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Comparing the Ricker and θ-logistic models for estimating elk population growth

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Abstract

Conflicting evidence exists supporting linear and nonlinear density-dependent population growth when species have slow life histories. The Ricker (linear) and θ-logistic (nonlinear) models are commonly used to analyze survey data for these species, but no evaluation has examined whether these hypotheses can be differentiated with field data. We conducted a simulation exploring effects from shape of density dependence and variation in vital rates on the fit of these models. When vital rates had moderate to high variation, the models had similar fit. The θ-logistic model differed from the Ricker model and was biologically realistic ($\theta > 1$) when variation in vital rates was low and the growth response was nonlinear. Furthermore, the θ-logistic model has issues with model convergence when using vague priors and when variation in vital rates as high. These results indicate that the Ricker model is appropriate for population survey data of species with slow life histories.

Recommendations for Resource Managers

- The shape of the growth response (i.e., the relationship between abundance and population growth rate) depends on the shape of the relationships between abundance and vital rates (survival and pregnancy).

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- The variation in the environmental setting of a population over time, as well as the species life history traits, can influence whether linear or nonlinear models fit time series of population survey data.
- Random changes over time in the growth rate of a population can mask the shape of the relationship between abundance and growth rate.
- When modeling population dynamics of species with slow life histories, the Ricker model is often more appropriate than the θ-logistic model, especially when environmental variation over time is high or when using vague priors when fitting the models.

KEYWORDS

carrying capacity, *Cervus elaphus*, density dependence, hierarchical models, maximum intrinsic growth rate, simulation, stochastic temporal variation

1 | INTRODUCTION

Ecological systems are complex and uncertain, which complicates our ability to directly interpret patterns from field data and make predictions. Thus, ecologists often use quantitative models to approximate system dynamics to understand and predict ecological processes. Indeed, the use of models is ubiquitous in the field of population ecology. Ecologists have developed countless models that are tailored to specific systems to better approximate ecological system dynamics.

Two commonly used approximating models of population growth for species with slow life histories (i.e., traits including long-lived, late maturation, few offspring, and parental care; Gaillard et al., 1989; Sæther & Bakke, 2000; Salguero-Gómez et al., 2016) are the Ricker and θ-logistic models (Ferguson & Ponciano, 2015; Fowler, 1981; Owen-Smith, 2007). These models assume that resources are available to all competitors, and that individuals scramble to acquire resources first (i.e., scramble competition). At small population abundances, both the Ricker and θ-logistic models predict that a population will experience the highest possible rate of growth ($r_{\max}$) under density-independent conditions, similar to exponential growth. As a population reaches abundances near carrying capacity (K), both models predict that growth will slow due to density-dependent factors. It is the shape of density-dependent growth which distinguishes the Ricker from the θ-logistic model.

The Ricker model predicts a linear decrease in the population growth rate $\left(r = \ln\left(\frac{N_{t+1}}{N_t}\right)\right)$ as abundance increases, otherwise known as linear density dependence (Ricker, 1954). The simplicity of the Ricker model is an appealing advantage for modeling density-dependent population dynamics. Nonetheless, a more complex curvilinear relationship between abundance

and r may be more realistic (Gilpin & Ayala, 1973). Species with slow life histories have evolved in environments where competition for resources is keen and, consequently, reduce mortality rather than increase reproductive output (Gaillard et al., 1989; Sæther & Bakke, 2000; Salguero-Gómez et al., 2016). This results in a constant r over a wider range of abundances until r abruptly decreases when the population is near K, generating a convex relationship between abundance and r (Fowler, 1981; McCullough, 1979). The θ-logistic model can capture this functional form (convex; $\theta > 1$), along with a linear ($\theta = 1$) or concave ($\theta < 1$) relationship between abundance and r because of the additional shape parameter (θ).

Although the θ-logistic is perhaps more intuitive for studying density-dependent population dynamics (Fowler, 1981), its added complexity may outweigh its practical advantages for several reasons. First, the additional parameter makes the θ-logistic model less parsimonious than the Ricker model. Second, this model predicts strongly intensifying density-dependent feedback when the population's abundance surpasses K (Fowler, 1981). Third, $r_{\max}$ and θ estimates can be correlated, and ridges and multiple peaks can occur in the likelihood profile of $r_{\max}$ and θ, which may result in biologically implausible and imprecise estimates of these parameters (Clark, Brook, Delean, Reşit Akçakaya, & Bradshaw, 2010; Delean, Brook, & Bradshaw, 2013; Polansky, de Valpine, Lloyd-Smith, & Getz, 2009).

In time series of population survey data for species with slow life histories, some studies indicate a linear growth response is sufficient while other studies support a convex growth response (Boyce, 1989; Clark et al., 2010; Fowler, 1981; McCullough, 1979; Sibly, Barker, Denham, Hone, & Pagel, 2005; Weckerly, 2017; Wicklund, 2001). These inconsistent findings might be partially due to a lack of comparison between the two models (i.e., typically only one model is fit to the population survey data). It is therefore, difficult to assess why one model might fit a time series of population survey data better than the other (McCullough, 1979). The shape of the growth response (i.e., linear or nonlinear) and stochasticity in population dynamics are two plausible reasons for why one model may fit the time series of population survey data for species with slow life histories better than the other.

We conducted a simulation exercise to explore when and why the Ricker or θ-logistic model was more likely to fit a time series of population survey data. We used a simulation to manipulate the shape of density dependence and the amount of variation in the vital rates. We simulated an elk (*Cervus elaphus*) population because this species has a slow life history and data on its life history (i.e., vital rates, temporal variation) are abundant. We compared the Ricker and θ-logistic models because they are commonly used for modeling the dynamics of ungulate populations, and because scramble competition is likely a realistic assumption for elk populations (Weckerly, 1998). The simulation explored how the amount of stochasticity in vital rates and the shape of density dependence in vital rates influence population growth and thus the fit of the Ricker and θ-logistic models. We hypothesized that higher amounts of stochasticity would obscure the shape of the density-dependent growth such that both models would fit the simulated data similarly.

2 | METHODS

2.1 | Simulation

We explored how combinations of two shapes of density dependence and five levels of stochasticity in vital rates of simulated populations affected the fit of the Ricker and θ-logistic models.

Stochasticity in vital rates was measured by temporal variation (i.e., process variance). The main steps in the simulation are as follows, with further details below; first, we started with an initial total population abundance, which was divided into age classes. Second, we determined the probabilities for survival and pregnancy for each age class in the current year. Third, we determined the number of individuals in each age class in the following year, the population abundance in the following year, and the population growth rate (r). Fourth, we repeated these steps for a total of 30 years, and conducted 600 iterations of the simulation. Fifth, we fit the Ricker and θ-logistic models to each iteration of the simulation and evaluated the fit of the two models.

The populations began in the first year with an abundance drawn from the uniform distribution $N_1 \sim Uniform(150, 200)$ rounded to the nearest individual, where N_1 was the population abundance in the first year. We selected this range of possible initial abundance values to avoid the high variation in population growth rates at small population sizes due to demographic stochasticity. The number of individuals in each age class in the first year was determined from the stable age distribution when the population was experiencing density-independent growth, which preliminary analyses showed was 65% adults, 3% subadults, and 32% juveniles. A sex ratio of 1:1 was assumed at birth.

The probabilities of survival and pregnancy (i.e., vital rates) of each age class in the current year were dependent on the population abundance that year relative to K, which was fixed at 1,000 animals. All vital rates decreased as population abundance increased toward K. Each vital rate for each age class had different ranges. Maximum and minimum values for the range of each vital rate and each age class (Table 1) were based on published elk population vital rates (Bender, Cook, Cook, & Hall, 2008; Bender, Davison, Cook, Cook, & Hall, 2006; Coughenour & Singer, 1996; Eberhardt, Eberhardt, Tiller, & Cadwell, 1996; Murphy, 1963; Raithel, Kauffman, & Pletscher, 2007; Sargeant & Oehler, 2007). Although a substantial amount of research has estimated probabilities of survival and pregnancy and the variance around these probabilities across age classes for elk, few have estimated these for each sex and no clear pattern in survival probabilities between the sexes is evident (Toïgo & Gaillard, 2003). Due to lower confidence in vital rates and variance in vital rates for each sex, our model was age-structured but not sex-structured. All adults were pooled into one age class (≥3 years), so the maximum and minimal adult vital rates spanned estimates presented in the literature for adult and senescent adult age classes.

Vital rates were drawn from a beta distribution with the mean vital rates defined as

$$X_t = X_{\max} + \frac{X_{\min} - X_{\max}}{1 + \left(\frac{D_t}{p}\right)^b}, \tag{1}$$

TABLE 1 Range of vital rates used in the simulation

Vital rate	Minimum	Maximum
Adult survival	0.85	0.95
Subadult survival	0.7	0.95
Juvenile survival	0	0.7
Adult pregnancy	0.7	0.95
Subadult pregnancy	0	0.5

Note: The minimum and maximum are the probability of survival or pregnancy when the population abundance is near K and near 0, respectively. These ranges were based on published elk population vital rates.

where X_t was the mean probability of survival or pregnancy for a given age class in year t, and X_{max} and X_{min} were the mean probabilities of survival or pregnancy for a given age class when the population abundance was near 0 and near K, respectively. The density of the population at time t was $D_t = \frac{N_t}{K}$, p was used to calculate the inflection point (I) of the curve, and b was the steepness of the curve. We fixed p to 1, and varied b to manipulate the shape of density dependence. This method is similar to what Robinson, McGowan, and Devers (2017) used for another species with a slow life history (American black ducks, *Anas rubripes*), and is especially useful for manipulating the strength and shape of density dependence in simulated data. We then used the mean and variance of vital rates and the beta method of moments to calculate the shape parameters, which we used when sampling from a beta distribution during the simulations.

We conducted the simulation with relatively linear ($b = -1.5$) and nonlinear ($b = -5$) density dependence for all vital rates (Figure 1). We selected this amount of nonlinearity to reflect estimates of nonlinear growth responses of elk published in the literature (Boyce, 1989). We simulated these two shapes of density dependence under five levels of temporal variation (see Table 2), resulting in a total of 10 scenarios. Each vital rate experienced different amounts of temporal variation for each of the five levels based on the amount of variation expected for the vital rate and age class (Table 2). The mid level of temporal variation included coefficients of variation equal to what has been reported in previous studies (Bender et al., 2006; Raithel et al., 2007). The low-mid and low levels of temporal variation represent 60% and 20% of the mid level of temporal variation, respectively. The high-mid and high levels of temporal variation represent 150% and about 200% of the mid level of temporal variation, respectively. These five levels of temporal variation were selected to encompass the variation across years in coefficients of variation for vital rates as reported by Bender et al. (2006). The coefficients of variation for juvenile survival and subadult pregnancy when doubled were too large for the beta distribution with a mean equal to the maximum vital rate because the distribution is bounded by 0 and 1. So, we used the maximum

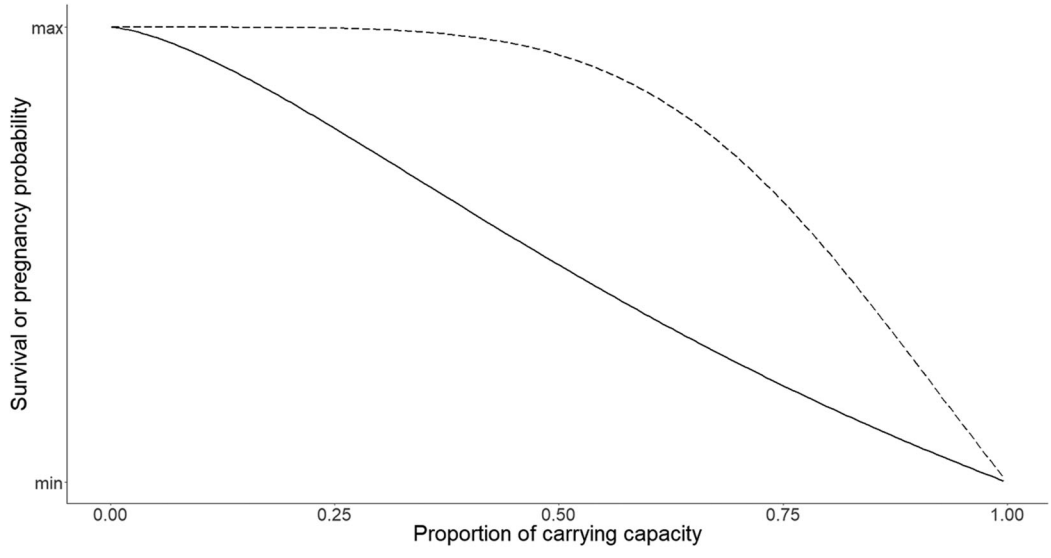

FIGURE 1 The shapes of relatively linear ($b = -1.5$; solid line) and nonlinear ($b = -5$; dashed line) density-dependent vital rates used in the simulation of elk population growth, where b was the steepness of the curve (see Equation (7)). The maximum and minimum values will vary across age classes and between vital rates

TABLE 2 Coefficients of variation for vital rates used in the simulation under five levels of temporal variation

Vital rate	Low	Low-mid	Mid	High-mid	High
Adult survival	0.014	0.050	0.080	0.120	0.160
Subadult survival	0.014	0.050	0.070	0.105	0.140
Juvenile survival	0.110	0.330	0.550	0.600	0.650
Adult pregnancy	0.022	0.066	0.110	0.165	0.220
Subadult pregnancy	0.120	0.370	0.620	0.810	1.000

Note: These levels of variation were based on published elk population vital rate means and standard deviations.

coefficient of variation possible for the distribution as the high level of temporal variation for these two vital rates (Table 2).

The number of surviving animals in each age class was calculated using a binomial process with the number of animals in that age class and the probability of survival of that age class. The number of female adults and subadults was calculated using a binomial process with the number of animals in that age class and a probability of 0.5 (i.e., assuming a 1:1 sex ratio). The number of pregnant adults and subadults was calculated using a binomial process with the number of female animals in that age class and the probability of pregnancy of that age class.

The number of adults in the following year was calculated as the sum of the number of surviving adults and subadults in the current year. The number of subadults in the following year was equal to the number of surviving juveniles in the current year. The number of juveniles in the following year was calculated as the sum of pregnant adults and subadults in the current year. The population abundance in the following year was calculated as the sum of the number of adults, subadults, and juveniles in the following year. The population growth rate (r) was calculated as $r = \ln\left(\frac{N_{\text{tot}_{t+1}}}{N_{\text{tot}_t}}\right)$, where $N_{\text{tot}_{t+1}}$ is the population abundance in the following year, and N_{tot_t} is the population abundance in the current year.

We generated elk population abundance time series for a total of 30 years. Although time series of elk population abundances from real-world monitoring efforts tend to be shorter than this, we chose to simulate a longer period to allow the simulated populations would approach K so that the number of data points would be sufficient to fit the models. We generated 1,000 iterations for each scenario, and randomly selected a subset of 600 iterations to keep, ensuring that these iterations reached abundances above 800 for more than 5 years. We kept 600 iterations because preliminary analyses showed that this was enough iterations to achieve agreement in parameter estimates across the iterations of each scenario.

We plotted the population growth rates in each year of each iteration as a function of the population abundance as a proportion of K to visualize the shape of the growth response under the 10 scenarios of the shape of density dependence and the level of temporal variation. For each of the 10 scenarios, we also fitted both the Ricker and θ-logistic models, as described below.

2.2 | Model fitting

We fitted the Ricker and θ-logistic models using Bayesian analysis and Markov Chain Monte Carlo algorithms with three chains, 500,000 iterations, a burn-in period of 200,000, an

adaptation period of 200,000, and no thinning. Convergence among chains was determined by whether the Gelman Rubin statistic ($\hat{R}$) was near 1 (Gelman et al., 2004; Kery, 2010). The Ricker model was fit as the following discrete equation (Cook, 1965):

$$\bar{N}_{e_{i+1}} = N_{e_i} e^{r_{\max}\left(1-\frac{N_{e_i}}{K}\right)}, \tag{2}$$

where $\bar{N}_{e_{i+1}}$ was the mean estimated true abundance from year i and N_{e_i} was the estimated true abundance from year i. These are described in further detail below. The θ-logistic model was fit as the following discrete equation (Gilpin & Ayala, 1973):

$$\bar{N}_{e_{i+1}} = N_{e_i} e^{r_{\max}\left(1-\left(\frac{N_{e_i}}{K}\right)^{\theta}\right)}. \tag{3}$$

We fit these hierarchical models using a state-space formulation and incorporated process variance using a Poisson distribution. We drew the population abundance in the first year from the Poisson distribution $N_{e_1} \sim Poisson(\lambda_1)$, where N_{e_1} was the population abundance in the first year estimated by the model, and λ_1 was the count for the first year with uncertainty around the count included, $\lambda_1 \sim Uniform(150, 200)$. We used the estimated abundance in each year (N_{e_i}) to calculate population abundance in the next year ($\lambda_{e_{i+1}}$) for the next 29 years using both the Ricker and θ-logistic models. We incorporated process variance in each year using a Poisson distribution such that the estimated abundance in the next year was $N_{e_{i+1}} \sim Poisson(\lambda_{e_{i+1}})$.

We first fit the models using vague priors to test the predictive abilities of the models with simulated data but no prior information. When using vague priors, we drew the prior for $r_{\max}$ from a uniform distribution ranging from 0 to 2. These represent lower and upper limits of $r_{\max}$ that are far beyond what is biologically realistic for elk (Eberhardt et al., 1996; McCorquodale, Eberhardt, & Eberhardt, 1988; Murphy, 1963; Sargeant & Oehler, 2007). We drew the prior for θ from another uniform distribution ranging from 0.0001 to 10, which also represent lower and upper limits far beyond what is biologically realistic for elk (Boyce, 1989). We drew the prior for K from a gamma distribution (i.e., shape = 0.01, rate = 0.01).

We also fit the models using informed priors because they can improve the accuracy and precision of parameter estimates (Delean et al., 2013). We based our informed priors on estimates of these same population dynamic parameters for elk population in the literature, because this is likely what would inform priors when fitting these models to real time series. We drew the prior for r_{max} from a beta distribution that had a mean of 0.275 and standard deviation of 0.075. We chose these parameters because previous studies of elk populations estimated $r_{\max}$ ranging from roughly 0.20 to 0.30, with more estimates toward the higher end of this range (Eberhardt et al., 1996; McCorquodale et al., 1988; Murphy, 1963; Sargeant & Oehler, 2007). We drew the prior for θ from a gamma distribution with a mean of 3.25 and a standard deviation of 2.25. This prior is positive because when $\theta > 0$, the population birth and death rates both increase with population size, with the death rate increasing faster than the birth rate (Ross, 2009), which is expected. We chose this mean because Boyce (1989) estimated θ parameters of 3.027 and 3.5 for two elk populations. The gamma distribution had a large standard deviation because few studies have estimated the θ parameter in elk populations. However, even when using informed priors, we used vague priors for K since there is rarely prior information about a specific population's K, unlike $r_{\max}$ and θ, which tend to be similar across conspecific populations. Thus, we once again drew the prior for K from a gamma distribution (i.e, shape = 0.01, rate = 0.01).

We measured the predictive abilities of the two models using root mean square predicted error (RMSPE). The RMSPE was an intuitive metric as it is an average of the deviation between estimated and predicted abundances. We directly estimated RMSPE as a derived parameter in the model to incorporate the uncertainty associated with each model parameter. We began with the estimated abundance in the first year, then used the parameters estimated by each model (i.e., $r_{\max}$, K, and θ) to predict the abundances (N_{p_i}) for the rest of the time series based solely on this initial abundance. We compared these predicted abundances, excluding the first year, to the abundances estimated by each model as follows:

$$\text{RMSPE} = \sqrt{\frac{\sum(N_{e_i} - N_{p_i})^2}{n-1}}, \tag{4}$$

where N_{e_i} was the estimated abundance from each model for year i, N_{p_i} was the predicted abundance of year i, and n was the length of the time series.

We reported the mean and confidence interval of parameters and of the RMSPE for each model estimated in each simulation. We restricted our inferences to only model runs that indicated convergence was achieved, but kept track of the number of iterations with convergence issue for each scenario. We conducted these analyses in the Rjags program in RStudio (R Version 3.5.0, www.r-project.org, accessed 26 April 2018; JAGS Version 4.0.0, www.sourceforge.net, accessed 24 January 2018). For simulation and model fitting code, see Appendix A.

3 | RESULTS

The simulations generated relatively linear and nonlinear growth responses and the stochastic variation in growth rates increased as the temporal variation in vital rates increased (Figure 2). When fitting the models with vague priors, both models, but especially the θ-logistic model, had issues with model convergence (Table 3). In particular, the θ-logistic model had convergence issues at all levels of variation and under both shapes of growth response, whereas the Ricker model only had convergence issues at mid- to high levels of variation when the growth response was linear. For scenarios in which both models had convergence issues, parameter estimates of the θ-logistic model converged for fewer iterations of the scenarios than the Ricker model. The θ-logistic model still had slight convergence issues even when fitting the model with informative priors.

When using informative priors and considering only the iterations that converged, the Ricker and θ-logistic models had similar predictive abilities, as measured by RMSPE, at all levels of temporal variation and under both shapes of growth response (Figure 3). However, when the growth response was linear, the θ-logistic model estimated $\theta < 1$ at low levels of temporal variation and $\theta = 1$ at mid- to high-levels of temporal variation. A concave growth response (generated when $\theta < 1$) is unrealistic for species with slow life histories, and a linear growth response (generated when $\theta = 1$) is equivalent to the Ricker model. When the growth response was nonlinear, the θ-logistic model estimated $\theta > 1$ at low levels of temporal variation and $\theta = 1$ at mid- to high-levels of temporal variation. Thus, the θ-logistic model was only realistic and different from the Ricker model at low levels of temporal variation when the growth response was nonlinear. However, it had similar predictive abilities as the Ricker model.

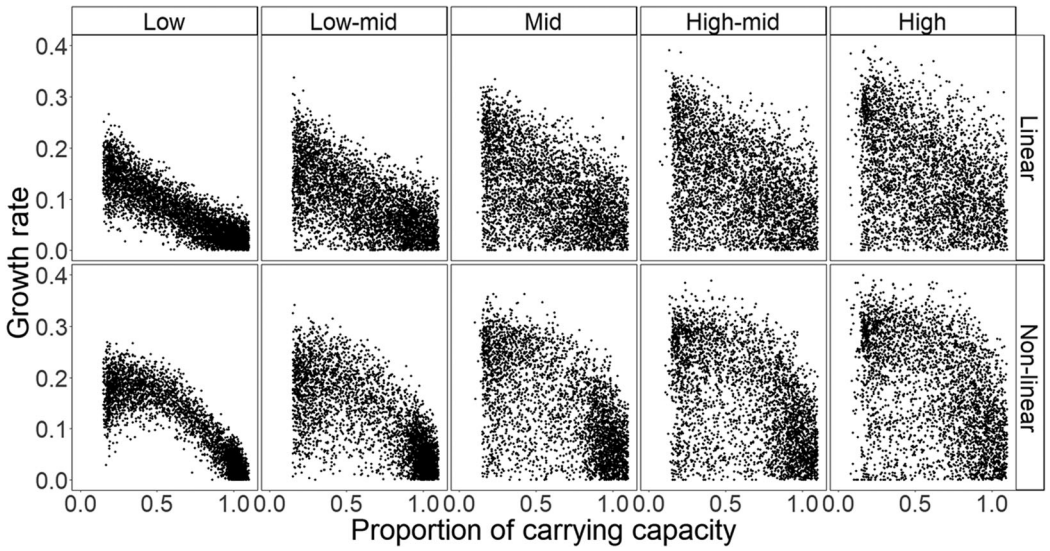

FIGURE 2 Simulated elk population growth rates (r) as population abundance increases over 30 years toward the carrying capacity (K); 300 iterations are shown. Simulations were run with relatively linear and nonlinear density-dependent vital rates (see Figure 1), and with five levels of temporal variation in vital rates (see Table 2)

4 | DISCUSSION

There is evidence to support both linear and nonlinear density-dependent growth in a variety of ungulate populations. Weckerly (2017) showed a linear population growth response in two elk populations in northern California, and Street, Rodgers, Avgar, and Fryxell (2015) fit a linear regression between population density and growth rate in moose (*Alces alces*) in Ontario, Canada.

TABLE 3 Number (and percent) of iterations of the simulation for which parameter estimates of the Ricker and θ-logistic models did not converge

		Vague priors		Informed priors	
Density dependence	**Temporal variation**	**Ricker**	**θ-logistic**	**Ricker**	**θ-logistic**
Linear	Low	0 (0.0)	12 (2.0)	0 (0.0)	0 (0.0)
	Low-mid	0 (0.0)	36 (6.0)	0 (0.0)	0 (0.0)
	Mid	1 (0.2)	46 (7.7)	0 (0.0)	0 (0.0)
	High-mid	10 (1.7)	27 (4.5)	0 (0.0)	0 (0.0)
	High	11 (1.8)	25 (4.2)	0 (0.0)	2 (0.3)
Nonlinear	Low	0 (0.0)	38 (6.3)	0 (0.0)	0 (0.0)
	Low-mid	0 (0.0)	12 (2.0)	0 (0.0)	0 (0.0)
	Mid	0 (0.0)	2 (0.3)	0 (0.0)	0 (0.0)
	High-mid	0 (0.0)	8 (1.3)	0 (0.0)	0 (0.0)
	High	0 (0.0)	5 (0.8)	0 (0.0)	1 (0.2)

Note: The models were fit using either vague or informed priors to simulated data with either linear or nonlinear density dependence and a range of levels of temporal variation.

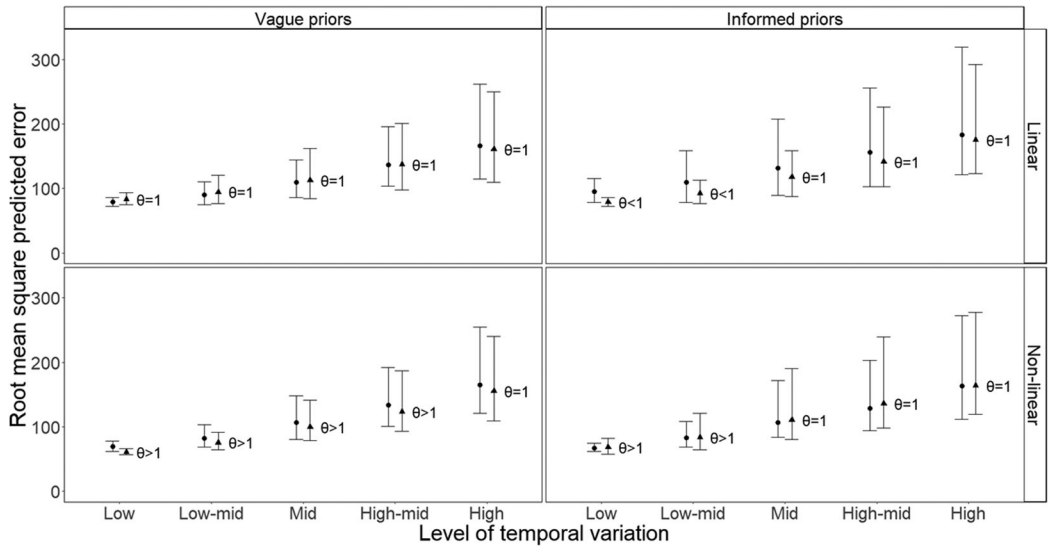

FIGURE 3 Root mean square predicted error of the Ricker model (circles) and θ-logistic model (triangles) fit to 10 scenarios. Simulations were run with either informed or vague priors, either linear or nonlinear density dependence, and with one of five levels of variation (see Table 2) in vital rates. RMSPE, root mean square predicted error

Owen-Smith (2006) estimated an essentially linear population growth response for a population of kudu (*Tragelaphus strepsiceros*) using a wide range of population abundances and an age-structured model but a nonlinear population growth response in two wildebeest (*Connochaetes taurinus*) populations. The nonlinear population growth response in wildebeest was consistent with the findings of Fryxell, Mosser, Sinclair, and Packer (2007), who fit the θ-logistic model to population survey data from another wildebeest population. The differences in the shapes of the growth response between the kudu and wildebeest populations was generated by changes in vital rates; all vital rates in the kudu population indicated linear density dependence, resulting in a linear growth response (Owen-Smith, 2006). In contrast, nonlinear density dependence occurring in adult mortality of one wildebeest population and in fecundity in the other resulted in both populations fitting a nonlinear growth response (Owen-Smith, 2006). Whether linear or nonlinear models fit time series of population survey data seems to be influenced by more than simply whether the species displays slow life history; there is also a dimension of the environmental setting that the population experiences (Wang et al., 2006, 2008).

We conducted a simulation to explore how the Ricker and θ-logistic models fit elk population growth data under linear and nonlinear density dependence in vital rates with varying levels of temporal variation. In both the linear and nonlinear growth response simulations, as the temporal variation in vital rates increased, the variation in growth rates also increased, which can mask the shape of the growth response. Increased variation can obscure the impact of the shape of the growth responses such that the θ-logistic model was equivalent to the Ricker model at high levels of temporal variation (i.e., $\theta = 1$). These results indicate that variation in the environmental setting, as well as life history traits of the species, influence the fit of the two models. Although the θ parameter has been shown to be estimated with less bias at high levels of temporal variation (Barker & Sibly, 2008), our simulation reveals that this does not increase the predictive abilities of the θ-logistic model past those of the Ricker model.

Consequently, even when some nonlinearity occurs in the growth response, high temporal variation in the vital rates, and thus in the growth rate, can mask the shape of the growth response. This results in both models predicting similar estimates of r_{max}, K, and abundances.

The variability generated in the simulations was well within the range of biological plausibility for elk, and we assumed perfect counting (i.e., we did not include sampling error). Given the presence of sampling error in almost all time series, our results are a conservative estimate. We would expect the variability in the growth response to increase as the variation in sampling efficiency increases.

The θ-logistic model was only realistic and different from the Ricker model (i.e., $\theta > 1$) under nonlinear density dependence with low levels of temporal variation. Nevertheless, the θ-logistic model had similar predictive abilities as the Ricker model under these conditions. These results suggest that the additional shape parameter in the θ-logistic model is rarely useful for improving the model's ability to predict population dynamics, which is a central purpose of population models.

Furthermore, when using vague priors, the θ-logistic model had convergence issues across all levels of temporal variation for both linear and nonlinear density dependence. Convergence issues were more pronounced when fitting the θ-logistic model than the Ricker model. Even with informed priors, the θ-logistic model did not converge for all iterations of the simulation at high levels of variation. Given this lack of convergence of the θ-logistic model, the simplicity of the Ricker model appears to make it a more robust model to fit, especially when temporal variation is high or when using vague priors.

Our simulation did not impose differences in survival between females and males. Lower male survival rates are commonly but not always found in size-dimorphic ungulates (Raithel et al., 2007; Toïgo & Gaillard, 2003). Nonetheless, the conclusion from our simulation that more temporal variation can mask nonlinear population growth is probably sound; the key feature of the simulations was the shape of density dependence of the abundance and vital rates (i.e., linear vs. nonlinear relationships). Lower male survival rates would simply have been an additional linear or nonlinear relationship with varying amounts of temporal variation. This should not have changed linear or nonlinear growth responses of simulation populations.

The structure of the two models that we examined are very similar to each other, and are also similar to other density-dependent models. This is unsurprising as most density-dependent models are related. For example, the θ-logistic model can be considered a less restrictive Ricker model. The close relationship between these and other models makes them hard to evaluate, except through simulations. However, seemingly slight differences in model structures can generate profoundly divergent ecological outcomes. The results of simulations studies are directly related to the models used in the simulations, so ecological processes need to be carefully considered when developing simulation exercises to evaluate models. For this reason, we examined the effect of linear and nonlinear density dependence, which is the difference between the Ricker and θ-logistic models.

When temporal variation is high, the shape of density dependence can be masked such that the θ-logistic model is equivalent to the Ricker model. Under all levels of temporal variation, both models fit the data similarly and parameter estimates from both models are likely to be in agreement. Thus, we suggest that the Ricker model is a more useful approximating model due to its parsimony and the convergence issues of the θ-logistic model. We recommend that when management decisions are based on estimates from a model of population dynamics, the Ricker model is likely a better choice, especially when temporal environmental variation is high or when using vague priors. Despite the intuitive appeal of the θ-logistic model to summarize large

mammal population growth, the accumulation of evidence continues to show the practical utility of the parsimonious Ricker model.

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AUTHOR CONTRIBUTIONS

L. J. K., A. D., and F. W. W. conceived of the ideas and analyzed the data; L. J. K. led the writing of the manuscript. All authors contributed critically to the paper.

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REFERENCES

Barker, D., & Sibly, R. M. (2008). The effects of environmental perturbation and measurement error on estimates of the shape parameter in the theta-logistic model of population regulation. *Ecological Modelling*, *219*, 170–177.

Bender, L. C., Cook, J. G., Cook, R. C., & Hall, P. B. (2008). Relations between nutritional condition and survival of north american elk *Cervus elaphus*. *Wildlife Biology*, *14*(1), 70–80.

Bender, L. C., Davison, M. A., Cook, J. G., Cook, R. C., & Hall, P. B. (2006). Assessing elk population status and potential performance in the nooksack area, washington. *Northwest Naturalist*, *87*(2), 98–106.

Boyce, M. S. (1989). *The jackson elk herd: Intensive wildlife management in north america*. Cambridge: Cambridge University Press.

Clark, F., Brook, B. W., Delean, S., Reşit Akçakaya, H., & Bradshaw, C. J. A. (2010). The theta-logistic is unreliable for modelling most census data. *Methods in Ecology and Evolution*, *1*, 253–262.

Cook, L. M. (1965). Oscillation in the simple logistic growth model. *Nature*, *207*, 316.

Coughenour, M. B., & Singer, G. J. (1996). Elk population processes in yellowstone national park under the policy of natural regulation. *Ecological Applications*, *6*(2), 573–593.

Delean, S., Brook, B. W., & Bradshaw, C. J. A. (2013). Ecologically realistic estimates of maximum population growth using informed bayesian priors. *Methods in Ecology and Evolution*, *4*, 34–44.

Eberhardt, L. E., Eberhardt, L. L., Tiller, B. L., & Cadwell, L. L. (1996). Growth of an isolated elk population. *The Journal of Wildlife Management*, *60*(2), 369–373.

Ferguson, J. M., & Ponciano, J. M. (2015). Evidence and implications of higher-order scaling in the environmental variation of animal population growth. *Proceedings of the National Academy of Science of the United States of America*, *112*(9), 2782–2787.

Fowler, C. W. (1981). Density dependence as related to life history strategy. *Ecology*, *62*(3), 602–610.

Fryxell, J. M., Mosser, A., Sinclair, A. R., & Packer, C. (2007). Group formation stabilizes predator-prey dynamics. *Nature*, *449*, 1041–1043.

Gaillard, J.-M., Pontier, D., Allainé, D., Lebreton, J. D., Trouvilliez, J., & Clobert, J. (1989). An analysis of demographic tactics in birds and mammals. *Oikos*, *56*(1), 59–76.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2004). *Bayesian data analysis*. Boca Raton, FL: Chapman and Hall/CRC.

Gilpin, M. E., & Ayala, F. J. (1973). Global models of growth and competition. *Proceedings of the National Academy of Science of the United States of America*, *70*(12), 3590–3593.

Kery, M. (2010). *Introduction to winbugs for ecologists*. Burlington, MA: Academic Press.

McCorquodale, S. M., Eberhardt, L. L., & Eberhardt, L. E. (1988). Dynamics of a colonizing elk population. *The Journal of Wildlife Management*, *52*(2), 309–313.

McCullough, D. R. (1979). *The george reserve deer herd: Population ecology of a k-selected species*. Ann Arbor, MI: University of Michigan Press.

Murphy, A. (1963). A captive elk herd in missouri. *The Journal of Wildlife Management*, *27*(3), 411–414.

Owen-Smith, N. (2006). Demographic determination of the shape of density dependence for three african ungulate populations. *Ecological Monographs*, *76*(1), 93–109.

Owen-Smith, N. (2007). *Introduction to modeling in wildlife and resource conservation*. Oxford: Blackwell Publishing.

Polansky, L., deValpine, P., Lloyd-Smith, J. O., & Getz, W. M. (2009). Likelihood ridges and multimodality in population growth rate models. *Ecology*, *90*(8), 2313–2320.

Raithel, J. D., Kauffman, M. J., & Pletscher, D. H. (2007). Impact of spatial and temporal variation in calf survival on the growth of elk populations. *The Journal of Wildlife Management*, *71*(3), 795–803.

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, *11*(5), 559–623.

Robinson, O. J., McGowan, C. P., & Devers, P. K. (2017). Disentangling density-dependent dynamics using full annual cycle models and bayesian model weight updating. *Journal of Applied Ecology*, *54*, 670–678.

Ross, J. V. (2009). A note on density dependence in population models. *Ecological Modelling*, *220*, 3472–3474.

Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., ... Buckley, Y. M. (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Science of the United States of America*, *113*(1), 230–235.

Sargeant, G. A., & Oehler, M. W. (2007). Dynamics of newly established elk populations. *The Journal of Wildlife Management*, *71*(4), 1141–1148.

Sibly, R. M., Barker, D., Denham, M. C., Hone, J., & Pagel, M. (2005). On the regulation of populations of mammals, birds, fish, and insects. *Science*, *309*, 607–610.

Street, G. M., Rodgers, A. R., Avgar, T., & Fryxell, J. M. (2015). Characterizing demographic parameters across environmental gradients: A case study with ontario moose (*Alces alces*). *Ecosphere*, *6*(8), 1–13.

Sæther, B.-E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, *81*(3), 642–653.

Toïgo, C., & Gaillard, J.-M. (2003). Causes of sex-biased adult survival in ungulates: Sexual size dimorphism, mating tactic or environment harshness?*Oikos*, *101*(2), 376–384.

Wang, G., Hobbs, N. T., Boone, R. B., Illius, A. W., Gordon, I. J., Gross, J. E., & Hamlin, K. L. (2006). Spatial and temporal variability modify density dependence in populations of large herbivores. *Ecology*, *87*(1), 95–102.

Wang, G., Hobbs, N. T., Twombly, S., Boone, R. B., Illius, A. W., Gordon, I. J., & Gross, J. E. (2008). Density dependence in northern ungulates: Interactions with predation and resources. *Population Ecology*, *51*(1), 123–132.

Weckerly, B. (2017). *Population ecology of roosevelt elk: Conservation and management in redwood national and state parks*. Reno, NV: University of Nevada Press.

Weckerly, F. W. (1998). *Sexual segregation and comeptition in Roosevelt elk*, Northwest. *Naturalist*, *79*(3), 113–118.

Wicklund, C. G. (2001). Food as a mechanism of density-dependent regulation of breeding numbers in the merlin, *Falco columbarius*. *Ecology*, *82*(3), 860–867.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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