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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 (DD) based on two 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, in priority on the intrinsic growth rate, is highly recommended.

Methods for detecting DD in life history traits are generally conservative, i.e. tend to
underestimate the strength of DD. 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 DD 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.

KEYWORDS Animal demography, Bayesian methods, Density-dependence, Kalman filter, Population dynamics, State-space models, Wildlife

INTRODUCTION

The i-state philosophy (Diekmann 1985) 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, in particular, not affected by a trend), the population growth is exponential, generally after damping of the effect of initial population structure, as well known for instance for matrix models (Caswell 2001) and their stochastic generalizations (Tuljapurkar, 1990). The key paradigm of exponential growth in population dynamics (Turchin 1981) is thus intimately linked to the i-state philosophy.

It has been recognized for more than two centuries (Malthus 1798) that exponential growth is impossible in the long term (Turchin 1981), as exponential growth leads to large population sizes that unavoidably induce depletion of resources and in turn of individual performance.

This is a broad definition of Density-Dependence (DD hereafter), as a phenomenon that explicitly has to do with resource and individual performance. In passing, as most authors in this context, we loosely use the word density for population size or local population size, e.g. in the term DD itself.

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, e.g., matrix models that translate individual parameters into population level consequences. There has been a continuous tension since the XIXth century between phenomenological and mechanistic approaches to density-dependence (see Krebs 1995, Murdoch 1994) and continuing discussions (e.g. Berryman 2004) on the role of limitation by resource availability - an individual level phenomenon – as supposedly opposed to regulation by DD, a population level result.

A key question is whether DD is present in a population, and if so, how to measure its intensity. As usual, even if one relies on some statistical significance for detection, one has indeed in mind some biological significance, i.e. the idea that DD 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 2012). Indeed the measurement phase is often linked with the idea that population projections accounting for DD go one step beyond those based on constant parameters: there is still a strong assumption of stationarity in the projection 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 DD 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 50s (Andrewartha and Birch 1954, Lack 1954).

Not surprisingly, the tension between phenomenological / population and mechanistic / individual approaches has been pervasive in the issue of detection / estimation of DD, would

72 it be only because the data themselves can be at the population level only (e.g. population
73 surveys) or at the level of individual traits only (e.g. body weight data). Finally, statistical
74 difficulties arise as the arrow of time induces dependencies that cannot be handled by naive
75 statistical approaches. While a comprehensive review of the literature would be beyond reach,
76 it is clear that the issue of detection / measurement of DD has alternatively raised optimistic
77 and pessimistic points of view, and has been a subject of “frustration” (Dennis and Taper
78 1994). Can we take series of data and estimate in a simple fashion how many show density-
79 dependence, as done by Brook and Bradshaw (2006) for 1198 species, or should we conclude
80 with Krebs (1995) that DD is an unattainable holy grail?

81 The purpose of this paper is to attempt to review the subject of detection and estimation of
82 DD with specific reference to these difficulties and the resulting confusing state of the art.
83 Although we will use many equations, as “if you are faced by a difficulty or a controversy in
84 science, an ounce of algebra is worth a ton of verbal argument” (a conviction of
85 J.B.S.Haldane, according to Maynard-Smith 1965), this review will attempt to avoid technical
86 developments (for a more technical review, see Lebreton 2009).

87 We will first review the methods for detection and estimation of DD based on population size
88 estimates, in three steps: a) an attempt to formalize the role of resource and density, b)
89 methods in the absence of uncertainty in population size, c) methods accounting for
90 uncertainty in population size, a key feature for wild animal populations. Then we will review
91 methods based on analyses of individual traits, demographic or not. We will then discuss new
92 modeling opportunities and perspectives.

93 Calculations were done using our own Matlab ® code, carefully validated by a series of cross-
94 checks, and WinBUGS (Lunn et al. 2000). The Matlab ® code is made available as
95 supplementary material.

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 $x_t = \text{Ln}(N_t)$ and $r = \text{Ln}(\lambda)$:

$$x_{t+1} = r + (1-b)x_t \quad [1]$$

As recalled by Lebreton (2009), $r = \text{Ln}(\lambda)$ is the growth rate for $N = 1$, while the growth rate for $N = 0$ is infinite. 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

$$x_{t+1} = r + x_t \quad [2]$$

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:

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

$$x_{t+1} = r + x_t + \varepsilon_t \quad [4]$$

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 as, 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 DD either by a test of model [3] vs model [4], such as a likelihood ratio test, or by a test of $H_0 \ b = 0$ in model [3], e.g. as a Wald

test. The latter approach is usually preferred as it can easily be easily implemented as a one-tailed test of $H_0 \ b = 0$ vs $H_1 \ b > 0$, 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:

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

As DD 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 left, 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,

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

While 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” (see e.g. Fuller 1987). In practice, the latent variable l_t is unknown and so is $var(\varsigma_t)$: model [6] cannot be readily used instead of [3]. What are the consequences of the error-in-variable problem on detection and estimation of DD 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 DD when present, remain to be explored.

Methods for detecting DD 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 (Hamilton 1994 p.123; Dennis and Taper 1994 p. 209; 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} wrt 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 at all the usual linear regression model: the same variable appears both as independent and dependent variable, with a shift in time, i.e. we are in a so-called autoregressive model. In figure 1, we illustrate what happens under H_0 $b = 0$: the joint distribution of the pairs (x_{t+1}, x_t) is aligned along the line $y = r + x$. Samples of this distribution thus have on the average 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 DD. Despite repeated warnings as early as the 70s (e.g. Maelzer, 1970), few people realize this bias is present indeed in the absence of uncertainty on population size (e.g. Freckleton et al. 2006, item 2 of summary) as can be seen for abscissa 0 in figure 2. Asymptotically, the estimate is not biased, just because the regression line in Figure 1 comes closer and closer to the line $y = r + x$ as the scatter of

points become more and more elongated since $\text{var}(x_t) \rightarrow \infty$ when $t \rightarrow \infty$ (Figure 1) while $\text{var}(x_{t+1} / x_t) = \text{var}(\varepsilon_t)$ 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:

a) Using simulation (i.e. parametric bootstrap) (Dennis and Taper 1994). Basically, one generates pseudo-samples using estimates under $H_0 \ b = 0$ and use 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 and Taper (1994) use it with a slightly different, nonlinear, model in which the approach also overcomes the absence of distributional results.

b) 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 the resulting test-level is sufficiently close to the nominal α . A bias-corrected estimate can indeed be also directly derived from the general study of the bias of the autocorrelation coefficient by Kendall (1954, in Sawa 2002) for a time series of length T , as $\tilde{b} = \hat{b} - \frac{4 - 3\hat{b}}{T}$.

Naive approaches are still commonly used (e.g. Saether 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 DD coefficient induces an overestimation of the prevalence of density-dependence. Based on the impossibility of long term exponential growth, one gets then 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:

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

$$y_{t+1} = x_{t+1} + \eta_{t+1} \quad [8]$$

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

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

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. Figure 2, based on simulations, clearly shows how the faked evidence for DD (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.

The ad hoc tests proposed by Bulmer 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 equation [7] and an observation equation [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 it possible to obtain the likelihood of the model, based on a series of observations $(y_1, y_2, \dots, y_T)$, 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 (Figure 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 (2002), based on the model presentation in equation (10).

Moreover, the distribution of the ML estimate under H_0 $b = 0$ cannot be easily obtained (Dennis et al. 2006). It cannot thus be used without care for a test of DD. 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 . Knappe and de Valpine (2011) go one step further with this approach by implementing a test of DD based on the likelihood ratio statistic between model [7] 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), and, e.g., use 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 DD - 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 (figure 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 two levels of uncertainty (process + sampling) and the dependency over time (Eq. [10]) they induce. The estimate of the process and sampling standards errors, $se(\varepsilon_t)$ and $se(\eta_t)$ are also highly correlated, although to a lesser degree than the estimates of r and b , while the correlation among the two 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 (Figure 4): over 1000 iterative searches starting from random initial values, only 21 did not fully converge in 1000 iterations; 15 had indeed practically 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 (0.9990), and the MLE of r , 0.3191, seems unrealistic (Table 2, second row) as it corresponds to a 37.6 % increase per year. These two features combined make the estimate of the coefficient of DD 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 , that are indeed 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 DD, or a weaker intrinsic growth rate and a low DD (see figure 5, below). The set of four parameters nearly appears as a set of two macro-parameters, one for the deterministic trajectory, the other one for the uncertainty. Based on our simulations (Figure 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, e.g., when the population size estimates come from capture-recapture (e.g. Dennis and Oten 2000, who do not account for this uncertainty in their analysis), from stratified sampling (as it 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 DD, and because of the unrealistic value 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 DD 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) to constrain r to a realistic value for such a species (Niel and Lebreton 2005 Table 2) did improve the results (Table 1, second and third row) and provided evidence of very weak DD, 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, i.e. of its coefficient of variation is 0.0607, comparable in magnitude to the field estimate (10 % or less, Gauthier et al. 2007 p. 1422). This fairly good precision limited the bias of the naïve regression approach (Table 1 first row), with a 95 % confidence interval for the coefficient of DD 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 DD by reducing the estimate for the process standard error.

Contrary to Dennis et al. (2006) and Knape and de Valpine (2011), 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 (Figure 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 reasonable to consider as a fair evidence for DD a value of $\hat{b}$ significantly differing from 0 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:

- 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 DD (e.g. Lebreton 1990).
- Age structure, e.g. with delayed recruitment, may require considering dependency over several time steps in components of population size.
- Further structure such as spatial cells may have to be considered, e.g. to model local density-dependence (Murdoch 1994) or dependence on some components of population size.
- The response to density may 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 DD and the corresponding tests or diagnostics of DD.

While in the original presentation by Bulmer (1975) the minimal model was presented as quite a specific statistical object, the state-space model point of view opens a number of perspectives (de Valpine 2002). For instance, it is relatively easy to generalize the state equation to account for an environmental covariate z_t , as $x_{t+1} = r + (1 - b)x_t + cz_t + \varepsilon_t$. 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 DD 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 the MLE as a consequence often 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. REML approaches based on first order differences found promising by Dennis et al (2006) could be useful, but have still to be investigated in such a more complex setting. A Bayesian approach seems the most straightforward treatment. As an alternative to MCMC 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 such approach such as the regression of “observed growth rate” $y_{t+1} - y_t$ vs observed population size y_t as well illustrated by Freckleton et al. (2006 Figure 1c). The resulting bias is particularly vicious in meta-analyses, in which the estimated proportion of populations subject to DD will unavoidably be overestimated. This was suspected in the analysis by Brook and Bradshaw (2006) by Lebreton (2009) and demonstrated for these same data by Knape and De Valpine (2011). Brook and Bradshaw conclude to DD in more than 75% of the cases studied, while, accounting for uncertainty in population size estimates and using a Bayesian approach, Knape and de Valpine conclude to significant DD in only 16 % of the case studied. Similarly, based on reliable tools, Jamieson and Brooks (2004) conclude to weak to moderate DD 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) and to develop specific models accounting for environmental covariates, age structure etc., and testing thus for DD 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 two-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 DD 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 the goal to remain 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 DD 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. Aslhey et al. 1998). Despite the current development of experimental ecology, few really manipulative experiments of densities have ever taken place. The few such studies with nest boxes (Torok and Toth, 1988, Alatalo and Lundberg 1984), 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 with several replicates.

The traits investigated in a search for DD 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 *C.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 paper. 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_{ij} :

$$z_{ij} = a + bx_t + \varepsilon_t + \eta_{ij} \quad [11]$$

The model may have to incorporate further effects, as the two-level sampling (individuals and years) 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 example; Catchpole et al. 2000 for survival; Crespin et al. 2006 for recruitment; Gaillard et al. 1996 for morphometric traits). 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 $y_t = x_t + \zeta_t$. When using the regression model $z_{ij} = a + by_t + \varepsilon_t + \eta_{ij}$, 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 DD is not overestimated, which is good news. As we usually have not 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:

- 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;
- Correct for bias. Barker et al. (2002), develop such an approach in the context of capture-recapture survival models. They develop two examples with seabird data that provide no evidence for DD.
- Use information on the precision of population estimates, i.e. in the notation above an estimate (or a prior distribution) for $var(\zeta_t)$ to improve identifiability in the error-in-variable model.

- Recast the capture-recapture model as a state-space model (Gimenez et al. 2007) and consider besides the observation equations needed for representing the recapture process an observation equation $y_t = x_t + \zeta_t$. 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.
- 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, ζ_t and correlated with true population size. Alternative, 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 for what concerns the use of capture-recapture methodology, the assessment of DD based on traits is relatively straightforward.

DISCUSSION

The first part of our review, on methods for detecting DD based on population size surveys, leads first to several straightforward recommendations, to avoid the pervasive risk of overestimating the strength of DD. The first one 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, particular functional form of DD, etc... 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 DD when population size surveys only are available, a common situation for managed wildlife populations. There is however little power for time series with fewer than, say, 30 time steps, i.e., in most cases, years. 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 DD or no DD on the basis of a random number.

When moving from methods based on population size surveys to methods for detecting DD 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 DD, which means that the evidence for DD 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 DD. While they can thus be used more confidently than approaches based on population size surveys, methods for DD 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 DD in different traits of the Mauritius Kestrel *Falco punctatus* by integrating these different traits and their DD 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 DD 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 DD whether from population surveys or in studies of traits, it is clear that the future of DD modeling lies with state-space modeling.

One can easily foresee what could be a state-space model incorporating DD 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:

- 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;
- Equations to iterate a population vector submitted to demographic stochasticity.

The corresponding observation equations are:

- Discrete variables such as Bernoulli for the capture-recapture process;

- 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. (submitted). Rotella et al ; (2009) go also one step in this direction by examining Weddell Seal 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 DD and the estimated intrinsic growth rate is not given.

The first consequence of this evolution is that detecting and estimating DD 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, with state-space models derive from the classical phenomenological approach to population dynamics reviewed here (e.g., Stephens et al. 2002).

This evolution is fortunate as DD 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 DD 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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666

667 Table 2: sampling correlations between Maximum Likelihood Estimates of the parameters of
 668 the stochastic Gompertz model for the Greater Snow Goose data

Parameters (as rows and columns)	Sampling standard error $se(\eta_t)$	Process standard error $se(\varepsilon_t)$	Intrinsic growth rate r	Coefficient of DD b
$se(\eta_t)$	1.0000	-0.7063	0.2955	0.2910
$se(\varepsilon_t)$	-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

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670

671

672 Table 2: Estimation of parameters r , b , $var(\varepsilon_t)$, and $var(\eta_t)$ of the density dependent
 673 model $x_{t+1} = r + (1-b)x_t + \varepsilon_t$ with uncertainty on log-population size represented as
 674 $y_t = x_t + \eta_t$, applied to spring population surveys of the greater Snow Goose (data from
 675 Gauthier 2007).

676 First row: naïve regression approach on log population size, neglecting uncertainty in
 677 population size.

678 Second row: Maximum Likelihood estimation of the model accounting for uncertainty in
 679 population.

680 Third row: Bayesian approach of that same model with a Gaussian prior distribution for r
 681 with mean 0.20 and standard error 0.06 and uninformative priors for the other parameters.

682 Fourth row: Bayesian approach of that same model with a Gaussian prior distribution for r
 683 with mean 0.20 and standard error 0.06, explicit posterior normal distribution

Parameter Method	Process Standard Error $\sqrt{\text{var}(\varepsilon_t)}$	Observation Standard Error $\sqrt{\text{var}(\eta_t)}$	Growth rate r	Coef- ficient of DD b	Corr ($\hat{r}, \hat{b}$)	Deter- ministic equilibriu m $\hat{r} / \hat{b}$
Naïve regression neglecting uncertainty in population size	0.1398	-	0.5044 [-0.5446, 1.5533]	0.0357 [-0.0469, 0.1184]	0.9988	14.12
Model with uncertainty in population size: Maximum Likelihood Estimate and, in brackets, 95 % CI	0.1041	0.0607	0.3191 [-0.2731, 0.9112]	0.0210 [-0.0258, 0.0678]	0.9990	15.21
idem, Bayesian approach with prior constraining r : posterior distribution of parameters, Mean and, in brackets, 2.5 % and 97.5 % quantiles (MCMC)	0.1210	0.0528	0.2022 [0.0865, 0.2413]	0.0118 [0.0019, 0.0151]	0.931	17.19
Idem, based on normal distribution	0.1022	0.0628	0.2024 [0.1201, 0.2847]	0.0118 [0.0049, 0.0187]	0.951	17.15

684

686 Legends of figures

687

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

694

695 Figure 2: Estimated strength of density dependence (ordinate) in absence of density
696 dependence, when uncertainty in population size (as a coefficient of variation, abscissa) is
697 neglected. The bias in the estimated strength of DD strongly increases with the uncertainty in
698 population size.

699 Simulated data based on the density independent model $x_{t+1} = r + x_t + \varepsilon_t$ with uncertainty on
700 log-population size represented as $y_t = x_t + \eta_t$. The estimated strength of DD (ordinate) is the
701 Maximum Likelihood estimate of b in the model $y_{t+1} = r + (1-b)y_t + \varepsilon_t$ over 30 time steps
702 in which y is treated as the “true” log population size. In abscissa, $\text{se}(y_t / x_t) = \text{se}(\eta_t)$ is the
703 coefficient of variation of the estimated population size. Dotted line: Mean estimate $\bar{b}$ (5000
704 replicates each), vertical lines; 95% limits of the 5000 replicates.

705

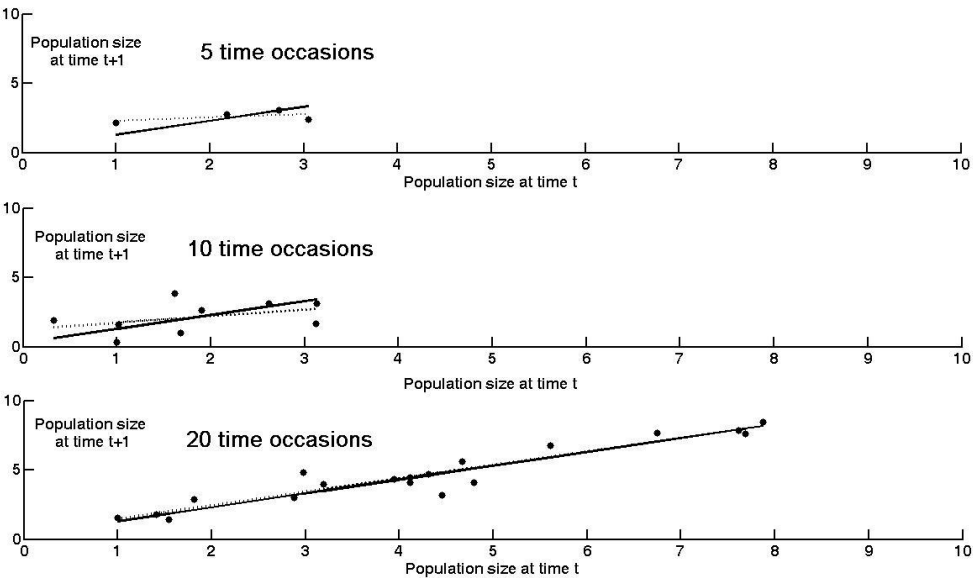
Figure 3: Deviance ($-2 \times \log\text{-likelihood}$) contours of simulated trajectories of increasing number of time steps ($T=10, 20, 50$ and 100) of the density dependent model $x_{t+1} = r + (1-b)x_t + \varepsilon_t$ with uncertainty on log-population size represented as $y_t = x_t + \eta_t$. The parameters used in the simulations are $r = 0.1$, $b = 0.3$, $\text{sd}(\varepsilon_t) = 0.2$, $\text{sd}(\eta_t) = 0.4$. The deviance is represented under $\text{sd}(\varepsilon_t) = 0.2$, $\text{sd}(\eta_t) = 0.4$ 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 a) the likelihood and the maximum likelihood estimates are well behaved in the absence of model misspecification; b) for 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 vs high intrinsic growth rate and strong density-dependence.

Figure 4: Profile Deviance for parameter r 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 2007). For each value of r the deviance is maximized with respect to the three other parameters b , $\text{var}(\varepsilon_t)$, and $\text{var}(\eta_t)$.

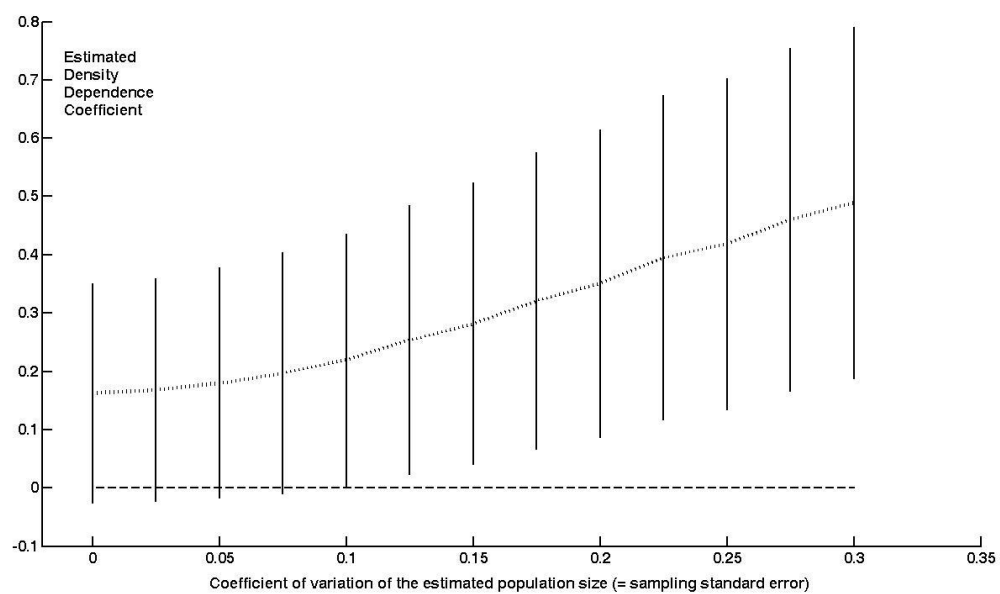
Figure 5: reconstructed log spring population size for the Greater Snow Goose, based on the relationship $x_{t+1} = r + (1-b)x_t$. Plain line: MLEs of r and b ; dotted line: Estimates under a Gaussian prior distribution for r with mean 0.20 and standard error 0.06 . The ability to discriminate among pairs of values (r, b) is obviously very low, as different pairs of values give closely similar curves.

729 Figure 1



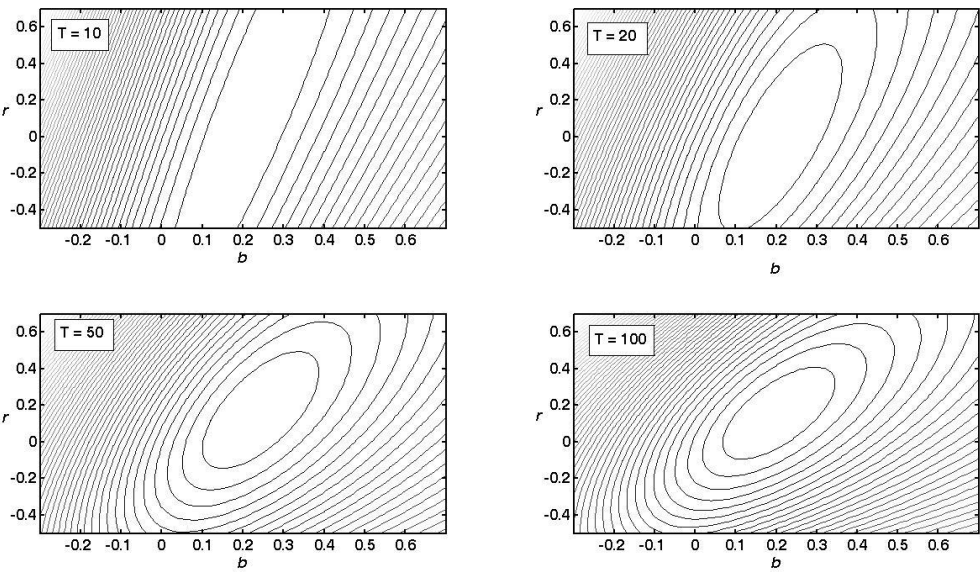
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732 Figure 2

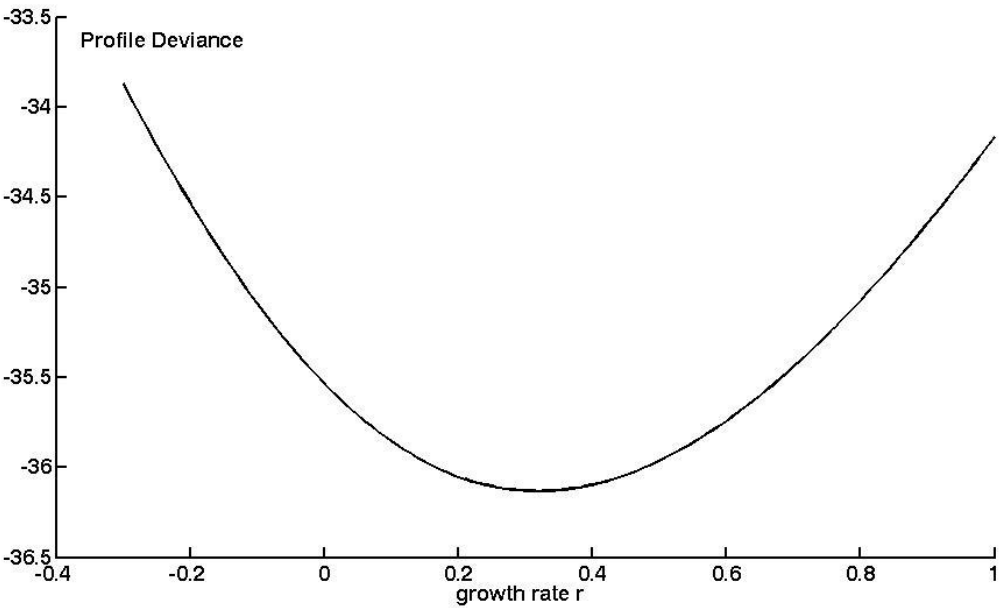


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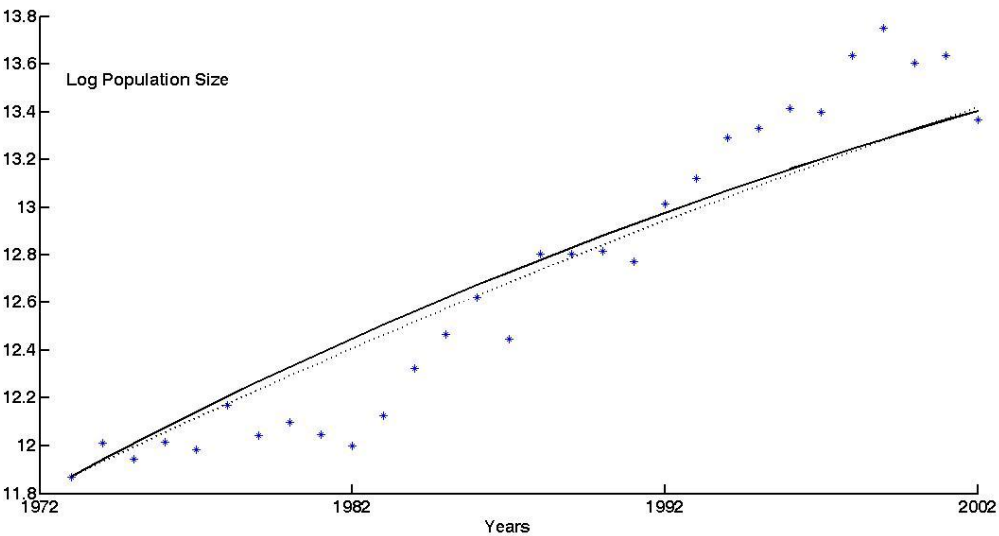
738 Figure 4



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741 Figure 5



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