The North Atlantic Oscillation, climate change and the ecology of British insects

A thesis submitted for the degree of Doctor of Philosophy

By Angus R. Westgarth-Smith

Institute for the Environment,

Brunel University,

Uxbridge, Middlesex,

UB8 3PH, UK

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Declaration

The work described in this thesis was carried out between 2000 and 2012 at Brunel University. This work was done independently and has not been submitted for any other degree.

Abstract

Evidence is accumulating that climate change is having a significant effect on a wide range of organisms spanning the full range of biodiversity found on this planet. This study investigates the ecological role of climate change, the North Atlantic Oscillation (NAO) and habitat change on British insect populations. Despite the NAO having a considerable effect on British weather, the role of the NAO on British insects has not previously been studied in great detail. The World's two best entomological time series datasets were used – the United Kingdom Butterfly Monitoring Scheme (UKBMS) and the Rothamsted Insect Survey of aphids – both surveys with very large sample sizes and high quality data.

Summary of main findings:

1. Warm weather associated with a positive NAO index caused the spring migration of the green spruce aphid (*Elatobium abietinum*), a pest species of spruce trees (*Picea*) to start earlier, continue for longer and contain more aphids. An upward trend in the NAO index during the period 1966-2006 is associated with an increasing population size of *E. abietinum*.

2. The NAO does not affect the overall UK butterfly population size. However, the abundance of bivoltine butterfly species, which have a longer flight season, were more likely to respond positively to the NAO compared to univoltine species, which show little or a negative response.

3. A positive winter NAO index was associated with warmer weather and earlier butterfly flight dates. For bivoltine (two generations in a year) species, the NAO affects the phenology of the first generation, and then the timing of the second generation is indirectly controlled by the timing of the first generation. The NAO influences the timing of the butterfly flight seasons more strongly than it influences population size.

4. Butterfly data from Monks Wood National Nature Reserve in Cambridgeshire showed that the NAO does not affect the abundance of the whole butterfly community, but it does affect the population size of some species. The NAO

does not affect butterfly diversity, but there were decreases in butterfly diversity and number of species with time.

5. The total number of butterflies counted at Monks Wood was constant for most of the time series. However, the population size of the ringlet (*Aphantopus hyperantus*) increased from very low numbers to more than half the total number of butterflies counted each year. Therefore the total population size of all the other species has decreased considerably.

6. The NAO was more important than climate change in determining the flight phenology of the meadow brown butterfly (*Maniola jurtina*) at Monks Wood.

In conclusion, the NAO affects the abundance of some species of British butterfly, and an aphid species, with a stronger effect on the timing of flight rather than abundance. There was evidence for a long-term decrease in the biodiversity of butterflies at Monks Wood and this decrease is likely to continue.

Acknowledgements

I would like to thank my supervisors, Professor John Sumpter and Dr Alan Tucker and co-authors of papers including Dr Philip Collins, Dr Richard Harrington, Martin Scholze, Professor Suzanne Leroy and Dr David Roy.

This study used data from two insect databases – the Rothamsted Insect Survey and the United Kingdom Butterfly Monitoring Scheme (UKBMS). Rothamsted Research receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom. The suction trap network is also supported by the Lawes Agricultural Trust. I am indebted to all the volunteer recorders and local co-ordinators who have contributed to the UKBMS. The UKBMS is a partnership between Butterfly Conservation and the Natural Environment Research Council, Centre for Ecology & Hydrology. The UKBMS is funded by a multi-agency consortium led by Defra, and including the Countryside Council for Wales, the Joint Nature Conservation Committee, Forestry Commission, Natural England, the Natural Environment Research Council, the Northern Ireland Environment Agency and Scottish Natural Heritage.

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Chapter 1

Introduction

1.1 Overview

Britain has a temperate maritime climate warmed by the Gulf Stream. The climate is subject to long term change due to changes in the composition of gases, including carbon dioxide, methane, nitrous oxides and aerosols in the atmosphere, which are causing changes in radiative forcing. The climate is also subject to shorter term fluctuations caused by the North Atlantic Oscillation (NAO).

Carbon dioxide is one of the main greenhouse gases that are responsible for the warming, and the rate of increase in atmospheric concentration of this gas is accelerating. Projected temperature increase due to climate change by 2100 AD for most of Europe is in the range 4 to 8°C and for the Arctic Ocean is >10°C. Projected temperature increases for the UK may be slightly lower, in the range of 2-6°C.

The NAO has a considerable influence on the weather over a large geographical area, including the North Atlantic, Europe, Mediterranean, Scandinavia and the UK. The NAO controls the route taken by depression systems crossing the Atlantic, thereby influencing the temperature and precipitation in the UK, especially during the autumn and winter months. The NAO is described by an NAO index, which is calculated from air pressures in Iceland and a location within the Azores high pressure area.

Climate change appears to be having an increasing effect on the ecology of organisms, including changes to distribution and phenology. Less has been published regarding the ecological effects of the NAO, although there is evidence that the NAO affects a range of different groups of organisms.

Increasing atmospheric carbon dioxide concentrations can have other ecological effects on invertebrates through changing the carbon to nitrogen ratios in plants. A reduced proportion of nitrogen in plants can reduce their nutritional value to insects.

Carbon dioxide can dissolve in seawater to cause ocean acidification. There are very few marine insect species however there are potentially severe consequences for other invertebrates as the acidification affects the ability of corals and molluscs to produce carbonate based skeletons and shells.

The ecological effects of climate change are already apparent and with projected increases in atmospheric carbon dioxide concentrations the effects of ocean acidification on marine biodiversity are likely to be apparent by 2030-2050 so the need for meaningful reductions in the production of greenhouse gases is urgently needed. There are attempts to reduce carbon dioxide emissions through international agreements, technological developments and public pressure. However, it is uncertain whether any meaningful reduction in emissions will be achieved as the global human population size is increasing rapidly and more people means more pressure to burn fossil fuels.

UK insect populations are also responding to changes in land management, including changes in forestry and livestock grazing, pressures from introduced organisms, diseases and air pollution. While some new insect species have colonised the UK recently, the overall pattern is one of a decrease in insect abundance and there is evidence that this decrease is also found in some non-insect invertebrate groups. It is likely that this decrease in insect population size is contributing to a reduction in population size of insectivorous organisms.

1.2 Factors influencing the UK weather

The UK has a temperate maritime climate, which means that its latitude and the surrounding sea reduce the extremes of weather that might be encountered further into mainland Europe, where continentality causes the weather to be more extreme. UK weather is influenced by the Gulf Stream (O’Hare, 2011), which is part of the thermohaline circulation that brings considerable amounts of heat energy to the North Atlantic. Westerly winds then carry this warmth and evaporated water into the UK and Western Europe, which causes winters to be warmer and wetter than would be expected for this latitude (Ahrens, 2000). For example, winter weather at the same latitude on the eastern coast of the USA, which is not warmed by the Gulf Stream, is much colder.

UK climate is also affected by climate change and the North Atlantic Oscillation (NAO). Climate change is caused by a range of substances that are mainly of anthropogenic origin and most of which are gases, which cause radiative forcing resulting in meteorological changes, including an increase in temperature. The NAO is an oscillatory weather system, causing changes in temperature and precipitation across the North Atlantic region and surrounding continental areas, including the UK.

1.3 Atmospheric radiative forcing

Radiative forcing is the difference in the solar energy that comes down to the Earth and its atmosphere compared to the amount of energy that leaves – if more energy comes in than leaves, due to a change in atmospheric concentration of greenhouse gases, then temperatures increase and climate change is occurring. Radiative forcing is measured in Wm^{-2} (IPCC, 2007). Solomon *et al*. (2007) lists eighteen greenhouse gases including carbon dioxide, methane, nitrous oxide and the Montreal gases, which include chloroflurocarbons. Anthropogenic sources of greenhouse gases include: carbon dioxide from burning fossil fuels, deforestation and cement manufacture; methane sources include agriculture, landfill and leaks from natural gas distribution; nitrous oxides come from the burning of fossil fuels and fertilisers; chloroflurocarbons used in refrigerators. The Montreal gases are now subject to control through the Montreal Protocol and there has been negligible change in their atmospheric concentrations between 1998 and 2005 (Table 1.1; Solomon *et al*., 2007). Water vapour is an important greenhouse gas, but there is no direct human control over emissions. Other factors that reduce radiative forcing, include some aerosols and the reflection of heat by ice and clouds (Figure 1.1).

Figure 1.1 gives an indication of the relative magnitude of the effect of different substance on radiative forcing, and also indicates whether they increase or decrease global temperature. Table 1.1 takes four of the most important greenhouse gases – carbon dioxide, methane, nitrous oxide and the Montreal gases - and puts their radiative forcing in to context with changes in their atmospheric concentrations.

1.4 Greenhouse gases causing climate change

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The atmospheric concentrations of carbon dioxide, methane and nitrous oxide have been fairly constant from the years 0 to 1800 AD (Solomon *et al*., 2007). However, in the last two hundred years, the atmospheric concentration of carbon dioxide has increased by 35%, methane by 157% and nitrous oxide by 19% (Figure 1.2). The increase in concentrations of these gases is associated with human population growth, industrialisation and agriculture.

Carbon dioxide is now regarded as the most important greenhouse gas as it causes more radiative forcing than the other gases, and also because it has increased from pre-industrial concentrations of about 280 ppm (Solomon *et al*., 2007) to over 390 ppm in 2011 (Figure 1.3; Tans, 2011). The annual rate of increase in atmospheric carbon dioxide concentration has doubled during the period 1959-2010 and appears still to be increasing (Figure 1.4), with the current rate of increase at slightly more than 2 ppm year^{-1}. This includes a 29% increase in emissions from fossil fuels between 2000 and 2008 (Le Quéré *et al*., 2009). The slowing in the rate of increase of the atmospheric carbon dioxide concentration in the early 1990s was partly due to an economic recession (Connor, 2010). Shepherd (2009) suggests that atmospheric carbon dioxide concentrations will exceed 500 ppm by the middle of this century and be approaching 1000 ppm by 2100.

Although carbon dioxide is the most important greenhouse gas, Table 1.1 suggests that nitrous oxides may increasingly contribute to climate change as a smaller increase in atmospheric nitrous oxide concentration than carbon dioxide concentration has produced a similar percentage change in radiative forcing. Increasing fertiliser use or increasing combustion of fossil fuels associated with an expanding human population has the potential to increase the atmospheric concentration of nitrous oxides.

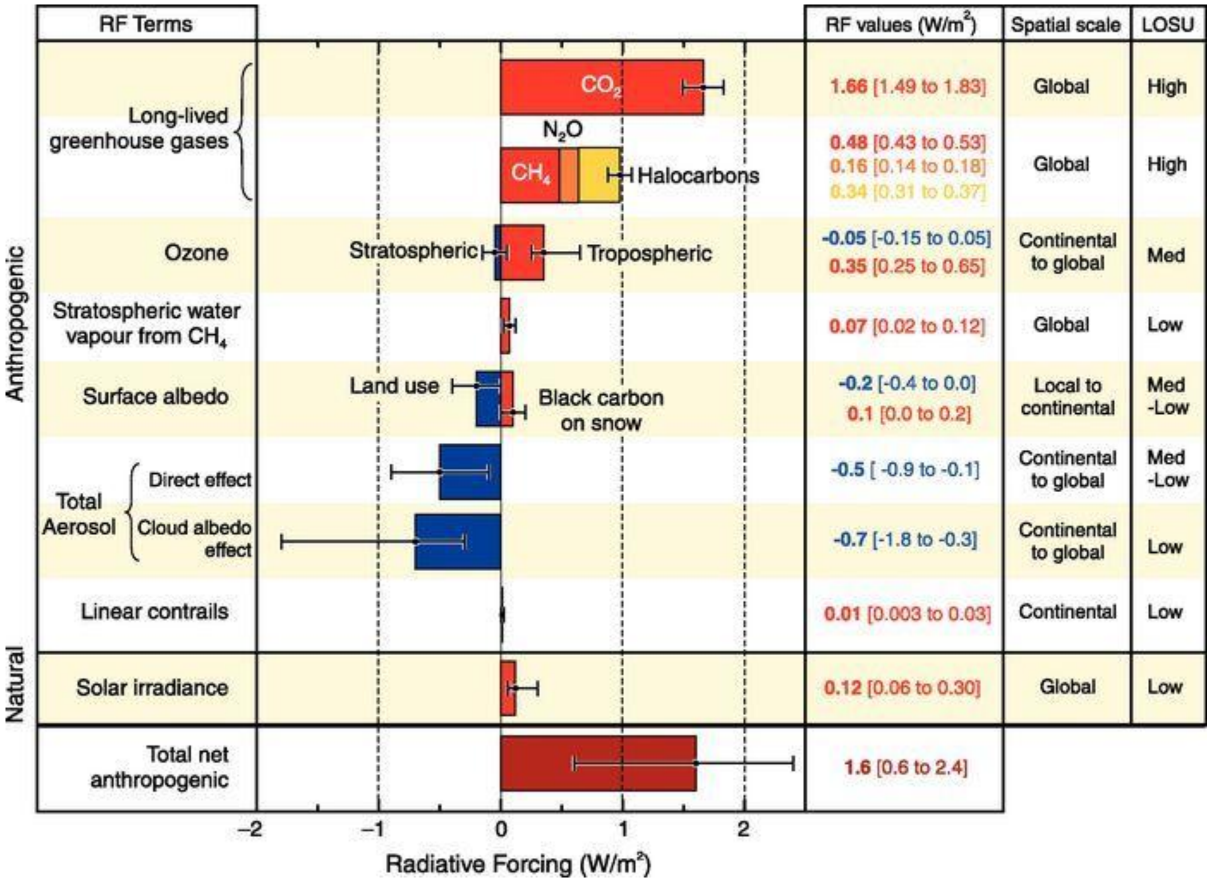


Figure 1.1. Global average radiative forcing (RF) components in 2005 compared to 1750 (pre-industrial) for carbon dioxide, methane and nitrous oxide. LOSU means level of scientific understanding (IPCC, 2007).

Gas	Concentration in 2005	Change in concentration since 1998	Radiative forcing (Wm^{-2})	Change in radiative forcing since 1998 (%)
Carbon dioxide	379 ppm	13 ppm	1.66	13
Methane	1774 ppb	11 ppb	0.48	ND
Nitrous oxide (N_2O)	319 ppb	5 ppb	0.16	11
Montreal gases	ND	ND	0.32	-1

Table 1.1. Some of the greenhouse gases, their change in atmospheric concentration and radiative forcing. Note change between ppm and ppb. ND = no data. Adapted from Solomon *et al*. (2007).

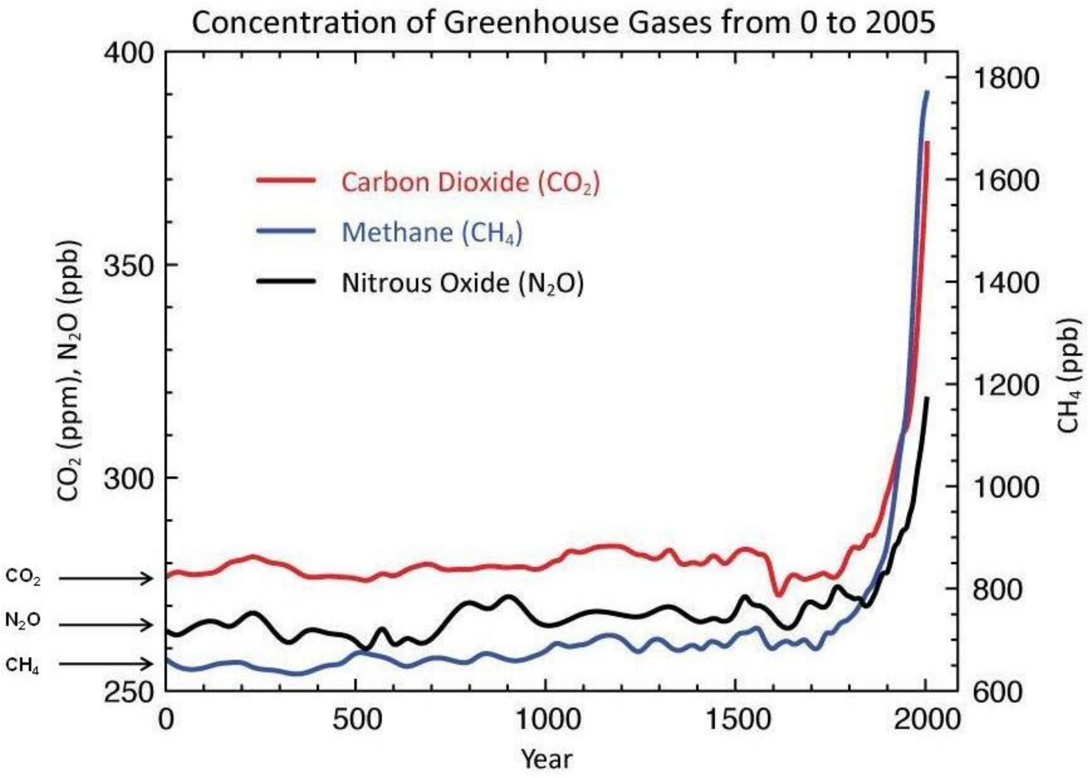


Figure 1.2. Changes in atmospheric concentrations of carbon dioxide, methane and nitrous oxide during the last 2000 years (Solomon *et al*., 2007).

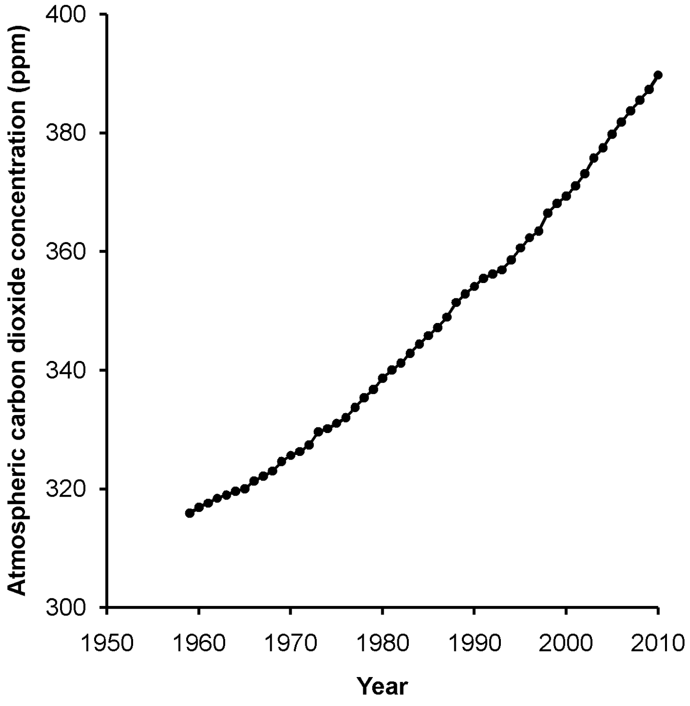


Figure 1.3. Mean annual atmospheric carbon dioxide concentration between 1959 and 2010 at Mauna Loa Observatory, Hawaii. Plotted by AWS using data from Tans and Keeling (2011).

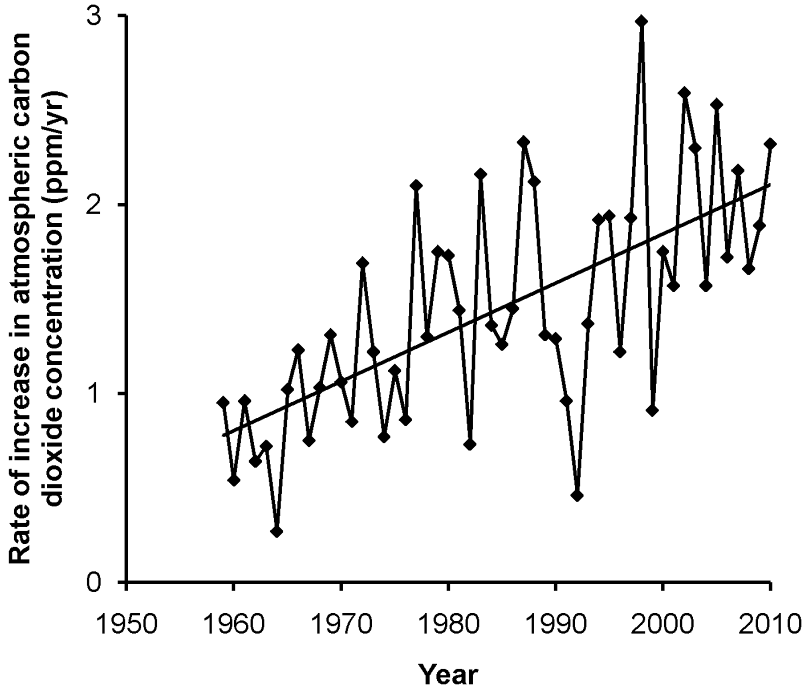


Figure 1.4. Annual rate of increase in atmospheric carbon dioxide concentration between 1959 and 2010 at Mauna Loa Observatory, Hawaii. Graph includes a linear trendline. Plotted by AWS using data from Tans and Keeling (2011).

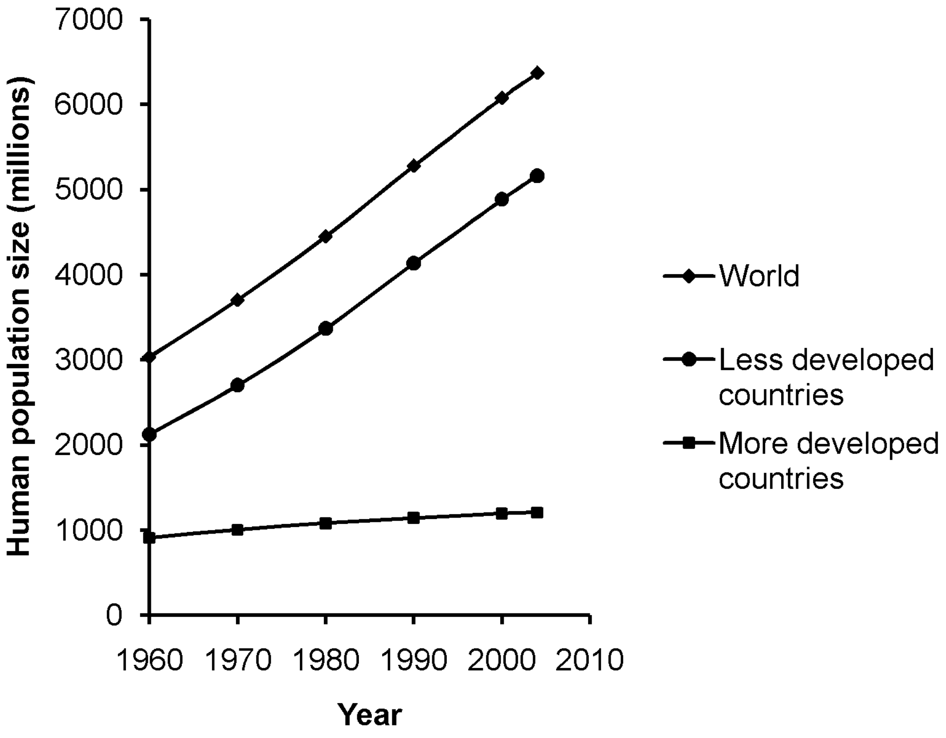


Figure 1.5. Human population growth for the World, less developed countries and more developed countries. Adapted by AWS from National Statistics (2005).

Human population size is increasing rapidly (Figure 1.5) and is expected to reach over 9 billion people by 2050 (United Nations Population Division, 2009), which would be a 50% population growth in 45 years, although the rate of growth may slow during the 21st century (US Census Bureau, 2011). The increase in atmospheric carbon dioxide concentration is associated with human population growth (Figures 1.2, 1.3, 1.4 and 1.5). Most of the population growth is in less developed countries, and as the populations of some of these countries gain in wealth, they may buy more fossil fuel powered products, such as cars, and also use more nitrogenous fertilisers for agriculture, so it is likely that the atmospheric concentration of greenhouse gases will continue to increase.

It is difficult to see any credible means of controlling greenhouse gas emissions with such a large predicted population increase. Trenberth (2011) suggests that the actions needed to ‘decarbonise the economy’ are so ‘revolutionary as to be highly unlikely to be achieved’ and Lovelock (2006), suggests that working to control the quality of the atmosphere suitable for life would be difficult and could become impossible. Melton (2011) is slightly more positive, suggesting that the use of renewable energy sources would increase if they were cheaper than fossil fuels, and that to achieve this financially would require economies of scale. ‘Health co-benefits’ might in part compensate for the costs of dealing with climate change. For example, healthcare costs could be reduced by more cycling and walking which would reduce the number of patients with heart disease and more fuel efficient stoves would reduce premature deaths from air pollution in India (Ganten *et al*., 2010; Roberts and Stott, 2010).

1.5 Aerosols

Atmospheric aerosols can be naturally present in the atmosphere (e.g. sea salt or dust) or be of anthropogenic origin (e.g. soot, or black carbon produced by combustion) and they can affect the amount of energy passing through the atmosphere by reflecting or absorbing radiation or by acting as condensation nuclei, thereby causing cloud formation. These clouds can then reflect radiation back into space and change precipitation patterns. So while some aerosols reduce, and some increase, radiative forcing, the overall effect of all aerosols is to reduce radiative forcing. However, the pattern can be complex as aerosols are much less equally distributed around the World and can be removed from the atmosphere much more quickly than greenhouse gases (Earth System Research Laboratory, 2011). Lovelock (2006) comments that aerosol pollution is keeping the Earth cool by reflecting solar energy, but that this is dependent on pollution sources and is a transient protection from extreme heat, with the potential to disappear relatively quickly – he suggests in days – if the pollution sources are removed.

Atmospheric black carbon is an aerosol that has the effect of absorbing solar energy and causing warming (Earth System Research Laboratory, 2011). In Lithuania, atmospheric black carbon was found to be more concentrated during the period October to April due to domestic heating, although black carbon also comes from road traffic and wildfires (Bycenkiene *et al*., 2011). Atmospheric black carbon has been decreasing in the UK since the 1960s, in part due to less domestic coal fires, although since the 1990s this decrease has been partly offset by increasing use of diesel cars (Novakov and Hansen, 2004). Therefore the atmospheric concentration of black carbon varies with time, both on an annual and a multi-decadal pattern, and as a result radiative forcing will change. Will future changes in black carbon concentrations result from the introduction of diesel particulate filters in car exhausts and will this slightly reduce the rate of climate change?

Aerosols can have other ecological effects. For example, Chameides *et al*. (1999) showed that in China aerosol haze can reduce solar radiation reaching crop plants, reducing yield by between 5 to 30%. Air quality control might increase agricultural production to meet the increasing demand for food, but improved air quality could increase the rate of local climate change, as less heat would be reflected.

1.6 The projected scale of global climate change

Climate change is expected to result in different temperature increases in different locations during the 21st century: the Atlantic and Pacific oceans are expected to increase by up to 4°C; most continental areas (Europe, Asia, Africa, USA and Antarctica) by 4-8°C; the tundra area of northern Canada and Russia increasing by

8-10°C; the Arctic Ocean by 10+°C. The tropical rainforest area of Brazil in the River Amazon basin is also predicted to increase by 10+°C (Hadley Centre, 2003, reproduced in Gregory, 2011). As this is an area of high species diversity, including insect diversity, the consequences might be severe. High temperature increases are predicted for Arctic areas, partly due to snow and sea ice melting (Perovich and Richter-Menge, 2009), as demonstrated by a record minimum sea ice extent in 2007 (Turner and Overland, 2009) and therefore reduced albedo (Notz, 2009), so less heat will be reflected. Stendel *et al*. (2008) predict that specific areas along the eastern coast of Greenland will increase by 18°C as a result of the retreat of sea ice.

Temperature change on this scale may have serious ecological and humanitarian consequences (Lowe *et al*., 2006). Bale and Hayward (2010) suggest that climate change could raise summer temperatures in Europe to 40+°C in 50-75 years, which is close to the upper lethal temperature limit for some insects. Lovelock (2006) presents an extreme example, suggesting that climate change will turn large areas of tropical land into scrub and desert, so reducing land available for food production. This scenario might lead to a grim situation of attempting to keep agriculture going as long as possible, followed by a societal breakdown and then 80% of the World's human population dying by the end of the 21st century (J. Lovelock quoted in Aitkenhead, 2008). A considerable reduction in the human population has the potential to reduce further emissions of greenhouse gases and allow the restoration of ecosystems, although Lovelock (2006) says the recovery might be slow, with a timescale of 100000 years.

1.7 Climate change in the UK

Figure 1.6 shows how mean annual temperature has increased in the UK from about 9.1°C in 1900 to about 10.3°C in 2009. The trend has not been constant throughout this time period, with considerable annual variation and a period of cooling during the 1950s and 1960s, which might have been due to aerosol pollution. Temperatures are expected to continue to increase, with Woodward *et al*. (2010) giving a range of mean annual temperature rises for Ireland, starting in the year 2000 with a mean of approximately 9.6°C, then rising to between 10.5°C and 17°C by 2100 based on a range of atmospheric carbon dioxide concentrations between 520 ppm and 920 ppm.

These different carbon dioxide concentrations are based on different predictions of human population growth, economic growth and use of clean technologies. The temperature increase predictions in Woodward *et al*. (2010) are corroborated by Solomon *et al*. (2007), who predict that northern European temperatures will increase by between 2 and 6°C by 2100.

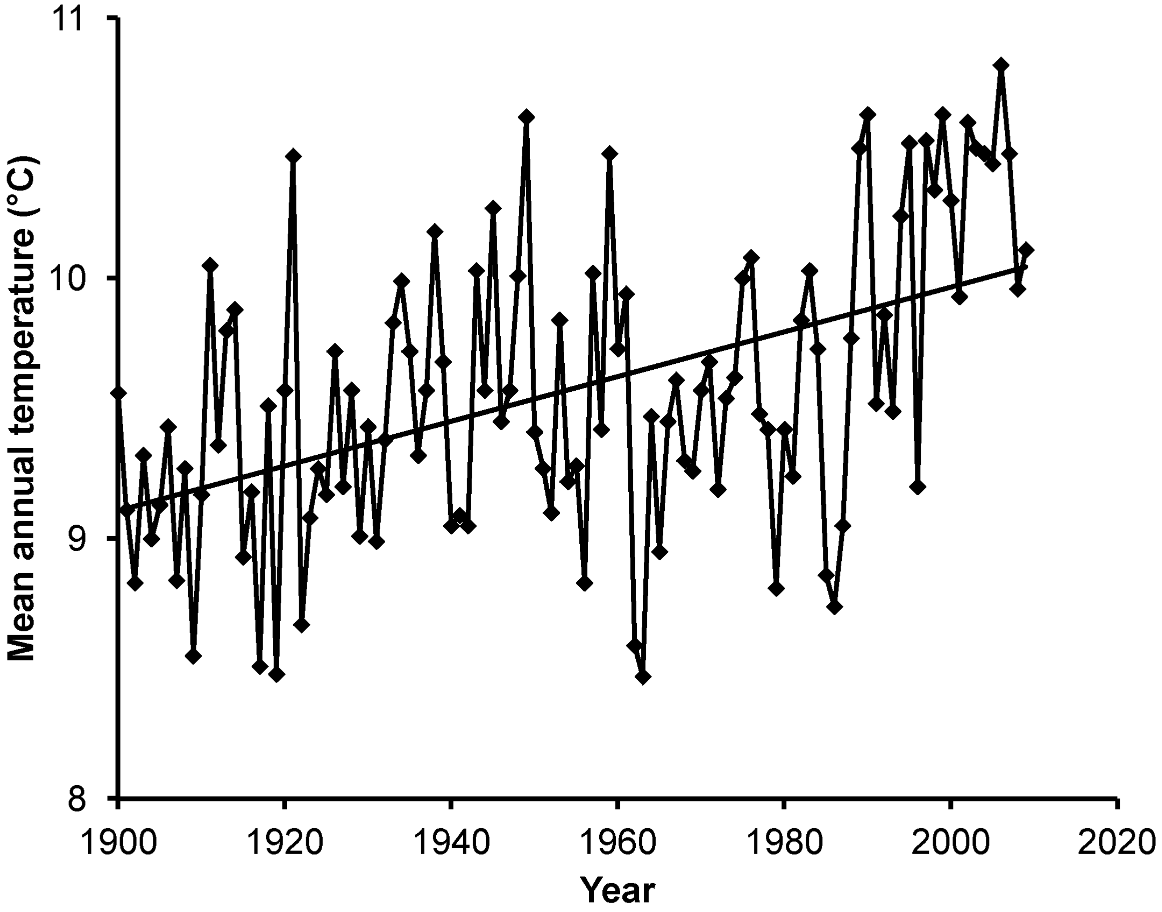


Figure 1.6. Mean annual temperature rise in England between 1900 and 2009 (r^2 = 0.2371, *r* = 0.480, *P* = <0.001) Plotted by AWS from Central England Temperature Series data.

1.8 The North Atlantic Oscillation

The North Atlantic Oscillation (NAO) has a considerable influence on the weather over a large geographical area (Figure 1.7) covering the North Atlantic, Scandinavia, the Mediterranean basin, North Africa, North America and Greenland (Mehta *et al*., 2000 and Nesje *et al*., 2000). The NAO affects the flow rate of the Euphrates and Tigris Rivers (Cullen and deMenocal, 2000) and the Indian monsoon (Kakade and Dugam, 2000).

The North Atlantic Oscillation is described by the NAO index, which is calculated from air pressures in Iceland and a location within the Azores high pressure region. The southern pressure data can come from the Azores, Lisbon or Gibraltar, with the exact choice of location being of little importance (Osborn, 2000). The present study uses NAO indices from the Climate Research Unit (CRU) at the University of East Anglia, UK (Climate Research Unit, 2004 and Osborn, 2010). CRU NAO indices are calculated from air pressure data from Iceland and Gibraltar (Climate Research Unit, 2004).

A positive NAO index is associated with depression systems taking a more northerly route across the Atlantic, resulting in warmer and wetter autumn and winter weather in the British Isles, whereas a negative NAO index is associated with the depression systems travelling along a more southerly route across the Atlantic, resulting in colder and drier conditions in north-west Europe (Hurrell, 1995 and Osborn, 2000). During high, positive, NAO index winters the westerly winds in Europe are over 8 ms^{-1} stronger than low NAO index winters (Hurrell, 1995). Weaker westerly winds associated with a negative NAO index allow colder northerly winds to dominate over northern Europe (Edwards *et al*., 2001).

The NAO causes contrasting weather in different regions, so a positive NAO index is associated with wet weather in north-west Europe and relatively dry weather in the Mediterranean, and a negative NAO index results in the UK being drier, but the Mediterranean wetter. A negative NAO results in cold weather in northern Europe, and south-east USA and warm weather in southern Greenland. Therefore there are oscillations in weather between both sides, and between higher and lower latitudes, on both sides of the North Atlantic (Figure 1.7).

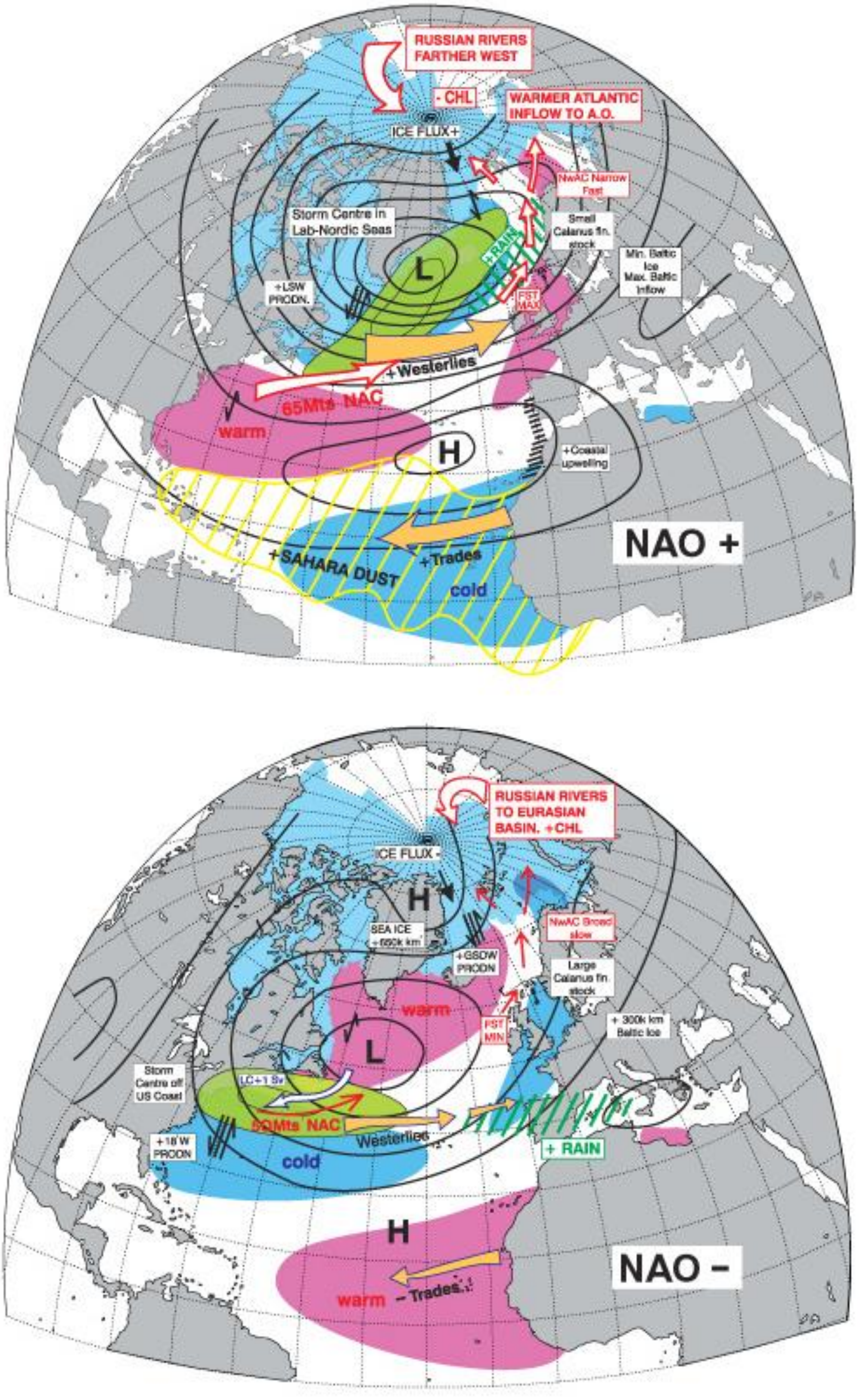


Figure 1.7. Meteorological effects associated with a positive (NAO+) and a negative (NAO-) NAO index. (Provided to AWS in 2002 by S. Leroy. Originally from CLIVAR, Climate Variability & Predictability, World Climate Research Programme).

1.9 Calculation of the NAO index

1.9.1 Calculation of monthly NAO indices from air pressure data

The CRU NAO index is calculated using monthly average air pressures in Gibraltar and Iceland. T. Osborn of the Climate Research Unit at the University of East Anglia gave me instructions on this calculation. I have used this equation to calculate monthly NAO indices from monthly air pressure data, and confirmed that the calculations were correct by checking the calculated NAO indices with the published NAO indices.

$$\text{NAO index} = PG_{\text{normalised}} - PI_{\text{normalised}}$$

$$\text{NAO index} = \left(\frac{PG - PG_{\text{mean}}}{PG_{\text{SD}}}\right) - \left(\frac{PI - PI_{\text{mean}}}{PI_{\text{SD}}}\right)$$

PG = Mean air pressure for any one specific month in one specific year.

$PG_{\text{normalised}}$ = Gibraltar normalised air pressure for any one specific month in one specific year.

PG_{mean} = Gibraltar mean monthly air pressure for the years 1951 – 1980. Calculated for January, February, March, etc.

PG_{SD} = Gibraltar standard deviation of monthly air pressures for the years 1951 – 1980. Calculated for January, February, March, etc.

PI, $PI_{\text{normalised}}$, PI_{mean} and PI_{SD} are the same as for PG, but instead of Gibraltar they refer to Iceland, hence the letter ‘I’ instead of ‘G’.

1.9.2 Calculation of seasonal NAO indices

It is possible to calculate NAO indices for any group of months or a year. The most useful NAO indices are the winter NAO index calculated as a mean of the NAO indices for January, February and March and the extended winter NAO index for December, January, February and March. The winter NAO index has the advantage that it avoids temporal overlap of data in calculations – for example, a correlation calculated between the extended winter NAO index and mean annual temperature data, where the December NAO index involved in calculating the extended winter NAO index describes the NAO that is controlling temperature in December of the previous year.

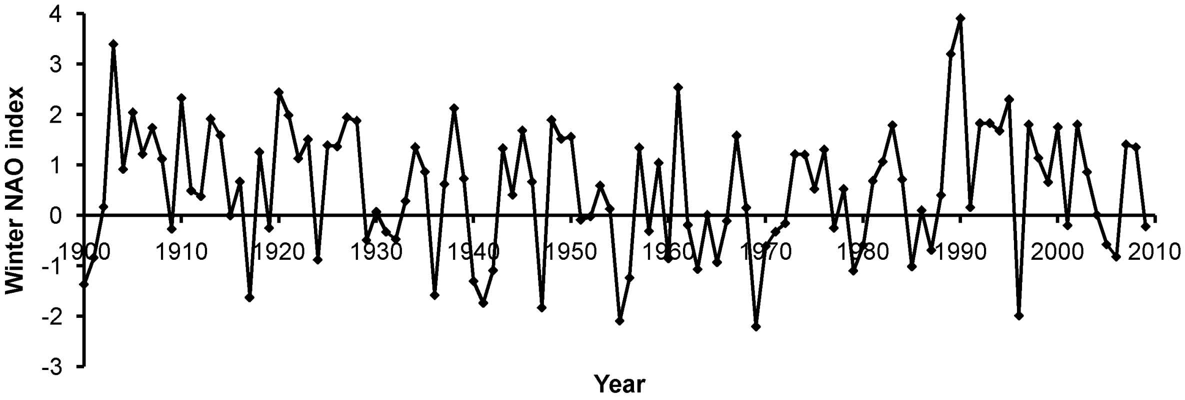


Figure 1.8. The winter NAO index between 1900 and 2009.

Figure 1.8 shows the winter NAO index between 1900 and 2009. Edwards *et al*. (2001) suggest that 'a large part' of the warming trend during the 1990s was due to the winter NAO index becoming more positive rather than just due to an increase in greenhouse gases. There is also evidence that temperatures were lower (Figure 1.6) during the period 1960 to the late 1980s, when the winter NAO index was lower. However during the period 1900-1930, temperatures were lower than during the period 1990-2009, although the NAO was approximately the same, so it appears that there is an interaction between climate change and the NAO in influencing temperature.

Figure 1.9 shows the association between the winter NAO index and mean annual temperature from the Central England Temperature Series, with more positive NAO indices associated with higher temperatures. During the period 1900-2009, the winter NAO index was associated with 21.8% of the variability in temperature. Coefficients of determination (and correlation coefficients) are vulnerable to changes in the time window examined, with the percentage of the variability in temperature associated with the winter NAO rising to 30.2% for the period 1966-2009, which is the range of years used in the present study. For comparison, a coefficient of determination for changing temperature with time (Figure 1.6) used as a proxy for climate change is 23.7% for 1900-2009 and 39.1% for 1966-2009. Therefore both climate change and the NAO have a considerable influence on temperature, with the NAO having a *relative* affect to climate change of about 77-92%.

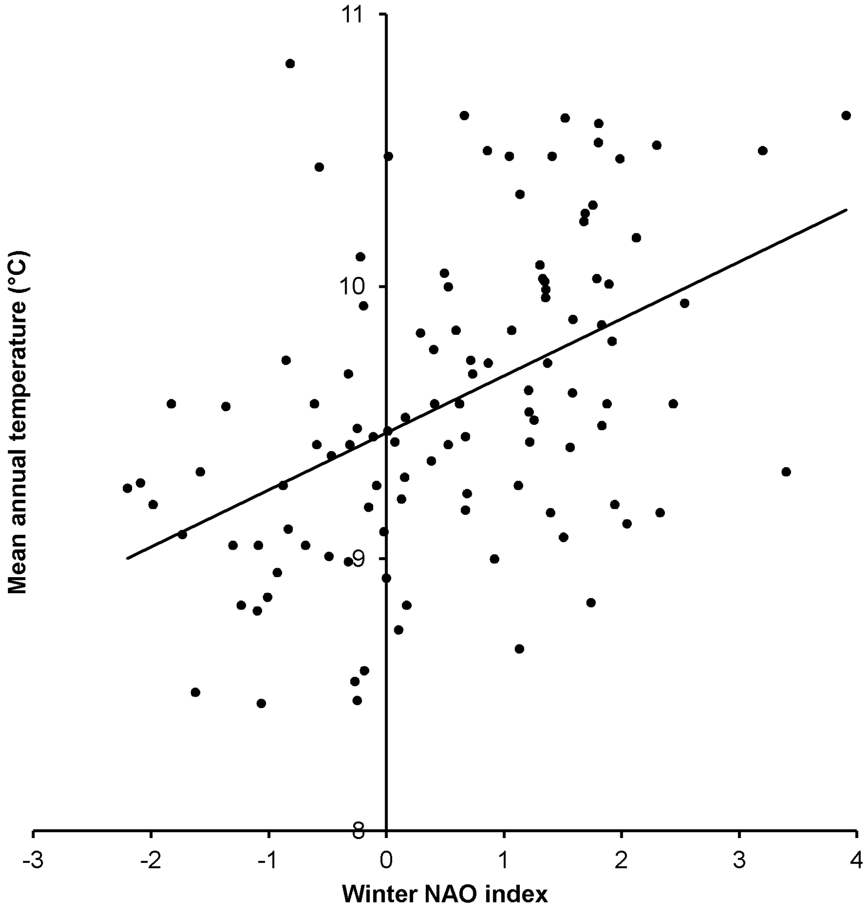


Figure 1.9. Mean annual temperature from the Central England Temperature Series plotted against the winter NAO index. Data for the years 1900-2009. (r^2 = 0.2178, *r* = 0.467, *P* = <0.001).

1.10 The effect of climate change on organisms

1.10.1 Climate change and insects

Climate change appears to be affecting the flight phenology of social hymenoptera. Sparks *et al*. (2010) have investigated changes in the timing of honeybee (*Apis mellifera* L.) first cleansing flight (when faeces are removed) in Poland. During the period 1985 to 2009, the timing of the first cleansing flight advanced by over one month. An earlier first cleansing flight was associated both with higher January to March temperatures and higher June to September temperatures in the previous year. Higher temperatures during the previous summer result in larger colonies which stay warmer during the winter, which means that brood rearing can occur and more food is consumed, resulting in more faecal waste that needs eliminating sooner. Tryjanowski *et al*. (2010) investigated the influence of climate change on two social wasps – *Vespula germanica* (Fabricius) and *V. crabro* (L.) – and found that *V. germanica* workers appeared up to 26 days earlier over the period 1981 to 2009, but *V. crabro* workers and queens of both species had not advanced their flight dates. Explanations for the different responses to temperature increases may include sex-specific cooling mechanisms, as well as a role of light intensity in controlling wasp activity. There was also some evidence that warmer weather in April caused an earlier flight season, but higher precipitation in April delayed the flight season.

Aphids are a group of insects that are especially well studied as many of them are agricultural pests. Climate change is causing the green peach aphid (*Myzus persicae* Sulzer) (Harrington *et al*., 2007) and the green spruce aphid (*Elatobium abietinum* Walker) (Westgarth-Smith *et al*., 2007), to fly earlier. Climate change may lead to increases in aphid pests of *Ribes* (L.) crops in the UK, through increased over-wintering survival and longer seasonal activity, a problem which may be exacerbated by increased cropping densities and stricter pesticide restrictions (Mitchell *et al*., 2011). Increased atmospheric carbon dioxide concentrations can influence insect herbivory of plants, including by increasing the carbon to nitrogen ratio (Holopainen, 2002). Hence, cotton aphids (*Aphis gossypii* Glover) produce more honeydew in a higher carbon dioxide environment, as they need to ingest more phloem sap to obtain sufficient amino acids (Sun *et al*., 2009). The Chinese lacewing (*Chrysopa* *sinica* Tjeder) is a predator of *Aphis gossypii* and higher carbon dioxide concentrations affect *C. sinica* by increasing the larval development rate and reducing predatory ability (Gao *et al*., 2010).

A mountain species can be trapped by altitude, as they may be unable to move northwards to track climate change because the low lying areas between the mountains are too warm, and becoming warmer. If insects are unable to move to track climate change, then factors that enable them to thermoregulate and survive the temperature increase become important (Turlure *et al*., 2010). Vegetation type can have a role in maintaining a constant thermal environment, for example hummocks of *Sphagnum* (L.) moss are used in Belgium by the glacial relict cranberry fritillary butterfly (*Boloria aquilonaris* Stichel), which has reduced larval survival at higher temperatures. Hummocks of *Sphagnum* are more thermally buffered than *Polytrichum* (Hedw.) moss. The surface temperature of both species of moss ranged from 5°C to 30°C through the day, but at 30 cm depth, *Sphagnum* provided a stable thermal environment of 12°C, whereas at 30 cm depth under *Polytrichum* the temperature ranged from 8-18°C. It appeared that the larvae were more abundant in *Sphagnum* hummocks that were more thermally buffered. Thermal buffering was higher in more humid conditions and lower nearer trees, because trees resulted in drier conditions. Peat bogs can gradually change into heathlands through succession, and this process might accelerate as a result of climate change. Climate change may require the butterfly larvae to go further into the hummocks, as thermal buffering will decrease due to less water as well as ambient temperatures increasing. Therefore habitat management to maintain populations of *B. aquilonaris* would involve maintaining early successional stages that are relatively wet (Turlure *et al*., 2010). This example illustrates the complex associations between climate change and responses of animals to that change. These responses may not be easy to predict with any degree of confidence.

Mountains are good environments in which to investigate the effects of climate change, as changes in temperature with altitude can act as models for climate change. The mountain specialist butterfly, *Parnassius apollo* (L.), uses more open habitats at higher altitudes in mountains in central Spain as open microhabitats were warmer, and this compensates for the lower temperatures found at higher altitude.

Climate change may cause habitat heterogeneity to be important for the conservation of *P. apollo*, as it will provide greater opportunities for larval thermoregulation as well as protecting against changes in food plant availability. Increasing altitude also caused a 5.3 – 7.0 day delay in phenology per 100 m increase in altitude (Ashton *et al*., 2009). Wilson *et al*. (2005) have shown that the lower elevational limit for 16 Spanish mountain butterfly species has risen by an average of 212 m in a 30 year period. During this 30 year period, the temperature increased by 1.3°C, which was equivalent to an altitude increase of 225 metres. This increase in altitude reduces the area of land available to the butterflies by about a third, with the prediction of a 50-80% loss during the 21st century.

There is an association between altitude and the number of generations that an insect is able to complete. *Rhagoletis pomonella* (Walsh) (the apple maggot, Diptera: Tephritidae) is a pest of apples in the Southern Appalachian Mountains in Carolina, USA. At altitudes of more than 630 metres, *R. pomonella* was univoltine, with most of the adult activity restricted to two months, whereas at altitudes of 300 metres *R. pomonella* was bivoltine, with adults active for five to six months (Meck *et al*., 2008).

Butterfly mating behaviour is temperature sensitive, so climate change may cause important behavioural changes. For example, male small copper butterflies (*Lycaena phlaeas daimio* L.) in Japan use both patrolling and perching mate-location strategies. Patrolling involves flying over a large area searching for females, whereas perching involves remaining stationary and waiting for a female to fly past. Patrolling was more common in high light intensity conditions, whereas perching appeared more independent of environmental conditions, so the chasing of insects increased when light intensity was highest. In cool weather the thoracic temperature of patrolling males was lower than perching males, so it appears that patrolling can increase heat loss whereas perching allows for easier heat regulation through basking. Although patrolling is used by males less frequently in colder weather, it can also become a more successful mating strategy as colder weather reduces the flight activity of females, so a perching male may encounter less females than a patrolling male (Ide, 2010). Consequently, climate change might result in patrolling behaviour being a more frequent mate finding strategy than perching.

More butterflies have the northern limit of their distribution in the UK - there are only four British butterfly species that have the southern limit of their geographical range in the UK, and therefore might decline as climate change causes the southern limit of their range to move northwards or increase in altitude. These species are the large heath (*Coenonympha tullia* Müller), Scotch argus (*Erebia aethiops* Esper), mountain ringlet (*Erebia epiphron* Knoch) and northern brown argus (*Aricia artaxerxes* Fabricius). Although all four species have declined due to habitat loss, only the Mountain Ringlet has disappeared from low altitude sites while remaining present at high altitudes (Thomas, 2010).

Isaac *et al*. (2011) have attempted to predict the abundance of UK butterfly species in 2080 by assuming that UK temperatures increase by 2.8°C in northern England and 3.6°C in southern England. They predicted that out of 45 butterfly species, 9 species would increase in numbers and 36 species would decline, with over half the species declining by more than 50%. They also suggest that the total number of butterflies will increase by 21%, with the meadow brown (*Maniola jurtina* L.) likely to make up half of all butterflies recorded by the UKBMS as a result of a predicted 68% increase in abundance. In contrast, Roy *et al*. (2001) suggested that climate change will result in only one species declining - the large white (*Pieris brassicae* L.) – and other species increasing or remaining stable, but Isaac *et al*. (2011) suggested that *P. brassicae* will increase by 15.8%. Therefore the most important message from both Roy *et al*. (2001) and Isaac *et al*. (2011) seems to be that butterfly population changes due to climate change are likely, and could be considerable, but that predicting which species will benefit, and which will not, is currently difficult. Potential sources of discrepancy include Isaac *et al*. (2011) using data for just England whereas Roy *et al*. (2001) used data for all of Britain - although there are relatively few UKBMS sites in Scotland and Wales. There were also different time windows in the two studies, with Roy *et al*. (2001) using fifteen years of data from 1976-90 and Isaac *et al*. (2011) apparently basing their analysis on five years of data from 2002-2006. It is also arguable that both papers are trying to analyse too many species without looking closely at the biology of individual species. Furthermore, neither paper considered habitat changes associated with changing climate.

Distribution maps plotted using NBN Gateway data (National Biodiversity Network, 2011a) can be used to show changes in distribution due to climate change. Species with a nationwide distribution need more than about 300000 records to form a clear map (pers. obs.), although species with a more restricted distribution can be plotted with less data. For example, the northern range boundary of the comma butterfly (*Polygonia c-album* L.) in the UK has moved northwards, probably in response to climate change (Figure 1.10). However, an associated increase in population size may not occur if there has also been a decrease in habitat quality. For example, Asher *et al.* (2001) say that the large skipper butterfly (*Ochlodes venata* Bremer and Grey) has increased in range, but there has been a decline in the area of suitable habitat within this range, due to agricultural intensification and hedgerow removal, with a reduction in suitable flight area for *O. venata* in Wales by over 70% since 1901.

However, not all species appear to move geographically to track climate change. For example, the black hairstreak butterfly (*Satyrium pruni* L.), which has a very restricted distribution in the UK, has not shown a distributional change that might be associated with climate change although there has been a decrease in the number of sites (Figure 1.11). This suggests that there is a considerable variation in the ability to move and track climate change between butterfly species, which might make *S. pruni* more vulnerable to extinction than *P. c-album*. Lawton *et al*. (2010) point out that not all species will be able to move at the same rate that weather patterns move, due to limits in their dispersal ability, geographical barriers or because other organisms which act as food sources or breeding sites are unable to keep pace with climate change.

Therefore, each species has a range of climatic conditions that it can live within, and hence as the climate changes the species may either move to remain within the right climatic conditions or if they cannot move, they could become endangered or extinct as the climate becomes unsuitable. Parmesan (2008) points out that this creates an important practical conservation issue as it is quite possible that many nature reserves will no longer have the climate conditions for the species that they were originally established to conserve and ‘a nation’s carefully planned reserve system will not work as intended’.

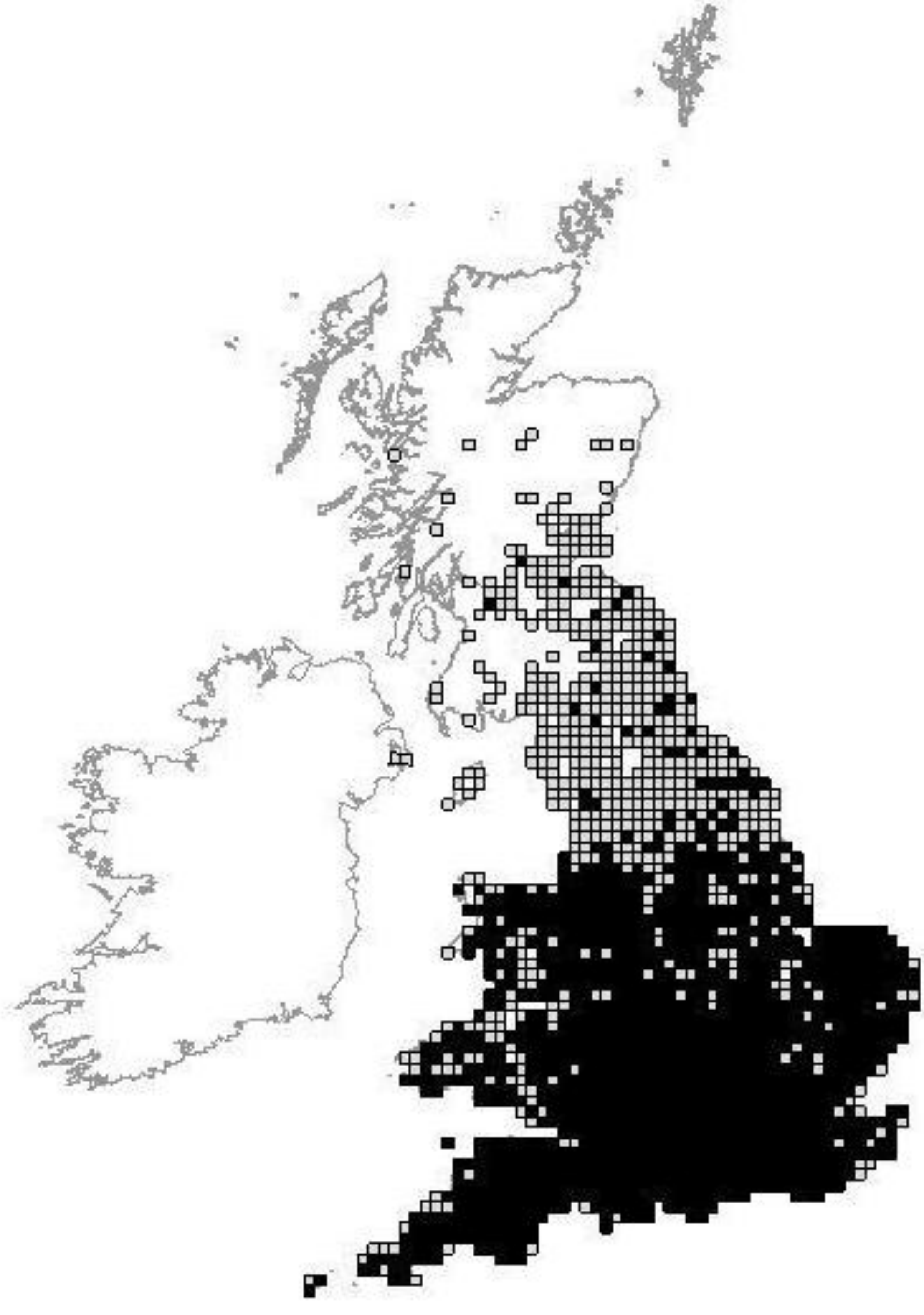


Figure 1.10. The apparent effect of climate change on the distribution of the comma butterfly (*Polygonia c-album*) at a 10 km square resolution in Great Britain and Ireland. Black squares are all records up to 1990 and grey squares are all records up to 2011. Illustration prepared by AWS using data from the NBN Gateway (National Biodiversity Network, 2011a). © Crown copyright. All rights reserved NERC 100017897 2004.

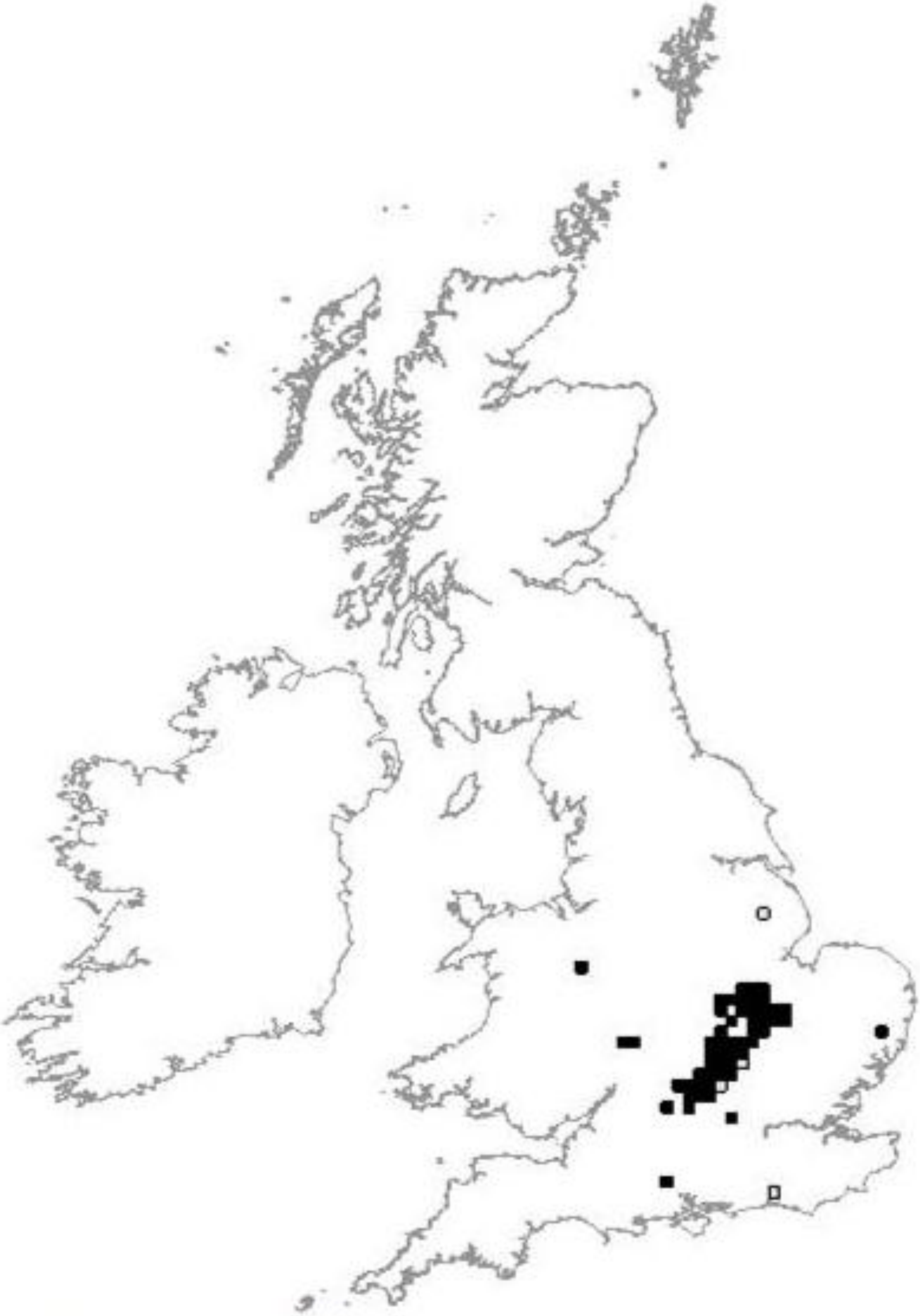


Figure 1.11. The distribution of the black hairstreak butterfly (*Satyrium pruni*) at a 10 km square resolution in Great Britain and Ireland. Black squares are all records up to 1990 and grey squares are all records up to 2011. Illustration prepared by AWS using data from the NBN Gateway (National Biodiversity Network, 2011a). © Crown copyright. All rights reserved NERC 100017897 2004.

1.10.2 Climate change and other organisms

Climate change affects the phenology, or timing, of biological events. Climate change has resulted in the advance of the timing of the spring migration of eight wading bird species in the Czech Republic and Slovakia. However, changes in the timing of the autumn migration was more variable with three species advancing their migration, three species delaying their migration and two species did not change the timing of their migration (Adamik and Pietruszkova, 2008). Todd *et al*. (2011) show that a 1.2°C increase in night-time temperatures associated with climate change is affecting the time of breeding of amphibians in South Carolina, USA, with two autumn breeding species now breeding later and two winter breeding species now breeding earlier, with phenological change in the range 5.9 to 37.2 days in one decade. Climate change appears to influence different groups of organisms by different amounts, with trees advancing their phenology by about 3 days per decade, invertebrates, amphibians and birds advancing by 4-6 days per decade, and zooplankton 7-8 days per decade (Richardson, 2008), with the potential to cause a mis-timing of biological events (Thackeray *et al*., 2010), for example associations between a predator and its prey.

There is a debate over whether climate change is (Aars and Ims, 2002), or is not (Brommer *et al*., 2010), preventing a 3-4 year cyclicity (Hornfeldt, 2004) in the population size of small mammals in Scandinavia. Aars and Ims (2002) suggest that a mechanism for climate change to negatively affect small mammal populations was for the ground to be covered by ice due to alternate melting and freezing in warmer winters rather than snow cover. Ice reduces insulation, access to food and causes flooding during the spring thaw. Hornfeldt (2004) discusses several other factors that might cause the loss of the cyclical pattern, including the decline of the red fox (*Vulpes vulpes* L.) due to the spread of the disease sarcoptic mange (*Sarcoptes scabei* De Geer). Although foxes eat small mammals, the small mammal population did not increase when the fox population declined, because foxes also eat stoats (*Mustela erminea* L.) and weasels (*Mustela nivalis* L.), both of which are more efficient predators of voles than foxes, so as stoats and weasels increased in numbers, the vole numbers decreased.

The magnitude of climate change is expected to vary geographically and therefore have a different magnitude of effect on species depending on where they live. For example, climate change is expected to be more pronounced in Arctic regions than elsewhere (Stendel *et al*., 2008), which may be detrimental to the Pacific walrus (*Odobenus rosmarus divergens* L.) (Jay *et al*., 2011). Polar bears (*Ursus maritimus* Phipps) may need to swim further to reach ice, if ice recedes, although this species is capable of swimming huge distances. A radio-tracked polar bear has been recorded swimming continuously for 687 km over 9 days, although this involves high energetic costs, may reduce reproductive fitness (Durner *et al*., 2011) and makes bears vulnerable to drowning in stormy conditions (Monett and Gleason, 2006). One response to climate change might be to relocate species to areas where their habitat may still exist, although introducing organisms to an area where they do not normally live can have negative ecological consequences. Parmesan (2008) suggests that the polar bear could be introduced into Antarctica as sea ice is being lost there at a lower rate than in the Arctic, but points out that penguins might be particularly vulnerable to increased predation as they are not adapted to defend themselves against terrestrial predators, because they cannot fly.

Climate change can interact with organisms through their parasites and symbionts. Fasciolosis is a parasitic disease of sheep and cattle caused by the liver fluke (*Fasciola hepatica* L.), which reduces growth, economic productivity and can be fatal. The area of Britain where Fasciolosis occurs has increased during the period 1970 to 2000, possibly associated with climate change, and if trends continue there might be serious epidemics from about 2020. However, predictions of infection rates are not straightforward. There is a relationship between both temperature and precipitation as droughts can dessicate and kill both *F. hepatica* and its intermediate host, a freshwater snail, *Lymnaea truncatula* (Müller), reducing the infection risk, but also drought conditions can force livestock to feed in damp areas where the infection risk is higher (Fox *et al*., 2011). Climate change can effect gut symbionts in two stink bug species, *Acrosternum hilare* (Say) and *Murgantia histrionic* (Hahn). These symbionts live normally at 25°C but disappear or die within two generations at 30°C, reducing the fitness of the host and causing a lower stink bug population growth rate (Prado *et al*., 2010).

Climate change also affects plants. Fitter and Fitter (2002) have shown that the first flowering dates of 385 British plants advanced by 4.5 days in 10 years during the 1990s and 16% of these plant species advanced their flowering date by 15 days in one decade. Annual species were more likely to flower earlier than perennials and insect pollinated species were more likely to flower earlier than wind pollinated flowers. Sparks *et al*. (2011) show that botanical phenology in the spring has advanced and botanical phenology in the autumn has become later as a result of climate warming. Sparks and Carey (1995) have used 211 years of data from the Marsham phenological record to predict that an increase in winter temperature of 3.5°C accompanied by an increase in temperature in spring, summer and autumn of 3°C and a 10% increase in rainfall would cause the flowering dates of four British plants to advance by 20-25 days and the leafing dates of 13 tree and shrub species to advance by 13-24 days. Importantly, Sparks and Carey (1995) are trying to compensate for climate change affecting the seasons by different amounts and affecting both temperature and precipitation. Unusual winter warming events on sub-Arctic heathland can cause a reduction in berry production, root growth and more than a 50% increase in shoot mortality and more than 50% reduction in gross primary production of dwarf shrub species such as *Empetrum hermaphroditum*, *Vaccinium vitis-idaea* (L.) and *Vaccinium myrtillus* (L.). Arctic areas are warming faster in winter than in the summer, so climate change might have serious consequences for these plant species, and possibly also birds which eat the berries (Bokhorst *et al*., 2011).

1.11 The effect of the NAO on organisms

The NAO has advantages as a measure of weather parameters that might influence the ecology of organisms as it is a "multi-month average that holds information on rainfall, wind speed and temperature", whereas monthly meteorological data may be too precise to describe the ecological event (Hallett *et al*., 2004) and fail to take into consideration the range of meteorological variables acting together on an organism.

1.11.1 The NAO and invertebrates

Zooplankton biomass during the spring and early summer in the Baltic Sea was found to be higher following positive NAO (mild) winters (Hansson *et al*., 2010). The population size of the copepod, *Calanus finmarchicus* (Gunnerus), in the North Sea and eastern North Atlantic is linked to the NAO, with the mechanisms including air temperature and wind stress affecting both sea surface temperature and phytoplankton production, which then affect *C. finmarchicus* abundance. *C. finmarchicus* can also affect the population size of *C. helgolandicus* (Claus) through competition (Fromentin and Planque, 1996).

Corals can record fluctuations in climate over considerable periods of time. Oxygen isotope records provided a 245 year record from a coral from the northern Red Sea (Felis *et al*., 2000), and strontium to calcium ratios were used in corals from Bermuda (Cohen *et al*., 2004). In both cases these corals showed evidence of the NAO as well as indicating the considerable geographical area influenced by the NAO. Geological evidence for the NAO has also been found in the thickness of annual bands in stalagmites from NW Scotland, with the change in thickness being linked to changes in precipitation (Proctor *et al*., 2000 and 2002).

There is evidence that the NAO influences the phenology and abundance of the green spruce aphid (*Elatobium abietinum*) (Westgarth-Smith *et al*., 2007) and affects butterfly ecology (Westgarth-Smith *et al*., 2005a, 2005b and 2005c).

1.11.2 The NAO and vertebrates

Warren and Bradford (2010) found that the abundance of four species of plethodontid salamanders (*Desmognathus* spp. Baird) in the Southern Appalachian mountains, USA, is positively associated with the NAO index. The Southern Appalachian mountains are at a similar latitude to parts of North Africa and the Mediterranean, so positive NAO phases result in warmer and wetter winters – that is weather associated with the NAO is in phase with north-west Europe and out of phase with the Mediterranean. These salamanders are completely dependent on gas exchange through their moist skin as they do not have lungs, and perhaps this is why their abundance is higher in wetter years.

The NAO appears to affect the population size of small mammal species in southern Finland (Solonen and Ahola, 2010), with significant and highly significant associations, that were positive for shrews and mice, but negative for bank voles. Significant associations between monthly NAO values rather than seasonal averages suggest that there are “critical periods of time” which may be “species-specific” and “quite short”.

Weather associated with the NAO affects Soay sheep (*Ovies aries* L.) on the island of Hirta, St Kilda, Scotland. After positive NAO index winters, which were characterised by warm, wet and windy weather, sheep were more likely to give birth to one rather than two lambs, which were born earlier with lower birthweights and take longer to reach maturity. However, while positive NAO index years reduced reproductive success, it also resulted in increased adult survival (Forchhammer *et al*., 2001). A more positive NAO index was also found to be associated with lower bodyweight of reindeer (*Rangifer tarandus* Smith) calves in Norway (Weladji and Holand, 2003).

The spring arrival date of short-distance bird migrants to Estonia was strongly linked to the NAO, but this association was much weaker for the long distance migrants (Palm *et al*., 2009). A positive NAO index being associated with an earlier arrival time of spring migrant wader species (Adamik and Pietruszkova, 2008). However, the timing of arrival of migrant birds that fly across the Sahel to the Mediterranean region in the spring is associated with vegetation growth in their over-wintering and passage areas, rather than the NAO and whether they take a western or an eastern route through the Mediterranean (Robson and Barriocanal, 2011). It therefore appears that the arrival time of spring migrant birds into European countries is controlled by both the meteorological and ecological conditions in the countries that they have over-wintered in, flown through and are arriving in. With so many variables involved, there is the potential for a mis-match in timing with ecological conditions in the breeding area.

The NAO has an effect on cod (*Gadus morhua* L.) recruitment in the North Atlantic, but this effect is complex, depends on the location of the population, sea temperature, salinity, oxygen and turbulence and the density of stocks. The demography of the fish stocks is heavily influenced by fishing and this also influences recruitment (Stige *et al*., 2006).

1.12 Atmospheric carbon dioxide and ocean acidification

As well as causing climate change, increased atmospheric carbon dioxide concentration is causing ocean acidification, with a calculated change from pH 8.2 to 8.1 between 1750 (pre-industrial) and 2009. If atmospheric carbon dioxide concentrations continue to rise, then by 2100 there is a predicted change in pH of 0.5 units. There are very few marine insect species, so the effect of ocean acidification on insects is small. However ocean acidification is discussed here as the potential future consequences for the conservation of marine invertebrates and their predators is serious.

Increasing acidity is expected to disrupt the calcification process used by invertebrates such as corals to make coral reefs and molluscs to make shells (Raven, 2005; Parliamentary Office of Science and Technology, 2009). Species that might be affected include the edible mussel (*Mytilus edulis* L.), Pacific oyster (*Crassostrea gigas* Thunberg) (Gazeau *et al*., 2007), *Nucella lamellosa* (Gmelin) (Nienhuis *et al*., 2010) and Sydney rock oyster (*Saccostrea glomerata* Gould) (Watson *et al*., 2009). Changes to mollusc shells are a problem, as Bibby *et al*.

(2007) suggest that thinner shells caused by ocean acidification may increase the predation risk for common periwinkles (*Littorina littorea* L.).

Kawaguchi *et al*. (2011) found that 2000 ppm concentrations of carbon dioxide prevented larval Antarctic krill (*Euphausia superba* Dana) from hatching by disrupting development before gastrulation. It is not clear if Antarctic krill have developed any hardened calcareous structures prior to gastrulation, so perhaps acidification disrupts more physiological processes other than just calcification. The authors predict that sea water carbon dioxide concentration might reach 1400 ppm by 2100. Whales and seals in the seas around Antarctica are dependent on krill for food (Food and Agriculture Organisation of the United Nations, 2012), so a reduction in krill populations could have severe consequences for Antarctic ecosystems.

The effect of ocean acidification can be made worse by other environmental factors. Ocean acidification and increased temperature, both caused by increased atmospheric carbon dioxide concentrations, can combine in effect to cause bleaching, reduced productivity and reduced calcification in corals (Anthony *et al*. (2008). Anthony *et al*. (2011) suggests that corals become vulnerable at carbon dioxide concentrations of 450-500 ppm, which might be during the years 2030-2045. Reduced calcification may make corals more vulnerable to storm damage (Madin *et al*., 2008). Ocean acidification can alter sperm performance in broadcast spawners such as the sea urchin, *Strongylocentrotus franciscanus* (L.), leading to low fertilisation rates, especially in locations where there are low population densities or high water turbulence (Reuter *et al*., 2011).

1.13 Mitigating the effects of climate change

Climate change mitigation is fascinating as it spreads into a range of areas including politics, environmental activism and technological development and it requires interaction with an entire cross section of society, as almost everyone uses fossil fuels and is therefore likely to be involved in the response to climate change. A Royal Society report (Raven, 2005) very bluntly states that carbon dioxide emission reduction needs to happen “now” and involve “all” possible means to “avoid the risk of irreversible damage to the oceans” from acidification, as well as help control climate change. Trenberth (2011) says that a response to climate change should be ‘multifaceted’ requiring ‘mitigation’ including new energy infrastructure, ‘adaptation’ to cope with the consequences of climate change and ‘communication’ with the public.

Lowe *et al*. (2006) suggest that the public is “uncertain about whether and when climate change will occur”, and Weber and Stern (2011) suggest that climate change is ‘challenging’ for the public to understand. For example, in only one month, May 2011, the BBC News web site (www.bbc.co.uk) carried 43 articles relating to climate change, with topics as wide ranging as wind turbines, international electricity cables, ocean currents, food prices and legal action against protestors. Climate change has become a very wide ranging topic for a non-specialist to cope with, so the environmental movement might be more successful in organising campaigns against the effects of increased carbon dioxide concentration on ocean acidification rather than climate change. The message, *carbon dioxide makes the oceans acid which kills corals*, might be quicker and easier for the public to understand rather than the complexities of climate change. For example, Murray (2011) has demonstrated that it is possible to summarise ocean acidification in a 1.25 minute animation.

Whether or not society succeeds in mitigating or even halting emissions of anthropogenic greenhouse gases will have profound effects on global ecology. Mitigation could confound ecological predictions due to changes in the rates of emissions of greenhouse gases and associated weather patterns, which could alter predictions of climate change. The potential ecological costs of failure to mitigate climate change could be very high.

There are international agreements on climate change, such as the Kyoto Protocol of 1997, which allows for emissions trading, also called the carbon market (United Nations, 1998). The Copenhagen Accord 2009 aims to keep the increase in global temperature below 2°C (United Nations, 2010), although does not make it clear what the baseline year is from which to measure this increase. The United Nations Framework Convention on Climate Change 2010, which took place in Cancun, Mexico and resulted in an international agreement for a “Green Climate Fund” to support less affluent countries in financing emission reduction and adaptation. There might be a relevant debate on whether this money should be spent on reducing emissions in the more affluent countries that produce most of the emissions. The United Nations Framework Convention 2011, which took place in Durban, South Africa (United Nations Framework Convention on Climate Change, 2011) and resulted in an international legally binding agreement to reduce emissions of carbon dioxide. The date that this agreement will come into effect seems a bit uncertain, with press reports of 2015-2020, and a suggestion that it will be insufficient to keep climate change below 2°C (Gray, 2011).

There was significant environmental protest activity in London associated with these United Nations negotiations, including a Climate Camp at Blackheath, in August 2009 (Bird and Booth, 2009). ‘The Wave’ protest march (Figure 1.12) of between 20000 and 50000 people (Siddique, 2009) coincided with the Copenhagen meeting in December 2009, a protest march with a few thousand people that coincided with the Cancun negotiations and a protest march of a few hundred people at the same time as the Durban conference. It is not clear why there were less people on each of the successive demonstrations, unless interest was reducing. Protest marches can be contradictory with banners opposing short haul internal flights and opposing the proposed high speed rail link between London, Birmingham, Manchester and Leeds (High Speed Two Ltd, 2012) – a rail link that might reduce carbon dioxide emissions from internal flights, although the proposed route may damage wildlife habitats.

Figure 1.12. The ‘Wave’ climate change protest march opposite the United States Embassy in Grosvenor Square, London. Photograph taken by AWS.

International conventions and agreements are incorporated into UK legislation, including the Climate Change Act 2008, which requires a 34% reduction in carbon dioxide emissions by 2020 and an 80% reduction by 2050 compared with a 1990 baseline (Department of Energy and Climate Change, 2011).

Recent technological developments aim to reduce the use of fossil fuels in buildings. For example, ground and air source heat pumps, wood chip fired heating systems, photovoltaic and water heating solar panels and insulation products ranging from sheep’s wool to plants that can be grown on roofs (Ecobuild, 2011). Plants on roofs have a dual use, as climate change may increase the severity of rainfall events and the plants reduce the rate of storm water run-off and hence mitigate flood risk.

However, Lomas (2009) shows that the task of retro-fitting energy use reduction products to existing houses by 2050 is huge, as there are about 24 million homes in the UK and this would be the equivalent of refurbishing a city the size of Cambridge each month, requiring an estimated 23000 teams of trained workers. Also even if building design was improved, Janda (2011) points out that it is people rather than buildings that use energy, and people can be highly variable in their energy usage and there may be a need for public awareness training on how to use buildings in an energy efficient manner. Also increased energy efficiency can result in higher usage, as people can afford to use more energy (Nature Editorials, 2011).

Climate change mitigation policy is directed at the user, not the supplier, of fossil fuels, whereas in some other industries that harvest environmental products, for example, fishing, the control regulations are directed at the fishing fleet, rather than the consumer. It might be more appropriate to restrict the extraction and supply of fossil fuels although this would increase prices and directly affect the ability of people to commute to work and heat their houses. During the unusually cold winter of 2010-2011 there were 25700 excess deaths in England and Wales (BBC, 2011), so restricting energy supplies as a climate change mitigation strategy has the potential to increase human mortality.

Geoengineering techniques which include reflecting solar radiation back into space and removing carbon dioxide from the atmosphere (Shepherd, 2009) may become necessary, as there is little confidence that political efforts (Seitz, 2011) to cause sufficient carbon dioxide emission reductions needed to avoid ‘unmanageable’ (Ridgwell *et al*., 2009) and ‘dangerous’ (Shepherd, 2009) climate change will succeed. As an example of a geo-engineering technique that reflects solar energy, Seitz (2011) has investigated creating hydrosols by producing small bubbles in sea water, which doubles the albedo. Microbubble production technology is increasingly available as it is used in paints and to reduce the drag of ships hulls as they move through the sea. Doubling the albedo of a 1 hectare reservoir would reflect heat, offset some carbon dioxide emissions and would reduce water loss by evaporation by about 1 mm day^{-1}, which is the equivalent of 3600 m^3 yr^{-1} and potentially could be powered by a photovoltaic system. At present it is difficult to imagine geo-engineering techniques on a scale able to alter the planet’s temperature, but microbubble technology may have the potential to reduce the temperature increase experienced by localised populations of aquatic or marine organisms that might otherwise be vulnerable to climate change.

Other techniques to increase reflection of solar energy include using crop plants that have a higher albedo due to glossier leaves, perhaps including genetic modification of leaf waxes, although this extra reflectivity should not reduce photosynthesis, as this would reduce crop yield (Ridgwell *et al*., 2009).

Examples of geo-engineering techniques that remove carbon dioxide from the atmosphere include increased forestry cover and ocean fertilisation. Ocean fertilisation works by increasing the rate of growth of phytoplankton by adding additional nutrients to the oceans. These phytoplankton die, or are eaten by zooplankton, which in turn die or defecate and the resulting material sinks to the sea bed, where it may remain as a carbon store or may be decomposed by bacteria, releasing the carbon dioxide, some of which may then return to the atmosphere. Removal of atmospheric carbon dioxide has extra benefits compared to reflecting solar energy as it addresses the actual cause of climate change and ocean acidification (Shepherd, 2009). Carbon dioxide capture and storage can be used to prevent carbon dioxide entering the atmosphere from power stations (Schrag, 2009).

1.14 Other factors causing insect population changes in the UK

UK invertebrate population sizes appear to be changing, with increasing evidence of declines. This can be a complex topic, because of the wide range of taxonomic groups involved and range of environmental factors. Also, while there is evidence of declines, some species are colonising the UK and increasing in distribution, partly due to climate change. This issue is further complicated by variation in the level of knowledge of different groups and the number of people with the specialist skills to identify and study them.

70% of UK butterflies are in decline (Thomas *et al*., 2004), mainly due to the loss, degradation and isolation of habitats. These changes are thought to be caused mainly by agricultural intensification, declines in woodland coppicing or by myxomatosis, which reduced rabbit grazing in the 1950s, causing grasslands to grow taller and denser, but less florally diverse. British butterfly populations are highly monitored and are sensitive to environmental change, so they may be good indicators of changes in the population sizes of other insect groups (Thomas, 2010).

British macro-moths are monitored through the Rothamsted Insect Survey. Out of 337 species that are monitored, two thirds have declined during a recent period of 35 years and 71 species declined by more than 30% in a ten year period (Conrad, *et al*., 2006). However, there have also been moth species that have newly colonised the UK, partly associated with non-native plants, with over 60 moth species recorded as new to Britain since 2000 and at least some confirmed as breeding and increasing in range (Fox *et al*., 2010). Many causes of moth declines are probably similar to other insect species, however most moth species are nocturnal and can be adversely effected by “light pollution” (Settele, 2009), which is probably of little or no relevance to daylight active species. If it was possible to stop species declining or becoming extinct, then with some species colonising diversity might increase, unless the new arrivals occupy an identical niche and cause competitive exclusion.

Mr S. Roberts from the University of Reading Centre for Agri-Environmental Research says two-thirds of British bee species are in decline. So a 66-70% of species in decline appears to be found in butterflies, moths and bees and may well be an indicator of the percentage of species declining in other, less well monitored, insect groups. Many flower visiting insects act as pollinators, although bees are particularly important. A decline in pollination services can have implications for agricultural productivity and possibly the conservation of insect pollinated wildflowers.

Causes of butterfly declines can be quite complex. For example, the high brown fritillary (*Argynnis adippe* Denis and Schiffermüller) has declined considerably in distributional area in the UK (Figure 1.13). *A. adippe* may now be Britain's most endangered butterfly and is becoming "conservation dependent" (Barnett and Warren, 1995). Causes of this decline include a decline in both woodland coppicing and grazing of more open habitats that contain bracken (*Pteridium aquilinum* (L.) Kuhn). When grazing stops the litter layer can become deeper preventing the growth of violets (*Viola* spp.), which are their larval food plants (Barnett and Warren, 1995). The reasons for these land management changes add further complexity, as they include the economics of rough grazing and a decline in requirement for coppice products, although the demand for wood for fuel may increase (Broome *et al*., 2011), as it can be used as a renewable energy source that can reduce greenhouse gas emissions from energy production (Karp *et al*., 2011). However, an increase in short rotation coppice involving a glyphosphate herbicide application is unlikely to be beneficial as it may kill the violets. The example of *A. adippe*, emphasises the complexity of identifying the factors which influence changes in invertebrate population size and distribution.

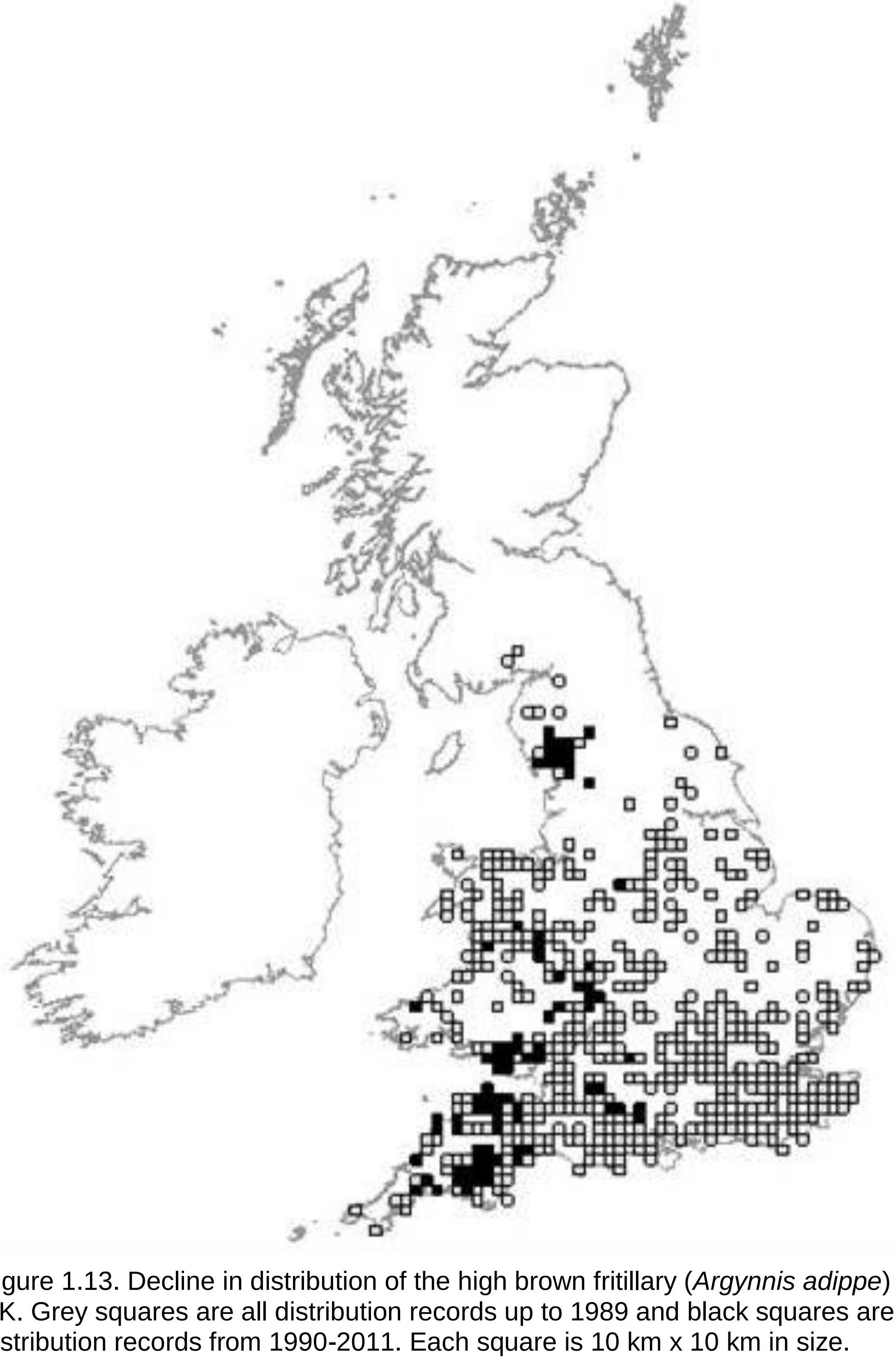


Figure 1.13. Decline in distribution of the high brown fritillary (*Argynnis adippe*) in the UK. Grey squares are all distribution records up to 1989 and black squares are all distribution records from 1990-2011. Each square is 10 km x 10 km in size. Illustration prepared by AWS using data from the NBN Gateway (National Biodiversity Network, 2011a). © Crown copyright. All rights reserved NERC 100017897 2004.

The decline in insects probably represents a considerable decline in overall insect biomass, as cars used to have dried ‘fly-splatter’ on the windscreens (Bennett and Gilchrist, 2010), but rarely do nowadays. However, even this apparently simple indicator of insect density is difficult to interpret as it can be difficult to separate the effect of car design, non-stick paintwork, insect population size and insect splatter. A. Saunders (email 2 February 2011) described butterfly splatter in the 1980s in the mid-West USA and said that some of this was due to cars having front grills at that time, as well as being in a ‘Lepidopteran rich region’. Munguira and Thomas (1992) have investigated butterfly mortality caused by cars and estimated that a busy road in southern England resulted in the death of 0.8-6.8% of a roadside verge population of butterflies. This included 92 individuals of *Pieris rapae* killed out of an estimated total population of 1350 individuals, although this number is much less than is likely to be killed by predators or parasitoids.

Agricultural productivity will need to increase to feed a human population size that is expected to increase considerably during the 21st century (Devine and Furlong, 2007; Figure 1.5) and this is likely to involve an increasing use of agrochemicals. Unfortunately, insect decline has occurred due to agrochemical usage, with insecticides killing the insects, herbicides killing the insect food plants and fertilisers reducing floral diversity by increasing the soil nutrient status. The loss of flowers means less nectar and pollen for honeybees (Decourtye *et al*., 2010), bumblebees and butterflies. Insects that feed on nectar and pollen need flowers available throughout the flight season, and some species of bumblebee can be quite specific about the shape of the flower (the corolla) that they can obtain nectar from, so they will not visit all flower species. Therefore a loss of floral abundance and diversity can mean that nectar is not available for the entire flight season (Corbet and Westgarth-Smith, 1992).

Agrochemicals can also drift away from the target crops. Estimates of how far pesticides can drift vary, for example 10 m (Longley and Sotherton, 1997) to 200 m and also depend on whether chemicals were applied from ground based machinery or from aircraft, with aerial applications able to drift several kilometres (Cox, 1995).

Consequently insecticides can affect non-target insects in habitats a considerable distance from agricultural land, and in the UK, where nature reserves can be small, potentially the whole reserve may be vulnerable to contamination.

Habitat loss has been considerable, although can be difficult to interpret due to changing habitat classifications and changes in survey area – for example surveys of England and Wales or Britain. Also the skills base of the surveyors and the technologies available to them have changed. However, there has been a 97% loss of unimproved lowland pasture between 1930 and 1984 (Fuller, 1987) and 45% of ancient woodland has been cleared or converted to plantations between 1930 and 1985 (Spencer and Kirby, 1992), although there has been a 23% increase in broadleaved woodland since 1945 (Lawton *et al*., 2010). Habitat loss continues to the present day with 26000 km of hedgerows lost between 1998 and 2007 (Countryside Survey, 2009 cited in Lawton *et al*., 2010).

Habitats have gained legal protection, so more than 50% of species rich grasslands now have Site of Special Scientific Interest (SSSI) status, but this is less than 2% of this habitat that would have been present in 1930 and 74% of heathlands are currently SSSIs, however this is only 10-15% of the heathland area that existed in the 19th century (Lawton *et al*., 2010). This is because unprotected habitats have been lost and by the time the legal protection was available it was too late for many sites.

European grassland butterfly species have declined by 70% between 1990 and 2009, due to agricultural intensification and abandonment of grazing, particularly in Eastern and Southern Europe, as people migrate to cities or as rough grazing becomes no longer economically viable. Habitat fragmentation and isolation has also affected grassland butterfly species. Europe has 436 butterfly species and 88% of them are found on grasslands at some time (Van Swaay *et al*., 2010; Van Swaay and Warren, 2006) making conservation of grasslands possibly the single most important factor in maintaining butterfly populations. The downward trend in the European grassland butterfly index is still continuing in 2009, so grassland butterflies are continue to decline.

1.15 Consequences of insect population change for insectivorous predators

Many organisms eat insects and other invertebrates, so a decline in insect population size could have negative consequences for the population size of insectivores. Conrad *et al*. (2006) has described the decline in moths as an ‘insect biodiversity crisis’, and that it could have serious consequences for birds and bats, which eat the moths. There is evidence of UK population declines for insectivorous birds: spotted flycatchers (*Muscicapa striata* Pallas) have declined by 85% during the period 1970-2008 (Eaton *et al*., 2010) and pied flycatchers (*Ficedula hypoleuca* Pallas) have declined by 50% during the period 1995-2008 (Hernandez, 2009). Both these flycatcher species are migratory (Hernandez, 2009), so factors outside the UK might be affecting their population size and make reserve-based management an inefficient conservation tool (Goodenough *et al*., 2009). Furthermore, flycatchers are vulnerable to climate change related mis-timing between the time of arrival and breeding and availability of their insect prey (Both *et al*., 2006).

Haysom *et al*. (2010) says that ‘many’ species of bats in Europe have suffered serious population declines during the 20th century. However it is possible that bat populations were much higher before the start of the 20th century as Gilbert White (1902) described in a letter written in 1767 that while travelling in a boat from Richmond to Sunbury he saw “*myriads of bats…the air swarmed with them…hundreds were in sight at a time*”. Bat population trends may be quite complex, with Kervyn *et al*. (2009) reporting that five species of bats had declined and four species have increased in Belgium. In Britain, the common pipistrelle (*Pipistrellus pipistrellus* Schreber) shows a 35.6% decrease in colony counts and a 54.7% increase in field counts during the period 1999-2006 (Bat Conservation Trust, 2008). This might be due to less bats spending more time feeding, as food is harder to obtain and therefore bats are counted more often when in flight and feeding. An alternative explanation is that the bat survey has not been running for enough years to produce reliable trends. AWS has been a member of Berkshire and South Buckinghamshire Bat Group (2011) since 1989 and has seen how the number of people interested in bats and bat surveys has increased and the monitoring technology has improved during this time – all factors that could influence bat recording data. It may also be difficult to separate out the effect of changes in insect population size from the effect of changing timing of insect activity due to climate change, which may influence food availability as Altermatt *et al*. (2010a) has suggested that climate change is causing moth species flying before the summer to fly earlier and species that fly after the hottest part of the year to fly later, potentially reducing the number of moths flying during the summer, which may be detrimental to insectivores such as bats.

Declines are also occurring in non-insect invertebrate groups in the UK. Between 1999 and 2008, 38 out of 87 land snail species, 11 out of 35 freshwater snail species and 10 out of 28 freshwater bivalve species have declined (Killeen, 2010). This may have negative consequences for the population size of song thrushes (*Turdus philomelos* Brehm), which eat terrestrial gastropod molluscs. Song thrush population size decreased by 48% between 1970 and 2008, although there might have been a partial reversal recently in this decline, as a 27% increase was recorded between 1995 and 2008. There is also evidence of reduced reproductive success, with a 48% decline in the ratio of juvenile to adult song thrushes (Eaton *et al*., 2010), but it is not clear whether this change is due to a lack of food (Westgarth-Smith, 1998).

The hedgehog (*Erinaceus europaeus* L.) population size in Britain has dropped from an estimated 30 million in the 1950s, to 1.5 million in 1995, and numbers are continuing to decrease. There are a range of reasons for this decline, including agricultural intensification, predation by badgers (*Meles meles* L.) (National Biodiversity Network - Hedgehog Street, 2011b) and road traffic accidents (Holsbeek *et al*., 1999), but caterpillars, beetles and earthworms have been found to comprise 55% of hedgehog food (Yalden, 1976), so the decline in the number of hedgehogs could be a consequence of a decline in their invertebrate food.

1.16 Air pollution and insects

Many types of invertebrates, including butterflies, use pheromones to detect mates and to assess whether the potential mates have, or have not, copulated (Thomas, 2011). Nectar feeding insects use floral scents to locate plants, and it is possible that butterflies travelling, or migrating longer distances, use smell to locate suitable habitat areas. Pheromones and floral scents travel through the air and are vulnerable to degradation by pollutants, including oxidation by low altitude ozone, reducing the distance that these chemicals can travel and still be detected (Arndt, 1995; McFrederick *et al*., 2009).

McFrederick *et al*. (2008) has shown how the scent trail from flowers has changed from several kilometres during pre-industrial environments with no air pollution to <200 m in the present day, with more polluted environments. This means that in a more polluted environment, a pollinating insect may need to travel further before finding a scent trail that can be followed to flowers. More time and energy spent foraging could reduce the energy that an insect can invest in reproduction. Pollination success could also be reduced if insects cannot find flowers so easily, which might cause plant communities in polluted areas to include less species that are insect pollinated and more species that are wind or self pollinated.

1.17 Diseases and introduced organisms

Diseases can also affect butterfly food plants, which may then affect butterfly populations. Dutch elm disease is caused by the fungus *Ophiostoma novo-ulmi* (Brasier) and the vectors are two species of bark beetles, *Scolytus scolytus* (Fabricius) and *S. multistriatus* (Marsham) (Harwood *et al*., 2011). The white-letter hairstreak butterfly (*Satyrium w-album* Knoch) breeds only on elm (*Ulmus* L.) trees. The population size of *S. w-album* at Monks Wood was small, although possibly partly due to under-recording, as this is a tree canopy species. However, this small population dropped abruptly in 1980, probably due to Dutch elm disease (Figure 1.14). Nationally, populations of *S. w-album* are starting to recover as a result of breeding on elm sucker regrowth (Asher *et al.*, 2001), but there is no evidence of this population recovery at Monks Wood.

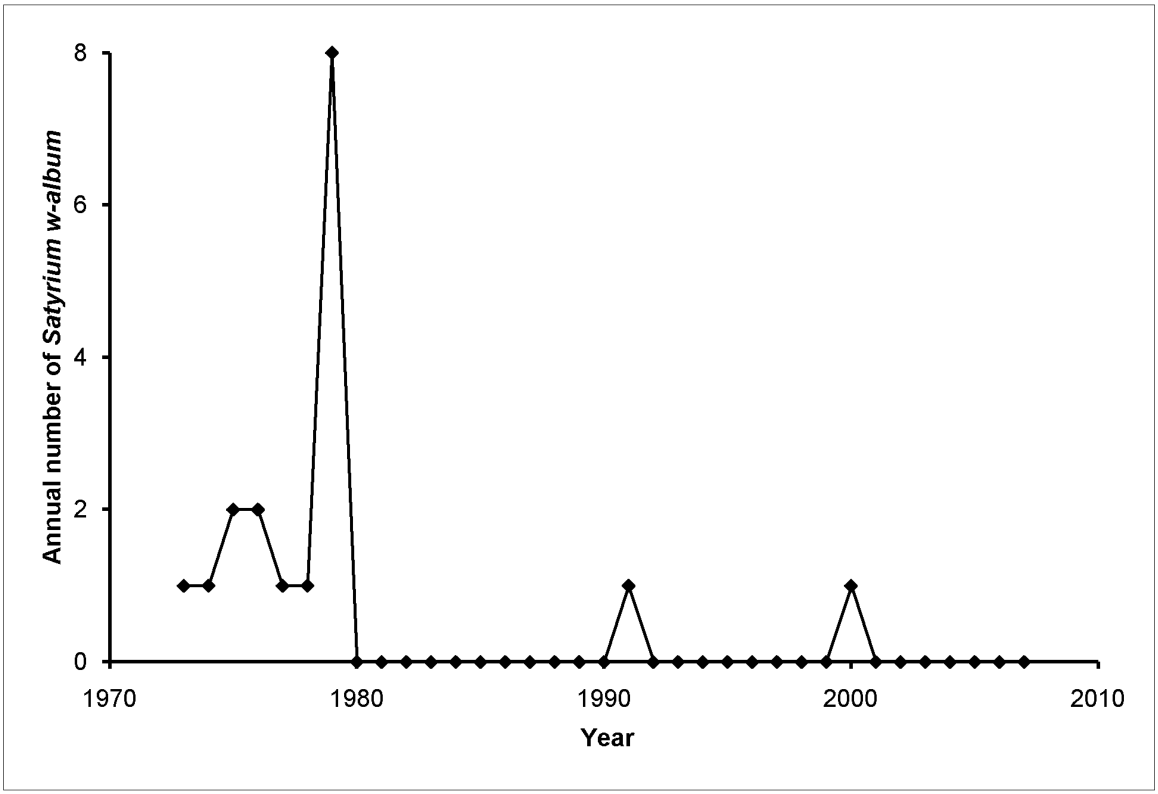


Figure 1.14. Annual numbers of white-letter hairstreak (*Satyrium w-album*) counted at Monks Wood between 1973 and 2007.

Sudden oak death is caused by the fungus *Phytophthora ramorum* (Dehnen-Schmutz *et al*., 2010) and was first recorded in the UK in 2002 (Xu *et al*., 2009). Oak (*Quercus robur* L.) is the larval food plant for the purple hairstreak butterfly (*Neozephyrus quercus* L.) (Thomas, 1975), so if this disease was to spread it might threaten the purple hairstreak.

The importation of plant diseases or insect pests can have serious consequences for native species. Dehnen-Schmutz *et al*. (2010) demonstrate that the horticultural industry is international, and is becoming a global market with an increasing risk of moving plant pathogens around the World. A globalised horticultural trade can be beneficial in achieving food security for an increasing global human population and may also be needed for agricultural plants to track a changing climate, but this needs to be balanced with the need for improved biosecurity mechanisms.

Non-native plant species can be a problem for insect populations as native insect species may not be able to live on them and so the area of land occupied by these plant species can become unavailable for native insect species. Non-native plants that are of concern include *Rhododendron ponticum* (L.), Japanese knotweed (*Fallopia japonica* Houtt) (Westgarth-Smith, 1994) and Himalayan balsam (*Impatiens glandulifera* Royle), although bumblebees feed from Rhododendron and Himalayan balsam flowers.

The harlequin ladybird (*Harmonia axyridis* Pallas) was introduced to Europe from Asia between 1995 and 2002 for biological control of aphids and coccids, and is now present in thirteen European countries. The first record for the UK was in 2004 (Brown *et al*., 2008). *H. axyridis* has increased in numbers, and is now up to 40% of the ladybird population in some parts of the UK, which makes it the most abundant ladybird species in the UK. At the same time, native ladybirds have declined, partly because *H. axyridis* is competing with them for food and eating their eggs, larvae and pupae (Brown *et al*., 2011). Therefore, it appears that *H. axyridis* is having a ‘seriously detrimental impact’ on native coccinellids (Brown *et al*., 2008).

The population size of the small tortoiseshell butterfly (*Aglais urticae* L.) has recently declined considerably in the UK. This decline might partly be due to a parasitic fly, *Sturmia bella* Meig. (Diptera: Tachinidae), which was first recorded in the UK in 1998 (Gripenberg *et al*., 2011).

The muntjac deer (*Muntiacus reevesi* Ogilby), which was introduced to the UK from China (Lu *et al*., 2007) may have a negative effect on the white admiral butterfly (*Limentis camilla* L.), because *L. camilla* lays its eggs low down on honeysuckle (*Lonicera periclymenum* L.) where muntjac can eat the leaves, eggs and larvae. Muntjac deer colonised Monks Wood nature reserve in the early 1970s, and by 1985 they were effecting the regrowth of coppiced hazel (*Corylus avellana* L.), field maple (*Acer campestre* L.) and ash (*Fraxinus excelsior* L.), such that by 1995 coppicing was stopped in Monks Wood (Cooke and Farrell, 2001). Therefore muntjac may have contributed to stopping coppicing, a woodland management practice that is important for butterfly conservation (Warren, 1993), on a National Nature Reserve.

1.18 Long term biodiversity surveys

Long term surveys of the abundance and timing of insect species are especially valuable to determine the effect of environmental change. These need to be accompanied by long term meteorological datasets. The UK has the World’s two best insect datasets - the United Kingdom Butterfly Monitoring Scheme (2010) and the Rothamsted Insect Survey (Harrington and Woiwood, 2007), both of which were used in the present study. The Rothamsted Insect Survey started in 1966 and the UKBMS was piloted at Monks Wood from 1973 and became a national survey from 1976. Both butterfly and aphid data are now being collected in continental European countries using the same methodologies as in the UK. However, relatively few mainland European aphid datasets have time series as long as that available from Rothamsted. Distributional data (Figures 1.10, 1.11 and 1.13) are also available for 10267 vertebrate, invertebrate and plant species in the British Isles from the National Biodiversity Network (2011a).

The 4th July Butterfly Count is run by the North American Butterfly Association (2010). The survey started in 1975 and data now come from about 450 sites (Ries, 2008), so it is comparable in size and duration to the UKBMS. Like the UKBMS, the number of years of data from each site was very variable. The 4th July Butterfly Count collects annual data, so it is not possible to detect phenological change. 4th July Butterfly Count data have been used in studies of butterfly mimicry (Ries and Mullen, 2008) and migrant butterflies, including the monarch (*Danaus plexippus* L.) and painted lady (*Vanessa cardui* L.) (Vandenbosch, 2003 and 2007). AWS tried using 4th July Butterfly data provided by L. Ries, University of Maryland, USA, for two butterfly species from the eastern coastal states, but no evidence of the NAO could be detected in the abundance of these butterflies.

The UK also has long term meteorological data, including the Central England Temperature Series, which are monthly data from 1659 to the present (Parker *et al*., 1992 and Met Office Hadley Centre observation datasets, 2009). Monthly precipitation data from the England and Wales Precipitation dataset (Alexander and Jones, 2001 and Met Office Hadley Centre observation datasets HadUKP, 2010).

The British Atmospheric Data Centre (2011) and University of East Anglia Climatic Research Unit (2011) are also excellent sources of data.

1.19 Conclusions

Changes in the atmospheric composition of anthropogenic gases are already causing climate change and are predicted to cause further considerable changes to temperature by 2100. Climate change is already causing changes in the phenology, abundance and distribution of organisms and predicted future change is large. Climate change can operate through complex, and difficult to predict, ecological mechanisms. The NAO is a meteorological system that causes oscillations in weather conditions over the North Atlantic and surrounding continental areas. Much less is known about the ecological effects of the NAO than climate change, so this presents an opportunity to contribute to the ecological understanding of how the NAO affects insect populations.

Increasing concentrations of carbon dioxide do not solely affect invertebrates through climate change. Increased carbon dioxide contributes to other ecological mechanisms including increasing the carbon to nitrogen ratio in food plants and by causing ocean acidification. Ocean acidification has the potential to cause a considerable reduction in global biodiversity as acidification effects organisms that have a calcareous skeleton, and this includes coral reefs, which are areas of very high biodiversity. The ecological consequences of climate change are now apparent and the ecological consequences of ocean acidification are likely to become apparent by about 2030 to 2050.

There are ongoing attempts to reduce the emissions of greenhouse gases through international agreement and technological developments, accompanied by pressure from environmental campaign groups, although there is no evidence that this is reducing the rate of increase in the atmospheric concentration of carbon dioxide or that it will succeed against a rapidly increasing human population size. The failure to decisively find ways to reduce greenhouse gas emissions to a sustainable level is likely to have considerable negative consequences for global biodiversity.

UK insect populations are not just responding to climate change and the NAO, they are also responding to a range of environmental changes including habitat loss, agrochemicals, air pollution, disease and introduced organisms. While the population size of some insects is increasing, more species of insects are declining than are increasing. 60-70% of butterfly, moth and bee species are in decline in the UK. As this percentage is consistent across three major groups of insects it suggests that similar declines might be found in less well studied insect groups. Declines on this scale have potential negative consequences for populations of insectivores and crop pollination. These population declines mean that studies of insect ecology, including the present study, may have a conservation value, as they contribute to our knowledge of potentially vulnerable organisms.

1.20 Hypothesis and research questions

The present study investigates the role of the NAO and climate change in influencing the population size and flight timing of individual insect species and communities of insect species. The insects used include the green spruce aphid (*Elatobium abietinum* Walker) and a range of butterfly species. The analysis is at different spatial scales, including site specific and national data.

The hypothesis for this thesis is: the NAO affects insect populations in the UK. This hypothesis was tested with the following research questions.

1. What effect does the NAO and climate change have on meteorological conditions?
2. Does climate change and the NAO affect the population size and timing (phenology) of insects?
3. Is there an association between the NAO and certain life history characteristics, including the number of generations (voltinism) or the length of the flight season?
4. In what ways do the highly variable insect population sizes influence the accuracy of the results, and is it possible to control for the effect of population size fluctuations by identifying minimum sample sizes?
5. What is the relative magnitude of meteorological and non-meteorological factors on butterfly populations?
6. Can the NAO be used as a predictor of insect population size or flight timing?
7. Having described how the NAO, climate change and other environmental factors influence insect ecology, is it possible to predict what future changes might occur?

Chapter 2

Materials and methods

2.1 Introduction

The present study investigates the effect of the NAO on meteorological parameters including temperature and precipitation, and the effect of these variables on the abundance and flight timing of aphids and butterflies. Entomological data came from the World's best insect datasets, which have both local and national resolutions. Sample sizes were exceptionally large. A range of statistical tests were used to interpret the data.

2.2 Entomological datasets

Insect population data were obtained from the Rothamsted Insect Survey (2011) and the UK Butterfly Monitoring Scheme (UKBMS) (United Kingdom Butterfly Monitoring Scheme, 2010). The aphid data were from a trap at Rothamsted Research, Harpenden, Hertfordshire, UK, so although the data were from a site-specific trap, aphids were blown in from the surrounding area. The UKBMS analysis included the use of national data and site specific data from Monks Wood, Cambridgeshire, UK. Data for one species, the ringlet (*Aphantopus hyperantus*), from two other locations, Chippenham Fen and Holme Fen in Cambridgeshire, were also used.

2.3 Why use entomological datasets?

Some advantages of using insects to detect weather-related changes in abundance or phenology are listed below.

1. Insects are poikilothermic, with a large surface area to volume ratio and although some species can partially regulate their internal temperature, they are much less effective at doing this than homeothermic organisms such as mammals. Consequently, poikilotherms are much more likely to respond to changes in their thermal environment than homeotherms.

2. Aphids and butterflies can fly, although the mobility of adult butterflies varies between species. Therefore they are able to change their distribution in response to climate change.
3. Butterflies usually have one (univoltine) or two (bivoltine) generations per year. They are therefore likely to be directly influenced by weather within the preceding 12 months, unlike a large mammal with a life cycle of many years or decades, making it likely that there will be lag effects between weather and population size.
4. Many species of butterflies are active during the winter months, including larval feeding, whereas some mammals, for example badgers (*Meles meles*), hibernate in well insulated deep underground burrows at the time of year when the NAO affects the weather. There are also some butterflies (e.g. the peacock, *Inachis io*) that hibernate as adults in the winter and thus will be inactive at that time.
5. UK butterflies are a good group to study, because they have been extensively researched, so baseline information such as life histories have been accurately established.

2.4 What is the quality and size of the datasets used?

Below are listed some reasons why the Rothamsted Insect Survey and the UK Butterfly Monitoring Scheme are very high quality datasets.

1. The Rothamsted Insect Survey data was a very large dataset, as it was daily resolution counts of aphid species from a suction trap at Rothamsted Research at Harpenden, Hertfordshire, UK. The dataset covered a very long time period from 1966 to the present, with almost no missing days.
2. AWS visited Rothamsted Research and met R. Harrington who coordinates the survey. AWS also saw that there was a team of experienced aphid identification staff working in what appeared to be a dedicated laboratory, so identification accuracy should be very high.
3. The Butterfly Monitoring Scheme datasets are large, come from many sites. In addition, many of the species are fairly distinctive, minimising the risk of mis-

identification. Weekly, site-specific data are also available from the UK Butterfly Monitoring Scheme (2010) website for all transect sites. A total of 1465 transect sites have been used by the UKBMS, although different sites were operational for different numbers of years, and therefore not all the sites were monitored for the whole time series.

4. The best single site out of all the UKBMS sites was Monks Wood, Cambridgeshire, as there were continuous data from 1973 to the present day, whereas the earliest start date for all other sites was 1976. The Monks Wood dataset has very few missing weeks.

2.5 Disadvantages of entomological datasets

There are also problems with long-term entomological datasets:

1. The United Kingdom Butterfly Monitoring Scheme (2010) provides access to weekly butterfly count data from 1465 sites. The regional distribution of these sites is England 1253 sites, Wales 81 sites, Scotland 119 sites and Northern Ireland 12 sites. This bias towards England may reflect the distribution of people who count butterflies, as well as the greater abundance and diversity of butterflies in southern England.
2. The use of Rothamsted Insect Survey and UKBMS data involves developing an analysis using data that has already been collected - it is not possible to influence the data collection methodology, whereas most other strategies involve designing the experiments to provide the necessary data.
3. The earliest start date for most UKBMS sites was 1976, however Monks Wood has data back to 1973, as this was where the survey was piloted. At the time of data analysis (March 2010), the most recent year where ‘Ind’ totals (‘Ind’ = ‘individuals’ = the total number of individuals of a species counted in a year and may involve estimates if there are missing weeks of data) had been uploaded onto the UKBMS website was 2007, so providing 34 years of data. Clutton-Brock and Sheldon (2010) indicate that you need three to four decades of data to explain why population sizes change, and they refer to Jane Goodall’s study of chimpanzees (*Pan troglodytes*), which needed 50

years to obtain sufficient data. However, they do point out that the number of years of data required depends on how long the species lives. Butterflies have a much shorter life cycle than chimpanzees, and hence will be able to respond much more quickly to environmental change. Yet butterfly population size can fluctuate considerably from year to year, creating ‘noisy’ data. Consequently the number of years of data available from Monks Wood was probably within the lower end of an acceptable range. However, there were no longer duration high quality butterfly datasets available.

4. The Butterfly Monitoring Scheme was one of several datasets considered for investigating the role of the NAO in the control of insect populations. Dr L. Ries, University of Maryland, USA, provided data for two species from the 4th July Butterfly Survey in the USA. In this scheme, butterflies are counted close to the 4th July, so data covers only one or a few days per year, whereas the UKBMS scheme uses a weekly survey that runs over many months. Like the UKBMS, the 4th July Butterfly Survey data involves differerent numbers of years of data for different sites. Aphid data was also investigated from one suction trap in Valence, France, but the number of aphids caught was too low to be used.

2.6 Locations of research sites

The present study uses aphid data from Rothamsted Research, Hertfordshire, UK and UKBMS data were mainly from Monks Wood, although data for one species, the ringlet (*Aphantopus hyperantus*), also came from Chippenham Fen and Holme Fen, all in Cambridgeshire (Figure 2.1). National resolution UKBMS data were also used.

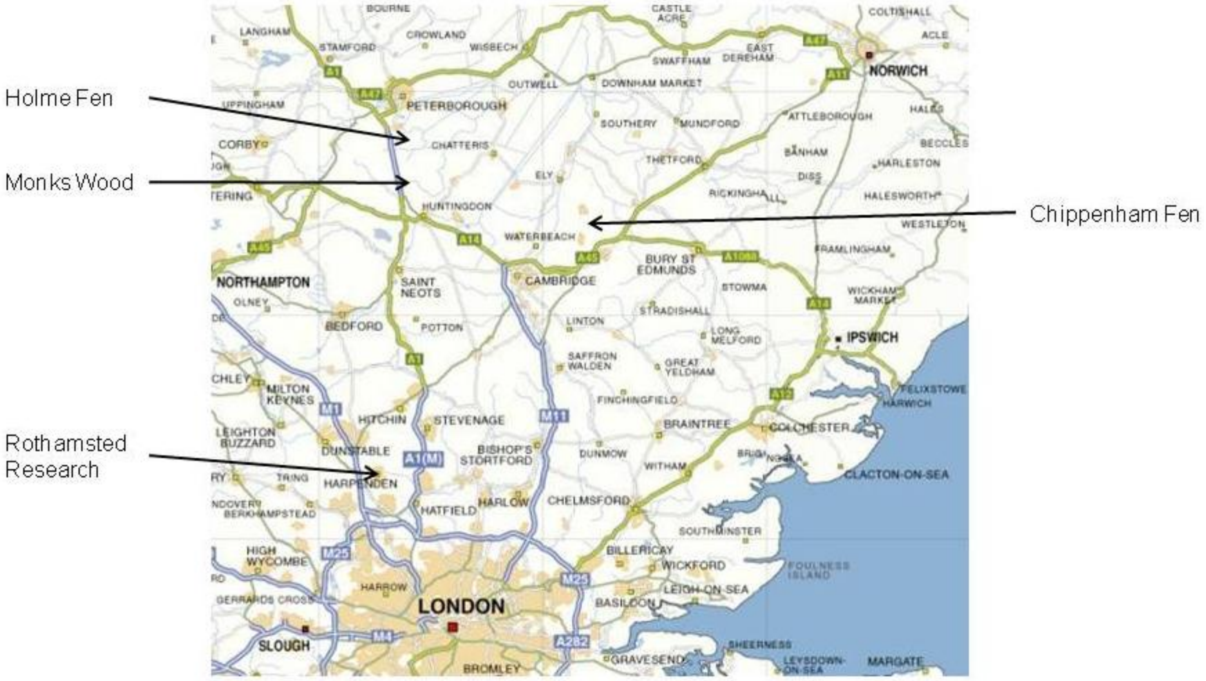


Figure 2.1. Map of part of the Midlands and East Anglia, UK, showing the location of survey sites. Grid lines are at 50 km intervals (www.streetmap.co.uk).

2.7 Introduction to the Rothamsted Insect Survey

The Rothamsted Insect Survey uses 12.2 metre tall suction traps (Macaulay *et al*., 1988) which suck in 0.75 m^3 of air per minute (Figure 2.2). The trap aperture is 12.2 m above the ground surface so that the catch is less likely to be affected by turbulence and convection caused by surrounding vegetation. There are 16 of these traps operational in the UK and a total of 73 traps in Europe and Scandinavia. The traps operate all year, although during April to mid-November when aphids are most active the traps are sampled daily, whereas for the rest of the year they are sampled weekly (Harrington and Woiwood, 2007).

The aphid data used in the present study was from the suction trap at Rothamsted Research, which has a long, continuous, dataset from 1966 to the present. Rothamsted Research is near Harpenden, Hertfordshire, UK, which is approximately 30 km north of London (Figure 2.1) and at an altitude of approximately 120 m – 130 m. Rothamsted Research is an agricultural research station surrounded by arable land, suburban housing, some small woodlands, golf courses and recreational parks, including cricket pitches (Figures 2.3 and 2.4). Aphid counts from suction traps are representative of large areas, with similarities in the numbers caught between traps hundreds of kilometres apart (Cocu *et al*., 2005).

Following consultation with Dr R. Harrington, who coordinates the Rothamsted Insect Survey, data were provided for the green spruce aphid (*Elatobium abietinum*), as this species has a relatively short-duration flight period and compared to other aphid species caught at Rothamsted the flight period was early in the year, nearer the time when the NAO has most effect on the weather. In the UK, *E. abietinum* is active and feeds during mild winters, whereas in continental Europe it is more likely to over-winter as an egg (Rothamsted Insect Survey, 2011). This mobility through the winter might increase the chance that this species would be influenced by weather associated with the NAO. Dr Harrington arranged for the data to be checked and sent to AWS.

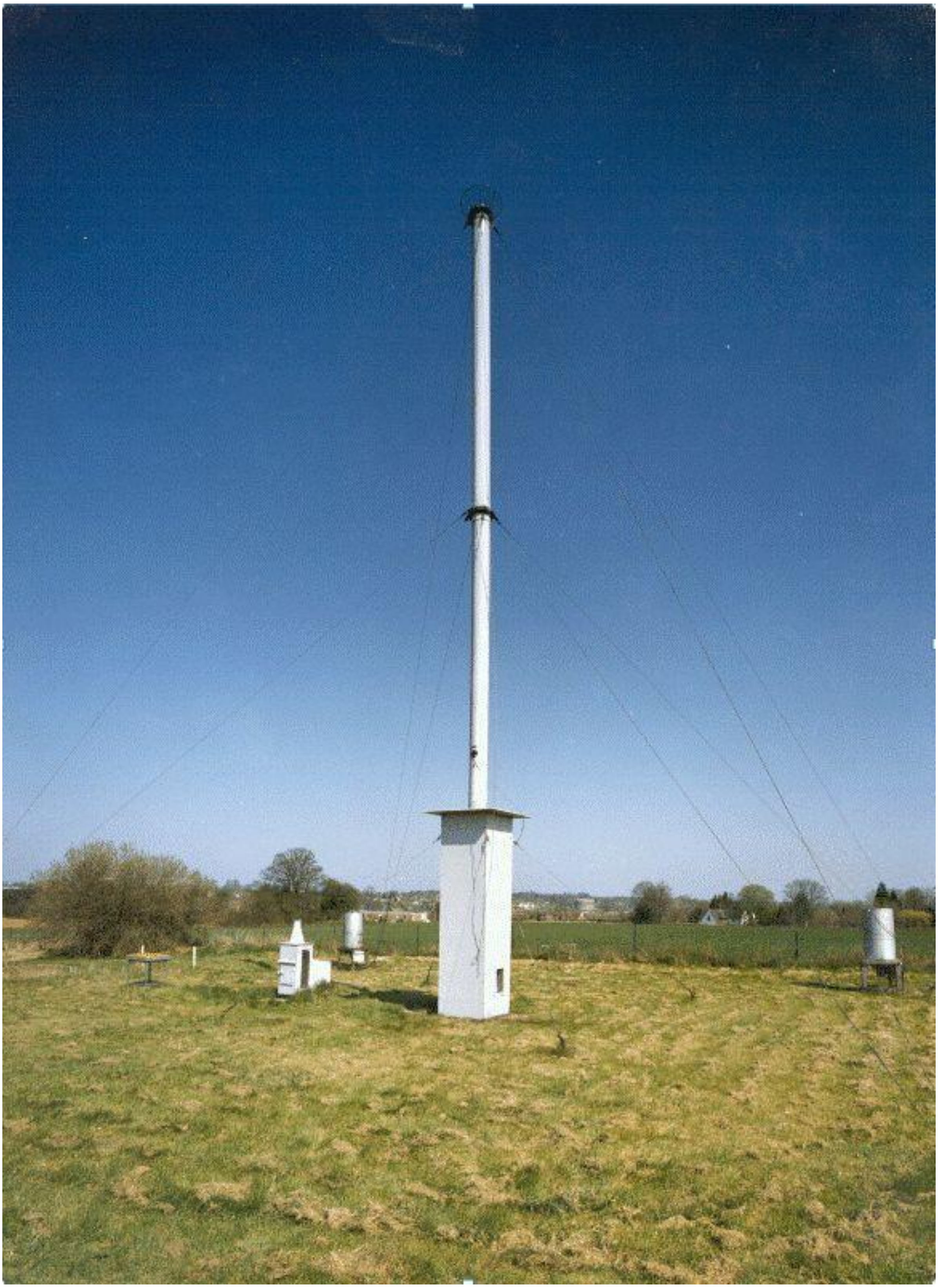


Figure 2.2. An aphid suction trap. (Photograph provided to AWS by Dr R. Harrington).

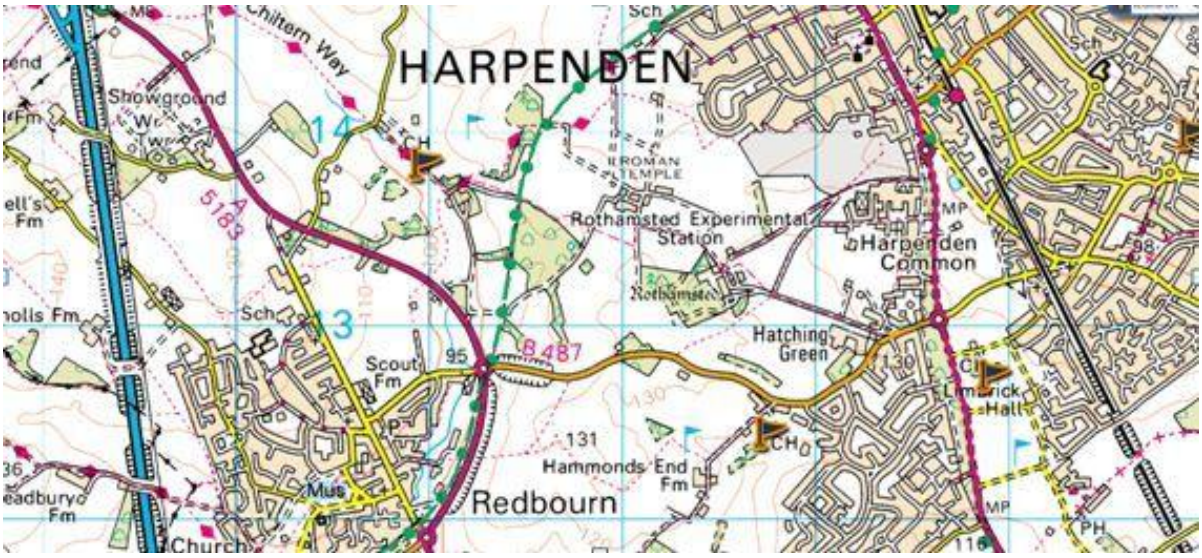


Figure 2.3. Map showing the location of Rothamsted Research, formerly Rothamsted Experimental Station (www.streetmap.co.uk). This map provides some information on land use.

Figure 2.4. Satelite image of Rothamsted Research (main buildings located in top, right of image) showing surrounding land use. Note the small woodlands, suburban gardens with large numbers of trees and arable fields, some of which appear to be subdivided into many research areas (www.google.co.uk).

2.8 Butterfly Monitoring Scheme methodology

The UK Butterfly Monitoring Scheme methodology involves walking a transect on a weekly basis from 1 April to 29 September. Transect lengths vary, although the transect at Monks Wood is 3 km long and takes between 60 and 90 minutes to complete. The transect widths are usually about 5 m, although this can vary depending on the width of the paths followed. Some observers count the butterflies in an imaginary 5 m x 5 m quadrat as they walk the transect. Transects are done between 10.15 and 15.45 British Summer Time and require that shade temperature should be over 17°C, or if 60% of the route is sunny then transects can be done down to temperatures of 13°C (Pollard and Yates, 1993).

Although the methodology has been designed to be relatively straightforward, there are some potential problems. Habitats can change with time, for example trees can grow and the increased shading from them can exclude butterflies as well as making it impossible for the observer to move through increasingly dense vegetation. The aim is to count the butterflies once in each of the 26 weeks, between 1 April and 29 September. However, in practice this may not happen due to bad weather, observer illness or holidays. There can be identification problems: for example, distinguishing between small (*Thymelicus sylvestris*) and Essex skippers (*T. lineola*) and small (*Pieris rapae*) and green-veined whites (*P. napi*) (Pollard and Yates, 1993) is not easy, particularly if the butterfly is in flight.

2.9 Sources and formats of UKBMS data

UKBMS data were available in a range of formats. Weekly counts from each transect site were available from the United Kingdom Butterfly Monitoring Scheme (2010) web site. National annual collated indices for each species were provided by Dr D. Roy of the UK Centre for Ecology and Hydrology. A multi-species collated index was calculated using data from the UKBMS, but obtained from the UK Joint Nature Conservation Committee (2010). JNCC uses the multi-species index as a UK biodiversity indicator.

2.10 Introduction to the three UKBMS sites used

2.10.1 Monks Wood

Monks Wood is located in Cambridgeshire, UK, between Huntingdon and Peterborough (Figure 2.1). It is a National Nature Reserve (NNR) and Site of Special Scientific Interest, although the condition of the SSSI is described as ‘unfavourable recovering’ (Nature on the Map, 2011). Monks Wood is an ash (*Fraxinus*) and oak (*Quercus*) woodland (Natural England, 2011a) that is 157 hectares in size and is the largest wood in Cambridgeshire. It was historically managed as coppice with standards. ‘Much of’ Monks Wood was clear-felled at the end of the First World War. Monks Wood was bought in 1953/4 by the Nature Conservancy (Cooke and Farrell, 2001). The Nature Conservancy changed its name, first to English Nature, and then Natural England.

Monks Wood ranges in altitude from 10 m to 40 m. Figures 2.5 and 2.6 show that Monks Wood is a fragmented area of woodland surrounded by agricultural land. Most of the agriculture is arable, and the colours of the fields in Figure 2.6 suggest cereal crops close to harvest. Further evidence for the photograph being taken in the summer (when cereal fields would be pale in colour) includes the trees having a full canopy of leaves and evidence of soil patterns, including ridges and furrows and possible trackways which would be more visible when the soil is dry, as differential drainage and water holding becomes apparent in vegetation in hot, dry conditions. Figure 2.7 shows the UKBMS transect route in Monks Wood and it is possible to identify the woodland rides followed by the transect in the satellite image (Figure 2.6). Monks Wood Experimental Station is also visible in Figures 2.5 and 2.5. This was the site of the Monks Wood meteorological station, as well as the base for the scientists who developed the UKBMS, although the site is now closed.

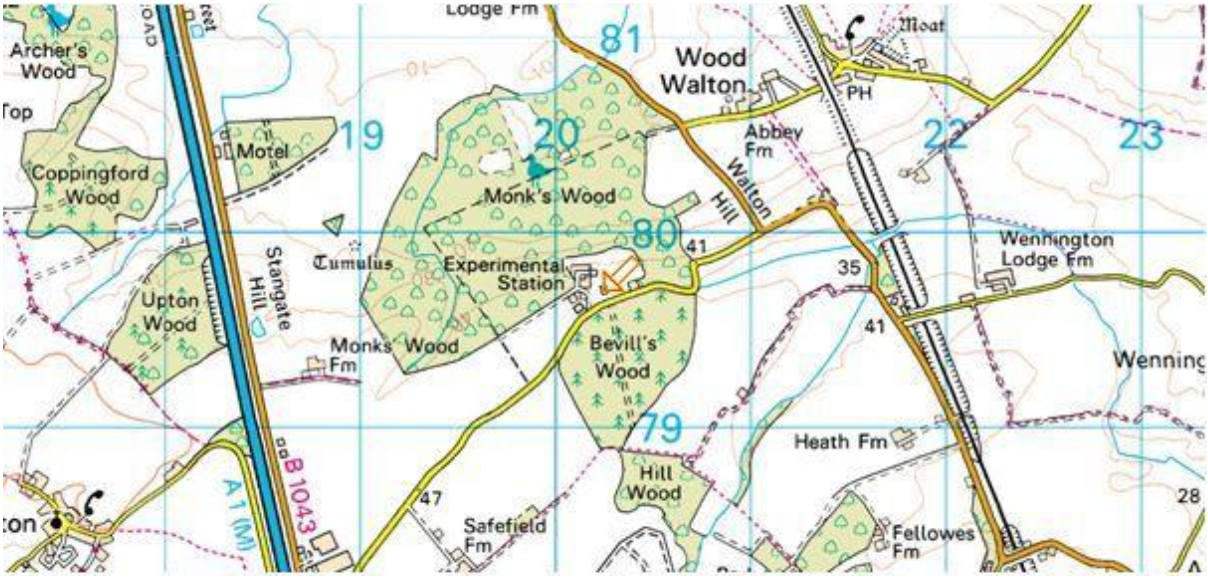


Figure 2.5. Map of Monks Wood National Nature Reserve. Scale: Grid lines are at 1 km intervals (www.streetmap.co.uk).

Figure 2.6. Satelite image of Monks Wood National Nature Reserve showing the fragmented nature of the woodlands surrounded by agricultural land (www.google.co.uk).

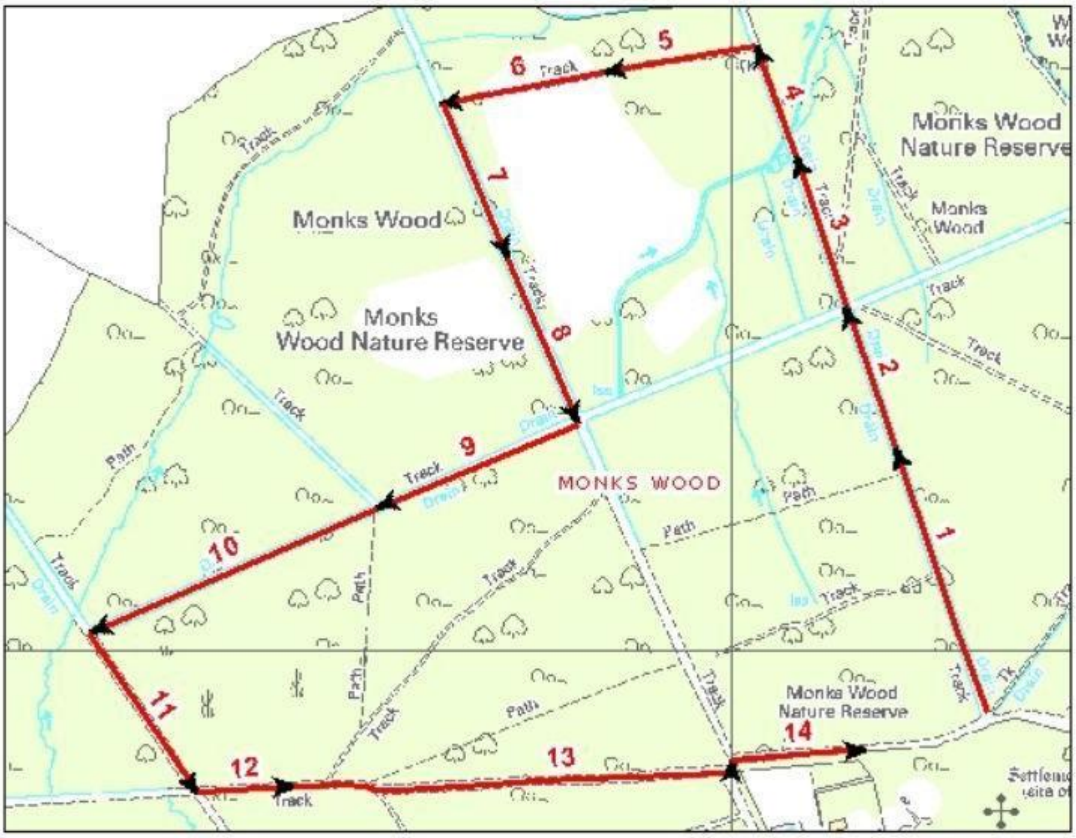


Figure 2.7. Map showing the Butterfly Monitoring Scheme transect route at Monks Wood (United Kingdom Butterfly Monitoring Scheme, 2010).

2.10.2 Chippenham Fen and Holme Fen

Chippenham Fen is located 6 km to the north of Newmarket in Cambridgeshire, UK, (Figures 2.1, 2.8 and 2.9). It is a National Nature Reserve, a Site of Special Scientific Interest (English Nature, 1999) and a Ramsar wetland site (Joint Nature Conservation Committee, 2008). Chippenham Fen is 117 hectares in size (Natural England, 2011b) and is described by the UKBMS (2010) as an area of fen, swamp and marsh with freshwater edges.

Holme Fen is located 9 km south of Peterborough, in Cambridgeshire, UK (Figures 2.1, 2.10 and 2.11). It is an area of mature broadleaved woodland (UKBMS, 2010). Holme Fen is a National Nature Reserve with an area of 266 hectares (Natural England, 2011c) and is part of the Great Fen project, which aims to restore 3000 hectares of fenland, thereby linking Holme Fen with Woodwalton Fen National Nature Reserve (Great Fen, 2011).

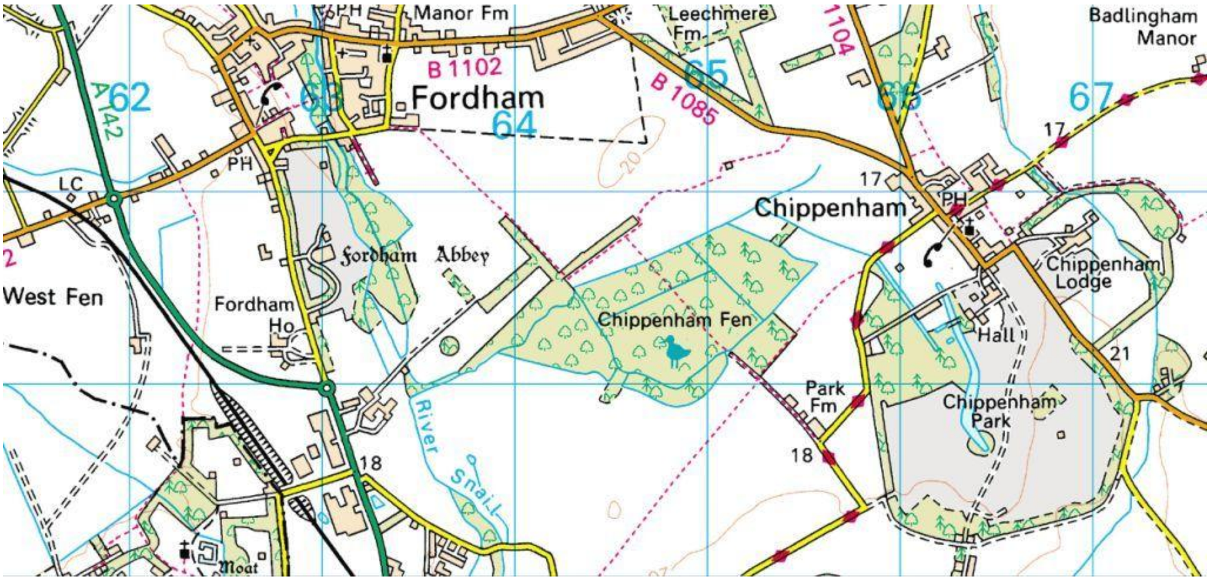


Figure 2.8. Map showing the location of Chippenham Fen. Gridlines are at 1 km intervals (www.streetmap.co.uk).

Figure 2.9. Satellite image of Chippenham Fen (www.google.co.uk).

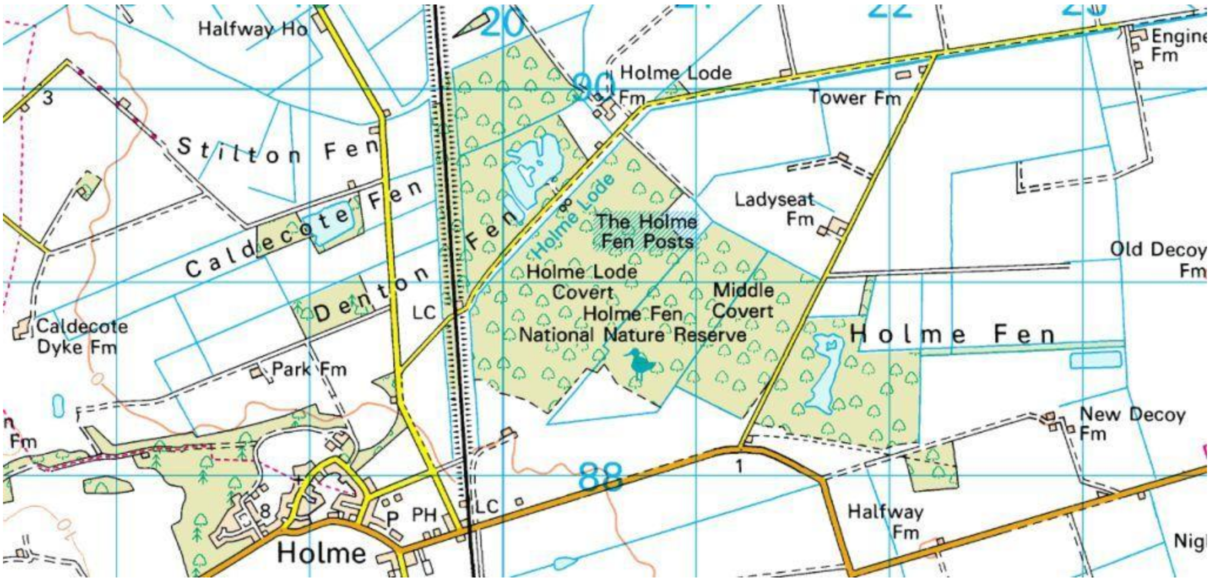


Figure 2.10. Map showing the location of Holme Fen. Gridlines are at 1 km intervals (www.streetmap.co.uk).

Figure 2.11. Satellite image of Holme Fen (www.google.co.uk).

2.11 Meteorological datasets

2.11.1 North Atlantic Oscillation index

The NAO index used throughout this analysis was published by the Climate Research Unit, University of East Anglia, UK (Climate Research Unit, 2004 and Osborn, 2010), which is based on air pressure data from Iceland and Gibraltar (Osborn, 2000). This NAO index was available in a monthly format, from which mean NAO indices for longer time periods were calculated - in particular a winter NAO index based on the mean of the January, February and March NAO indices.

2.11.2 National meteorological datasets

Monthly mean temperature data were obtained from the Central England Temperature Series (Parker *et al*., 1992 and Met Office Hadley Centre observation datasets, 2009). The Central England Temperature Series is “representative of a roughly triangular area of the UK enclosed by Lancashire, London and Bristol” (Met Office Hadley Centre for Climate Change, 2011). Monthly precipitation data were obtained from England and Wales Precipitation (Alexander and Jones, 2001 and Met Office Hadley Centre observation datasets HadUKP, 2010).

2.11.3 Local meteorological datasets

Monthly mean temperature data and monthly precipitation data for the Rothamsted meteorological station were provided to AWS by Dr R. Harrington for the period 1966 to 2006. This meteorological station is at the same location as the suction trap used to catch the *E. abietinum*.

Meteorological data were obtained for Monks Wood from the British Atmospheric Data Centre (2010), but this dataset was found to be incomplete. S. Martin, Weather Desk Advisor, Met Office, UK, provided meteorological data from the National Institute for Agricultural Botany (NIAB), located on the outskirts of north-west Cambridge. These data were in the form of monthly mean maximum temperatures, monthly mean minimum temperatures, monthly days of air frost, monthly precipitation and monthly total sunshine duration (Met Office Historic Station Data, 2010).

2.12 Statistical tests

SPSS was used to calculate Pearson correlation coefficients (r) and the associated probability (P). EXCEL was used to calculate coefficients of determination (r^2), although it is unable to calculate P values. The r^2 value is a measure of the percentage of the variability that has been explained, so $r^2 = 0.4$ means that 40% of the original variability has been described, leaving 60% residual variability (StatSoft, 2010). The coefficient of determination (r^2) is the Pearson correlation coefficient (r) squared. Pearson correlation coefficients indicate whether a gradient is positive or negative, but the squaring process removes negative values so r^2 does not indicate a positive or negative gradient. A graph is useful to identify the effect of outliers with both r and r^2 values and to determine whether a gradient is positive or negative with r^2.

Multiple linear regression calculations were used to identify the relative influence of weather for up to twelve months previously on butterfly flight timing. Multiple linear regression analysis has an advantage compared to Pearson correlations, because collinearity diagnostics were available, in particular variance inflation factors (VIF). A VIF of >5.0 was considered to be too high a risk of collinearity.

Binary logistic regression coefficients, β, were calculated when one variable was discontinuous – as with the number of butterfly generations.

The generalised linear equation, $y = mx + c$, was used to obtain the value for the gradient, m. Multiplying m by number of years was used to determine how many weeks flight timing had advanced due to climate change.

The statistical software, C^2 (Juggins, 2007 and 2010), was used to construct the multi-proxy graphs.

Assistance was provided by M. Scholze, Brunel University, with statistical path analysis using the SAS procedure PROC TCALIS (SAS Institute Inc., Cary, NC, USA).

2.13 Shannon-Wiener diversity index (*H*)

Shannon-Wiener diversity indices (*H*) have been used in other butterfly studies (Munguira and Thomas, 1992) and were calculated using the formula:

$$H = - (p_1 log_e p_1 + p_2 log_e p_2 + \ldots.. p_i log_e p_i)$$

Where P_i is the proportion of the i^{th} species in the sample. The Shannon-Wiener diversity index has the effect of weighting the contribution to the sample made by the relative abundance of each species (Ricklefs, 1990). Shannon-Wiener diversity indices were calculated for each year from 1973 to 2007 at Monks Wood.

2.14 Correspondence analysis

Correspondence analysis (CA) is a form of multivariate analysis, which was done using the statistical package C^2 (Juggins, 2007 and 2010). Correspondence analysis produces species and sample scores that explain different proportions of the variation in the data, with sample scores representing years. Species scores can be plotted against each other to search for clumping or outliers and identify whether fluctuations in the population sizes of different species were similar or different to other species or groups of species. Sample scores can be plotted against each other to identify specific years or groups of years where butterfly species are different or similar. Eigenvalues result from the correspondence analysis in C^2, and give an indication of how much variation is described by each score. However, when calculated in C^2, they are not percentages. The eigenvalues for the species scores and the sample scores are the same numbers (Steve Juggins, pers. comm.).

Correspondence analysis can be vulnerable to producing an arch effect and detrended correspondence analysis (DCA) can be used to eliminate this. DCA divides the graphical output up into segments and then repositions each segment to remove this arch effect. This has been described as ‘inelegant’ (Palmer, 2010). As an arch effect did not occur in the Monks Wood data when analysed with CA, DCA was not used.

Chapter 3

Temporal variations in English populations of a forest insect pest, the green spruce aphid (*Elatobium abietinum*), associated with the North Atlantic Oscillation and global warming

This chapter has been published as: Westgarth-Smith, A.R., Leroy, S.A.G., Collins, P.E.F. and Harrington, R. (2007) Temporal variations in English populations of a forest insect pest, the green spruce aphid (*Elatobium abietinum*), associated with the North Atlantic Oscillation and global warming. *Quaternary International* 173-174: 153-160.

Westgarth-Smith *et al*. (2007) was reviewed in *Nature Reports Climate Change* (Newton, 2008) and has received press coverage in nine publications. By January 2012, Westgarth-Smith *et al*. (2007) had been cited nine times.

Temporal variations in English populations of a forest insect pest, the green spruce aphid (*Elatobium abietinum*), associated with the North Atlantic Oscillation and global warming

3.1 Introduction

Abrupt, sometimes persistent changes in Holocene terrestrial ecosystems are well known: for example the mid-postglacial declines in European elm (*Ulmus* L.) (e.g. Peglar 1993; Parker *et al*. 2002) and hemlock (*Tsuga canadensis* (L.) Carr.) (Haas and McAndrews, 2000). Both these examples have been linked to insect pests and associated pathogens (e.g. Girling and Greig, 1985; Bhiry and Filion, 1996; Clark and Edwards, 2004) but there is still uncertainty over what made apparently stable forest populations vulnerable to such pests. Climatic forcing may well be a significant contributing factor, either by directly weakening the trees, or by enhancing insect population growth and dispersal. A more detailed understanding of the relationship between climate change and insect populations is clearly of relevance to palaeoecological studies, and in the context of the current phase of global warming.

Here the response of *Elatobium abietinum* (Walker) (green spruce aphid) to short-term climatic forcing over the last 41 years is examined. Although detailed records of individual climatic variables (temperature, precipitation etc.) are available, the influence of the North Atlantic Oscillation (NAO) is used as a proxy for a range of climatic conditions. In the mid-latitude, temperate, study area of southern England, ecosystems respond to the combined effects of several climatic variables rather than being dominated by a single variable.

The NAO has a considerable influence on the weather in north-west Europe, Scandinavia, the Mediterranean basin, eastern side of North America and Greenland. The NAO is described by the NAO index, which is calculated from air pressure at two locations. The northern location is usually in Iceland, but the southern location can be in the Azores, Lisbon or Gibraltar, the choice of location being of little importance (Osborn, 2000).

A positive NAO index is associated with depression systems taking a more northerly route across the Atlantic, resulting in warmer autumn and winter weather in the British Isles, whereas a negative NAO index is associated with the depression systems travelling in a more southerly route across the Atlantic (Osborn, 2000). Consequently the NAO index shows a strong, positive association with temperatures at Rothamsted, in Hertfordshire, U.K., between October and March and a weaker association with temperatures in April and May. The NAO has a much weaker control over precipitation, with an almost significant correlation between the January NAO index and January precipitation, but no significant correlations between the winter (January to March) NAO index and precipitation averaged over several months (Table 3.1).

3.1.1 NAO and organisms

Weather conditions associated with the NAO have been shown to have an influence on a range of different groups of organisms. Marine Copepod population size in the Eastern North Atlantic and North Sea is influenced by winter temperature and wind speed, with meteorological factors interacting with interspecific competition (Fromentin and Planque, 1996). Cod (*Gadus morhua* L.) recruitment in the North Atlantic increased during the sustained negative phase of the NAO index in the 1960s and then recruitment decreased during the more positive phase of the NAO index in the 1990s with water temperature as the most likely controlling factor (Parsons and Lear, 2001). Soay Sheep (*Ovis aries* L.) populations on Hirta, part of the St Kilda archipelago, Scotland, appear to be influenced by precipitation in March (Catchpole *et al*., 2000). Red Deer (*Cervus elaphus* L.) in Norway are affected by the NAO before birth, with warmer winters resulting in smaller birth size than those born following cold winters (Post *et al*., 1997). Reindeer and Caribou (both *Rangifer tarandus* L.) in Greenland and Russia show synchronous population changes associated with the NAO despite being geographically separated by a minimum of 3300 km (Post and Forchhammer, 2006). Butterflies (Lepidoptera) appear to be influenced in a complex manner by weather, life history characteristics and morphological characteristics associated with partial thermoregulation (Westgarth-Smith *et al*., 2005a, b and c).

3.1.2 *Elatobium abietinum* and its hosts

Elatobium abietinum was selected for this study, as high temporal resolution data, extending over 41 years, are available. This species was chosen for study from the range of species caught in a suction trap at Rothamsted, U.K., as it is one of the earliest aphid species to undertake its winged migration each year, and would therefore be flying nearer the time of year when the NAO influences U.K. weather. Also *E. abietinum* has a single, well-defined flight period (Figure 3.1), which is about two months in duration and so relatively short compared to many other aphid species. In the U.K., *E. abietinum* is continuously parthenogenetic, over-wintering in the active stages.

Elatobium abietinum lives on *Picea* spp., especially *P. sitchensis* (Bong.) Carr., but also *P. abies* (L.) H. Karst., *P. pungens* Engelm. and less frequently on *Abies* Mill. spp. (Harrington and Pickup, 2005). These tree species are not native to the British Isles. *Picea sitchensis* was introduced into the British Isles in 1831, *P. abies* was probably introduced before 1500 AD, different varieties of *P. pungens* were introduced between 1862 – 1912 and *Abies alba* (Mill.) was introduced in 1603 (Mitchell, 1978).

There is a practical relevance in understanding the ecology of *E. abietinum*, as this species is a significant pest of *Picea* spp. For example, Straw *et al*. (2000) found that *P. sitchensis*, grown in Wales, suffered 38.5% defoliation and 22.4% reduced height increment when artificially infested with *E. abietinum* at population densities equivalent to a moderate to severe outbreak. Furthermore a high infestation rate can reduce productivity in the following year as the aphids disrupt bud formation, which reduces the quality of foliage and photosynthetic ability, causing 12.2% decrease in the stem diameter increment and 23.8% decrease in the stem volume increment.

Trees in the U.K. are rarely killed by *E. abietinum* (Williams *et al.*, 2005). However *E. abietinum* has been introduced into the south-western USA (Campbell, 2005) where it can cause 24 - 41% mortality of *Picea engelmannii* (Parry) Engelm. and a combined infection with *E. abietinum* and the mistletoe, *Arceuthobium microcarpum*

(Engelm.) Hawksworth and Wiens, can cause 70% mortality of *P. pungens* (Lynch, 2004).

Associations between climate and tree pest species are of interest to palaeoecologists. For example, the summer drought related decline of hemlock (*Tsuga canadensis*) in eastern North America which occurred 5700 – 5100 years ago may be due to drought weakened trees being attacked by insect pests (Haas and McAndrews, 2000), especially the hemlock looper (*Lambdina fiscellaria* (Guen.)) and the spruce budworm (*Choristoneura fumiferana* (Clem.)) (Bhiry and Filion, 1996). Similarly the mid-Holocene elm (*Ulmus*) decline appears to be a combined effect of elm disease which is an infection by the ascomycete fungus, *Ophiostoma* (*Ceratocystis*) *ulmi* (Buisman) carried by elm bark beetles, *Scolytus scolytus* (F.) and *S. multistriatus* (M.), as well as climate change and human activities (Parker *et al*., 2002).

Insect pest associated changes in tree growth rates are used to identify historical records of pest outbreaks in forests. For example, *Choristoneura occidentalis* (Freeman), another spruce budworm, outbreaks on Douglas-fir (*Pseudotsuga menziesii* var. *glaucha* Mirb. Franco) growing in British Columbia, Canada (Campbell *et al*., 2005) and the larch budmoth (*Zeiraphera diniana* Guénée) defoliation of larch (*Larix decidua* Mill.) in the French Alps (Rolland *et al*., 2001).

Palaeoecology uses organism population changes as a proxy for meteorological changes, however, butterflies (Lepidoptera) in the U.K. show complex associations between their life history characteristics and the NAO index, such that species that are more positively correlated with the NAO index are more likely to have two generations per year (bivoltine) rather than one generation per year (univoltine) and have a longer flight season. This is because positive NAO index years tend to be warmer, allowing more time to complete two generations and for a longer flight period. There are also associations with the over-wintering stage such that species of butterfly that hibernate as adults show much less association with the NAO index than species that over-winter as larvae, this is probably because adult butterflies have completed their feeding before the onset of NAO controlled autumn and winter weather, whereas larvae will feed on warm winter days (Westgarth-Smith *et al*., 2005a, b and c).

Analyses by Westgarth-Smith *et al*. (2005a, b and c) of the effect of the NAO index on butterfly populations were based on an annual collated index of butterfly population size. We wanted to extend this work to use a daily insect dataset, in particular to examine the influence of the NAO on phenology. Phenology is of particular current interest with biological events reportedly happening earlier in the spring, and also later in the autumn as a response to global warming. For example Roy and Sparks (2000) suggest that climate warming of 1°C could advance butterfly appearance by 2-10 days.

We hypothesise that there is a correlation between the NAO index and the timing and size of the spring migration of the green spruce aphid, *Elatobium abietinum* (Walker). These associations may be of interest to foresters responsible for spruce (*Picea*) plantations and palaeoecologists investigating the associations between climate, tree population size and insect pests.

3.2 Materials and methods

Daily counts have been made of aphids since 1966 from a 12.2 m high suction trap (Macaulay *et al*., 1988) at Rothamsted Research near Harpenden, 30 km north of London, U.K. Air is sucked into the trap at a constant rate every day of the year and the traps operate with a very high level of reliability, such that trap breakdown events are exceptionally rare. With 41 years of data available, this is one of the longest invertebrate ecological datasets available in the World. This trap is one of a network of 16 suction traps distributed throughout England and Scotland, operated by the Rothamsted Insect Survey (Harrington and Woiwod, 2007). As part of their life cycle, aphids undergo a period of flight. This winged migration takes place at different times of year depending on the species.

From the daily aphid data it was possible to calculate a total number of *E. abietinum* caught per year and to obtain the first and last date of capture. The dates were recorded as Julian calendar dates, where, for example, 1 January is day 1 and 1 June is day 152. The flight period is the inclusive number of days between the first and last date of capture.

The mean flight day number was calculated by multiplying the number of aphids caught each individual day by the Julian date. These numbers were then summed for each year and divided by the total number of aphids caught in that year.

Monthly NAO indices were obtained from the Climate Research Unit (2004) and Osborn (2006). This NAO index is based on atmospheric pressures in Iceland and Gibraltar and is available in a monthly form. The winter NAO index was calculated as a mean of the January, February and March NAO indices and an autumn and winter (October to March) NAO index, used in Table 3.1 only, was calculated from the mean of all monthly NAO indices from October to March.

Monthly mean temperature data and monthly precipitation data were obtained from the Rothamsted meteorological station.

The generalised linear equation $y=mx+c$ was used to describe the trend lines for first flight day number and mean flight day number, when plotted against the winter NAO index. The gradient, m, was used to calculate the change in the day number associated with a change in the winter NAO index. The intercept, c, can be used to estimate the day number for the first day of flight or mean flight day number at Rothamsted for a winter NAO index of zero.

3.3 Results

The total number of *E. abietinum* caught per year in the Rothamsted suction trap ranged from 5 to 592. Log_{10} total numbers of *E. abietinum* caught per year suggest an upward trend with time, but with considerable oscillations from year to year (Figure 3.2). There is a significant positive correlation (Pearson correlation coefficient = 0.387, *P*. = 0.012) between the winter NAO index and the $\log_{10}$ total number of *E. abietinum* caught per year (Figure 3.3).

There is a significant negative correlation between the winter NAO index and the first date of capture of *E. abietinum* (Pearson correlation coefficient = -0.407, *P*. = 0.008, Figure 3.4), but not the date of last capture (Pearson correlation coefficient = -0.034, *P*. = 0.834, Figure 3.4). As a result, the flight period is significantly positively correlated with the NAO index (Pearson correlation coefficient = 0.334, *P*. = 0.033, Figure 3.5). Mean flight date is significantly negatively correlated with the winter NAO index (Pearson correlation coefficient = -0.402, *P*. = 0.009, Figure 3.6). During the period 1966 to 2006, the first date of capture has advanced by 29.7 days, the mean flight day number has advanced by 17.5 days and the last date of capture by 19.7 days (Figure 3.7).

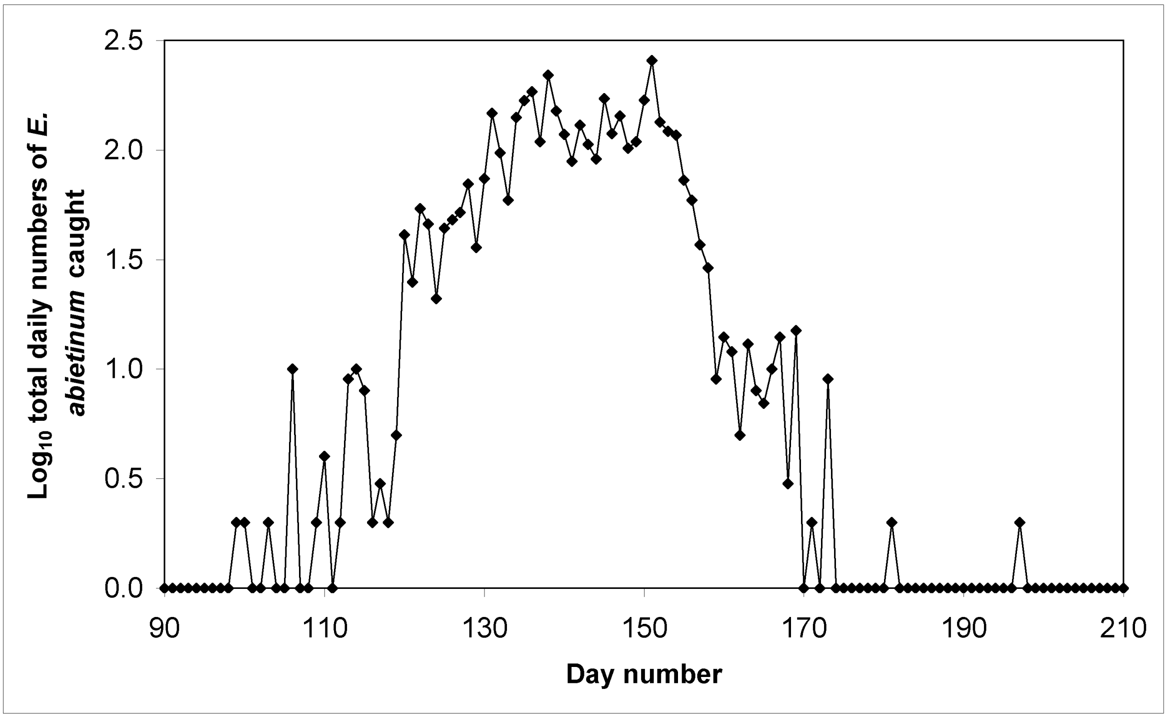


Figure 3.1. Annual migration pattern for *E. abietinum*. Graph of $\log_{10}$ total daily counts for 1966-2006 against day number.

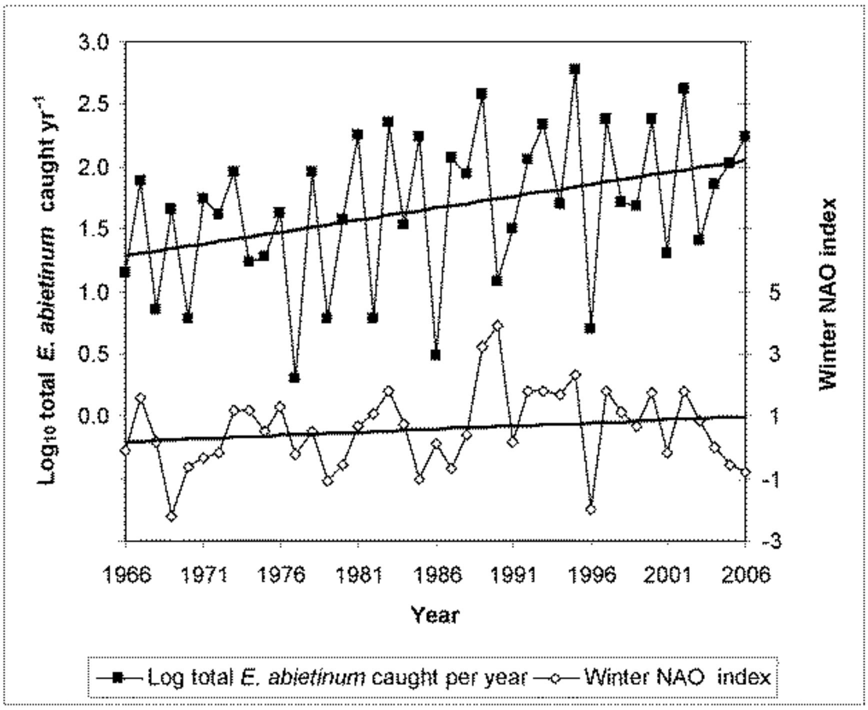


Figure 3.2. Log_{10} total number of *E. abietinum* caught per year and the winter NAO index for the years 1966-2006.

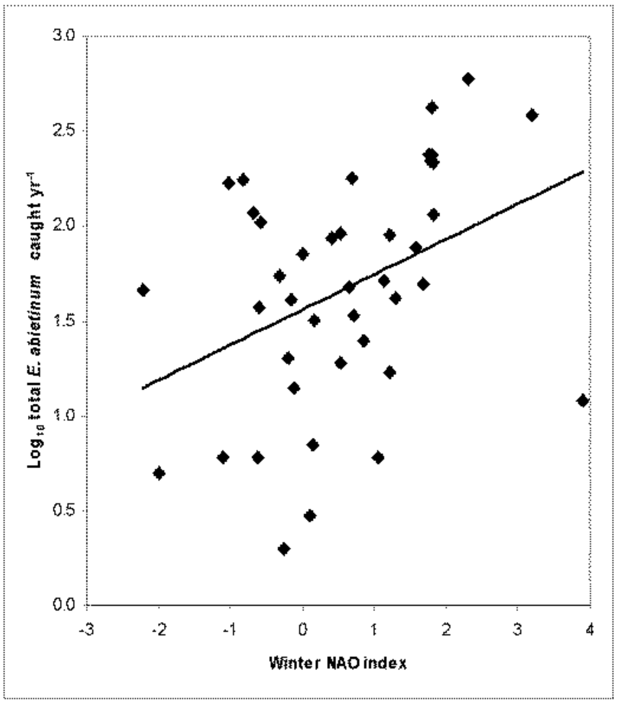


Figure 3.3. Relationship between the $\log_{10}$ total number of *E. abietinum* plotted against the winter NAO index. Pearson correlation coefficient = 0.387, *P*. = 0.012.

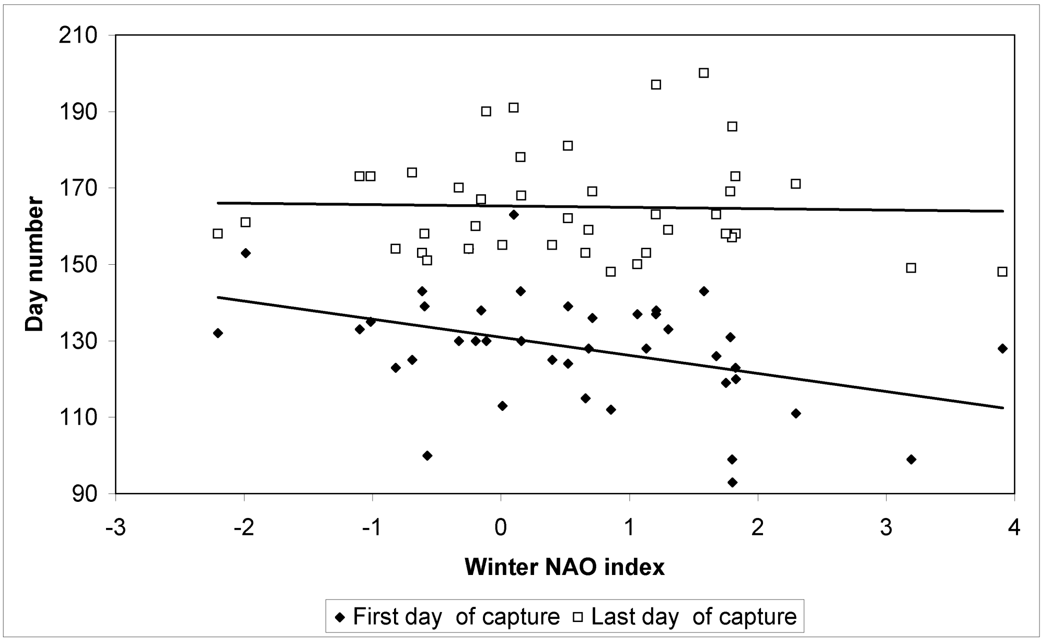


Figure 3.4. Relationship between first day of capture of *E. abietinum* and the winter NAO index (Pearson correlation coefficient = -0.407, *P*. = 0.008) and between the last day of capture of *E. abietinum* and the winter NAO index (Pearson correlation coefficient = -0.034, *P*. = 0.834). The linear equation for the trend line for the first day of capture is y = -4.7322x + 130.96.

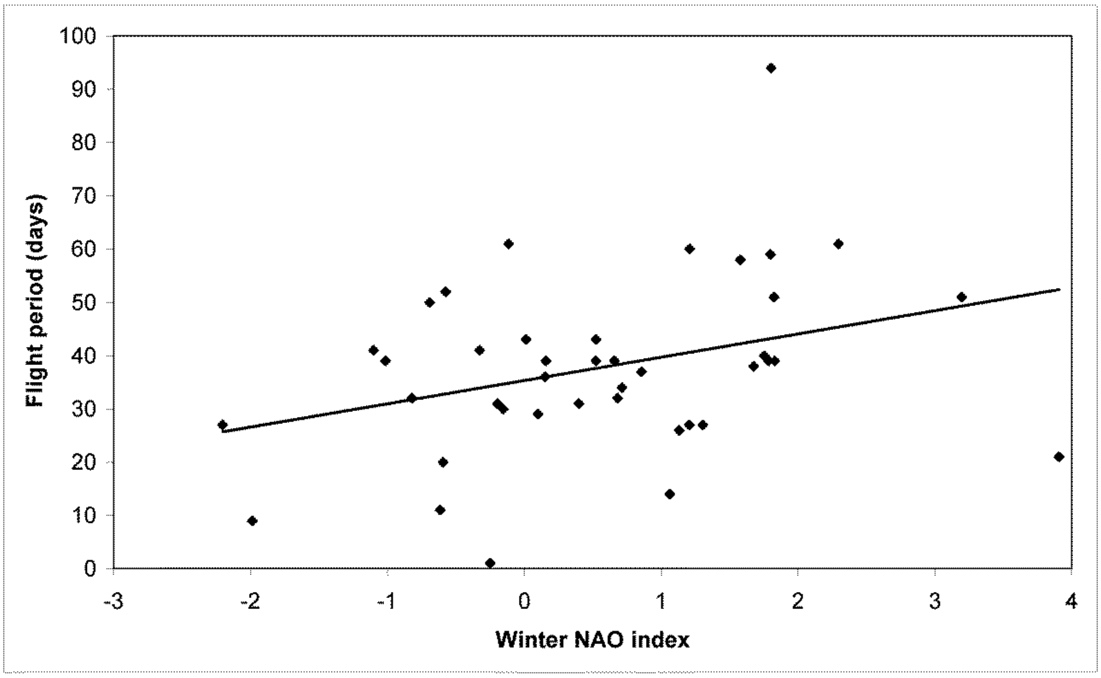


Figure 3.5. Relationship between the total flight period of *E. abietinum* in each year and the winter NAO index (Pearson = 0.334, *P*. = 0.033).

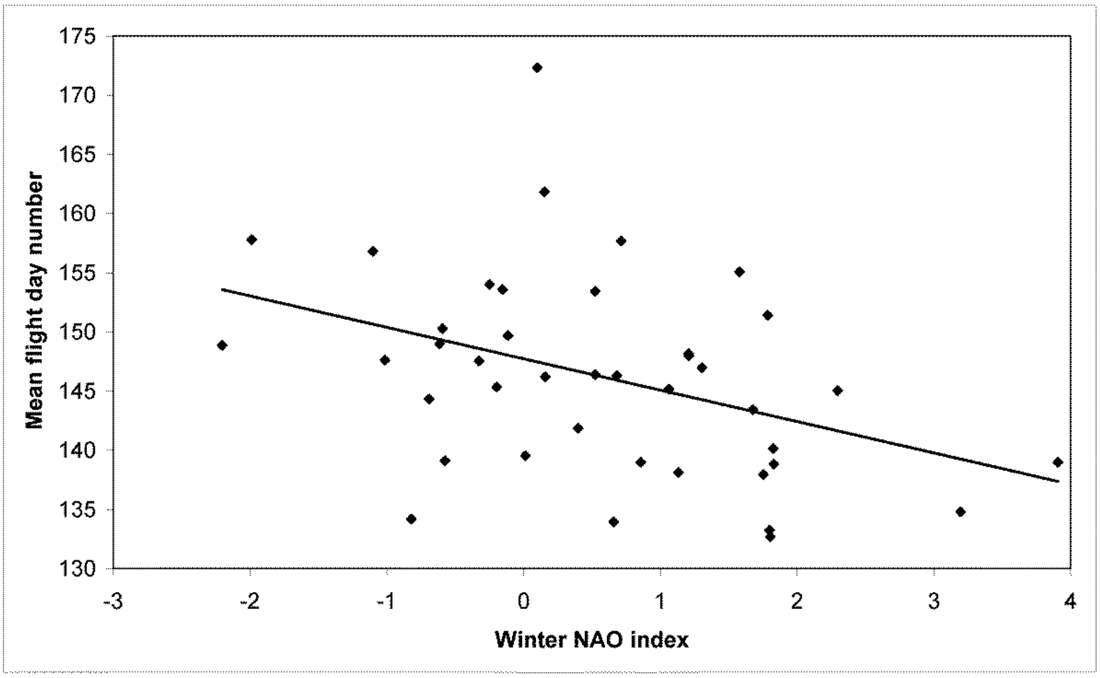


Figure 3.6. Relationship between the mean flight day number of *E. abietinum* and the winter NAO index (Pearson correlation coefficient = -0.402, *P*. = 0.009). The linear equation for the trend line is y = -2.6575x + 147.74.

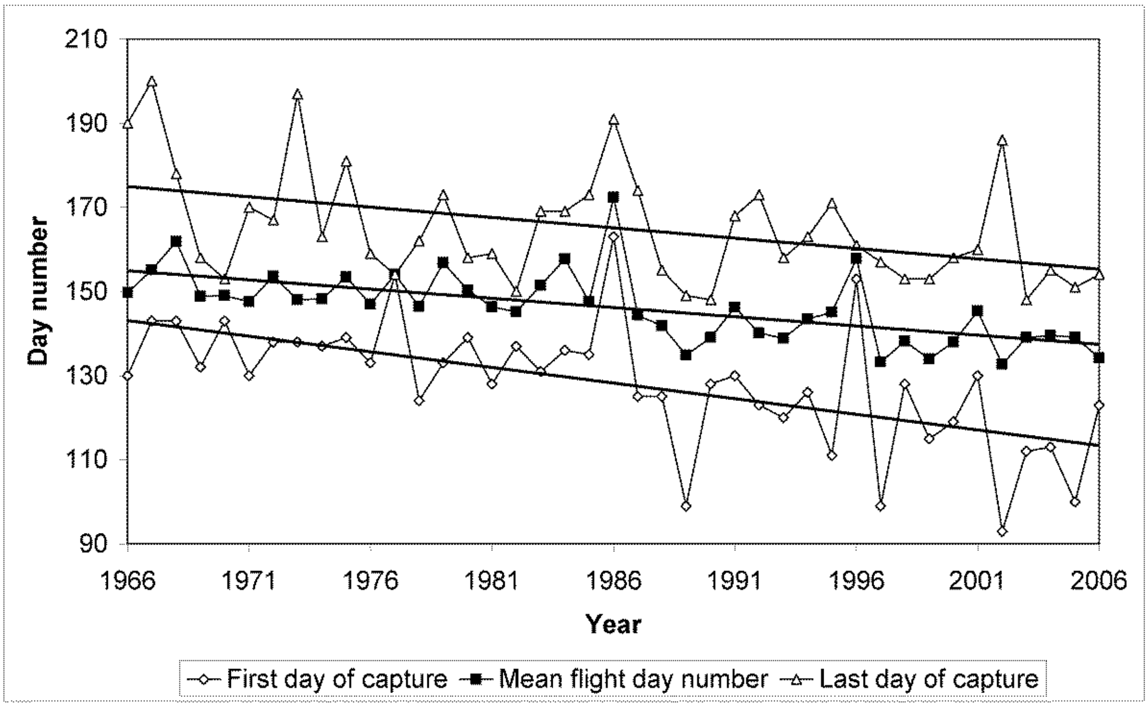


Figure 3.7. First date of capture, mean flight date and last date of capture of *E. abietinum* for the period 1966-2006.

	Winter NAO index		Log$_{10}$ annual total *E. abietinum*	
	Correlation coefficient	Probability	Correlation coefficient	Probability
Mean October to April temperature	0.351	0.024	0.517	0.001
Mean October to April precipitation	-0.023	0.888	-0.241	0.129
Mean January to April temperature	0.646	<0.001	0.458	0.003
Mean January to April precipitation	-0.015	0.927	-0.242	0.127
Mean May to June temperature	0.296	0.060	0.207	0.194
Mean May to June precipitation	-0.110	0.492	0.081	0.615
Winter NAO index			0.387	0.012
October to March NAO index			0.485	0.001

Table 3.1. Pearson correlation coefficients showing the relationships between temperature and precipitation at different times of year and the log$_{10}$ annual total number of *E. abietinum* caught in the Rothamsted suction trap. An October to March NAO index was used in calculating correlation coefficients with mean October to April temperature and precipitation and the winter (January to March) NAO index was used in calculating correlation coefficients with the mean January to April and mean May and June temperature and precipitation.

There are highly significant positive correlations between the $\log_{10}$ annual total number of *E. abietinum* and the mean October to April temperature (Pearson correlation coefficient = 0.517, *P*. = 0.001) and with the mean January to April temperature (Pearson correlation coefficient = 0.458, *P*. = 0.003). However the annual total number of aphids is not significantly correlated with the mean May to June temperature (Pearson correlation coefficient = 0.207, *P*. = 0.194). There are no significant correlations between the total annual capture of *E. abietinum* and precipitation (Table 3.1).

The data were tested for 1st order temporal autocorrelations and the only relationship found was a negative association for $\log_{10}$ annual total *E. abietinum* in successive years (Pearson correlation coefficient = -0.371, *P*. = 0.018).

3.4 Discussion

The warmer weather associated with a positive NAO index appears to result in *E. abietinum* starting to fly earlier in the year with an earlier peak in flight activity, also as the NAO index has become more positive with time, the flight season for *E. abietinum* has tended to start sooner. The last date of flight is unchanged by the NAO, so the more positive the NAO index, the longer the flight period. The lack of an association between the last date of flight and the NAO might be due to a much weaker link between weather and the NAO this late in the year, or to the fact that the end date of aphid flight is controlled by some other factor, including possibly a change in the nutritional quality of the phloem sap (Day *et al*., 2004).

The highly significant correlation between the total annual capture of *E. abietinu*m and mean January to April temperatures indicates that temperature during this period is important in controlling the population size of this species. A slight increase in the significance level of the correlation coefficient for mean October to April temperatures, when compared to mean January to April temperatures, might indicate that both autumn and winter temperatures are important. Temperatures in May and June do not appear to affect the population size of *E. abietinum*, which suggests that the population size was determined before the migration and also validates the suction traps as a census method as the number of aphids caught is not a function of temperature determined flight ability. Moreover, precipitation appears to have no effect on *E. abietinum* population size. As the NAO has a much greater influence over temperature rather than precipitation (Table 3.1), it seems that the mechanism for control of *E. abietinum* population size by the NAO is through temperature rather than precipitation.

These results suggest that the winter NAO index can be used as a proxy for the population size of *E. abietinum* in the Rothamsted area. Furthermore the winter NAO index can be used to predict the timing of the winged migration of *E. abietinum* with an increase of 1.0 in the winter NAO index resulting in a 4.7 day advance in first flight date and a 2.7 day advance in mean flight day number (Figures 3.4 and 3.6). For the Rothamsted area it is possible to calculate the actual date by using the intercept as a reference point. So with a winter NAO index of zero, it would be expected that *E. abietinum* would start flying on about Julian day number 131 (11 May) and the mean flight day number would be day 148 (28 May). The aphid data for Rothamsted is considered to be representative of an area of 80 km radius (Harrington and Woiwod, 2007), so it would be necessary to recalculate this predictive model for different areas. With the winter NAO index predicting the scale and timing of the migration of *E. abietinum*, it may be possible to use the winter NAO index as a proxy for the amount of *E. abietinum* damage to *Picea* populations.

A general upward trend in the number of *E. abietinum* caught per year occurs during the period 1966-2006. During the same period, the winter NAO index has become more positive (Figure 3.2), the mean annual temperature at Rothamsted increased by 1.46ºC and the mean annual temperature from the Central England Temperature Series increased by 1.19ºC Series (Manley, 1974 and Hadley Centre, 2003). It is possible that the global warming trend will be manifested in the U.K. by an increasingly more positive NAO index, which will in turn be associated with greater flight activity of *E. abietinum* and probably increasing aphid damage to spruce trees. While it is possible that this upward trend in the population of *E. abietinum* in part reflects an increase in the percentage of coniferous forests that has occurred in Great Britain during the period 1950 – 1990, the majority of the increase in sitka spruce has been in Scotland (Forestry Commission, 2005). However the percentage of conifers has been considerably reduced during the 1990s, but an associated decline in *E. abietinum* is not apparent (Figure 3.2).

The dataset used for this chapter has some limitations, including a very large range in sample size. A future line of enquiry might include averaging aphid data for years with similar NAO indices. Flight times could be calculated for years with a winter NAO index of 0.00 to 0.99, 1.00 to 1.99, etc. This would eliminate datapoints based on very small sample sizes. It may also be possible to merge data from nearby suction traps, although there are likely to be latitudinal differences in the weather. The effect of latitudinal temperature differences on flight timing could be a surrogate for climate change and make it possible to investigate the interaction of the NAO and climate change on the ecology of *E. abietinum*.

3.5 Conclusion

The present study has shown a strong link between the winter NAO index and the phenology of the aphid, *E. abietinum*. A positive NAO index is associated with larger populations that start flying earlier in the year and which have a longer flight period. Furthermore there is evidence that global warming is resulting in the winter NAO index becoming more positive, therefore high population sizes of *E. abietinum* may become more common. The winter NAO index has considerable potential as a predictor of the scale and timing of infestations of *E. abietinum* and the associated damage to *Picea*, as well as the potential for use as a proxy in palaeoecological studies of insect pest damage to trees.

Chapter 4

The role of the North Atlantic Oscillation in controlling UK butterfly population size and phenology

This chapter is a manuscript currently under review for publication in the journal *Ecological Entomology*: Westgarth-Smith, A.R., Roy, D.B., Scholze, M., Tucker, A. and Sumpter, J.P. The role of the North Atlantic Oscillation in controlling UK butterfly population size and phenology.

The role of the North Atlantic Oscillation in controlling UK butterfly population size and phenology.

4.1 Introduction

Climate change is affecting UK butterfly populations, with the northern distributional limits of some species moving northwards (Hill *et al*., 2002; Asher *et al*., 2001; Asher *et al*., 2011) and most species flying earlier (Sparks and Yates, 1997; Roy and Sparks, 2000). It is predicted that projected climate change might cause future population changes (Roy *et al*., 2001). Insects are excellent organisms to investigate the influence of weather as they are poikilothermic and are therefore strongly influenced by climatic conditions. The present study investigates the effect of the North Atlantic Oscillation (NAO) on butterfly ecology, using data from the United Kingdom Butterfly Monitoring Scheme (2010), which currently contains 16.4 million butterfly records and is one of the best long-term biodiversity datasets in the World.

The North Atlantic Oscillation (NAO) exerts a considerable control on the weather in the North Atlantic, Mediterranean, Europe and Scandinavia (Hurrell and Desser, 2010). The NAO is described by the NAO index, which is calculated from air pressures in Iceland and a location within the region of the Azores high pressure area. The NAO exerts a stronger control on temperature than on precipitation and has its greatest influence on weather in the autumn and winter. A positive NAO index is associated with depression systems taking a more northerly route across the Atlantic, so UK weather is milder with slightly higher precipitation – in other words slightly more maritime in nature and a negative NAO index is associated with depression systems taking a more southerly route, so UK weather tends to be colder and drier, or slightly more continental in nature (Osborn, 2000).

The NAO index is associated with a range of meteorological factors including temperature, precipitation, cloud cover and storms, and so can be a more useful means of describing the variability of the weather experienced by an organism than a single variable such as temperature (Stenseth, *et al*., 2003, Hurrell and Deser, 2010). In effect, the NAO index is a synthesis of a range of weather features that interact to affect organisms. The NAO exerts most of its control on the weather before the butterfly flight season (Table 4.1), making it potentially more useful than mean annual temperature to explain butterfly ecology, as mean annual temperature is the mean for all 12 months, including months that are later in the year, after the butterflies have finished flying.

A study of the spring arrival time of 81 migratory bird species in Finland showed that most species arrived earlier in years with a positive NAO index, and therefore characterised by mild, rainy, weather. This association was significant for 79% of the species and the correlations were stronger for earlier, rather than later, phases of the migration (Vähätalo *et al*., 2004). Spring migrant birds have also been found to arrive earlier in years with a positive NAO index in the Czech Republic (Hubalek, 2003) and on Helgoland (Hüppop and Hüppop, 2003). However, the arrival time of trans-Saharan migrant birds to the Mediterranean area can also be influenced by factors including vegetation growth in their over-wintering and passage areas and different weather conditions, depending on whether they take a western or an eastern route through the Mediterranean (Robson and Barriocanal, 2011), indicating that there can be many environmental variables in different geographical regions that can control the phenology of migrant species.

In freshwater habitats, warmer water associated with a positive NAO index results in earlier emergence of sea trout (*Salmo trutta* L.) fry in the English Lake District (Elliott *et al*., 2000). Graphs in that paper suggest that the NAO is associated with about a 3ºC variation in water temperature, which is associated with about five weeks of variation in the emergence date. Mayfly (Ephemeroptera) nymphs in Wales were found to grow faster during positive phases of the NAO, as the water temperature of the streams that they inhabit is warmer (Briers *et al*., 2004).

In England, warm weather associated with a positive NAO index causes the spring migration of the green spruce aphid, *Elatobium abietinum* (Walker), to start earlier, continue for longer and contain more aphids (Westgarth-Smith *et al*., 2007). There is also preliminary evidence that the NAO influences UK butterfly population size (Westgarth-Smith *et al*., 2005a, 2005b and 2005c).

In marine environments, Copepod population size in the Eastern North Atlantic and North Sea is affected by the NAO through temperature and wind speed interacting with interspecific competition between two species of Copepod (Fromentin and Planque, 1996). Jellyfish (Cnidaria: Scyphozoa) population size in the North Sea appears to be negatively associated with the North Atlantic Oscillation index (Lynam *et al*., 2004), although the controlling mechanism is unclear.

The NAO also affects plants, with highly significant negative associations between the NAO index and the leafing dates of eleven tree species and the flowering dates of nine plant species in the UK (D'Odorico *et al*., 2002). The NAO has an impact on UK agriculture, as demonstrated by the association between the NAO index and the quality and economic value of wheat (*Triticum* spp.) (Kettlewell *et. al*. 1999).

The aims of the present study were to investigate whether the NAO influenced butterfly abundance and phenology and whether there was an interaction with life history variables, including the number of generations and duration of the flight season. Was it possible to identify a mechanism where weather associated with the NAO in specific months influenced butterfly phenology, and if so, was the mechanism different for univoltine (one generation per year) and bivoltine (two generations per year) species?

4.2 Materials and methods

4.2.1 Meteorological datasets

Monthly NAO indices were obtained from the Climate Research Unit (2004) and Osborn (2010). This NAO index uses air pressure data from Iceland and Gibraltar. A winter NAO index was calculated as a mean of the January, February and March NAO indices. Monthly mean temperature data were obtained from the Central England Temperature Series (Parker *et al*., 1992 and Met Office Hadley Centre observation datasets, 2009) and monthly precipitation data were from England and Wales Precipitation (Alexander and Jones, 2001 and Met Office Hadley Centre observation datasets HadUKP, 2010).

4.2.2 The UK Butterfly Monitoring Scheme

The UK Butterfly Monitoring Scheme was piloted in Monks Wood in Cambridgeshire, UK, during 1973-75, and was then extended nationally from 1976, with a steadily expanding number of survey sites in the UK. The technique involves walking a standard line transect on a weekly basis from the start of April to the end of September when weather conditions are suitable for butterfly activity. All butterflies seen by the observer in a 5 metres wide strip are identified and counted (Pollard and Yates, 1993; United Kingdom Butterfly Monitoring Scheme, 2010).

Butterfly data for 1976-2009 are available as a multi-species annual collated index, calculated from UK abundance data for 49 species (Brereton *et al*., 2011) and annual collated indices for each species. These collated indices are calculated from all Butterfly Monitoring Scheme sites in the UK and are a national, annual index of abundance. Weekly butterfly counts are also available from each Butterfly Monitoring Scheme transect site (United Kingdom Butterfly Monitoring Scheme, 2010). The peak flight week was the week when the most butterflies were seen for the entire national dataset.

Butterfly life history information, including the typical number of generations per year and the usual months when adults fly, was obtained from Pollard and Yates (1993).

4.2.3 Choice of species

Although species-level annual collated indices were available for most UK species (n = 57), those species that do not have data for the entire time series from 1976-2009 were excluded from the present study. Also the three main migrants - *Colias croceus* (Geoffroy), *Vanessa atalanta* (L.) and *V. cardui* (L.) - were excluded as these species spend part of their life cycle outside the UK and therefore in different meteorological conditions. Therefore annual collated indices for 35 species were used in the current study. Of these 35 species, 23 species are univoltine and 12 are bivoltine. Bivoltine species may be more strongly affected by the NAO as their two generations are spread through a longer period of the year than univoltine species, and so are more active at times of the year when the NAO affects the weather.

None of the 35 species had precisely defined peak flight weeks in all 34 years between 1976 and 2009. It can, for example, be difficult to precisely identify a peak flight week if a similar number of butterflies were counted in two adjacent weeks. However, abundant, univoltine species with shorter flight seasons resulted in more accurately defined peak flight weeks in more years than species that were bivoltine, less abundant or had a longer flight season. Accurate determination of the peak flight week for some bivoltine species was reduced if one generation was quite small, or by the presence, in some years, of a third generation. Voltinism is also affected by latitude, so a species can be bivoltine in southern Britain and univoltine further north. Thus, high quality datasets suitable for analysis of flight timing are available for only a rather limited number of butterfly species, most of which are univoltine, and only two are bivoltine.

Six butterfly species were chosen to investigate the association between the NAO and peak flight week. These species had enough high quality data throughout the entire time period studied. These were four univoltine species: *Anthocharis cardamines* (orange tip), *Melanargia galathea* (marbled white), *Aphantopus hyperantus* (ringlet), *Pyronia tithonus* (gatekeeper or hedge brown); and two bivoltine species: *Lasiommata megera* (wall brown) and *Polyommatus icarus* (common blue). The four univoltine species chosen cover two seasons of the year, with *A. cardamines* flying in the spring when the NAO has the maximum control over the weather, but not so early that too many butterflies are missed because they are flying before the survey starts, or the weather is too unstable to calculate an accurate peak flight week. *M. galathea*, *A. hyperantus* and *P. tithonus* fly in the summer. The first generations of *L. megera* and *P. icarus* fly in the late spring and their second generations in the summer (Figure 4.1). Therefore, all six species peak at different times, and hence should provide an indication of how the NAO affects butterfly populations throughout the spring and summer.

4.2.4 Statistical analysis of data

Pearson correlation coefficients (r) and probabilities (P) were used. Percentage control of variability was calculated using a coefficient of determination (r^2) multiplied by 100. Multiple linear regression analysis was used to identify which month's weather had the most influence on peak flight week - regression coefficients (*b*), probabilities (*P*) and overall model coefficients of determination (r^2) were calculated. Variance inflation factors (VIF) were used as a test for collinearity, with a VIF of <5.0 considered to be free from collinearity. Binary logistic regression coefficients (*β*) were calculated when using the number of generations, as this was a discontinuous variable.

Associations between the winter NAO index and the first and second generation peak flight week numbers were investigated by path analysis. Here we considered two models with the following direct and indirect dependencies: (i) second generation peak flight week numbers are connected only indirectly to the winter NAO index (winter NAO index → first generation → second generation), and (ii) they are connected directly and indirectly to the winter NAO index (winter NAO index → first generation → second generation and winter NAO index → second generation).

The software used for Pearson correlation coefficients, multiple linear regression analysis and binary regression analysis was SPSS. Coefficients of determination were calculated using Excel. The statistical software, C^2 (Juggins, 2007 and 2010), was used to construct the multi-proxy graphs (Figures 4.1 and 4.2A). Statistical path analysis was performed using SAS procedure PROC TCALIS (SAS Institute Inc., Cary, NC, USA).

4.3 Results

4.3.1 The NAO, climate change and weather

During the period 1976 to 2009, mean annual temperature recorded in the Central England Temperature Series increased by 1.22 °C. Although the winter NAO index fluctuated considerably during this period, there was no overall increase or decrease (Figure 4.2A).

There was a highly significant Pearson correlation between the winter NAO index and mean annual temperature ($r = 0.544$, $P = 0.001$, Figure 4.2B). To identify the months in which the NAO affects the weather in the UK, Pearson correlation coefficients were calculated between monthly NAO indices, mean monthly temperatures and monthly precipitation. There were highly significant positive Pearson correlation coefficients (*P* = <0.001) between monthly NAO indices and mean monthly temperatures in December to February and significant positive correlations (*P* = <0.050) in October, March and April (Table 4.1). The correlation for November was not quite significant (*P* = 0.059). The association between the NAO and precipitation was weaker, although there were significant positive correlations between monthly NAO indices and monthly precipitation in January (*P* = 0.026) and February (*P* = 0.021) (Table 4.1).

	Temperature		Precipitation	
	r	*P*	*r*	*P*
October	0.446	0.008	0.052	0.769
November	0.327	0.059	0.228	0.195
December	0.649	<0.001	0.226	0.199
January	0.568	<0.001	0.381	0.026
February	0.727	<0.001	0.395	0.021
March	0.367	0.033	-0.068	0.704
April	0.362	0.036	-0.011	0.949
May	0.219	0.213	0.085	0.631
June	0.048	0.790	-0.342	0.048
July	-0.020	0.911	-0.116	0.515
August	0.169	0.341	-0.100	0.574
September	0.193	0.273	-0.324	0.062

Table 4.1. Pearson correlation coefficients (*r*) and probabilities (*P*) between monthly NAO indices, mean monthly temperatures and monthly precipitation. September is the last month of the year when butterflies are counted by the UK Butterfly Monitoring Scheme, so the table runs from October of the previous year (dataset used was 1975-2008) to September of the current year (dataset used was 1976-2009).

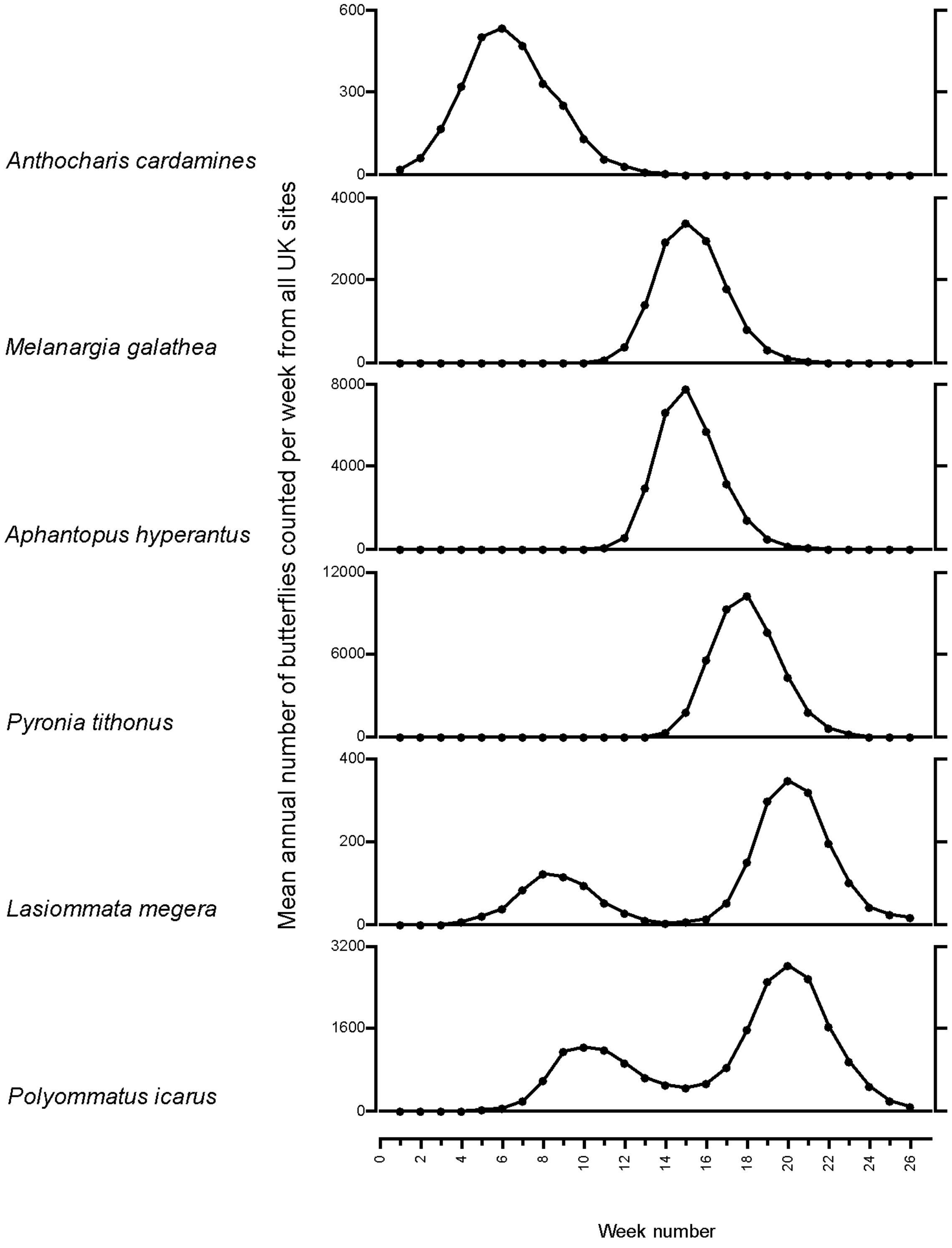


Figure 4.1. Flight seasons of four univoltine butterfly species, *A. cardamines*, *M. galathea*, *A. hyperantus*, *P. tithonus* and two bivoltine species, *L. megera* and *P. icarus*. Data are annual mean number of each species counted per week from all UK Butterfly Monitoring Scheme sites for 1976-2009. The week numbers are those used by the United Kingdom Butterfly Monitoring Scheme (2010), so week 1 is the first week of April and week 14 is the first week of July.

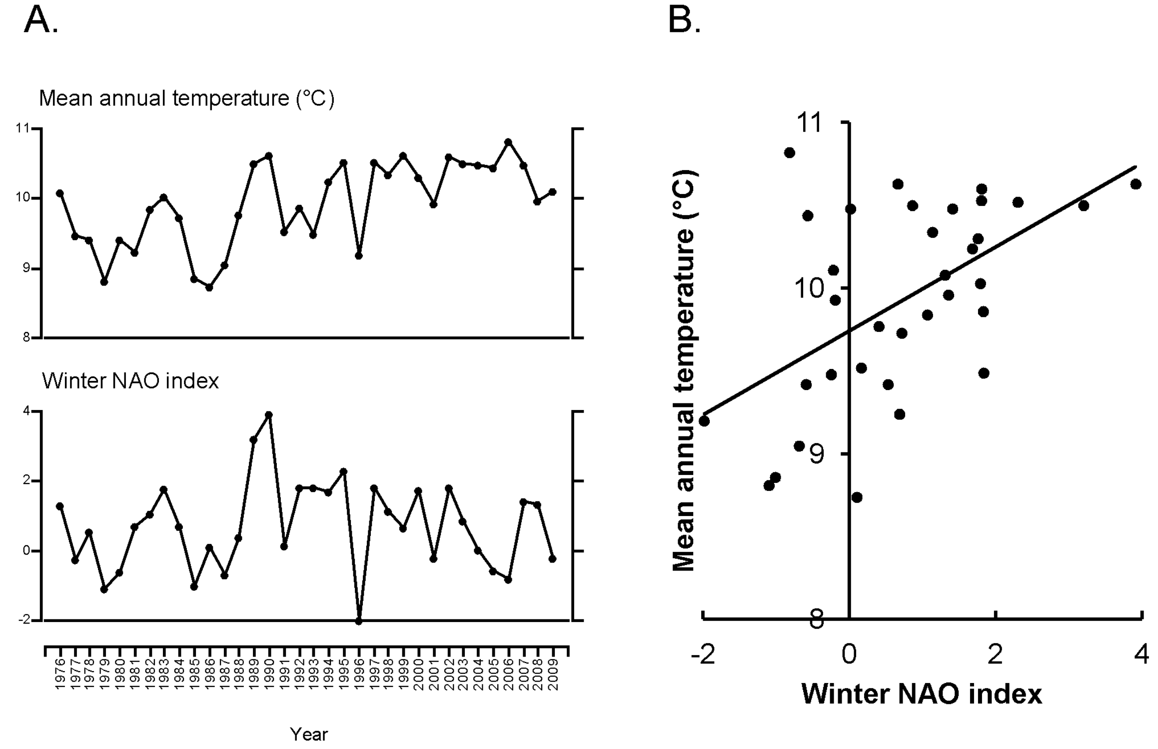


Figure 4.2. Mean annual temperature and the winter NAO index between 1976 and 2009. (A) Mean annual temperature has increased by 1.22 °C (*r* = 0.620, *P* = <0.001) between 1976 and 2009. (B) Association between the mean annual temperature and the winter NAO index (*r* = 0.544, *P* = 0.001).

4.3.2 The relationship between the NAO and butterfly abundance

The multi-species collated index was used to assess the association between the collective abundance of many species and the winter NAO index. There was no significant association between the winter NAO index and the multi-species annual collated index (*r* = 0.137, *P* = 0.439, r^2 = 0.0189), suggesting that the NAO does not affect the total population size of all butterfly species in the UK.

Pearson correlation coefficients were calculated between the annual collated indices for all 35 individual species and the winter NAO index, to determine if there were associations for individual species. Only one species, *L. megera*, showed a significant positive correlation (*r* = 0.348, *P* = 0.043). However, bivoltine species (*β* =

10.346, *P* = 0.006) and those with a longer flight period (*r* = 0.248, *P* = 0.151) tended to have a stronger positive correlation between the population index and the winter NAO index (Table 4.2).

					Months when flying												
Scientific name	Common name	*r*	*P*	Number of generations	J	F	M	A	M	J	J	A	S	O	N	D	Total months
Lasiommata megera (L.)	Wall Brown	0.348	0.043	2					●	●	●	●					4
Anthocharis cardamines (L.)	Orange Tip	0.310	0.074	1				●	●	●							3
Lycaena phlaeas (L.)	Small Copper	0.304	0.080	2					●	●	●	●					4
Pararge aegeria (L.)	Speckled Wood	0.277	0.113	2				●	●	●	●	●	●	●			7
Celastrina argiolus (L.)	Holly Blue	0.257	0.142	2				●	●	●	●	●					5
Polyommatus icarus (Rott.)	Common Blue	0.237	0.178	2					●	●	●	●					4
Pieris rapae (L.)	Small White	0.235	0.181	2					●	●	●	●					4
Pieris napi (L.)	Green-veined White	0.185	0.296	2					●	●	●	●					4
Aphantopus hyperantus (L.)	Ringlet	0.135	0.447	1							●	●					2
Hipparchia semele (L.)	Grayling	0.125	0.482	1							●	●					2
Erynnis tages (L.)	Dingy Skipper	0.111	0.532	1					●	●							2
Coenonympha pamphilus (L.)	Small Heath	0.106	0.552	2					●	●	●	●	●				5
Ochlodes sylvanus (Esper)	Large Skipper	0.103	0.563	1						●	●						2
Boloria selene (D. & S.)	Small Pearl-bordered Fritillary	0.102	0.566	1					●	●	●						3
Maniola jurtina (L.)	Meadow Brown	0.101	0.570	1						●	●	●	●				4
Thymelicus sylvestris (Poda.)	Small Skipper	0.101	0.571	1						●	●	●					3
Neozephyrus quercus (L.)	Purple Hairstreak	0.085	0.631	1							●	●					2
Aglais urticae (L.)	Small Tortoiseshell	0.083	0.639	2				●	●	●	●	●	●	●			7
Pieris brassicae (L.)	Large White	0.058	0.743	2					●	●	●	●					4
Polygonia c-album (L.)	Comma	0.035	0.844	2				●	●	●	●	●	●	●			7
Pyronia tithonus (L.)	Gatekeeper or Hedge Brown	0.017	0.925	1							●	●					2
Satyrium w-album (Knoch)	White-letter Hairstreak	0.008	0.963	1							●	●					2
Inachis io (L.)	Peacock	0.003	0.987	1					●	●	●	●					4
Callophrys rubi (L.)	Green Hairstreak	-0.017	0.924	1					●	●							2
Boloria euphrosyne (L.)	Pearl-bordered Fritillary	-0.023	0.895	1					●	●							2
Pyrgus malvae (L.)	Grizzled Skipper	-0.033	0.851	1					●	●							2
Aricia agestis (D. & S.)	Brown Argus	-0.057	0.750	2					●	●	●	●					4
Melanargia galathea (L.)	Marbled White	-0.079	0.658	1							●	●					2
Leptidea sinapis (L.)	Wood White	-0.106	0.553	1					●	●							2
Argynnis aglaja (L.)	Dark Green Fritillary	-0.157	0.374	1						●	●	●					3
Polyommatus coridon (Poda.)	Chalk-hill Blue	-0.163	0.356	1							●	●	●				3
Limentis camilla (L.)	White Admiral	-0.172	0.332	1						●	●	●					3
Argynnis paphia (L.)	Silver-washed Fritillary	-0.221	0.209	1						●	●	●					3
Thymelicus lineola (Ochsenheimer)	Essex Skipper	-0.235	0.181	1							●	●					2
Gonepteryx rhamni (L.)	Brimstone	-0.250	0.154	1				●	●	●	●	●	●				6

Table 4.2. 35 species of butterflies ranked by the Pearson correlation coefficient (*r*) between their annual collated indices and the winter NAO index. The table also includes the typical number of generations per year and the duration of the flight season in months. Species with a more positive association with the winter NAO index were more likely to be bivoltine (β = 10.346, *P* = 0.006) and have a longer flight period (*r* = 0.248, *P* = 0.151).

4.3.3 The relationship between the NAO and butterfly phenology

The analysis so far has concentrated on the effect of the winter NAO on butterfly abundance, based on collated indices. However, the NAO might also affect the timing, or phenology, of the butterfly flight period.

The six species chosen to investigate the effect of the NAO on phenology had large sample sizes: *A. cardamines* ranging from 348 individuals counted in 1976 to 7715 individuals counted in 2009 and the number of sites ranged from 24 in 1976 to 617 in 2009; *M. galathea* ranged from 694 individuals in 1978 to 48092 in 2006 and the number of sites ranged from 11 in 1976 to 377 in 2007; *A. hyperantus* ranged from 623 individuals in 1977 to 111994 individuals in 2009 and the number of sites ranged from 25 in 1977 to 740 in 2009; *P. tithonus* ranged from 6845 individuals counted in 1978 to 107994 individuals in 2004 and the number of sites ranged from 33 in 1976 to 647 in 2008; *L. megera* ranged from 484 individuals counted in 1977 to 4600 in 1990, and the number of sites ranged from 33 in 1976 to 187 in 2004. *L. megera* is in decline in the UK (Asher *et al*., 2011), hence explaining the maximum count being relatively early in the time series, despite the number of survey sites increasing after 1990; *P. icarus* ranged from 1610 individuals counted in 1977 to 65165 in 2003 and the number of sites ranged from 35 in 1976 to 781 in 2009.

The peak flight timing for all four univoltine species and both generations of the two bivoltine species was earlier in years with a more positive winter NAO index (Figures 4.3 and 4.4). The winter NAO is associated with variations in the peak flight week of: 3.50 weeks for *A. cardamines* (r = -0.429, P = 0.011); 1.46 weeks for *M. galathea* (r = -0.284, P = 0.103); 1.76 weeks for *A. hyperantus* (r = -0.375, P = 0.029); 1.86 weeks for *P. tithonus* (r = -0.424, P = 0.012); 3.66 weeks for the first generation of *L. megera* (r = -0.577, P = <0.001); 3.03 weeks for the second generation of *L. megera* (r = -0.606, P = <0.001); 2.72 weeks for the first generation of *P. icarus* (r = -0.382, P = 0.026); 2.58 weeks for the second generation of *P. icarus* (r = -0.405, P = 0.018). Each of the correlation coefficients calculated between the peak flight week and the winter NAO index (Figures 4.3 and 4.4) showed stronger associations than the correlation coefficients between the annual collated indices and the winter NAO index (Table 4.2) for the same species.

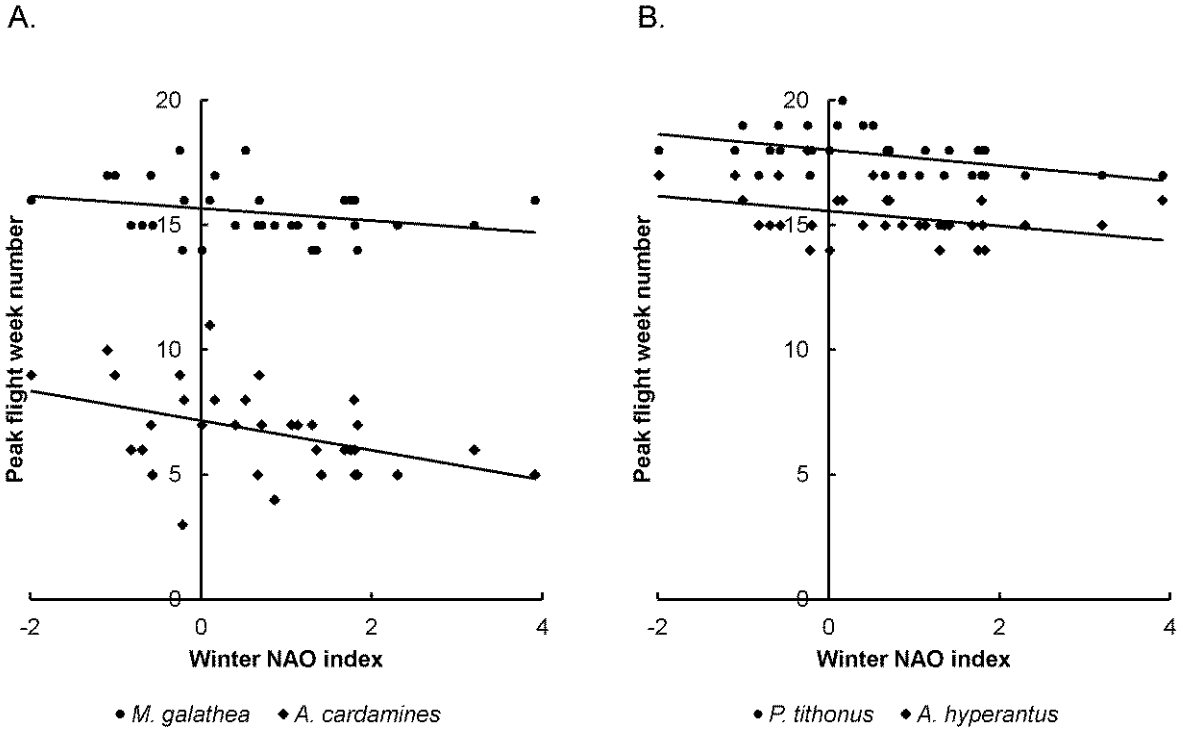


Figure 4.3. Flight phenology and the winter NAO index for the four univoltine species. (A) The relationship between the peak flight week for *M. galathea* (*r* = -0.284, *P* = 0.103) and *A. cardamines* (*r* = -0.429, *P* = 0.011) and the winter NAO index and (B) the relationship between the peak flight week for *P. tithonus* (*r* = -0.424, *P* = 0.012) and *A. hyperantus* (*r* = -0.375, *P* = 0.029) and the winter NAO index. Each data point is the annual peak flight week number for 1976 to 2009.

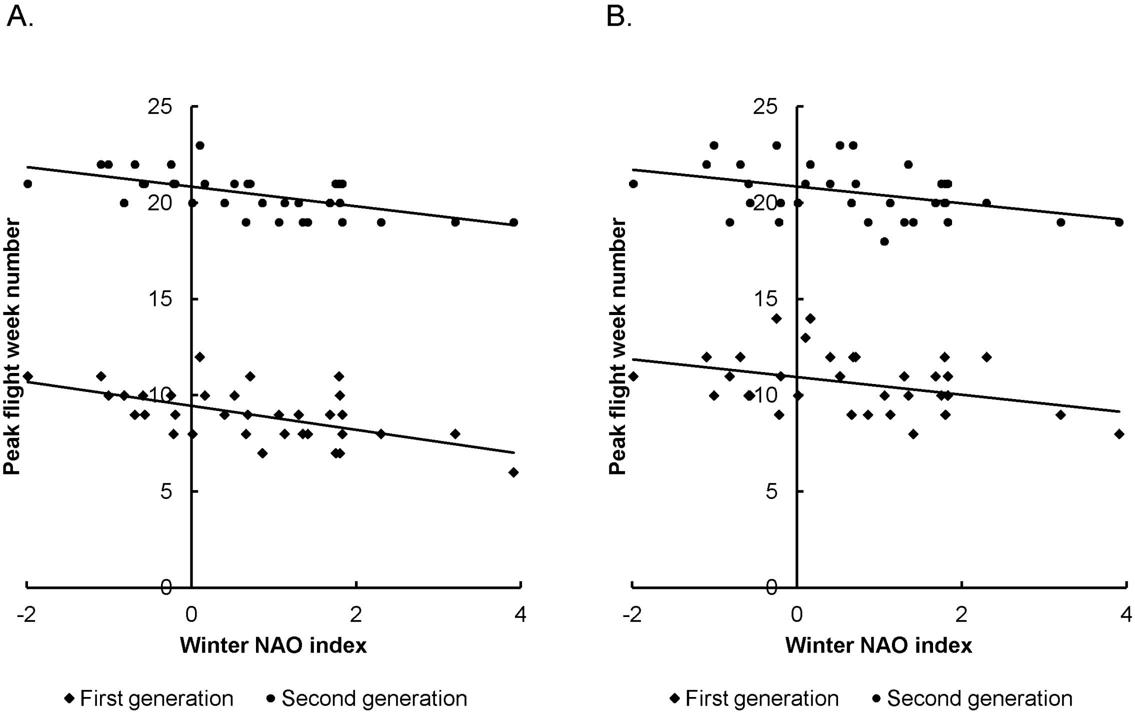


Figure 4.4. Flight phenology and the winter NAO index for the two bivoltine species. (A) The relationship between the first (*r* = -0.577, *P* = <0.001) and second generation (*r* = -0.606, *P* = <0.001) peak flight weeks for *L. megera* and the winter NAO index and (B) the relationship between the first (*r* = -0.382, *P* = 0.026) and second generation (*r* = -0.405, *P* = 0.018) peak flight weeks for *P. icarus* and the winter NAO index. Each data point is the annual peak flight week number for 1976 to 2009.

L. megera and *P. icarus* are bivoltine species with the first generation flying nearer the time when weather is affected by the NAO than the second generation, yet both generations showed significant or highly significant correlations between the timing of the peak flight weeks and the winter NAO index. Therefore an analysis was made of the role of the timing of the first generation with respect to the timing of the second generation (Figure 4.5). There were highly significant Pearson correlations between the timing of the first and second generations for *L. megera* (*r* = 0.676, *P* = <0.001) and for *P. icarus* (*r* = 0.528, *P* = 0.001). *L. megera* and *P. icarus* path coefficients for the model I direct path (winter NAO index → first generation peak flight week → second generation peak flight week) were higher than for the model II direct and indirect paths (winter NAO index → first generation peak flight week → second generation peak flight week and winter NAO index → second generation peak flight week), suggesting that the primary cause of the timing of the second generation of both species was the affect of weather associated with the winter NAO on the timing of the first generation. All path coefficients, variance estimates and *P* values are shown in Table 4.3.

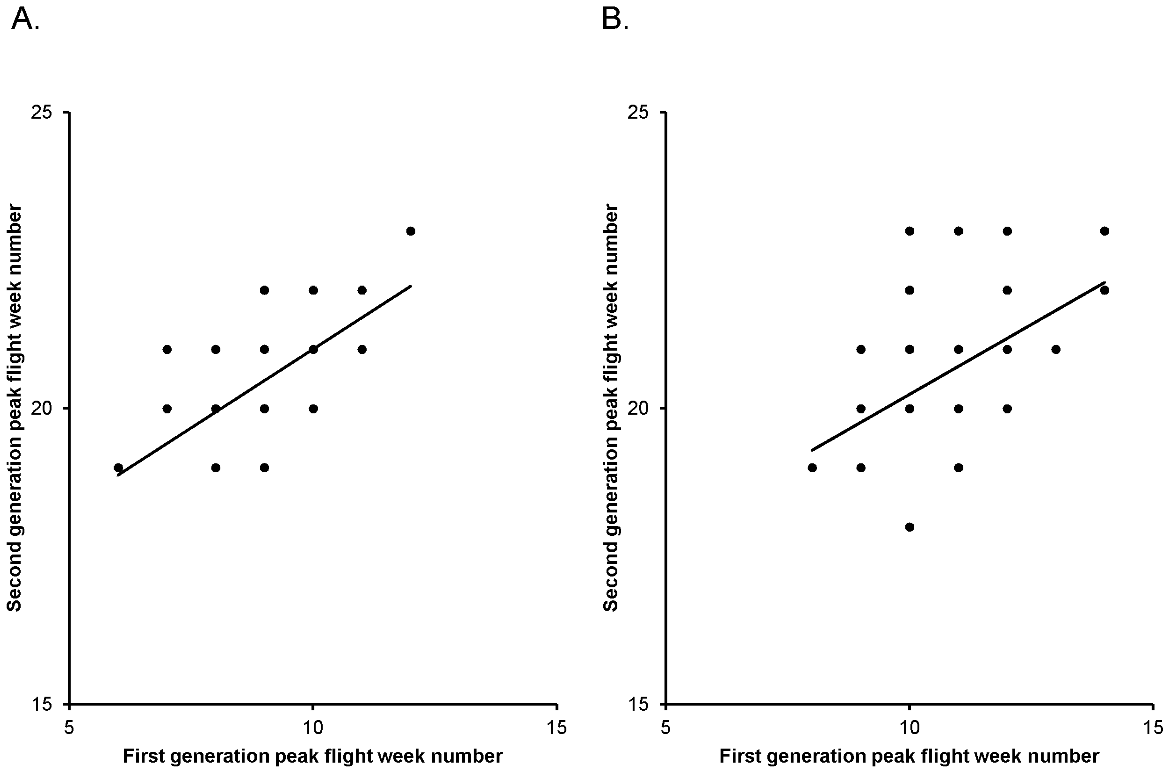


Figure 4.5. Second generation peak flight week number against first generation peak flight week number for (A) *Lasiommata megera* (*r* = 0.676, *P* = <0.001) and (B) *Polyommatus icarus* (*r* = 0.528, *P* = 0.001). Data are from all UK sites between 1976 and 2009. Each datapoint is for one year, but some datapoints are superimposed.

	Lasiommata megera		*Polyommatus icarus*	
	Model I	Model II	Model I	Model II
Path coefficients (SE, P-value)				
NAO index → peak 1	**-0.62**	**-0.62**	**-0.46**	**-0.46**
	(0.15;<0.01)	(0.15;<0.01)	(0.19;0.017)	(0.19;0.017)
Peak 1 → peak 2	**0.53**	**0.39**	**0.47**	**0.39**
	(0.10;<0.01)	(0.12;<0.01)	(0.13;<0.01)	(0.14;<0.01)
NAO index → peak 2	-	**-0.27**	-	-0.26
		(0.12;0.028)		(0.17;0.12)
Variance estimates (SE)				
NAO index	1.63 (0.40)	1.63 (0.40)	1.63 (0.40)	1.63 (0.40)
Peak 1	1.25 (0.31)	1.25 (0.31)	2.02 (0.50)	2.02 (0.50)
Peak 2	0.63 (0.16)	0.55 (0.14)	1.36 (0.34)	1.27 (0.31)

Table 4.3. Path analysis. Model I: winter NAO index → peak 1 → peak 2; Model II: winter NAO index → peak 1 → peak 2 and winter NAO index → peak 2; peak 1 = first generation peak flight week number; peak 2 = second generation peak flight week number; SE = standard error; path coefficients in bold are statistically significant at the 5% level.

The winter NAO index was a mean for a three month period, because it was calculated from the January to March NAO indices. Therefore, multiple linear regression analysis was used to increase the resolution to specific months when weather influenced phenology. Overall model r^2 values were higher for monthly temperatures than for monthly precipitation. This analysis showed significant and highly significant negative regressions between the peak flight weeks and mean monthly temperatures for *A. cardamines* in April, *M. galathea* and *A. hyperantus* in April, May and June and *P. tithonus* in June and July (Table 4.4). The first generation peak flight week for *L. megera* showed negative regressions with P = <0.100 for all four months between February and May and the second generation for *L. megera* showed a significant negative regression with May temperature. First generation *P. icarus* showed a significant regression with June and July temperatures (Table 4.5).

There was a highly significant positive association between March precipitation and the peak flight week for *A. cardamines* and a significant positive association between

February precipitation and the peak flight week for *M. galathea*. There were no significant regressions between monthly precipitation and the peak flight week for *A. hyperantus*, *P. tithonus* or the first or second generation peak flight weeks for *L. megera* and *P. icarus* (Tables 4.4 and 4.5).

		Temperature			Precipitation		
		r^2	*b*	*P*	r^2	*b*	*P*
A. cardamines	October	0.715	0.113	0.451	0.371	-0.015	0.077
	November		0.151	0.429		0.003	0.727
	December		-0.095	0.505		-0.003	0.764
	January		-0.169	0.132		0.002	0.833
	February		-0.156	0.343		0.006	0.574
	March		-0.189	0.325		0.031	**0.004
	April		-0.941	**<0.001		0.010	0.315
	May		-0.204	0.439		0.004	0.674
M. galathea	October	0.726	0.256	*0.017	0.384	-0.001	0.854
	November		0.124	0.358		0.002	0.802
	December		0.025	0.794		0.004	0.583
	January		-0.058	0.479		<0.001	0.939
	February		0.054	0.674		0.016	*0.033
	March		0.208	0.153		0.010	0.130
	April		-0.434	**0.004		0.005	0.420
	May		-0.412	*0.050		0.002	0.763
	June		-0.320	*0.037		0.005	0.432
	July		0.012	0.934		-0.007	0.307
	August		-0.157	0.337		-0.001	0.903
A. hyperantus	October	0.744	0.231	0.015	0.405	-0.004	0.451
	November		0.022	0.854		0.002	0.688
	December		-0.052	0.538		0.001	0.925
	January		0.033	0.648		0.005	0.371
	February		0.033	0.774		0.011	0.100
	March		-0.055	0.663		0.012	0.065
	April		-0.375	**0.005		-0.004	0.526
	May		-0.382	*0.041		0.002	0.736
	June		-0.322	*0.019		0.005	0.372
	July		-0.057	0.666		-0.011	0.075
	August		-0.050	0.727		0.001	0.847
P. tithonus	October	0.734	0.136	0.120	0.298	0.001	0.850
	November		0.062	0.585		-0.001	0.857
	December		0.065	0.427		0.002	0.761
	January		-0.069	0.319		0.003	0.598
	February		-0.077	0.482		0.005	0.475
	March		0.152	0.215		0.005	0.398
	April		-0.099	0.394		0.006	0.330
	May		-0.163	0.343		-0.002	0.764
	June		-0.270	*0.036		0.008	0.153
	July		-0.343	*0.011		0.007	0.276
	August		-0.028	0.836		0.004	0.457

Table 4.4. Multiple linear regression analyses between mean monthly temperatures, monthly precipitation and the peak flight week for the univoltine species - *A. cardamines*, *M. galathea*, *A. hyperantus* and *P. tithonus*. r^2 = overall model coefficient of determination, *b* = regression coefficient, *P* = probability, * = probability <0.05, ** = probability <0.01.

		Temperature			Precipitation		
		r^2	*b*	*P*	r^2	*b*	*P*
L. megera - first generation	October	0.786	0.061	0.561	0.246	-0.007	0.315
	November		-0.178	0.183		0.002	0.825
	December		-0.093	0.351		0.002	0.761
	January		-0.059	0.459		-0.003	0.682
	February		-0.207	0.077		-0.008	0.375
	March		-0.269	0.062		0.012	0.159
	April		-0.283	0.054		-0.009	0.292
	May		-0.462	*0.025		0.007	0.462
	June		0.045	0.762		-0.003	0.655
L. megera - second generation	October	0.743	-0.036	0.724	0.312	-0.002	0.797
	November		-0.031	0.814		0.003	0.680
	December		0.060	0.518		0.006	0.415
	January		-0.209	*0.014		-0.005	0.416
	February		-0.082	0.516		-0.006	0.405
	March		0.037	0.790		0.003	0.657
	April		-0.149	0.273		0.004	0.531
	May		-0.484	*0.024		0.005	0.498
	June		0.006	0.968		-0.004	0.511
	July		-0.182	0.222		-0.004	0.630
	August		0.013	0.934		-0.001	0.851
	September		0.109	0.471		-0.013	0.063
P. icarus - first generation	October	0.573	-0.193	0.249	0.297	<0.001	0.970
	November		0.035	0.867		-0.001	0.887
	December		-0.042	0.789		0.005	0.582
	January		-0.022	0.862		0.001	0.866
	February		-0.221	0.224		-0.003	0.777
	March		-0.210	0.347		0.018	0.059
	April		-0.422	0.068		-0.002	0.808
	May		-0.287	0.358		-0.004	0.715
	June		-0.316	0.185		-0.015	0.080
P. icarus - second generation	October	0.784	0.012	0.920	0.225	-0.009	0.263
	November		0.069	0.657		0.007	0.467
	December		0.057	0.604		-0.006	0.526
	January		0.108	0.246		0.007	0.375
	February		-0.218	0.145		0.011	0.313
	March		-0.176	0.283		0.019	0.065
	April		-0.290	0.074		0.010	0.323
	May		-0.120	0.612		0.005	0.638
	June		-0.700	**<0.001		0.003	0.755
	July		-0.472	*0.011		-0.001	0.917
	August		0.031	0.865		<0.001	0.958
	September		0.119	0.500		-0.003	0.710

Table 4.5. Multiple linear regression analyses between mean monthly temperatures, monthly precipitation and the peak flight week for each of the two generations for the bivoltine species - *L. megera* and *P. icarus*. r^2 = overall model coefficient of determination, *b* = regression coefficient, *P* = probability, * = probability <0.05, ** = probability <0.01.

4.4 Discussion

4.4.1 The NAO, climate change and weather

Identification of when the NAO has the most effect on temperature and precipitation were pre-requisites to describe how the NAO influences butterfly populations. The NAO influenced temperatures from October to April, with the strongest association between December and February. The NAO had a greater influence over temperature than precipitation, but showed significant influence over precipitation in January and February (Table 4.1).

Butterflies have emerged earlier with recent climate warming (Roy and Sparks, 2000; Sparks and Yates, 1997) and mean annual temperature in the UK has increased by 1.22 °C during the period 1976-2009 (Figure 4.2). Although there was a highly significant correlation between the winter NAO index and mean annual temperature ($r = 0.544$, $P = 0.001$), the winter NAO index did not show an upward trend during the time series, so would appear not to have made a major contribution to the overall temperature increase. The NAO is an oscillatory set of weather parameters, and is different from climate change. Conclusions as to whether there is an association between rising temperatures due to climate change and the NAO can be influenced by the time window studied, particularly with shorter time series. It is likely that climate change and the NAO combine to influence the phenology of butterfly flight, although Wallisdevries and Van Swaay (2006) hypothesise that climate warming combined with high nitrogen deposition can advance spring plant growth, leading to microclimatic cooling, which can effect butterfly species that hibernate as eggs or larvae. Such suggestions indicate that the relationship between weather and butterflies can be complex.

4.4.2 The role of the NAO in butterfly abundance

The multi-species collated index did not show an association with the winter NAO index. However, multi-species indices are averages of the response of many species to a range of environmental factors, and hence could mask effects on some individual species, so Pearson correlation coefficients were calculated to investigate the relationship between the annual collated indices for each of 35 individual species with the winter NAO index (Table 4.2). A significant relationship was found for only one species (*L. megera*), but bivoltine species tended to have stronger associations with the winter NAO than univoltine species. Similarly, the population abundance of species with relatively long flight periods tended to be more positively associated with the NAO.

An explanation for bivoltine species showing positive associations with the winter NAO is that warmer weather, associated with a positive NAO index, provided a longer time to complete two or more generations. Altermatt (2010b) has shown that climatic warming increases voltinism in European butterflies and moths and Välimäki *et al*. (2008) discuss the issue of seasonal weather, time constraint and number of generations. The low correlations with univoltine species may imply that as the flight season is shorter, weather is less important in providing sufficient time to complete this life stage and the negative associations shown by some univoltine species suggest these species require cold winters, perhaps for dormancy. It is possible that the winter NAO index can be used to predict the relative abundance of univoltine and bivoltine species, and it is also possible that increased temperatures associated with climate change might favour bivoltine species more than univoltine species.

Therefore, the NAO appears to have a complex relationship with butterfly life cycle parameters and abundance, which was difficult to detect using multi-species indicators. As the NAO plays such an important role in UK weather, then it is perhaps questionable how suitable multi-species indices are for monitoring ecological change. There may be an important, and difficult, practical dilemma to develop an index of entomological population change that integrates complex ecological traits and can identify conservation problems.

4.4.3 The role of the NAO in butterfly phenology

The NAO influenced the timing, or phenology, of the butterfly flight season for all six species studied in detail. The peak flight weeks for *A. cardamines*, *M. galathea*, *A. hyperantus*, *P. tithonus* (Figure 4.3) and the peak flight weeks for both the first and second generations for *L. megera* and *P. icarus* (Figure 4.4) were earlier in positive

NAO index years. These results were similar to those found for the green spruce aphid, *E. abietinum*, which flew earlier in years with a more positive winter NAO index (Westgarth-Smith *et al*., 2007). The higher correlation coefficients between peak flight week and the winter NAO index rather than annual collated indices and the winter NAO index indicated that the NAO had a stronger relationship with butterfly phenology than abundance. The NAO index is very difficult to predict, and hence although the winter NAO index can be used to predict flight timing, it would be difficult to predict the winter NAO index in December, but by the end of March it would be feasible to predict the flight timing, because by then the winter NAO index is known.

Temperature had a greater effect on flight timing than precipitation. Warmer temperatures during the period April to July resulted in all six species of butterfly flying earlier, with temperatures in later months being associated with later flying species. Previous studies (Sparks and Yates, 1997; Roy and Sparks, 2000) have also found that warmer spring weather is associated with earlier butterfly flight timing and Sparks and Yates (1997) showed how flight timing of four UK butterfly species was earlier in years when temperatures in April were higher. The present study also suggested that higher precipitation in February and March can delay the flight timing of two of the univoltine species. The NAO is significantly positively correlated with both temperature and precipitation in February (Table 4.1), so to some extent the effect of higher temperature making a flight season earlier should be partly offset by higher precipitation, making the flight season later. However, as temperatures were more strongly correlated with the NAO for more months than precipitation, the mechanism for control of the flight timing by the NAO was probably mainly through temperature. So while other authors have shown associations between weather in specific months and flight timing, our new contribution has been to link these associations to the NAO.

It appears that a factor in determining the timing of the second generation of bivoltine species is the timing of the first generation and was presumably due to the length of time needed for eggs laid in the first generation to hatch, develop as larvae, pupate and then emerge as adults, rather than weather conditions at the time of, or shortly before, the second generation emerged as adults. Effectively the NAO indirectly controlled the phenology of the second generation by controlling the phenology of the first generation. We believe that this is the first time an association between the timing of the first and second generations for bivoltine species has been described using butterfly ecological datasets.

In conclusion, the use of multi-species indicators hides the complexity of response of individual species. Butterfly species that were bivoltine and had a longer flight period were more likely to respond positively to the NAO than univoltine species with a short flight period. Warmer weather associated with a more positive winter NAO index caused butterflies to fly earlier. With bivoltine species, the NAO controls temperature, which controls the timing of the first generation, then the timing of the first generation controls the timing of the second generation.

Chapter 5

The North Atlantic Oscillation and butterfly ecology at Monks Wood, Cambridgeshire, UK

5.1 Introduction

This chapter investigates the role of the NAO in butterfly ecology at a single site, Monks Wood National Nature Reserve in Cambridgeshire, UK. Brief mention is also made of the populations of *Aphantopus hyperantus* (ringlet) at Chippenham Fen and Holme Fen, also both in Cambridgeshire. Monks Wood is the UKBMS site with the longest time series and the highest quality data of any site within the survey. This puts Monks Wood at the global leading edge of potential long term invertebrate survey sites, the only equivalent schemes of a similar quality in the UK are the Rothamsted Insect Survey of aphids and some of the bird surveys organised by the British Trust for Ornithology (British Trust for Ornithology, 2011 and Eaton *et al*., 2010). I tried using data from the 4th July Butterfly Survey run by the North American Butterfly Association (2010), but found that the UKBMS data are of significantly higher quality, as the UKBMS uses weekly data whereas the 4th July count is for a few days close to 4th July.

Monks Wood is provided with considerable legal protection as a National Nature Reserve and Site of Special Scientific Interest, yet it also represents a fragmented area of woodland habitat in an intensively farmed landscape. Chamberlain *et al*. (2000) demonstrated how the area sprayed with herbicides in England and Wales increased from the 1960s, the area of insecticide application increased from the mid-1970s and the area of fallow land, which might have contained more larval food plants and nectar sources, decreased during the 1970s. Insecticides and herbicides can drift in the wind into nature reserves such as Monks Wood (Lawton *et al*., 2010). The UKBMS dataset matches the same time period as this period of agricultural intensification and meant that Monks Wood was surrounded by an environment that was increasingly less hospitable to butterflies through the time of the survey. Thomas *et al*. (2004) describe how a higher percentage of butterfly species as compared to plants and birds have suffered declines in Britain.

The Monks Wood dataset consists of weekly counts, with large sample sizes for some species, and so is an excellent resource to investigate the potential effect of climate change and the NAO on the phenology of flight. While analyses of national datasets have the advantages of even larger sample sizes and the elimination of site-specific vagaries, changes may be occurring at a local level that are not obvious when the national resolution annual collated indices are analysed. Site-specific analyses also have some other major advantages that are discussed below.

5.1.1 The advantages of an analysis of site-specific Butterfly Monitoring Scheme data from Monks Wood

The Butterfly Monitoring Scheme was piloted in Monks Wood National Nature Reserve from 1973-1975 (Pollard, 1977), and then butterflies have been counted at this site from 1976 to the present. The earliest start date for any of the other UKBMS sites was 1976, so Monks Wood has the longest time series of any site. Most UKBMS sites contain some missing weeks of data due, for example, to the person counting the butterflies being on holiday or ill. However, Monks Wood has very few missing weeks of data. Therefore Monks Wood is the best survey site in the World's best butterfly survey scheme.

A site-specific study of butterflies means that it was possible to make a reliable assessment of the NAO on total flight period. In contrast, progressively more sites have been added to the national dataset over the years, and more sites mean more butterflies counted, which has the effect of increasing the estimate of the length of the flight season. Butterfly phenology is influenced by latitude, so if more northern sites were counted in one year, this would alter estimates of the flight timing. By using data from one site, this latitudinal effect was removed.

Site-specific studies allow calculation of a mean flight week number, which is more accurate than a peak flight week number. Calculating a mean flight week number using the entire national database is difficult, because different numbers of sites were being counted in each week. Also calculation of the mean flight week number requires that the UKBMS survey period is longer than the flight period for the butterfly species. For example, in the national database there are reports of meadow brown (*Maniola jurtina*) butterflies still flying in the last week of September, so some will probably still be flying in the first week of October and will not be counted by the UKBMS, which finishes at the end of September, however none were counted in the final week at Monks Wood during the period 1973-2007.

The national dataset includes about 1500 transect sites that were operational for different numbers of years. Consequently it is likely that several thousand people have taken part in the survey during the period 1976 to the present. Many of these will be highly skilled naturalists, all of them are making a significant contribution through their time and effort in taking part in the survey, and without their help the excellent UKBMS database would not exist. However, there will be some recorders whose identification skills will be less good, but at Monks Wood, the transect was supervised and surveyed by some of the most senior professional entomologists in the UK, so identification quality should be very high.

Single site studies enable the use of a range of mathematical tools, including diversity indices, multivariate analysis, and correlations involving total number of species or total number of butterflies of all species – all of which are exceedingly difficult to do with data from different numbers of sites in each year.

5.1.2 Research questions

The following hypothesis was tested in this chapter: do the NAO and climate change affect the weather and ecology of butterflies at Monks Wood? This hypothesis was investigated through the following specific research questions:

1. What influence does the NAO have on the weather at Monks Wood?
2. Is there any evidence of climate change at Monks Wood?
3. Is the relative abundance of butterflies at Monks Wood changing with time?
4. Does the NAO have an effect on the overall diversity or abundance of the butterfly community at Monks Wood?
5. How does sample size influence the ability to estimate the timing of the flight season, and therefore which species might be more appropriate to investigate the potential influence of the NAO?
6. Is it possible to estimate the relative magnitude of the effect of climate change compared to the effect of the NAO on flight timing?

5.2 Materials and Methods

Weekly butterfly counts for Monks Wood were obtained from the United Kingdom Butterfly Monitoring Scheme (2006) web site for the period 1973 to 2007. At the time that this analysis was done, the UKBMS web site showed weekly counts to 2009, but the calculation of annual totals (the ‘Ind’ or ‘individuals’ column) was complete only up to and including 2007, so this analysis does not use data for 2008 and 2009. The annual totals (‘Ind’) for each species were usually the same number as the total of weekly counts unless a week had been missed, when it could include estimated numbers for the missing week. In the rare situation where it was not possible to calculate an ‘Ind’ then ‘NI’ (‘no index’) was recorded. Data quality was excellent, with butterflies counted in almost every week from the first week of April to the last week of September in every year.

Meteorological data were obtained for Monks Wood from the British Atmospheric Data Centre (2010), but this dataset was found to be incomplete. Sarah Martin, Weather Desk Advisor, Met Office, UK, provided meteorological data from the National Institute for Agricultural Botany (NIAB), located on the outskirts of north-west Cambridge. These data were in the form of monthly mean maximum temperature, monthly mean minimum temperature, monthly days of air frost, monthly precipitation and monthly total sunshine duration (Met Office Historic Station Data, 2010).

There were no data for mean monthly temperatures. As mean temperatures would probably be a better indication of the conditions affecting insect growth and development than mean maximum and minimum temperatures, mean monthly temperatures (Tmean) were calculated as a mean of the mean monthly minimum (Tmin) and mean monthly maximum temperatures (Tmax) for each month. Mean annual maximum temperatures, mean annual minimum temperatures and mean annual temperature were calculated as a mean of twelve monthly values. Annual precipitation, annual numbers of days of air frost and annual sun hours were calculated as a total of twelve months.

The NAO index data used was from the Climate Research Unit (2004).

5.3 Results

5.3.1 Associations between the NAO and NIAB meteorological data

To find what effect the NAO has on weather, Pearson correlation coefficients were calculated between monthly and winter NAO indices and meteorological parameters obtained from the National Institute for Agricultural Botany in Cambridge.

Month	Tmax		Tmin		Tmean	
	Pearson	Probability	Pearson	Probability	Pearson	Probability
January	0.812	<0.001	0.737	<0.001	0.786	<0.001
February	0.767	<0.001	0.662	<0.001	0.732	<0.001
March	0.536	0.001	0.273	0.113	0.442	0.008
April	0.344	0.043	0.335	0.049	0.383	0.023
May	0.414	0.014	0.455	0.006	0.484	0.003
June	0.269	0.119	-0.067	0.704	0.160	0.358
July	<0.001	1.000	-0.019	0.912	-0.006	0.971
August	0.271	0.115	0.158	0.366	0.244	0.158
September	0.302	0.077	-0.009	0.961	0.180	0.300
October	0.423	0.011	0.380	0.024	0.420	0.012
November	0.294	0.086	0.232	0.179	0.273	0.112
December	0.712	<0.001	0.489	0.003	0.614	<0.001

Table 5.1. Pearson correlation coefficients and probabilities between monthly NAO indices and monthly mean maximum temperatures (Tmax), monthly mean minimum temperatures (Tmin) and monthly mean temperatures (Tmean) for the period 1973-2007 at the National Institute for Agricultural Botany, Cambridge.

	Precipitation		Days of air frost		Total sunshine duration	
	Pearson	Probability	Pearson	Probability	Pearson	Probability
January	0.207	0.234	-0.787	<0.001	0.384	0.023
February	0.286	0.095	-0.644	<0.001	0.315	0.065
March	-0.131	0.454	-0.304	0.075	0.588	<0.001
April	-0.038	0.830	-0.238	0.169	0.187	0.282
May	0.237	0.170	-0.174	0.316	0.219	0.205
June	-0.354	0.037	No frost	No frost	0.477	0.004
July	-0.130	0.456	No frost	No frost	0.128	0.463
August	-0.291	0.090	No frost	No frost	0.423	0.011
September	-0.222	0.200	No frost	No frost	0.523	0.001
October	-0.043	0.806	-0.303	0.077	0.011	0.950
November	0.186	0.286	-0.314	0.066	0.001	0.996
December	-0.109	0.534	-0.465	0.005	0.284	0.099

Table 5.2. Pearson correlation coefficients and probabilities between monthly NAO indices and monthly precipitation, monthly days of air frost and monthly sunshine duration for the period 1973-2007 at the National Institute for Agricultural Botany, Cambridge.

	Pearson	Probability
Mean annual maximum temperature	0.524	0.001
Mean annual minimum temperature	0.478	0.004
Mean annual temperature	0.536	0.001
Annual precipitation	0.060	0.734
Annual days of air frost	-0.678	<0.001
Annual total sunshine duration	0.364	0.032

Table 5.3. Pearson correlation coefficients between the winter NAO index and mean annual maximum, mean annual minimum and mean annual temperatures, annual precipitation, annual days of air frost and annual total sunshine duration for the period 1973-2007 at the National Institute for Agricultural Botany, Cambridge.

There were significant and highly significant positive Pearson correlation coefficients between monthly NAO indices and monthly mean maximum temperatures, monthly mean minimum temperatures and monthly mean temperatures in all except one case for January to May inclusive, October and December (r = 0.335-0.812, P = <0.001-0.049, Table 5.1).

No significant correlation coefficients were found between monthly NAO indices and monthly temperatures for June to September, although the correlation coefficient between the September NAO index and September mean maximum temperature is almost significant (r = 0.302, P = 0.077, Table 5.1).

There appeared to be very little association between monthly NAO indices and monthly precipitation, although the correlation for February is close to significant (r = 0.286, P = 0.095), and a significant correlation for June precipitation (r = -0.354, P = 0.037). However, this apparent association might be random, as this is an unusual time of year for the NAO to influence the weather (Table 5.2).

There were highly significant correlations between monthly NAO indices and the number of days of air frost for January, February and December (r = -0.465 to -0.787, P = <0.001-0.005) and significant and highly significant correlations between monthly NAO indices and sunshine duration in January, March, June and September (r = 0.384 – 0.588, P = <0.001-0.023) (Table 5.2).

The winter NAO index showed highly significant correlation coefficients between mean annual maximum, mean annual minimum and mean annual temperatures (r = 0.478-0.536, P = 0.001-0.004) and annual number of days of air frost (r = -0.678, P = <0.001) . There was a significant correlation between the winter NAO index and annual total sunshine duration (r = 0.364, P = 0.032), but not annual precipitation (r = 0060, P = 0.734) (Table 5.3).

5.3.2 Climate change in Cambridge

Temperature data from the National Institute for Agricultural Botany (NIAB), Cambridge, were plotted against year to investigate whether there was evidence of climate change.

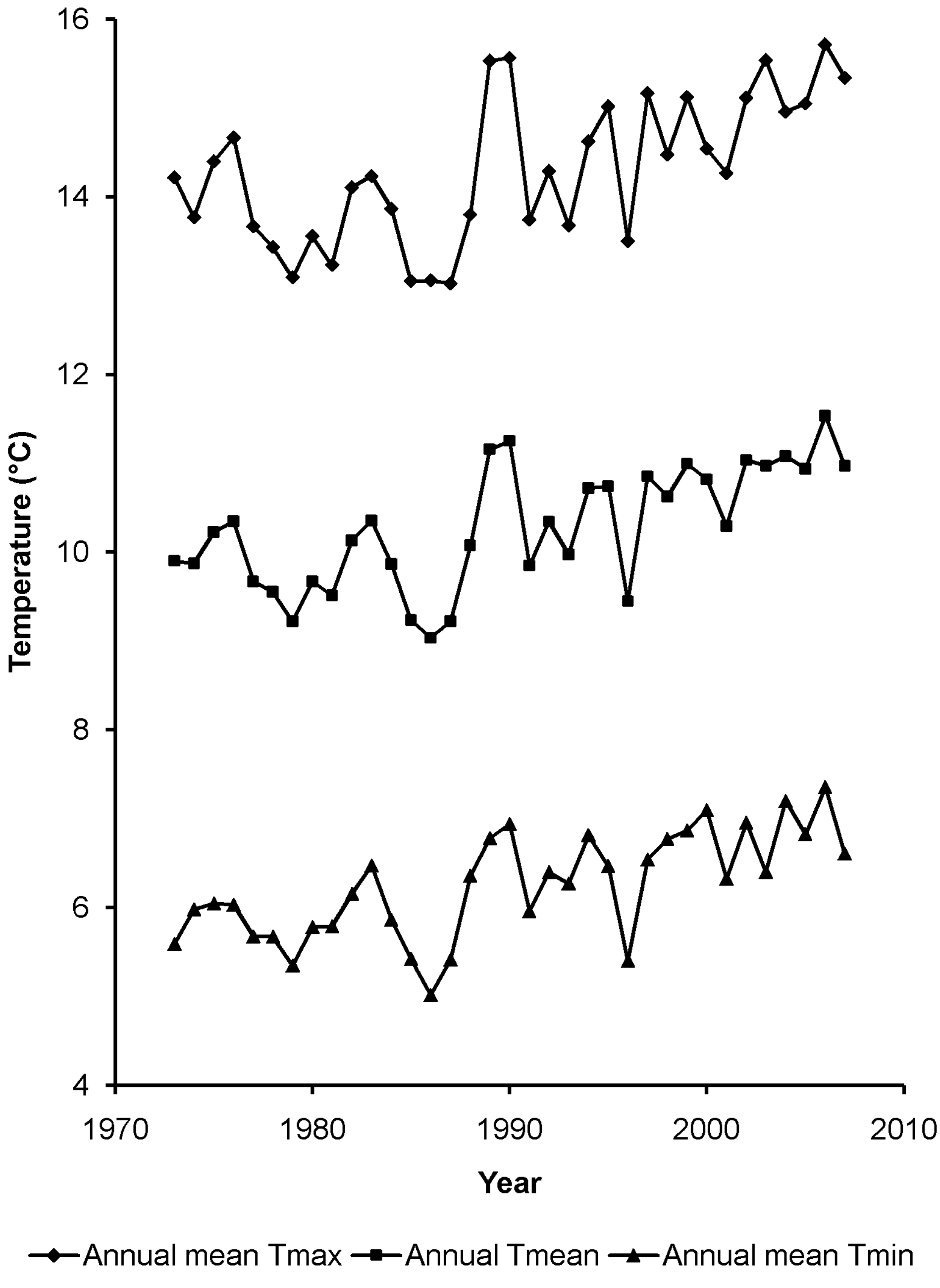


Figure 5.1. Change in annual mean maximum (*r* = 0.605, *P* = <0.001), and mean minimum (*r* = 0.675, *P* = <0.001) and annual mean (*r* = 0.655, *P* = <0.001) temperatures for 1973-2007 at the National Institute for Agricultural Botany, Cambridge.

Figure 5.1 shows highly significant evidence (*P* = <0.001) for a warming trend at NIAB, with increases in annual mean maximum temperature, annual mean minimum temperature and mean annual temperature. However, the warming trend has not been consistent throughout the time series, as there was some evidence for cooling between 1976 and 1986 or 1987.

5.3.3 Total number of individuals of each butterfly species counted at Monks Wood

Figure 5.2 gives the relative abundance of each species of butterfly at Monks Wood, which was useful information in identifying the species with the largest sample sizes and therefore those species more suitable for detecting trends associated with the NAO.

The Butterfly Monitoring scheme recorded individuals of 33 species of butterfly at Monks Wood during the period 1973-2007, although data for two species, *Thymelicus sylvestris* and *T. lineola*, were combined as these species were considered difficult to distinguish from each other (Pollard and Yates, 1993). The five most frequently counted species, in declining order, were *Aphantopus hyperantus*, *Maniola jurtina*, *Pieris napi*, *Pyronia tithonus* and *Pararge aegeria*. Figure 5.2 shows the total number of each species counted from 1973-2007, although the annual numbers counted for some species, for example *Aphantopus hyperantus*, changed considerably through the time series.

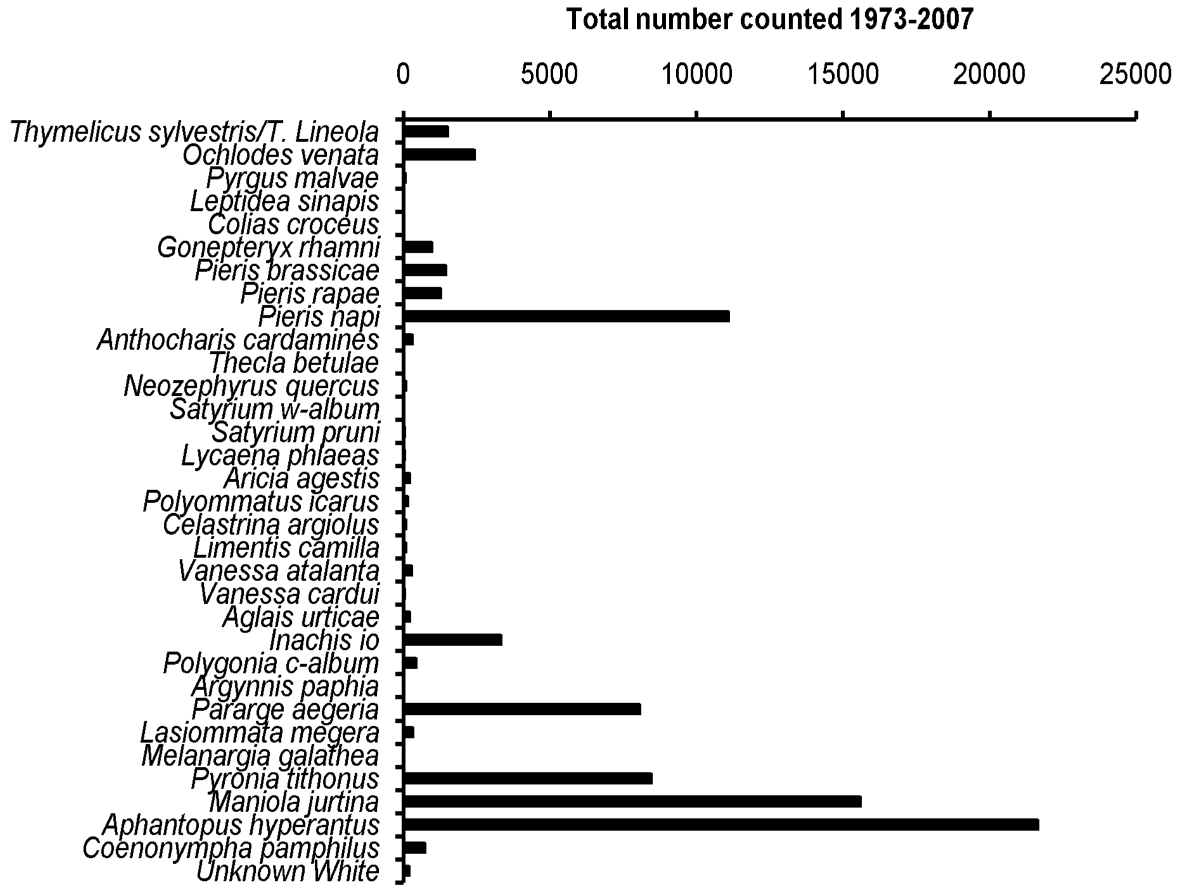


Figure 5.2. Total number of individuals of each species of butterfly recorded at Monks Wood by the UKBMS during the period 1973-2007. There was an overall total of 79284 butterflies for the entire time series.

5.3.4 Total number of butterfly species and total number of butterflies at Monks Wood

The annual total number of butterfly species and the annual total number of butterflies of all species were plotted against year (Figures 5.3 and 5.4). The population size of one species, *A. hyperantus*, increased considerably during the time series (Figure 5.5) and the annual total count of all species, excluding *A. hyperantus* decreased (Figure 5.6). This was a considerable change in the butterfly community at Monks Wood, so populations of *A. hyperantus* at two other Cambridgeshire nature reserves (Chippenham Fen and Holme Fen) were also investigated (Figures 5.7 and 5.8).

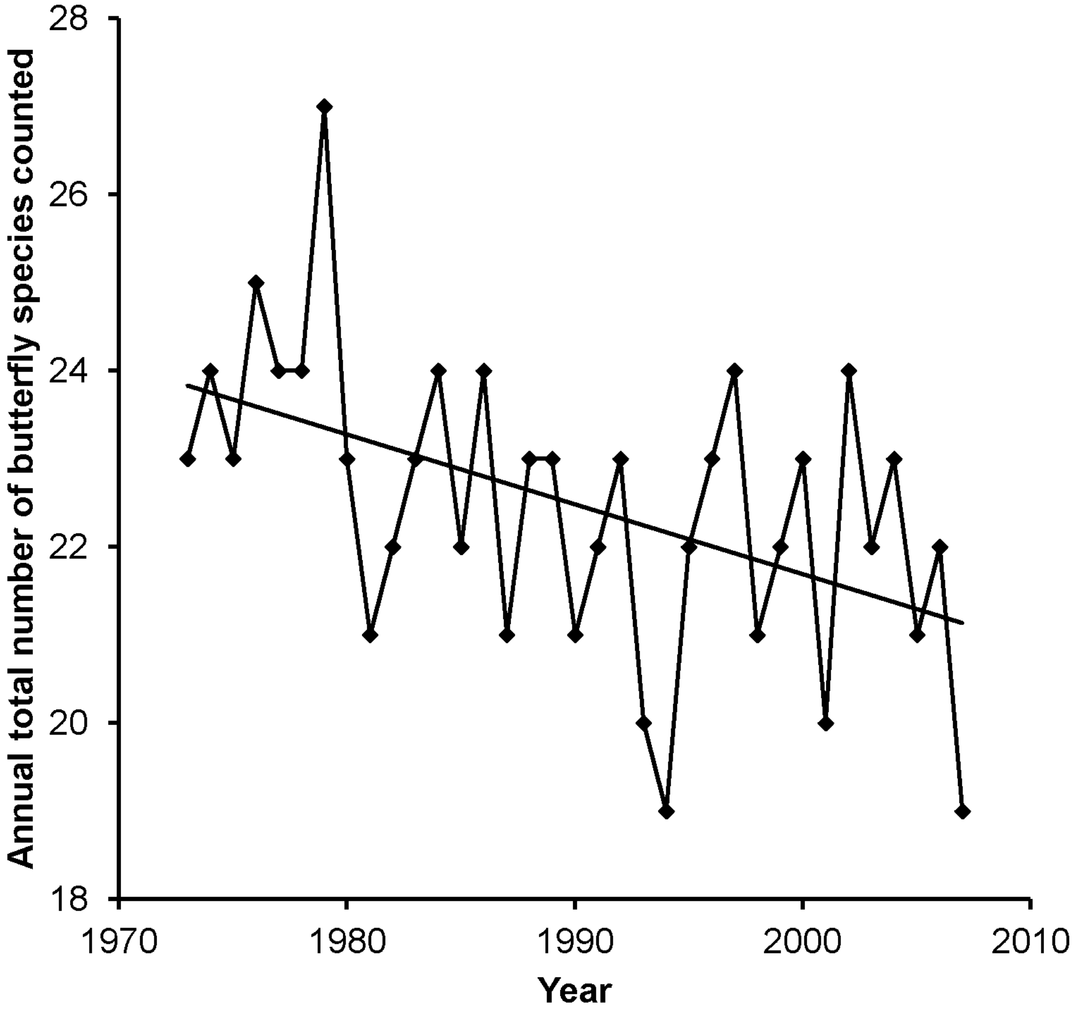


Figure 5.3. Total number of butterfly species recorded each year at Monks Wood between 1973 and 2007 (r^2 = 0.2368, r = -0.487, P = 0.003, m = -0.0793).

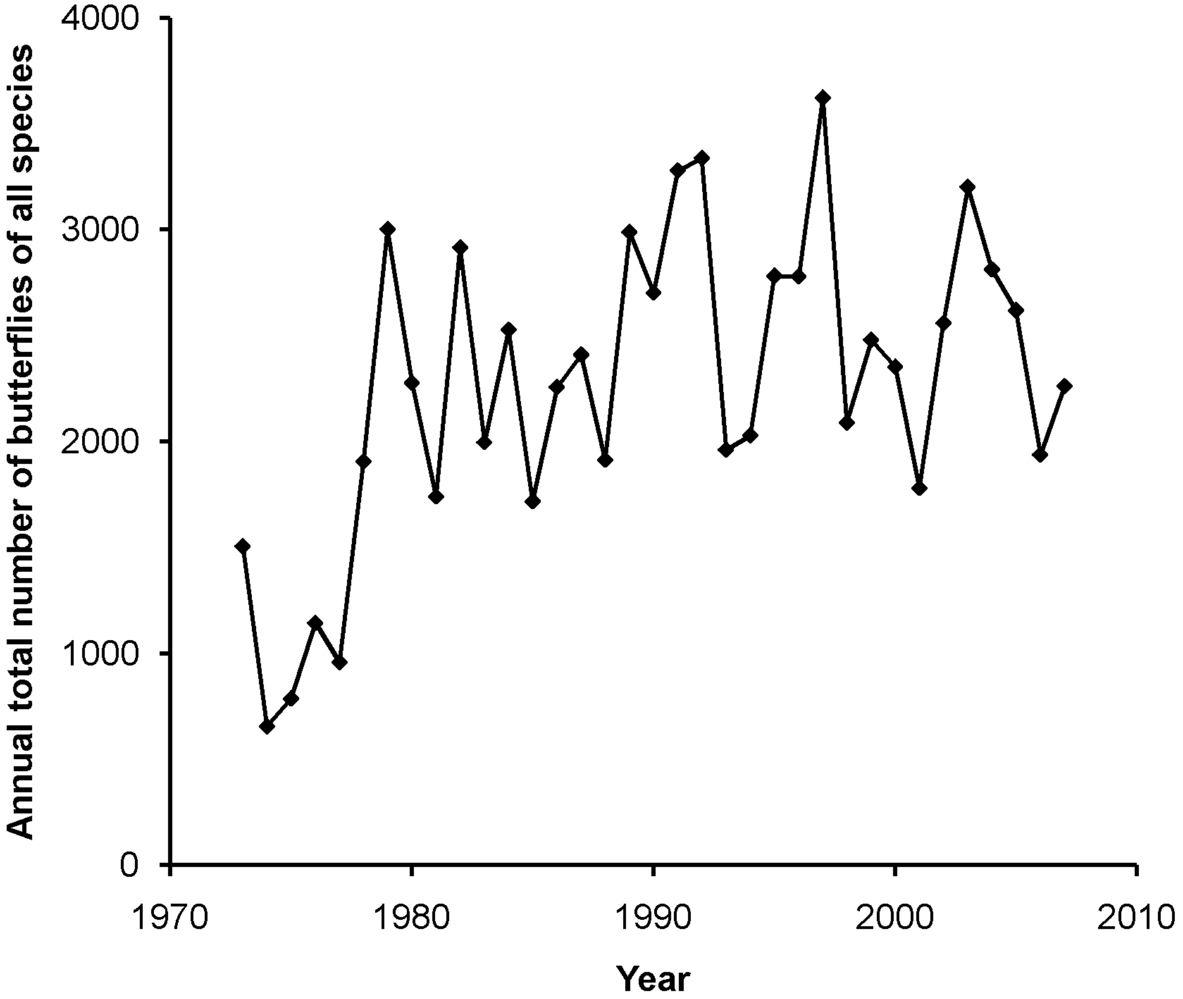


Figure 5.4. Total number of butterflies of all species recorded at Monks Wood each year. The correlation coefficient for the period 1978-2007 inclusive is *r* = 0.138, *P* = 0.466, data from 1973-1977 was excluded from this correlation as there appeared to be a gradient change at 1977-78, with the annual number of butterflies counted between 1973 and 1977 being less than half the annual number counted from 1978 onwards.

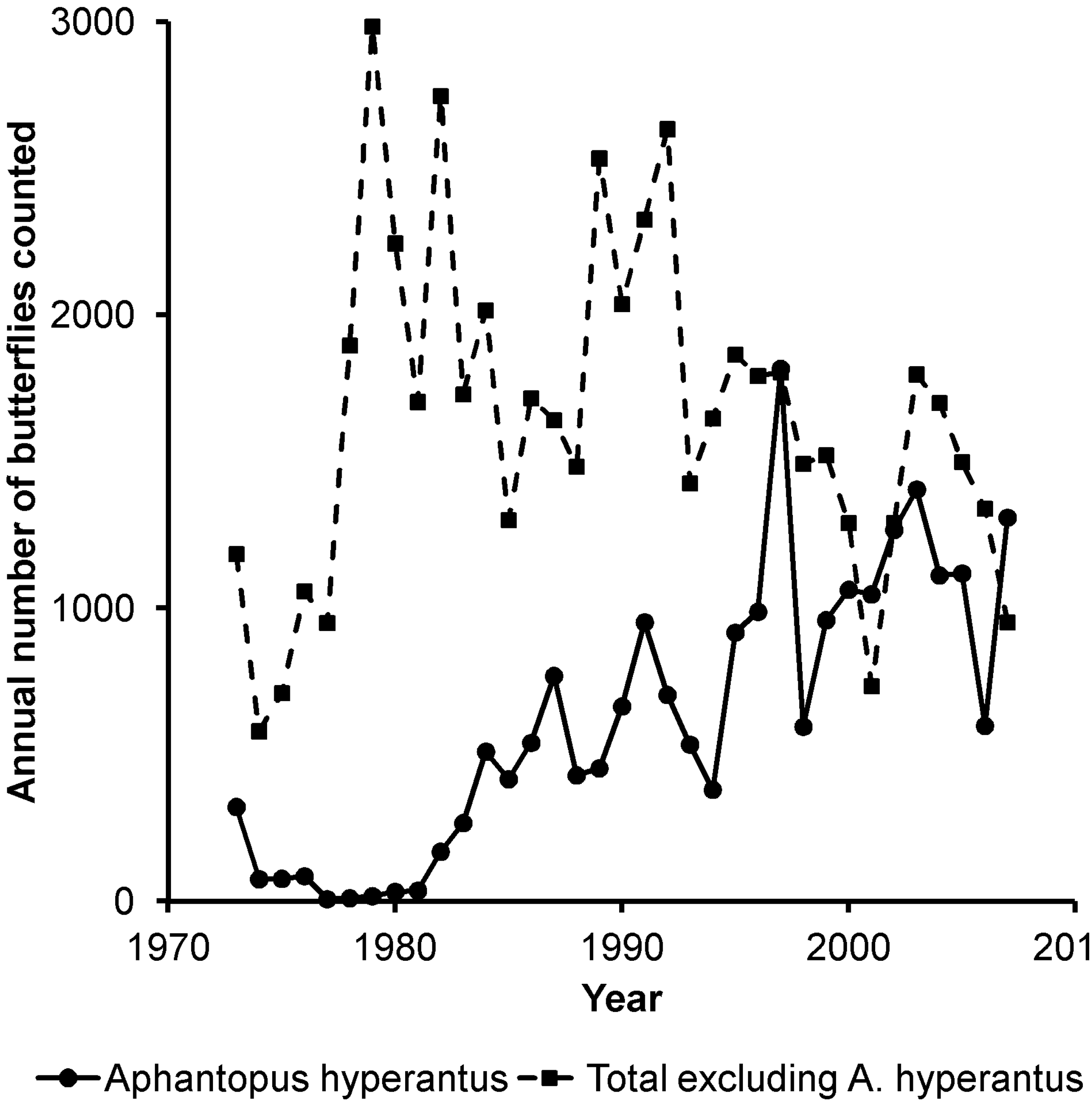


Figure 5.5. Total number of all species of butterfly excluding *Aphantopus hyperantus* and total number of *A. hyperantus* only counted at Monks Wood each year between 1973 and 2007. There were more *A. hyperantus* counted in 1997, 2001 and 2007 than all butterfly species excluding *A. hyperantus*.

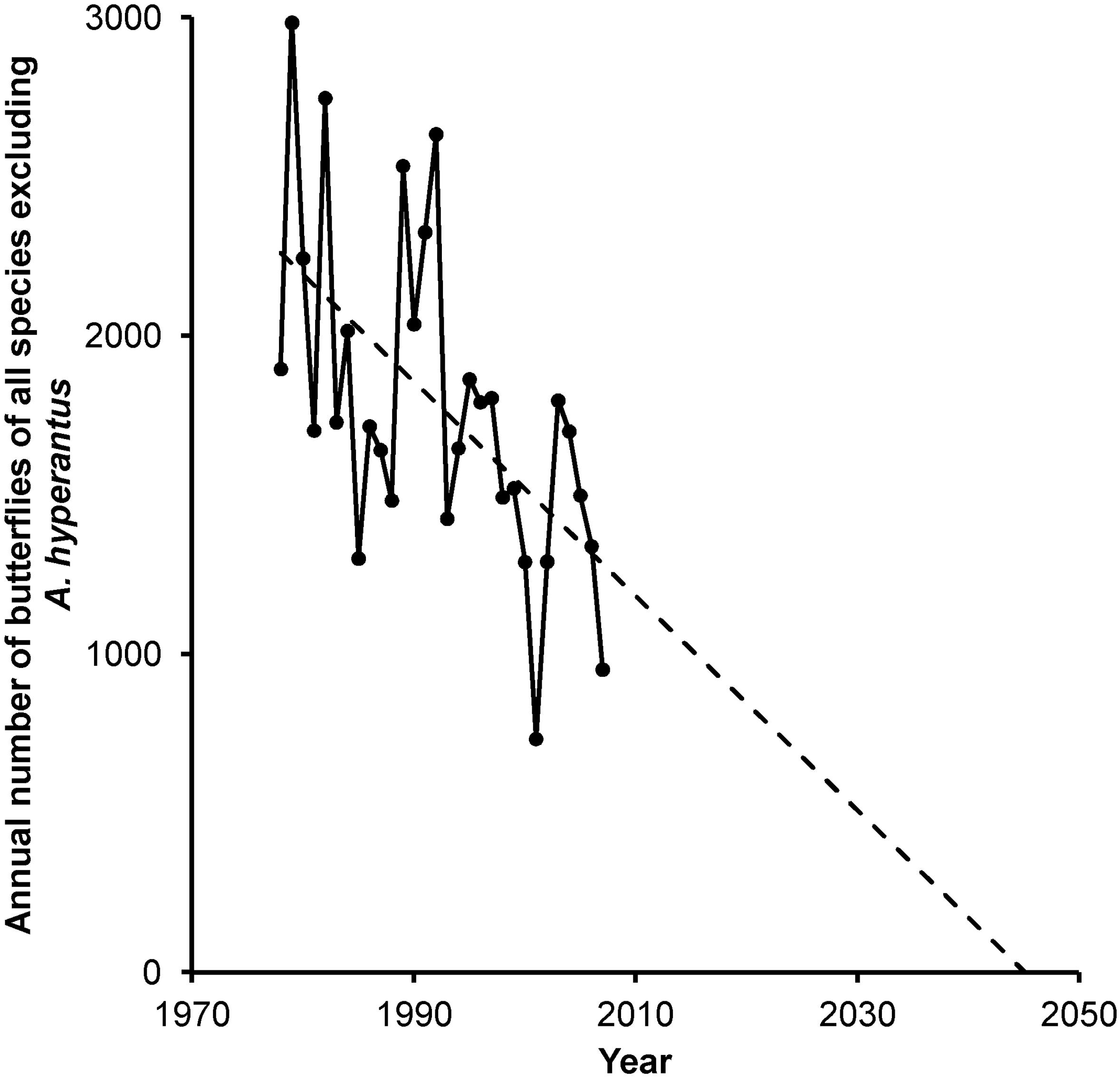
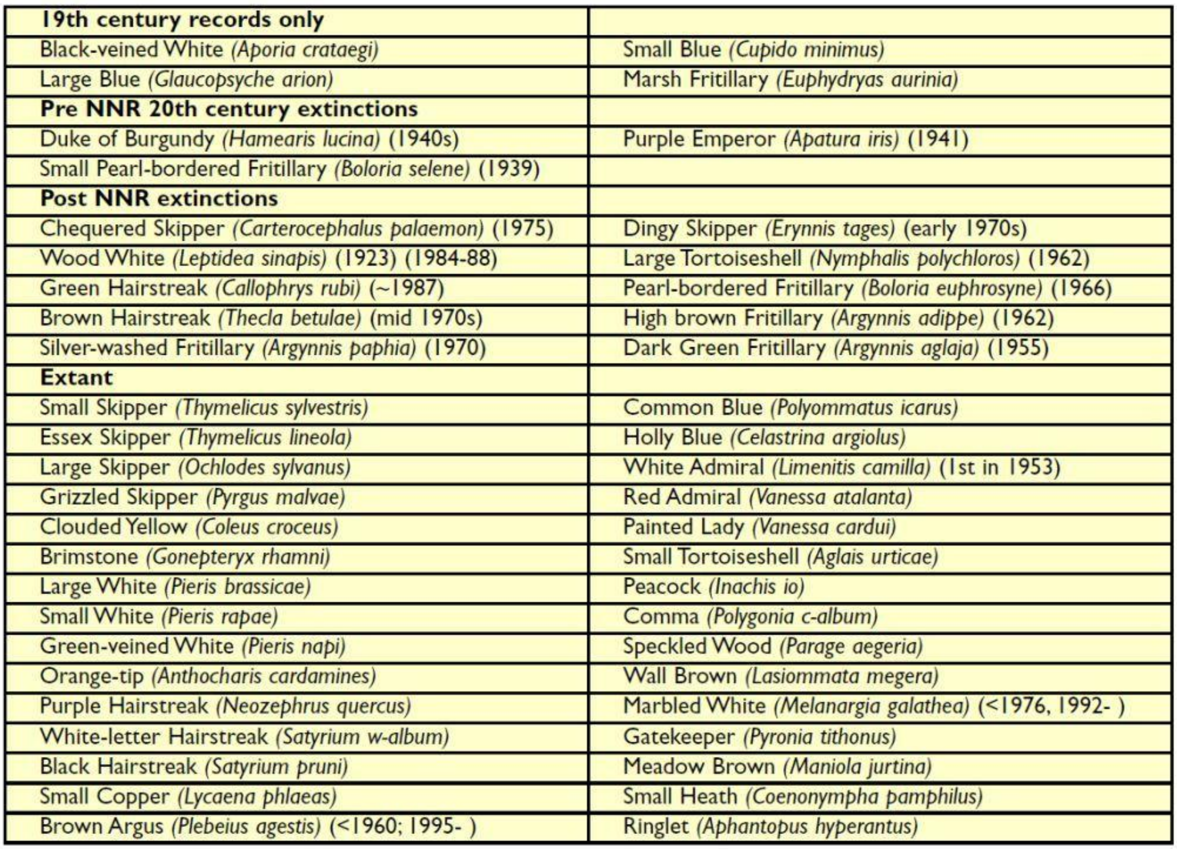


Figure 5.6. Annual total of all species excluding *A. hyperantus* from 1978 to 2007 with a possible prediction of future changes (r^2 = 0.3386, *r* = -0.582, P = 0.001). A linear trendline is included and extrapolated to zero.



19th century records only	
Black-veined White *(Aporia crataegi)*	Small Blue *(Cupido minimus)*
Large Blue *(Glaucopsyche arion)*	Marsh Fritillary *(Euphydryas aurinia)*
Pre NNR 20th century extinctions	
Duke of Burgundy *(Hamearis lucina)* (1940s)	Purple Emperor *(Apatura iris)* (1941)
Small Pearl-bordered Fritillary *(Boloria selene)* (1939)	
Post NNR extinctions	
Chequered Skipper *(Carterocephalus palaemon)* (1975)	Dingy Skipper *(Erynnis tages)* (early 1970s)
Wood White *(Leptidea sinapis)* (1923) (1984-88)	Large Tortoiseshell *(Nymphalis polychloros)* (1962)
Green Hairstreak *(Callophrys rubi)* (~1987)	Pearl-bordered Fritillary *(Boloria euphrosyne)* (1966)
Brown Hairstreak *(Thecla betulae)* (mid 1970s)	High brown Fritillary *(Argynnis adippe)* (1962)
Silver-washed Fritillary *(Argynnis paphia)* (1970)	Dark Green Fritillary *(Argynnis aglaja)* (1955)
Extant	
Small Skipper *(Thymelicus sylvestris)*	Common Blue *(Polyommatus icarus)*
Essex Skipper *(Thymelicus lineola)*	Holly Blue *(Celastrina argiolus)*
Large Skipper *(Ochlodes sylvanus)*	White Admiral *(Limenitis camilla)* (1st in 1953)
Grizzled Skipper *(Pyrgus malvae)*	Red Admiral *(Vanessa atalanta)*
Clouded Yellow *(Coleus croceus)*	Painted Lady *(Vanessa cardui)*
Brimstone *(Gonepteryx rhamni)*	Small Tortoiseshell *(Aglais urticae)*
Large White *(Pieris brassicae)*	Peacock *(Inachis io)*
Small White *(Pieris rapae)*	Comma *(Polygonia c-album)*
Green-veined White *(Pieris napi)*	Speckled Wood *(Parage aegeria)*
Orange-tip *(Anthocharis cardamines)*	Wall Brown *(Lasiommata megera)*
Purple Hairstreak *(Neozephrus quercus)*	Marbled White *(Melanargia galathea)* (<1976, 1992-)
White-letter Hairstreak *(Satyrium w-album)*	Gatekeeper *(Pyronia tithonus)*
Black Hairstreak *(Satyrium pruni)*	Meadow Brown *(Maniola jurtina)*
Small Copper *(Lycaena phlaeas)*	Small Heath *(Coenonympha pamphilus)*
Brown Argus *(Plebeius agestis)* (<1960; 1995-)	Ringlet *(Aphantopus hyperantus)*

Table 5.4. Records of butterflies that have been present at Monks Wood in the past. For locally extinct species, the last year that it was recorded is given in brackets. Two species – the brown argus (*Aricia* (*Plebeius*) *agestis*) and the marbled white (*Melanargia galathea*) became extinct and then recolonised Monks Wood (Greatorex-Davies *et al*., 2006).

The total number of butterfly species recorded by the UKBMS at Monks Wood each year during the period 1973 to 2007 varies from19 to 27, but there has been a highly significant decline in the number of species recorded per year from an average of 24 to 21 species per year (r = -0.487, P = 0.003). An average rate of one less butterfly species being seen at Monks Wood every 12.6 years (Figure 5.3). The species that appear to have become locally extinct at Monks Wood, based on UKBMS data are: *Pyrgus malvae*, *Leptidea sinapsis*, *Satyrium w-album* and *Lasiommata megera*, although Greatorex-Davies *et al*. (2006, Table 5.4) suggests that three of these species are extant with only *L. sinapsis* locally extinct – which suggests that it can be quite difficult to demonstrate a local extinction. Species that have decreased include *Gonepteryx rhamni* and *Coenonympha pamphilus*. Species that appear to have colonised Monks Wood are *Aricia agestis* and *Melanargia galathea*. Species that have increased in numbers are *Thymelicus sylvestris*/*T. lineola*, *Ochlodes venata*, *Neozephyrus quercus*, *Polygonia c-album*, *Pararge aegeria*, and *Aphantopus hyperantus*. Species only recorded once were *Colias croceus* and *Argynnis paphia*.

Since the 19th century, about 17 species of butterfly have become extinct at Monks Wood (Greatorex-Davies *et al*., 2006, Table 5.4), with most of the known local extinction dates being in the 1960s and 1970s. However, the UKBMS data suggests that a further three of the extant species have more recently become extinct. This suggests that there were 46 species in the 19th century, 7 became extinct before Monks Wood was designated an NNR, and after designation as an NNR an additional 13 species have become locally extinct and one species (*Limentis camilla*) has colonised. This is the equivalent of a 30% loss of species while Monks Wood has been managed as a National Nature Reserve. There are limitations to the accuracy of these species numbers when Monks Wood was designated as a NNR in 1953 as illustrated by Greatorex-Davies *et al*. (2006) suggesting that there were 39 or 40 species and Thomas (2010) saying that there were 35 species.

The total number of individuals of all species increased during the 1970s and then there was no significant change from 1978 to 2007 ($r = 0.138$, $P = 0.466$, Figure 5.4). However, one species, *Aphantopus hyperantus* has increased considerably, such that in 2001 and 2007 there were more *A. hyperantus* than the combined total of all the other species (Figure 5.5). The total annual count of all species excluding *A. hyperantus* has dropped from 2984 in 1979 to 734 in 2001 and 952 in 2007- a 68-75% decrease (Figure 5.6). Figure 5.6 shows the total number of individuals of all species, excluding *A. hyperantus*, from 1978 onwards extrapolated using a linear trendline to the point where it reaches zero. The graph was started from 1978, rather than the peak of 1979, as the high population size in 1979 might unreasonably increase the gradient of the graph. The population would appear to reach zero before 2050, suggesting all species of butterfly would be extinct by this point, except for *A. hyperantus*. However, there are currently other species that are increasing in numbers, such as *O. venata* and *T. lineola*/*T. sylvestris*, so perhaps the predicted 2050 date is the date of complete replacement of one butterfly community with another community?

The population size of *A. hyperantus* and all butterflies excluding *A. hyperantus* was also investigated at Chippenham Fen and Holme Fen (Figure 5.7 and 5.8). These sites were chosen because they are in the same county as Monks Wood and have high quality data. Both sites had over 500 *A. hyperantus* counted in at least one year, suggesting that they contain reasonably good *A. hyperantus* habitat. Chippenham Fen, Holme Fen and Monks Wood (Figures 5.7 and 5.8) all showed increases in *A. hyperantus* populations in the 1980s and this also occurred in the national data (Figure 5.9). However, numbers at Chippenham Fen and Holme Fen did not reach 50% of the total butterfly population size, as occurred at Monks Wood. Also, the numbers of *A. hyperantus* at Chippenham Fen declined from the early 1990s and at Holme Fen they declined in the late 1980s. There was no evidence of a decline at Monks Wood or in the annual collated index.

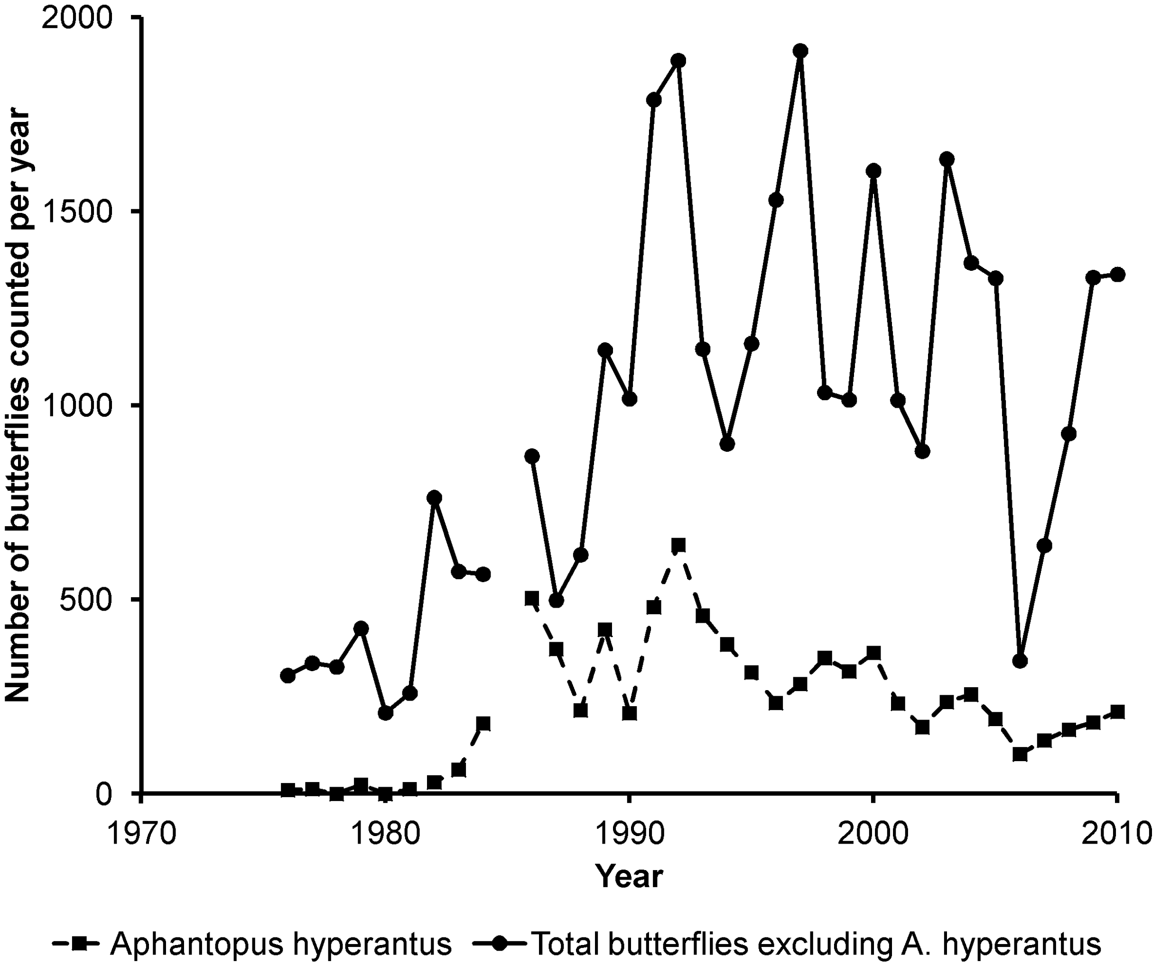


Figure 5.7. Total number of *A. hyperantus* and total number of all species excluding *A. hyperantus* at Chippenham Fen, Cambridgeshire, UK. No data were available for 1985.

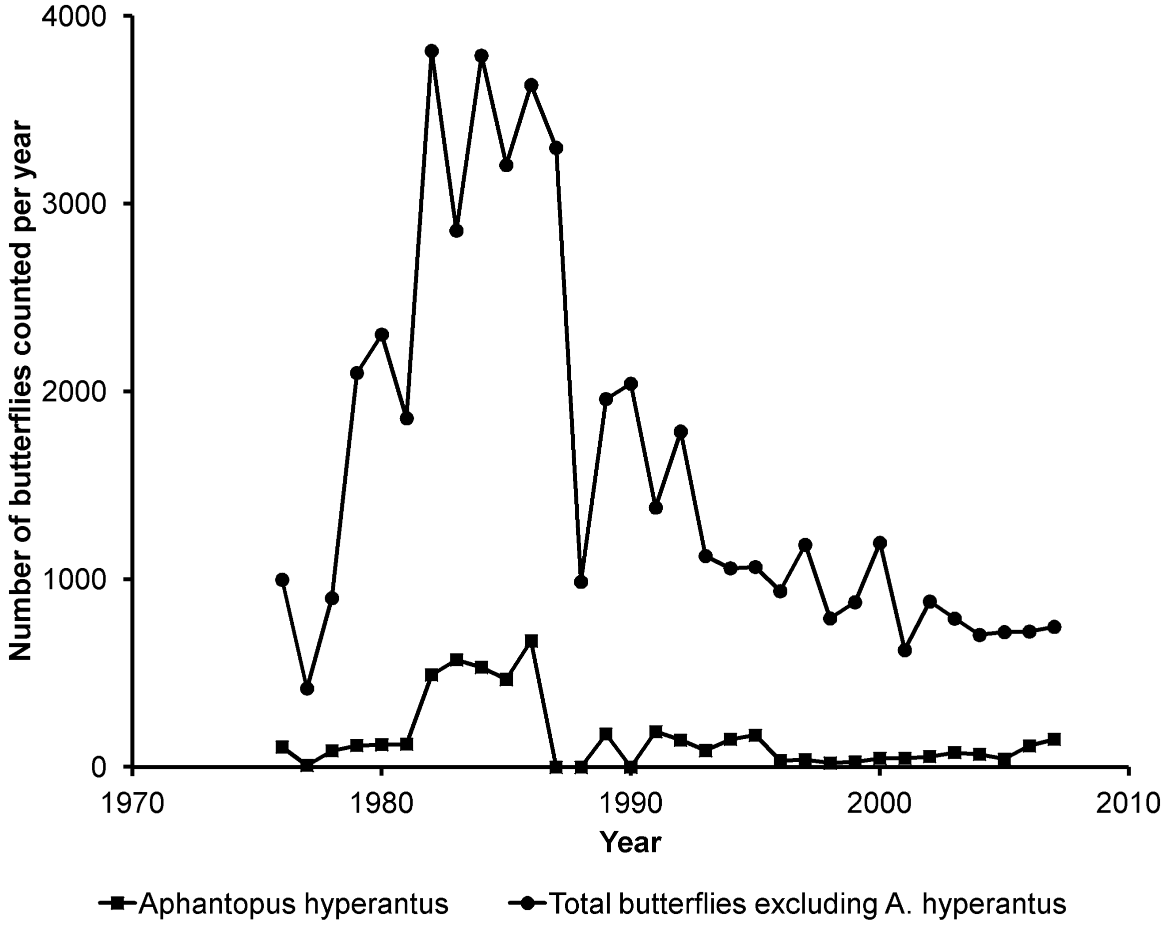


Figure 5.8. Total number of *A. hyperantus* and total number of all species excluding *A. hyperantus* at Holme Fen, Cambridgeshire, UK.

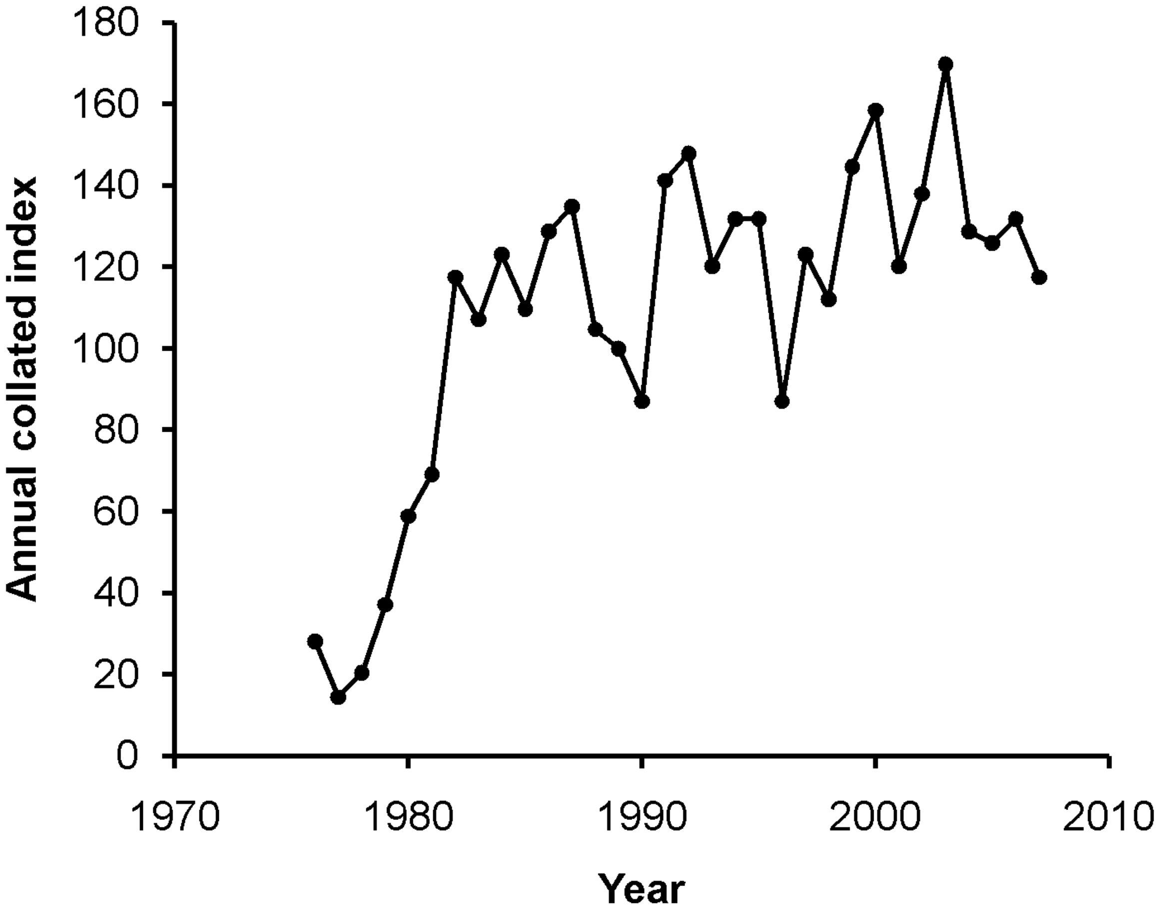


Figure 5.9. Changes in the national, annual collated index for *A. hyperantus* between 1976 and 2007. National collated indices are only available from 1976 onwards as this was when the butterfly survey was expanded from the pilot site of Monks Wood to a national survey.

5.3.5 The NAO and the total number of butterfly species and total population size of all butterfly species

The total number of butterfly species and total number of butterflies of all species at Monks Wood were plotted against the winter NAO index to investigate whether weather associated with the winter NAO can control the number of species or the total number of butterflies.

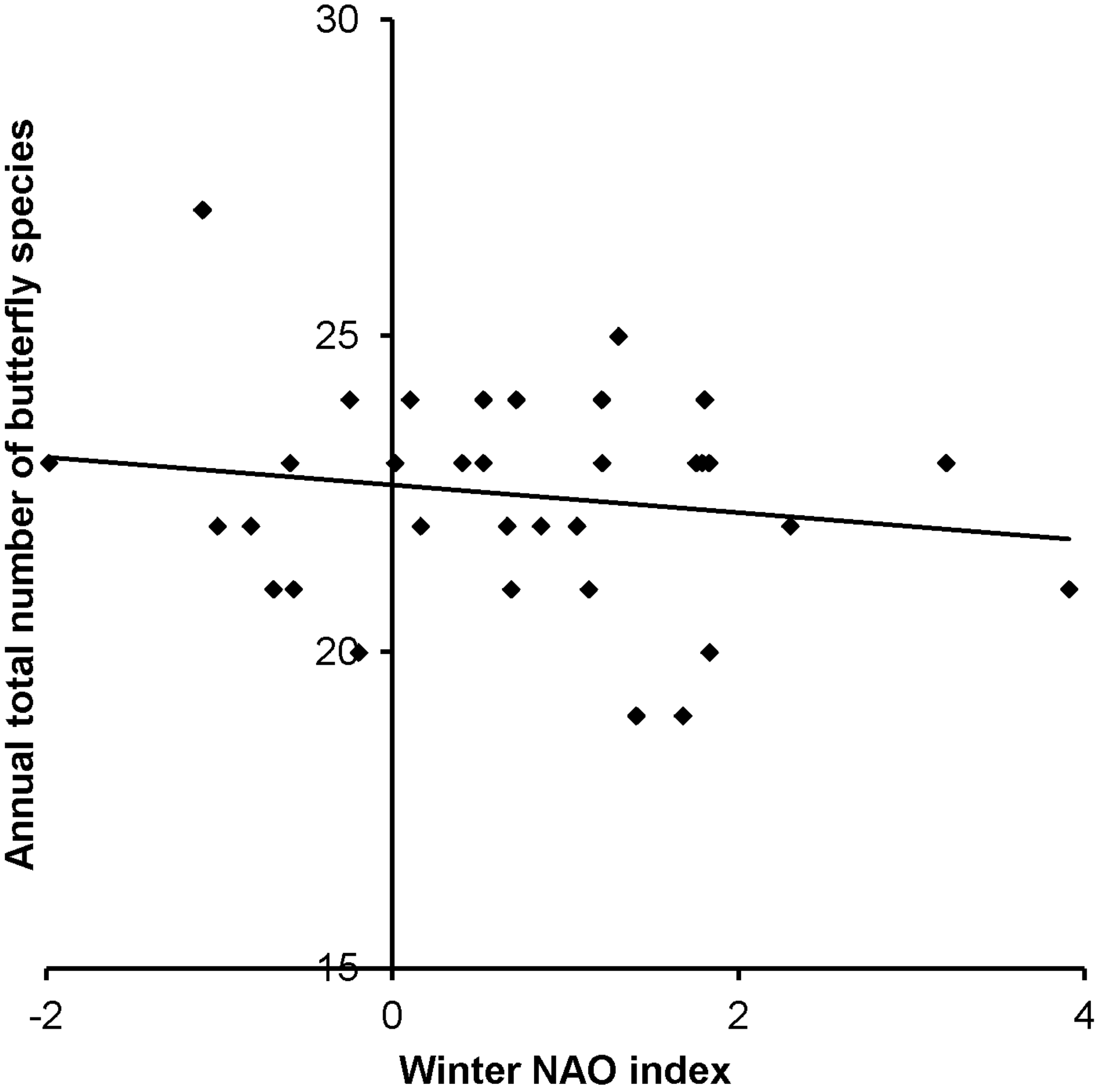


Figure 5.10. The association between the total number of butterfly species recorded at Monks Wood and the winter NAO index (r^2 = 0.0268, r = -0.164, P = 0.347).

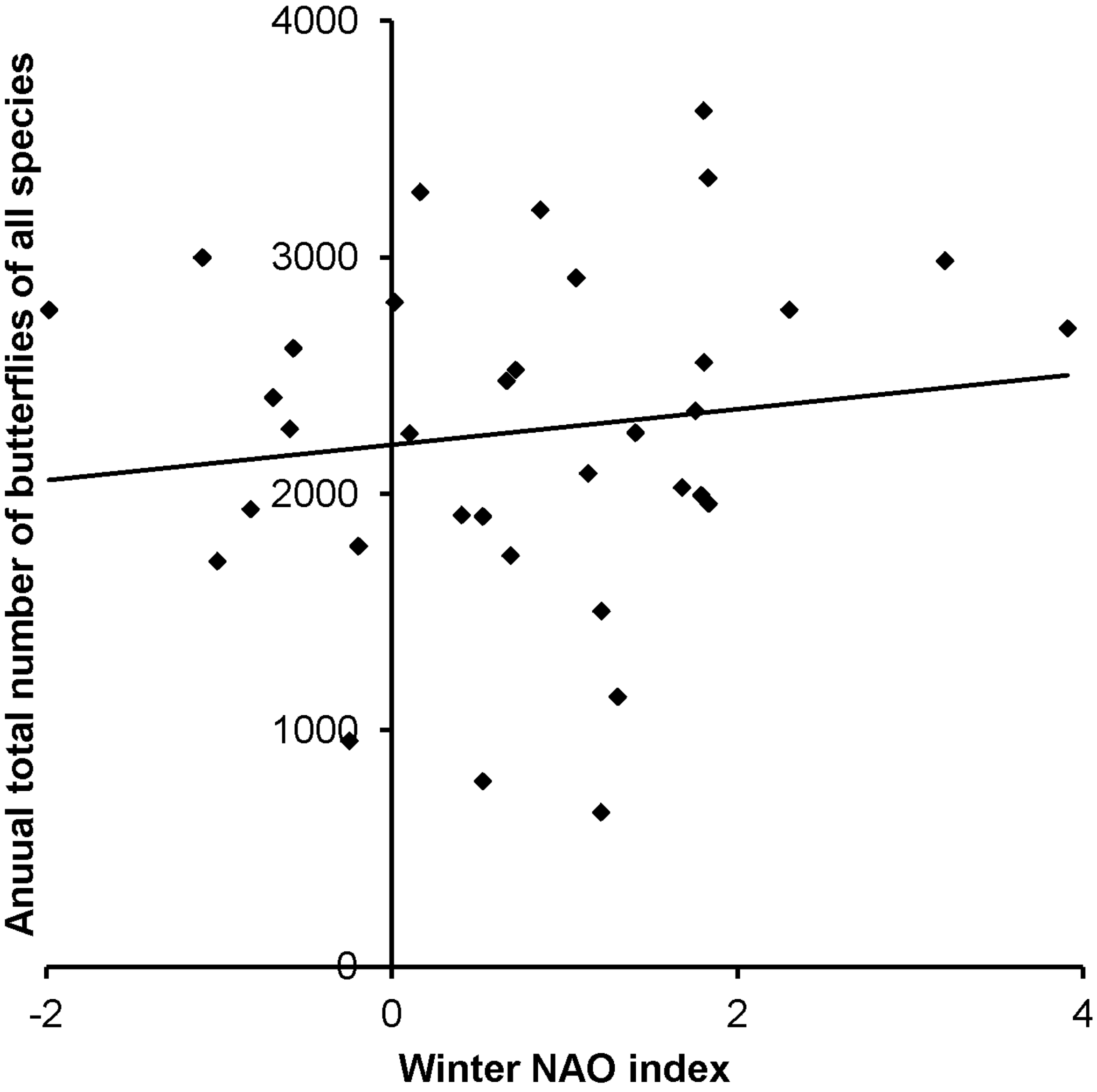


Figure 5.11. The association between the total number of butterflies of all species counted per year at Monks Wood and the winter NAO index ($r^2 = 0.0169$, $r = 0.130$, $P = 0.455$).

Weather associated with the NAO did not appear to influence the total number of butterfly species seen each year (Figure 5.10) or the total number of butterflies of all species counted per year (Figure 5.11).

5.3.6 Shannon-Wiener diversity index (*H*)

Shannon-Wiener diversity indices were calculated for each year from 1973-2007 at Monks Wood.

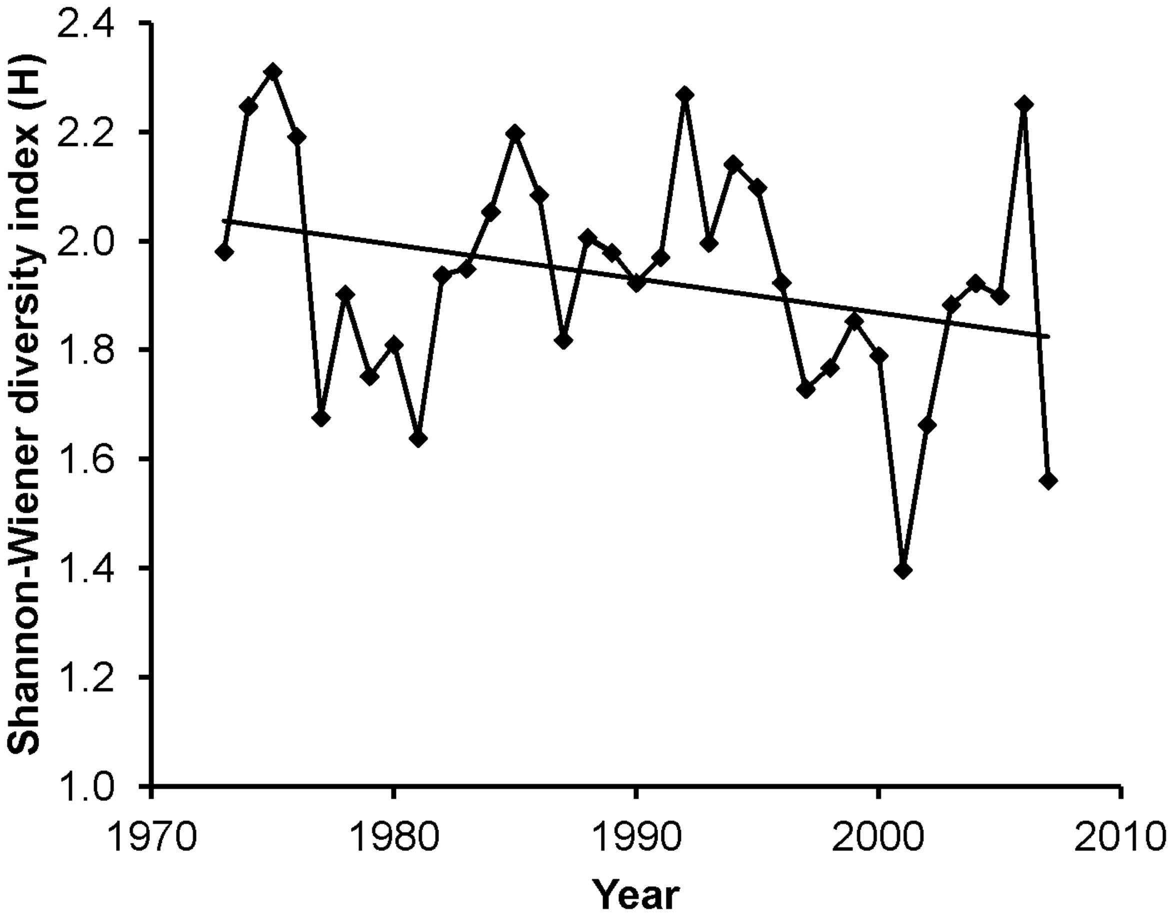


Figure 5.12. The Shannon-Wiener diversity index between 1973 and 2007 at Monks Wood National Nature Reserve (r^2 = 0.091, r = -0.302, P = 0.078).

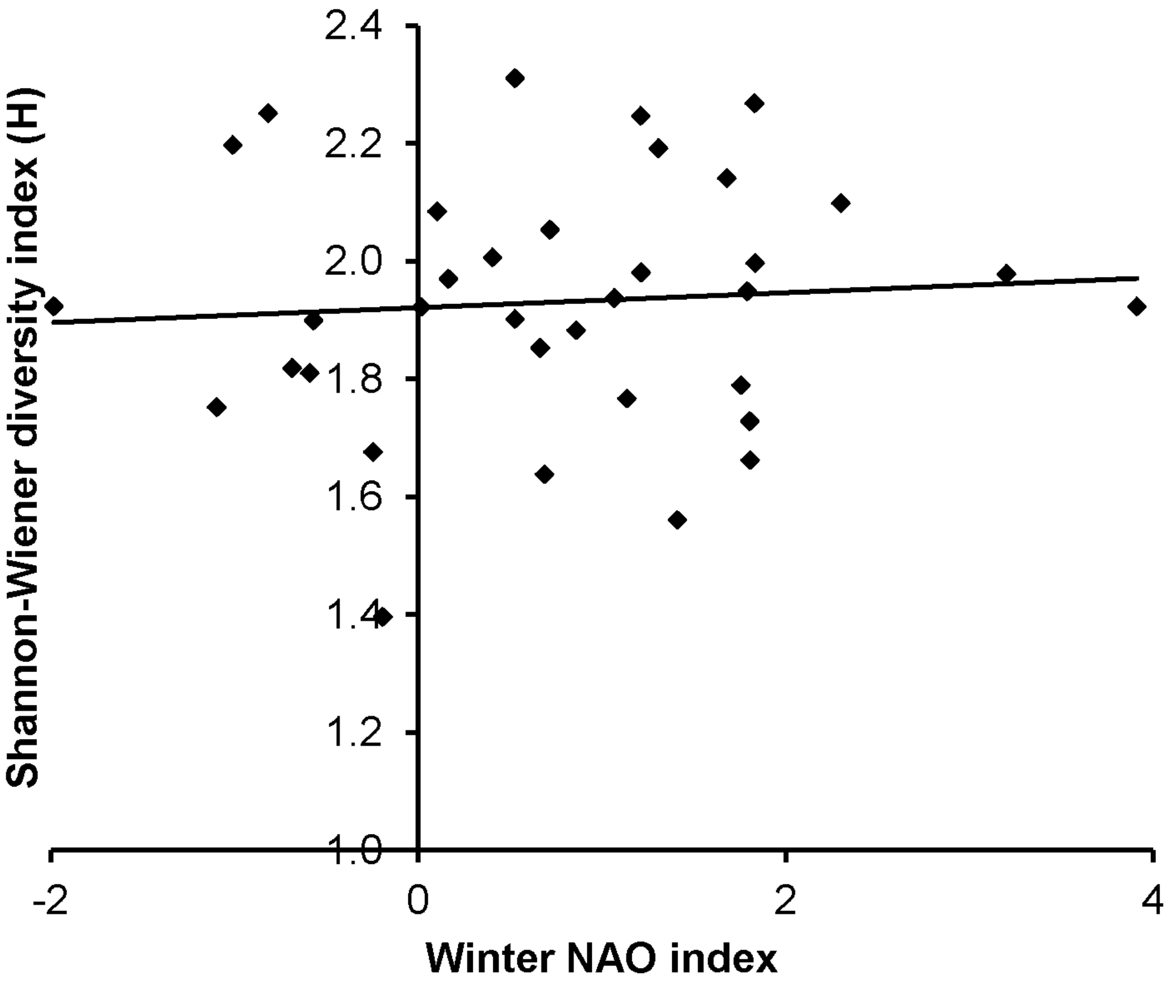


Figure 5.13. The association between the Shannon-Wiener diversity indices for butterflies at Monks Wood and the winter NAO index for the period 1973-2007. (r^2 = 0.0055, r = 0.075, P = 0.669).

The Shannon-Wiener diversity index appeared to be decreasing through the time series, although this decrease is not significant and there was considerable annual variation (r = -0.302, P = 0.078, Figure 5.12). Diversity would be expected to be decreasing as the number of species is decreasing (Figure 5.3) and one species (*A. hyperantus*) has increased in number to become a very large proportion of the butterfly community (Figure 5.5). A community where one species is especially abundant will have a lower diversity. There was no significant association between the Shannon-Wiener diversity index and the winter NAO index (r = 0.075, P = 0.669, Figure 5.13).

5.3.7 Associations between the population sizes of individual species of butterfly at Monks Wood and the winter NAO index

Annual count data for each species of butterfly at Monks Wood were correlated with the winter NAO index and then detrended butterfly count data were correlated with a detrended winter NAO index (Table 5.5). The detrending method used was to subtract the previous annual butterfly count, or the previous winter NAO index, from the current year. So the detrended data were the *change* from one year to the next.

	Not detrended		Detrended	
	r	*P*	*r*	*P*
Thymelicus sylvestris/T. lineola	-0.125	0.474	-0.071	0.688
Ochlodes venata	0.017	0.921	0.171	0.333
Pyrgus malvae	-0.180	0.300	-0.012	0.946
Leptidea sinapis	-0.313	0.067	-0.246	0.161
Colias croceus	0.144	0.410	0.132	0.455
Gonepteryx rhamni	-0.097	0.586	0.121	0.509
Pieris brassicae	0.077	0.660	0.066	0.710
Pieris rapae	0.075	0.669	0.285	0.102
Pieris napi	0.030	0.863	0.248	0.158
Anthocharis cardamines	-0.150	0.389	-0.121	0.495
Neozephyrus quercus	0.194	0.263	*0.397	0.020
Satyrium w-album	-0.236	0.172	-0.162	0.359
Satyrium pruni	-0.153	0.380	0.062	0.728
Lycaena phlaeas	*0.362	0.033	*0.406	0.017
Aricia agestis	-0.182	0.294	-0.105	0.555
Polyommatus icarus	**0.476	0.004	0.232	0.186
Celastrina argiolus	-0.154	0.376	**-0.503	0.002
Limentis camilla	0.016	0.929	0.141	0.425
Vanessa atalanta	-0.043	0.805	-0.053	0.767
Vanessa cardui	*-0.412	0.014	**-0.554	0.001
Aglais urticae	0.157	0.369	0.014	0.936
Inachis io	0.004	0.981	0.068	0.713
Polygonia c-album	-0.021	0.904	0.066	0.709
Argynnis paphia	0.128	0.462	-0.057	0.749
Pararge aegeria	0.211	0.223	0.213	0.227
Lasiommata megera	**0.498	0.002	*0.374	0.029
Melanargia galathea	-0.173	0.319	-0.079	0.658
Pyronia tithonus	-0.174	0.326	*-0.360	0.040
Maniola jurtina	0.090	0.607	-0.001	0.994
Aphantopus hyperantus	0.107	0.539	0.243	0.165
Coenonympha pamphilus	-0.190	0.273	-0.014	0.937
Total number of butterflies	0.130	0.455	0.189	0.285
Total number of species	-0.164	0.347	0.127	0.475

Table 5.5. Pearson correlation coefficients between non-detrended and detrended butterfly monitoring scheme counts for each species at Monks Wood and the winter NAO index. * = significant correlations, ** = highly significant correlations. *Thecla betulae* was excluded as there was insufficient data for this species.

Of the 31 species investigated, seven species (Table 5.5) showed significant Pearson correlation coefficients (P = <0.05) between the winter NAO index and the annual count of each species. There were four significant associations with non-detrended data and six with detrended data. Three of the seven species had significant associations with both non-detrended and detrended data.

A total of 62 correlation coefficients were calculated between individual species abundance and the winter NAO index (Table 5.5). If the data were completely random, then 5% of Pearson correlation coefficients might be expected to be significant at the 5% level, by chance. Therefore three correlations might be significant, by chance alone. However, as 10 correlations involving seven species showed statistically significant relationships, it is likely that the associations between abundance of these species and the winter NAO index were not due to chance.

5.3.8 Correspondence analysis

Correspondence analysis using the software C^2 was used to analyse the annual butterfly count data (the ‘Ind’ values). Unfortunately C^2 will not accept columns of species abundance data with any missing values. The Monks Wood dataset had some missing values, including both *Gonepteryx rhamni* and *Inachis io* in 2001, probably caused by access restrictions to the site due to an outbreak of foot and mouth disease in farm animals. *Pyronia tithonus* had one data point missing for 2007, presumably due to data missing for one week (week 17), in mid-flight season, for a species that can be present in very large numbers. These three missing values were replaced with the mean of the number counted in the year before and the year after the missing value. There were no data, other than an ‘NI’ (no index), for *Thecla betulae* and there were 27 years of missing data for unknown whites, so both *T. betulae* and unknown whites were excluded from the correspondence analysis.

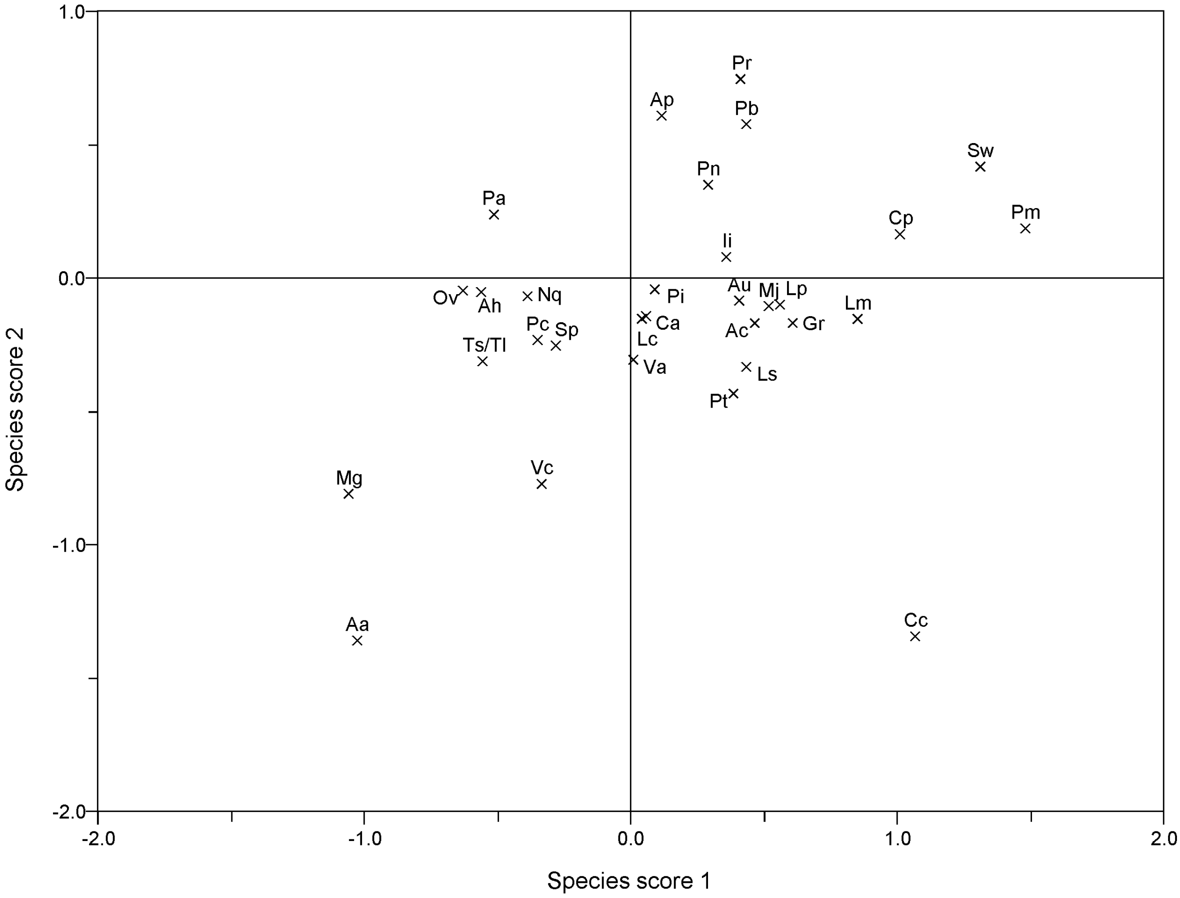


Figure 5.14. Correspondence analysis: species score 2 against species score 1 for the Monks Wood butterfly data. Eigenvalue for species score 1 is 0.2482 and species score 2 is 0.0707. Ts/Tl, *Thymelicus sylvestris*/*T. lineola*; Ov, *Ochlodes venata*; Pm, *Pyrgus malvae*; Ls, *Leptidea sinapsis*; Cc, *Colias croceus*; Gr, *Gonepteryx rhamni*; Pb, *Pieris brassicae*; Pr, *Pieris rapae*; Pn, *Pieris napi*; Ac, *Anthocharis cardamines*; Nq, *Neozephyrus quercus*; Sw, *Satyrium w-album*; Sp, *Satyrium pruni*; Lp, *Lycaena phlaeas*; Aa, *Aricia agestis*; Pi, *Polyommatus icarus*; Ca, *Celastrina argiolus*; Lc, *Limentis camilla*; Va, *Vanessa atalanta*; Vc, *Vanessa cardui*; Au, *Aglais urticae*; Ii, *Inachis io*; Pc, *Polygonia c-album*; Ap, *Argynnis paphia*; Pa, *Pararge aegeria*; Lm, *Lasiommata megera*; Mg, *Melanargia galathea*; Pt, *Pyronia tithonus*; Mj, *Maniola jurtina*; Ah, *Aphantopus hyperantus*; Cp, *Coenonympha pamphilus*.

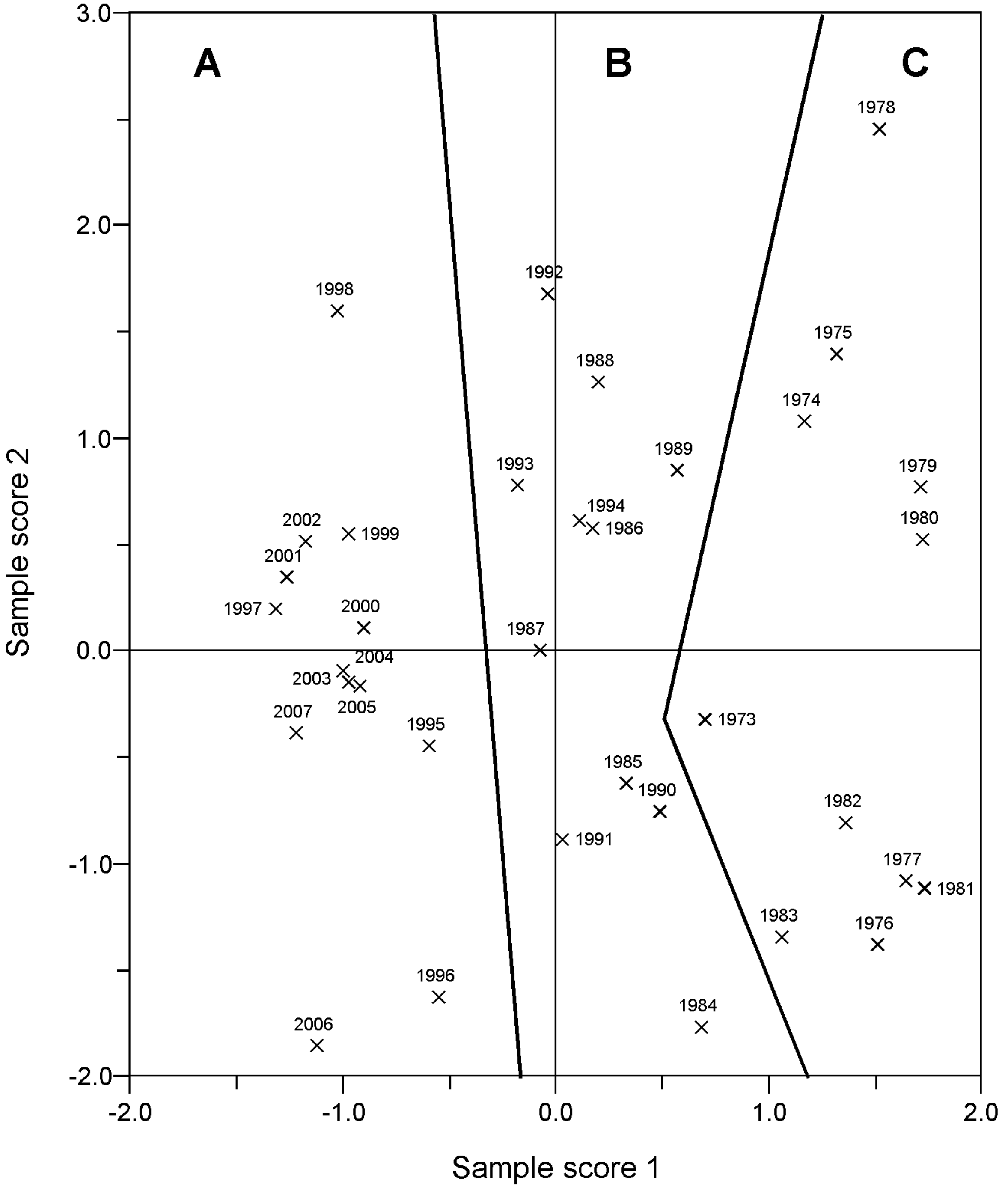


Figure 5.15. Correspondence analysis: sample score 2 against sample score 1 for the Monks Wood butterfly data. Contour lines have been added to show the change with time. A = years 1995-2007, B = years 1984-1994, C = years 1973-1983. Eigenvalue for sample score 1 is 0.2482 and sample score 2 is 0.0707.

Most of the species in the species score graph appeared as one group, suggesting that the abundance of most butterfly species at Monks Wood fluctuated in a relatively similar manner (Figure 5.14). The main outlier species were *Melanargia galathea*, *Aricia agestis* and *Colias croceus*. These species had many years when no individuals were counted, so it is likely to be the very low numbers of these species, rather than necessarily any unusual behaviour, that has resulted in them being outliers.

Sample score analyses suggest that the butterfly species composition at Monks Wood has been changing in a fairly consistent manner throughout the time series (Figure 5.15). Contours have been drawn on the graph to make it easier to see this change. This change with time is described by sample score 1, which has a relatively high eigenvalue of 0.2482, which means that points that are distributed along this axis represent an important proportion of the change in species composition and abundance. Replacing the labels showing years in the sample score graph to labels showing the winter NAO index showed no evidence of a pattern.

5.3.9 The NAO and flight phenology at Monks Wood

Total weekly count data for a single species, *Maniola jurtina*, at Monks Wood were used to investigate how weather associated with the winter NAO index affected the phenology of the flight season. *M. jurtina* was chosen because it was the second most abundant species at Monks Wood (Figure 5.2). By selecting species on the basis of abundance, bias in species choice was minimised. *M. jurtina* flies during the summer and numbers can be higher than spring species. Also it is a relatively abundant, easy-to-see species, as it flies low down, perching on grass or flowers, unlike some hairstreaks, that fly high in the canopy, and hence can be considerably more difficult to both see and accurately identify.

The most abundant species at Monks Wood was *A. hyperantus*, but the sample size varied considerably through the time series and this sample size variation had too large an influence on estimates of flight duration, with a longer flight time associated with more individuals counted (Figure 5.16). Also, the association between flight duration and number of individuals counted appearing to change for less than, and more than, about 300 individuals per year (Figure 5.17).

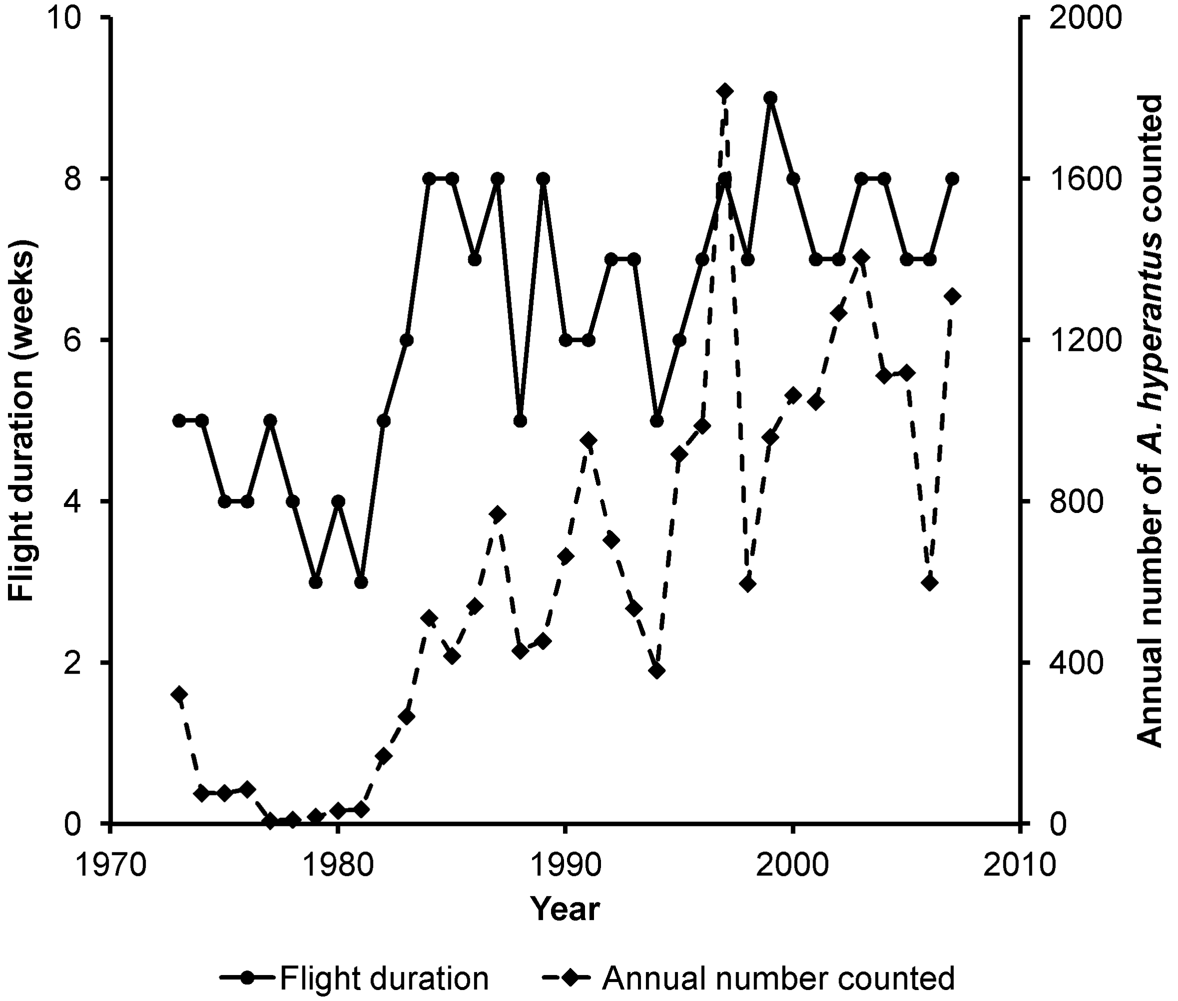


Figure 5.16. The flight duration of *Aphantopus hyperantus* and the annual number of this species counted at Monks Wood between 1973 and 2007.

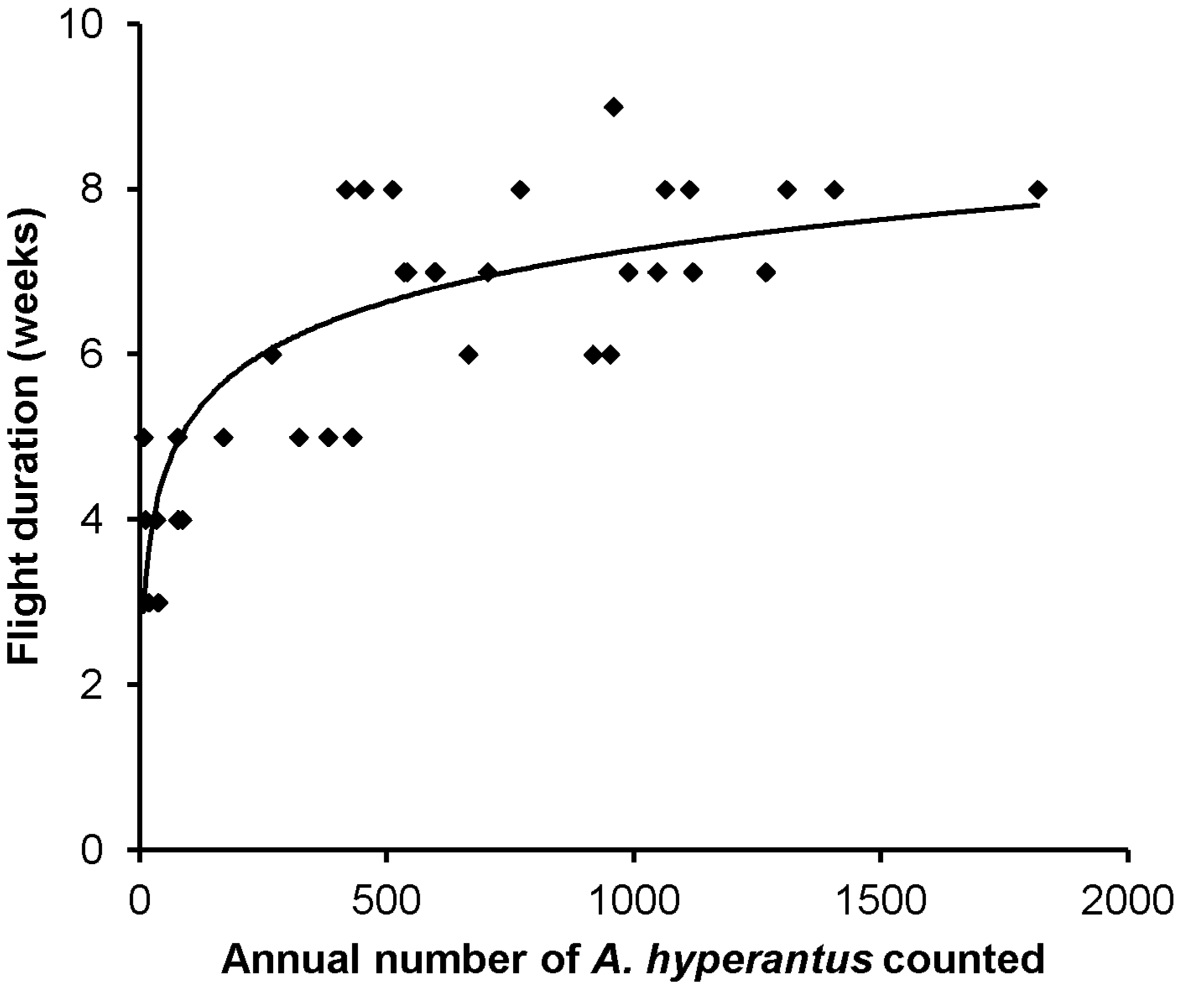


Figure 5.17. The flight duration of *A. hyperantus* plotted against the annual number counted. The trendline is a $\log_{10}$ trendline (r^2 = 0.6549).

M. jurtina had the advantage that it was not recorded on the first survey week, so the problem found with species such as *G. rhamni*, *A. urticae*, *I. io* and *P. c-album*, that were already flying at the start of each year's survey, and therefore too early to obtain a first flight week, was eliminated. This problem of describing phenological changes for species with hibernating adults, including *A. urticae* and *G. rhamni*, was identified by van Strien *et al*. (2008) using data from the Dutch Butterfly Monitoring Scheme. As these species fly so close to the months that the NAO influences UK weather, it is unfortunate that the UKBMS does not start earlier in the year, as these species might show strong associations with the NAO. The species that fly early in the year usually do not fly in large enough numbers on individual sites to investigate phenological change and the numbers recorded each week can be highly variable due to variable weather early in the year.

The week number of first and last flight for *M. jurtina* was obtained for each year, from which it was possible to calculate the flight duration. The mean flight week was calculated by multiplying the number counted in each week by the week number. These numbers were then summed and divided by the total number of butterflies counted in that year. The total number of butterflies was the total from all weeks, not the total from the ‘Ind’ column, which is in part based on predictions of the number of butterflies in any weeks with missing data. There were few missing data at Monks Wood, so the ‘Ind’ column is similar to the total obtained from summing the weekly data.

5.3.10 *Maniola jurtina* and the NAO

This section investigates whether there is evidence for weather associated with the winter NAO or climate change controlling the flight timing of *M. jurtina*. *M. jurtina* is univoltine and the second most abundant species at Monks Wood.

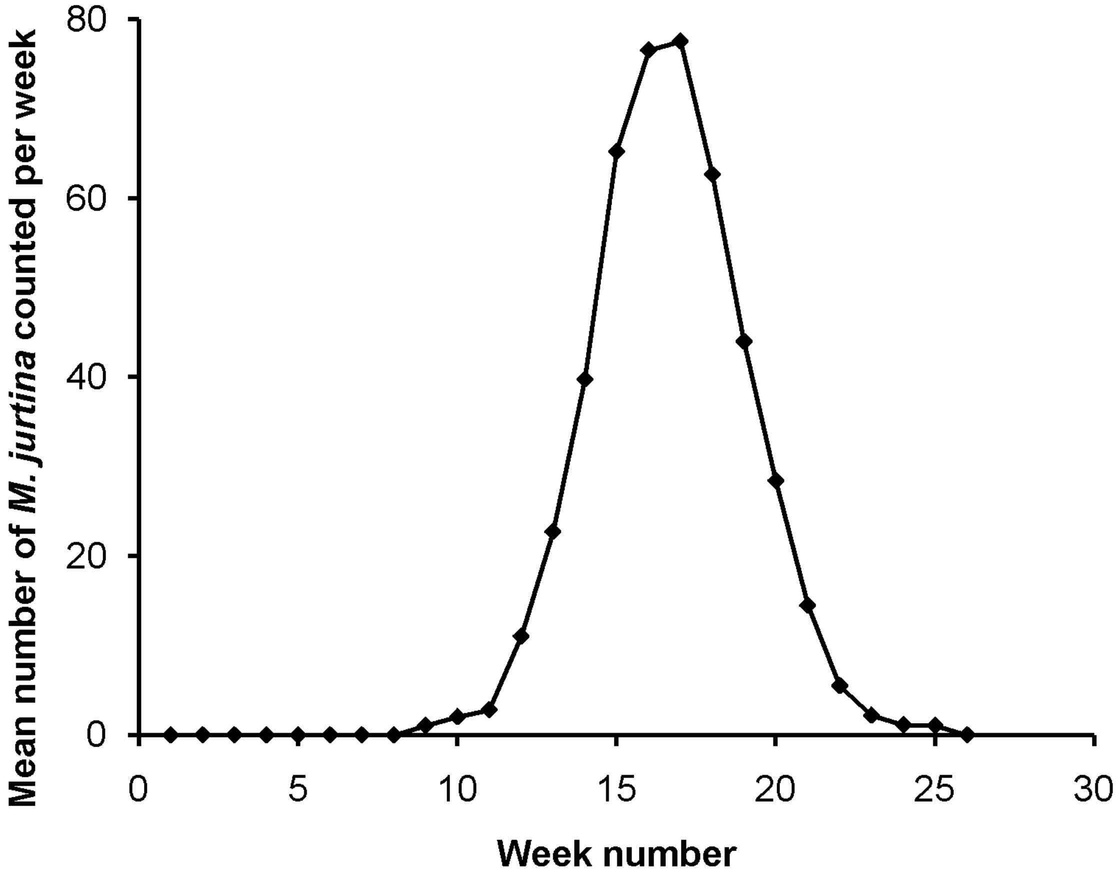


Figure 5.18. The flight season of *Maniola jurtina*, demonstrated by plotting the mean number of *M. jurtina* counted per week for 1973-2007 against the time of year (week 1 represents the first week of April, and week 26 is the last week of September.

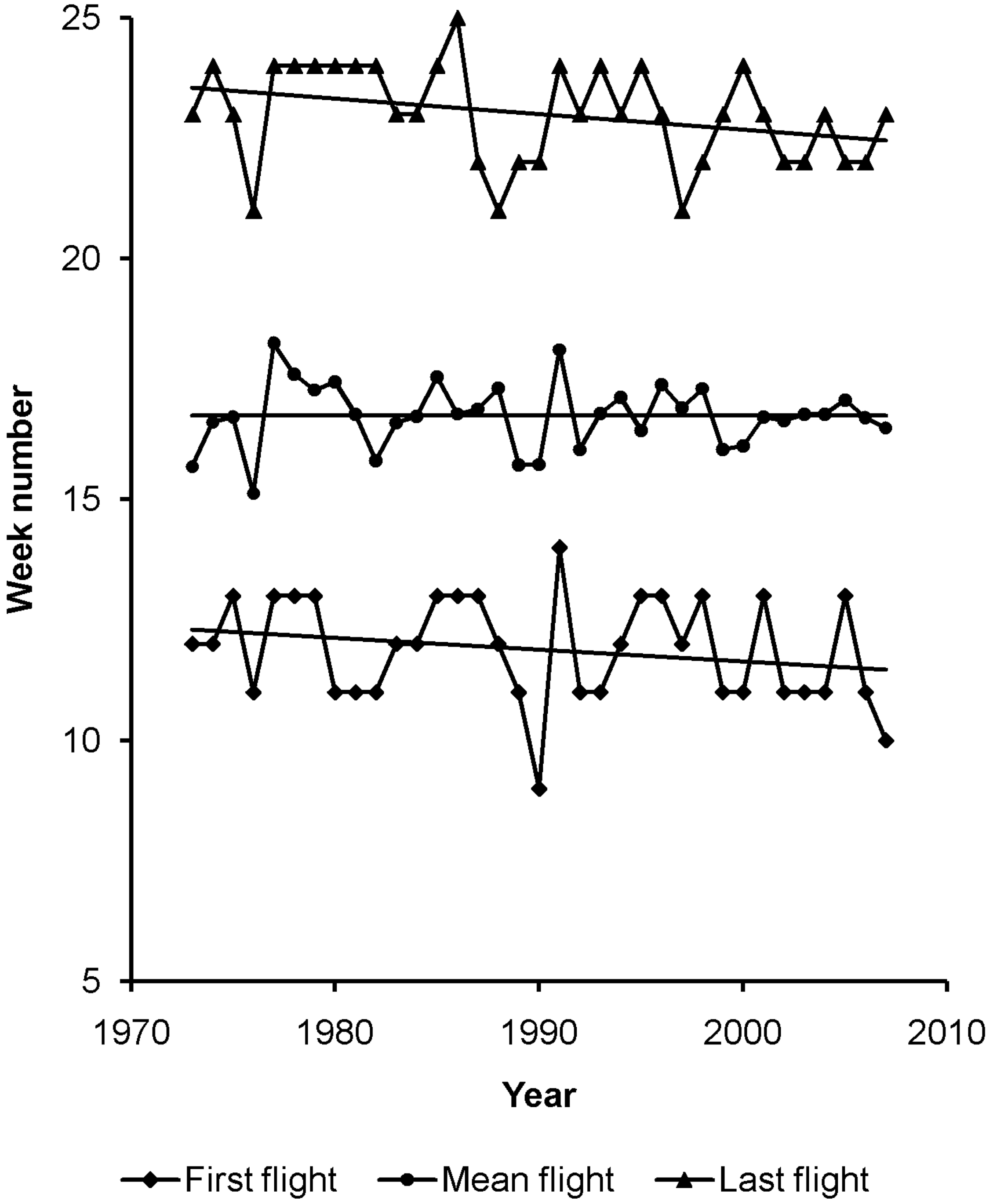


Figure 5.19. Changes in the flight season of *M. jurtina* with time at Monks Wood National Nature Reserve. The first (*r* = -0.226, *P* = 0.192), mean (*r* = -0.001, *P* = 0.996) and last (*r* = -0.321, *P* = 0.060) flight weeks are plotted against the year.

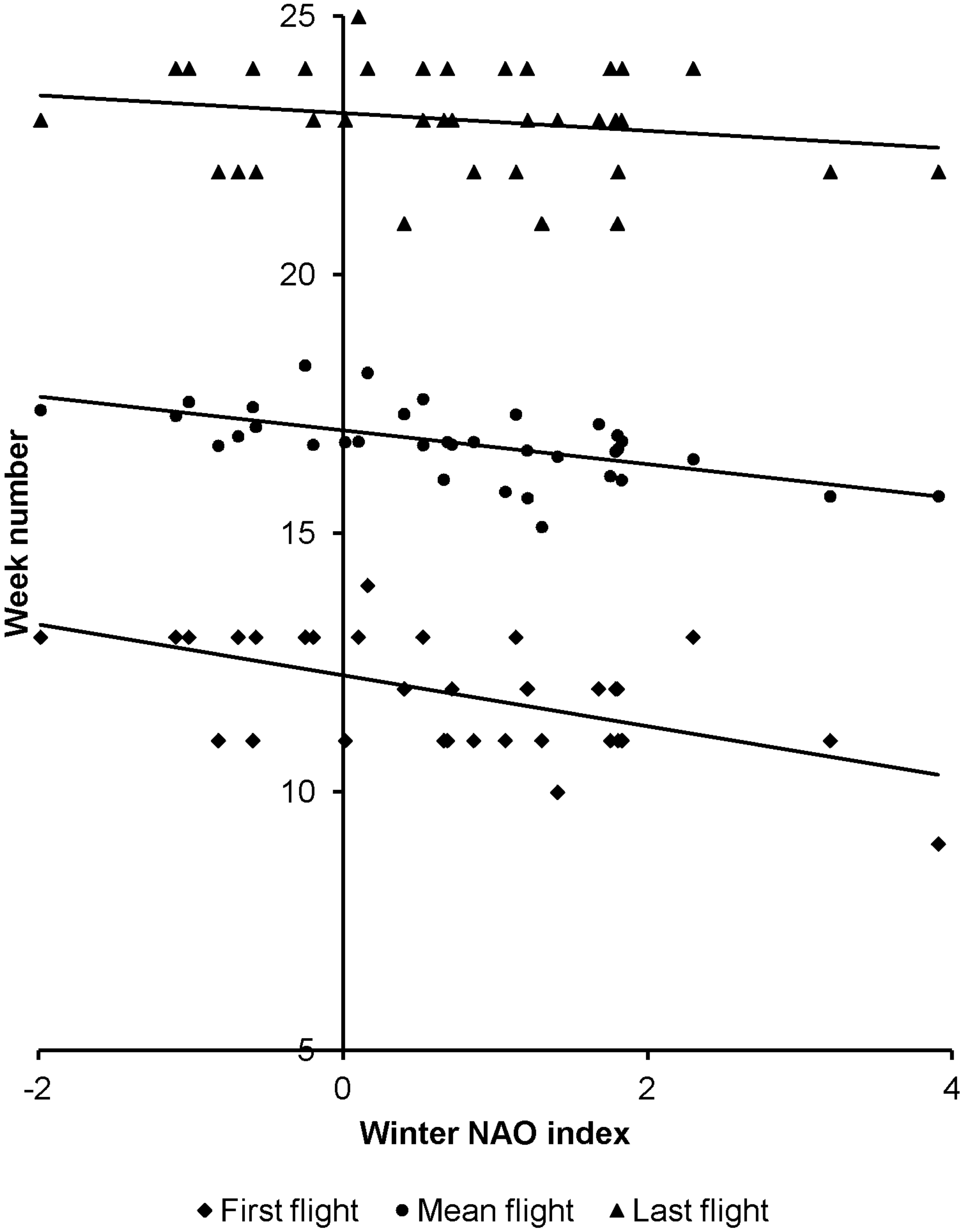


Figure 5.20. The relationship between flight time of *M. jurtina* and the winter NAO index at Monks Wood National Nature Reserve. The week of first flight (r^2 = 0.3078, r = -0.555, P = 0.001, m = -0.4921), mean flight (r^2 = 0.3551, r = -0.596, P = <0.001, m = -0.3274) and last flight (r^2 = 0.0432, r = -0.208, P = 0.231, m = -0.1716) are plotted against the winter NAO index using data from 1973-2007.

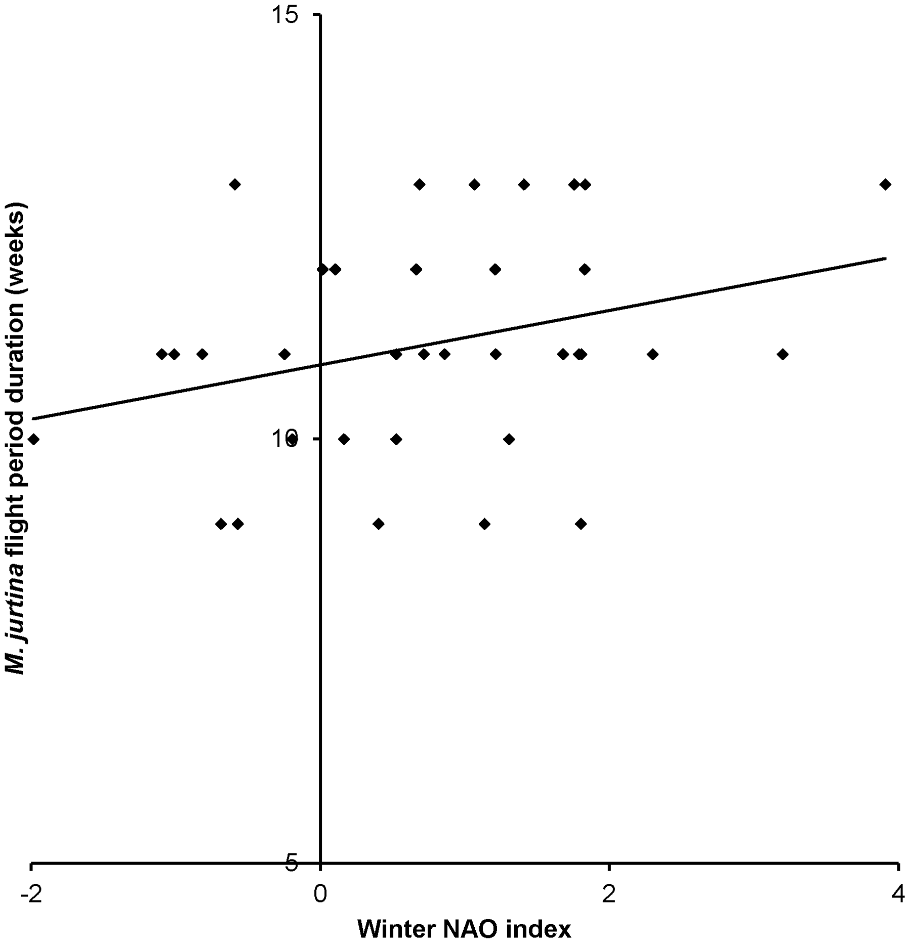


Figure 5.21. The relationship between the flight period of *M. jurtina* and the winter NAO index. Data for 1973-2007 (r^2 = 0.0943, *r* = 0.307, *P* = 0.073).

Weekly data for 1973-2007 from Monks Wood showed that *M. jurtina* is univoltine, with a clearly defined flight period starting at about week 9 and finishing at about week 25 (Figure 5.18). There is limited evidence for a role of climate change; although the first (*r* = -0.226, *P* = 0.192) and last flight weeks (*r* = -0.321, *P* = 0.060) have become earlier through the time series, the mean flight week has not changed (*r* = -0.001, *P* = 0.996) (Figure 5.19).

M. jurtina appears to fly earlier in years with a more positive winter NAO index. This association is strongest with both mean (*r* = -0.596, *P* = <0.001) and first flight (*r* = -0.555, *P* = 0.001), whereas the association with the date of last flight was not significant (*r* = -0.208, *P* = 0.231) (Figure 5.20). The gradient was steepest for the week of first flight (*m* = -0.4921), less for the mean flight (*m* = -0.3274) and least for the last date of flight (*m* = -0.1716). Therefore the association between the winter NAO index and phenology for *M. jurtina* appears to diminish later in the year and further from the winter period, when the NAO has the strongest effect on the weather.

The mean flight week had a slightly higher Pearson correlation coefficient with the winter NAO index than the week of first flight. This may be because first and last flight week numbers were influenced by small numbers of butterflies at the extremes of the flight season. Mean flight dates were influenced more by weeks containing larger numbers of butterflies and which were nearer the peak of the flight season.

The time interval between the first and last flight was used to calculate a flight season duration which was plotted against the winter NAO index. As the NAO index becomes more positive, both the first and last flight start earlier, but as the gradient of first flight is steeper, the flight duration increases. So the more positive the winter NAO index, the longer the flight season although the relationship was not quite significant at the 5% level (*r* = 0.307, *P* = 0.073, Figure 5.21).

5.3.11 Relative magnitude of the effect of the NAO compared to climate change on the flight timing of *Maniola jurtina* at Monks Wood

Coefficients of determination were calculated for *M. jurtina* flight timing against year (as a proxy for climate change) and against the winter NAO index and were converted into a percentage of the variability explained by climate change and the winter NAO index.

Species or group of species	Event	Percentage of variability explained by climate change	Percentage of the variability explained by the winter NAO
Maniola jurtina	First flight	5.11	30.78
	Mean flight	<0.01	35.51
	Last flight	10.30	4.32

Table 5.6. Percentage of the variability in flight timing explained by climate change and by the winter NAO.

Table 5.6 suggests that for *M. jurtina* the winter NAO has a stronger effect than climate change on first and mean flight, but not last flight week numbers.

5.4 Discussion

5.4.1 What influence does the NAO have on the weather at Monks Wood?

The NAO appeared to control temperature between October and May, with the strongest degree of control of temperatures from December to February inclusive. As the NAO controls temperature, it also influences the number of days of air frost during the period December to February inclusive. The NAO appeared to exert a weak control of precipitation in February and sunshine duration in February, March, August and September.

The winter NAO index showed a highly significant correlation with annual temperatures and annual days of air frost, a significant correlation with annual total sunshine hours and no association with precipitation. The correlation coefficient between the winter NAO index and air frost days has a higher correlation coefficient than the correlation between the winter NAO index and annual temperatures, because most of the air frost days are in the months when the NAO has the largest influence on the weather.

5.4.2 Is there any evidence of climate change at Monks Wood?

Annual temperatures appeared to decrease during the period 1973-1986 and then to increase until the end of the data series in 2007. The initial decrease in temperatures may be due to sulphate aerosol pollution causing increased reflection of radiation back into space and therefore causing cooling (Bauer *et al*., 2008; Earth System Research Laboratory, 2011). The temperature increase from 1986 onwards is due to climate change and a reduction in aerosol pollution in part due to clean air legislation.

The Copenhagen Accord (United Nations Framework Convention on Climate Change, 2009) “*recognises the scientific view that the increase in global temperature should be below 2 degrees Celsius*” although it does not seem to specify the baseline reference year. The mean annual temperature rise at NIAB between 1973 and 2007 was 1.5ºC, and if trends continue would be 2ºC by 2018, so to be meaningful the actions resulting from the Copenhagen Accord must be very swift and effective, and as far as Cambridge is concerned, this target is highly unlikely to be met. If the rate of temperature increase remains constant then by 2100 mean annual temperature in Cambridge would be about 5.6°C higher than 1973, however this is assuming a linear increase and could be an underestimate as the annual rate of increase in carbon dioxide in the atmosphere is increasing (Figure 1.3), so there might be an increasing rate of temperature increase.

A >5°C warming would be the equivalent of a change in latitude between Cambridgeshire and southern Europe or North Africa, which might mean that the temperature at Monks Wood would be less suitable for the English oak (*Quercus robur*) and more appropriate for the cork oak (*Quercus suber* L.) – which currently grows in Spain (Lacambra *et al*., 2010; AWS pers. obs.).

5.4.3 Is the relative abundance of butterflies at Monks Wood changing with time?

There was considerable variation in the relative abundance of some species of butterfly at Monks Wood. The most abundant species was *Aphantopus hyperantus*, followed by *Maniola jurtina*. However, *A. hyperantus* went from being relatively uncommon to comprising over 50% of the butterflies counted during the time series. This population increase may be due to increasing atmospheric nitrogen deposition, which can change grassland plant communities by increasing coarse grasses (e.g. *Brachypodium sylvaticum* (Huds.) Beauv.) and reducing floral abundance and diversity (Pollard *et al*., 1998) to Monks Wood. The low population size in the mid-1970s is in part due to the effect of the 1976 drought (Sutcliffe *et al*., 1997), although populations were low in 1974 when annual precipitation was high. Populations of *A. hyperantus* at two other East Anglian National Nature Reserves initially showed the increase seen at Monks Wood, but then they declined, whereas the population at Monks Wood did not decline, suggesting that site-specific factors can also influence population size. Further enquiries might relate to patterns of nitrogenous fertiliser usage in surrounding fields, as Chippenham Fen is a Ramsar wetland and it is possible that less fertilisers are used in a buffer zone.

The low total number of butterflies of all species counted during the 1970s might be an effect of testing the recording technique at that time. When the route was being piloted it was sometimes walked more than once per week and average weekly numbers were calculated. Averaging can remove extreme high and extreme low values. However, low butterfly numbers were also recorded at Chippenham and Holme Fens in the 1970s and early 1980s, suggesting the involvement of a national, not local, factor. In 1974, the Nature Conservancy Council started to manage Monks Wood for butterfly conservation, including by widening the rides (woodland tracks) (Pollard, 1982), and this might also have contributed to the increase in butterfly numbers. Monks Wood has, however, gone from low total butterfly abundance with high species diversity, to a higher butterfly abundance but with a lower diversity.

As the total number of butterflies of all species has remained fairly constant from 1978, this means that the total number of butterflies of all other species excluding *A. hyperantus* is in decline. Extrapolating a trendline suggests that all other species might be extinct by the mid-2040s, although as some species, such as *Ochlodes venata*, are also increasing, a complete local extinction of all species other than *A. hyperantus* is unlikely.

Thomas (2010) says that when Monks Wood was designated a nature reserve in 1953, it had 35 species of butterflies (although this might be 39-40 species; Table 5.4; Greatorex-Davies *et al*., 2006). However, within 30 years, eleven of these butterfly species had become locally extinct and were no longer present at Monks Wood, although none of their larval food plants had declined (Thomas, 2010). However, plants are also needed for nectar, as shown by the fact that butterfly diversity on roadside verges correlates with nectar availability (Munguira and Thomas, 1992). Further, nectar source plant decline viewed at a national scale has been shown to be a problem for bumblebees (Carvell *et al*., 2006), so perhaps butterfly population size is limited by adult food supply than larval food supply?

Unfortunately the extinction rate was highest before the UKBMS started, limiting the ability of the UKBMS to describe historical biodiversity loss. During the period of the UKBMS one less butterfly species was seen on average every 12.6 years, however Greatorex-Davies *et al*. (2006, Table 5.4) suggests that the last extinctions were in the mid-1970s, so perhaps some of the lower number of species recorded in some years from 1993 to 2007 was due to the lower probability of seeing a declining species rather than an actual extinction (Figure 5.3). The changing number of species with time at Monks Wood is known, although when accompanied by 35 species present in 1953 represents one of the longest published time series of insect decline – although Corke (1999) has published a two century decline in Epping Forest, Essex, UK. What appears new with the present study is to publish an average extinction rate for Monks Wood.

With most of the butterfly extinctions at Monks Wood happening during the 1960s and 1970s, it suggests that they were associated with agricultural intensification, and therefore indicating that butterflies at Monks Wood are vulnerable to what happens in the surrounding countryside. There could be various mechanisms for this vulnerability including pesticides and fertilisers blowing into the reserve, or the loss of ability of butterflies from surrounding areas to fly into the nature reserve. An important question is, which, if any, butterfly species can survive in an isolated nature reserve. Insect metapopulations usually require a combination of large habitat size, good habitat quality and reduced habitat isolation (Samways, 2007). Binzenhöfer *et al*. (2008) show that for the small blue butterfly (*Cupido minimus* Fuessly) living in a fragmented landscape, this process is complex with long term survival of metapopulations in lower habitat quality compensated for by higher connectivity within habitat patches.

5.4.4 Does the NAO have an effect on the overall diversity or abundance of the butterfly community at Monks Wood?

The NAO does not appear to have an effect on the abundance of the whole butterfly community, although it does have an effect on the population sizes of some species. The NAO also does not have an effect on overall butterfly biodiversity, but there have been decreases in diversity and number of species with time. I believe that this is the first time that it has been shown that for butterfly community abundance and diversity, long term environmental changes are ecologically more important than the NAO.

Weather associated with the winter NAO appears to influence the population size of the same species at the site-specific level of Monks Wood (Table 5.5) as it does at the national level using annual collated indices (Table 4.2). Butterfly abundance data from Monks Wood were used in calculating the annual collated indices, but so also were data from very many other UKBMS sites. Therefore it appears that the pattern of changes in the population sizes of individual species associated with the NAO at Monks Wood was probably not due to chance. Hence, it was possible to detect the influence of the NAO on butterfly abundance at the resolution level of a species but not at the community level.

Other authors (Conrad *et al*., 2002; 2004 and Greatorex-Davies *et al*., 2006) have described how the population sizes of insect species have changed with time. However, the new contribution of this work is to use multi-species statistics – total number of species, total butterflies, diversity indices and correspondence analysis - to look for evidence of an association with the winter NAO index.

5.4.5 How does sample size influence the ability to estimate the flight season timing, and therefore which species might be more appropriate to investigate the potential influence of the NAO?

Larger sample sizes enable more accurate determination of the mean flight week number. The most abundant butterfly species was *A. hyperantus*; however, the annual numbers counted of this species varied considerably, and the relationship between numbers counted and estimated flight period changes at lower numbers. This problem was resolved by using data for *M. jurtina*, which was the second most abundant species at Monks Wood to investigate possible effects at the species level. Future work might include merging weekly data for *M. jurtina* from several sites to further increase sample size. A larger sample size for *M. jurtina* might demonstrate a significant correlation between the winter NAO index and total flight period.

As many species of butterfly are declining in numbers, this could mean that site-specific butterfly monitoring scheme data will reduce in value for understanding butterfly ecology, because the sample sizes may become too small.

5.4.6 Is it possible to estimate the relative magnitude of the effect of climate change compared to the effect of the NAO on flight timing?

M. jurtina flew earlier and for longer in more positive NAO index years. This species flies during the summer, well after the period when the weather is affected by the NAO, so weather associated with the NAO is presumably affecting the non-adult life stages. Although other authors have shown associations between temperature and the behaviour of *M. jurtina* (Cormont *et al*., 2011), this is the first time that evidence of an association between the NAO and *M. jurtina* flight timing and flight season duration has been published.

For *M. jurtina*, the NAO appears more important than climate change in determining flight phenology. This is the first time that an attempt has been made to estimate the relative effects of climate change and the NAO on a butterfly species. However, whether other species of butterfly are similarly more affected by the NAO than by climate change, or the reverse, is currently unknown.

5.5 Summary

Both the NAO and climate change affect the weather at Monks Wood. The total number of butterflies recorded at Monks Wood was low from 1973-1977, but then increased and remained fairly constant from 1978 to 2007, although the total number of species, and probably also diversity, have declined. One species, *A. hyperantus*, has increased considerably in population size, suggesting declines in some of the remaining species. The effect of the NAO is difficult to detect in the abundance and diversity of the whole butterfly community, but is detectable in the abundance of some bivoltine species. The NAO influences the flight timing of *Maniola jurtina* at Monks Wood. 30% of butterfly species have become locally extinct at Monks Wood while it has been classified as a National Nature Reserve, with the highest rate of extinction being during the 1960s and 1970s. This was a period of agricultural intensification and suggests that the butterflies of Monks Wood are vulnerable to agricultural practices outside the reserve. Unfortunately, the UKBMS started too late to record this main period of butterfly species loss. It is possible that a similar magnitude species loss has occurred in other, much less well monitored, invertebrate groups at Monks Wood.

Chapter 6

General discussion

6.1 Overview

The main aim of this study was to use long-term butterfly and aphid population datasets to assess whether the North Atlantic Oscillation affects UK insect populations. National and local resolution data as well as single and multi-species data were used. Warm weather associated with a positive NAO index causes insects to fly earlier and also influences the population size of some species. There is an interaction between the NAO and butterfly life cycles which determines how much influence the NAO has on population size. Evidence is also presented showing the role of climate change and long-term environmental change on insect populations, and an evaluation has been made of the relative ecological importance of these effects.

6.2 The NAO and insects

The NAO affects UK weather from October to May, although its main influence is from December to March, and it exerts a greater control on temperature than precipitation. A positive NAO index is associated with warmer weather, slightly more rain and slightly more sunshine. As a result of the effect of the NAO on temperature, there is also a significant positive association between the winter NAO index and the number of frost-free days.

Warmer weather in years with a positive winter NAO index causes both butterflies and the green spruce aphid, *E. abietinum*, to fly earlier. The NAO causes both warmer and wetter weather which can work against each other, with wetter weather associated with later flight. The warmer weather that causes the change in phenology can occur before the flight season. The warmer weather associated with a positive NAO index can also act indirectly, by influencing the flight timing of the first generation of the bivoltine butterfly species, *Lasiommata megera* and *Polyommatus icarus*, which in turn can affect the flight timing of the second generation. The NAO influences the flight date of *M. galathea*, *A. hyperantus*, *P. tithonus* and *M. jurtina* by affecting the non-adult stages as the adult stages are after the time of year when the NAO affects the weather. Further investigation might include laboratory studies of the sensitivity of larvae, pupae and the process of metamorphosis to temperature.

There is a stronger association between the date of first flight of *E. abietinum* and *M. jurtina* and the winter NAO index than the date of last flight and the winter NAO index. This is due to the first flight date being nearer the time of year when weather is influenced by the NAO, and results in the flight season having a longer duration in more positive NAO years – this association was found to be significant for *E. abietinum* and almost significant for *M. jurtina*. Further work might include adding data from several sites for *M. jurtina*, to determine if the association between the NAO index and total flight season is significant with a larger sample size.

The NAO affects the population size of *E. abietinum* and some, but not all, butterfly species. Thus it is not possible to detect the influence of the NAO on butterflies at a community level through number of species, total number of butterflies, Shannon-Wiener diversity index or correspondence analysis. Longer-term population changes of individual species could, however, be detected with these methods, suggesting that long-term community level changes are of a greater magnitude than weather associated with the NAO.

The NAO influences butterflies in a complex manner, with species that are bivoltine and have a longer flight season being more likely to have a population size associated with the NAO. The reason for this may be that bivoltine species need a longer summer season to complete two generations, and weather associated with the NAO can influence the length of the flight season.

E. abietinum is a forestry pest species and a positive NAO index is associated with a larger population size and probably more damage to spruce trees. *Pieris brassicae* and *P. rapae* are two butterfly species that are pests (Cartea *et al*., 2009), but neither species show significant associations between their population size and the NAO. It is very difficult to predict the NAO index in advance, but by March, when the winter NAO index is known, there is potential to use the NAO as a predictor of flight timing and population size. Further work would include the effect of the NAO on the growth rate of spruce trees and butterfly parasitoid population size. Faster tree growth could mask the effect of more *E. abietinum*, and more butterfly parasitoids could mask the effect of an association between the NAO and butterfly pest population size.

6.3 Climate change and insects

Climate change has caused an increase in temperature at Rothamsted of 1.46°C during the period 1966-2006 which has caused the mean flight date for *E. abietinum* to advance by 17.5 days. This means that aphids have advanced their flight by 11.99 days°C^{-1}. If UK temperatures increased by 6°C, then this might lead to a 72 day change in aphid flight date. This could have serious consequences for butterflies, because as nectar source flowers become rarer in the countryside, aphid honeydew (a food source for some butterfly species) might make up a higher proportion of butterfly energy sources and such a large change in phenology might cause a mis-timing of honeydew availability for butterflies. Increasing atmospheric carbon dioxide concentrations could increase the carbon to nitrogen ratio of sap and therefore might reduce the nutritional value of honeydew as a butterfly food source. Therefore climate change can have a double effect on nutrition by causing mis-timing and reducing food quality. Further investigations might be on the effect of a reduced protein, higher sugar diet on butterfly growth and osmotic balance.

If climate change continues at the same rate, then this has the potential to lead to considerable ecological changes. However, predicting temperatures to the end of the 21st century is difficult especially as atmospheric carbon dioxide concentration is increasing in an accelerating manner. It also assumes that there are no phase shifts, perhaps associated with changes in the thermohaline circulation or a different range of atmospheric aerosol pollutants. Some butterfly species are likely to increase the number of generations per year as temperature increases, but this can create difficulties in monitoring the effect of climate change on phenology, as distinguishing between the second and third generations can be difficult.

6.4 Long-term butterfly population changes

The total number of butterflies at Monks Wood was low in the mid-1970s, but then increased and remained fairly constant from the 1980s onwards. However, the total number of butterfly species and probably also butterfly species diversity has declined at Monks Wood. *A. hyperantus* has increased from very low numbers to making up more than 50% of the entire butterfly population. Therefore Monks Wood has gone from a relatively low abundance, high diversity site in the mid-1970s to a higher abundance, lower diversity site towards the end of the time series.

The loss of species diversity suggests that either Monks Wood is too small or too isolated to be independent of environmental change in the intensively farmed East Anglian countryside, or that it is vulnerable to changes in woodland management, in particular the decline in coppicing. Monks Wood is the largest area of woodland in Cambridgeshire, so if it is too small to maintain biodiversity, then most woodlands in Cambridgeshire are probably too small. For butterfly conservation to be effective, existing woodlands may need inter-connecting in a manner similar to the Great Fen project. Lawton *et al*. (2010) summarise future conservation of habitats with the words: "*more, bigger, better and joined*" and environmental restoration needs to be large – on a "*landscape scale*". However it can take many decades, if not centuries, for recently planted woodland to develop into woodland with the habitat characteristics needed to support butterflies, so it may be a long time before woodland planting will benefit butterflies through increased habitat area and connectivity.

Future research might try and identify the minimum size of woodland needed to sustain a diverse butterfly population and identify the width of a buffer zone needed to exclude edge effects, such as those caused by nitrogen fertilisers, insecticides and road pollution. Corke (1999) suggests that the loss of butterfly species from Epping Forest might be due to particulate pollution from coal fires, so diesel particulates might also influence butterfly population size. As well as being surrounded by intensively farmed agricultural areas, Monks Wood is only 600 m to the east of the A1(M) road, and as the prevailing wind is from the south-west, this means that road vehicle pollution will be blown onto the reserve.

Butterfly population size is very variable from one year to the next. Presumably this means that there is a relatively high chance of local extinction, which means that effective conservation requires a network of inter-connected smaller populations within a woodland - so metapopulation dynamics are important. This network would be superimposed on a dynamic woodland system. To maintain several areas of woodland at each of these changing stages means that quite a large woodland would be needed.

Monks Wood is continuing to lose butterfly species, although species loss was fastest during the 1960s and 1970s, which corresponds to a period of agricultural intensification just before the UKBMS started. The rate of extinction may now have reduced, but this could be a result of the more vulnerable species becoming extinct first, and it is not clear if local extinctions will stop when the butterfly population has reduced to the range of species capable of surviving in woodland in an intensively farmed area. Monks Wood has lost 30% of its butterfly species while classified as a National Nature Reserve. If butterflies can be used as indicators of general insect diversity, then Monks Wood may also have lost 30% of non-butterfly insect species since becoming an NNR. UKBMS data are disproportionately based on ‘good’ butterfly sites rather than the wider countryside, and so the annual collated indices probably underestimate the loss of total number of individual butterflies at a landscape scale.

It is questionable how long a site can retain classification as a National Nature Reserve and Site of Special Scientific Interest with such a large species loss. It is not clear what the political and social accountability is to deal with wildlife conservation that is funded by the taxpayer, and which seems ultimately to be failing. Viewed at the scale of England, Lawton *et al*. (2010) say that species and habitats are continuing to be lost, yet is also correct in saying that “*conservation efforts have not been a waste of time - without them the losses would have been even greater*”. However, he did not point out that conservation efforts can create a societal perception that the situation is under control and therefore fail to make the “*step-change in nature conservation*”, which they correctly identify is needed. It might also be interesting to calculate a national rate of biodiversity loss with and without the actions of nature conservationists – it is possible that the differences between both these rates might be quite small and the relative influence of farming practices may be much larger than the role of conservation activities.

This loss of both species and biomass is probably occurring in other, non-butterfly, insect groups and is probably an international problem, with the potential to negatively affect populations of insectivorous organisms. The international dimension is relevant because some of our insectivorous birds (and some butterflies) migrate across many countries. We value some of these insectivores highly – for example, garden song birds. A response to this problem might require some scientists to make the cultural shift from describing and explaining what is happening to the political process of implementing change or working in teams with people with these skills. As an example of teamwork, the successful re-introduction of the large blue butterfly (*Maculinea arion*) in south-west England involved 23 organisations and individuals with different skills (National Trust, 2011). The scientific community and the peer-reviewed literature are international, and this might facilitate a response to international problems. Furthermore, the political process now has a strengthening international dimension through European legislation (e.g. the European Union Directive 92/43/EEC on the conservation of natural habitats of wild fauna and flora), international conventions (e.g. the Bern Convention on the Conservation of European Wildlife and Natural Habitats) and the United Nations, so perhaps the framework is developing for a response to international environmental problems. However, if conservation measures are on balance failing in the UK, what is the chance of success at an international level where the habitats concerned are geographically further away from the decision makers?

Butterfly conservation at Monks Wood might benefit from reinstating coppicing. This would require control of deer populations and perhaps development of a larger market for coppice products – possibly including burning the coppiced wood in a power station. However this should be hazel (*Coryllus avellana*) coppice with standards, probably oak, (*Quercus robur*), rather than short rotation coppice using high yielding varieties of willow (*Salix* L.) and poplar (*Populus* L.), which would be densely planted without standards, require the use of glyphosphate herbicides (Defra, 2004), and be harvested with large machines that create pollution, crush soil and vegetation. Pollution within woodlands can be reduced by using horse transport, but the main practical option for moving timber from woodlands to power stations requires the use of lorries.

Future conservation work could be to re-introduce locally extinct butterfly species into Monks Wood, both to replace species and possibly ‘assisted colonisation’ of species such as the black-veined white (*Aporia crataegi* L.) and mazarine blue (*Polyommatus semiargus*) as a response to climate change (Carroll *et al*., 2009). However, re-introduced organisms can be genetically different, as they come from different geographical regions (Porter and Ellis, 2011), and re-introducing species is pointless if the factors that caused the original extinction have not been identified and corrected. Re-introduction programmes can concentrate on colourful, distinctive, organisms but ignore small, non-distinctive organisms such as flies (Diptera). It is possible that the habitat restoration prior to re-introducing a butterfly species may help less distinctive species, but habitat restoration can be a significant change, for example felling trees to re-instate coppicing, and accompanied by microclimatic changes of opening the canopy, this could cause extinction of poorly monitored species.

Two of the most important butterfly habitats are grasslands and coppiced woodland, both of which are maintained by human activities. What butterfly species composition would be expected several thousand years ago before humans started grazing and coppicing and when human population densities were low? Were grasslands and open areas in woodlands maintained by fire, grazing by deer and perhaps beaver (*Castor fiber* L.), or were butterfly populations much lower? Are we now reducing butterfly populations back to what they were prior to human activity?

Butterfly extinction was probably highest at Monks Wood during the 1960s and 1970s, during the period of agricultural intensification. Species loss was occurring at Epping Forest from at least 1805 (Corke, 1999). Does this mean that to reinstate butterfly populations, agricultural techniques need to return to what they were in the 1950s (or perhaps pre-World War II) or even to eighteenth century techniques? The human population size has now grown. Could improved, modern, organic farming techniques make it possible to feed a higher population density?

6.5 The relative magnitude of parameters affecting insect populations

Many factors affect butterfly populations – the NAO is just one of these factors. However, it is possible to put several of these environmental effects into a relative order using the size of the correlation coefficients. Long-term environmental change (includes habitat loss) appears to have the greatest magnitude of effect on butterflies, followed by the influence of the NAO and climate change on flight phenology. However, temperatures associated with the NAO are more important than precipitation. Finally, of lowest magnitude, the effect of the NAO on butterfly population size with the relative magnitude of the effect being higher for bivoltine species with a longer flight season.

In declining order, the relative magnitude for *E. abietinum* is the effect of climate change on phenology, followed by the effect of the NAO on phenology, which is about the same magnitude as long term population change, which might be due to a range of factors including climate change, and finally the effect of the NAO on population size, with temperature between October and April having more effect than precipitation.

6.6 Long-term insect surveys

The UKBMS and the Rothamsted Insect Survey of aphids are probably the World's two best insect surveys. The UKBMS started in 1973 at Monks Wood and 1976 at other sites, and the Rothamsted Insect Survey started in 1966, and both surveys provide enough years of data to assess trends. The minimum number of years depends on the consistency of trends, but might be about 30 years. Therefore, both surveys have just a few more than the minimum number of years. More years of data would statistically strengthen conclusions, but environmental factors might change with time, and the rate of change might accelerate, making the identification of trends more complex. This problem already exists, with low numbers of butterflies counted at Monks Wood in the 1970s, which then increased in the 1980s.

There is a significant split in the UKBMS data between site-specific data and the national, annual collated index. Brereton *et al*. (2011) have used indices for separate habitats in England and Scotland to show long term butterfly population changes. There are parallels with the European butterfly indicator for grassland species (Van Swaay *et al*., 2010) and the bird multi-species indicators, which are divided into birds that occupy farms, woodlands, water and wetland birds and seabirds (Eaton *et al*., 2010). Habitat specific analyses are useful as they allow prioritisation of conservation activity and funding on specific habitat types.

The analysis done by Brereton *et al*. (2011) could be extended to include more multi-species statistical techniques such as correspondence analysis and the Shannon-Wiener diversity index. At present these techniques can be used more easily on site-specific data rather than the annual collated index. However, a multi-site data format needs developing that can be analysed using multi-species statistical techniques. A multi-site index might be the sum or mean of the butterflies from several sites, but would be vulnerable to bias through the choice of which sites to include or exclude. However, bias can be reduced by selecting sites by duration of the dataset. A National Nature Reserves multi-site species indicators could be developed to evaluate whether the National Nature Reserve system is, or is not, succeeding in maintaining UK butterfly populations.

The fastest rate of loss of butterfly species appears to have been before the start of the UKBMS, which limits the value of the UKBMS to describe species loss and perhaps provide information that may eventually be used to re-introduce these species. Butterfly species loss in Epping Forest, near London, was underway by 1805 (Corke, 1999), so it would be useful to understand butterfly population change during the past two centuries. Although some older distributional records are accessible via the NBN Gateway, a useful project would be to find naturalists notebooks from before the start of the UKBMS, scan them and make them available on the internet. Where possible, this information should be accompanied by old photographs showing habitats, old maps or other historical documents as this information might facilitate future habitat restoration. Older naturalists who were making observations prior to agricultural intensification, and if possible before World War II, could be interviewed - a process that could be done in conjunction with human geographers who have specialist skills in interviewing techniques and validating the quality of verbal information.

Long-term biological surveys are high value resources for identifying changes in species ecology. It is important to maintain surveys on sites and to avoid periods when data are not collected. The closure of the Monks Wood experimental station potentially made this survey vulnerable, although fortunately the butterfly recording has continued, but the meteorological recording has been of a variable standard. Losing good quality meteorological data from the site of probably the World's best butterfly survey is a considerable loss. Hopefully the UKBMS will be maintained for decades to come, but as the organisations that support this survey keep being changed (for example the Nature Conservancy being renamed English Nature and then Natural England, and the Institute of Terrestrial Ecology being renamed Centre for Ecology and Hydrology. Monks Wood Experimental Station being closed and staff relocated to Wallingford), this continuity may not be easy to maintain. That the UKBMS has survived these changes suggests considerable dedication on behalf of those managing the scheme and the many thousands of volunteer recorders, but with so many major changes in the past, it is reasonable to assume that there will be future changes, and it is hoped that the UKBMS will continue to operate.

6.7 General conclusions

1. The NAO is positively associated with UK temperatures between October and May, with the strongest control between December and March. There is also a strong, positive association between the NAO and the number of frost days and a weak positive association with precipitation and sunshine duration.
2. The NAO is positively associated with the population size of the green spruce aphid, *Elatobium abietinum*, and some butterfly species. The population sizes of butterfly species that are bivoltine, and have a longer flight season, are more likely to be positively associated with the winter NAO index than are those of univoltine species.
3. The NAO does not affect the total population size of all butterfly species, number of species, species diversity or correspondence analysis for butterflies.
4. the NAO cannot be detected at a butterfly community level. Longer term environmental change has a greater effect at a butterfly community resolution than weather associated with the NAO.
5. The NAO has a stronger effect on flight phenology rather than abundance of *E. abietinum* and butterflies.
6. Both *E. abietinum* and butterfly species fly earlier in positive NAO index years, because the weather is warmer. Higher precipitation can delay the butterfly flight season. As a positive NAO is associated with higher temperatures and higher precipitation, so precipitation can partly offset the effect of temperature, making the flight season earlier.
7. Both *E. abietinum* and probably also *M. jurtina* have a longer flight season in positive NAO index years.
8. There is evidence of climate change in East Anglia, with temperatures increasing by 1.46°C at Rothamsted during the period 1966-2006, 1.5°C at the National Institute of Agricultural Botany during the period 1973-2007 and the Central England Temperature Series shows an increase of 1.22°C during the period 1976-2009. This rate of increase suggests that, if trends continue, Cambridge could exceed the Copenhagen Accord maximum increase of 2°C in temperature by 2018.

9. Climate change is causing *E. abietinum* to fly earlier, with a 17.5 day advance in flight timing associated with a 1.46°C temperature increase during the period 1966-2006. Aphid honeydew is an important energy source for some butterfly species and if temperatures continue to rise a phenological change of this magnitude might lead to a mis-timing between honeydew availability and phenology of butterfly flight.
10. For one species, *Maniola jurtina* at Monks Wood, the NAO appears to have a greater effect on flight timing than climate change.
11. The total number of butterflies at Monks Wood has remained relatively constant since 1980. However, one species, *Aphantopus hyperantus*, has increased considerably and now accounts for over 50% of the butterflies counted, which means that the population size of other species has decreased.
12. On average, one less species of butterfly is seen at Monks Wood every 12.6 years, and there is some evidence that species diversity is reducing. Species loss has been under-recorded by the UKBMS as the fastest rate of species loss was before the UKBMS started.

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