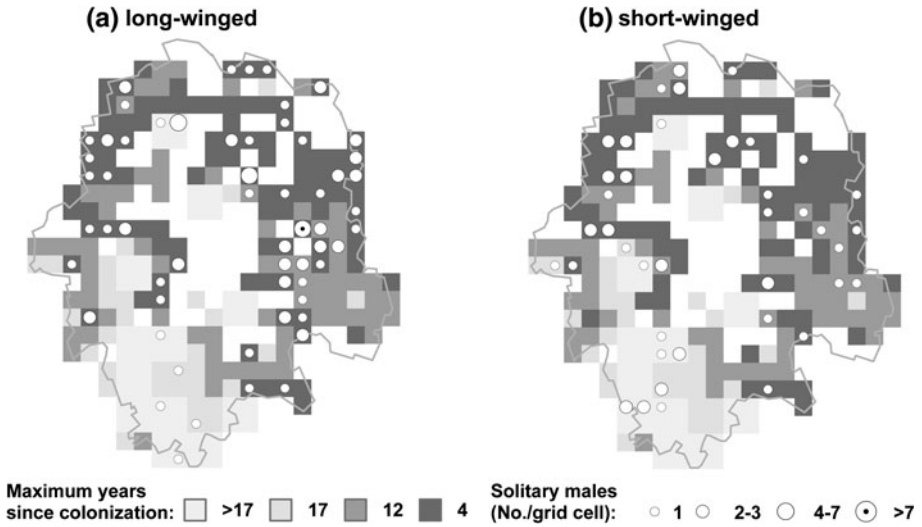


Fig. 2 Grid-based distribution of solitary **a** long-winged and **b** short-winged males of *Metrioptera roeselii* for the municipal area of Münster (NW Germany) in 2009. Symbol size (*white circles*) represents the number of documented solitary males per grid cell. *Grid cells* are graded differently depending on the years since colonisation (References: Passlick 1992; Tumbrinck and Passlick 1997; Wissmann et al. 2009; this study; see also Fig. 1); *white grid cells* = no records of *M. roeselii*

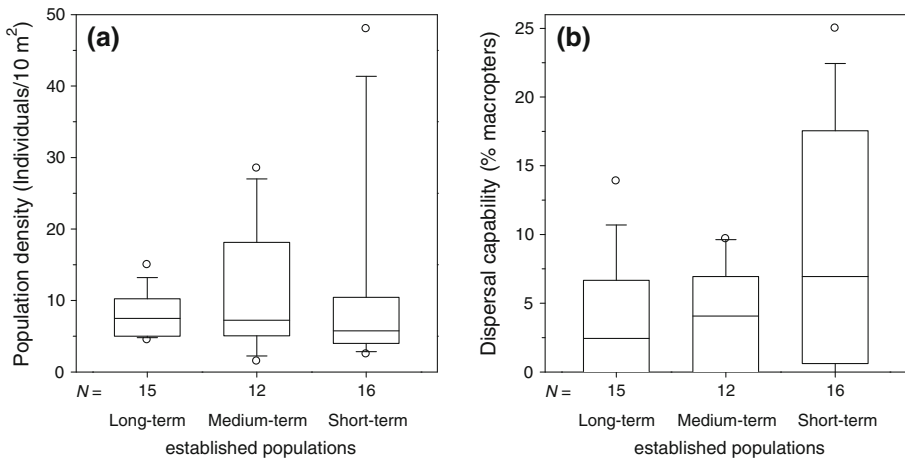


Fig. 3 Comparison of **a** population density (individuals/10 m²) and **b** dispersal capability (% macropters) among populations of *Metrioptera roeselii* characterised by different colonisation histories in 2009. *Box plots* show 10th and 90th percentile (*whiskers*), 25th and 75th percentile (boundary of the *box*), median (*line*), and outliers (*open dots*). For sampling design, see Table 1

Moreover, (2) the bush cricket has shown distinctly higher dispersal capability (% macropters) in expanding range margin populations (short-term established) than in populations characterised by medium- or long-term establishment (Fig. 3).

Table 2 Likelihood ratio test statistics of GLMM: Relationship between ‘dispersal capability’ (% macropters) (response variable) as well as ‘population density’ (individuals/10 m²) and ‘colonisation history’ (short-, medium- and long-term established) (predictor variables)

Variable	χ^2	df	P	Pseudo R ²
Population density	16.976	1	<0.001	0.76
Colonisation history	37.458	2	<0.001	
Population density × colonisation history	3.2595	2	0.196	

The goodness-of-fit of the model can be derived from the Pseudo R² (Nagelkerke’s). For more information and sampling design, see Table 1

Distribution of solitary males

Macropters appear to be the driving force for the range expansion, which is documented by the large number of solitary long-winged individuals at the range margin. In newly colonised grid cells, significantly more macropters were observed than in grid cells with longer established populations.

There might be two reasons for this pattern. (1) The higher number of solitary long-winged males in recently settled grid cells may have resulted from a higher proportion of macropters within range margin source populations (see below) and, therefore, a higher potential of nearby dispersal events. (2) The dispersal of macropters over long distances to unsettled suitable habitats might have occurred. In contrast to their short-winged conspecifics, macropterous *M. roeselii* are capable of flight (Smith 2007) and thus are able to reach new uncolonised habitats far away from the nearest population (Gardiner 2009). Genetic assignment tests for *M. roeselii* revealed maximum dispersal distances up to 19 km (Hochkirch and Damerou 2009). As has been shown here and in many other studies, orthopterans are strongly affected by density stress, which leads not only to the development of mobile macropters (Higaki and Ando 2003; Poniatowski and Fartmann 2009, 2011b), but also to a high emigration pressure (Brunzel 2002; Poniatowski and Fartmann 2011a). It is conceivable that stressed macropters dispersed from various source populations, which differ in age and distance, with the aim of reaching unoccupied habitats. However, it is noteworthy that one-third of solitary males were short-winged. Even though these individuals are flightless, we should not undervalue their dispersal potential. Short-winged individuals may walk over several hundred meters (Kindvall et al. 1998; Poniatowski and Fartmann 2011a), and linear structures such as road margins can act as dispersal corridors (Berggren et al. 2001, 2002).

Dispersal capability and evolutionary changes at expanding range margins

Corresponding with the results of other studies (Thomas et al. 2001; Simmons and Thomas 2004), we observed significantly higher proportions of long-winged individuals in recently established populations at the range margin than in longer established populations. Simmons and Thomas (2004) explain this pattern by transient evolutionary changes in dispersal: at expanding range margins, there are selective benefits to long-winged individuals colonising vacant habitat patches, whereas the more fertile brachypters dominate in longer-established populations closer to the range core. However, Simmons and Thomas (2004) did not mention what exactly happened at the expanding range margin and they observed—in contrast to our study—negative density dependence. Our findings are

consistent with the idea that macroptery results from both density stress, as has been shown for other wing-dimorphic species (Ando and Hartley 1982; Higaki and Ando 2003; Poniatowski and Fartmann 2009, 2011c), and a change in the genetic predisposition to become macropterous (i.e. it is a combination of both ecological and evolutionary effects).

More precisely, the dispersal process at expanding range margins may be characterised by the following scenario: due to their capability of flight (Higaki and Ando 2003; Smith 2007), macropters are able to colonise vacant habitats at the range margin, which are situated outside the range of their short-winged conspecifics. Consequently, the likelihood that macropters mate with other macropters is rather high. Because the tendency to become macropterous at high population densities is partly determined by genes (REF), this assortative mating might result in a higher mean sensitivity to density stress in these outlying populations, which in turn could lead to an increase in the production of long-winged individuals (cf. Harrison 1980; Poniatowski and Fartmann 2009). It is likely that most of these stressed macropters disperse, and therefore, that the persistence of the population is maintained by the less mobile and more reproductive short-winged individuals. These brachypters, in turn, produce predominantly short-winged offspring, and thus, the frequency of long-winged individuals in established populations decreases with time (cf. Roff 1986).

Conclusion

Our study illustrates that macropterous individuals are the driving force of the recent range expansion of *M. roeselii* because they increasingly occur within expanding range margin populations and as dispersers into uncolonised areas. These results are probably not only applicable to *M. roeselii* but also to some other wing-dimorphic orthopterans, such as *Chrysochraon dispar*. The species can regularly be found as a long-winged morph, and like *M. roeselii*, *C. dispar* is shifting its range northwards in large parts of Central Europe (Hochkirch 2001). It is conceivable that—beside a high frequency of macropters (see introduction)—low habitat specificity is of particular importance for the range expansion of these wing-dimorphic species (cf. Poniatowski and Fartmann 2011c). It has been noted that many species are potentially able to shift their range, but a high level of habitat fragmentation does not allow range shifts (Hill et al. 2001; Wilson et al. 2009). As a consequence, no range shifts have currently been observed for wing-dimorphic habitat specialists (Simmons and Thomas 2004). Therefore, it is reasonable to suggest that in these species, selection for decreased dispersal has taken place (Travis and Dytham 1999; van Dyck and Matthysen 1999). Taking this into account, the effects of climate change and habitat fragmentation on transient evolutionary changes in dispersal will be an important area of research to understand the rates at which species will be able to shift their distributions in response to environmental change.

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