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# Climate variation and regional gradients in population dynamics of two hole-nesting passerines

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Latitudinal gradients in population dynamics can arise through regional variation in the deterministic components of the population dynamics and the stochastic factors. Here, we demonstrate an increase with latitude in the contribution of a large-scale climate pattern, the North Atlantic Oscillation (NAO), to the fluctuations in size of populations of two European hole-nesting passerine species. However, this influence of climate induced different latitudinal gradients in the population dynamics of the two species. In the great tit the proportion of the variability in the population fluctuations explained by the NAO increased with latitude, showing a larger impact of climate on the population fluctuations of this species at higher latitudes. In contrast, no latitudinal gradient was found in the relative contribution of climate to the variability of the pied flycatcher populations because the total environmental stochasticity increased with latitude. This shows that the population ecological consequences of an expected climate change will depend on how climate affects the environmental stochasticity in the population process. In both species, the effects will be larger in those parts of Europe where large changes in climate are expected.

**Keywords:** climate change; density dependence; great tit; North Atlantic Oscillation; pied flycatcher; stochastic population dynamics

## 1. INTRODUCTION

The relative importance of density dependence and stochastic factors for variation in size of natural populations has, since the publication of the influential books by Andrewartha & Birch (1954) and Lack (1954), been one of the most central problems in ecology (reviewed in Turchin 1995). In recent years this question has again received increased attention because of the need to predict the ecological impact of the expected changes in climate. In spite of this increased focus, few hypotheses have been presented under which conditions stochastic variation in the

environment is expected to have large influence on the dynamics of natural populations.

One reason for why so few general hypotheses have been developed for predicting variation in the effects on the population fluctuations of stochastic variation in the environment may be that two types of stochasticity affect the population dynamics, which is difficult to separate by using traditional time-series analysis. Demographic stochasticity is caused by random variation among individuals in their contribution to fitness, whereas environmental stochasticity arises from random effects that affect the whole or parts of the population at the same time (Lande *et al.* 2003). These stochastic effects affect the variance in population size differentially: demographic variance  $\sigma_d^2$  is most important at smaller population sizes, whereas the effects of the environmental variance  $\sigma_e^2$  increase with the

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square of population size and thus are important in large populations as well (Lande 1998). In addition, small variations in parameters specifying the deterministic component of the population dynamics, e.g. the specific growth rate, may also affect the population characteristics (May 1976; Lande *et al.* 2003). Hence, a proper understanding of the effects of environmental variation on population fluctuations must include estimates of parameters describing the deterministic as well as the stochastic components of the dynamics.

Basically, two alternative hypotheses can be derived, under which conditions stochastic variation in an environmental variable is expected to have a greater influence on the dynamics of a population. One hypothesis may be that a large effect of variation in the environment may be expected in populations where the stochastic components of the population dynamics are large. Alternatively, environmental stochasticity may more strongly affect the fluctuations of populations with a small stochastic component because in highly variable populations, the effects of climate variability will be cancelled out by other factors (see Pimm (1991) for a similar line of argument).

Many important features of the environment relate to variation in climate. The North Atlantic Oscillation (NAO) is one such large-scale climate phenomenon that is correlated to annual variation in local climate over large areas (Hurrell 1995; Mysterud *et al.* 2002). The NAO represents changes in the subtropical atmospheric high-pressure zone centred over the Azores and the low-pressure zone over Iceland, and may also be interrelated with other large-scale climate patterns (Visbeck *et al.* 2001). In general, high values of the NAO-index during winter are associated with strong wind circulation in the North Atlantic causing an increase in temperatures and precipitation in northern Europe but dry weather in the Mediterranean region (Hurrell 1995). By contrast, negative values of the NAO are associated with a decrease in temperature and precipitation in northwestern Europe.

Several studies have documented that variation in climate may affect demographic characteristics of small passerines (McCarty 2001; Stenseth *et al.* 2002; Walther *et al.* 2002). For instance, an advance in laying date with increase in spring temperature has occurred in many populations of the great tit (*Parus major* L. (Winkel & Hudde 1997; McCleery & Perrins 1998; Visser *et al.* 2003)) and the pied flycatcher (*Ficedula hypoleuca* L. (Winkel & Hudde 1997; Both & Visser 2001; Sanz *et al.* 2003)), which also may be explained by variation in the NAO (Forchhammer *et al.* 1998; Sanz 2002, 2003). However, population dynamical responses to changes in climate have been more difficult to document (but see Sæther *et al.* 2000).

In this paper we will, using a newly developed theoretical framework (Lande *et al.* 2003), relate fluctuations in the size of great tit and pied flycatcher populations distributed across Europe to variation in the NAO. We will then try to derive latitudinal gradients in the population dynamical characteristics of the two species, especially focusing on how the NAO affects the noise structure of the population process. Our aim will be to examine whether these effects will be similar in the sedentary great tit and the migratory pied flycatcher, suggesting general relationships for how a large-scale climate phenomenon

such as the NAO affects the population dynamics within the distributional range of a species.

## 2. POPULATION MODEL

Let  $N$  be the population size in a given year and  $N + \Delta N$  the population size the following year. The stochasticity in the population dynamics is then given by  $\text{var}(\Delta N | N) = N^2 \sigma_e^2 + N \sigma_d^2$ , where  $\sigma_e^2$  and  $\sigma_d^2$  denote the environmental and demographic variance, respectively. The logistic model (May 1981)  $E(\Delta N) = rN(1 - N/K)$ , where  $r$  is the mean specific population growth rate and  $K$  the carrying capacity has been found to describe the density regulation in many bird species quite well (Sæther & Engen 2002). Thus, for small and moderate fluctuations in population size, we find, writing  $X = \ln N$  and using the first-order approximation  $\Delta X \approx \Delta N/N$ , that the expected change in log population size is

$$E(\Delta X | X) = s + \alpha e^X - \frac{1}{2} \sigma_d^2 e^{-X}, \quad (2.1)$$

where the stochastic population growth rate  $s = r - 1/2 \sigma_e^2$  and  $\alpha = -r/K$ .

We then partition the environmental variance  $\sigma_e^2$  into a component  $Z$  due to linear effects of the NAO and a residual component  $\sigma_{\text{res}}^2$  (Engen *et al.* 1998; Sæther *et al.* 2000) so that the environmental stochastic component of the change in log population size becomes  $U \sigma_e = \beta_{\text{NAO}} Z + V \sigma_{\text{res}}$ , where  $Z$  is the NAO-index,  $U$  and  $V$  are standardized variables with zero mean and unit variance and  $\beta_{\text{NAO}}$  is the regression coefficient. Hence the total environmental variance is

$$\sigma_e^2 = \beta_{\text{NAO}}^2 \text{var} Z + \sigma_{\text{res}}^2 = \sigma_{\text{NAO}}^2 + \sigma_{\text{res}}^2. \quad (2.2)$$

Using  $Z$  as a known covariate we then obtain the model

$$E(\Delta X | X) = s - \frac{1}{2} \sigma_d^2 e^{-X} + \alpha e^X + \beta_{\text{NAO}} Z \quad (2.3a)$$

and

$$\text{var}(\Delta X | X) = \sigma_{\text{res}}^2 + \sigma_d^2 e^{-X}. \quad (2.3b)$$

## 3. METHODS

### (a) Population data

We compiled long-term (10 years or more) time-series of population fluctuations of the great tit and pied flycatcher from different parts of Europe (figure 1). Only study sites with artificial nest-boxes were included, resulting in more precise population estimates than are usually recorded in studies of natural populations. To avoid problems with  $N = 0$ , we include only populations where the estimate of  $K$  was larger than 10. For estimates of the population parameters see Appendix A.

### (b) Climate data

The NAO is a global climate phenomenon (Visbeck *et al.* 2001), and is expressed by an index based on the difference of normalized sea level pressures between Ponta Delgada, Azores, Portugal, and Stykkisholmur, Iceland, from 1864 through to 2002 for the winter period, December through to March (<http://www.cgd.ucar.edu/cas/climind>).

### (c) Estimation of parameters

The demographic variance  $\sigma_d^2$  was estimated from data on individual variation among females in their fitness contributions

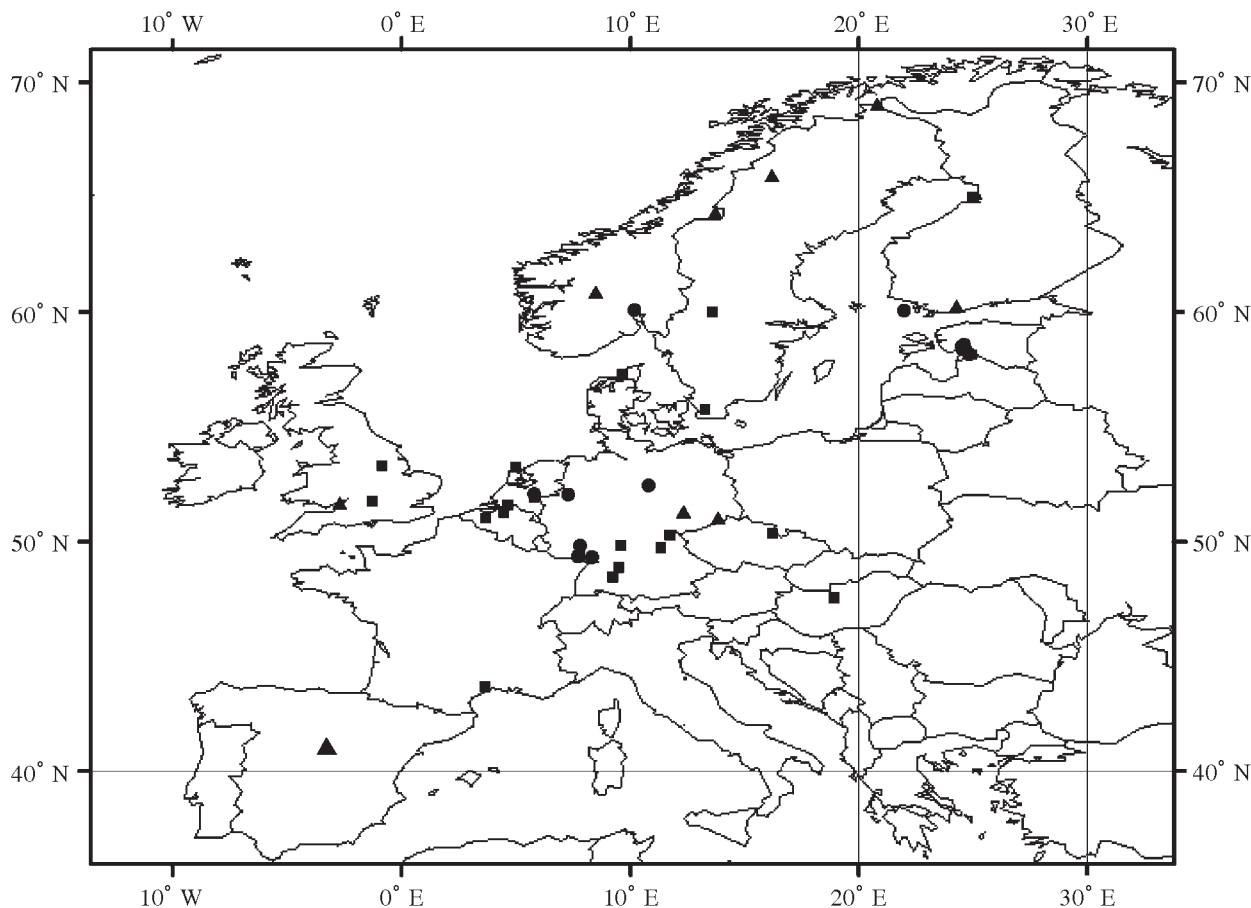


Figure 1. Location of the study areas. Triangles represent pied flycatcher study sites, squares represent study sites with great tit populations, and circles represent study sites where time-series of both species were present. Some adjacent study sites are represented only by one symbol.

to the following generations (Lande *et al.* 2003). The total contribution of a female  $i$  in year  $t$  ( $R_i$ ) is the number of female offspring born during the year that survive for at least 1 year, plus 1 if the female survives to the next year (Sæther *et al.* 1998). The demographic variance was estimated (Lande *et al.* 2003) as the weighted mean across years of  $\sigma_{\hat{a}}^2(t) = E(1/a-1) \Sigma(R_i - \bar{R})^2$ , where  $\bar{R}$  is the mean contribution of the individuals and  $a$  is the number of recorded contributions in year  $t$ . Estimates of  $\sigma_{\hat{a}}^2$  were obtained for 10 great tit populations and three pied flycatcher populations (see Appendix A). When no individual data were available, the species-specific mean of  $\hat{\sigma}_{\hat{a}}^2$  was used.

The other parameters in equations (2.3) were estimated by maximum likelihood using the full-likelihood function for the process obtained by assuming that  $\Delta X$  conditioned on  $X$  is normally distributed. Uncertainties in the estimates were found by parametric bootstrapping simulating new sets of data from the fitted model (Efron & Tibshirani 1995). To test the hypothesis that  $\beta = 0$  we first carried out the estimation for the reduced model with  $\beta = 0$  and performed bootstrap simulations using the parameters estimated from this model and  $\beta = 0$ . The  $p$ -value for the test is then obtained as the fractions of the simulations giving an estimate of  $\beta$  larger than  $\hat{\beta}$ . The results of the tests are presented in Appendix A.

The diffusion approximation to the quasi-stationary distribution of population sizes

$$f(N; N_0) = G(N, N_0) / \int_1^{\infty} G(N, N_0) du \quad (3.1)$$

can be derived following Lande *et al.* (2003). Here,  $G(N, N_0)$  is the Green function or the sojourn time starting from an initial size  $N_0$ . The Green function expresses the expected cumulative time spent at each population size before extinction (Karlin & Taylor 1981). We first computed the variance in the quasi-stationary distribution using  $N_0 = K$  that can be explained by variation in the NAO,  $V_{\text{NAO}}$ , using  $\sigma_{\text{NAO}}^2$  and then repeated the computation with  $\sigma_{\text{res}}^2$  to get the residual variance  $V_{\text{res}}$ . The relative contribution to the variance in the quasi-stationary distribution of variation in the NAO then becomes  $V_{\text{NAO}} / (V_{\text{NAO}} + V_{\text{res}})$ . To facilitate the comparison among populations all variances were standardized in relation to  $K$ .

#### 4. RESULTS

The stochastic population growth rate  $s$  (defined by equation (2.1)) differed significantly between the two species (table 1;  $F = 21.27$ , d.f. = 1,67,  $p < 0.001$ ), with a smaller mean value of  $s$  in the pied flycatcher than in the great tit populations. No significant ( $p > 0.1$ ) interspecific variation was present in  $K$  or in any components of the environmental variance  $\sigma_e^2$ .



Table 1. The mean ( $\bar{x} \pm \text{s.d.}$ ) of the estimated population parameters for the two species.

( $s$  is the stochastic specific growth rate,  $\sigma_d^2$  the demographic variance,  $\sigma_e^2$  the environmental variance,  $\sigma_{\text{NAO}}^2$  the component of  $\sigma_e^2$  due to variation in the NAO-index,  $\sigma_{\text{res}}^2$  the residual component not explained by the NAO and  $n$  the number of study populations.)

	great tit			pied flycatcher		
	$\bar{x} \pm \text{s.d.}$	range	$n$	$\bar{x} \pm \text{s.d.}$	range	$n$
$s$	$0.89 \pm 0.38$	0.10–1.58	40	$0.49 \pm 0.31$	0.14–0.89	28
$K$	$56 \pm 49$	11–216	40	$60 \pm 58$	13–290	28
$\sigma_d^2$	$0.48 \pm 0.15$	0.30–0.77	10	$0.40 \pm 0.14$	0.31–0.56	3
$\sigma_e^2$	$0.070 \pm 0.049$	0.002–0.250	40	$0.052 \pm 0.047$	0.010–0.211	28
$\sigma_{\text{NAO}}^2$	$0.009 \pm 0.013$	0.00–0.042	40	$0.006 \pm 0.008$	0.000–0.035	28
$\sigma_{\text{res}}^2$	$0.061 \pm 0.046$	0.002–0.209	40	$0.045 \pm 0.041$	0.007–0.176	28

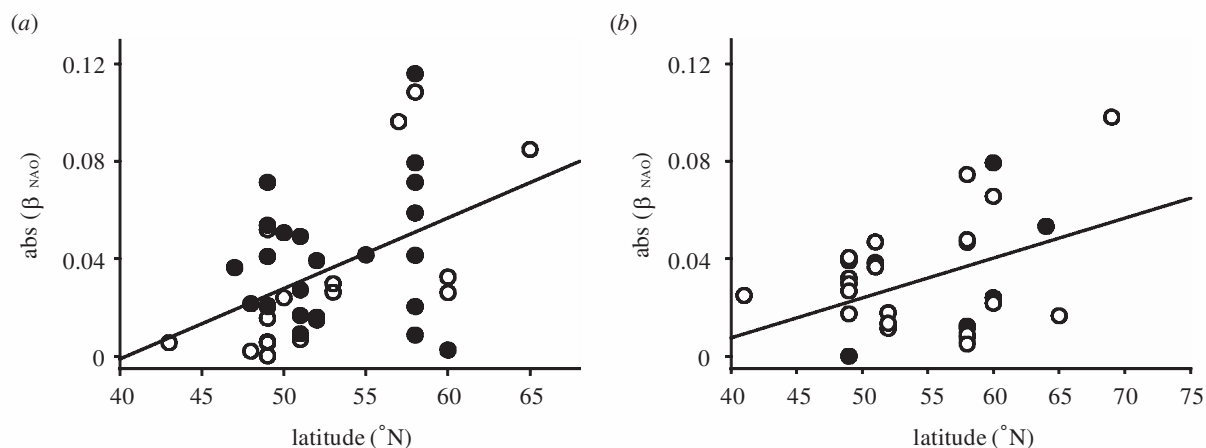


Figure 2. Latitudinal gradients in the absolute value of the regression coefficient of the NAO effect  $\beta_{\text{NAO}}$  in (a) great tit and (b) pied flycatcher populations across Europe. Filled circles denote positive values and open circles denote negative values of  $\beta_{\text{NAO}}$ .

Intraspecific variation in  $\sigma_e^2$  or in its two components was not significantly ( $p > 0.1$ ) related to  $s$  in any of the species. This is in contrast to previous cross-species comparisons in birds, where a close relationship between parameters describing the deterministic characteristics and the environmental stochasticity have been documented (Sæther & Engen 2002; Sæther *et al.* 2002).

We then examined variation in the component of the environmental stochasticity due to fluctuations in the NAO. Variation in the NAO was able to explain a significant proportion of the variance in population size in 20% ( $n = 40$ ) of the great tit and in 21% ( $n = 29$ ) of the pied flycatcher populations. A latitudinal gradient was present in the relative contribution of the NAO to the population fluctuations of both species because there was an increase in the absolute value of the regression coefficient  $\beta_{\text{NAO}}$  with latitude (figure 2; correlation coefficient = 0.463,  $p = 0.003$ ,  $n = 40$  and correlation coefficient = 0.378,  $p = 0.048$ ,  $n = 29$  in the great tit and pied flycatcher, respectively). However, the sign of the effects of the NAO differed in both species over relatively short distances (figure 2): in some populations a positive relationship was present, whereas in others  $N$  decreased with increasing NAO. Hence, the correlation coefficient with latitude after including the sign of  $\beta_{\text{NAO}}$  was insignificant (correlation coefficient =  $-0.153$ ,  $n = 40$  and correlation coefficient =  $0.038$ ,  $n = 29$ ,  $p > 0.34$  in the great tit and pied flycatcher, respectively).

These effects of the NAO were associated with latitudinal gradients in the effects of environmental stochasticity on the population dynamics. In both the great tit and pied flycatcher  $\sigma_{\text{NAO}}^2$  increased with latitude (figure 3a,b; correlation coefficient = 0.439,  $p = 0.005$ ,  $n = 40$  and correlation coefficient = 0.487,  $p = 0.007$ ,  $n = 29$  in the great tit and pied flycatcher, respectively). In the pied flycatcher, the residual component remaining after accounting for the NAO,  $\sigma_{\text{res}}^2$ , increased with latitude (figure 3d; correlation coefficient = 0.454,  $p = 0.013$ ,  $n = 29$ ), resulting in a latitudinal gradient in environmental stochasticity in this species (figure 3f; correlation coefficient = 0.478,  $p = 0.009$ ,  $n = 29$ ). By contrast,  $\sigma_{\text{res}}^2$  and  $\sigma_e^2$  were independent of latitude in the great tit (figure 3c,e; correlation coefficient =  $-0.003$  and correlation coefficient = 0.114,  $p > 0.48$ ,  $n = 40$  for  $\sigma_{\text{res}}^2$  and  $\sigma_e^2$ , respectively). Consequently, the relative contribution of variation in the NAO to  $\sigma_e^2$  of the great tit increased with latitude (figure 3g; correlation coefficient = 0.334,  $p = 0.035$ ,  $n = 40$ ), whereas no such significant relationship was present in the pied flycatcher (figure 3h; correlation coefficient =  $-0.179$ ,  $p > 0.35$ ,  $n = 29$ ). As a consequence, the contribution of the NAO to the variance in the quasi-stationary distribution of population sizes (equation (3.1)) increased with latitude in the great tit (correlation coefficient = 0.326,  $p = 0.034$ ,  $n = 40$ ). Finally, the variance in the population size explained by variation in the NAO increased in both species with the residual compo-

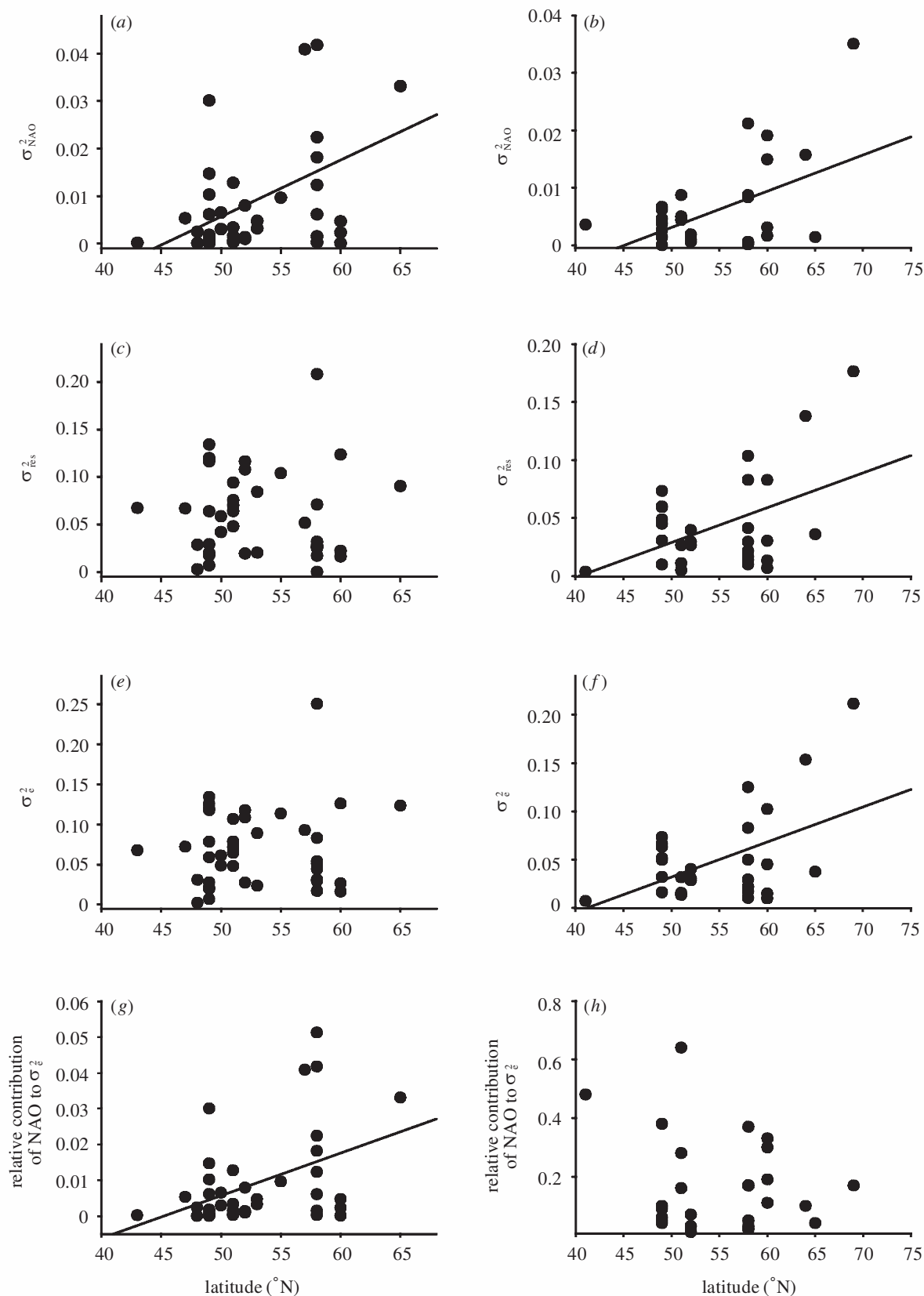


Figure 3. Latitudinal gradients in the component of the environmental stochasticity explained by: (a,b) variation in the NAO  $\sigma_{NAO}^2$ ; (c,d) in residual component of the environmental stochasticity  $\sigma_{res}^2$ ; (e,f) in total environmental variance  $\sigma_e^2$ ; and (g,h) in proportion of  $\sigma_e^2$  explained by variation in the NAO in great tit (a,c,e,g) and pied flycatcher (b,d,f,h) populations across Europe.

ment of the environmental variance in population size (correlation coefficient = 0.475,  $p = 0.002$ ,  $n = 40$  and correlation coefficient = 0.636,  $n = 29$ ,  $p < 0.001$  in the great tit and pied flycatcher, respectively). This shows that con-

tributions of large-scale climate patterns to variation in population size increased with increasing influence of environmental stochasticity on the population fluctuations.

## 5. DISCUSSION

Our results show that in both the great tit and pied flycatcher the NAO affects the population dynamics (figure 2*a,b*) and that this influence increases with latitude (figure 3*a,b*). However, the regional variation in the contribution of the NAO to the population fluctuations differed between the two species. In the great tit, the proportion of the annual variation in population change explained by the NAO increased with latitude (figure 3*g*). By contrast, in the pied flycatcher both  $\sigma_{\text{NAO}}^2$  and  $\sigma_{\text{res}}^2$  were large at high latitudes (figure 3*b,d*), resulting in a latitudinal increase in the stochastic component of the population dynamics (figure 3*e*).

The European pied flycatcher is a trans-Saharan migrant that winters in western Africa (Wernham *et al.* 2002), whereas the great tit is a stationary species over most of its breeding range. In spite of these differences in migratory behaviour, a large-scale climate phenomenon acting during winter affected the population dynamics of both species. One reason for this may be that wintering conditions for the pied flycatcher in West Africa are related to variation in the NAO. Some evidence does in fact suggest a tele-connection between several large-scale climate patterns (Hoerling *et al.* 2001). However, even in sedentary tit species it has been difficult to relate fluctuations in population size to winter climate (Slagsvold 1975*a*). Another explanation is that the NAO affects local winter climate, which in turn influences the phenological development of the environment. Thus, several reproductive traits of both pied flycatcher and great tit are influenced by annual variation in the phenological development of the environment (Slagsvold 1975*b*, 1976). Accordingly, it has been suggested that the effects of spring warming will be greater in populations experiencing a short period of peak in the food supply for the nestlings than in the habitats with greater variance around the mean date of peak food supply (Visser *et al.* 2003).

Although the contribution of the NAO to the fluctuations in population size increased with latitude (figure 3), the sign of the regression coefficient of change in popu-

lation size on the NAO differed over relatively short distances at the same latitude (figure 2). This suggests that microgeographical variation in how large-scale climate phenomena are related to fluctuations in local weather may generate differences in local population dynamics over short distances. Accordingly, the relationship between the NAO and different reproductive traits show regional variation in both species (Sanz 2002, 2003). Similarly, Mysterud *et al.* (2000) showed that the relationship between snow depth in March that affected the sex ratio in red deer (*Cervus elaphus* L.) and the NAO differed over short distances, dependent on local topographical conditions.

Cross-species comparisons of avian population dynamics have shown that the effects of environmental stochasticity on the population fluctuations are related to parameters (e.g. specific growth rate, form of density dependence) characterizing the deterministic component of the population dynamics (Sæther & Engen 2002; Sæther *et al.* 2002). No such relationship was, however, present among populations of either the great tit or the pied flycatcher. One reason for this may be that large uncertainties in  $\hat{r}$  (table 1) mask any such relationship because of the relatively short time-series used in the analysis.

Modelling has shown large regional variation in the magnitude of the expected changes in climate that are expected in the future (Houghton *et al.* 2001). Some of the largest changes are expected to occur at high latitudes. Our analyses (figures 2 and 3) suggest a particularly strong influence of climate on the population dynamics of great tit and pied flycatcher in those areas likely to be most strongly affected by an expected climate change.

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## APPENDIX A

The estimates of the parameters characterizing the population dynamics of the great tit (GT) and the pied flycatcher (PF) at the different study sites.

(For locations see figure 1. GER, Germany; SE, Sweden; NO, Norway; BE, Belgium; HU, Hungary; UK, United Kingdom; NL, The Netherlands; EST, Estonia; FI, Finland; DK, Denmark; FR, France; ES, Spain.)

locality	species	°N	'N	$s$	$K$	$\sigma_d^2$	$\sigma_{\text{res}}^2$	$\sigma_{\text{NAO}}^2$	$\sigma_c^2$
Allmenwald, GE	GT	49	19	0.801	51	—	0.02	$2 \times 10^{-7}$	0.02
Allmenwald, GE	PF	49	20	0.764	47	—	0.045	0.005	0.05
Amarnäs, SE	PF	65	57	0.264	141	—	0.036	0.001	0.038
Amseldell, GER	GT	49	21	1.262	22	—	0.12	0.006	0.126
Amseldell, GER	PF	49	21	0.319	13	—	0.049	0.003	0.052
Antonihof, GER	GT	49	21	1.32	27	—	0.064	0.015	0.079
Averøya, NO	PF	60	6	0.224	24	0.31	0.083	0.019	0.102
Averøya, NO	GT	60	6	0.81	13	0.35	0.022	0.005	0.027
Bad Kreuznach, GER	GT	49	50	0.59	27	—	0.134	$2 \times 10^{-4}$	0.134
Bad Kreuznach, GER	PF	49	50	0.616	20	—	0.074	$2 \times 10^{-9}$	0.074
Boswachter, BE	GT	51	16	0.817	49	0.41	0.075	0.003	0.079
Budapest, HU	GT	47	32	0.429	35	—	0.067	0.005	0.072

(Continued.)

locality	species	°N	'N	$s$	$K$	$\sigma_d^2$	$\sigma_{res}^2$	$\sigma_{NAO}^2$	$\sigma_c^2$
Buhlbronn, GER	GT	48	51	0.801	132	—	0.029	0.002	0.031
Finsterbrunnertal, GER	GT	49	21	0.715	24	—	0.116	0.001	0.118
Forest of Dean, UK	PF	51	40	0.264	62	—	0.011	0.004	0.016
Frankfurt, GER	GT	50	21	1.168	183	—	0.042	0.007	0.049
Ghent, BE	GT	51	0	0.567	36	0.48	0.048	$5 \times 10^{-4}$	0.048
Harthausen, GER	GT	49	18	1.04	85	—	0.007	$10^{-4}$	0.007
Harthausen, GER	PF	49	18	0.44	60	—	0.031	0.001	0.032
Hemsedal, NO	PF	60	52	0.138	30	—	0.007	0.003	0.01
Hoge Veleuwe, NL	GT	52	5	0.937	116	0.39	0.117	0.001	0.118
Hoge Veleuwe, NL	PF	52	5	0.399	90	0.33	0.027	0.002	0.028
Hollenbach, GER	GT	49	44	0.599	101	—	0.018	0.01	0.028
Illu, EST	GT	58	31	0.565	15	—	0.071	0.012	0.083
Illu, EST	PF	58	31	0.257	110	—	0.017	$5 \times 10^{-4}$	0.017
Kilingi, EST	GT	58	9	1.152	97	—	0.028	0.001	0.03
Kilksama, EST	GT	58	28	1.571	13	—	0.032	0.022	0.054
Kilksama, EST	PF	58	28	1.448	21	—	0.041	0.009	0.05
Kilpisjärvi, FI	PF	69	3	0.592	30	—	0.176	0.035	0.211
Künnametsa, EST	GT	58	35	1.345	11	—	0.017	$3 \times 10^{-4}$	0.017
Künnametsa, EST	PF	58	35	0.63	42	—	0.03	$10^{-4}$	0.03
Kaas, DK	GT	57	17	0.152	64	—	0.052	0.041	0.093
La Hiruela, ES	PF	41	4	0.560	75	0.56	0.004	0.004	0.007
Langdell, GER	GT	49	20	0.827	18	—	0.118	0.002	0.12
Langdell, GER	PF	49	20	0.256	23	—	0.06	0.007	0.067
Lauvsjøen, NO	PF	64	20	0.22	17	—	0.138	0.016	0.154
Leipzig, GER	PF	51	17	0.863	50	—	0.027	0.005	0.032
Lemsjøholm, FI	GT	60	5	1.579	19	—	0.124	0.002	0.126
Lemsjøholm, FI	PF	60	5	0.886	39	—	0.013	0.002	0.015
Liesbos, NL	GT	51	35	1.043	40	0.345	0.064	$3 \times 10^{-4}$	0.065
Lingen, GER	GT	52	3	0.795	99	—	0.108	0.001	0.109
Lingen, GER	PF	52	3	0.408	92	—	0.04	$6 \times 10^{-4}$	0.04
Linnebejer, SE	GT	55	44	1.212	47	0.593	0.104	0.01	0.114
Matapere, EST	GT	58	20	1.036	31	—	0.025	0.006	0.031
Matapere, EST	PF	58	20	0.596	73	—	0.022	$4 \times 10^{-4}$	0.022
Neubruich, GE	PF	49	20	0.513	13	—	0.01	0.006	0.016
Niidu, EST	GT	58	23	1.447	67	—	0.026	0.018	0.044
Niidu, EST	PF	58	23	0.093	114	—	0.014	0.008	0.022
Osterhout, NL	GT	51	55	0.476	29	0.634	0.094	0.013	0.107
Oti, EST	PF	58	28	0.345	27	—	0.083	$2 \times 10^{-4}$	0.083
Oulu, FI	GT	65	0	0.963	23	—	0.09	0.033	0.123
Pfullingen, GER	GT	48	26	1.183	51	—	0.003	$2 \times 10^{-5}$	0.003
Pillnitz, GER	PF	51	1	0.118	14	—	0.005	0.009	0.014
Riitskulli, EST	GT	58	10	1.686	14	—	0	0.051	0.051
Riitskulli, EST	PF	58	10	0.973	115	—	0.01	$6 \times 10^{-4}$	0.011
Rothense, GE	GT	49	20	0.955	14	—	0.02	0.001	0.021
Rothense, GE	PF	49	20	0.586	18	—	0.059	0.004	0.063
Rouviere, FR	GT	43	40	0.767	35	—	0.068	$2 \times 10^{-4}$	0.068
Råde, SE	GT	60	0	0.994	91	—	0.016	$4 \times 10^{-5}$	0.016
Sanga, EST	GT	58	24	0.1	23	—	0.209	0.042	0.25
Sanga, EST	PF	58	24	0.727	53	—	0.104	0.021	0.125
Simmertal, GER	GT	49	49	0.819	35	—	0.029	0.03	0.059
Siuntio, FI	PF	60	15	0.425	62	—	0.03	0.015	0.045
Theresienstein, GER	GT	50	16	1.012	16	—	0.059	0.003	0.062
Tresswell, UK	GT	53	18	0.493	35	0.300	0.02	0.003	0.024
Vlieland, NL	GT	53	15	0.153	134	0.769	0.084	0.005	0.089
Wolfsburg, GER	GT	52	27	0.651	100	—	0.019	0.008	0.027
Wolfsburg, GER	PF	52	27	0.313	290	—	0.03	$9 \times 10^{-4}$	0.031
Wytham Wood, UK	GT	51	46	0.719	216	0.565	0.07	0.002	0.072



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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.