Macropters can be common in field populations, for example, in Essex, 2 to 30% of individuals can be macropters (Table 1). This contrasts with published studies from other countries where macropters are assumed to be at 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 macropters for this bushcricket, with it not uncommon to find > 20% of individuals in a population with long wings.

Macropters 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 macropters 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 macropters *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. Flies 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 macropters 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 macropters in the range expansion of *M. roeselii* in Essex, UK, and to relate this to climate change and landscape structure.
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 into 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 special note has been made of the discovery of macropterus individuals, so we have a very good idea of the occurrence of this form in the county. The bushcricket is also one of the most commonly sighted orthopterans in the county, approximately 16% of records being of this species (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, 2008). It has successfully spread away from its strongholds on the coast (east Essex) and has moved westwards over the last 30 years to colonize inland habitats, often on farmland (Gardiner & Benton in press, Gardiner et al. 2008).

During the systematic study of the distribution of Orthoptera, Alan Wake examined a wide variety of published material from the Essex Naturalist and national entomological journals to chart the history of M. roeselii recording and the occurrence of macropterus in the county. The first county record was in 1912, and Alan amassed details of a considerable number of sightings for the period 1912-1979. Recording in the county during this 68-year period was patchy (Wake 1997), but 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 (Whittle 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 was 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 was 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 1880-2000 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/km². 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.

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

<table>
<thead>
<tr>
<th>Study reference</th>
<th>Year</th>
<th>Location</th>
<th>% individuals with long wings</th>
<th>Recorder</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burr (1936)</td>
<td>1933</td>
<td>South Benfleet</td>
<td>30</td>
<td>K.G. Blair</td>
</tr>
<tr>
<td>Gardiner &amp; Haines (2008)</td>
<td>2007</td>
<td>Mardyke Valley</td>
<td>7</td>
<td>T. Gardiner</td>
</tr>
<tr>
<td>Gardiner (2008a)</td>
<td>2007</td>
<td>Good Easter</td>
<td>20</td>
<td>T. Gardiner</td>
</tr>
</tbody>
</table>
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 allow an analysis of the range expansion of *M. roeselii* in the county, 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 1992-2008 using Chi-square ($\chi^2$) to determine the overall range expansion over the last 100 y. 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) that macropters were recorded in, for 1912-1979 and 1992-2008.

The mean number of field boundaries removed/km² 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).

The 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, which supports the evidence presented in the study by Wissmann *et al.* (2009) indicate that macropterous individuals only play a minor role in the dispersal of this species due to their low incidence (< 2% of individuals) in populations, and 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 undoubtedly 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

**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 ($\chi^2 = 9.65$, 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 bushcricket (records for period 1912-1979) did not differ significantly from 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 ($\chi^2 = 11.64$, 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 was reflected by a significant increase ($\chi^2 = 20.57$, d.f. = 1, P<0.01) in the number of 1-km squares in which they were sighted (Table 2; Fig. 1). These data suggest that macropters have become increasingly common and more widespread since 1980. Indeed, for the period 1912-1979, macropters were only sighted at two coastal locations (Fig. 1). However, for the period 1980-1995, macropters were sighted 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. Indeed, 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 only play a minor role in the dispersal of this species due to their low incidence (< 2% of individuals) in populations, and that walking is the main method by which new areas are colonized.
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.

(Richmond 2001). Populations of newly colonized habitats are likely to have a high proportion of macropterous individuals; as breeding colonies develop 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 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

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

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>All <em>M. roeselii</em> data</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. 10-km squares occupied N</td>
<td>27 (47)a</td>
<td>46 (81)</td>
<td>55 (96)b</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>Macropter data</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean no. reports of macropters/yr (total no.)</td>
<td>&lt;0.1 (3)a</td>
<td>0.7 (11)</td>
<td>1.5 (19)b</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>Cumulative no. 1-km squares recorded in (total new squares)</td>
<td>2 (2)a</td>
<td>12 (10)</td>
<td>26 (14)b</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>Landscape features</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean field boundary loss/km² for newly recorded range ± SE</td>
<td>28 ± 3a</td>
<td>34 ± 3a</td>
<td>54 ± 10b</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>Climate data*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean annual temperature (°C) ± SE</td>
<td>9.7 ± 0.1a</td>
<td>10.0 ± 0.1a</td>
<td>10.7 ± 0.1b</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>Mean annual rainfall (mm) ± SE</td>
<td>562 ± 4</td>
<td>593 ± 20</td>
<td>584 ± 35</td>
<td>NS</td>
</tr>
</tbody>
</table>

*climate data for period 1943-2008
**statistical differences indicated in each row by a different letter, NS = not significant
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 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. However, 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), indicates 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 (indeed 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 mid summer cutting (Gardiner & Hill 2006). The cut material was also not collected and was left to rot on the ground over winter, this would have provided cover for bushcrickets that survived mowing. The non-removal 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 Coun-


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

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 macropterus form of *M. roeselii*, the following table shows that the majority of individuals found were of the wingless form. 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).

<table>
<thead>
<tr>
<th>Grass margin width (m)</th>
<th>Estimated no. individuals/ha</th>
<th>Dominant grass species</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>10</td>
<td><em>Dactylis glomerata</em></td>
</tr>
<tr>
<td>4</td>
<td>21</td>
<td><em>Dactylis glomerata</em></td>
</tr>
<tr>
<td>2</td>
<td>9</td>
<td><em>Dactylis glomerata</em></td>
</tr>
<tr>
<td>0 (no margin)</td>
<td>9</td>
<td><em>Lolium perenne</em></td>
</tr>
<tr>
<td>Arable field</td>
<td>0</td>
<td><em>Triticum</em> spp.</td>
</tr>
</tbody>
</table>

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).
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 R² = 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).

Acknowledgements

The author would like to thank Alan Wake, the previous County Recorder for Orthoptera, and the Essex Field Club for supporting the collection of county records. Alan was a true pioneer of Orthoptera recording in the county and brought together many historical records which allow us to understand how orthopterans have spread their range. Over 100 recorders have sent in their sightings over the years, but those who have contributed significantly to the observation of bushcrickets include Ted Benton, Jerry Bowdrey, Peter Harvey, Neil Harvey and Roger Payne. Martin Heywood maintained the weather station at Writtle College and made the data available in report format which facilitated easier analysis. A special thank you must be made to Dr Kevin Judge who provided invaluable guidance and input on statistical issues, and to Dr Glenn Morris who made important suggestions for improvements to the paper.

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