

Climate patterns and the stochastic dynamics of migratory birds

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We analyse time series data of 17 bird species trapped at Ottenby Bird Observatory, Sweden, during spring migration 1972–1999. The species have similar demography but respond differently to variation in the North Atlantic Oscillation (NAO) – a strong determinant of winter climate in the northern Hemisphere. Species wintering in northern Europe, compared to species having winter quarters in the Mediterranean area, tend to respond positively to variation in NAO. The variation within each group is high due to wide-ranging winter-distribution in many species, probably smoothing out the effect of spatial variation in NAO. Whereas mild winters (high NAO) are benign for many – but not all – birds wintering in northern Europe, the effect of drier-than-normal conditions in the Mediterranean area during high NAO index winters is uncertain. The work presented here goes beyond simple correlative studies and help identifying which species that are most affected by variation in winter climate. This is a first important step that calls for a more mechanistic approach when analysing possible changes to climate change.

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Most ecologists seem to agree on a synthetic view of population regulation (Kendall et al. 1999, Turchin 1999) acknowledging the importance of both endogenous (biotic interactions) and exogenous (e.g. weather and climate) factors for explaining population fluctuations (Elton 1924, Higgins et al. 1997, Leirs et al. 1997, Forchhammer et al. 1998a, Grenfell et al. 1998, Stenseth et al. 1999a, b). The need for a better understanding of how exogenous and endogenous factors shape observable population dynamics is motivated by the narrow focus on deterministic theory permeating ecology (Lundberg et al. 2000), as well as the urgent need to formulate stochastic population models intended for implementation in the decision-making process inevitably needed in conservation biology and management (Hilborn and Mangel 1997).

A key issue further sparking the interest in stochastic theory is the concern about global change, exemplified

by numerous recent publications investigating the ecological ramifications of large-scale abiotic phenomena such as the North Atlantic Oscillation (NAO) and El Niño (Hofgaard et al. 1999). The majority of these studies have focussed on how climate change correlates with phenology (Beebe 1995, Crick et al. 1997, Brown et al. 1999, Sparks 1999) or reproduction (Stevenson and Bryant 2000, Both and Visser 2001), and only a handful have explicitly linked climate and population change (see review by Post et al. 1999). Among the few studies actually devoted to the interaction between large scale climate patterns and population dynamics, there is a strong bias towards either large mammals inhabiting northern latitudes (Forchhammer et al. 1998a, Post and Stenseth 1998, Stenseth et al. 1999b) or marine systems (e.g. Fromentin and Planque 1996). To our knowledge, only three studies have explicitly incorporated climate indices in population models for bird

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species (Forchhammer et al. 1998b, Sæther et al. 2000, Sillet et al. 2000). The relationship between regional and local weather and population dynamics in birds has, however, been studied (Winstanley et al. 1974, Hjort and Lindholm 1978, Cave 1983, Lindholm et al. 1983, Svensson 1985, Jones 1987, Peach et al. 1991, Catchpole et al. 1999) and overviews have been given by Burton (1995) and Newton (1998). Local weather is likely to respond to global climate change, and NAO is probably an important component of global change (Dickson 1997) and therefore of great interest to ecology (Post et al. 1999).

Migratory birds are interesting because the dynamic consequences of climate change, e.g., a trend towards warmer winters in Europe, are equivocal. For instance, if a warm winter increases the survival, this effect may be counteracted by density dependence on the breeding ground. In a range of bird species, the existence of density dependent reproduction has been clearly verified (Newton 1998) and has been studied on levels ranging from individual behaviour to population dynamics (e.g. Both 1998). Furthermore, the very fact that migratory birds are mobile should affect how they react to climate patterns on both short and long time scales (Sutherland 1998). Since birds are often used as bio-indicators in population monitoring programmes (Greenwood et al. 1993), there is a need for a better understanding of climatic effects on the dynamics of migratory bird populations.

Here we present a time series analysis of passerine birds with winter quarters mainly in northern Europe or the Mediterranean area. Based on a priori models we sort out the effect of density dependence and winter climate in explaining the observed fluctuations. As an index of winter climate we use the annual variation in

the North Atlantic Oscillation – a strong determinant of the climatic winter conditions in the northern Hemisphere (Hurrell et al. 2001).

Material and methods

Data

We used spring ringing figures for 17 passerine species (Table 1) trapped according to a standardised procedure at Ottenby Bird Observatory (56° 12' N, 16° 24' E), Sweden, generally between 15 March and 15 June 1972–1999. In 1972–1979, the start of trapping varied between 19 March and 1 April. In the earliest arriving species, some birds would have been missed in some of these first years. Normally, however, only small numbers are trapped in March, also of the earliest arriving species. We therefore consider trapping data from the whole study period to be comparable, but we also took the somewhat unbalanced sampling scheme into account during the analysis.

Birds were trapped in 9 mistnets (in total 66 m) and two large traps (Helgoland-type) positioned at the same sites throughout the study. Nets and traps were in operation daily from 30 min before dawn to 11.00. On days with many birds, trapping went on further, until no or very few birds were trapped (the birds normally move out of the trapping area during the day). Trapping data similar to ours have been shown to reflect the local migratory intensity of birds (Zehnder and Karlsson 2001).

The species are similar to each other in terms of being relatively short-lived and reproducing at age 1 yr. However, they differ with respect to migration distance

Table 1. Lean body mass (LBM, in gram) and parameter estimates for the second-order autoregressive model with NAO as a covariate: $r_t = a_0 + a_1x_{t-1} + a_2x_{t-2} + b \text{ NAO}_t + \varepsilon_t$. Here, a_0 is a constant, a_1 and a_2 are the estimates of the strength of direct and delayed density dependence, respectively, b is the regression coefficient with respect to NAO, and ε_t is a noise term. The deviations between model and $\log_e(\text{data})$ are assumed to be normally distributed and σ is the maximum likelihood estimate of the standard deviation. "E" and "M" refer to the main winter area, where E = northern Europe and M = the Mediterranean. Mean and SD (= standard deviation) are given for numbers trapped between 15 March and 30 June 1972–1999.

Species	Latin	Mean	SD	LBM		a_0	a_1	a_2	b	σ
blackbird	<i>Turdus merula</i>	149	62	90	E	4.8	−0.76	−0.21	0	0.4
blue tit	<i>Parus caeruleus</i>	17	14	10	E	0.85	−0.79	0.4	0.14	0.66
brambling	<i>Fringilla montifringilla</i>	15	9	21	E	2.2	−0.87	−0.02	0.04	0.66
chaffinch	<i>Fringilla coelebs</i>	145	62	20	E	5.27	−1.18	0.14	−0.08	0.33
fieldfare	<i>Turdus pilaris</i>	10	5	100	E	1.58	−0.81	0.03	0.08	0.52
goldcrest	<i>Regulus regulus</i>	219	129	5	E	4.57	−0.84	−0.06	0.15	0.57
great tit	<i>Parus major</i>	55	43	17	E	3.15	−0.76	−0.04	−0.08	0.73
greenfinch	<i>Carduelis chloris</i>	39	15	26	E	3.53	−0.91	−0.07	0.03	0.37
linnet	<i>Carduelis cannabina</i>	45	39	17	E	1.44	−0.5	−0.04	0.36	0.73
reed bunting	<i>Emberiza schoeniclus</i>	15	8	19	E	2.18	−0.65	−0.26	0.1	0.62
wren	<i>Troglodytes troglodytes</i>	84	36	8	E	2.25	−0.81	0.27	0.09	0.47
yellowhammer	<i>Emberiza citrinella</i>	21	15	26	E	3.48	−1.24	−0.01	0.09	0.62
black redstart	<i>Phoenicurus ochruros</i>	14	6	14	M	2.14	−0.89	0.11	−0.03	0.34
dunnoek	<i>Prunella modularis</i>	79	59	17	M	4.5	−1.01	−0.07	0.05	0.55
European robin	<i>Erithacus rubecula</i>	1787	669	14	M	8.02	−1.09	0	0	0.34
redwing	<i>Turdus iliacus</i>	40	17	55	M	2.33	−0.8	0.17	−0.05	0.41
song thrush	<i>Turdus philomelos</i>	118	58	65	M	3.07	−0.77	0.11	0.02	0.41

and hence wintering area. Based on ringing recoveries, we divided the species into two groups: birds wintering in northern Europe (north of the Pyrenees and the Alps) and birds wintering in the Mediterranean (south of the Pyrenees and the Alps, and north of the Atlas mountains). Some species (e.g. chaffinch, dunnock, European robin and redwing) have such wide-ranging winter distribution that the decision of placing them in the northern Europe or Mediterranean group is somewhat tentative. We nevertheless decided to make this grouping and keeping the underlying complexities in mind when interpreting the results.

Even though all the species in a given group have similar demography and winter quarters, they may still respond differently to climatic variation as measured by NAO. We use lean body mass (LBM, measured in gram) as one way of spreading the species along a one-dimensional niche axis. Possibly different responses to NAO may be caused by physiological processes related to size (e.g. temperature regulation), size related differences in diet choice, and competitive ability through dominance.

As a measure of winter climate we used the December–March index of the North Atlantic Oscillation (NAO) based on the difference of normalised pressure between Lisbon (Portugal) and Stykkishólmur/Reykjavík (Iceland). The NAO is characterised by an inter-annual and decadal oscillation of atmospheric mass between the Arctic and the subtropical Atlantic (Hurrell 1995, Hurrell et al. 2001), which influences the winter climate over vast areas in the northern Hemisphere (Lamb and Pepler 1987). When NAO is in “high phase”, strong westerly winds are prevalent that transport heat and moisture across the Atlantic, resulting in relatively warm and humid winters in northern coastal Europe (Hurrell et al. 2001) and drier-than-normal conditions in central and southern Europe including the Mediterranean. For further details, see Hurrell (1995). Data on NAO are available from the homepage of the Climate Analysis Section (Colorado) at <http://www.cgd.ucar.edu/cas/>.

Theoretical framework

A general single-species model in discrete time can be written

$$N_t = N_{t-1}g(\cdot) \quad (1)$$

where N_t is population density at time t , and g is a function translating density from one time step to the next. If we define the logarithmic per capita rate of change as

$$r_t = \log_e(N_t) - \log_e(N_{t-1}) = \log_e(g(\cdot)) = f(\cdot) \quad (2)$$

it is clear that the function f is of crucial importance and may contain previous densities (so-called density dependence), as well as other biotic or abiotic input. For instance, if f is the sum of a constant a_0 and a random element,

$$f = a_0 + \varepsilon_t \quad (3)$$

the population undergoes an unbiased random walk ($a_0 = 0$) or a random walk with drift ($a_0 \neq 0$). A random walk is the relevant null-model when testing for statistical significant density dependence because it implies no regulation (Dennis and Taper 1994, Berryman and Turchin 2001). Often, r_t will be assumed to be a linear function of density. Assuming a linear relationship has the advantage of avoiding the choice between a variety of possible non-linear models. Furthermore, judging non-linearity on the basis on, e.g., the response surface methodology, may sometimes be difficult (Lindström et al. 1999). One should consider the linear model as an approximation of a non-linear model evaluated around the deterministic equilibrium point (e.g. Roughgarden 1975). The choice is now between regressing r_t on density or log density. We will take the Gompertz model approach (Gompertz 1825) and regress r_t on log density (x) as

$$r_t = a_0 + a_1x_{t-1} + a_2x_{t-2} + \dots + a_px_{t-p} + \varepsilon_t \quad (4)$$

that can (remembering eq. 2) be rearranged to

$$x_t = a_0 + (1 + a_1)x_{t-1} + a_2x_{t-2} + \dots + a_px_{t-p} + \varepsilon_t \quad (5)$$

Here, a_1, a_2, \dots, a_p are estimates of the strength of statistical density dependence. If ε_t is assumed to be independent and from an identical symmetric distribution, eq. 5 is an autoregressive model of order p , (AR(p); Royama 1992). This is a family of statistical time-series models with well-known properties and a good track-record in population dynamics (Stenseth 1999).

The task is now to estimate the effect and importance of NAO in explaining population fluctuations. In practice, this means that we have to decide how to incorporate NAO in the model (eq. 4) as well as determine the structure of density dependence, i.e. the order of the process. The bird species we are interested in are all short-lived with early maturation and not predated upon by any specialist (species unique) predator. Hence, we have no a priori reason to assume a higher order than one. However, we do not know anything about other possible strong dynamic interactions, for example with parasites or generalist predators – another possible source of second-order dynamics (Bjørnstad et al. 2001). We therefore decided to keep an extra term taking care of possible delayed density ef-

fects. The effect of previous winter was estimated by including NAO as a covariate (Forchhammer et al. 1998a). Some previous studies have demonstrated lagged effects of NAO, e.g. in the northern fulmar (*Fulmarus glacialis*) (Thompson and Ollason 2001) and ungulates (Post and Stenseth 1998). However, the bird species studied here are short-lived and there is no reason to expect any lagged response to NAO through e.g. cohort effects. Hence, we only include NAO with lag 0 giving the model

$$r_t = a_0 + a_1 x_{t-1} + a_2 x_{t-2} + b \text{NAO}_t + \varepsilon_t \quad (6)$$

where b is the regression coefficient with respect to NAO, and ε_t is a noise term lumping together all factors (including observation error) not included in the model. We hypothesise that b should be positive for the group of birds wintering in northern Europe since mild winters (high NAO) are likely to increase survival and vice versa. The b -value of the species in the Mediterranean group should mirror whether drier-than-normal (high NAO) or wetter-than-normal conditions (low NAO) is beneficial to the species spending the winter in that region.

Finally, the AR models describe stationary processes, but some of the time series violate that assumption by showing a trend. However, detrending may remove long-term fluctuations caused by NAO, which is the focus of this study. Fortunately, it turned out that our general results and conclusions were not affected by whether we detrended the data or not. Hence, we present results based on the analysis of the log_e-transformed data and indicate the exceptional cases when detrending produced a different result.

Evaluation

The parameters were estimated by minimising the sum of squared deviations between model and data. Observation error is of course present and its potential effect here is to bias the estimate of density dependence. However, we are not interested in the exact point estimates, but rather in comparing species. When comparing the relative effect of NAO and density dependence we are aware of this problem. Furthermore, we have no reason to believe that observation error differs significantly between the selected species. Relative differences therefore remain.

While the regression coefficient with respect to NAO gives a first hint about the importance of NAO, we will also compare the full model (eq. 6) with simpler nested models including or excluding the effect of NAO. The Akaike information criterion corrected for small sample, AIC_c (Hurvich and Tsai 1989), guided model selection. AIC_c provides an estimator of the relative Kullback-Leibler (K-L) information – the information

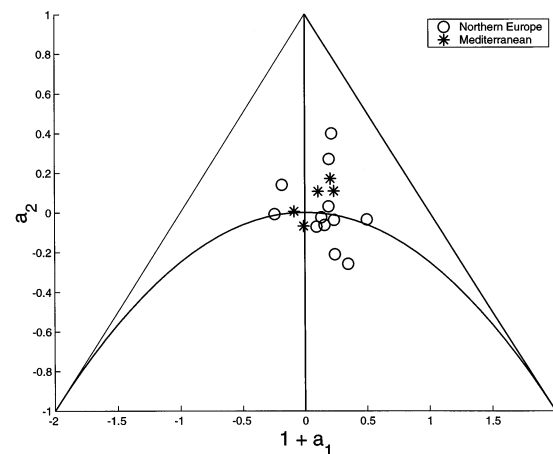


Fig. 1. Location of the estimated AR parameters estimated by fitting the model $r_t = a_0 + a_1 x_{t-1} + a_2 x_{t-2} + b \text{NAO}_t + \varepsilon_t$ to each time series. Here, a_0 is a constant, a_1 and a_2 are the estimates of the strength of direct and delayed density dependence, respectively, b is the regression coefficient with respect to NAO, and ε_t is a noise term. Parameter values inside the triangle give rise to point stability or damped fluctuations in a deterministic world. However, the presence of stochasticity changes the dynamics and below the parabola, the dynamics will be cyclic. For a detailed explanation of the dynamic properties depending on location of the AR parameters, see Royama (1992).

lost when using a model for approximating full reality (Burnham and Anderson 1998). We then calculated AIC_c differences (Δ_i) for each model such that $\Delta_i = AIC_c(i) - \min(AIC)$, scaling the AIC_c values to give the model with minimum AIC_c a value of zero. Finally, for each of the r models, we calculated the likelihood of the model given data and normalised each value according to

$$w_i = \exp(-0.5\Delta_i) / \sum \exp(-0.5\Delta_r) \quad (7)$$

The normalised likelihood for each model, w_i is the Akaike weight (Burnham and Anderson 1998).

Results

In Table 1 we present the point estimates of all parameters when fitting the full model (eq. 6) to each time series. The AR parameter estimates are also plotted in $(1 + a_1, a_2)$ space in Fig. 1. Overall, the AR parameter estimates are distributed around $a_1 = -1$ and $a_2 = 0$, suggesting first order dynamics for most species (see also Fig. 4).

We find the 7 species with highest regression coefficient with respect to NAO (b) in the northern Europe group and 9 of the 12 species have positive b . In the Mediterranean group the b estimates are distributed around zero with some positive and some negative

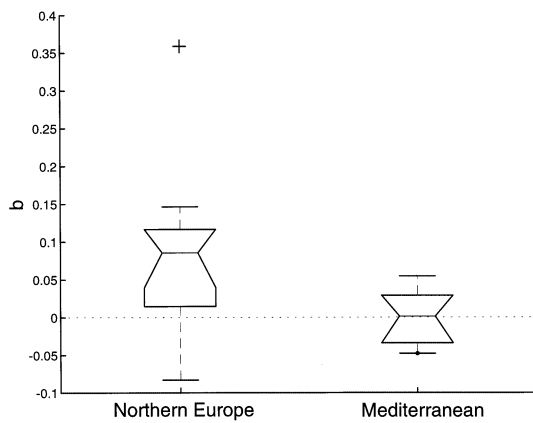


Fig. 2. Boxplot of the regression coefficient b in the model $r_t = a_0 + a_1x_{t-1} + a_2x_{t-2} + bNAO_t + \varepsilon_t$. The whiskers extend to 1.5 times the interquartile range and the “+” signs indicate outliers. There is no significant difference between the two groups at the 5% level (Kruskal-Wallis: $\chi^2 = 2.5$, $df = 1$, $P = 0.11$, $n = 17$).

values. There is, however, no significant difference between the two groups at the 5% level (Kruskal-Wallis: $\chi^2 = 2.5$, $df = 1$, $P = 0.11$, $n = 17$; see Fig. 2). We also regressed b on \log_{10} (lean body mass). Though there was a tendency of a negative association (Fig. 3), the relationship was not significant at the 5% level ($F = 1.15$, $n = 17$, $P = 0.3$).

In Fig. 4, the Akaike weight (or the normalised likelihood) for each of 6 nested models is shown. Among the 12 species mainly wintering in northern Europe, a model including NAO is best in four (blue tit, chaffinch, goldcrest and linnet), practically indistinguishable from the best model in two (fieldfare and wren) and almost as good as the best in two (reed bunting and yellowhammer). Only the blue tit had

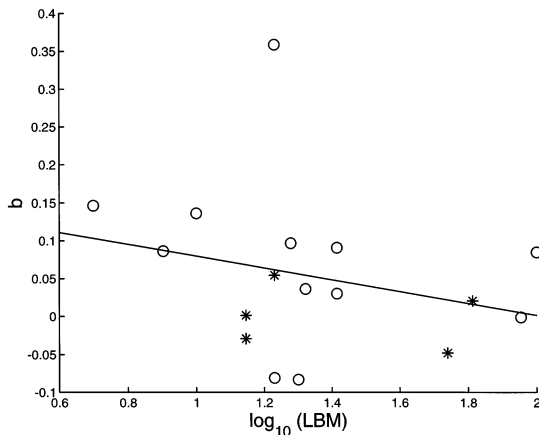


Fig. 3. The regression coefficient b in the model $r_t = a_0 + a_1x_{t-1} + a_2x_{t-2} + bNAO_t + \varepsilon_t$ plotted against \log_{10} (LBM). LBM = lean body mass. The straight line represents the least squares regression and the equation is $y = -0.078x + 0.16$. $F = 1.15$, $n = 17$, $P = 0.30$.

second order effects in the best model. No species wintering in the Mediterranean has NAO included in the most parsimonious model.

When analysing detrended data, only reed bunting had second-order effects in the best model, and an AR(1) model with NAO as a covariate was the best description of the blue tit data. All other results from the previous analysis remained. We also tried to account for the somewhat unbalanced sampling scheme before 1980 by only including birds trapped between 1 April and 30 June. That resulted in almost identical results. However, the most parsimonious model in blue tit turned out to be AR(1) (compared to AR(2) + NAO before), whereas in the great tit, the model selection procedure suggested an AR(1) + NAO as the best model (compared to AR(1) before).

In conclusion, despite similarities among species in terms of demography – as illustrated by the AR parameters – we found a variety of responses to NAO ranging from negative to positive. The general pattern is that the species most positively affected by NAO are found in northern Europe rather than in the Mediterranean group. However, NAO is included in the most parsimonious model only in 33% of the species in the northern Europe group. The model uncertainty is, however, considerable. There was also a (non-significant) tendency of small birds responding more positively to variation in NAO than larger birds.

Discussion

Putting the global climate change on the political agenda has forced scientists – including ecologists – to come up with forecasts and risk assessment for decision making. A number of recent studies have focussed on how phenology patterns have changed in relation to climate parameters (Beebe 1995, Crick et al. 1997, Brown et al. 1999, Both and Visser 2001). Such studies are important but nobody really knows how changes such as a trend towards earlier breeding in animals translates into population dynamics – the level where the potential effects of climate change become interesting for conservation and management.

We have tried to evaluate the effect of climate pattern directly on the population level, thereby ignoring a lot of details. Our results are reasonably straightforward: the 17 bird species studied here, similar in demography, respond differently to variation in NAO. We argue that the reason why many species wintering in northern Europe are more positively affected by NAO than species mainly wintering in the Mediterranean is due to the spatial pattern of NAO. A high NAO winter index results in mild and wet winters in northern Europe, but drier-than-normal conditions in central and southern Europe. It is reasonable to believe

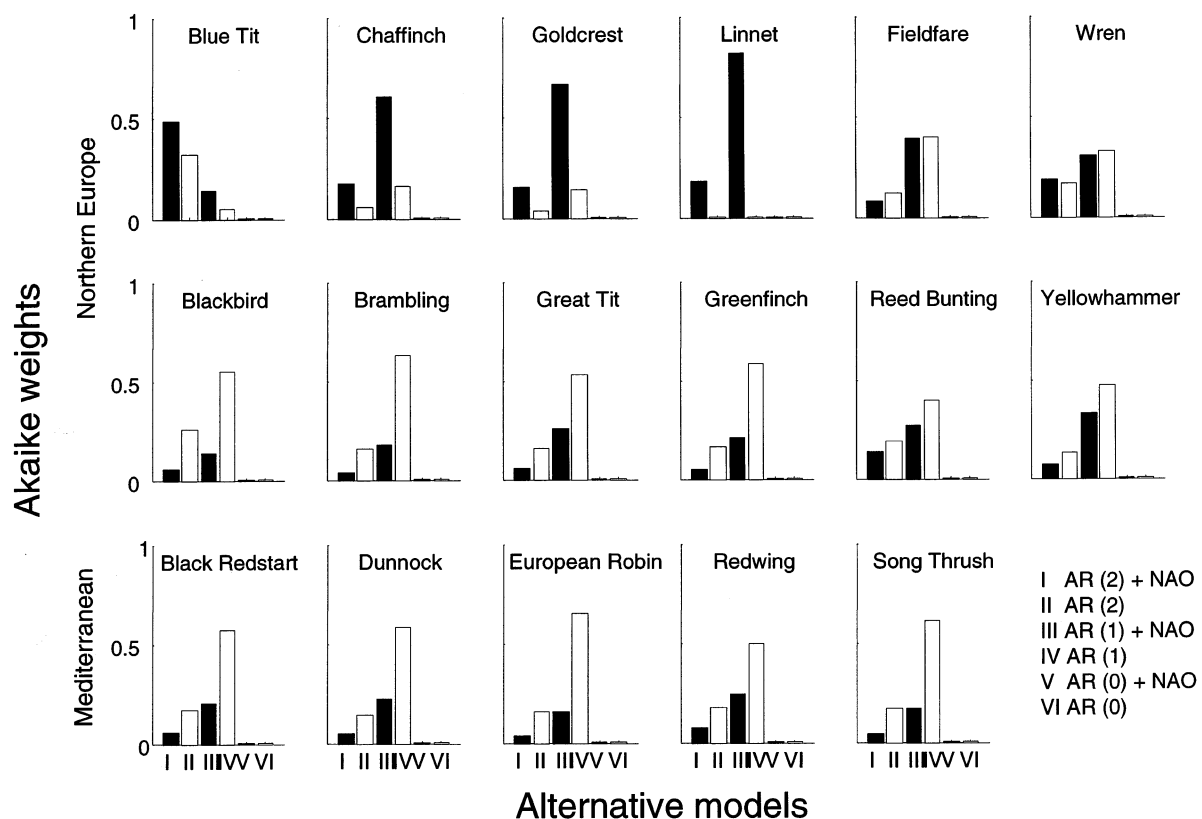


Fig. 4. The likelihood of each model given data normalised such that they sum to one (the Akaike weight) for each species. The 6 nested models are: (I) $r_t = a_0 + a_1x_{t-1} + a_2x_{t-2} + bNAO_t + \varepsilon_t$, (II) $r_t = a_0 + a_1x_{t-1} + a_2x_{t-2} + \varepsilon_t$, (III) $r_t = a_0 + a_1x_{t-1} + bNAO_t + \varepsilon_t$, (IV) $r_t = a_0 + a_1x_{t-1} + \varepsilon_t$, (V) $r_t = a_0 + bNAO_t + \varepsilon_t$, (VI) $r_t = a_0 + \varepsilon_t$. The black and white bars give the Akaike weight of models including or excluding NAO, respectively.

that winter survival among birds at northern latitudes is increased during mild winters, whereas the effect of relative drought in the Mediterranean on survival is less clear. Hence, the pattern revealed in this study seems to confirm that winter climate affects the population rate of change in migratory birds (e.g. Peach et al. 1991) and our results indicate that climate driven winter survival is an important factor behind long-term population fluctuations, often appearing as trends in short time series. The pattern would probably be even clearer if the species could be sorted into non-overlapping winter ranges, which is unfortunately not the case. However, the variation between species is interesting per se and our approach helps to identify which species that are most affected by variation in winter climate. It seems logical that small species wintering in northernmost Europe have NAO in the most parsimonious model (blue tit and goldcrest) or, as is the case with the wren, in the second best and almost indistinguishable from the most parsimonious model. However, it would have been difficult to guess that NAO should be such a strong predictor of rate of change in the linnet.

Whereas detrending did not affect the inference on the effect of NAO, excluding the birds trapped in

March – due to the unbalanced trapping in March in the 1970s – gave different results for great tit and blue tit. This may be due to the fact that both species are among the earliest migrants in spring at Ottenby, being relatively common in March, and the lack of March trapping data in some years could yield misleading results. We note, however, that our general results and inference about the role of NAO were not affected by the irregular trapping scheme in March 1972–1979.

The approach followed in this paper, i.e. autoregressive modelling with NAO as a covariate and an objective information criterion to rank the credibility of alternative models, is a reasonable way of tackling the problem at hand. For instance, we avoid some fundamental problems occurring when calculating cross-correlation between stochastic factors such as NAO and population indices (Royama 1992, Ranta et al. 2000). For an alternative and non-linear approach, see Pascual and Ellner (2000).

To sort out the relative effects of environmental fluctuations and demography (i.e. how to estimate AR parameters) requires that environmental stochasticity becomes an integral part of the models we are using (Lundberg et al. 2000). That can be accomplished by

including relevant environmental factors as covariates in for example AR models, as has been done in this study. The question remains, however, exactly how to define “environment” when it in fact encompasses both abiotic changes, such as day-to-day rainfall or long-term fluctuations as the NAO, and the entire biotic feedback environment (e.g. Jonzén et al. 2002).

We have shown that climate variation as described by the North Atlantic Oscillation may affect species differently, between as well as within geographical areas. A challenge for future studies is to build more mechanistic models of how climate variation affects different population processes and how these translate into observable population dynamics. The prediction of such models can be tested against population abundance data, the level where the effects of climate variation ultimately must be understood. The work presented here sets the stage for merging detailed studies of how climate affects population processes in birds and other organisms, and the statistical properties of population fluctuations.

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