

# Parameter estimation in a generalized discrete-time model of density dependence

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**Abstract** Flexible discrete-time per-capita-growth-rate models accommodating a variety of density-dependent relationships offer parsimonious explanations for the variation of population abundance through time. However, the accuracy of standard approaches to parameter estimation and confidence interval construction for such models has not been explored in a generalized setting or with consideration of limited sample sizes typical for ecology. Here, we use simulated data to quantify the relative effects of sample size, population perturbations, and environmental stochasticity on statistical inference. We focus on the key parameters that inform population dynamic predictions in a generalized Beverton–Holt model. We find that reliable parameter estimation requires data spanning ranges where both low and high density dependence act. However, the

asymptotic distribution of the likelihood ratio test statistic can be fairly accurate for constructing confidence regions even when point estimation is poor. Consideration of the joint profile likelihood surface is shown to be useful for assessing reliability of point estimates and dynamical population predictions.

**Keywords** Density dependence · Beverton–Holt · Time series analysis · Statistical inference · Per capita growth rate · Discrete-time population model

## Introduction

Time series analysis has emerged as a fundamental approach to understanding core questions in population ecology (Bjornstad and Grenfell 2001). One such scientific endeavor, the identification of patterns in time series data that are consistent with population regulation, has particularly benefited from this approach. For example, theoretical population models without density dependence predict unbounded growth or decline and the simplest models capturing long-term dynamics in regulated populations must include a term that reflects density-dependent influences on population rates of change (Turchin 1995). Testing theoretical models against time series data with statistical modeling and inference is important for addressing central questions about the way in which density dependence acts, even in the face of limited sample sizes and noisy data, and motivates the research here.

The starting point for evaluating the way in which density dependence acts is a time series of observed densities (or a proxy)  $N^T = \{n_t\}_{t=1}^T$  of length  $T$ , where  $n_t$  is the density (proxy) of individuals in a population at time

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*t*. A simple stochastic framework for relating  $n_{t+1}$  to  $n_t$  that includes a general notion of density dependence is given by

$$n_{t+1} = rn_t g(n_t) e^{\nu_t}, \quad (1)$$

where the density-independent growth rate parameter  $r$  is the product of the per capita birth rate (young born per adult per generation) and the probability of survival from birth to maturity,  $g(n_t)$  accounts for the effects of density and  $\nu_t$  is as commonly assumed (e.g., Dennis and Taper 1994) a normally distributed random variable representing environmental stochasticity with mean  $\mu=0$  and standard deviation  $\sigma>0$ . The product  $rg(n)$  is sometimes referred to as the per-capita-growth-rate (*pgr*) curve, where  $r$  is the density-independent component and  $g(n)$  a density-dependent modifier that may take a variety of forms. We refer to the region where  $g(n)$  is close to one, for small  $n$ , as the (approximately) density-independent region.

With increased computing power and availability of long-term datasets, population ecologists are beginning to consider general models for  $g(n)$  and aiming to estimate the shape as well as the strength of density dependence in population studies (Bellows 1981; Myers et al. 1999; Saether et al. 2000, 2002a, b, 2007; Sibly et al. 2005; Owen-Smith 2006). Generalized density-dependent models are highly flexible in describing the shape of the decline of the *pgr* curve with increasing population density and can increase realism substantially by allowing the effects of density dependence to set in around some critical population size (Fig. S1; Bellows 1981; Getz 1996). Using least-squares methods to compare the fits of several density-dependent models, including both general and restricted Ricker and Beverton–Holt (BH) models, Bellows (1981) concluded that the generalized BH models most often described a wide range of insect populations but did not expand the research to address general issues of statistical inference for such models.

Efforts to estimate point values and confidence intervals for the parameters of generalized density-dependent models face several recognized challenges: observation error (Doncaster 2006; Freckleton et al. 2006), model misspecification (Getz and Lloyd-Smith 2006), lack of informative data (Myers et al. 1999), and sample size (Saether et al. 2000). In this paper, we focus on the issues embodied in the latter two concerns using frequentist likelihood methods. To investigate rates of convergence of parameter estimates for models with form given by Eq. 1, we choose a generalized BH density-dependent model (described below). In particular, we examine how different true *pgr* curves, sample sizes, levels of environmental stochasticity  $\sigma$ , and population perturbations affect statistical inference on the growth rate and shape parameters in a generalized BH model of density dependence. Our qualitative findings will hold generally for other common models

of density dependence, including the Ricker, theta-logistic, and Gompertz models, because the asymptotic distributional results discussed below apply to biologically plausible density-dependent models (i.e., the *pgr* decreases with increased density) of the form of Eq. 1 which define stationary distributions and are differentiable with respect to their parameters (Tong 1990).

## Model

The generalized BH density-dependent model has a long history in population ecology (e.g., Maynard Smith and Slatkin 1973; Bellows 1981; Getz 1996) and has a close relationship to the continuous-time logistic growth model (Turchin 2003). A generalized BH density-dependent process defines  $g(n)$  as

$$g(n) = K^\gamma / (K^\gamma + n^\gamma) \quad (2)$$

where  $K$  is the half-saturation parameter that determines the density of  $n$  at which the change  $g'(n)$  is maximized, and  $\gamma>0$  is a parameter controlling the shape of density dependence. Equations 1 and 2 define a stochastic process satisfying properties guaranteeing the existence of a stationary distribution, the long-term limiting distribution of  $n_t$  (Tong 1990).

In addition to a fixed-point equilibrium at  $n^* = K(r-1)^{1/\gamma}$ , the deterministic model ( $\sigma=0$ ) defined by Eq. 1 with  $g(n)$  as in Eq. 2 exhibits a rich variety of dynamics in its population trajectories and has a relatively well-understood phase plane that includes both fixed-point and cyclic attractors that depend on the values of  $r$  and  $\gamma$  (Maynard Smith and Slatkin 1973; Getz 1996; Schoombie and Getz 1998); bifurcation from damped to stable oscillations occurs at the boundary  $r = 2/(\gamma - 2)$  (Getz 1996).

## Statistical inference

Likelihood-based statistical inference is used widely in ecology (Hilborn and Mangel 1997) and is the approach we take here to understand parameter estimation properties of the generalized BH model with sample sizes and some scenarios typical for ecology. Use of the likelihood to estimate parameters, ascertain confidence intervals, and test hypotheses rests on a rigorous foundation based on asymptotic theory (Severini 2000). We follow convention in denoting the vector of model parameters by  $\theta=(r, K, \gamma, \sigma)$  in the space  $\Theta$  of all possible parameter values (nonzero  $\mu$  can be expressed as  $\mu=0$  with an appropriate change in  $r$ , so for the remainder of the paper and without loss of generality  $\mu$  is fixed at 0 in all simulation and estimation equations).

Given a time series of population densities  $\mathbf{N}^T$ , let  $x_t = \log_e(n_t)$ . Assuming the random variables  $\nu_1, \nu_2, \dots$  in Eq. 1 are independent and normally distributed with  $\mu=0$  and standard deviation  $\sigma>0$ , the log-likelihood function for the model of Eqs. 1 and 2 is given by

$$\ell(\theta) = (T - 1) \log_e \left( \frac{1}{\sigma\sqrt{2\pi}} \right) - \frac{1}{2\sigma^2} \times \sum_{t=1}^{T-1} [x_{t+1} - \log_e(r) - x_t + \log_e(1 + (\exp(x_t)/K)^\gamma)]^2. \tag{3}$$

The maximum likelihood (ML) estimators of the structural parameters  $r, K,$  and  $\gamma$  obtained by maximizing Eq. 3 are the same as those obtained by a least-squares fit of the one-step-ahead prediction error.

Typically discussed in the context of independent, identically distributed data, several desirable properties (e.g., consistency, efficiency, and asymptotic normality) of the ML estimate  $\hat{\theta}$  also hold for non-linear discrete-time models such as Eq. 3 (Tong 1990). In particular, using Taylor series approximations of  $\ell(\theta)$  around the true value  $\theta_0=(r_0, \gamma_0, K_0, \sigma_0)$  and large-sample convergence, it can be shown that

$$W = 2 \left( \ell(\hat{\theta}) - \ell(\theta_0) \right) \sim \chi_d^2, \tag{4}$$

where  $d$  is the number of free parameters in the model (Tong 1990). Thus, for example, given an estimate  $\hat{\theta}$  and a desired test size  $\alpha$ , a  $(1-\alpha)$  confidence region is defined as the set of  $\theta$  such that  $W$  is less than the  $(1-\alpha)$  quantile of the chi-squared distribution with  $d$  degrees of freedom. Related asymptotic results (e.g., the Rao score or Wald statistics) approximate the likelihood surface as quadratic, with subsequent construction of confidence intervals based on an estimate of the parameter variance–covariance matrix at the ML point (Severini 2000). Such methods result in elliptical confidence regions and turn out to be a liability for the model considered here.

### Testing large-sample results on realistic sample sizes

We simulated data with known parameter values (Table 1) to evaluate the accuracy of ML point estimates using Eq. 3 and confidence regions using Eq. 4. The source of variation in population fluctuations (e.g., external noise vs. over-compensatory population growth rates) and  $pgr$  data at low population densities are expected to be important for parameter estimation (Schaffer et al. 1986; Kendall 2001; Saether et al. 2002b). The impacts of both are considered in this study. Throughout, the fixed-point equilibrium of the deterministic trajectories of the generating model was kept constant at  $n^*=1$  by setting the half-saturation parameter  $K_0 = (r_0 - 1)^{1/\gamma_0}$  for different choices of  $r_0$  and  $\gamma_0$ .

We initially focus on data generated from all possible  $(r_0, \gamma_0)$  pairs where  $r_0$  takes values from the set  $\{1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5\}$  and  $\gamma_0$  takes values from the set  $\{1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5\}$  (Table 1). Each pair uniquely determines the stability of  $n^*$  (Getz 1996) with stronger instability typically generating larger variance of the stationary distribution. These choices of  $(r_0, \gamma_0)$  focus on biologically realistic systems ( $n^*>0$ ) in which the form of density dependence is allowed to be initially concave up (relatively strong) or down (relatively weak; Figs. S1 and S2) and such that the overall effects of density dependence are both weak and strong around  $n^*$  and result in either absent, damped, or persistent oscillations in the deterministic population trajectories (Fig. S2). Other choices for the values of  $r_0$  and  $\gamma_0$  would likely produce similar parameter estimation properties for  $\hat{\theta}$  as those values of  $r_0$  and  $\gamma_0$  considered here as a result of similar deterministic predictions about population trajectories. The set of  $(r_0, \gamma_0)$  values considered here also spans the range of least-squares parameter estimates for several insect populations (Bellows 1981). To emphasize the effect of deterministic density-dependent variation, we set the environmental stochasticity at a relatively low value  $\sigma_0=0.05$ .

Not all of the stationary distributions for the scenarios above are expected to contain population densities that are sufficiently low so that the influence of density-independent growth is present. Thus, we considered two additional

**Table 1** Parameter values used to generate different datasets with Eqs. 1 and 2

Parameters	Data		
	Stationary with small environmental stochasticity	Stationary with large environmental stochasticity	Perturbed
$r_0$	1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5	3	3
$\gamma_0$	1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5	1, 5	1, 5
$\sigma_0$	0.05	0.25	0.05

For each unique combination of parameters across the rows of each column and for each value of  $T$  equal to 10, 20, and 50, we generated 300 time series to obtain data  $\mathbf{N}^T$ .  $K_0$  was set at  $(r_0 - 1)^{1/\gamma_0}$  in all simulations to keep  $n^*=1$ . See text for a discussion of the biological implications for each set of generating parameter values  $(r_0, \gamma_0, K_0, \sigma_0)$ .

sources of variation in time series data  $\mathbf{N}^T$ : increased environmental stochasticity with  $\sigma_0=0.25$  and perturbations, described below, with  $\sigma_0=0.05$  (Table 1). For the other parameters of the generating model, we chose two  $(r_0, \gamma_0)$  pairs, (3, 1) and (3, 5), to represent the stable and unstable regions of parameter space, respectively. For  $r_0=3$ , when  $\gamma_0=1$  the attractor has a stable equilibrium point at  $n^*$  and for  $\gamma_0=5$  the attractor is cyclic with period three, a minimum population density of  $0.23n^*$ , and a maximum population density of  $1.57n^*$ .

The two choices for  $\sigma_0$  gave a feel for the relative role of environmental stochasticity in the types of models and data considered here. The relationship between the one-step-ahead expected population trajectory and the stochastic one, with the parameters chosen here, is that approximately 68% of the time the value of  $n_{t+1}$  will be within  $100\sigma_0\%$  of its expected value, and approximately 95% of the time it will be within  $200\sigma_0\%$  of the expected value.

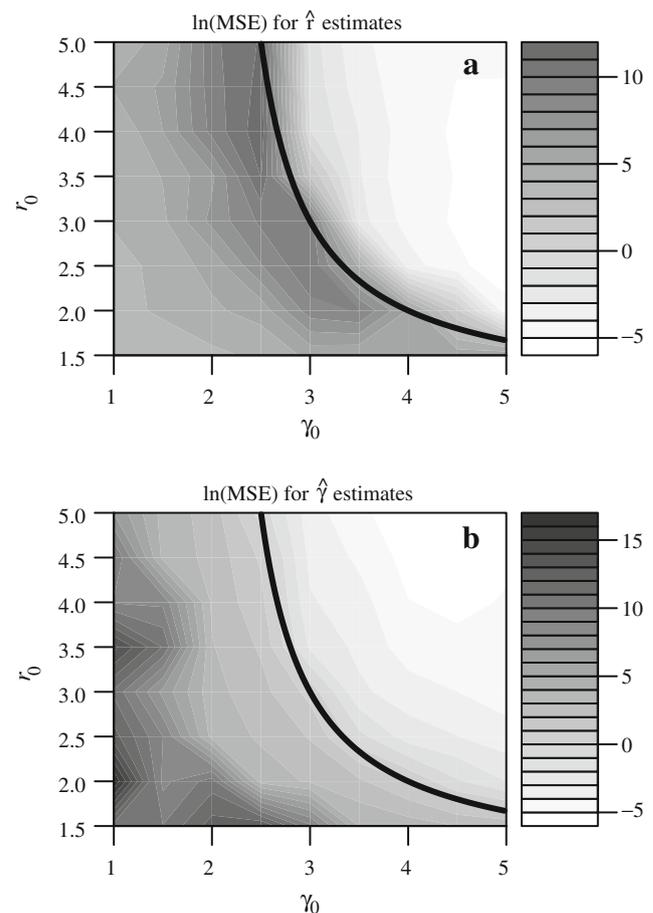
For each of the generating models discussed above and summarized in Table 1, we generated 300 time series of length 1,050, reusing the stochastic terms when changing the structural parameters  $r_0$  and  $\gamma_0$  to keep the environmental stochasticity constant across changes in the deterministic component of population variation. The initial population density  $n_0$  for each simulation was set at 0.1, corresponding to 10% of the deterministic fixed-point equilibrium. Sampling the final 10, 20, and 50 values produce a time series associated with the stationary distribution. Sampling from the first 10, 20, and 50 points provided a time series associated with a return toward the stationary distribution following a perturbation. The choices of sample size were motivated by data in the Global Population Dynamics Database (National Environment Research Council (NERC) Centre for Population Biology 1999) from which 3,269 time series considered by (Sibly et al. 2005) had mean length 16.5 and a standard deviation of 14.2.

Maximizing  $\ell(\theta)$  in Eq. 3 for each sample gave 300 independent ML point estimates for each scenario. We maximized Eq. 3 using both the Nelder–Mead and BFGS algorithms as implemented in R 2.6.0 (R Development Core Team) with multiple restarts. The robustness of this approach for finding the maximum of Eq. 3, sometimes difficult when the likelihood surfaces had extended ridges of similar values around the maximum, was tested using several diagnostic runs. We evaluate point estimation properties by calculating the bias, variance about the mean, and the mean squared error (MSE, equal to variance plus squared bias) of the point estimates.

To explore the efficacy of using the asymptotic distribution in Eq. 4 as a means for constructing accurate confidence regions, we compare it with the distribution of  $W$  formed from the 300 resulting ML estimates for each scenario using the two representative  $(r_0, \gamma_0)$  pairs. In this

case, the degrees of freedom  $d$  equals 4, corresponding to the number of parameters being estimated. By calculating the proportion of samples for which the theoretically defined confidence interval contained the true parameter value, we obtained a measure of the actual coverage for confidence intervals calculated using Eq. 4.

The joint profile likelihood of two parameters in a multiparameter model is useful for interpreting the overall estimation problem and the shape of the confidence regions (Tong 1990). This surface of values is constructed by varying the two parameters of interest over a grid of values and repeatedly maximizing  $\ell(\theta)$  in the remaining two free parameters. Given a relatively accurate approximation of the likelihood ratio test (LRT) statistic to its limiting distribution in Eq. 4, it is possible to approximate confidence regions at specified  $p$  values, while also detecting likelihood ridges, by transforming this surface accordingly (i.e., taking twice the difference between the value  $\ell(\hat{\theta})$  and each of the maximized joint profile likelihood values) and plotting



**Fig. 1** MSE contour plots (*shading*) and the bifurcation boundary (*line*) from damped to sustained oscillations (*lower left* and *upper right*, respectively) for point estimates of  $\hat{r}$  in panel **a** and  $\hat{\gamma}$  in panel **b** from stationary time series with  $T=20$  and  $\sigma_0=0.05$ . The values of the generating pair  $(r_0, \gamma_0)$  are given on the  $y$  and  $x$  axes

contours at levels defined by quantiles of a chi-square distribution with 2 *df*.

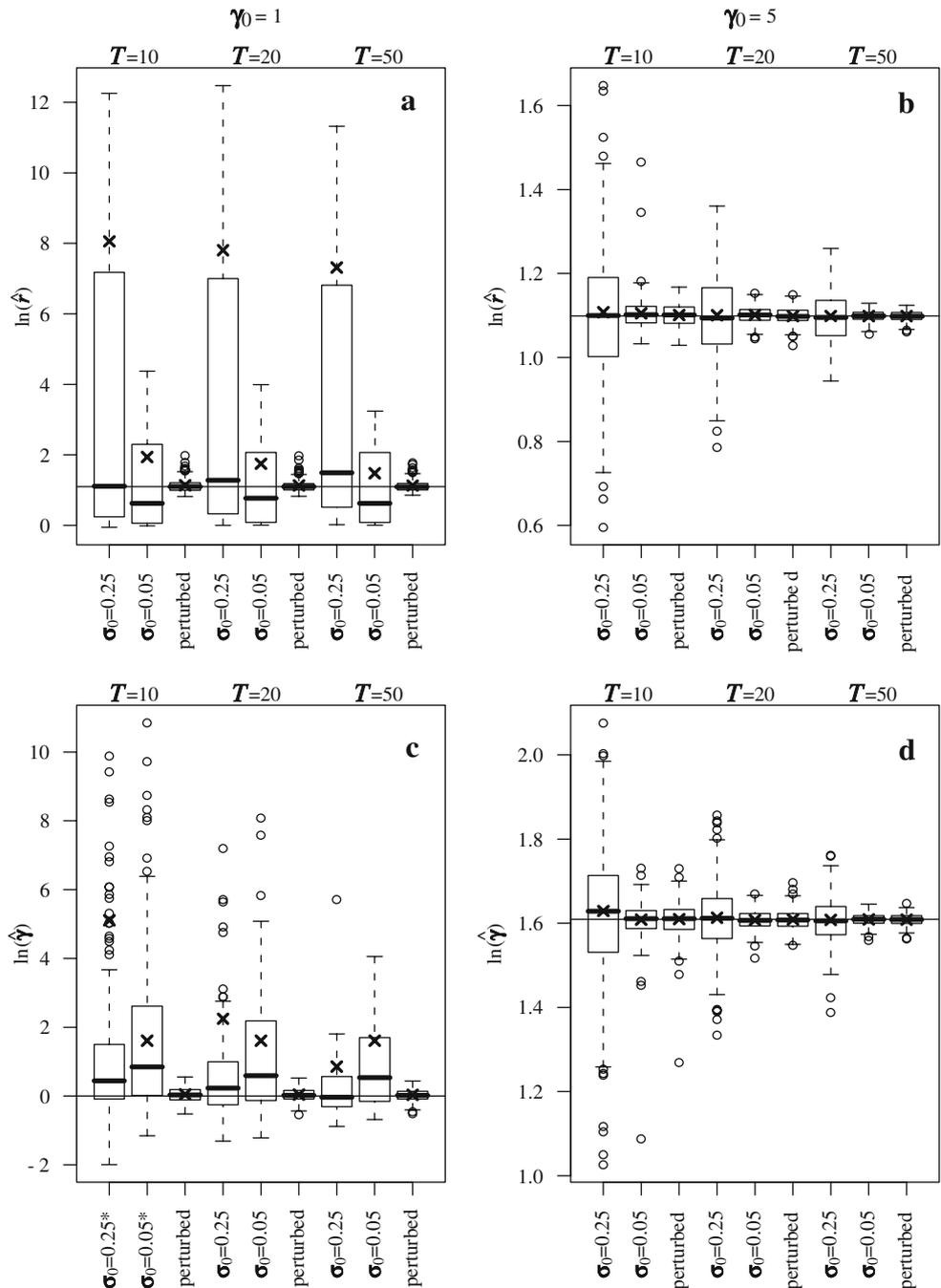
**Results**

The type of deterministic population dynamics defined by the values  $r_0$  and  $\gamma_0$  had substantial effects on point estimation properties (Fig. 1; Tables S1–S18 of the Supporting Information). Notably, as the  $(r_0, \gamma_0)$  pair moves from the

stable region  $r_0 < 2/(\gamma_0 - 2)$  to the bifurcation line (i.e., deterministic oscillations around  $n^*$  take longer to dampen out), estimates of  $r_0$  become increasingly worse and estimates of  $\gamma_0$  increasingly better. Sharp improvement in estimation of both parameters is made when  $(r_0, \gamma_0)$  pairs produce sustained population fluctuations.

Focusing on the representative  $(r_0, \gamma_0)$  pairs (3, 1) and (3, 5) used to evaluate the importance of other sources of data variation, parameter estimation was also highly improved when populations experienced perturbations and

**Fig. 2** Tukey box plots with whiskers extending to 1.5 times the interquartile range of natural logarithmic-transformed point estimates of  $\hat{r}$  (panels **a** and **b**) and  $\hat{\gamma}$  (panels **c** and **d**), for the representative  $(r_0, \gamma_0)$  pairs (3, 1) and (3, 5). Open circles give locations of values beyond 1.5 times the interquartile range. The perturbed data were simulated with  $\sigma_0=0.05$ . Sets of three correspond to sample size  $T$  values shown above each panel. Panel column **a, c** uses  $\gamma_0=1$  and panel column **b** and **d** uses  $\gamma_0=5$  to generate data (see Table 1). Asterisks indicate that the plot omitted inclusion of negative estimates of  $\gamma_0$ , which only occurred with stationary data, once with  $\sigma_0=0.05$  and twice with  $\sigma_0=0.25$ . The **x** denotes the natural logarithmic-transformed mean of all parameter estimates, and the thick horizontal line is at the median of transformed parameter estimates included in the plot. The thin horizontal lines are drawn at the true values of  $r_0$  or  $\gamma_0$



a subsequent return to growth rates typical of the stationary distribution (Fig. 2, Table S19), regardless of the  $\gamma_0$  value. When populations experience temporal changes that cover both weak and strong density-dependent effects (perturbed samples or  $(r_0, \gamma_0)=(3, 5)$  at either level of  $\sigma_0$ ), point estimation is improved dramatically (Table S19, Fig. 2); the likelihood function has a well-defined global maximum in the region of the correct parameter estimates (Fig. 3a, b), and the covariance between structural parameters is small (Table S20). In contrast, with the absence of large perturbations or persistent cycles in the endogenous dynamics ( $(r_0, \gamma_0)=(3, 1)$  at either level of  $\sigma_0$ ), ML point estimates could be extremely erroneous (Table S19, Fig. 2), are associated with a ridge of highly similar likelihood values over a wide range of parameters (Fig. 3c, d), and exhibit relatively strong covariance between structural parameters (Table S21).

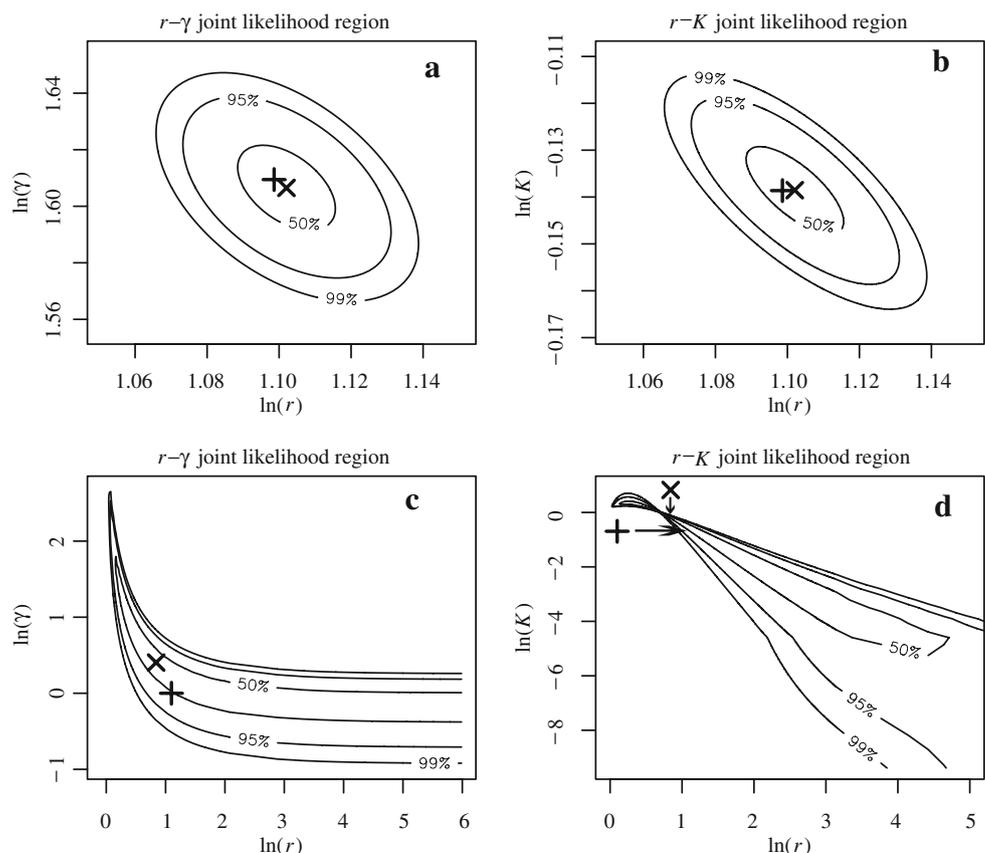
Sample size had some influence on overall characteristics of point estimation, particularly for population data without endogenous cycles or external perturbations (Tables S1–S19, Fig. 2). The most pronounced effect was the removal of especially poor estimates, which reduced the variance and MSE considerably (Fig. 2), but the problem of flat likelihood surfaces containing ridges of similar likelihood values (Fig. 3c, d) remained. Increasing sample size also removed obvious multimodalities in the likelihood

surface for three cases in which stochastic impacts created unusual sequences of data points in short time series ( $T=10$ ) for which  $\hat{\theta}$  describes a *pgr* that increases with density.

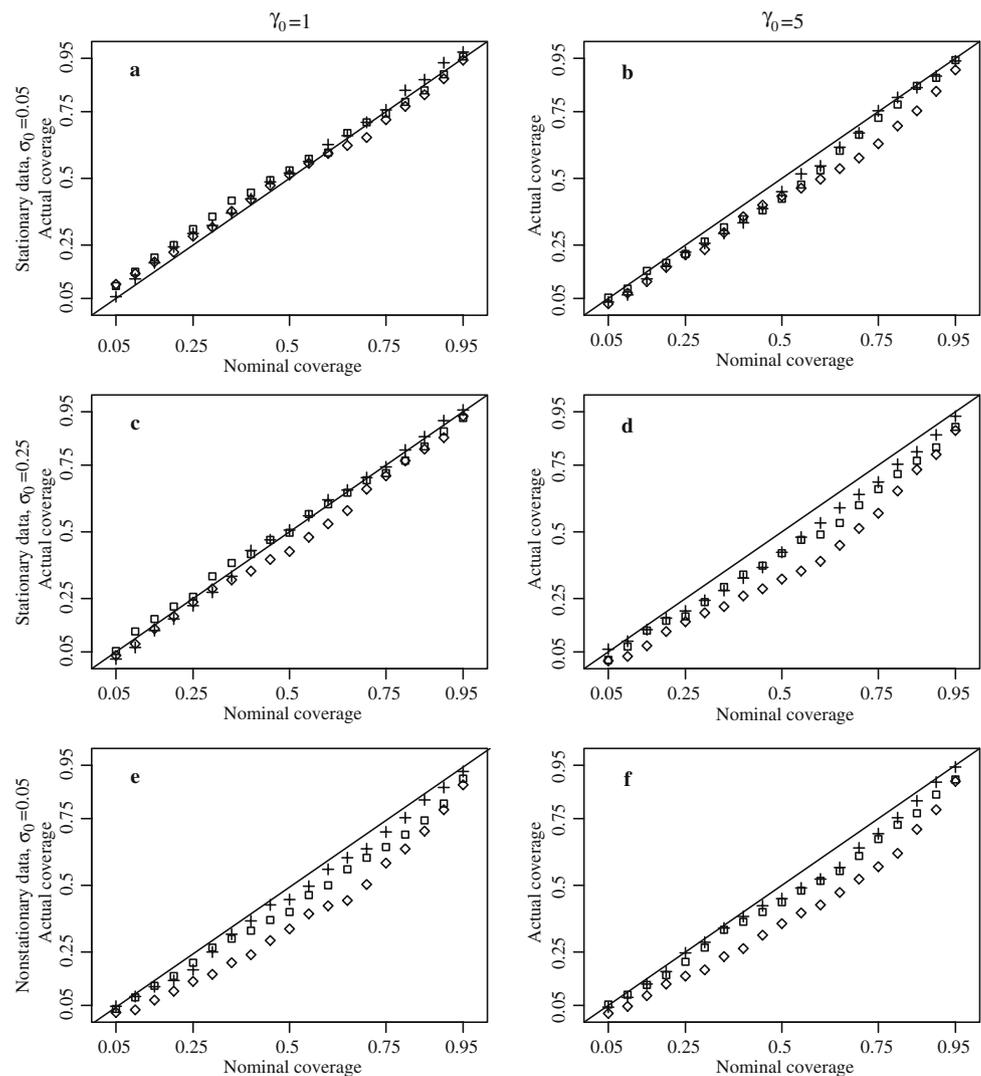
With weak regulation  $(r_0, \gamma_0)=(3, 1)$  and  $N^T$  obtained from a stationary distribution, increased levels of noise had opposite effects on parameter estimation properties for  $r_0$  and  $\gamma_0$ , yielding worse estimates for  $r_0$  but better estimates for  $\gamma_0$  (Table S19, Fig. 2), similar to the effect of increased instability in  $n^*$ . However, the distribution of population densities driven by environmental stochasticity alone (at the levels and sample sizes considered here) was not sufficient to produce informative estimates of *pgr* curves. For the already informative perturbed or cyclic populations, increased levels of stochasticity had the expected effect of worsening estimation of both  $r_0$  and  $\gamma_0$  (Table S19, Fig. 2).

The plots in Fig. 4 compare the accuracy of using quantiles from the theoretical distribution of Eq. 4 to define coverage probabilities. In all scenarios, nominal (approximated) coverage was not too far from the actual coverage for the 0.95 level but could substantially overestimate actual coverage at smaller levels for some scenarios with smaller sample sizes and larger  $\sigma_0$ . Nonstationary data had the expected effect of worsening approximations using the asymptotic derived distribution in Eq. 4.

**Fig. 3** Transformed (see text) joint profile likelihood contour plots for two simulated time series depict the typical geometry of the likelihood function in Eq. 3. Both time series are from the stationary distribution with  $r_0=3, K_0 = (r_0 - 1)^{1/\gamma_0}, T=50$ , and  $\sigma_0=0.05$ , but the time series in **a** and **b** has  $\gamma_0=5$  and for **c** and **d**  $\gamma_0=1$ . The location of the ML estimate  $(\hat{r}, \hat{\gamma})$  or  $(\hat{r}, \hat{K})$  is denoted by  $X$  and the generating pair  $(r_0, \gamma_0)$  or  $(r_0, K_0)$  is denoted by  $+$  pluses. Contour lines are drawn at the nominal 0.5, 0.95, and 0.99 quantiles for a  $\chi^2_2$  distribution, giving the approximate 50%, 95%, and 99% confidence regions. Note the different axis limits for different graphs. Joint profile likelihood surfaces with data from perturbed populations tend to be comparable to **a** and **b**, regardless of the values for the generating pair  $(r_0, \gamma_0)$



**Fig. 4** Actual vs. nominal coverage probabilities using a  $\chi^2_4$  distribution to define nominal quantiles for different scenarios with time series of length 10 (diamonds), 20 (squares) and 50 (pluses) for the representative  $(r_0, \gamma_0)$  pairs in Table 1. Left and right panel columns correspond to generating values of  $\gamma_0=1$  and 5, respectively, where panels **a** and **b** give the results for data obtained with stationary data and  $\sigma_0=0.05$ ; panels **c** and **d** give the results for data obtained with stationary data and  $\sigma_0=0.25$ ; panels **e** and **f** give the results for data obtained with perturbed data and  $\sigma_0=0.05$ . Points near the identity line indicate that  $p$  values defined by the associated theoretical quantiles in the distribution of Eq. 4 are accurate approximations of true coverage



## Discussion

The roles of deterministic complexity, noise, perturbations, and model choice on detecting biological processes from time series has a rich and valuable history in ecology (e.g., Schaffer et al. 1986; Nychka et al. 1992; Ellner and Turchin 1995; Kendall 2001), often focusing on the identification of system measures such as Lyapunov exponents under different combinations of these factors. In particular, for detecting the presence of density dependence, Murdoch (1994) points out that observed population densities far from the carrying capacity are needed to detect factors regulating growth. In this research, we extend these types of results in several ways. First, we explicitly consider the relationship between sample sizes typical of ecological time series to both point convergence of ML parameter estimates (Eq. 3) and distributional convergence of the LR test statistic (Eq. 4). Second, we quantify how different levels of noise affect parameter estimates for a particular model of density

dependence. Finally, we show that an explicit consideration of the joint profile likelihood surface, as opposed to a quadratic approximation giving an elliptical region such as from a Wald test, provides insight into the estimation problem and the uncertainty in parameter estimates.

Our tests of the performance of statistical inference under different sources of variation in the data revealed that the primary determinant influencing parameter point estimation is not sample size or stationarity (i.e., all  $\theta_0$  considered here produce stationary distributions) of the sample but rather the variance of observed population sizes. Datasets derived from populations with variation driven by endogenous processes or from a population approaching the stationary distribution following a perturbation can be expected to yield estimates with superior properties (lower bias and variance, narrower confidence regions) to those obtained from longer datasets with lower variation. The negative effects of environmental stochasticity and weak density-dependent regulation on estimation of the shape parameter in the theta-logistic model

have been found in several previous case studies (Saether et al. 2000, 2002a, 2007), but shape estimation has not been quantified in relationship to sample size until now.

A cluster of uninformative data (Schaffer et al. 1986) often emerges when noise is added to a dynamical system with a fixed-point equilibrium. Consider such a cluster of *pgr* data at approximately the constant  $a$  across the different values in  $\mathbf{N}^T$ . The modeled *pgr* curve is  $rK^\gamma/(K^\gamma + N_t^\gamma)$  and therefore should be  $\approx a$  for  $t=1, \dots, T-1$ . Thus, for  $K \ll 1$  and  $r = a/K^\gamma$ , the modeled *pgr* is  $\approx a/N_t^\gamma$ . Choosing  $\gamma$  to be sufficiently large (the exact choice depending on the range of  $\mathbf{N}^T$  and  $a$ ), the modeled *pgr* curve will be flat through the cluster of *pgr* data. Hence, a continuum of  $(r, K)$  estimates can produce similar *pgr* curves that have approximately the same support, allowing estimates of  $r_0$  that are essentially arbitrarily large as estimates of  $K_0$  approach zero (Fig. 3c).

It is encouraging that the limiting distribution of the LRT statistic (Eq. 4) is often a fairly accurate approximation and therefore useful for constructing confidence limits with limited sample sizes. In contrast, methods for constructing confidence intervals that assume elliptical contours, such as the score or Wald statistics (Severini 2000), would be expected to provide poor approximations of coverage given the absence of an ellipsoidal likelihood surface in the region of the ML estimate.

Statistical inference based on Bayesian methods is an alternative approach to evaluate density-dependent population models (de Valpine and Hilborn 2005; Saether et al. 2007; Lillegard et al. 2008). For the relatively simple model studied here, Bayesian analyses using uninformative prior parameter distributions would be expected to give similar results, on average. For data resulting in elongated ridges in the likelihood surface (Fig. 4a, c), posterior parameter distributions would have inaccurate location (e.g., mean, median, or mode) summaries of the “true” parameter and probability mass distributed over a wide interval. For data resulting in a likelihood surface with a well-defined unimodal peak, posterior parameter distributions would be expected to give accurate location summaries, have highly concentrated probability mass, and be approximately normal.

Population biologists have realized the importance of employing more complicated stochastic models accommodating multiple sources of stochastic variability arising, for example, at both the process level and additionally through observation error (de Valpine and Hastings 2002; de Valpine and Hilborn 2005; Dennis et al. 2006; Saether et al. 2007; Lillegard et al. 2008). For models of  $g(n)$  that do not allow transformation to linear state-space models, parameter estimation can rely on simulation based approaches to estimate Bayesian posterior distributions (Saether et al. 2007) or numerical procedures such as those described by de Valpine and Hastings (2002) and Kitagawa (1987) to

obtain and maximize likelihood values. One natural direction of future research to extend the findings here would be to use stochastic simulations to evaluate and compare frequentist and Bayesian methods under different scenarios of process model complexity, environmental stochasticity, and observation error.

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