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Density Dependence Special Section

Detecting and Estimating Density Dependence in Wildlife Populations

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ABSTRACT We review methods for detecting and assessing the strength of density dependence based on 2 types of approaches: surveys of population size and studies of life history traits, in particular demographic parameters. For the first type of studies, methods neglecting uncertainty in population size should definitely be abandoned. Bayesian approaches to simple state-space models accounting for uncertainty in population size are recommended, with some caution because of numerical difficulties and risks of model misspecification. Realistic state-space models incorporating features such as environmental covariates, age structure, etc., may lack power because of the shortness of the time series and the simultaneous presence of process and sampling variability. In all cases, complementing the population survey data with some external information, with priority on the intrinsic growth rate, is highly recommended. Methods for detecting density dependence in life history traits are generally conservative (i.e., tend to underestimate the strength of density dependence). Among approaches to correct for this effect, the state-space formulation of capture–recapture models is again the most promising. Foreseeable developments will exploit integrated monitoring combining population size surveys and individual longitudinal data in refined state-space models, for which a Bayesian approach is the most straightforward statistical treatment. One may thus expect an integration of various types of models that will make it possible to look at density dependence as a complex biological process interacting with other processes rather than in terms of a simple equation; modern statistical and modeling tools make such a synthesis within reach. © 2012 The Wildlife Society.

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The i-state philosophy (Diekmann 2005) describes demography at the individual level based on life-cycle stages. This philosophy naturally leads to describe death, fecundity, and more generally any transition between stages such as recruitment or dispersal, through per capita parameters. If such individual parameters are constant or at least stationary (in the sense of stochastic processes: affected by random effects that can be shifted over time and, as such, not affected by a trend), the population growth is exponential, generally after a dampening of the effect of initial population structure, as in matrix models (Caswell 2001) and their stochastic generalizations (Tuljapurkar 1990). The key paradigm of exponential growth in population dynamics (Turchin 2001) is thus intimately linked to the i-state philosophy.

For more than 2 centuries (Malthus 1798), scientists have recognized that exponential growth is impossible in the long term (Turchin 2001), as exponential growth leads to large population sizes that unavoidably induce depletion of resources and, in turn, individual performance. This is a broad definition of density dependence, as a phenomenon that explicitly has to do with resource and individual performance. We loosely use the word density for population size or local population size (e.g., in the term density dependence).

Density dependence became a key subject in population dynamics with the well-known logistic growth curve (Verhulst 1838). One of the discrete time counterparts is the discrete time Gompertz model $N_{t+1} = \lambda N_t^{-b} N_t$ with $b > 0$. Such models are phenomenological, as they describe only the population level and do not explicitly consider the individual level, contrary to mechanistic models, such as matrix models that translate individual parameters into population level consequences. Since the 19th century, researchers have debated phenomenological and mechanistic approaches to density dependence (see Murdoch 1994, Krebs 1995) and discussions continue (e.g., Berryman 2004) on the role of limitation by resource availability, an individual level phenomenon, as supposedly opposed to regulation by density dependence, a population level result.

A key question is whether density dependence is present in a population, and if so, how to measure its intensity. As usual,

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even if one relies on some statistical significance for detection, one has some biological significance in mind (i.e., the idea that density dependence is or is not negligible for the future fate of the population or relative to other sources of variation) and thus bears a relationship to its management (Guthery and Shaw 2012). Indeed, the measurement phase is often linked with the idea that population projections accounting for density dependence go one step beyond those based on constant parameters; a strong assumption of stationarity in the projection still exists but rather than "as if parameters were the same as up to now", it is "as if parameters were varying with density as they have been shown to do up to now." Estimating the strength of density dependence is also central in discussions of the relative role and magnitude of density dependent and density-independent variation in population size, the subject of a famous controversy in the 1950s (Andrewartha and Birch 1954, Lack 1954).

Not surprisingly, the tension between population and individual level approaches has been pervasive in the issue of detection and estimation of density dependence, possibly because the data themselves can be at the population level only (e.g., population surveys) or at the level of individual traits only (e.g., body weight data). Finally, statistical difficulties arise as the arrow of time induces dependencies that cannot be handled by naïve statistical approaches. Although a comprehensive review of the literature would be beyond reach, the issues of detection and measurement of density dependence have alternatively raised optimistic and pessimistic points of view, and have been a subject of frustration (Dennis and Taper 1994). Can we take series of data and estimate in a simple fashion how many show density dependence, as done by Brook and Bradshaw (2006) for 1,198 species, or should we conclude with Krebs (1995) that density dependence is an unattainable holy grail?

The purpose of this article is to attempt to review the subject of detection and estimation of density dependence with specific reference to these difficulties and the resulting confusion. However, we heed the advice of J. B. S. Haldane, "if you are faced by a difficulty or a controversy in science, an ounce of algebra is worth a ton of verbal argument" (Maynard Smith 1965). Although we will use many equations, this review will attempt to avoid technical developments (for a more technical review, see Lebreton 2009).

We will first review the methods for detection and estimation of density dependence based on population size estimates, in 3 steps: 1) an attempt to formalize the role of resource and density, 2) methods in the absence of uncertainty in population size, and 3) methods accounting for uncertainty in population size, a key feature for wild animal populations. Then we will review methods based on analyses of individual traits, demographic or not. Finally, we will discuss new modeling opportunities and perspectives.

We completed calculations using our own Matlab® (MathWorks, Natick, MA) code, carefully validated by a series of cross-checks, and WinBUGS (Lunn et al. 2000). The Matlab® code is made available online at www.onlinelibrary.wiley.com.

DETECTING AND ESTIMATING DENSITY DEPENDENCE BASED ON POPULATION SIZE ESTIMATES

The Gompertz model $N_{t+1} = \lambda N_t^{-b} N_t$ becomes linear on a log scale. Denoting $x_t = \mathrm{Ln}(N_t)$ and $r = \mathrm{Ln}(\lambda)$:

$$x_{t+1} = r + (1 - b)x_t \tag{1}$$

As recalled by Lebreton (2009), $r = \mathrm{Ln}(\lambda)$ is the growth rate for $N = 1$, whereas the growth rate for $N = 0$ is infinite negative. This bears no consequences on our treatment of this model and related ones, and we will speak of r as the intrinsic growth rate.

Under $b = 0$ (i.e., density independence) the model reduces to

$$x_{t+1} = r + x_t \tag{2}$$

As the world is not deterministic, a straightforward stochastic generalization considers some extra random variation to represent demographic and environmental stochasticity, leading under density independence and density dependence, respectively, to:

$$x_{t+1} = r + (1 - b)x_t + \varepsilon_t \tag{3}$$

$$x_{t+1} = r + x_t + \varepsilon_t \tag{4}$$

The random terms, represented by Greek letters, have expectations equal to 0 and, unless otherwise stated, are assumed to be normally distributed. The latter model is a random walk; besides the shift r, x_t varies through independent additive increments. Because of their simplicity, these models have been used by a number of authors over the years (see Dennis et al. 2006, Lebreton 2009). One can equivalently test for density dependence either by a test of model (3) versus model (4), such as a likelihood ratio test, or by a test of H_0 $b = 0$ in model (3) (e.g., a Wald test). The latter approach is usually preferred as it can easily be implemented as a one-tailed test of H_0 $b = 0$ versus H_1 $b > 0$, the alternative of biological interest.

Density Dependence and Resource Dependence

By rewriting (3) one can make a per capita growth rate $r - bx_t + \varepsilon_t$ appear:

$$x_{t+1} = (r - bx_t + \varepsilon_t) + x_t \tag{5}$$

As density dependence occurs through the depletion of resource of some kind, in the per capita growth rate, the log population size x_t is a proxy for something else. Let's assume a single latent variable l_t, such as the amount of a key resource used, is the actual determinant of the growth rate. Assuming l_t can be expressed on the same scale as x_t, the actual growth rate is then $r - bl_t + \varepsilon_t$. The log-population size x_t is then a proxy for l_t, with a relationship necessarily modified by some random variation, $l_t = x_t + \varsigma_t$, as the proxy and the latent variable cannot be expected to be perfectly correlated over time. The random term ς_t has a null expectation (i.e., $E(\varsigma_t) = 0$). Note that this issue has nothing to do with uncertainty on x_t, a problem that will be examined later.

One should thus use $x_{t+1} = (r - bl_t + \varepsilon_t) + x_t$ or, alternatively,

$$x_{t+1} = (r - b(x_t + \varsigma_t) + \varepsilon_t) + x_t \tag{6}$$

Although model (5) (or equivalently 3) is analogous to a linear regression of x_{t+1} on x_t (to an extent that will be discussed later), model (6) is affected by an error-in-variable (e.g., Fuller 1987). In practice, the latent variable l_t is unknown and so is var(ς_t); model (6) cannot be readily used instead of (3). What are the consequences of the error-in-variable problem on detection and estimation of density dependence when using (3)? Under H_0 $b = 0$, model (6) reduces to $x_{t+1} = (r + \varepsilon_t) + x_t$ (i.e., model 4). The distribution of any estimator of b under H_0 remains thus unaffected by the error-in-variable problem. So, although density dependence is strictly a model concept, testing for it is equivalent to a test of dependence on resource depletion, at least in the simplistic setting considered here. As far as we know, the consequences on the estimated slope under H_1 $b > 0$ (i.e., the estimated strength of density dependence when present) remain to be explored.

Methods for Detecting Density Dependence in the Absence of Uncertainty on Population Size

Model (3) $x_{t+1} = r + (1 - b)x_t + \varepsilon_t$ can easily be treated by maximum likelihood, preferably conditional on x_1, which plays no role in the estimation of b (Dennis and Taper 1994:209, Hamilton 1994:123, Lebreton 2009). Because of the linear structure of the model, the maximum likelihood estimator (MLE) of $1 - b$ is obtained by the formula for estimating the slope of the ordinary linear regression of x_{t+1} with respect to x_t. This apparent simplicity is quite unfortunate, as the estimator does not benefit from the properties of the regression estimator, because the underlying statistical model is not the usual linear regression model; the same variable appears both as an independent and dependent variable, with a shift in time (i.e., autoregressive model). We illustrate what happens under H_0 $b = 0$ (Fig. 1); the joint distribution of the pairs (x_{t+1}, x_t) is aligned along the line $y = r + x$. Samples of this distribution thus, on the average, have a major axis with slope 1. The regression estimate is then necessarily, on the average, below 1. As a consequence, the estimator of b is positively biased (i.e., the naïve approach tends to detect too often density dependence). Despite repeated warnings as early as the 1970s (e.g., Maelzer 1970), few people realize this bias is present in the absence of uncertainty on population size (e.g., see abscissa 0 in Fig. 2 and item 2 of the summary in Freckleton et al. 2006). Asymptotically, the estimate is not biased, just because the regression line comes closer and closer to the line $y = r + x$ as the scatter of points become more and more elongated since var(x_t) $\to \infty$ when $t \to \infty$ (Fig. 1) while var(x_{t+1}/x_t) = var(ε_t) remains constant. As, in studies of wild animal populations, the time series are usually fairly short, the asymptotic absence of bias offers little consolation.

Two approaches have been proposed to account for this bias:

1) Using simulation (i.e., parametric bootstrap; Dennis and Taper 1994). Basically, one generates pseudo-samples using estimates under H_0 $b = 0$ and uses the appropriate percentiles of the empirical distribution of the resulting estimates of b to accept or reject H_0. In our model, this approach would amount to a bias correction, but Dennis

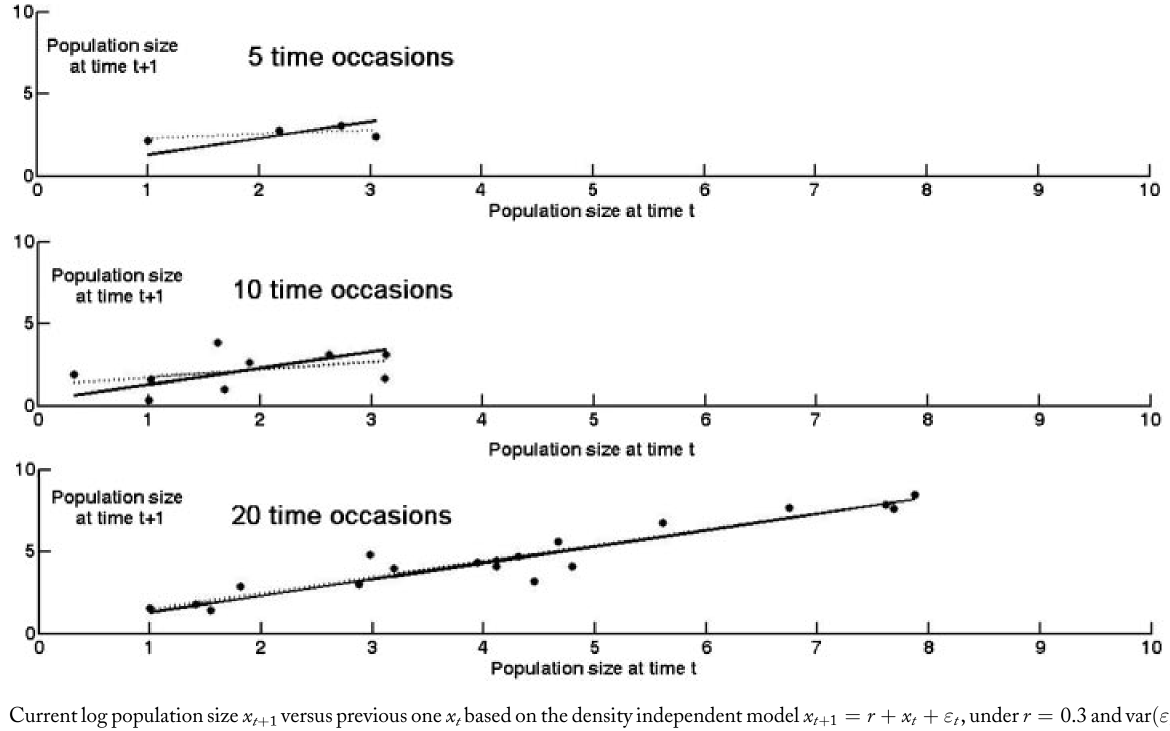

Figure 1. Current log population size x_{t+1} versus previous one x_t based on the density independent model $x_{t+1} = r + x_t + \varepsilon_t$, under $r = 0.3$ and var(ε_t) = 0.64. From top to bottom, simulations over 5, 10, and 20 time occasions, respectively. The regression line of x_{t+1} versus x_t (dotted lines) progressively converges to the line $x_{t+1} = r + x_t$ (plain lines) as var(x_t) $\to \infty$ (i.e., the regression slope progressively converges to 1). For all finite sample sizes, this approach points to a model $x_{t+1} = r + (1 - b)x_t + \varepsilon_t$ with $b > 0$ (i.e., to density dependence).

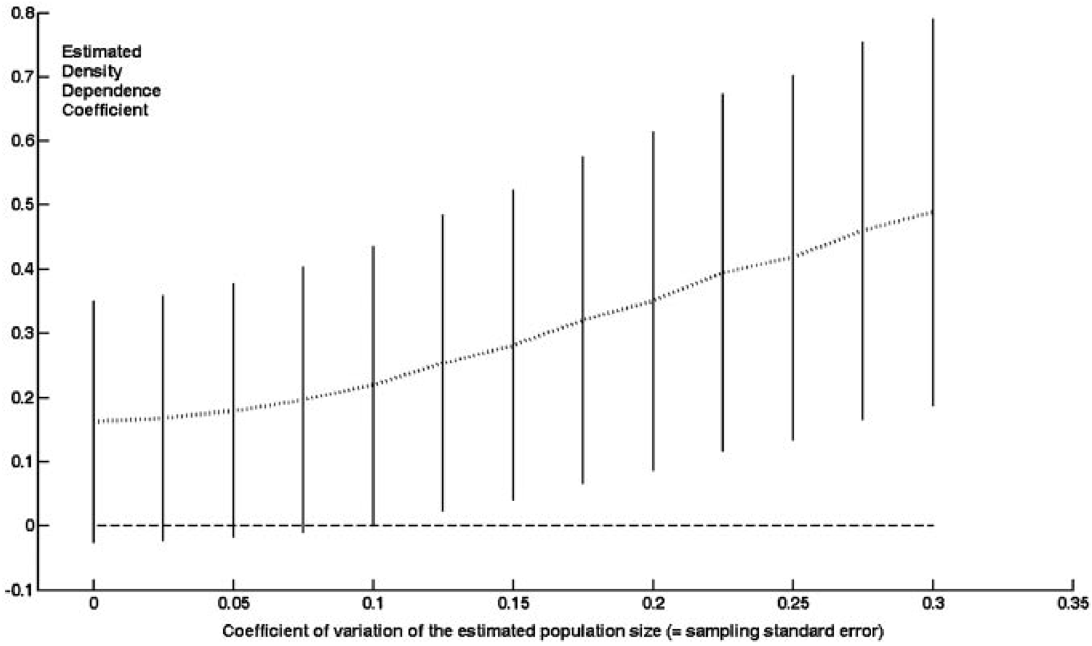

Figure 2. Estimated strength of density dependence (ordinate) in absence of density dependence, when uncertainty in population size (as a coefficient of variation, abscissa) is neglected. The bias in the estimated strength of density dependence strongly increases with the uncertainty in population size. The simulated data is based on the density independent model $x_{t+1} = r + x_t + \varepsilon_t$ with uncertainty on log-population size represented as $y_t = x_t + \eta_t$. The estimated strength of density dependence (ordinate) is the maximum likelihood estimate of b in the model $y_{t+1} = r + (1 - b)y_t + \varepsilon_t$ over 30 time steps in which y is treated as the true log population size. In abscissa, $\mathrm{SE}(y_t/x_t) = \mathrm{SE}(\eta_t)$ is the coefficient of variation of the estimated population size. Dotted line: Mean estimate $\hat{b}$ (5,000 replicates each), vertical lines: 95% limits of the 5,000 replicates.

and Taper (1994) use it with a slightly different, nonlinear, model in which the approach also overcomes the absence of distributional results.

2) Obtaining an expression for the bias. Lebreton (2009), reformulating results by Saint-Amant (1970), develops a bias corrected t-test of H_0 $b = 0$, and checks if the resulting test-level is sufficiently close to the nominal α. A bias-corrected estimate can also be directly derived from the general study of the bias of the autocorrelation coefficient by Kendall (1954, in Sawa 1978) for a time series of length T, as $\tilde{b} = \hat{b} - ((4 - 3\hat{b})/T)$.

Naïve approaches are still commonly used (e.g., Sæther et al. 2005, Sibly et al. 2005, among others). For a particular study, they can lead to grossly misleading results. In meta-analyses, the bias on the density dependence coefficient induces an overestimation of the prevalence of density dependence. Based on the impossibility of long-term exponential growth, one gets a faked statistical confirmation of a plausible result! However, the corrections to bias mentioned above do not appear to be a general solution to be recommended. Indeed, they largely amount to a useless statistical exercise, as the assumption of no uncertainty in x_t is very stringent and far from met for most animal population surveys. We thus strongly recommend approaches not accounting for uncertainty in population size are abandoned. Handling this uncertainty is the subject of the next section.

Methods Accounting for Uncertainty in Population Size

Bulmer (1975) was the first author to formulate the linearized Gompertz model with uncertainty in population size. In this formulation, the state of the population is described by model (3) above, and only a time series of estimated log-population size y_t is observed:

$$x_{t+1} = r + (1 - b)x_t + \varepsilon_t \tag{7}$$

$$y_{t+1} = x_{t+1} + \eta_{t+1} \tag{8}$$

Bulmer (1975), in a direct treatment of the model, rewrote it as

$$y_{t+1} = r + (1 - b)y_t + \eta_{t+1} - (1 - b)\eta_t + \varepsilon_t \tag{10}$$

which clearly shows a further dependency over time induced by the presence of η_t both in the equation for y_{t+1} and that for y_t.

Neglecting it (i.e., treating y_t by the previous regression-like method) induces a severe bias (Bulmer 1975) that has rarely if ever been illustrated. Simulations clearly show how the faked evidence for density dependence (i.e., the bias in $\hat{b}$) increases with the uncertainty in population size, over a range of realistic values of the coefficient of variation for the estimated population size (Fig. 2).

The ad hoc tests proposed by Bulmer (1975) were criticized by Den Boer and Reddingius (1989), in particular because they are not optimal, statistically speaking. However one clearly distinguishes in the model above a state (7) and an observation (8) (i.e., a linear Gaussian state-space model), which can be treated by specific methods such as the Kalman filter, as noted by Lebreton (1989). The Kalman filter makes obtaining the likelihood of the model possible, based on a series of observations $(y_1, y_2, \ldots, y_T)$, as presented in a clear and detailed way by Dennis et al. (2006). The MLE adequately exploits the statistical information available and is definitely preferable to any ad hoc estimate such as the regression estimate from the previous model or the explicit formulas proposed by Bulmer (1975). The MLE has to be obtained numerically, with, according to Dennis et al. (2006), special care because of potential multiple minima in the likelihood (see also Polansky et al. 2009). This approach removes the substantial bias that would have been present by ignoring the uncertainty in population size (Fig. 2). However, the MLE is again only asymptotically unbiased (i.e., suffers from some bias for realistic sample sizes). As in the absence of sampling error, some bias corrections could be obtained from the results on the autocorrelation coefficient bias, extended to autocorrelated random errors by Sawa (1978), based on the model presentation in (10).

Moreover, the distribution of the MLE under H_0 $b = 0$ cannot be easily obtained (Dennis et al. 2006). Thus, it cannot be used without care for a test of density dependence. Dennis et al. (2006) also discuss alternative estimation methods, based in particular on the first-order differences of the estimated log-population sizes (y_t). Knape and De Valpine (2012) go one step further with this approach by implementing a test of density dependence based on the likelihood ratio statistic between model (7, 8) and its density independent version, obtaining its distribution under H_0 $b = 0$ by parametric bootstrap, exactly as Dennis and Taper (1994) did for the model without uncertainty on population size. To avoid distributional problems with the test statistics, one can use a Bayesian approach, easily implemented in WinBUGS (Lunn et al. 2000) or in R via JAGS (Plummer 2003) using, for example, a 95% credible interval as an admissible set of parameter values. Bayesian approaches also allow for flexibility in the functional form of the state equation (i.e., the shape of density dependence) and in the distribution of the random terms. These approaches currently seem the most reliable and the handiest ones, even if the underlying properties of the models (e.g., the degree to which the various parameters are separately identifiable) do not depend on the estimation method and still remain often problematic.

Let us briefly examine the performance of these approaches, first by simulation. Deviance contours from simulated data (Fig. 3) show no evidence of local minima at the scale considered. However the estimates of r and b are strongly correlated for realistic lengths of the time series. They behave as the estimated intercept and slope of a regression when the dependent variable values are on a same side of the origin, to an even greater extent because of the 2 levels of uncertainty (process + sampling) and the dependency over time (equation 10) they induce. The estimate of the process and sampling standards errors, $\mathrm{SE}(\varepsilon_t)$ and $\mathrm{SE}(\eta_t)$, are also highly correlated, although to a lesser degree than the estimates of r and b, whereas the correlation between the 2 parameter subsets remain moderate. How does this translate in a real world example?

Let us use as an illustrative example the spring population surveys of greater snow geese (*Chen caerulescens atlantica*) in Quebec from 1973 to 2002 (Gauthier et al. 2007). The deviance did not show local minima. Out of over 1,000 iterative searches starting from random initial values, only 21 did not fully converge in 1,000 iterations; 15 had practi-

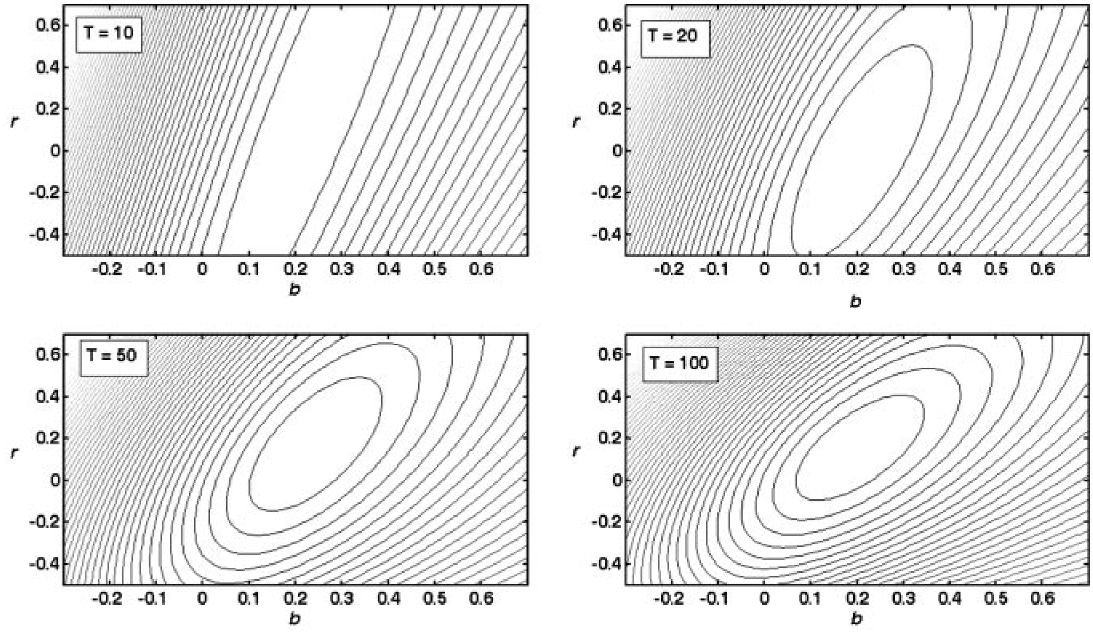

Figure 3. Deviance ($-2 \times$ log-likelihood) contours of simulated trajectories of increasing number of time steps ($T = 10$, 20, 50, and 100) of the density-dependent model $x_{t+1} = r + (1 - b)x_t + \varepsilon_t$ with uncertainty on log-population size represented as $y_t = x_t + \eta_t$. The parameters used in the simulations are $r = 0.1$, $b = 0.3$, $\mathrm{SE}(\varepsilon_t) = 0.2$, and $\mathrm{SE}(\eta_t) = 0.4$. The deviance is represented under $\mathrm{SE}(\varepsilon_t) = 0.2$, $\mathrm{SE}(\eta_t) = 0.4$ as a function of b (in abscissa, from -0.3 to 0.7) and r (in ordinate, from -0.5 to 0.7). The contours clearly show that in presence of uncertainty on population size, the likelihood and the maximum likelihood estimates are well behaved in the absence of model misspecification; and for a realistic number of time steps (<50), the estimates of r and b will be strongly positively correlated, making it difficult to distinguish between low intrinsic growth rate and light density dependence versus high intrinsic growth rate and strong density dependence.

Table 1. Sampling correlations between the maximum likelihood estimate of the parameters of the stochastic Gompertz model for the greater snow goose data from Gauthier et al. (2007).

Parameters (as rows and columns)	Sampling standard error, SE(η_t)	Process standard error, SE(ε_t)	Intrinsic growth rate, r	Coefficient of density dependence, b
SE(η_t)	1.0000	−0.7063	0.2955	0.2910
SE(ε_t)	−0.7063	1.0000	−0.2947	−0.2900
r	0.2955	−0.2947	1.0000	0.9989
b	0.2910	−0.2900	0.9989	1.0000

cally converged; and 6 were still not at the global optimum. They concerned searches starting from large sampling standard error and small process standard error, a combination mimicking a short, instable time series.

The MLEs of r and b are highly correlated (0.9989, Table 1), and the MLE of r (0.3191) seems unrealistic (Table 2, second row) as it corresponds to a 37.6% increase per year. These 2 features combined make the estimate of the coefficient of density dependence (b) suspicious.

The correlations between estimates (Table 1) emphasize the difficulty to separately estimate the sampling and process variance, and even more, r and b, which are nearly not separately estimable. The latter point makes practical sense; similar population trajectories can arise as the result of a high intrinsic growth rate and a strong density dependence, or a weaker intrinsic growth rate and a low density dependence (Fig. 4). The set of 4 parameters nearly appears as a set of 2 macro-parameters, 1 for the deterministic trajectory, the other 1 for the uncertainty. Based on our simulations (Fig. 3) and a variety of unpublished examples, we think this situation is general. It immediately leads to consider the use of external information to improve the identifiability. Bayesian approaches using appropriate prior distributions on the parameters appear then as a necessity, rather than just an algorithmic convenience.

An estimate of the sampling standard error will often be available, for example, when the population size estimates come from capture–recapture (e.g., Dennis and Otten 2000, who do not account for this uncertainty in their analysis), from stratified sampling (as is the case with the greater snow goose), or more directly, through replicated population sampling (Dennis et al. 2010). However, because of the high correlation with the estimated coefficient of density dependence, and because of the unrealistic estimate often obtained, as in the snow goose example, the main target for external information is certainly the intrinsic growth rate, r. We strongly suspect that a fair part of published examples correspond to unrealistic estimates of r, without being able to check, as the estimates of r are rarely given in published examples because of the focus on the coefficient of density dependence, b.

Assuming in the snow goose example a Gaussian prior distribution for r with mean 0.20 and standard error 0.06 (i.e., with 95% of the density between 0.12 and 0.28), constraining r to a realistic value for such a species (Niel and Lebreton 2005, their Table 2) did improve the results (Table 2, third and fourth row) and provided evidence of very weak density dependence, with nearly no biological significance.

The population size survey appeared as fairly precise, as the MLE of the standard error of the log population size (coefficient of variation was 0.0607) was comparable in magnitude to the field estimate (10% or less; Gauthier et al. 2007:1422). This fairly good precision limited the bias of the naïve regression approach (Table 2, first row), with a 95% confidence interval for the coefficient of density dependence encompassing 0, despite its bias. Accounting for uncertainty in population size not only removes a bias, but also increases the precision on the coefficient of density dependence by reducing the estimate for the process standard error.

Contrary to Dennis et al. (2006) and Knape and De Valpine (2012), we found no pervasive presence of local minima in the likelihood, although we agree that care should be exercised on this point (Knape 2008). The sampling correlation between the estimates of r and b and the resulting near non-identifiability is, for us, the main problem. Results from simulated data (Fig. 3, and unpublished results on shorter time series) and a few other unpublished examples indicate similar general properties of what remains in the words of Dennis et al. (2006) a "minimal model." The improvement brought by using a prior for the intrinsic population growth rate encourages refining the model and combining it with further pieces of external information, to improve its moderate performance. It gives a central role to Bayesian approaches, which also bring a great deal of flexibility. We do not think considering a value of $\hat{b}$ significantly differing from 0 as a fair evidence for density dependence without checking if the associated $\hat{r}$ value makes sense. We currently recommend, as a minimal step, a careful look at the estimated intrinsic growth rate, and the use of a prior for r based on comparative demography approaches (e.g, Niel and Lebreton 2005).

From a Minimal to Realistic Models

Besides the difficulties just mentioned, the minimal model above may be inappropriate in practice for a variety of reasons (Lebreton 2009). The most prominent issues are:

1) Environmental covariates have to be taken into account to reduce the residual standard error and enhance power and, if negatively autocorrelated, to distinguish their effect from that of density dependence (e.g., Lebreton 1990).
2) Age structure (e.g., with delayed recruitment) may require considering dependency over several time steps in components of population size.
3) Further structure such as spatial cells may have to be considered, for example, to model local density dependence

Table 2. Estimation of parameters r, b, $\mathrm{var}(\varepsilon_t)$, and $\mathrm{var}(\eta_t)$ of the density-dependent model $x_{t+1} = r + (1 - b)x_t + \varepsilon_t$ with uncertainty on log-population size represented as $y_t = x_t + \eta_t$, applied to spring population surveys of the greater snow goose (data from Gauthier et al. 2007). First row: naïve regression approach on log population size, neglecting uncertainty in population size. Second row: maximum likelihood estimation (MLE) of the model accounting for uncertainty in population. Third row: Bayesian approach of that same model with a Gaussian prior distribution for r with mean 0.20 and standard error 0.06 and uninformative priors for the other parameters. Fourth row: Bayesian approach of that same model with a Gaussian prior distribution for r with mean 0.20 and standard error 0.06, explicit posterior normal distribution.

Parameter method	Process standard error, $\sqrt{\mathrm{var}(\varepsilon_t)}$	Observation standard error, $\sqrt{\mathrm{var}(\eta_t)}$	Growth rate, r	Coefficient of density dependence, b	$\mathrm{Corr}(\hat{r}, \hat{b})$	Deterministic equilibrium, $(\hat{r}/\hat{b})$
Naïve regression neglecting uncertainty in population size (95% CI)	0.1398		0.5044 (−0.5446, 1.5533)	0.0357 (−0.0469, 0.1184)	0.9988	14.12
MLE of model with uncertainty in population size (95% CI)	0.1041	0.0607	0.3191 (−0.2731, 0.9112)	0.0210 (−0.0258, 0.0678)	0.9990	15.21
Bayesian approach with prior constraining r (2.5% and 97.5% quantiles from MCMC[a] methods)	0.1210	0.0528	0.2022 (0.0865, 0.2413)	0.0118 (0.0019, 0.0151)	0.931	17.19
Bayesian approach based on normal distribution (2.5% and 97.5% quantiles from MCMC methods)	0.1022	0.0628	0.2024 (0.1201, 0.2847)	0.0118 (0 0049, 0.0187)	0.951	17.15

[a] Markov chain Monte Carlo.

(Murdoch 1994) or dependence on some components of population size.

4) The response to density may be nonlinear and more complex functional forms may have to be considered (e.g., Dennis et al. 2006). Comparative explorations of the functional form based on naïve regressions neglecting uncertainty in population size (Sibly et al. 2005) appear as highly questionable.

Neglecting any of these issues may result in a model misspecification, and thus in biases of the estimate of the intensity of density dependence and the corresponding tests or diagnostics of density dependence.

Although in the original presentation by Bulmer (1975) the minimal model was presented as a specific statistical object, the state-space model point of view opens a number of perspectives (De Valpine 2002). For instance, generalizing the state equation to account for an environmental covariate, z_t, as $x_{t+1} = r + (1 - b)x_t + cz_t + \varepsilon_t$ is relatively easy. Good examples are provided by Jacobson et al. (2004) and Pasinelli et al. (2011). It is also possible to adapt the model to particular life cycles. A good example of a model with a seasonal life cycle is provided by Stenseth et al. (2003). In all such models, the main potential bias of the slope for density dependence is removed by incorporating the population size uncertainty in the observation equation. However, the slope remains biased for finite sample sizes to an unknown degree. The likelihood for such models can be multimodal (Polansky et al. 2009) and as a consequence the MLE can often be difficult to obtain.

Parametric bootstrap for such realistic models (e.g., with age structure, with covariates) may be tedious and remain thus confidential until a specialized user-friendly piece of software is produced. Restricted maximum likelihood approaches based on first order differences found promising by Dennis et al. (2006) could be useful, but have yet to be investigated in such a more complex setting. A Bayesian approach seems the most straightforward treatment. As an alternative to Markov chain Monte Carlo algorithms, the posterior distributions can be obtained through numerical integration (De Valpine and Hastings 2002), and explicitly in simple cases under Gaussian distributions.

An Overview of Methods Based on Time Series of Estimated Population Sizes

The first clear recommendation is to abandon all methods not accounting for uncertainty in population size, as they are unavoidably biased when used with real world, noisy estimates of population size. This conclusion, although developed here based on a simple model, applies to any similar approach, such as the regression of observed growth rate, $y_{t+1} - y_t$, versus observed population size y_t as well illustrated by Freckleton et al. (2006; Fig. 1c). The resulting bias is particularly vicious in meta-analyses, in which the estimated proportion of populations subject to density dependence will unavoidably be overestimated. This was suspected in the analysis of Brook and Bradshaw (2006), by Lebreton (2009), and demonstrated for these same data by Knape and De Valpine (2012). Brook and Bradshaw conclude

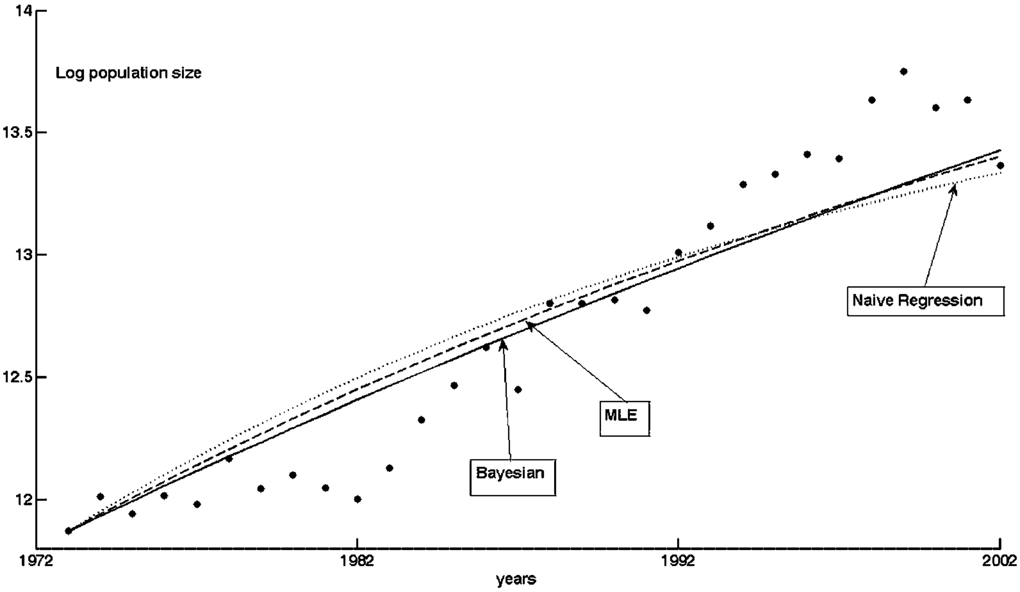

Figure 4. Reconstructed log spring population size for the greater snow goose, based on the relationship $x_{t+1} = r + (1 - b)x_t$. Plain line: maximum likelihood estimates of *r* and *b*; dotted line: estimates under a Gaussian prior distribution for *r* with mean 0.20 and standard error 0.06. The ability to discriminate among pairs of values (*r*, *b*) is obviously very low, as different pairs of values give closely similar curves.

density dependence in more than 75% of the cases studied, whereas, accounting for uncertainty in population size estimates and using a Bayesian approach, Knape and De Valpine conclude significant density dependence in only 16% of the case studied. Similarly, based on reliable tools, Jamieson and Brooks (2004) conclude weak to moderate density dependence among American ducks. We still suspect part of these conclusions would not resist a close examination of the resulting intrinsic growth rate estimates.

The state-space model formulation provides a sensible approach to account for uncertainty in population size (Dennis et al. 2006), to develop specific models accounting for environmental covariates, age structure, etc., and to test these models for density dependence in presence of such potentially confounding effects.

Two intermingled issues severely limit the potential of such models if used by themselves:

1) Numerical issues (multiple maxima to the likelihood or sensitivity to priors, depending on the type of algorithms used) and problems of bias associated with finite sample size, which currently make such models difficult to use without specific help from a specialist.
2) Low power and identifiability problems as a result of the shortness of the time series and the 2-level uncertainty, in particular if further complexities are brought in the model, at an unavoidable cost in terms of number of parameters to be estimated. We would rarely expect evidence for density dependence with fewer than 30 points and we think external information on the intrinsic growth rate has to be seriously considered in any such analysis, unless one wishes to keep the grail inaccessible.

The situation is somewhat similar to that of capture–recapture models for closed populations, whose status rapidly moved in the last few years from an innocuous, fairly standard approach to that of delicate, specialized models with severe issues of bias and robustness (Link 2003).

We will come back in greater detail in the general discussion to the potential of state-space models.

DETECTING AND ESTIMATING DENSITY DEPENDENCE BASED ON TRAITS

By contrast, one clear type of evidence for density dependence concerns the response of life history traits to changes in population size. Surprisingly, most such studies are observational, correlative studies relating particular traits to observed changes in population size over time. Some qualify as quasi-experiments, as based on a clear population crash or explosion (e.g., Ashley et al. 1998). Despite the current development of experimental ecology, few manipulative experiments of densities have ever taken place. The few such studies with nest boxes (Alatalo and Lundberg 1984, Torok and Toth 1988), although quite convincing, do not take full advantage of an experimental setting, notably in terms of block design and replication (see also Newton 1994). Bartmann et al. (1992) provide a good example of an experimental study of density-dependent compensatory mortality in the mule deer (*Odocoileus hemionus*) with several replicates.

The traits investigated in a search for density dependence can be morphological, such as body weight (e.g., Gaillard et al. 1996), and are then relatively simple to study. Demographic traits, such as fecundity, can be studied in a similar fashion (e.g., Arcese and Smith 1988). Demographic traits less directly measurable, such as survival, require more sophisticated approaches such as capture–recapture models (Lebreton et al. 1992, roe deer [*Capreolus capreolus*]; Catchpole et al. 2000, Soay sheep). A full review of studies relating estimated population size to life history traits, whether demographic or not, is beyond the purpose of this article. Bonenfant et al. (2009) provide a broad review of density dependence in mammals, discussing trait response to density, as well as different responses by different segments of the population, such as males and females or age classes. Newton (1998) reviews a number of trait–density or trait–resource relationships in birds.

In all analyses of traits, one has to deal with some kind of linear model between the density or population size (possibly transformed, to log, to discrete categories), x_t, and the trait at time t in individual j, z_{tj}:

$$z_{tj} = a + bx_t + \varepsilon_t + \eta_{tj} \tag{11}$$

The model may have to incorporate further effects, as the 2-level sampling (individuals and yrs) raises some specific issues (whether for instance the same individuals are sampled over several years or not). Environmental covariates can easily be incorporated as additive effects (Lebreton et al. 1992, roe deer; Gaillard et al. 1996 for morphometric traits; Catchpole et al. 2000 for survival; Crespin et al. 2006 for recruitment). The prominent point common to all approaches is again that the density is always a proxy for something else and is always known with some uncertainty (i.e., we are again faced with an error-in-variable problem). Model (11) should be accompanied by an observation equation, $y_t = x_t + \varsigma_t$. When using the regression model $z_{tj} = a + by_t + \varepsilon_t + \eta_{tj}$, attenuation of the slope estimate towards 0 (McArdle 2003) is unavoidable. Clearly, any test on the slope will be conservative (i.e., contrary to methods based on population size, the presence and intensity of density dependence is not overestimated), which is good news. As we usually do not have much control on the uncertainty in population size, several possibilities are available to account for the error-in-variable problem, of which most remain to be explored:

1) Use an error-in-variable model (Fuller 1987); however, all such models are weakly identifiable, through stringent distributional assumptions, as they exploit differences in distribution in the ε and the η terms to estimate their relative effect on the variation in the response variable.
2) Correct for bias. Barker et al. (2002), develop such an approach in the context of capture–recapture survival models. They develop 2 examples with seabird data that provide no evidence for density dependence.
3) Use information on the precision of population estimates, that is, an estimate or a prior distribution for $\mathrm{var}(\varsigma_t)$, to improve identifiability in the error-in-variable model.
4) Recast the capture–recapture model as a state-space model (Gimenez et al. 2007) and consider an observation equation $y_t = x_t + \varsigma_t$ in addition to the observation equations needed for representing the recapture process. In such an approach, survival for instance is represented as state equations made of Bernoulli (0/1) random variables, and the detection/recapture process as observation equations also made of 0/1 random variables.
5) Use instrumental variables, a tool commonly used in econometrics (e.g., Stock 2001). An instrumental variable will be, in our context, a variable uncorrelated with the random term for estimated population size, ς_t, and correlated with true population size. Alternatively, independent estimates of population size could be good candidates (for an example using multiple surveys; see Fromentin et al. 2001).

The impact of the error-in-variable problem is clearly relatively limited and, although some statistical care should be exercised (notably with capture–recapture methodology), the assessment of density dependence based on traits is relatively straightforward.

DISCUSSION

The first part of our review, on methods for detecting density dependence based on population size surveys, leads first to several straightforward recommendations, to avoid the pervasive risk of overestimating the strength of density dependence. The first recommendation is that methods neglecting uncertainty in population size should definitely be abandoned. The second is that the Bayesian approach to simple state-space models, such as the linearized Gompertz model, accounting for uncertainty in population size should be used, with some caution because of practical difficulties. We recommend also a reasonable prior based on external comparative information is used for the population growth rate. Even when these difficulties are correctly handled, which may require the assistance of an applied statistician with good knowledge of these models and their tricks, the simplest models may remain strongly misspecified because they neglect a number of features such as environmental covariates, age structure, and a particular functional form of density dependence. Moving away from such minimal models is alike moving from simple regression to more sophisticated linear or nonlinear models. One cannot avoid a trade-off between the improvement brought by a better adaptation of a more complex model to the data (such as a decrease in residual variance), and the loss of precision implied by a greater number of parameters: modeling remains the art of oversimplification. Again, in this context, a Bayesian approach is probably the preferable approach, with caution exercised. In spite of their statistical and practical difficulties, methods based on population size surveys remain very attractive as they immediately translate into population projections. They are often the only practicable analyses of density dependence when population size surveys only are available, a common situation for managed wildlife populations. However, time series with fewer than, say, 30 time steps (i.e., in most cases, yrs) have little power. One has to recall that when the power drops down to values close to the test level α, the analysis boils down to deciding for density dependence or no density dependence on the basis of a random number.

When moving from methods based on population size surveys to methods for detecting density dependence on traits, one is, in some sense, moving from pattern to process (Swihart et al. 2002). The most straightforward methods for traits, such as using density as a covariate in capture–recapture models, are conservative (i.e., tend to underestimate the strength of density dependence), which means that the evidence for density dependence is reliable when present. Several perspectives to correct for the conservative effect of uncertainty in population size will probably be explored in the near future. The most promising is the use of the state-space formulation of capture–recapture models (Gimenez et al. 2007), completed by an observation equation for population size to properly model density dependence. Although they can thus be used more confidently than approaches based on population size surveys, methods for density dependence in traits do not easily lead to population projections. Even when the traits under study are demographic, they can only be translated into projections through a projection model such as a matrix model. Nevoux et al. (2011) examine the consequences of density dependence in different traits of the Mauritius kestrel (*Falco punctatus*) by integrating these different traits and their density-dependent relationships into a nonlinear discrete time model, studied independently from the trait analyses. In the absence of correction for attenuation, the results of such models should be looked at with a critical eye. Moreover, deterministic models do not account for the interplay of density dependence and various forms of stochasticity.

As the state-space formulation can easily encompass projection models (e.g., Gauthier et al. 2007) and as it brings decisive advantages for assessing density dependence whether from population surveys or in studies of traits, the future of density dependence modeling clearly lies with state-space modeling.

One can easily foresee what could be a state-space model incorporating density dependence in a wildlife population, based on integrated monitoring covering both population size surveys and individual longitudinal data (i.e., capture-mark-recapture data in the broad sense). Such a model has to combine different types of state equations with, possibly at some stage, the need to account for the lack of independence between the marked individuals and the overall population:

1) Multinomial distributions of individual trajectories on a Markov chain (reducing to Bernoulli equations in the case of survival), with parameters possibly dependent on population size (i.e., density dependent).
2) Equations to iterate a population vector submitted to demographic stochasticity.

The corresponding observation equations are:

1) Discrete variables such as Bernoulli for the capture–recapture process.
2) Equations for the uncertainty in the observation for population size (as a vector or total number).

A model on these lines is proposed by Abadi et al. (2012). Rotella et al. (2009) go one step in this direction by examining Weddell seal (*Leptonychotes weddellii*) population size estimates derived together with demographic parameters from a capture–recapture analysis within a stochastic Gompertz model. The demographic parameters are, however, not examined for density dependence and the estimated intrinsic growth rate is not given.

The first consequence of this evolution is that detecting and estimating density dependence has already started moving from a push-button procedure to a full size modeling exercise. A second consequence is that the gap between projection models and statistical models is progressively filled. In such a promising state of the art, one may also expect a progressive integration of models based on mechanism at the individual levels, in the spirit of individual-based models, but based on state-space models deriving from the classical phenomenological approach to population dynamics reviewed here (e.g., Stephens et al. 2002).

This evolution is fortunate because density dependence as a complex biological phenomenon has no reason to be uniformly reduced to a simple omnibus model, apart from a theoretical point of view that makes the logistic growth curve (Verhulst 1838) so useful. We have to think of density dependence as a complex biological process interacting with other processes rather than in terms of a simple equation; modern statistical and modeling tools make such a synthesis within reach.

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