

Population Dynamical Consequences of Climate Change for a Small Temperate Songbird

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Predicting the effects of an expected climatic change requires estimates and modeling of stochastic factors as well as density-dependent effects in the population dynamics. In a population of a small songbird, the dipper (*Cinclus cinclus*), environmental stochasticity and density dependence both influenced the population growth rate. About half of the environmental variance was explained by variation in mean winter temperature. Including these results in a stochastic model shows that an expected change in climate will strongly affect the dynamics of the population, leading to a nonlinear increase in the carrying capacity and in the expected mean population size.

A central question in ecology for decades has been how to quantify the relative importance of stochastic and density-dependent factors for fluctuations in population size (1). This question has received increased attention because of the need to predict the biological consequences of climate change (2). To answer this question, we must obtain separate estimates of different forms of stochasticity, such as demographic and environmental variances (3) and the strength of density dependence, and use these estimates to model the impact of a climate change on the population fluctuations. Several studies have predicted changes in species ranges, demographic rates, or average population sizes in response to climate change (4). However, missing are quantitative analyses that explicitly link climate change and population fluctuations in a mechanistic population model. Here we provide such a link and obtain predictions of markedly altered population dynamics for a songbird, mediated primarily through winter temperature.

Modeling the dynamics of populations in a stochastic environment involves estimating the separate effects of density regulation and stochastic factors. The variance of the change in population size can be split into the demographic and environmental variances (5). The demographic variance is caused by stochastic variation among individuals in their contribution to the next generation, whereas the environmental variance is due to stochasticity similarly affecting a certain group of individ-

uals at a certain time (3). Several studies (6) have now shown that knowledge of demographic as well as environmental stochasticity is important for understanding temporal fluctuations in population size. Thus, quantifying the effects and predicting the consequences of an expected climate change, which possibly involves changes in both the mean and the variance of several climatic variables, will require estimates of how these changes will affect the behavior of the population dynamic processes. The dipper (*Cinclus cinclus*), a 50- to 60-g passerine species widely distributed in aquatic habitats close to running water all over the Palearctic region (7), is suitable for studying those questions because at northern latitudes the amount of ice strongly affects which areas have available winter feeding habitats. Thus, this relation provides a possible link between population dynamics and climate.

We studied a population of dippers in southern Norway (8), where a large proportion of all individuals was color-ringed for individual recognition (9) over a 20-year period (1978–97). Large fluctuations in population size occurred during the study period (Fig. 1A), from a minimum of 27 pairs in 1982 to a maximum of 117 pairs in 1993. The

recruitment rate of the population, $R_t = \frac{X_{t+1}}{X_t}$,

where X_t is the size of the breeding population in year t , also showed large annual variation (Fig. 1B). The recruitment rate decreased with increasing population size ($r = -0.49, n = 18, P < 0.05$) (Fig. 1B). Accounting for annual variation in the number of immigrants M_{t+1} (10), no significant density-dependent decrease was found in the net re-

productive rate $NR_t = \frac{X_{t+1} - M_{t+1}}{X_t}$, ($r = -0.27, n = 18, P > 0.1$) (Fig. 1B). Thus, the

decrease in recruitment rate was mainly due to a reduction of the immigration rate $IR_t =$

$\frac{M_{t+1}}{X_t}$ with increasing population size ($r = -0.56, n = 18, P < 0.05$) (Fig. 1C). However, no significant density dependence in the absolute number of immigrating females was found ($r = 0.27, n = 18, P > 0.1$).

To estimate parameters, we modeled the dynamics of the population by assuming that the change in the logarithm of the net recruitment rate ($\Delta \ln NR_t$) was normally distributed

$$\Delta \ln NR_t = \ln \left(\frac{X_{t+1} - M_{t+1}}{X_t} \right) \sim N \left(r - \alpha X_t + \beta C_t, \sigma_e'^2 + \frac{\sigma_d^2}{X_t} \right) \quad (1)$$

where C_t is the climatic variable (11, 12), $\sigma_e'^2$ is the residual environmental variance not accounted for by the variation in C_t , σ_d^2 is the demographic variance estimated from individual-based data (13), α is the strength of density regulation, and β denotes the strength of dependency on the climatic variable. Observations of mean winter temperatures C_t were centered such that the expectation $E(C_t) = 0$ for the whole period with available climate data (38 years). It follows that the

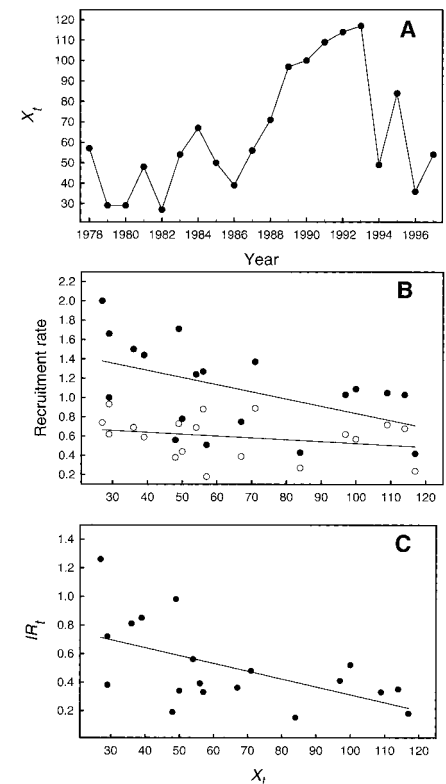


Fig. 1. (A) The annual variation in population size (X_t). (B) The recruitment rate R_t (solid circles) and the net recruitment rate NR_t (open circles) and (C) the immigration rate IR_t in relation to population size (X_t).

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environmental variance is about

$$\sigma_c^2 = \sigma_e'^2 + \text{var}(\beta C_t) = \sigma_e'^2 + \beta^2 \text{var}(C_t) \quad (2)$$

The number of immigrants was correlated with the winter temperature ($r = 0.62, n = 18, P = 0.003$) (Fig. 2A). To incorporate this in the model used for estimation and prediction, we assumed that M_t was Poisson-distributed with parameter λ_t , with each λ_t being independently lognormally distributed with expectation depending on mean winter temperature by letting each

$$\log(\lambda_t) \sim N(\mu_0 + \mu_1 C_t, \sigma_\lambda^2) \quad (3)$$

where σ_λ^2 is the variance in the log of the immigration rate, μ_0 is the mean log immigration rate at $C_t = 0$ and μ_1 measures the dependence of the immigration rate on temperature.

To facilitate modeling of the effects of a climatic change, we used mean winter (January to March) temperature (°C) and total winter precipitation as C_t in Eqs. 1 and 3. These variables were chosen because they

are commonly used when developing climatic scenarios (2). We estimated the posterior distribution (quantifying degree of belief in alternative parameter values conditional on the data) for parameters in the model (Eqs. 1 and 3) by Markov Chain Monte Carlo methods (14). These analyses showed that variation in the logarithm of the net reproductive rate was influenced by population density and by climate (Table 1). Low recruitment occurred in years with high population densities. Furthermore, fewer individuals for a given population size were recruited after cold winters (Fig. 2B). This may be because mean winter temperature was closely correlated with the annual variation in the number of days with ice cover in the study area ($r = -0.83, n = 38, P < 0.001$). However, the recruitment rate was not significantly correlated with winter precipitation ($r = 0.13, n = 12, P > 0.1$). On the basis of the annual variation in mean winter temperature C_t over the past 40 years (SD = 2.09°C) and the estimate of the parameters substituted into Eq. 2, we find that about half of the total environmental variance was explained by variation in winter temperature (Table 1). The slope (μ_1) in the regression of $\log(\lambda_t)$ on C_t was of similar magnitude but somewhat smaller than the slope (β) in the regression of the log net recruitment rate on C_t (Table 1), indicating that cold winters have similar effects on the survival of both dispersing and nondispersing individuals.

The deterministic carrying capacity K was found numerically (for each realization from the posterior) by setting X_t and X_{t+1} equal to K and M_t equal to its expectation and then solving for K .

In the Northern Hemisphere, climatic conditions during winter are often determined by annual variation in large-scale fluctuations in atmospheric mass between the subtropic and the subpolar North Atlantic regions, the North Atlantic Oscillation (NAO). The NAO index is an integrated

measure that influences a large number of climatic variables that affect the winter weather over large areas of the Northern Hemisphere (15). For instance, a high positive NAO index is, in general, associated with relatively warm winters with much precipitation in northern Atlantic coastal Europe (16). Variation in the NAO index is closely correlated with global fluctuations in temperature (17). Because the net recruitment rate is positively correlated with the NAO index (Fig. 2C), such large-scale climatic changes are likely to affect the dynamics of the local dipper population.

The Intergovernmental Panel on Climate Change (IPCC) has developed different scenarios of future greenhouse gas and aerosol precursor emissions on the basis of socioeconomic assumptions for the period 1990–2100 (2). These predicted emissions were then used to project atmospheric concentrations of greenhouse gases and aerosols and their effects on natural radiation processes. When these effects are entered into climatic models, some scenarios suggest an increase in mean winter temperature of 2° to 3°C in the region in which our study population is located (2), although the quantitative effects of the anthropogenic influences on the atmosphere must be considered uncertain (18). To examine the effects of the fluctuations in climate and a change in long-term mean on the dipper population dynamic, we model the climatic process C_t as a first-order autoregressive process (19)

$$C_{t+1} - c \sim N[a(C_t - c), \sigma_c^2] \quad (4)$$

where c and σ_c^2 are the mean and variance, respectively, and a determines the return time in the process. According to the scenarios from IPCC for the region (2), we model the change in the long-term mean winter temperature by setting $c = 2.5$ in Eq. 4. We find that an increase in mean winter temperature is likely to strongly affect the population dynamics of the dipper in the study area. The expected carrying capacity (K) increased by

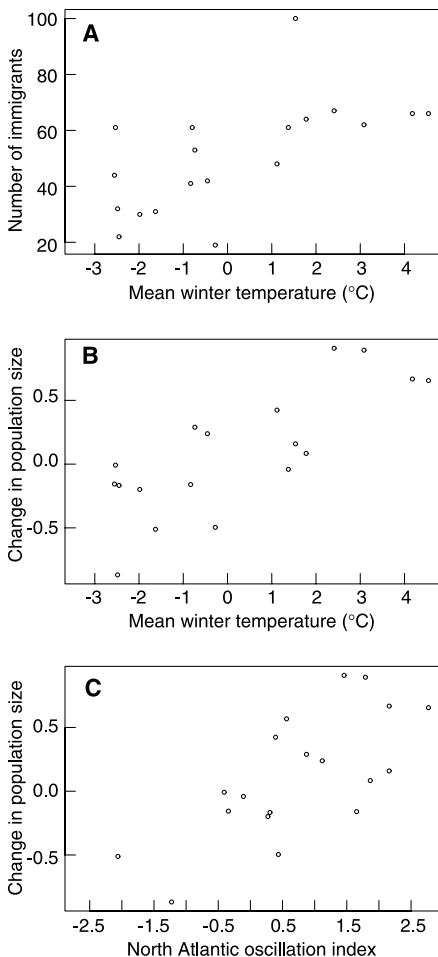


Fig. 2. The number of immigrants plotted against mean winter temperature (A) and the relative change in population size in relation to mean winter temperatures that were centered (B) and the NAO index (C).

Table 1. The estimates of the parameters describing the population dynamics ($\log NR_t$, see Eq. 1) of the dipper *Cinclus cinclus* in southern Norway and posteriori probabilities (degree of belief conditional on the observed data) of some hypotheses.

Parameter	Estimate (mean ± SD)	Posteriori probabilities
Population growth rate (r)	-0.086 ± 0.186	$P(r > 0) = 0.31$
Density regulation (α)	0.0042 ± 0.0014	$P(\alpha > 0) = 0.998$
Effects of winter temperature (β)	0.15 ± 0.03	$P(\beta > 0) = 0.9999$
Total environmental variance (σ_e^2)	0.21 ± 0.06	
Environmental variance from winter temperature ($\sigma_{e_w}^2$)	0.10 ± 0.05	
Residual environmental variance ($\sigma_e'^2$)	0.11 ± 0.04	
Demographic variance (σ_d^2)	0.268 ± 0.018	
Expected number of immigrants at $c = 0$	50.4 ± 4.4	
at $c = 2.5$	67.7 ± 7.5	
Slope in Poisson regression for M_t (μ_1)	0.11 ± 0.03	$P(\mu_1 > 0) = 0.999$

58% (Fig. 3A), from $K = 115$ (SD = 10) for $c = 0$ to $K = 182$ (SD = 22) for $c = 2.5$. Similarly, such an increase in mean temperature increased the expectation of the stationary distribution of the population size X_t from 117 to 184 (Fig. 3B). When we run the model, assuming no relation between climate and immigration rate, the effect of a change from $c = 0$ to $c = 2.5$ on K was still large [$K = 167$ (SD = 20) for $c = 2.5$]. Thus, the major effect of a change in winter climate on the dipper population will occur through an influence on the local dynamics.

To quantitatively examine how the magnitude of a change in mean winter temperature affected the population dynamics of the dipper, we computed the change in carrying capacity K (evaluated at the estimated mean of all model parameters) over a range of -2.5° to 2.5°C for the mean value of c in Eq. 4. Our analysis suggests a nonlinear relation between the carrying capacity K and change in mean temperature c (Fig. 3C). Thus, for $c = -2.5$, K will decrease to about 45 pairs, whereas a similar increase in the temperature will increase K considerably more, to about 178 pairs.

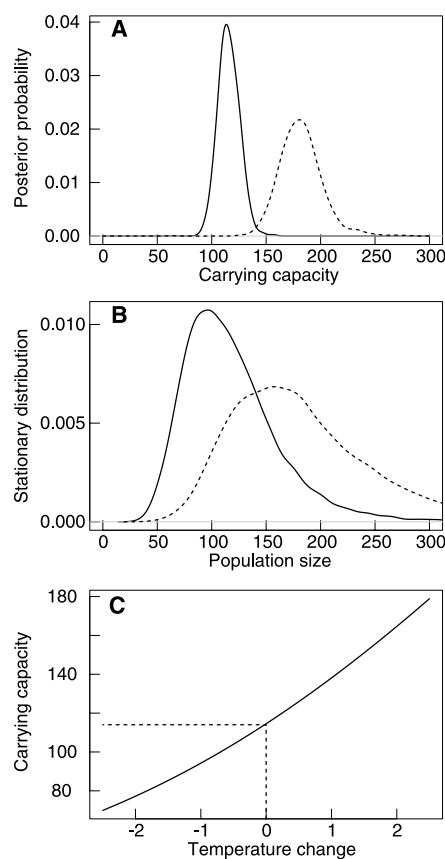


Fig. 3. (A) The posterior distribution of the deterministic carrying capacity (K) and (B) the stationary distribution of the population size (X_t) before (solid lines) and after (dashed lines) an increase in winter temperature of 2.5°C . (C) The change in the carrying capacity (K) as a function of a change in mean winter temperature ($^\circ\text{C}$).

Several studies have documented effects of changes in climate on several demographic characteristics of birds and mammals. For instance, many temperate bird species lay eggs earlier in the year, probably because of warmer springs (20, 21). Similarly, the spawning dates of amphibians such as *Rana* spp. were positively correlated with the NAO index (20). Our study complements those results by showing that climatic changes may also strongly affect the dynamical characteristics of a population (Figs. 2 and 3). These large effects on the population dynamics of relative small changes in climate (Fig. 3) were due to an effect on the local dynamics as well as higher immigration rate in mild winters. These interactions between processes operating at different geographical scales suggest that climate changes may have major consequences for the pattern of fluctuations in bird populations over space and time (22).

References and Notes

1. P. W. Turchin in *Population Dynamics: New Approaches and Synthesis*, N. Cappuccino and P. W. Price, Eds. (Academic Press, San Diego, 1995), pp. 19–40.
2. Intergovernmental Panel on Climate Change, *Climate Change 1995. The Science of Climate Change* (Cambridge University Press, Cambridge, 1996).
3. S. Engen, Ø. Bakke, A. Islam, *Biometrics* **54**, 840 (1998).
4. A. E. Dunham, in *Biotic Interactions and Global Change*, P. M. Kareiva, J. G. Kingsolver, R. B. Huey, Eds. (Sinauer Associates, Sunderland, MA, 1993), pp. 95–119; A. R. Ives and G. Gilchrist, in *Biotic Interactions and Global Change*, P. M. Kareiva, J. G. Kingsolver, R. B. Huey, Eds. (Sinauer Associates, Sunderland, MA, 1993), pp. 120–146; C. Solbreck, in *Population Dynamics: New Approaches and Synthesis*, N. Cappuccino and P. W. Price, Eds. (Academic Press, San Diego, 1995), pp. 279–301; B.-E. Sæther, *Trends Ecol. Evol.* **12**, 143 (1997); I. Newton, *Population Limitation in Birds* (Academic Press, San Diego, 1998); E. P. Post and N. C. Stenseth, *Ecology* **80**, 1322 (1999).
5. M. S. Bartlett, *Stochastic Population Models* (Methuen, London, 1960); K. B. Athreya and S. Karlin, *Ann. Math. Stat.* **42**, 1499 (1971); R. M. May, *Am. Nat.* **107**, 621 (1973); R. Lande, *Oikos* **83**, 353 (1998).
6. S. Engen and B.-E. Sæther, *Oikos* **83**, 345 (1998).
7. S. J. Ormerod and S. J. Tyler, *The Dippers* (Poysner, London, 1994).
8. The study population was located along the lower parts of the river Lygna in the county of Vest-Agder in southern Norway ($58^\circ15'N$, $7^\circ15'E$). The study area covers about 60 km from the mouth of the river to the inland.
9. The population size was estimated by searching the banks of the river for occupied nest sites on almost every day of the breeding season. A large fraction of the breeding adults were individually color-ringed. In addition, a large proportion of the fledglings were ringed. Because of the large proportion of ringed individuals and the conspicuous behavior of the adults, the bias in population estimate is low and the recapture rates are high. Thus, during the 1988–96 period, 94% (SD = 4) of all known breeding females on average were ringed by the end of the breeding season.
10. The number of immigrants M_t was recorded as the number of previously unbanded (non-ringed) individuals in the population.
11. Data on the number of days with ice cover were

collected by local representatives of the Norwegian Water Resources and Electricity Directorate.

12. Climate data (monthly means of temperature and precipitation) were collected at the weather station Kongsno during the period 1964–98 by the Norwegian Institute of Meteorology. The NAO index was obtained from the Climate Analysis Section of the University Corporation for Atmospheric Research (Boulder, CO); additional information is available at <http://www.cgd.ucar.edu/cas/climind>.
13. To model the separate effects of density dependence and stochastic factors, we estimated (3) the demographic variance in year T , $\sigma_{d,T}^2 = E \frac{1}{n-1} \sum (R_i - \bar{R})^2$, where R_i is the contribution of an individual i to the next generation, \bar{R} is the mean contribution of the individuals, and n is the number of recorded contributions in year T . The total contribution of a female in year T (R_t) is the number of female offspring born that year that is recorded the following or a later year breeding in the population plus 1 if the female survives to the next year. In contrast to the great tit *Parus major* (23), $\sigma_{d,T}^2$ was not related to population size ($r = 0.02$, $n = 20$, $P > 0.1$). Thus, we estimated the demographic variance as the weighted mean across years (23). On the basis of observation of population sizes X_t (Fig. 1A), number of migrants M_t , and variation in the climate C_t , combined with estimates of the demographic variance ($\sigma_{d,T}^2$) from individually based data (3, 23), the posterior distribution for all unknown parameters was computed numerically with the BUGS package [D. J. Spiegelhalter, A. Thomas, N. Best, W. Gilks, *BUGS 5.0 Bayesian Inference Using Gibbs Sampling. Version 5.0* (MRC Biostatistical Unit, Cambridge, UK, 1996)]. This is a general software package carrying out Bayesian inference with Markov Chain Monte Carlo methods (14, 24). A model similar to that of Tufto *et al.* (25) was used, but with noninformative or diffuse scale and location priors assigned directly to the demographic parameters and with an additional climate term, as in Eq. 1, incorporating the effect of winter temperature. For other details, see (25).
14. W. Gilks, S. Richardson, D. Spiegelhalter, Eds., in *Markov Chain Monte Carlo in Practice* (Chapman and Hall, London, 1996), pp. 1–20.
15. P. J. Lamb and R. A. Pepler, *Bull. Am. Meteorol. Soc.* **68**, 1218 (1987); J. W. Hurrell, *Science* **269**, 676 (1995).
16. J. C. Rogers, *Mon. Weather Rev.* **112**, 1999 (1984); J. W. Hurrell and H. Van Loon, *Clim. Change* **36**, 301 (1997).
17. M. E. Schlesinger and N. Ramankutty, *Nature* **367**, 723 (1994).
18. S. Corti, F. Molteni, T. N. Palmer, *Nature* **398**, 799 (1999); D. T. Shindell, R. L. Miller, G. A. Schmidt, L. Pandolfo, *Nature* **399**, 452 (1999).
19. C. Chatfield, *The Analysis of Time Series: An Introduction* (Chapman and Hall, London, ed. 3, 1996).
20. M. C. Forchhammer, E. C. Post, N. C. Stenseth, *Nature* **391**, 29 (1998).
21. H. Q. P. Crick, C. Dudley, D. E. Glue, D. L. Thomson, *Nature* **388**, 526 (1997); R. H. McCleery and C. M. Perrins, *Nature* **391**, 30 (1998).
22. E. Ranta, V. Kaitala, J. Lindström, in *Modeling Spatio-temporal Dynamics in Ecology*, J. Bascompte, R. V. Solé, Eds. (Springer-Verlag, Berlin, 1998), pp. 47–62; O. N. Bjørnstad, R. A. Ims, X. Lambin, *Trends Ecol. Evol.* **14**, 427 (1999); R. Lande, S. Engen, B.-E. Sæther, *Am. Nat.* **154**, 271 (1999).
23. B.-E. Sæther, S. Engen, A. Islam, R. McCleery, C. Perrins, *Am. Nat.* **151**, 441 (1998).
24. J. O. Berger, *Statistical Decision Theory and Bayesian Analysis* (Springer-Verlag, New York, 1985).
25. J. Tufto *et al.*, *Oikos* **88**, 273 (2000).
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