

ORIGINAL ARTICLE

Local population dynamics of gray wolves *Canis lupus* and Eurasian lynx *Lynx lynx* exhibit consistency with intraspecific contest competition models

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Abstract

In Europe, the gray wolf and Eurasian lynx populations are recovering after various levels of persecution. The two species differ in their social structure and spatial patterns of aggregation. Using model selection, we investigated the consistency of the available time series data on local wolf and lynx subpopulations with a number of single-species population growth models that pertain to two types of intraspecific competition, namely, scramble (SC) and contest competition (CC), and reflect random (R) or aggregated (A) distribution of individuals. The applied models of population growth—the Ricker (SCR), Skellam (CCR), Hassell (SCA), and Beverton–Holt (CCA) models—were all parameterized in terms of intrinsic growth rate and carrying capacity with unified definitions. The projected carrying capacity was allowed to show a temporal trend, which was justified by an observed increase in prey abundance in recent decades. For both species, the models pertaining to contest competition outperformed the scramble competition models, and the Beverton–Holt model had the greatest weight. However, for the lynx, the difference of performance between the scramble and contest competition models was considerably smaller than that for the wolves. In most of the models, when it was meaningful, an optional time lag operator was added to account for a delay in individual maturity and reproduction. However, the models with a time lag had a worse fit than the models without it. This study promotes the application of population models that reflect intraspecific competition for modeling population dynamics in a single- or multi-species framework.

KEYWORDS

Canis lupus, contest competition, *Lynx lynx*, population dynamics, scramble competition

1 | INTRODUCTION

It is common practice to adopt single-species models when investigating certain aspects in population dynamics, such as time lags (Ruan, 2006), density dependence

(Boukal & Berec, 2002), and environmental conditions (Liu & Wang, 2009). The important intraspecific factors affecting population growth also include aspects of the nature of competition (Brännström & Sumpter, 2005). As indicated by simulation experiments in previous studies

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(e.g., Johst et al., 2008), population dynamics may reflect intraspecific competition patterns and resource partitioning. By recognizing these factors and selecting an appropriate population model, one may improve the projection of population dynamics for more appropriate management and effective conservation.

After previous persecution and deliberate eradication, populations of large carnivores have been recovering and locally re-emerging due to internationally binding legislation favoring conservation and reintroduction efforts (Boitani et al., 2015; Chapron et al., 2014). As the availability of remote wilderness areas is limited, the future of large carnivores depends on sustainable human–wildlife coexistence in the human-dominated landscape (Chapron et al., 2014; Everatt et al., 2019; Lennox et al., 2018; Linnell et al., 2001; López-Bao et al., 2017). Under such circumstances, viable population management should be based on understanding the characteristics of carnivore population dynamics and the functional form of population growth.

Two extremes of intraspecific competition, namely, scramble and contest competition, are generally distinguished (Getz & Owen-Smith, 2011; Hassell, 1975; Krebs, 2014; Nicholson, 1954). Scramble competition involves equal or random resource partitioning among all of the individuals in the population. In contrast, contest competition implies monopolistic resource utilization by the successful competitors among the local population; the remaining resources (i.e., leftovers) are insufficient to sustain more individuals, which ultimately fail to reproduce and are forced to leave the area, live as floaters, or die from the lack of necessary resources. Although some authors (e.g., Rockwood, 2015) have suggested that dividing intraspecific relationships into either scramble or contest competition may not be realistic, the assumptions of scramble and contest competition have been applied in studies of a broad range of organisms such as fish (Petersson & Järvi, 2000), birds (Rieucan & Giraldeau, 2008), and mammals (Dammhahn & Kappeler, 2010; Luo et al., 2020). Sibly et al. (2007) examined 634 populations of mammals, birds, fish, and insects. Their results indicate that contest competition, rather than scramble competition, reflects the status of the species examined. However, some of the existing studies, which consider, for example, birds (Black-throated blue warblers; Rodenhouse et al., 2003) and ungulates (Tibetan antelopes; Luo et al., 2020), conclude that certain species exhibit scramble competition. There is a large amount of accumulated empirical and theoretical knowledge regarding cases in which primates exhibit both types of intraspecific competition (e.g., Howlett & Wheeler, 2021; Isbell, 1991; Janson & Van Schaik, 1988; Kappeler & van Schaik, 2002; Knott et al., 2008; van Schaik, 1989). To the best of the

authors' knowledge, the applications of intraspecific competition models for large carnivores are limited.

Phenomenological discrete time models $N_{t+1} = f(N_t)$, which predict population size at time step $t + 1$ (e.g., reproductive season or year) as a function of the population size at the previous time step t according to the scramble or contest competition scenarios, can be derived from Verhulst's logistic equation (Johst et al., 2008; Royama, 1992) or by other means (e.g., Hassell, 1975). Meaningful derivations are obtained according to predefined fundamental processes, resource partitioning, and individual interaction (e.g., Anazawa, 2019; Eskola & Geritz, 2007; Geritz & Kisdi, 2004). The site-based framework provides general underlying principles for developing population models that predict population size within a network of sites based on initial number of individuals and the expected number of remaining individuals and offspring, which is determined according to explicit assumptions about intraspecific competition and individual clustering (Anazawa, 2009; Brännström & Sumpter, 2005; Johansson & Sumpter, 2003). Both the distribution of individuals in habitat sites (random or aggregated) and their interactions (scramble or contest) are incorporated in the site-based framework. Four such models that employ only two parameters, which can be expressed as functions of the intrinsic growth rate and carrying capacity (i.e., equilibrium density), are listed in Table 1. These models pertain to scramble or contest competition and assume Poisson or geometric probability distribution for the number of individuals at the sites. Regarding intraspecific competition, the Ricker (1954) and Hassell (1975) models reflect scramble competition while the Skellam (1951) and Beverton–Holt (Beverton & Holt, 1957) models reflect contest competition. Regarding spatial patterns, the Ricker and Skellam models are associated with random (i.e., Poissonian) individual distribution while the Hassell and Beverton–Holt models assume the aggregation of individuals according to the geometric distribution and a considerable proportion of the unoccupied sites within the area.

This study aims to examine the consistency of intraspecific carnivore population dynamics using scramble and contest population models. This knowledge may be relevant when justifying the choice of a particular population model to predict the population dynamics of a certain species. For example, the Ricker model has typically been applied in various cases (Hall, 1988; Hamada, 2024; Šuba et al., 2023), but territorial animals, for example, gray wolves *Canis lupus*, are generally supposed to reflect contest competition (Mech & Boitani, 2003). Such an examination is of particular interest as both carnivore species reproduce seasonally but differ in their social structure. Therefore, we used model selection and multi-

TABLE 1 Two-parameter (α_i and β_i) single-species population models derived according to site-based framework.

Model name	Expression	Competition type	Distribution of individuals at sites
Ricker	$\alpha_R N_t \exp(-\beta_R N_t)$	Scramble	Random
Skellam	$\alpha_S (1 - \exp[-\beta_S N_t])$	Contest	Random
Hassell	$\alpha_H N_t / (1 + \beta_H N_t)^2$	Scramble	Aggregated
Beverton–Holt	$\alpha_{BH} N_t / (1 + \beta_{BH} N_t)$	Contest	Aggregated

model inference to investigate whether the population dynamics of carnivore species are more consistent with contest competition. We used available census and culling (i.e., hunting) data on the gray wolf and Eurasian lynx *Lynx lynx* populations in Latvia obtained over the last six decades. Additional assumptions were also considered. As the prey populations for both species in Europe have been increasing in recent decades (Apollonio et al., 2010; Carpio et al., 2021), we investigated whether an increase in carrying capacity would contribute to the growth of the local wolf and lynx populations independently of their intrinsic growth rates. Previous studies on wolf and lynx dynamics in Latvia (Kawata, 2008), and on wolf dynamics in neighboring Lithuania (Balčiauskas & Kawata, 2009), have found that a time lag due to delayed maturity was significant for the wolf population growth. Therefore, we also considered model versions with different values for the time lag operator. Lastly, it is known that observation noise and bias in time series data can affect estimates of density dependence and, consequently, carrying capacity if not explicitly accounted for (Knape, 2008). As the game census data are often subject to overestimation and contain process errors of unknown magnitude, we also investigated the effect of abundance estimation bias and the additional noise of known magnitude on parameter estimates.

2 | MATERIALS AND METHODS

2.1 | Study species

In Europe, the distribution ranges of the gray wolf and Eurasian lynx populations are currently largely overlapping (Linnell et al., 2008). Wolves have been capable of recovering after drastic reductions by natural recolonization (Hayes & Harestad, 2000; Linnell et al., 2005; Pletscher et al., 1997; Reinhardt et al., 2019; Szewczyk et al., 2019;

Vilà et al., 2003) or artificially facilitated acclimatization (Smith et al., 2003). Reintroduction efforts have played a more significant part in the lynx recolonization of several areas in central and western Europe due to the inferior dispersal capabilities of lynx (Breitenmoser, 1998; Breitenmoser et al., 1998; von Arx et al., 2004). The social structures of gray wolves and Eurasian lynx are different. The wolves form family packs which consist of a monogamous pair, their offspring before reproductive age, and newborn pups (Mech, 1970). The lynx males and nonreproductive females are solitary, while reproductive females accompany and nurse their cubs until they become independent (Breitenmoser et al., 2000). Wolf packs defend their territories from intruding conspecifics (Jędrzejewska & Jędrzejewski, 1998; Mech, 1970), whereas the home ranges of neighboring lynx males or members of opposite sexes may overlap to some extent (Schmidt et al., 1997).

The so-called Baltic wolf and lynx populations, to which the Latvian sub-populations belong, are thriving wolf and lynx populations in Europe (Chapron et al., 2014). In Latvia, wolves and lynx have never been totally exterminated (Bagrade et al., 2016; Ozoliņš, Bagrade, et al., 2017; Ozoliņš, Žunna, et al., 2017; Šuba et al., 2021). The implemented hunting praxis for wolves and lynx has varied historically (Ozoliņš et al., 2008, 2016). Before Latvia became a member state of the European Union in 2004, wolves were legally hunted all year round (Ozoliņš, Bagrade, et al., 2017). After joining the EU, a closed season and an annual quota were introduced in compliance with the Habitat Directive (European Council, 1992). Lynx have always been a protected species in Latvia, and illegal killings have been penalized. Moderate hunting and lethal control of this species have been conducted according to strict supervision by game surveillance authorities (Bagrade et al., 2016; Ozoliņš, Žunna, et al., 2017). In the hunting season of 2021/2022, the hunting of lynx was no longer permitted, and a permanent hunting ban on this species was introduced in 2022 (Ozoliņš et al., 2022). In our analysis, we focused on annual transitions, which are not affected by seasonal variations in hunting activity. The poaching of wolves and lynx in Latvia is rare, and its share within the total number of intentionally removed wolf and lynx individuals can be considered to be negligible as the majority of hunters are motivated to report the killings in compliance with approved legal culling (J. Ozoliņš, personal communication).

2.2 | Abundance estimates and culling data

The datasets used in this study contained the estimated population (i.e., number of individuals) of wolves and

lynx and the numbers of culled individuals in Latvia from 1958 to 2022. Such data are available on the Latvian State Forest Service website (www.vmd.gov.lv) and in previous publications (e.g., Andersone-Lilley & Ozolins, 2005; Kawata, 2008; Vanags, 2010). The numbers of wolves and lynx are estimated for every regional game management district at the closure of the hunting season, that is, 31 March or 30 April, and added together to calculate the total abundance over larger game management territories and the whole country. This estimate can be understood as the abundance before reproduction. However, it is prone to overestimation as the home ranges of large carnivores are likely to encompass several adjacent hunting districts (e.g., Herfindal et al., 2005), and the individual animals may have been accounted for more than once. The extent of this overestimation bias is unknown. Other studies (Ozoliņš, Bagrade, et al., 2017; Ozoliņš, Žunna, et al., 2017; Šuba et al., 2021) suggest that the actual abundance differs from the reported number by less than 50%. To examine the potential effects on model performance caused by biased population estimates, we investigated the tested models with adjusted abundance estimates using $X_t = cN_t$, where the reported abundance estimates N_t were multiplied by a factor of $c = 0.7, 0.8, 0.9$, or 1.1 to account for potential bias, or by setting $c = 1$ if no bias was assumed.

The effects of potential observation errors in the abundance data on the model statistics and parameter values were investigated using 5000 simulated datasets per species. These datasets were created by multiplying the original wolf and lynx data by a set of independent log-normally distributed annual random numbers, with 1 as the expected value (parameters $\mu = -1/2\sigma^2_{\text{noise}}$ and $\sigma^2 = \sigma^2_{\text{noise}}$), and by setting σ_{noise} to 0.1. While we do not know the true level of noise in the data, this reflects a realistic level, which at least helps to identify the occurrence and direction of bias due to observation errors and also gives a rough clue about the level of bias in the different parameters. The parameter estimates were also bias-corrected by subtracting the levels of bias (estimated in the simulations) from the originally estimated parameter values. The approach used here for exploring the effect of simulated additional observation error, and using that for bias correction, applies the idea of simulation extrapolation (i.e., SIMEX), which is thoroughly explicated in Cook and Stefanski (1994) and Stefanski and Cook (1995).

2.3 | Models and parameters

In this study, we applied phenomenological single-species discrete time population models that use

parameters related to intrinsic growth rate, carrying capacity, and residual variance. The analyses were carried out separately for each species. The intrinsic growth rate was parameterized as an instantaneous (i.e., logarithmic) rate r_0 instead of a finite (i.e., geometric) rate λ_0 (Skalski et al., 2005). The effects on population growth following the removal of known individuals due to culling, in relation to the abundance estimate before breeding and culling X_t , were accounted for by adding the total number of culled individuals h_t to the estimated abundance at the closure of the hunting season X_{t+1} , obtained in the spring of the following calendar year, that is, $X_{t+1} + h_t = f(X_t)$ or $X_{t+1} = f(X_t) - h_t$ (Eberhardt, 1987). The annual logarithmic per capita growth rate was calculated as $r_t = \ln(X_{t+1} + h_t) - \ln(X_t)$. A monotonic multiplicative change in the projected carrying capacity over the study period was allowed by expressing K_t as a function of year t and using the two parameters a and b ; the latter expressed the temporal trend as

$$K_t = \exp(a + bt). \quad (1)$$

Hence, the abundance of wolves or lynx during the temporal transition from year t to year $t + 1$ was modeled according to the focal species' abundance before breeding X_t , the number of culled individuals h_t , the intrinsic growth rate r_0 , the parameters a and b (which defines the carrying capacity at year t), and the stochastic parameter ε_t , quantifying the residual variation due to errors, uncontrolled environmental factors, and demographic stochasticity:

$$X_{t+1} = f(X_t, t | r_0, a, b) e^{\varepsilon_t} - h_t. \quad (2)$$

The error term ε_t was treated as a normally distributed random variable (see Ruokolainen et al., 2009). Setting its mean and variance as $-1/2\sigma_\varepsilon^2$ and σ_ε^2 , respectively, ensures that the expected value of a log-normally distributed ratio $\frac{X_{t+1} + h_t}{f(X_t, t | r_0, a, b)}$ equals unity and therefore provides unbiased parameter estimates. Furthermore, although the model itself is a first-order autoregression, we allowed the residuals to be serially autocorrelated according to a first-order linear autoregressive process with the autocorrelation coefficient φ .

A significant proportion of the wolf and lynx populations in Latvia consists of juveniles and subadults (Bagrade et al., 2016; Šuba et al., 2021). Hence, a time lag operator τ , represented by a non-negative integer, was applied to account for the effect of delayed reproduction due to maturity. In previous studies, $0 < \tau \leq 3$ improved the model fitting to the observed wolf dynamics in Latvia and Lithuania (Balčiauskas & Kawata, 2009;

Kawata, 2008). A time lag of $\tau = 0, 1, 2, 3, 4$ was introduced into the Ricker, Hassell, and Beverton–Holt models (see Equations 3, 5, and 6); this introduction was similar to that carried out in Kawata (2008) and Balčiauskas and Kawata (2009). The Skellam model requires only a single term with the explanatory variable (Table 1). Hence, the introduction of $\tau > 0$ into this model was incompatible with a first-order autoregressive process. Rearrangements of the Ricker, Skellam, Hassell, and Beverton–Holt equations are given in Equations (3–6), and a description of their derivation is given in Appendix 1 (a more detailed description of the modified Skellam model is also provided by Šuba et al., 2023).

$$f_R(X_t, X_{t-\tau}, t | r_0, a, b, \tau) = X_t \exp \left(r_0 \left[1 - \frac{X_{t-\tau}}{\exp(a + [t - \tau]b)} \right] \right). \quad (3)$$

$$f_S(X_t, t | r_0, a, b) = \exp(a + bt) \frac{1 - \exp \left(-X_t \frac{1 + e^{-r_0} W(-\exp\{r_0 - e^{r_0}\})}{e^{a+bt-r_0}} \right)}{1 + e^{-r_0} W(-\exp\{r_0 - e^{r_0}\})}. \quad (4)$$

$$f_H(X_t, X_{t-\tau}, t | r_0, a, b, \tau) = \frac{X_t \exp(r_0)}{\left(1 + \left[\exp\left(\frac{r_0}{2}\right) - 1 \right] \frac{X_{t-\tau}}{\exp(a + [t - \tau]b)} \right)^2}. \quad (5)$$

$$f_{BH}(X_t, X_{t-\tau}, t | r_0, a, b, \tau) = \frac{X_t \exp(r_0)}{1 + \left[\exp(r_0) - 1 \right] \frac{X_{t-\tau}}{\exp(a + [t - \tau]b)}}. \quad (6)$$

2.4 | Fitting procedure and model selection

To fit the investigated models to the data and to find the maximum likelihood estimates for r_0 , a , b , σ_ϵ^2 , and φ , numerical optimization and generalized least squares (GLS) techniques were applied. Nonlinear numerical optimization using the Nelder–Mead simplex algorithm was used to estimate the parameters φ , r_0 , or b , which depended on the particular model. The remaining parameters could be estimated analytically—during each iteration of the optimization algorithm—using the GLS techniques. The discrete parameter τ was given by the model setting, that is, its value was assessed in terms of model uncertainty.

To assess the consistency of the investigated models with the data, we applied model selection and assessed individual model weights (Aho et al., 2014; Symonds &

Moussalli, 2011; Wagenmakers & Farrell, 2004). For each species, we evaluated a set of 16 candidate models with optimized parameter values. The set included the modifications of the Ricker, Hassell, and Beverton–Holt models described above, each with the time lag τ of 0, 1, 2, 3, or 4, as well as the Skellam model. In our case, as the number of parameters was the same for every model ($k = 5$), the penalty terms of the model complexity would be constant in information criteria such as $\text{AIC}_{(C)}$ and BIC, and the differences in the performances of the models would in all cases be determined solely by differences in $-2\ln(L) = \ln(L^{-2})$, where L is the maximized likelihood function value. Hence, model selection results that are determined according to the Bayesian or Akaike information criterion provide essentially the same differences between the models, that is, $\Delta\text{BIC} = \Delta\text{AIC}_{(C)} = \Delta\ln(L^{-2})$.

The standard errors (SEs) for the estimated model parameters (r_0 , \hat{a} , b , σ_ϵ^2 , and φ) were calculated by presuming that the inverse Hessian matrices of the negative log-likelihood function provided the variance–covariance matrix of the parameters. Confidence intervals (95%) were constructed by adding $1.96 \times \text{SE}$ to or subtracting it from the parameter estimates. All the calculations were conducted using the programming environment R (R Core Team, 2017, see [Supporting Information](#) for the code).

3 | RESULTS

The Latvian wolf and lynx abundance data exhibited an overall increasing trend with considerable fluctuations over the last six decades (Figure 1a,c), but with a decrease in the calculated annual growth rate over time (Figure 1b,d). The mean observed annual per capita growth rates \bar{r}_t for the wolf and lynx populations in Latvia were 0.577 (SD = 0.425, $n = 58$) and 0.225 (SD = 0.260, $n = 58$), respectively.

The estimates of the intrinsic growth rate, the parameters a and b that determined the projected carrying capacity $K_t = \exp(a + bt)$, the residual variance σ_ϵ^2 , and the autocorrelation coefficient φ according to the investigated population models are given in Tables 2 and 3. The unconditional parameter estimates according to full-model averaging by the model weights w are given in Table 4. The model-averaged estimates of the residual parameters were $\bar{\sigma}_\epsilon^2 = 0.0387$ and $\bar{\varphi} = 0.5939$ for the wolf population models and $\bar{\sigma}_\epsilon^2 = 0.0386$ and $\bar{\varphi} = 0.2671$ for the lynx population models, respectively. The Beverton–Holt model with $\tau = 0$ was found to be the best performing model, with parameter values of $r_0 = 1.3903$ (SE = 0.1509), $\hat{a} = 5.9272$ (SE = 0.3458), and $b = 0.0245$ (SE = 0.0072) for the wolves and $r_0 = 0.7581$

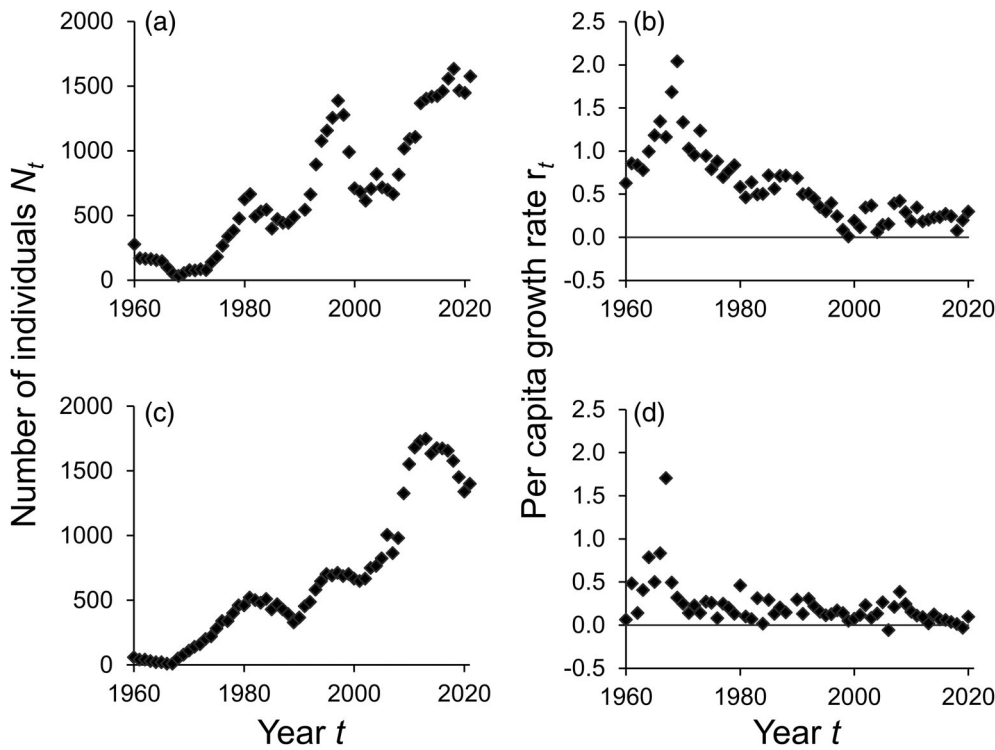


FIGURE 1 Population dynamics of wolves (top panels a, b) and lynx (bottom panels c, d) in Latvia during the last six decades in terms of pre-breeding and pre-culling abundance N_t (panels a, c) and annual per capita growth rate $r_t = \ln(N_{t+1} + h_t) - \ln(N_t)$ (panels b, d).

TABLE 2 Summary of estimated intrinsic growth rate r_0 and parameters determining the projected carrying capacity $K_t = \exp(a + bt)$, residual variance, autocorrelation coefficient, and information-theoretic statistics of tested models describing wolf population dynamics in Latvia from 1963 to 2021.

Model	τ	\hat{r}_0	\hat{a}	\hat{b}	$\hat{\sigma}_\epsilon^2$	$\hat{\varphi}$	$\ln(L)$	$\Delta \ln(L^{-2})$	w
Ricker	0	1.092	6.169	0.019	0.053	0.693	21.1	8.1	0.013
Ricker	1	1.068	6.174	0.019	0.051	0.651	19.3	11.6	0.002
Ricker	2	0.970	6.587	0.013	0.063	0.689	16.0	18.3	<0.001
Ricker	3	1.027	6.143	0.021	0.060	0.697	17.9	14.6	0.001
Ricker	4	0.890	7.012	0.007	0.082	0.768	15.3	19.6	<0.001
Skellam	0	1.249	5.946	0.023	0.044	0.640	22.9	4.5	0.078
Hassell	0	1.228	5.997	0.023	0.045	0.642	22.8	4.6	0.074
Hassell	1	1.190	6.057	0.021	0.042	0.574	20.8	8.6	0.010
Hassell	2	1.077	6.358	0.017	0.050	0.614	16.8	16.7	<0.001
Hassell	3	1.129	6.129	0.021	0.052	0.645	18.8	12.6	0.001
Hassell	4	0.942	7.005	0.007	0.075	0.742	15.6	19.0	<0.001
Beverton–Holt	0	1.390	5.927	0.025	0.037	0.593	25.1	0.0	0.743
Beverton–Holt	1	1.321	6.042	0.022	0.035	0.489	22.8	4.7	0.072
Beverton–Holt	2	1.244	6.203	0.019	0.041	0.488	18.3	13.7	0.001
Beverton–Holt	3	1.222	6.221	0.019	0.045	0.605	20.0	10.3	0.004
Beverton–Holt	4	1.000	6.991	0.007	0.068	0.727	16.0	18.3	<0.001

(SE = 0.1234), $\hat{a} = 5.3668$ (SE = 0.2844), and $\hat{b} = 0.0381$ (SE = 0.0062) for the lynx. The most obvious difference between the parameter estimates for the two species was a higher intrinsic growth rate for the wolves compared to that of the lynx. The model fit with the data and the trend

in the projected carrying capacity of studied wolf and lynx populations are illustrated in Figures 2a–h and 3a–h, respectively.

For the populations of both carnivore species, the models that implied contest competition (i.e., the

TABLE 3 Summary of estimated intrinsic growth rate r_0 and parameters determining the projected carrying capacity $K_t = \exp(a + bt)$, residual variance, autocorrelation coefficient, and information-theoretic statistics of tested models describing lynx population dynamics in Latvia from 1963 to 2021.

Model	τ	\hat{r}_0	\hat{a}	\hat{b}	$\hat{\sigma}_e^2$	$\hat{\varphi}$	$\ln(L)$	$\Delta \ln(L^{-2})$	w
Ricker	0	0.645	5.422	0.037	0.040	0.294	13.3	3.4	0.088
Ricker	1	0.581	5.562	0.035	0.042	0.207	10.9	8.3	0.007
Ricker	2	0.555	5.603	0.034	0.044	0.230	10.0	10.0	0.003
Ricker	3	0.571	5.487	0.036	0.044	0.296	10.9	8.3	0.007
Ricker	4	0.464	6.037	0.026	0.049	0.313	8.1	13.8	<0.001
Skellam	0	0.687	5.405	0.037	0.039	0.280	13.9	2.1	0.163
Hassell	0	0.693	5.403	0.037	0.039	0.277	14.1	1.9	0.187
Hassell	1	0.619	5.539	0.035	0.041	0.184	11.4	7.2	0.013
Hassell	2	0.583	5.601	0.034	0.043	0.214	10.3	9.4	0.004
Hassell	3	0.597	5.496	0.036	0.043	0.288	11.1	7.8	0.010
Hassell	4	0.473	6.089	0.026	0.049	0.309	8.2	13.6	0.001
Beverton–Holt	0	0.758	5.367	0.038	0.037	0.263	15.0	0.0	0.471
Beverton–Holt	1	0.666	5.510	0.036	0.040	0.159	12.1	5.8	0.026
Beverton–Holt	2	0.614	5.602	0.035	0.042	0.197	10.7	8.6	0.006
Beverton–Holt	3	0.625	5.511	0.036	0.043	0.281	11.4	7.3	0.012
Beverton–Holt	4	0.482	6.152	0.025	0.048	0.305	8.3	13.5	0.001

TABLE 4 Unconditional estimates of intrinsic growth rate r_0 and parameters determining the projected carrying capacity $K_t = \exp(a + bt)$ for wolf and lynx population dynamics in Latvia from 1963 to 2021 (the estimates are model-averaged values of the Ricker, Skellam, Hassell, and Beverton–Holt models according to model weights; numbers in brackets are parameter standard errors).

Population	\hat{r}_0	\hat{a}	\hat{b}
Wolf	1.354 (0.160)	5.949 (0.357)	0.024 (0.007)
Lynx	0.711 (0.123)	5.400 (0.289)	0.037 (0.006)

Beverton–Holt and Skellam models) had a greater cumulative model weight (0.899 for the wolf population and 0.679 for the lynx population) compared to the models of the scramble competition (i.e., the Hassell and Ricker models). The 95% confidence set of models describing wolf population dynamics included the Beverton–Holt model with $\tau = 0$ ($w = 0.743$), the Skellam model ($w = 0.078$), the Hassell model with $\tau = 0$ ($w = 0.074$), and the Beverton–Holt model with $\tau = 1$ ($w = 0.072$). For the lynx population, the 95% confidence set included the Beverton–Holt model with $\tau = 0$ ($w = 0.471$), the Hassell model with $\tau = 0$ ($w = 0.187$), the Skellam model ($w = 0.163$), the Ricker model with $\tau = 0$ ($w = 0.088$), the Beverton–Holt model with $\tau = 1$ ($w = 0.026$), the Hassell model with $\tau = 1$ ($w = 0.013$), and the Beverton–Holt model with $\tau = 3$ ($w = 0.012$). The models that assumed a random

distribution of individuals at sites (i.e., the Ricker and Skellam models) had a lower cumulative model weight (0.093 for the wolf population and 0.269 for the lynx population) than the models involving non-random distribution and individual clustering (i.e., the Hassell and Beverton–Holt models). The models that contained a time lag operator τ (i.e., the models with $\tau > 0$) had a low cumulative model weight (0.092 for the wolf population and 0.091 for the lynx population). Hence, in further analyses, we focused on models with $\tau = 0$.

Multiplying the abundance estimates by a bias factor $c = \{0.7, 0.8, 0.9, 1, 1.1\}$ indicated that overestimation would have influenced the relative performances of the candidate models (Figure 4a–f). When overestimation was assumed for the lynx population, the model weights of the Beverton–Holt model with $\tau = 0$ were greater compared to the assumption of no bias or when assuming underestimation of the abundance data (Figure 4d); these results therefore provided robust support in favor of this model. The opposite pattern was observed for the worst performing models (Figure 4e,f). For the wolf population, the weights of the models with assumed bias in the abundance data changed to a lesser extent (Figure 4a–c), again suggesting that the results from the model selection would, in practice, be the same regardless of the bias in the abundance estimates.

The potential effect of observation errors was investigated by testing the models' performance in 5000

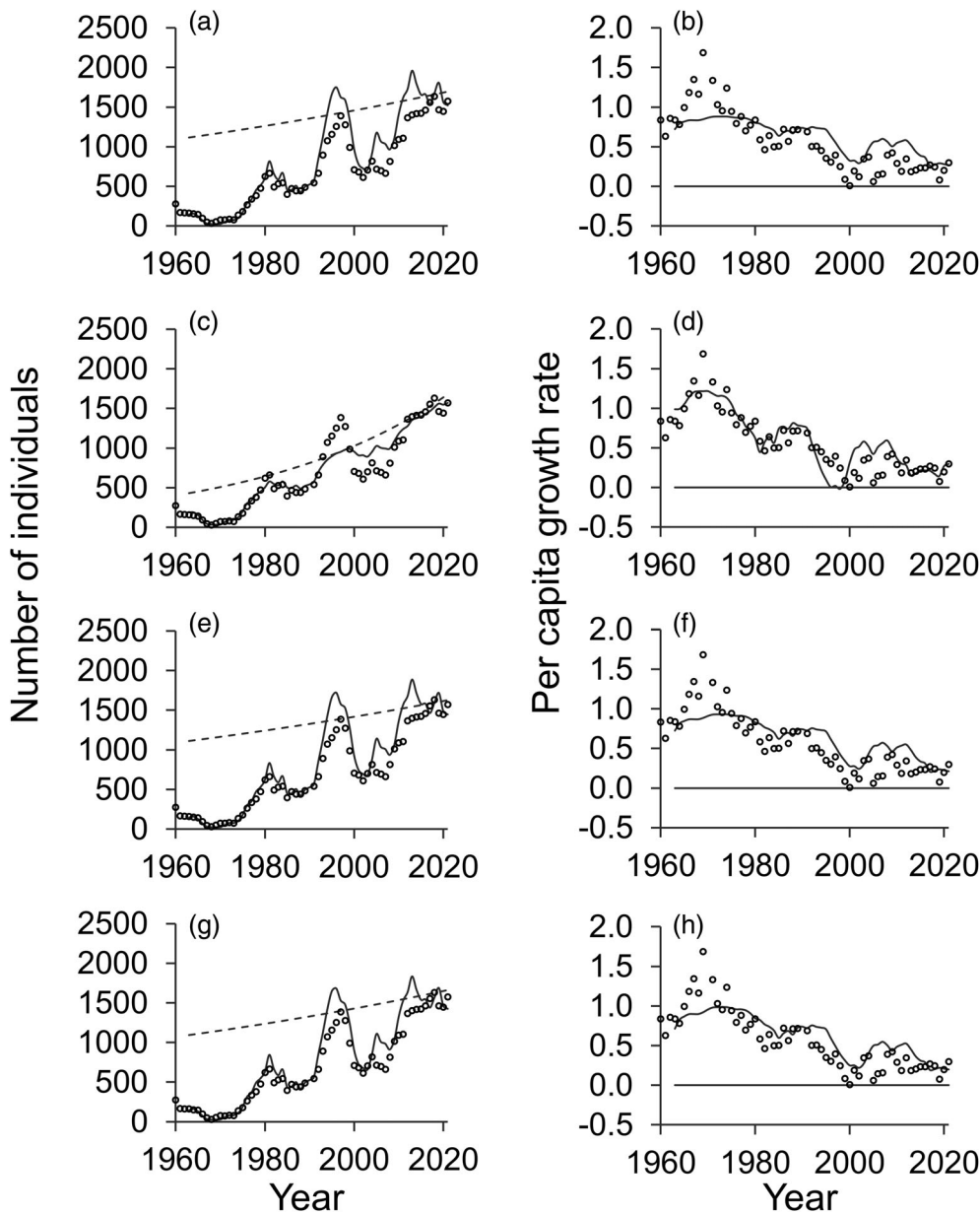


FIGURE 2 Fit of the tested scramble and contest competition models (solid line) with temporally increasing carrying capacity (dashed line) to the pre-culling abundance estimates (left panels) and corresponding observations and estimates of instantaneous per capita growth rate (right panels) of the wolf population in Latvia during the last six decades: Ricker model (panels a, b), Skellam model (panels c, d), Hassell model (panels e, f), and Beverton–Holt model (panels g, h).

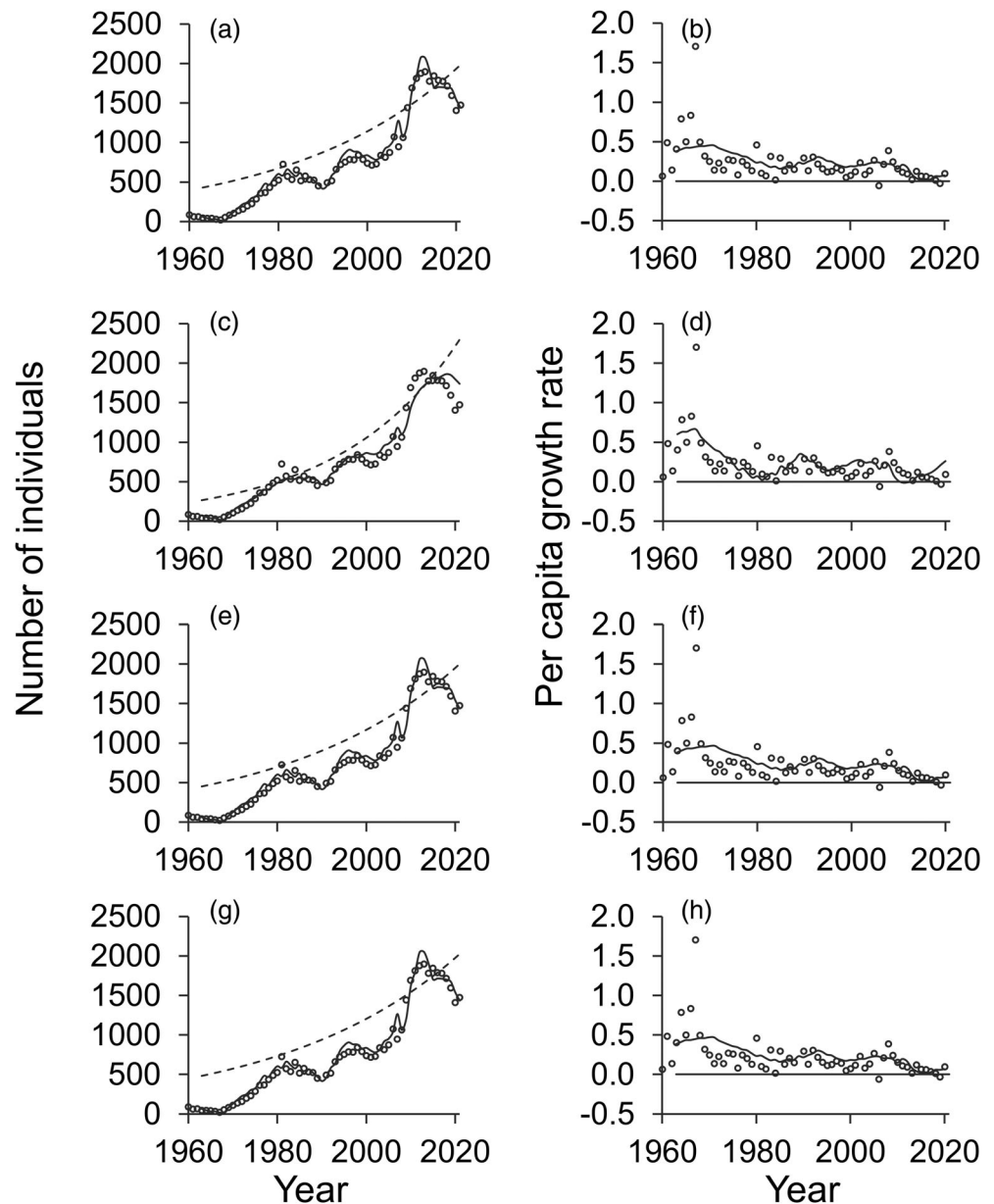
simulated datasets, where a log-normally distributed noise was added to the original data. The performance of the Beverton–Holt model for the wolf time series remained superior according to the mean values of the model weights (Figure 5a–c). In the lynx time series, however, the mean value of the model weights considerably decreased for the Beverton–Holt and Hassell models and increased for the Ricker and Skellam models (Figure 5d–f).

The assumptions about bias in the abundance data affected the estimates of the intrinsic growth rate and the constant parameter defining the carrying capacity (Figure 6a–f). As the bias factor was increased from 0.7 to 1.1, the intrinsic growth rate decreased for both wolves and lynx. In contrast, the constant parameter \hat{a} (level

of K_t) increased for lynx, but less so for wolves. The trend parameter \hat{b} (a logarithmic trend in K_t) remained largely unaffected by bias in the abundance estimates, particularly when related to the parameter uncertainty that was measured as the confidence interval range.

The introduction of noise into the original data mainly increased the error variance and decreased the autocorrelation (Figure 7a–j). It also had a considerable effect on the parameter estimates that determined the growth rate and the carrying capacity of the wolf population. In particular, the added noise increased the estimates of parameters r_0 and \hat{b} and decreased that of the parameter \hat{a} . However, the additional noise had no significant effect on the parameter estimates of the lynx population.

FIGURE 3 Fit of the tested scramble and contest competition models (solid line) with temporally increasing carrying capacity (dashed line) to the pre-culling abundance estimates (left panels) and corresponding observations and estimates of instantaneous per capita growth rate (right panels) of the lynx population in Latvia during the last six decades: Ricker model (panels a, b), Skellam model (panels c, d), Hassell model (panels e, f), and Beverton–Holt model (panels g, h).



4 | DISCUSSION

Gray wolves and Eurasian lynx, as with large carnivores in general, are territorial animals, albeit with different social structures. The differences in individual interaction are expected to conform to the different functional forms of the models describing population dynamics. The main difference between the scramble and contest competition models, as determined by their functional forms is related to the predicted response when the expected abundance $N_{t+1} = f(N_t)$ exceeds the carrying capacity of the initial abundance N_t due to an influx of individuals from elsewhere. In scramble competition, under such circumstances, the resulting abundance decreases due to density dependence and overcompensation, whereas in contest competition, the abundance asymptotically approaches a

certain level as individuals attack each other and the excess individuals are killed or forced to leave the sites (e.g., Brännström & Sumpter, 2005; Eskola & Geritz, 2007).

In this study, we investigated the consistency of the time series data with a range of phenomenological single-species population models that are derivable from first principles (i.e., a mechanistic bottom-up manner of deriving population models based on the process at an individual level) according to site-based frameworks (Anazawa, 2009; Brännström & Sumpter, 2005; Johansson & Sumpter, 2003). The models were rearranged to contain the same set of parameters, namely, the intrinsic growth rate and the carrying capacity. The Ricker and Beverton–Holt population models assume scramble competition and a random distribution of

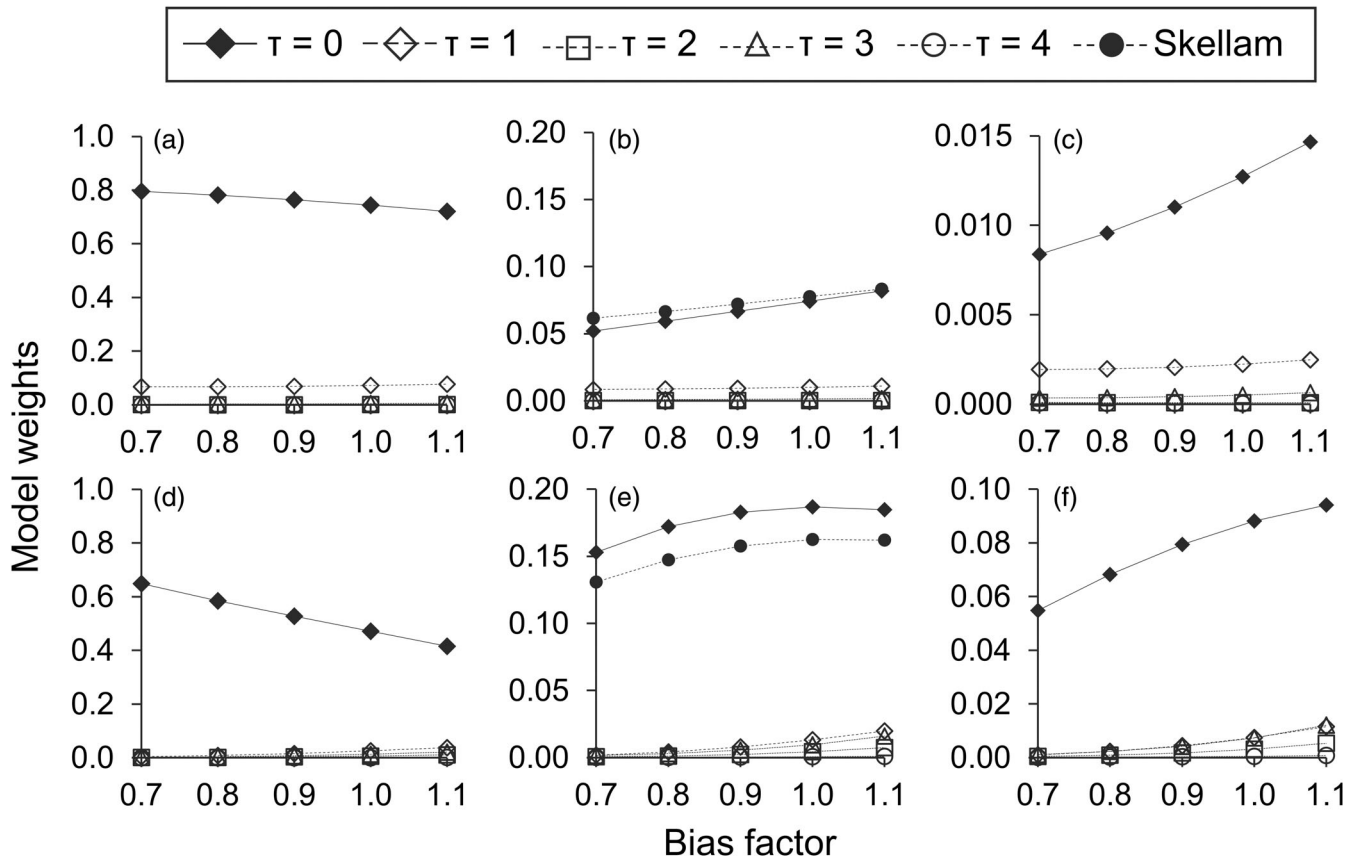


FIGURE 4 Effect of overestimation ($c < 1$) and underestimation bias ($c > 1$) in abundance estimates $X_t = cN_t$ on the weights of the candidate models describing wolf (top panels a–c) and lynx (bottom panels d–f) population dynamics: Beverton–Holt model (panels a, d), Hassell and Skellam models (panels b, e), Ricker model (panels c, f); τ values correspond to introduced time lags from 0 to 4 years to account for the effect of delayed reproduction due to maturity.

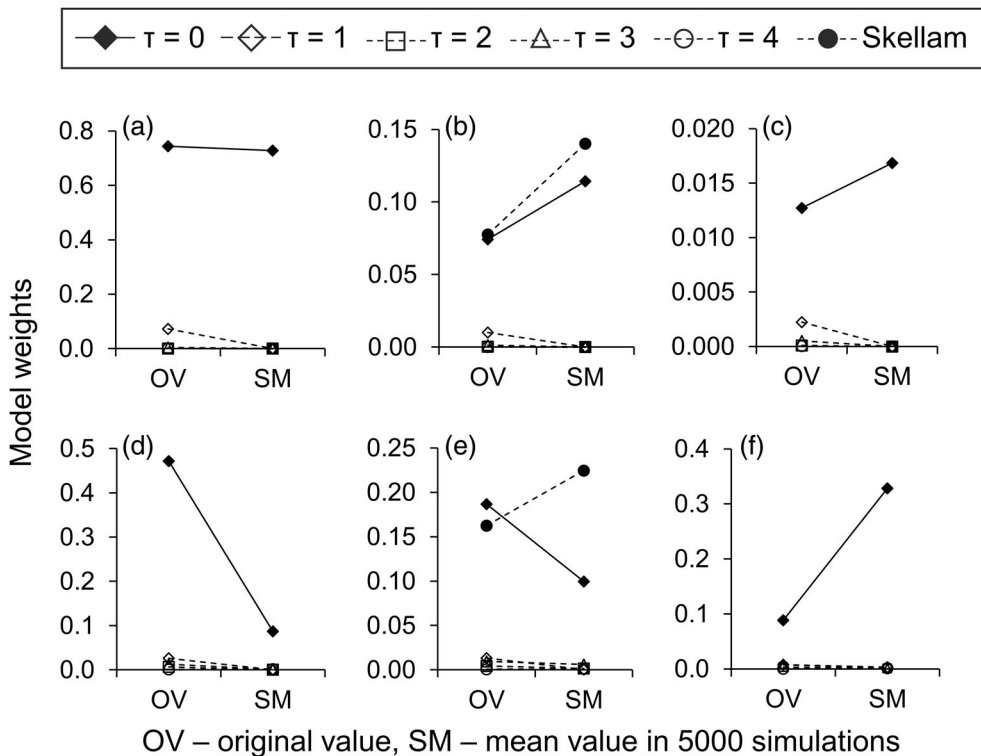


FIGURE 5 Effect of introduced noise in the data in 5000 simulations, multiplying original values by a log-normally distributed variable with $\mu = -1/2\sigma^2_{\text{noise}}$ and $\sigma^2 = \sigma^2_{\text{noise}}$ set to 0.1, on the weights of the candidate models describing wolf (top panels a–c) and lynx (bottom panels d–f) population dynamics: Beverton–Holt model (panels a, d), Hassell and Skellam models (panels b, e), Ricker model (panels c, f); τ values correspond to introduced time lags from 0 to 4 years to account for the effect of delayed reproduction due to maturity.

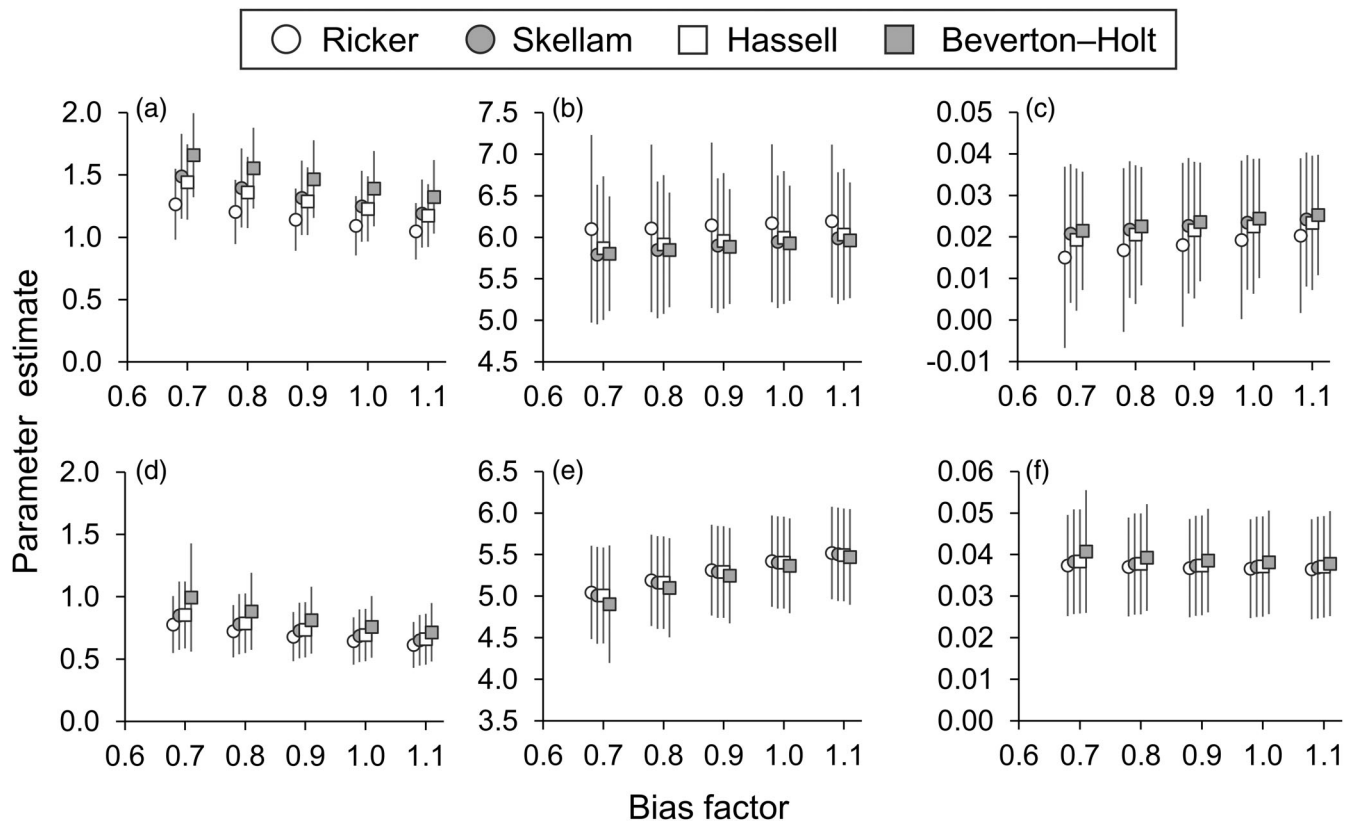
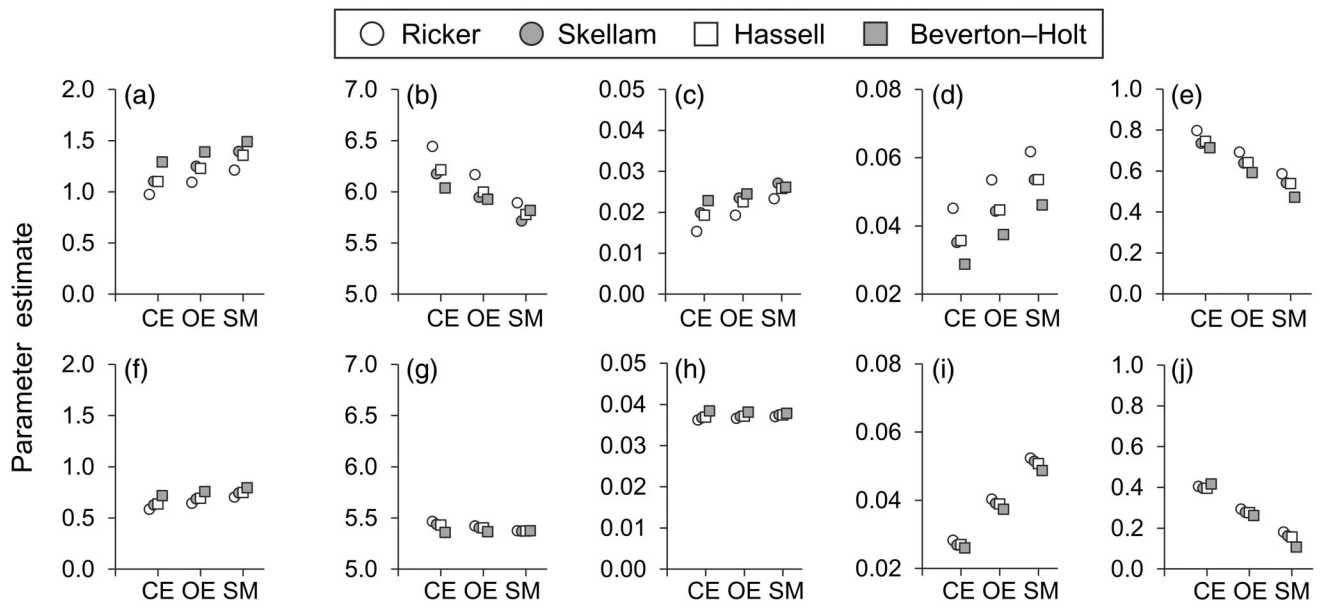


FIGURE 6 Effect of overestimation ($c < 1$) and underestimation bias ($c > 1$) in abundance estimates $X_t = cN_t$ on estimated model parameters describing wolf (top panels a–c) and lynx (bottom panels d–f) population dynamics: Intrinsic growth rate r_0 (panels a, d) and parameters \hat{a} (panels b, e) and \hat{b} (panels c, f) determining the projected carrying capacity $K_t = \exp(a + bt)$ (whiskers indicate 95% confidence intervals).

individuals at habitat sites and contest competition and individual aggregation, respectively. The Hassell and Skellam models assume other combinations of underlying assumptions, namely scramble competition and individual aggregation and contest competition and a random distribution of individuals (Table 1). Our study confirmed the different performances of the investigated models in describing the population dynamics of the wolf and lynx population in Latvia between 1963 and 2021, as well as the superior performance of the other models (Tables 2 and 3) when compared to the frequently applied Ricker model (Hamada, 2024). Specifically, the changes in wolf abundance were more consistent with the models that assumed contest competition and spatial aggregation and matched the expectations related to their territorial behavior and assemblage into packs. For lynx, the Beverton–Holt model with $\tau = 0$ also had the highest model weights, but differed from that of the other models to a lesser extent. Moreover, the differences between the contest and scramble competition scenarios were less clear when the other models were considered. This may be explained by the fact that the territorial behavior of lynx is not as extensive and competitive as it is for wolves.

Although individuals in neighboring territories tend to avoid each other, lynx males may share 30%–75% of their home ranges with other individuals (Schmidt et al., 1997), whereas wolf packs violently attack and pursue intruding conspecifics, and the overlapping of neighboring territories is rare (Mech, 1970).

The investigated population models pertain to somewhat extreme cases of individual spatial distribution (i.e., random or extremely clustered cases). The inclusion of a parameter that quantifies spatial clustering (e.g., Anazawa, 2009; Brännström & Sumpter, 2005) was deliberately avoided due to the general scope of this study and the focus on parameters associated with intrinsic growth rate and carrying capacity. However, the differences in individual aggregation are undoubtedly significant enough to require a quantitative scaling. Moreover, ideal scramble and ideal contest competition can be regarded as extreme cases in intraspecific competition. Anazawa (2009) has developed a general population model with a parameter β that quantifies deviation from the ideal contest competition scenario and ranges between zero and one (i.e., $\beta = 0$ for the ideal contest competition and $\beta = 1$ for the ideal scramble



CE – corrected estimate assuming no noise, OE – original estimate, SM – mean value in 5000 simulations

FIGURE 7 Effect of introduced noise in the data in 5000 simulations, multiplying original values by a log-normally distributed variable with $\mu = -\frac{1}{2}\sigma^2_{\text{noise}}$ and $\sigma^2 = \sigma^2_{\text{noise}}$ set to 0.1, on estimated model parameters describing wolf (top panels a–e) and lynx (bottom panels f–j) population dynamics: Intrinsic growth rate r_0 (panels a, f) and parameters \hat{a} (panels b, g) and \hat{b} (panels c, h) determining the projected carrying capacity $K_t = \exp(a + bt)$ as well as error variance $\hat{\sigma}_\varepsilon^2$ (panels d, i) and autocorrelation coefficient $\hat{\varphi}$ (panels e, j).

competition). A general population model with additional parameters may be worth exploring in further studies. This may be relevant when considering the various possibilities of social aggregation and territorial behavior since the lynx case in this study demonstrated less conformity with the ideal contest competition scenario.

A viable population is expected to grow at densities below the carrying capacity, which is frequently treated as a constant. This was an underlying assumption in previous investigations of the wolf and lynx populations in Latvia (Kawata, 2008) and of the wolf population in Lithuania (Balčiauskas & Kawata, 2009). The previous estimates of the carrying capacities for wolves and lynx in Latvia, which used the same dataset until the year 2005 but applied a quadratic population growth model, were 1066–1092 and 971–1188 individuals, respectively (Kawata, 2008). In this study, however, the projected carrying capacity or equilibrium density K_t was allowed to increase, as suggested by the increase in prey abundance observed locally (Ozoliņš et al., 2016) and regionally (Apollonio et al., 2010; Carpio et al., 2021). Prey biomass has been called the most important factor affecting wolf population dynamics (Fuller et al., 2003). For lynx, an increasing prey density would allow smaller home ranges (Herfindal et al., 2005). We assumed an exponential function according to the growth process and defined the carrying capacity as $K_t = \exp(a + bt)$. In the majority of

models, zero was beyond the 95% confidence limits of the parameter b , supporting the validity of the assumption regarding the increase in the carrying capacity (Figure 6c,f). Consequently, the estimates of intrinsic growth rate r_0 were higher than the estimates provided by Kawata (2008), which assumed a constant carrying capacity (1.354 vs. 0.962 for the wolf population and 0.711 vs. 0.399 for the lynx population).

Apart from the increasing trend, the population dynamics of both species also exhibited a fluctuating pattern (Figure 1a,c), which may have been caused by changes in the carrying capacity (e.g., fluctuations in prey availability) or stochastic factors. Moreover, in the overcompensatory models, oscillations between stable states and chaotic dynamics may occur with elevated growth rates (e.g., May, 1974, 1976). As this is not the case for contest competition, which limits the population density, the fluctuations in population density under the assumption of contest competition are expected according to changes in the limiting factors associated with the carrying capacity. Although a temporally increasing and oscillating carrying capacity may be introduced into the models by applying a periodical function and adding parameters that determine the period and range of the oscillations, we treated the fluctuations in population density as autocorrelated noise to avoid overparameterization of the models.

The model-averaged intrinsic growth rates \bar{r}_0 for the wolf and lynx population in Latvia were 1.354 and 0.711

(Table 4), respectively. These rates are associated with stable population dynamics and would correspond to the geometric growth rates (λ_0) of 3.87 and 2.04, respectively. The intrinsic growth rates of both species are expected to differ due to different fecundity. The mean litter sizes of gray wolves and Eurasian lynx in Europe vary from 4.4 to 7.7 (on average, 5.9, Jędrzejewska et al., 1996) and from 2.08 to 2.12 (Nilsen et al., 2012), respectively. In Latvia, prenatal fecundity for wolves and lynx during the last two decades has been 6.1 (Šuba et al., 2021) and 3.2 (Bagrađe et al., 2016), respectively. This matches well with the difference in growth rates observed between the two species. Assuming mean wolf and lynx litter sizes of 5.9 and 2.1, which may account for postnatal mortality, equal sex ratio, and the complete survival of the recruited individuals, the annual geometric growth rates of 3.87 and 2.04 could be achieved if 97.4% of all wolf females and 98.7% of all lynx females reproduced. This estimate is based on the assumption that the proportion of reproducing females in the population under the stated circumstances equals $2(\lambda_0 - 1)/y$, where y corresponds to the mean number of offspring per female (see Kelker, 1947). In this study, the mean observed annual growth rates \bar{r}_t were 0.577 for wolves and 0.225 for lynx. These rates correspond to geometric growth rates λ_t of 1.78 and 1.25, respectively. As reproductive output decreases due to density dependence, the litter size or the proportion of reproductive females may remain high to counterbalance additional mortality. During the last two decades, 63.1% and 87% of the wolf and lynx adult females culled in Latvia contained traces of reproduction (Bagrađe et al., 2016; Šuba et al., 2021). Such proportions were lower than expected in the absence of competition, but comparable to other areas with considerable hunting pressure (Frank & Woodroffe, 2001; Fuller et al., 2003; López-Bao et al., 2019; Mech et al., 2016).

Wolf and lynx individuals usually become mature later than their first or second year of life (Fuller et al., 2003; Nilsen et al., 2012). Therefore, the effect of delayed reproduction on the population growth rate has been considered in previous studies on wolf and lynx population dynamics by introducing a time lag operator τ (Balčiauskas & Kawata, 2009; Kawata, 2008). This approach estimates the growth rate at year t by considering only mature individuals, that is, all the individuals at year $t - \tau$ would have become mature by the year t and capable of producing offspring. In this study, we applied a time lag operator for the models where meaningful introduction of τ was possible (i.e., for all the models but the Skellam model). Unlike in previous research, the models with $\tau > 0$ had significantly lower model weights than the models with $\tau = 0$. Conversely, in previous studies, the quadratic model describing wolf dynamics was

the most consistent with the data in the case of $\tau = 3$ (Balčiauskas & Kawata, 2009; Kawata, 2008). As mentioned above, the previous studies also differed from the present one in that they assumed a constant carrying capacity. As different results may arise from different underlying assumptions, our findings do not dismiss the potential significance of delayed maturity in modeling wolf dynamics altogether. Rather they demonstrate that it had an insignificant impact on determining wolf population growth under the modeling circumstances applied here, which included an unstructured model, a carrying capacity with a temporal trend, and autocorrelated residuals.

As the abundance data used in this study likely included a considerable overestimation bias, we investigated whether such bias could have influenced the model performance. Assuming overestimation up to 42.9% and an unlikely underestimation down to -9.1% , the abundance estimates for both species were multiplied by a bias factor c , which varied between 0.7 and 1.1 (i.e., $c = 1$ assumed no bias, $c < 1$ assumed overestimation in the abundance data, and $c > 1$ assumed underestimation). We found that such bias affected not only the parameter values but also the model performance in terms of model weights. In both species, the greatest weight was observed for the Beverton–Holt model with $\tau = 0$. Changes in the bias factor did not significantly influence the weight of this model for wolves, but for lynx, the weight of the Beverton–Holt model increased as the assumed overestimation was increased. However, the weights of the other models displayed an inverse trend according to the changes in the bias factor. Therefore, the likely overestimation in the wolf and lynx abundance data indicated a greater correspondence with the Beverton–Holt model, and the model selection results were robust regardless of the existence of estimation bias.

The effect of unknown observation errors was investigated by examining 5000 simulated datasets, in which a log-normally distributed noise was added to the original data. This treatment had almost no effect on the average performance of the Beverton–Holt model with $\tau = 0$ for the wolf population as the mean value of the model weight was similar to the original value. For the lynx population, this was not the case as the mean value of the model weight in the simulations increased for the models of spatially random individual distribution and scramble competition. As the bias correction is the opposite of adding more noise, when a parameter value decreases with an added observation error, then the true value is on average larger than the original estimate (and vice versa). Therefore, when the model weights decreased with added noise, the contest competition models would be supported even more strongly than was observed.

This study examined the consistency of wolf and lynx population dynamics with the models based on scramble or contest competition. The differences found in model performance may be relevant when considering the application of models other than the most popular ones, such as the Ricker model, to study and predict changes in population dynamics in single- or multi-species frameworks. In our case, the contest competition models, such as the Beverton–Holt model, showed better fit. Hence, these models may be better suited for predicting carnivore population dynamics. The time series used in our study, which spanned more than six decades, contained no additional information on age structure or on the proportion of males and females within the studied populations. As more detailed demographic data become available, we believe that age- or stage-structured population models will be more appropriate for species like wolves and lynx. Matrix models are adaptable and can include density dependence (e.g., Miller et al., 2002), or multiple age or stage classes can be introduced into population models such as the Ricker model (Shelton et al., 2012). Whether and how such models reflect the intraspecific competition remains an open question for further studies.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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APPENDIX 1: EXPRESSION OF TWO-PARAMETER POPULATION MODELS IN TERMS OF INTRINSIC GROWTH RATE AND CARRYING CAPACITY

To estimate the carrying capacity and intrinsic growth rate of wolf and lynx populations by fitting the selected models to the data, the parameters α_i and β_i of the Ricker ($i = R$), Skellam ($i = S$), Hassell ($i = H$), and Beverton–Holt ($i = BH$) model equations (Table 1) were expressed in terms of carrying capacity and intrinsic growth rate. Intrinsic growth rate is the maximum population growth rate in the absence of competition. It can be formulated as a finite rate λ_0 or an instantaneous rate r_0 . For species such as the gray wolf and Eurasian lynx, which reproduce once per year during a breeding season, λ_0 may be preferred as it is analogous to the annual or geometric growth rate $\lambda_t = N_{t+1}/N_t$. The analytical expression of λ_0 in terms of the given model parameters was derived as:

$$\lambda_0 = \lim_{N_t \rightarrow 0} \frac{f(N_t | \alpha_i, \beta_i)}{N_t}. \quad (\text{A1})$$

Parameter K pertaining to carrying capacity was derived from the expected equilibrium density:

$$\left. \frac{f(N_t | \alpha_i, \beta_i)}{N_t} \right|_{N_t=K} = 1. \quad (\text{A2})$$

Solving parameters α_i and β_i for the Ricker, Hassell, and Beverton–Holt models according to Equations (A1) and (A2) provided $\alpha_R = \alpha_H = \alpha_{BH} = \lambda_0$ and $\beta_R = \ln(\lambda_0)/K$, $\beta_H = (\sqrt{\lambda_0} - 1)/K$, and $\beta_{BH} = (\lambda_0 - 1)/K$, respectively. For the Skellam model, Equation (A1) yielded:

$$\alpha_S = \frac{\lambda_0}{\beta_S}. \quad (\text{A3})$$

Combining Equations (A2) and (A3) and conducting algebraic rearrangements provided a nonlinear equation:

$$(\beta_S K - \lambda_0) e^{\beta_S K - \lambda_0} = -\frac{\lambda_0}{e^{\lambda_0}}. \quad (\text{A4})$$

The parameter β_S was found by applying Lambert's W function (also called the omega function or product logarithm) to Equation (A4):

$$\beta_S = \frac{\lambda_0 + W\left(-\frac{\lambda_0}{e^{\lambda_0}}\right)}{K}. \quad (\text{A5})$$

Rearranged equations of the applied population models in terms of λ_0 and K are given in Table A1. Certain calculations are facilitated by applying instantaneous growth rates. Ultimately, using $r_0 = \ln(\lambda_0)$ was found to be more convenient for our study.

TABLE A1 Expression of Ricker, Skellam, Hassell, and Beverton–Holt population models in terms of intrinsic geometric growth rate λ_0 and carrying capacity K .

Model	Expression $f(N_t \lambda_0, K)$
Ricker	$N_t \lambda_0^{1 - \frac{N_t}{K}}$
Skellam	$K \frac{1 - \exp\left(-\left[\lambda_0 + W\left(-\frac{\lambda_0}{e^{\lambda_0}}\right)\right] \frac{N_t}{K}\right)}{1 + \lambda_0^{-1} W\left(-\frac{\lambda_0}{e^{\lambda_0}}\right)}$
Hassell	$\frac{N_t \lambda_0}{(1 + [\sqrt{\lambda_0} - 1] \frac{N_t}{K})^2}$
Beverton–Holt	$\frac{N_t \lambda_0}{1 + (\lambda_0 - 1) \frac{N_t}{K}}$