

# Generation time and temporal scaling of bird population dynamics

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Theoretical studies have shown that variation in density regulation strongly influences population dynamics<sup>1</sup>, yet our understanding of factors influencing the strength of density dependence in natural populations still is limited<sup>2</sup>. Consequently, few general hypotheses have been advanced to explain the large differences between species in the magnitude of population fluctuations<sup>3–6</sup>. One reason for this is that the detection of density regulation in population time series is complicated by time lags induced by the life history of species<sup>7,8</sup> that make it difficult to separate the relative contributions of intrinsic and extrinsic factors to the population dynamics. Here we use population time series for 23 bird species to estimate parameters of a stochastic density-dependent age-structured model. We show that both the strength of total density dependence in the life history and the magnitude of environmental stochasticity, including transient fluctuations in age structure, increase with generation time. These results indicate that the relationships between demographic and life-history traits in birds<sup>9,10</sup> translate into distinct population dynamical patterns that are apparent only on a scale of generations.

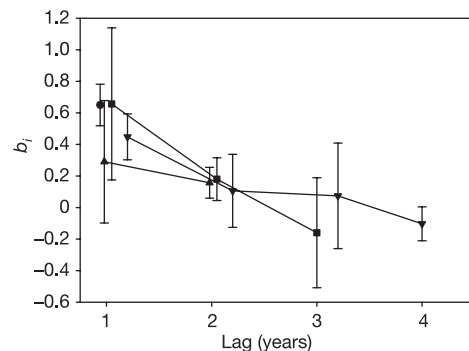
Analyses of density dependence in natural populations are usually based on autoregression of population time series in which regression coefficients are assumed to represent both direct and delayed density dependence<sup>11</sup>. This approach neglects the basic fact that the life history can produce time lags in the population dynamics<sup>8</sup> that will wrongly be interpreted as delayed density dependence<sup>12,13</sup>. In the Soay sheep (*Ovis aries*) lagged responses in life history were shown to be important for explaining temporal variation in population fluctuations<sup>14</sup>. In a simple deterministic model with no age structure, de Kroon *et al.*<sup>15</sup> defined the strength of density dependence  $\gamma$  as the negative elasticity of the population growth rate  $\lambda$  with respect to changes in population size  $N$ , evaluated at the carrying capacity  $K$ ,  $\gamma = -(\partial \ln \lambda / \partial \ln N)_K$ . Lande *et al.*<sup>16</sup> extended this approach to show that in a generalized life-history model structured by age and dependent on density, total density dependence in the life history,  $D$ , should be defined as the negative elasticity of the population growth rate per generation,  $\lambda^T$ , with respect to the change in the size of the adult population when fluctuating around the carrying capacity, so that

$$D = - \left( T \frac{\partial \ln \lambda}{\partial \ln N} \right)_K \quad (1)$$

where  $T$  is the generation time. Thus, the rate of return to equilibrium then becomes  $\gamma = D/T$ . This definition facilitates a comparison of the strength of density dependence between species with different life-history characteristics.

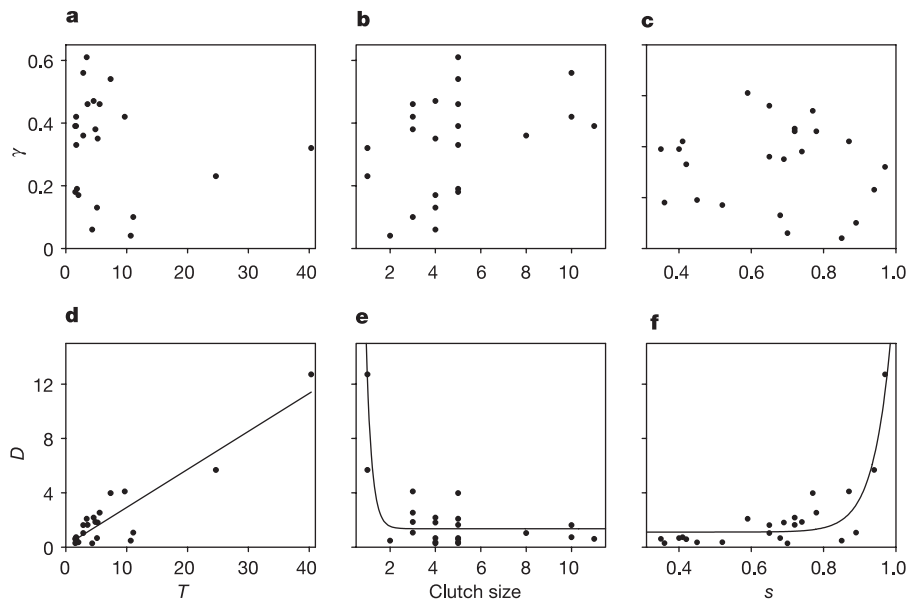
Here we use the general definition of density dependence in equation (1) to model the stochastic density-dependent population dynamics of different bird species. For simplicity we assume that the expected adult annual survival and fecundity rates are independent of age. Furthermore, it is assumed that density dependence is exerted by the adult fraction of the population on any combination of juvenile and adult vital rates, which encompasses general features of the dynamics of many bird populations<sup>17</sup>. Finally, deviations of the adult population at time  $t$  from equilibrium,  $x(t) = N(t) - K$ , are expected to be small or moderate. In our data set, the coefficient of variation in the time series is generally less than 30%, which has been shown<sup>5,18</sup> to fit our theoretical approach well. On the basis of these assumptions, we obtain<sup>16</sup> a linearized autoregressive model with time delays from 1 to  $\alpha$  years, namely

$$x(t) = \sum_{i=1}^{\alpha} b_i x(t-i) + \omega(t) \quad (2)$$



**Figure 1 | Autoregression coefficients  $b_i$  for different lags in the population dynamics in relation to variation in age at maturity.** Circles represent species that mature at 1 year, triangles age at maturity at 2 year, squares age at maturity at 3 years and reversed triangles species that mature at 4 years or older. Results are means  $\pm$  s.d.

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**Figure 2 | Strength of density dependence in relation to life history variation in birds.** The strength of density dependence in annual population

fluctuations,  $\gamma$  (a–c), and the total life history,  $D$  (d–f), in relation to generation time  $T$  (a, d), clutch size (b, e) and adult survival rate  $s$  (c, f).

where  $\omega(t)$  is a noise term with a mean of zero and variance  $\sigma_\omega^2$ , describing environmental stochasticity, including transient fluctuations in age structure and autocorrelations due to long-term fluctuations in the biotic or abiotic environment.

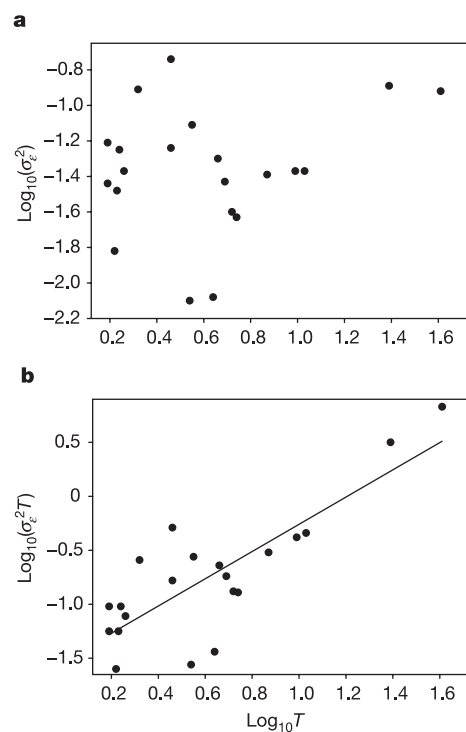
In our data set the mean of the autoregression coefficients  $b_i$  for species with age at maturity  $\alpha \geq 2$  decreased with time lag (Fig. 1), indicating that the effects of the previous years' population sizes on current population size decreased with time. However, these autoregression coefficients  $b_i$  do not directly reveal the strength of delayed density dependence because they depend on both life-history parameters and density dependence in the vital rates<sup>5,18</sup>. For instance, in a species with  $\alpha > 1$ , with no density dependence in subadult or adult survival rates,  $b_1$  equals the adult annual survival rate  $s$ . Similarly, in a species that matures at 1 year, if  $b_1 = 0$  the population autocorrelations for all time lags will be zero, corresponding to a white-noise process for the population size,  $N(t)$ , that indicates strong density dependence. However, on the basis of the general definition of density dependence (equation (1)), there is a relationship<sup>16</sup> between total density dependence in the life history and the autoregression coefficients:

$$(1 - s)D = 1 - \sum_{i=1}^{\alpha} b_i \quad (3)$$

Using this theoretical framework, we find a large interspecific variation in the density dependence in bird population dynamics. The strength of density dependence varied from  $\gamma = 0.04$  in the South Polar skua (*Catharacta macrorhynchos*) to  $\gamma = 0.61$  in the Eurasian sparrowhawk (*Accipiter nisus*), resulting in differences in return times to equilibrium from about 1.7 to 22.5 years. These density-dependent effects were independent of generation time (Fig. 2a; correlation coefficient =  $-0.15$ ,  $P > 0.5$ ) as well as clutch size (Fig. 2b; correlation coefficient =  $0.40$ ,  $P = 0.06$ ) and adult survival rate (Fig. 2c; correlation coefficient =  $-0.09$ ,  $P > 0.69$ ). As a consequence, the stationary variance in the time series  $\sigma_N^2$  was also independent of life history (the absolute value of the correlation coefficients between  $\sigma_N^2$  and  $T$ , clutch size,  $s$  and  $\alpha$  were all less than 0.10;  $P > 0.7$ ).

Our analyses reveal that the magnitude of annual fluctuations in size of age-structured bird populations cannot be predicted from estimates of generation time or from a knowledge of life-history traits such as clutch size and adult survival rate. However, previous

comparative analyses have shown that many avian demographic traits such as clutch size and age at maturity scale closely with adult life span<sup>9,19,20</sup>. As expected from this, we find that several features of population dynamics measured on a time scale of generations can be predicted from life-history characteristics. The strength of total density dependence in the life history,  $D$ , increased with generation time  $T$  (Fig. 2d; correlation coefficient =  $0.92$ ,



**Figure 3 | Residual variation in avian population fluctuations after accounting for density dependence in relation to generation time  $T$ .** a, The residual variance in a first-order process,  $\sigma_\epsilon^2$ , describing environmental stochasticity and transient fluctuations in age structure as well as long-term autocorrelations in the environment. b, The total residual variance  $\sigma_\epsilon^2 T$  over a period of one generation.

$n = 23$ ,  $P < 0.001$ ) and adult survival rate (Fig. 2f; correlation coefficient = 0.62,  $n = 23$ ,  $P = 0.002$ ) but decreased with clutch size (Fig. 2e; correlation coefficient =  $-0.45$ ,  $n = 23$ ,  $P = 0.03$ ). Although this relationship was strongly influenced by the two long-lived seabird species southern fulmar (*Fulmarus glacialisoides*) and lesser snow-petrel (*Pagodroma nivea*), a significant relationship was still present after excluding those two species from the analyses involving  $T$  (correlation coefficient = 0.47,  $n = 21$ ,  $P = 0.034$ ) and adult survival rate (correlation coefficient = 0.57,  $n = 21$ ,  $P = 0.007$ ), whereas no significant effect was present for clutch size (correlation coefficient =  $-0.20$ ,  $n = 21$ ,  $P > 0.1$ ). An increase in strength of density dependence with longevity when the censuses were taken at intervals of one generation has also been previously recorded in British birds<sup>21</sup>. This implies that the effect on the population growth rate per generation of a change in population size was larger for long-lived species than for short-lived species. Consequently, the rate of return to equilibrium measured in generations decreases with generation time  $T$  (correlation coefficient of  $\log_{10}$ -transformed values =  $-0.73$ ,  $P < 0.001$ ,  $n = 23$ ).

To compare the residual variation in the population process we must account for interspecific variation in age at maturity that will cause differences in the lag-structure of the population dynamics<sup>16</sup>. We first estimate (see Methods) the variance in the stationary distribution of the population sizes  $\sigma_N^2$  in our model (equation (2)) and then calculate the variance in the noise of a first-order process with a single time lag of one year,  $\sigma_\epsilon^2$ , that will give the same stationary variance in population size as in the full model. The variance of this white noise process for species with age at maturity larger than 1 year should be approximately equal to the environmental variance (R.L., S.E., B.-E.S., and T. N. Coulson, unpublished observations). In our data set  $\log_{10}\sigma_\epsilon^2$  was independent of  $\log_{10} T$  (Fig. 3a, correlation coefficient = 0.24,  $P > 0.3$ ,  $n = 23$ ). In contrast, there was a highly significant linear increase in  $\log_{10}(\sigma_\epsilon^2 T)$  (Fig. 3b; correlation coefficient = 0.82,  $P < 0.001$ ,  $n = 21$ ; correlation coefficient = 0.56,  $n = 19$ ,  $P = 0.013$  after omitting the southern fulmar and lesser snow-petrel). Furthermore, the environmental variance for this process per generation ( $\sigma_\epsilon^2 T$ ) was closely related to life-history characters; that is,  $\sigma_\epsilon^2 T$  decreased with clutch size (correlation coefficient of  $\log_{10}$ -transformed values =  $-0.71$ ,  $P < 0.001$ ,  $n = 21$ ; no longer significant after removing the two extreme values, correlation coefficient =  $-0.25$ ,  $n = 19$ ,  $P > 0.3$ ) but increased with adult survival rate (correlation coefficient of  $\log_{10}$ -transformed values = 0.70,  $P < 0.001$ ,  $n = 21$ ; correlation coefficient = 0.63,  $n = 19$ ,  $P = 0.004$  after omitting the two outliers). This indicates that environmental stochasticity per generation might be greater for long-lived species than for species with short life expectancies. In contrast, interspecific differences in avian demographic stochasticity per generation are independent of life-history variation<sup>22</sup>.

Comparative studies have shown that density dependence strongly influences population dynamics, and especially that of small passerine birds<sup>17</sup>. Increasing evidence suggests that density dependence also occurs frequently in long-lived species. For instance, in long-lived seabirds competition for breeding space or food can cause density dependence in their population dynamics<sup>23</sup>. Similarly, environmental fluctuations strongly influence variation in population size<sup>24</sup> and age structure<sup>25,26</sup> of many long-lived species and often generate lagged effects in the population dynamics<sup>27</sup>. Although the effects of density dependence and environmental fluctuations may be small in long-lived species on a yearly basis<sup>19</sup>, their accumulated influence on the population growth rate over one generation may still be large. Despite large differences between species in sensitivity of population growth rate per generation to changes in population density and environmental effects (Figs 2d and 3b), the lack of trend in Fig. 3a indicates that life histories might have evolved to produce comparable environmental variance in both short-lived and long-lived

species, with similar impacts on their rates of population growth in the long run<sup>5</sup>.

Our results indicate that understanding population dynamical patterns in birds might require accounting for generation time. Because many bird species are long-lived it will be necessary for the progress of basic ecology to secure continuity of long-term demographical studies. For population viability analyses of rare or endangered species, in which it is often not feasible to obtain detailed demographic data, the development of empirical scaling relationships between stochastic population parameters such as demographic and environmental variances and generation time may provide useful information for extinction risk assessment as well as conservation and restoration planning.

## METHODS

**Data.** This study is based on 23 time series longer than 15 years. Estimates of population parameters based on time series analyses are strongly influenced by the precision in the population estimates<sup>28</sup>. We therefore included only studies in which uncertainties in population estimates are negligible compared with the environmental variance; that is, studies based on total counts of nests or colour-ringed birds<sup>29</sup>. The average population size  $\bar{N}$  should be much larger than  $\sigma_d^2/\sigma_\epsilon^2$  to avoid the influence of demographic stochasticity<sup>5</sup>, where  $\sigma_d^2$  is the environmental variance. No estimates of the demographic variance  $\sigma_d^2$  were available for many of the species. Because demographic stochasticity has the largest influence on the population dynamics of small passerines with estimated values of  $\sigma_d^2$  about 0.50 (ref. 22), we included only time series of passerines with mean values of more than 50 individuals.

Demographic data were extracted from studies of individual species (see Supplementary Information). Age at maturity  $\alpha$  refers to the age at which regular breeding of females first occurred. Generation time  $T$  was calculated<sup>5</sup> as  $T = \alpha + [s/(1-s)]$ , where  $s$  is the expected adult survival rate. Survival estimates were based either on capture–recapture analysis or calculated as the return rate of individually known adults from one breeding season to another.

**Estimation of parameters.** As described in ref. 16, the maximum-likelihood estimates of the autoregression coefficients  $b_i$  in equation (2) are found by inverting the Yule–Walker equations<sup>30</sup> for the time series. These estimators are biased because population size at a given time enters the regression as both a dependent variable and an independent variable<sup>13</sup>. This bias can be estimated and corrected by using computer simulations<sup>16</sup>. Those simulations also can be used for significance testing and calculation of confidence intervals of the estimates<sup>16</sup>.

**Calculation of variance in the noise.** For a stationary time series such as equation (2) the autocovariances  $C(\tau) = \text{cov}(N_t, N_{t+\tau})$ ,  $\tau = 0, 1, \dots$ , are determined by the Yule–Walker equations<sup>30</sup>

$$C(j) - \sum_{i=1}^{\alpha} b_i C(j-i) = \begin{cases} \sigma_\epsilon^2 & \text{for } j=0 \\ 0 & \text{for } j>0 \end{cases}$$

where the variance in the noise  $\sigma_\epsilon^2$  is estimated by maximum likelihood<sup>30</sup> and  $C(0) = \sigma_N^2$ . Using the fact that  $C(\tau) = C(-\tau)$ , this is a set of linear equations that can be solved with respect to the variance in the stationary distribution  $C(0)$  as well as  $C(1)$ ,  $C(2)$ , ... We calculate the residual variance of a first-order process with the same stationary variance as in equation (2), namely  $\sigma_\epsilon^2 = C(0)(1 - b_1^2)$ , provided that for this first-order process  $|b_1| < 1$ .

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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