The apparent influence of climatic change on recent changes of range by European insects (Lepidoptera, Orthoptera)

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Abstract

For several years I have been collecting data concerning changes in the ranges of European insects, especially Lepidoptera and Orthoptera. The vast majority of those species which have altered their ranges since 1850 have spread to the north, north-west or west (e.g. 96% of the Lepidoptera expanding their ranges). Of the smaller number of species where the range has contracted, the majority (e.g. 75% of the Lepidoptera) have retreated southwards, south-westwards or south-eastwards.

I have attempted to correlate these range changes with the main climatic fluctuations from 1850 to the present. Throughout this long period of predominately warming climate in Europe, those insect species which have been expanding their ranges have done so in steadily increasing numbers, especially since 1975, thus coinciding with the marked increase in temperatures worldwide associated with the anthropogenic greenhouse effect.

Key words: climate change, range change, Europe, insects, Lepidoptera, Orthoptera, greenhouse effect.

Introduction and climatic background

This paper is concerned with the apparent influence of climate changes on changes in range by European insects over the past century and particularly with current trends. However, it is necessary to view such relatively recent events against the background of the climatic history of the interglacial period within which we are living.

It is, of course, well known that during the Pleistocene ice ages the fauna and flora of the northern hemisphere retreated southwards when the climate cooled and caused the ice sheets to expand outwards from the North Pole, advancing northwards again as the ice retreated during those frequent periods when, to a greater or lesser degree, the climate warmed up again (Beirne 1952). The whole process went into reverse when next the climate cooled and so on. Because warm and cold interludes of variable durations and extent have alternated right up to the present time, this back and forth process has continued to some degree ever since the ice-sheets massively retreated at the end of the last (or Weichselian) glaciation, some 10 000 years ago, and the present Holocene interglacial epoch, commonly known as the post-glacial, began.

Following the 500 years or so of the ‘little ice age’, which was at its coldest in the 17th century and did not finally end until about 1850, we have experienced a climatic amelioration which lasted till about 1950, followed by another climatic deterioration that caused some climatologists and others (Calder 1974) to predict the end of our interglacial and the onset of a new ‘ice age’ (glaciation). At the time, this did not seem at all improbable as some warm interludes between the most recent glaciations were of similar length to that attained by the present one. However, these predictions proved unfounded when the present climatic warming became evident about 1975. This warming is, of course, attributed, with much justification, to the pollution caused by human activities which has resulted in the anthropogenic greenhouse effect.

Europe’s flora and fauna have responded to such climatic fluctuations as they have always done in the past, the extent depending upon the severity of the climate. Many of the consequences of the gradual climatic amelioration after 1850 are, fortunately, well documented. This warmer, but generally wetter phase reached its peak in the 1930s and 1940s when the summers became hotter and drier, and the winters distinctly colder. It enabled many species of birds and insects, for example, to extend their breeding ranges northwards and/or north-westwards, sometimes at the expense of closely related northern species which, at the same time, withdrew the southern limits of their ranges northwards as well (Burton 1995, 1998, Parmesan et al. 1999, Williamson 1975). The largely maritime-type climate did not suit all species with a Central European or Mediterranean centre of distribution; except in the drier 1930s and 1940s, these tended to contract their ranges eastwards or south-eastwards where conditions were drier and more stable. Examples among insects include the lepidopterans *Aporia crataegi* (Linnaeus, 1758) and *Tyta luctuosa* (Denis & Schiffermüller, 1775), the tettigoniid *Ephippiger ephippiger* (Fiebig, 1775), the gryllid *Gryllus campestris* Linnaeus, 1758 and the acridid grasshopper *Psophus stridulus* (Linnaeus, 1758) (Burton 1975, Heath & Emmet 1983, Kleukers 1997, Pratt 1983). From 1950, when the climate of the northern hemisphere, particularly that of the Arctic and Subarctic, began to cool and hard winters also became more frequent farther south in Europe, there was again a trend to a southwards expansion of the ranges of northern zone species and a contraction southwards of those of the temperate zone, although a good many species which had been expanding northwards in response to the earlier amelioration continued to do so, carried along by the momentum of their expansion. So this north-south movement and back of animals in reaction to strong climatic oscillations was nothing new, but a continuation of a process which has been happening, to a greater or lesser extent, throughout the ice ages.

About 1975 the anthropogenic greenhouse effect began to neutralize the previous, apparently natural, climatic deterioration; by 1980, the global warming it produced was beginning to overwhelm it in at least some regions of the northern hemisphere (Burton 1995, Gribbin 1990). Not surprisingly, the complex and, for a time, opposing climatic trends have been reflected in correspondingly complex, even apparently paradoxical, effects on birds, insects and other wildlife. Since 1980, however, most of the temperate-zone and Mediterranean-zone species have recovered from the set-backs they suffered during the climatic deterioration and have resumed their advance northwards, while some of the arctic and other northern species have retreated again. Those advancing north have been joined by a large number of other species, especially by those whose breeding range is centred on the Mediterranean.

Figure 1
Roesel's bush-cricket *Metrioptera roeseli*, a rapidly expanding species in Britain and north-western Europe. Photo Roy Kleukers.

Problems involved in assessing the responses to climate change

In this paper I have concentrated on the apparent effects on European insects of climate changes since about 1850. It is, of course, not easy to prove that observed changes in the behaviour of animals are, in fact, due to climate change rather than other causes. Man's growing influence on the terrestrial environment as well as on the climate is now so profound and complex that it has greatly complicated the situation compared with that existing prior to historic times. It is, for instance, difficult to unravel the precise causes of changes in the distribution of species when so many other factors are involved, such as habitat fragmentation and loss, the intensification of agriculture, afforestation and disafforestation, horticultural expansion (including the introduction of alien plants), industrial pollution and the use of insecticides. It is probable that in many cases climate change is not the sole factor; a combination of two or more factors may be involved. The reponses of animal species may take the form of alterations not only in breeding range and abundance, but also in such factors as migration patterns, number of annual generations, overwintering abilities, interactions with other organisms, and phenology. Because of the specific theme of this colloquium, I have confined myself in this paper to describing changes in distribution.

Changes in geographical range since 1850

For space reasons, I am obliged to restrict my examples to a few of the more notable species of the Lepidoptera, Orthoptera and Hymenoptera which are altering their ranges, apparently as a consequence of climate warming.

Lepidoptera

Of 245 species of Macrolepidoptera and Pyralidae whose breeding distributions have, to my knowledge, altered since 1850, 201 (82%) have expanded their ranges at some time or another in one or more directions, the vast majority, 193 species (96%) to the north, north-west or west. Of the 77 species which have contracted their ranges, 58 (75%) have retreated southwards, south-westwards or south-eastwards. The reason why the combined total of expanding and contracting species is greater than the total number of species (245) involved is that, within this lengthy period, some species (like the butterflies *Pararge aegeria* (Linnaeus, 1758) and *Polygonia c-album* (Linnaeus, 1758)) have both contracted and expanded their ranges at different times. Moreover, some other species (like *Parnassius apollo* Linnaeus, 1758) and *Lycaena tityrus* (Poda, 1761)) have expanded their ranges at the northern limit and contracted at the southern limit during the same period of time (Parmesan et al. 1999).

A further analysis of the 201 species which have expanded their ranges reveals that 68 (34%) were doing so in the period of gradual climatic warming from 1850-1949, 105 (52%) in the years 1950-1974 (a period of climatic deterioration in western Europe) and 169 (84%) in the years from 1975-1999 inclusive, a period of escalating climatic warming fuelled by a marked increase in the influence of the anthropogenic greenhouse effect. An examination of the 77 species which have contracted their ranges since 1850 shows that 32 (42%) were doing so in the period from that year to 1949, 30 (38%) in the years 1950-1974 and 35 (45%) in 1975-1999 inclusive. Thus the number of species contracting their ranges has been fairly uniform from 1850 to the present.

On the whole, those species which began expanding their ranges after 1850 continued to do so and were joined by many more species as the climatic amelioration became more noticeable after 1920. It appears that, as a consequence of the impetus built-up during the very warm decades of the 1930s and 1940s (apart from the winters), the majority of these species maintained their range expansions in spite of the temporary checks resulting from the relatively brief climatic deterioration from about 1950 to 1975.

Davis (1989) remarked that for ‘most species, constraints on dispersal will cause a time-lag between the climate becoming suitable for establishment and their actual appearance’. My own study of the influences of climatic change on European birds (Burton 1995) tended to to confirm this as does my current work on European Lepidoptera. I believe the responses of so many species, and the directions in which they are expanding, strongly suggest that climate change is the main factor operating. It is probably working also on other species which have yet to reveal any obvious tendency to alter their present ranges. Some of them may be inhibited from expansion through ecological competition with closely related species which already occupy the territory into which they might otherwise expand.

Regardless of the factors, or combination of factors, involved, it is clear from the foregoing details that the vast majority of European Lepidoptera that altered their geographical distributions to a greater or lesser extent since 1850 expanded them in a northerly direction. Furthermore, a majority of those that contracted their breeding ranges since that year did so in a southerly direction. This, in itself, and taking into account the known fluctuations of the European climate during the same period, indicates that climatic factors are involved in some way. It appears that these species have been, and still are, responding to the climatic warming that has occurred for the greater part of the period. Bearing in mind the known responses of animal and plant species to the glaciations and their aftermath during the ice ages, this is to be expected.

The general results so far obtained from my own investigations are similar to those of Parmesan et al. (1999) who, in a sample of 35 non-migratory species of European butterflies, found that in the 20th century 63% have extended their ranges to the north by 35-240 km and only 3% to the south. These percentages compare fairly closely with mine for the same period for 231 species of European Lepidoptera (butterflies and moths) of which 75% have extended northwards and 1% southwards.

As Parmesan et al. (1999) found in their study of European butterflies, many of those species expanding their ranges have done so across large tracts of unsuitable territory and in spite of habitat fragmentation and loss. In this respect, my findings support their conclusion that ‘several of these species have extended northwards across heavily cultivated landscapes that are clearly less suitable for those species than they were a hundred years ago’. For example, such species of Lepidoptera as *Brenthis ino* (Rottemburg, 1775), *Coenonympha tullia* (Müller, 1764) and *Deltote bankiana* (Fabricius, 1775) have expanded their ranges in Europe in spite of significant habitat loss. On the other hand, other species (like *Hecatera dysodea* (Denis & Schiffermüller, 1775) and *Hypena rostralis* Linnaeus, 1758) that have contracted theirs have done so without any obvious loss of habitat (Burton 1998b).

Although analyses of my data strongly suggest the influence of climatic change on the observed alterations in the distributions of European Lepidoptera, other factors, such as habitat change may, nevertheless, also play a part. I have attempted to look for this: for instance, I have begun analyses of those Lepidoptera expanding their ranges whose larvae feed on coniferous trees and also of those that feed on a variety of cultivated plants, because it is sometimes stated (for instance by Owen & Duthie 1982, concerning the spread of *Lithophane leautieri hesperica* Boursin, 1957) that the range expansions of some of these species can be wholly explained by the increasing cultivation and therefore spread of such plants into new areas. However, my results so far do not support the contention that this is the sole cause. They suggest the same link to climatic fluctuations since 1850 as found for the majority of other species investigated; in fact, reflecting the same general pattern in time and direction. As concluded by Parmesan et al. (1999): ‘Consistency across taxa and continents indicates that butterfly species in the northern hemisphere are shifting generally northwards in response to a common environmental change’.

As also pointed out by Parmesan and her cooperators, Europe has warmed by about 0.8°C during the 20th century, shifting the climatic isotherms northwards by an average of 120km and ‘nearly all population-dynamic studies have concluded that butterflies, and insects in general, are sensitive to temperature’. They commented further that, although the correlational nature of their study limited their ability to determine causal factors, the sum of knowledge of butterfly biology, including numerous experimental studies, implied that the northwards shifts represented responses to increased temperatures.

I have only sufficient space to mention a few of the most notable examples of species altering their geographical ranges in response to climate warming and I have therefore decided to single out two butterflies with a characteristically Mediterranean-South European centre of distribution. As with several species of North African birds, the butterfly *Danaus chrysippus* (Linnaeus, 1758) has considerably increased and extend-

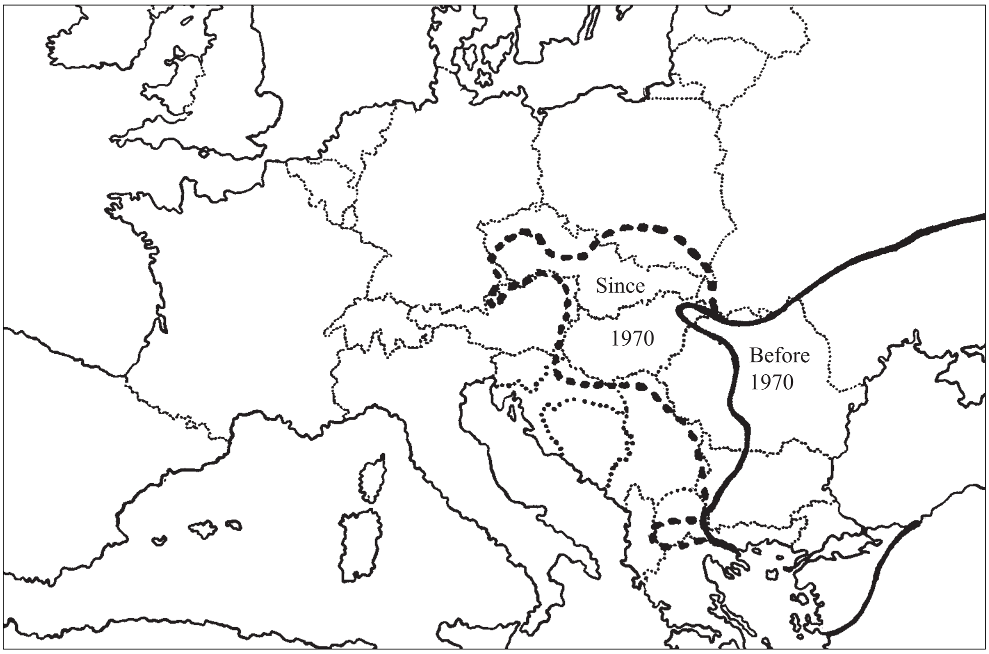

Figure 2
The range expansion of the butterfly *Colias erate*. The continuous line indicates the approximate limit of its distribution before 1970 and the broken line its expansion up to 31 January 2000 (Burton 1988, updated from Kudrna 2000 with his permission)

ed its range in the North African coastal regions in the past two decades, and from there has colonised parts of the southern coastal regions of Spain, Corsica, Sardinia, Italy, Malta, Greece and elsewhere along the 'underbelly' of Europe (Bretherton 1984, Borgo et al. 1992, Hensle 2000, Kleinekuhle 1999, Martin & Gurrea 1988, Owen 1991). Another North African butterfly *Colotis evagore nouana* (Lucas, 1849) has also begun the colonisation of the Spanish south coast (Tarrier & Leestmans 1997).

With regard to those Lepidoptera of truly European origin, the following are examples of a number of species that are currently spreading northwards or north-westwards (since the 1970s or earlier) on the European mainland, apparently in response to recent climatic warming: the Lepidoptera *Apamea illyria* Freyer, 1852, *Araschnia levana* (Linnaeus, 1758), *Autographa buraetica* (Staudinger, 1892), *A. mandarina* (Freyer, 1845), *Brenthis ino*, *Chlorantha (Actinotia) hyperici* (Denis & Schiffermüller, 1775), *Colias erate* (Esper, 1805) (fig. 2), *Cucullia artemisiae* (Hufnagel, 1766), *C. fraudatrix* Eversmann, 1837, *Erebia ligea* (Linnaeus, 1758), *Libythea celtis* (Laicharting in Fuessly, 1782), *Lithophane leautieri hesperica*, *Lycaena tityrus*, *Macdunnoughia confusa* (Stephens, 1850), *Opigena polygona* (Denis & Schiffermüller, 1775), *Pararge aegeria*, *Polygonia c-album* and *Staurophora celsia* (Linnaeus, 1758) (Burton 1992, 1997, 1998b, Emmet & Heath 1989, Hill et al. 1999, Hreblay et al. 1991, Schulze 1993, 1995). Some of these species seem to be on the point of attempting the colonisation of south-east England, as many others have done during the 20th century (Burton 1997).

Orthoptera
Grasshoppers, bush-crickets and their allies are very sensitive to temperature and are especially characteristic of hot, sunny regions. Their numbers and species diversity decline the farther north one travels. Only a few species occur as far

Figure 3
The distribution and expansion of range of the tettigoniid *Conocephalus discolor* in north-western Europe. Black area and black circles: distribution before 1980; open circles: records from 1 January 1980 to 1995; dotted line: records from 1996 to 31 December 2000 (updated from Kleukers et al. 1996 with records from Roy Kleukers and John Widgery, and reproduced by courtesy of Roy Kleukers and the Editor of the Entomologist's Gazette).

north as the subarctic zone or at high altitudes in alpine regions. Therefore, the Orthoptera are particularly good indicators of climate change.

One of the best examples of an almost certain response to the warming of the climate in north-western Europe since 1975 is the small tettigoniid *Conocephalus discolor* (Thunberg, 1815) (fig. 3) which has considerably expanded its range to the north in western Europe (Kleukers et al. 1996). Up to that year it was confined in Britain to a few footholds on the extreme south coast of England, but has since broken out of them to spread northwards at a remarkable speed towards and beyond the River Thames (Burton 1991). It has now reached Suffolk and even south-east Wales (Widgery 2000a, b). The advanced 'guards' often prove to be very long-winged and more mobile individuals capable of extended flights which develop as a result of overcrowding (Ando & Hartley 1982).

Another tettigoniid that has been expanding its previously limited range in Britain and increasing rapidly is Roesel's bush-cricket *Metrioptera roeselii* (Hagenbach, 1822) (fig. 1). Up to about 1980 it was mainly confined to grassland, especially in marshes, around the estuaries of south-eastern England as far north as the Humber. Since that year, however, it has been spreading farther inland, colonising much of the Home Counties as far west as Oxfordshire, and even penetrating into Wiltshire, Gloucestershire and Somerset and north-west to the Lancashire coast. In mainland Europe, the steady northward advances over the past two decades of the tettigoniids *Phaneroptera falcata* (Poda, 1761), *Meconema meridionale* Costa, 1860, *Conocephalus discolor*, and *Oecanthus pellucens* (Scopoli, 1763), and the acridid grasshopper *Chorthippus mollis* (Charpentier, 1825) (Kleukers et al. 1996, Kleukers 1997) are thought to be associated with the present climate warming, although *M. meri-*

dionale is known to obtain transport on vehicles (Kleukers et al. 1996), as I have seen for myself with my own car. The distributions of this and *Oecanthus pellucens* are centred on the Mediterranean, but they now extend as far north as the Low Countries and North-central Germany.

In Britain, the acridid grasshopper *Chorthippus albomarginatus* (De Geer, 1773), which formerly had a mainly coastal distribution, often sharing the same low-lying habitats as Roesel's bush-cricket, has been spreading farther inland in England since the early 1980s, especially in the Midland counties, and also farther northwards in Yorkshire (Burton 1991, Widgery 1999).

Over the past decade there has been increasing evidence that several other species with previously limited distributions are expanding their ranges in England, including the tettigoniids *Meconema thalassinum* (De Geer, 1773), *Platycleis albopunctata* (Goeze, 1778), *Tettigonia viridissima* Linnaeus, 1758 and *Conocephalus dorsalis* (Latreille, 1804), the acridids *Stenobothrus lineatus* (Panzer, 1796) and *Omocestus rufipes* (Zetterstedt, 1821), and the tetrigid *Tetrix subulata* (Linnaeus, 1758) (Widgery 2000a).

Hymenoptera

A number of species of Hymenoptera have expanded their ranges north and north-westwards in Britain in recent years, including the hornet *Vespa crabro* Linnaeus, 1758, the wasps *Dolichovespula media* (Retzius, 1783), *D. saxonia* (Fabricius, 1775), the bee wolf-wasp *Philanthus triangulum* (Fabricius, 1775) (fig. 4) and the sphecid wasp *Nitela borealis* Valkeila, 1974 (Else 1991-1997). *Dolichovespula media*, *D. saxonia* and *Nitela borealis* have all colonised South-east England from the European mainland. The very large bee *Xylocopa violacea* (Linnaeus, 1758), a mainly southern European species, has been spreading north-westwards in Germany since 1936 and especially since 1985 in central Europe in general (Otten et al. 1995), so it is not unexpected that it is now appearing almost annually in England and may be attempting to colonise (Else 1991-1999). Likewise, the wasps *Dolichovespula media* and *D. saxonia* have also been spreading northwards in Germany since the 1980s and elsewhere in Central Europe, as has the wasp *Polistes dominulus* (Christ, 1791) (Otten et al. 1995).

Figure 4
The bee wolf-wasp *Philanthus triangulum*, a species which has expanded its range northwards in Britain in recent years. Photo Aart Noordam.

Concluding remarks

These accounts of alterations in the geographical ranges of various insects do not in themselves prove without doubt that such distributional changes are due to the effects of climate change, but their broad correlation with known climatic oscillations over the past two centuries, as documented by climatologists, is highly suggestive that climate has been a primary influence in many cases, if not all. Absolute proof is difficult to obtain, but the circumstantial evidence is, I believe, strong. For instance, the similar directional changes in the distribution of a wide range of species, whether they are closely related to each other or not, indicates that climate change is a highly probable cause and driving force, even though other factors, such as habitat loss and fragmentation, afforestation and the cultivation of potential larval foodplants in new areas, may be involved to some extent. As mentioned earlier, some species at least have spread in spite of loss of habitat. If warming continues, it is a reasonable guess that further species will invade Britain from the European mainland.

As has been pointed out by various authors (Barkham 1994, Moss 1998), a warming climate will inevitably cause changes in habitats in the British Isles and elsewhere in Europe, particularly in montane regions and along low-lying coasts where inundation by the sea due to rising sea-levels will be a growing problem. Therefore, more changes in distribution can be anticipated. Without doubt, the current changes in the climate are providing plenty of opportunities for interesting study, not only by professional biologists, but also by amateur naturalists, especially when in co-operation with the professionals.

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