

A Perfect Storm: The Combined Effects on Population Fluctuations of Autocorrelated Environmental Noise, Age Structure, and Density Dependence

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ABSTRACT: While it is widely appreciated that climate can affect the population dynamics of various species, a mechanistic understanding of how climate interacts with life-history traits to influence population fluctuations requires development. Here we build a general density-dependent age-structured model that accounts for differential responses in life-history traits to increasing population density. We show that as the temporal frequency of favorable environmental conditions increases, population fluctuations also increase provided that unfavorable environmental conditions still occur. As good years accumulate and the number of individuals in a population increases, successive life-history traits become vulnerable to density dependence once a return to unfavorable conditions prevails. The stronger this ratcheting of density dependence in life-history traits by autocorrelated climatic conditions, the larger the population fluctuations become. Highly fecund species, and those in which density dependence occurs in juvenile and adult vital rates at similar densities, are most sensitive to increases in the frequency of favorable conditions. Understanding the influence of global warming on temporal correlation in regional environmental conditions will be important in identifying those species liable to exhibit increased population fluctuations that could lead to their extinction.

Environmental stochasticity has long been recognized by ecologists as an important modulator of population dynamics (Andrewartha and Birch 1954). Developing a mechanistic understanding of how variation and correlation in the environment influence population fluctuations, however, has only recently gained momentum among demographers as human modification of natural ecosystems results in an increasingly variable world (Boyce et al. 2006). As such, current work has been devoted to understanding the interaction between environmental autocorrelation and density dependence in nonstructured population models (Halley 1996; Ripa and Lundberg 1996, 2000; Morales 1999; Heino et al. 2000; Lundberg et al. 2000; Inchausti and Halley 2003), between environmental autocorrelation and age- or size-dependent vital rates in density-independent models (Tuljapurkar and Haridas 2006), and between density dependence and vital rates in stochastic environments (Grant 1997; Grant and Benton 2000). Many economically and ecologically important species, such as predatory fish and large mammals, however, are influenced by all three factors (i.e., environmental autocorrelation, density dependence, and structured vital rates) simultaneously. In order to better understand the influence of climatic variability on these species, therefore, we investigate how interactions among all three factors affect population dynamics.

Identifying the drivers of animal population fluctuations is crucial for a number of reasons. Extinction due to Allee effects, inbreeding, disease, demographic stochasticity, and catastrophes are each more likely to occur in smaller rather than larger populations. Thus, the higher the frequency and/or the larger the amplitude of fluctuations, the more likely a population will go through a low point and become extinct. Furthermore, effective population size is reduced each time a population goes through a bottleneck, lowering genetic diversity and possibly reducing the evolutionary

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potential for that species. From a community perspective, highly variable resources may attract different consumers than relatively stable ones (Wilmers et al. 2003), resulting in differences in food-web composition and structure (Ostfeld and Keesing 2000).

Nearly 30 years ago, Eberhardt (Eberhardt 1977) proposed that vital rates of different stages of long-lived vertebrates change in a sequence as population density increases. Juvenile survival declines first, followed by an increase in age at first reproduction, fecundity of adult females, and lastly, survival of adults. While Eberhardt's original hypothesis was formulated for marine mammals, it has been primarily tested in ungulates, where studies generally confirm this sequence (Gaillard et al. 1998), with some exceptions for South African ungulates (Owen-Smith and Mason 2005). This sequence is most likely due to differential responses in age-class specific vital rates to diminishing food resources (Coulson et al. 2004). Therefore, in variable environments, this progression of vital rate decline may differ substantially from year to year depending on interactions between density and environmental correlation. Good conditions generally allow a population to increase, perhaps affected by only mild density dependence in juvenile survival. A sequence of favorable years allows the population to expand until unfavorable conditions potentially lead to density dependence in one or more vital rates, causing a population decline. The magnitude and frequency of population fluctuations, therefore, may critically depend on how many favorable years occur before an unfavorable one.

Research using nonstructured population models has shown that positive environmental autocorrelation tends to increase or decrease the magnitude of population fluctuations depending on whether density dependence is under or over compensatory (Ripa and Heino 1999). Empirical analysis of 554 populations of 123 species has also shown that the larger the temporal correlation in environmental variation, the greater the population variation and the shorter the time to extinction (Inchausti and Halley 2003). However, this can critically depend on the magnitude of the variance in environmental noise and on the degree of overcompensating density dependence (Schwager et al. 2006). To our knowledge, however, the effects of environmental autocorrelation on density-dependent structured models have not been investigated.

Many environmental drivers of animal population dynamics are now changing due to anthropogenic effects. From mesoscale (2–2,000 km) changes in temperature and precipitation to disturbances such as hurricanes (Emanuel 2005; Katz et al. 2005), general circulation models (GCMs) predict both increased and decreased climatic variability over much of the earth (Easterling et al. 2000; Houghton et al. 2001). Increases in climatic variability in positively

autocorrelated environments may result in longer-lasting sequences of favorable or unfavorable conditions for individual species as climatic conditions spend more time in the extremes of their distributions rather than simple increases in maximum and/or decreases in minimum favorability (Houghton et al. 2001). Developing a mechanistic understanding of how populations respond to autocorrelation in environmental conditions, therefore, will be important to predicting and mitigating the influence of global climate change on animal populations. Our search for mechanism, therefore, led us to formalize Eberhardt's well-supported hypothesis into a mathematical model to test the effects of environmental autocorrelation on the propensity of age-structured populations to fluctuate.

Methods

We model the dynamics of an age-structured population using a modified Leslie matrix (Leslie 1945) with a yearly time step and density dependence in the transition probabilities. The population is represented by an age class vector $\mathbf{x} = (x_1, \dots, x_n)$, where the elements x_i are the number of individuals in each age class i and x_n is the number of individuals who are n years old or older. The population in year $t + 1$ is given by

$$\mathbf{x}(t + 1) = \mathbf{A}(t)\mathbf{x}(t), \quad (1)$$

where \mathbf{A} is a transition matrix of fecundities f and survival probabilities p of the form

$$\mathbf{A}(t) = \begin{bmatrix} 0 & p_2(t)f_2(t) & \cdot & \cdot & p_n(t)f_n(t) \\ p_1(t) & 0 & & & \\ & \cdot & \cdot & & \\ & & \cdot & 0 & \\ & & & p_{n-1}(t) & p_n(t) \end{bmatrix}. \quad (2)$$

We employ the commonly used Maynard Smith-Slatkin (Maynard Smith and Slatkin 1973) form of density dependence for our vital rates, modified to include resources (Wilmers and Getz 2004). This function is highly flexible, allowing for a wide variety of density-dependent curve shapes (Getz 1996), and it has been shown to yield a good fit to empirical data (Bellows 1981). In addition, we include a cohort effect in the model because cohort effects have been shown to be prevalent in many age-structured populations (Rose et al. 1998) and because they often impact population fluctuations (Lindström and Kokko 2002). Following Lindström and Kokko (2002), we define a cohort effect as any influence on the subsequent survival or reproduction of individuals based on the environmental conditions during their birth year.

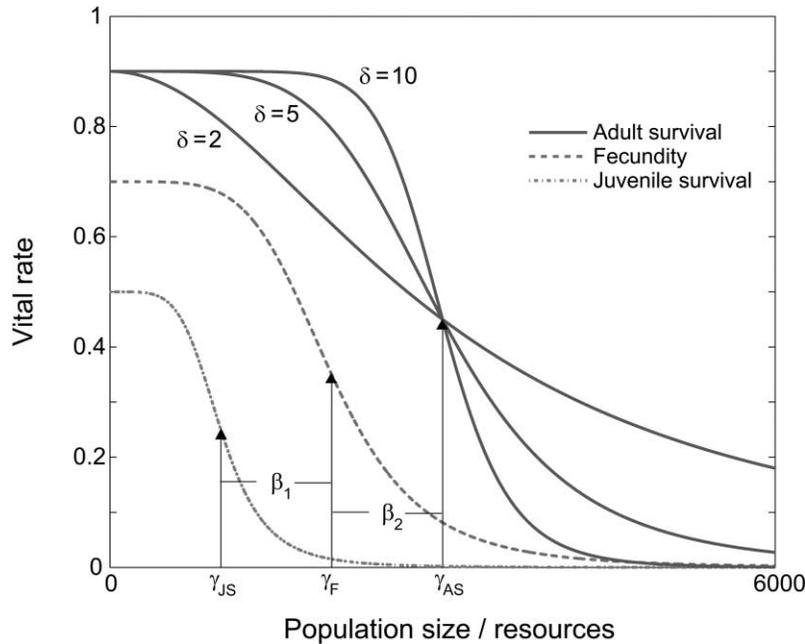


Figure 1: Effects of increased population density on vital rates reflecting Eberhardt’s (1977, 2002) hypothesis. As the ratio of population size to resources grows, juvenile survival declines first, followed by fecundity and finally by adult survival. The shape parameter δ determines the speed with which density dependence occurs as population increases, as illustrated here for adult survival. γ is the half-saturation constant for juvenile survival (JS), fecundity (F), and adult survival (AS). β_1 and β_2 are the differences in γ_{JS} and γ_F and γ_F and γ_{AS} , respectively. A color version of this figure is available in the online edition of the *American Naturalist*.

We define R as the resource pool, γ as the half-saturation parameter that sets the resource-weighted total density at the point at which maximum survival or fecundity is reduced by half, σ as the shape parameter that determines the onset of density dependence (Getz 1996), and b as the maximum fecundity or survival probability. The functional form g for the survival probability ($p_i = g_{i,1}$) or fecundity ($f_i = g_{i,2}$) of age class i is given by

$$g_{i,j}(t) = \frac{b_{i,j}(t)\gamma_{i,j}^{\delta_{i,j}}}{\gamma_{i,j}^{\delta_{i,j}} + \left[\frac{\sum_{k=1}^n x_k(t)}{R(l,t)} \right]^{\delta_{i,j}}}, \quad (3)$$

where l and t are the birth year of a cohort and current year respectively. Note that the combined density of all age classes affects the vital rates of each age class. The total effect of resources in a cohort’s birth year and the current year on survival is given by

$$R(l,t) = \alpha \times r(l) + (1 - \alpha) \times r(t) \text{ for } 0 \leq \alpha \leq 1, \quad (4)$$

where $r(m)$ is the quality of resources in year m (see Lindström and Kokko 2002). When $\alpha = 1$, a cohort’s sensitivity to current density is determined solely by conditions

it experienced in its birth year, and when $\alpha = 0$, sensitivity to current density is determined exclusively by current environmental conditions. The juvenile and adult age classes are given by $i = 1$ and $i > 1$, respectively. Parameters in equations for juvenile survival (JS), adult survival (AS), and fecundity (F) are subsequently indexed by these abbreviations. For the simulations considered here, all adult age classes share the same parameter values (e.g., δ_{AS} refers to the survival probability shape parameter for all adults).

Eberhardt’s hypothesis is incorporated into the model by constraining the half-saturation parameters such that $\gamma_{JS} < \gamma_F < \gamma_{AS}$. This ensures that density dependence in juvenile survival sets in before density dependence in fecundity, and in turn, adult survival, for most parameter combinations and densities (fig. 1). We also define parameters β_1 and β_2 , which are simply the difference between half saturation in adult fecundity and juvenile survivorship and between adult survivorship and fecundity, respectively (fig. 1). For simplicity, we only present results for $n = 2$ (i.e., for only two age classes: juveniles and adults), although the results are qualitatively similar for $n > 2$, and we do not include changes in age at first reproduction, which was part of Eberhardt’s original hypothesis. In addition, while many long-lived species are also structured

according to sex as well as to age, our primary purpose here is to understand how environmental variability interacts with age structure. As such, we leave exploration of sex structure to future research.

Simulations and Sensitivity Analysis

Many of the dominant atmospheric teleconnection patterns, such as the North Atlantic Oscillation (NAO) and the Pacific-North American and west Pacific teleconnections, have been shown to behave like first-order Markov processes (Feldstein 2000). In order to explore the relationship between environmental autocorrelation and population dynamics, therefore, we simulate climate using a simple Markov chain model, which allows us to explore different levels of environmental autocorrelation. We assume that each year is either unfavorable ($r = 1$) or favorable ($r = 4$) for population growth. The probability of having a good year (g) or a bad year (b) is represented by the transition matrix

$$\mathbf{P} = \begin{bmatrix} P_{gg} & P_{gb} \\ P_{bg} & P_{bb} \end{bmatrix}, \quad (5)$$

where P_{ij} is the probability that if a given year is of type j , it will be followed by a year of type i . Note that each column of the Markov matrix sums to 1; therefore, $P_{bg} = 1 - P_{gg}$ and $P_{bb} = 1 - P_{gb}$.

We first perform a sensitivity analysis (details explained in the appendix) to explore the structure and response of the model to changes in parameter values under environmental conditions that are either generally favorable or unfavorable. We then explore the dynamics of the model to changes in key parameters identified by the sensitivity analysis under differing levels of environmental autocorrelation.

Results and Discussion

Our sensitivity analysis revealed that in general, population fluctuations and mean population size were most sensitive to changes in the cohort effect α , changes in the difference between half saturation in juvenile survival and fecundity β_1 , and differences between fecundity and adult survival β_2 (table A1). A few key differences emerged in sensitivities when the environment was on average unfavorable versus favorable to population growth. When a low frequency of favorable years prevailed, the population fluctuated very little. This resulted in a statistically significant but small influence of α , δ_{js} , and β_1 on the coefficient of variation (CV) of the overall time series. A measure of year-to-year fluctuations, ϕ (eq. [A1]), under these conditions was

mainly influenced by changes in β_1 because poor environmental conditions never allowed the population to grow to the point where β_2 became influential. Cohort effects were also negligible. When a high frequency of favorable years prevailed, however, population fluctuations became influenced by β_1 , β_2 , and the cohort effect α .

When the environment is dominated by a low frequency of favorable years, strong density dependence in juvenile survival each time there is a bad year prevents the population from recruiting enough new individuals to grow. Since there is little population growth, densities are never high enough for the population to experience strong density dependence in adult vital rates. This results in dynamics characterized by small fluctuations at low population size (fig. 2a). When an intermediate frequency of favorable conditions exists, strings of a few good years in a row are experienced, releasing the population from density dependence and allowing it to grow to higher densities. When a bad year strikes, density dependence is felt strongly in juvenile survival and fecundity, causing the population to decline (fig. 2b). When a high frequency of favorable conditions is the norm, strings of many good years in a row are experienced, causing the population to grow until it begins to level off due to density dependence in juvenile survival and fecundity. When a bad year strikes, strong density dependence is experienced in all three vital rates, resulting in a dramatic crash in the population (fig. 2c). Populations that experience large crashes in bad years after a succession of good years decline to lower densities and take longer to recover than populations experiencing crashes after a succession of fewer good years (e.g., cf. fig. 2b, 2c). The decline to lower densities is due to the larger magnitude in density dependence in adult survivorship between the two scenarios. This also reduces the number of reproductive adults in the population, thus delaying time to recovery.

The influence of autocorrelation in environmental conditions is revealed in figure 3. When conditions are positively correlated from year to year, conditions in the current year are more likely to resemble conditions in the previous year. This leads to an increased likelihood of successive years of favorable or unfavorable conditions resulting in large population fluctuations (fig. 3a, 3b) such as those experienced in the intermediate and high frequency of good-year scenarios (fig. 2b, 2c). When conditions are negatively correlated, however, conditions in the current year are more likely to be different than the previous year, preventing the population from ever building up and leading to low-amplitude dynamics (fig. 3c, 3d) such as those experienced under the low frequency of good-year conditions (fig. 2a). While the mechanism leading to large population fluctuations is a succession of good years followed by bad, this pattern is

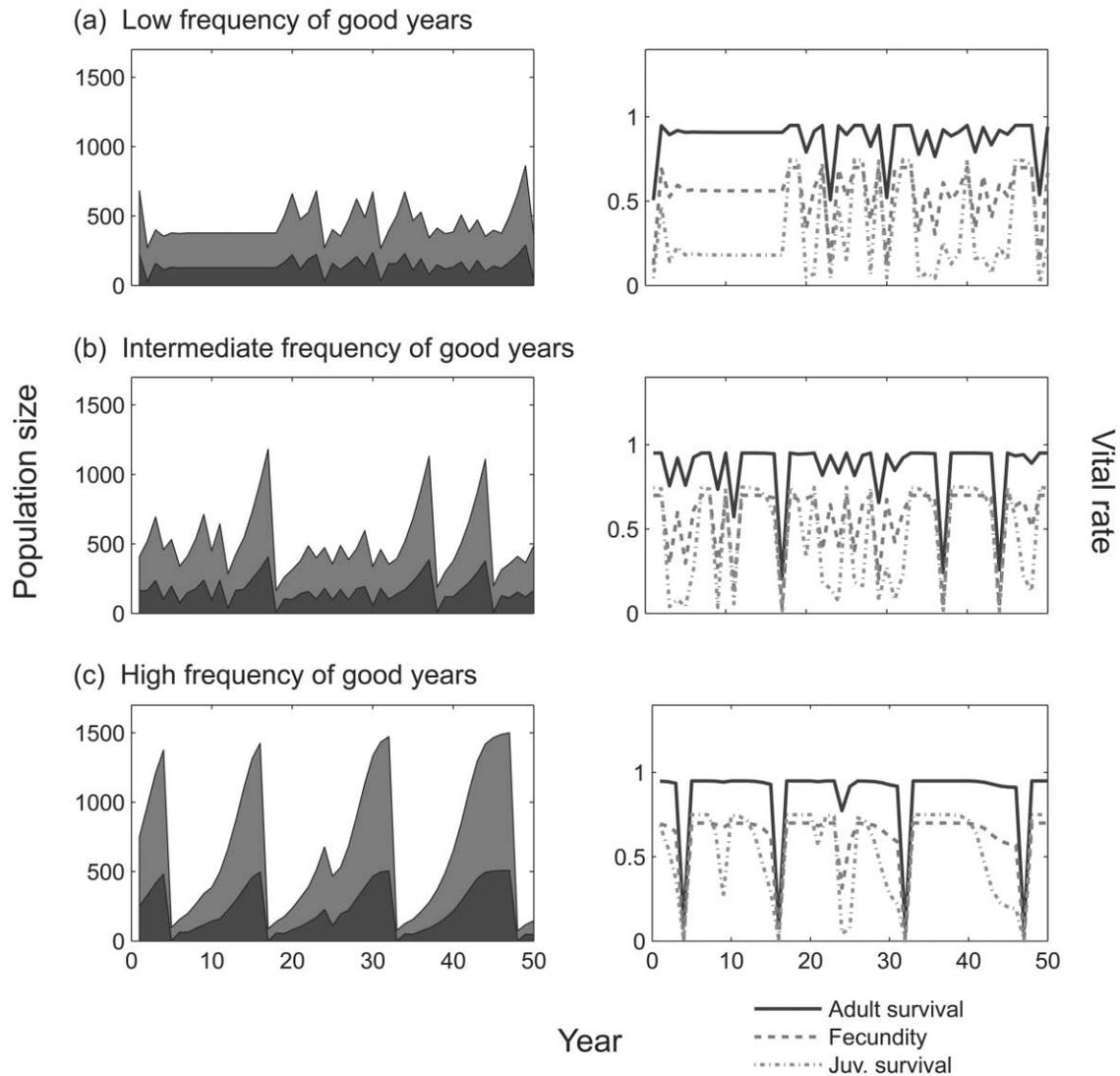


Figure 2: Changing the relative frequency of favorable versus unfavorable environmental conditions influences the magnitude of population fluctuations. The left panels display total population size broken down into adult (*above*) and juvenile (*below*) components, while the right panels display vital rates for each year. Yearly environmental conditions were generated from a Markov matrix (see “Methods”) using the following parameter values: *a*, $P_{gg} = 0.2$, $P_{gb} = 0.2$; *b*, $P_{gg} = 0.5$, $P_{gb} = 0.5$; *c*, $P_{gg} = 0.8$, $P_{gb} = 0.8$. Model parameters for this figure and all subsequent figures were as follows unless otherwise indicated: $\delta_{js} = \delta_i = \delta_{AS} = 5$, $\gamma_{js} = 300$, $\alpha = 0.1$, $\beta_1 = \beta_2 = 200$, $b_1 = 0.75$, $b_2 = 0.95$, $c_1 = 0$, and $c_2 = 0.7$. A color version of this figure is available in the online edition of the *American Naturalist*.

more likely to manifest in positively rather than negatively correlated environments.

Highly fecund species are more likely to exhibit pronounced population fluctuations than less fecund species given equivalent temporal correlation in environmental conditions. Varying the height of the asymptote of the fecundity curve in figure 1 while maintaining the same level of autocorrelation in environmental conditions results in a strong positive correlation between fecundity and both measures of population fluctuations, CV ($r =$

0.96 , $P < .01$) and ϕ ($r = 0.98$, $P < .01$). The more quickly a population increases during periods of favorable conditions, the fewer good years in a row that are required for the population to reach densities at which a return to unfavorable conditions causes strong density dependence in all three vital rates, precipitating a population crash. Highly fecund species that are able to grow quickly during sequences of good years are vulnerable to lower levels of positive correlation, therefore, than less fecund species.

In nonstructured models exhibiting compensatory den-

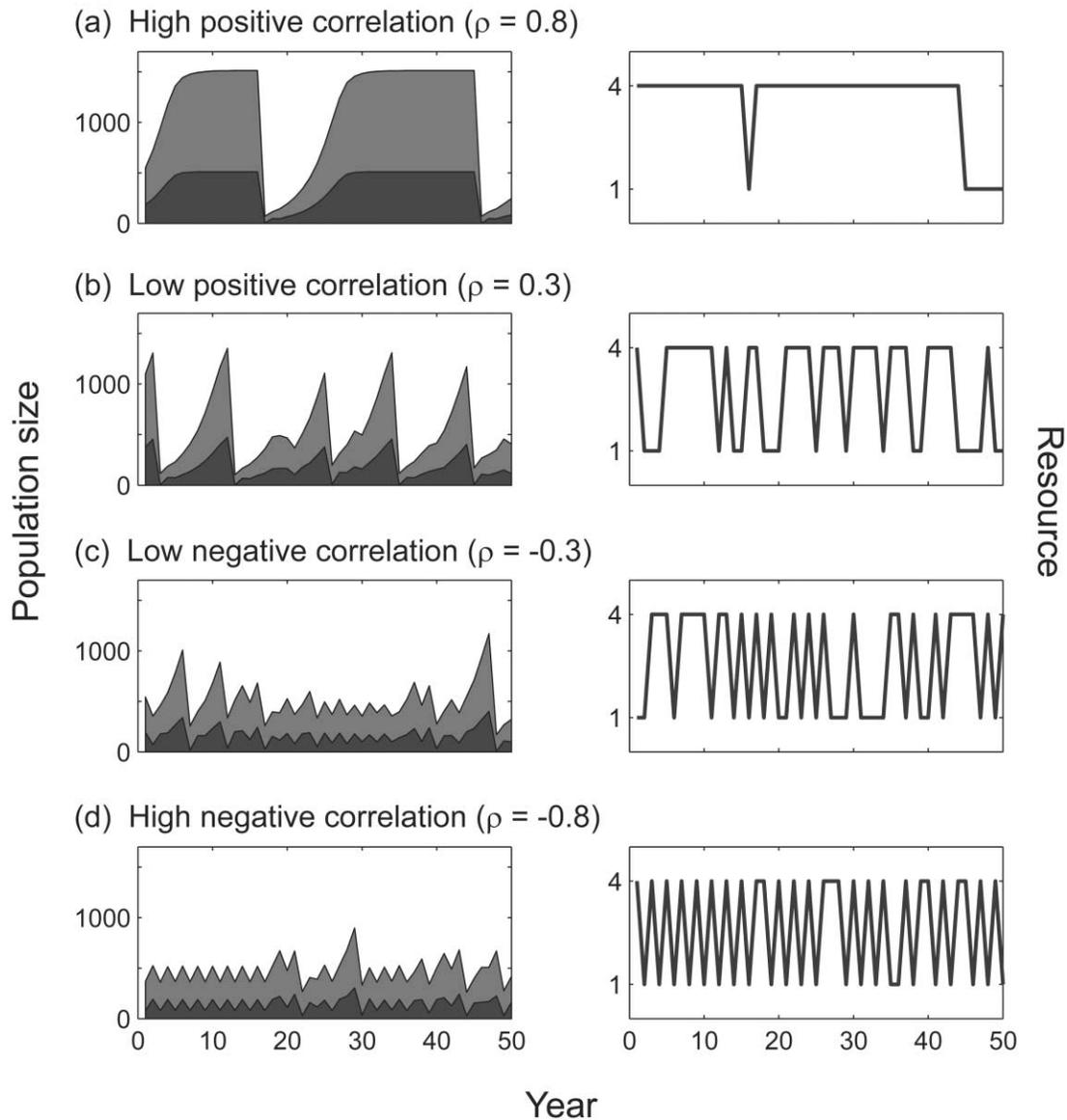


Figure 3: Influence of environmental autocorrelation on population fluctuations ranging from high positive to high negative autocorrelation. The left panels represent population size as described in figure 2. Yearly environmental conditions (*right panels*) were generated from a Markov matrix using the following parameter values: *a*, $P_{gg} = 0.9$, $P_{gb} = 0.1$; *b*, $P_{gg} = 0.7$, $P_{gb} = 0.4$; *c*, $P_{gg} = 0.3$, $P_{gb} = 0.6$; *d*, $P_{gg} = 0.1$, $P_{gb} = 0.9$. Correlation coefficients ρ , given by the subdominant eigenvalue of the Markov matrix, are shown. A color version of this figure is available in the online edition of the *American Naturalist*.

sity dependence (these can be thought of as representing populations that are slow trackers of environmental conditions), positive autocorrelation is more devastating than negative autocorrelation because long strings of bad years put the population at greater risk of decline to low densities (Ripa and Heino 1999). In our age-structured model, conversely, positive autocorrelation increases the probability of a crash to low densities because long strings of good

years act as a ratchet on density dependence in successive life-history traits as the population grows causing a steep crash in the population once a return to bad years prevails. In nonstructured models exhibiting overcompensatory density dependence (fast trackers of environmental conditions), negative autocorrelation is more devastating than positive autocorrelation because in each year the population “overreacts to the current environment, faces in the

next time step a totally different environment, overreacts again, and so on” (Ripa and Heino 1999, p. 221). Positive autocorrelation, conversely, is less devastating because a good year that causes the population to exceed its resources and then “want” to crash will be followed by another good year that then impedes the crash. In the age-structured model, negative autocorrelation in environmental conditions never allows the population to grow to the point that there is significant density dependence in adult survival, and thus the population is relatively stable.

The degree to which a population fluctuates is influenced not only by the degree of environmental autocorrelation but also by the magnitude of the difference in onset of density dependence in juvenile survival and adult fecundity, β_1 , and in adult fecundity and adult survival, β_2 . Setting β_1 and β_2 to be large has the effect of removing density dependence in fecundity and adult survival, respectively. Conversely, setting these parameters to be small results in strong density dependence in each vital rate. As long as β_1 and β_2 are relatively small, populations will tend to fluctuate as a sequence of good years allows the population to grow to the point at which substantial levels of density dependence occur in fecundity and adult survivorship, causing crashes when poor conditions return. In figure 4a, both β_1 and β_2 are relatively low, leading to density dependence in all three vital rates and thus steep declines in density at various times. In figure 4b, we set β_2 to be high, which keeps the adult segment of the population immune to the effects of density dependence in survival. This erases the large declines. As β_1 increases, populations become regulated by density dependence in juvenile survivorship alone, thus leading to very small interannual fluctuations. In figure 4c, we set both β_1 and β_2 to be high, thus removing the effects of density dependence in both fecundity and adult survival. This removes much of the year-to-year fluctuation in the time series.

Lindström and Kokko (2002) showed that when the deterministic dynamics of an age-structured population are stable, cohort effects combined with environmental noise result in increased fluctuations. Conversely, when the deterministic dynamics are unstable, they showed that cohort effects combined with environmental variation result in reduced population fluctuations. We demonstrate that when environmental variation is assumed, increased cohort effects lead to reduced fluctuations in the population (table A1). This is because as the cohort effect becomes stronger and stronger, it increasingly restricts the effects of climate to one age class per year rather than to all age classes. The influence of cohort effects on reducing population fluctuations, therefore, becomes noticeable only when α is near unity, thus limiting the effects of environmental variation to one age class per year. When cohort effects are small or intermediate, climate still in-

fluences all age classes, and thus the influence of the cohort effect on population fluctuations is outweighed by other factors.

Our results suggest a possible mechanism by which climate change may impact age-structured populations. In areas where climate change leads to an increase in positive correlation in environmental conditions or more generally to an increase in the frequency of favorable conditions (with occasional poor years still occurring), populations that are limited by resources will fluctuate more dramatically and be more prone to extinction as a result.

The phenomenon of ungulate population irruptions often observed in predator-free environments, such as islands, displays dynamics similar to those predicted by our model. Reindeer (*Rangifer tarandus*), for instance, were introduced to St. Matthew Island in the Bering Sea in 1944 (Klein 1968). The population grew from 29 introduced animals to 6,000 individuals in 1960 before crashing to fewer than 42 individuals the next year. Klein (1968) suggested that food supply, through interaction with climate, was the dominating population-regulating factor for reindeer on St. Matthew Island, ruling out other factors of population control such as disease, parasites, or predation. Favorable environmental conditions over a number of years allowed the population to increase until the winter of 1960, when harsh climatic conditions coincided with high densities leading to density-dependent mortality in all age classes and a sharp crash in the population. This is much like the dynamics exhibited by our model in figure 2c. Notably, on its introduction to the island, the population comprised exclusively two-year-olds, whereas during the increase and before the population crash, a composition count in 1957 revealed the population consisted of 21% calves, 14% yearlings, and 65% adults; moreover, the most abundant age class among carcasses was 8+-year-olds (Klein 1959).

The moose (*Alces alces*) and wolf (*Canis lupus*) populations of Isle Royale have been carefully monitored on a yearly basis since 1959. In 1980 an outbreak of canine parvovirus on the island decimated the wolf population (Peterson et al. 1998; Peterson 1999), thereafter releasing moose from top-down control (Wilmers et al. 2006). Before 1980, the moose population growth rate was uncorrelated with the NAO, which is the dominant atmospheric circulation pattern influencing climate on Isle Royale. After the crash of the wolf population in 1980, moose became regulated from the bottom up and their growth rate became highly correlated with the NAO (Wilmers et al. 2006). From the early 1980s to 1995, the NAO was in a positive phase leading to favorable growing conditions for moose on Isle Royale before reversing course in 1996, becoming strongly negative, and leading to unfavorable conditions for moose. The moose population during this

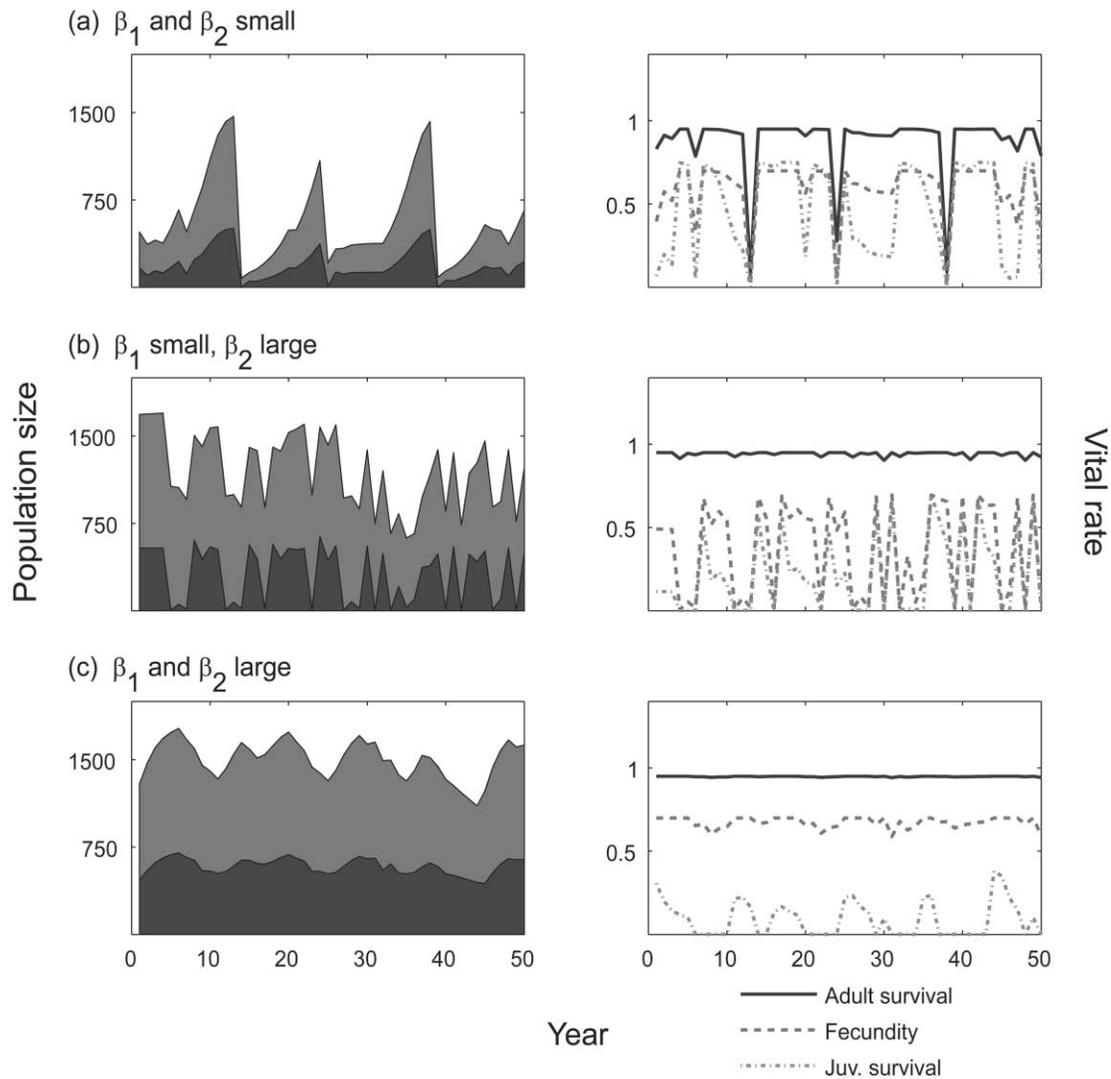


Figure 4: Illustrating the progressive effects of increasing the difference between half saturation in adult fecundity and juvenile survivorship β_1 and between adult survivorship and fecundity β_2 on population fluctuations (*left*) and vital rates (*right*). *a*, $\beta_1 = 200$, $\beta_2 = 200$. *b*, Increasing β_2 to 2,000 minimizes the effects of density dependence in adult survival and removes large population crashes. *c*, Increasing β_1 and β_2 to 2,000 minimizes the effects of both adult fecundity and survivorship, thus removing small year-to-year fluctuations in addition to large crashes. The resulting fluctuations in the time series are almost completely determined by juvenile survivorship. Environmental variation in resources is driven by low positively correlated noise ($\rho = 0.3$), with the Markov matrix values given by those in figure 3*b*. A color version of this figure is available in the online edition of the *American Naturalist*.

time interrupted nearly two-and-a-half-fold to record high densities and then crashed dramatically in 1996. Our model suggests that an unusually long period of favorable conditions allowed the moose population to grow to such high densities that when a bad year came along, density dependence was strongly felt in all three vital rates, leading to a crash in the moose population.

Conclusion

We have demonstrated that the fluctuations exhibited by age-structured populations are strongly influenced by an interaction between population density, age-class-specific vital rates, and the degree of temporal correlation in environmental conditions. Populations that are resource lim-

ited and live in negatively autocorrelated environments in which a succession of many favorable years in a row are likely to be relatively stable, whereas those populations living in positively autocorrelated environments, in which sequences of many good years in a row occur, are more likely to experience dramatic increases and crashes.

Understanding how increases in global temperatures will impact autocorrelation in environmental conditions and the relative frequency of favorable and unfavorable conditions will therefore be important in understanding the effects of climate change on the dynamics of age-structured populations. Our analysis suggests that if future warming leads to an increase in the autocorrelation of environmental noise or the frequency of favorable conditions (with occasional bad years still occurring), increasingly violent population fluctuations could result, paradoxically putting species, particularly highly fecund ones, at increased risk of extinction.

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APPENDIX

Results of Sensitivity Analysis

To conduct the sensitivity analysis, we used Monte Carlo methods to assess the relative effects of several parameters on model statistics (Wisdom et al. 2000; Cross and Beissinger 2001; Wilmers and Getz 2004). Although analytical approaches to sensitivity analysis have been developed for linear deterministic (Caswell 2001), stochastic (Tuljapurkar 1990), and density-dependent models at equilibrium (Grant and Benton 2000), nonlinear models, where population sizes are often far away from equilibrium, require a simulation approach to evaluate sensitivities. As such, we generated 1,000 random parameter sets by choosing parameters from uniform distributions bounded by the values shown in table 1A. Each parameter set was used to run the model

once, for a total of 1,000 runs. Mean population size \bar{N} , coefficient of variation CV, and a statistic ϕ given by

$$\phi = \frac{\frac{1}{(yr-1)} \sum_{t=1}^{yr-1} [N(t+1) - N(t)]^2}{\frac{1}{yr} \sum_{t=1}^{yr} [N(t)]^2}, \quad (A1)$$

where N is total population size and yr is the total number of years in the simulation, were recorded for each run and used as the dependent variables in linear regressions in which the model parameters were the explanatory variables. Whereas the CV of the population time series quantifies overall variability, the statistic ϕ is more sensitive to year-to-year fluctuations in the time series. For instance, two time series might fluctuate in a sawtooth pattern between 100 and 1,000 individuals, one on a yearly basis, the other on a decadal basis. Over the long term, both will have similar CVs, but the former will have a much higher ϕ .

The larger the magnitude of the slope and the greater the r^2 value, the more influential that parameter is on affecting the output statistic. In order to assess whether sensitivities are different in generally favorable versus unfavorable environments, we performed the sensitivity analysis under both a low frequency of good years ($P_{gg} = P_{gb} = 0.2$) and high frequency of good years ($P_{gg} = P_{gb} = 0.8$). In all cases, we ran the model for 100 years and discarded the first 20 years in order to remove transitory effects. All simulations were run in Matlab 7.

Initially we conducted sensitivity analyses by allowing the survivorship and fecundity parameters b_i and c_i to also change from run to run. This resulted in nearly all of the explained variation in ϕ , CV, and mean population size \bar{N} to be dominated by changes in the maximum adult survivorship parameter b_2 . This is because when b_2 is low, the population either becomes extinct ($N \leq 0$) or hovers around a low equilibrium, unable to respond to good resource conditions through increased survival and population growth. Conversely, when b_2 is high the population easily responds to good resource conditions by surviving and growing. In order to gain insight, therefore, into the effects of the other model parameters on population dynamics, we held the maximum survival and fecundity parameters fixed.

Table A1: Results of sensitivity analysis

Parameter	Description	Range	ϕ^a				CV ^a				\bar{N}^a			
			r^2	SRC	r^2	SRC	r^2	SRC	r^2	SRC				
α	Cohort effect	0–3	.00	.14	.02	-.38	.05	.10	.23	-.31	.00	.09	.05	.30
δ_{js}	Density dependence onset in juvenile survivorship	1–10	.00	.03	-.02	-.18	.11	.05	.33	-.22	.06	.02	-.24	-.12

Table A1 (Continued)

Parameter	Description	Range	ϕ^a				CV ^a				\bar{N}^a			
			<i>r</i> ²	<i>r</i> ²	SRC	SRC	<i>r</i> ²	<i>r</i> ²	SRC	SRC	<i>r</i> ²	<i>r</i> ²	SRC	SRC
δ_f	Density dependence onset in fecundity	1–10	.04	.03	.19	.18	.00	.02	.06	.15	.00	.00	.01	-.03
δ_{AS}	Density dependence onset in adult survivorship	1–10	.07	.00	.27	.06	.00	.01	.05	.08	.20	.02	.45	.14
γ_{15}	Juvenile survival half saturation	200–400	.06	.08	.24	.29	.00	.10	.06	.31	.10	.13	.31	.37
β_1	Difference in juvenile survival and fecundity half saturation	0–1,000	.41	.26	-.64	-.51	.03	.21	-.17	-.46	.37	.34	.61	.58
β_2	Difference in fecundity and adult survival half saturation	0–1,000	.00	.10	.03	-.32	.00	.23	-.02	-.48	.10	.18	.32	.43

Note: We report the sensitivity of population fluctuation (ϕ), coefficient of variation (CV), and mean population size (\bar{N}) to changes in model parameters. Results presented here are for fixed values of $b_1 = .75$, $b_2 = .95$, $c_1 = .1$, and $c_2 = .7$. Statistical significance at the 0.01 level is indicated by boldface values of the standardized regression coefficient (SRC). The SRCs are slope estimates from the least squares fit of the data multiplied by the ratio of the standard deviations in the independent to dependent variables. Nonitalic values are the results of sensitivity runs with a low frequency of favorable years ($P_{gg} = .2$, $P_{gb} = .2$), whereas italic values are the results of sensitivity runs with a high frequency of favorable years ($P_{gg} = .8$, $P_{gb} = .8$).

^a Variables log transformed to meet normality assumptions. Each response variable was graphed against each parameter for each run of the model to visually inspect for linearity.

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