
ARTICLES

Mechanisms for the control of U.K. Butterfly abundance by the North Atlantic Oscillation**Angus R. Westgarth-Smith¹, Suzanne A.G. Leroy^{1&2}, Philip E.F. Collins¹ and David B. Roy³**¹ Department of Geography and Earth Sciences, Brunel University, Uxbridge, Middlesex, UB8 3PH, U.K.² Institute for the Environment, Brunel University, Uxbridge, Middx, UB8 3PH, U.K.³ NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire, PE28 2LS, U.K.

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Introduction

The North Atlantic Oscillation (NAO) is a fluctuation in air pressure and is described by the NAO index. This index is calculated from the difference between the air pressures in Iceland and the sub-tropical area centred on the Azores. There are several published NAO indices, which differ in the location of the weather station used for the sub-tropical pressure data, with pressure data from the Azores, Lisbon or Gibraltar, although the choice of location for the sub-tropical pressure data makes little difference (Osborn, 2000). We use the Climate Research Unit NAO index (Climate Research Unit, 2004), which uses pressure data from Gibraltar.

The NAO has a particularly strong effect on the weather in Scandinavia, north-west Europe and the Mediterranean basin. A positive NAO index means that air pressure in the sub-tropical region is higher than over Iceland and depression systems take a more north-easterly route into northern Europe and Scandinavia. During periods with a negative NAO index depressions cross the Atlantic on a more easterly route, resulting in colder and drier winters in north-west Europe (Osborn, 2000).

There are studies of the effect of the NAO on terrestrial vertebrates (Catchpole *et al.*, 2000; Post *et al.*, 1997) and fish (Parsons & Lear, 2001). Studies of the effect on invertebrates are rare, but include work on freshwater and marine copepods (George, 2000; Fromentin & Planque, 1996). There is an absence of work on the NAO and terrestrial invertebrates, although there is a paper on U.K. weather and butterfly populations (Roy *et al.* 2001), but this does not discuss the role of the NAO.

Methods

Our study uses data from the U.K. Butterfly Monitoring Scheme (BMS) from the period 1977–2001. This dataset is based on counts of butterflies on transects on up to 130 sites throughout the U.K. Transect lengths vary, but as an example, the

transect at Monks Wood, Cambridgeshire, U.K., is 3 km long. An observer walks the transect every week from 1st April to the 29th September recording all the butterflies seen in a five-metre wide strip. This data is used to calculate an annual collated index for each butterfly species.

The majority of the butterflies are identified 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 *Thymelicus sylvestris* and *T. lineola* and also *Pieris rapae* and *P. napi*. Data for *T. sylvestris* and *T. lineola* have been combined as *T. sylvestris* (Pollard and Yates 1993).

Further details of the BMS, and the survey techniques used, can be found in Pollard & Yates (1993) and Greatorex-Davies (2003). Moss and Pollard (1993) describe methods for calculating annual collated indices. The considerable scale of this survey in terms of number of years, large number of sites and weekly monitoring make the BMS one of the best insect datasets in the World.

Monthly NAO indices were obtained from the Climate Research Unit, University of East Anglia, U.K. (2004). This NAO index is based on atmospheric pressures in Iceland and Gibraltar. Monthly mean temperature data was obtained from the Central England Temperature Series (Manley, 1974 and Hadley Centre, 2003a) and monthly precipitation data was obtained from England and Wales Precipitation (Hadley Centre 2003b).

While it is known that there is a link between the NAO index and winter weather, it is necessary to identify the links between monthly NAO indices and winter weather for the same years as the butterfly data, therefore Pearson correlation coefficients were calculated between monthly NAO indices and monthly temperatures and precipitation. These calculations were done for the monthly weather data in the same month as the NAO index and in subsequent months, from October of the preceding year until September of the current year. This time period was used as the NAO starts to affect the weather strongly from October and the butterfly survey period finishes at the end of September.

Multiple linear regression calculations were made between the butterfly annual collated index, monthly NAO indices, monthly temperatures and monthly precipitation from October of the previous year to September in the year that the butterflies were counted. Each multiple linear regression calculation involved one species of butterfly and twelve monthly weather variables.

Results

Monthly NAO indices show significant and highly significant positive correlations with mean monthly temperatures in the same months for the period October to March excluding November (Table 1). The Pearson correlation coefficients between monthly NAO indices and mean monthly temperatures in December, January and

Table 1. Pearson correlation coefficient probabilities for the NAO index in each month correlated with mean monthly temperatures for all months.

		NAO INDEX IN THESE MONTHS											
		O	N	D	J	F	M	A	M	J	J	A	S
CORRELATED WITH THE MEAN TEMPERATURES FOR THESE MONTHS	October	1P	*	*	*	*	*	*	*	*	*	*	*
	November	-	10P	*	*	*	*	*	*	*	*	*	*
	December	-	-	0.1P	*	*	*	*	*	*	*	*	*
	January	10N	-	-	0.1P	*	*	*	*	*	*	*	*
	February	-	-	-	-	0.1P	*	*	*	*	*	*	*
	March	5N	-	-	10P	1P	5P	*	*	*	*	*	*
	April	-	5P	-	-	10P	10N	10P	*	*	*	*	*
	May	-	-	-	-	5P	10P	-	10P	*	*	*	*
	June	-	-	-	-	-	-	-	-	-	*	*	*
	July	-	-	-	5P	-	-	-	-	-	-	*	*
August	-	-	-	-	0.1P	-	-	-	-	-	-	*	
September	-	-	-	-	5P	10N	-	-	-	10N	-	-	

Key
 0.1, 1 etc Numbers are probabilities from Pearson Correlation coefficient calculations expressed as a percentage.
 * Correlation not calculated as monthly NAO after month in which temperature data in Table 1 and precipitation data in Table 2. was measured.
 - $P > 0.10$ (10%)
 P Positive correlation
 N Negative correlation

Table 2. Pearson correlation coefficient probabilities for the NAO index in each month correlated with monthly precipitation for all months. Key to letters, numbers and symbols in Table 1.

		NAO INDEX IN THESE MONTHS											
		O	N	D	J	F	M	A	M	J	J	A	S
CORRELATED WITH PRECIPITATION IN THESE MONTHS	October	-	*	*	*	*	*	*	*	*	*	*	*
	November	-	-	*	*	*	*	*	*	*	*	*	*
	December	-	-	-	*	*	*	*	*	*	*	*	*
	January	-	-	-	5P	*	*	*	*	*	*	*	*
	February	-	-	-	-	5P	*	*	*	*	*	*	*
	March	-	-	-	-	10N	-	*	*	*	*	*	*
	April	-	-	-	-	-	-	-	*	*	*	*	*
	May	-	-	-	-	-	-	5N	-	*	*	*	*
	June	-	-	-	10N	-	-	-	-	-	*	*	*
	July	-	-	-	-	-	-	-	-	-	-	*	*
August	-	-	-	-	1N	-	-	-	-	-	-	*	
September	-	-	-	1P	5P	-	-	-	-	10N	-	-	

February are significant at $P = < 0.001$. November, April and May show correlation coefficients between monthly NAO indices and mean monthly temperatures with $P = < 0.10$. There are fewer significant correlation coefficients between the monthly NAO indices and monthly precipitation (Table 2) than for mean monthly

temperatures, however there are significant correlations ($P. = <0.05$) between the monthly NAO indices and monthly precipitation in January and February.

There are significant correlation coefficients between the monthly NAO indices and mean monthly temperature in months later in the year (Table 1). For example the January NAO index shows correlation coefficients with probabilities in the range 0.01 – 0.10 with July temperatures and June, August and September precipitation. The February NAO index shows correlation coefficients with probabilities in the range 0.001 – 0.10 for temperatures in March, April, May, August and September and also for precipitation in March (Table 2).

Most of the associations between monthly NAO indices and butterfly annual collated indices are positive with September, February and May being the months with the most regressions with $P. = <0.10$ (Table 3).

Butterflies show both positive and negative associations between monthly temperatures (Table 4). The month with the most linear regression probabilities of <0.10 between the annual collated indices and mean monthly temperature is June, followed by April, October and January. There is a tendency for the associations between temperature and butterfly numbers to move from being negative in December to positive during the spring and summer.

More of the linear regressions between the butterfly annual collated indices and precipitation are negative (Table 5), than the associations with temperature (Table 4). The month with the most linear regression probabilities of $P. = <0.10$ between the annual collated index and monthly precipitation is March followed by February, June, April and then January.

Collinearity is a potential problem with weather variables correlating significantly with each other (Tables 1 and 2), so variance inflation factors (VIF) were calculated (Table 6). The VIF is an indicator which can vary from zero to infinity, and the higher the value for the VIF, the higher the risk of collinearity, with a VIF >5.0 considered too high a risk of collinearity. All VIF values for multiple linear regression calculations with monthly NAO indices and monthly precipitation are <4.0 . VIF values for regressions with mean monthly temperatures are <3.0 , except February, March, May and August that show a VIF in the range 4.0-5.0.

Discussion

The NAO appears to have a stronger effect on U.K. temperature rather than precipitation (Tables 1 and 2). The NAO exerts a direct effect on monthly temperatures from October to May although the control on temperature is strongest in December to February. The NAO has a direct effect on precipitation in January and February. There is some evidence for an indirect effect of the NAO, with the NAO during winter months affecting weather later in the year. The mechanism for this may be thermal buffering by the sea, as North Atlantic sea surface temperature (SST) in January and February can be used to produce a forecast, issued in March, of temperature and rainfall in north-west Europe during the subsequent July and August (Meteorological Office, 2003).

Table 3. Significance levels resulting from multiple linear regression calculations between monthly NAO indices and annual collated indices for butterflies.

Family	Species	Probabilities from multiple linear regression analysis with monthly NAO indices											
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
Hesperiidae	<i>Thymelicus sylvestris</i> (Poda.)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Ochlodes venata</i> (Br. & Grey)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Erynnis tages</i> (L.)	10P	-	-	-	-	-	-	-	-	-	-	10P
	<i>Pyrgus malvae</i> (L.)	-	-	10N	-	-	-	-	1N	-	10N	-	5P
Pieridae	<i>Gonepteryx rhamni</i> (L.)	-	-	-	-	-	10N	-	-	-	-	-	-
	<i>Pieris brassicae</i> (L.)	-	-	-	-	-	-	-	1P	-	10P	5P	-
	<i>Pieris rapae</i> (L.)	-	-	-	-	-	-	-	10P	-	-	-	-
	<i>Pieris napi</i> (L.)	-	-	-	-	5P	-	-	5P	10N	-	-	-
	<i>Anthocharis cardamines</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
Lycaenidae	<i>Callophrys rubi</i> (L.)	-	10P	-	-	10P	-	-	-	-	-	-	5N
	<i>Lycaena phlaeas</i> (L.)	-	-	-	-	5P	-	-	-	-	-	-	-
	<i>Polyommatus icarus</i> (Rott.)	-	-	-	10P	10P	-	-	-	-	-	-	-
	<i>Polyommatus icarus</i> (Rott.) (N)	-	-	10N	5P	-	-	-	-	-	-	-	5P
	<i>Aricia agestis</i> (D. & S.)	-	-	-	-	10P	-	-	-	-	-	-	-
	<i>Polyommatus coridon</i> (Poda.)	-	-	-	-	10P	-	-	-	-	-	-	-
	<i>Celastrina argiolus</i> (L.)	-	10N	-	-	10P	-	5P	-	-	-	-	-
Nymphalidae	<i>Limenitis camilla</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Vanessa atalanta</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Vanessa cardui</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Aglais urticae</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Inachis io</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Polygonia c-album</i> (L.)	-	-	-	-	5P	-	-	5P	-	-	-	-
	<i>Boloria selene</i> (D. & S.)	-	-	-	-	-	-	-	-	-	-	-	10P
	<i>Boloria euphrosyne</i> (L.)	-	-	5N	-	-	-	-	-	-	10N	-	1P
	<i>Argynnis aglaja</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Argynnis paphia</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-
Satyridae	<i>Lasiommata megera</i> (L.)	-	-	-	5P	-	-	-	-	-	-	-	10P
	<i>Pararge aegeria</i> (L.)	-	-	-	-	1P	-	-	5P	-	-	-	5N
	<i>Melanargia galathea</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	5N
	<i>Hipparchia semele</i> (L.)	-	-	-	10P	-	-	-	-	-	-	-	-
	<i>Pyronia tithonus</i> (L.)	-	-	-	-	-	10N	-	-	-	-	-	-
	<i>Maniola jurtina</i> (L.)	-	-	-	-	-	10N	-	-	-	-	-	-
	<i>Coenonympha pamphilus</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	1P
	<i>Aphantopus hyperantus</i> (L.)	-	-	10P	-	-	-	-	-	-	-	-	1N
Number of regressions at each probability Level per month	Number of 1P	0	0	0	0	1	0	0	1	0	0	0	2
	Number of 5P	0	0	0	2	3	0	1	3	0	0	1	2
	Number of 10P	1	1	1	2	5	0	0	1	0	1	0	3
	Number of 10N	0	1	2	0	0	3	0	0	1	2	0	0
	Number of 5N	0	0	1	0	0	0	0	0	0	0	0	3
	Number of 1N	0	0	0	0	0	0	0	1	0	0	0	1
Total with <i>P</i> : less than 10%		1	2	4	4	9	3	1	6	1	3	1	11

Key

- 1, 5, 10 Numbers are probabilities from multiple linear regression calculations expressed as a percentage. *P*. is less than the percentage shown
- *P*. >0.10 (10%)
- P Positive correlation
- N Negative correlation
- P. icarus* Southern bivoltine (two generations per year) form of this species.
- P. icarus* (N) Northern univoltine form

Table 4. Significance levels resulting from multiple linear regression calculations between mean monthly temperatures and annual collated indices for butterflies. Key to letters, numbers and symbols in Table 3.

Family	Species	Probabilities from multiple linear regression analysis with mean monthly temperatures											
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
Hesperiidae	<i>Thymelicus sylvestris</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Ochlodes venata</i>	-	-	-	-	-	-	-	-	5P	-	-	-
	<i>Erynnis tages</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pyrgus malvae</i>	-	-	-	-	10P	-	-	-	-	-	-	-
Pieridae	<i>Gonepteryx rhamni</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pieris brassicae</i>	-	-	-	10N	-	5P	-	-	5P	-	-	-
	<i>Pieris rapae</i>	-	-	-	5N	-	-	-	-	10P	-	-	-
	<i>Pieris napi</i>	-	-	-	-	-	-	-	-	5P	-	-	-
Lycaenidae	<i>Anthocharis cardamines</i>	10P	-	-	-	-	-	5P	-	-	-	-	-
	<i>Callophrys rubi</i>	-	-	-	-	-	-	-	-	10P	-	-	-
	<i>Lycaena phlaeas</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Polyommatus icarus</i>	-	-	-	-	-	-	-	-	5P	5P	-	-
	<i>Polyommatus icarus</i> (N)	-	-	-	-	-	-	10N	-	-	-	-	-
	<i>Aricia agestis</i>	1P	-	5N	5P	-	-	-	1N	1P	10P	-	10P
	<i>Polyommatus coridon</i>	1P	-	-	-	-	-	1P	-	10P	-	-	-
<i>Celastrina argiolus</i>	5P	-	-	-	-	-	-	-	-	-	-	-	
Nymphalidae	<i>Limenitis camilla</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Vanessa atalanta</i>	-	-	10N	-	-	-	-	-	10P	-	-	-
	<i>Vanessa cardui</i>	1P	-	5P	-	-	-	-	-	-	-	-	-
	<i>Aglais urticae</i>	-	-	10N	-	-	-	-	-	-	10P	-	-
	<i>Inachis io</i>	5P	-	10N	-	-	-	5P	-	5P	-	-	-
	<i>Polygonia c-album</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Boloria selene</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Boloria euphrosyne</i>	-	-	-	-	5P	-	5N	-	5N	-	-	-
	<i>Argynnis aglaja</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Argynnis paphia</i>	1P	-	-	-	-	-	1P	-	1P	-	-	-
Satyridae	<i>Lasiommata megera</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pararge aegeria</i>	-	-	-	-	-	5P	5P	-	5P	-	-	-
	<i>Melanargia galathea</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Hipparchia semele</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pyronia tithonus</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Maniola jurtina</i>	-	-	-	10N	-	-	-	-	-	-	-	-
	<i>Coenonympha pamphilus</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Aphantopus hyperantus</i>	-	-	-	-	-	-	10P	-	-	-	-	-
Number of regressions at each probability Level per month	Number of 1P	4	0	0	0	0	0	2	0	2	0	0	0
	Number of 5P	2	0	0	2	1	2	3	0	6	1	0	0
	Number of 10P	1	0	0	0	1	0	1	0	4	1	1	1
	Number of 10N	0	0	2	2	1	0	1	0	0	0	0	0
	Number of 5N	0	0	1	1	0	0	1	0	1	0	0	0
	Number of 1N	0	0	0	0	0	0	0	1	0	0	0	0
Total with P. less than 10%		7	0	3	5	3	2	8	1	13	2	1	1

Table 5. Significance levels resulting from multiple linear regression calculations between monthly precipitation and annual collated indices for butterflies. Key to letters, numbers and symbols in Table 3.

Family	Species	Probabilities from multiple linear regression analysis with monthly precipitation											
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
Hesperiidae	<i>Thymelicus sylvestris</i>	-	-	-	-	5N	5N	5N	10N	5N	10N	-	-
	<i>Ochlodes venata</i>	-	-	-	-	1N	5N	1N	-	5N	-	-	-
	<i>Erynnis tages</i>	-	-	-	-	-	-	5N	-	-	-	-	-
	<i>Pyrgus malvae</i>	10N	-	-	-	5P	-	-	-	5P	-	-	-
Pieridae	<i>Gonepteryx rhamni</i>	-	-	-	-	10N	-	-	-	-	-	-	-
	<i>Pieris brassicae</i>	10N	-	-	-	-	-	-	-	-	-	-	-
	<i>Pieris rapae</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pieris napi</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Anthocharis cardamines</i>	-	-	10P	-	-	1N	-	-	-	-	-	-
Lycaenidae	<i>Callophrys rubi</i>	-	-	-	-	-	5N	-	-	-	-	-	-
	<i>Lycaena phlaeas</i>	-	-	-	-	-	-	-	-	-	10N	10N	-
	<i>Polyommatus icarus</i>	-	-	-	10N	5N	1N	5N	10N	1N	5N	-	-
	<i>Polyommatus icarus</i> (N)	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Aricia agestis</i>	-	-	-	-	-	5N	-	-	-	10N	-	-
	<i>Polyommatus coridon</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Celastrina argiolus</i>	-	-	-	-	-	10N	-	5N	-	-	-	-
Nymphalidae	<i>Limenitis camilla</i>	-	-	-	-	1N	10N	5N	-	5N	-	-	-
	<i>Vanessa atalanta</i>	-	-	-	10N	-	10N	-	5N	10N	-	-	-
	<i>Vanessa cardui</i>	-	-	-	-	-	-	-	-	10N	-	-	-
	<i>Aglais urticae</i>	-	-	-	10N	-	-	1N	-	-	-	-	-
	<i>Inachis io</i>	-	-	-	-	-	10N	-	-	-	-	-	-
	<i>Polygonia c-album</i>	-	-	-	5N	-	5N	-	-	-	-	-	-
	<i>Boloria selene</i>	5N	-	10N	10P	10P	-	-	-	-	-	-	-
	<i>Boloria euphrosyne</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Argynnis aglaja</i>	5N	5P	-	-	-	-	5N	-	-	-	-	-
	<i>Argynnis paphia</i>	-	-	-	-	-	-	-	-	-	-	-	-
Satyridae	<i>Lasiommata megera</i>	-	-	-	-	-	-	-	-	-	-	10N	-
	<i>Pararge aegeria</i>	-	-	-	-	-	-	10P	-	-	-	-	-
	<i>Melanargia galathea</i>	-	-	-	-	-	5N	-	-	-	-	-	-
	<i>Hipparchia semele</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pyronia tithonus</i>	-	-	-	-	10N	5N	-	-	10N	-	-	-
	<i>Maniola jurtina</i>	-	-	-	5N	1N	1N	-	5N	5N	-	-	-
	<i>Coenonympha pamphilus</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Aphantopus hyperantus</i>	-	-	-	10N	5N	5N	-	-	-	-	-	-
Number of regressions at each probability level per month	Number of 1P	0	0	0	0	0	0	0	0	0	0	0	0
	Number of 5P	0	1	0	0	1	0	0	0	1	0	0	0
	Number of 10P	0	0	1	1	1	0	1	0	0	0	0	0
	Number of 10N	2	0	1	4	2	4	0	2	3	3	2	0
	Number of 5N	2	0	0	2	3	8	5	3	4	1	0	0
	Number of 1N	0	0	0	0	3	3	2	0	1	0	0	0
Total with P. less than 10%	4	1	2	7	10	15	8	5	9	4	2	0	

Table 6. Variance inflation factors for multiple linear regression calculations between butterfly annual collated indices and monthly NAO indices, mean monthly temperature and monthly precipitation.

Month	Variance inflation factors		
	NAO index	Temperature	Precipitation
October	1.785	1.921	2.668
November	1.753	1.850	1.738
December	1.739	1.981	2.002
January	1.915	2.695	2.060
February	1.436	4.819	3.542
March	1.703	4.222	1.524
April	1.339	1.786	1.608
May	1.280	4.908	1.928
June	1.329	2.010	2.382
July	1.517	2.515	1.394
August	1.766	4.491	1.432
September	1.643	1.762	1.973

The NAO in February appears to have a particularly strong effect on U.K. weather, and with nine linear regressions, with $P. < 0.10$, between the butterfly annual collated indices and the February NAO index, it would appear that the February NAO index has the potential to be used as a predictor of U.K. butterfly population size later in the year. As six of these associations between the February NAO index and butterfly annual collated indices are for the Lycaenidae, it would appear that there is a particular potential for using this as a predictor of abundance in this family.

There is a gradation from negative associations between December and January monthly temperatures and butterfly abundance to more positive associations in February and March (Table 4). It is possible that low temperatures are needed in December for winter dormancy, or to reduce the activity of damaging organisms, such as fungi. The positive associations between butterfly abundance and temperatures in October, February and March, may, for species that over-winter as larvae, be due to larvae using periods of warmer weather in the early autumn and late winter for feeding.

Almost all the regressions with $P. = < 0.10$ between the butterfly annual collated index and monthly precipitation are negative, except for some associations between *Pyrgus malvae*, *Anthocharis cardamines*, *Boloria selene*, *Argynnis aglaja* and *Pararge aegeria* and precipitation where there are some positive regressions (Table 5). It has been suggested that one of these species, *P. aegeria*, benefits from improved vegetation quality associated with increased precipitation (Hill *et al.*, 1999).

There is an increasing number of negative associations between precipitation and butterfly abundance from December to March (Table 5), which might suggest that larvae in sheltered dormancy sites are unaffected by rainfall but in February and March they become more vulnerable to rain perhaps while feeding on the exposed surfaces of leaves. However *P. c-album* over-winters as an adult, but still shows significant ($P. = < 0.05$) negative associations with January and March precipitation.

This is unlikely to be explained by moving from a sheltered site to feed in an exposed site, so perhaps the mechanism for an adverse effect of precipitation is through an increased risk of fungal infection in wet weather, with the increasing number of associations between rainfall and precipitation between December and March being due to warmer and wet weather towards the end of this period being particularly favourable conditions for fungal growth.

Temperatures in May, July and August appear important for *Aricia agestis*, *Polyommatus icarus* and *Aglais urticae* (Table 3). Consequently it would appear that the NAO is indirectly controlling these species through the influence of sea surface temperature. Butterflies are particularly affected by temperature in June, when most species are in adult form, however temperature in June appears to be independent of the NAO. Precipitation in May, June and August also appears to be indirectly controlled by the NAO (Table 2), through SST, and precipitation in these months has a negative effect on twelve species (Table 5).

To conclude, there is evidence that the NAO affects U.K. autumn and winter weather, which then affects butterfly populations. Also the NAO appears to be able to affect the weather several months later, through the effect of sea surface temperature, and this then influences butterfly population size. There is a potential for using the NAO index, especially the February NAO index, as a predictor for butterfly population size in the summer.

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