UNIVERSITY OF SOUTHAMPTON

FACULTY OF MEDICINE, HEALTH AND LIFE SCIENCES

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The Effects of Climate and Habitat on Butterfly Populations

by

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ABSTRACT

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Biodiveristy is threatened globally and there is a need to monitor and understand future changes. Rigourous assessment of trends in insect populations is difficult because they are a species-rich, yet little known taxa. Butterflies are among the most practical insect group to study, given their extensive long-term, large-scale datasets.

The effects of climate and habitat of butterfly populations are examined to understand the implications of environmental change for these, and other, insect taxa. It is found that first appearance (phenology) of most British butterflies has advanced in the last two decades and is strongly related to climate. Further warming is predicted to advance appearance by 2 to 6 days per 1°C temperature increase. Despite this strong relationship between appearance dates and temperature over time, a comparable geographical relationship between temperature and timing was not detected for over a third of species analysed, suggesting their populations may be adapted to their local climates.

A seasonal switch in egg-laying requirements of the butterfly, *Polyommatus bellargus*, demonstrates an interaction between niche requirements and climate determine fluctuations in populations. The effect of climate on populations of other butterflies was studied using national weather records and indices of population change since 1976. Strong associations between weather and population fluctuations were found in 28 out of 31 species studied. Models derived from these associations predict that most species will increase in abundance under warmer climates.

Large scale habitat modification is known to have profoundly affected butterfly populations over the last century. Data from a farm scale evaluation of the effects of management for genetically modified herbicide-tolerant (GMHT) crops showed that effects on vegetation cover and flowering at this scale has marked knock-on effects for butterflies and other mobile, nectar feeding insects.

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1 Introduction

In response to global declines in biodiversity (Groombridge & Jenkins, 2002) and the resulting global threat to ecosystem goods and services (Ceballos & Ehrlich, 2002), international governments have endorsed the Convention on Biological Diversity (CBD) pledge to *"achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on earth".* The European Union (EU) has identified the need for more specific action and intends "*to protect and restore habitats and natural systems and halt the loss of biodiversity by 2010*" and its member nations have endorsed the "Message from Mallahide" (2004) to:

- *"Improve and apply the knowledge base for the conservation and sustainable use of biodiversity*
- *"Implement an agreed set of biodiversity indicators to monitor and evaluate progress towards the 2010 targets, with the potential to communicate biodiversity problems effectively to the general public and to decision-makers and provoke appropriate policy responses*".

Meeting these commitments requires a critical evaluation of existing measures of the state of wildlife in the face of data uncertainty, critical gaps and sampling biases. Determining rates of change require that at least two measurements have been taken, yet many habitats, species, populations and ecosystems lack even a baseline assessment. Further, the best data to assess changes in biodiversity are biased towards charismatic vertebrate species, that are important for cultural reasons but do not generally provide other ecosystem services which transforming natural assets (soil, plants and animals, air and water) into resources for other components of the sytem. Ecosystem services are poorly defined but cover a range of aspects such as pollination, maintenance of soil fertility and health and water filtration, absorption and breakdown.

Not withstanding the paucity of data that exists for many non-vertebrate groups, analyses to assess changes in biodiversity need to be expanded to the vast diversity of invertebrate, fungal and microbial species that do play a major role in determining ecosystem integrity. Of the non-vertebrate groups, invertebrates offer the greatest scope for contributing towards the 2010 goal of assessing rates of biodiversity loss, particularly for groups such as butterflies (and other lepidopera) where population assessments are available for a variety of ecosystems in a number of regions of the world. Although they do not directly contribute much in the way of ecosystem services, butterflies are likely to respond more rapidly to change and be more representative than higher taxa of the status and trends of other invertebrates (Thomas, 2005).

1.1 Effects of climate and weather on butterfly populations

Global climates warmed by approximately 0.5 °C during the 20th Century, and are predicted to continue warming by up to 5.8 °C this century (Houghton *et al.*, 2001). For species to persist during rates of change unprecedented during the last millennium (Houghton *et al.*, 2001), local populations must either adapt (unlikely with rapid change), disperse to new regions where they can function, or be replaced by immigrant genotypes of the same species. Evidence from the Quaternary palaeontological record show that many taxa, including insects (Coope, 1995) and plants (Huntley, 1991) are predicted to shift their distributions to keep track of these climate changes, rather than adapt or go extinct.

Assessment of the impact of climate change on wildlife have been based on the response of four aspects of populations (de Groot, Ketner & Ovaa, 1995; Hughes, 2000; McCarty, 2001; Pollard & Relton, 1970; Walther *et al.*, 2002): changes in abundance or geographic distribution of species or the communities which they form (Hengeveld, 1995; Huntley, 1995; Parmesan *et al.*, 1999; Thomas *et al.*, 1999), changes in species' phenology (reviewed in Peñuelas & Filella, 2001), changes in inter-specific interactions (Harrington, Woiwod & Sparks, 1999) and changes in physiology (Körner, 1993). Reviews of empirical studies from around the globe also suggest that the impacts of climate change are already detectable on a range of biota (Parmesan & Yohe, 2003; Root *et al.*, 2003). In these meta-analyses, butterfly studies predominate among the evidence for the impacts of climate change on insects. The effects of weather and climate on three aspects of butterfly populations (phenology, abundance and distribution) are discussed in the following sections in more detail.

1.1.1 Phenology

The timing of biological events has been enthusiastically recorded since the late 18th Century (Clarke, 1936). This long history gives phenology a high prominence in the assessment of the 'fingerprint' of global climate change (Parmesan *et al.*, 2003; Root *et al.*, 2003); the earliest abundance and distribution monitoring schemes providing information on the distribution and abundance of species only date back to the 1960s. Changes have been detected in the timing of a wide range of phenological events from a range of taxonomic groups across large parts of the globe (Peñuelas *et al.*, 2001) and climatic effects have been implicated as the cause in many cases. Reports have demonstrated advances in the timing of growth and flowering of plants (Bradley *et al.*, 1999; Fitter & Fitter, 2002; Menzel & Fabian, 1999; Peñuelas, Filella & Comas, 2002), adult emergence of insects (Zhou *et al.*, 1995), migration in birds and insects (Inouye *et al.*, 2000; Sparks, 1999), and reproduction in amphibians and birds (Beebee, 1995; Crick *et al.*, 1997; Dunn & Winkler, 1999; Gibbs & Breisch, 2001).

As ectotherms, butterflies are predicted to benefit from the direct impact of a rise in temperature (Dennis, 1993). Positive effects are predicted for all stages of the life-cycle, leading to changes in the timing of phenological events. In particular, development rates of early stages are likely to be accelerated by warmer temperatures (Bryant, Thomas & Bale, 1997), thereby reducing exposure to predators (Pollard, 1979) and possibly leading to advanced eclosion as well as additional broods of bi- and multivoltine species such as *Coenonympha pamphilus* (Lees, 1962), *Aglais urticae* (Dennis, 1985b; Pullin, 1986), and *Parage aegeria* (Shreeve, 1986).

As predicted, warmer climates over the past two decades have coincided with changes in the timing of adult emergence of Lepidoptera across Europe. A survey of the average peak flight dates of 104 common species of Microlepidoptera in the Netherlands, revealed an advancement of 12 days over the period of 1975-1994 in response to warmer spring temperatures (Ellis, Donner & Kuchlein, 1997). Long-term data from a light-trapping network in Britain also demonstrate an increasing tendency, consistent with climate change, for some species of Macrolepidoptera to now emerge up to three weeks or more earlier than in the mid 1970s (Woiwod, 1997).

Analyses of butterfly phenology show similar patterns. A clear relationship between the first appearance of the male *Gonepteryx rhamni* and early spring temperatures has been demonstrated from one of the oldest, and longest, phenological records (Sparks & Carey, 1995). Sparks and Yates (1997) investigated the mean first appearance of a wider set of butterflies in Britain by examining data from the phenological reports of the Royal Meteorological Society (RMS) over the period 1883-1947 and from the current United Kingdom Butterfly Monitoring Scheme (UKBMS) for the years 1976-1993. They demonstrated a clear relationship between spring temperatures and timing of first appearance, and predict that butterflies will appear 5-7 days earlier for every 1°C of climate warming. Comparable effects of temperature on butterfly phenology are also apparent in the northwest Mediterranean Basin (Stefanescu, Penuelas & Filella, 2003). Over a fifteen year period (1988-2002) there has been a tendency for earlier first appearance dates in all 17 butterfly species examined, with significant advances in mean flight dates in 8 out of 19 species (Stefanescu *et al.*, 2003). These changes paralleled a 1 to 1.5°C increase in spring and early summer temperatures in the region over the same time period.

As well as the timing of adult appearance, voltinism of butterflies is closely associated with climatic conditions. Work suggests that the voltinism of several butterfly species can change rapidly in response to artificial selection (Lees, 1962, 1965; Lees & Archer, 1980; Pullin, 1986). Long-term monitoring has also shown that voltinism is flexible in response to annual fluctuations in climate (Pollard & Yates, 1993). Species such as *Coenonympha pamphilus* and *Polyommatus icarus* produce an additional generation in warm years. With successive warm years, there is evidence that normally univoltine populations (eg *Polyommatus icarus* in Scotland) are producing second generations with increasing frequency.

1.1.2 Abundance

Most European butterflies have discreet, non-overlapping generations due to the seasonality of temperate latitudes. Changes in the numbers of individuals in successive generations therefore describe the population dynamics of most species. For some species, population density remains fairly constant over time, whereas others show wide variation from one generation to the next (Pollard & Yates, 1993; Thomas *et al.*, 1998a). The dynamics of populations depend on a number of factors including climate, natural enemies, and the quality and distribution of natural resources. These factors effect intrinsic population parameters such as birth, death and migration rates through both density-dependent (varying according to local population density) and density-independent processes.

Density-dependent population regulation is hard to detect (Dempster & McLean, 1998) but evidence from long-term datasets suggests that it is a widespread phenomenon in the Lepidoptera (Pollard, Rothery & Yates, 1996; Woiwod & Hanski, 1992). Both resource limitation (Dempster & Pollard, 1981) and natural enemies (Dempster, 1983; Ehrlich, 1984) are thought to be important potential agents of density-dependence.

Density-independent factors such as weather conditions and climate affect butterfly population dynamics in a variety of ways. At the broad scale, butterfly populations fluctuate in synchrony over hundreds of kilometres (Pollard, 1991b; Pollard, Van Swaay & Yates, 1993; Pollard & Yates, 1993), presumably due to regionally correlated weather conditions. The degree of synchrony declines with distance between populations and depends on a species' mobility (Sutcliffe, Thomas & Moss, 1996). Population sizes of sedentary species are governed more by local habitat conditions than is the case for dispersive species that move more freely through the landscape. Local habitat conditions and butterfly dispersal enhance synchrony at local scales, up to 1-2km for sedentary species and up to around 4km for more mobile species (Sutcliffe *et al.*, 1996). Beyond this distance up to at least 200km, populations showed low but decreasing levels of synchrony. In a comparable study of moths and aphids, the large scale levels of synchrony were greater but declined more steeply, possibly due to the greater dispersal ability of these groups (Hanski & Woiwod, 1993).

Although synchrony in populations is apparent at large distances (Pollard, 1991b; Pollard *et al.*, 1993a; Pollard & Yates, 1993), generation-to-generation fluctuations in population size is greater towards a species' geographic range margin that it is towards the core (Thomas, Moss & Pollard, 1994). At geographic margins, populations become increasingly localised to favourable microclimates (Gutiérrez & Menéndez, 1995; Thomas, 1993) as climatic requirements limit their distribution (Dennis, 1993); such populations are less buffered against climatic variation.

The importance of weather on butterfly populations has been demonstrated through a range of studies of individual species. Through a variety of mechanisms, weather interacts with resources to change the carrying capacity of sites for butterfly populations from generation to generation. Inter-specific variation in the effects of weather is therefore apparent; the same weather produces contrasting effects among species due to differences in phenologies and habitat requirements (Pollard, 1988). Some generalities are apparent however. Most bivoltines, and some univoltine species become more abundant during warm, dry summers, because development is faster and there is more suitable weather for flight. Species such as *Gonepteryx rhamni*, *Inachis io* and *Aglais urticae* that overwinter as adults also benefit from warm summers. They tend to be more abundant in the year following favourable conditions, perhaps because an extended feeding period prior to hibernation increases over-winter survival (Pullin, 1987). In contrast, species like *Aphantopus hyperantus* and *Pararge aegeria*, which breed in partially shaded habitats, tend to be more abundant in years following cool, moist summers.

Conditions may affect particular butterfly populations directly through extremes such as flooding (Webb & Pullin, 1996) and unseasonal frosts (Singer & Thomas, 1996), but is more commonly through interactions with other species, such as predators, parasites and foodplants. Of greatest importance are weather effects on host plants since many aspects of the life history of butterflies are strongly related to the hostplants they use (Dennis *et al.*, 2004). In particular, a number of species are susceptible to drought effects on their foodplants. Autecological studies of *Maculinea arion*, *Lysandra bellargus*, *Aricia agestis* and the ant *Myrmica sabuleti* indicate that although warm summers are generally beneficial, drought can catastrophically reduce population size (Bourn & Thomas, 1993; Morecroft *et al.*, 2002; Thomas, 1983). The summer generation of small tortoiseshell *Aglais urticae* populations is more abundant when preceded by cool wet weather (Pollard, Greatorex-Davies & Thomas, 1997), because high water and nitrogen contents in its host plant *Urtica dioica* increase larval growth rate (Pullin, 1987). *Aphantopus hyperantus* populations contracted to core areas following drought conditions (Sutcliffe, Thomas & Peggie, 1997) and this is believed to be a more widespread phenomenon: several thermophilous species experienced population crashes on thin-soiled sites following some of the warmest (but driest) summers of recent years (Thomas *et al.*, 1998c).

It is clear that the main effects of weather on butterfly population abundance is through habitats and the condition of foodplants; other effects such as through interacting species (predators, parasites) and weather effects on butterfly behaviour are likely to be secondary (Dennis and Shreeve, 1991). For species that require a variety of habitat types for their persistence, the interaction between weather and population dynamics can be complex. *Euphydryas editha bayensis* has been the subject of intensive study in California by a number of researchers over a number of years. Its populations depend on complex interactions between rainfall, temperature and the timing of host plant growth and senescence (Dobkin, Olivieri & Ehrlich, 1987; Ehrlich *et al.*, 1980; Ehrlich *et al.*, 1975; Singer, 1972; Weiss *et al.*, 1993; Weiss, Murphy & White, 1988). The larvae of *E. editha bayensis* develop on *Plantago erecta*, an annual plant which germinates in winter and sets seed in early summer. The success or failure of pre-diapause larvae to reach their forth instar before host plant senescence is the major cause of mortality and therefore determines the adult population size the following year (Ehrlich *et al.*, 1975; Singer, 1972). Larval development rate and timing depend on the interaction between weather and the location where eggs are laid. In hot, dry years when host plants senesce rapidly, eggs laid on cooler north-facing slopes fair best. However, adults resulting from eggs laid on north-facing slopes in wet, cool years are too late to lay their eggs on non-senescent plants (Weiss & Murphy, 1988; Weiss *et al.*, 1993).

1.1.3 Distribution

The range and distribution of butterflies is closely linked to climate (Dennis, 1977; Stefanescu, Herrando & Paramo, 2004; Turner, Gatehouse & Corey, 1987) and rarely limited by hostplant distributions (Quinn, Gaston & Roy, 1998). It is physiological tolerances, life-history, behavioural and morphological factors that ultimately determine distributions at the large scale (Dennis, 1993); for ectotherms such as butterflies, most of these attributes are closely linked to aspects of weather and climate. Detailed investigation of the direct effects of climatic factors on physiology, behaviour etc. is unfeasible for all but a few species, but broad-scale expansion and contraction of species' distributions is the ultimate effect of major environmental change and is the focus of conservationists and policy makers.

The evolutionary history of British butterflies can be traced back through numerous glaciations, interglacials, stadials and interstadials that have occurred over the past two million years, but the arrival of contemporary butterfly species is believed to have occurred during the latter half of the last glacial stage (the Devensian), beginning some 15 000 years BP (Dennis, 1977, 1992). The main 'invasion' of butterflies to the British Isles occurred after the post glacial period after the Loch Lomond Stadial (or Younger Dryas) however, and the environmental changes during the subsequent Flandrian period (Holocene) have subsequently had profound effects on their distribution.

Following the retreat of ice and rising temperatures, temperate butterflies of open habitats expanded during the pre-boreal phase, but were then curtailed by woodland expansion during the late Boreal and Atlantic phases. In contrast, woodland butterflies that require mature tree hostplants spread widely during the Boreal and Atlantic climax forests. From around 5000 years BP, forest clearance began under Neolithic cultures and grew apace during the Bronze, Iron and later cultures with contrasting effects on open habitat vs woodland species. Despite the subsequent increases in the human population and resulting pressure on the land, agricultural practices were non-intensive and weeds were allowed to persist, extensive areas were left fallow, herb-rich pastures thrived and widespread enclosure created new semi-natural habitat in hedgerows (Mitchell, 1965).

The favourable habitat conditions and relative warmth during the medieval period (10th to 14th C) probably made this period the heyday for British butterflies. Even though the subsequent climatic downturns of the Sub-Atlantic and of the Little Ice Age (around 1450 till 1850) would have caused range retractions in both woodland

and open-habitat butterflies, the availability of suitable habitats in the south and lowland areas would have allowed populations to persist. Many British butterfly species that are dependent on early successional habitats were maintained by traditional agriculture and forestry practices during this period (Thomas, 1993). The major loss and degradation of habitats and the resulting decline in many specialist butterflies in Britain has occurred since the end of the eighteenth century as arable practices have intensified and urban areas have expanded. However, since the beginning of the 20th Century the climate in Britain has warmed, with rapid warming being apparent since around 1970, giving opportunity for ectotherms such as butterflies the potential to expand their distributions.

Consistent with predictions, certain butterflies have expanded northwards (Hill, Thomas & Huntley, 1999; Parmesan *et al.*, 1999) and to higher latitudes (Parmesan, 1996) and altitudes (Konvicka *et al.*, 2003) with warmer climates in recent decades. In Europe, a study of 35 butterfly species showed that more than 60% had shifted northwards by 35-240km during a period when temperature isotherms had shifted northwards by 120km (Parmesan *et al.*, 1999). In Britain, most butterflies have a southerly distribution and reach the northern limit to their ranges in Britain. These species would be expected to benefit from warmer temperatures over the last 30 years and indeed around 20% of butterflies have increased their ranges between the 1970s and late 1990s, with expanding species shifting northwards by 32-220km. Notable examples include *Polygonia c-album*, *Pararge aegeria*, *Thymelicus lineola* and *Aricea agestis* (Asher *et al.*, 2001). However, over the same time period, three-quarters of butterflies in Britain declined. For these species, the negative consequences of habitat loss have outweighed the positive effects of climate warming (Warren *et al.*, 2001). Sedentary species and those with specific habitat requirements have fared significantly worse than more mobile ones with more general requirements. Even the expansion of mobile species has been constrained by available habitat; they have not expanded into all the areas predicted to be suitable under the current, warmer climates (Hill *et al.*, 2002).

As predicted, most species are moving to keep track of changing climate rather than adapting *in situ*. However, for some species, there is evidence that ecological and evolutionary changes are accelerating the rate of expansion northwards. In expanding populations of *Pararge aegeria*, increased dispersal is associated with reduced investment in reproduction (Hughes, Hill & Dytham, 2003) and two bush cricket species have shown increased fractions of longer-winged, dispersive individuals in recently founded populations (Thomas *et al.*, 2001a). Such dispersive phenotypes will increase the speed at which species respond to changing environments. The expansion of two butterfly species (*Aricia agestis* and *Hesperia comma*) has similarly been accelerated by an increase in the variety of habitat types they can exploit.

Both long-term distributional changes (e.g. over last ~15k years Dennis, 1992) and recent expansions of range are strongly interlinked with changes in both climates and the extent and condition of habitats. Although studies have identified patterns of change amongst butterflies and other taxa that are consistent with a climate explanation at global (Parmesan *et al.*, 2003; Root *et al.*, 2003), European (Parmesan *et al.*, 1999) and British (Hill *et al.*, 2002; Warren *et al.*, 2001) scales, the interaction between climate suitability and the availability, spatial distribution and quality of habitat is key to determining species responses (Hill *et al.*, 2001; Hill *et al.*, 1999; Thomas *et al.*, 2001a; Thomas *et al.*, 1999; Warren *et al.*, 2001).

1.2 Effects of habitat on butterfly populations

Biodiversity is threatened by a range of environmental pressures (Sala *et al.*, 2000), including climate change, pollution, land-use change, the harvesting and persecution of species and the introductions of alien species and genotypes. There are few predictions about how the full range of pressures will impact on biodiversity (Petit *et al.*, 2001; Tilman *et al.*, 2001), but climate change and habitat destruction have been identified as two of the greatest threats to global biodiversity (Travis, 2003). For UK butterflies, habitat and climate have been identified as opposing forces for change (Warren *et al.*, 2001).

1.2.1 Habitat loss and modification

Over the last two centuries, the landscape of Britain has undergone profound changes. Until the 18th Century, the net effect of human impact was probably beneficial to butterflies. Many British species are dependent on early successional habitats which were maintained by traditional agriculture and forestry practices (Thomas, 1993). Since the end of the eighteenth century, land management practices have changed dramatically and human impact has become increasingly unfavourable, particularly during the last 50 years. Specialist butterflies have suffered through loss of rough marginal land, draining of wetlands, reclamation of heathland and improvement of downland. As the same time as the unprecedented loss of habitat since 1939 (Rackham, 1986), changes in habitat management have also affected the quality of remaining habitat. Decreases in grazing of chalk grassland and the decline in coppicing and clearance of woodlands have had the most notable effect (Warren, 1993a, b).

The long history of biological recording in Britain has allowed the effects of habitat changes over the last century and a half to be well documented. British Butterflies have been collected and studied since before the Victorian era, with the first account of their status being provided by Christopher Merrett in 1666. Systematic documentation of the status of British butterflies began with publication of the distribution of Lepidoptera within geographical provinces (Fust, 1868) and this was followed by the publication of incomplete distribution maps in 1949 (Ford, 1949). The first national census of the distribution of all British butterflies at the 10km x 10km square scale was published in the *Atlas of butterflies in Britain and Ireland* (Heath, Pollard & Thomas, 1984) and repeated during an intensive period of recording between 1995 and 1999 for *The millennium atlas of butterflies in Britain and Ireland* (Asher *et al.*, 2001). Together, these sources provide a detailed account of the changing status of British butterflies over the last 150 years.

Since recording began more than 150 years ago, five resident species have gone extinct: *Aporia crataegi* in the 1920s; *Lycaena dispar* in 1864; *Polyommatus semiargus* in 1904; *Maculinea arion* in 1979 although reintroduced since 1983; and *Nyphalis polychlorus* in the 1980s. The ranges of many other butterfly species have contracted dramatically over the same time period. Although the timing, rate and cause of changes vary markedly between species, most have suffered from habitat loss and degradation. Drainage of fenland was one of the first major causes of habitat loss with less than 3% of fens remaining by the early 1900s, accounting for the extinction of *L. dispar* and the restricted range of *Papilio machaon*. Similarly, drainage and destruction of bog vegetation seriously reduced the habitat of *Coenonympha tullia.*

Unlike other semi-natural habitats, the total area of woodland has been steadily increasing during the 20th Century. However, half the area of managed ancient woodland has been lost since the 1940s (Council, 1984), a habitat important for at least three-quarters of Britain's resident butterflies, and the sole habitat of 16 species (Asher *et al.*, 2001). In particular, the decline in coppice management of broad-leaved woodland has affected violet-feeding fritillaries such as *Argynnis adippe*, *Boloria euphrosyne*, *Boloria selene*, *Melitaea athalia* and two other species, the *Leptidea sinapis* and *Hamearis lucina*, that require clearing and open rides to persist.

The biggest change affecting butterflies during the last century has been the loss or agricultural improvement of semi-natural grasslands. Herb-rich grasslands are an important habitat for almost three-quarters of British butterflies (43 out of 59 resident species, Asher *et al.*, 2001), yet estimates suggest that 97% of the area of this habitat has been lost from lowland Britain since the 1940s (UK Biodiversity Steering Group, 1995). Ploughing, fertilising and cultivation has typically replaced flower-rich swards, rich in a range of larval foodplants, with vegetation dominated by a narrow range of grasses. Butterflies affected by the wholesale loss and damage to semi-natural grasslands include *Hesperia comma*, *Cupido minimus*, *Pyrgus malvae*, *Plebeius argus*, *Polyommatus bellargus*, *Euphydryas aurinia* and *Melitaea cinxia* and to a less extent species such as *Erynnis tages*, *Callophrys rubi*, *Aricia artaxerxes*, *Polyommatus coridon* and *Hipparchia semele.*

There is no longer dramatic loss of semi-natural habitats in Britain, and the area covered by such habitats has remained relatively stable over the past two decades (Haines-Young *et al.*, 2000). The threats to habitats in Britain and much of north-west Europe now come from wide-ranging effects that affect quality rather than the quantity. The most notable threats come from nutrient enrichment (Dalton & Brand-Hardy, 2003), succession and overgrazing (Haines-Young *et al.*, 2000), and the impact of alien species and climate change. Given that widescale habitat recreation is unlikely in densely populated countries such as Britain, improvements in the ecological quality of arable land is seen as having great potential for wildlife.

1.2.2 Arable habitats

Agricultural modernization has caused a widespread decline of organisms in agricultural landscapes across Europe (Benton, Vickery & Wilson, 2003; Krebs *et al.*, 1999). Most focus has been on reductions in the abundance of some arable weeds (Preston, Pearman & Dines, 2002; Robinson & Sutherland, 2002) and birds (Chamberlain *et al.*, 2000; Siriwardena *et al.*, 1998) but concurrent losses in other taxa are likely (Robinson *et al.*, 2002).

Although arable habitats generally support an impoverished butterfly fauna, field margins and other uncultivated areas are often the only suitable habitat for woodland and grassland species in intensive arable landscapes. They provide both breeding sites and vital links between suitable habitat patches (Dover, Clark & Rew, 1992) as well as other features that are important for butterflies, e.g. shelter, isolation and nectar resources (Clausen, Holbeck & Reddersen, 2001; Dover, 1996). Hedgerow structure, adjacent land use and floral diversity of field margins also have an important effect on butterfly numbers (Dover, Sparks & Greatorex-Davis, 1997; Sparks & Parish, 1995), as does the availability of perennial nectar sources (Feber, Smith & MacDonald, 1996).

Given the mounting evidence of the negative effects of current agricultural practices on wildlife, proposals for novel agricultural practices are subject to great scrutiny, not least the potential for wide-scale planting of genetically modified crops. By late 1998, the first genetically modified herbicide-tolerant (GMHT) crops had cleared most of the regulatory hurdles needed before commercial growing could be permitted in the U.K. Varieties of these crops, maize *Zea mays* L., beet *Beta vulgaris* L., spring oilseed rape and winter oilseed rape, or canola *Brassica napus* L. have been modified to make them tolerant to broad spectrum herbicides. Maize and oilseed rape varieties were made resistant to glufosinate-ammonium and the beet to glyphosate. While these crops have been assessed as safe in terms of human health and direct impacts upon the environment, insufficient research had been conducted on the potential effects on wildlife from how these crops were managed. The four GMHT varieties that have been developed all have the potential to allow greater flexibility in the timing of herbicide use (Dewar *et al.*, 2002; Firbank & Forcella, 2000), to facilitate the control of herbicide-tolerant weeds and to reduce reliance on persistent and relatively hazardous chemicals. The regimes used for GMHT versus conventional varieties differ in timing and specificity; the herbicides glyphosate and glufosinate-ammonium are broad-spectrum and can be applied later in the development of tolerant crops than herbicides applied to non-tolerant crops.

Concerns have been raised that this change in weed management might exacerbate the recent declines in biodiversity of arable fields, but this indirect risk to the environment of using such herbicides on crops had not been considered specifically under the existing regulatory system. Control of weeds in GMHT crops tolerant to broad-spectrum herbicides might be so efficient that it could help to clean up previously weedy fields (Watkinson *et al.*, 2000), worsening long-term declines in weeds and reduce numbers of invertebrates that feed on them, together with their predators (hails 2000). By contrast, GMHT crops might ameliorate affects on wildlife by delaying and reducing herbicide use (Firbank & Forcella, 2000) or allowing weeds and associated wildlife to remain in fields for longer (Dewar *et al.*, 2002).

The UK Farm Scale Evaluations (FSEs) were established because of concerns that the introduction of genetically modified herbicide-tolerant (GMHT) crops could have negative impacts upon farmland biodiversity (Firbank *et al.*, 2003). For each of the four crop (beet, maize, spring and winter oilseed rape), the FSE aimed to test the null hypothesis that there is no difference between the management of GMHT varieties and that of comparable conventional varieties in their effect on the abundance and diversity of arable plants and invertebrates. Full details of the experimental design and statistical analysis are given by Perry *et al.* (2003).

To assess the effect of management of GMHT crops on wildlife, indicator taxa were chosen to represent larger groups of organisms or to identify ecological processes that may result in important changes over larger scales of time and space. Farmland can support a substantial proportion of the UK butterfly fauna (Feber & Smith, 1995), but rarely does; its suitability as habitat is highly dependent upon management (Feber *et al.*, 1996). The differences in the timing and types of herbicides applied to

GMHT versus conventional crop varieties are likely to have marked effects on the flora of arable fields and surrounding margins. Changes in the abundance and distribution of plant species may in turn affect higher trophic levels such as associated invertebrates. As nectar feeders, butterflies will be most sensitive to effects on the abundance of flowering weeds in arable landscapes. Although butterflies can travel considerable distances in search of resources (Pollard & Yates, 1993), any changes to agricultural practices on a broad geographic and temporal scale is likely to have profound effects on even such mobile species.

1.3 Aims and structure of the thesis

This thesis is concerned with the application of butterflies as indicator species to assess the effect of habitat modification and climate change. Chapters two and three investigate the effects of climate and weather on the spatial and temporal trends in the phenology of British butterflies. The recording of the timing of naturally recurring events has a long history and provides some of the longest running biological time series. Analysis of such phenology data has been widely used to provide evidence of the impact of climate change on biodiversity (Hughes, 2000; Parmesan *et al.*, 2003; Peñuelas *et al.*, 2001). Chapter two utilises extensive data on the flight periods of butterflies from the Butterfly Monitoring Scheme, the UK's national monitoring network. The primary aim is to detect temporal trends in the timing of the first and peak appearance dates and length of flight-periods of adult butterflies over the period 1976-98 and relate these to changes in weather over the same period. First appearance dates are used in most studies of phenology, but these dates may represent atypical, extreme events and not correspond to the average timing of the overall population. A secondary aim, therefore, is to examine the inter-relation between timing of first and peak appearance.

Few phenology studies have examined spatial trends in phenological events but, given the often-reported strong relationship between timing and temperature, it is expected that events such as the appearance of adult butterflies will occur later in the north of their range than in the warmer south. However, previously published data for the butterfly *Pyronia tithonus* (Brakefield, 1987; Pollard, 1991a) show no clear trend in the timing of the flight period with latitude over its British range.

Conversely, anecdotal evidence suggests that other butterfly species fly later in the north, as expected (Warren, 1992). The aim of chapter 3 is to quantify spatial trends in butterfly phenology using data from a major survey of their distribution in Britain, to determine the extent to which appearance is synchronized across regions.

Chapter four examines the intra-annual variation in niche requirements and population dynamics of a habitat specialist species in response to seasonal variation in climate. It has been established that at higher latitudes and altitudes in Europe, the immature stages of many ground-dwelling species of insect become restricted to patches of habitat where the micro-climate is especially hot, such as the earliest seral stages of woodland, heath and grassland (Thomas, 1993; Thomas *et al.*, 1999). In contrast, the same species occupy different and broader niches near the centre of range. Recent field evidence (Thomas *et al.*, 2001a) has shown that certain types of thermophilous insects have expanded to occupy broader niches near their northern range margins during some of the warmer summers of recent years. Understanding the mechanisms responsible for these shifts is important to predict how species' populations may respond to climate warming (Warren *et al.*, 2001) and to ensure that appropriate management is applied to maintain optimal habitat structures for threatened species under different local climates (Thomas *et al.*, 2001b; Thomas *et al.*, 1998b).

Bivoltine butterfllies, that have two generations per year, experience larger and more predictable alterations of climate during their two development periods and provide a useful system for understanding these processes. This paper examines the niche requirements of the summer and autumn/spring generations of the bivoltine butterfly *Polyommatus bellargus* Rott. whose autumn-spring larvae are known to exploit only a minority of the foodplants (*Hippocrepis comosa*) within their sites, being restricted to the hottest available spots (Thomas, 1983; Thomas *et al.*, 2001b). However, the summer niche has not been studied. Given the different climatic conditions likely to be experienced by the two generations, we predict that the niches utilised by the summer compared to spring/autumn butterflies will differ markedly with likely knock-on consequences for the site carrying capacities at different times of the year for this species.

Chapter five models the effect of weather on the size of British butterfly populations and the future effects of climate change. The UK Butterfly Monitoring Scheme is one of the longest-running time series of insect populations and is used to test the association between butterfly abundance and weather and climate. In a preliminary analysis, Pollard (1988) used the BMS data from 1976 to 1986 to test for significant associations between butterfly abundance and climatic variables. The most striking association was an increase in abundance with warm, dry summers. There was also an association of increased numbers and high rainfall early in the previous year, but winter temperature and rainfall showed no strong associations with butterfly abundance. This paper extends this approach further. Given the length of the time series available, models are developed using the first part of the series (1976-90) and then tested with observed weather patterns to predict butterfly numbers in the later period (1991-1997). The predictions were then compared with the observed data. This independent test is important for verifying the models, an approach that is rarely used in similar studies. Where good predictive success is achieved with models relating fluctuations in butterfly populations to changes in weather conditions, past butterfly numbers are predicted using historical weather data spanning the last two centuries and compated with documented declines and expansions of populations; a further test of the models. Models are also used to predict future trends in population levels using a range of climate scenarios.

Chapter six details the response of butterflies and a range of other fauna, and flora associated with field margins to a new agriculture technique – Genetically Modified Herbicide-Tolerant (GMHT) crops. Field margins are an important resource for plants and animals in the farmed landscape (Marshall & Moonen, 2002) and are strongly influenced by the management of the adjacent cropped areas of fields. The aim of this paper is to compare the effects of management of GMHT and non-GMHT crops on key groups of flora and fauna in adjacent field margins; effects within the cropped area of the field are reported in accompanying papers on vegetation (Heard *et al.*, 2003a; Heard *et al.*, 2003b) and invertebrates (Brooks *et al.*, 2003; Haughton *et al.*, 2003). For beet (*Beta vulgaris* ssp. *vulgaris* (L.), maize (*Zea mays* (L.) and spring oilseed rape (*Brassica napus* ssp. *Oleifera* (DC.) crops, a specific null hypothesis is tested: that there is no difference between the management of GMHT varieties and that of comparable conventional varieties in their effects on the cover, flowering and seeding of vegetation, and the abundances of bees, butterflies, slugs and snails, and other invertebrates in the field margins. Where treatment effects are significant, their magnitude is estimated and the implications for farmland biodiversity of growing these GMHT crops is discussed.

2 Phenology of British butterflies and climate change

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2.1 Abstract

Data from a national butterfly monitoring scheme were analysed to test for relationships between temperature and three phenological measures, duration of flight period and timing of both first and peak appearance. First appearances of most British butterflies has advanced in the last two decades and is strongly related to earlier peak appearance and, for multi-brooded species, longer flight period. Mean dates of first and peak appearance are examined in relation to Manley's central England temperatures, using regression techniques. We predict that, in the absence of confounding factors, such as interactions with other organisms and land-use change, climate warming of the order of 1°C could advance first and peak appearance of most butterflies by 2 to 6 days.

2.2 Introduction

Since the late 18th Century, the timing of biological events has been enthusiastically recorded (Clarke, 1936). With increasing evidence for human-induced global climate change (Houghton *et al.*, 1996), phenology has taken on greater importance as an indicator of species' response to the changing environment. In order to predict future responses of species to a changed climate we first need to discover how species have responded to climate in the past. Studies covering a diverse range of taxonomic groups and biological events have demonstrated strong relationships between phenological events and climate. Analyses of long-term datasets have shown earlier nesting and arrival from migration for birds (Crick *et al.*, 1997; Sparks, 1999), an extended growing season across Europe (Menzel *et al.*, 1999) and advanced first flowering of plants (Fitter *et al.*, 1995). Although invertebrates make up a large fraction of terrestrial biodiversity (Groombridge, 1992), datasets on their phenology are limited. However, analyses of long-term phenological records have shown that climate warming of the order of 3°C could advance butterfly appearance by two to three weeks (Sparks & Carey, 1995; Sparks & Yates, 1997).

Butterflies are good organisms for studying the effects of environmental change. As poikilothermic animals their activity is closely controlled by weather and many species are constrained by climate (Dennis, 1993; Pollard, 1979, 1988; Turner *et al.*, 1987), mostly occupying a small part of the range of their host plants (Dennis & Shreeve, 1991; Quinn *et al.*, 1998). They are fecund, have high dispersal ability and an annual or more frequent life cycle, so changes in abundance and distribution can be detected over a relatively short time scale (Parmesan, 1996; Pollard & Yates, 1993). Butterflies are also an ideal group for phenological recording, being conspicuous and having a high public profile. Also, there is a large amount of data on the flight-periods of butterflies in the British Butterfly Monitoring Scheme (BMS), a national monitoring network.

A previous study has used data from the BMS to demonstrate the effects of spring temperatures on the timing of first and mean appearance for twelve species of British butterflies (Sparks & Yates, 1997) between 1976 and 1993. In the current paper, we examine the effects of temperature on the phenology of 35 British butterflies over a longer time period, 1976-1998, using data from the BMS. The main aims of this study are to (1) detect temporal trends in timing of first and peak appearance and flight-period length, (2) examine inter-relationship between timing of first and peak appearance and flight-period length, (3) predict the effects of temperature on first and peak appearance. Latin names have been used throughout this paper; common English names are listed in Table 1.

2.3 Methods

2.3.1 Butterfly Monitoring Scheme (BMS)

The BMS was established in 1976 to monitor the abundance of butterflies in the British Isles (Pollard, 1977). The methods used in the BMS have been described in detail elsewhere (Pollard & Yates, 1993). Briefly, at over 100 sites throughout the country, observations are taken at least weekly from April until September each year. Butterflies are counted on fixed transect routes under defined weather conditions. We have abstracted data on 35 out of a total of 51 species covered by the BMS for the years 1976 until 1998. Species present in less than 20 years or with a mean of less than five sites recorded per year were excluded. Data for each species have been summarised for each year to provide simple parameters to describe flight-period characteristics. The following measures have been derived across all sites: mean first appearance date, mean peak abundance date, mean length of flight period and mean number of sites. Parameters were calculated for 30,710 individual flight periods. For individual species, the number of flight periods ranges from 115 for *Lysandra bellargus* to over 1700 for *Maniola jurtina.*

To simplify comparison between species and because we do not want to make any distributional assumptions, we measure duration of flight period as the interval between the first and last counts. Previous studies used the standard deviation of flight days as a measure of the length of the flight period (Brakefield, 1987; Pollard, 1991a). They suggested that the interval between first and last counts, as used in this analysis, was variable and liable to distortion by a single individual which lived a week or more longer than the rest of its cohort. However, this is unlikely to seriously effect the estimates derived from a large number of flight periods as used here.

Butterfly species that are migrant in the UK such as *Vanessa atalanta* and *Cynthia cardui* have been included in the following analyses. Although they do not emerge from pupae in this country, timing of first and peak appearance and duration of flight period at BMS sites is of interest. Trends over time and temperature effects have been demonstrated in timing and patterns of migrating birds in Britain (Sparks, 1999).

2.3.2 Temperature data

The Central England Temperature (CET) series constructed by Manley (Manley, 1974), provides monthly mean surface air temperatures for a region representative of central England for each year from 1659 to 1973. The series was extended to 1991 by Parker *et al.* (1992) and is now regularly updated by the Meterological Office Hadley Centre (http://www.cru.uea.ac.uk/~mikeh/datasets/uk/cet.htm). Data from the CET series have been shown to be broadly representative of temperature in other parts of the UK (Duncan, 1991).

2.3.3 Analysis

Trends over time in mean first appearance, peak appearance and length of flight period were examined using regression with year as the explanatory variable. The relationship between mean first appearance date and other measures of flight periods (mean flight date and length of flight period) were examined using correlation coefficients to test for linear trends.

A stepwise regression approach was used to relate changes in first and peak appearance to temperature data. Potential explanatory variables included monthly temperatures for the year preceding overall mean first and peak appearance dates and a year index (for unexplained changes over time). For example, for a species such as *M. jurtina* with a mean first appearance month of June, monthly temperature for July-December of the previous year and Jan-June of the current year were included. Only significant months were included in the final model. Weather in both the current and previous year may be important for the timing of appearance of butterfly species. Pollard (1988) has shown a positive association between temperature in the previous summer and current butterfly numbers, particularly for spring-flying species such as *Erynnis tages* and *Pyrgus malvae*. Smoothed lines on figures are produced using the LOWESS (locally weighted scatterplot smoother) process.

2.4 Results

2.4.1 Trends over time

Between 1976 and 1998 central England spring temperature increased by approximately 1.5°C and summer temperature by approximately 1°C (Figure 1), even though 1976 was the warmest summer. Table 1 summarises trends in mean first appearance date, peak flight date and length of flight period over the same time period. The first appearance of most species (26 species) is earlier in recent years. This relationship is significant for 13 species, most notably *Anthocharis cardamines* and *V. atalanta* where appearance has advanced by 17.5 and 36.3 days respectively over the period 1976 to 1998 (Figure 2). Mean peak appearance is also earlier in recent years for most species (27 species), but the relationship is significant for only three species. Twelve species have a significant relationship with mean flight period length over time. With the exception of *Hipparchia semele*, this relationship is for a longer flight period in later years. The most marked increase in duration of flight period over the period 1976 to 1998 are for *V. atalanta* (39.8 days), *Pieris napi* (23.5 days), *L. bellargus* (30.6 days) and *Polygonia c-album* (30.1 days).

From the significant relationships of mean first appearance and mean length of flight period over time, a number of species show the same pattern: earlier first appearance and longer flight period (Table 1). This effect is strongest in the *P. napi* and *V. atalanta* (Figure 2), but is also apparent in *L. bellargus*, *Gonepteryx rhamni*, *P. c-album*, *Erynnis tages*, *Inachis io* and *Aphantopus hyperantus*.

2.4.2 Relationships with first appearance

All 35 species analysed have a positive correlation coefficient between mean first appearance date and mean peak flight date (Table 2). With the exception of *L. bellargus*, *Coenonympha pamphilus* and *Pararge aegeria*, the relationship is significant: for all univoltines the relationship is highly significant. Almost all species (32) also have a negative relationship between mean first appearance date and length of flight period. Early first appearance results in an extended flight period and for the majority of species the relationship is significant: for all multivoltine species the relationship is highly significant.

There is a clear relationship between three attributes of flight period: dates of first and peak appearance and length of the flight period. For single-brooded species such as *Thymelicus sylvestris*, *Limenitis camilla* and *Callophrys rubi* early first appearance results in an early peak flight date, but no lengthening of the flight period. For multi-brooded species such as *P. aegeria*, *L. bellargus* and *P. napi* early first appearance results in a longer flight period, but not a significantly earlier peak flight date (Figure 3).

2.4.3 Relationships with weather

Table 3 gives a summary of regression models relating mean first appearance and mean peak flight date to temperature. For almost all species, there is a highly significant relationship with weather of both first appearance date and peak flight date. Almost all temperature components had a negative effect; warmer weather tended to produce earlier first and peak appearance. The most striking result is that many species showed earlier first and peak appearance with warm spring temperature, particularly February (e.g. *A. cardamines* and *Polyommatus icarus*,

Figure 4), or with summer temperature (e.g. *Melanargia galathea* and *M. jurtina*, Figure 4). Trend with calendar year was apparent for a number of species, reflecting changes over time not accounted for by the examined temperature variables. Where trend over time was apparent, the effect was negative, suggesting that these species have appeared earlier. In the absence of trend the more reliable models suggest that a 1°C rise in temperature could advance both mean first and peak appearance by 2-10 days.

2.5 Discussion

The foregoing analyses support recent research suggesting that the timing of many natural events is occurring earlier in recent years (e.g. Crick *et al.*, 1997; Menzel *et al.*, 1999) and that climate is the most likely cause of change (Beebee, 1995; Sparks & Crick, 1999; Sparks, 1999; Sparks, Carey & Combes, 1997). We have demonstrated that first appearance of most British butterflies has advanced over the last two decades and that there is a strong relationship between these changes and temperature. The Butterfly Monitoring Scheme is probably the longest running such scheme in the World. However, 23 years is still a relatively short time series with which to detect change and we are excited with the consistency of results reported here.

Together with early emergence, there is a concurrent advancement of peak appearance and longer flight duration. Therefore, advanced first appearance results in a more asymmetrical flight period distribution rather than a forward shift: for univoltine species the tail of the flight period is lengthened; for multivoltine species extra generations per year may be produced. As well as increasing the duration of each generation, earlier appearance may allow those species capable of multivoltinism to increase the frequency with which this occurs. Voltinism of several butterfly species can change in response to artificial selection (Lees, 1962, 1965; Lees *et al.*, 1980; Pullin, 1986), and it is likely that similar changes would occur with climate change. Species such as the *P. icarus* and *C. pamphilus* have flexible voltinism in southern Britain; in warm years there are two generations. Certain species which are univoltine in Britain, have more than one generation in warmer parts of their range, e.g. *I. io* has two generations in central Europe (Pullin, 1986). Duration of flight-period has also been shown to be longer in open (grassland) compared to closed (woodland) biotopes for *M. jurtina* and *C. pamphilus* (Pollard & Greatorex-Davies, 1997). Other implication of earlier emergence of British butterflies may include increased abundance and range expansion northward for species currently restricted geographically by climate (Pollard, Moss & Yates, 1995). Pollard (1991a) has shown a longer flight period and earlier mean flight date for the *Pyronia tithonus* during a period of range expansion.

Clearly, early emergence is an effective measure of other flight period characteristics, but it is not clear how advanced first appearance is related to population abundance. This question is complicated by the probabilistic argument that increased abundance in a given year may lead to first appearance being observed earlier, i.e. less chance of an isolated, early individual being overlooked. This is only likely to be a problem with less apparent species undergoing large annual population changes. Resolving the link between population size and first observation is not trivial and is probably best approached through simulation studies.

Regression analyses suggest a relationship between temperature and timing of first and peak appearance for most species. In particular, a positive effect of February temperature on first appearance was detected for the majority of species. Over the last twenty years, this month has shown greatest variation in temperature in the UK compared to other periods of the year. Although this may increase the likelihood of detecting an effect, spring is a critical time for larval development for many species and increased temperatures over this period are likely to advance emergence. Whilst some of the effects reported may be spurious due to the large number of comparisons being made, the dominance of negative relationships with spring temperatures (warmer springs linked to earlier appearance) cannot be denied. Predictions of advanced timing of appearance of British butterflies mostly vary between 1-10 days per °C. With each additional °C, the advanced nesting of long-tailed tit, *Aegithalos caudatus*, by 4.1 days, early arrival of blackcap, *Sylvia atricapilla*, from migration by 2.3 days and early leafing of oak, *Quercus robur*, by 7.8 days reported by Sparks and Crick (1999) also fall within this range. However, there are clearly a large number of confounding factors such as food supply, desiccation, predation, possibly most strongly land use change, which will modify the impact of climate change as suggested here.

The effects of temperature on other aspects of butterfly ecology such as diversity, range and abundance are well recognised (Dennis, 1993; Pollard, 1988; Turner *et al.*, 1987). Most predicted effects of climate change on butterflies are likely to be positive, mainly through the increase in flight-dependant activities such as mate-location, egg laying, nectaring, predator-evasion and dispersal (Dennis *et al.*, 1991). However, the propensity for drought associated with climate change predictions may have negative effects on some butterfly species. Dry summers are likely to affect egg survival, host plant growth and habitat structure (Dennis *et al.*, 1991; Pollard, 1988).

Interactions with other organisms as well as abiotic factors add further complexity to prediction of the response of individual butterfly species to increased temperatures (Harrington *et al.*, 1999). A driving force for climate warming is elevated levels of 'greenhouse gases', notably CO_2. As well as indirectly raising temperature, increased levels of this gas have been shown to raise photosynthetic activity (Keeling, Chin & Whorf, 1996). This in turn can affect plant-insect herbivore interactions (Bazzaz, 1990; Bezemer & Jones, 1998). Studies of Lepidoptera, however, have shown that the *A. cardamines* is likely to remain synchronised with one of its foodplants, garlic mustard *Alliaria petiolata* (Sparks and Yates, 1997) and a similar synchrony is apparent between winter moth *Operophtera brumata* (L.) larvae and oak budburst (Buse & Good, 1996).

Most studies of the effects of climate change on the timing of biological events have utilised avian and botanical datasets. This paper has shown that historical change in the phenology of butterfly species demonstrate an impressive response to only two decades of climate change.

Table 2.1. Trends over time (1976-1998) for mean first appearance, peak flight date and length of flight period. Table reports R^2 and significance values from regressions of flight period characteristics on year. Values for change per decade are number of days. (ns $p > 0.05$, * $0.05 > p > 0.01$, ** $0.01 > p > 0.001$, *** $0.001 > p$).

		Mean first appearance date			Mean peak appearance date			Mean length of flight period		
		R^2 (%)	sig.	Change (+10yr)	R^2 (%)	sig.	Change (+10yr)	R^2 (%)	sig.	Change (+10yr)
a) species with one flight period each year										
Thymelicus sylvestris (Poda.)	small skipper	0	ns	-1.4	0	ns	-1.6	0	ns	-0.9
Ochlodes venata (Br. & Grey)	large skipper	11	ns	-3.7	1	ns	-2.3	31	**	4.4
Erynnis tages (L.)	dingy skipper	17	*	-5.1	6	ns	-3.4	18	*	4.3
Pyrgus malvae (L.)	grizzled skipper	28	**	-6.0	11	ns	-4.4	12	ns	3.4
Anthocharis cardamines (L.)	orange tip	50	***	-7.6	39	**	-7.0	1	ns	1.2
Callophrys rubi (L.)	green hairstreak	23	*	-4.3	21	*	-4.7	0	ns	-0.2
Quercusia quercus (L.)	purple hairstreak	0	ns	-1.7	7	ns	-3.8	0	ns	-0.4
Lysandra coridon (Poda)	chalk-hill blue	0	ns	0.0	0	ns	-0.3	0	ns	0.0
Limenitis camilla (L.)	white admiral	7	ns	-3.1	4	ns	-2.5	0	ns	0.4
Clossiana selene (D. & S.)	small pearl-bordered fritillary	0	ns	-1.8	0	ns	-0.5	0	ns	1.6
Clossiana euphrosyne (L.)	pearl-bordered fritillary	27	**	-6.7	11	ns	-4.7	0	ns	1.8
Argynnis aglaja (L.)	dark green fritillary	0	ns	0.0	0	ns	-0.5	0	ns	-1.8
Argynnis paphia (L.)	silver-washed fritillary	12	ns	-4.4	0	ns	-2.3	14	*	3.5
Melanargia galathea (L.)	marbled white	23	*	-4.6	9	ns	-3.2	6	ns	1.7
Hipparchia semele (L.)	grayling	0	ns	0.4	4	ns	-2.7	30	**	-4.6
Pyronia tithonus (L.)	hedge brown (gatekeeper)	0	ns	-1.6	2	ns	-2.0	0	ns	-1.1
Maniola jurtina (L.)	meadow brown	1	ns	-2.0	0	ns	-0.8	6	ns	2.1
Aphantopus hyperantus (L.)	ringlet	23	*	-4.6	10	ns	-3.2	28	**	4.6
b) species with two flight periods, but only one generation										

		Mean first appearance date			Mean peak appearance date			Mean length of flight period		
		R^2 (%)	sig.	Change (+10yr)	R^2 (%)	sig.	Change (+10yr)	R^2 (%)	sig.	Change (+10yr)
Gonepteryx rhamni (L.)	brimstone	24	*	-5.3	0	ns	-2.6	20	*	5.7
Inachis io (L.)	peacock	36	**	-12.8	15	*	-8.1	18	*	10.4
c) species with two or more flight periods representing different generations										
Pieris brassicae (L.)	large white	0	ns	3.7	8	ns	5.2	0	ns	-1.9
Pieris napi (L.)	green-veined white	32	**	-6.6	0	ns	0.6	45	***	10.2
Pieris rapae (L.)	small white	3	ns	3.6	13	ns	5.6	0	ns	-2.1
Lycaena phlaeas (L.)	small copper	0	ns	0.1	0	ns	0.3	0	ns	1.1
Aricia agestis (D. & S.)	brown argus	0	ns	2.2	0	ns	0.9	0	ns	-2.4
Polyommatus icarus (Rott.)	common blue	0	ns	0.2	0	ns	1.3	0	ns	0.1
Lysandra bellargus (Rott.)	Adonis blue	15	*	-11.2	2	ns	-5.0	15	*	13.3
Celastrina argiolus (L.)	holly blue	0	ns	-2.9	0	ns	-4.1	0	ns	3.6
Vanessa atalanta (L.)	red admiral	40	***	-15.8	0	ns	-1.6	38	**	17.3
Cynthia cardui (L.)	painted lady	5	ns	-8.3	0	ns	-2.3	5	ns	9.8
Aglais urticae (L.)	small tortoiseshell	0	ns	-2.5	0	ns	-0.7	0	ns	1.8
Polygonia c-album (L.)	comma	36	**	-13.2	0	ns	-1.2	24	*	13.1
Pararge aegeria (L.)	speckled wood	13	ns	-5.2	6	ns	5.2	26	**	8.9
Lasiommata megera (L.)	wall brown	0	ns	2.9	4	ns	-3.4	7	ns	-6.1
Coenonympha pamphilus (L.)	small heath	0	ns	-1.0	0	ns	1.6	0	ns	1.2

Table 2.2. Correlation between mean first appearance 1976-1998 and i) peak flight date ii) mean length of flight period. (ns p > 0.05, * 0.05 > p > 0.01, ** 0.01 > p > 0.001, *** 0.001 > p).

	peak flight date		length of flight period	
a) species with one flight period each year				
Thymelicus sylvestris	0.92	***	0.08	ns
Ochlodes venata	0.93	***	-0.43	*
Erynnis tages	0.94	***	-0.66	***
Pyrgus malvae	0.87	***	-0.21	ns
Anthocharis cardamines	0.96	***	-0.13	ns
Callophrys rubi	0.93	***	0.08	ns
Quercusia quercus	0.90	***	-0.36	ns
Lysandra coridon	0.91	***	-0.69	***
Limenitis camilla	0.95	***	0.01	ns
Clossiana selene	0.91	***	-0.24	ns
Clossiana euphrosyne	0.90	***	-0.34	ns
Argynnis aglaja	0.82	***	-0.46	*
Argynnis paphia	0.90	***	-0.13	ns
Melanargia galathea	0.93	***	-0.17	ns
Hipparchia semele	0.88	***	-0.35	ns
Pyronia tithonus	0.89	***	-0.14	ns
Maniola jurtina	0.85	***	-0.73	***
Aphantopus hyperantus	0.95	***	-0.54	**
b) species with two flight periods, but only one generation				
Gonepteryx rhamni	0.59	**	-0.55	**
Inachis io	0.67	***	-0.93	***
c) species with two or more flight periods representing different generations				
Pieris brassicae	0.61	**	-0.90	***
Pieris napi	0.41	*	-0.83	***
Pieris rapae	0.60	**	-0.88	***
Lycaena phlaeas	0.57	**	-0.90	***
Aricia agestis	0.72	***	-0.91	***
Polyommatus icarus	0.51	*	-0.91	***
Lysandra bellargus	0.34	ns	-0.83	***
Celastrina argiolus	0.77	***	-0.67	***
Vanessa atalanta	0.54	**	-0.96	***
Cynthia cardui	0.76	***	-0.91	***
Aglais urticae	0.61	**	-0.86	***
Polygonia c-album	0.54	**	-0.87	***
Pararge aegeria	0.26	ns	-0.93	***
Lasiommata megera	0.58	**	-0.87	***
Coenonympha pamphilus	0.39	ns	-0.76	***

Table 2.3. Summary of regression models relating mean first appearance and mean peak flight date to temperature data. Terms are included in the order they entered the model; values represent CET month number with those from the previous year being negative, ie 2 = February of current year, -11 = November of previous year. All coefficients with temperature are negative, except those marked with $^{+}$. The figures in parenthesis adjacent to 'Yr' indicate the per year coefficient associated with the significant trend over time. Values for change per +1°C are number of days. Number of years in all models, n=23. (ns $p > 0.05$, * $0.05 > p > 0.01$, ** $0.01 > p > 0.001$, *** $0.001 > p$).

	First appearance date				Peak flight date			
	Terms included	R^2 (%)	sig.	Change (+1 °C)	Terms included	R^2 (%)	sig.	Change (+1 °C)
a) species with one flight period each year								
Thymelicus sylvestris	6,2	82	***	-4.9	6,7,2,1^{+}	85	***	-6.7
Ochlodes venata	2,6	79	***	-5.1	6,2	73	***	-5.0
Erynnis tages	2,4,1	78	***	-6.2	4,5	73	***	-8.7
Pyrgus malvae	2,Yr(0.05),-9^{+}	69	***	0.7	2,-9^{+}	67	***	0.1
Anthocharis cardamines	Yr(-0.08),2	75	***	-1.7	2,Yr(-0.05),-11^{+},4,1,5	91	***	-5.7
Callophrys rubi	2,Yr(-0.04),-8^{+}	83	***	-1.8	2,Yr(-0.04),-7	79	***	-2.7
Quercusia quercus	6,2	62	***	-2.1	2,6	51	**	-4.9
Lysandra coridon	6,3	73	***	-7.7	6,8	68	***	-7.3
Limenitis camilla	6,2	65	***	-4.8	6,2	63	***	-4.5
Clossiana selene	2	36	**	-1.9	2,6	46	**	-3.7
Clossiana euphrosyne	2,Yr(-0.07)	54	***	-1.9	2	56	***	-2.9
Argynnis aglaja	2,3^{+}	47	**	-0.3	6,2	45	**	-3.1
Argynnis paphia	2,7,6	58	**	-5.9	2,7	63	***	-5.5
Melanargia galathea	5,6,Yr(-0.05)	77	***	-4.7	6,5,7,4	86	***	-8.7
Hipparchia semele	6,2	46	**	-3.3	2,6	40	**	-3.5
Pyronia tithonus	6,7,5,4	91	***	-7.0	6,7,2	88	***	-5.7
Maniola jurtina	2,6	83	***	-4.7	6,2,7	79	***	-5.4
Aphantopus hyperantus	6,Yr(-0.05),-10^{+},2	77	***	-3.0	6,2,-10^{+},Yr(-0.03)	78	***	-2.1

	First appearance date				Peak flight date			
	Terms included	R^2 (%)	sig.	Change (+1 °C)	Terms included	R^2 (%)	sig.	Change (+1 °C)
b) species with two flight periods, but only one generation								
Gonepteryx rhamni	Yr(-0.08)	28	**	-4.4	2	31	**	-3.4
Inachis io	Yr(-0.15),-8	55	***	-6.6	2,-12,6	34	***	-9.9
c) species with two or more flight periods representing different generations								
Pieris brassicae	5,Yr(0.09),-7^{+},-11,-6	90	***	-9.3	6,Yr(0.11),2	56	**	-2.4
Pieris napi	2,Yr(-0.08),-6^{+}	69	***	-0.4	6	22	*	-2.8
Pieris rapae	5,3^{+}	56	***	-3.9	6,Yr(0.11),2	59	**	-5.8
Lycaena phlaeas	2	23	*	-2.4	7^{+},6	37	**	1.0
Aricia agestis	-8	23	*	-3.7	5	21	*	-5.2
Polyommatus icarus	2	42	**	-2.5	7^{+},2	43	**	1.3
Lysandra bellargus	3,-8	54	***	-11.8	5	19	*	-9.2
Celastrina argiolus					7^{+}	39	**	8.5
Vanessa atalanta	Yr(-0.19),6,2	77	***	-9.2	6	27	*	-3.7
Cynthia cardui	None				none			
Aglais urticae	2	21	*	-1.9	1	26	*	-3.0
Polygonia c-album	Yr(-0.26),-9,3^{+}	65	***	-5.4	none			
Pararge aegeria	5,4	77	***	-10.2	none			
Lasiommata megera	2,6,Yr(0.10)	60	***	-8.2	2	55	***	-2.8
Coenonympha pamphilus	2	60	***	-2.5	7^{+},5	54	***	1.8

Figure 2.1. Time trends in spring and summer Central England Temperature (CET), 1976-1998. Open circles are spring temperatures (mean February-April CET) and solid circles are summer temperatures (mean May-July CET).

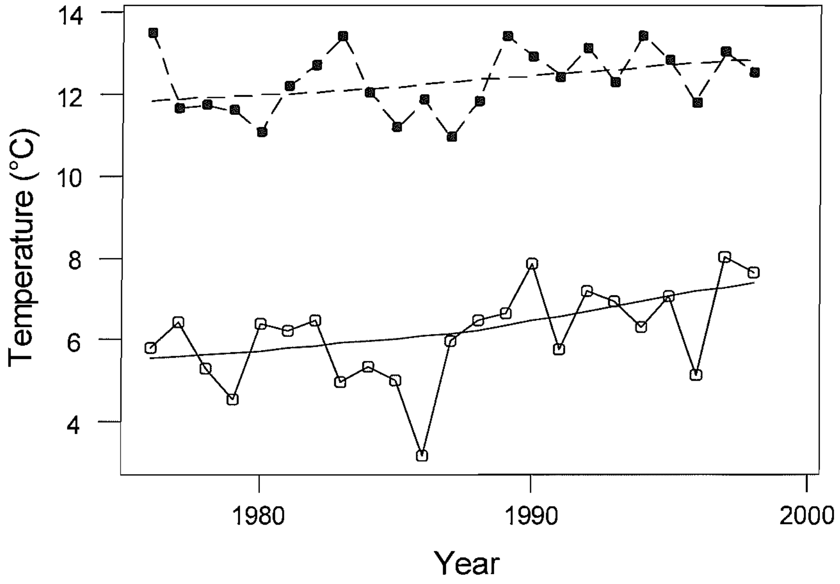
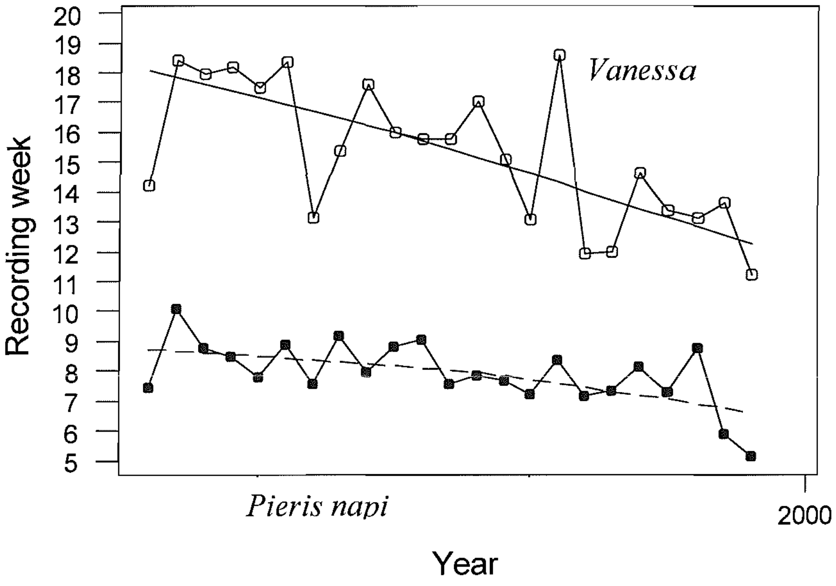


Figure 2.2. Time trends for (a) first appearance and (b) duration of flight period for Vanessa atalanta and Pieris napi. Week 1 is the first week in April.

a)



b)

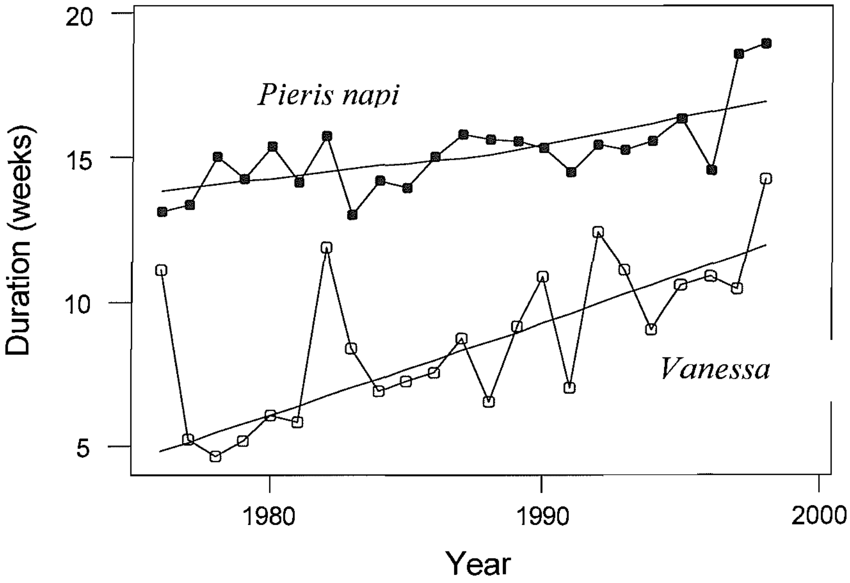
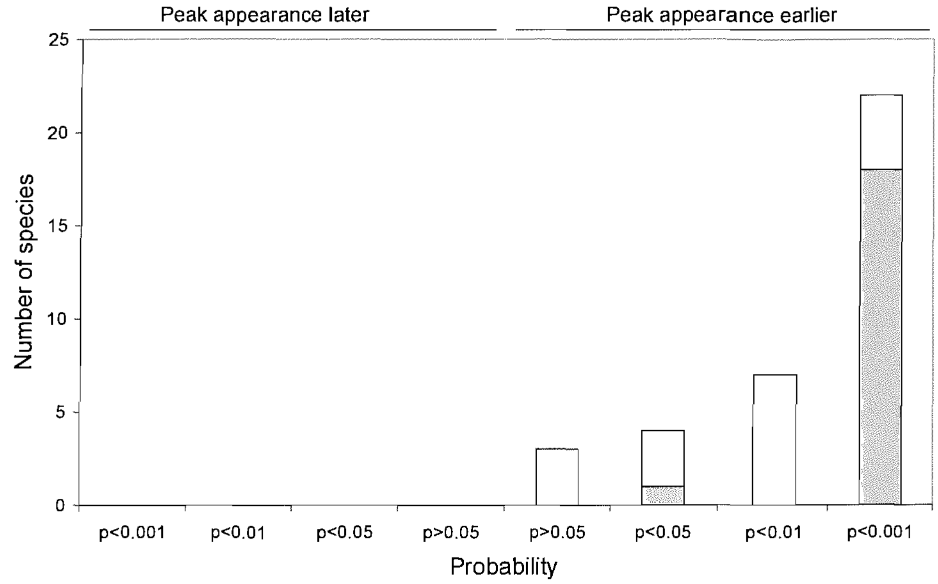


Figure 2.3. Correlations with first appearance. Frequency distribution of P values of correlation between first appearance and (a) peak appearance and (b) length of flight period. Univoltine species are shown in grey, multivoltine in white.

a)



b)

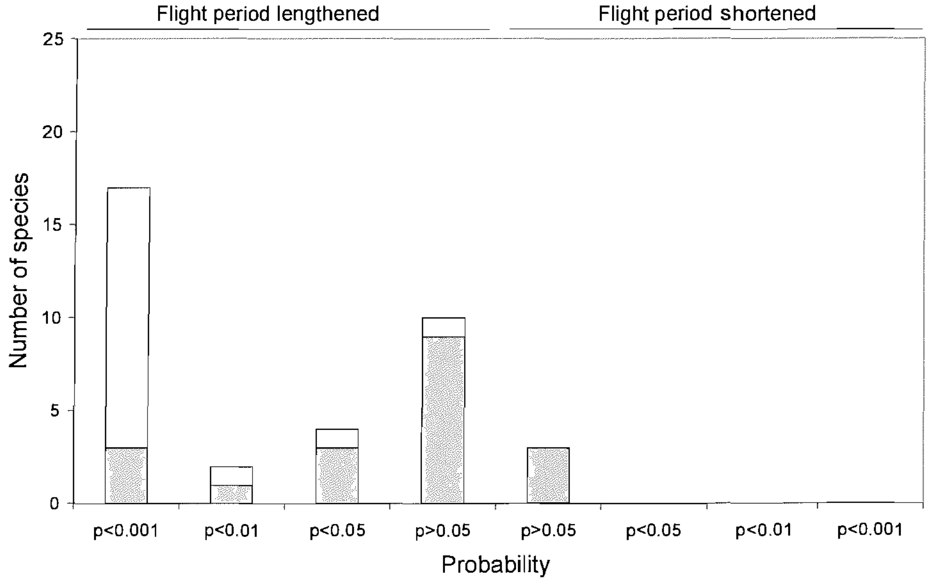
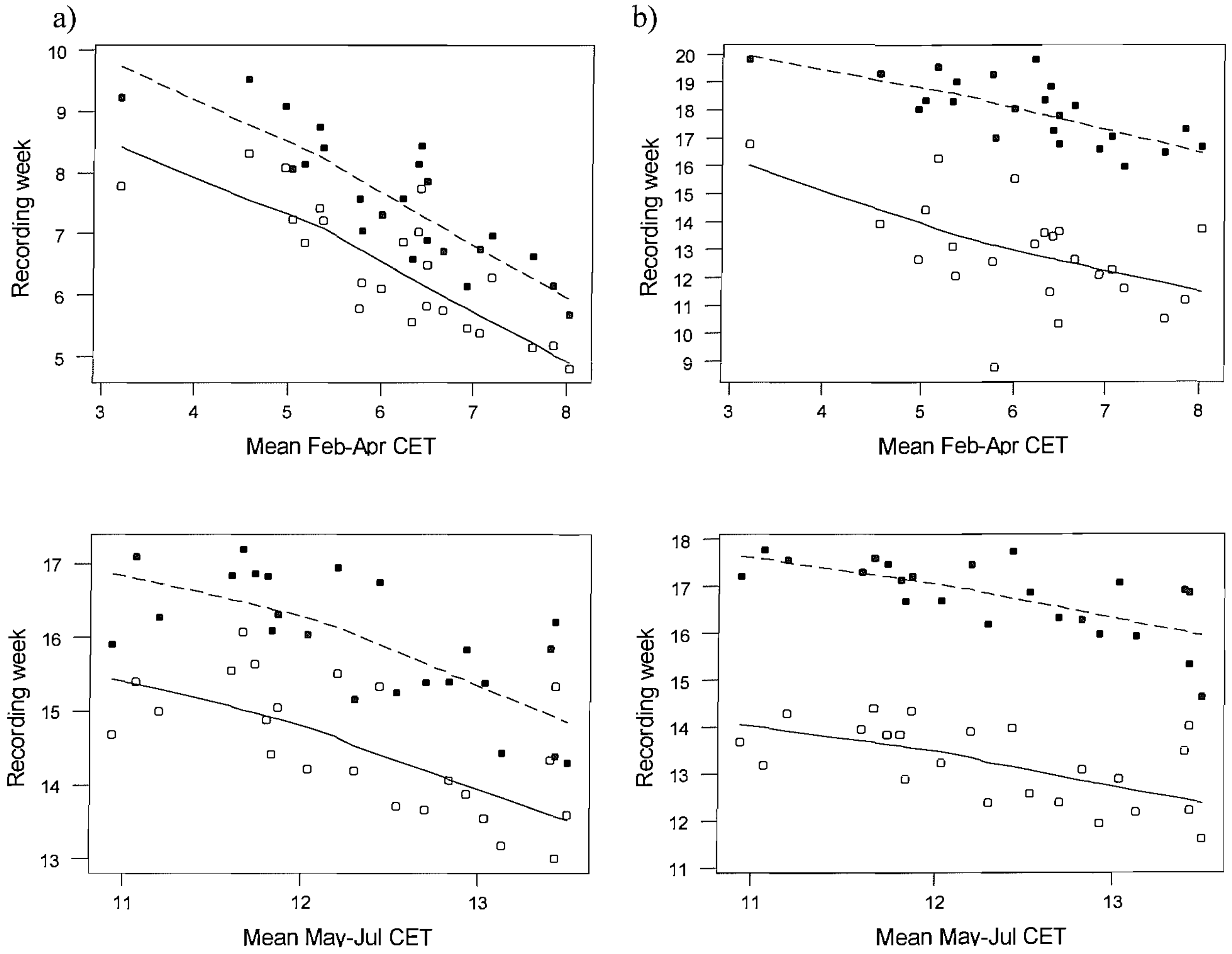


Figure 2.4. Relationships between mean first and mean peak appearance dates and temperature. Open circles are first appearance dates, solid circle are peak appearance and are related to mean spring temperature (mean February-April Central England Temperature, CET) for a) *Anthocharis cardamines* and b) *Polyommatus icarus* and summer temperature (mean May-July Central England Temperature, CET) for c) *Melanargia galathea* and d) *Maniola jurtina*. Week 1 is the first week of April.



3 Spatial trends in the sighting dates of British butterflies

Roy, D.B. & Asher, J. (2003) Spatial trends in the sighting dates of British butterflies. *International Journal of Biometeorology*, **47**, 188-192.

3.1 Abstract

A strong relationship between appearance dates and temperature has been demonstrated over two decades for most British butterflies. Given this relationship over time, this paper tests whether comparable spatial trends in timing are also apparent. A major survey of British butterflies is used to calculate mean sighting dates of adults across the country, and compared with geographic patterns in temperature. With the use of regression techniques, we calculated latitudinal (south-north) and longitudinal (east-west) gradients in sighting date and temperature. The majority of butterflies appear later in the east of Britain where temperatures are lower during summer, but not the rest of the year. Most butterflies are also seen later in the cooler north of the country, by upto 3-4 days per 100km. However, a geographical relationship between temperature and timing of appearance was not detected for over a third of the species analysed, suggesting their populations may be adapted to their local climates. We suggest possible mechanisms for this and discuss the implications of such adaptation for the ability of butterfly species to respond to rapid climate warming.

3.2 Introduction

Recent evidence suggests that responses to global warming are consistent across a range of taxonomic groups, organisational levels and throughout all major biomes (e.g. Hughes, 2000; Walther *et al.*, 2002). Phenological changes have proved particularly sensitive (Peñuelas and Filella 2001), and well studied, with numerous aspects of plant and animal life cycles showing marked trends with warmer temperatures across Europe and North America (e.g. Bradley *et al.*, 1999; Menzel *et al.*, 1999).

Most phenological studies report climate-related changes over time in events such as bird migration (Sparks, 1999) and egg laying (Crick & Sparks, 1999), plant growth and flowering (Abu-asab *et al.*, 2001) and insect life cycles (Zhou *et al.*, 1995). Similarly, on average, the appearance of British butterflies has advanced by 2-10 days per 1 °C increase in temperature over a twenty-three year period (Roy & Sparks, 2000).

Fewer studies have examined spatial trends in phenological events, but given the often reported strong relationship between timing and temperature, it is expected that events such as appearance of adults butterflies will occur later in the north of their range than the warmer south. However, previously published data for the butterfly *Pyronia tithonus* (Brakefield, 1987; Pollard 1991) showed no clear trend in the timing of the flight-period with latitude over its British range. Conversely, anecdotal evidence suggests that other butterfly species fly later in the north as expected (Warren, 1992). The aim of this paper is to quantify spatial trends in butterfly phenology using data from a major survey of their distribution in Britain, to determine the extent to which appearance is synchronized across regions.

3.3 Methods

Latitudinal and longitudinal trends in temperatures across Britain were calculated using 10km x 10km climate summaries available from the UK Climate Impacts Programme (Hulme & Jenkins, 1998). Monthly, seasonal and annual mean temperatures were calculated for each 100km x 100km for which butterfly sighting data was available. Trends in temperature were calculated by multiple linear regressions with easting and northing as explanatory variables. Although the temperature data used is a mean of values for 1960 to 1990, the spatial trends in temperatures across the country are likely to be applicable to recent years.

Timing of butterfly sightings across Britain was derived from distributional records (1.5 million records) collected over a five-year period, 1995-1999 (Asher *et al.*, 2001). The mean sighting date per 100km x 100km grid square was calculated to reduce local effects of variation in recording intensity. Recording continued throughout periods where adult butterflies were active and mean sighting date is taken to represent an average flight-period time. Species with more than one generation per year were excluded to overcome the difficulty in separating generations for multivoltine species. Non-resident species such as *Vanessa atalanta* and *Cynthia cardui* were also excluded as their appearance within Britain is dependent on conditions in breeding areas further south. Twenty-nine remaining species were suitable for analysis. Trends over space in mean sighting date were examined using linear regression with easting and northing as separate explanatory variables, but models were weighted by the number of sightings per grid square to accommodate variation in recording intensity and density.

3.4 Results

Unsurprisingly there are clear east-west and north-south gradients in temperature across Britain (Table 1) reflecting global latitudinal gradients from the equator to the pole. Annual, monthly and seasonal temperatures are constantly warmer by approximately 0.4°C per 100km from the north to the south. Longitudinal gradients in temperature are not consistent throughout the year however. The west is warmer than the east in the winter and spring months, by upto 0.42°C warmer per 100km, but the gradient is reversed during the summer months, but with a less marked gradient, 0.23°C per 100km in July.

There is a significant trend towards later sighting date in the north for over a third of the butterflies analysed (Table 2) reflecting the north-south temperature gradient in Britain (Table 1). Habitat specialists with a northern (e.g. *Limentis Camilla, Argynnis aglaja*) or southern range margin in Britain (e.g. *Coenonympha tullia, Aricia artaxerxes*), as well more wide-ranging species (*Anthocharis cardamines* – Figure 1a, *Thymelicus sylvestris*) are seen as adults earlier in the southern compared to the northern parts of their range. These species also have a range of life histories, overwintering as eggs, caterpillars or chrysalis. A further eleven species had a positive, but non-significant, trend towards earlier sighting date in the south. *Callophrys rubi* was the only species with a significantly negative relationship between timing and distance north (Table 2). This species has an extended flight period, and late mean flight date, in the most southerly parts of its range (Asher *et al.*, 2001). Ten species have a negative relationship between northing and mean sighting date and there is little variation in mean sighting date of *Pyronia tithonus* (Figure 1b) from the south to north parts of its range, as noted by previous authors (Brakefield, 1987; Pollard, 1991a).

Mean sighting date is earlier in the east for most species (Table 2), and significantly so for almost a quarter of species. The reverse pattern with significantly earlier sighting date in western Britain is found in only two species, *Ochlodes venata* and *Hipparchia semele*. Temperatures are warmer in eastern Britain during summer, but not the rest of the year (Table 1) and we may expect this to effect timing of appearance differently for spring- and summer-emerging species. However, the direction of east-west relationships do not relate to overall timing of flight-period. For example, spring-emerging species such as *Anthocharis cardamines* and *Pyrgus malvae* do not appear significantly earlier in the west even though autumn and spring temperatures are warmer in this part of the country during important periods for development of immature stages for these species.

3.5 Discussion

As expected, the flight-period of most butterflies is earlier in the warmer south than the cooler north of Britain. This relationship is predicted by the year-to-year response between temperature and timing of butterfly appearance reported for most British species (Roy & Sparks, 2000), and the tendency for timing to be later at high, and cooler, altitudes (Gutiérrez and Menéndez 1998). However, for a number of species, the mean sighting date of records appears synchronized across latitude, supporting the findings of Brakefield (1987) and Pollard (1991a) for *Pyronia tithonus*; the latitudinal gradient in temperature is not mirrored by butterfly phenology. This finding raises important questions, such as how is the synchrony of flight-periods achieved and what are the implications for butterfly populations under climate warming?

Synchrony in appearance across temperature gradients may provide evidence for local adaptation of butterfly populations to regional climates, and possible mechanisms include behavioural, morphological, physiological and developmental characteristics.

Lepidopteran larvae can attain temperatures 5°-20° above ambient by adjusting posture and orientation, exploiting thermal heterogeneity within the environment, and minimizing convective heat losses (Weiss *et al.*, 1988). Larvae can also exhibit positive phototaxy within the host canopy which tends to put them in high radiation microsites. These behaviours may be well developed in cooler parts of a species' range. Butterfly populations are also more localised at the northern range margin (Asher *et al.*, 2001) as the suitable habitat patches available are typically smaller, more isolated and short-lived (Bourn & Thomas, 2002) compared to those at its core. Thomas (1993) argues that many species of insect in the Palaearctic have been living a few hundred kilometres north of their 'natural' climatic limits during recent centuries or millennia because of an ability to exploit unnaturally warm microclimates generated within semi-natural biotopes by traditional forms of agriculture and silviculture. In contrast, the same species occupy different and broader niches near their centres of range, particularly mid-late seral stages of ecosystems (Thomas, 1993). Such exploitation of warmer microclimates in the north may allow comparable larval development times, and resulting synchronised emergence dates of adults, between populations in different parts of a species' range.

Compensation for cooler temperatures may also be achieved by reduced size in the north of the range. Ayres and Scriber (1994) report smaller larvae and adults in Alaskan vs. Michigan populations of *P. canadensis*, and a similar size clines has been suggested for a number of butterflies in Sweden with individuals measured from museum collections being smaller in the north of the country due to a shorter growing season and therefore reduced development time (Nylin & Svard, 1991). However, butterflies may compensate for limited development time in seasonal environments by accelerated growth rates. Several species of fish exhibit faster increases in growth with temperature in northern as opposed to southern populations (Conover & Present, 1990; Schultz, Reynolds & Conover, 1996) and similar results have been documented for ectothermic organisms (Conover & Schultz, 1995; Nylin & Gotthard, 1998). The adaptive explanation for such a counter-gradient in growth rate is that temperatures favourable for growth and development occur during a shorter period in northern areas, yet high growth rates are associated with fitness costs (Conover *et al.*, 1990). An analysis of the phenology of four butterflies in Sweden demonstrated that growth rate of these species is indeed finely tuned depending on season, but also that larvae can both hibernate and aestivate when extra time is available (Wickman, Wiklund & Karlsson, 1990).

If local adaptation to temperature occurs widely, as suggested here, this has implications for the conservation of butterflies by introductions from one locality to another where extinction has occurred. Butterflies moved from a cooler to a warmer locality may emerge earlier in the season with possible consequences for survival. Similarly, a locally adapted butterfly may be unable to cope with the rapid climate warming predicted for much of Europe. Evidence suggests that mobile, wide-ranging butterflies are already expanding in range and increasing in abundance within Britain due to climate warming, yet sedentary habitat specialist species are becoming increasingly restricted due to habitat loss and degredation (Roy *et al.*, 2001; Warren *et al.*, 2001). It is unclear which mechanism(s) allow synchronised emergence of butterflies in Britain, and different strategies may be operating in different species, yet this intriguing phenomenon deserves more attention to enable more accurate predictions of the future response of butterflies to climate warming.

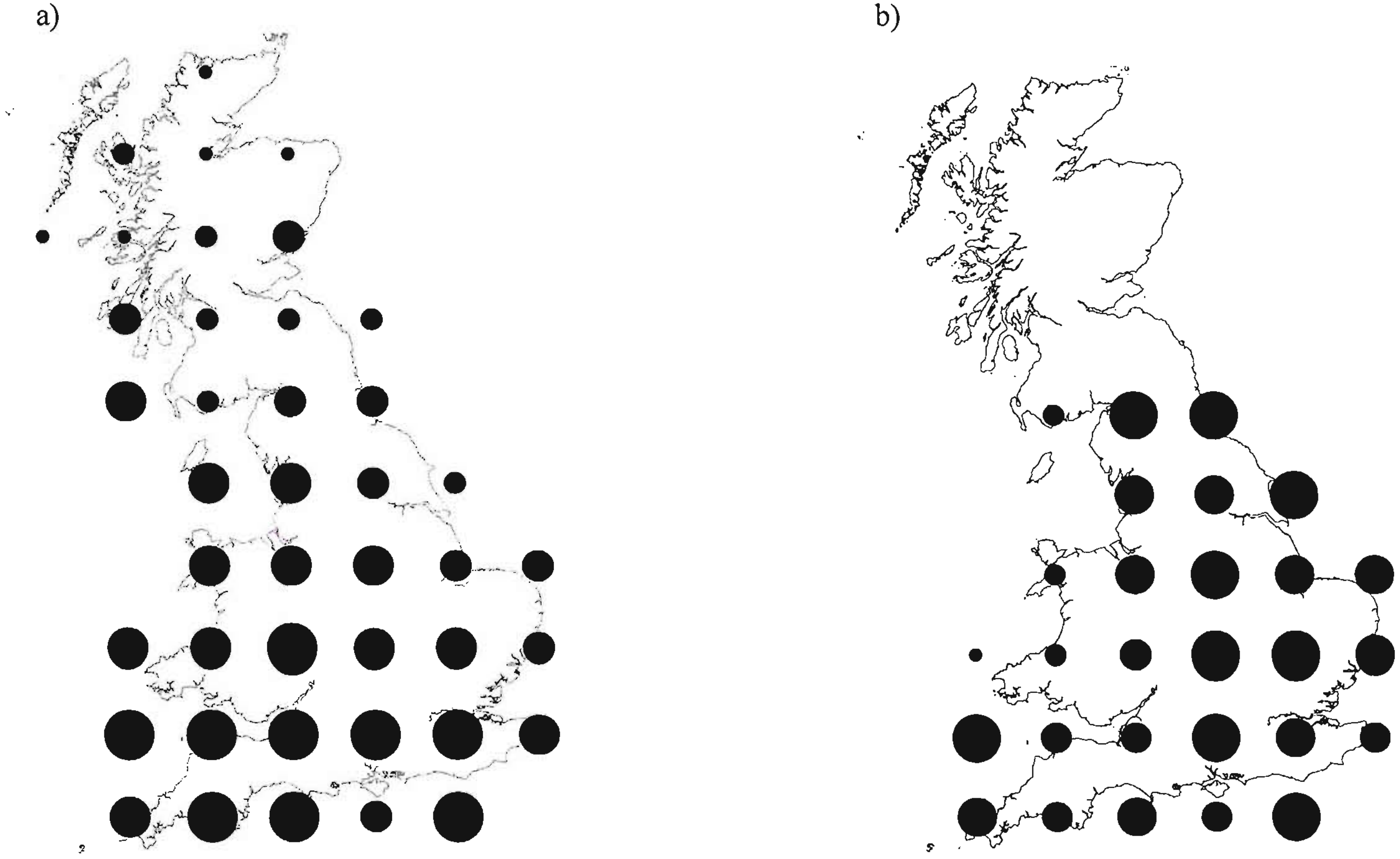
Table 3.1. Spatial trends (1960-90) in temperature. T_{EAST} and T_{NORTH} are the regression coefficients (se) from a multiple linear regression of east-west and south-north effects (per 100Km) on monthly, seasonal and annual temperature. Seasons are defined as three-month periods with winter as November, December, January. n = 47. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Period	T_{EAST}	T_{NORTH}
Month		
January	-0.42 (0.08) ***	-0.33 (0.04) ***
February	-0.32 (0.08) ***	-0.31 (0.04) ***
March	-0.16 (0.06) *	-0.31 (0.03) ***
April	-0.07 (0.03)	-0.32 (0.03) ***
May	0.06 (0.04)	-0.34 (0.02) ***
June	0.16 (0.03) ***	-0.36 (0.02) ***
July	0.23 (0.04) ***	-0.43 (0.02) ***
August	0.22 (0.04) ***	-0.43 (0.02) ***
September	0.13 (0.06) *	-0.43 (0.03) ***
November	-0.29 (0.08) **	-0.41 (0.04) ***
December	-0.42 (0.08) ***	-0.36 (0.05) ***
Season		
Winter	-0.39 (0.04) ***	-0.34 (0.04) ***
Spring	-0.06 (0.05)	-0.33 (0.03) ***
Summer	0.21 (0.04) ***	-0.41 (0.02) ***
Autumn	-0.07 (0.07)	-0.42 (0.04) ***
Annual	-0.08 (0.05)	-0.37 (0.03) ***

Table 3.2. Spatial trends (1995-99) for mean date (julian day) of butterfly sightings per 100km x 100km grid cell of the British Ordinance Survey grid. n is the number of grid cells analysed; B_{EAST} and B_{NORTH} are the regression coefficients (se) from a multiple linear regression of east-west and south-north effects (per 100Km) on mean sighting date. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Common name	n	B_{EAST}	B_{NORTH}
Thymelicus sylvestris	Small skipper	28	-0.94 (0.41)*	2.34 (0.38)***
Thymelicus lineola	Essex skipper	17	-0.60 (0.79)	0.82 (0.74)
Ochlodes venata	Large skipper	32	2.13 (0.54)***	-0.42 (0.45)
Erynnis tages	Dingy skipper	29	1.26 (1.94)	1.42 (1.30)
Pyrgus malvae	Grizzled skipper	18	-0.01 (1.05)	0.36 (1.11)
Anthocharis cardamines	Orange tip	41	0.54 (0.33)	2.15 (0.20)***
Callophrys rubi	Green hairstreak	39	-2.84 (0.83)**	-2.07 (0.49)***
Lysandra coridon	Chalkhill blue	11	-1.59 (0.77)	-2.10 (0.91)
Limenitis camilla	White admiral	15	-1.21 (0.39)**	1.11 (0.47)*
Clossiana selene	Small pearl-bordered fritillary	35	0.97 (1.24)	2.19 (0.46)***
Clossiana euphrosyne	Pearl-bordered fritillary	25	0.79 (1.21)	3.75 (0.55)***
Argynnis aglaja	Dark green fritillary	45	1.62 (0.88)	1.22 (0.42)**
Argynnis paphia	Silver-washed fritillary	19	-2.80 (0.77)**	0.88 (0.80)
Melanargia galathea	Marbled white	19	0.39 (0.76)	-0.16 (0.73)
Hipparchia semele	Grayling	40	2.02 (0.58)**	-0.32 (0.32)
Pyronia tithonus	Gatekeeper	28	-0.80 (0.29)*	0.16 (0.31)
Maniola jurtina	Meadow brown	47	-0.70 (0.46)	-0.08 (0.25)
Aphantopus hyperantus	Ringlet	38	0.70 (0.39)	0.36 (0.26)
Apatura iris	Purple emporer	6	-2.78 (0.96)	-1.00 (1.15)
Aricia artaxerxes	Northern Brown argus	13	1.70 (1.85)	3.65 (0.94)**
Coenonympha tullia	Large heath	24	2.18 (1.32)	2.64 (0.62)***
Erebia aethiops	Scotch argus	13	-0.07 (0.97)	1.15 (0.56)
Eurodryas aurinia	Marsh fritillary	18	-6.19 (2.31)*	-1.50 (1.26)
Hamearis lucina	Duke of Burgundy	12	-0.94 (1.09)	1.51 (0.83)
Hesperia comma	Silver-spotted skipper	6	0.22 (1.09)	-1.55 (2.83)
Plebejus argus	Silver-studded blue	12	1.52 (1.13)	-1.64 (1.57)
Strymonidia w-album	White letter hairstreak	22	-1.46 (1.00)	2.55 (0.76)**
Thecla betulae	Brown hairstreak	11	0.27 (2.30)	0.32 (3.11)
Quercusia quercus	Purple hairstreak	29	-2.25 (0.60)**	2.30 (0.46)***
Number of significantly *negative* relationships			7	1
Number of significantly *positive* relationships			2	10

Figure 3.1. Geographic patterns in mean date (julian day) of butterfly sightings for a) *Anthocharis cardamines* and b) *Pyronia tithonus* within 100km x 100km grid square of the British Ordinance Survey grid. Symbol, in decreasing size, represent mean dates as follows a) 206-210, 210-212, 212-214, 214-216, 216-219; b) 125-130, 130-135, 135-140, 140-145, 145-151.



a)

b)

4 Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin

Roy, D.B. & Thomas, J.A. (2003) Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia*, **134**, 439-444.

4.1 Abstract

We investigated the niche requirements of the summer and autumn/spring generations of the bivoltine butterfly, *Polyommatus bellargus* Rott., and their implications for population dynamics at sites occurring near its northern range margin. The larvae of this species are sedentary, and the turf height and shelter of *Hippocrepis comosa* foodplants selected for egg-laying accurately predict larval distributions within United Kingdom (UK) sites. We found a significant shift between the plants used for egg-laying in each generation, with the niche occupied by summer-feeding larvae being broader and different to the autumn one. Measurements of soil temperature confirmed that the short, sheltered foodplants selected by ovipositing females in autumn placed the autumn/spring-feeding generation of larvae in the warmest available microclimates within sites. In late spring, egglaying females avoided the hottest spots but extended egglaying into taller, less sheltered (relatively cool) turf where the microclimate was similar to that experienced by autumn/spring-feeding larvae. Using each generations' definition of niche requirement, we analysed surveys of foodplant populations available on 24 UK sites for *P. bellargus*, and estimated that nearly twice as many plants were available to the summer-feeding larvae compared to those feeding in the autumn. Annual adult population counts match these seasonal differences in site carrying capacity; first generation counts (from autumn-laid eggs) were generally half as abundant as in the second generation, and more variable. These results suggest that the seasonal cycle of niche switches represents an annual (autumn-spring) bottleneck for populations of this butterfly at its northern range margin. Under climate warming we predict that the inter-generational difference in niche availability, carrying capacity and population size will be reduced. We recommend revised management requirements for this threatened species under current and predicted climates in northern Europe.

4.2 *Introduction*

Climatic constraints determine the latitudinal and altitudinal range margins of many Holarctic plants and ectotherms (Dennis 1993; Parmesan *et al.* 1999; Pigott and Pigott 1993; Warren *et al.* 2001), although the 'envelope' that a species can inhabit is frequently extended by an ability to exploit locally warm microhabitats near the northern edge of its range and locally cool spots in the south (Thomas 1983, 1993). Thus at higher latitudes in Europe, the immature stages of many grounddwelling species of insect become restricted not only to sheltered south-facing slopes of unusual local warmth, but also to patches within them where the micro-climate is exceptionally hot, such as in the earliest seral stages of woodland, heath and grassland (Thomas 1993; Thomas *et al.* 1999). In contrast, the same species occupy different and broader niches near their centres of range, encompassing a diversity of other aspects and the (often more abundant) mid-late seral stages of ecosystems (Thomas 1991, 1993). Consequently, the habitat patches available to an ectotherm are typically smaller, more isolated and more ephemeral (Bourn and Thomas 2002, Thomas *et al.* 1999), and populations are more localised (Asher *et al.* 2001), near its northern margin compared to those at its core.

Recent field evidence (Thomas *et al.* 2001a) supports theoretical predictions (Thomas *et al.* 1999) that certain types of thermophilous insects have expanded to occupy broader niches, and hence larger patch sizes, near their northern range margins during some of the warmer summers of recent years. Understanding the mechanisms responsible for these shifts is important not just to predict how species' populations and ranges may respond to climate warming (Roy *et al.* 2001; Thomas *et al.* 2001a; Warren *et al.* 2001) but also, in conservation, to ensure that appropriate management is applied to maintain optimal habitat and metapopulation structures for threatened species under different local climates (Thomas 1996; Thomas *et al.* 1998, 2001b).

Bivoltine butterflies, that have two generations per year, experience larger and more predictable alternations of climate during their two developmental periods, and might provide a clearer paradigm for understanding the above processes. For example, the first generation of larvae of the butterfly *Polyommatus bellargus*_Rott. develop during summer in southern England (at its northern range limit), but the second generation develop during autumn and spring, when mean regional air temperatures are 4°C cooler (Hulme and Barrow 1997). It was already known that the autumn-spring larvae of *P. bellargus* exploit only a minority of the foodplants (*Hippocrepis comosa*) within their sites, being restricted to those growing in the most sheltered and shortest turf, representing the hottest available spots (Thomas 1983; Thomas *et al.* 2001b). However, the summer niche had not been studied. Here, we describe how the summer niche of *P. bellargus* differs substantially in term of vegetation structure from its spring/autumn one in the United Kingdom (UK); we also estimate the consequences of the observed niche switches in alternate generations on foodplant availability, site carrying capacities and the population dynamics and management requirements of this Red Data list species.

4.3 Materials and methods

4.3.1 Study species and site

Polyommatus bellargus is a spectacular butterfly of calcareous grassland. Although still common in surviving 'unimproved' grassland across central-southern Europe, it becomes increasingly localised towards its northern limit across Germany, Belgium and south England (Tolman and Lewington 1997), where it is restricted to south-facing downlands with abundant *Hippocrepis comosa* growing in short (<4 cm), very sheltered patches of turf (Thomas 1983; Thomas *et al.* 2001b). During the past 25 years, *P. bellargus* is reported to have declined in 42% of recorded European countries (and to have increased in none); it is currently a Red Data listed species (IUCN status: Endangered, Vulnerable, Rare or Intermediate) in 14 of the 32 European countries in which it is resident (van Swaay and Warren 1999). *P. bellargus* is obligately bivoltine throughout Europe, apart from possible univoltine populations in south Greece (Tolman and Lewington 1997). In Britain, first generation adults emerge in mid- May and typically reach peak abundance in early June (see Fig. 2). Eggs laid in early summer develop mainly during June and July, emerging as adults in late August and September. Larvae from the second generation eggs, laid mainly in September, feed for 6–8 weeks until mid October, and resume feeding during the following March and April (Thomas and Lewington 1991). Our study site, Five Mary's Tumuli, Dorset, is a south-facing slope of chalk downland in southern England, about 100 km south of *P. bellargus*' current northern range margin. The site was stocked with cattle during winter and lightly grazed by rabbits during spring and summer 2000, when our study was made.

4.3.2 Niche measurements

Niche preferences were recorded for both summer (late May–June) and autumn (early September) generations of *P. bellargus* larvae on the study site by measuring two attributes (turf height, shelter) of the *H. comosa* plants selected for egg-laying already known to describe 99% of variation in autumn/spring egg and larval distributions on neighbouring UK sites (Thomas *et al.* 2001b) (few larvae move >10 cm from eggsites). The eggs, which are laid singly, were located by following egg-laying females throughout the flight period; their presence on the marked plants was confirmed before the height and the shelter category of every chosen plant was measured. Sward height was measured using the 'direct method', which accurately measures turf height both in uneven terrain and in very short, as well as tall, vegetation (Stewart *et al.* 2001). The extent to which *H. comosa* was growing in a suntrap was assessed into one of three categories after Thomas (1983): (1) open downland with even, unsheltered terrain; (2) limited shelter from tracks, scrapes and depressions; and (3) complete shelter in tracks, scrapes, hoofprints and similar depressions.

The structure of the foodplant population available for *P.bellargus* was assessed using the same criteria for the whole site during both egg-laying periods. The height of sward and shelter categories around all *H. comosa* plants was recorded in 700 locations across the site for four strata: top, mid and lower sections of the downland slope and within chalk scrapes.

Soil temperature was monitored during the summer (June–July) and autumn (September–October) larval development periods: a total of 18 Tiny Talk temperature data loggers were buried under *H. comosa* representative of the range of turf heights selected by *P. bellargus* for summer and autumn/spring larvae; due to insufficient loggers, all were restricted to shelter category 2. The exact location of data loggers was determined by recorded egg-laying by the first generation (4–6 cm turf) and based on literature information on microhabitat use (Thomas 1983; Thomas *et al.*

2001b) by the second generation females (1–3 cm turf). The loggers measured hourly variation in temperature in the top 1 cm of soil, a reasonable approximation to the variation experienced by *P. bellargus* larvae, which live either on the soil surface or just beneath it in cells constructed by mutualistic ants (Thomas 1983).

4.3.3 Seasonal variation in habitat availability within sites

Having defined the summer and autumn egg-laying niches of *P. bellargus* in terms of different combinations of turf height and shelter categories, it was possible to assess what proportion of the foodplant population was available to each generation of larvae on typical UK sites. We analysed data from 24 other *P. bellargus* sites in Dorset and Wiltshire, where the height and shelter category of all *H. comosa* plants in 30–50 random 1 m^2 quadrats per site (total area 920 m2) had previously been recorded (Bourn *et al.* 2000; Thomas 1983; Thomas *et al.* 2001b). We scored every plant sampled on each site into one of four categories of suitability for: (1) summerfeeding larvae alone, (2) autumn-feeding larvae alone, (3) both summer and autumn-feeding larvae, and (4) neither generation.

4.3.4 Population dynamics

Fluctuations in the size of *P. bellargus* populations were derived from the Butterfly Monitoring Scheme (BMS), which has accurately recorded variation in the abundance of most UK butterfly species, using fixed transect counts, from the beginning of April to the end of September since 1976 (see Pollard and Yates 1993 and Thomas 1983, respectively, for details and validation of the general method and its suitability for P. bellargus populations). An index of abundance was calculated separately for each generation of *P. bellargus* in each year. We restricted analyses to sites (i.e. populations) with a run of population index values for both generations for at least five consecutive years and calculated the coefficient of variation (CV) as a measure of annual variability in population indices, separately for each generation.

4.4 Results

4.4.1 Differences in summer and autumn/spring larval niches

P. bellargus females were followed from a number of different starting points and flew freely across the site. Eggs were typically laid singly and followed by a short flight before the next oviposition. Plants were often rejected for egg-laying.

Forty-six eggs were seen laid by female *P. bellargus* in September. All were restricted to *H. comosa* plants growing in short turf, <3 cm (mean 2.06 cm, SE 0.14) and within sheltered locations (shelter categories 2, 3) (Fig. 1a), as described on other UK sites (Bourn *et al.* 2000; Thomas 1983; Thomas *et al.* 2001b). In contrast, the 53 eggs recorded by following ovipositing females in late May–June were laid on *H. comosa* growing in taller vegetation, up to 7 cm (mean 4.65 cm, SE 0.21), in situations with limited shelter (mainly categories 1, 2). Not only was the summer niche broader than the spring one (Fig. 1: 14 out of 21 possible height-shelter combinations used in summer compared to 8 in autumn), it also showed a significant shift away from the plants used in autumn (height $t_{df=89} = 10.3$, $P<0.001$; shelter $X^2_{df=2} = 25.3$, $P<0.001$). No summer eggs were laid in the shortest turf or in the most sheltered spots available.

This dichotomy does not reflect differences between the structure of the foodplant population in each season. Indeed, the *H. comosa* plants were generally shorter in the spring (mean 3.73 cm, SE 0.11) than in late summer (mean 4.03 cm, SE 0.17), but not significantly different ($t_{df=385} = 1.51$, n.s.).

As before (Thomas 1983), we found that the soilsurface temperature during the autumn generation of *P.bellargus* larvae (September and early October) was significantly warmer ($t_{df=4} = 5.9$, $P<0.01$) under the preferred short-turf (1–2 cm) than under more rank vegetation (4–6 cm) (Table 1). In contrast, we found no difference between soil-surface temperature under these two categories of sward height during the development period of summer larvae in June and July ($t_{df=6} = 0.12$, n.s.); both were slightly warmer than the warmest (shortturf) plants available to autumn-feeding larvae. Thus the autumn generation of adults selected the warmest microclimates for egg-laying whereas the summer generation had a wider choice.

4.4.2 Habitat availability and population dynamics

Over a range of 24 UK sites, there were, on average, nearly twice as many *H. comosa* plants available to the summer-feeding generation of larvae compared to the autumn-feeding one (Table 2: 70% cf. 36% respectively), based on the criteria for seasonal suitability identified in Fig. 1. The shift, as opposed to the broadening, of *P. bellargus*' niche in summer is illustrated by the calculation that one-third of the individual plants that were suitable for autumn-feeding larvae were unsuitable for the summer generation; only 23% of the *H. comosa* populations were suitable for both generations of *P. bellargus* compared to 83% of plants that were suitable for one or other generation (Table 2).

The scale of this seasonal alternation in the number of foodplants available to *P. bellargus* larvae suggests that its populations may experience substantial bottlenecks during their autumn/spring-feeding periods. This prediction is consistent with observed seasonal fluctuations of the adult butterfly (Fig. 2). Ten time-series with five or more years of consecutive population indices (from eight sites) were reliably monitored for *P. bellargus* by the BMS. Mean peak numbers of second generation adults (from summer-feeding larvae) were nearly twice as high as those resulting from autumn-feeding larvae. If we assume that an annual bottleneck does occur in site carrying capacities for *P. bellargus*, set by the reduced number of plants available each autumn-spring, then the relative increase over summer in a typical site's carrying capacity can also be calculated: this predicted increase closely matches the recorded increase in adult butterflies resulting from eggs laid in June (Fig. 2). Numbers in spring were also more variable than those in late summer (mean (SE) CV: generation 1 = 0.32 (0.048) generation 2 = 0.23 (0.024); $P<0.05$).

4.5 Discussion

These results confirm earlier observations (Thomas 1983) that the autumn/spring-feeding larval population of *P. bellargus* is restricted, near its northern limit of range, to a minority of *H. comosa* plants that grow both in short (<4 cm) vegetation and in sheltered spots within occupied sites. They also demonstrate that, as well as displaying variation in niche requirements between core and marginal populations (Thomas *et al.* 1999), thermophilous butterflies may differ in niche breadth between generations: in this example, the eggs laid in early summer occupy a broader niche that overlaps only partly with the spring one, involving a shift towards taller, less sheltered *H. comosa* plants. We suggest that the seasonal cycle in foodplant availability resulting from these niche shifts represents an annual (autumn-spring) bottleneck for *P. bellargus* populations in this part of its range, a hypothesis that is strengthened by the similarity of the ratios of estimated site carrying capacities and fluctuations in *P. bellargus* numbers between the two seasons (Fig. 2). We would not expect an exact match between these values because each cohort of larvae is likely to experience unrelated variation in seasonal survival (different interactions with enemies, mutualistic ants etc.); nor will populations necessarily increase to occupy all the vacant habitat every summer. Nevertheless, the parallel between the cycles of habitat availability and population dynamics is intriguing.

Our results also confirm that the foodplants selected for egg-laying in early autumn grow in a significantly warmer microclimate than those that the females reject, and show for the first time that no such distinction is detectable across the distribution of summer eggs, when all selected *H. comosa* plants have a similar (slightly warmer) micro-environment to those preferred in autumn. Moreover, the differences in autumn plants would probably have been amplified had we also measured variation in micro-temperatures across the three shelter categories, with category 3 plants expected to be warmer than category 1 plants (Morris *et al.* 1994). As with other thermophilous insects studied near their range edges (e.g. Bourn and Thomas 2002; Cherrill and Brown 1992; Thomas 1991, 1993; Thomas *et al.* 2001a), we believe that these results reflect the direct effect of temperature on *P. bellargus*' oviposition behaviour and larval fitness rather than indirect effects on the foodplant. Although we did not examine seasonal variation in the quality of *H. comosa* from different microhabitats on *P. bellargus*, our experience of rearing many larvae suggests that leaves from short and tall plants are equally palatable, resulting in pupae of similar size. Moreover, if there were a local shift in the palatability of *H. comosa* during the year, as described for *Lotus corniculatus* the foodplant of *Polyommatus icarus* (Dennis 1984), we would expect to observe the opposite pattern of egg-laying (resembling that of *P. icarus*) to that recorded for *P. bellargus* (Fig. 1b), with summer eggs being laid preferentially on the recently-cropped (short regenerating) plants rather than on the older (tall) leaves.

Unlike the foodplants of *P. icarus*, *H. comosa* is a deep rooted perennial adapted to withstand the normal summer soil-water deficits of its thin-soiled sites (Smith 1980). Only in exceptional years of drought does *H. comosa* become noticeably unpalatable for *P. bellargus* (Thomas and Merrett 1980; Thomas 1983); years which account for most of the occasional declines recorded in its second adult generation. However, populations do not decline further over winter, suggesting site carrying capacity rather than increased over-winter mortality limits first generation counts. Similar extreme drought effects are reported in other butterfly species (Pollard *et al.* 1997), due to higher larval mortalities when water content and nitrogen levels in foodplants are low (Pullin 1987).

Climate warming is likely to be beneficial to *P. bellargus* across northern Europe, where warmer summers are currently predicted (Hulme and Jenkins 1998). Already, its average appearance date in the UK has advanced during the last two decades, suggesting that warmer climates have accelerated larval development during spring (Roy and Sparks 2000). Like the univoltine butterfly *Hesperia comma* in the same UK landscapes (Thomas *et al.* 2001a), *P. bellargus* is expected to expand into sites with cooler microclimates, confirming the need to conserve high habitat heterogeneity for butterfly populations to persist under changeable weather (Bourn and Thomas 1993; Singer 1972; Sutcliffe *et al.* 1997; Thomas *et al.* 1996; Weiss *et al.* 1988). Habitat heterogeneity may also help mitigate the increased incidence of droughts predicted for southern England (Hulme and Jenkins 1998), by providing microsites for *H. comosa* plants to grow in taller turf less susceptible to desiccation. After decades of steep decline, UK *P. bellargus* populations have indeed increased in abundance and more than doubled in number during the past 20 years within those landscapes that it already occupied (Asher *et al.* 2001; Bourn *et al.* 2000), but how much of this recovery is due to targeted conservation management following our original recommendations (Thomas 1983), how much to the fortuitous return of rabbit grazing to many sites, and how much to climate change is unclear. We also predict that the difference in abundance between first and second adult generations of *P. bellargus* (Fig. 2) will diminish under warmer climates, if our hypothesis about an annual bottleneck in site carrying capacities is correct. However, this has yet to be detected in the BMS time-series.

The main constraint on the exploitation of new habitat by *P. bellargus* under warmer climates is likely to be its ability to reach new sites in vacant landscapes. The adults in UK populations are extremely sedentary (Thomas 1983) and patches of calcareous grassland containing *H. comosa* are highly fragmented across most of *P. bellargus*' northern range margin in Europe. Certainly, no northward spread has been detected in *P. bellargus* to date, in contrast to several of the more mobile butterfly species of Europe (Hill *et al.* 1999; Parmesan *et al.* 1999; Warren *et al.* 2001). Even within the core UK landscape where *P. bellargus* is most abundant, site isolation quite strongly explains which individual patches of calcareous grassland are occupied by its populations, although the density of autumn-spring growth forms of *H. comosa* within these patches is an even stronger (independent) explanatory factor (Thomas *et al.* 2001b). Our studies in this landscape suggest that this latter variable, which, through grazing, is largely under human control, can alter the carrying capacity of occupied sites by >100-fold, making existing populations more persistent in habitat of optimal quality, as well as greatly increasing both the number of emigrants in the landscape and the probability that invading females will establish successfully after reaching a new patch (Thomas *et al.* 2001b).

To achieve optimum habitat for *P. bellargus*, we now provide a different recommendation for summer management to our original prescription (Thomas 1983). While it remains paramount to ensure that an abundance of shortcropped sheltered turf exists for the presumed population bottleneck every autumn-spring (even in the warm, late- 1990s, UK *P. bellargus* densities were strongly correlated with variation in autumn habitat: Thomas *et al.* 2001b) uniformly close-cropped swards are no longer recommended for the summer brood, because these females avoid the shortest foodplants. Instead, we recommend a regime that provides short turf in March and April, light or no grazing throughout May to late July, and sufficient grazing from late July onwards not only to restore the average sward height to <3 cm tall, but to allow time for the bitten-back *H. comosa* plants to regenerate fresh leaves for September oviposition. Not only should this regime maximise *P. bellargus* populations, it also removes the current conflict of grazing conservation grasslands intensively in May–July, now allowing most plants to flower and seed, and the invertebrates of later seral stages to co-exist with *P. bellargus*.

Table 4.1. Mean soil surface temperature beneath *Hippocrepis comosa* plants growing under two categories of turf height. Data is for the first 6 weeks following egg-laying by first (summer development) and second brood (autumn development) *Polyommatus bellargus* adults

Development Period	Sward height category (cm)	Mean temperature (SE) (°C)
Summer	1–2	17.5 (0.33)
Summer	4–6	17.6 (0.15)
Autumn	1–2	18.0 (0.08)
Autumn	4–6	17.4 (0.05)

Table 4.2. The mean proportion of *H. comosa* plants on 24 UK sites scored, using egg distributions from Figure 1, for their suitability for *P. bellargus* at different times of the year.

Period of the year	Mean proportion (SE) of *H. comosa* plants
Autumn	0.13 (0.02)
Summer	0.47 (0.05)
Autumn and summer	0.23 (0.04)
None	0.17 (0.04)

Figure 4.1. The distribution of eggs laid on *Hippocrepis comosa* in A autumn generation and B summer by *Polyommatus bellargus* females in different heights of turf within three categories of shelter: 1 unsheltered, 2 limited shelter, 3 complete shelter. Black Plants used in summer only, dark grey autumn only, white both summer and autumn

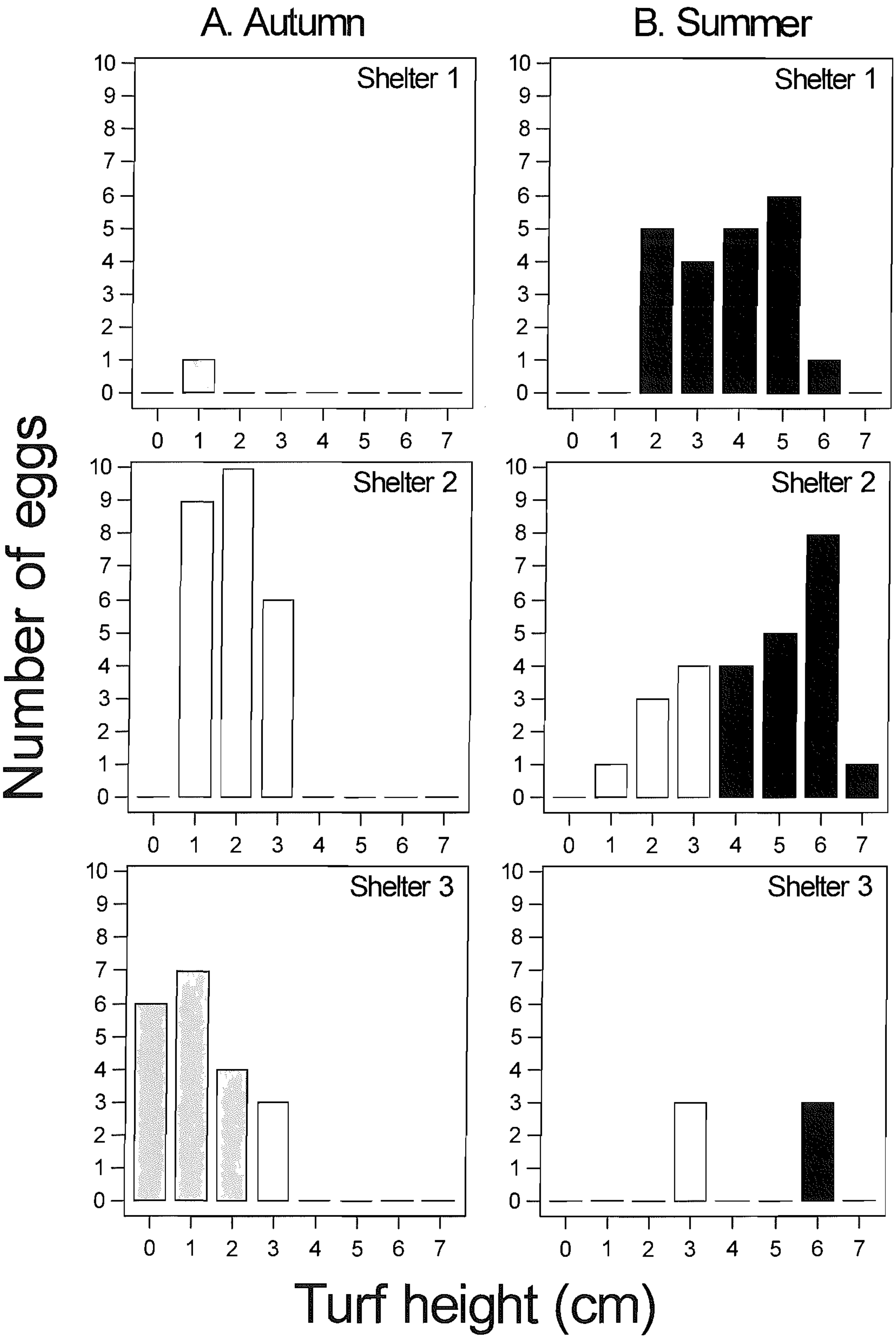
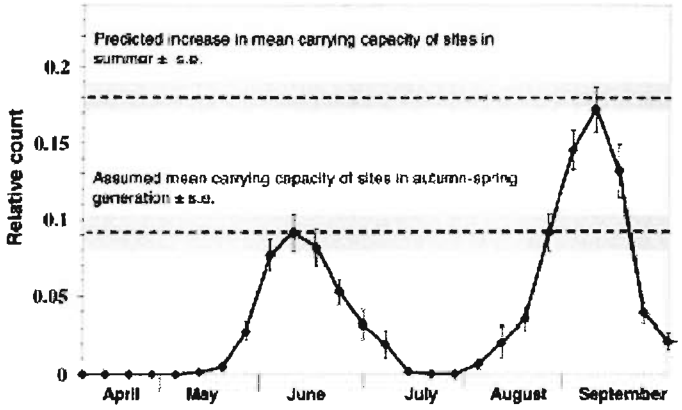


Figure 4.2. Mean BMS count per site of *P. bellargus* adults (solid line) expressed as a proportion of annual site totals in 1976–2000. Dashed lines (SE in grey) indicate seasonal differences in the mean predicted carrying capacities of *P. bellargus* sites, based on the availability of *H. comosa* (Table 2) to the young stages of each adult generation, with the spring-autumn value fitted to the peak of the May–June adult emergence, on the assumption that this represents an annual bottleneck for *P. bellargus* populations



5 Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change

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5.1 Abstract

1. The effect of weather on the size of British butterfly populations was studied using national weather records and the Butterfly Monitoring Scheme (BMS), a national database that has measured annual changes in abundance since 1976.

2. Strong associations between weather and population fluctuations and trends were found in 28 out of 31 species studied. The main positive associations were with warm summer (especially June) temperature during the current and previous year, low rainfall in the current year and high rainfall in the previous year. Most bivoltine species benefited from warm June weather in the current year, three spring species and two that overwinter as adults benefited from warm weather in the previous summer, and most species with moist or semi-shaded habitats increased following high rainfall and cooler weather in the previous year.

3. Simple models incorporating weather variables and density effects were constructed for each species using the first fifteen years' population data (1976-90). These fitted the observed data for that period well (median $R^2 = 70\%$). Models were less good at predicting changes in abundance over the next seven years (1991-97), although significant predictive success was obtained.

4. Parameter values of models were then adjusted to incorporate the full 22-year data-run. For the eight species whose models had best predicted population changes or fitted the data well ($R^2 > 85\%$), models were run from 1767 to 1997, using historical weather records, to "predict" trends in abundance over the past two centuries. For three species it was possible to compare predicted past trends

with contemporary accounts of abundance since 1800. In each case, the match between predictions and these qualitative assessments was good.

5. Models were also used to predict future changes in abundance, using three published scenarios for climate change. Most, but not all, species are predicted to increase in the UK under warmer climates, a few species stayed stable, and only one species - the agricultural pest *Pieris brassicae* (Cabbage White) - is predicted to decline.

5.2 Introduction

There is mounting evidence of human-induced global climate change attributable to increased levels of 'greenhouse gases'. Mean surface air temperatures are reported to have increased globally by 0.3-0.6 °C in the 20th century, of which 0.2-0.3 °C has been within the past 40 years. Current predictions for warming at the end of the next century range from 1-3.5 °C, with a "best estimate" of 2 °C (Houghton *et al.*, 1996). Changes in precipitation have not been observed so clearly and are more difficult to predict, but most models agree that winter precipitation is likely to increase in northern latitudes (Houghton *et al.*, 1996).

The challenge to predict the possible effects of climate change on plants and animals has concerned ecologists since the mid-1980's. In addition to changes in biodiversity (e.g. de Groot *et al.*, 1995; Markham, 1996), the impacts of such effects on man's activities may include direct economic and health impacts on, for example, agricultural production (Parry, 1992; Rosenzweig & Hillel, 1998), forestry (Schwartz, 1992), insect pests (Cannon, 1998; Sutherst, 1995), disease vectors (Lindsay & Birley, 1996; Sutherst, 1998) and the incidence of climate-related diseases (Langford & Bentham, 1995). The ecological effects can be broadly grouped into four categories (de Groot *et al.*, 1995): changes in abundance or geographical distribution of species or the communities which they form (e.g. Hengeveld, 1995; Huntley, 1995; Parmesan *et al.*, 1999; Thomas *et al.*, 1999), changes in species' phenology (e.g. Crick *et al.*, 1999), changes in inter-specific interactions, and changes in physiology (Körner, 1993).

Butterflies are an ideal group for studying the effects of climate change because, as poikilothermic organisms, their life-cycle, activity, distribution and abundance are influenced by temperature (Dennis, 1993; Pollard, 1979, 1988; Roy *et al.*, 2000; Turner *et al.*, 1987). Furthermore, unusually accurate long-term (1976-97) population data for developing models are available from the UK's Butterfly Monitoring Scheme (BMS) (Pollard & Yates, 1993). Finally, records and anecdotal accounts of change in the distribution and abundance of certain UK butterflies during the past two centuries are detailed enough to test the longer-term predictive ability of models, at least for species whose habitats have remained comparatively stable.

In a preliminary analysis, Pollard (1988) used the BMS data from 1976-86 to test for significant associations between butterfly abundance and climatic variables. The most striking association was an increase in abundance with warm, dry summers. There was also an association of increased numbers and high rainfall early in the previous year, but winter temperature and rainfall showed no strong associations with butterfly abundance. For one species, *Pyronia tithonus*, historical patterns of changing abundance since 1800 were shown to correspond roughly to backward predictions from a simple model based on these associations (Pollard & Eversham, 1995).

The opportunity is taken now to use eleven further years' data to reassess the association between butterfly abundance, weather and climate. The range of types of model was widened, and predictive models, developed using part of the time period available (1976-90), were used with observed weather data to predict butterfly numbers in 1991-97. The predictions were then compared with the observed data. For species where agreement between fitted and observed population levels was good, past and future butterfly numbers were predicted using historical weather data spanning the last two centuries and various climate change scenarios.

5.3 Methods

5.3.1 Butterfly counts and calculation of collated index values

The BMS is based on transect counts at sites throughout Britain. There were 34 sites in 1976, rising to over 100 from 1979 onwards. At each site, an observer recorded all butterflies seen within prescribed limits along a fixed route (for details and validation of the method see Pollard & Yates, 1993). Counts were made in 26 weeks from the beginning of April until the end of September, provided that weather conditions met specified criteria.

An index of abundance for each species on each site was calculated by addition of the weekly counts (Pollard & Yates, 1993). For species with more than one discrete flight period per year, a separate index was obtained for each period and that for the second flight-period was used in this study. The index values for all sites were collated to produce a regional trend. The method is based on ratios of counts in successive years using those sites recorded in both years. The collated index for a given year is then calculated by multiplying an initial arbitrary value (100) by successive ratio estimates, i.e. the collated index for year *t* is given by $I_t = 100r_{12}r_{23}. . . r_{(t-1)t}$ The present analysis used a modified method which downweights the contributions from sites with larger numbers (Moss & Pollard, 1993).

5.3.2 Weather Data

The analysis used monthly Central England Temperature (CET) data (Manley, 1974; Parker *et al.*, 1992); and England and Wales Precipitation (EWP) data (Jones & Conway, 1997; Wigley, Lough & Jones, 1984). The recording period included the exceptionally hot and dry summer of 1976 and three winters with very cold periods (January 1978-79, December 1981-82 and February 1985-86). There were cool summers from 1977-80, followed by warmer summers from 1982 to 1984, 1983 being the warmest. The summers in 1985, 1986 and 1993 were cool. In general, the warm summers were dryer than cool summers. Mean temperature for January-April and May-August (excluding 1976) showed similar significant increases (Table 1, Figure 1). Throughout this paper we define summer as the months June-August and winter as December, January and February.

5.3.3 Analysis and modelling of associations with weather

Data from the first 15 years of the BMS (1976-90) were used to develop predictive models for individual species, then data for the next 7 years (1991-97) were used to test the models. Analyses were restricted to 31 species that are recorded from a sufficient number of sites and years to produce an all-sites collated index. Species that are migrant in Britain, *Vanessa atalanta* and *Cynthia cardui*, were excluded.

The analysis of changes in butterfly numbers and weather is based on a Gompertz model for log index (or first-order autoregressive scheme) with weather variables as covariates (Pollard, 1988; Pollard & Lakhani, 1985). For a model with one weather variable, changes in the log index are given by

$$Y_{t+1} = a + b_0 Y_t + b_1 W_t + Z_t$$

where Y_t denotes the $\log_{10}$ collated index in year *t* and W_t is the value of the weather variable associated with the change in the index from year *t* to year *t* +1, which may include weather in either the current or previous year. The last term, Z_t, denotes a random component of change in the index.

The effect of the previous year's index is included for two reasons. First, in the chaining method the index in year *t* +1 is calculated as the index in year *t* multiplied by the ratio of the counts for sites monitored in both years (r_t), i.e. $I_{t+1} = r_t I_t$ and $Y_{t+1} = \log r_t + Y_t$. Second, the growth rate may be density dependent being lower at higher population densities: this is allowed for in the model by the slope coefficient b_0 of less than unity.

The model describes changes in butterfly abundance at the regional level, although these changes occur as the result of changes at the local site level. A justification for analysing overall change is the observed widespread synchrony in butterfly population fluctuations on a large spatial scale, which is partially ascribed to weather-related regional stochasticity (Pollard, Hall & Bibby, 1986; Pollard & Yates, 1993; Sutcliffe *et al.*, 1996). The effects of density-dependent processes operating on a local scale are included implicitly in the model through their indirect effects on population change at the regional scale.

An alternative formulation to the above is the first-order discrete logistic model in which successive values of the index are related by

$$I_{t+1} = I_t \exp(a + b_0 I_t + b_1 W_t + Z_t)$$

where I_t denotes the index for year t, W_t is the weather variable and Z_t is a random effect. In this model the underlying relationship between change in log index is linear in the index, rather than log index as in the Gompertz model. A preliminary analysis showed that there was little to choose between models. However, the Gompertz model accounted for more variation in the change in log index in 15 out of 19 non-tied cases, so it was used for the main analysis reported below.

When the model was extended to several weather variables a basic problem was which variables to include - there are 40 variables to choose from and only 15 years data (1976-90). With so many potential subsets of variables, some reduction in the number of variables was necessary. We used the following preliminary selection procedure based on the empirical evidence and the biology of each species. 1) The model was fitted to the data using each of the weather variables in turn; any variable which was statistically significant at the 10% level was considered as a candidate for further consideration. This also involved fitting quadratic effects in weather variables and graphical examination of any apparent trends. At this stage we chose a fairly liberal threshold to reduce the chances of missing effects, accepting the inflated Type 1 error. The number of variables for inclusion then varied between two and ten, depending on the species. 2) Biologists EP and JAT examined the sets of selected variables and eliminated any that seemed to have no reasonable biological explanation. The approach took into account the direction of the effects in the months either side of the one under consideration. This subjective approach, taken to reduce the number of spurious weather variables, may have been at the cost of losing a few variables that had real but counter-intuitive effects. The full range of weather variables can be seen as they are presented prior to the development of models.

For each species, the selected set of weather variables was further analysed by fitting models containing different combinations of variables, using best subsets regression to find the best-fitting models (i.e. largest R^2) for a specified number of variables. We used the Akaike Information Criterion (AIC), with correction for small sample size

(Hurvich & Tsai, 1989), to compare the fit of models containing different numbers of weather variables.

Models were tested against the 1991-97 data by predicting the log index values. Predictions were made (1) stepwise using the observed value of the previous index, and (2) free-running starting with the observed index in 1990. Predictive success was measured using the root mean square error and the Pearson correlation between observed and predicted values.

5.3.4 Past and Future Prediction

Historical weather data and climate change scenarios were used to predict past and future population changes for eight species for which models based on the earlier BMS period (1976-90) either gave predictive success ($P < 0.05$) for the later period (1991-1997) or both fitted the data for the earlier period closely ($R^2 > 85\%$) and gave some predictive success ($r > 0.3$). For these species, regression models, using values from the full BMS time-series (1976-1997), were applied to monthly weather summaries of the Central England Temperature series and England and Wales Precipitation series spanning the last two centuries (1767-1997), to predict past fluctuations in butterfly numbers. To test predictions, attempts were also made to reconstruct the major shifts in status recorded for each species over the same period, from the many local atlases and regional accounts of British butterflies that have been compiled in recent years. Predicted patterns of past abundance were then compared with the historical record.

Due to the anecdotal, and mainly qualitative, nature of most early butterfly records, we scored past changes in status simply as an 'increase' or decrease' in a particular year, decade, or longer using the following criteria. 'Increase' equals any report of exceptional local abundance or increase in numbers, or the local colonisation of new sites or an extension of range. 'Decrease' represents any of the opposite changes. The following sources were used for the historical reconstructions: (Arnold *et al.*, 1997; Baker, 1994; Bristow, Mitchell & Bolton, 1993; Collins, 1995; Corke, 1998; Duddington & Johnson, 1983; Emmet & Heath, 1989; Fox & Asher, 1999; Frost & Madge, 1991; Gay & Gay, 1996; Hall, 1991; Harrison & Sterling, 1985; Heath *et al.*, 1984; Horton, 1994; Mabbett & Williams, 1993; Mendel & Piotrowski, 1986;

Morgan, 1989; Philp, 1993; Pratt, 1981; Rafe & Jefferson, 1983; Sawford, 1987; Smith, 1997; Sutton & Beaumont, 1989; Thomas *et al.*, 1998c; Thomas & Webb, 1984; Thomson, 1980; Whalley, 1997).

Climate change scenarios for the United Kingdom (UKCIP98 Hulme *et al.*, 1998) were used to predict future changes in butterfly numbers. Four scenarios that span a range of possible future UK climates predict change from a baseline climate of 1961-1990 at three future time periods: 2020s, 2050s and 2080s. Regression models based on the full BMS time series (1976-1997) were used to predict the theoretical mean population levels of butterfly species for each scenario at each future time periods. In addition, simulations of future butterfly numbers were performed to incorporate the year-to-year variability in past weather. The medium-high UKCIP98 climate change scenario was used to calculate the predicted increment in monthly weather values up to 2080. These increments were added to the weather from a year chosen at random from the CET and EWP series from 1767 to 1997. For each year from 2000 to 2080, historical weather was chosen one hundred times at random and the predicted butterfly numbers calculated. From these predictions the mean and 90% interval values were derived.

5.4 Results

5.4.1 Assocations with Weather

For the 1976-97 period the frequency of significant linear weather associations at the 5% level (Tables 2 & 3) is significantly greater than expected for both temperature (12.8%) and rainfall (7.8%). Corresponding values for 1976-86 were 8.1% and 5.2% (Pollard, 1988), reflecting the greater statistical power by using the longer series. The excess of significant associations was due mainly to the frequency of positive associations with temperature (8.9%) and negative associations with rainfall (6.1%). The frequency of positive associations for rainfall (1.8%) was no more than expected by chance. Significant quadratic relationships were few and were not considered further.

The patterns of association between index values and monthly temperature and rainfall (Tables 2 & 3) generally confirmed the findings of Pollard (1988) and can be summarised as follows.

(1) One group of species, including *Melanargia galathea*, *Pyronia tithonus* and *Aglais urticae,* showed significant increases associated with warm, dry summers in both the current year and previous years. The beneficial effect of warm weather only in the current summer was especially marked for several bivoltine species, including the lycaenids *Lycaena phlaeas*, *Polyommatus icarus* and *Aricia agestis*. For the bivoltine pierid species *Pieris brassicae* and *P. napi*, the associations were strongest with warm spring weather.

(2) Beneficial effects of warm and/or dry summer weather in the previous year, but not in the current year, were shown by *Gonepteryx rhamni* and *Inachis io*, which overwinter as adults, by the spring-flying species *Pyrgus malvae* and *Clossiana euphrosyne*, and by *Argynnis aglaja*.

(3) In contrast *Aphantopus hyperantus*, *P. napi*, *Lasiommata megera*, *Polygonia c-album*, and *Pararge aegeria* showed significantly reduced index values associated with higher temperature in the previous summer and *P. aegeria* also showed a significant increase associated with wet weather in the previous summer. All these species apart from *L. megera* have moist or semi-shaded habitats.

Index values generally decreased with high rainfall in the current year and the latter part of the previous year, especially November, but increased, often significantly, with high temperature and to a lesser extent with high rainfall for some months in the early part of the previous year. Recall, however, that the total number of positive associations with rainfall was not significantly different from that expected by chance.

There were some significant associations with weather during the winter, with increases associated with cold months for *Erynnis tages*, *M. galathea*, *Limenitis camilla*, *G. rhamni* and *I. io* (the last two over-winter as adults) and with wet months for *L. camilla*.

5.4.2 Model Selection and Prediction

Table 3 shows the weather variables chosen for best subsets regression using data for 1976-90 and applying the preliminary selection procedure based on considerations of statistical and biological significance (see Methods). Of the 31 species analysed, no weather variables were selected using these criteria for *I. io*, *Lysandra coridon* and *A. urticae*. Model selection was based on a reduced number of years to enable independent prediction for the later years. However, regression models used for historical and future predictions were based on the full time series (1976-1997).

The ability of fitted models to describe the fluctuations in population indexes during 1976-90 is shown in Fig. 2 and Table 4. For many species the models fit rather well, with the percentage variation accounted for (R^2) exceeding 70% in 18 out of 29 cases. Three notable exceptions are *Anthocaris cardamines*, *Callophrys rubi* and *A. aglaja* with values of R^2 between 30-35%, perhaps because models for these species were based on low counts per transect and, in the case of *C. rubi* and *A. aglaja*, on a comparatively small number of sites. In general, models for species with indexes based on large counts were the most successful in prediction.

The fits of stepwise and free-running predictions for individual years during 1991-97 are summarised in Table 4 and illustrated in Fig. 3. Overall the mean correlations were: stepwise $r = 0.243$ +/- 0.072 (S.E.) and free-running $r = 0.150$ +/- 0.081. The former was significantly greater than zero (Wilcoxon matched pairs test, $p < 0.004$) while the latter just failed to reach significance ($p = 0.068$), suggesting some, albeit small, overall predictive success. There is a positive relationship between observed and predicted mean log population index during 1991-97 ($r = 0.19$) (Fig. 3).

Positive associations with summer temperature were retained in the final models (Table 5), with June temperature in particular appearing in 13 models. Associations of increases with dry summer weather, both in previous and current years featured quite strongly in the models, with seven recorded for the previous summer and eight for the current summer. There were rather few associations retained with wet weather in the previous spring, but in four cases a hot previous June or July was associated with decreases in numbers (*Argynnis paphia*, *A. hyperantus*, *L. megera* and *P. aegeria*).

The positive associations with cold or dry winters noted for the full data set, were now represented only by the *E. tages* and *L. camilla.*

For some species there was a relatively weak relationship between successive values of the log index. Those with estimated slope coefficients less than 0.2 were *E. tages, P. rapae* and *P. napi*. All these species typically occur at low densities on sites or have open populations, and are less likely to show strong within-population trends or density dependence.

5.4.3 Predicting the Abundance of Butterflies

Of the 28 species found to have a strong association between weather and abundance (Table 5), only eight butterflies gave models that met our further criteria for predictive ability and fit with the original data. The analyses and models for six of these species (*Ochlodes venata, P. brassicae, P. napi, P. icarus, P. tithonus* and *L. megera*) were based on large data-sets of population change (110-143 sites per species); those for *M. galathea* and *P. malvae* were based on changes in 67 and 37 populations respectively. Despite reservations about the sample size of *P. malvae*, we felt able to employ these eight models to predict abundance beyond the recording period using various scenarios for climate change to predict future changes. Fluctuations in past populations were predicted for three species (*M. galathea, P. tithonus* and *L. megera*), which have a large body of documentation on historic changes in status and range. Evidence of past population fluctuations for other species was considered too anecdotal to validate our models. In both sets of predictions, it is important to note that we assume the same availability of biotopes and species' habitats in the UK as in 1976-97, although to some extent the effect of weather variation on both the fundamental and realised niche – and hence on the growth rates and carrying capacity of sites - for individual species is expressed as variation in the empirical (BMS) population data from which the models are derived.

5.4.3.1 Historical patterns of abundance

Predicted fluctuations in past population levels are large for *M. galathea, P. tithonus,* and *L. megera,* with log index values typically varying from less than 1.5 to over 2.5 (Fig. 4). There is no clear evidence of a trend (of increasing abundance) in these species; they are predicted to have experienced alternating periods of above-average abundance and troughs since 1767, each of which often lasted for a decade or longer. The incidence of predicted peaks and troughs is similar for *M. galathea* and *P. tithonus*, with a period of comparative abundance in the late eighteenth and early nineteenth centuries being followed by marked troughs during the 1820s and early '30s (especially for *M. galathea*), by further troughs towards the end of the nineteenth century and during the first three decades of the twentieth century, followed by predominantly above-average abundance from the 1940s onwards.

M. galathea, P. tithonus, and *L. megera* occupy broad niches (all within the later seral stages of grassland) which have remained comparatively abundant in recent centuries (Thomas & Lewington, 1991). All three species experienced substantial well-documented fluctuations in status and range since records began; these fluctuations are plotted above our predictions of former abundance (Fig. 4). In each case, predicted and reported abundance are in broad accord. For *M. galathea,* 31 out of 36 recorded changes in status since 1820 are in the same direction as that predicted by its model ($P < 0.001$); for *P. tithonus,* 27 out of 30 historical records are in accord with predictions ($P < 0.001$), and for *L. megera,* 49.5 out of 61 records match predictions ($P < 0.001$).

Both the model and contemporary records suggest that *M. galathea* declined and experienced many local extinctions after the early decades of the 19th century, when it not only disappeared from much of the northern and eastern parts of its former range (e.g. Corke, 1998; Heath *et al.*, 1984; Mendel *et al.*, 1986; Sutton & Beaumont, 1989) but was also 'very uncommon' and localised in current strongholds such as Cornwall (Smith, 1997). Further periods of local decline and range contraction occurred in the late nineteenth and early decades of the twentieth century. From about 1940 onwards, there has been a recovery, during which *M. galathea* increased locally (e.g. Heath *et al.*, 1984; Mabbett *et al.*, 1993; Philp, 1993; Sawford, 1987; Smith, 1997; Thomas *et al.*, 1984) and expanded in range both around its northern refuge in the Yorkshire Wolds and along the main 'front' of its northern limit, across the Midlands, Cambridgeshire and in East Anglia (Arnold *et al.*, 1997; Fox *et al.*, 1999; Rafe *et al.*, 1983; N Greatorex-Davies *pers. comm.*).

Model predictions and regional accounts also indicate that *Pyronia tithonus* declined and contracted greatly in range after the early nineteenth century, and again during the 1870s and c.1920-1940. As with *M. galathea*, a recovery occurred throughout its recorded range, accompanied by a substantial northwards expansion during the 1970s-late 1990s during which it re-occupied much of its former English range (Corke, 1998; Dunn & Parrack, 1986; Emmet *et al.*, 1989; Fox *et al.*, 1999; Harrison *et al.*, 1985; Heath *et al.*, 1984; Pollard, 1991a; Pollard & Eversham, 1995; Pratt, 1981; Sutton *et al.*, 1989; Thomson, 1980; Whalley, 1997).

Throughout its range, *L. megera* has been noted for extreme fluctuations in local abundance, extinction and recolonisation (e.g. Dennis & Bramley, 1985; Thomas *et al.*, 1991) consistent with the variability predicted by our model (Fig. 4). As with *M. galathea* and *P. tithonus*, patterns of local extinction and recovery are more apparent (and hence better documented) in the northern half of its range, where populations are more locally distributed. Thus *L. megera* populations reached their historical peak in the mid 19th century in Scotland (Thomson, 1980) and in north-east England, where it was often the most abundant satyrid (Emmet *et al.*, 1989). A major decline began towards the end of that century, resulting in widespread extinctions throughout the north. Ten major shifts in abundance are predicted during the twentieth century, which again generally match contemporary reports, with local recovery and expansions in the 1940s and other favourable periods (e.g. Dunn *et al.*, 1986). However, the prediction is of below-average numbers during the twentieth century, consistent with the extraordinary decline experienced by this once common species during recent decades throughout most of its British range (Fox *et al.*, 1999).

We therefore conclude that our models are successful in predicting broad medium-term trends in abundance for three species which have (a) models which show good fits to recorded date and/or some success in short-term prediction, (b) occupy niches which have remained relatively stable (Fig. 4).

5.4.3.2 Future predictions involving climate change

The mean population level of four of the eight species modelled under climate change scenarios is predicted to increase (Table 6, Fig. 5). The log index for *P. icarus, P. tithonus* and *M. galathea* are expected to become 50% greater by 2080 under a high climate change scenario (Table 6). There is almost no change in index predicted for *P. malvae* even under the most extreme scenario, while *M. megera* shows an initial increase for five years before stabilising at a level fractionally below its mean national density in 1976, at the start of the BMS recording period. In contrast, a substantial decline is predicted for the pest species, *P. brassicae*, under all scenarios of climate change.

Models were more successful at predicting qualitative trends in historical abundance than at predicting precise annual population size. Although we do not publish figures for the next eight best species, this larger sample gave the same qualitative predictions as the original eight butterflies under scenarios of climate change: four additional species (*Thymelicus sylvestris, Clossiana selene, M. jurtina, A. agestis*) increased throughout the simulation period, one (*P. aegeria*), like its close relative *L. megera*, briefly increased before stabilising, and three species (*A. cardamines, G. rhamni, L. camilla*) showed no trend. As with the original eight species, we detect no pattern among species that are predicted to increase, apart from the beneficial effect of warm summer temperatures on most. Thus this group includes representatives from all the main butterfly families; both univoltine and bivoltine species; species living both near their edges and centres of range; and species that inhabit a diverse range of biotopes.

5.5 Discussion

5.5.1 Assocations with Weather

Our analysis shows statistically significant associations between the abundance of most UK butterfly species and monthly rainfall and temperature, and that the number of associations has increased with the additional of 11 years' data since Pollard's (1988) original study.

It is possible to provide speculative reasons for almost any association found between abundance and weather. Here we limit discussion to the clearest patterns of associations, to reduce the danger of unwarranted speculation. The discussion is based mainly on the independent associations with weather for individual months, rather than the reduced number of variables selected for the models.

The strongest associations, based on the whole 22-year period, were with current summer temperature, so strengthening the similar conclusion by Pollard (1988), based on 11 years' data. This result is also consistent with Turner *et al.*'s (1987) demonstration that the northern boundaries of the ranges of most European butterfly species are most closely correlated with June-July isotherms. Since about 80% of resident UK butterflies reach their northern range limits somewhere in the UK (Thomas, 1995a), it is not unexpected that a positive association would be found between local abundance and June temperatures among British butterfly species as a whole (Pollard & Yates, 1993). Moreover, Parmesan *et al.* (1999) list the stability or changes of 65 European butterfly species at their northern limits in recent years: 12 of the species we found to have a positive association between population size and warm summers (Table 3) have experienced major northward expansions in Europe coinciding with recent warmer summers, whereas just three of these species are reported as having had stable northern range boundaries.

In our analyses of population trends in 1976-90, June temperature showed most significant results, and the importance of June temperature was increased amongst variables selected for the full predictive models. For the univoltine species with such associations, June is the period of late larval and pupal development, suggesting that survival of these stages was greater when high temperatures increased development rate. For the bivoltine species, which showed the strongest associations with warm summers, the benefit may be spread more widely over the life-cycle, perhaps including improved oviposition by adults of the spring generation. Another possibility, during warm summers, is that a higher proportion of individuals in populations develops into second generation adults among species which display partial bivoltinism, such as *P. icarus* and *Coenonympha pamphilus*. For all bivoltine species, further analysis using the indexes for both generations is possible and may help to clarify the timing of weather effects.

For *P. tithonus* and *M. galathea*, there were quite strong associations with weather in both current and previous summers. These were also shown in the predictive models based on the shorter period (Table 4) and largely validated by the historical predictions and reconstructions (Fig. 4). In the case of *M. galathea*, this association is presumably due to improved oviposition, as the larvae enter hibernation immediately on hatching. *P. tithonus* has similar oviposition dates, but also exhibits larval growth prior to hibernation; the significant association with warm September (Table 4) weather suggests a beneficial effect at this stage. Both are among the species that have expanded their northern range limits most notably in recent years (Fig. 4), and are predicted to increase further under all scenarios of climate change that we investigated (Table 6).

Three species over-wintering as adults, *G. rhamni*, *I. io* and *A. urticae* showed positive associations between temperature in the previous summer and increased index values. Pullin (1987) showed that limiting the feeding time of adults of the last two species reduced over-winter survival; this may explain the results found here.

A group of species is thought to be susceptible to desiccation of food-plants through drought (Pollard, 1988). These species especially include *A. hyperantus* and *P. aegeria*, which show strong associations between decreased abundance and warm and/or dry weather in the previous summer. It is perhaps significant that the larvae of these satyrids respectively prefer moist and semi-shaded habitats.

Although there has long been a view that butterflies benefit greatly from cold winters (e.g. Beirne, 1955), Pollard (1988) found very few significant associations with winter weather. This remains the case, although the five significant associations that were recorded did show beneficial effects of cold and/or dry weather. Note however, that some of these associations were lost in the final predictive models.

5.5.2 Prediction

Despite the marked associations with weather and the good fit of models to the data for 1976-90, predictions of the patterns of fluctuations during 1991-97 were rather poor, although overall, there was statistically significant success in predicting annual population values. On the other hand, we had greater success in predicting mean levels (Fig. 3) and predictions made by the 22-year models matched qualitative historical records of changing abundance well for some species (Fig. 4).

The generally poor success of initial models to predict species' fluctuations in 1991-97 was disappointing yet salutary. Butterflies were considered amongst the most promising groups for short-term prediction of effects of climate change. Their population data are amongst the best available for any terrestrial invertebrate, and most stages in their life-cycles have been shown to be strongly affected by weather. To date, it has been rare for predictions describing population changes in any taxon to be tested against observed data in this way. If claims of good predictive power are made, they should be tested against real data.

Possible explanations for the limited success of the 1991-97 predictions are: (1) The analysis has omitted factors other than weather and density effects that may be driving population fluctuations. It is also possible that other measures of weather could be explored and would perform better. (2) There may be bias in the initial model selection procedure. (3) The models may be based on too few years' data or applied to changes on too large a spatial scale. However, similar analyses, made at finer scales of UK regions and single sites are likely to be subject to the confounding effects of site management. (4) The weather variables used are adequate to show associations with weather, but inadequate for the much more difficult task of prediction.

Our models appear adequate to predict qualitative rather than quantitative long-term changes, and this may be all that is achieved from models based on correlations between BMS data and weather variables. However, for most purposes, qualitative predictions of major changes in the abundance of species are all that are required by policy makers, farmers and conservationists. Our historical predictions seem to confirm the important role of weather in driving the major shifts in abundance and range of *M. galathea*, *P. tithonus* and *L. megera* during the past two centuries. Our models (Table 5) suggest that there have been considerable increases due to favourable weather in the status of many species during the second half of the twentieth century. This supports Pollard & Eversham's (1995) hypothesis that many of the steep declines among UK butterflies caused by habitat loss over this period would have been even more severe were it not for the mitigating effect of favourable weather on surviving populations. It may also explain the paradox of several species that have simultaneously expanded in range over the past 60 years whilst experiencing major declines, through habitat loss, within their former ranges (Heath *et al.*, 1984).

Further increases are predicted for most UK butterflies under the most widely accepted scenarios for climate change. This is consistent with predictions that increased areas of habitat will become available to poikilothermic species that currently live near their northern range limits in the UK (Thomas *et al.*, 1999). This prediction may not hold under alternative scenarios in which increased temperatures are accompanied by reduced rainfall (e.g. Pollard *et al.*, 1997b). Nor does the BMS adequately sample the few alpine species whose southern range limits occur in north Britain: it is logical that these would decline (Thomas *et al.*, 1999). These provisos apart, the best available data suggest that the only species for which a substantial decline is predicted under climate warming is *P. brassicae,* the main agricultural pest among UK butterflies, whilst all the benign species of butterfly will increase or, in a few cases, remain. Despite the attractiveness of this conclusion, we urge that it be adopted with caution until more precise models giving quantitative predictive success become available.

Table 5.1. Summary of estimated trends in temperature and rainfall 1976-97.
* $P < 0.05$. [a] excluding hot summer of 1976.

Month	Estimated slope (s.e.)	
	Temperature (°C)	Rainfall (mm)
Jan	0.072(0.065)	0.19(1.40)
Feb	0.077(0.070)	0.40(1.20)
Mar	0.071(0.046)	-2.20(1.00) *
Apr	0.062(0.033)	0.57(0.95)
May [a]	0.028(0.039)	-0.85(0.93)
Jun [a]	0.046(0.035)	-1.00(1.30)
Jul [a]	0.073(0.044)	0.34(1.00)
Aug [a]	0.100(0.048) *	-0.95(1.20)
Sep	-0.031(0.030)	-0.01(1.40)
Oct	-0.004(0.048)	-0.78(1.30)
Nov	-0.011(0.050)	0.38(1.10)
Dec	0.005(0.064)	-1.20(1.40)
Jan-Apr	0.070(0.034) *	-0.27(0.56)
May-Aug [a]	0.063(0.023) *	-0.64(0.57)
Sep-Dec	-0.010(0.210)	-0.40(0.61)
Annual [a]	0.038(0.021)	-0.44(0.27)

Table 5.2. Number of significant effects ($P < 0.05$) for monthly weather variables after allowing for previous index (percentage in parenthesis) for 31 species and 608 tests. Comparison with number expected by chance using a chi-square test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Positive	Negative	Overall
Temperature	54 (8.9) ***	24 (3.9) *	78 (12.8) ***
Rainfall	11 (1.8)	37 (6.1) ***	48 (7.8) **

Table 5.3. Patterns of positive and negative associations between index values and monthly temperature (a) and rainfall (b), after allowing for previous year's index (1976-1997). Double symbol - $P < 0.05$; double symbol bold - $P < 0.01$. Shaded weather variables are included in best subsets and stepwise regression models. These combinations of weather variables were selected based on statistical association ($P < 0.1$) after allowing for previous index (1976-1990) and biological significance.

(a)

Species	Previous year												Current year							
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
Group (a) - species with one flight period in each year																				
Thymelicus sylvestris	++	+	++	+	+	-	+	+	+	-	-	-	+	-	+	-	+	+	++	+
Ochlodes venata	+	--	+	-	-	-	+	-	-	-	+	-	-	-	-	-	+	++	+	+
Erynnis tages	-	--	+	**--**	-	-	-	-	+	+	+	-	**--**	-	-	+	-	+		
Pyrgus malvae	+	-	-	-	-	+	**++**	+	-	++	+	-	-	+	-	+	-	-		
Anthocharis cardamines	+	+	+	--	++	+	+	+	-	+	+	+	-	+	+	+	-	-		
Callophrys rubi	+	-	+	-	-	+	+	+	-	-	+	-	-	+	-	++	+	+		
Polyommatus icarus (N)	+	+	++	-	+	-	-	+	+	-	+	-	+	+	+	-	+	+	+	+
Lysandra coridon	+	-	++	-	+	-	+	+	-	+	+	-	-	+	-	+	-	+	+	+
Limenitis camilla	+	-	+	-	-	-	+	+	+	-	+	-	-	**--**	**--**	+	-	+	+	-
Clossiana selene	++	+	+	-	-	-	++	+	-	+	+	-	+	+	+	-	+	+		
Clossiana euphrosyne	+	-	+	--	-	+	+	+	-	+	+	-	-	+	-	+	+	-		
Argynnis aglaja	++	-	+	-	-	+	+	+	-	+	+	-	-	+	-	+	-	+	+	+
Argynnis paphia	+	-	+	+	-	--	+	+	-	+	+	-	+	+	-	+	+	++	+	+
Melanargia galathea	++	+	++	-	+	-	++	**++**	+	+	+	--	+	+	+	-	-	+	++	++
Hipparchia semele	+	-	+	--	+	-	-	-	+	+	+	-	-	+	+	-	+	+	+	+
Pyronia tithonus	++	+	++	-	+	-	+	++	+	+	+	-	+	+	+	-	-	+	++	++
Maniola jurtina	+	+	**++**	-	+	-	-	+	+	-	+	-	+	-	+	-	+	+	++	+
Aphantopus hyperantus	-	-	+	-	-	**--**	--	-	+	-	+	+	-	-	-	+	+	+	+	+
Group (b) - species with two flight periods representing different generations (only second generation used in analysis)																				
Pieris brassicae	-	-	++	+	-	**--**	-	-	+	-	-	+	+	+	+	-	++	**++**	-	-
Pieris rapae	+	-	+	-	-	-	+	-	+	+	+	+	-	+	+	-	+	+	++	+
Pieris napi	-	-	+	+	--	**--**	-	-	+	-	-	+	+	+	+	+	**++**	**++**	+	+
Lycaena phlaeas	+	+	++	-	+	-	-	+	+	+	+	+	+	+	+	-	+	++	**++**	**++**
Polyommatus icarus	+	+	++	-	+	-	-	-	+	-	+	+	+	+	+	-	+	**++**	**++**	++
Aricia agestis	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	-	-	++	**++**	++
Lasiommata megera	-	+	+	-	+	--	-	-	+	-	-	+	+	+	+	-	+	++	+	+
Group (c) – species with two flight periods, but only one generation (adults overwintering)																				
Gonepteryx rhamni	+	+	+	+	+	+	++	**++**	+	-	+	--	+	-	-	+	-	+	+	-
Inachis io	++	+	++	-	-	-	+	++	+	+	+	--	-	+	+	+	+	+	+	+

Species	Previous year												Current year							
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
Group (d) species with two or more flight periods, but only a single annual index is used because the flight periods are not readily separated																				
Aglais urticae	+	-	+	-	--	-	+	++	+	+	+	-	-	+	-	+	+	+	+	++
Polygonia c-album	+	-	+	-	-	--	-	-	+	+	+	+	-	+	-	+	+	+	+	+
Pararge aegeria	-	-	+	+	-	--	--	--	-	-	-	+	+	+	+	+	++	++	+	+
Coenonympha pamphilus	+	-	+	--	-	-	+	+	+	+	-	-	-	+	-	-	+	+	+	+

(b)

Species	Previous year												Current year							
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
Group (a)																				
Thymelicus sylvestris	+	+	-	+	-	+	-	--	+	-	--	-	+	+	+	-	-	-	--	-
Ochlodes venata	+	-	+	++	+	-	+	-	+	-	-	-	+	-	-	-	-	-	+	+
Erynnis tages	-	-	+	+	+	-	++	+	-	-	+	+	-	-	-	-	+	+		
Pyrgus malvae	+	+	-	-	+	--	+	-	-	-	+	+	-	+	--	-	-	++		
Anthocharis cardamines	+	+	-	+	-	--	+	+	-	-	+	+	-	+	--	+	-	+		
Callophrys rubi	-	-	+	++	+	-	+	-	+	-	+	+	-	-	--	-	-	+		
Polyommatus icarus (N)	+	+	+	+	-	-	+	-	+	+	-	-	-	+	+	-	-	-	-	-
Lysandra coridon	+	+	-	+	+	-	-	--	+	-	--	-	-	-	-	-	-	-	-	+
Limenitis camilla	+	-	-	+	+	+	-	-	+	-	+	-	+	--	+	+	+	-	+	+
Clossiana selene	-	+	-	+	-	-	+	-	+	+	-	-	+	+	-	-	-	-		
Clossiana euphrosyne	+	+	+	+	+	--	++	-	-	-	-	+	-	+	-	--	--	++		
Argynnis aglaja	+	+	-	+	+	--	--	-	+	-	+	-	-	+	-	--	-	+	-	-
Argynnis paphia	+	+	-	+	-	-	-	-	-	--	-	-	-	-	-	-	-	-	+	+
Melanargia galathea	+	+	-	+	-	-	+	--	+	-	-	-	+	+	-	-	-	+	--	-
Hipparchia semele	-	-	+	+	+	-	++	-	-	-	-	+	-	+	+	-	-	+	--	-
Pyronia tithonus	+	+	+	+	-	-	+	--	+	-	--	-	+	+	-	-	-	-	--	-
Maniola jurtina	+	+	+	+	-	+	+	-	-	-	--	-	-	-	+	-	-	-	-	-
Aphantopus hyperantus	+	+	+	+	+	+	+	+	-	-	-	+	-	-	+	-	+	+	+	-
Group (b)																				
Pieris brassicae	-	+	+	+	-	+	+	+	-	-	-	-	-	-	+	+	+	-	+	+
Pieris rapae	+	+	+	+	-	-	+	-	-	--	-	+	+	+	-	-	-	-	-	-
Pieris napi	+	+	+	+	-	+	+	+	-	-	-	-	-	-	+	-	-	-	+	+
Lycaena phlaeas	+	+	+	+	-	-	-	-	-	-	--	-	-	+	-	-	-	-	--	-
Polyommatus icarus	+	+	-	+	+	+	+	-	-	-	--	+	-	-	-	+	+	-	-	-
Aricia agestis	+	-	+	+	+	-	-	-	+	-	--	+	-	-	-	+	+	-	--	-
Lasiommata megera	-	+	++	+	-	+	+	+	-	-	--	-	-	-	+	+	-	-	-	-
Group (c)																				
Gonepteryx rhamni	+	+	-	-	-	-	-	--	++	+	-	-	+	-	-	+	-	-	-	+
Inachis io	+	+	-	-	-	-	-	--	+	-	-	-	-	-	-	-	-	-	-	+
Group (d)																				
Aglais urticae	+	+	+	+	+	-	+	-	-	-	-	-	-	-	-	--	-	+	-	+
Polygonia c-album	+	+	+	+	+	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-
Pararge aegeria	-	+	+	+	-	++	+	+	--	-	-	-	-	-	+	+	-	-	+	-
Coenonympha pamphilus	+	+	+	+	+	-	++	-	-	-	--	-	-	+	+	-	-	+	-	+

Table 5.4. Application of models developed using data for 1976-90 to predict log index values for 1991-97. For details of models see Table 4. Stepwise predictions use observed index in previous year; free-running predictions only use observed index in 1990. Predictive power measured by the root mean square error (rmse) and the Pearson correlation coefficient between observed and predicted values (r). Values of r for fitted model using 1976-90 data given for comparison. (* $p < 0.01$). Models for species in bold are used to predict historical and future change.

Species	1976-90	1991-97		1991-97	
	Fitted model	Stepwise prediction		Free-running prediction	
	r	rmse	r	rmse	r
Group (a)					
Thymelicus sylvestris	0.94	0.171	-0.28	0.208	-0.33
Ochlodes venata	0.81	0.067	0.80 *	0.075	0.79 *
Erynnis tages	0.84	0.277	0.12	0.237	0.025
Pyrgus malvae	0.87	0.114	0.85 *	0.126	0.82 *
Anthocharis cardamines	0.59	0.064	0.47	0.067	0.41
Callophrys rubi	0.55	0.226	-0.42	0.231	-0.42
Polyommatus icarus (N)	0.93	0.503	-0.11	0.49	-0.09
Limenitis camilla	0.82	0.199	0.41	0.228	0.36
Clossiana selene	0.67	0.056	0.23	0.054	0.31
Clossiana euphrosyne	0.89	0.344	0.35	0.529	-0.31
Argynnis aglaja	0.59	0.252	0.06	0.263	0.070
Argynnis paphia	0.82	0.270	0.06	0.299	-0.12
Melanargia galathea	0.92	0.17	0.39	0.144	0.45
Hipparchia semele	0.84	0.20	-0.55	0.272	-0.78
Pyronia tithonus	0.98	0.115	0.31	0.171	0.22
Maniola jurtina	0.86	0.148	0.01	0.154	-0.59
Aphantopus hyperantus	0.98	0.25	-0.12	0.465	0.13
Group (b)					
Pieris brassicae	0.69	0.168	0.81 *	0.169	0.81
Pieris rapae	0.77	0.218	0.16	0.222	0.12
Pieris napi	0.90	0.142	0.54	0.144	0.52
Lycaena phlaeas	0.89	0.272	0.49	0.273	0.49
Polyommatus icarus	0.95	0.173	0.63	0.166	0.69
Aricia agestis	0.86	0.228	0.57	0.241	0.51
Lasiommata megera	0.98	0.256	0.76 *	0.544	0.11
Group (c)					
Gonepteryx rhamni	0.84	0.133	0.35	0.132	0.31
Group (d)					
Polygonia c-album	0.77	0.389	0.15	0.568	0.073
Pararge aegeria	0.88	0.168	0.59	0.237	0.52
Coenonympha pamphilus	0.98	0.25	-0.34	0.271	-0.25

Table 5.5. Summary of models relating log collated index to previous log collated index and weather variables selected by the Akaike Information Criterion (AIC) for models with subsets of the weather variables given in Table 3 (1976_1997). *S* denotes residual standard deviation. Statistical significance of weather variables: $^{+}$ P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001.

Species	Fitted model				
	Intercept & Previous Index	Temperature Effects	Rainfall Effects	R^2 (%)	*S*
Group (a)					
Thymelicus sylvestris	0.62 +0.58Y	+ 0.036Jun_1	- 0.0023Jul_1 *	62.6	0.110
Ochlodes venata	0.28 +0.45Y	+ 0.065Jun_1	+ 0.0014Apr_1 **	65.2	0.087
Erynnis tages	1.36 +0.15Y	- 0.036Jan_1 *	- 0.0010Jul_0	36.9	0.137
Pyrgus malvae	1.31 +0.44Y		- 0.0026Jun_0 ** - 0.0039Jul_0 **	74.1	0.117
Anthocharis cardamines	1.63 +0.28Y		- 0.0016Mar_1 **	38.5	0.076
Callophrys rubi	1.46 +0.34Y		- 0.0016Jul_0	17.1	0.155
Polyommatus icarus (N)	-0.33 +0.53Y	+ 0.06Jul_1	- 0.0012Aug_0	46.8	0.205
Limenitis camilla	1.26 +0.36Y		- 0.0039Feb_1 **	50.7	0.169
Clossiana selene	0.21 +0.44Y	+ 0.043Jul_0 *		42.9	0.120
Clossiana euphrosyne	0.50 +0.70Y		- 0.0033Jun_0 *	67.0	0.175
Argynnis aglaja	1.22 +0.38Y	- 0.018Mar_1		17.1	0.179
Argynnis paphia	1.94 +0.80Y	- 0.123Jun_0 **	+ 0.0023Apr_0 *	56.4	0.130
Melanargia galathea	-1.10 +0.67Y	+ 0.076Aug_0 ** + 0.045Jun_1		76.8	0.111
Hipparchia semele	0.72 +0.67Y		- 0.0026Jul_1 *	58.2	0.123
Pyronia tithonus	0.51 +0.60Y	+ 0.054Jun_1 **	- 0.0030Aug_0 *** - 0.0024Aug_1 ** - 0.0012Jul_1 $^{+}$	87.7	0.076
Maniola jurtina	0.25 +0.59Y	+ 0.044Jun_1 $^{+}$		52.4	0.101
Aphantopus hyperantus	1.50 +0.92Y	- 0.085Jun_0 *	+ 0.0011Mar_0 - 0.0016Oct_0	84.7	0.149
Group (b)					
Pieris brassicae	3.42 +0.27Y	- 0.135Jun_1 ***		50.7	0.149
Pieris rapae	2.38 - 0.41Y	+ 0.047Jun_1	- 0.0019Oct_0 $^{+}$	38.1	0.155
Pieris napi	0.40 +0.12Y	+ 0.067May_1 ** + 0.070Jun_1 *		61.6	0.102
Lycaena phlaeas	0.13 +0.28Y	+ 0.10Jul_1 **	- 0.0038Nov_0 *	60.8	0.168
Polyommatus icarus	-3.50 +0.29Y	+ 0.174Jun_1 *** + 0.095Jul_1 ** + 0.052Aug_1 $^{+}$		84.1	0.137
Aricia agestis	-0.52 +0.39Y	+ 0.141Jun_1 **	- 0.0056Jul_1 **	67.1	0.170
Lasiommata megera	0.83 +0.86Y	- 0.115Jul_0 *** + 0.128Jun_1 **	- 0.0039Nov_0 ** - 0.0021Aug_1 $^{+}$	86.8	0.134
Group (c)					
Gonepteryx rhamni	1.36 +0.42Y		- 0.0024Aug_0 ***	46.5	0.096

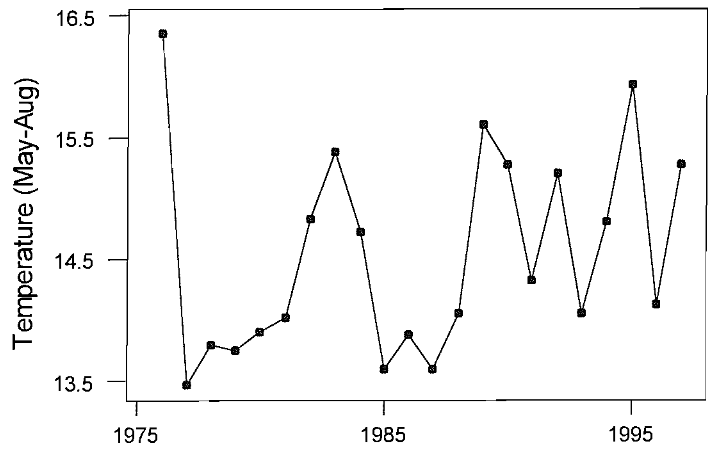
Species	Fitted model				
	Intercept & Previous Index	Temperature Effects	Rainfall Effects	R^2 (%)	*S*
Group (d)					
Vanessa atalanta	-1.85 +0.40Y	+ 0.20Jun_1 *	+ 0.0023Jun_1	43.7	0.280
Polygonia c-album	0.59 +0.65Y		+ 0.0022Mar_0	39.3	0.262
Pararge aegeria	0.47 +0.72Y	- 0.059Jul_0 * + 0.079Jun_1 *		73.8	0.132
Coenonympha pamphilus	0.96 +0.48Y		+ 0.0003Mar_1 - 0.0019Jul_1 $^{+}$	40.4	0.122

Table 5.6. Predicted change in log index values with four UK climate change scenarios (low, medium-low, medium-high and high) at three future time periods (2020s, 2050s and 2080s).

Species	Scenario	2020s	2050s	2080s
Ochlodes venata	Low	0.060	0.090	0.124
	Medium-low	0.105	0.154	0.214
	Medium-high	0.135	0.199	0.263
	High	0.150	0.229	0.293
Pyrgus malvae	Low	0.001	0.000	0.002
	Medium-low	0.001	0.001	0.004
	Medium-high	0.001	0.003	0.004
	High	0.001	0.004	0.004
Melanargia galathea	Low	0.249	0.339	0.500
	Medium-low	0.430	0.580	0.857
	Medium-high	0.521	0.828	1.021
	High	0.578	0.956	1.139
Pyronia tithonus	Low	0.249	0.339	0.500
	Medium-low	0.430	0.580	0.857
	Medium-high	0.521	0.828	1.021
	High	0.578	0.956	1.139
Pieris brassicae	Low	-0.097	-0.143	-0.199
	Medium-low	-0.167	-0.245	-0.342
	Medium-high	-0.215	-0.318	-0.420
	High	-0.240	-0.366	-0.468
Pieris napi	Low	0.083	0.115	0.160
	Medium-low	0.143	0.196	0.274
	Medium-high	0.176	0.276	0.396
	High	0.195	0.319	0.441
Polyommatus icarus	Low	0.269	0.377	0.560
	Medium-low	0.464	0.644	0.962
	Medium-high	0.574	0.894	1.129
	High	0.638	1.031	1.258
Lasiommata megera	Low	-0.060	-0.012	-0.183
	Medium-low	-0.092	-0.011	-0.318
	Medium-high	-0.037	-0.233	-0.128
	High	-0.042	-0.275	-0.138

Figure 5.1. Fluctuations and trends in temperature and rainfall data: (a) mean temperature January-April; (b) mean temperature June-August.

a)



b)

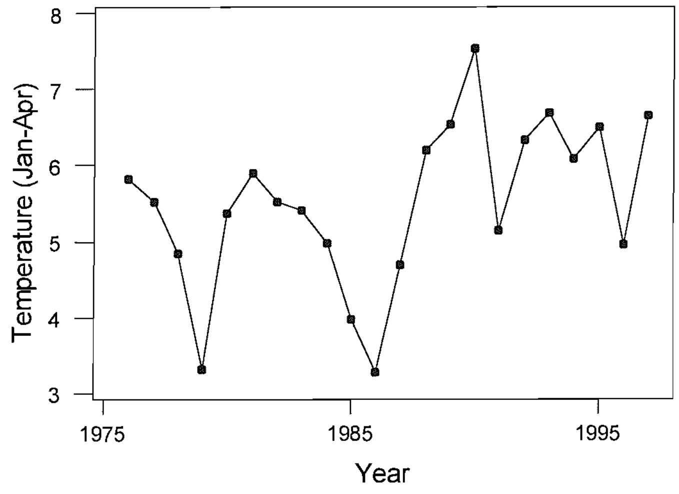
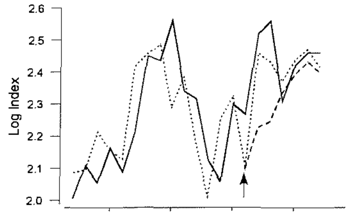


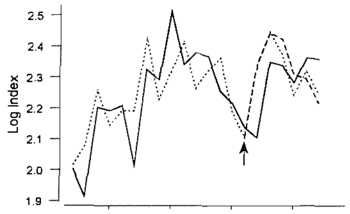
Figure 5.2. Observed fluctuations in collated butterfly index (solid line) together with fitted model values 1976-90, stepwise predictions 1991-97 using observed log index in the previous year (dotted line) and free-running predictions 1991-97 using observed log index in 1990 only (dashed line). Arrows indicate first year of free-running predictions (1991).

[Plots are shown on next two pages]

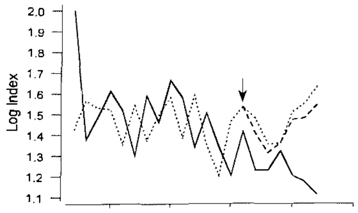
i) *Thymelicus sylvestris*



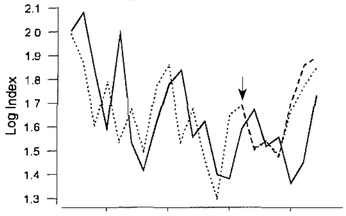
ii) *Ochlodes venata*



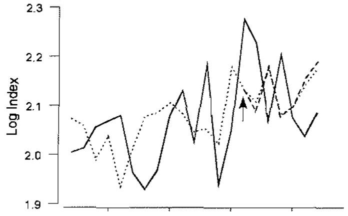
iii) *Erynnis tages*



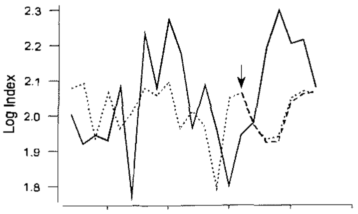
iv) *Pyrgus malvae*



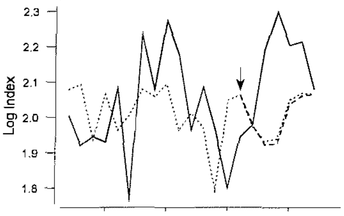
v) *Anthocharis cardamines*



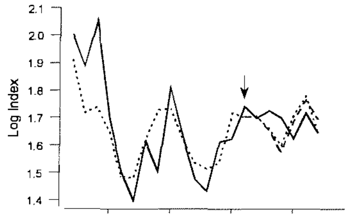
vi) *Callophrys rubi*



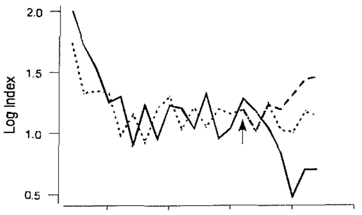
vii) *Limenitis*



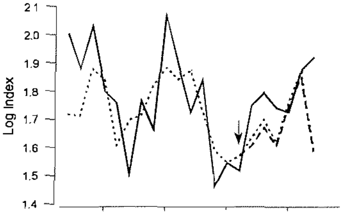
viii) *Clossiana selene*



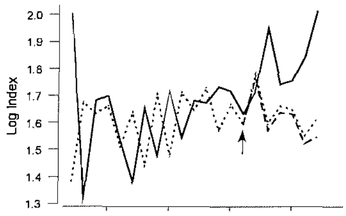
ix) *Clossiana euphrosyne*



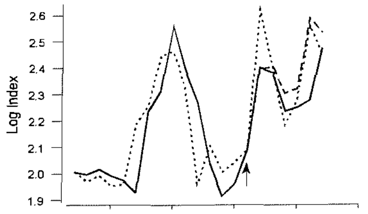
x) *Argynnis aglaja*



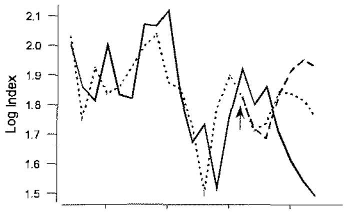
xi) *Argynnis paphia*



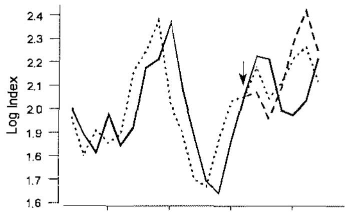
xii) *Melanargia galathea*



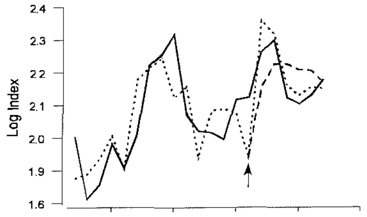
xiii) *Hipparchia*



xiv) *Pyronia*

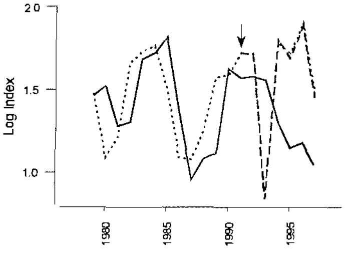


xv) *Maniola*



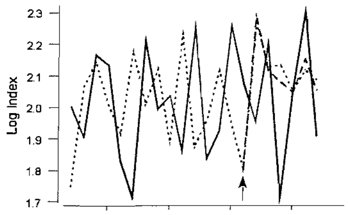
xvi) *Aphantopus hyperan*

xvii) *Polyommatus icarus*

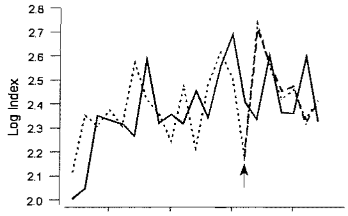


xviii) *Pieris*

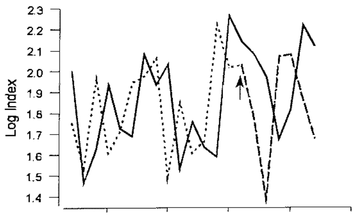
xix) *Pieris rapae*



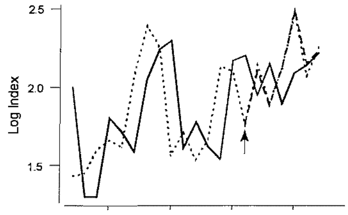
xx) *Pieris napi*



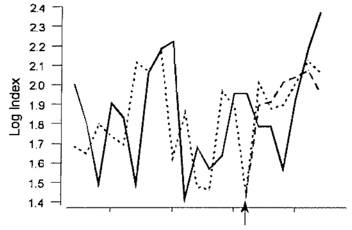
xxi) *Lycaena phlaeas*



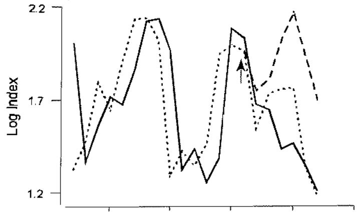
xxii) *Polyommatus*



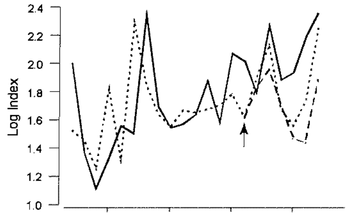
xxiii) *Aricia agestis*



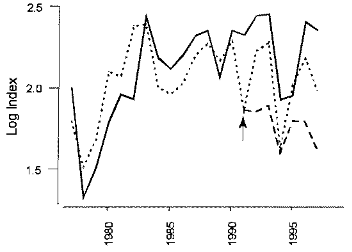
xxiv) *Lasiommata*



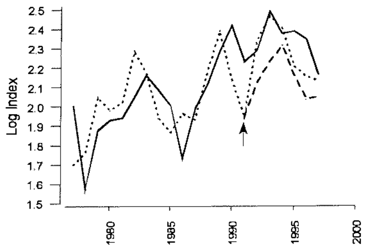
xxv) *Vanessa*



xxvi) *Polygonia c-*



xxvii) *Pararge*



xxviii) *Coenonympha*

Figure 5.3. Summary measures of model predictive success. Relationships between mean observed and predicted log index values 1991-97. Observed within 20% of predicted (broken line); observed within 50% of predicted (solid line). Data labels are as follows: smsk - *Thymelicus sylvestris*; lsk - *Ochlodes venata*; dsk - *Erynnis tages*; gsk - *Pyrgus malvae*; ot - *Anthocharis cardamines*; ghs - *Callophrys rubi*; wa - *Limenitis camilla*; swf - *Argynnis paphia*; pbf - *Clossiana euphrosyne*; spbf - *Clossiana selene*; dgf - *Argynnis aglaja*; mw - *Melanargia galathea*; gr - *Hipparchia semele*; hb - *Pyronia tithonus*; mb - *Maniola jurtina*; ring - *Aphantopus hyperantus*; cbn - *Polyommatus icarus* (N); lw - *Pieris brassicae*; smw - *Pieris rapae*; gvw - *Pieris napi*; sc - *Lycaena phlaeas*; cb - *Polyommatus icarus*; ba - *Aricia agestis*; wa - *Lasiommata megera*; br - *Gonepteryx rhamni*; com - *Polygonia c-album*; spw - *Pararge aegeria*; smh - *Coenonympha pamphilus*.

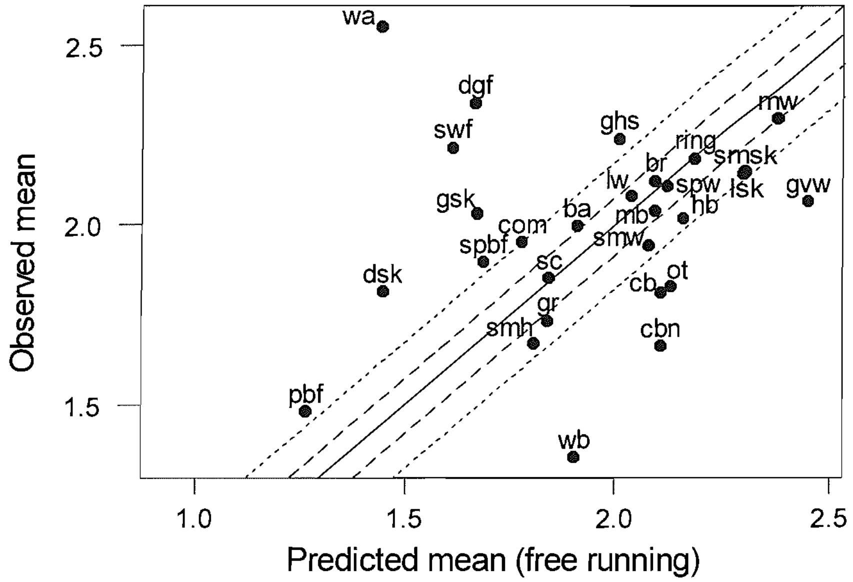
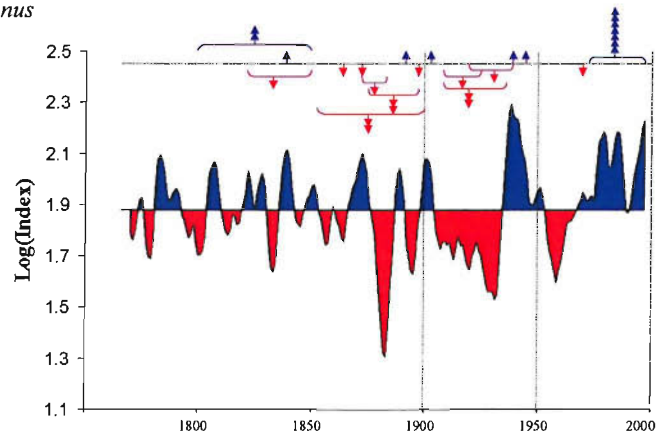
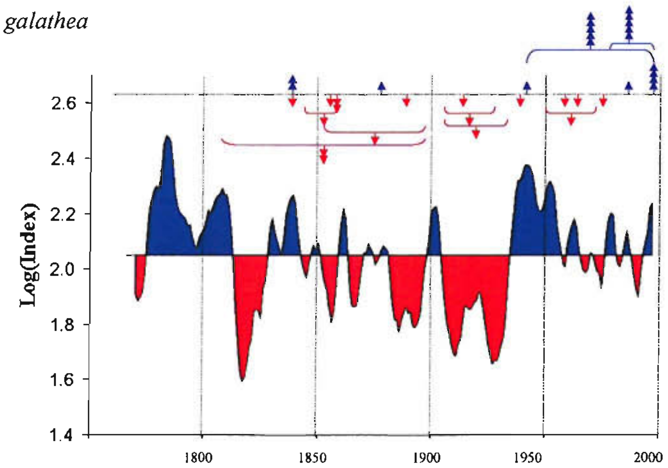


Figure 5.4. Predicted historical fluctuations in the 10-year running mean butterfly numbers 1767-1997 for i) *Pyronia tithonus*, ii) *Melanargia galathea* and iii) *Lasiommata megera*. The mean index level over the period is shown by a horizontal line with above average values in blue and below average values in red. Major shifts in status reported in the literature are shown at the top of each figure. Changes are scored as an 'increase' (up arrow in blue) or 'decrease' (down arrow in red) in a particular year, decade or longer span of years.

i) Pyronia tithonus



ii) Melanargia galathea



iii) Lasiommata megera

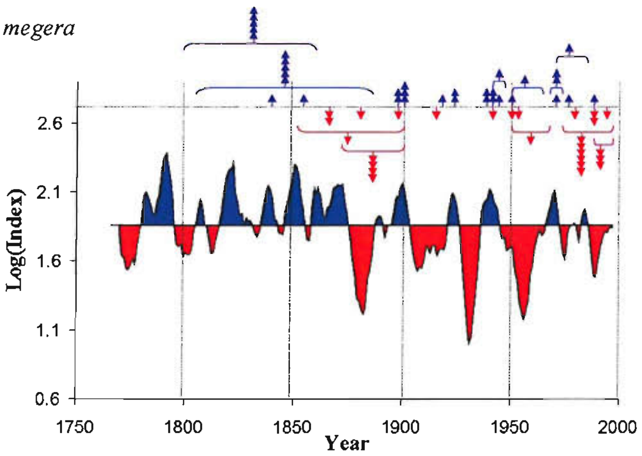
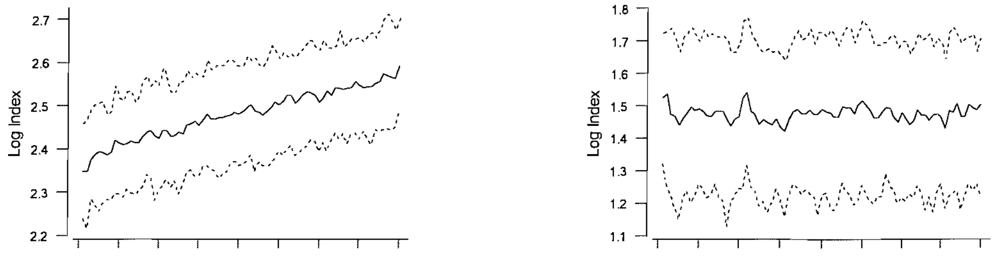
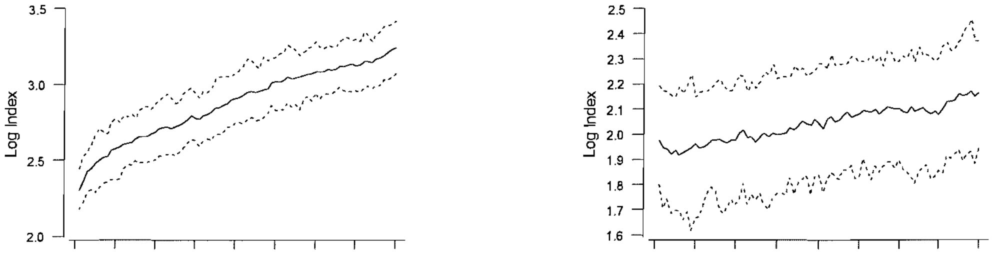


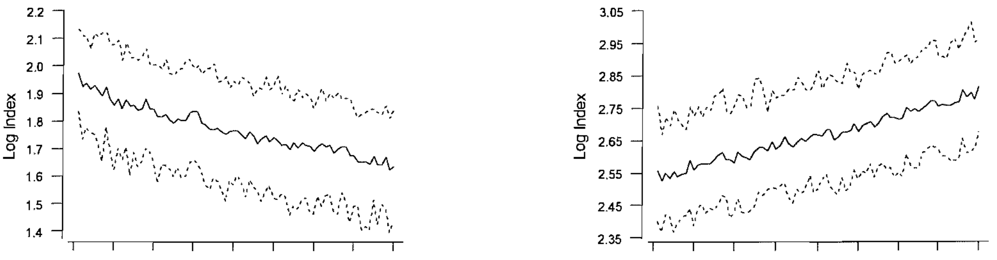
Figure 5.5. Simulated future fluctuations in butterfly index 2000-2080 under a medium-high UKCIP98 climate change scenario. Solid lines are mean population level and dotted lines are 90% confidence intervals derived from 100 simulations. i) *Ochlodes venata*; ii) *Pyrgus malvae*; iii) *Melanargia galathea*; iv) *Pyronia tithonus*; v) *Pieris brassicae*; vi) *Pieris napi*; vii) *Polyommatus icarus*; viii) *Lasiommata megera*.


i) *Ochlodes venata*

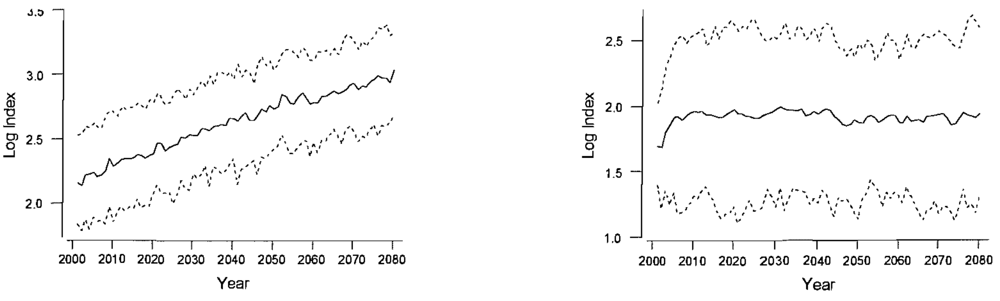
ii) *Pyrgus malvae*


iii) *Melanargia galathea*

iv) *Pyronia tithonus*


v) *Pieris brassicae*

vi) *Pieris napi*


vii) *Polyommatus icarus*

viii) *Lasiommata*

6 Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops

Roy, D.B., Bohan, D.A., Haughton, A.J., Hill, M.O., Osborne, J.L., Clark, S.J., Perry, J.N., Rothery, P., Scott, R.J., Brooks, D.R., Champion, G.T., Hawes, C., Heard, M.S., & Firbank, L.G. (2003) Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1879 - 1898.

6.1 Abstract

The effects of management for genetically modified herbicide-tolerant (GMHT) crops on adjacent field margins were assessed for 59 maize, 66 beet and 67 spring oilseed rape sites. Fields were split into halves, one being sown with a GMHT crop and the other with the equivalent conventional non-GMHT crop. Margin vegetation was recorded in three components of field margins (figure 1). Most differences were in the tilled area, with fewer, smaller effects mirroring them in the verge and boundary. In spring oilseed rape fields, the cover, flowering and seeding of plants were 25%, 44% and 39% lower, respectively, in the GMHT uncropped tilled margins. Similarly, for beet, flowering and seeding were 34% and 39% lower in the GMHT margins. For maize, the effect was reversed, with plant cover and flowering 28% and 67% greater in the GMHT half. Effects on butterflies mirrored these vegetation effects, with numbers 24% less in margins of GMHT spring oilseed rape. The likely cause is the lower nectar supply in GMHT tilled margins and crop edges. Few large treatment differences were found for bees, gastropods or other invertebrates. Scorching of vegetation by herbicide spray drift was on average 1.6% on verges beside conventional crops and 3.7% beside GMHT crops, the difference being significant for all three crops.

6.2 Introduction

Management for genetically modified herbicide-tolerant (GMHT) crops differs from that for conventional crops mainly in the type and timing of herbicides applied to the cropped area of fields (Champion *et al.*, 2003). Field margins are, however, an important resource for plants and animals in the arable landscape (Marshall & Moonen, 2002; Way

& Greig-Smith, 1987), and the effects of new management techniques on this component of agro-ecosystems need to be assessed.

Field margins can support a high diversity of plant species and are of conservation importance within farmed landscapes of Europe (Barr *et al.*, 1993) and North America (Freemark, Boutin & Keddy, 2002). Field margins also provide a habitat for numerous invertebrates (Dover & Sparks, 2000; Frank, 1998; Morris & Webb, 1987), a food resource for mammals (Tew, Todd & MacDonald, 1994) and birds (Lack, 1992), and a refuge for beneficial parasitoids (Powell, 1986) and predators, e.g. carabid beetles (Bohan *et al.*, 2000; Symondson *et al.*, 1996). Margins provide resources for birds (Bradbury *et al.*, 2000; Brickle *et al.*, 2000; Peach *et al.*, 2001; Potts, 1986) and bees (Fussell & Corbet, 1992b; Svensson, Lagerlof & Svensson, 2000), and may be the only source of nectar and pollen in arable landscapes through much of the season.

The interactions between field margins and crops can have detrimental as well as positive agronomic impacts. While margins provide overwintering sites for insects beneficial for pest control (Sotherton, 1985), some slug species migrate into fields from the boundary, causing significant crop damage around field edges (Frank, 1998). The depredations of rabbits are notorious (Sheail, 1972) and field-margin plants commonly harbour pests and pathogens (Norris & Kogan, 2000).

Many declining farmland species are found within edges of fields. Conservation concern has focused on farmland birds (Brickle *et al.*, 2000; Chamberlain *et al.*, 2000; Donald & Vickery, 2001; Evans *et al.*, 1995; Potts, 1986) but other species groups are also affected (Robinson & Sutherland, 2002; Sotherton & Self, 2000). The UK Countryside Survey 2000 showed that over a 20-year period, the vegetation of hedgerows had become on average less species-rich and more dominated by tall, competitive plants associated with fertile conditions (Haines-Young *et al.*, 2000). Over a longer time period, many plants that have shown the greatest declines in distribution since the 1950s in the British Isles are those that are usually found in arable fields (Preston *et al.*, 2002; Wilson, 1992). The common butterflies of the farmed countryside have also suffered declines (Cowley *et al.*, 1999). In arable environments this is mainly as a result of deterioration in both quality and quantity of field margins

(Asher *et al.*, 2001). Bumble bees have reacted likewise, particularly in arable regions (Williams, 1986).

Owing to their proximity to cropped land, field margins receive direct and indirect applications of pesticides. The effects of such spray drift are often small (Marrs & Frost, 1997) but misplaced applications of herbicide can reduce plant cover and diversity (de Snoo, 1997; de Snoo & van der Poll, 1999), and may significantly reduce the abundance of ground beetles (Carabidae), spiders (Araneae), and true bugs (Heteroptera) (Haughton *et al.*, 1999a; Haughton *et al.*, 1999b) through lower sward height and increased amount of dead vegetation (Haughton *et al.*, 2001).

The aim of this paper is to compare the effects of management for GMHT and non-GMHT crops on key groups of flora and fauna in adjacent field margins; effects within the cropped area of the field are reported in accompanying papers on vegetation (Heard *et al.*, 2003a, b) and invertebrates (Brooks *et al.*, 2003; Haughton *et al.*, 2003). For beet (*Beta vulgaris* ssp. *vulgaris* (L.), maize (*Zea mays* (L.) and spring oilseed rape (*Brassica napus* ssp. *oleifera* (DC.) crops, we test a specific null hypothesis: that there is no difference between the management of GMHT varieties and that of comparable conventional varieties, in their effects on the cover, flowering and seeding of vegetation, and the abundance of bees, butterflies, slugs and snails, and other invertebrates. Where treatment effects are significant, we estimate their magnitude and consider the implications for farmland biodiversity of growing these GMHT crops. The main ecological effects of GMHT varieties are likely to be from the direct effects of herbicide regimes on vegetation, with knock-on indirect effects on associated invertebrate groups (Haughton *et al.*, 2003).

6.3 Methods

The experimental design and statistical justification for the number of sites used in the trials have been outlined in detail elsewhere (Perry *et al.*, 2003). The experiment ran from 2000 to 2002. Fields were selected from a pool on the basis that they satisfied a number of criteria relating to biodiversity, management regimes and agricultural intensity to provide a sample of sites broadly representative of current British agriculture (Champion *et al.*, 2003). In each field, the treatments (GMHT or conventional cropping) were allocated at random to each half.

The experiment contrasts the effects of crop type management regimes (Haughton *et al.*, 2003). The main difference in crop management between treatments was mostly restricted to herbicide regimes. Differences in pesticide use, rotations, field margin management or cultivation were allowed between half-fields if there were good agronomic reasons. In practice, management activities performed on field margins such as mowing of verges, cutting of hedgerow and ditch clearance are almost exclusively performed outside the cropping.

6.3.1 The structure of field margins

Various definitions and nomenclature are used to describe field margins. We follow the definitions of Marshall & Moonen (2002) who distinguished the crop edge (outer few metres of the crop), any margin strip present and the semi-natural habitat associated with the boundary. For the Farm Scale Evaluations, cropped areas of fields were not treated as part of the field margin. Treatment effects in this part of fields are reported in accompanying papers (Brooks *et al.*, 2003; Haughton *et al.*, 2003; Heard *et al.*, 2003a, b). The three components of the field margin are defined as follows (figure 1). The ***tilled margin*** is the cultivated but uncropped strip at the edge of the field; a subset of the 'crop edge' as defined by Marshall & Moonen (2002). The ***field verge*** is defined as the strip of grassy or herbaceous vegetation between the edge of the plough and the field boundary, termed a 'margin strip' by Marshall & Moonen (2002). The ***field boundary*** is taken to be any physical feature that is an interface between the field and another land cover type, as defined by Marshall & Moonen (2002). A boundary is typically a hedge, wall, fence, ditch or embankment, but may be absent if two arable crops abut directly.

For those positions at which margin vegetation was recorded (figure 2) the widths of the tilled margin and verge were measured. At the ends of the twelve transects used for sampling vegetation in the crop, the presence or absence of a boundary hedge or ditch was noted within a 10 m length of margin (figure 2, Heard *et al.*, 2003a).

6.3.2 Sampling vegetation

The vegetation of field margins was recorded using plots located at the ends of three of the twelve transects used for sampling vegetation in the crop (figure 2, Heard *et al.*, 2003a). Each group of margin plots included a sample within the three field margin types defined above (boundary, field verge and tilled margin), provided that these features were present. The standard size of plot (10 × 1 m) was chosen to coincide with that used in a national survey of the UK countryside (Haines-Young *et al.*, 2000), but the plots were often in practice narrower, especially within the tilled margin. The full width of the tilled margin, verge or boundary was sampled when it was narrower than 1 m. Where no boundary existed (i.e. one crop was sown up against another) or where the verge was greater than 30 metres wide (e.g. game cover or set-aside), no boundary sample was taken.

Three types of vegetation record were made within each plot: vegetation cover was sampled in June; flowering and herbicide spray damage were assessed in June, July and August (with an additional sample in May for beet); and records of seeding vegetation were taken in July and August. The timings were chosen to coincide with invertebrate sampling.

Estimates of total cover of green plant material were made using the Braun-Blanquet scale (Lepš & Hadincová, 1992; Mueller-Dombois & Ellenberg, 1974). The cover, b_{ijkl}, of a species k (in plot l of treatment i at site j) was measured on a scale of 1 to 6 as follows:

$b_{ijkl} = 1$ if species present, cover <1%;
$b_{ijkl} = 2$ if cover 1-5%;
$b_{ijkl} = 3$ if cover 5.1-25%;
$b_{ijkl} = 4$ if cover 25.1-50%;
$b_{ijkl} = 5$ if cover 50.1-75%; and
$b_{ijkl} = 6$ if cover >75%.

An overall estimate of cover was given for all grass species.

Flowering of species k was measured by two values, f_{ijkl}, the frequency of flowering (the number of 1-m^2 subplots, out of ten, of the 10-m^2 plot l of treatment i at site j)

and the extent of flowering e_{ijkl}, which was measured on a scale of 1 to 4 as follows, referring only to those subplots where species k was flowering:

$e_{ijkl} = 1$ if < 10 individual blooms & < 1% cover of blooms;
$e_{ijkl} = 2$ if ≥ 10 individual blooms & < 1% cover of blooms;
$e_{ijkl} = 3$ if blooms had 1-5% cover; and
$e_{ijkl} = 4$ if blooms had > 5% cover.

Flowers of grasses, sedges and rushes were not recorded to species.

Assessments of herbicide spray drift damage refer only to that part of the plot that was (or recently was) vegetated. It does not include any bare ground in the plot. Thus 100% damage implies that all vegetation was browned (but there may be bare ground also). Likewise, 50% damage + 50% bare ground implies that 50% of the ground is bare, 25% is vegetated and still green, and 25% is vegetated but browned by herbicide. Seed presence as ripe fruits on plants, including grasses, was recorded as a frequency out of ten 1 m segments.

6.3.3 Sampling bees and butterflies

Bees and butterflies were counted using the line transect method developed for the UK Butterfly Monitoring Scheme (BMS, Pollard & Yates, 1993) and adapted as a standard method for bee surveys (Banaszak, 1980). Transects were walked in June, July and August for all crops, with an additional sample in May for beet. Where possible, transects were walked beside maize and spring oilseed rape when the crop was in flower. The two halves of a split field were walked on the same day, the order being randomized because time of day affects flight activity. Walks were carried out between 10.00 hrs and 17.30 hrs when weather conformed to BMS standards (wind speed < 5.5 ms^{-1}, not raining, temperature > $17^{o}C$ if sky overcast or > $13^{o}C$ if sky at least 60% clear). Three separate 100 m sections along the field margin were sampled, one on each side of the half-field in a standard field (figure 2). These sections were centred on the mid vegetation transect of each side of the half-field used to sample within-crop vegetation (figure 2, Heard *et al.*, 2003a). Transect walks were conducted twice for each treatment with bees counted in one direction and butterflies counted in the opposite direction, the order being chosen at random. Bees were counted in field margins within 2 m of the crop edge and butterflies within 5 m. Transects were also walked within the crop at the same time and are reported in Haughton *et al.* (2003).

Given the need to identify bees whilst on the wing, counts were made for groups of bumble bee (*Bombus*) species based on colour type (according to Prys-Jones & Corbet, 1991). Each colour group contains one or two species that are common in southern Britain and one or two rare and localised species, which are difficult to separate without capturing the insects. The common species in each colour group are shown in brackets: black and red tail (*B. lapidarius*); brown/ginger (*B. pascuorum*); one or two yellow bands with red tail (*B. pratorum*); two yellow bands with white or buff tail (*B. terrestris*/*B. lucorum*); three yellow bands with white tail (*B. hortorum*). Separate counts were also made for honey bees, cuckoo bees (*Psithyrus*) and solitary bees. In all cases, only actively foraging individuals or nest-searching queens were counted. The flowering species on which the bees were foraging were listed. Counts were made separately for all butterfly species.

6.3.4 Sampling slugs and snails

Slugs and snails (gastropods) were counted in twelve areas around the field, located at the end of transects used for sampling vegetation in the crop (figure 2, Heard *et al.*, 2003a). Where the verge was up to 1 m wide, each sampling area consisted of a 2 m length of the verge to the width of the verge. Where this feature was over 1 m wide, a 2 × 1 m sampling area was used. Within each sampling area, a visual search was made for four minutes. The vegetation within the plot was gently parted, by hand, to reveal any slugs and snails present. Those found during the four-minute search were retained for identification at the end of the search. All gastropods collected were identified *in situ*, where possible. However, some were removed to the laboratory for later identification. The searches took place after, but within one week of, the vegetation sampling. The timing of sampling was adjusted, where possible, so that the forecast daily air temperature was in the region 10 - 18°C, the weather overcast and the soil surface and vegetation visibly moist.

6.3.5 Sampling other invertebrates using a suction sampler

Invertebrates were sampled using a Vortis suction sampler (Arnold, 1994). The Vortis sampler has an aperture diameter of 15.5 cm and is comparable to the bulkier D-vac suction sampler. Such devices have been used widely in similar entomological field studies (e.g. Haughton *et al.*, 2001; Maudsley *et al.*, 1997; Moreby, Sotherton & Jepson, 1997) and were used for invertebrate assessments within the crop (Haughton *et al.* 2003). Although extraction efficiency is always less than 100%, suction samples represent a consistent proportion of the population present and thus allow direct statistical comparison of abundance between treatments for the same habitat.

Samples comprised five 10-second sub-samples taken one metre apart in the verge. These were taken at three locations around each half of the field in June and August. Samples were taken from dry vegetation and sampling positions and timings coincided as closely as possible with those for vegetation sampling (figure 2). The area of verge sampled in each half-field per year was approximately equal to 0.56 m^2. Invertebrate samples were placed in labelled polythene bags, in a cool box containing frozen blocks during transit from the field, and then stored in a freezer in the laboratory. The invertebrates were separated from other organic matter and soil particles by repeated flotation prior to being counted and identified to the taxonomic level specified for each major group (table 1).

6.3.6 Analysis

6.3.6.1 Response variables

All analyses were based on totals per half-field. Indices of plant species density, flowering and seeding were calculated for the three components of the field margin (tilled margin, field verge and boundary). Indices of flowering and seeding were also calculated for separate months.

The index of plant cover, C_{ij}, was calculated as the sum of the cover scores of the n_s species recorded per half-field as,

$$C_{ij} = \sum_{k=1}^{n_s} \sum_{l=1}^{3} b_{ijkl}$$

where bijkl is the cover score (1 to 6) of species k in plot l for treatment i at site j.

An index of flowering of vegetation, Fij, was calculated as the sum of the product of frequency and extent of flowering of ns species recorded per half-field as,

$$F_{ij} = \sum_{k=1}^{n_s} \sum_{l=1}^{3} f_{ijkl} \times e_{ijkl}$$

where fijkl is the frequency of flowering (in ten 1 m2 subplots of the 10 m2 plot) and eijkl (out of four) is the extent of flowering of species k in plot l for treatment i at site j. A flowering index was calculated separately for plant families (Asteraceae, Brassicaceae, Fabaceae, Lamiaceae, Rosaceae, Scrophulariaceae) that have previously been identified as being important nectar sources for bees and/or butterflies (Feber *et al.*, 1996; Fussell & Corbet, 1992a; Meek *et al.*, 2002).

A seeding index was calculated as the frequency of species recorded seeding within the same plots

$$S_{ij} = \sum_{k=1}^{n_s} \sum_{l=1}^{3} s_{ijkl}$$

where s_{ijkl} is the frequency of seeding (in ten 1 m^2 subplots of the 10 m^2 plot) of species k in plot l for treatment i at site j.

Bee and butterfly counts were analysed as totals summed over individual months and for the whole season. The responses of honey bees (*Apis mellifera*), bumble bees (*Bombus* spp. and *Psithyrus* spp.) and a subgroup of long-tongued bumble bees (*B.hortorum*, *B.pascuorum* and bees in the same colour groups) were also analysed separately. Long-tongued bumble bees were chosen because they are selective about the plants they feed on, and may be particularly sensitive to any reduction in floral resources in farmland. The response of *Pieris* and non-*Pieris* butterflies were analysed separately for spring oilseed rape as cultivated brassicas such as this crop are foodplants of small white (*P. rapae*) and large white (*P. brassicae*). Totals from spring and autumn slugs and snails samples were analysed separately as well as combined season totals. Totals of invertebrates sampled by suction sampler were also analysed as counts from separate sampling occasions in addition to totals over the whole season. The following taxonomic groups were analysed: ground beetles (Carabidae: family and selected species), true bugs (Heteroptera: sub-order, herbivores and predators), spiders (Araneae: order and selected species), and springtails (Collembola: order and families). Invertebrates sampled by suction sampler were assigned to functional groups based on their role in the movement of resource from primary production to decomposition (herbivores, predators, parasitoids) (Lindeman 1942; Hawes *et al.* 2003). Numbers of these functional groups were analysed, as was a groups of invertebrates identified as important food resource for birds (table 1, Wilson *et al.*, 1999).

6.3.6.2 *(ii)* Statistical analysis

A description of the experimental design has been given in detail elsewhere (Perry *et al.*, 2003) and is only summarised briefly here. Records for each variate analysed were obtained from systematic samples within half-fields of three spring crops, in a randomised block experimental design, in which the blocks were paired halved-fields. The total count, c_{ij}, per half-field, for treatment i at site j, was transformed to $l_{ij} = \log (c_{ij}+1)$. To give an approximate indication of abundance, geometric means for each treatment i were calculated from backtransformed arithmetic means of l_{ij}. The standard analysis of abundance was a randomised block ANOVA of the transformed values, l_{ij}, termed the lognormal model by Perry *et al.* (2003). The null hypothesis was tested with a paired randomisation test, using as a test statistic $d = \Sigma_j [l_{2j} - l_{1j}] / n$ for n sites, the mean of the differences between the GMHT and conventional treatments on a logarithmic scale. The treatment effect was measured as R, the multiplicative ratio of the GMHT treatment divided by the conventional, calculated as $R = 10^d$; confidence intervals about R were obtained by back-transformation of the confidence interval of d on the logarithmic scale, derived from the standard error of d and $t_{(0.05)}$. Response variables were analysed separately for each occasion and for all occasions totalled over the season. Where differences in treatment effects between occasions were minimal, results are given for all occasions totalled over the entire season. Sites, j, for which the whole-field total count, $c_{1j} + c_{2j}$, was zero or unity were removed from analyses. For analysis of margin attributes and vegetation scorching, all sites were analysed and differences in arithmetic means were assessed using a paired t-test.

We present *p*-values of individual tests together with estimates of treatment effects and errors of estimation. The justification for not applying techniques (such as Bonferroni) to adjust significance levels when numerous tests are performed is given in Firbank *et al.* (2003).

Where large treatment effects were found ($p < 0.05$), separate covariate analyses were done to test for consistency of treatment effects between years, in relation to the weed status of sites, between environmental regions and between sugar beet and fodder beet. The potential density of weeds from an initial sample of the seedbank (Heard *et al.*, 2003a) was taken as a measure of the overall potential weed status of each site. The six Environmental Zones (Firbank *et al.*, 2003; Haines-Young *et al.*, 2000) of the ITE Land Classification of Great Britain (Bunce *et al.*, 1996) were used to group sites with similar topography and climate.

6.4 Results

6.4.1 Characteristics of the field margin

No differences were found in the frequency of hedgerow or ditch on margins adjacent to any of the three crops (table 2). The average width of tilled margins were 1.2 m, 0.8 m and 0.7 m for beet, maize and spring oilseed rape, and did not differ between treatments. Verges were on average 0.9 m, 1.1 m and 1.2 m wide for beet, maize and spring oilseed rape, respectively, and again did not differ between treatments (table 2).

6.4.2 Treatment effects on vegetation

Common nettle (*Urtica dioica*), common couch (*Elytrigia repens*), creeping thistle (*Cirsium arvense*) and cleavers (*Galium aparine*) were frequent within all three margin plot types, occurring with the tilled margin, field verge and boundary of over 70% of plots sampled. The plant composition of the tilled margin was similar to that found in the cropped area of the field. The twelve most frequent and abundant weed species found within the crop (Heard *et al.*, 2003b), also occurred within tilled margins of more than 60% of plots sampled.

6.4.2.1 Cover

For spring oilseed rape, the indices of plant cover in the tilled margin, field verge and boundary of the GMHT half were 25%, 19% and 25% lower, respectively, than on the conventional half (table 3*a*). In maize, the index of cover was greater in GMHT halves by 28% and 15% in tilled margin and field verge samples, but no differences were found in boundary plots. There was no treatment difference in plant cover for any of the field edge plots sampled adjacent to beet.

6.4.2.2 Flowering

The plants recorded flowering in field margins were similar for all three crops. Species flowering in more than 20% of tilled margin plots were common field-speedwell (*Veronica persica*), shepherd's-purse (*Capsella bursa-pastoris*), field pansy (*Viola arvensis*) and groundsel (*Senecio vulgaris*). Within verge plots, common nettle, cleavers, hogweed (*Heracleum sphondylium*) and creeping thistle were most frequently flowering and bramble (*Rubus fruticosus*), common nettle and cleavers flowered in more than 20% of boundary plots.

Over the whole season, the flowering resource available within tilled margins was greatest adjacent to spring oilseed rape crops, but of similar magnitude beside beet crops (table 3*b*). The average, whole field, geometric mean count for beet and spring oilseed rape was 72.3 and 83.6, respectively. The flowering index was less than half this amount on average in tilled margins of maize. For this crop, flowering was greatest within field verge samples.

For all three crops studied, differences in flowering were found within the tilled margins of fields. Flowering adjacent to beet and spring oilseed rape was lower adjacent to GMHT halves of fields, but greater for maize.

The most consistent effects were found for the tilled margins of spring oilseed rape, with less flowering throughout the season. The greatest difference was found in July with a 53% lower flowering index in GMHT tilled margins (table 3*b*, figure 3). Flowering index was also lower in June verge samples of GMHT halves of the same crop, by 34% (table 3*b*) but not for other months sampled. Flowering of plant families that are important nectar sources for bees and butterflies was also lower throughout the season in tilled margins of spring oilseed rape (table 4). No differences in flowering were found in boundaries of spring oilseed rape.

Over the whole season, tilled margins of GMHT halves of beet fields had 34% less flowering than conventional halves (table 3*b*). Differences were greatest in July, 54% lower on GMHT halves, and comparable to those found in spring oilseed rape tilled margins at the same time of the year (table 3*b*, figure 3). The flowering index of Asteraceae was similarly reduced in GMHT tilled margins in July (table 4). Flowering differences were also found in August for Asteraceae and Brassicaceae but in opposite directions; a greater flowering index was found in GMHT tilled margins for Brassicaceae but a lower index for Asteraceae. No differences were found in flowering in field verge or boundary samples for this crop.

Flowering in tilled margins of maize crops was greater in GMHT halves of fields, by 98% in August and 67% over the whole season (table 3*b*). The flowering index of Brassicaceae, Fabaceae and Scrophulariaceae was also greater in GMHT tilled margins in August and when totalled over the season (table 4). Differences were also found in boundary samples for this crop, with 118% more flowering in GMHT halves of fields in August and 32% more over the whole season (table 3*b*).

6.4.2.3 Seed set

The frequency of seeding species was three to four times higher in field verges compared to tilled margins and field boundaries (table 3*c*). There was a large treatment effect in seeding within tilled margins of beet and spring oilseed rape fields, with 39% and 35% less seed over the whole season in GMHT compared to conventional halves of fields. August seeding was also lower in GMHT tilled margins for these crops, by 37% for beet and 32% for spring oilseed rape. Fewer seeding species in field verges adjacent to GMHT beet crops were also found in August (table 2*c*), despite no effects on flowering or plant species density in this component of field margins for this crop (table 2*a*,*b*). No differences in seeding were found in field margin samples adjacent to maize crops.

6.4.2.4 Spray damage

Differences in the amount of scorched vegetation were found in the tilled margins of all three crops (table 5). Effects were most marked in beet with a higher percentage of vegetation scorched from June onwards, with 4.4% more overall and reaching a maximum in July of 6.7% more. The amount of bare ground was also different between treatments within tilled margins of beet fields, with 22% for GMHT compared to 17% for conventional halves on average. Less overall scorching was found in the field verge and boundary for beet, with 2.8% and 0.5%, but again considerably more was found in GMHT halves (table 5).

A higher proportion of vegetation was also scorched in GMHT field margins adjacent to maize and spring oilseed rape. Differences were greater in tilled margins than within the verge, with 3.1% compared to 1.5% more scorching in maize and 2.5% versus 2% in spring oilseed rape. Within the season, effects were found in June and July for maize, but only in June for spring oilseed rape (table 5).

6.4.3 Bees and butterflies

For all three crops sampled, small white (*Pieris rapae*) was the most abundant butterfly species recorded, making up over half of all individuals seen on edges of spring oilseed rape crops and approximately a quarter of those seen on margins of beet and maize crops. Large white (*Pieris brassicae*), meadow brown (*Maniola jurtina*), small tortoiseshell (*Aglais urticae*) and green-veined white (*Pieris napi*) were also commonly found, together comprising 45%, 44% and 34% of individuals recorded on beet, maize and spring oilseed rape tilled margins, respectively. The most consistent treatment effects on butterfly numbers were found for spring oilseed rape crops (table 6, figure 3). For *Pieris*, non-*Pieris* and the two combined, over the whole season counts were lower on margins of GMHT halves of fields. Differences were greater for non-*Pieris* than *Pieris* species with 37% compared to 19% lower densities, respectively, on GMHT margins compared to conventional ones. Within the season, counts were lower on GMHT margins by the greatest amount in July for Pieris, 39%, but in August for non-Pieris, 40%. Counts for all eight individual species analysed were also consistently lower on spring oilseed rape GMHT margins. Over the whole season, the total numbers of butterflies on margins were not different for beet. However, butterfly numbers recorded in July samples from this crop were less in margins adjacent to GMHT halves of the field by 27% (table 6, figure 3). Numbers of small tortoiseshell over the whole season were also lower in GMHT beet than in conventional. No differences in butterfly densities were found on margins around maize crops (table 6).

The bumble bee (*Bombus*) species *B. terrestris*, *B. lucorum*, *B. lapidarius* and *B. pascuorum* and the honey bee *Apis mellifera* were the most frequently recorded bees in all crops. They were recorded visiting 66 different plant genera from 30 families. In the margins of all three crops, they were most often recorded on thistles (*Cirsium* spp.), hogweed (*Heracleum sphondylium*) and bramble (*Rubus fructicosus*). For all three crops, counts were low and variable and no differences were found in total density of all bees between margins of GMHT and conventional halves of fields (table 7). However, differences were found between groups of bees in margins of beet crops in June. Counts of bumble bee and long-tongued bee groups were greater by 74% and 71% in GMHT margins at this time of the year, but lower by 52% for honey bee; no difference was found in total bee numbers. Honey bee density was greater by 182% in August in GMHT margins of maize, but no other differences in bees were found for this crop. Bee counts were highest in July, and the density of bees was much greater on margins next to spring oilseed rape compared to those adjacent to beet and maize crops, but no treatment differences in bee densities were found on these margins.

6.4.4 Other invertebrates

6.4.4.1 Slugs and snails

Three main gastropod species found in field verges of all three crops were the snails *Monacha cantiana* and *Cepea hortensis*, and the slug *Deroceras reticulatum*. No treatment effects were found for gastropods within any of the three crops sampled (table 8).

6.4.4.2 Ground beetles (Carabidae)

The most abundant ground beetles were *Bembidion lampros*, *Trechus quadristriatus* and *Demetrias atricapillus* and represented 12%, 14% and 5% in beet; 19%, 6% and 8% in maize; and 16%, 7% and 12% in spring oilseed rape field verges, respectively. Of the species analysed, although counts were low, abundance of *B. lampros* was shown to be 105% higher, while that of *D. atricapillus* was 44% lower, in field verges of GMHT maize (table 9a). No other species showed treatment effects.

6.4.4.3 True bugs (Heteroptera)

There were no treatment effects for total numbers of true bugs in any of the three crops. Samples were dominated by nymphs, which restricted species-level identification. The abundance of herbivorous true bugs was 50% lower in June, but not August, samples in the field verge adjacent to GMHT beet (table 9a). No differences in abundance were found on field verges beside maize or spring oilseed rape.

6.4.4.4 Springtails (Collembola)

More than 98% of the springtails comprised the Entomobryidae, Isotomidae and Sminthuridae families, which represented 58%, 35% and 6% in beet; 53%, 33% and 12% in maize; and 56%, 28% and 15% in spring oilseed rape field verges, respectively. In August samples, total springtail numbers in the field verge were 37% more in GMHT maize than in conventional, and Sminthuridae abundance was 69% greater in the field verge beside GMHT spring oilseed rape (table 9a).

6.4.4.5 Spiders (Araneae)

Treatment effects on total spider numbers were detected only in maize, where there were 16% fewer in the GMHT treatment. Sheet web spiders (Linyphiidae) represented 26%, 30% and 37% total adult spiders in beet, maize and spring oilseed rape field verges, respectively, and the abundance of this groups of spiders, were 29% lower in GMHT maize than in conventional over the whole season and 33% lower in GMHT spring oilseed rape in June.

6.4.4.6 Functional groups

Treatment differences for herbivores and parasitoids were found in August samples in field verges beside beet, where abundance was 28% lower in the GMHT treatment for both groups (table 9b). There were no treatment effects for predators or invertebrate bird food items in any of the three crops (table 9b).

6.4.5 Consistency of treatment effects: treatment by covariate interactions

Excluding analyses of vegetation scorching and margin attributes, of the 64 significant treatment effects found (tables 3, 4, 6, 7, 8, 9) seven showed a significant treatment by year interaction. In all but one of these cases, the magnitude, but not the direction of the effect differed in one of the three years analysed. There was no consistent pattern in the year that differed. For one effect, cover index of vegetation in tilled margins of maize, the effect was only apparent in the third year, and the treatment difference was slight but in different directions for the first two years.
For all significant treatment effects no interaction between treatment and the weed status of sites was found, nor were differences in treatment effects apparent between sugar beet and fodder beet. Treatment effects were found to differ between Environmental Zones of Great Britain in two out of 64 analyses conducted. These cases are counts of total butterflies and counts of the dominant species small white, and the direction of the treatment difference was reversed for the Scottish lowlands (Environmental Zone 4) compared to sites in England.

6.5 Discussion

The management of GMHT crops had significant effects on the plants and invertebrates of field margins. The main effects were found on the vegetation within the non-cropped, tilled margin of fields, which is situated between the crop and the field verge. The overall cover of plant species and the degree of flowering and seeding of these species were all affected, but the response differed between the three crops studied. Less plant cover, which produced fewer flowers and less seed, were found on tilled margins of GMHT halves of spring oilseed rape fields throughout the season. The tilled margins of GMHT halves of beet also had less flowering and seeding, though this effect was only apparent in July and August. The converse was found on tilled margins of maize fields, with more flowering found on GMHT halves. The effects on tilled margins of adoption of GMHT management are therefore likely to be markedly different depending on the crop grown.

Although not part of the cropped area of fields, the tilled margin was cultivated and likely to be managed in a similar way to the adjacent crop. Herbicide may be applied directly. Consequently, effects on weeds in this area of fields were similar to those within the crop where the density and biomass of weeds, including reproductive individuals, were greater within GMHT maize crops, but less within beet and spring oilseed rape crops (Heard *et al.*, 2003a). The effects on weeds found within the crop reflect the relative efficacy of GMHT compared to conventional herbicide regimes. In particular, lower weed densities in conventional maize were attributed to the widespread use of herbicides such as atrazine that persist in soil for long periods (Heard *et al.* 2003*a*). Although the main effects of management of GMHT crops on the vegetation of adjacent margins were within the often narrow (0.9 m on average) tilled margin strip, differences were also found in other components of field margins, situated further away from the crop. Notably, the cover of vegetation and amount of flowering within the field verge and boundary was reduced beside GMHT spring oilseed rape in June. This reduction in flowering did not persist into July and August however, even though flowering effects within tilled margins were marked at these times of the year. Although greater cover of vegetation was found in field verges beside GMHT maize in June, no resultant effects on flowering and seeding were found. Compared to the tilled margin, vegetation effects in the field verge and boundary were therefore fewer in number and smaller in magnitude, and for flowering and seeding, were not found throughout the season.

As well as affecting vegetation in the tilled margin, management of GMHT crops also had significant effects on invertebrates found along field margins. The greatest effects were on butterflies, and were most marked in margins adjacent to spring oilseed rape. The overall density of butterflies was greatest in this crop and counts were consistently lower on GMHT margins throughout the season. These differences were mirrored within the cropped area of the field (Haughton *et al.*, 2003) where butterfly counts were also lower in the GMHT half. The magnitude of these effects on butterfly density was also remarkably similar with 34% lower numbers within the crop and 32% less within adjacent margins. Effects on butterfly numbers were also found in margins of beet crops but these differed through the season; fewer butterflies were found on GMHT margins in July, but not earlier in the season. Within the crop however, butterfly numbers were lower in the GMHT half only in August (Haughton *et al.*, 2003). Counts of butterflies in margins adjacent to maize were not different between treatments despite differences being apparent within the field (Haughton *et* *al.*, 2003). Compared to spring oilseed rape and beet, maize tilled margins had less overall flowering that only differed between treatments in August.

For mobile insects such as bees and butterflies, it is likely that densities on margins and within the adjacent crop are closely related, but there was also a good match between effects on butterfly numbers on margins and flowers within tilled margins throughout the season. It therefore seems likely that these mobile, nectar-feeding insects were simply responding to availability of forage resource. Flower density has been shown to affect the density of butterflies on field margins (Clausen *et al.*, 2001; Dover, 1996; Feber *et al.*, 1996; Meek *et al.*, 2002; Sparks & Parish, 1995). These studies highlight the importance of particular plants for nectar, many of which are Asteraceae (e.g. thistles) one of the plant families with reduced flowering in tilled margins of beet and spring oilseed rape GMHT crops. Related work has also shown the importance of nectar resource in arable system for bees (Backman & Tiainen, 2002; Dramstad & Fry, 1995; Fussell & Corbet, 1992a; Saville, 1993) but we did not detect comparable effects of GMHT management on this group of species. This could be due, in part, to low and variable counts, and in spring oilseed rape, a buffering effect of the crop, which provides copious nectar and pollen on both treatments when in flower.

In arable ecosystems, weeds are an important source of pollen and nectar for invertebrates. This study has suggested that weeds within the tilled, non-cropped component of field margins, and within the crop edge, may be important for the following reasons. Field margin vegetation adjacent to the cropped area of fields, at least within the first 20 cm (Kleijn, 1996), is likely to capture fertilisers applied to the crop. As well as having increased productivity, vegetation in this part of the boundary has a higher percentage of annual species (Kleijn & Verbeek, 2000). Plants growing in such a habitat, in the absence of crop plants, are also more likely to flower and produce seed due to less competition. Equally, an important trait of plants that predominate in such situations is the production of a large number of flowers. Although flowering of any particular species may be over a short period, the temporally separate flowering phenologies of a diverse weed community can provide a regular supply of pollen and nectar, particularly for generalist feeders. In addition, plants in the tilled margin may be particularly important to larger flower-visiting insects, as they are likely to be more apparent than similar resources within the crop. Butterflies may also benefit from the proximity of this nectar supply to boundaries, which provide shelter, larval foodplants and to a lesser extent insulation for these species (Dover *et al.*, 2000).

It is likely that the effects observed on butterflies were mostly, but not solely, due to differences in nectar resources provided by arable plants. The availability of larval food resources in margins may be important for some species (Feber *et al.*, 1996) but the consistency of effects found for the separate butterfly species, which have different larval foodplant requirements, suggests a mechanism common to all species. Effects on butterfly numbers could also be caused by differences in toxic effect of herbicides, or insecticides, used between the two halves of the field. Applications of insecticides were almost always the same for the two halves of the field (Champion *et al.*, 2003) and there are few examples of direct toxic effects of herbicides on invertebrates (Norris *et al.*, 2000). The most important effects of herbicides on invertebrates are likely to be through the indirect effects on the host plants, by modification of food resource and habitat (Potts, 1986). The GMHT and conventional crop may also differ in other aspects important for butterflies. Whether the two varieties differ in attractiveness cannot be assessed from these Farm Scale Evaluations, but previous work suggests this is unlikely, at least for bees (Osborne, Carreck & Williams, 2001; Picard-Nizou *et al.*, 1995). Differences in flowering duration of conventional and GMHT crops are also unlikely to be important. Beet did not provide nectar or pollen, because it was not allowed to flower (Champion *et al.*, 2003) and the effects observed in spring oilseed rape were found in July and August after the crop had finished flowering. Further, no differences were found in the overall frequency of crop flowering between GMHT and conventional spring oilseed rape (Hawes *et al.*, 2003).

From the results of this experiment, it is not possible to make direct conclusions about the impact of GMHT management on the long-term dynamics of butterfly populations. We have no measurement of densities at sites in subsequent years and all the common species are highly mobile. The effects on butterfly numbers relating to nectar resources in tilled margins demonstrate a foraging choice. If sufficient forage resource is available elsewhere in the landscape, then populations of this mobile species group will be buffered against the effects of changes in herbicide management, but not if such forage reductions occur over large contiguous areas. Of the butterfly species commonly found in arable ecosystems, those with lower dispersal ability (e.g. hedge brown - *Pyronia tithonus*) are likely to be most vulnerable to changes in the availability of nectar plants. For these species in particular, but also for butterfly populations in general, landscape structure is likely to be more important than the farming system (Sherratt & Jepson, 1993; Weibull, Bengtsson & Nohlgren, 2000). Loss and degradation of field margins associated with agricultural intensification has been suggested as a cause of decline in butterflies in the UK (Asher *et al.*, 2001) and other European countries (Maes & van Dyck, 2001; van Swaay, 1990), but the relative importance of these versus other suitable habitats such as road verges and wasteplaces has not been quantified. Whether resources for adult (nectar) and/or larval (foodplants) butterflies are limited in agro-ecosystems is not known, and scaling up the results of this experiment poses similar problems to those identified for predicting the effects of GMHT on skylark populations (Watkinson *et al.*, 2000).

This experiment has demonstrated the indirect effects of herbicide management on butterflies; similar effects may be expected for other flower and nectar-feeding groups such as solitary bees, moths, hoverflies and other flies, and less frequently beetles and wasps (Vespidae species and larger parasitic groups such as the Ichneumonidae). Effects to such a range of species groups could have implications for the pollination of arable plants (Allen-Wardell *et al.*, 1998). The effects on seeding may also have knock-on effects for arable food webs. Differences in the frequency of species which set seed in tilled margins, mirrored effects on seed rain found within the crop (Heard *et al.*, 2003a) whereby seeding was lower in GMHT beet and spring oilseed rape but greater in GMHT maize. The longer-term implications of such changes depend upon rotational cropping patterns, yet may be important to birds of conservation concern whose densities are related to availability of dietary seed (Firbank *et al.*, 2003; Moorcroft *et al.*, 2002; Robinson *et al.*, 2002).

The amount of herbicide drift was not measured in this experiment, but the level of scorched vegetation was low in field margins adjacent to both GMHT and conventional halves of fields. Although drift of agrochemicals is dependent on a number of factors, levels reported under normal conditions range from 1 to 15% of the amount applied to the crop at 1m from the last nozzle (Marrs *et al.*, 1989). Differences in the amount of scorched vegetation were found particularly within tilled margins, being greater in GMHT treatments for all crops. The management of the GMHT allowed the use of herbicides to be applied later in the development of tolerant crops than in conventional non-tolerant varieties (Champion *et al.*, 2003). The spray boom was therefore higher, and the potential for spray drift likely to be greater, when herbicide was applied to GMHT halves of fields. At this later stage of the season, more plants will also be actively growing (e.g. less still dormant) and therefore susceptible to drift, but the structure of vegetation will also affect deposition of spray droplets; drift may penetrate less distance into field margins when the sward is taller (Marrs, Frost & Plant, 1991).

The effects of herbicide spray drift on field margin plants and animals have proved hard to measure and predict (Marrs *et al.*, 1997). Scorching of vegetation was greater on GMHT field margins, notably within tilled margins where fifteen of the twenty-two effects on vegetation were found. Less evidence for marked treatment effects were found in field verge or boundary vegetation. Plant cover was lower in these components of field margins in GMHT spring oilseed rape when sampled in June however, the time of the year when spray damage effects were greatest. Flowering was also lower in GMHT spring oilseed rape verges at this time, but not later in the season when spray damage effects were reduced. Seeding of vegetation was also not affected, suggesting some recovery by the vegetation. Experimental studies have suggested that drift of herbicides has less severe effects on field margin vegetation compared to drift of fertiliser applications (Kleijn & Snoeijing, 1997).

Slugs, snails and other invertebrates sampled directly from the field verge showed few differences. Where effects were detected for these taxa, abundance was affected both negatively and positively in GMHT treatments. Taxa, where abundance was lower under GMHT crop management, were mainly those that utilise vegetation directly as food plants, such as the herbivorous true bugs (Heteroptera) (Southwood & Leston, 1959) and other arthropods, and those that use plants as structures for web-spinning (e.g. many Linyphiidae, Alderweireldt, 1994) and climbing in search of prey (e.g. *Demetrias atricapillus*, Forsythe, 2000). The lower density of the functional groups, herbivores and predators, in August samples from GMHT beet reflect differences found for these groups within-field, albeit at lower magnitudes (Hawes *et al.*, 2003). Biomass of weeds in the crop was also lower at this time of the season in GMHT beet (Heard *et al.*, 2003), but differences were not detected in the vegetation of the verge for this crop. There may be movement of individuals between the crop and field verge for these groups. The lower counts of web sheet spiders (Linyphiidae) in GMHT spring oilseed rape verges may relate directly to vegetation differences found in the verge however. Many of these spiders utilise plants in web-building and reductions in vegetation height have been shown to lead to a lower abundance of one such species, *Lepthyphantes tenuis* (Haughton *et al.* 2001). Less vegetation cover may have provided fewer potential web-building sites for these spiders.

The lack of a difference in the response between fodder and sugar beet suggested that the management of these crops is sufficiently similar that they may be treated as one crop for analysis. The consistency of the treatment effects of sites within a range of environmental regions and with differing degrees of overall weediness implied that they could be scaled up to a wider population of sites across the UK. However, the effects on field margins differed between the three crops studied and predicting the potential implications of commercial growing of GMHT spring-sown crops on farmland biodiversity requires an approach that considers the entire farmed landscape (Firbank *et al.*, 2003).

In conclusion, this experiment has shown that effects of GMHT management on the plants of field margins are most marked in the non-cropped, tilled strip between the crop and field verge, and carry over to a lesser extent to the verge and field boundary. Vegetation in this component of field margins receives most if not all the herbicide sprays applied to weeds in the crop, and pronounced treatment differences in flowering had knock-on effects on butterfly abundance. The effects differed between the three crops studied however, with less flowering and butterflies on margins of GMHT spring oilseed rape and beet, but more flowering on maize GMHT margins yet no butterfly differences for this crop. Although scorching of vegetation through spray drift was greater on GMHT field verges, the overall percentage of vegetation affected was very low. No other marked effects were found on plants and invertebrates living in the field verge or boundary. Of the invertebrate groups sampled, butterflies have been shown to be particularly sensitive to differences in vegetation, and highlight their importance as a key indicator species in future studies of agro-ecosystems.

Figure 6.1. Cross-section of a field margin. Vegetation plots were recorded within the boundary, field verge and tilled margin.

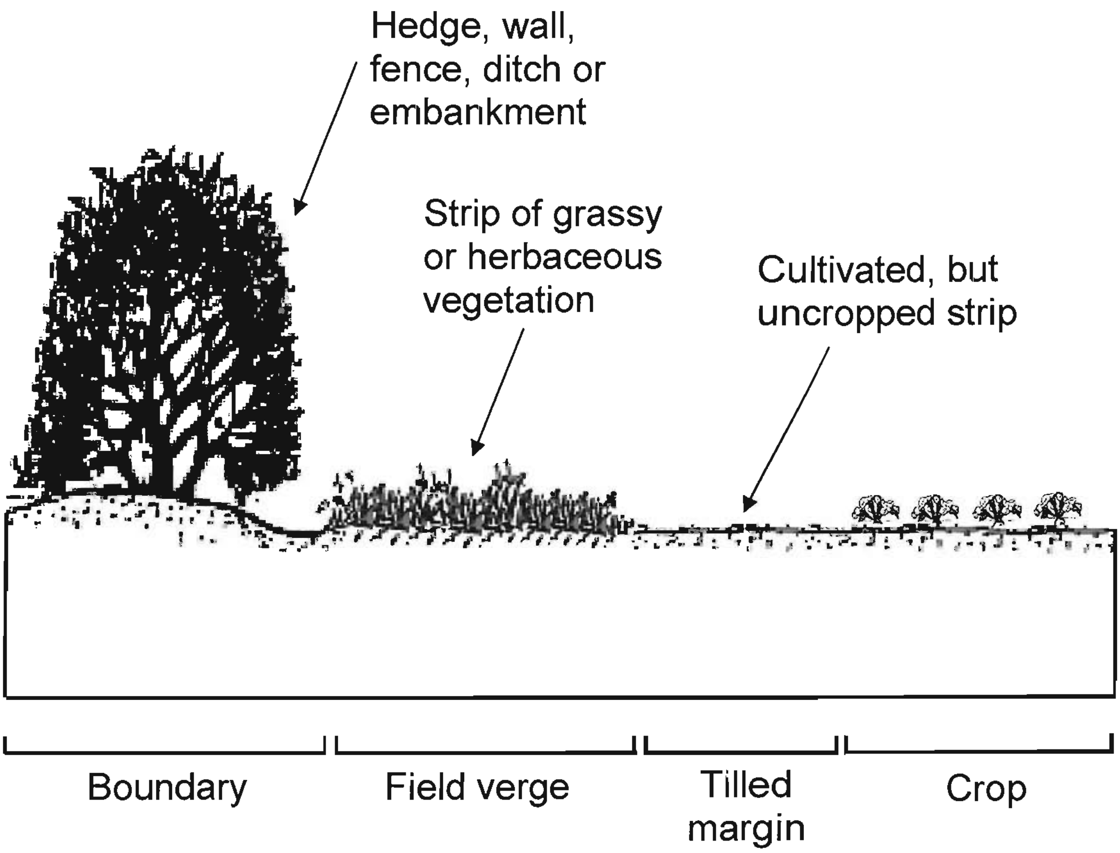


Figure 6.2. Location of margin sample points in a standard half-field. Symbols indicate sampling locations as follows: ✱ gastropod searches, and margin attribute samples; + suction samples; --- bee/butterfly transects; location of vegetation plots are labelled.

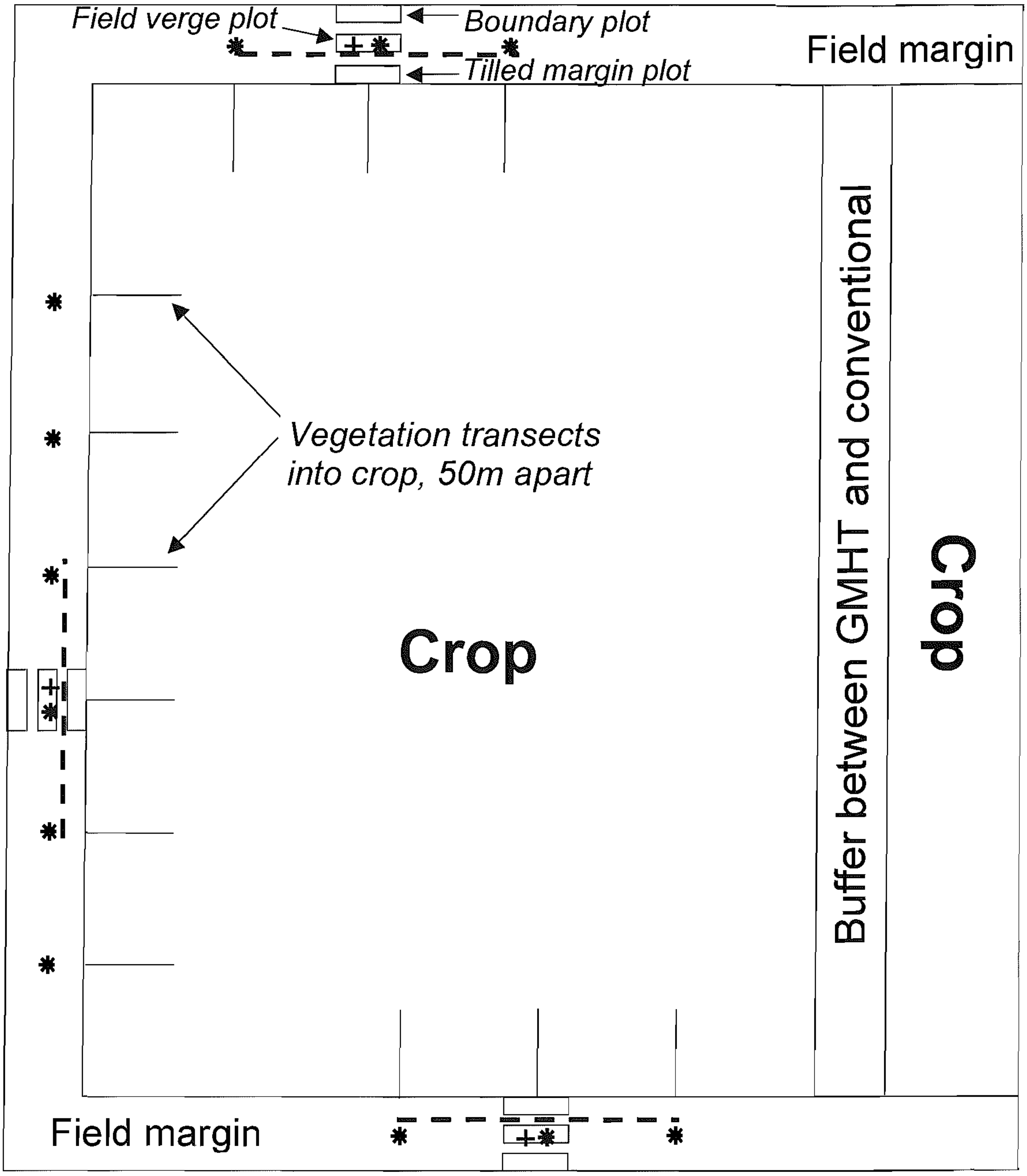
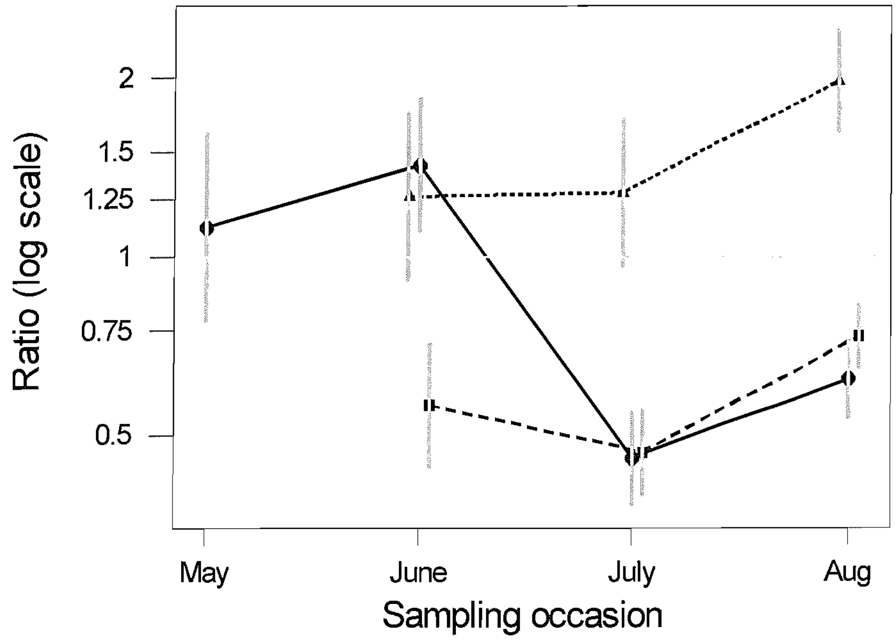


Figure 6.3. Main effects of treatment on (a) flowering in tilled margins and (b) butterflies expressed as a ratio (GMHT/conventional) for each month. Symbols (line style) for different crops: circle (solid) beet, triangle (dot) maize, square (dash) spring oilseed rape. Error bars are one standard error.

(a)



(*b*)

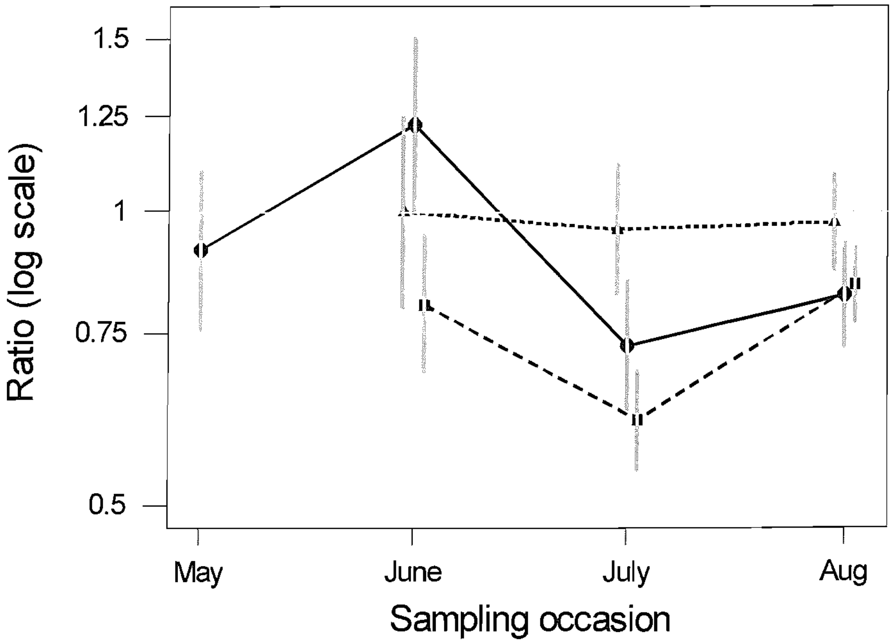


Table 6.1. Level of identification and assigned major functional groups of suction sampled invertebrates in the field margins. Collembola are not assigned to a functional group. Invertebrates identified as important food resource for birds follow Wilson *et al.* (1999).

taxa	level of identification	functional group			
		predator	herbivore	parasitoid	bird food
Collembola	family				
Orthoptera	order				y
Hemiptera:					
Heteroptera	species	y	y		y
Auchenorrhyncha	species		y		y
Aphidoidea	super-family		y		y
Neuroptera	order	y			
Lepidoptera:					
larvae	order		y		y
Diptera	order				y
Hymenoptera:					
Symphyta larvae	sub-order		y		y
Parasitica	super-family			y	
Coleoptera:					
Coccinellidae	species	y	y		
Curculionidae	family		y		y
Staphylinidae	family	y			y
Carabidae	species	y			y
others	order				
Araneae:					
Linyphiidae	family	y			y
Lepthyphantes tenuis	species	y			y
Erigone	genera	y			y
Oedothorax	genera	y			y
Lycosidae	family	y			y
others	order	y			y

Table 6.2. Attributes of field margins. Hedge and ditch frequencies (out of 12) are given as mean values, width of tilled margin and field verge are median values in metres. Arithmetic means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are values per 10 m^2 for *n* sites included in the analysis.

crop / margin location	*n*	arithmetic mean count		difference between treatments (95% c.i.)	*p*-value
		C	GMHT		
beet					
tilled margin width	66	0.98	1.37	1.22 (-0.31 - 2.76)	0.12
field verge width	66	0.93	0.95	0.45 (-0.35 - 1.25)	0.26
hedge frequency	66	4.50	4.86	0.36 (-0.53 - 1.25)	0.42
ditch frequency	66	2.33	2.03	-0.30 (-0.93 - 0.33)	0.34
maize					
tilled margin width	59	0.85	0.84	0.03 (-0.07 - 0.12)	0.59
field verge width	59	1.08	1.21	0.39 (-0.57 - 1.35)	0.42
hedge frequency	59	5.66	5.34	-0.32 (-1.26 - 0.61)	0.49
ditch frequency	59	2.05	1.81	-0.24 (-0.94 - 0.47)	0.50
spring oilseed rape					
tilled margin width	67	0.63	0.68	0.84 (-0.49 - 2.16)	0.21
field verge width	67	1.29	1.04	-0.32 (-2.38 - 1.73)	0.75
hedge frequency	67	5.72	5.24	-0.48 (-1.34 - 0.39)	0.27
ditch frequency	67	2.54	3.21	0.67 (-0.17 - 1.51)	0.11

Table 6.3. Margin vegetation in relation to treatments in each half-field for (*a*) index of plant cover; (*b*) index of flowering; (*c*) index of seeding. Geometric means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are values per 10 m^2 for *n* sites included in the analysis. Multiplicative treatment ratio, $R = 10^d$, where *d* is the mean of the differences between GMHT and conventional treatments on the logarithmic scale; confidence limits for *R* are back-transformed from those for *d*. *$p<0.05$, **$p<0.01$, ***$p<0.001$.

(*a*)

crop / margin location	*n*	geometric mean		*R* (95% c.i.)	*p*-value
		C	GMHT		
beet					
tilled margin	62	7.49	7.71	1.03 (0.79 - 1.33)	0.84
verge	61	10.6	11.1	1.04 (0.79 - 1.38)	0.77
boundary	62	6.68	6.49	0.97 (0.67 - 1.41)	0.88
maize					
tilled margin	48	7.54	9.73	1.28 (1.06 - 1.54)	0.006 **
verge	49	14.2	16.3	1.15 (1.03 - 1.27)	0.012 *
boundary	48	10.0	11.8	1.17 (0.89 - 1.55)	0.27
spring oilseed					
tilled margin	64	9.31	6.85	0.75 (0.62 - 0.90)	<0.001 ***
verge	64	13.7	11.1	0.81 (0.70 - 0.94)	0.004 **
boundary	65	9.60	7.14	0.75 (0.59 - 0.96)	0.016 *

(*b*)

crop / margin location	period	*n*	geometric mean		*R* (95% c.i.)	*p*-value
			C	GMHT		
beet						
tilled margin	year	66	87.3	57.2	0.66 (0.50 - 0.86)	<0.001 ***
	May	23	2.31	2.63	1.12 (0.52 - 2.41)	0.76
	June	42	4.70	6.85	1.43 (0.83 - 2.44)	0.19
	July	62	29.8	13.5	0.46 (0.32 - 0.66)	<0.001 ***
	Augus	64	47.3	29.3	0.62 (0.46 - 0.85)	0.002 **
field verge	year	66	65.7	61.5	0.94 (0.66 - 1.32)	0.71
	May	36	19.1	14.5	0.76 (0.49 - 1.19)	0.22
	June	50	26.1	23.5	0.90 (0.58 - 1.41)	0.66
	July	63	25.0	19.8	0.79 (0.53 - 1.18)	0.25
	Augus	62	17.9	16.5	0.92 (0.65 - 1.32)	0.67
boundary	year	66	20.1	21.0	1.04 (0.66 - 1.65)	0.87
	May	33	7.11	9.39	1.31 (0.65 - 2.64)	0.44
	June	48	10.8	10.7	1.00 (0.59 - 1.69)	0.99
	July	58	9.09	6.75	0.75 (0.46 - 1.23)	0.25
	Augus	55	5.41	8.12	1.47 (0.89 - 2.44)	0.14
maize						
tilled margin	year	58	25.7	43.1	1.67 (1.16 - 2.40)	0.009 **
	June	33	2.38	3.09	1.26 (0.65 - 2.47)	0.47
	July	50	8.04	10.4	1.28 (0.72 - 2.30)	0.38
	Augus	55	15.3	30.5	1.98 (1.32 - 2.97)	<0.001 ***
field verge	year	58	87.0	94.9	1.09 (0.95 - 1.25)	0.20
	June	48	31.4	29.4	0.94 (0.71 - 1.23)	0.63
	July	54	28.2	30.4	1.07 (0.89 - 1.30)	0.44
	Augus	55	23.0	30.0	1.30 (1.00 - 1.69)	0.056
boundary	year	57	35.8	47.2	1.32 (1.03 - 1.68)	0.018 *
	June	47	17.0	18.9	1.11 (0.73 - 1.69)	0.64
	July	52	11.1	12.2	1.09 (0.77 - 1.55)	0.64
	Augus	52	4.15	9.41	2.18 (1.36 - 3.49)	0.002 **
spring oilseed						
tilled margin	year	67	101	66.1	0.66 (0.54 - 0.80)	<0.001 ***
	June	48	8.87	4.84	0.56 (0.35 - 0.91)	0.019 *
	July	64	39.7	18.4	0.47 (0.33 - 0.66)	<0.001 ***
	Augus	66	42.5	31.2	0.74 (0.57 - 0.95)	0.027 *
field verge	year	67	105	87.6	0.83 (0.68 - 1.02)	0.083
	June	57	34.0	22.2	0.66 (0.49 - 0.88)	0.005 **
	July	64	33.3	30.5	0.92 (0.67 - 1.26)	0.59
	Augus	66	27.3	25.7	0.94 (0.72 - 1.23)	0.66
boundary	year	67	41.7	36.6	0.88 (0.64 - 1.20)	0.43
	June	57	16.8	12.0	0.72 (0.46 - 1.12)	0.15
	July	64	10.8	9.44	0.88 (0.55 - 1.41)	0.60
	Augus	64	6.90	6.90	1.00 (0.63 - 1.58)	1.00

(*c*)

crop / margin location	period	*n*	geometric mean		*R* (95% c.i.)	*p*-value
			C	GMHT		
beet						
tilled margin	year	6	4.19	2.41	0.61 (0.43 - 0.86)	0.007 **
	July	3	2.04	1.29	0.68 (0.42 - 1.12)	0.13
	August	5	3.15	1.86	0.63 (0.43 - 0.91)	0.015 *
field verge	year	6	16.0	12.0	0.76 (0.57 - 1.01)	0.062
	July	6	6.91	5.41	0.79 (0.59 - 1.07)	0.13
	August	6	9.46	6.13	0.66 (0.48 - 0.91)	0.004 **
boundary	year	6	3.94	4.03	1.02 (0.69 - 1.52)	0.92
	July	4	2.48	1.85	0.77 (0.47 - 1.26)	0.29
	August	5	2.73	2.82	1.03 (0.67 - 1.58)	0.88
maize						
tilled margin	year	4	2.58	3.72	1.40 (0.87 - 2.23)	0.15
	July	2	1.49	1.29	0.89 (0.52 - 1.54)	0.68
	August	4	2.06	3.07	1.42 (0.86 - 2.33)	0.16
field verge	year	5	21.0	23.6	1.12 (0.94 - 1.34)	0.21
	July	5	8.78	9.40	1.07 (0.85 - 1.34)	0.56
	August	5	13.4	14.3	1.06 (0.88 - 1.28)	0.52
boundary	year	5	4.28	5.76	1.32 (0.93 - 1.88)	0.12
	July	4	2.12	2.09	0.99 (0.66 - 1.48)	0.97
	August	4	3.33	5.06	1.47 (0.98 - 2.22)	0.057
spring oilseed						
tilled margin	year	6	6.26	3.97	0.65 (0.51 - 0.84)	0.002 **
	July	4	2.19	1.47	0.71 (0.46 - 1.11)	0.13
	August	6	4.56	2.98	0.68 (0.52 - 0.88)	0.005 **
field verge	year	6	18.3	20.0	1.09 (0.92 - 1.31)	0.35
	July	6	6.20	6.63	1.07 (0.83 - 1.37)	0.64
	August	6	11.5	12.1	1.05 (0.86 - 1.27)	0.70
boundary	year	6	6.77	5.74	0.86 (0.63 - 1.16)	0.30
	July	4	3.43	2.58	0.77 (0.50 - 1.21)	0.25
	August	5	4.66	4.52	0.97 (0.69 - 1.37)	0.87

Table 6.4. Index of flowering within tilled margins for plant families important for nectar and pollen for bees and butterflies. Geometric means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are values per 10 m^2 for n sites included in the analysis. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and conventional treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. *$p<0.05$; **$p<0.01$; ***$p<0.001$.

crop / plant group	period	n	geometric mean		R (95% c.i.)	p-value
			C	GMHT		
beet						
Asteraceae	year	64	12.0	6.04	0.52 (0.34 - 0.79)	0.004 **
	June	19	1.41	2.40	1.57 (0.58 - 4.22)	0.27
	July	53	5.94	1.88	0.35 (0.22 - 0.57)	<0.001 ***
	Augus	61	6.78	3.43	0.53 (0.34 - 0.83)	0.005 **
Brassicaceae	year	58	4.93	6.13	1.23 (0.79 - 1.91)	0.34
	June	20	1.35	3.79	2.44 (1.09 - 5.48)	0.027 *
	July	45	3.24	2.75	0.86 (0.49 - 1.52)	0.60
	Augus	53	2.22	3.83	1.63 (1.01 - 2.66)	0.045 *
Fabaceae	year	52	1.93	1.91	0.99 (0.63 - 1.55)	0.97
	June	17	0.56	1.32	1.86 (0.65 - 5.31)	0.23
	July	39	1.75	0.57	0.44 (0.27 - 0.71)	0.004 **
	Augus	44	0.80	0.98	1.15 (0.71 - 1.87)	0.57
Scrophulariaceae	year	56	5.59	5.37	0.96 (0.61 - 1.51)	0.87
	June	22	1.15	2.00	1.57 (0.73 - 3.41)	0.27
	July	43	3.81	2.46	0.67 (0.38 - 1.19)	0.18
	Augus	46	3.75	2.83	0.78 (0.45 - 1.32)	0.33
maize						
Asteraceae	year	51	5.72	5.69	1.00 (0.61 - 1.62)	0.99
	June	11	0.75	2.00	2.15 (0.90 - 5.10)	0.12
	July	40	2.70	1.83	0.71 (0.38 - 1.34)	0.34
	Augus	48	4.09	3.29	0.82 (0.46 - 1.46)	0.52
Brassicaceae	year	45	1.70	6.59	3.41 (1.90 - 6.11)	<0.001 ***
	June	11	1.07	1.53	1.33 (0.23 - 7.52)	0.73
	July	27	1.78	2.60	1.39 (0.56 - 3.46)	0.47
	Augus	40	0.91	4.49	3.88 (2.02 - 7.43)	<0.001 ***
Fabaceae	year	36	0.86	3.50	3.22 (1.67 - 6.20)	0.002 **
	June	7	0.37	0.49	1.17 (0.40 - 3.46)	0.82
	July	23	0.36	2.41	3.98 (1.60 - 9.88)	0.009 **
	Augus	31	0.65	3.01	3.41 (1.82 - 6.38)	0.002 **
Scrophulariaceae	year	41	1.11	5.79	4.24 (2.33 - 7.73)	<0.001 ***
	June	12	0.79	0.74	0.95 (0.39 - 2.34)	0.91
	July	27	0.85	3.67	3.38 (1.63 - 6.98)	0.002 **
	Augus	37	0.71	4.49	4.61 (2.52 - 8.46)	<0.001 ***
spring oilseed						
Asteraceae	year	67	15.3	7.60	0.51 (0.36 - 0.72)	<0.001 ***
	June	25	1.95	0.51	0.37 (0.19 - 0.70)	0.005 **
	July	61	4.71	2.25	0.51 (0.32 - 0.83)	0.008 **
	Augus	65	8.31	4.33	0.54 (0.38 - 0.76)	0.002 **
Brassicaceae	year	66	8.36	5.60	0.68 (0.47 - 0.98)	0.030 *
	June	34	2.49	1.13	0.52 (0.30 - 0.90)	0.015 *
	July	56	6.05	2.92	0.51 (0.33 - 0.80)	0.003 **

crop / plant group	period	*n*	geometric mean		*R* (95% c.i.)	*p*-value
			C	GMHT		
	Augus	54	2.72	2.37	0.89 (0.6 - 1.31)	0.53
Fabaceae	year	51	3.49	2.86	0.84 (0.50 - 1.40)	0.50
	June	16	1.88	1.01	0.61 (0.23 - 1.61)	0.32
	July	39	2.38	1.41	0.64 (0.38 - 1.10)	0.094
	Augus	48	1.66	1.57	0.96 (0.57 - 1.61)	0.89
Scrophulariaceae	year	52	8.41	4.35	0.54 (0.35 - 0.82)	0.007 **
	June	28	3.20	1.24	0.45 (0.25 - 0.80)	0.013 *
	July	43	3.91	1.94	0.54 (0.31 - 0.92)	0.026 *
	Augus	45	3.92	2.14	0.58 (0.37 - 0.93)	0.026 *

Table 6.5. Scorching of vegetation in field margins. Arithmetic means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are percent vegetation scorched per 10 m^2 for *n* sites included in the analysis. *$p<0.05$; **$p<0.01$; ***$p<0.001$.

crop / margin location	period	*n*	arithmetic mean count		difference between treatments (95% c.i.)	*p*-value
			C	GMHT		
beet						
tilled margin	year	66	1.12	5.49	4.37 (2.97 - 5.77)	<0.001 ***
	May	34	0.72	1.86	1.14 (-1.28 - 3.57)	0.34
	June	42	1.29	4.06	2.85 (0.51 - 5.18)	0.018 *
	July	60	1.48	8.44	6.67 (4.54 - 8.79)	<0.001 ***
	Augus	63	0.91	5.06	4.15 (2.06 - 6.24)	<0.001 ***
field verge	year	64	1.35	4.24	2.50 (1.74 - 3.26)	<0.001 ***
	May	34	0.68	1.94	1.26 (-0.26 - 2.78)	0.10
	June	40	1.39	4.25	2.24 (1.01 - 3.47)	<0.001 ***
	July	58	1.48	4.98	3.64 (2.18 - 5.11)	<0.001 ***
	Augus	60	1.11	3.46	2.34 (1.15 - 3.52)	<0.001 ***
boundary	year	61	0.16	0.89	0.65 (0.19 - 1.11)	0.007 **
	May	32	0.05	0.02	-0.04 (-0.15 - 0.08)	0.54
	June	39	0.37	0.87	0.24 (-0.10 - 0.58)	0.17
	July	53	0.15	0.96	0.80 (0.11 - 1.50)	0.025 *
	Augus	56	0.17	0.83	0.67 (0.01 - 1.34)	0.047 *
maize						
tilled margin	year	58	1.24	4.32	3.09 (1.59 - 4.59)	<0.001 ***
	June	43	2.18	6.61	4.53 (1.61 - 7.45)	0.003 **
	July	52	1.43	5.07	3.94 (1.56 - 6.33)	0.002 **
	Augus	51	0.47	0.46	0.00 (-0.50 - 0.51)	0.99
field verge	year	58	1.63	3.10	1.47 (0.60 - 2.35)	<0.001 ***
	June	43	2.68	4.79	2.08 (0.28 - 3.88)	0.024 *
	July	51	1.42	3.81	2.50 (1.18 - 3.83)	<0.001 ***
	Augus	51	1.03	0.89	-0.06 (-0.74 - 0.62)	0.87
boundary	year	58	0.43	0.56	0.13 (-0.17 - 0.44)	0.39
	June	42	0.63	1.10	0.53 (0.05 - 1.00)	0.030 *
	July	50	0.34	0.53	0.20 (-0.31 - 0.71)	0.43
	Augus	50	0.15	0.17	0.03 (-0.07 - 0.12)	0.59
spring oilseed						
tilled margin	year	64	1.02	3.75	2.54 (1.56 - 3.52)	<0.001 ***
	June	52	2.01	8.18	6.06 (3.37 - 8.75)	<0.001 ***
	July	54	1.26	2.96	1.66 (-0.11 - 3.43)	0.065
	Augus	61	0.22	0.49	0.28 (-0.13 - 0.68)	0.18
field verge	year	64	1.99	3.96	2.02 (1.01 - 3.03)	<0.001 ***
	June	51	2.96	6.74	3.87 (1.49 - 6.26)	0.002 **
	July	54	2.68	4.23	1.38 (-0.22 - 2.97)	0.09
	Augus	60	0.59	1.28	0.72 (-0.21 - 1.65)	0.12
boundary	year	65	1.08	1.73	0.35 (-0.36 - 1.06)	0.33
	June	49	0.91	1.93	-0.02 (-0.51 - 0.48)	0.94
	July	53	1.26	1.81	0.13 (-0.54 - 0.80)	0.71
	Augus	58	0.36	0.59	0.26 (-0.50 - 1.01)	0.50

Table 6.6. Butterfly counts on field margins in relation to treatments in each half-field. Year totals are based on four visits for beet sites, and three visits for maize and spring oilseed rape sites. Geometric means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are numbers per 300 m of transect for n sites included in the analysis. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and conventional treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. *$p<0.05$; **$p<0.01$; ***$p<0.001$.

crop / taxa	period	n	geometric mean		R (95% c.i.)	p-value
			C	GMHT		
beet						
total butterflies	year	66	11.4	9.09	0.82 (0.66 -	0.064
	May	25	2.14	1.86	0.91 (0.61 -	0.60
	June	22	1.24	1.75	1.23 (0.79 -	0.35
	July	54	5.19	3.51	0.73 (0.54 -	0.042 *
	August	58	5.30	4.17	0.82 (0.64 -	0.14
Pieris brassicae	year	37	2.30	2.11	0.94 (0.65 -	0.78
Pieris rapae	year	51	4.06	3.32	0.85 (0.66 -	0.25
Pieris napi	year	24	1.74	1.79	1.02 (0.68 -	0.94
Aglais urticae	year	31	3.57	1.29	0.50 (0.31 -	0.005 **
Inachis io	year	16	2.50	1.08	0.59 (0.32 -	0.11
Maniola jurtina	year	34	2.34	2.29	0.99 (0.74 -	0.93
maize						
total butterflies	year	56	11.6	11.3	0.98 (0.79 -	0.88
Pieris brassicae	year	32	1.90	2.79	1.31 (0.94 -	0.12
Pieris rapae	year	44	3.78	3.15	0.87 (0.69 -	0.22
Pieris napi	year	14	2.85	1.94	0.76 (0.46 -	0.22
Aglais urticae	year	27	2.54	1.90	0.82 (0.52 -	0.36
Inachis io	year	18	1.57	1.19	0.85 (0.51 -	0.53
Pyronia tithonus	year	23	2.26	1.71	0.83 (0.47 -	0.53
Maniola jurtina	year	36	2.26	2.68	1.13 (0.80 -	0.45
Aphantopus	year	16	1.72	1.96	1.09 (0.60 -	0.81
spring oilseed rape						
total butterflies	year	67	24.5	18.3	0.76 (0.64 -	0.003 **
	June	42	2.84	2.08	0.80 (0.58 -	0.17
	July	57	9.37	5.34	0.61 (0.48 -	<0.001
	August	64	13.2	10.9	0.84 (0.70 -	0.055
Pieris species	year	67	16.7	13.2	0.81 (0.67 -	0.024 *
	June	37	2.68	2.06	0.83 (0.57 -	0.36
	July	51	5.44	2.94	0.61 (0.48 -	0.002 **
	August	61	10.4	9.77	0.95 (0.76 -	0.62
non-*Pieris* species	year	61	7.20	4.12	0.63 (0.50 -	<0.001
	June	7	1.03	1.03	1.00 (0.39 -	1.00
	July	48	4.96	2.92	0.66 (0.48 -	0.013
	August	47	3.55	1.75	0.60 (0.48 -	<0.001
Pieris brassicae	year	52	4.05	3.59	0.91 (0.66 -	0.55
Pieris rapae	year	65	10.9	8.91	0.83 (0.70 -	0.034 *
Pieris napi	year	31	2.61	1.15	0.60 (0.40 -	0.011 *
Inachis io	year	16	2.23	0.98	0.61 (0.36 -	0.090
Aglais urticae	year	29	2.65	1.41	0.66 (0.41 -	0.084
Pyronia tithonus	year	13	3.42	1.36	0.53 (0.29 -	0.073
Maniola jurtina	year	31	2.56	1.87	0.81 (0.53 -	0.28
Aphantopus	year	23	3.60	2.07	0.67 (0.41 -	0.11

Table 6.7. Bees on field margins in relation to treatments in each half-field. Year totals are based on four visits for beet sites, and three visits for maize and spring oilseed rape sites. Geometric means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are numbers per 300 m of transect for n sites included in the analysis. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and conventional treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. *$p<0.05$; ***$p<0.001$.

crop / taxa	period	n	geometric mean		R (95% c.i.)	p-value
			C	GMHT		
beet						
total bees	year	63	9.12	8.12	0.90 (0.66 - 1.23)	0.50
	May	19	1.52	1.09	0.83 (0.46 - 1.51)	0.53
	June	35	2.18	3.22	1.33 (0.86 - 2.04)	0.17
	July	47	4.04	4.01	1.00 (0.69 - 1.44)	0.98
	Augus	44	3.46	2.34	0.75 (0.47 - 1.18)	0.21
Apis mellifera	year	26	2.36	2.63	1.08 (0.61 - 1.93)	0.79
	June	13	2.58	0.71	0.48 (0.25 - 0.91)	0.044 *
	July	13	1.28	2.95	1.73 (0.73 - 4.08)	0.18
bumble bees	year	63	7.43	6.43	0.88 (0.65 - 1.2)	0.43
	May	15	1.65	0.93	0.73 (0.36 - 1.48)	0.34
	June	30	1.49	3.32	1.74 (1.17 - 2.59)	0.013 *
	July	46	3.61	3.32	0.94 (0.64 - 1.37)	0.70
	Augus	41	3.36	2.15	0.72 (0.45 - 1.17)	0.20
long-tongued bees	year	45	3.02	2.75	0.94 (0.63 - 1.39)	0.71
	June	18	0.83	2.14	1.71 (1.09 - 2.70)	0.028 *
	July	19	2.08	1.64	0.86 (0.46 - 1.58)	0.59
	Augus	27	1.82	1.33	0.83 (0.47 - 1.47)	0.50
maize						
total bees	year	54	7.48	7.60	1.01 (0.75 - 1.37)	0.92
Apis mellifera	year	27	2.00	3.58	1.53 (0.95 - 2.47)	0.081
	June	11	1.91	1.63	0.91 (0.44 - 1.88)	0.80
	July	10	3.14	2.79	0.92 (0.31 - 2.75)	0.87
	Augus	15	0.54	3.35	2.82 (1.63 - 4.90)	<0.001 ***
bumble bees	year	53	6.08	5.48	0.92 (0.68 - 1.24)	0.55
long-tongued bees	year	35	2.31	1.72	0.82 (0.57 - 1.20)	0.32
spring oilseed rape						
total bees	year	67	14.1	13.5	0.96 (0.76 - 1.22)	0.75
Apis mellifera	year	50	3.29	3.61	1.07 (0.75 - 1.53)	0.68
bumble bees	year	67	9.69	9.46	0.98 (0.77 - 1.25)	0.87
long-tongued bees	year	50	2.36	2.36	1.00 (0.75 - 1.33)	1.00

Table 6.8. Gastropods totalled over two sampling occasions, in relation to treatments in each half-field. Geometric means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are numbers per 24 m^2 for *n* sites included in the analysis. Multiplicative treatment ratio, $R = 10^d$, where *d* is the mean of the differences between GMHT and conventional treatments on the logarithmic scale; confidence limits for *R* are back-transformed from those for *d*.

crop / taxa	*n*	geometric mean		*R* (95% c.i.)	*p*-value
		C	GM		
beet					
total Gastropods	64	54.1	57.3	1.06 (0.84 - 1.34)	0.64
slugs	61	10.0	7.95	0.81 (0.64 - 1.03)	0.080
snails	61	35.3	37.8	1.07 (0.81 - 1.41)	0.65
maize					
total Gastropods	58	86.1	82.7	0.96 (0.81 - 1.14)	0.65
slugs	54	10.7	8.93	0.85 (0.68 - 1.06)	0.15
snails	58	53.0	49.3	0.93 (0.73 - 1.20)	0.56
spring oilseed rape					
total Gastropods	66	86.9	75.7	0.87 (0.70 - 1.09)	0.24
slugs	58	13.2	10.9	0.84 (0.63 - 1.12)	0.25
snails	60	61.0	54.4	0.89 (0.68 - 1.17)	0.41

Table 6.9. Invertebrates sampled by suction sampling of the field verge, in relation to treatments in each half-field for (*a*) taxonomic groups, and (*b*) functional groups. Geometric means for conventional (C) and genetically modified herbicide-tolerant (GMHT) treatments are numbers per 0.56 m^2 for *n* sites included in the analysis. Multiplicative treatment ratio, $R = 10^d$, where *d* is the mean of the differences between GMHT and conventional treatments on the logarithmic scale; confidence limits for *R* are back-transformed from those for *d*. $^*p<0.05$; $^{**}p<0.01$.

(*a*)

crop / taxa	period	*n*	geometric mean		*R* (95% c.i.)	*p*-value
			C	GMHT		
beet						
total Carabidae	year	60	4.34	3.56	0.85 (0.69 - 1.06)	0.16
total Araneae	year	64	17.9	15.9	0.89 (0.73 - 1.10)	0.26
total Heteroptera	year	58	10.6	8.71	0.84 (0.63 - 1.13)	0.24
herbivorous	year	40	1.84	1.52	0.89 (0.59 - 1.33)	0.55
	June	12	2.23	0.60	0.50 (0.26 - 0.95)	0.024 *
	Aug	34	1.46	1.43	0.99 (0.64 - 1.54)	0.98
total Collembola	year	64	113	125	1.10 (0.81 - 1.50)	0.51
maize						
total Carabidae	year	51	3.46	3.65	1.04 (0.83 - 1.32)	0.72
B. lampros	year	22	0.65	2.38	2.05 (1.37 - 3.07)	0.003 **
D. atricapillus	year	9	2.61	1.03	0.56 (0.38 - 0.83)	0.027 *
total Araneae	year	57	24.4	20.3	0.84 (0.71 - 1.00)	0.046 *
Linyphiidae	year	55	8.30	5.64	0.71 (0.58 - 0.88)	0.003 **
total Heteroptera	year	54	12.7	12.1	0.96 (0.77 - 1.21)	0.73
total Collembola	year	57	152	170	1.12 (0.87 - 1.43)	0.38
	June	52	64.9	74.6	1.15 (0.85 - 1.55)	0.38
	Aug	53	73.9	101	1.37 (1.02 - 1.84)	0.049 *
spring oilseed rape						
total Carabidae	year	58	3.16	2.83	0.92 (0.73 - 1.16)	0.50
total Araneae	year	65	14.3	13.2	0.93 (0.74 - 1.16)	0.53
Linyphiidae	year	60	6.36	5.28	0.85 (0.69 - 1.06)	0.14
	June	41	3.21	1.81	0.67 (0.49 - 0.91)	0.019 **
	Aug	53	4.19	4.34	1.03 (0.80 - 1.33)	0.83
total Heteroptera	year	47	7.57	6.65	0.89 (0.71 - 1.13)	0.35
total Collembola	year	65	105	113	1.07 (0.84 - 1.37)	0.55
Sminthuridae	year	54	8.31	12.8	1.48 (0.91 - 2.43)	0.12
	June	45	8.80	11.6	1.29 (0.68 - 2.44)	0.43
	Aug	36	2.23	4.46	1.69 (1.08 - 2.63)	0.027 *

(*b*)

species group	period	*n*	geometric mean C	GM	*R* (95% c.i.)	*p*-value
beet						
herbivores	year	64	51.8	41.5	0.81 (0.63 - 1.03)	0.077
	June	56	17.4	18.8	1.07 (0.79 - 1.46)	0.66
	Aug	62	30.4	21.7	0.72 (0.55 - 0.96)	0.023 *
predators	year	64	27.9	24.9	0.90 (0.76 - 1.06)	0.20
parasitoids	year	64	38.2	30.4	0.80 (0.64 - 1.01)	0.060
	June	56	10.1	11.0	1.09 (0.84 - 1.41)	0.55
	Aug	62	27.0	19.1	0.72 (0.55 - 0.94)	0.017 *
bird food	year	64	58.3	51.3	0.88 (0.71 - 1.09)	0.25
maize						
herbivores	year	57	63.0	68.5	1.09 (0.88 - 1.34)	0.43
predators	year	57	33.9	31.9	0.94 (0.81 - 1.09)	0.42
parasitoids	year	57	41.4	41.5	1.00 (0.84 - 1.20)	0.99
bird food	year	57	76.3	83.4	1.09 (0.91 - 1.30)	0.34
spring oilseed						
herbivores	year	65	37.4	41.5	1.11 (0.92 - 1.33)	0.27
predators	year	65	20.8	19.5	0.94 (0.79 - 1.13)	0.54
parasitoids	year	65	41.3	41.7	1.01 (0.87 - 1.17)	0.91
bird food	year	65	48.8	49.1	1.01 (0.87 - 1.16)	0.89

7 Supplementary, co-authored, papers

7.1 *The implications of spring-sown genetically modified herbicide-tolerant crops for farmland biodiversity*

1. Firbank, L.G., Heard, M.S., Woiwod, I.P., Hawes, C., Haughton, A.J., Champion, G.T., Scott, R.J., Hill, M.O., Dewar, A.M., Squire, G.R., May, M.J., Brooks, D.R., Bohan, D.A., Daniels, R.E., Osborne, J.L., Roy, D.B., Black, H.I.J., Rothery, P., & Perry, J.N. (2003) An introduction to the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops. *Journal of Applied Ecology*, **40**, 2-16.
2. Haughton, A.J., Champion, G.T., Hawes, C., Heard, M.S., Brooks, D.R., Bohan, D.A., Clark, S.J., Dewar, A.M., Firbank, L.G., Osborne, J.L., Perry, J.N., Rothery, P., Roy, D.B., Scott, R.J., Woiwod, I.P., Birchall, C., Skellern, M.P., Walker, J.H., Baker, P., Browne, E.L., Dewar, A.J.G., Garner, B.H., Haylock, L.A., Horne, S.L., Mason, N.S., Sands, R.J.N., & Walker, M.J. (2003) Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1863 - 1877.
3. Hawes, C., Haughton, A.J., Osborne, J.L., Roy, D.B., Clark, S.J., Perry, J.N., Rothery, P., Bohan, D.A., Brooks, D.R., Champion, G.T., Dewar, A.M., Heard, M.S., Woiwod, I.P., Daniels, R.E., Young, M.W., Parish, A.M., Scott, R.J., Firbank, L.G., & Squire, G.R. (2003) Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1899 - 1913.
4. Heard, M.S., Hawes, C., Champion, G.T., Clark, S.J., Firbank, L.G., Haughton, A.J., Parish, A.M., Perry, J.N., Rothery, P., Roy, D.B., Scott, R.J., Skellern, M.P., Squire, G.R., & Hill, M.O. (2003) Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. II. Effects on individual species. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1833 - 1846.
5. Squire, G.R., Brooks, D.R., Bohan, D.A., Champion, G.T., Daniels, R.E., Haughton, A.J., Hawes, C., Heard, M.S., Hill, M.O., May, M.J., Osborne, J.L., Perry, J.N., Roy, D.B., Woiwod, I.P., & Firbank, L.G. (2003) On the rationale and interpretation of the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1779 - 1799.

7.2 *Effects of climate on phenology*

1. Rothery, P. & Roy, D.B. (2001) Application of generalized additive models to butterfly transect count data. *Journal of Applied Statistics*, **28**, 897-909.

7.3 Effects of climate and habitat on butterfly abundance and range size

1. Cowley, M.J.R., Thomas, C.D., Roy, D.B., Wilson, R.J., LeonCortes, J.L., Gutierrez, D., Bulman, C.R., Quinn, R.M., Moss, D., & Gaston, K.J. (2001) Density-distribution relationships in British butterflies. I. The effect of mobility and spatial scale. *Journal of Animal Ecology*, **70**, 410-425.
2. Dennis, R.L.H., Hodgson, J.G., Grenyer, R., Shreeve, T.G., & Roy, D.B. (2004) Host plants and butterfly biology. Do host-plant strategies drive butterfly status? *Ecology Entomology*, **29**, 12-26.
3. Shreeve, T., Dennis, R.L.H., Roy, D.B., & Moss, D. (2001) An ecological classification of British butterflies: ecological attributes and biotope occupancy. *Journal of Insect Conservation*, **5**, 145-161.
4. Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T., & Lawton, J.H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, 303, 1879-1881.
5. Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414, 65-69.
6. Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B., & Kunin, W.E. (2004) Spatial patterns in species distributions reveal biodiversity change. Nature, 432, 393-396.

8 Discussion

The five papers within this thesis each contain a specific discussion. This chapter reviews the main findings from each piece of work and gives an expanded discussion. The use of butterflies as indicator species is also reviewed and additional areas of work are identified.

8.1 The effects of climate on butterfly phenology

Paper 1 – Chapter 2

> This paper analyses the relationship between mean monthly temperatures and three measures of phenology – the duration of flight periods and the timing of first and peak appearance dates. First appearances of most British butterflies has advanced in the last two decades and is strongly related to earlier peak appearance and, for multibrooded species, longer flight period. Mean dates of first and peak appearance are strongly related to temperatures: a 1 °C rise in temperature equating to advanced first and peak appearance of 2-10 days on average.

This paper supports other work on Lepidoptera that shows many species of butterfly and moth to be appearing on the wing significantly earlier now than they did a decade or more ago (Ellis *et al.*, 1997; Forister & Shapiro, 2003; Sparks & Carey, 1995; Sparks *et al.*, 1997; Stefanescu *et al.*, 2003; Woiwod, 1997). Most studies have concentrated on the effects of a single variable (e.g. temperature) on one life-stage of a species and have mostly ignored the range of possible ecological interactions with other organisms (Harrington *et al.*, 1999). For Lepidoptera, a key question is how interactions with their host plants are affected by changes in climate. One of the main driving forces for climate warming is elevated levels of CO2, which has been shown to increase photosynthetic activity (Keeling *et al.*, 1996) as well as indirectly raising temperatures. This in turn can affect plant chemistry and ultimately plant-insect herbivore interactions (Bazzaz, 1990; Bezemer *et al.*, 1998).

Two mechanisms have been proposed for maintaining synchrony between insects and their hostplants (Harrington *et al.*, 1999). There is little evidence for the first of these - a direct link between the physiological status of the host plant and initiation of insect feeding. An alternative solution is for the herbivore to use the same cues to initiate feeding as those used by the host plant to initiate growth. There are few systems where cues have been quantified for different trophic levels, but the most detailed work has focused on timing of tree budburst and commencement of feeding by insect pests. Winter moth (*Operophtera brumata*) which attacks oak (*Quercus* spp.) is a well-studied example. In experimental conditions of ambient temperatures compared to elevated temperatures (+3°C), Buse and Good (1996) found no effect of increased temperature on the degree of synchronisation of *O. brumata* hatching and *Quercus* bud burst. Using field data and experimental studies, Visser and Holleman (2001) reached the opposite conclusion for this system, suggesting that recent warm springs without a decrease in the incidence of freezing spells in winter have disrupted the synchrony between *O. brumata* feeding and oak bud burst. Buse and Good (1996) did not include winter chilling in their experiments. Visser and Holleman (2001) suggest that changing weather patterns, rather than global warming per se may affect ecosystem interactions more strongly.

The synchrony of insect-host plant interactions will clearly be subject to selection pressure. Natural selection should favour the maintenance of synchrony over the whole range of natural conditions. In the case of *O. bumata*, annual shifts in oak bud burst should result in a corresponding shift in egg hatching. Visser and Holleman (2001) attribute the mis-timing of winter moth egg hatching to extreme temperature patterns (higher temperatures and low number of frost days) observed in the late 1990s that have not been apparent over the last 25 years. Rapid climate change may therefore disrupt species interactions because selection on response mechanisms may be slow (Vantienderen & Koelewijn, 1994) and result in maladaptive behaviour (Dewar & Watt, 1992). However over a 65 year period from 1883 to 1947, the mean date of first appearance of the butterfly *Anthocharis cardamines* (Orange Tip) and the first flowering date of one of its host plants, *Alliaria petiolata* have a similar relationship to spring temperature suggesting that loss of synchrony for this butterfly under climate warming is unlikely (Sparks & Yates, 1997). Evidence is lacking on whether widespread de-synchronisation will occur between the different levels of multitrophic interactions but highly synchronous interactions where the environmental cues occur in different seasons or are based on different climatic factors (e.g. frost vs temperature) are most likely to be affected.

> This paper quantifies the latitudinal (south– north) and longitudinal (east–west) gradients in sighting date of butterflies in Britain. Most species appear later in the west of Britain where temperatures are lower during summer, but not the rest of the year. Sighting dates for the 2/3 of butterflies are also seen later in the cooler north of the country, by up to 3–4 days/100 km. However, no geographical relationship between temperature and timing of appearance was detected for over a third of the species analysed, suggesting their populations may be adapted to their local climates.

As well as trends in phenology between years (temporal trends), within-year (spatial) trends in the timing of adult appearance are apparent for most butterfly species. Within any year, butterflies emerge earlier in the south versus the north of Britain in relation to climatic differences across the country. However, evidence suggests that a few species are fairly well synchronized in their appearance dates across Britain; populations emerge over the same period within each year, but this overall date of emergence varies between years. Evidence for this phenomenon presented by this paper provides evidence of adaptation to local climates.

One such adaptation may be thermoregulatory behaviour and selective egg-laying to exploit warmer microclimates in northern populations and escape the constraints of local climate. It is known that thermophilous butterflies with sedentary larvae oviposit selectively in warm microclimates near their northern limits (Thomas, 1993; Thomas *et al.*, 1998b); a phenomenon observed in edge of range species in southern Britain, i.e. *L. bellargus* (Thomas, 1983) and *Hesperia comma* (Thomas *et al.*, 1986). Compensation for cooler temperature may also be achieved by reduced size in the north of range; a slower growth-rate in a cool climate could produce a small adult in the same time as rapid growth could produce a larger adult in the south (Nylin *et al.*, 1991). Such morphological changes are evident from the fossil record for small mammals that may compensate for temperature changes by alterations in body size, rather than through range changes (Smith & Betancourt, 1998).

Perhaps the most likely explanation for synchronisation of appearance is a lower threshold for larval activity and growth in the north, enabling more rapid development in those populations. Several species of fish exhibit faster increases in growth with temperature in northern as opposed to southern populations (Conover *et al.*, 1990; Schultz *et al.*, 1996) and similar results have been documented for ectothermic organisms (Conover *et al.*, 1995; Nylin *et al.*, 1998). The adaptive explanation for such a counter-gradient in growth rate is that temperature favourable for growth and development occur during a shorter period in northern areas, yet high growth rates are associated with fitness costs (Conover *et al.*, 1990). Gotthard *et al.* (2000) take this adaptive hypothesis further and demonstrate that individuals within a *Lasiommata megera* population can vary their growth rate in response to temperature and time-stress (i.e. day length); the scheduling of growth is state-dependent (McNamara & Houston, 1996).

8.2 The effects of climate on butterfly abundance

Paper 3 – Chapter 4

> This paper investigated the niche requirements of the two generations of the bivoltine butterfly, Adonis Blue (*Polyommatus bellargus*), and their implications for its population dynamics. There is a significant shift between plants used for egg-laying in each generation, with the niche occupied by the summer-feeding larvae being broader and different to the autumn one. Females laid eggs in the warmest available microclimates in the autumn, but these locations were avoided for egg-laying in spring, when taller, less sheltered turf was used. Vegetation surveys at existing sites for this species revealed that almost twice as many plants were available to the summer-feeding larvae compared to those feeding in the autumn. This seasonal difference in foodplant availability closely matched differences in butterfly numbers; second generation counts are, on average, twice as large as those for the first generation. These results suggest a seasonal cycle of niche switches with an over-winter bottleneck for populations of this butterfly at its northern range margin.

Butterflies, and other ectothermic animals, at the edge of their geographic range are generally constrained by temperature. Populations at the northern range boundary are therefore restricted to warm locations, such as sheltered south-facing slopes of early successional grassland (Bourn *et al.*, 2002; Thomas *et al.*, 1999; Thomas *et al.*, 1986). These conditions are frequently recognised in the prescriptions for habitat management to conserve such species, but often assume that such requirements are constant. This paper demonstrates that the ideal habitat conditions for certain species can vary within a year, and habitat management designed to maintain favourable locations may be too restrictive. This supports other empirical studies that species near their northern range margins are also utilising a wider range of habitat types (Thomas *et al.*, 2001a), shifting their realised niche in response to climate warming.

Paper 4 – Chapter 5

> This paper analyses the effect of weather on the size of British butterfly populations. Strong associations between weather and population fluctuations were found in most species (28 out of 31 species) with the main positive associations being with warm temperatures in both the current and previous summers, low rainfall in the current year and high rainfall in the previous year. Most bivoltine species benefited from warm June weather in the current year, three spring species and two that overwinter as adults benefited from warm weather in the previous summer, and most species with moist or semi-shaded habitats increased following high rainfall and cooler weather in the previous year. Models of association between weather and butterfly numbers predict that almost all species are predicted to increase in the UK under predicted warmer climates.

Despite the marked associations with weather and the good fit of models to the data for the early part of the time series (1976-1990), predictions of the patterns of the fluctuations during 1991-97 were poor. The limited success of prediction may be due to a number of factors. For example, important additional factors, other than weather and density effects, may be driving population fluctuations. Also, the time scale for building and testing models may be too short and better predictive success may be achieved if such analyses are repeated with a longer run of monitoring data.

The generally poor success of initial models to predict species' fluctuations was salutary. Butterflies are considered among the most promising groups for short-term prediction of effects of climate change (Thomas, 2005). Their population data are among the best available for any terrestrial invertebrate, and most stages in their life-cycles have been shown to be strongly affected by weather. To date, it has been rare for predictions describing population changes in any taxon to be tested against observed data in this way. If claims of good predictive power are made, they should be tested against real data.

Despite these reservations, these models allow prediction of qualitative rather than quantitative long-term changes, and that this may be all that is achieved from models based on correlations between monitoring data and weather variables. Such analyses also highlight differences between groups of species in their response to weather. Overall, trends in specialist and generalist species of butterflies (for definitions see Pollard & Eversham, 1995) show a marked divergence. Mobile and habitat generalist species have increased over the last few decades, supporting predictions of the positive effects of warming temperatures, whereas over the same time period habitat specialist have declined, being susceptible to habitat modification (Warren *et al.*, 2001). In addition, grassland species have shown an increasing population trend since 1976 whereas woodland species have declined. Although this is related to warming climates, for many grassland species this positive trend has resulted from targeted conservation management (Bourn *et al.*, 2000).

8.3 The effects of changes in farmland management on butterfly populations

Paper 5 - Chapter

This paper analyses the effects of management of genetically modified herbicide-tolerant (GMHT) crops (maize, beet and spring oilseed rape) on adjacent field margins. Effects on plants and invertebrates were assessed in three components of field margins; most differences were found in the tilled area with fewer, smaller effects mirroring them in the verge and boundary. In spring oilseed rape fields, the cover, flowering and seeding of plants were 24%, 44% and 39% lower respectively, in the GMHT uncropped tilled margins. Similarly, for beet, flowering and seeding were 34% and 39% lower, respectively in the GMHT margins. For maize, the effect was reversed, with plant cover and flowering 28% and 67% greater, respectively, in the GMHT half. With the exception of butterflies, few large treatment differences were found for invertebrates (bees, gastropods or other groups). Effects on butterflies mirrored the vegetation effects, with 24% fewer butterflies in margins of GMHT spring oilseed rape, with lower nectar supply in this treatment being the likely cause.

This paper is one of a series of eight papers that report the finding of the Farm Scale Evaluations (FSE) of genetically modified herbicide-tolerant (GMHT) crops. The FSC evaluated the changes in management of GMHT cropping on farmland biodiversity. The management of GMHT crops differs from that of conventional crops mainly in the type of timing of herbicides applied to the cropped area of fields (Champion *et al.*, 2003). The herbicide regimes associated with the spring-sown GMHT beet, maize and spring oilseed rape all had direct effects on weeds (Heard *et al.*, 2003a,b) and knock-on, indirect effects on invertebrate abundance and diversity (Brooks *et al.*, 2003; Haughton *et al.*, 2003; Hawes *et al.*, 2003; Roy *et al.*, 2003). Broadly similar effects were also found in an accompanying evaluation of winter-sown spring oilseed rape (Bohan *et al.*, 2005).

Out of the invertebrate groups sampled in the FSE, butterflies have been shown to be particularly sensitive to differences in vegetation, both with the cropped area of field and the adjacent field margins. The overall abundance of butterflies tended to be less within the cropped area of GMHT beet and spring oilseed treatments, by 32% and 22% respectively, when compared to their conventional equivalent (Haughton *et al.*, 2003). The effects were similar in adjacent margins, where overall butterfly numbers were 18% and 24% less in GMHT beet and spring oilseed rape treatments respectively. Effects were comparable for individual butterfly species. Although relative densities of butterflies were less within cropped areas versus margins of arable fields – 50%, 21% and 38% for beet, maize and spring oilseed rape respectively – the results from the FSC demonstrate the potential importance of forage resource provided by weed plants within fields. Although the resources in the field may be widely spread, because the cultivated area is so much greater than that of the uncultivated boundaries, they may be important on a landscape scale.

The effects on butterflies found in the Farm Scale Evaluations (FSC) of genetically modified herbicide-resistant (GMHT) crops demonstrate that mobile nectar-foraging insects can respond rapidly to changes in the distribution of flowering plants. Similar results have been found in a range of studies on butterflies in agricultural systems (e.g. Clausen *et al.*, 2001; Dover, 1996, 1997; Feber *et al.*, 1997; Feber *et al.*, 1996; Meek *et al.*, 2002; Pywell *et al.*, 2004; Sparks & Parish, 1995) and supports studies that have demonstrated the importance of nectar plants and vegetation diversity for butterfly populations in a range of habitats (e.g. Brakefield, 1982; Holl, 1995; Loertscher, Erhardt & Zettel, 1995; Manguira & Thomas, 1992; Peterson, 1997).

Although supported by a number of studies, the relationship between butterfly numbers and flowering plants does not allow direct conclusions about the effects of nectar availability on the long-term dynamics of butterfly populations. The relationship demonstrates a clear feeding choice of mobile species, but if sufficient forage resource is available elsewhere in the landscape, then populations will be buffered against changes. Whether resources for adults (nectar, shelter etc.) are/or larval (foodplant availability and quality) butterflies are limited in agro-ecosystems is not known. Whatever the exact mechanism however, changes to agriculture over a long period have been suggested as the major cause of substantial declines in abundance, major range contractions and several extinctions of butterflies documented throughout Europe (Asher *et al.*, 2001; Heath, 1981; Pullin, 1995; Saarinen, Lahti & Marttila, 2003; Thomas, 1984; Thomas, 1995a; van Swaay & Warren, 1999; van Swaay, 1990; Warren, 1993a).

In the main, the loss and damage to habitats from changes in agricultural practices can be traced back to the eighteenth century. These agricultural improvements gathered pace during the early twentieth century but were sharply accelerated after 1939. Yields per hectare of the main cereal crops increased by around 1% per year during the twentieth century (Evans, 1993), as did the amount and variety of agro-chemical use increase after the 1960s; together, these killed a range of arable weed. From the 1970s, a major shift occurred in the timing of tillage and sowing, from spring to autumn, so that by 2000 more than 75% of crops were sown in the autumn and thereby covering land and absorbing sunlight, water and nutrients for much longer each year. The continued intensification of agriculture over a long period has led to declines in fauna and flora of farmland (Chamberlain *et al.*, 2000; Ewald & Aebischer, 2000; Preston *et al.*, 2002).

The promotion of agri-environment schemes in Europe is seen as the best option for addressing concerns over the environmental impact of agriculture across the continent. The main aims of such schemes are to reduce nutrient and pesticide emissions, protect biodiversity, restore landscapes and prevent rural depopulation. There are currently agri-environment schemes in 26 out of 44 European countries, but it has proved impossible to give a general judgment on their effectiveness (Kleijn & Sutherland, 2003); schemes lack clear objectives on which to judge success and omit to include rigorous evaluation programmes. Notwithstanding these difficulties, individual studies can be used to assess effects on particular taxa. A comparison of trends in butterfly populations showed the positive effect of sites managed under agri-environment schemes, with 10 out of 13 (five significant) habitat-specialist species increasing on agri-environment sites when compared to other sites. In general, the diversity and abundance of arthropods appears to be easier to enhance through implementation of agri-environment schemes than other groups (Kleijn *et al.*, 2003); their rapid response may indicate longer-term improvements in taxa that are slower to respond such as birds and plants.

8.4 Butterflies as indicator taxa

Insects comprise more than half of all known species of organism and represent the majority of animal taxa in the United Kingdom. Estimates also predict that 75-90% of species that remain to be discovered could be insects. With such a diverse group that lacks baseline knowledge across most of the globe, monitoring wholesale change is unfeasible. Assessing change in the status of insects relies on generalisation from a few well-studied taxa and the need for reliable indicator species is paramount.

Indicator species are thought to either signal the presence / abundance of other species, or to signal chemical / physical change in the environment through changes in their own presence or abundance (Landres, Verner & Thomas, 1988; Simberloff, 1998). The second of these types of indicators is referred to as an ecological indicator (McGeoch, 1998). A number of criteria for selecting indicator species have been proposed (Landres *et al.*, 1988) which can be distilled into four general categories: baseline information; location information; niche and life history attributes; and other (Hilty & Merenlender, 2000). Although it is recognised that not all useful indicator taxa will fit all criteria, they should satisfy multiple criteria, as is the case for Lepidoptera.

In many regions of the world, Lepidoptera are recognised as ecological indicators of ecosystem health (Beccaloni & Gaston, 1995; New, 1997; Oostermeijer & Van Swaay, 1998; Rosenberg, Danks & Lehmkuhl, 1986), and meet a number of the criteria laid out by Hilty and Merenlender (2000). Butterflies have a fairly clear taxonomy, and their life history and biology are well defined, particularly in Britain and Europe (Thomas *et al.*, 1991; Tolman & Lewington, 1997). For a small number of species their physiological tolerances, such as light, temperature, and habitat requirements, have been quantified (Greatorex-Davies *et al.*, 1993; Oostermeijer *et al.*, 1998; Pollard *et al.*, 1998b; Sparks *et al.*, 1996; Thomas & Harrison, 1992; Warren, 1985) and correlation with changes in ecosystem conditions have been demonstrated in both northern temperate (Bowman *et al.*, 1990; Pollard *et al.*, 1998b; Pullin, 1996; Sparks *et al.*, 1996; Thomas *et al.*, 1992) and tropical habitats (Hamer *et al.*, 2003; Hill *et al.*, 2003; Spitzer *et al.*, 1997). In addition, butterflies are small, have high reproductive rates, and are at a low trophic level. As with many other insects, a high proportion of butterfly species are restricted to specific micro-habitats in relatively small areas of semi-natural habitat (Thomas, 1993, 1995b). Subtle changes in these habitats may substantially diminish insect diversity, but may not significantly impact upon higher trophic levels (e.g. bird populations) that are often used as Biodiversity Indicators (Thomas, 1995b). Together, these attributes allow butterflies to respond quickly to environmental stress; butterflies have undergone more regional extinctions than plants or birds over a similar period in the UK (Thomas *et al.*, 2004c).

Butterflies also have limitations as ecological indicators. A number of species are mobile and may be able to tolerate some levels of disturbance because of their ability to move and find resources. Their ability to respond to change in habitat condition can be a hindrance in areas with high climatic variability, as changes detected in their abundance may be in response to a climate condition instead of ecosystem structure (Pollard & Yates, 1993). Hambler and Speight (2004) have argued that, as warmth-loving herbivores, butterflies are atypical invertebrates and have experienced amplified losses in Britain compared to other insects. Based on analysis of the British

Red Data Book for Insects (Shirt, 1987) they show that extinction rate per century is >5% for butterfly species, yet only 0.4% overall for the 14,000 insects species covered (Hambler & Speight, 1996). Thomas and Clarke (2004) refute this claim by arguing that inequalities in the level of historical recording has led to biases when comparing extinction rates between taxonomic groups (May, Lawton & Stork, 1995). Within a given taxonomic group, common and widespread species tend to be discovered first (Gaston, Blackburn & Loder, 1995), before the rare and local species that are most prone to extinction (May *et al.*, 1995). Rare and localised species may not be known before they have gone extinct. Studies of extinction rates in relation to recording history appear to support this theory. McKinney (1999) established a strong relationship between the proportion of species recorded as being globally extinct against the proportion of species that was estimated to have been discovered. A comparable relationship has been demonstrated for a range of British invertebrate groups (Thomas, 2005; Thomas & Clarke, 2004). The dates of discovery of individual butterfly species are strongly correlated with their range sizes. Butterflies have a longer history of recording (by over 200 years) than most other invertebrate groups and if their extinction is assessed since 1900, the rate is halved and is inline with other invertebrate groups when assessed from the same date (Thomas, 2005; Thomas & Clarke, 2004). Although extinction rates are a crude measure of change, Thomas and Clarke (2004b) argue that, given the rigour of early butterfly recording in Britain, their documented declines were not atypical when compared to other invertebrates.

8.5 Futher work

This thesis has considered a number of potential ecological effects on butterfly populations of climate change and habitat modification. Given the broad subject area, each chapter has only addressed a few aspects and there is considerable scope for further work leading directly from these analyses.

There is scope for future work on phenology that concentrates on the spatial aspects of the timing of naturally recurring events. Geographic patterns in flight-periods have been studied in very few butterfly species (Brakefield, 1987; Dennis, 1985a; Pollard, 1991a), yet the large body of data from the Butterfly Monitoring Scheme (currently over 50,000 individual flight periods) is ideal to investigate many key aspects of the life-cycle. Some of the immediate priorities for hypotheses to test include:

1. Most butterflies fly earlier in response to warmer weather, and the degree of this response is related to life history and geographic location.
2. Most butterflies fly later in the north, but the flight periods of a few species are well synchronized across Britain.
3. The duration of the flight period is shorter in the north with important implications for population dynamics (Thomas *et al.*, 1994).
4. Butterfly species may become de-coupled from their foodplant resource due to changes in phenology.
5. Early emergences and/or additional broods are correlated with high numbers and expansions of range (Brakefield, 1987; Dennis, 1985a; Pollard, 1991a).

Building on the work presented in chapters 4 and 5 of this thesis, future work on the effects of climate and weather on population abundance is recommended. More detailed analysis of the response of butterfly populations to different components of the climate system is needed. Climate change is complex and is not simply a steady increase in mean air temperatures. Minimum temperature is rising at twice the rate of maximum temperature (Karl *et al.*, 1993); precipitation is changing in quantity, seasonality and severity across the globe (Groisman *et al.*, 1999); the growing season is lengthening (Menzel *et al.*, 1999); the frequency of extreme events is increasing (Houghton *et al.*, 2001). There is considerable scope for assessing the effects of some of these weather effects. In particular, analyses of the response of different generations of bivoltine species are likely to greatly improve our understanding of the effects of weather at different times of year. Analyses of weather effects on bivoltine species has concentrated on the larger, summer-autumn generation but quantifying the change in population size between spring and summer-autumn generations will allow over-winter and over-summer survival rates to be estimated. This will expand upon the approach developed in chapter 5 of this thesis that utilised the predictable seasonal alterations of climate during the two development periods of bivoltine species such as *Polyommatus icarus* to provide a useful system for understanding processes of population expansion and contraction. Some specific hypotheses to test include:

1. For bivoltine species, over-winter and over-summer survival rates differ and are strongly related to weather conditions.
2. Over-winter survival rate is related to distance from range margins (Crozier, 2003).
3. Some multivoltine species produce extra generations as the weather warms, others keep rigidly to two, while some species switch rather suddenly between one and two generations at an apparent geographical cut-off. These variations in voltinism will be quantified and, with other aspects of phenology, will be related to life-history traits and to the ecology of larval foodplants.
4. Sensitivities to drought will differ among species with different life-history traits, e.g. the timing of larval feeding period.
5. Drought effects will be amplified on sites with homogeneous aspects and habitats.

As well as further work arrising directly from the chapters presented in this thesis, the large-scale, long-term datasets used are invaluable for further investigation of other effects of broad-scale phenomenum on wildlife, particularly climate change. Two potential new areas that utilise these data are the effects of climate on patterns of migration of butterflies, and the interaction of climate and habitat on the spatial configoration of butterfly populations. These two aspects are outlined in the following sections.

8.5.1 Migration

The migration of butterflies and other insects, over hundreds or even thousands of kilometers, is a remarkable feat. The most famous example is the travels of the Monarch butterfly, *Danaus plexippus*, that aggregates over winter in great numbers in a small area of Mexico, yet the adults produced in the following spring migrate as far north as Canada. Although less spectacular, migrants to Britain are considered to be those butterflies which breed but don't overwinter here so their contribution to the following year's population is negligible. The three most common of these migratory butterflies are *Vanessa atalanta*, *Cynthia cardui* and *Colias crocea*, in declining order of average frequency. Although individual *V. atalanta* have been known to hibernate in Britain, this is still probably a rare occurrence. Another group of butterflies is known to range widely over large areas of countryside and some of these have been seen in large numbers, apparently on migration, at sea or on the coast. This group includes the *Inachis io* and *Aglais urticae*, but paramount amongst them are *Pieris brassicae* and *Pieris rapae*.

Migration has both advantages and costs. A species may benefit by exploiting new vegetation growth and prey abundance and by escaping from natural predators (Pollard *et al.*, 1998a). Some of the main disadvantages of migration include delayed onset of reproduction and the need for increased development of larger wings and flight muscles. The balance of these factors affecting migrants will be influences by changing climatic conditions.

There is a large amount of data on the distribution of abundance of migratory butterflies in Britain. These could be used to can be used to test the hypothesis that migrants are becoming more abundant and breeding at higher latitudes as a consequence of warming. Sparks *et al.* (2005) found a strong correlation between the abundance of migrant lepidoptera arriving in Britain and temperatures in France, suggesting that climatic conditions are important throughout the migration route.

8.5.2 The effects of climate on spatial variation in butterfly populations

All populations vary from year-to-year and across geographic areas (Andrewartha & Birch, 1954; Gilpin & Hanski, 1991), but a key question facing theoretical and practical ecologists is how do temporal and spatial patterns co-vary? Within species, it has been suggested that population density tends to be greatest in the centre of the range and declines gradually towards the boundaries, and that species usually become more localized towards the range margin (Brown, 1984). It has been shown that butterfly populations are more variable at the edge of their geographic range (Thomas *et al.*, 1994). What has not been examined is how the spatial distribution of species changes with changing population abundance.

The structure of the Butterfly Monitoring Scheme allows these aspects of the spatial variation in butterfly populations to be addressed. The scheme is designed to have small spatial units (sections) nested within a site (transect), within a national dataset. The intra-site data will be used to address the question of whether populations expand into neighboring habitats in years or generations of high abundance, or do they increase in numbers within existing areas. Conversely, in generations of low abundance, do populations contract to 'refuge' locations, and are refuges the same areas in different years or do they shift?

8.6 Conclusions

The loss of biodiversity is a global problem (Balmford *et al.*, 2005). Current rates of species extinction are estimated to be at least three orders of magnitude above rates observed in the fossil record (Pimm *et al.*, 1995), and are predicted to increase. Within groups whose conservation status has been comprehensively assessed (birds, amphibians, conifers and cycads), around twenty percent of species are at risk of global extinction by the end of the 21st Century (Baillie, Hilton-Taylor & Stuart, 2004).

Biodiversity is threatened by a range of environmental pressures (Sala *et al.*, 2000), including climate change, pollution, land-use change, the harvesting and persecution of species and the introductions of alien species and genotypes. There are few predictions about how the full range of pressures will impact on biodiversity (Petit *et al.*, 2001; Tilman *et al.*, 2001), but climate change and habitat destruction have been identified as two of the greatest threats to global biodiversity (Travis, 2003). More than half of all natural habitat on agriculturally useable land has already been cleared for cropland or permanent pasture, and much of the rest has been altered by temporary grazing (Groombridge *et al.*, 2002). Models predict that between 15 to 37% of species are 'committed to extinction' by 2050 under a mid-range scenario of climate-warming, leading to the conclusion that anthroprogenic climate warming ranks alongside other threats to biodiversity and is likely to be the greatest in many parts of the world (Thomas *et al.*, 2004a).

Given this multitude of threats, the conservation (and restoration) of biodiversity requires an ability to understand the integrated impact of natural and anthropogenic drivers of change on species' populations and ecosystem structure and function.

Exploiting the extensive datasets on butterfly populations available in the UK, this thesis demonstrates clear affects of climate change and changing agricultural practices on a range of attributes of populations.

References

Abu-asab, M.S., Peterson, P.M., Shetler, S.G., & Orli, S.S. (2001) Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. *Biodiversity and Conservation*, **10**, 597-612.

Alderweireldt, M. (1994) Prey selection and prey capture strategies of linyphiid spiders in high-input agricultural fields. *Bulletin of the British Arachnological Society*, **9**, 300-308.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D.W., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., & Nabhan, G.P. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crops and yields. *Conservation Biology*, **12**, 8-17.

Andrewartha, H.G. & Birch, L.C. (1954) *The distribution and abundance of animals* Chicago University Press.

Arnold, A.J. (1994) Insect suction sampling without nets, bags or filters. *Crop Protection*, **13**, 73-76.

Arnold, V.W., Baker, C.R.B., Manning, D.V., & Woiwod, I.P. (1997) *The butterflies and moths of Bedfordshire.* Bedfordshire Natural History Society, Bedford.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G., & Jeffcoate, S. (2001) *The millennium atlas of butterflies in Britain and Ireland* Oxford University Press, Oxford.

Ayres, M.P. & Scriber, J.M. (1994) Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera, Papilionidae). *Ecological Monographs*, **64**, 465-482.

Backman, J.P.C. & Tiainen, J. (2002) Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera : Bombus and Psithyrus). *Agriculture, Ecosystems and Environment*, **89**, 53-68.

Baillie, J.E.M., Hilton-Taylor, C., & Stuart, S.N. (2004) *IUCN Red List of threatened species. A global species assessment* IUCN, Gland.

Baker, B.R. (1994) *The butterflies and moths of Berkshire* Hedera Press, Wallingford.

Balmford, A., Crane, P., Dobson, A., Green, R.E., & Mace, G.M. (2005) The 2010 challenge: data availability, information needs and extraterrestrial insights. *Philosophical Transactions of the Royal Society B*, **360**, 221-228.

Banaszak, J. (1980) Studies on methods of censusing the numbers of bees (Hymenoptera, Apoidea). *Polish Ecological Studies*, **6**, 355-366.

Barr, C.J., Bunce, R.G.H., Clarke, R.T., Fuller, R.M., Furse, M.T., Gillespie, M.K., Groom, G.B., Hallam, C.J., Hornung, M., Howard, D.C., & Ness, M.J. (1993) *Countryside Survey 1990: main report* HMSO, London.

Bazzaz, F.A. (1990) The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology and Systematics*, **21**, 167-196.

Beccaloni, G.W. & Gaston, K.J. (1995) Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation*, **71**, 77-86.

Beebee, T.J.C. (1995) Amphibian breeding and climate. *Nature*, **374**, 219-220.

Beirne, B.P. (1955) Natural fluctuations in the abundance of British Lepidoptera. *Entomologists Gazette*, **6**, 21-52.

Benton, T.G., Vickery, J.A., & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182-188.

Bezemer, T.M. & Jones, T.H. (1998) Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. *Oikos*, **82**, 212-222.

Bohan, D.A., Boffey, C.W.H., Brooks, D.R., Clark, S.J., Dewar, A.M., Firbank, L.G., Haughton, A.J., Hawes, C., Heard, M.S., May, M.J., Osborne, J.L., Perry, J.N., Rothery, P., Roy, D.B., Scott, R.J., Squire, G.R., Woiwod, I.P., & Champion, G.T. (2005) Effects on weed and invertebrate abundance and diversity of herbicide management in genetically modified herbicide-tolerant winter-sown oilseed rape. *Proceedings of the Royal Society B.*, **272**, 463-474.

Bohan, D.A., Bohan, A.C., Glen, D.M., Symondson, W.O.C., Wiltshire, C.W., & Hughes, L. (2000) Spatial dynamics of predation by carabid beetles on slugs. *Journal of Animal Ecology*, **69**, 367-379.

Bourn, N.A.D., Pearman, G.S., Goodger, B., Warren, M.S., & Thomas, J.A. (2000). Changes in the status of two endangered butterflies over two decades and the influence of grazing management. In *Grazing management* (eds A.J. Rook & P.D. Penning), pp. 141-146. British Grassland Association, Okehampton.

Bourn, N.A.D. & Thomas, J.A. (1993) The ecology and conservation of the brown argus butterfly *Aricia agestis* in Britain. *Biological Conservation*, **63**, 67-74.

Bourn, N.A.D. & Thomas, J.A. (2002) The challenge of conserving butterflies at range margins in Europe. *Biological Conservation*, **104**, 285-292.

Bowman, D.M., Woinarski, J.C., Sands, D.P., Wells, A., & McShane, V.J. (1990) Slash-and-burn agriculture in the wet coastal lowland of Papua New Guinea: response of birds, butterflies and reptiles. *Journal of Biogeography*, **17**, 227-239.

Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J., & Wilson, J.D. (2000) Habitat associations and breeding success of yellowhammers on lowland farmland. *Journal of Applied Ecology*, **37**, 789-805.

Bradley, N.L., Leopold, A.C., Ross, J., & Heffaker, W. (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 9701-9704.

Brakefield, P.M. (1982) Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution and dispersal. *Journal of Animal Ecology*, **51**, 713-726.

Brakefield, P.M. (1987) Geographical variability in, and temperature effects on, the phenology of *Maniola jurtina* (Lepidoptera, Satyridae) in England and Wales. *Ecological Entomology*, **12**, 139-148.

Brickle, N.W., Harper, D.G.C., Aebischer, N.J., & Cockayne, S.H. (2000) Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. *Journal of Applied Ecology*, **37**, 742-755.

Bristow, C.R., Mitchell, S.H., & Bolton, D.E. (1993) *Devon butterflies* Devon Books, Tiverton.

Brooks, D.R., Bohan, D.A., Champion, G.T., Haughton, A.J., Hawes, C., Heard, M.S., Clark, S.J., Dewar, A.M., Firbank, L.G., Perry, J.N., Rothery, P., Scott, R.J., Woiwod, I.P., Birchall, C., Skellern, M.P., Walker, J.H., Baker, P., Bell, D., Browne, E.L., Dewar, A.J.G., Fairfax, C.M., Garner, B.H., Haylock, L.A., Horne, S.L., Hulmes, S.E., Mason, N.S., Norton, L.R., Nuttall, P., Randle, Z., Rossall, M.J., Sands, R.J.N., Singer, E.J., & Walker, M.J. (2003) Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. I. Soil-surface-active invertebrates. *Philosophical*

Transactions of the Royal Society of London Series B-Biological Sciences, **358**, 1847 - 1862.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255-279.

Bryant, S.R., Thomas, C.D., & Bale, J.S. (1997) Nettle-feeding nymphalid butterflies: temperature, development and distribution. *Ecological Entomology*, **22**, 390-398.

Bunce, R.G.H., Barr, C.J., Gillespie, M.K., & Howard, D.C. (1996). The ITE land classification: providing an environmental stratification of Great Britain. In *Global to local: ecological land classification* (eds R.A. Sims, I.G.W. Corns & K. Klinka), pp. 39-46. Kluwer, Dordrecht.

Buse, A. & Good, J.E. (1996) Synchronization of larvae emergence is winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change. *Ecological Entomology*, **21**, 335-343.

Cannon, R.J.C. (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology*, **4**, 785-796.

Ceballos, G. & Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. *Science*, **296**, 904-907.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771-788.

Champion, G.T., May, M.J., Bennett, S., Brooks, D.R., Clark, S.J., Daniels, R.E., Firbank, L.G., Haughton, A.J., Hawes, C., Heard, M.S., Perry, J.N., Randle, Z., Rossall, M.J., Rothery, P., Skellern, M.P., Scott, R.J., Squire, G.R., & Thomas, M.R. (2003) Crop management and agronomic context of the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1801 - 1818.

Clarke, J.E. (1936) The history of British phenology. *Quarterly Journal of the Royal Meterological Society*, **62**, 19-23.

Clausen, H.D., Holbeck, H.B., & Reddersen, J. (2001) Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. *Biological Conservation*, **98**, 167-178.

Collins, G.A. (1995) *Butterflies of Surrey* Surrey Wildlife Trust, Woking.

Conover, D.O. & Present, T.M.C. (1990) Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, **83**, 316-324.

Conover, D.O. & Schultz, E.T. (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology and Evolution*, **10**, 248-252.

Coope, G.R. (1995) The effects of quaternary climatic changes in insect populations: lessons from the past. *Symposium - Royal Entomological Society of London*, **17**, 30.

Corke, D. (1998) *The butterflies of Essex* Lopinga Books, Wimbish.

Council, N.C. (1984) *Nature Conservation in Great Britain* Nature Conservancy Council, Shrewsbury.

Cowley, M.J.R., Thomas, C.D., Thomas, J.A., & Warren, M.S. (1999) Flight areas of British butterflies: assessing species status and decline. *Proceedings of the Royal Society of London B.*, **266**, 1587-1592.

Crick, H.Q.P., Dudley, C., Glue, D.E., & Thomson, D.L. (1997) UK birds are layer eggs earlier. *Nature*, **388**, 526.

Crick, H.Q.P. & Sparks, T.H. (1999) Climate change related to egg-laying trends. *Nature*, **399**, 423-424.

Crozier, L. (2003) Winter warming facilitates range expansion: cold tolerance of the butterfly Atalopedes campestris. *Oecologia*, **135**, 648-656.

Dalton, H. & Brand-Hardy, R. (2003) Nitrogen: the essential public enemy. *Journal of Applied Ecology*, **40**, 771-781.

de Groot, R.S., Ketner, P., & Ovaa, A.H. (1995) Selection and use of bio-indicators to assess the possible effects of climate change in Europe. *Journal of Biogeography*, **22**, 935-943.

de Snoo, G.R. (1997) Arable flora in sprayed and unsprayed crop edges. *Agriculture, Ecosystems and Environment*, **66**, 223-230.

de Snoo, G.R. & van der Poll, R.J. (1999) Effect of herbicide drift on adjacent boundary vegetation. *Agriculture, Ecosystems and Environment*, **73**, 1 - 6.

Dempster, J.P. (1983) The natural control of populations of butterflies and moths. *Biological Reviews*, **58**, 461-481.

Dempster, J.P. & McLean, I.F.G., eds. (1998) *Insect populations in theory and practice. 19th Symposium of the Royal Entomological Society.* Kluwer Academic Publishers, Dordrecht, The Netherlands.

Dempster, J.P. & Pollard, E. (1981) Fluctuations in resource availability and insect populations. *Oecologia*, **50**, 412-416.

Dennis, R.L.H. (1977) *The British Butterflies. Their origin and establishment.* E.W. Classey, Faringdon, Oxford, UK.

Dennis, R.L.H. (1985a) British butterfly distributions: space-time predictability. In Proceedings of the 3rd congress of Europian Lepidoptery, pp. 50-62, Cambridge 1982.

Dennis, R.L.H. (1985b) Voltinism in British *Aglais urticae* (L.) (Lep: Nymphalidae): Variation in space and time. *Proceedings and Transactions of the British Entomological and Natural History Society*, **18**, 51-61.

Dennis, R.L.H. (1992). An evolutionary history of British butterflies. In *The Ecology of Butterflies in Britain* (ed R.L.H. Dennis), pp. 217-245. Oxford Science Publications, Oxford.

Dennis, R.L.H. (1993) *Butterflies and climate change.* Manchester University Press, Manchester.

Dennis, R.L.H. & Bramley, M.J. (1985) The influence of man and climate on dispersion patterns within a population of adult *Lasiommata megera* (L.) (Satyridae) at Brereton Heath, Cheshire (U.K.). *Nota Lepidopterologica*, **8**, 309-324.

Dennis, R.L.H., Hodgson, J.G., Grenyer, R., Shreeve, T.G., & Roy, D.B. (2004) Host plants and butterfly biology. Do host-plant strategies drive butterfly status? *Ecology Entomology*, **29**, 12-26.

Dennis, R.L.H. & Shreeve, T.G. (1991) Climatic-change and the British butterfly fauna - opportunities and constraints. *Biological Conservation*, **55**, 1-16.

Dewar, A.M., May, M.J., Woiwod, I.P., Haylock, L.A., Champion, G.T., Garner, B.H., Sands, R.J.N., Qi, A., & Pidgeon, J.D. (2002) A novel approach to the use of genetically modified herbicide tolerant crops for environmental benefit. *Proceedings of the Royal Society of London, B.*

Dewar, R.C. & Watt, A.D. (1992) Predicted changes in the synchrony of larval emergence and budburst under climatic warming. *Oecologia*, **89**, 557-559.

Dobkin, D.S., Olivieri, I., & Ehrlich, P.R. (1987) Rainfall and the interaction of microclimate with larval resources in the population dynamics of checkerspot butterflies (*Euphydryas editha*) inhabiting serpentine grassland. *Oecologia*, **71**, 161-166.

Donald, P.F. & Vickery, J.A. (2001) *The ecology and conservation of Skylarks Alauda arvensis* RSPB, Sandy.

Dover, J. & Sparks, T.H. (2000) A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management*, **60**, 51-63.

Dover, J.W. (1996) Factors affecting the distribution of satyrid butterflies on arable farmland. *Journal of Applied Ecology*, **33**, 723-734.

Dover, J.W. (1997) Conservation headlands: effects on butterfly distribution and behaviour. *Agriculture, Ecosystems and Environment*, **63**, 31-49.

Dover, J.W., Clark, S.A., & Rew, L. (1992) Habitats and movement patterns of Satyrid butterflies (Lep: Sartyridae) on arable farmland. *Entomologists Gazette*, **43**, 29-44.

Dover, J.W., Sparks, T.H., & Greatorex-Davis, J.N. (1997) The importance of shelter for butterflies in open landscapes. *Journal of Insect Conservation*, **1**, 89-97.

Dramstad, W. & Fry, G. (1995) Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land. *Agriculture, Ecosystems and Environment*, **53**, 123-135.

Duddington, J. & Johnson, R. (1983) *The butterflies and larger moths of Lincolnshire and south Humberside* Lincolnshire Naturalists' Union, Lincoln.

Duncan, K. (1991) A comparison of the temperature records of Edinburgh and central England. *Weather*, **46**, 169-173.

Dunn, P.O. & Winkler, D.W. (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings- Royal Society of London B*, 2487-2490.

Dunn, T.C. & Parrack, J.D. (1986) The butterflies and moths of Northumberland and Durham. Part 1: Macolepidoptera. *The Vasculum (Supplement 2).*

Ehrlich, P.R. (1984). The structure and dynamics of butterfly populations. In *The Biology of Butterflies* (eds R.I. Vane-Wright & P.R. Ackery). Academic Press, London.

Ehrlich, P.R., Murphy, D.D., Singer, M.C., Sherwood, C.B., White, R.R., & Brown, I.L. (1980) Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia*, **46**, 101-105.

Ehrlich, P.R., White, R.R., Singer, M.C., McKeohnie, S.W., & Gilbert, L.E. (1975) Checkerspot butterflies: a historical perspective. *Science*, **188**, 221-228.

Ellis, W.N., Donner, J.H., & Kuchlein, J.H. (1997) Recent shifts in phenology of Microlepidoptera, related to climatic change (Lepidoptera). *Ent. Ber. Amst.*, **57**, 66-72.

Emmet, A.M. & Heath, J., eds. (1989) *The Moths and Butterflies of Great Britain and Ireland, Vol. 7, The Butterflies.* Harley Books, Colchester.

Evans, A., Appleby, M., Dixon, J., Newbery, P., & Swales, V. (1995) What future for lowland farmland birds in the UK? *RSPB Conservation Review*, **9**, 32-40.

Evans, L.T. (1993) *Crop evolution, adaptation and yield* Cambridge University Press, Cambridge.

Ewald, J.A. & Aebischer, N.J. (2000) Trends in pesticide use and efficacy during 26 years of changing agriculture in southern England. *Environmental Monitoring Assessment*, **64**, 493-529.

Feber, R.E., Firbank, L.G., Johnston, P.J., & MacDonald, D.W. (1997) The effects of organic farming on pest and non-pest butterfly abundance. *Agriculture, Ecosystems and Environment*, **64**, 133-139.

Feber, R.E. & Smith, H. (1995). Butterfly conservation on arable farmland. In *Ecology and conservation of butterflies* (ed A.S. Pullen), pp. 84-97. Chapman & Hall in association with Butterfly Conservation, London.

Feber, R.E., Smith, H., & MacDonald, D.W. (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology*, **33**, 1191-1205.

Firbank, L.G., Barr, C.J., Bunce, R.G.H., Furse, M.T., Haines-Young, R., Hornung, M., Howard, D.C., Sheail, J., Sier, A., & Smart, S.M. (2003a) Assessing stock and change in land cover and biodiversity in GB: an introduction to Countryside Survey 2000. *Journal of Environmental Management*, **67**, 207-218.

Firbank, L.G., Bennett, S., Bohan, D.A., Brooks, D.R., Champion, G., Clark, S.J., Daniels, R.E., Davidson, H.E., Dewar, A., Fairfax, C., Haughton, A.J., Hawes, C., Haylock, L., Heard, M.S., Hill, M.O., Hulmes, S., Lovell, L., May, M., Nuttall, P., Osborne, J.L., Parish, A., Perry, J.N., Randall, Z., Rossall, M.J., Rothery, P., Roy, D.B., Scott, R.J., Singer, E., Skellern, M.P., Squire, G., Todd, A.D., Woiwod, I.P., & Young, M. (2003b) The potential implications of spring-sown GMHT crops on farmland biodiversity. Defra: London.

Firbank, L.G. & Forcella, F. (2000) Genetically modified crops and farmland biodiversity. *Science*, **289**, 1481-1482.

Firbank, L.G., Heard, M.S., Woiwod, I.P., Hawes, C., Haughton, A.J., Champion, G.T., Scott, R.J., Hill, M.O., Dewar, A.M., Squire, G.R., May, M.J., Brooks, D.R., Bohan, D.A., Daniels, R.E., Osborne, J.L., Roy, D.B., Black, H.I.J., Rothery, P., & Perry, J.N. (2003c) An introduction to the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops. *Journal of Applied Ecology*, **40**, 2-16.

Fitter, A.H. & Fitter, R.S.R. (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689-1691.

Fitter, A.H., Fitter, R.S.R., Harris, I.T.B., & Williamson, M.H. (1995) Relationship between first flowering date and temperature in the flora of a locality in central England. *Functional Ecology*, **9**, 55-60.

Ford, E.B. (1949) *Butterflies* Collins, London.

Forister, M.L. & Shapiro, A.M. (2003) Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, **9**, 1130-1135.

Forsythe, T.G. (2000) *Ground beetles* Richmond Publishing Company, Slough, UK.

Fox, R. & Asher, J. (1999) *Butterflies for the New Millenium 1999, Provisional Atlas 2nd edition* Butterfly Conservation, Wareham.

Frank, T. (1998) The role of different slug species in damage to oilseed rape bordering on sown wildflower strips. *Annals of Applied Biology*, **133**, 483-493.

Freemark, K.E., Boutin, C., & Keddy, C.J. (2002) Importance of farmland habitats for conservation of plant species. *Conservation Biology*, **16**, 399-412.

Frost, M.P. & Madge, S.C. (1991) *Butterflies in south-east Cornwall* Caradon Field and Natural History club, Caradon.

Fussell, M. & Corbet, S.A. (1992a) Flower usage by bumble-bees: a basis for forage plant management. *Journal of Applied Ecology*, **29**, 451-465.

Fussell, M. & Corbet, S.A. (1992b) The nesting places of some British bumble bees. *Journal of Apicultural Research*, **31**, 32-41.

Fust, H.J. (1868) On the distribution of Lepidoptera in Great Britain and Ireland. *Transactions of the Royal Entomological Society London*, **4**, 417-517.

Gaston, K.J., Blackburn, T.M., & Loder, N. (1995) Which species are described first - the case of North-American butterflies. *Biodiversity and Conservation*, **4**, 119-127.

Gay, J. & Gay, P. (1996) *Atlas of Sussex butterflies* Butterfly Conservation, Lower Beeding.

Gibbs, J.P. & Breisch, A.R. (2001) Climate warming and calling phenology of frogs near Ithaca, New York, 1900-1999. *Conservation Biology*, **15**, 1175-1178.

Gilpin, M. & Hanski, I. (1991) *Metapopulation Dynaimcs: Empirical and theoretical investigations* Academic Press, London.

Gotthard, K., Nylin, S., & Wiklund, C. (2000) Individual state controls temperature dependence in a butterfly (*Lasiommata maera*). *Proceedings of the Royal Society of London B*, **267**, 589-593.

Greatorex-Davies, J.N., Sparks, T.H., Hall, M.L., & Marrs, R.H. (1993) The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. *Biological Conservation*, **63**, 31-41.

Groisman, P.Y., Karl, T.R., Easterling, D.R., Knight, R.W., Jamason, P.F., Hennessy, K.J., Suppiah, R., Page, C.M., Wibig, J., Fortuniak, K., Razuvaev, V.N., Douglas, A., Forland, E., & Zhai, P.M. (1999) Changes in the probability of heavy precipitation: Important indicators of climatic change. *Climatic Change*, **42**, 243-283.

Groombridge, B., ed. (1992) *Global biodiversity: status of the Earth's living resources*, pp xx + 594. Chapman and Hall, London.

Groombridge, B. & Jenkins, M.D. (2002) *World atlas of biodiversity* Berkeley.

Gutiérrez, D. & Menéndez, R. (1995) Distribution and Abundance of Butterflies in a Mountain Area in the Northern Iberian Peninsula. *Ecography*, **18**, 209-216.

Haines-Young, R., Barr, C.J., Black, H.I.J., Briggs, D.J., Bunce, R.G.H., Clarke, R.T., Cooper, A., Dawson, F.H., Firbank, L.G., Fuller, R.M., Furse, M.T., Gillespie, M.K., Hill, R., Nornung, M., Howard, D.C., McCann, T., Morecroft, M.D., Petit, S., Sier, A.R.J., Smart, S.M., Smith, G.M., Stott, A., Stuart, R.C., &

Watkins, J.W. (2000). Accounting for nature: assessing habitats in the UK countryside. CEH/DETR, London.

Hall, M.R. (1991) *An atlas of Norfolk butterflies, 1984-88* British Butterfly Conservation, Norwich.

Hambler, C. & Speight, M.R. (1996) Extinction rates in British nonmarine invertebrates since 1900. *Conservation Biology*, **10**, 892-896.

Hambler, C. & Speight, M.R. (2004) Extinction rates and butterflies. *Science*, **305**, 1563.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M., & Chey, V.K. (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, **40**, 150-162.

Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, **62**, 656-668.

Harrington, R., Woiwod, I., & Sparks, T.H. (1999) Climate change and trophic interactions. *Trends in Ecology and Evolution*, **14**, 146-149.

Harrison, F. & Sterling, M.J. (1985) *Butterflies and moths of Derbyshire part 1* Derbyshire Entomological Society, Derby.

Haughton, A.J., Bell, J.R., Boatman, N.D., & Wilcox, A. (1999a) The effects of different rates of the herbicide glyphostae on spiders in arable field margins. *Journal of Arachnology*, **27**, 249-254.

Haughton, A.J., Bell, J.R., Boatman, N.D., & Wilcox, A. (2001) The effect of the herbicide glyphosate on non-target spiders: Part II. Indirect effects on Lepythphantes tenuis in field margins. *Pest Management Science*, **57**, 1037-1042.

Haughton, A.J., Champion, G.T., Hawes, C., Heard, M.S., Brooks, D.R., Bohan, D.A., Clark, S.J., Dewar, A.M., Firbank, L.G., Osborne, J.L., Perry, J.N., Rothery, P., Roy, D.B., Scott, R.J., Woiwod, I.P., Birchall, C., Skellern, M.P., Walker, J.H., Baker, P., Browne, E.L., Dewar, A.J.G., Garner, B.H., Haylock, L.A., Horne, S.L., Mason, N.S., Sands, R.J.N., & Walker, M.J. (2003) Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1863 - 1877.

Haughton, A.J., Wilcox, A., K., C., & Boatman, N.D. (1999b) The effects of different rates of glyphosate on non-target invertebrates in field margins. *Aspects of Applied Biology*, **54**, 185 - 190.

Hawes, C., Haughton, A.J., Osborne, J.L., Roy, D.B., Clark, S.J., Perry, J.N., Rothery, P., Bohan, D.A., Brooks, D.R., Champion, G.T., Dewar, A.M., Heard, M.S., Woiwod, I.P., Daniels, R.E., Young, M.W., Parish, A.M., Scott, R.J., Firbank, L.G., & Squire, G.R. (2003) Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1899 - 1913.

Heard, M.S., Hawes, C., Champion, G.T., Clark, S.J., Firbank, L.G., Haughton, A.J., Parish, A.M., Perry, J.N., Rothery, P., Roy, D.B., Scott, R.J., Skellern, M.P., Squire, G.R., & Hill, M.O. (2003a) Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. II. Effects on individual species. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1833 - 1846.

Heard, M.S., Hawes, C., Champion, G.T., Clark, S.J., Firbank, L.G., Haughton, A.J., Parish, A.M., Perry, J.N., Rothery, P., Scott, R.J., Skellern, M.P., Squire, G.R., & Hill, M.O. (2003b) Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. I. Effects on abundance and diversity. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1819 - 1832.

Heath, J. (1981) *Threatened Rhopalocera (butterflies) of Europe* Council of Europe, Strasbourg.

Heath, J., Pollard, E., & Thomas, J. (1984) *Atlas of butterflies in Britain and Ireland.* Penguin, Harmondsworth, U.K.

Hengeveld, R. (1995). Species response to climate change. In *Impacts of climate change on ecosystems and species: environmental context* (eds J. Pernetta, R. Leemans, D. Elder & S. Humphrey), pp. 27-42. IUCN, Gland.

Hill, J.K., Collingham, Y.C., Thomas, C.D., Blakeley, D.S., Fox, R., Moss, D., & Huntley, B. (2001) Impacts of landscape structure on butterfly range expansion. *Ecology Letters*, **4**, 313-321.

Hill, J.K., Hamer, K.C., Dawood, M.M., Tangah, J., & Chey, V.K. (2003) Rainfall but not selective logging affect changes in abundance of tropical forest butterfly in Sabah, Borneo. *Journal of Tropical Ecology*, **19**, 35-42.

Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J., & Huntley, B. (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings- Royal Society of London B*, 2163-2172.

Hill, J.K., Thomas, C.D., & Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1197-1206.

Hilty, J. & Merenlender, A. (2000) Faunal indicator taxa selection for monitoring ecosystem health. *Biological Conservation*, **92**, 185-197.

Holl, K.D. (1995) Nectar resources and their Influence on butterfly communities on reclaimed coal surface mines. *Restoration Ecology*, **3**, 76-85.

Horton, G.A.N. (1994) *Monmouth Lepidoptera* Images Publishing, Malvern.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Da, X., Maskell, K., & Johnson, C.A., eds. (2001) *Climate Change 2001: The Scientific Basis*. Cambridge University Press, New York.

Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A., & Maskell, K., eds. (1996) *Climate change 1995: the science of climate change.*, pp xii+572. Cambridge University Press, Cambridge.

Hughes, C.L., Hill, J.K., & Dytham, C. (2003) Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, S147-S150.

Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent. *Trends in Ecology and Evolution*, **15**, 56-61.

Hulme, M. & Jenkins, G. (1998) *Climate change scenarios for the United Kingdom: summary report* Climate Research Unit, Norwich.

Huntley, B. (1991) How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany*, **67 (Suppl. 1)**, 15-22.

Huntley, B. (1995). How vegetation responds to climate change: evidence from palaeovegetation studies. In *The impact of climate change on ecosystems and* *species: terrestrial ecosystems* (eds J. Pernetta, R. Leemans, D. Elder & S. Humphrey), pp. 43-63. IUCN, Gland.

Hurvich, C.M. & Tsai, C.L. (1989) Regression and time series model selection in small samples. *Biometrik*, **76**, 297-307.

Inouye, D.W., Barr, B., Armitage, K.B., & Inouye, B.D. (2000) Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 1630-1633.

Jones, P.D. & Conway, D. (1997) Precipitation in the British Isles: an analysis of area-average data updated to 1995. *International Journal of Climatology*, **17**, 427-438.

Karl, T.R., Jones, P.D., Knight, R.W., Kukla, G., Plummer, N., Razuvayev, V., Gallo, K.P., Lindseay, J., Charlson, R.J., & Peterson, T.C. (1993) A New Perspective on Recent Global Warming - Asymmetric Trends of Daily Maximum and Minimum Temperature. *Bulletin of the American Meteorological Society*, **74**, 1007-1023.

Keeling, C.D., Chin, J.F.S., & Whorf, T.P. (1996) Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature*, **382**, 146-149.

Kleijn, D. (1996) The use of nutrient resources from arable fields by plants in the field boundaries. *Journal of Applied Ecology*, **33**, 1433-1440.

Kleijn, D. & Snoeijing, G.I.J. (1997) Field boundary vegetation and the effects of agrochemical drift: botanical change caused by low levels of herbicide and fertilizer. *Journal of Applied Ecology*, **34**, 1413-1425.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947-969.

Kleijn, D. & Verbeek, M. (2000) Factors affecting the species composition of arable boundary vegetation. *Journal of Applied Ecology*, **37**, 256-266.

Konvicka, M., Maradova, M., Benes, J., Fric, Z., & Kepka, P. (2003) Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography*, **12**, 403-410.

Körner, C. (1993). CO_2 fertilization: the great uncertainty in future vegetation development. In *Vegetation dynamics and global change* (eds A.M. Solomon & H.H. Shugart), pp. 53-70. Chapman & Hall, London.

Krebs, J.R., Wilson, J.D., Bradbury, R.B., & Siriwardena, G.M. (1999) The second silent spring? *Nature*, **400**, 611-612.

Lack, P.C. (1992) *Birds on lowland farms* HMSO, London.

Landres, P.B., Verner, J., & Thomas, J.W. (1988) Ecological Uses of Vertebrate Indicator Species: A Critique. *Cons. Biol.*, **2**, 316-328.

Langford, I.H. & Bentham, G. (1995) The potential effects of climate-change on winter mortality in England and Wales. *International Journal of Biometeorology*, **38**, 141-147.

Lees, E. (1962) On the voltinism of *Coenonympha pamphilus* (L.) (Lep., Satyridae). *Entomologist*, **95**, 5-6.

Lees, E. (1965) Further observations on the voltinism of *Coenonympha pamphilus* (L.) (Lep., Satyridae). *Entomologist*, **98**, 43-45.

Lees, E. & Archer, D.M. (1980) Diapause in various populations of *Pieris napi* from different parts of the British Isles. *Journal of Research on the Lepidoptera*, **89**, 18-19.

Lepš, J. & Hadincová, V. (1992) How reliable are our vegetation analyses? *Journal of Vegetation Science*, **3**, 119-124.

Lindsay, S.W. & Birley, M.H. (1996) Climate change and malaria transmission. *Annals of Tropical Medicine and Parasitology*, **90**, 573-588.

Loertscher, M., Erhardt, A., & Zettel, J. (1995) Microdistribution of butterflies in a mosaic-like habitat - the role of nectar sources. *Ecography*, **18**, 15-26.

Mabbett, R. & Williams, M. (1993) *The butterflies and moths of the west Midlands and Gloucestershire: a five year review* Butterfly Conservation, Kenilworth.

Maes, D. & van Dyck, H. (2001) Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation*, **99**, 263-276.

Manguira, M.L. & Thomas, J.A. (1992) Use of road verges by butterfly and burnet populations and the effects of roads on adult dispersal and mortality. *Journal of Animal Ecology*, **29**, 316-329.

Manley, G. (1974) Central England temperatures: monthly means 1659 to 1973. *Quarterly Journal of the Royal Meterological Society*, **100**, 389-405.

Markham, A. (1996) Potential impacts of climate change on ecosystems: A review of implications for policymakers and conservation biologists. *Climate Research*, **6**, 179-191.

Marrs, R.H. & Frost, A.J. (1997) A microcosm approach to detection of the effects of herbicide spray drift in plant communities. *Journal of Environmental Management*, **50**, 369-388.

Marrs, R.H., Frost, A.J., & Plant, R.A. (1991) Effects of herbicide spray drift on selected species of nature conservation interest: The effects of plant age and surrounding vegetation structure. *Environmental Pollution*, **69**, 223-235.

Marrs, R.H., Williams, C.T., Frost, A.J., & Plant, R.A. (1989) Assessment of the effects of herbicide spray drift on a range of plant species of conservation interest. *Environmental Pollution*, **59**, 71-86.

Marshall, E.J.R. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture Ecosystems & Environment*, **89**, 5-21.

Maudsley, M.J., West, T.M., Rowcliffe, H.P., & Marshall, E.J.P. (1997). Spatial variability in plant and insect (Heteroptera) communities in hedgerows in Great Britain. In *Species Dispersal and Land Use Processes* (eds A. Cooper & J. Power), pp. 229-236. IALE, Coleraine.

May, R.M., Lawton, J.H., & Stork, N.E. (1995). Assessing extinction rates. In *Extinction rates* (eds J.H. Lawton & R.M. May), pp. 1-24. Oxford University Press, Oxford.

McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology*, **15**, 320-331.

McGeoch, M.A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*, **73**, 181-201.

McKinney, M.L. (1999) High rates of extinction and threat in poorly studied taxa. *Conservation Biology*, **13**, 1273-1281.

McNamara, J.M. & Houston, A.I. (1996) State-dependent life histories. *Nature*, **380**, 215-221.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., & Nowakowski, M. (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, **106**, 259-271.

Mendel, H. & Piotrowski, S.H. (1986) *The butterflies of Suffolk* Suffolk Naturalists Society, Ipswich.

Menzel, A. & Fabian, P. (1999) Growing season extended in Europe. *Nature*, **397**, 659.

Mitchell, J.B. (1965) *Historical Geography* Universities Press, London.

Moorcroft, D., Whittingham, M.J., Bradbury, R.B., & Wilson, J.D. (2002) The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *Journal of Applied Ecology*, **39**, 535-547.

Moreby, S.J., Sotherton, N.W., & Jepson, P.C. (1997) The effects of pesticides on species of non-target Heteroptera inhabiting cereal fields in southern England. *Pesticide Science*, **51**, 39-48.

Morecroft, M.D., Bealey, C.E., Howells, O., Rennie, S., & Woiwod, I.P. (2002) Effects of drought on contrasting insect and plant species in the UK in the mid-1990s. *Global Ecology and Biogeography*, **11**, 7-22.

Morgan, I.K. (1989) *A provisional review of the butterflies of Carmarthenshire* Nature Conservancy Council, Aberystwyth.

Morris, M.G. & Webb, N.R. (1987). The importance of field margins for the conservation of insects. In *Field Margins* (eds J.M. Way & P.W. Greig-Smith), pp. 53-65. British Crop Protection Council, Thornton Heath, UK.

Moss, D. & Pollard, E. (1993) Calculation of collated indices of abundance of butterflies based on monitored sites. *Ecological Entomology*, **18**, 77-83.

Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and methods in vegetation ecology* John Wiley, New York.

New, T.R. (1997) Are Lepidoptera an effective 'umbrella group' for biodiversity conservation? *Journal of Insect Conservation*, **1**, 5-12.

Norris, R.F. & Kogan, M. (2000) Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems. *Weed Science*, **48**, 94-158.

Nylin, S. & Gotthard, K. (1998) Plasticity in life-history traits. *Annual Review of Entomology*, **43**, 63-83.

Nylin, S. & Svard, L. (1991) Latitudinal patterns in the size of European butterflies. *Holarctic Ecology*, **14**, 192-202.

Oostermeijer, J.G.B. & Van Swaay, C.A.M. (1998) The relationship between butterflies and environment indicator values: a tool for conservation in a changing landscape. *Biological Conservation*, **86**, 271-280.

Osborne, J.L., Carreck, N., & Williams, I.H. (2001) How far do honey bees fly to *Brassica napus* (oilseed rape) crops? In Proceedings of Apimondia, Durban, South Africa.

Parker, D.E., Legg, T.P., & Folland, C.K. (1992) A new daily central England temperature series, 1772-1991. *International Journal of Climatology*, **12**, 317-342.

Parmesan, C. (1996) Climate change and species' range. *Nature*, **382**, 765-766.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.

Parry, M. (1992) The potential effect of climate changes on agriculture and land use. *Advances in Ecological Research*, **22**, 63-91.

Peach, W.J., Lovett, L.J., Wotton, S.R., & Jeffs, C. (2001) Countryside stewardship delivers cirl buntings (Emberiza cirlus) in Devon, UK. *Biological Conservation*, **101**, 361-373.

Peñuelas, J. & Filella, I. (2001) Responses to a warming world. *Science*, **294**, 793-795.

Peñuelas, J., Filella, I., & Comas, P. (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, **8**, 531-544.

Perry, J.N., Rothery, P., Clark, S.J., Heard, M.S., & Hawes, C. (2003) Design, analysis and statistical power of the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops. *Journal of Applied Ecology*, **40**, 17-31.

Peterson, M.A. (1997) Host plant phenology and butterfly dispersal: causes and consequences of uphill movement. *Ecology*, **78**, 167-180.

Petit, S., Firbank, L., Wyatt, B.K., & Howard, D. (2001) MIRABEL: Models for Integrated Review and Assessment of Biodiversity in European Landscapes. *Ambio*, **30**, 81-88.

Philp, E.G. (1993) *The butterflies of Kent* Kent Field Club, Sittingbourne.

Picard-Nizou, A.L., Pham-Delegue, M.H., Kerguelen, V., Doualt, P., Marilleau, R., Olsen, L., Grison, R., Toppan, A., & Masson, C. (1995) Foraging behaviour of honey bees (*Apis mellifera* L.) on transgenic oilseed rape (*Brassica napus* L. var. *oleifera*). *Transgenic Research*, **4**, 270-276.

Pimm, S.L., Russell, G.J., Gittleman, J.L., & Brooks, T.M. (1995) The future of biodiversity. *Science*, **209**, 347-350.

Pollard, E. (1977) A method of assessing changes in the abundance of butterflies. *Biological Conservation*, **12**, 115-134.

Pollard, E. (1979) Population ecology and change in range of the White Admiral butterfly *Ladoga camilla*. L. in England. *Ecological Entomology*, **4**, 61-74.

Pollard, E. (1988) Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*, **25**, 819-828.

Pollard, E. (1991a) Changes in the flight period of the Hedge Brown butterfly *Pyronia tithonus* during range expansion. *Journal of Animal Ecology*, **60**, 737-748.

Pollard, E. (1991b) Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos*, **60**, 7-10.

Pollard, E. & Eversham, B.C. (1995a). Butterfly monitoring: interpreting the changes. In *Ecology and conservation of butterflies* (ed A.S. Pullin), pp. 23-36. Chapman & Hall in association with Butterfly Conservation, London.

Pollard, E. & Greatorex-Davies, J.N. (1997a) Flight-periods of the Small Heath butterfly, *Coenonympha pamphilus* (Linnaeus) (Lepidoptera: Nymphalidae, Satyrinae) on chalk downs and in woodland in southern England. *Entomologist's Gazette*, **48**, 3-7.

Pollard, E., Greatorex-Davies, J.N., & Thomas, J.A. (1997b) Drought reduces breeding success of the butterfly Aglais urticae. *Ecological Entomology*, **22**, 315-318.

Pollard, E., Hall, M.L., & Bibby, T.J. (1986). Monitoring the abundance of butterflies 1976-1985. Nature Conservancy Council, Peterborough.

Pollard, E. & Lakhani, K.H. (1985). Butterfly Monitoring Scheme: effects of weather on abundance. In *Institute of Terrestrial Ecology, Annual Report 1984*, pp. 54-56.

Pollard, E., Moss, D., & Yates, T.J. (1995b) Population trends of common British butterflies at monitored sites. *Journal of Applied Ecology*, **32**, 9-16.

Pollard, E. & Relton, J. (1970) Hedges. V. A study of the small mammals in hedges and cultivated fields. *Journal of Applied Ecology*, **7**, 899-912.

Pollard, E., Rothery, P., & Yates, T.J. (1996) Annual growth rates in newly established populations of the butterfly *Pararge aegeria*. *Ecological Entomology*, **21**, 365-369.

Pollard, E., Van Swaay, C.A.M., Stefanescu, C., Lundsten, K.E., Maes, D., & Greatorex-Davies, J.N. (1998a) Migration of the painted lady butterfly *Cynthia cardui* in Europe: evidence from monitoring. *Diversity and Distributions*, **4**, 243-253.

Pollard, E., Van Swaay, C.A.M., & Yates, T.J. (1993a) Changes in butterfly numbers in Great Britain and the Netherlands 1900-1991. *Ecological Entomology*, **18**, 93-94.

Pollard, E., Woiwod, I.P., Greatorex-Davies, J.N., Yates, T.J., & Welch, R.C. (1998b) The spread of coarse grasses and changes in numbers of lepidoptera in a woodland nature reserve. *Biological Conservation*, **84**, 17-24.

Pollard, E. & Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation.* Chapman and Hall, London.

Potts, G.R. (1986) *The partridge: pesticides, predation and conservation* Collins, London.

Powell, W. (1986). Enhancing parasitoid activity in crops. In *Insect parasitoids* (eds J. Waage & D. Greathead), pp. 319-335. Academic press, London.

Pratt, C. (1981) *A history of the butterflies and months of Sussex* Booth Museum, Brighton.

Preston, C.D., Pearman, D.A., & Dines, T.D., eds. (2002) *New Atlas of the British and Irish flora.* Oxford University Press, Oxford.

Prys-Jones, O.E. & Corbet, S.A. (1991) *Bumblebees*, 2nd edn. Richmond Publishing Company, Slough, UK.

Pullin, A.S. (1986) Effect of photoperiod and temperature on the life-cycle of different populations of the peacock butterfly *Inachis io*. *Entomol. exp. appl.*, **41**, 237-242.

Pullin, A.S. (1987) Changes in leaf quality following clipping and regrowth in *Urtica dioicia* , and consequences for a specialist insect herbivore *Aglais urticae*. *Oikos*, **49**, 39-45.

Pullin, A.S. (1995) *Ecology and conservation of butterflies* Chapman and Hall, London.

Pullin, A.S. (1996) Restoration of butterfly populations in Britain. *Restoration Ecology*, **4**, 71-80.

Pywell, R.F., Warman, E.A., Sparks, T.H., Greatorex-Davies, J.N., Walker, K.J., Meek, W.R., Carvell, C., Petit, S., & Firbank, L.G. (2004) Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation*, **118**, 313-325.

Quinn, R.M., Gaston, K.J., & Roy, D.B. (1998) Coincidence in the distribution of butterflies and their foodplants. *Ecography*, **21**, 279-288.

Rackham, O. (1986) *The history of the countryside* Dent, London.

Rafe, R.W. & Jefferson, R.G. (1983) The status of *Melanargia galathea* (Lepidoptera: Satyridae) in the Yorkshire Wolds. *Naturalist, Hull*, **108**, 3-7.

Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157-176.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-60.

Rosenberg, D.M., Danks, H.V., & Lehmkuhl, D.M. (1986) Importance of insects in environmental impact assessment. *Environmental Management*, **10**, 773-783.

Rosenzweig, C. & Hillel, D. (1998) *Climate change and the global harvest: Potential impacts of the greenhouse effect on agriculture.* Oxford University Press, Oxford.

Roy, D.B., Bohan, D.A., Haughton, A.J., Hill, M.O., Osborne, J.L., Clark, S.J., Perry, J.N., Rothery, P., Scott, R.J., Brooks, D.R., Champion, G.T., Hawes, C., Heard, M.S., & Firbank, L.G. (2003) Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **358**, 1879 - 1898.

Roy, D.B., Rothery, P., Moss, D., Pollard, E., & Thomas, J.A. (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201-217.

Roy, D.B. & Sparks, T.H. (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407-416.

Saarinen, K., Lahti, T., & Marttila, O. (2003) Population trends of Finnish butterflies (Lepidoptera : Hesperioidea, Papilionoidea) in 1991-2000. *Biodiversity and Conservation*, **12**, 2147-2159.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. (2000) Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774.

Saville, N.M. (1993) *Bumblebee ecology in woodlands and arable farmland.* Ph.D., Cambridge University Press, Cambridge.

Sawford, B. (1987) *The butterflies of Hertfordshire* Castlemead, Ware.

Schultz, E.T., Reynolds, K.E., & Conover, D.O. (1996) Countergradient variation in growth among newley hatched *Fundulus heterclitus*: geographical differences revealed by common-environment experiments. *Functional Ecology*, **10**, 366-374.

Schwartz, M.W. (1992) Potential effects of global climate change on the biodiversity of plants. *Forestry Chronicle*, **68**, 462-471.

Sheail, J. (1972) *Rabbits and their history* Country Book Club, Newton Abbot, UK.

Sherratt, T.N. & Jepson, P.C. (1993) A metapopulation approach to modelling the long-term impact of pesticides on invertebrates. *Journal of Applied Ecology*, **30**, 696-705.

Shirt, D.B., ed. (1987) *British Red Data Books, 2, Insects.* Nature Conservancy Council, Peterborough.

Shreeve, T.G. (1986) The Effect of Weather on the Life-Cycle of the Speckled Wood Butterfly Pararge-Aegeria. *Ecological Entomology*, **11**, 325-332.

Simberloff, D. (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation*, **83**, 247-257.

Singer, M.C. (1972) Complex components of habitat suitability within a butterfly colony. *Science*, **176**, 75-77.

Singer, M.C. & Thomas, C.D. (1996) Evolutionary responses of a butterfly metapopulation to human- and climate-caused environmental variation. *American Naturalist*, **148**, S9-S39.

Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H., & Wilson, J.D. (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, **35**, 24-43.

Smith, F.A. & Betancourt, J.L. (1998) Response of bushy-tailed woodrats (Neotoma cinerea) to late Quaternary climatic change in the Colorado Plateau. *Quaternary Research*, **50**, 1-11.

Smith, F.H.N. (1997) *The moths and butterflies of Cornwall and the Isles of Scilly* GEM, Wallingford.

Sotherton, N.W. (1985) The distribution and abundance of predatory coleoptera overwintering in field boundaries. *Annals of Applied Biology*, **106**, 17-21.

Sotherton, N.W. & Self, M.J. (2000). Changes in plant and arthropod biodiversity on lowland farmland: an overview. In *Ecology and conservation of lowland farmland birds* (eds N.J. Aebischer, A.D. Evans, P.V. Grice & J.A. Vickery), pp. 26-35. British Ornithologists' Union, Tring.

Southwood, T.R.E. & Leston, D. (1959) *Land and Water Bugs of the British Isles* Frederick Warne, London.

Sparks, T. & Crick, H. (1999) The times they are a-changing? *Bird Conservation International*, **9**, 1-7.

Sparks, T.H. (1999) Phenology and the changing pattern of bird migration in Britain. *International Journal of Biometerology*, **42**, 134-138.

Sparks, T.H. & Carey, P.D. (1995) The response of species to climate over two centuries: an analysis of the Marsham phenological record 1736-1947. *Journal of Ecology*, **83**, 321-329.

Sparks, T.H., Carey, P.D., & Combes, J. (1997a) First leafing dates of trees in Surrey between 1947 and 1996. *The London Naturalist*, **76**, 15-20.

Sparks, T.H., Greatorex-Davies, J.N., Mountford, J.O., Hall, M.L., & Marrs, R.H. (1996) The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. *Forest Ecology and Management*, **80**, 197-207.

Sparks, T.H. & Parish, T. (1995) Factors affecting the abundance of butterflies in field boundaries in Swavesey Fens, Cambridgeshire, UK. *Biological Conservation*, **73**, 221-227.

Sparks, T.H. & Yates, T.J. (1997) The effect of spring temperature on the appearance dates of British butterflies 1883-1993. *Ecography*, **20**, 368-374.

Spitzer, K., Jaros, J., Havelka, J., & Leps, J. (1997) Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation*, **80**, 9-15.

Stefanescu, C., Herrando, S., & Paramo, F. (2004) Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *Journal of Biogeography*, **31**, 905-915.

Stefanescu, C., Penuelas, J., & Filella, I. (2003) Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, **9**, 1494-1506.

Sutcliffe, O.L., Thomas, C.D., & Moss, D. (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, **65**, 85-95.

Sutcliffe, O.L., Thomas, C.D., & Peggie, D. (1997) Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. *Oecologia*, **109**, 229-234.

Sutherst, R.W. (1995). The potential advance of pests in natural ecosystems under climate change: implications for planning and management. In *The impact of climate change on ecosystems and species: terrestrial ecosystems* (eds J. Pernetta, R. Leemans, D. Elder & S. Humphrey), pp. 83-98. IUCN, Gland.

Sutherst, R.W. (1998) Implications of global change and climate variability for vector borne diseases: generic approaches to impact assessments. *International Journal for Parasitology*, **28**, 935-945.

Sutton, S.L. & Beaumont, H.E. (1989a) *The butterflies and moths of Yorkshire* Yorkshire Naturalists Union, Doncaster.

Sutton, S.L. & Beaumont, H.E. (1989b) *Butterflies and moths of Yorkshire : distribution and conservation* Yorkshire Naturalists' Union, Leeds.

Svensson, B., Lagerlof, J., & Svensson, B.G. (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems and Environment*, **77**, 247-255.

Symondson, W.O.C., Glen, D.M., Wiltshire, C.W., Langdon, C.J., & Liddell, J.E. (1996) Effects of cultivation techniques and methods of straw disposal on predation by Pterostichus melanarius (Coleoptera: Carabidae) upon slugs (Gastropoda: Pulmonata) in an arable field. *Journal of Applied Ecology*, **33**, 741-753.

Tew, T.E., Todd, I.A., & MacDonald, D.W. (1994). Field margins and small mammals. In *Field margins: Integrating agriculture and conservation* (ed N.D. Boatman), Vol. BCPC Monograph 58, pp. 85-94. The British Crop Protection Council, Farnham, UK.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., & Conradt, L. (2001a) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577-581.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., & Williams, S.E. (2004a) Extinction risk from climate change. *Nature*, **427**, 145-148.

Thomas, C.D. & Harrison, S. (1992) Spatial dynamics of a patchily distributed butterfly species. *J.Anim.Ecol.*, **61**, 437-446.

Thomas, C.D., Jordano, D., Lewis, O.T., Hill, J.K., Sutcliffe, O.L., & Thomas, J.A. (1998a). Butterfly distributional patterns, processes and conservation. In *Conservation in a changing world: integrating processes into priorities for actions* (eds G.M. Mace, A. Balmford & J.R. Ginsberg), pp. 107-138. Cambridge University Press, Cambridge.

Thomas, J.A. (1983) The ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lycaenidae) in Britain. *Journal of Applied Ecology*, **20**, 59-83.

Thomas, J.A. (1984). The conservation of butterflies in temperate countries; past, present and lessons for the future. In *The Biology of Butterflies* (eds R.I. Vane-Wright & P.R. Ackery). Academic Press, London.

Thomas, J.A. (1991). Rare species conservation: case studies of European butterflies. In *The scientific management of temperate communities for conservation* (eds I.F. Spellerberg, F.B. Goldsmith & M.G. Morris), pp. 149-197. Blackwell, Oxford.

Thomas, J.A. (1993) Holocene climate changes and warm man-made refugia may explain why a 6th of British butterflies possess unnatural early-successional habitats. *Ecography*, **16**, 278-284.

Thomas, J.A. (1995a) The conservation of declining butterfly populations in Britain and Europe: Priorities, problems and successes. *Biological Journal of the Linnean Society*, **56**, 55-72.

Thomas, J.A. (1995b) Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. *Ibis*, **137**, S112-S119.

Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 339-357.

Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R., & Goodger, B. (2001b) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London Series B*, **268**, 1791-1796.

Thomas, J.A. & Clarke, R.T. (2004) Extinction rates and butterflies. *Science*, **305**, 1563-1564.

Thomas, J.A. & Lewington, R. (1991) *The butterflies of Britain and Ireland* Dorling Kindersley, London.

Thomas, J.A., Moss, D., & Pollard, E. (1994) Increased fluctuations of butterfly populations towards the northern edges of species ranges. *Ecography*, **17**, 215-220.

Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D., & Webb, N.R. (1999) Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, **13**, 55-64.

Thomas, J.A., Simcox, D.J., Wardlaw, J.C., Elmes, G.W., Hochberg, M.E., & Clarke, R.T. (1998b) Effects of latitude, altidude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *Journal of Insect Conservation*, **2**, 39-46.

Thomas, J.A., Surry, R., Shreeves, W., & Steele, C. (1998c) *New atlas of Dorset butterflies* Dorset Natural History & Archaeological Society, Dorchester.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T., & Lawton, J.H. (2004c) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**, 1879-1881.

Thomas, J.A., Thomas, C.D., Simcox, D.J., & Clarke, R.T. (1986) Ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology*, **23**, 365-380.

Thomas, J.A. & Webb, N.R. (1984) *Butterflies of Dorset* Dorset Natural History & Archaeological Society, Dorchester.

Thomson, G. (1980) *The butterflies of Scotland* Croom Helm, London.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science*, **292**, 281-284.

Tolman, T. & Lewington, R. (1997) *Butterflies of Britain and Europe* Harper Collins, London.

Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London B.*, **270**, 467-473.

Turner, J.R.G., Gatehouse, C.M., & Corey, C.A. (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, **48**, 195-205.

UK Biodiversity Steering Group (1995) *Biodiversity: the UK Steering Group Report* HMSO, London.

van Swaay, C. & Warren, M.S. (1999) *Red data book of European butterflies (Rhopalocera).* Nature and Environment, No. 99. Council of Europe, Strasbourg.

van Swaay, C.A.M. (1990) An assessment of the changes in butterfly abundance in The Netherlands during the 20th Century. *Biological Conservation*, **52**, 287-302.

Vantienderen, P.H. & Koelewijn, H.P. (1994) Selection on Reaction Norms, Genetic Correlations and Constraints. *Genetical Research*, **64**, 115-125.

Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 289-294.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Guldberg, O.H., & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389-395.

Warren, M.S. (1985) The influence of shade on butterfly numbers in woodland rides with special reference to the Wood White, *Leptidea sinapis. Biological Conservation*, **33**, 147-164.

Warren, M.S. (1992). Butterfly populations. In *The Ecology of Butterflies in Britain* (ed R.L.H. Dennis), pp. 354. Oxford Science Publications, Oxford.

Warren, M.S. (1993a) A review of butterfly conservation in Central Southern Britain (1) Protection, evaluation and extinction on prime sites. *Biological Conservation*, **64**, 25-35.

Warren, M.S. (1993b) A review of butterfly conservation in Central Southern Britain (2) Site management and habitat selection of key species. *Biological Conservation*, **64**, 37-49.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65-69.

Watkinson, A.R., Freckleton, R.P., Robinson, R.A., & Sutherland, W.J. (2000) Predictions of biodiversity response to genetically modified herbicide-tolerant crops. *Science*, **289**, 1554-1557.

Way, J.M. & Greig-Smith, P.W., eds. (1987) *Field margins*. British Crop Protection Council, Thornton Heath, UK.

Webb, M.R. & Pullin, A.S. (1996) Larval survival in populations of the large copper butterfly Lycaena dispar batavus. *Ecography*, **19**, 279-286.

Weibull, A.-C., Bengtsson, J., & Nohlgren, E. (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, **23**, 743-750.

Weiss, S.B. & Murphy, D.D. (1988a) Fractal geometry and caterpillar dispersal: or how many inches can inch-worms inch? *Functional Ecology*, **2**, 116-118.

Weiss, S.B., Murphy, D.D., Ehlich, P.R., & Metzler, C.F. (1993) Adult emergence phenology in Checkerspot butterflies: the effects of macroclimate, topoclimate and population history. *Oecologia*, **96**, 261-270.

Weiss, S.B., Murphy, D.D., & White, R.R. (1988b) Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology*, **69**, 1486-1496.

Whalley, P. (1997) *Butterflies of Gwynedd* First Hydro, Llanberis.

Wickman, P.O., Wiklund, C., & Karlsson, B. (1990) Comparative phenology of four satyrine butterflies inhabiting dry grasslands in Sweden. *Holarctic Ecology*, **13**, 238-246.

Wigley, T.M.L., Lough, J.M., & Jones, P.D. (1984) England and Wales precipitation: a discussion of recent changes in variability and an update to 1985. *Journal of Climatology*, **4**, 1-25.

Williams, P.H. (1986) Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World*, **67**, 50-61.

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., & Bradbury, R.B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment*, **75**, 13-30.

Wilson, P.J. (1992) Britain's arable weeds. *British Wildlife*, **3**, 149-161.

Woiwod, I.P. (1997) Detecting the effects of climate change on Lepidoptera. *Journal of Insect Conservation*, **1**, 149-158.

Woiwod, I.P. & Hanski, I. (1992) Patterns of density dependance in moths and aphids. *Journal of Animal Ecology*, **61**, 619-629.

Zhou, X.L., Harrington, R., Woiwod, I.P., Perry, J.N., Bale, J.S., & Clark, S.J. (1995) Effects of Temperature on Aphid Phenology. *Global Change Biology*, **1**, 303-313.