

# Comparative population dynamics of large and small mammals in the Northern Hemisphere: deterministic and stochastic forces

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Deterministic feedbacks within populations interact with extrinsic, stochastic processes to generate complex patterns of animal abundance over time and space. Animals inherently differ in their responses to fluctuating environments due to differences in body sizes and life history traits. However, controversy remains about the relative importance of deterministic and stochastic forces in shaping population dynamics of large and small mammals. We hypothesized that effects of environmental stochasticity and density dependence are stronger in small mammal populations relative to their effects in large mammal populations and thus differentiate the patterns of population dynamics between them. We conducted an extensive, comparative analysis of population dynamics in large and small mammals to test our hypothesis, using seven population parameters to describe general dynamic patterns for 23 (14 species) time series of observations of abundance of large mammals and 38 (21 species) time series for small mammals. We used state-space models to estimate the strength of direct and delayed density dependence as well as the strength of environmental stochasticity. We further used phylogenetic comparative analysis to detect differences in population dynamic patterns and individual population parameters, respectively, between large and small mammals. General population dynamic patterns differed between large and small mammals. However, the strength of direct and delayed density dependence was comparable between large and small mammals. Moreover, the variances of population growth rates and environmental stochasticity were greater in small mammals than in large mammals. Therefore, differences in population response to stochastic forces and strength of environmental stochasticity are the primary factor that differentiates population dynamic patterns between large and small mammal species.

Understanding the forces that create variability in the abundance of organisms is a central, organizing goal of population ecology (Krebs 2003, Turchin 2003, Hastings 2010). Sources of population variability include deterministic and stochastic processes that interact to generate complex patterns of animal abundance over time and space (Turchin 2003, Coulson et al. 2004, Boyce et al. 2006, Melbourne and Hastings 2009). These patterns result in part from stochastic demographic responses to temporally varying environments (i.e. environmental stochasticity) and in part deterministic, direct and delayed feedbacks from population density to population growth rate (hereafter, direct and delayed density dependence) (Forchhammer et al. 1998, Ives et al. 2003, Lande et al. 2003, Coulson et al. 2004). Density dependence results from competitive interactions within a population (Forchhammer et al. 1998), whereas the causes of environmental stochasticity include extrinsic stochastic forces, such as climate, interspecific interactions, and anthropogenic disturbances (Ives et al. 2003, Coulson et al. 2004). Therefore, multivariate analysis of the deterministic

and stochastic forces together is needed to understand how the two forces shape the dynamics of animal populations.

Organisms differ inherently in their demographic responses to fluctuating environments owing to differences in life histories (Saether et al. 1996). Body size is a predictor of many of these life history traits (Read and Harvey 1989, Sibly and Brown 2007, Fagan et al. 2010), and as a result, it is reasonable to expect that large- and small-sized animals should exhibit fundamentally different responses to environmental variation (Caughley and Krebs 1983, Sinclair 1989, Krebs 2009). Small and large mammals differ by orders of magnitude in their body mass and, as a result, offer a particularly useful model system for examining how characteristics of species entrain population dynamics (Sinclair 2003, Sibly and Brown 2007, Fagan et al. 2010). Small mammals have greater intrinsic rates of population increase and shorter lifespan than do large mammals. As a result, small mammal populations have higher turnover rates and greater temporal variability relative to large mammal populations (Perrin 1989, Sinclair and Krebs 2002). On the other hand, large

mammals have physiological and behavioral traits that attenuate effects of environmental fluctuations in resources and it is believed that these traits should act to reduce temporal variance in population abundances (Lindstedt and Calder 1981, Erb et al. 2001). As a general rule, ungulates are capital breeders, fattening their body, storing energy in autumn for winter survival and reproduction, and producing one or a few offspring in a year (Gaillard et al. 2000, Erb et al. 2001). In contrast, most small mammals have little physiologically buffering capacity against environmental fluctuations as income breeders (Perrin 1989, Innes and Millar 1994). Therefore, small mammals are adapted to changing resource availability or environments, and their populations are predicted to have greater environmental stochasticity than those of large mammals.

Recent studies have shown that density dependence is common in large and small mammal populations (Erb et al. 2001, Lima et al. 2006, Bonenfant et al. 2009). With a high intrinsic rate of increase, small mammal populations can increase dramatically within a season or a year under favorable conditions. Rapid increases in abundances may deplete food or other resources, result in intraspecific competition for food and space, and immediately reduce survival and breeding efforts (Ostfeld et al. 1993). In the long run, density dependence may be manifested more frequently and more strongly in small mammals with more dramatic fluctuations of population sizes than in large mammals with relatively stable population dynamics. Therefore, it is plausible to hypothesize that the strength of direct and delayed density dependence is stronger in small mammals than in large mammals. Alternatively, observed predictable long-term trends may suggest strong direct density dependence, but weak delayed density dependence in large mammals.

Despite the intuitive appeal of these predictions, few empirical studies have investigated how differences in life history between large and small mammals create differences in their population trajectories. Erb et al. (2001) found that the abundance of large mammal populations tends to remain relatively stable, whereas small mammal populations are temporally variable; they ascribed these differences to direct and delayed density dependence. For example, stronger delayed density dependence may create greater population variation, and high intrinsic rate of increase and strong nonlinear density dependence may result in chaotic patterns in small mammal populations (Erb et al. 2001). However, these authors did not directly estimate the strength or variance of environmental stochasticity. It remains unknown how differences in environmental stochasticity shape the dynamic patterns of large and small mammal populations (Coulson et al. 2004, Boyce et al. 2006). Furthermore, the regulation of population dynamics is multifactorial. Little is known about the set of population parameters (i.e. population growth rates, density dependence, and (or) environmental stochasticity) that differentiate population dynamic patterns between large and small mammals.

Resolving these questions requires an extensive, comparative analysis of population dynamics in large and small mammals. We compared a suite of seven population parameters to identify fundamental differences in trajectories of large and small mammal populations and related these differences to life history characteristics. Our objectives were to: 1) test

the hypothesis that the effects of environmental stochasticity and density dependence are stronger in small mammal populations relative to their effects in large mammal populations and thus differentiate the patterns of population dynamics between them; and 2) test the hypothesis that direct density dependence stabilizes mammal population dynamics (i.e. an inverse relationship between the strengths of environmental stochasticity and direct density dependence), whereas delayed density dependence destabilizes mammal population dynamics. We used state-space time series models to separate measurement error from process error or environmental stochasticity. In addition, we used phylogenetic comparative analysis to account for phylogenetic interdependence or inertia when comparing population parameters between large and small mammals. Therefore, our study provided general insight into the role of life history characteristics (predicted by body sizes) in shaping dynamics of large and small mammal populations.

## Methods

### Population time series

We re-analyzed a total of 61 time series of annual population counts or indices for 14 species of large mammals and 21 species of small mammals, including 23 large herbivore populations and 38 small mammal populations. Large herbivores included alpine ibex *Capra ibex*, bighorn sheep *Ovis canadensis*, bison *Bison bison*, elk *Cervus elaphus*, caribou *Rangifer tarandus*, fallow deer *Dama dama*, moose *Alces alces*, mule deer *Odocoileus hemionus*, muskox *Ovibos moschatus*, red deer *Cervus elaphus*, reindeer *Rangifer tarandus*, roe deer *Capreolus capreolus*, sika deer *Cervus nippon*, and Soay sheep *Ovis aries*. The 23 large herbivore population time series were animal counts on foot or from air (Wang et al. 2009a). We used small mammal population time series that were collected from live-trapping or kill-trapping studies. Locations, study periods, trapping and estimation methods, and references or sources of small mammal data are listed in Supplementary material Appendix 1, Table A1. The 61 time series used in our analyses were made available for this study through previous collaboration. We did not choose a specific set of species, populations, and study locations from a larger pool of data sets for our analyses. Inclusion of more time series would improve the generality of our conclusions.

### Statistical analysis

We fit the Gompertz population model (Gompertz 1825) to each population time series to estimate the parameters measuring the strengths of direct density dependence, delayed density dependence, and environmental stochasticity. Forchhammer et al. (1998) found that the Gompertz model tended to outperform the Ricker model for the population time series of red deer in Norway. Three models derived from the global model  $\ln(N_t) = a + (1 + b) \ln(N_{t-1}) + c \ln(N_{t-2})$  were fit to each time series of annual log-transformed population abundances, where  $a$  is the intercept,  $1 + b$  measures the strength of direct density dependence, and  $c$  measures

the strength of delayed density dependence (Royama 1992). When  $b$  is negative (or  $[1 + b]$  is  $<1$ ), increases in the magnitude of  $b$  (or decreases in  $[1 + b]$ ) indicate increasingly strong, direct, negative effects of population densities on per capita population growth rates. Likewise, if  $c < 0$ , increases in the magnitude of  $c$  suggest increasingly strong, delayed, negative effects of population densities on per capita population growth rates. The three models were: a) the exponential growth model ( $b = 0, c = 0$ ); b) the order 1 autoregressive (AR) model ( $c = 0$ ); and c) the global model, i.e. AR (2) model. Model selection was done using corrected Akaike information criterion ( $AIC_c$ ), and model uncertainty was measured with the Akaike weight (Burnham and Anderson 2002).

Estimates of animal abundance have inherent measurement errors that may bias estimates of the strength of density dependence (Stenseth et al. 2003). To account for measurement errors, we used the classic Kalman filter (KF; Kalman 1960), a state-space model, to analyze time series of annual population abundance ( $N_t$ ). In state-space models, a true state variable or true abundance  $X_t$  is unobservable; however, the observation  $Y_t (= \ln N_t)$  of apparent population size is the true size ( $X_t$ ) plus a random measurement error ( $u_t$ ), i.e.  $Y_t = X_t + u_t$ . Therefore, the structural form of the AR(2) Gompertz model (Royama 1992) is given by:

$$X_t = a + (1 + b)X_{t-1} + cX_{t-2} + e_t \quad (1)$$

$$Y_t = X_t + u_t \quad (2)$$

Error terms  $e_t$  and  $u_t$  are assumed to be normal and conditionally independent of each other and independent over time, i.e.  $e_t \sim N(0, \sigma_e^2)$ ,  $u_t \sim N(0, \sigma_u^2)$ ,  $\text{Corr}(e_t, u_t) = 0$ . Equations (1) and (2) were cast into the KF (Wang et al. 2006). The variance  $\sigma_e^2$  represents the effects of environmental stochasticity. However, we noted that animal counts may be a biased index of population sizes or abundances. For example, counts of alpine ibex in Belledune, France underestimated ibex population sizes, particularly at large population sizes (Gaillard et al. 2003). The estimation bias of population sizes may result in the bias in estimation of population parameters. State-space models do not correct for potential estimation bias of population parameters from the biased estimates or indices of population sizes.

Model parameters  $a, b, c, \sigma_u^2$  and  $\sigma_e^2$  were estimated using maximum likelihood methods. We maximized the complete data log-likelihood function yielded by the KF (Shumway and Stoffer 2000) using the expectation-maximization (EM) algorithm (Dempster et al. 1977). The maximized likelihood was used to compute  $AIC_c$  and Akaike weights (Burnham and Anderson 2002). Akaike weights were used to compute model-averaged estimates of parameters  $b, c$  and  $\sigma_e^2$  to account for model selection uncertainty. For example, the model-averaged estimate ( $\bar{b}$ ) of the parameter  $b$  was computed as the weighted average of maximum likelihood estimates ( $\hat{b}_r$ ) from the three candidate models (i.e. the exponential, AR(1), and AR(2) models):

$$\bar{b} = \sum_{r=1}^3 w_r \hat{b}_r$$

where  $w_r$  is the Akaike weight for model  $r$ . We also calculated relative importance indices of direct density dependence and delayed density dependence by summing the Akaike weights over all models that include direct density dependence and delayed density dependence terms, respectively.

We assumed lognormal distributions for population time series data (Halley and Inchausti 2002). We applied natural logarithm-transformations on all population time series to normalize the data. We checked the model assumptions on model errors following Harvey (1989: 259). Inspection of the sample autocorrelation function (ACF) plot indicated that the residuals were not serially correlated. Quantile-quantile (Q-Q) plots were consistent with the assumption of normally distributed residuals (Sokal and Rohlf 1995).

We estimated seven population parameters plus latitude of population habitats to characterize dynamics of large and small mammal populations (Table 1 for the definitions of the seven parameters). We determined the patterns of population dynamics using the location of the parameters  $1 + b$  and  $c$  in the parameter space/plane of the AR(2) model (Fig. 1; Royama 1992). A location of the parameter pair  $(1 + b, c)$  in region I indicates that a population increases or decreases to a stable trajectory. If the parameter pair is located in the region II, a population has a two-year cycle. A location in the region III or IV below the parabolic curve ( $b^2 + 4c = 0$ ) inside the triangle (defined by the lines  $1 + b - c = 0$ ,  $1 - b - c = 0$ , and  $1 + c = 0$ ) is statistical evidence supporting multi-annual cyclic fluctuations of a population conforming to the AR(2) model (Fig. 1; Royama 1992, Stenseth 1999).

We used phylogenetic comparative analysis to detect differences in the pattern of population dynamics between large and small mammals, accounting for potential phylogenetic dependence in the estimates of a population parameters among the 35 mammal species (Freckleton et al. 2002, Freckleton 2009). We first obtained the sequences of the cytochrome (cyt)  $b$  gene from GenBank ([www.ncbi.nlm.nih.gov/nuccore](http://www.ncbi.nlm.nih.gov/nuccore)) to reconstruct the phylogenetic tree of the 35 mammal species (Supplementary material Appendix 2 for the methods and results of the phylogeny reconstruction). Then we used phylogenetic multivariate analysis of variance (MANOVA) to test for differences in general population dynamic patterns depicted by the seven population parameters (Freckleton 2009, Harmon et al. 2009). If the null hypothesis was rejected in phylogenetic MANOVA, we applied phylogenetic generalized estimating equations (GEE) to detect differences in individual population parameters between large and small mammals (Paradis and Claude 2002). Phylogenetic GEE are a general extension of phylogenetic generalized least square (PLGS) models, with a fixed correlation matrix derived from a known phylogenetic tree to account for phylogenetic dependence (Paradis and Claude 2002). Phylogenetic MANOVA uses randomization procedures to simulate a large number of data sets ( $n = 2000$  in our study) of compared characters on a phylogenetic tree under the Brownian motion model for the evolution of compared characters and then applies classical MANOVA to each set of simulated data to construct an empirical null distribution of Wilks' test static for testing the null hypothesis (Garland et al. 1993, Harmon et al. 2009). However, phylogenetic GEE do not assume a specific model for the evolution of

Table 1. Definitions of the parameters used to characterize the patterns of mammal population dynamics.

Name of parameter	Symbol	Definition
Coefficient $b$	$b$	the coefficient of the term $X_{t-1}$ in the Gompertz model
Coefficient $c$	$c$	the coefficient of the term $X_{t-2}$ in the Gompertz model
Latitude	lat	latitude of habitat
Population growth rate	pgr	the difference of log population sizes between years $t$ and $t-1$ , i.e. $X_t - X_{t-1}$
Relative importance of density dependence	DD	the variable importance of density dependence, calculated as the sum of Akaike weights over all models that have density dependence terms
Relative importance of delayed density dependence	IDD	the variable importance of delayed density dependence, calculated as the sum of Akaike weights over all models that have delayed density dependence terms
Variance of population growth rate	var1	the sample variance of population growth rates over the study period
Variance of environmental stochasticity	var2	the variance of process error that represents all unspecified stochastic variation in the Gompertz population model

compared characters (Paradis and Claude 2002). We used the mean of the population-specific estimates of a population parameter for a mammal species in our phylogenetic comparative analyses if the species had several population time series, as we did not have the cyt  $b$  sequence for each of those populations.

We also conducted principal component analysis (PCA) to illustrate differences in general patterns of population dynamics between large and small mammals. Principal component analysis is a dimension-reducing technique, using a set of principal components fewer than the original vari-

ables to model variability in original multivariate data and to illustrate any grouping of the original data in a reduced dimensional space (e.g. 2–3 principal components). Principal components are linear combinations of original variables and are perpendicular to one another (orthogonal). We tested the multivariate-normality assumption for our multivariate data used in the PCA using chi square probability plots described by Everitt (2004). The chi square plot of our data was approximately linear, suggesting the normality of our data.

We also investigated relationships between log-transformed variance of environmental stochasticity and coefficients  $1 + b$  and  $c$  using phylogenetic GEE. We used the quasi likelihood information criterion (QIC), an equivalent of AIC, to select the best approximating GEE (Pan 2001). The best model has the lowest QIC value among a set of four candidate models: 1) M1 with intercept only, i.e. the null model; 2) M2 with intercept and direct density dependent term ( $1 + b$ ); 3) M3 with intercept and delayed density dependent term ( $c$ ); and 4) M4 with intercept, direct density dependent term ( $1 + b$ ), and delayed density dependent term ( $c$ ). We carried out phylogenetic MANOVA and GEE using the R package GEIGER (Harmon et al. 2009) and APE (Paradis et al. 2004), respectively, in the R ver. 2.13.0 (R Development Core Team).

## Results

Population-specific estimates of the strength of direct and delayed density dependence and the variances of environmental stochasticity and population growth rates tended to be greater in small mammals than in large mammals (Fig. 2). Values of coefficient  $c$  for delayed density dependence ranged from  $-0.06$  to  $0.38$  in large mammal populations, but from  $-0.86$  to  $0.63$  in small mammal populations. All 23 large mammal populations were located in the region I of the Royama parameter plane (Fig. 3a), indicating a steady increase or decrease in population abundance, whereas small mammal populations were distributed in all four regions (Fig. 3b).

Phylogenetic MANOVA showed that general patterns of population dynamics, which were described by the seven population parameters, differed between large and small mammals (Wilks  $\lambda = 0.37$ ,  $p = 0.0005$ ). However, only two population parameters differed between large and small mammals in the univariate tests for individual parameters. The variances of population growth rate and environmental stochasticity were greater in small mammals than in large mammals (variance of population growth rate:  $p = 0.0$ ,  $DF = 18.5$ ; and variance of environmental stochasticity:  $p = 0.03$ ,  $DF = 18.5$ ). Average population growth rates and the strength of direct and delayed density dependence did not differ between small and large mammals (population growth rates:  $p = 0.96$ ,  $DF = 18.5$ ; direct density dependence:  $p = 0.19$ ,  $DF = 18.5$ ; and delayed density dependence:  $p = 0.54$ ,  $DF = 18.5$ ). Additionally, the first two principal components explained 54% the total variability. Although large and small mammal populations were not tightly clustered in the biplot of first two principal components (Fig. 4), the two groups were somewhat separated along the direction of the variances of population growth

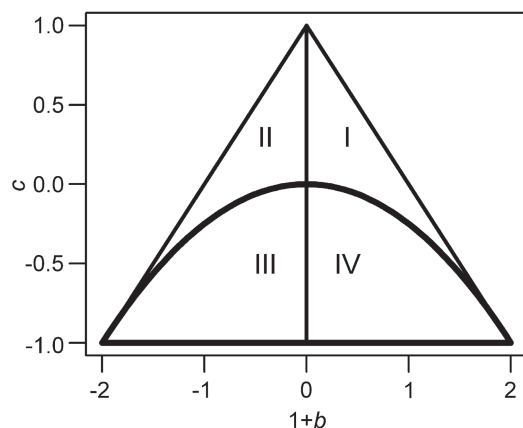


Figure 1. The Royama parameter plane of the order-2 autoregressive population models. The ordinate is the value of coefficient  $1 + b$  measuring the strength of direct density dependence. The abscissa is the value of coefficient  $c$  measuring the strength of delayed dependent dependence.



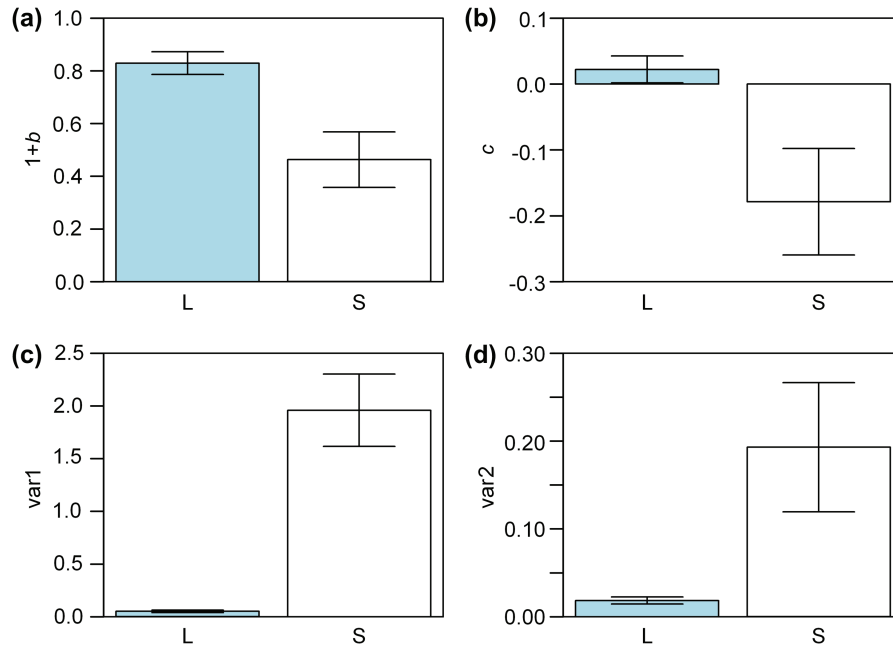


Figure 2. Comparisons of strength of density dependence and delayed density dependence and variances of environmental stochasticity and population growth rates between large and small mammals. The symbols  $1 + b$ ,  $c$ ,  $\text{var1}$ , and  $\text{var2}$  represent the coefficient of direct density dependence, the coefficient of delayed density dependence, the variance of population growth rate, and the variance of environmental stochasticity, respectively.

rate and environmental stochasticity, as indicated by the arrows for the variance of population growth rate ( $\text{var1}$ ) and the variance of environmental stochasticity ( $\text{var2}$ ) in Fig. 4.

The QIC values of models M1, M2, M3, and M4 (see the method section for the GEE model notation) were 125.3, 93.5, 117.2, and 93, respectively. Among the four candidate models, the models with intercept and direct density dependence (M2) and with intercept, direct density dependence, and delayed density dependence (M4) received more support from data, with QIC weights being 0.437 and 0.562, respectively. The two competing were of the forms: M2:  $\text{lvar2} = -1.44 - 2.36(1 + b)$  and M4:  $\text{lvar2} = -1.69 - 2.09(1 + b) - 1.01c$  respectively. Symbol  $\text{lvar2}$  was the log-transformed variance of environmental

stochasticity. The standard errors of regression coefficients were 0.56 (for  $1 + b$ ) in M2 and 0.61 (for  $1 + b$ ) and 0.89 (for  $c$ ) in M4, respectively. Thus, our results of model selection showed substantial support for the inverse relationships between the values of  $\text{lvar2}$  and  $c$  and between the values of  $\text{lvar2}$  and  $(1 + b)$ .

## Discussion

The results we offer here add to a growing body of work that seeks to understand how population dynamics are shaped by internal feedbacks from population density to population growth rate and by external forcing from stochastic influences,

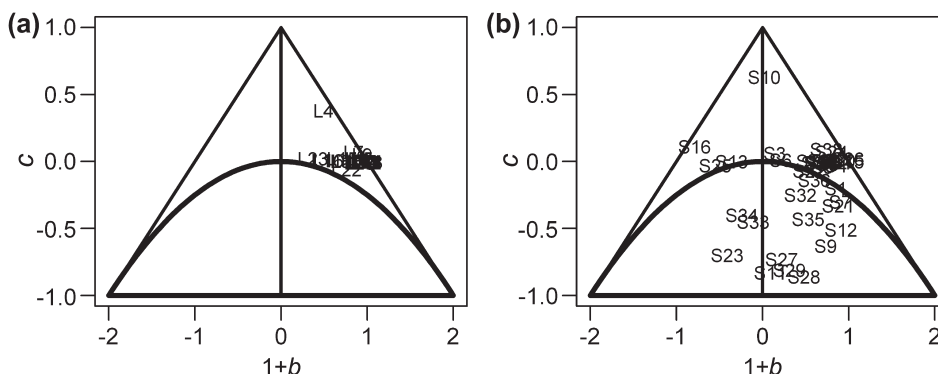


Figure 3. The parameter plane of the second order autoregressive Gompertz models of (a) 23 large mammal populations and (b) 38 small mammal populations. Symbols L1–L23 and S1–S38 represent coefficient pairs  $(1 + b, c)$  in the parameter space for 23 large mammal and 38 small mammals populations, respectively; symbol  $1 + b$  is the coefficient of direct density dependence; and letter  $c$  is the coefficient of delayed density dependence. Populations below the parabola and in the range from 0 to 1 on the horizontal axis  $1 + b$  have multi-annual cycles.



primary factor that differentiates the patterns of population dynamics between large and small mammals, while variation in the strength of density dependence alone fails to explain these differences in population dynamics. Strengths of direct and delayed density dependence are positively related to the strength of environmental stochasticity of mammal populations.

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Supplementary material (Appendix E7156 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1–2.