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Macropterism of Roesel's bushcricket Metrioptera roeselii in relation to climate change and landscape structure in eastern England

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Abstract

There has been a considerable range expansion for Roesel's bushcricket *Metrioptera roeselii* in Essex since 1980, and it is often assumed that the macropterous (long-winged) form (*f. diluta*) has played an important role. A systematic study of the occurrence and distribution of this bushcricket in the county shows that this range expansion has corresponded with a significant increase in air temperature and the availability of tall grassland on farmland, due to the introduction of set-aside and agri-environment schemes such as Countryside Stewardship. These tall grasslands are particularly important for *M. roeselii* in areas of the county (*e.g.*, the northwest) where hedgerow removal has been severe since the 1940s. This study indicates that the previous year's air temperature may be the most crucial climatic determinant of macroptery, hot weather leading to successful breeding and high population densities in the following year. These populations may then produce macropterous individuals in response to overcrowding; this may explain the occurrence of long-winged *M. roeselii* in years with cool and damp weather. However, this study fails to provide conclusive evidence of this due to a lack of quantitative macropter data. Nevertheless, a clear link is established between high temperatures and the early appearance of macropters, hot weather from April to July leading to accelerated nymphal development and earlier sightings of macropterous bushcrickets.

Key words

macropters, dispersal, temperature, rainfall, climate change, set-aside, field margin

Introduction

Roesel's bushcricket *Metrioptera roeselii* (Orthoptera: Tettigoniidae) has been recorded in Essex (southeast England) since the early 1900s (Wake 1997). Indeed, one of its main strongholds in the UK was the Essex coast for much of the 20th century. The first evidence of a range expansion for this species was in the 1940s, when it was recorded 20 km away from the coast in Chelmsford by J.A. Whellan (Wake 1997). The spread of this normally brachypterous bushcricket is often attributed to the macropterous (long-winged) form (*f. diluta*), which apparently appears in long, hot summers (Marshall & Haes 1988) when high-density populations can occur, and render advantageous, dispersal to new less-crowded habitats (Zera & Denno 1997). However, the production of long wings has energetic costs and can lead to low fecundity in Orthoptera (Ritchie *et al.* 1987).

Macropters can be common in field populations: for example, in Essex up to 30% of individuals (Table 1). This contrasts with published studies from other countries where macropterism has a much lower incidence: typically < 2% of individuals are long-winged (Vickery 1965, Wissmann *et al.* 2009). Studies in Essex suggest a much higher occurrence of macropterism for this bushcricket, with it not uncommon to find > 20% of individuals in a population with long wings.

Macropterism in crickets may be influenced by a reduction in degradation of juvenile hormones (JH), particularly in the final instar. This reduced degradation delays the usual drop in the JH titer, ultimately leading to a prolonged period of high JH titer; this inhibits the metamorphosis of flight muscles and wings, leading to the production of a brachypter (Zera & Denno 1997). This classic hypothesis implies that environmental factors that influence macropterism in crickets (Gryllidae) may be particularly important in the final instar, which for *M. roeselii* is in June/early July in most years (Marshall & Haes 1988).

Although most orthopterans in the UK do not fly strongly, flights often covering only 2-3 m (Marshall & Haes 1988), Smith (2007) observed macropterous *M. roeselii* being taken up by air currents to a considerable height on a set-aside field in Highwood, where they were eaten by birds of prey. Fliers that survive predators could be carried large distances on air currents, a fact underlined by the capture of the range-expanding Lesser Marsh Grasshopper *Chorthippus albomarginatus* in a balloon trap at an altitude of 200 m (Chapman *et al.* 2004).

The main assumption underlying the range expansion of *M. roeselii* in the UK is that long hot summers promote the development of macropterous individuals, leading to increased dispersal. However, macropters have been seen in apparently unfavorable 'cool and damp' summers in Essex (Gardiner & Benton in press), prompting speculation about the causes of macropterism in this bushcricket. Range expansion of *M. roeselii* may also be directly linked to landscape connectivity and structure (Berggren 2008), with destruction of grassland habitats and removal of arable field boundaries since 1945 (the end of World War II) (Rackham 1986) potentially leading to fragmentation of populations of this bushcricket in the UK. This could have inhibited the range expansion of this species since 1945. Indeed, government policy, coupled with increasing mechanisation of agriculture, initiated large-scale removal of hedgerows and ploughing of unimproved grasslands (for conversion to arable cropping); these activities were particularly severe during the 1960s (Pollard *et al.* 1974). The result was a landscape of large fields with few hedgerows and very limited availability of ancient grassland (Rackham 1986), a landscape unlikely to be favorable for orthopterans such as *M. roeselii*.

The primary aim of this paper is to examine the importance of macropterism in the range expansion of *M. roeselii* in Essex, UK, and to relate this to climate change and landscape structure.

Table 1. Percentage of the total number of *M. roeselii* individuals that were macropterous (*f. diluta*) in various studies in Essex.

Study reference	Year	Location	% individuals with long wings	Recorder
Burr (1936)	1933	South Benfleet	30	K.G. Blair
Gardiner (2006)	2004	Writtle College	2	T. Gardiner
Gardiner & Haines (2008)	2007	Mardyke Valley	7	T. Gardiner
Gardiner (2008a)	2007	Good Easter	20	T. Gardiner
Benton (2008)	2007	Colchester	30	T. Benton

Method

Orthoptera surveys.—An in-depth survey of the Orthoptera of Essex was initiated by Alan Wake in 1980. Some 5000 records were accumulated from 1980 to 1995, and led to the publication of the first county atlas in 1997 (Wake 1997). Approximately 3000 records have been collected since 1995 and have been input to a database (MapMate); interactive distribution maps for Orthoptera (and many other insect orders) are available online from the Essex Field Club website (www.essexfieldclub.org.uk).

M. roeselii has been recorded every year from 1980 to 2008. Recorders have visited most areas of the county, and made special note of the discovery of macropterous individuals, so we have a good idea of the occurrence of this form. The species is also one of the most commonly sighted orthopterans in the county, comprising approximately 16% of records (Wake 1997). It has a wide distribution and has been recorded from over 95% of the 10 × 10-km grid squares (hereafter referred to as 10-km squares) in the county since 1980. It occurs in a wide range of habitats including tall grasslands such as field margins, roadside verges, ungrazed grassland, woodland rides and hay meadows (Gardiner & Pye 2001). Nymphs appear in April in most years, becoming adult in late June/early July (Gardiner 2003, 2004). It has successfully spread away from its strongholds on the coast (east Essex) and has moved westwards over the last 30 y to colonize inland habitats, often on farmland (Gardiner & Benton in press, Gardiner *et al.* 2008).

During his systematic study Alan Wake examined a variety of published material from the Essex Naturalist and national entomological journals to chart a history of *M. roeselii* records and the occurrence of macropters. From the first county record in 1912, details of a considerable number of sightings were obtained for the period 1912-1979. Though recording in the county during this 68-year period was patchy (Wake 1997), it provided an accurate baseline range, against which the subsequent range expansion, commencing in the 1980s, could be compared. Authors such as Payne (1957) stated that the bushcricket was mainly restricted to the Thames Estuary and Essex coastline, without any substantial evidence of any northwards or westwards range expansion into inland areas. For the purposes of this paper, data on the range of *M. roeselii*, climate and landscape structure are divided into three main periods: 1912-1979, 1980-1995 and 1996-2008.

Climate data.—The Writtle College Weather Station is situated in mid Essex (Ordnance Survey grid ref: TL 6707) and has collected climate data since 1943 (Writtle College 2002). Standardised meteorological recording methods were used in the collection of rainfall and temperature data for every day of the year. The meteorological data were sent to the Met Office to input into national statistics. All recording instruments were kept in a Stevenson Screen (to provide protection from direct radiation and wind), a wooden box painted white to reflect heat. The box was mounted on four legs at a height from the ground of 1.25 m and located approximately 30 m from the nearest building. Temperature data were collected using maximum and minimum thermometers situated inside the screen, whereas rainfall was measured in millimetres using a rain gauge. These are standard Met Office recording methods used nationally (Overton 2007). Climatic measurements were taken once daily at 0900 h.

Landscape structure data.—The impact of landscape structure (e.g., connectivity) was assessed using data kindly provided by Essex County Council's Historic Environment Branch of the number of field boundaries removed on a large number of land holdings. The data were collected by examination of the 1880 (1:10560 scale First Edition maps) and 2000 Ordnance Survey (OS) maps, using MapInfo (Version 8.0), a Geographic Information Systems (GIS) software package (MapInfo Corporation 2005). The field boundaries from the 1880 OS map for a large number of land holdings (N = 42241) were plotted on MapInfo and then compared with the 2000 edition to see how many field boundaries had been removed. The Historic Environment Branch did not differentiate between field boundaries with or without hedgerows (therefore boundaries that are ditches without hedgerows were included in the analysis). The number of field boundaries lost between 1880 and 2000 were calculated for a small random selection of these farms (N = 72) and standardized between the area of each holding, to give the number of field boundaries removed/ha. These figures were then scaled up to give a standardized number of field boundaries removed/km^2. The mean field boundary loss was then compared for the 1912-1979 range of *M. roeselii* in the county and the range extension (new 10-km squares recorded outside of existing range) for the bushcricket for 1980-1995 and 1996-2008. This allowed an analysis of the landscape structure in the areas that the species had colonized since 1980.

Since 1980, government funding for agricultural land management has changed significantly. Due to problems with agricultural overproduction leading to surplus crop and livestock output in Europe, set-aside was introduced by the UK government in 1993 (Centre for Rural Economics Research 2001). They stipulated that a specific area of arable land (generally 10% of land holding) must be taken out of agricultural production each year and left fallow. Typically, set-aside took two forms: rotational (different fields are left fallow each year) and permanent (a specific area is left fallow for 10 years, allowing more stable vegetation communities to establish). Set-aside grassland was abolished for harvest 2008 due to rising grain prices; it is unclear if it will return in future.

Several voluntary government schemes have been introduced to provide funding to landowners for environmental enhancements. In 1987, the Environmentally Sensitive Areas (ESA) scheme was introduced to encourage landowners to adopt agricultural practices that would safeguard and enhance parts of England that are of particularly high value for wildlife. In Essex the coast was designated as an ESA. In 1991 the government piloted the Countryside Stewardship Scheme (CSS), which was formally introduced in 1996 across England. Under this scheme farmers received payments linked to environmental enhancements such as the creation of grass margins around arable fields and restoration of hedgerows. In 2005 the scheme was superseded by Environmental Stewardship, the main component of this being the Entry Level Scheme (ELS) which was open to all landowners.

Land under set-aside (particularly permanent set-aside) and entered into agri-environment schemes is likely to be beneficial to *M. roeselii,* due to the introduction of tall grassland on otherwise intensively managed farms. Therefore data on the land area (in million ha) of both set-aside and agri-environment schemes were taken from the DEFRA and Natural England websites for the period 1993-2006. It has not been possible to get accurate figures on land use for Essex, so the data do not directly relate to the county.

Statistical analysis.—To test the range expansion of *M. roeselii* in the county over the last 100 y, the number of 10-km squares in which the bushcricket was recorded (total number of 10-km squares for Essex = 57) for 1912-1979 was compared against the period 1996-2008 using Chi-square (χ^2). Chi-square was also used to compare the number of reports of macropters and the cumulative number of 1 × 1-km squares (hereafter referred to as 1-km squares) within which macropters were recorded for 1912-1979 and 1996-2008.

The mean number of field boundaries removed/km^2 was compared for the baseline range (1912-1979, N = 25) and the newly colonized range (outside of existing range boundaries) for the periods 1980-1995 (N = 36) and 1996-2008 (N = 11), using a one-way ANOVA. Data were square-root transformed to correct for non-normality before analysis using this parametric test (Heath 1995).

Mean annual air temperature (°C) and total annual rainfall (mm) were compared between the three time periods using a one-way ANOVA; data were square-root transformed before analysis. Climate data were only available from the Writtle Weather Station from 1943 onwards. To determine if macropters were being produced earlier in the year in response to seasonal temperature during nymphal development, mean air temperature for the period April-July was compared against the date (numerical date, *e.g.,* 1 January = 1; 31 December = 365; dates corrected for leap year where necessary) of the year that macropters were sighted, using linear regression. Where there was more than one sighting in a year, a mean date was used in the analysis. Reports of macropters in 1983 did not include precise dates, therefore this year was excluded from the analysis. Data were square-root transformed before linear regression to correct for non-normality.

For the purposes of the following analysis, data for the main period of occurrence of *M. roeselii* nymphs and adults (April-September) were used (Gardiner 2008b). Mean air temperature, and total rainfall for this six-month period were used to predict the occurrence of macropterous individuals for all years 1980-2008 inclusive. The macropterous form was sighted in 1983-84, 1986, 1992-97, 2003-05 and 2007-08 (a total of 14 y). Macropters were not recorded in the remaining 15 y. To ascertain whether the previous summer's weather had any impact on the occurrence of macropters, the previous year's mean air temperature (April-September) and rainfall were included as independent variables, with the current year's mean air temperature and rainfall in a logistic model with the occurrence of macropters (0 = no, 1 = yes) as the binary dependent variable. For the purposes of the binary logistic regression, the data were not transformed prior to analysis due to a normal distribution in the dataset. Data were analysed using SPSS Version 16.0 (SPSS 2007), except for the logistic regression, which used Version 10.0.

Results and Discussion

M. roeselii has been recorded in 55 10-km squares (96% of Essex total) since the first county record in 1912. There was a significant difference (χ^2 = 9.65, d.f. = 1, P<0.01) between the number of 10-km squares in which the bushcricket was recorded for its historic range (1912-1979) and the 1996-2008 period (Table 2). This suggests a doubling of the range of this species since 1980, and a steady colonization of inland areas to the north and west of its traditional stronghold on the Essex coast (Fig. 1).

The field boundary removal rate in the historic range of the bush-cricket (records for period 1912-1979) did not differ significantly from that in the newly recorded range for the species in the period 1980-1995. However, field boundary loss was significantly higher (F = 5.31, P<0.01) than in the previously recorded range, in the areas colonized by *M. roeselii* in 1996-2008 (Table 2), indicating that by the late 1990s/early 2000s, the species was able to move into the northwest of the county, where (historic) hedgerow removal was at its most severe (Fig. 1). Only a very small portion of the county in the extreme northwest remains uncolonized.

It is highly likely that macropters have been pivotal in this range expansion, as there has been a significant increase (χ^2 = 11.64, d.f. = 1, P<0.01) in the sightings of long-winged *M. roeselii* since 1980 (Table 2). This increase in the number of reports is reflected in a significant increase (χ^2 = 20.57, d.f. = 1, P<0.01) in the number of 1-km squares where they were sighted (Table 2, Fig. 1). These data suggest that macropters have become increasingly common and more widespread since 1980. Indeed, though for the period 1912-1979, macropters were only sighted at two coastal locations (Fig. 1), for the period 1980-1995, macropters were seen in five new locations outside of their historic range in the newly colonized areas of Essex (Fig. 1). Two of these new locations were in Epping Forest, where the bushcricket was recorded for the first time in 1982, macropters being reported in 1983 and 1984 (Hanson 1992). This indicates that macropters were colonizing new habitats in Epping Forest, which is within 10 km of the boundary of the historic 1912-1979 range, as early as 1983. The two sites where macropters were reported in the Forest were within 1 km of each other, which supports the evidence presented in the study by Wissmann *et al.* (2009) that suggests dispersal by long-winged *M. roeselii* tends to be very small-scale, over relatively short distances (< 10 km). The clustering of sightings of macropters in the Colchester area in northeast Essex (Fig. 1) also lends weight to this assertion. However, Wissmann *et al.* (2009) indicate that macropterous individuals play only a minor role in the dispersal of this species, due to their low incidence (< 2% of individuals) in populations, and assert that walking is the main method by which new areas are colonized. Studies from Essex indicate that the proportion of macropterous individuals in a population can be much higher (20-30% in 2007; Table 1) and is likely to be a significant factor in the colonization of new areas.

Macropterous individuals are probably important in the colonization of new areas; for example, the first individuals of *M. roeselii* sighted in Norfolk in 1997 and 1999 were long-winged (Richmond 2001). Populations of newly colonized habitats are likely to have a high proportion of macropterous individuals: as populations establish in an area and dispersal becomes less important, it is probable that macropterism becomes rarer due to the high energetic costs and reduced fecundity associated with the production of wings in

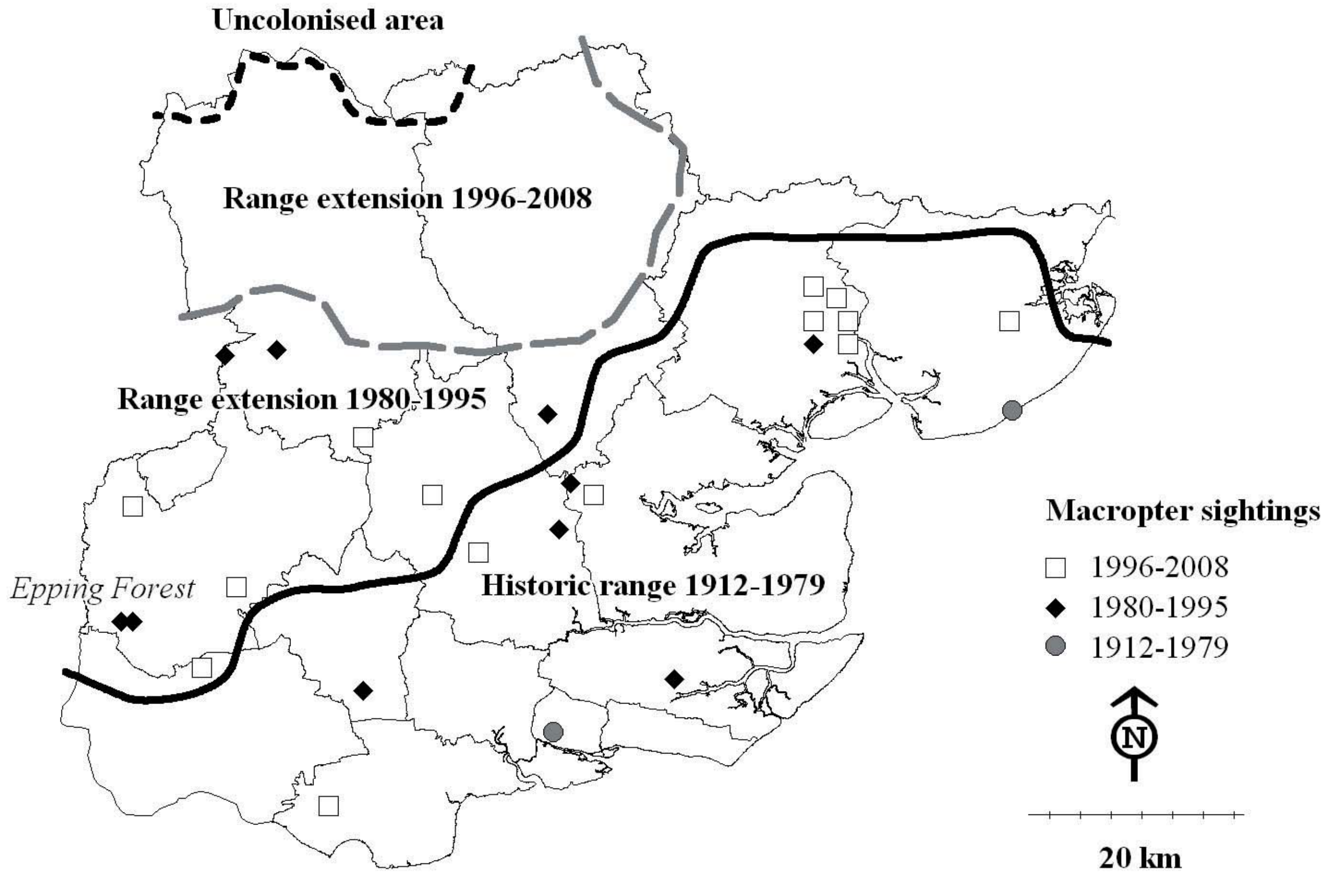

Fig.1. Range expansion of *M. roeselii* in Essex showing the distribution of macropter sightings; range extensions show areas that have been colonized outside of existing range within the time period indicated.

brachypterous species (Thomas *et al.* 2001).

It is likely that *M. roeselii* has been able to respond to the increased availability of tall grassland on farmland due to the introduction of set-aside in 1993 and agri-environment schemes in 1987. There were three clear periods of macropterism in the county during the systematic survey: 1983-1986 (exclusive of 1985), 1992-1997 and 2003-2008 (exclusive of 2006). The first period of macropterism in the 1980s was before the introduction of compulsory set-aside and agri-environment schemes such as ESAs and CSS. However, *M. roeselii* colonized large areas of central and western Essex, which appeared to escape the worst effects of historic field boundary removal (particularly of hedgerows) (Table 2). In these areas it would be expected that the establishment of set-aside and agri-environment habitats (such as grass field margins) would be less crucial to insect survival than in the extreme northwest of the county, where landscape connectivity was severely reduced by hedgerow removal (Table 2, Fig. 1).

The second period of macropterism in the 1990s coincided

Table 2. *M. roeselii* range expansion and macropter data in relation to climate change and landscape structure since 1912.

Factors	Years 1912-1979	1980-1995	1996-2008	Significance**
All *M. roeselii* data				
No. 10-km squares occupied N = 57 (% of N)	27 (47)a	46 (81)	55 (96)b	χ^2 =9.65 (P<0.01)
Macropter data only				
Mean no. reports of macropters/yr (total no.)	<0.1 (3)a	0.7 (11)	1.5 (19)b	χ^2 =11.64 (P<0.01)
Cumulative no. 1-km squares recorded in (total new squares)	2 (2)a	12 (10)	26 (14)b	χ^2=20.57 (P<0.01)
Landscape features				
Mean field boundary loss/km^2 for newly recorded range ± SE	28 ± 3a	34 ± 3a	54 ± 10b	F=5.31 (P<0.05)
Climate data*				
Mean annual temperature (°C) ± SE	9.7 ± 0.1a	10.0 ± 0.1a	10.7 ± 0.1b	F=16.83 (P<0.01)
Mean annual rainfall (mm) ± SE	562 ± 4	593 ± 20	584 ± 35	F=0.83 NS

*climate data for period 1943-2008

**statistical differences indicated in each row by a different letter, NS = not significant

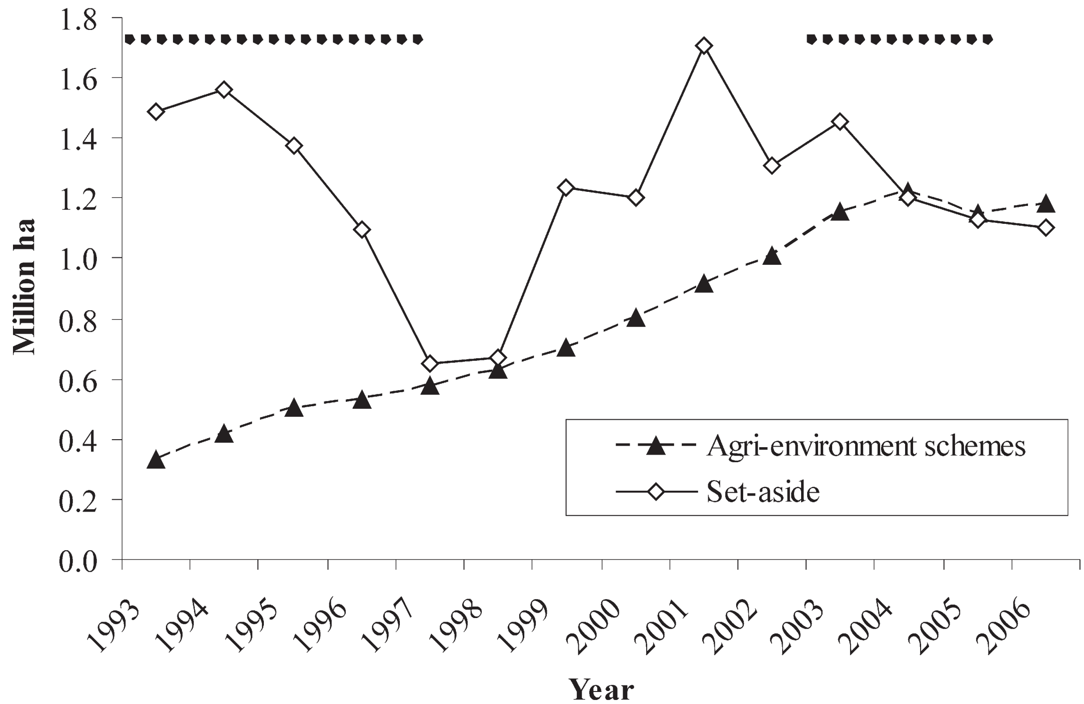

Fig. 2. Area of land under set-aside and agri-environment schemes (Countryside Stewardship and Environmentally Sensitive Areas combined) in England 1993-2006 (dotted lines indicate periods of macropterism in Essex).

almost exactly with the introduction of set-aside in 1993 (Fig. 2), when the area of set-aside exceeded 1 million ha until a decline in 1997. Then the area of set-aside recovered in the late 1990s and early 2000s. The high level of set-aside throughout the mid-1990s was not matched by the area of land under management through agri-environment schemes such as Countryside Stewardship (Fig. 2), as funding and uptake were probably limited at the time. Evidence of the high importance of blocks of permanent set-aside for *M. roeselii* is highlighted by a study undertaken at Writtle College (Table 3).

The data collected in 1999 from open-quadrat sampling at Writtle College in central Essex (Gardiner 1999, Gardiner & Pye 2001), indicate that large populations of *M. roeselii* were sustained in permanent set-aside fields (*ca* 300 individuals/ha), but not in Countryside Stewardship grass field margins that were 2-6 m wide and connected with the set-aside (no *M. roeselii* were recorded in either grass field margin, Table 3). An extremely large population (*ca* 1000 individuals/ha) was recorded in a hay meadow adjacent to one of the set-aside fields, and it is likely that extensive areas of grassland were important for this bushcricket, which was otherwise scarce on farmland in the area.

Sward heights of the two set-aside fields varied with their botanical composition. Field 1 was comprised of Perennial Rye-grass *Lolium perenne* and had a relatively short sward height (< 50 cm), whereas field 2 was dominated by Timothy *Phleum pratense*, with sward height exceeding 70 cm (Table 3).

Management of set-aside grasslands may have been particularly suited to this bushcricket, as cutting (topping) was forbidden from 1 May to 15 July, a time when this species is in its nymphal and early adult stages (Marshall & Haes 1988). Cutting of the Writtle set-aside fields was undertaken as late as possible in the summer (August onwards) to avoid significant mortality of mammals and insects that may occur during midsummer cutting (Gardiner & Hill 2006). The cut material was uncollected and was left to rot on the ground over winter; this would have provided cover for bushcrickets that survived mowing. The nonremoval of mown vegetation would also have meant that eggs laid in grass stems (Ingrisch 1984) would have been left on site in readiness for hatching in following seasons.

Footpaths next to grass field margins established in 2005 under the Environmental Stewardship Scheme (which replaced Countryside Stewardship), were found to support small populations of this bushcricket on intensively managed (high-N fertilizer input, pesticides regularly used) farmland in central Essex in the following season (Table 4). The adjacent margins tended to be composed of tall growing grasses such as Cocks-foot, *Dactylis glomerata*, ideal habitat for this insect to colonize.

Table 3. Set-aside grasslands sampled in 1999 at Writtle College for *M. roeselii* using open quadrats (data sources: Gardiner 1999, Gardiner & Pye 2001).

Site	Date habitat established	Estimated no. individuals/ha	Dominant grass species	Mean sward height (cm)
Permanent set-aside 1	1997	313	*Lolium perenne*	45
6-m grass field margin	1996	0	*Poa trivialis*	50
Arable field	1998	0	*Triticum* spp.	70
Permanent set-aside 2	1996	278	*Phleum pratense*	73
2-m grass field margin	1996	0	*Dactylis glomerata*	65
Hay meadow	1990	1111	*Arrhenatherum elatius*	80

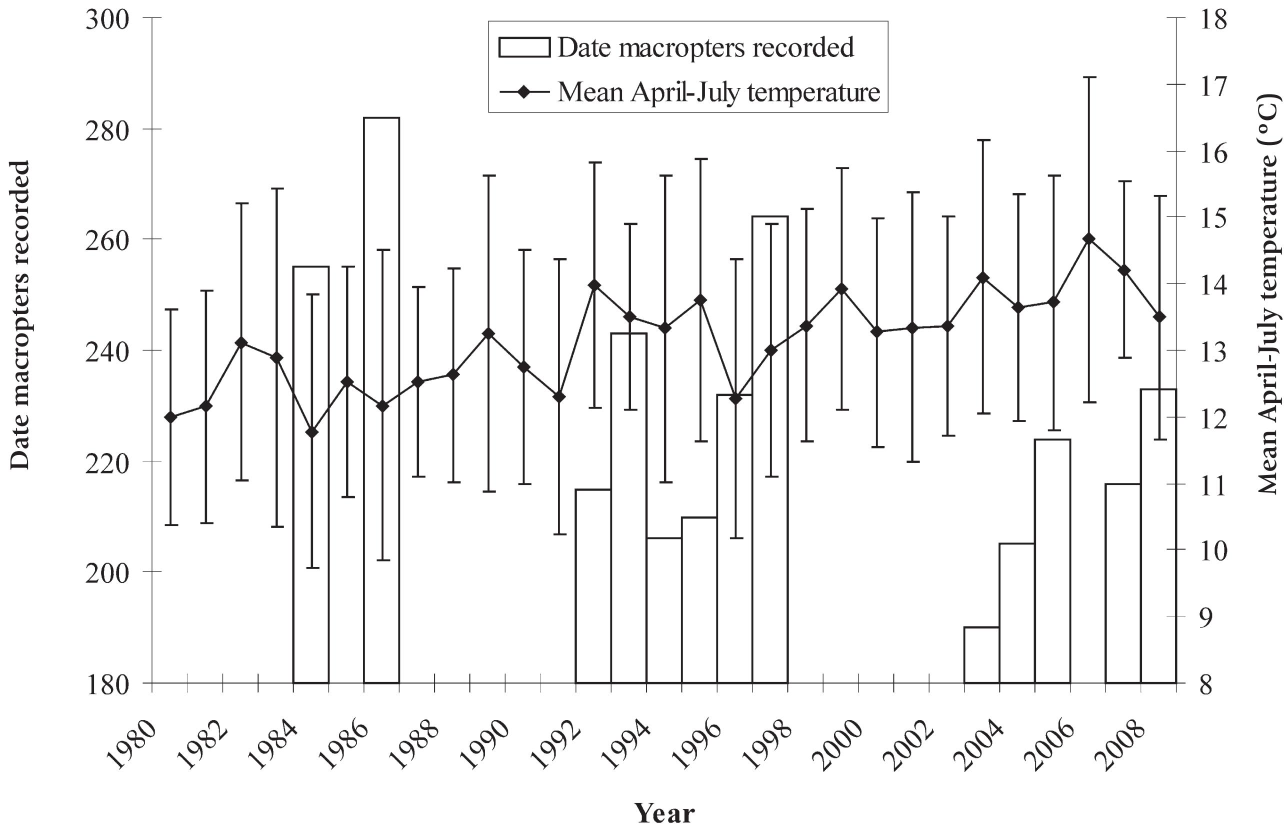

Fig. 3. Mean air temperature (SE bars shown) for the main period of nymphal development (April-July) in relation to the date macropters were recorded in that year; data are averaged for years with more than one sighting (*e.g.*, there were 11 records in 2004).

By 2006, the area of land entered into agri-environment schemes was at an equivalent level to the amount of set-aside in England (Fig. 2). The third period of macropterism from 2003-2008 (exclusive of 2006) coincided with the increased availability of land managed under agri-environment schemes and the relatively large area of land still under set-aside (Fig. 2). This may have enabled *M. roeselii* to colonize the extreme northwest of the county during the period 1996-2008 (Fig. 1), where hedgerow removal had been extremely severe (Table 2) and creation of grass field margins and restoration of hedges could have started to re-establish landscape features destroyed since 1945.

Berggren (2001, 2005, 2008) states that landscape corridors increase connectivity of habitats and can reduce the incidence of inbreeding which often results in smaller body size. Small individuals produce a comparatively low number of offspring, therefore decreasing the genetic viability of isolated populations (Berggren 2008). However, there is a trade-off as the energy needed to produce a larger body reduces the immune response of the insect. Increased connectivity of habitats in the county through restoration of field boundary vegetation may be beneficial in producing and maintaining an optimal body size in *M. roeselii*, despite the potential lowering of immune response.

Table 4. *M. roeselii* abundance in summer 2006 from transect counts on footpaths next to Environmental Stewardship grass field margins established in 2005 on intensively managed farmland (data source: Gardiner 2007).

Grass margin width (m)	Estimated no. individuals/ha	Dominant grass species
6	10	*Dactylis glomerata*
4	21	*Dactylis glomerata*
2	9	*Dactylis glomerata*
0 (no margin)	9	*Lolium perenne*
Arable field	0	*Triticum* spp.

The current study shows that landscape structure and climate change were probably the main drivers behind the range expansion of *M. roeselii* in Essex. Firstly, there was a significant increase ($F = 16.83$, $P<0.01$) in mean air temperature for the period 1996-2008 (Table 2), which coincided with the increases in range, macropter incidence/distribution, and the spread of the insect into the northwest of the county (Fig. 1) where historic hedgerow removal was extremely severe. Despite the increase in temperature, there has been no significant ($F = 0.83$, $P = 0.44$) change in rainfall levels since 1943 (Table 2).

I failed to detect an effect of either the current year's mean temperature and rainfall or the previous year's mean temperature and rainfall on the occurrence of macropters of *M. roeselii* (logistic regression R2 = 4.43, d.f. = 4, p = 0.35). These four predictors combined to explain approximately 18.9% of the variation in macropter occurrence (Nagelkerke's R2 = 0.19). The previous year's mean temperature was the strongest of the four independent variables (Wald statistic = 2.34, d.f. = 1, p = 0.13) although it was not statistically significant.

Despite the perceived occurrence of the macropterous form of *M. roeselii* in long hot summers (Marshall & Haes 1988), it seems that there is no such relationship in Essex as seasons with macropters were not warmer or drier (Fig. 3). Admittedly, they were present in hot, dry seasons such as 1983, 1995 and 2003; but it is likely that the appearance of macropters is determined by the previous summer's air temperature, hot weather leading to successful breeding (a large number of eggs are then laid which hatch in the following spring) and high population densities in the following year. These large populations may produce macropterous individuals (which disperse to colonize new habitat) in response to population over-crowding; this could explain the sightings of long-winged *M. roeselii* in summers with apparently cool and damp weather, such as 2008.

A crucial influence of air temperature within the season may be to accelerate nymphal development (which occurs from April-July), leading to the earlier production of macropters. The significant relationship (linear regression $R^2 = 0.55$, $P<0.05$) between mean air temperature for the main period of nymphal development and the date that macropters were sighted in a particular year (Fig. 3) adds weight to this assertion. High temperatures from April-July are likely to be crucial accelerants of nymphal development and the production of macropters in the final instars before maturation (Zera & Denno 1997). Macropters that appear earlier in the summer are at a substantial advantage to those that are produced later in the year (*e.g.*, in September), as they will be able to quickly colonize new areas in the hottest weather and successfully mate once those habitats are reached. It seems that the significant benefit of climate change for *M. roeselii* may be earlier maturation and production of macropters in response to enhanced spring and summer temperatures.

It is important to remember that microclimate may be crucial along with local habitat conditions in providing warm temperatures for development of large populations and macropterous bushcrickets. Sites acting as hot 'sun traps' have been found to be favorable for Orthoptera, and include the south (Marshall & Haes 1988) and east sides of hedgerows (Gardiner & Dover 2008). Therefore, overall 'crude' climatic data may be a poor indicator of the occurrence of macropterous bushcrickets. This study must also be viewed with some caution due to the lack of quantitative data, and the possibility that macropterous individuals went unreported to the county co-ordinator or were simply overlooked, which is surprisingly easy even with large bushcrickets (Harvey & Gardiner 2006).

Whatever the causes of macropterism in *M. roeselii*, it is no doubt important in the range expansion of this bushcricket. This is underlined by the comparative rarity of the long-winged form of bushcrickets such as the short-winged conehead *Conocephalus dorsalis* (*f. burri*), only sighted in 1983, 1984, 2004 and 2007 in the period of study and restricted to coastal areas of Essex, with no significant range expansion since 1980. The macropterous form of the meadow grasshopper *Chorthippus parallelus* (*f. explicatus*) has never been sighted in the county, although it was noted nationally in 1983-84 (Ritchie *et al.* 1987, Marshall & Haes 1988).

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References

Benton T. 2008. Grasshoppers, Bush-crickets and their Allies: an Up-date for N E Essex. Nature in North East Essex. Colchester Natural History Society, Colchester.

Berggren A. 2001. Colonization success in Roesel's bush-cricket *Metrioptera roeseli*: the effects of propagule size. Ecology 82: 274-280.

Berggren A. 2005. The effect of propagule size and landscape structure on morphological differentiation in asymmetry in experimentally introduced Roesel's bush-crickets. Conservation Biology 19: 1095-1102.

Berggren A. 2008. The effects of population and landscape ecology on body size in orthopterans. Journal of Orthoptera Research 17: 183-188.

Burr M. 1936. British Grasshoppers and their Allies: a Stimulus to their Study. Janson, London.

Centre for Rural Economics Research. 2001. Economic Evaluation of Set-aside. University of Cambridge, Cambridge.

Chapman J.W., Reynolds D.R., Smith A.D., Smith E.T., Woiwod I.P. 2004. An aerial netting study of insects migrating at high altitude over England. Bulletin of Entomological Research 94: 123-136.

Gardiner T. 1999. The Grasshoppers and Bush-crickets of the Writtle College Estate. Writtle College, Chelmsford.

Gardiner T. 2003. Orthoptera and allied insects of Essex 2002. Essex Naturalist (N.S.) 20: 62-66.

Gardiner T. 2004. Orthoptera and allied insects of Essex 2003. Essex Naturalist (N.S.) 21: 69-74.

Gardiner T. 2006. The impact of grassland management on Orthoptera populations in the UK. Unpublished PhD thesis, University of Essex, Colchester, UK.

Gardiner T. 2008a. Orthoptera and allied insects of Essex 2007. Essex Naturalist (N.S.) 25: 72-75.

Gardiner T. 2008b. The Overlooked Orthoptera: an Introduction to Grasshoppers and Bush-crickets. British Naturalists' Association Guide: www.bna-naturalists.org/ident.htm

Gardiner T., Benton T. in press. The effects of climate change on Orthoptera in Essex.

Gardiner T., Dover J. 2008. Is microclimate important for Orthoptera in open landscapes? Journal of Insect Conservation 12: 705-709.

Gardiner T., Haines K. 2008. Intensive grazing by horses detrimentally affects orthopteran assemblages in floodplain grassland along the Mardyke River Valley, Essex, England. Conservation Evidence 5: 38-44.

Gardiner T., Hill J. 2006. Mortality of Orthoptera caused by mechanised mowing of grassland. British Journal of Entomology & Natural History 19: 38-40.

Gardiner T., Hill J., Marshall E.J.P. 2008. Grass field margins and Orthoptera in eastern England. Entomologist's Gazette 59: 251-257.

Gardiner T., Pye M. 2001. Habitats of Orthoptera on the Writtle College Estate in Essex. Bulletin Amateur Entomologists' Society 60: 154-160.

Gardiner T. 2007. Orthoptera of crossfield and headland footpaths in arable farmland. Journal of Orthoptera Research 16: 127-133.

Hanson M.W. 1992. Epping Forest – Through the Eye of the Naturalist. Essex Field Club, Stratford.

Harvey P., Gardiner T. 2006. Pitfall trapping of scarce Orthoptera at a coastal nature reserve in Essex, UK. Journal of Insect Conservation 10: 371-373.

Heath D. 1995. An Introduction to Experimental Design and Statistics for Biology. UCL Press, London.

Ingrisch S. 1984. The influence of environmental factors on dormancy and duration of egg development in *Metrioptera roeseli* (Orthoptera: Tettigoniidae). Oecologia 61: 254-258.

MapInfo Corporation. 2005. MapInfo Professional Version 8.0. MapInfo Corporation, London.

Marshall J.A., Haes E.C.M. 1988. Grasshoppers and Allied Insects of Great Britain and Ireland. Harley Books, Colchester.

Overton A.K. 2007. A guide to the siting, exposure and calibration of automatic weather stations for synoptic and climatological observations. www.rmets.org
Payne R.M. 1957. The distribution of grasshoppers and allied insects in the London area. London Naturalist 37: 102-115.
Pollard E., Hooper M.D., Moore N.W. 1974. Hedges. Collins, London.
Rackham O. 1986. The history of the countryside. J.M. Dent, London.
Richmond D. 2001. Grasshoppers and Allied Insects of Norfolk. Norfolk and Norwich Naturalists' Society, Norwich.
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.
Smith G. 2007. Bush crickets on the menu. Essex Field Club Newsletter 54: 8-9.
SPSS. 2007. SPSS Version 16.0. SPSS Inc, Chicago.
Thomas C., Bodsworth T., Wilson R., Simmons A., Davies Z., Musche M., Conradt L. 2001. Ecological and evolutionary processes at expanding range margins. Nature 411: 577-581.
Vickery V.R. 1965. Factors governing the distribution and dispersal of the recently introduced grasshopper, *Metrioptera roeseli* (Hgb.) (Orthoptera: Ensifera). Annales Entomological Society of Québec 10: 165-171.
Wake A. 1997. Grasshoppers and Crickets (Orthoptera) of Essex. Colchester Natural History Society, Colchester.
Wissmann J., Schielzeth H., Fartmann T. 2009. Landscape-scale expansion of Roesel's bush-cricket *Metrioptera roeselii* at the north-western range limit in Central Europe (Orthoptera: Tettigoniidae). Entomologia Generalis 31: 317-326.
Writtle College. 2002. Writtle College Annual Weather Report. Writtle College, Chelmsford.
Zera A.J., Denno R.F. 1997. Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology 42: 207-230.