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1 DETECTING AND ESTIMATING DENSITY DEPENDENCE IN WILDLIFE
2 POPULATIONS

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7 **ABSTRACT** We review methods for detecting and assessing the strength of density
8 dependence (DD) based on two types of approaches: surveys of population size and studies of
9 life history traits, in particular demographic parameters.

10 For the first type of studies, methods neglecting uncertainty in population size should
11 definitely be abandoned. Bayesian approaches to simple state-space models accounting for
12 uncertainty in population size are recommended, with some caution because of numerical
13 difficulties and risks of model misspecification. Realistic state-space models incorporating
14 features such as environmental covariates, age-structure, etc., may lack power because of the
15 shortness of the time series and the simultaneous presence of process and sampling
16 variability. In all cases, complementing the population survey data with some external
17 information, in priority on the intrinsic growth rate, is highly recommended.

18 Methods for detecting DD in life history traits are generally conservative, i.e. tend to
19 underestimate the strength of DD. Among approaches to correct for this effect, the state-space
20 formulation of capture-recapture models is again the most promising.

21 Foreseeable developments will exploit integrated monitoring combining population size
22 surveys and individual longitudinal data in refined state-space models, for which a Bayesian
23 approach is the most straightforward statistical treatment. One may thus expect an integration

24 of various types of models that will make it possible to look at DD as a complex biological
25 process interacting with other processes rather than in terms of a simple equation: modern
26 statistical and modeling tools make such a synthesis within reach.

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

29

30 **INTRODUCTION**

31 The i-state philosophy (Diekmann 1985) describes demography at the individual level based
32 on life-cycle stages. This philosophy naturally leads to describe death, fecundity, and more
33 generally any transition between stages such as recruitment or dispersal, through per capita
34 parameters. If such individual parameters are constant or at least stationary (in the sense of
35 stochastic processes: affected by random effects that can be shifted over time, and, as such, in
36 particular, not affected by a trend), the population growth is exponential, generally after
37 damping of the effect of initial population structure, as well known for instance for matrix
38 models (Caswell 2001) and their stochastic generalizations (Tuljapurkar, 1990). The key
39 paradigm of exponential growth in population dynamics (Turchin 1981) is thus intimately
40 linked to the i-state philosophy.

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

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

48 Density-Dependence became a key subject in population dynamics with the well known
49 logistic growth curve (Verhulst 1838). One of the discrete time counterparts is the discrete
50 time Gompertz model $N_{t+1} = \lambda N_t^{-b} N_t$ with $b > 0$. Such models are phenomenological, as they
51 describe only the population level and do not explicitly consider the individual level, contrary
52 to mechanistic models such as, e.g., matrix models that translate individual parameters into
53 population level consequences. There has been a continuous tension since the XIXth century
54 between phenomenological and mechanistic approaches to density-dependence (see Krebs
55 1995, Murdoch 1994) and continuing discussions (e.g. Berryman 2004) on the role of
56 limitation by resource availability - an individual level phenomenon – as supposedly opposed
57 to regulation by DD, a population level result.

58 A key question is whether DD is present in a population, and if so, how to measure its
59 intensity. As usual, even if one relies on some statistical significance for detection, one has
60 indeed in mind some biological significance, i.e. the idea that DD is or is not negligible for
61 the future fate of the population or relative to other sources of variation, and thus bears a
62 relationship to its management (Guthery 2012). Indeed the measurement phase is often linked
63 with the idea that population projections accounting for DD go one step beyond those based
64 on constant parameters: there is still a strong assumption of stationarity in the projection but
65 rather than “*as if parameters were the same as up to now*”, it is “*as if parameters were*
66 *varying with density as they have been shown to do up to now*”. Estimating the strength of DD
67 is also central in discussions of the relative role and magnitude of density-dependent and
68 density-independent variation in population size, the subject of a famous controversy in the
69 50s (Andrewartha and Birch 1954, Lack 1954).

70 Not surprisingly, the tension between phenomenological / population and mechanistic /
71 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.

96 **DETECTING AND ESTIMATING DENSITY DEPENDENCE BASED ON**
97 **POPULATION SIZE ESTIMATES**

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

100
$$x_{t+1} = r + (1-b)x_t \quad [1]$$

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

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

105
$$x_{t+1} = r + x_t \quad [2]$$

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

109
$$x_{t+1} = r + (1-b)x_t + \varepsilon_t \quad [3]$$

110
$$x_{t+1} = r + x_t + \varepsilon_t \quad [4]$$

111 The random terms, represented by Greek letters, have expectations equal to 0 and, unless
112 otherwise stated, are assumed to be normally distributed. The latter model is a random walk
113 as, besides the shift r , x_t varies through independent additive increments. Because of their
114 simplicity, these models have been used by a number of authors over the years (see Dennis et
115 al. 2006, Lebreton 2009). One can equivalently test for DD either by a test of model [3] vs
116 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

117 test. The latter approach is usually preferred as it can easily be easily implemented as a one-
118 tailed test of $H_0 b = 0$ vs $H_1 b > 0$, the alternative of biological interest.

119 **Density-dependence and resource-dependence**

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

$$121 \quad x_{t+1} = (r - bx_t + \varepsilon_t) + x_t \quad [5]$$

122 As DD occurs through the depletion of resource of some kind, in the per capita growth rate,
123 the log population size x_t is a proxy for something else. Let's assume a single latent variable
124 l_t , such as the amount of a key resource left, is the actual determinant of the growth rate.

125 Assuming l_t can be expressed on the same scale as x_t , the actual growth rate is then

126 $r - bl_t + \varepsilon_t$. The log-population size x_t is then a proxy for l_t , with a relationship necessarily
127 modified by some random variation, $l_t = x_t + \zeta_t$, as the proxy and the latent variable cannot
128 be expected to be perfectly correlated over time. The random term ζ_t has a null expectation,
129 i.e. $(E(\zeta_t) = 0)$. Note that this issue has nothing to do with uncertainty on x_t , a problem that
130 will be examined later.

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

$$132 \quad x_{t+1} = (r - b(x_t + \zeta_t) + \varepsilon_t) + x_t \quad [6]$$

133 While model [5] (or equivalently [3]) is analogous to a linear regression of x_{t+1} on x_t (to an
134 extent that will be discussed later), model [6] is affected by an "error-in-variable" (see e.g.
135 Fuller 1987). In practice, the latent variable l_t is unknown and so is $var(\zeta_t)$: model [6]
136 cannot be readily used instead of [3]. What are the consequences of the error-in-variable
137 problem on detection and estimation of DD when using [3]? Under $H_0 b = 0$, model [6]

138 reduces to $x_{t+1} = (r + \varepsilon_t) + x_t$, i.e. model [4]. The distribution of any estimator of b under H_0
139 remains thus unaffected by the error-in-variable problem. So, although density-dependence is
140 strictly a model concept, testing for it is equivalent to a test of dependence on resource
141 depletion, at least in the simplistic setting considered here. As far as we know, the
142 consequences on the estimated slope under H_1 $b > 0$, i.e. the estimated strength of DD when
143 present, remain to be explored.

144 **Methods for detecting DD in the absence of uncertainty on population size**

145 Model [3] $x_{t+1} = r + (1-b)x_t + \varepsilon_t$ can easily be treated by maximum likelihood, preferably
146 conditional on x_1 which plays no role in the estimation of b (Hamilton 1994 p.123; Dennis
147 and Taper 1994 p. 209; Lebreton 2009). Because of the linear structure of the model, the
148 Maximum Likelihood Estimator (MLE) of $1-b$ is obtained by the formula for estimating the
149 slope of the ordinary linear regression of x_{t+1} wrt x_t . This apparent simplicity is quite
150 unfortunate, as the estimator does not benefit from the properties of the regression estimator,
151 because the underlying statistical model is not at all the usual linear regression model: the
152 same variable appears both as independent and dependent variable, with a shift in time, i.e. we
153 are in a so-called autoregressive model. In figure 1, we illustrate what happens under H_0 $b=0$
154 : the joint distribution of the pairs (x_{t+1}, x_t) is aligned along the line $y = r + x$. Samples of
155 this distribution thus have on the average a major axis with slope 1. The regression estimate is
156 then necessarily on the average below 1. As a consequence, the estimator of b is positively
157 biased, i.e. the naïve approach tends to detect too often DD. Despite repeated warnings as
158 early as the 70s (e.g. Maelzer, 1970), few people realize this bias is present indeed in the
159 absence of uncertainty on population size (e.g. Freckleton et al. 2006, item 2 of summary) as
160 can be seen for abscissa 0 in figure 2. Asymptotically, the estimate is not biased, just because
161 the regression line in Figure 1 comes closer and closer to the line $y = r + x$ as the scatter of

162 points become more and more elongated since $\text{var}(x_t) \rightarrow \infty$ when $t \rightarrow \infty$ (Figure 1) while
163 $\text{var}(x_{t+1} / x_t) = \text{var}(\varepsilon_t)$ remains constant. As, in studies of wild animal populations, the time
164 series are usually fairly short, the asymptotic absence of bias offers little consolation.

165 Two approaches have been proposed to account for this bias:

166 a) Using simulation (i.e. parametric bootstrap) (Dennis and Taper 1994). Basically, one
167 generates pseudo-samples using estimates under H_0 $b = 0$ and use the appropriate percentiles
168 of the empirical distribution of the resulting estimates of b to accept or reject H_0 . In our
169 model, this approach would amount to a bias correction, but Dennis and Taper (1994) use it
170 with a slightly different, nonlinear, model in which the approach also overcomes the absence
171 of distributional results.

172 b) Obtaining an expression for the bias. Lebreton (2009), reformulating results by Saint-
173 Amant (1970), develops a bias corrected t-test of H_0 $b = 0$, and checks the resulting test-level
174 is sufficiently close to the nominal α . A bias-corrected estimate can indeed be also directly
175 derived from the general study of the bias of the autocorrelation coefficient by Kendall (1954,
176 in Sawa 2002) for a time series of length T , as $\tilde{b} = \hat{b} - \frac{4 - 3\hat{b}}{T}$.

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

185 not accounting for uncertainty in population size are abandoned. Handling this uncertainty is
186 the subject of the next section.

187 **Methods accounting for uncertainty in population size**

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

$$191 \quad x_{t+1} = r + (1-b)x_t + \varepsilon_t \quad [7]$$

$$192 \quad y_{t+1} = x_{t+1} + \eta_{t+1} \quad [8]$$

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

$$194 \quad y_{t+1} = r + (1-b)y_t + \eta_{t+1} - (1-b)\eta_t + \varepsilon_t \quad [10]$$

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

197 Neglecting it, i.e. treating y_t by the previous regression-like method induces a severe bias
198 (Bulmer 1975) that has rarely if ever been illustrated. Figure 2, based on simulations, clearly
199 shows how the faked evidence for DD (i.e. the bias in \hat{b}) increases with the uncertainty in
200 population size, over a range of realistic values of the coefficient of variation for the estimated
201 population size.

202 The ad hoc tests proposed by Bulmer were criticized by Den Boer and Reddingius (1989), in
203 particular because they are not optimal, statistically speaking. However one clearly
204 distinguishes in the model above a state equation [7] and an observation equation [8], i.e. a
205 linear Gaussian state-space model, which can be treated by specific methods such as the

206 Kalman filter, as noted by Lebreton (1989). The Kalman filter makes it possible to obtain the
207 likelihood of the model, based on a series of observations (y_1, y_2, \dots, y_T) , as presented in a
208 clear and detailed way by Dennis et al. (2006). The MLE adequately exploits the statistical
209 information available and is definitely preferable to any ad hoc estimate such as the regression
210 estimate from the previous model or the explicit formulas proposed by Bulmer (1975). The
211 MLE has to be obtained numerically, with, according to Dennis et al. (2006), special care
212 because of potential multiple minima in the likelihood (see also Polansky et al. 2009). This
213 approach removes the substantial bias that would have been present by ignoring the
214 uncertainty in population size (Figure 2). However, the MLE is again only asymptotically
215 unbiased, i.e. suffers from some bias for realistic sample sizes. As in the absence of sampling
216 error, some bias corrections could be obtained from the results on the autocorrelation
217 coefficient bias, extended to autocorrelated random errors by Sawa (2002), based on the
218 model presentation in equation (10).

219 Moreover, the distribution of the ML estimate under H_0 $b = 0$ cannot be easily obtained
220 (Dennis et al. 2006). It cannot thus be used without care for a test of DD. Dennis et al. (2006)
221 also discuss alternative estimation methods, based in particular on the first-order differences
222 of the estimated log-population sizes y_t . Knappe and de Valpine (2011) go one step further
223 with this approach by implementing a test of DD based on the likelihood ratio statistic
224 between model [7] and its density-independent version, obtaining its distribution under H_0
225 $b = 0$ by parametric bootstrap, exactly as Dennis and Taper (1994) did for the model without
226 uncertainty on population size. To avoid distributional problems with the test statistics, one
227 can use a Bayesian approach, easily implemented in WinBUGS (Lunn et al. 2000) or in R via
228 JAGS (Plummer 2003), and, e.g., use a 95 % credible interval as an admissible set of parameter
229 values. Bayesian approaches also allow for flexibility in the functional form of the state
230 equation – i.e. the “shape” of DD - and in the distribution of the random terms. These

231 approaches currently seem the most reliable and the handiest ones, even if the underlying
232 properties of the models, e.g., the degree to which the various parameters are separately
233 identifiable do not depend on the estimation method and still remain often problematic.

234 Let us briefly examine the performance of these approaches, first by simulation. Deviance
235 contours from simulated data (figure 3) show no evidence of local minima at the scale
236 considered. However the estimates of r and b are strongly correlated for realistic lengths of
237 the time series. They behave as the estimated intercept and slope of a regression when the
238 dependent variable values are on a same side of the origin, to an even greater extent because
239 of the two levels of uncertainty (process + sampling) and the dependency over time (Eq. [10])
240 they induce. The estimate of the process and sampling standards errors, $se(\varepsilon_t)$ and $se(\eta_t)$ are
241 also highly correlated, although to a lesser degree than the estimates of r and b , while the
242 correlation among the two parameter subsets remain moderate. How does this translate in a
243 real world example?

244 Let us use as an illustrative example the spring population surveys of Greater Snow Geese
245 *Chen caerulescens atlantica* in Quebec from 1973 to 2002 (Gauthier et al . 2007). The
246 deviance did not show local minima (Figure 4): over 1000 iterative searches starting from
247 random initial values, only 21 did not fully converge in 1000 iterations; 15 had indeed
248 practically converged, and 6 were still not at the global optimum. They concerned searches
249 starting from large sampling standard error and small process standard error, a combination
250 mimicking a short, instable, time series.

251 The MLEs of r and b are highly correlated (0.9990), and the MLE of r , 0.3191, seems
252 unrealistic (Table 2, second row) as it corresponds to a 37.6 % increase per year. These two
253 features combined make the estimate of the coefficient of DD b suspicious.

254 The correlations between estimates (Table 1) emphasize the difficulty to separately estimate
255 the sampling and process variance, and even more, r and b , that are indeed nearly not
256 separately estimable. The latter point makes practical sense: similar population trajectories
257 can arise as the result of a high intrinsic growth rate and a strong DD, or a weaker intrinsic
258 growth rate and a low DD (see figure 5, below). The set of four parameters nearly appears as
259 a set of two macro-parameters, one for the deterministic trajectory, the other one for the
260 uncertainty. Based on our simulations (Figure 3) and a variety of unpublished examples, we
261 think this situation is general. It immediately leads to consider the use of external information
262 to improve the identifiability. Bayesian approaches using appropriate prior distributions on
263 the parameters appear then as a necessity, rather than just an algorithmic convenience.

264 An estimate of the sampling standard error will often be available, e.g., when the population
265 size estimates come from capture-recapture (e.g. Dennis and Oten 2000, who do not account
266 for this uncertainty in their analysis), from stratified sampling (as it is the case with the
267 Greater snow Goose), or more directly, through replicated population sampling (Dennis et al.
268 2010). However, because of the high correlation with the estimated coefficient of DD, and
269 because of the unrealistic value often obtained, as in the snow Goose example, the main target
270 for external information is certainly the intrinsic growth rate r . We strongly suspect that a
271 fair part of published examples correspond to unrealistic estimates of r , without being able to
272 check, as the estimates of r are rarely given in published examples because of the focus on
273 the coefficient of DD b .

274 Assuming in the snow Goose example a Gaussian prior distribution for r with mean 0.20 and
275 standard error 0.06 (i.e. with 95 % of the density between 0.12 and 0.28) to constrain r to a
276 realistic value for such a species (Niel and Lebreton 2005 Table 2) did improve the results
277 (Table 1, second and third row) and provided evidence of very weak DD, with nearly no
278 biological significance.

279 The population size survey appeared as fairly precise, as the MLE of the standard error of the
280 log population size, i.e. of its coefficient of variation is 0.0607, comparable in magnitude to
281 the field estimate (10 % or less, Gauthier et al. 2007 p. 1422). This fairly good precision
282 limited the bias of the naïve regression approach (Table 1 first row), with a 95 % confidence
283 interval for the coefficient of DD encompassing 0, despite its bias. Accounting for uncertainty
284 in population size not only removes a bias, but also increases the precision on the coefficient
285 of DD by reducing the estimate for the process standard error.

286 Contrary to Dennis et al. (2006) and Knape and de Valpine (2011), we found no pervasive
287 presence of local minima in the likelihood, although we agree that care should be exercised on
288 this point (Knape 2008). The sampling correlation between the estimates of r and b and the
289 resulting near non-identifiability is for us the main problem. Results from simulated data
290 (Figure 3, and unpublished results on shorter time series) and a few other unpublished
291 examples indicate similar general properties of what remains in the words of Dennis et al.
292 (2006) a “minimal model”. The improvement brought by using a prior for the intrinsic
293 population growth rate encourages refining the model and combining it with further pieces of
294 external information, to improve its moderate performance. It gives a central role to Bayesian
295 approaches, which also bring a great deal of flexibility. We do not think reasonable to
296 consider as a fair evidence for DD a value of \hat{b} significantly differing from 0 without
297 checking if the associated \hat{r} value makes sense. We currently recommend as a minimal step a
298 careful look at the estimated intrinsic growth rate, and the use of a prior for r based on
299 comparative demography approaches (e.g; Niel and Lebreton 2005).

300 **From a minimal to realistic models**

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

- 303 • Environmental covariates have to be taken into account to reduce the residual standard
304 error and enhance power, and, if negatively autocorrelated, to distinguish their effect
305 from that of DD (e.g. Lebreton 1990).
- 306 • Age structure, e.g. with delayed recruitment, may require considering dependency
307 over several time steps in components of population size.
- 308 • Further structure such as spatial cells may have to be considered, e.g. to model local
309 density-dependence (Murdoch 1994) or dependence on some components of
310 population size.
- 311 • The response to density may nonlinear and more complex functional forms may have
312 to be considered (e.g. Dennis et al. 2006). Comparative explorations of the functional
313 form based on naïve regressions neglecting uncertainty in population size (Sibly et al.
314 2005) appear as highly questionable.

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

317 While in the original presentation by Bulmer (1975) the minimal model was presented as
318 quite a specific statistical object, the state-space model point of view opens a number of
319 perspectives (de Valpine 2002). For instance, it is relatively easy to generalize the state
320 equation to account for an environmental covariate z_t , as $x_{t+1} = r + (1 - b)x_t + cz_t + \varepsilon_t$. Good
321 examples are provided by Jacobson et al. (2004) and Pasinelli et al. (2011). It is also possible
322 to adapt the model to particular life cycles. A good example of a model with a seasonal life
323 cycle is provided by Stenseth et al. (2003).

324 In all such models, the main potential bias of the slope for DD is removed by incorporating
325 the population size uncertainty in the observation equation. However, the slope remains

326 biased for finite sample sizes to an unknown degree. The likelihood for such models can be
327 multimodal (Polansky et al. 2009) and the MLE as a consequence often difficult to obtain.
328 Parametric bootstrap for such realistic models (e.g., with age structure, with covariates) may
329 be tedious and remain thus confidential until a specialized user-friendly piece of software is
330 produced. REML approaches based on first order differences found promising by Dennis et al
331 (2006) could be useful, but have still to be investigated in such a more complex setting. A
332 Bayesian approach seems the most straightforward treatment. As an alternative to MCMC
333 algorithms, the posterior distributions can be obtained through numerical integration (de
334 Valpine and Hastings, 2002), and explicitly in simple cases under Gaussian distributions.

335 **An overview of methods based on time series of estimated population sizes**

336 The first clear recommendation is to abandon all methods not accounting for uncertainty in
337 population size, as they are unavoidably biased when used with real world, “noisy”, estimates
338 of population size. This conclusion, although developed here based on a simple model,
339 applies to any such approach such as the regression of “observed growth rate” $y_{t+1} - y_t$ vs
340 observed population size y_t , as well illustrated by Freckleton et al. (2006 Figure 1c). The
341 resulting bias is particularly vicious in meta-analyses, in which the estimated proportion of
342 populations subject to DD will unavoidably be overestimated. This was suspected in the
343 analysis by Brook and Bradshaw (2006) by Lebreton (2009) and demonstrated for these same
344 data by Knape and De Valpine (2011). Brook and Bradshaw conclude to DD in more than
345 75% of the cases studied, while, accounting for uncertainty in population size estimates and
346 using a Bayesian approach, Knape and de Valpine conclude to significant DD in only 16 % of
347 the case studied. Similarly, based on reliable tools, Jamieson and Brooks (2004) conclude to
348 weak to moderate DD among American ducks. We still suspect part of these conclusions
349 would not resist a close examination of the resulting intrinsic growth rate estimates.

350 The state-space model formulation provides a sensible approach to account for uncertainty in
351 population size (Dennis et al. 2006) and to develop specific models accounting for
352 environmental covariates, age structure etc., and testing thus for DD in presence of such
353 potentially confounding effects.

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

355 1) Numerical issues (multiple maxima to the likelihood or sensitivity to priors,
356 depending on the type of algorithms used) and problems of bias associated with finite
357 sample size which currently make such models difficult to use without specific help
358 from a specialist;

359 2) Low power and identifiability problems as a result of the shortness of the time
360 series and the two-level uncertainty, in particular if further complexities are brought in
361 the model, at an unavoidable cost in terms of number of parameters to be estimated.
362 We would rarely expect evidence for DD with fewer than 30 points and we think
363 external information on the intrinsic growth rate has to be seriously considered in any
364 such analysis unless the goal to remain inaccessible.

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

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

370 **DETECTING AND ESTIMATING DENSITY DEPENDENCE BASED ON TRAITS**

371 By contrast, one clear type of evidence for DD concerns the response of life history traits to
372 changes in population size. Surprisingly, most such studies are observational correlative

373 studies relating particular traits to observed changes in population size over time. Some
374 qualify as quasi-experiments, as based on a clear population crash or explosion (e.g. Aslhey et
375 al. 1998). Despite the current development of experimental ecology, few really manipulative
376 experiments of densities have ever taken place. The few such studies with nest boxes (Torok
377 and Toth, 1988, Alatalo and Lundberg 1984), although quite convincing, do not take full
378 advantage of an experimental setting, notably in terms of block design and replication (see
379 also Newton 1994). Bartmann et al. (1992) provide a good example of an experimental study
380 of density dependent compensatory mortality in the Mule Deer with several replicates.

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

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

395
$$z_{ij} = a + bx_t + \varepsilon_t + \eta_{ij} \quad [11]$$

396 The model may have to incorporate further effects, as the two-level sampling (individuals and
397 years) raises some specific issues (whether for instance the same individuals are sampled over
398 several years or not). Environmental covariates can easily be incorporated as additive effects
399 (Lebreton et al. 1992, Roe Deer example; Catchpole et al. 2000 for survival; Crespin et al.
400 2006 for recruitment; Gaillard et al. 1996 for morphometric traits). The prominent point
401 common to all approaches is again that the density is always a proxy for something else and is
402 always known with some uncertainty, i.e. we are again faced with an error-in-variable
403 problem. Model [11] should be accompanied by an observation equation $y_t = x_t + \zeta_t$. When
404 using the regression model $z_{ij} = a + by_t + \varepsilon_t + \eta_{ij}$, attenuation of the slope estimate towards 0
405 (McArdle 2003) is unavoidable. Clearly, any test on the slope will be conservative, i.e.,
406 contrary to methods based on population size, the presence and intensity of DD is not
407 overestimated, which is good news. As we usually have not much control on the uncertainty
408 in population size, several possibilities are available to account for the error-in-variable
409 problem, of which most remain to be explored:

- 410 • Use an error-in-variable model (Fuller 1987); however, all such models are weakly
411 identifiable, through stringent distributional assumptions, as they exploit differences in
412 distribution in the ε and the η terms to estimate their relative effect on the variation in
413 the response variable;
- 414 • Correct for bias. Barker et al. (2002), develop such an approach in the context of
415 capture-recapture survival models. They develop two examples with seabird data that
416 provide no evidence for DD.
- 417 • Use information on the precision of population estimates, i.e. in the notation above an
418 estimate (or a prior distribution) for $var(\zeta_t)$ to improve identifiability in the error-in-
419 variable model.

- 420 • Recast the capture-recapture model as a state-space model (Gimenez et al. 2007) and
421 consider besides the observation equations needed for representing the recapture
422 process an observation equation $y_t = x_t + \zeta_t$. In such an approach, survival for
423 instance is represented as state equations made of Bernoulli (0/1) random variables,
424 and the detection/recapture process as observation equations also made of 0/1 random
425 variables.
- 426 • Use instrumental variables, a tool commonly used in econometrics (e.g. Stock 2001).
427 An instrumental variable will be in our context a variable uncorrelated with the
428 random term for estimated population size, ζ_t and correlated with true population
429 size. Alternative, independent estimates of population size could be good candidates
430 (for an example using multiple surveys, see Fromentin et al. 2001).

431 The impact of the error-in-variable problem is clearly relatively limited, and, although some
432 statistical care should be exercised, notably for what concerns the use of capture-recapture
433 methodology, the assessment of DD based on traits is relatively straightforward.

434 **DISCUSSION**

435 The first part of our review, on methods for detecting DD based on population size surveys,
436 leads first to several straightforward recommendations, to avoid the pervasive risk of
437 overestimating the strength of DD. The first one is that methods neglecting uncertainty in
438 population size should definitely be abandoned. The second is that the Bayesian approach to
439 simple state-space models, such as the linearized Gompertz model, accounting for uncertainty
440 in population size should be used, with some caution because of practical difficulties. We
441 recommend also a reasonable prior based on external comparative information is used for the
442 population growth rate. Even when these difficulties are correctly handled, which may require
443 the assistance of an applied statistician with good knowledge of these models and their tricks,

444 the simplest models may remain strongly misspecified because they neglect a number of
445 features such as environmental covariates, age structure, particular functional form of DD,
446 etc... Moving away from such minimal models is alike moving from simple regression to
447 more sophisticated linear or nonlinear models: one cannot avoid a trade-off between the
448 improvement brought by a better adaptation of a more complex model to the data (such as a
449 decrease in residual variance), and the loss of precision implied by a greater number of
450 parameters: modeling remains the art of oversimplification. Again, in this context, a Bayesian
451 approach is probably the preferable approach, with caution exercised. In spite of their
452 statistical and practical difficulties, methods based on population size surveys remain very
453 attractive as they immediately translate into population projections. They are often the only
454 practicable analyses of DD when population size surveys only are available, a common
455 situation for managed wildlife populations. There is however little power for time series with
456 fewer than, say, 30 time steps, i.e., in most cases, years. One has to recall that when the power
457 drops down to values close to the test level α , the analysis boils down to deciding for DD or
458 no DD on the basis of a random number.

459 When moving from methods based on population size surveys to methods for detecting DD
460 on traits, one is, in some sense, moving from pattern to process (Swihart et al. 2002). The
461 most straightforward methods for traits, such as using density as a covariate in capture-
462 recapture models, are conservative, i.e. tend to underestimate the strength of DD, which
463 means that the evidence for DD is reliable when present. Several perspectives to correct for
464 the conservative effect of uncertainty in population size will probably be explored in the near
465 future. The most promising is the use of the state-space formulation of capture-recapture
466 models (Gimenez et al. 2007), completed by an observation equation for population size to
467 properly model DD. While they can thus be used more confidently than approaches based on
468 population size surveys, methods for DD in traits do not easily lead to population projections.

469 Even when the traits under study are demographic, they can only be translated into projections
470 through a projection model such as a matrix model. Nevoux et al. (2011) examine the
471 consequences of DD in different traits of the Mauritius Kestrel *Falco punctatus* by integrating
472 these different traits and their DD relationships into a nonlinear discrete time model, studied
473 independently from the trait analyses. In the absence of correction for attenuation, the results
474 of such models should be looked at with a critical eye. Moreover, deterministic models do not
475 account for the interplay of DD and various forms of stochasticity.

476 As the state-space formulation can easily encompass projection models (e.g. Gauthier et al.
477 2007) and as it brings decisive advantages for assessing DD whether from population surveys
478 or in studies of traits, it is clear that the future of DD modeling lies with state-space modeling.

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

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

489 The corresponding observation equations are:

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

491 • Equations for the uncertainty in the observation for population size (as a vector or total
492 number).

493 A model on these lines is proposed by Abadi et al. (submitted). Rotella et al ; (2009) go also
494 one step in this direction by examining Weddell Seal population size estimates derived
495 together with demographic parameters from a capture-recapture analysis within a stochastic
496 Gompertz model. The demographic parameters are however not examined for DD and the
497 estimated intrinsic growth rate is not given.

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

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

510

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514 **LITERATURE CITED**

515 Abadi, F., O. Gimenez, W. Jakober, R. Arlettaz, and M. Schaub. Submitted. Estimating the
516 strength of density-dependence in the presence of observation errors using integrated
517 population models.

518 Alatalo, R. V., and A. Lundberg. 1984. Density-Dependence in breeding success of the pied
519 flycatcher (*Ficedula hypoleuca*). *Journal of Animal Ecology* 53:969-977.

520 Andrewartha, H. G., and L. C. Birch. 1954. *The distribution and abundance of animals.*
521 University of Chicago Press, Chicago.

522 Arcese, P., and J. N. M. Smith. 1988. Effects of population density and supplemental food on
523 reproduction in song sparrows. *Journal of Animal Ecology* 57:119-136.

524 Ashley, E. P., G. B. McCullough, and J. T. Robinson. 1998. Morphological responses of
525 white-tailed deer to a severe population reduction *Canadian Journal of Zoology* 76:1-
526 5.

527 Barker, R., D. Fletcher, and P. Scofield. 2002. Measuring density dependence in survival from
528 mark-recapture data. *Journal of Applied Statistics* 29:305-313.

529 Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a
530 Colorado Mule Deer population. *Wildlife Monographs* 121: 1-39.

531 Berryman, A. A. 2004. Limiting factors and population regulation. *Oikos* 105:667-670.

532 Bonenfant, C., J. M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe,
533 P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit, and P. Duncan. 2009.

534 Empirical Evidence of Density-Dependence in Populations of Large Herbivores.

535 Pages 313-357 in H. Caswell, editor. *Advances in Ecological Research*, Vol 41.

536 Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in
537 abundance time series of 1198 species. *Ecology* 87:1445-1451.

538 Bulmer, M. G. 1975. The statistical analysis of density-dependence. *Biometrics* 31:901-911.

539 Caswell, H. 2001. Matrix population models. 2nd edition, in press edition. Sinauer,
540 Sunderland, Mass.

541 Catchpole, E. A., B. J. T. Morgan, T. N. Coulson, S. N. Freeman, and S. D. Albon. 2000.
542 Factors influencing Soay sheep survival. *Journal of the Royal Statistical Society Series*
543 *C-Applied Statistics* 49:453-472.

544 Crespin, L., M. P. Harris, J.-D. Lebreton, M. Frederiksen, and S. Wanless. 2006. Recruitment
545 to a seabird population depends on environmental factors and on population size.
546 *Journal of Animal Ecology* 75:228-238.

547 De Valpine, P. 2002. Review of methods for fitting time-series models with process and
548 observation error and likelihood calculations for nonlinear, non-Gaussian state-space
549 models. *Bulletin Of Marine Science* 70:455-471.

550 De Valpine, P., and A. Hastings. 2002. Fitting population models incorporating process noise
551 and observation error. *Ecological Monographs* 72:57-76.

552 Dennis, B. and M. R. M. Otten. 2000. Joint effects of density dependence and rainfall on
553 abundance of San Joaquin kit fox. *Journal of Wildlife Management* 64: 388-400.

554 Dennis, B., and M. L. Taper. 1994. Density-dependence in time-series observations of natural
555 populations - Estimation and testing. *Ecological Monographs* 64:205-224.

556 Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. 2006. Estimating
557 density dependence, process noise, and observation error. *Ecological Monographs*
558 76:323-341.

559 Diekmann, O. 2005. On the Mathematical synthesis of physiological and behavioural
560 mechanisms and population dynamics. Centre for Mathematics and Computer Science.

561 Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland. 2006. Census error
562 and the detection of density dependence. *Journal of Animal Ecology* 75:837-851.

563 Fromentin, J. M., R. A. Myers, O. N. Bjornstad, N. C. Stenseth, J. Gjosaeter, and H. Christie.
564 2001. Effects of density-dependent and stochastic processes on the regulation of cod
565 populations. *Ecology* 82:567-579.

566 Fuller, W. A. 1987. *Measurement error models*. Wiley, New-York.

567 Gaillard, J. M., D. Delorme, J. M. Boutin, G. VanLaere, and B. Boisaubert. 1996. Body mass
568 of roe deer fawns during winter in 2 contrasting populations. *Journal of Wildlife*
569 *Management* 60:29-36.

570 Gauthier, G., P. Besbeas, B. J. T. Morgan, and J.-D. Lebreton. 2007. Population growth in
571 Snow Geese: A modeling approach integrating demographic and survey information.
572 *Ecology* 88:1420-1429.

573 Gimenez, O., V. Rossi, R. Choquet, C. Dehais, B. Doris, H. Varella, J.-P. Vila, and R. Pradel.
574 2007. State-space modelling of data on marked individuals. *Ecological Modelling*
575 206:431-438.

576 Guthery, F. S., and J. H. Shaw. 2012. Density-Dependence: applications in wildlife
577 management. *Journal of Wildlife Management* In press.

578 Hamilton, J. D. 1994. *Time series analysis*. Princeton, NJ, Princeton University Press.

579 Jacobson, A. R., A. Provenzale, A. von Hardenberg, B. Bassano and M. Festa-Bianchet. 2004.
580 Climate forcing and density-dependence in a mountain ungulate population. *Ecology*
581 85: 1598–1610.

582 Jamieson, L.E. and S. P. Brooks. 2004. Density dependence in North American ducks.
583 *Animal Biodiversity and Conservation* 27:113-128.

584 Knappe, J. 2008. Estimability of density-dependence in models of time-series data. *Ecology*
585 89:2994-3000.

586 Knappe, J., and P. De Valpine. In revision. Are patterns of density dependence in the Global
587 Population Dynamics Database driven by observation errors?

588 Krebs, C. J. 1995. Two paradigms of population regulation. *Wildlife Research* 22:1-10.

589 Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.

590 Lebreton, J.-D. 1989. Statistical methodology for the study of animal populations. *Bull.*
591 *International Statistical Institute* 53:267-282.

592 Lebreton, J.-D. 1990. Modelling density-dependence, environmental variability, and
593 demographic stochasticity from population counts: an example about Wytham Great
594 tits. Pages 89-102 in J. Blondel, A. Gosler, J.-D. Lebreton, and R. McCleery, editors.
595 *Population biology of passerine birds an integrated approach*. Springer, Berlin.

596 Lebreton, J.-D. 2009. Assessing density-dependence: where are we left? Modeling
597 demographic processes in marked populations. T. D. L., E. G. Cooch and M. J.
598 Conroy, Springer. 3: 19-42.

599 Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and
600 testing biological hypotheses using marked animals: a unified approach with case
601 studies. *Ecological Monographs* 62:67-118.

602 Link, W. A. 2003. Nonidentifiability of population size from capture-recapture data with
603 heterogeneous detection probabilities. *Biometrics* 59:1123-1130.

604 Lunn, D.J., A. Thomas, A., N. Best, and D. Spiegelhalter (2000) WinBUGS -- a Bayesian
605 modelling framework: concepts, structure, and extensibility. *Statistics and Computing*,
606 10:325-337.

607 Maelzer, D. A. 1970. The regression of $\log(N_{t+1})$ on $\log(N_t)$ as a test of density-dependence:
608 an exercise with computer constructed density independent populations. *Ecology*
609 51:810-822.

610 Malthus, T. R. 1798. An essay on the principle of population. Pages 4-16 in G. Hardin, editor.
611 *Population, evolution, and birth control: a collage of controversial ideas* (1964).
612 Freeman, San Francisco.

613 Maynard Smith, J. 1965. Professor J. B. S. Haldane, FRS. *Nature* 206:239-240.

614 McArdle, B. H. 2003. Lines, models, and errors: Regression in the field. *Limnology and*
615 *Oceanography* 48:1363-1366.

616 Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271-287.

617 Nevoux, M., O. Gimenez, D. Arlt, M. Nicoll, C. Jones, and K. Norris. 2011. Population
618 regulation of territorial species: both site dependence and interference mechanisms
619 matter. *Proceedings of the Royal Society B-Biological Sciences* 278:2173-2181.

620 Newton, I. 1994. Experiments on the limitation of bird breeding densities - a review. *Ibis*
621 136:397-411.

622 Newton, I. 1998. Population limitation in birds. Academic Press, London.

623 Pasinelli, G., M. Schaub, G. Hafliger, M. Frey, H. Jakober, M. Muller, W. Stauber, P.
624 Tryjanowski, J. L. Zollinger and L. Jenni. 2011. Impact of density and environmental
625 factors on population fluctuations in a migratory passerine. *Journal of Animal Ecology*
626 80: 225-234.

627 Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using
628 Gibbs Sampling, . ISSN 1609-395X. *Proceedings of the 3rd International Workshop*
629 *on Distributed Statistical Computing DSC 2003*, March 20-22, , Vienna, Austria.

630 Polansky, L., P. de Valpine, J. O. Lloyd-Smith, and W. M. Getz. 2009. Likelihood ridges and
631 multimodality in population growth rate models. *Ecology* 90: 2313-2320.

632 Reddingius, J., and P. J. Denboer. 1989. On the stabilization of animal numbers - problems of
633 testing. 1. Power estimates and estimation errors. *Oecologia* 78:1-8.

634 Rotella, J. J., W. A. Link, J. D. Nichols, G. L. Hadley, R. A. Garrott, and K. M. Proffitt. 2009.
635 An evaluation of density-dependent and density-independent influences on population
636 growth rates in Weddell seals. *Ecology* 90: 975-984.

637 Saether, B. E., R. Lande, S. Engen, H. Weimerskirch, M. Lillegard, R. Altwegg, P. H. Becker,
638 T. Bregnballe, J. E. Brommer, R. H. McCleery, J. Merila, E. Nyholm, W. Rendell, R.
639 R. Robertson, P. Tryjanowski, and M. E. Visser. 2005. Generation time and temporal
640 scaling of bird population dynamics. *Nature* 436:99-102.

641 Sæther, B.-E., S. Engen, R. Lande, C. Both, and M. E. Visser. 2002. Density dependence and
642 stochastic variation in a newly established population of a small songbird. *Oikos*
643 99:331-337.

644 Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of
645 populations of mammals, birds, fish, and insects. *Science* 309:607-610.

646 Stenseth, N. C., H. Viljugrein, T. Saitoh, T. F. Hansen, M. O. Kittilsen, E. Bølviken, and F.
647 Glöckner. 2003. Seasonality, density dependence, and population cycles in Hokkaido
648 voles. *Proceedings of the National Academy of Sciences USA* 100:11478–11483.

649 Stephens, P. A., F. Frey-Roos, W. Arnold, and W. J. Sutherland. 2002. Model complexity and
650 population predictions. The alpine marmot as a case study. *Journal of Animal Ecology*
651 71:343-361.

652 Swihart, R. K., J. B. J. Dunning, and P. M. Waser. 2002. Gray matters in ecology: dynamics
653 of pattern, process and scientific progress. *Bulletin of the Ecological Society of*
654 *America* 83:149-155.

655 Torok, J., and L. Toth. 1988. Density dependence in reproduction of the collared flycatcher
656 (*Ficedula albicollis*) at high population levels. *Journal of Animal Ecology* 57:251-
657 258.

658 Tuljapurkar, S. 1990. *Population dynamics in variable environments*. Springer, New-York.

659 Turchin, P. 2001. Does population ecology have general laws? *Oikos* 94:17-26.

660 Verhulst. 1838. Notice sur la loi que suit la population dans son accroissement (English
661 translation). *in* E. J. Kormondy, editor. (1965) *Readings in ecology*. Prentice-
662 Hall, Englewood Cliffs, New-Jersey.

663 Wang, G., N. T. Hobbs, S. Twombly, R. B. Boone, A. W. Illius, I. J. Gordon, and J. E. Gross.
664 2009. Density dependence in northern ungulates: interactions with predation and
665 resources. *Population Ecology* 51: 123-132.

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

669

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 $var(\varepsilon_t)=0.64$. 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 $var(x_t) \rightarrow \infty$,
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, $se(y_t / x_t) = se(\eta_t)$ 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

706 Figure 3: Deviance ($-2 \times \log$ -likelihood) contours of simulated trajectories of increasing
707 number of time steps ($T=10, 20, 50$ and 100) of the density dependent model
708 $x_{t+1} = r + (1-b)x_t + \varepsilon_t$ with uncertainty on log-population size represented as $y_t = x_t + \eta_t$.
709 The parameters used in the simulations are $r = 0.1$, $b = 0.3$, $s\mathcal{d}(\varepsilon_t) = 0.2$, $s\mathcal{d}(\eta_t) = 0.4$. The
710 deviance is represented under $s\mathcal{d}(\varepsilon_t) = 0.2$, $s\mathcal{d}(\eta_t) = 0.4$ as a function of b (in abscissa, from
711 -0.3 to 0.7) and r (in ordinate, from -0.5 to 0.7). The contours clearly show that in presence
712 of uncertainty on population size a) the likelihood and the maximum likelihood estimates are
713 well behaved in the absence of model misspecification; b) for realistic number of time steps (
714 < 50), the estimates of r and b will be strongly positively correlated, making it difficult to
715 distinguish between low intrinsic growth rate and light density-dependence vs high intrinsic
716 growth rate and strong density-dependence.

717

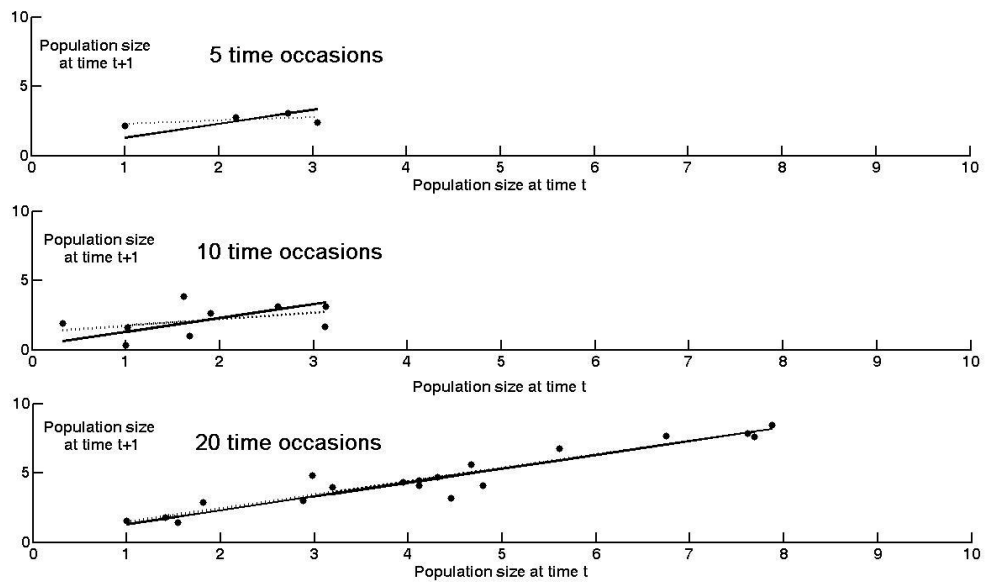
718 Figure 4: Profile Deviance for parameter r of the density dependent model

719 $x_{t+1} = r + (1-b)x_t + \varepsilon_t$ with uncertainty on log-population size represented as $y_t = x_t + \eta_t$,
720 applied to spring population surveys of the greater Snow Goose (data from Gauthier 2007).
721 For each value of r the deviance is maximized with respect to the three other parameters b ,
722 $var(\varepsilon_t)$, and $var(\eta_t)$.

723

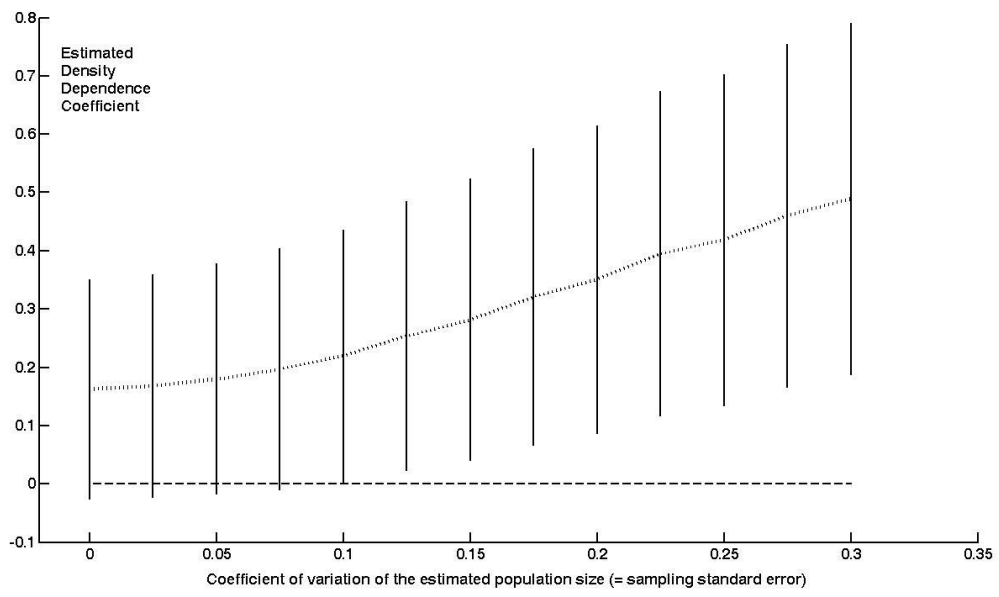
724 Figure 5: reconstructed log spring population size for the Greater Snow Goose, based on the
725 relationship $x_{t+1} = r + (1-b)x_t$. Plain line: MLEs of r and b ; dotted line: Estimates under a
726 Gaussian prior distribution for r with mean 0.20 and standard error 0.06 . The ability to
727 discriminate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

729 Figure 1



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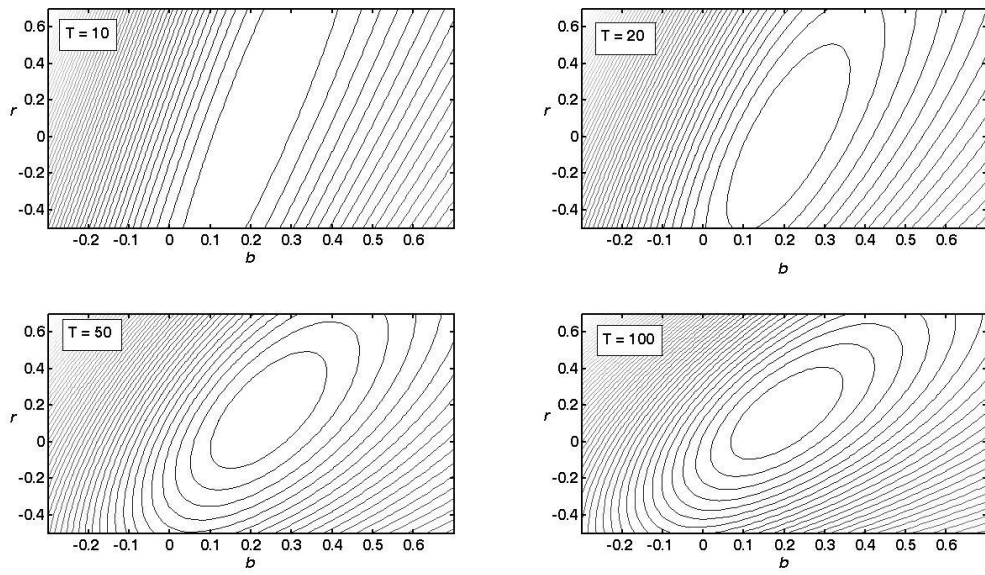
732 Figure 2



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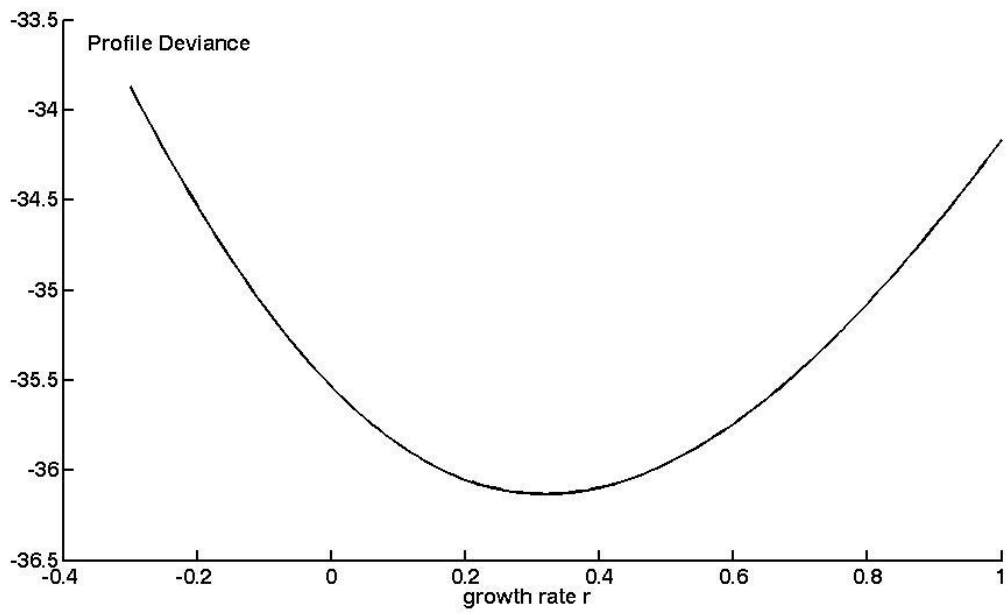
735 Figure 3



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737

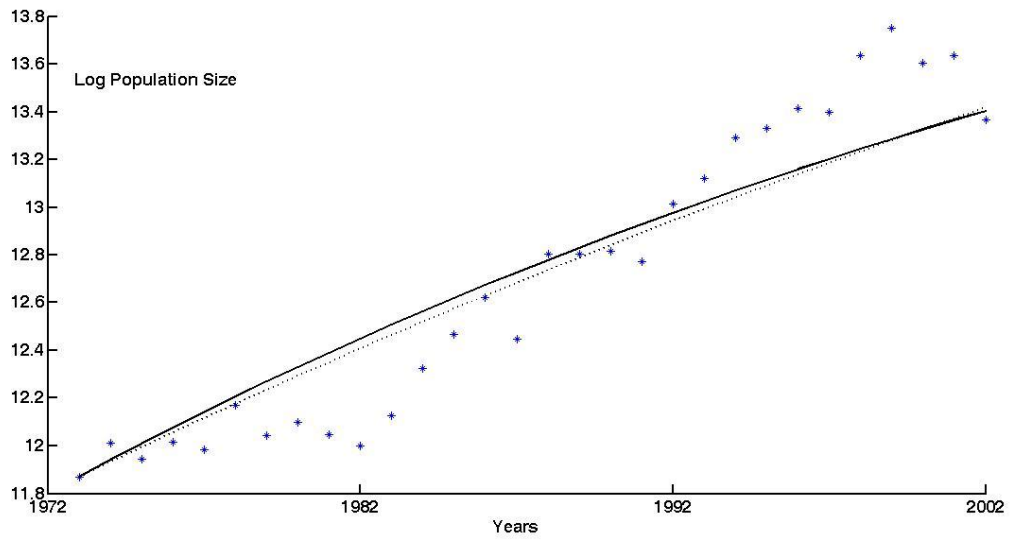
738 Figure 4



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740

741 Figure 5



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