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Landscape-scale Expansion of Roesel's bush-cricket Metrioptera roeselii at the North-western Range Limit in Central Europe (Orthoptera: Tettigoniidae)

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– – – [Note]

Range expansion linked to global warming is a widespread phenomenon among insects. This range expansion may be either gradual and on a broad-front or discontinuous following long distance dispersal. Many species of Orthoptera show a distinct wing-length dimorphism related to dispersal and rare long-wing individuals are assumed to contribute significantly to the colonisation of new habitat patches. Grid-based distribution surveys of Roesel's bush cricket *Metriopera roeselii* (Hagenbach 1822) at the edge of the species' range in NW' Germany were conducted in 1991, 1996 and 2004. Most newly colonised grid cells were directly adjacent to cells that were occupied in previous surveys or were connected to them by other colonised cells. The maximal distance between newly colonised grid cells and cells that were occupied in previous surveys was 6.3 km between 1991 and 1996 and 5.1 km between 1996 and 2004. The proportion of macropterous individuals sampled in 2004 was very low (1.4%). Macropterous individuals tended to occur in newly colonised, more isolated and low abundance grid cells. Hence, range expansion of *M roeselii* took place by short-distance colonisation from cells that were occupied in previous surveys rather than by single events of long-distance dispersal.

Key-words: *Metriopera roeselii* (Hagenbach 1822) – climate change – colonisation – dispersal – range expansion – wing-length polymorphism

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– – – [Mitteilung]

Arealausbreitungen in Verbindung mit Klimaveränderungen sind ein weit verbreitetes Phänomen bei Insekten. Derartige Arealververänderungen können entweder schrittweise und in breiter Front oder diskontinuierlich stattfinden, abhängig vom Dispersionsverhalten der Art. Viele Heuschrecken-Arten zeigen einen Flügellängen-Dimorphismus, der mit der Ausbreitungsfähigkeit in Zusammenhang steht. Von den meist selteneren, langflügeligen Individuen wird angenommen, daß sie wesentlich zur Kolonisierung neuer Habitate beitragen. Rasterbasierte Kartierungen von Roesels Beißschrecke *Metriopera roeselii* (Hagenbach 1822) an der Verbreitungsgrenze in Nordwestdeutschland zeigen eine Arealausweitung von 1991 über 1996 bis 2004. Die meisten neubesiedelten Rasterzellen befanden sich in direkter Nachbarschaft zu bereits früher besiedelten Rasterzellen oder waren über ebenfalls neubesiedelte Rasterzellen mit solchen verbunden.

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Die Maximaldistanz zwischen neubesiedelten und bereits früher besiedelten Rasterzellen betrug 6,3 km zwischen 1991 und 1996 bzw. 5,1 km zwischen 1996 und 2004. Der Anteil langflügeliger Individuen war sehr gering (1,4 %). Langflügelige Individuen traten eher in neu besiedelten und isoliert liegenden Rasterzellen und solchen mit geringer Individuendichte auf. Aus den Ergebnissen ist zu schließen, daß *M roeselii* sich im Untersuchungsgebiet vor allem über Kurzstrecken-Kolonisation ausbreitet. Es gibt keine Hinweise auf die Etablierung neuer Kolonien durch einzelne Ereignisse von Langstreckenkolonisation.

Schlüsselbegriffe: *Metrioptera roeselii* (Hagenbach 1822) – Arealerweiterung – Flügellängen-Polymorphismus – Klimawandel – Kolonisierung – Verbreitungsgebiet

1 Introduction

Distribution shifts of organisms are natural consequences of environmental changes. Biotic or abiotic conditions as well as dispersal ability can limit the distribution of species [GASTON 2003]. In Central Europe, many insect species reach their northernmost range limit [eg KUDRNA 2002, MAAS et al 2002]. Due to global warming many species have recently expanded their ranges N'wards (**Fig. 1**) [PARMESAN et al 1999, SIMMONS & THOMAS 2004, HICKLING et al 2005, HICKLING et al 2006, PARMESAN 2006], among these are several Orthoptera species [DETZEL 1998, FARTMANN 2004].

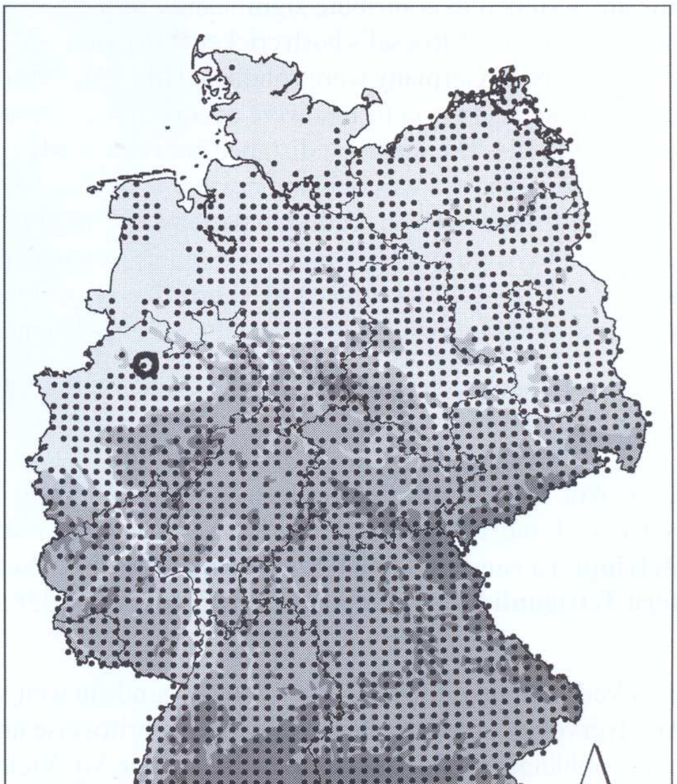

Fig 1: Distribution of *Metrioptera roeselii* (Hagenbach 1822) in Germany based on data collected between 1980 and 2007 [MAAS et al 2002, STAUDT in litt]. Münster is marked with a bold circle.

This does not necessarily mean that these species achieve a wider distribution, since range expansions on the N' limit of the distribution are sometimes accompanied by retraction on the S' range margin [PARMESAN et al 1999]. Although global warming is an obvious reason for N'ward range expansion of insects in Europe, this is not the only explanation for range shifts. For example, changes in land use practice or passive transportation might enable insects to expand their ranges [INGRISCH & KÖHLER 1998].

Many species of Central European Orthoptera show a distinct polymorphism in wing length. This polymorphism typically occurs in populations of usually short-winged (brachypterous) and hence flightless species with long-winged (macropterous) individuals being the rarer morph [INGRISCH & KÖHLER 1998]. Macropterous individuals are usually capable of flight, but this ability trades off with decreased fecundity [ZERA & DENNO 1997, INGRISCH & KÖHLER 1998, ROFF et al 1999, SIMMONS & THOMAS 2004]. Wing-length dimorphism has been demonstrated to be a heritable, threshold-based quantitative trait [MORI & NAKASUJI 1990, MATSUMURA 1996, ROFF et al 1999, but see INGRISCH & KÖHLER 1998]. Although the reaction norm to produce macropterous offspring is under genetic control, the actual development of long-winged individuals is influenced by environmental factors (eg population density) during larval development [INGRISCH & KÖHLER 1998, THOMAS et al 2001, BEHRENS & FARTMANN 2004]. Macropterous morphs are suspected to play an important role in colonising new habitat patches and are often more abundant near species range limits and in isolated outposts than in more continuously populated parts of the range [VICKERY 1965, THOMAS et al 2001, SIMMONS & THOMAS 2004].

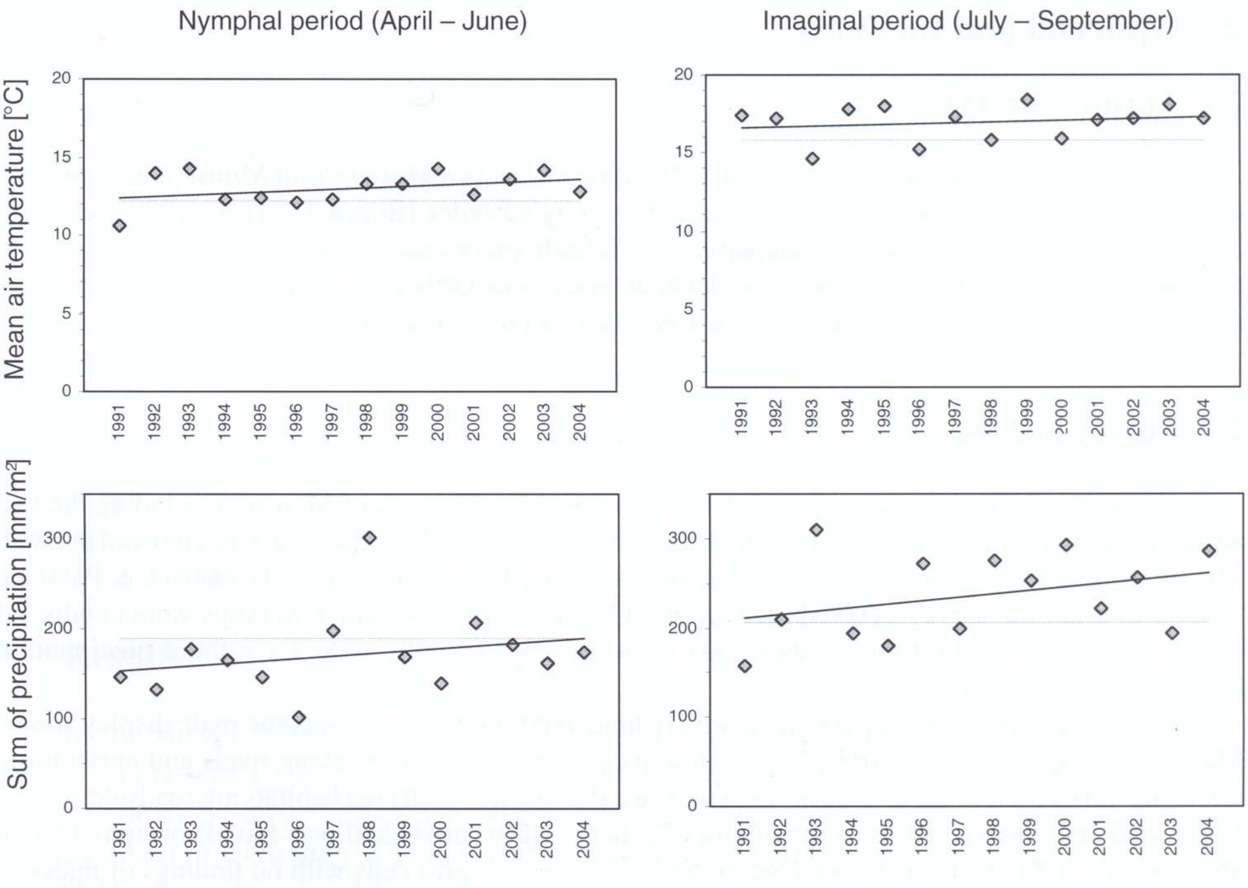

Fig 2: Trends in mean day temperature and sum of precipitation during the nymphal period (April-June) and the imaginal period (July–September) at Münster-Osnabrück. The continuous line shows the trend for the period 1991–2004 (Temperature nymphal period: $F_{1,12} = 1.73$, $P = 0.21$; Temperature imaginal period: $F_{1,12} = 0.47$, $P = 0.50$; Precipitation nymphal period: $F_{1,12} = 0.83$, $P = 0.38$; Precipitation imaginal period: $F_{1,12} = 1.55$, $P = 0.24$) The dotted line shows the long-term mean (1961–1990) for the station Münster-Zoo (c. 21 km SSW of the station Münster-Osnabrück). Data source: Deutscher Wetterdienst.

Here, the recent range expansion of Roesel's bush-cricket (*Metrioptera roeselii*) in Münster (51° 57' N, 7° 37' E, North Rhine-Westphalia, Germany) is documented based on three grid-based surveys conducted between 1990 and 2004. Although the species occurs in wide parts of Europe including locations further north like Great Britain, Scandinavia and North-eastern Europe [Detzel 1998], a local range limit runs through North Rhine-Westphalia and Lower Saxony, where it occurs in the Southeast while the Northwest is largely unoccupied [Volpers 1998, Grein 2000, Maas et al 2002: **Fig 1**]. Recently, the species has expanded its range in Western, Central and Northern Europe [Pettersson 1996, Kleukers et al 1997, Ivarsson 1998, Hochkirch 2002, Hochkirch 2004, Berggren 2005].

In Münster, *M roeselii* was first recorded in 1990 [Passlick 1992] and the range has been expanded since then, but the limits of its range are still within the city's borders. Spring and summer temperatures in Münster did not change significantly over the period considered here, but tended to be higher than in the period before 1991 (**Fig 2**). *M roeselii* is usually brachypterous and flightless, but macropterous morphs occur regularly in very low numbers [Vickery 1965, Detzel 1998, Berggren 2004]. Individuals were sampled from different parts of the species range in Münster to evaluate whether macropterous morphs are more common in isolated outposts or at the edge of the distribution compared to parts of more continuous distribution.

2 Material and methods

2.1 Former surveys

Orthoptera surveys in the 1940s and 1950s failed to record *M roeselii* in Münster, although the nearest colonised patch was just 3 km south of the city's border [Röber 1951]. In 1990 and 1991, Passlick [1992] conducted a complete survey of all Orthoptera based on a 2 × 2 km grid (referred to here as survey 1991). Between 1992 and 1996 all species of Orthoptera were surveyed again based on a 1 × 1 km grid [Tumbrinck & Passlick 1997, referred to here as survey 1996].

2.2 Survey in 2004

Since the two former surveys were limited to the municipal area of Münster (including the two adjacent nature reserves 'Venner Moor' und 'Bockholter Berge'), the same area was surveyed in 2004. The survey in 2004 was performed based on the same 1 × 1 km grid as used by Tumbrinck & Passlick [1997]. In total, the survey covered an area of 343 grid cells (= 343 km^2). Surveys were conducted between 19th July and 6th September 2004 on warm days (usually >18 °C) without precipitation between 10 am and 6 pm.

The surveys concentrated on the relatively loud and highly species-specific male display songs. Males were registered while travelling at slow pace by bike. Transects along roads and agricultural tracks are very efficient for finding *M roeselii*, since the species' preferred habitats are roadside verges. Every grid cell was visited for a maximum of 3 hours (if no individual was found) or until 15 min after the first individual was located. More time was spend in grid cells with no findings of males to secure that these cells were indeed unoccupied. As soon as the first individual was found, the time used to assess abundance was fixed to 15 min. Abundance was classified in four categories: 0 = not detected within 3 h, 1 = one male and no further males within an additional 15 min, 2 = a total of 2–5 males within 15 min after finding the first male, 3 = 6 or more individuals within 15 min after finding the first male.

When specimens were found in a grid cell, one to five males were located and categorised with respect to their wing-morph.

If wings were half as long as the abdomen or shorter, individuals were classified as brachypterous, while individuals with wings reaching the rear end of the abdomen were classified as macropterous. In three grid cells larger numbers of specimens were caught and classified according to their wing length (K 22, T 14, H 2, for locations of grid cells see **Fig 3**).

2.3 Statistical analysis

From the grid-based survey data, we calculated prevalence (number of grid cells with records of *M roeselii* divided by total number of grid cells) for each survey.

Furthermore, an index of isolation was calculated as the number of neighbouring cells that were occupied divided by the number of neighbouring cells that were surveyed [Maas et al 2002]. Neighbouring cells were defined according to the 'queens' neighbourhood, ie horizontally, vertically and diagonally neighbouring cells [Fortin & Dale 2005]. By taking into account the number of neighbouring cells that were surveyed, edge effects were controlled for in the calculation of the isolation index. However, when calculating colonisation distances of newly colonised grid cells (relative to the nearest grid cell that was occupied in previous surveys), one had to assume two extreme scenarios to deal with missing survey data outside of our study area. Hence, the results presented here are based on two extreme scenaries: all cells outside the study area were unoccupied (Scenario A) or occupied (Scenario B).

A randomisation procedure was used to test whether the occurrence of macropterous individuals was correlated with the isolation of grid cells, abundance class or time of population establishment (occupied in 1996 vs first recorded in 2004). Since five macropterous individuals were found in the here reported systematic surveys, the empirical test statistic (mean isolation index, abundance class and population establishment, respectively) was calculated of the five grid cells with macropterous individuals and compared this to the distribution of 10,000 randomisation runs, each sampling five grid cells from the pool of occupied grid cells and calculating the test statistic for each simulation. During sampling for the variation in individuals sampled per grid cell (1–5 individuals) was accounted by drawing the samples from a population with the same distribution of capture positions as in our empirical data (three macropterous individuals were captured as the first individual within the grid cell, one as the second and one as the third). Fisher's exact test was used to examine whether the local abundance within grid cells depended on former occupancy of the grid cell. Like the randomisation test, Fisher's exact test uses permutation of the data to calculate the probability of the observed or more extreme values to occur by chance alone. All *P* values presented are two-tailed and all calculations were conducted using the freely available software package R 2.4.0 [R Development Core Team 2005].

3 Results

In the survey 2004 *M roeselii* was found in 139 out of 343 grid cells (prevalence of 40.5%). This was a clearly higher prevalence than in 1991 (15.3%) and 1996 (20.1%). In comparison to the survey 1996 there were 71 grid cells occupied in 2004 only and one grid cell was occupied in 1996 only. The index of isolation was very similar in 1996 and 2004 (36.3% and 33.1%, respectively). Many of the newly colonised grid cells were directly adjacent to previously unoccupied cells (1996 compared to 1991: two 2 × 2 grid cells when assuming all cells outside the study area were unoccupied in 1991; 2004 compared to 1996: 30 out of 71 when assuming all cells outside the study area were unoccupied in 1996 = Scenario A, 35 out of 71 when assuming they were all occupied in 1996 = Scenario B).

Between 1991 and 1996 *M roeselii* expanded its range mainly in the southwest (**Fig 3a**) with two isolated outposts in the north (O3) and southeast (T15).

Between 1996 and 2004, the range expansion took place mainly in the southeast and to some degree in the west, while the central part was still largely unoccupied (**Fig 3b**). Isolated outposts in the north could be confirmed and several newly colonized grid cells were found in the north. Most of them, however, were connected by occupied cells to cells that were occupied in previous surveys, indicating an expansion from existing colonies. In 2004, there were only three grid cells (M3, Q3, O11) and one larger patch of occupied cells (F4–J2) that were isolated from presently occupied cells, and cells that were occupied in previous surveys. Calculating distances from mid grid cell points leads to a maximum of 4.0–5.1 km between 1996 and 2004 (range between Scenario B and Sencario A). The comparison of the surveys in 1991 and 1996 is less precise, since the 1991 survey was conducted on a 2 × 2 km grid. A similar estimation of the colonisation distance for the period 1991–1996 based on the 2 × 2 km grid yields a maximum distance of 2.8–6.3 km (range between Scenario B and Sencario A). One of the outposts in 1996 (a single individual in O3) was the only occurrence that could not be confirmed in 2004.

In most occupied grid cells (73%) more than five individuals were found in 2004, while 22% of all occurrences refer to low density populations (2–5 individuals) and 5% to single individuals (**Fig 4**). Low abundance grid cells (less than 6 individuals) were not more isolated than expected by chance (Randomisation test: $P = 0.17$), but were more common among newly colonised grid cells (ie unoccupied in survey 1996, Fisher's exact test: $P < 0.001$).

During systematic sampling of 1–5 males per occupied grid cell in 2004, a total of five macropterous individuals were found. Cells with macropterous individuals tended to be more isolated than expected by chance (Randomisation test: $P = 0.076$). Macropterous individuals also tended to occur in grid cells with low abundance, although this was statistically not significant (Randomisation test: $P = 0.11$). All macropterous individuals found in systematic surveys occurred in newly colonised grid cells (ie unoccupied in 1996 survey, Randomisation test: $P = 0.092$). More intense sampling in three grid cells with high abundance (in total 83 individuals) did reveal one additional long-winged individual (K 22: 1 macropterous vs 33 brachypterous, T 14: 28 brachypterous, H 2: 21 brachypterous individuals). Hence, the overall proportion of macropterous individuals was 1.4% (6 macropterous out of 426 individuals).

4 Discussion

Metrioptera roeselii showed a significant range expansion within the municipal area of Münster. The range expansion was unequally fast in different parts of study area. The southwest was colonised mainly in the early 1990s, while further range expansion till 2004 took mainly place in the southeast. Urban areas were clearly avoided. Most newly colonised grid cells were adjacent to cells occupied in previous surveys, indicating a range expansion by diffusion to new habitats from previously occupied cells. Only a few records in isolated grid cells indicate the establishment of colonies by long-distance dispersal. The overall proportion of macropterous individuals was low (1.4%). As expected, long-winged individuals were found mainly in grid cells that were formerly unoccupied, more isolated and of lower total abundance, but all these effects were statistically not significant. However, the lack of significance was probably due to the low total number of macropterous individuals, since the tested statistical distribution is more variable when sampling few data points.

Fragmentation and the loss of connectivity in cultivated landscapes are major factors that limit dispersal of animals [Lord & Norton 1990, Baguette et al 2000].

(a) Distribution in 1991 and 1992-1996 **(b) Distribution in 2004**

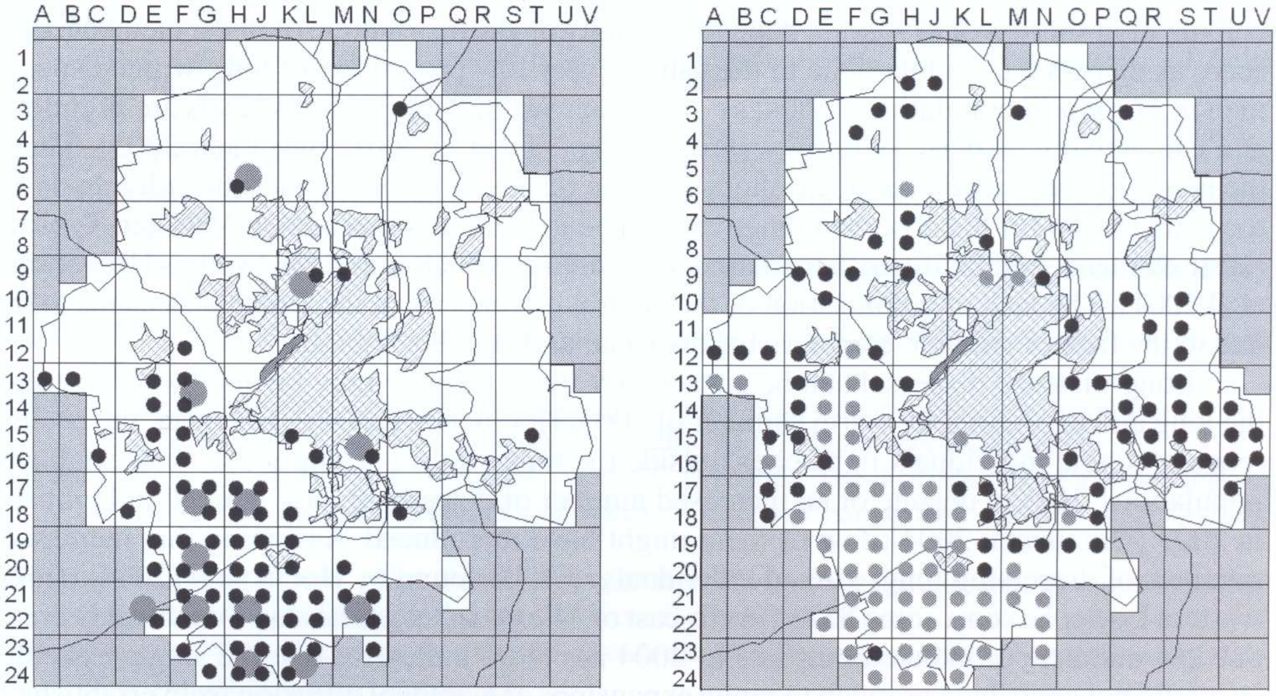

Fig 3: Distribution of *Metrioptera roeselii* (Hagenbach 1822) in the municipal area of Münster (North Rhine-Westphalia, Germany) in (a) 1990/91 (large grey dots based on a 2 × 2 km grid, Passlick 1992) and 1992–1996 (small black dots based on 1 × 1 km grid, Tumbrinck & Passlick 1997) and (b) 2004 (based on 1 × 1 km grid, this study). Black dots in figure (b) refer to newly colonized grid cells, while grey dots refer to confirmation of occurrences from 1996. Light grey hatching = urban areas, filled grey cells = not surveyed. Edge length of one square is two kilometers, maximum north-south extension of the study area is 24 km and maximum east-west extension is 21 km.

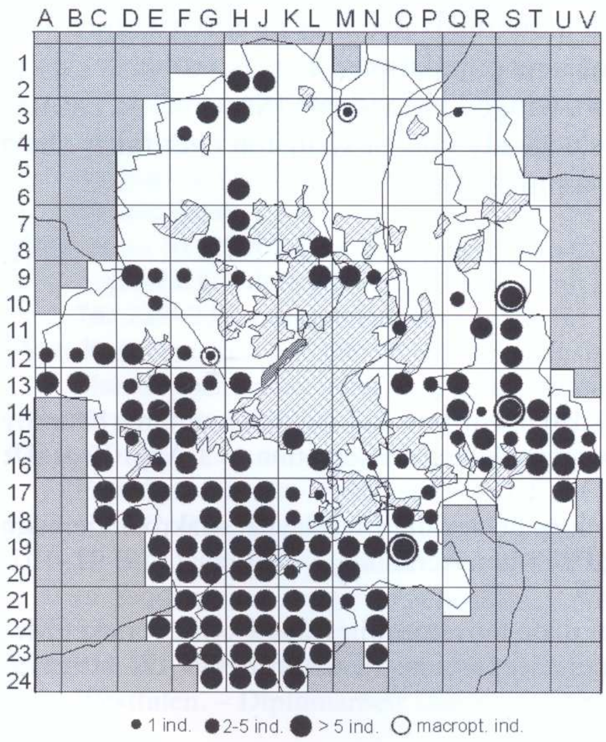

Fig 4: Abundance and discoveries of macropterous individuals of *Metrioptera roeselii* (Hagenbach 1822) in the municipal area of Münster (North Rhine-Westphalia, Germany) in 2004. Filled grey cells = not surveyed. Edge length of one square is two kilometers, maximum north-south extension of the study area is 24 km and maximum east-west extension is 21 km.

This is especially true for flightless species or morphs. Landscape connectivity depends on the composition and structure of appropriate habitats. BERGGREN et al [2001] showed that colonization success of *M roeselii* depends strongly on the distribution of linear elements that serve as dispersal corridors. Due to the usually very low proportion of long-winged specimen in *M roeselii* populations [VICKERY 1965] the vast majority of individuals are flightless and can actively disperse only by walking [BERGGREN et al 2001, BERGGREN 2005]. Thus, the here presented results indicate short-distance dispersal by brachypterous individuals as the main reason for the observed range expansion in the municipal area of Münster. Typical linear elements that facilitate dispersal of *M roeselii* are ditches and road verges [BERGGREN et al 2001]. The lack of colonisation of the central urban parts of the study area seems to be due to the lack of suitable corridors for dispersal and suitable habitats.

Long-distance dispersal can be particularly likely in extremely favourable years (like the long and exceptionally warm summer of 2003, HOCHKIRCH [2004]). However, the occurrence of single individuals in patches outside the range does not imply that they establish populations. Hence, despite of an increased number of dispersing long-winged individuals in 2003 [HOCHKIRCH 2004], few of them might have reproduced. Assuming that increased numbers of dispersing long-winged individuals in 2003 found by HOCHKIRCH [2004] (from western Lower Saxony, some 85 km north-east of Münster) holds true also for our study area, our low numbers of isolated outposts in 2004 are more indicative that the single extreme event did not contribute as much to range expansions as a gradual diffusion from established populations did. However, the life cycle of *M roeselii* can last one or two years [INGRISCH 1986], so that some effects of colonisation events in 2003 would not have been observed in 2004 but will be observed first in 2005.

Although not quite significant due to low sample size, the here presented findings of long-winged individuals in more isolated, newly established and low abundance sites are consistent with the predicted role of macropterous individuals as dispersal morphs [VICKERY 1965]. VICKERY [1965] observed the dynamics of *M roeselii* over seven years in a newly colonised site in eastern Canada, where the species has been introduced. In the first two years population size was low and nearly all specimens were long-winged. Population size increased strongly during the next year, while the proportion of macropterous specimens in following years decreased continuously. Based on more extensive surveys SIMMONS & THOMAS [2004] found that the proportion of long-winged individuals declines rapidly (within 5–10 years) to normal levels after the establishment of new populations. This is probably due to natural selection favouring the more fecund short-winged individuals [SIMMONS & THOMAS 2004]. Overall, the here reported results indicate a steady range expansion over fairly short distances with long-winged individuals playing a minor role.

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Wichard W & Weitschat W: – **Im Bernsteinwald** (2 Aufl 2005). – [168 Seiten, unzählige Farbfortos, einige Strichzeichnungen, 245 x 245 mm, Hartkart-Ebd, Schutzumschl]. – **Publ:** Vlg Gerstenberg, Hildesheim; **ISBN:** 3-8067-2551-9. – – – [EGR-Nr 3.075]

Ebenso wie in einem früheren Werk [Weitschat & Wichard 2001] bieten die Verfasser auch im vorliegenden prächtige makroskopische Farbaufnahmen von Bernstein-Einschlüssen dar: Pflanzen und Tiere werden zu einem vorzeitlichen Legespiel zusammengefügt, das den sagenumwobenen tropischen Bernsteinwald des nordeuropäischen Alttertiärs mit seiner vielfältigen Flora und Fauna vor Augen führt. Begleitet werden die eindrucksvollen Farbbilder von gegenübergestellten aufschlußreichen Strichzeichnungen und allgemeinverständlich erklärenden Texten so wie von sinnreichen Sprüchen und Zitaten, auch klassischer Autoren. Über den Dokumentationszweck hinaus erhebt dieses Werk keine wissenschaftlichen Ansprüche. Es vermittelt aber tiefe Eindrücke in vergangenes Erdenleben und vermag angehende Rezent- und Paläobiologen, besonders Entomologen, dazu anregen, sich mit der Erforschung dieser offenbarenden Funde zu befassen. So, wie dieses Werk bereits lobende Erwähnung in nicht-biologischen Zeitschriften gefunden hat, sollte es auch über den naturwissenschaftlichen Rahmen hinaus weiteren Zuspruch in Naturliebhaber-Kreisen erhalten.