Estimating density dependence in time-series of age-structured populations

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For a life history with age at maturity α, and stochasticity and density dependence in adult recruitment and mortality, we derive a linearized autoregressive equation with time-lags of from 1 to α years. Contrary to current interpretations, the coefficients for different time-lags in the autoregressive dynamics do not simply measure delayed density dependence, but also depend on life-history parameters. We define a new measure of total density dependence in a life history, D, as the negative elasticity of population growth rate per generation with respect to change in population size, $D = -\partial \ln \lambda^T / \partial \ln N$, where λ is the asymptotic multiplicative growth rate per year, T is the generation time and N is adult population size. We show that D can be estimated from the sum of the autoregression coefficients. We estimated D in populations of six avian species for which life-history data and unusually long time-series of complete population censuses were available. Estimates of D were in the order of 1 or higher, indicating strong, statistically significant density dependence in four of the six species.

Keywords: autoregression; density dependence; life history; stage structure; time-series

1. INTRODUCTION

Detection and estimation of density dependence is 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 & Liebhold 1995; Berryman & Turchin 1997), including interspecific ecological interactions (Turchin 1990, 1995; Royama 1992; Turchin & Taylor 1992; Kaitala *et al.* 1997; Ripa *et al.* 1998; Hansen *et al.* 1999). The life history of a species may largely determine the relative importance of intrinsic and extrinsic factors in contributing to time-lags in population dynamics. For short-lived species with high population growth rates, such as some insects, ecological interactions may best explain time-lags longer than a generation (Turchin 1990, 1995; Royama 1992). For long-lived species with low population growth rates, such as many vertebrates, most time-lags may occur within a generation because of life history (Jensen 1999; Coulson *et al.* 2001; Thompson & Ollason 2001). Understanding density dependence has been impeded by the lack of a general quantitative definition that would allow comparisons among species with different life histories and forms of density dependence (Murdoch 1994).

Time-lags in population dynamics caused by life history have not, to our knowledge, previously been incorporated into methods for detecting and estimating density dependence from population time-series (Bulmer 1975; Pollard *et al.* 1987; Turchin 1990, 1995; Royama 1992; Turchin & Taylor 1992; Hanski *et al.* 1993; Dennis & Taper 1994; Zeng *et al.* 1998). However, Jensen (1999) demonstrated by simulation that stochastic fluctuations in the life history of Walleye fish (*Stizostedion vitreum*) could produce the pattern of delayed density dependence detected by autoregression analysis. Coulson *et al.* (2001) and Thompson & Ollason (2001) showed that time-lags in life history are important in explaining temporal patterns of population fluctuations in Soay sheep (*Ovis aries*) and in Northern fulmars (*Fulmarus glacialis*).

Here, we analyse a density-dependent stage-structured life history to derive linearized autoregressive dynamics of small or moderate population fluctuations around a stable equilibrium. We estimate density dependence in observed time-series of avian populations reproducing at discrete annual intervals. Vertebrate species with mean adult body mass greater than 1 kg usually have $r_{\max} \leq 0.1$ per year (Charnov 1993) and, even for highly fecund species, such as many fishes, 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 & Redfearn 1988; Pimm 1991).

2. DEFINITION OF DENSITY DEPENDENCE

Consider a simple deterministic population model with no age structure, where individuals that reach the age of one year reproduce and then die, as for univoltine insects

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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 product of the probability of survival to maturity and 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 to within 10% if the coefficient of variation is as high as 30% (Lande *et al.* 1999). Denoting the equilibrium population size or carrying capacity as K and the deviation from equilibrium as $x(t) = N(t) - K$, Taylor expansion of λ produces the linearized dynamics

$$x(t) = (1 - \gamma)x(t-1), \tag{2.1a}$$

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

A new measure of total density dependence of the life history of an age-structured population can be defined by interpreting λ in equation (2.1a) 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 (Lande *et al.* 2002) indicates that the total density dependence in the life history, D, should be defined as the negative elasticity of population growth rate per generation, λ^T, with respect to change in population density of adults, 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). Because $\ln\lambda^T = T\ln\lambda$ and at equilibrium $\lambda = 1$ or $\ln\lambda = 0$, we find

$$D = -\left(\frac{\partial \ln\lambda^T}{\partial \ln N}\right)_K = -\left(T\frac{\partial \ln\lambda}{\partial \ln N} + \ln\lambda\frac{\partial T}{\partial \ln N}\right)_K$$
$$= -\left(T\frac{\partial \ln\lambda}{\partial \ln N}\right)_K. \tag{2.1b}$$

Equations (2.1a,b) 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 also applies in the stage-structured life history analysed below (§ 3), with density dependence in juvenile and adult survival as well as recruitment.

3. STAGE-STRUCTURED LIFE HISTORY

The limited duration of most population time-series requires analysis of a stage-structured life history to reduce the number of parameters to be estimated in comparison with a general age-structured life history (Lande *et al.* 2002). Avian populations often have life histories in which the annual survival and reproductive rates of adults are roughly constant and independent of age (Deevey 1947; Nichols *et al.* 1997). In such populations, most 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 (Sæther 1997). This 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.

Defining α as the age at first breeding and $N(t)$ as the number of adults (of age $\geq \alpha$) in year t, the stochastic density-dependent dynamics are described by the non-linear recursion

$$N(t) = s(N,t-1)N(t-1) + \phi(N,t-\alpha,..., \\ t-1)N(t-\alpha). \tag{3.1a}$$

The time dependence of population sizes on the right-hand side of (3.1a) is specified in the functional definitions (3.1b) and (3.1c), below. The probability of adult annual survival is s. The adult annual recruitment rate ϕ is the product of annual fecundity (female offspring per adult female per year) multiplied by first-year survival, f, and the probabilities of annual survival from age i to $i+1$ during the juvenile stages, s_i,

$$\phi(N,t-\alpha,...,t-1) = f(N,t-\alpha)\prod_{i=1}^{\alpha-1}s_{\alpha-i}(N,t-i). \tag{3.1b}$$

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

$$f(N,t) = \bar{f}[N(t)] + \varepsilon(t),$$
$$s_\tau(N,t) = \bar{s}_\tau[N(t)] + \delta_\tau(t) \text{ for } 1 \leq \tau \leq \alpha - 1,$$
$$s(N,t) = \bar{s}[N(t)] + \zeta(t). \tag{3.1c}$$

Similar models with or without stochasticity and density dependence have been applied to a variety of species (Caswell 2001, p. 192).

The coefficient of total density dependence in equation (2.1b) 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 using the generation time for this life history at equilibrium in the average environment, $T = \alpha + \bar{s}/(1 - \bar{s})$ (Lande 1988), produces

$$D = -\left(\frac{\partial \ln\bar{f}}{\partial \ln N} + \sum_{\tau=1}^{\alpha-1}\frac{\partial \ln\bar{s}_\tau}{\partial \ln N} + \frac{\bar{s}}{1 - \bar{s}}\frac{\partial \ln\bar{s}}{\partial \ln N}\right)_K$$
$$= -\left(\frac{\partial \ln\bar{\phi}}{\partial \ln N} - \frac{\partial \ln\bar{\mu}}{\partial \ln N}\right)_K = -\left(\frac{\partial \ln(\bar{\phi}/\bar{\mu})}{\partial \ln N}\right)_K, \tag{3.2a}$$

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.

From the Euler equation at the deterministic equilibrium with $\lambda = 1$, it can be seen that the recruitment rate
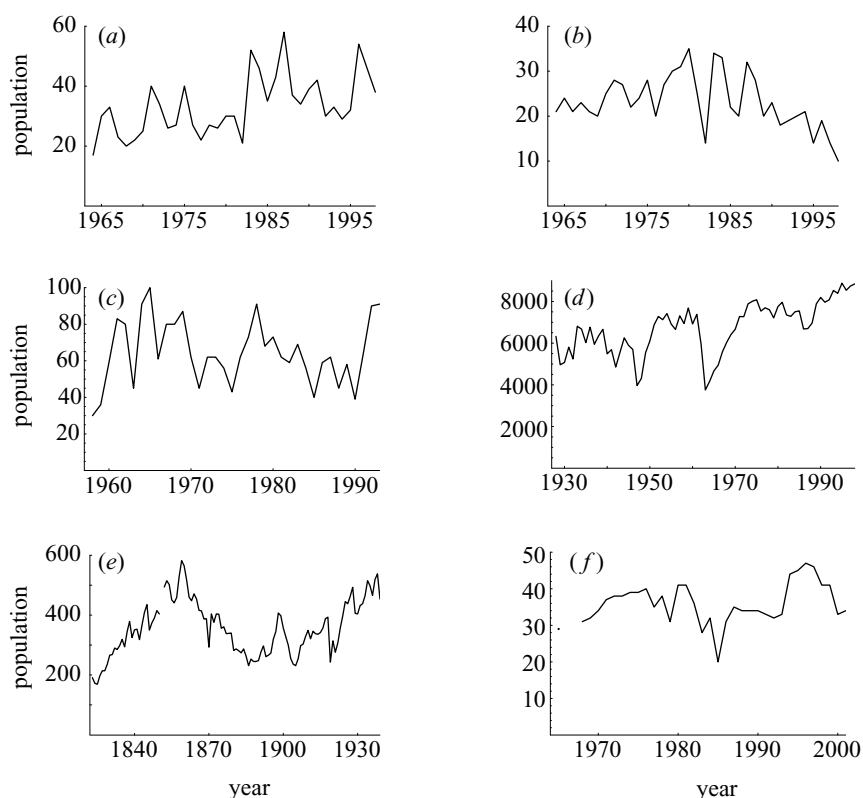
Figure 1. Time-series for annual census of adult population in six avian species. (a) Great tit (*Parus major*); (b) blue tit (*Parus caeruleus*); (c) tufted duck (*Aythya fuligula*); (d) grey heron (*Ardea cinerea*); (e) mute swan (*Cygnus olor*); (f) South Polar skua (*Catharacta maccormicki*).

of adults equals their mortality rate. Denoting equilibrium values as $\hat{s} = \bar{s}(K)$ and $\hat{\phi} = \bar{\phi}(K)$,

$$\hat{\phi} = 1 - \hat{s} = \hat{\mu}. \tag{3.2b}$$

Expanding the vital rates in equation (3.1a) in Taylor series around K, with the deviation from equilibrium denoted as $x(t) = N(t) - K$, gives the linearized autoregression with up to α time-lags

$$x(t) = \sum_{\tau=1}^{\alpha} b_{\tau} x(t - \tau) + \xi(t), \tag{3.3}$$

with constant coefficients

$$b_1 = \left[1 + \left(\frac{\partial \ln \bar{s}}{\partial \ln N}\right)_K\right]\hat{s} + \left(\frac{\partial \ln \bar{s}_{\alpha-1}}{\partial \ln N}\right)_K \hat{\phi},$$

$$b_{\tau} = \left(\frac{\partial \ln \bar{s}_{\alpha-\tau}}{\partial \ln N}\right)_K \hat{\phi} \text{ for } \tau = 2,...,\alpha - 1,$$

$$b_{\alpha} = \left[1 + \left(\frac{\partial \ln \bar{f}}{\partial \ln N}\right)_K\right]\hat{\phi}.$$

The noise term has time-lags of between one year and α years,

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

Hence, even with no autocorrelation in the vital rates, the noise in the autoregression—equation (3.3)—will be auto-correlated if the vital rates operating at different time-lags are cross-correlated at a given time.

For species with age at maturity of one year ($\alpha = 1$), the form of the autoregression and the interpretation of the regression coefficient is different, with the new b_1 being the sum of the old b_1 through b_{α}. Using equation (3.2b), the autoregressive equation is $x(t) = b_1 x(t - 1) + \xi(t)$, where $b_1 = 1 - \hat{\mu}D$ and the noise $\xi(t) = [\zeta(t-1) + \varepsilon(t-1)]K$ has only a single time-lag and no autocorrelation.

Statistical analysis of population dynamics frequently is performed using $\ln N$ rather than N (Royama 1992; Turchin 1995). The linearized autoregression for the dynamics of $\ln N$ is identical to that for N. This can be seen by dividing both sides of equation (3.3) by K, noting that, for small fluctuations, $x/K \approx \ln(1 + x/K) = \ln(N/K) = \ln N - \ln K$.

4. ESTIMATING DENSITY DEPENDENCE

The maximum-likelihood estimator of the autoregression coefficients is identical to the least-squares estimator for a standard regression, if we ignore end effects as proposed by Kendall et al. (1983). The autoregression coefficients can be expressed in terms of population auto-correlations for time-lag τ, denoted as ρ_{τ}. 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), $\boldsymbol{b} = P^{-1}\boldsymbol{\rho}$, where $\boldsymbol{\rho}$ and $\boldsymbol{b}$ are column vectors with elements $\rho_1,...,\rho_{\alpha}$ and $b_1,...,b_{\alpha}$, and P is the population autocorrelation matrix with elements $P_{ij} = \rho_{i-j}$ for i, $j = \{1,...,\alpha\}$ 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

Table 1. Bias-corrected estimates of total density dependence, D, with 95% confidence intervals in parentheses.
(Population time-series fitted to the stage-structured life-history model—equation (3.3)—with age of first reproduction α and annual adult survival rate $\hat{s}$ ($= 1 - \hat{\mu}$)) obtained from the literature (Clobert *et al.* 1988; Dhondt *et al.* 1990; Blums *et al.* 1993, 1996; Owen 1960; North & Morgan 1979; Bacon & Andersen-Harild 1989; Bacon & Perrins 1991; Jouventin & Guillotin 1979; H. Weimerskirch, unpublished data). **$p < 0.01$ for hypotheses that $\hat{\mu}D > 0$, by one-tailed test. CV, coefficient of variation; R^2, proportion of total variance explained.)

species	years	CV	α	$\hat{\mu}D$	R^2	$\hat{s}$	D
great tit	35	0.30	1	0.535** (0.184, 0.879)	0.16	0.46	0.99
blue tit	35	0.26	1	0.507** (0.157, 0.849)	0.15	0.49	0.99
tufted duck	36	0.27	1	0.564** (0.221, 0.907)	0.14	0.65	1.61
grey heron	71	0.18	2	0.081 (0.000, 0.246)	0.73	0.70	0.27
mute swan	116	0.26	4	0.062 (0.000, 0.184)	0.80	0.85	0.41
South Polar skua	35	0.16	5	0.397** (0.103, 1.114)	0.29	0.85	2.65

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 (Lande *et al.* 2002).

The autoregression coefficients in equation (3.3) do not directly reveal the strength of density dependence in population dynamics because the coefficients of density dependence in the vital rates also depend on the life-history parameters $\hat{\phi}$ and $\hat{s}$. For example, even in the absence of density dependence in adult fecundity, $\partial \ln f / \partial \ln N = 0$, the autoregression coefficient for lag α years is not zero but equals the adult recruitment rate at equilibrium, $b_\alpha = \hat{\phi}$.

The time-series analysis described above can be used with life-history estimates of adult annual survival and recruitment rates to determine where in the life cycle density dependence has acted. However, the limited duration of most ecological time-series reduces the statistical accuracy of such assessments (Lande *et al.* 2002).

There are α autoregression coefficients and, from equations (3.2) and (3.3), the product of the adult mortality rate and the total density dependence in the life history can be estimated, with reasonable accuracy, as one minus the sum of the autoregression coefficients,

$$\hat{\mu}D = 1 - \sum_{\tau=1}^{\alpha} b_\tau. \tag{4.1}$$

Time-series were analysed for six avian populations with three or more decades of accurate annual census data and few missing observations (figure 1). 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, are for the total adult population ($\geqslant 1$ year old). Counts of the tits are almost exact since nearly all pairs breed 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 ($\geqslant 2$ years old) in southern Britain, which therefore constitutes a relatively closed population. Counts of the mute swan (*Cygnus olor*) on the Thames, England, are for the total population minus fledglings. The time-series for the mute swan was truncated following

a period of no data during World War II, after which population large increases occurred in both adults and yearlings (Cramp 1972). Some of the mute swan annual counts may be biased (Birkhead & Perrins 1986) and fledglings were wing-clipped during the counts to reduce emigration (Cramp 1972); this series is included mainly for illustrative purposes because of its length. The South Polar skua (*Catharacta maccormicki*) population at Pointe Géologie archipelago, Terre Adélie, Antarctica, has significant recruits from outside of the archipelago. The strong territoriality of adults helps to ensure that all birds in the archipelago are ringed and the counts of breeding adults are exact. Years without a complete census were excluded from the analysis of the mute swan and South Polar skua.

Employing basic statistical methods for stationary autoregressive time-series analysis, we found evidence of density dependence in four out of the six species (table 1). Although the theory indicates that the noise in the population process may be autocorrelated—see equation (3.3)—so that, using life-history information, the population time-series could in principle be analysed as an autoregressive moving average process (ARMA, cf. 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.

5. DISCUSSION

Turchin (1990, 1995), Royama (1992), Turchin & Taylor (1992), Zeng *et al.* (1998) and others fitted nonlinear autoregressive models with time-lags of one, two or three years to population time-series. They interpreted a significant autoregression coefficient for a time-lag greater than one year as evidence for density dependence with a time-lag. However, their models are phenomenological and not based on explicit demographic mechanisms. Our results—see equation (3.3)—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. In the stage-structured model, density dependence operates with time-lags up to α years. Contrary to previous interpretations, the autoregression coefficients do not directly measure density dependence operating at particular lags. The autoregressive coefficients depend on parameters of the life history as well as density dependence of a particular stage class.

It is instructive to consider a species with $\alpha = 1$ and autoregression coefficient $b_1 = 0$, which implies that all autocorrelations are zero (except $\rho_0 = 1$), corresponding to a flat power spectrum or white noise process for the population. 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 tufted duck approaches this situation, having a low R^2 (table 1). Thus, statistical significance of autoregression coefficients is not a valid criterion for the detection of density dependence.

Total density dependence in the life history was significant in four out of the six species. Comparing the strength of total density dependence, D, between species requires correcting the estimates of $\hat{\mu}D$ in table 1, through division by the adult annual mortality rate, $\hat{\mu}$. In conjunction with the estimates of $\hat{\mu}D$ derived from autoregression analyses, adult annual survival rates $\hat{s}$ ($= 1 - \hat{\mu}$) obtained from life-history studies allow estimation of the total density dependence, D, in each of the populations (table 1). Strong density dependence occurs in each of the four populations in which significant estimates were obtained. Density dependence for the grey heron and the mute swan, which had the longest time-series, is relatively weak and not significant. The average value of the total density dependence in the six species is $\overline{D} = 1.16$. Thus, on average, a given proportional increase in adult population density, N, produces roughly the same proportional decrease in multiplicative growth rate of the population per generation, λ^T. Because the expected annual rate of return to the equilibrium population size is $\gamma = D/T$, stochastic perturbations from the equilibrium population size for the bird species analysed here all appear to have $0 < \gamma < 1$ and thus to be undercompensated (Begon *et al.* 1996, pp. 239–240), since even for species with age of maturity equal to one year the generation time is generally larger than D.

Autocorrelation of physical and biotic environments has been discussed as a cause of autocorrelated noise (Williams & Liebhold 1995; Berryman & 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—see equation (3.3). Observed correlations among vital rates (Sæther & 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 multiplied by first-year survival) are much more variable among years than estimates of adult mortality (Gaillard *et al.* 1998, 2000; Sæther & Bakke 2000), as observed in the tufted duck (Blums *et al.* 1996), grey heron (North & Morgan 1979) and mute swan (Cramp 1972; Bacon & Perrins 1991). This would tend to reduce the environmental covariance of vital rates in the stage-structured model—see equation (3.3). The present autoregression analysis, like previous studies (see, amongst others, Turchin 1990, 1995; Royama 1992; Turchin & Taylor 1992; Zeng *et al.* 1998), assumes 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. Time-series of at least an order of magnitude longer than the number of autoregression coefficients are required to estimate accurately the total density dependence.

Our results illustrate the advantages of applying demographic theory both to define the total density dependence quantitatively in a life history and to estimate it from population time-series.

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