

# Estimating Density Dependence from Population Time Series Using Demographic Theory and Life-History Data

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**ABSTRACT:** For populations with a density-dependent life history reproducing at discrete annual intervals, we analyze small or moderate fluctuations in population size around a stable equilibrium, which is applicable to many vertebrate populations. Using a life history having age at maturity  $\alpha$ , with stochasticity and density dependence in adult recruitment and mortality, we derive a linearized autoregressive equation with time lags from 1 to  $\alpha$  yr. Contrary to current interpretations, the coefficients corresponding to different time lags in the autoregressive dynamics are not simply measures of delayed density dependence but also depend on life-history parameters. The theory indicates that the total density dependence in a life history,  $D$ , should be defined as the negative elasticity of population growth rate per generation with respect to change in population size,  $D = -\partial \ln \lambda / \partial \ln N$ , where  $\lambda$  is the asymptotic multiplicative growth rate per year,  $T$  is the generation time, and  $N$  is adult population size. The total density dependence in the life history,  $D$ , can be estimated from the sum of the autoregression coefficients. We estimate  $D$  in populations of seven vertebrate species for which life-history studies and unusually long time series of complete population

censuses are available. Estimates of  $D$  were statistically significant and large, on the order of 1 or higher, indicating strong density dependence in five of the seven species. We also show that life history can explain the qualitative features of population autocorrelation functions and power spectra and observations of increasing empirical variance in population size with increasing length of time series.

**Keywords:** age structure, autocorrelation, autoregression, density dependence, stage structure, time series.

Density dependence limits populations at high density by decreasing population growth rate and its components of age- or stage-specific survival and reproduction. The history of ecological studies of density dependence progressed from debate about its occurrence (Andrewartha and Birch 1954) to its detection and measurement in experimental and observational studies (Harrison and Cappuccino 1995) and, by inference, from population time series (Bulmer 1975; Pollard et al. 1987; Hanski et al. 1993; Dennis and Taper 1994; reviewed by Turchin 1995). Ubiquitous stochastic fluctuations in population size tend to obscure simple deterministic patterns of density dependence in population dynamics. Detection and estimation of density dependence is further complicated because it usually operates with a time lag due to intrinsic factors in individual development and life history (May 1973, 1981; MacDonald 1978; Renshaw 1991; Nisbet 1997; Jensen 1999; Claessen et al. 2000) and extrinsic factors in an autocorrelated environment (Williams and Liebholt 1995; Berryman and Turchin 1997), including ecological interactions among species (Turchin 1990, 1995; Royama 1992; Turchin and Taylor 1992; Kaitala et al. 1997; Ripa et al. 1998; Hansen et al. 1999). The relative importance of intrinsic and extrinsic factors in contributing to time lags in population dynamics may depend on the life history itself. For short-lived species with high population growth rates, such as some insects, ecological interactions may best explain time lags longer than the generation time of the species (Turchin 1990, 1995; Royama 1992). For long-lived species with low population growth rates, such as large vertebrates, most time lags may be caused by life history (Jensen 1999; Coulson et al. 2001; Thompson and Ollason 2001). A major

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impediment to understanding density dependence has been the lack of a general quantitative definition that would allow comparisons among species with different life histories and forms of density dependence (discussed by Murdoch 1994).

It is widely appreciated that life history can produce time lags in population dynamics (see references above). The dynamics of age- or stage-structured populations often can equally well be described by univariate models with multiple time lags and by multivariate models without time lags (e.g., cf. Lotka 1924 and Leslie 1945; reviewed for stage-structured models in Nisbet 1997). However, this basic fact has not previously been incorporated into general methods for detecting and estimating density dependence from population time series (Bulmer 1975; Pollard et al. 1987; Turchin 1990, 1995; Royama 1992; Turchin and Taylor 1992; Hanski et al. 1993; Dennis and Taper 1994; Zeng et al. 1998). Jensen (1999) demonstrated by simulation that stochastic fluctuations in the life history of walleye fish could produce the pattern of delayed density dependence detected by autoregression analysis. Coulson et al. (2001) and Thompson and Ollason (2001) showed that time lags in life history are important in explaining temporal patterns of population fluctuations in Soay sheep and in northern fulmars.

Here, we analyze density-dependent age- or stage-structured life histories to derive linearized autoregressive dynamics of small or moderate population fluctuations around a stable equilibrium. We apply this theory to estimate density dependence in observed time series of vertebrate populations reproducing at discrete annual intervals. Vertebrate species with mean adult body mass  $>1$  kg usually have  $r_{\max} \leq 0.1/\text{yr}$  (Charnov 1993), and even for highly fecund species, such as many fish, insects, and plants, maximum population growth rates are limited by high density-independent mortality (Myers et al. 1999). Such species tend to show damped fluctuations around a stable equilibrium (May 1981) and often have a small or moderate coefficient of variation in population size (Pimm and Redfearn 1988; Pimm 1991).

Using a life history having age at maturity  $\alpha$ , with stochasticity and density dependence in adult recruitment and mortality, we derive a linearized autoregressive equation with time lags from 1 to  $\alpha$  yr. Contrary to current interpretations (Turchin 1990, 1995; Royama 1992; Turchin and Taylor 1992; Zeng et al. 1998; and many other authors), the coefficients corresponding to different time lags in the autoregressive dynamics are not simply measures of delayed density dependence but also depend on life-history parameters. The theory indicates that the total density dependence in a life history,  $D$ , should generally be defined as the negative elasticity of population growth rate per generation with respect to change in population size,

$D = -\partial \ln \lambda / \partial \ln N$ , where  $\lambda$  is the asymptotic multiplicative growth rate per year,  $T$  is the generation time, and  $N$  is adult population size. We demonstrate that total density dependence in the life history,  $D$ , can be estimated from the sum of the autoregression coefficients. We apply this theory to estimate  $D$  in populations of seven vertebrate species (six birds and one mammal) for which life-history studies and unusually long time series of complete population censuses are available. Estimates of  $D$  were statistically significant and large, on the order of 1 or higher, indicating strong density dependence in five of the seven species. We also show that life history can explain the qualitative features of population autocorrelation functions and power spectra, and observations of increasing empirical variance in population size with increasing length of time series, which are often used to describe temporal patterns of population fluctuations.

### Quantitative Definition of Density Dependence

Consider first a simple deterministic population model with no age structure, where individuals that reach the age of 1 yr, reproduce and then die, as for univoltine insects or annual plants with no seed bank. With population size in year  $t$  denoted as  $N(t)$ , the dynamics are given by  $N(t) = \lambda[N(t-1)]N(t-1)$  where  $\lambda[N(t-1)]$  is the density-dependent finite rate of population increase, the probability of survival to maturity times the mean fecundity. We assume that fluctuations in the population size are sufficiently small for a linearized model to have good accuracy. For populations without age structure, a linearized model gives results that are accurate within 10% if the coefficient of variation is as high as 30% (Lande et al. 1999). Let the equilibrium population size or carrying capacity be  $K$  and denote the deviation from equilibrium as  $x(t) = N(t) - K$ . Taylor expansion of  $\lambda$  produces the linearized dynamics,

$$x(t) = (1 - \gamma)x(t-1), \quad (1a)$$

where  $\gamma = -(\partial \ln \lambda / \partial \ln N)_K$  gives the rate of return toward the equilibrium. In the simple model with no age structure (and a generation time of 1 yr),  $\gamma$  can be used to define the strength of density dependence as the negative elasticity (de Kroon et al. 1986; Caswell 2001, p. 226) of population growth rate with respect to change in population density at equilibrium.

Density dependence in age- or stage-structured populations can be defined by interpreting  $\lambda$  in equation (1a) as the asymptotic multiplicative growth rate of the population per year. Analysis of a general age-structured life-history model with density dependence in age-specific fecundity and first year survival (see below) indicates that

the total density dependence in the life history,  $D$ , should be defined as the negative elasticity of population growth rate per generation,  $\lambda^T$ , with respect to change in population density, evaluated at equilibrium. The generation time,  $T$ , is the mean age of mothers of newborn individuals when the population is in a stable age distribution (Caswell 2001, p. 128). Using  $\ln \lambda^T = T \ln \lambda$  and that at equilibrium  $\lambda = 1$  or  $\ln \lambda = 0$ , we find

$$\begin{aligned} D &= -\left(\frac{\partial \ln \lambda^T}{\partial \ln N}\right)_K \\ &= -\left(T \frac{\partial \ln \lambda}{\partial \ln N} + \ln \lambda \frac{\partial T}{\partial \ln N}\right)_K \quad (1b) \\ &= -\left(T \frac{\partial \ln \lambda}{\partial \ln N}\right)_K. \end{aligned}$$

Together equations (1a) and (1b) show that, with age structure, the asymptotic rate of return to equilibrium is the total density dependence in the life history divided by the generation time at equilibrium,  $\gamma = D/T$ . This definition of total density dependence in the life history (eq. [1b]) also applies in the stage-structured life history analyzed below, with density dependence in juvenile and adult survival as well as recruitment.

### Stage-Structured Life History

Many wild bird and mammal populations have life histories in which the annual survival and reproductive rates of adults are roughly constant and independent of age (Deevey 1947; Gaillard et al. 1994; Nichols et al. 1997; Loison et al. 1999). In such populations the great majority of individuals die before reaching the age of senescence, which is therefore of little demographic consequence. We assume, as appears roughly accurate for some populations, that all density dependence is exerted by the adult population density. This assumption would apply, at least approximately, if juveniles do not compete with adults or if adults are long lived and juveniles compose a small fraction of the population. The number of adults is then a dynamically sufficient variable for the stage-structured life history.

We follow the standard methods of female-based demographic models (Caswell 2001). Defining  $\alpha$  as the age in years at first breeding and  $N(t)$  as the number of adults (individuals of age  $\geq \alpha$ ) in year  $t$ , the stochastic density-dependent dynamics are given by the nonlinear recursion

$$\begin{aligned} N(t) &= s(N, t-1)N(t-1) \\ &\quad + \phi(N, t-\alpha, \dots, t-1)N(t-\alpha). \quad (2a) \end{aligned}$$

The time dependence of population sizes on the right side of (2a) is specified in the successive functional definitions (2b) and (2c). The probability of adult annual survival is  $s$ . The adult annual recruitment rate  $\phi$  is the product of annual fecundity (female offspring per adult female per year) times first year survival,  $f$ , and the probabilities of annual survival from age  $i$  to  $i+1$  during the juvenile stages,  $s_i$ :

$$\phi(N, t-\alpha, \dots, t-1) = f(N, t-\alpha) \prod_{i=1}^{\alpha-1} s_{\alpha-i}(N, t-i). \quad (2b)$$

Environmental and demographic stochasticity affect these vital rates through additive perturbations  $\zeta(t)$ ,  $\varepsilon(t)$ , and  $\delta_\tau(t)$  with 0 means  $\bar{\zeta} = \bar{\varepsilon} = \bar{\delta}_\tau = 0$ ,

$$\begin{aligned} f(N, t) &= \bar{f}[N(t)] + \varepsilon(t), \\ s_\tau(N, t) &= \bar{s}_\tau[N(t)] + \delta_\tau(t), \quad \text{for } 1 \leq \tau \leq \alpha-1, \quad (2c) \\ s(N, t) &= \bar{s}[N(t)] + \zeta(t). \end{aligned}$$

Deterministic and stochastic versions of this stage-structured model, with or without density dependence, have been applied to a variety of species (Caswell 2001, p. 192).

The coefficient of total density dependence in equation (1b) can be derived by implicit differentiation of the deterministic Euler equation for this life history (Lande 1988),

$$\bar{\phi}(N)\lambda^{-\alpha} = 1 - \bar{s}(N)/\lambda,$$

where

$$\bar{\phi}(N) = \bar{f}(N) \prod_{i=1}^{\alpha-1} \bar{s}_i(N)$$

is the adult recruitment rate in the average environment. Finding  $\partial \lambda / \partial N$ , evaluating the result at equilibrium ( $N = K$  and  $\lambda = 1$ ), and finally using the generation time for this stage-structured life history at equilibrium in the average environment,  $T = \alpha + \bar{s}/(1 - \bar{s})$  (Lande 1988), gives

$$\begin{aligned}
 D &= -\left(\frac{\partial \ln \bar{f}}{\partial \ln N} + \sum_{\tau=1}^{\alpha-1} \frac{\partial \ln \bar{s}_\tau}{\partial \ln N} + \frac{\bar{s}}{1 - \bar{s}} \frac{\partial \ln \bar{s}}{\partial \ln N}\right)_K \\
 &= -\left(\frac{\partial \ln \bar{\phi}}{\partial \ln N} - \frac{\partial \ln \bar{\mu}}{\partial \ln N}\right)_K \\
 &= -\left[\frac{\partial \ln (\bar{\phi}/\bar{\mu})}{\partial \ln N}\right]_K.
 \end{aligned}
 \tag{3a}$$

where  $\bar{\mu} = 1 - \bar{s}$  is the adult mortality rate. Thus, density dependence in the stage-structured life history can be measured by the negative elasticity of the ratio of adult recruitment rate to mortality rate with respect to change in adult population density at equilibrium.

The expected lifetime production of female offspring per female is unity at the deterministic equilibrium, which implies that the recruitment rate of adults equals their mortality rate at equilibrium. Denoting equilibrium values as  $\hat{s} = \bar{s}(K)$  and  $\hat{\phi} = \bar{\phi}(K)$ ,

$$\sum_{i=0}^{\infty} \hat{s}^i \hat{\phi} = 1 \quad \text{or} \quad \hat{\phi} = 1 - \hat{s} = \hat{\mu}. \tag{3b}$$

This relation also can be obtained directly from the Euler equation at equilibrium with  $\lambda = 1$ .

Expanding the vital rates in equation (2a) in Taylor series around a deterministic equilibrium adult population size,  $K$ , with deviations from equilibrium denoted as  $x(t) = N(t) - K$ , gives the linearized autoregression for small fluctuations:

$$x(t) = \sum_{\tau=1}^{\alpha} b_\tau x(t - \tau) + \xi(t) \tag{4}$$

with constant coefficients

$$\begin{aligned}
 b_1 &= \left[1 + \left(\frac{\partial \ln \bar{s}}{\partial \ln N}\right)_K\right] \hat{s} + \left(\frac{\partial \ln \bar{s}_{\alpha-1}}{\partial \ln N}\right)_K \hat{\phi}, \\
 b_\tau &= \left(\frac{\partial \ln \bar{s}_{\alpha-\tau}}{\partial \ln N}\right)_K \hat{\phi} \quad \text{for} \quad \tau = 2, \dots, \alpha - 1, \\
 b_\alpha &= \left[1 + \left(\frac{\partial \ln \bar{f}}{\partial \ln N}\right)_K\right] \hat{\phi}.
 \end{aligned}$$

The noise term has time lags of 1 to  $\alpha$  years,

$$\xi(t) = \left[\zeta(t-1) + \hat{\phi} \sum_{i=1}^{\alpha-1} \frac{\hat{\delta}_{\alpha-i}(t-i)}{\hat{s}_{\alpha-i}} + \hat{\phi} \frac{\varepsilon(t-\alpha)}{\hat{f}}\right] K.$$

Hence, even with no autocorrelation in the vital rates, the noise in the autoregression (eq. [4]) will be autocorrelated if the vital rates operating at different time lags are cross correlated at a given time.

For species with age at maturity of 1 yr ( $\alpha = 1$ ), the form of the autoregression is different and the interpretation of the regression coefficient changes (the new  $b_1$  is the sum of the old  $b_1$  through  $b_\alpha$ ). Using (3b), the autoregressive equation is  $x(t) = b_1 x(t-1) + \xi(t)$ , where  $b_1 = 1 - \hat{\mu}D$  and the noise  $\xi(t) = [\zeta(t-1) + \varepsilon(t-1)]K$  with only a single time lag has no autocorrelation.

Statistical analysis of population dynamics is often carried out using  $\ln N$  rather than  $N$  (Royama 1992; Turchin 1995). The form of the linearized autoregression (each of the autoregression coefficients) for the dynamics of  $\ln N$  is identical to that for  $N$ . This can be shown by dividing both sides of equation (4) by  $K$  and noting that for small fluctuations  $x/K \approx \ln(1 + x/K) = \ln(N/K) = \ln N - \ln K$ .

#### *Population Autocorrelation and Spectral Density Functions*

A stationary time series without cycles or deterministic trends can be characterized either by its autocorrelation function (correlogram) or by its spectral density function (power spectrum), the Fourier transform of the autocorrelation function (Box et al. 1994; Chatfield 1996). The power spectrum for most populations shows a substantial “red shift” toward low frequencies in comparison to the flat power spectrum associated with “white noise” that would describe populations with no autocorrelation (Pimm 1991; Ariño and Pimm 1995). Deterministic population models in discrete time without age structure can produce chaotic dynamics as a consequence of high rates of population growth,  $r_{\max} > 1$  per unit time (May 1981), resulting in power spectra that are blue shifted (Cohen 1995), but real population dynamics usually are not chaotic (Hassell et al. 1976; Ellner and Turchin 1995). Ariño and Pimm (1995) also emphasized that the empirical (or observed) variance in population size tends to increase with length of the time series because of autocorrelation. We now show that the observed patterns of red-shifted power spectra and increasing empirical variance with time can be explained by a stochastic density-dependent life history producing damped population fluctuations around a stable equilibrium.

We applied analytical methods for linear autoregressive processes (Box et al. 1994) to derive the theoretical correlogram and power spectrum for adult population size in the stage-structured life history (app. A). Although density dependence limits population size and can confer stability on the dynamics, strong density dependence can produce noticeable cycles and instability (Beddington 1974; Caswell

1997; Neubert and Caswell 2000). For example, in a species with  $\alpha = 1$ , the autocorrelation function is  $\rho_\tau = b_1^{|\tau|}$  and the power spectrum, which is a function of the frequency  $\nu$ , is  $F(\nu) = 2/[1 + b_1^2 - 2b_1\cos(2\pi\nu)]$ . The power spectrum has an internal peak, corresponding to noticeable 2-yr cycles in population time series, and the appearance of negative autocorrelations at odd-numbered time lags, when  $b_1 < 0$  or

$$D > \frac{1}{\hat{\mu}}, \tag{5a}$$

which requires very strong density dependence.

As another example, consider a species with  $\alpha > 1$  and density dependence in  $f$ , the adult annual fecundity times first year survival, but not in survival beyond the first year. There are then only two nonzero autoregression coefficients,  $b_1$  and  $b_\alpha$ , with  $b_1 = \hat{s}$  the expected adult annual survival rate at equilibrium. The power spectrum has an internal peak, corresponding to noticeable cycles in population time series with the appearance of negative autocorrelations, when  $b_\alpha$  is sufficiently negative:  $b_\alpha < -b_1/[b_1 + (1 - b_1)\alpha]$  or

$$D = -\left(\frac{\partial \ln \bar{f}}{\partial \ln N_K}\right) > 1 + \frac{1/\hat{\mu}}{1 + \alpha\hat{\mu}/\hat{s}}. \tag{5b}$$

Figure 1 illustrates for this case how the strength of density dependence in fecundity influences the sample paths, the autocorrelation function, and the power spectrum of the adult population, also showing how the empirical variance in population size is expected to increase with length of the time series.

*Increase of Empirical Variance with Length of Series*

The empirical (or observed) variance in census population size tends to increase with the period of observation, over timescales as long as decades (Ariño and Pimm 1995). This occurs because of either autocorrelation or nonstationarity, both of which cause extreme population sizes to be undersampled in short time series. Nonstationarity in the form of a sustained population trend produces large negative autocorrelations at long time lags (Chatfield 1996). For a stationary time series of population sizes censused during  $L$  consecutive years, the expected empirical variance can be derived from a one-way ANOVA (Scheffé 1959) within and among replicate time series. Regardless of temporal autocorrelation, the variance of population size in an infinite series,  $\sigma_N^2$ , can be partitioned into the expected empirical variance within series of length  $L$ ,

$E[s_N^2]$ , plus the expected empirical variance of mean population size among series of length  $L$ ,  $\text{Var}[\bar{N}]$ ,

$$\begin{aligned} \text{Var}[\bar{N}] &= \text{Var}\left[\frac{1}{L}\sum_{t=1}^L N(t)\right] = \frac{\sigma_N^2}{L^2}\sum_{i=1}^L\sum_{j=1}^L \rho_{i-j} \\ &= \sigma_N^2\left[\frac{1}{L} + \frac{2}{L}\sum_{\tau=1}^L\left(1 - \frac{\tau}{L}\right)\rho_\tau\right], \end{aligned} \tag{6a}$$

where  $\rho_\tau$  is the autocorrelation of lag  $\tau$ , that is, the correlation of  $N(t)$  with  $N(t - \tau)$ . In the absence of autocorrelation this reduces to the standard formula for the sampling variance of the mean of  $L$  independent data points,  $\sigma_N^2/L$  (Kendall and Stuart 1977). The expected empirical variance in a stationary time series of length  $L$  depends directly on the autocorrelation function,

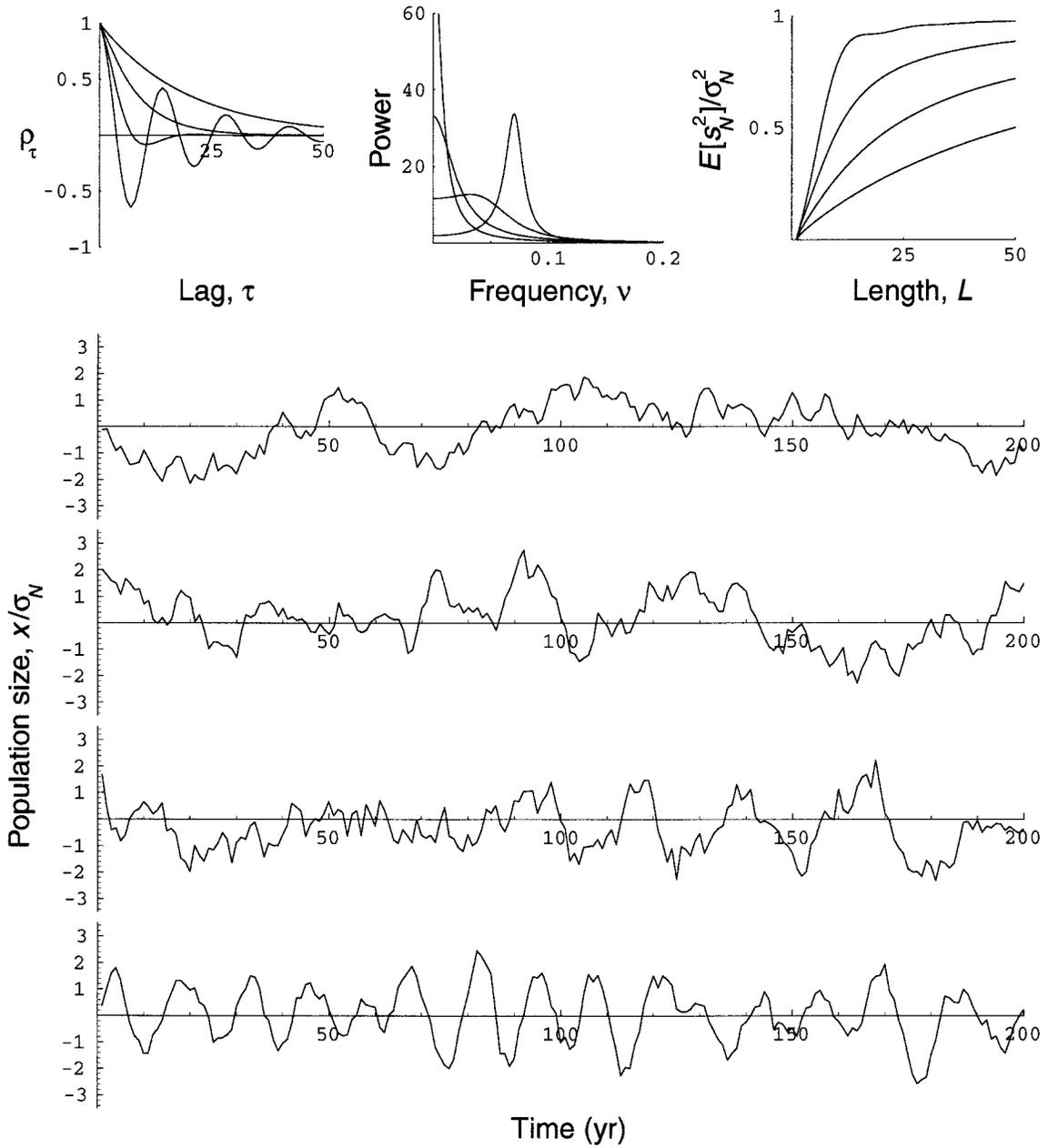
$$\begin{aligned} E[s_N^2] &= \sigma_N^2 - \text{Var}[\bar{N}] \\ &= \left[1 - \frac{1}{L} - \frac{2}{L}\sum_{\tau=1}^L\left(1 - \frac{\tau}{L}\right)\rho_\tau\right]\sigma_N^2. \end{aligned} \tag{6b}$$

This closely approaches its asymptotic value  $\sigma_N^2$  only when the length of the time series greatly exceeds the net autocorrelation,  $L \gg 1 + 2\sum_{\tau=1}^L \rho_\tau$ . A slow increase in empirical variance with increasing length of time series is a consequence of positive autocorrelations that, in the stage-structured life-history model, are enhanced by high adult annual survival and weak density dependence (fig. 1).

*Estimating Density Dependence*

The autoregression coefficients can be expressed in terms of population autocorrelations. The maximum likelihood estimator of the autoregression coefficients is identical to the least squares estimator for a standard regression (app. A). For  $\alpha = 1$  the autoregression coefficient is estimated by  $b_1 = \rho_1$ . More generally, the autoregression coefficients can be estimated as the solution of the Yule-Walker equations (Box et al. 1994),  $\mathbf{b} = \mathbf{P}^{-1}\boldsymbol{\rho}$ , where  $\boldsymbol{\rho}$  and  $\mathbf{b}$  are column vectors with elements  $\rho_1, \dots, \rho_\alpha$  and  $b_1, \dots, b_\alpha$ , and  $\mathbf{P}$  is the population autocorrelation matrix with elements  $P_{ij} = \rho_{i-j}$  for  $i, j = \{1, \dots, \alpha\}$ , and  $\rho_0 = 1$ . However, these estimators of the autoregression coefficients are biased because population sizes at a given time enter the autoregression as both dependent and independent variables. This time series bias can be removed and standard errors and significance tests on the autoregression coefficients can be obtained by computer simulation (see app. A).

It is important to realize that the autoregression coefficients in equation (4) do not directly reveal the strength of density dependence in population dynamics. The co-



**Figure 1:** Autocorrelation functions,  $\rho_\tau$ , power spectra, and sample paths for small fluctuations in adult population size around a density-dependent equilibrium in the stage-structured life history. In this illustration, all density regulation is exerted by the number of adults on the adult fecundity times first year survival,  $f$ , and all stochasticity occurs in this vital rate alone. The increase in expected empirical variance of population size with increasing length of the sample series is shown as a proportion of the stationary variance. Power spectra, as a function of frequency in cycles per year, are normalized to unit area. Population sizes are plotted as deviations from the mean and standardized to unit variance. Age at maturity is  $\alpha = 4$  yr. Adult vital rates are independent of age, with adult annual mortality rate  $\mu = 0.05$ . Different lines in each panel correspond to values of density dependence in fecundity  $D = -(\partial \ln \bar{f} / \partial \ln N)_K = 1, 2, 4, \text{ or } 8$ . Weak density dependence produces positive autocorrelations over long time lags and a red shift in the power spectrum. Increasing the strength of density dependence in recruitment gives rise to negative autocorrelations and a noticeable tendency to cycle in the sample paths, corresponding to an internal peak in the power spectrum that increases with the strength of density dependence.

efficients of density dependence in the vital rates are confounded with the life-history parameters  $\hat{\phi}$  and  $\hat{s}$  themselves. For species with  $\alpha = 1$ , there is only a single autoregression coefficient  $b_1 = 1 - \hat{\mu}D$  from which we can estimate  $\hat{\mu}D = 1 - b_1$ . For species with  $\alpha > 1$ , there are  $\alpha$  autoregression coefficients and from equations (3) and (4) the product of the adult mortality rate and the total density dependence in the life history can be estimated as one minus the sum of the autoregression coefficients:

$$\hat{\mu}D = 1 - \sum_{\tau=1}^{\alpha} b_{\tau}. \tag{7}$$

Time series for analysis were chosen from seven vertebrate populations based on having three or more decades of accurate annual census data with few missing observations (table 1; fig. 2). Counts of the great tit (*Parus major*) and blue tit (*Parus caeruleus*) at Ghent, Belgium, and the tufted duck (*Aythya fuligula*) at Engure Marsh, Latvia, include the total adult population ( $\geq 1$  yr old). The tit counts are almost exact since a high proportion of them reproduce in nest boxes, but there is considerable exchange of individuals with other populations. The grey heron (*Ardea cinerea*) counts are for the breeding adult population ( $\geq 2$  yr old that have built a nest) in southern Britain, which therefore represents a relatively closed population. The chamois (*Rupicapra rupicapra*) in the Swiss National Park in southwestern Switzerland is a nearly closed population; the counts are much more accurate than usual for ungulates but include calves and juveniles (calves composed 20%–33% of the population from 1967–1999). Counts of

the mute swan (*Cygnus olor*) on the Thames, England, are for the total population minus fledglings. We truncated the time series for the mute swan following a several year gap of no data during World War II, after which there were large increases in both adults and yearlings (Cramp 1972). Some of the mute swan annual counts may be biased (Birkhead and Perrins 1986) and fledglings were wingclipped during the counts to reduce emigration (Cramp 1972); this series is included mainly for illustrative purposes because of its length. The population of South Polar skua (*Catharacta maccormicki*) at Pointe Géologie archipelago (66°S, 140°E), Terre Adélie, Antarctica, has a significant input of recruits from outside the archipelago. The strong territorial behavior of adults helps to ensure that all birds in the archipelago are metal- and color-ringed and the counts of breeding adults are exact. Years when a complete census was not undertaken were excluded from the analysis of the chamois, mute swan, and South Polar skua.

The high accuracy of these population time series based on complete annual censuses implies that measurement errors are negligible in comparison to the magnitude of actual population fluctuations. We therefore have no need for elaborate techniques, such as state space models and Kalman filtering (Box et al. 1994), designed to deal with measurement error in population estimates. Using basic statistical methods for autoregressive time series analysis (app. A), we found evidence of density dependence in five of the seven species (tables 1 and 2). Although the theory (eq. [4]) indicates that the noise in the population process is autocorrelated, so that with life-history information the

Table 1: Bias-corrected parameter estimates ( $\pm$  SE or 95% CI) for population time series fitted to the stage-structured life-history model

Species	Years	CV	$\alpha$	$b_1$	$b_2$	$b_3$	$b_4$	$\hat{\mu}D$	$R^2$
Great tit	35	.30	1	.465 $\pm$ .159	...	...	...	.535** (.184, .879)	.21
Blue tit	35	.26	1	.493 $\pm$ .156	...	...	...	.507** (.157, .849)	.12
Tufted duck <sup>a</sup>	36	.27	1	.436 $\pm$ .156	...	...	...	.564** (.221, .907)	.21
Grey heron <sup>b</sup>	71	.18	2	.926 $\pm$ .127	-.006 $\pm$ .119	...	...	.081 (.000, .246)	.72
Chamois	69	.12	3	.728 $\pm$ .133	-.057 $\pm$ .157	.045 $\pm$ .130	...	.283** (.080, .573)	.42
Mute swan <sup>c</sup>	116	.26	4	.850 $\pm$ .100	.078 $\pm$ .127	-.002 $\pm$ .125	.011 $\pm$ .095	.062 (.000, .184)	.83

Note: See equation (4). Age of first reproduction  $\alpha$  obtained from the literature (Owen 1960; Clobert et al. 1988; Bacon and Andersen-Harild 1989; Dhondt et al. 1990; Loison et al. 1994; Blums et al. 1996).

<sup>a</sup> Reference: Blums et al. 1993.

<sup>b</sup> Reference: British Trust for Ornithology, unpublished data.

<sup>c</sup> Reference: Cramp 1972.

\*\*  $P < .01$  for hypothesis that  $\hat{\mu}D > 0$  by one-tailed test.

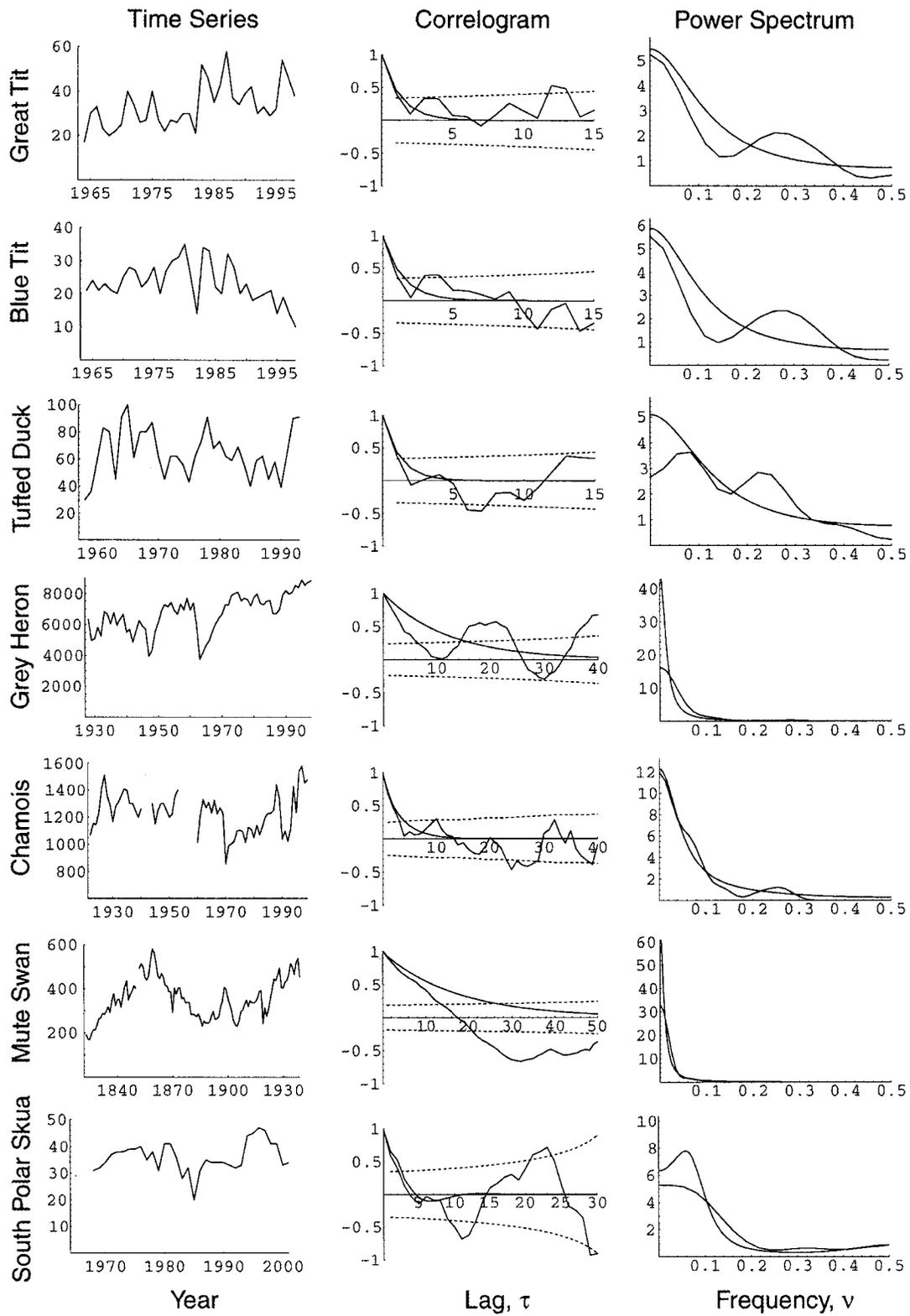


Figure 2: Time series, empirical correlogram, and power spectrum for annual census of adult population in seven vertebrate species. Theoretical autocorrelation function and power spectrum (smooth curves) were calculated for each species from autoregression coefficients in the stage-structured life-history model (eq. [4]; tables 1, 2; app. A).

**Table 2:** Bias-corrected parameter estimates ( $\pm$  SE or 95% CI) for the 35-yr population time series of the South Polar skua (CV 0.16) fitted to the stage-structured life-history model (eq. [4]), using different mean ages of first reproduction  $\alpha$

$\alpha$	$b_1$	$b_2$	$b_3$	$b_4$	$b_5$	$\hat{\mu}D$	$R^2$
3	.601 $\pm$ .186	.310 $\pm$ .193	-.299 $\pm$ .170			.388** (.107, .864)	.32
4	.582 $\pm$ .197	.334 $\pm$ .217	-.257 $\pm$ .200	-.070 $\pm$ .180		.411** (.137, 1.008)	.28
5	.587 $\pm$ .207	.339 $\pm$ .221	-.259 $\pm$ .211	-.078 $\pm$ .213	.014 $\pm$ .188	.397** (.103, 1.114)	.22

\*\*  $P < .01$  for hypothesis that  $\hat{\mu}D > 0$  by one-tailed test.

population time series could in principle be analyzed as an autoregressive moving-average process (ARMA; see Box et al. 1994), residuals from the simple autoregression showed no significant autocorrelations in the noise, justifying the approximation of independent errors in estimation and significance testing.

### Age-Structured Life History

Consider an age-structured life history with synchronized annual reproduction and individuals enumerated immediately before reproduction (Leslie 1966; Caswell 2001). Age structure in the population at a given time is represented by a column vector  $\mathbf{n}$  with elements  $n_1, \dots, n_\omega$ , where  $n_i$  denotes the number of individuals of age  $i$  and  $\omega$  is the maximum length of life. A nonlinear autoregressive equation for the first age class (yearlings) is

$$n_1(t) = \sum_{\tau=1}^{\omega} l_{\tau}(t-1) f_{\tau}(\mathbf{n}, t-1) n_1(t-\tau), \quad (8a)$$

where

$$l_{\tau}(t) = \prod_{i=1}^{\tau-1} s_i(t) \quad \text{for } \tau \geq 2$$

is the probability of survival to age  $\tau$  at time  $t$  from age 1 at time  $t-\tau+1$  and  $l_1(t) = 1$ . The probability of survival from age  $\tau$  to  $\tau+1$  in year  $t$ ,  $s_{\tau}(t)$ , is assumed to be density independent for  $\tau \geq 1$ . Evidently  $l_{\tau}(t)$  depends on the sequence of age-specific survival rates  $\tau-1$  yr into the past. The time dependence of age structure vectors on the right side of (8a) is specified in the functional definition (8b). For females of age  $\tau$ , the product of fecundity times the probability of offspring survival from age 0 to age 1 in year  $t$ ,  $f_{\tau}(\mathbf{n}, t)$ , may depend on the population densities of all age classes. The product  $l_{\tau} f_{\tau}$  is called the “net maternity function” (Keyfitz 1977; Caswell 2001, p. 220). Environmental and demographic stochasticity are assumed to add random perturbations  $\varepsilon_{\tau}(t)$  to the expected repro-

ductive rate and  $\delta_{\tau}(t)$  to the expected survival rate of age class  $\tau$  (with 0 means,  $\bar{\varepsilon}_{\tau} = \bar{\delta}_{\tau} = 0$ ),

$$f_{\tau}(\mathbf{n}, t) = \bar{f}_{\tau}[\mathbf{n}(t)] + \varepsilon_{\tau}(t),$$

$$s_{\tau}(t) = \bar{s}_{\tau} + \delta_{\tau}(t) \quad \text{for } \tau \geq 1. \quad (8b)$$

Letting a carat denote a deterministic equilibrium age structure,  $\hat{\mathbf{n}}$ , the linearized autoregression for the deviation from equilibrium of the first age class,  $x_1(t) = n_1(t) - \hat{n}_1$ , is (see app. B)

$$x_1(t) = \sum_{\tau=1}^{\omega} b_{\tau} x_1(t-\tau) + \xi(t) \quad (9a)$$

with constant coefficients

$$b_{\tau} = \hat{\phi}_{\tau} - D_{\tau}, \quad (9b)$$

where  $\hat{\phi}_{\tau} = \hat{l}_{\tau} \hat{f}_{\tau}$  represents the net maternity at age  $\tau$  at equilibrium in the average environment. The total net maternity is the expected lifetime production of female offspring per female, which at equilibrium equals unity,  $\sum_{\tau=1}^{\omega} \hat{\phi}_{\tau} = 1$ . The age-specific density dependence,  $D_{\tau}$ , is the negative elasticity of the finite rate of increase per generation,  $\lambda^T$ , with respect to changes in density of age class  $\tau$ , holding the densities of all other age classes constant,

$$D_{\tau} = - \left( \frac{\partial \ln \lambda^T}{\partial \ln n_{\tau} |_{\hat{\mathbf{n}}}} \right) = - \sum_{k=1}^{\omega} \left( T \frac{\partial \ln \lambda}{\partial \ln \bar{f}_k} \frac{\partial \ln \bar{f}_k}{\partial \ln n_{\tau} |_{\hat{\mathbf{n}}}} \right), \quad (9c)$$

where  $T$  is the generation time, or mean age of mothers of newborns at equilibrium,  $T = \sum_{\tau=1}^{\omega} \tau \hat{\phi}_{\tau}$ . The total effect of changes in relative density of age class  $\tau$  on the population growth rate is propagated through density effects exerted by this age class on all the age-specific fecundities (see Caswell 2001, p. 232). The elasticity in the fecundity at each age with respect to changes in the relative density

of age class  $\tau$  is multiplied by the elasticity of  $\lambda$  with respect to changes in the corresponding fecundity evaluated at equilibrium (Charlesworth 1994)

$$\left(\frac{\partial \ln \lambda}{\partial \ln f_k}\right)_{\hat{n}} = \frac{\hat{\phi}_k}{T}. \tag{9d}$$

As before in the stage-structured life history, even in the absence of environmental autocorrelation, the noise term  $\xi(t)$  in equation (9a) is autocorrelated when environmental stochasticity affects vital rates that operate with more than a single time lag, if these are cross correlated at a given time (app. B).

### Estimating Density Dependence

Assuming no environmental autocorrelation and neglecting autocorrelated noise caused by life history, the Yule-Walker equations  $\mathbf{b} = \mathbf{P}^{-1}\boldsymbol{\rho}$  provide estimators of the autoregression coefficients  $b_1, \dots, b_\omega$  in equation (9a) that can be corrected for time series bias by computer simulation (app. A). An estimate of the density dependence in age-specific fecundity can be obtained by subtracting the corresponding autoregression coefficient from the net maternity function at equilibrium (from eq. [9b]),

$$D_\tau = \hat{\phi}_\tau - b_\tau. \tag{10a}$$

The net maternity function at equilibrium summed over the life history equals unity, so the sum of the autoregression coefficients from (9a) can be used to estimate the total density dependence in fecundity and first year survival in an age-structured life history as

$$\sum_{\tau=1}^{\omega} D_\tau = 1 - \sum_{\tau=1}^{\omega} b_\tau. \tag{10b}$$

To compare the total density dependence in the stage-structured and age-structured life-history models, we note the following relation. Suppose that, in the age-structured model, all density dependence is exerted by a linear combination of the age classes,  $N = \sum_{\tau=1}^{\omega} c_\tau n_\tau$ , where  $c_\tau$  represents the relative competitive effect of an individual of age  $\tau$  (see Charlesworth 1994). Then  $\lambda$  is a function only of  $N$  and  $\partial N / \partial n_\tau = c_\tau$ , so that

$$\frac{\partial \lambda}{\partial n_\tau} = \frac{\partial \lambda}{\partial N} \frac{\partial N}{\partial n_\tau} = c_\tau \frac{\partial \lambda}{\partial N} \quad \text{or} \quad \frac{\partial \ln \lambda}{\partial \ln n_\tau} = \frac{c_\tau n_\tau}{N} \frac{\partial \ln \lambda}{\partial \ln N}.$$

Multiplying both sides by  $-T$  and summing using the first equality of (9c), evaluating the result at equilibrium yields

$$\sum_{\tau=1}^{\omega} D_\tau = - \sum_{\tau=1}^{\omega} \left(\frac{\partial \ln \lambda^\tau}{\partial \ln n_\tau}\right)_{\hat{n}} = - \left(\frac{\partial \ln \lambda^\tau}{\partial \ln N}\right)_K. \tag{11}$$

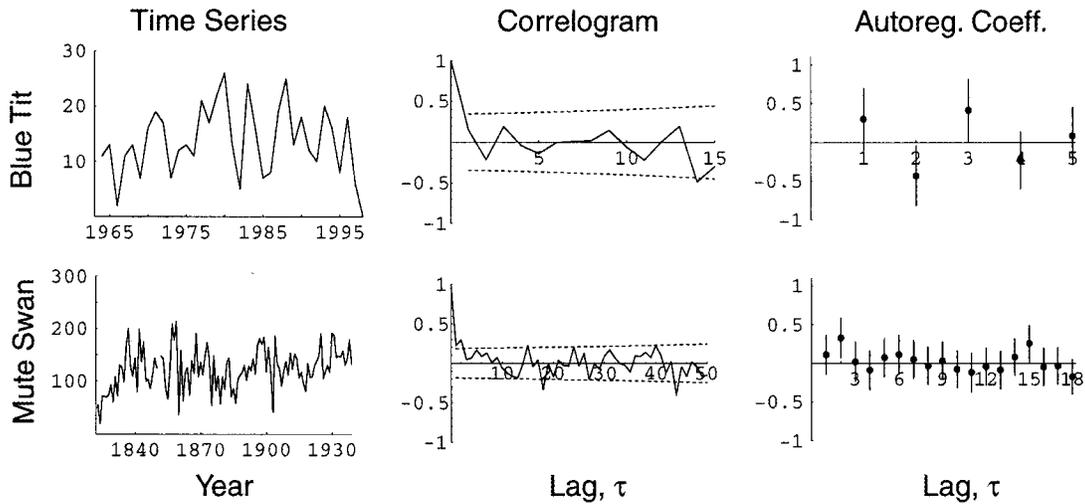
Thus  $D$  in the stage-structured model is analogous to the total density dependence in the age-structured model.

We applied the age-structured model to analyze time series data on yearling great tits and blue tits and fledgling mute swans from the same populations as in figure 2, assuming no density dependence in survivorship past age 1. Because annual survival rates of adult tits are about 50% (Clobert et al. 1988; Dhondt et al. 1990), few individuals live past  $\omega = 5$  yr. The longest recorded lifespan for a wild mute swan in southern Britain is 26 yr (Bacon and Andersen-Harild 1989). The bias correction algorithm did not converge for the great tit hence no estimates of the autoregression coefficients were obtained. For the mute swan, bias-corrected estimates of the autoregression coefficients could not be obtained for  $\omega > 18$  yr. Standard errors of the autoregression coefficients were large for both the blue tit and mute swan (fig. 3). We estimated the total density dependence in fecundity over the life history, which was not significant either for the blue tit,  $\sum_{\tau=1}^5 D_\tau = 0.86 \pm 0.45$ , or the mute swan,  $\sum_{\tau=1}^{18} D_\tau = 0.62 \pm 0.38$ .

### Discussion

We developed a demographic theory of stochastic fluctuations around a stable equilibrium for a stage-structured life history in which the vital rates depend on adult population density. We also derived a similar theory for an age-structured life history in which age-specific fecundities and first year survival may depend on the population densities of all age classes. This theory suggests that the total density dependence in a life history should be quantitatively defined as the negative elasticity of population growth rate per generation with respect to change in population size (eqq. [3a], [9c], [11]). The theory further specifies how density dependence can be estimated from linear autoregression equations, at least for populations with a small or moderate coefficient of variation. This theory is applicable to populations of many species with an annual breeding season, especially vertebrates with low intrinsic rates of increase and population dynamics that are not cyclic or chaotic; it facilitates the measurement and comparison of density dependence among species with different life histories and forms of density regulation.

Turchin (1990, 1995), Royama (1992), Turchin and Taylor (1992), Zeng et al. (1998), and others fitted nonlinear autoregressive models with time lags of one, two, and possibly three years to population time series. They interpreted a significant autoregression coefficient for a time lag  $>1$  yr as evidence of density dependence with a time lag. How-



**Figure 3:** Population time series and empirical correlogram for annual census of blue tit yearlings and mute swan fledglings from the same populations as in figure 2. Also shown are autoregression coefficients (*dots*)  $\pm 2$  SE (*bars*) for the age-structured life-history model (eqq. [9]; app. A).

ever, the form of their models is not based on an explicit demographic mechanism but is purely phenomenological, often a linear autoregression in the log of census population size. Our results (eqq. [4] and [9]) demonstrate that the interpretation of autoregression coefficients is clarified by deriving the form of the linearized autoregressive equation from a nonlinear stochastic life-history model. The form of the linearized autoregression (the vector of autoregression coefficients) is identical when  $\ln N$  is used instead of  $N$ . Contrary to the interpretation of previous authors, the autoregression coefficients do not directly measure density dependence operating at particular lags. Most important, in both the stage-structured and age-structured life-history models the autoregressive coefficients each may depend on parameters of the life history and density dependence of a particular stage or age class. The interpretation of autoregression coefficients differs fundamentally between the stage-structured and the age-structured models. In the stage-structured model, the autoregression coefficients of longer lags include density dependence in survivorships of younger stages exerted by adult population density, and density dependence in adult fecundity is included in the last autoregression coefficient,  $b_\alpha$  (eq. [4]). In the age-structured model, the autoregression coefficients of longer lags include the density dependence in  $\lambda$  exerted by the population density of older age classes, ramifying through their effects on fecundities of all ages (eqq. [9]).

It is instructive to consider a species with  $\alpha = 1$  and autoregression coefficient  $b_1 = 0$ , which implies that all autocorrelations are 0 (except  $\rho_0 = 1$ ) corresponding to a flat power spectrum or white noise process for the pop-

ulation. This would entail very strong density dependence,  $D = 1/\hat{\mu}$  (the inverse of the adult annual mortality rate), despite the regression explaining none of the total variance,  $R^2 = 0$ . The great tit, blue tit, and tufted duck approach this situation, having a relatively flat power spectrum with a small red shift and a low  $R^2$  (table 1; fig. 2). Using the stage-structured model to analyze the chamois with  $\alpha = 3$ , the autoregression coefficients  $b_2$  and  $b_3$  do not differ significantly from 0, yet this nevertheless allows the detection of significant total density dependence in the life history of this population (table 1). Thus statistical significance of autoregression coefficients is not a valid criterion for the detection of density dependence.

In the stage-structured model, density dependence operates with up to  $\alpha$  time lags. For the grey heron (North and Morgan 1979), chamois (Loison et al. 1994), and mute swan (Bacon and Perrins 1991) the estimated adult survivorships from life-history studies are, respectively,  $\hat{s} = 0.70, 0.96, \text{ and } 0.77$ . These are not significantly different from the respective estimates of the first autoregression coefficient  $b_1 = 0.93, 0.73, \text{ and } 0.85$  in table 1, and subsequent regression coefficients up to  $b_{\alpha-1}$  do not differ significantly from 0. Thus for these species we cannot reject the hypothesis of no density dependence in survival beyond the first year. Any differences between estimates of  $\hat{s}$  from life-history studies and autoregression estimates could, however, be due to different years of study or violation of assumptions in the stage-structured life-history model.

For the South Polar skua, the average age of first reproduction is 6 yr (Jouventin and Guillotin 1979; H. Weimerskirch, unpublished data). Estimates of the first three

autoregression coefficients and the total density dependence in the life history are rather insensitive to values of  $\alpha$  ranging from 3 to 5 yr (table 2), but for  $\alpha = 6$  the estimated autoregression coefficients became unreliable, with large standard errors, apparently because there were too many coefficients relative to the length of the series for accurate estimation (as discussed below for the age-structured life history). We used the results in table 2 for  $\alpha = 5$  in subsequent analyses. The estimated adult survivorship from life-history studies (H. Weimerskirch, unpublished data)  $\hat{s} = 0.85$  is significantly larger than the first autoregression coefficient  $b_1 = 0.59$  and the intermediate autoregression coefficients between  $b_1$  and  $b_\alpha$  include some substantial (although not significant) estimates, suggesting appreciable density dependence in survivorship beyond the first year in this species, possibly because of the strong territoriality.

Life history can explain the qualitative features of population autocorrelation functions and power spectra and observations of increasing empirical variance in population size with increasing length of time series (figs. 1, 2). Populations of all seven species in figure 2 have power spectra that display the usual red shift toward low frequencies in comparison to the flat power spectrum for white noise (Pimm 1991; Ariño and Pimm 1995). The most strongly red-shifted power spectra occur in populations with low adult mortality and weak density dependence corresponding to small values of  $\hat{\mu}D$ , regardless of age at maturity (see figures and tables). Discrepancies between the estimated autocorrelation functions and power spectra and their theoretical counterparts obtained from fitting the stage-structured life history (fig. 2) are attributable to sampling errors caused by the limited length of the time series, to violation of the assumption that the population is closed to immigration, and to specific factors that might produce nonstationarity in some of the time series. For example, an unusually harsh winter in 1963 caused the grey heron population to fall by nearly half (fig. 2). The 20-yr cycle in grey heron abundance suggested by the correlogram may be largely an artifact of this single catastrophe. Alternatively, this departure of the grey heron correlogram from that of the fitted stage-structured life-history model could be interpreted as evidence for environmental autocorrelation, which is assumed absent from the model. For the mute swan, significant negative autocorrelations at long time lags might be caused by a linear trend (Chatfield 1996) or a long-term cycle in the data; however, random long-term fluctuations that appear cyclic in time series of limited duration are typical of species with weak density dependence (see fig. 1, top sample path).

We detected strong total density dependence in five of the seven species. This is not surprising because some form of population regulation is required to maintain a low

coefficient of variation in population size over a long time in a fluctuating environment, and only strong density dependence is likely to be detected as statistically significant in time series of a few decades. Comparing the strength of total density dependence,  $D$ , between species requires correcting the estimates of  $\hat{\mu}D$  in tables 1 and 2 via division by the adult annual mortality rate,  $\hat{\mu}$ . For species with  $\alpha = 1$ , the adult annual survival rate  $\hat{s} = 1 - \hat{\mu}$  can be obtained from life-history studies, which for the great tit, blue tit, and tufted duck give estimates of  $\hat{s} = 0.46, 0.49,$  and  $0.65$ , respectively (Clobert et al. 1988; Dhondt et al. 1990; Blums et al. 1996). For the chamois and South Polar skua, the life-history estimates of  $\hat{s}$  are  $0.96$  (Loison et al. 1994) and  $0.85$  (H. Weimerskirch, unpublished data). The total density dependence within each of these five populations in order is then estimated as  $D = 0.99, 0.99, 1.61, 7.1,$  and  $2.65$ . The total density dependence appears to be strong to very strong in all of the populations in which significant estimates were obtained, especially for the chamois. Strong density dependence of recruitment is often observed in ungulates (Sæther 1997; Gaillard et al. 2000). Lack of significant density dependence for the grey heron and especially for the mute swan, which had the longest time series, suggests that density dependence is relatively weak in these species. Life-history estimates of  $\hat{s}$  for these two species are  $0.70$  and  $0.85$ , respectively (North and Morgan 1979; Bacon and Perrins 1991), which gives corresponding estimates of  $D = 0.27$  and  $0.41$ .

Autocorrelated noise presents a potential complication for the measurement of density dependence from population time series. Autocorrelation of physical and biotic environments have been discussed as causes of autocorrelated noise (Williams and Liebhold 1995; Berryman and Turchin 1997). The present theory reveals that environmental covariance in vital rates operating at different time lags, creates another source of autocorrelated noise, even in the absence of environmental autocorrelation (eqq. [4], [9]). Observed correlations among vital rates (Sæther and Bakke 2000) may be caused both by environmental covariances and by density dependence in the vital rates. Long-term life-history studies of vertebrate species often show that estimates of recruitment of yearlings (reproduction times first year survival) are much more variable among years than estimates of adult mortality (Gaillard et al. 1998, 2000; Sæther and Bakke 2000), as observed in the tufted duck (Blums et al. 1996), grey heron (North and Morgan 1979), and mute swan (Cramp 1972; Bacon and Perrins 1991). This would tend to reduce the environmental covariance of vital rates in the stage-structured model (eq. [4]). The present autoregression analyses, like previous studies (Turchin 1990, 1995; Royama 1992; Turchin and Taylor 1992; Zeng et al. 1998; and other authors), assume no autocorrelation of the noise. Residuals from

the autoregressions showed no significant autocorrelations, suggesting not only a negligible environmental autocorrelation, but also that environmental covariance of vital rates operating at different time lags is small.

With the age-structured life-history model, the density dependence in age-specific fecundity can in principle be estimated by autoregression of time series for yearlings (age class 1), in conjunction with life-history studies. The linear autoregression coefficient for time lag  $\tau$  equals the net maternity at age  $\tau$  minus the age-specific density dependence (eq. [9b]) measured by the negative elasticity population growth rate per generation with respect to change in the density of age class  $\tau$ , ramifying through all of the age-specific fecundities (eq. [9c]). This indicates that the autoregression coefficient for time lag  $\tau$  must be subtracted from the net maternity at age  $\tau$  to accurately estimate age-specific density dependence. However, because the net maternity function sums to unity at equilibrium, the total density dependence summed over the life history can be estimated from one minus the sum of the autoregression coefficients (eq. [10b]).

We applied the age-structured model (eqq. [9]) to analyze time series of great tit and blue tit yearlings and mute swan fledglings, assuming no density dependence in mortality beyond age 1 and a maximum lifespan of 5 yr for the tits and 26 yr for the mute swan (Bacon and Andersen-Harild 1989). The autoregression coefficients were unreliable, with large standard errors. For the great tit no estimates were obtained because the bias correction did not converge. For the mute swan, bias corrected estimates could not be obtained for  $\omega > 18$  yr (fig. 3). In an attempt to overcome these statistical limitations, we summed the autoregression coefficients to estimate the total density dependence for the life history, but in neither case were the results significant,  $\sum D_r = 0.86 \pm 0.45$  for the blue tit and  $0.62 \pm 0.38$  for the mute swan. Evidently, time series at least an order of magnitude longer than the number of autoregression coefficients,  $L \gg \omega$ , would be required to accurately estimate the total density dependence using the age-structured life-history model. This statistical limitation arises in an extreme form if the age-structured model is extended to include density dependence in survivorship past the first year, which causes the linearized autoregression to contain all possible time lags from 1 to infinity.

Our results illustrate the advantages and limitations of applying demographic theory both to quantitatively define density dependence and to estimate it from population time series. Our definition of density dependence as the negative elasticity of population growth rate per generation with respect to change in population size, can be evaluated at any population size as well as at equilibrium. Estimation of density dependence in population time series with large

fluctuations could be accomplished using nonlinear time series analysis (Tong 1990).

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## APPENDIX A

### Theoretical Correlogram and Power Spectrum

From theoretical autoregression coefficients in the stage-structured life history, contained in the column vector  $\mathbf{b}$  with elements  $b_1, \dots, b_\alpha$ , the first  $\alpha$  autocorrelations were obtained by joint numerical solution of the Yule-Walker equations,  $\boldsymbol{\rho} = \mathbf{P}\mathbf{b}$ , where  $\boldsymbol{\rho}$  is a column vector with elements  $\rho_1, \dots, \rho_\alpha$  and  $\mathbf{P}$  is the population autocorrelation matrix with elements  $P_{ij} = \rho_{i-j}$  for  $i, j = \{1, \dots, \alpha\}$  and  $\rho_0 = 1$ . A feasible (or physically possible) autocorrelation function must have an autocorrelation matrix that is positive semidefinite, meaning that the eigenvalues of  $\mathbf{P}$  (which are all real because the matrix is symmetric; Franklin 1968) must be nonnegative. The remaining autocorrelations were obtained from the general recursion  $\rho_\tau = \sum_{i=1}^{\alpha} b_i \rho_{\tau-i}$  for  $\tau > \alpha$ . For  $\alpha = 1$ , the autocorrelation function is  $\rho_\tau = b_1^{|\tau|}$ .

The spectral density function is the Fourier transform of the autocorrelation function, which has the general form  $F(\nu) = 2[1 + 2 \sum_{\tau=1}^{\alpha} \rho_\tau \cos(2\pi\tau\nu)]$ , with frequency in the range  $0 < \nu \leq 1/2$  cycles per year (Box et al. 1994; Chatfield 1996). In terms of the autoregression coefficients, it can be shown from equation (3.2.9) of Box et al. (1994, p. 57) that

$$F(\nu) = \frac{2}{1 + \sum_{\tau=1}^{\alpha} b_\tau [b_\tau - 2 \cos(2\pi\tau\nu)] + 2 \sum_{\tau=1}^{\alpha-1} \sum_{j=1}^{\alpha-\tau} b_j b_{j+\tau} \cos(2\pi\tau\nu)}. \quad (\text{A1})$$

If  $\alpha = 1$ , then  $F(\nu) = 2/[1 + b_1^2 - 2b_1 \cos(2\pi\nu)]$ .

*Empirical Correlogram and Power Spectrum*

In a sample time series for annual population census over  $L$  years, on the null hypothesis of a stationary time series with no temporal autocorrelation, small sample estimates of autocorrelation of lag  $\tau$  years are approximately unbiased with sampling variance  $1/(L - \tau)$  so that an estimated autocorrelation with a magnitude greater than  $2/\sqrt{L - \tau}$  can be considered significant with 95% confidence (Kendall et al. 1983). Formulas typically employed in analyzing time series data assume long series, much longer than the time lags of interest,  $L \gg \tau$ , for example, using just  $1/L$  as the sampling variance of an estimated autocorrelation (Chatfield 1996). However ecological time series usually have lengths measured in decades, and density-dependent life history can produce autocorrelations in population size on timescales much longer than the generation time of the population (figs. 1, 2). We therefore utilized the sampling variance  $1/(L - \tau)$  for small samples in testing the statistical significance of estimated autocorrelations, so in figure 2 the width of the confidence intervals on the correlograms increases with the lag  $\tau$ .

Consistent statistical estimation of the power spectrum from time series data requires that in the Fourier transformation of the empirical correlogram short time lags should be weighted much more heavily than long time lags, using a set of weights or "lag window," such as the Tukey or Parzen lag windows (Box et al. 1994; Chatfield 1996). For figure 2, we used a Parzen window with  $1.6\sqrt{L}$  points.

*Autoregression Statistics*

*Estimation.* Ignoring end effects as proposed by Kendall et al. (1983) the maximum likelihood estimates of autoregression coefficients are the same as those obtained by formulating the problem as a standard regression model, with the observations being used both as dependent and independent variables. The autoregression coefficients can thus be estimated as the solution of the Yule-Waker equations,  $\mathbf{b} = \mathbf{P}^{-1}\boldsymbol{\rho}$ . However, the autoregression model is very different from a standard regression model, which uses the assumption of independent observations, while the observations in a time series are likely to be strongly dependent, in particular when there is weak density dependence with slow return to equilibrium. The sampling properties of the estimators may therefore be rather different from those derived from standard regression models even if the noise terms are independent. In particular, the maximum likelihood estimates of the autoregression coefficients are biased (Caswell 2001, p. 142), and the uncertainty in the mean population size may be quite large for short time series (eq. [6a]).

*Bias Corrections.* Even for time series that are considered to be extremely long for ecological data, say 50–60 yr (Powell and Steele 1995), the bias of the maximum likelihood estimators may be substantial, often of the same order as the standard deviations. The bias leads to overestimation of the strength of density dependence. Bulmer (1975) gave a simple first order approximation for the bias in  $b_1$  when  $\alpha = 1$ . We estimated the bias by performing repeated stochastic simulations of the time series with estimation of parameters. Numerically, the bias has been corrected so that the mean value of  $\mathbf{b}$  from 10,000 estimates precisely matches the observed estimates. By performing the simulations with a fixed random number seed at the beginning of each set of 10,000 simulations, giving repeatable sequences of the stochastic variables, the problem can be solved numerically by iteration, using the fixed point method with initial values of  $\mathbf{b}$  from the Yule-Waker equations. Convergence of the bias corrected values usually is rapid, within a few iterations.

*Standard Errors.* Standard errors are estimated by parametric bootstrapping, simulating the processes using the bias corrected estimates.

*Significance Testing.* The test statistic for the hypothesis  $D > 0$  is the maximum likelihood estimate of  $D$  (bias correction is not necessary and not recommended here. The critical values will in any case be chosen so that the test has the required significance level). This statistic is simulated 10,000 times to determine the critical values. An interesting and important property of these models is that the distributions of the maximum likelihood estimators do not depend on the unknown variance of the noise term in the model (the total demographic and environmental variance). No correction corresponding to using the  $t$  distribution in regression is therefore required. However, in regression, the distribution of test statistics for regression coefficients does not depend on the other coefficients, that is, those not entering the definition of the null hypothesis. This is not the case in time series, and therefore the simulations must be performed using the bias corrected estimates for these parameters. The null hypothesis only specifies the value of  $D$  (or the sum of the betas), that is, only one out of  $\alpha$  parameters. The distribution of the test statistic will depend on the unspecified parameters, usually called nuisance parameters in statistical terminology, so this distribution can not be found exactly, not even by performing stochastic simulations. In practice, however, these parameter can be replaced by their estimates to obtain an approximation for the distribution. We have done this by keeping the ratios between the coefficients equal to their maximum likelihood estimates. However, we have

checked that the critical values only depend weakly on these parameters.

*Confidence Intervals.* Confidence intervals are found by stochastic simulations adopting the technique of Bølviken and Skovlund (1996). This utilizes the general relation between hypothesis testing and confidence intervals. The set of all parameter values that are not rejected by a test with significance level  $\gamma$  constitutes a confidence region with coverage  $1 - \gamma$ . However, we make the prior assumption that the model is stationary and do not include in the confidence intervals parameter sets corresponding to nonstationary time series. If the end of the interval turns out to be on the border of the stationary region ( $D = 0$ ) we cannot conclude with statistical significance that the series actually is stationary. The technique used by Bølviken and Skovlund (1996) is to perform each test by stochastic simulations from different null hypotheses. By performing the simulations with a given fixed seed for the random number generator the endpoints of the confidence interval can be found just by solving a numerical equation with respect to the parameter of interest. The nuisance parameters have been dealt with as in the tests described above.

APPENDIX B

Linearized Autoregression for Age-Structured Life History

The approximate dynamics of small fluctuations in the age structure,  $\mathbf{x}(t) = \mathbf{n}(t) - \hat{\mathbf{n}}$ , can be obtained by using Taylor expansions of the density-dependent fecundities in the average environment,

$$\bar{f}_k[\mathbf{n}(t)] = \hat{f}_k + \sum_{\tau=1}^{\omega} \left( \frac{\partial \bar{f}_k}{\partial n_{\tau} \hat{\mathbf{n}}} \right) x_{\tau}(t) + \dots$$

Substituting this into (8a) and linearizing produces

$$\begin{aligned} x_1(t) = & \sum_{\tau=1}^{\omega} \hat{\phi}_{\tau} x_1(t - \tau) \\ & + \sum_{k=1}^{\omega} \hat{\phi}_k \frac{\hat{n}_1}{\hat{f}_k} \left[ \sum_{\tau=1}^{\omega} \left( \frac{\partial \bar{f}_k}{\partial n_{\tau} \hat{\mathbf{n}}} \right) x_{\tau}(t - 1) + \varepsilon_k(t - 1) \right] \\ & + \hat{n}_1 \sum_{k=1}^{\omega} \sum_{\tau=1}^{k-1} \hat{\phi}_k \frac{\delta_{k-\tau}(t - \tau)}{\bar{s}_{k-\tau}}. \end{aligned}$$

All age classes can be reduced to yearlings in the past by using the basic demographic relation  $n_{\tau}(t) = l_{\tau}(t -$

$1)n_1(t - \tau + 1)$ , which can be linearized around the equilibrium  $\hat{n}_{\tau} = l_{\tau} \hat{n}_1$  to give

$$x_{\tau}(t) = \hat{l}_{\tau} x_1(t - \tau + 1) + \hat{n}_{\tau} \sum_{j=1}^{\tau-1} \frac{\delta_{\tau-j}(t - j)}{\bar{s}_{\tau-j}}.$$

Substituting this in the previous equation yields

$$x_1(t) = \sum_{\tau=1}^{\omega} \left[ \hat{\phi}_{\tau} + \sum_{k=1}^{\omega} \hat{\phi}_k \left( \frac{\partial \ln \bar{f}_k}{\partial \ln n_{\tau} \hat{\mathbf{n}}} \right) \right] x_1(t - \tau) + \xi(t), \quad (B1)$$

where

$$\begin{aligned} \xi(t) = & \hat{n}_1 \sum_{k=1}^{\omega} \hat{\phi}_k \left[ \frac{\varepsilon_k(t - 1)}{\hat{f}_k} + \sum_{\tau=1}^{k-1} \frac{\delta_{k-\tau}(t - \tau - 1)}{\bar{s}_{k-\tau}} \right. \\ & \left. + \sum_{\tau=1}^{\omega} \left( \frac{\partial \ln \bar{f}_k}{\partial \ln n_{\tau} \hat{\mathbf{n}}} \right) \sum_{j=1}^{\tau-1} \frac{\delta_{\tau-j}(t - j - 1)}{\bar{s}_{\tau-j}} \right]. \end{aligned}$$

Recognizing (9d) and using it to substitute for  $\hat{\phi}_k$  in (B1) gives (9a)–(9c).

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