The North Atlantic Oscillation and UK butterfly life cycles, pigmentation, morphology, behaviour and conservation

Angus R. Westgarth-Smith [1], *Suzanne A.G. Leroy* [2], *Philip E.F. Collins* [2] *and David B. Roy* [3]

[1] Department of Biological Sciences and Department of Geography and Earth Sciences, Brunel University, Uxbridge, Middlesex, UB8 3PH, U.K.;

[2] Department of Geography and Earth Sciences, Brunel University, Uxbridge, Middlesex, UB8 3PH, U.K.;

[3] NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire, PE28 2LS, U.K.

Correspondence: Angus Westgarth-Smith, Department of Geography and Earth Sciences, Brunel University, Uxbridge, Middlesex, UB8 3PH, U.K.
Email: Angus.Westgarth-Smith@Brunel.ac.uk.

Introduction

We examine the associations between the North Atlantic Oscillation and a range of butterfly life cycle, adult and larval pigmentation, larval morphology, behaviour and conservation parameters.

The North Atlantic Oscillation (NAO) is a fluctuation in air pressure between the sub-tropical area centred on the Azores and the sub-polar area centred on Iceland. The NAO is described by the NAO index, which is calculated from the air pressure difference between Iceland and the Azores, Gibraltar (Osborn, 2000) or Lisbon (Hurrell, 1995). The NAO has its greatest influence on weather during the winter. A high, or positive, NAO index means that the air pressure over the Azores is higher than over Iceland and westerly winds containing a lot of moisture take a more north-easterly route across the Atlantic resulting in relatively warm, moist winters in north-west Europe and Scandinavia. A low, or negative, NAO index results from the air pressures between Iceland and the Azores being more equal, the westerlies cross the Atlantic on a more easterly route, into the Mediterranean region, resulting in cold and dry winters in north-west Europe and Scandinavia (Hurrell, 1995) and wetter winters in the Mediterranean region (Osborn, 2000).

There is evidence for an affect of the NAO on marine vertebrates and invertebrates (Parsons and Lear, 2001; Lloret *et al.*, 2001; Fromentin and Planque, 1996); freshwater invertebrates (George, 2000) and terrestrial vertebrates (Catchpole *et al.*, 2000; Post *et al.*, 1997). There is less documented evidence for an effect of the NAO on terrestrial invertebrates, although Moller (2002) suggests that weather conditions associated with the NAO affect the vulnerability of insects to predation by Barn Swallows (*Hirundo rustica*). There have been no published studies of the influence of the NAO on butterflies, although Roy *et al.* (2001) have investigated the link between temperature and precipitation on U.K. butterfly populations, but did not relate this to the NAO.

In the UK, butterflies complete one (univoltine), two (bivoltine) and occasionally three generations per year. Some species will complete different numbers of generations per year depending on the variation in weather conditions from year to year and with latitude. In particular we distinguish between a bivoltine, southern form of *Polyommatus icarus* and a univoltine, northern form *P. icarus* (N). Different butterfly species can be seen flying as adults in different months each year and bivoltine species are more likely to be seen flying for more months of the year than univoltine species. Butterflies undergo complete metamorphosis, that is egg to larva to pupa to adult, and different species over-winter in different life cycle stages.

Butterfly larvae and adults are believed to use melanin in thermoregulation and basking. Melanin is a black pigment associated with the ability to absorb and emit infra-red radiation – a dark, surface will absorb and emit infra-red radiation faster than a bright surface (Duncan, 1975). Butterfly larvae can have a smooth surface or be covered in hairs. These hairs are either very short and straight or form long branching spikes such as in *Inachis io*. Long, straight hairs as found in the larva of the moth *Arctia caja* are not found in British butterflies. Hairs have been associated with thermal insulation in adult butterflies (Van Dyck *et al.*, 1998). While short larval hairs would probably not trap a boundary layer of air, spikes are up to half the diameter of the larval body and could insulate the larva. Spikes can make larvae unpalatable to birds, an adaptation that would be particularly valuable to a larva basking on an exposed leaf.

Male butterflies use perching or patrolling behaviour in mate finding. Perching involves waiting at a vantage point and flying up to intercept females whereas patrolling means actively searching for females involving long periods of flight. There is some evidence that this behaviour is temperature sensitive with species such as *P. aegeria* perching at lower temperatures and patrolling at higher temperatures, a possible explanation being that perching may provide more opportunities for basking at lower temperatures, whereas flight is easier at higher temperatures (Pollard and Yates, 1993).

There are significant concerns about the conservation of some UK butterfly species, with the geographic range of some species changing. In response to this, *English Nature*, the UK statutory conservation organisation, has established Biodiversity Action Plans for some species. Butterfly conservation priority is listed as low, medium and high in Asher *et al.* (2001), a priority rating based on Warren *et al.* (1997). The mobility of an organism is an important issue in wildlife conservation as more mobile species can disperse into areas of new habitat and recolonise sites where the species has become locally extinct.

Method

This study uses data from the Butterfly Monitoring Scheme (BMS), which started in 1976, and is still continuing in 2004. The BMS involves transect counts of butterflies at sites throughout Britain, with 34 sites in 1976, rising to over 100 sites by 1979 (Roy *et al.*, 2001) and 130 sites by 2003 (Greatorex-Davies, 2003). Transect lengths vary, but as an example, the transect at Monks Wood is three km long. An observer walks the transect recording all the butterflies seen in a strip five metres wide (Pollard and Yates, 1993). The transects are walked once a week from the 1st April to the 29th September (Pollard and Yates, 1993), and this weekly data is then used to calculate an annual collated index. Moss and Pollard (1993) describe methods for calculating collated indices.

While doing butterfly transects, the surveyor identifies the majority of the butterflies in flight or perched on plants. They are relatively rarely identified after capture in a net, although observers are recommended to catch butterflies where the identification is a problem, or, if still uncertain, to record the individual seen as the commoner of the two species. Two identification problems, include the separation of the Small Skipper (*Thymelicus sylvestris*) and Essex Skippers (*T. lineola*) and the Small White *(Pieris rapae)* and Green-veined Whites (*P. napi*). Data for *T. sylvestris* and *T. lineola* have been combined as *T. sylvestris* (Pollard and Yates, 1993).

Monthly NAO indices were obtained from the Climate Research Unit, University of East Anglia, UK (2004), this NAO index is based on atmospheric pressures in Iceland and Gibraltar. The monthly NAO indices were then converted into a January to March NAO index, by calculating the mean of the NAO indices for January, February and March (Figure 1). Annual mean temperature data was obtained from the Central England Temperature Series (Manley, 1974 and Hadley Centre, 2003). The January to March NAO index shows a Pearson correlation coefficient of 0.771, $p = <0.001$ with the mean annual temperature (Figure 1). Pearson correlation coefficients were calculated between the BMS annual collated indices for each butterfly species against the January to March NAO index, for the years 1977-2001. The butterflies were then put in rank order by this correlation coefficient (Tables 1 and 2).

Pollard and Yates (1993) was used to obtain information on the over-wintering stage of each species, the normal number of generations per year, total number of months when active as an adult, mobility and whether each species shows patrolling or perching behaviour. Information on changes to the geographical range, whether the species is subject to a Biodiversity Action Plan and butterfly conservation priority were obtained from Asher *et al.* (2001). Basal wing colour, larval colour and spikiness, were obtained by examining pictures in Burton (1973) (Tables 1 and 2).

Results

P. aegeria (Figure 2) and *P. napi* show highly significant positive correlations with the January to March NAO index and *L. phlaeus, P. icarus,* and *L. megera* show significant positive correlations (Tables 1 and 2). *V. cardui* shows a significant negative correlation coefficient with the January to March NAO index. More species show positive correlations with the January to March NAO index than negative correlations with 24 positive and 10 negative correlations.

Table 1. Butterfly species in rank order with the Pearson correlation coefficient between the annual collated index for each butterfly species and the January to March NAO index. This table also shows the probability (*p*.) Of the correlation coefficient, the usual number of generations per year, the usual total number of months when the adult may be seen flying, the over-wintering stage, colour of larvae and basal wing areas of adults. Black and dark brown pigmented larvae and basal wing areas are highlighted with asterisks.

Correlation coefficient with January to March NAO index	P.	Taxa	Typical number of generations per year	Length of flight period in months	Over-wintering stage	Larval colour Black and dark brown marked with asterisks	Basal wing colour - Dark colours marked with asterisks
0.553	0.004	*Pararge aegeria* (L.)	2	7	Larva/Pupa	Green	Brown
0.533	0.006	*Pieris napi* (L.)	2	4	Pupa	Green	Grey/white
0.491	0.013	*Lycaena phlaeas* (L.)	2	4	Larva	Green	Orange/brown
0.462	0.020	*Polyommatus icarus* (Rott.)	2	4	Larva	Green	Blue
0.446	0.025	*Lasiommata megera* (L.)	2	3	Larva	Green	Brown/orange
0.390	0.054	*Pieris rapae* (L.)	2	4	Pupa	Green	Grey/white
0.389	0.055	*Celastrina argiolus* (L.)	2	4	Pupa	Green	Dark blue
0.303	0.142	*Aphantopus hyperantus* (L.)	1	2	Larva	Brown	Brown
0.299	0.146	*Maniola jurtina* (L.)	1	4	Larva	Green	Brown/orange
0.299	0.147	*Polygonia c-album* (L.)	2	6	Adult	Brown/white	*Dark brown
0.261	0.208	*Pieris brassicae* (L.)	2	4	Pupa	Green/black	Grey/white
0.218	0.294	*Vanessa atalanta* (L.)	1	10	Adult	*Dark brown/Black	*Black
0.201	0.336	*Thymelicus sylvestris* (Poda.)	1	3	Larva	Green	Orange
0.189	0.364	*Anthocharis cardamines* (L.)	1	3	Pupa	Green	Grey/white
0.168	0.421	*Polyommatus icarus* (Rott.) (N)	1	3	Larva	Green	Blue
0.158	0.451	*Callophrys rubi* (L.)	1	2	Pupa	Green	*Dark brown
0.087	0.680	*Coenonympha pamphilus* (L.)	2	4	Larva	Green	Dark grey
0.066	0.755	*Aglais urticae* (L.)	2	6	Adult	*Dark brown/black	*Dark brown/black
0.061	0.770	*Argynnis paphia* (L.)	1	3	Larva	Brown	Yellow
0.055	0.793	*Pyronia tithonus* (L.)	1	2	Larva	Brown	Brown
0.053	0.802	*Polyommatus coridon* (Poda.)	1	3	Egg	Green	Blue/brown
0.048	0.821	*Boloria selene* (D. & S.)	1	2	Larva	*Black	Brown
0.045	0.830	*Hipparchia semele* (L.)	1	2	Larva	Brown	Brown
0.028	0.896	*Aricia agestis* (D. & S.)	2	4	Larva	Green	Brown
-0.004	0.985	*Melanargia galathea* (L.)	1	2	Larva	Brown	Dark grey/white
-0.024	0.909	*Ochlodes venata* (Br. & Grey)	1	2	Larva	Green	Orange
-0.047	0.823	*Inachis io* (L.)	1	4	Adult	*Dark brown/black	Dark red
-0.083	0.694	*Gonepteryx rhamni* (L.)	1	6	Adult	Green	Grey/yellow
-0.183	0.381	*Argynnis aglaja* (L.)	1	3	Larva	*Black	Pale brown
-0.224	0.281	*Boloria euphrosyne* (L.)	1	2	Larva	*Black	Brown
-0.252	0.224	*Erynnis tages* (L.)	1	2	Larva	Green	*Dark brown/black
-0.324	0.114	*Pyrgus malvae* (L.)	1	2	Pupa	Green/brown	*Black
-0.355	0.081	*Limenitis camilla* (L.)	1	3	Larva	Green	*Black
-0.405	0.044	*Vanessa cardui* (L.)	Multiple	8	All stages	Brown	Light brown

Table 2. Butterfly species in rank order with the Pearson correlation coefficient between the annual collated index for each butterfly species and the January to March NAO index. This table lists larval surface spikes, perching or patrolling behaviour, mobility and conservation status. Question marks are used as in Pollard and Yates (1993).

Taxa	Spiky larva Y = yes	Perch (Pe) and/or patrol (Pa)	Mobility	Changes to geographical range in UK	Biodiversity Action plan	Conservation priority
Pararge aegeria		Pe/Pa	Sedentary	Expanding		Low
Pieris napi		Pa	Intermediate	Stable		Low
Lycaena phlaeas		Pe	Intermediate	Stable		Low
Polyommatus icarus		Pe/Pa	Intermediate	Stable		Low
Lasiommata megera		Pe/Pa	?	Declining & spreading		Low
Pieris rapae		Pa	Wide-ranging	Stable		Low
Celastrina argiolus		?	Wide-ranging	Expanding		Low
Aphantopus hyperantus		Pa	Sedentary	Expanding		Low
Maniola jurtina		Pa	Sedentary	Stable		Low
Polygonia c-album	Y	Pe	Intermediate	Expanding		Low
Pieris brassicae		Pa	Wide-ranging	Stable		Low
Vanessa atalanta	Y	Pa	Wide-ranging	Migrant	Not assessed	Not assessed
Thymelicus sylvestris		Pa	Sedentary	Expanding		Low
Anthocharis cardamines		Pa	Intermediate	Expanding		Low
Polyommatus icarus (N)		Pe/Pa	Intermediate	Stable		Low
Callophrys rubi		Pe	Sedentary	Stable		Low
Coenonympha pamphilus		Pe/Pa	Sedentary	Stable		Low
Aglais urticae	Y	Pe	Wide-ranging	Stable		Low
Argynnis paphia	Y	Pa	Intermediate	Decline & re-expansion	Concern	Low
Pyronia tithonus		Pe/Pa	Sedentary	Expanding		Low
Polyommatus coridon		Pa	Sedentary	Declining	Concern	Low
Boloria selene	Y	Pa	Sedentary	Declining	Concern	Medium
Hipparchia semele		Pe	Sedentary	Declining		Low
Aricia agestis		Pe/Pa	Intermediate	Expanding		Low
Melanargia galathea		Pa	Sedentary	Expanding		Low
Ochlodes venata		Pe/Pa	Sedentary	Expanding		Low
Inachis io	Y	Pe	Wide-ranging	Expanding		Low
Gonepteryx rhamni		Pa	Wide-ranging	Expanding		Low
Argynnis aglaja	Y	Pa	Intermediate	Declining		Low
Boloria euphrosyne	Y	Pa	Sedentary	Declining	Priority	High
Erynnis tages		Pe	Sedentary	Declining		Low
Pyrgus malvae		Pe	Sedentary	Declining		Medium
Limenitis camilla	Y	Pe	Intermediate	Expanding		Low
Vanessa cardui	Y	Pe	Wide-ranging	Migrant	Not assessed	Not assessed

Species that correlate positively with the January to March NAO index tend to have a higher number of generations per year (Figure 3) and a longer flight period (Figure 4). Species that over-winter as adults are more likely to have low correlation coefficients with the January to March NAO index (Table 1).

Species with black or brown larvae and black or dark brown basal wing colouration tend to have low or negative correlation coefficients with the January to March NAO index, whereas green larvae tend to have positive correlation

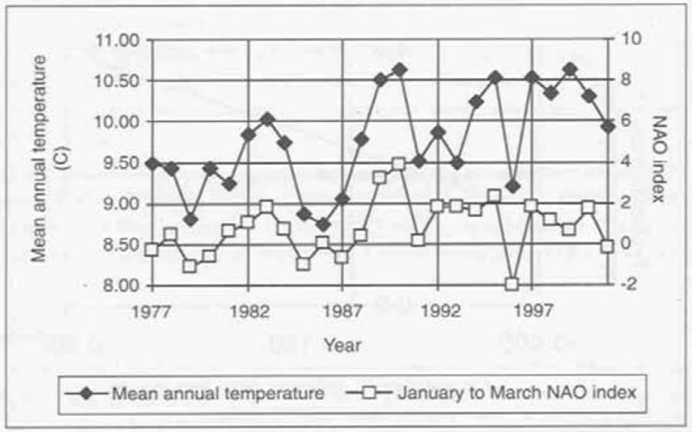

Figure 1.
Graph of mean annual temperature and January to March NAO index for the years 1977-2001.

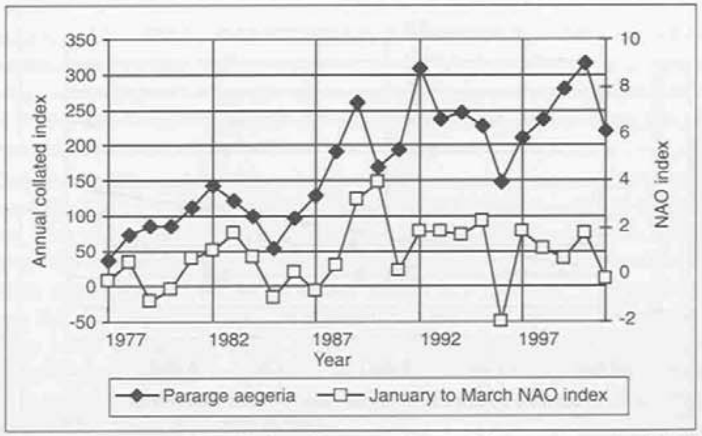

Figure 2. Graph of annual collated index of *Pararge aegeria* and the January to March NAO index for the years 1977-2001.

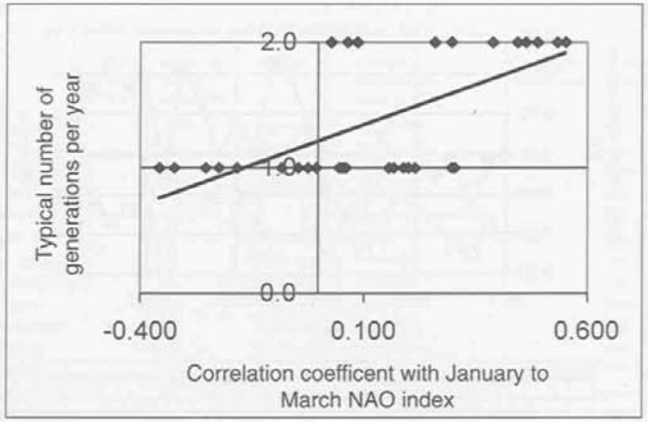

Figure 3. Graph of typical number of generations per year against the correlation coefficient with the January to March NAO index. *V. cardui* has been omitted as multiple generations. Pearson = 0.638, p = <0.001.

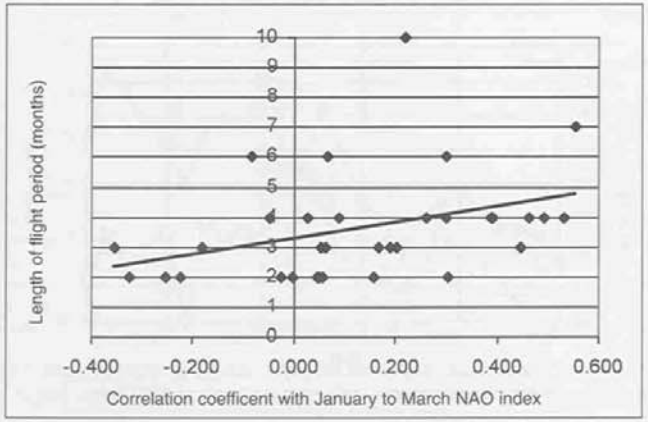

Figure 4. Graph of flight period in months against the correlation coefficient with the January to March NAO index. *V. cardui* omitted for consistency with figure 3. Pearson = 0.368, p = 0.035.

coefficients with the January to March NAO index (Tables 1 and 2). Spiky larvae are more likely to have a low or negative correlation coefficient with the January to March NAO index (Table 1).

There are no apparent patterns in the rank orders of perching and patrolling behaviours with the January to March NAO index. However all species, except *V. atalanta*, that show black or dark brown basal wing areas also show perching behaviour (Table 2).

Species are more likely to be declining in range, to be of conservation concern or to have a higher Butterfly Conservation Priority if they have a negative correlation coefficient with the January to March NAO index. Species with low or negative correlations with the January to March NAO index being more likely to be sedentary (Table 2).

Discussion

Species that are bivoltine or have longer flight periods are more likely to correlate positively with the January to March NAO index and annual temperature, because high NAO index years are warmer resulting in more weeks when the adult butterflies can fly and providing more time and a faster development rate to complete two generations. Also species that are active as adults for longer in the year will be more likely to be affected by the NAO as they are likely to be flying earlier and later in the year - nearer the time period when the NAO has a stronger influence on weather conditions.

Butterfly larvae need to feed to grow and develop, whereas adult butterflies have completed their growth and development. Butterflies that over-winter as larvae feed during warm weather in the late winter whereas species that over-winter as adults feed much less. Therefore species that over-winter as adults are much less affected by the NAO than species that over-winter as larvae.

Dark coloured larvae and species with black basal wing areas tend to be clustered around the low to negative correlation coefficients with the January to March NAO index. The low correlation coefficients suggest that they are using the melanin to absorb solar infra-red radiation and thermoregulate and negative correlations suggest that the melanin is causing an increased radiant heat loss. Bryant *et al.* (2002) has shown that the black larvae of *I. io* and *A. urtica* are capable of thermoregulating by basking in the sunlight on *Urtica dioica* leaves. The seven species at the top of the table have green larvae and so have less ability to thermoregulate, therefore they tend to be thermal conformers, with internal temperature and rates of development more directly related to air temperature.

Larval surface structure shows an association with the NAO index with spiky larvae being more likely to have low or negative correlation coefficients with the January to March NAO index. This could suggest some thermal independence from ambient temperatures caused by the spikes trapping a boundary layer of air and hence providing insulation. There is also evidence for an indirect role for spikes in thermoregulation through protecting basking larvae from bird predation as six of the ten spiky larvae are black. Black larvae require this protection as they are less camouflaged than green larvae and tend to bask on the exposed upper surfaces of leaves where they are more easily seen by birds.

Butterflies and other organisms are assumed to respond passively to climate change by changing their latitudinal or altitudinal distribution or becoming extinct. Here we suggest that melanin in butterfly larvae and adults and a larval spiky surface morphology can make butterfly species thermally independent of the NAO, which is a major factor in the control of UK weather. As such perhaps there should be more emphasis on identifying how butterflies can resist and cope with the effects of climate change?

Perching or patrolling behaviour does not appear to be linked to the NAO index. A possible explanation is that this is an adult activity and takes place only in the summer months when the control of the weather by the NAO index is lowest. However there does appear to be an association between basal wing colour and perching, such that all species, except *V. atalanta*, with black or dark brown basal wing colouration show perching behaviour. Possible explanations for this association include the use of the dark basal wing areas for basking while perched, or, as darker surfaces radiate heat more rapidly than lighter surfaces, then perhaps species with dark basal wing areas lose heat too rapidly in flight and need to return to a perch to bask.

The effect of the NAO is reversed in the Mediterranean basin, such that a positive NAO index results in higher precipitation in the UK and drier weather in the Mediterranean and vice versa during a period with a negative NAO. There is an area of equilibrium in central Europe where the NAO has little effect. *V. cardui* and *V. atalanta* are both long range migrants with *V.cardμui* migrating from North Africa and the Middle East and *V. atalanta* migrating from central Europe. *V. cardui* will therefore be breeding in regions where the effect of the NAO is reversed, whereas *V. atalanta* is migrating from areas relatively unaffected by the NAO – this might explain why *V. cardui* has the lowest negative correlation coefficient with the NAO index (Pearson = -0.405, $p = 0.044$) and *V. atalanta* has a low correlation coefficient (Pearson = 0.218, $p = 0.294$).

There is evidence for an association between conservation status, the January to March NAO index and mean annual temperature. Species that are declining in range, are of 'concern' or 'priority' for UK Biodiversity Action plans and are or of medium or high Butterfly Conservation priority tend to have low or negative correlation coefficients with the January to March NAO index. There appears to be an association between climate, dispersal ability and conservation as sedentary species are more likely to have a low or negative correlation coefficient with the January to March NAO index.

The January to March NAO index can be calculated by the end of March, and before most butterfly species have been seen in flight, therefore this NAO index has the potential to be used to predict the abundance of adult butterflies, particular for taxa such as *P. aegeria, P. napi, L. phlaeus, P. icarus, L. megera* and *V. cardui*. During the period 1977-2001, the NAO index was in a predominantly positive phase, and as more species show positive correlations with the January to March NAO index than negative correlations, it is possible that weather associated with the NAO has had the effect of mitigating the effects of other conservation problems such as habitat loss. A change to a sustained period with a negative NAO index might have severe consequences for U.K. butterflies.

Acknowledgements

The authors thank N. Greatorex-Davies from the Centre for Ecology and Hydrology, U.K., for providing butterfly annual collated index data.

References

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. (2001) *The Millennium Atlas of Butterflies in Britain and Ireland.* Oxford University Press, UK.

Bryant, S.R., Thomas, C.D. & Bale, J.S. (2002) The influence of thermal ecology on the distribution of three nymphalid butterflies. *Journal of Applied Ecology*, **39**, 43.

Burton, J. (1973) *The Oxford Book of Insects.* Oxford University Press, UK.

Catchpole, E.A., Morgan, B.J.T., Coulson, T.N., Freeman, S.N. & Albon, S.D. (2000) Factors influencing Soay sheep survival. *Applied Statistics*, **49**, 453-472.

Climate Research Unit (2004) *North Atlantic Oscillation.* University of East Anglia, UK. www.cru.uea.ac.uk/cru/data/nao.htm.

Duncan, T. (1975) *Advanced Physics: Fields, Waves and Atoms.* John Murray, London.

Fromentin, J.M. & Planque, B. (1996) *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus. Marine Ecology Progress Series*, **134**, 111-118.

George, D.G. (2000) The impact of regional-scale changes in the weather on the long-term dynamics of *Eudiaptomus* and *Daphnia* in Esthwaite Water, Cumbria. *Freshwater Biology*, **45**, 111-121.

Greatorex-Davies, J.N. (2003) *Butterfly Monitoring Scheme.* www.bms.ceh.ac.uk.

Hadley Centre (2003) *Central England Temperature Series.* www.meto.gov.uk/research/hadleycentre/CR_data/Daily/HadCET_act.txt.

Hurrell, J.W. (1995) Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. *Science*, **269**, 676-679.

Lloret, J., Lleoart, J., Sole, I. & Fromentin, J.-M. (2001) Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. *Fisheries Oceanography*, **10**, 33-50.

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

Moller, AP (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migrant passerine bird. *Journal of Animal Ecology*, **71**, 201-210.

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

Osborn, T. (2000) North Atlantic Oscillation. *Climate Research Unit: Information sheets.* www.cru.uea.ac.uk/cru/info/nao/. Accessed July 2004.

Parsons, L.S. & Lear, W.H. (2001) Climate variability and marine ecosystem impacts: a north Atlantic perspective. *Progress in Oceanography*, **49**, 167-188.

Pollard, E. & Yates, T.J. (1993) *Monitoring Butterflies for Ecology and Conservation.* Chapman and Hall, London, UK.

Post, E., Stenseth, N. Chr., Langvatn, R. & Fromentin, J.-M. (1997) Global climate change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society of London, Series B, Biological Sciences,* **264**, 1317-1324.

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

Van Dyck, H., Matthysen, E. & Wiklund, C. (1998) Phenotypic variation in adult morphology and pupal colour within and among families of the speckled wood butterfly *Pararge aegeria. Ecological Entomology,* **23**, 465-472.

Warren, M.S., Barnett, L.K., Gibbons, D.W. & Avery, M.I. (1997) Assessing national conservation priorities: an improved red list of British butterflies. *Biological Conservation,* **82**, 317-328.