

# Response of population size to changing vital rates in random environments

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**Abstract** Population size and population growth rate respond to changes in vital rates like survival and fertility. In deterministic environments change in population growth rate alone determines change in population size. In random environments, population size at any time  $t$  is a random variable so that change in population size obeys a probability distribution. We analytically show that, in a density-independent population, the proportional change in population size with respect to a small proportional change in a vital rate has an asymptotic normal distribution. Its mean grows linearly at a rate equal to the elasticity of the long-term stochastic growth rate  $\lambda_S$  while the standard deviation scales as  $\sqrt{t}$ . Consequently, a vital rate with a larger elasticity of  $\lambda_S$  may produce a larger mean change in population size compared to one with a smaller elasticity of  $\lambda_S$ . But a given percentage change in population size may be more likely when the vital rate with smaller elasticity is perturbed. Hence, the response of population size to perturbation of a vital rate depends not only on the elasticity of the population growth rate but also on the variance in change in population size. Our results provide a formula to calculate the probability that population size changes by a given percentage that works well even for short time periods.

**Keywords** Random environments · Stage-structured populations · Stochastic growth rate · Stochastic elasticity · Population size · Variance in population size · Normal distribution

## Introduction

Population ecologists have proposed and used various measures of response of population growth rate to changes in vital rates. For instance, in the absence of environmental variation, elasticity of the long-term growth rate  $\lambda$  to a vital rate (Caswell 2001) quantifies the proportional change in  $\lambda$  due to a small change in a vital rate when the population is in its stable stage distribution. Most studies using density-independent models have focused on how population growth rate, rather than population size, responds to changes in vital rates. However, temporal variation in the environment produces random fluctuations in population sizes so that an estimate of growth rate would not predict the variation in population size. Moreover, (unlike in deterministic environments), even a positive long-term stochastic growth rate  $\lambda_S$  may result in a decrease in population size and even extinction, with non-zero probability (Lande and Orzack 1988). This probability depends upon the variance in population size, so that  $\lambda_S$  alone may not accurately capture the stochastic dynamics. Further, in conservation/management scenarios, population size is often a better indicator of population status and managers target population size for recovery and control. For instance, Fox and Gurevitch (2000) states that “the concern of many conservation programs is to increase the population size rapidly so that stochastic events do not drive the population closer

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to extinction.” More importantly, management plans typically operate upon short time scales (3–10 years) (Fefferman and Reed 2006; Morris and Doak 2002), so that prediction of change in population size is necessary in short periods. There are other ecological scenarios where such short-term dynamics is critical: like plant–animal interactions (Maron et al. 2010) and the spread of an invasive species (Ramula et al. 2008). In density-independent stochastic models, population size  $N(t)$  in year  $t$  has an asymptotic log-normal distribution (Cohen 1977). As a result, the change in population size due to an increase/decrease in a vital rate is also random having a probability distribution. Thus, the question arises whether one could predict the effect of changing a vital rate on population size based on its effect on long-term stochastic growth rate alone. In other words, we are interested in the probability distribution of the change in population size  $\Delta N(t)$  (or  $\Delta N(t)/N(t)$ , the proportional change) resulting from a change in a vital rate.

We use recent results in stochastic elasticities (Haridas et al. 2009) to analytically show that, in density-independent models, the proportional change in population size  $\Delta N(t)/N(t)$  with respect to a small proportional change in a vital rate is asymptotically normally distributed. The mean of this distribution depends on  $t$  and is given by  $t E_S$ , where  $E_S$  is the elasticity of the long-term stochastic growth rate  $\lambda_S$ . For instance,  $E_S$  could be the elasticity to the mean or to the variance (Tuljapurkar et al. 2003) depending upon the type of change (mean/variance) in the vital rate. In other words, we show that the *elasticity of population size to a vital rate* has a normal distribution. This result is important for two reasons: Firstly, it provides an analytical tool to calculate the probability that the population size increases/decreases by a specific percentage due to a change in a vital rate. Secondly, the result shows that the effect of perturbing a vital rate on population size depends not only on the elasticity of  $\lambda_S$  to that vital rate (as it is in deterministic models) but also on the variance in the change in population size. This variance results from the variation in original population size generated by environmental stochasticity. Hence, in stochastic environments, an estimate of the change in total population size based on the elasticity of  $\lambda_S$  gives the mean change in population size while actual change could be less or more than this estimate. Elasticity of  $\lambda_S$  is often used to compare the relative effect of perturbing one vital rate over another on population growth rate. Our results show that a vital rate with a smaller elasticity of  $\lambda_S$  can produce a larger variance in the change in population size. Consequently, the probability of a given percentage change in population

size may be larger when the vital rate with smaller elasticity of  $\lambda_S$  is perturbed as compared to the vital rate with larger elasticity.

We illustrate our results using stochastic population models for two species: *Cucurbita pepo* (wild squash), a monoecious annual species native to south-central USA and northern Mexico (Wilson 1993; Cowan and Smith 1993), and *Fumana procumbens*, a perennial woody shrub species found in the baltic island of Öland (Bengtsson 1993). Though the change in population size attains a normal distribution only in the long-term, we show, using these examples, that our results can yield good approximations for relatively short (15–25 years) time periods.

### Elasticity of population size in random environments

Dynamics of a density-independent stage-structured population in random environments can be described by the equation

$$\mathbf{P}(t) = \mathbf{A}(t) \mathbf{P}(t-1), \quad (1)$$

where  $\mathbf{P}(t)$  is the  $k \times 1$  vector of population numbers in  $k$  stages at time  $t$  and  $\mathbf{A}(t)$  is the random  $k \times k$  projection matrix. Throughout this work, we assume that the underlying environmental process (which may be serially autocorrelated, e.g., as a Markov chain) is stationary and mixing and that the demographic matrices satisfy demographic weak ergodicity (Tuljapurkar 1990).

Let  $N(t)$  be the total population size in year  $t$  which is given by  $|\mathbf{P}(t)|$ , the sum of elements of the population vector  $\mathbf{P}(t)$ . Let  $\lambda(t) = N(t)/N(t-1)$  be the population growth rate in year  $t$ . Then, we can write

$$N(t) = \lambda(t)N(t-1). \quad (2)$$

Iterate Eq. 2, starting from  $t = 1$ , and then take logarithms to get

$$\log(N(T)) = \sum_{t=1}^T \log(\lambda(t)) + \log(N(0)), \quad (3)$$

where  $N(0)$  is the initial population size and  $N(T)$  is the population size in year  $T$ . The long-term stochastic growth rate  $\log \lambda_S$  is given by

$$\log \lambda_S = \lim_{T \rightarrow \infty} (1/T) \sum_{t=1}^T \log(\lambda(t)). \quad (4)$$

The asymptotic variance of  $\log(N(T))$  is  $T\sigma^2$ , where

$$\sigma^2 = \lim_{T \rightarrow \infty} (1/T) \text{Var}(\log(N(T))), \tag{5}$$

where  $\text{Var}(\log(N(T)))$  denotes the variance of  $\log(N(T))$ . Consider a small proportional change in a vital rate represented by a matrix element  $A_{(i,j)}(t)$ . Let  $A_{(i,j)}(t)$  change to  $A_{(i,j)}(t) \rightarrow A_{(i,j)}(t) + \epsilon C_{(i,j)}(t)$  in every year  $t = 1 \dots T$ , where  $\epsilon$  is small. Typical choices for  $C_{(i,j)}(t)$  are either of  $A_{(i,j)}(t)$  or  $\mu_{(i,j)}$  or  $A_{(i,j)}(t) - \mu_{(i,j)}$ , where  $\mu_{(i,j)}$  is the mean of  $A_{(i,j)}(t)$  (Tuljapurkar et al. 2003). Let population size at time  $T$  changes from  $N(T)$  to  $N(T) + \Delta N(T)$  as a result of this perturbation in rate  $A_{(i,j)}(t)$  in every year  $t = 1 \dots T$ . Then, the elasticity of population size at time  $T$  with respect to the vital rate  $A_{(i,j)}(t)$  is defined as  $\frac{\Delta N(T)/N(T)}{\epsilon}$  when  $\epsilon$  is small.

A heuristic approach to understand the distribution of  $\Delta N(T)/N(T)$  is as follows: Recall that  $\log(N(T))$  is asymptotically normally distributed with mean  $T \log \lambda_S$  and a variance  $T\sigma^2$  (Cohen 1977) and similarly  $\log(N(T) + \Delta N(T))$  is also asymptotically normally distributed. When  $\Delta N(T)$  is small,  $\log(N(T) + \Delta N(T)) - \log(N(T)) \approx \Delta N(T)/N(T)$ , which suggests that  $\Delta N(T)/N(T)$  is approximately normally distributed (being the difference of two normal random variables). However,  $\log(N(T))$  and  $\log(N(T) + \Delta N(T))$  are not statistically independent, and hence, this argument is not valid to derive the normality of  $\Delta N(T)/N(T)$ . In the next section, we use stochastic elasticities (Haridas et al. 2009) to analytically derive the distribution of elasticity of population size.

### Main results

To derive the elasticity of total population size to a vital rate  $A_{(i,j)}(t)$ , we make use of Eq. 3. This equation suggests that the elasticity of population size depends on the elasticities of the annual growth rate  $\lambda(t)$ ,  $t = 1, \dots, T$ . Let  $M(T)$  denote the elasticity of total population size. Then (see online Appendix A),

- (I) *The elasticity of total population size to a vital rate eventually grows at a rate given by the long-term elasticity of  $\lambda_S$ , i.e.,  $M(T) \approx T E_S$  for large  $T$ , where  $E_S$  stands for the long-term elasticity of  $\lambda_S$  to the vital rate  $A_{(i,j)}(t)$ . This could be the elasticity to the rate or its mean or variance, depending on the perturbation (Tuljapurkar et al. 2003).*

Further, let  $e_{(i,j)}(t)$  denote the elasticity of growth rate  $\lambda(t)$  with respect to the vital rate (Haridas et al.

2009) perturbed in years  $1 \dots t$ . Then (see online Appendix A)

$$M(T) = \sum_{t=1}^T e_{(i,j)}(t), \tag{6}$$

and

- (II) *The proportional change in total population size with respect to a vital rate has an asymptotic normal distribution whose mean is linear in the long-term elasticity  $E_S$  of  $\lambda_S$  and has a variance  $T\sigma_e^2$ . That is, the elasticity of total population size  $M(T) \approx \text{Normal}(T E_S, T\sigma_e^2)$ .*

Note that Haridas et al. (2009) discussed the estimation of elasticities of  $\lambda_S$  but did not show the relationship between response of population size to elasticities of  $\lambda_S$ .

### Implications

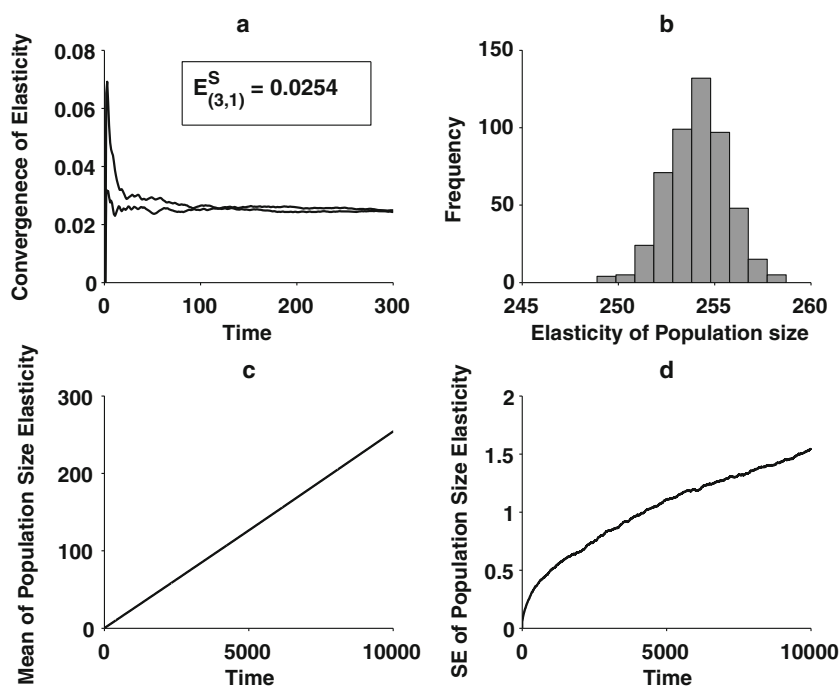
- From result (I), it follows that the elasticity of long-term stochastic growth rate  $\lambda_S$  is given by the slope of the regression line between the elasticity of population size and time (see Fig. 1c). Recall that  $\log \lambda_S$  itself is often estimated as the slope of the logarithmic population sizes against time (Dennis et al. 1991; Chevin 2010).
- Result (II) provides an easy tool to calculate the probability that the proportional change in population size is larger (smaller) than a target value, say  $\alpha$ . For instance, if  $\epsilon$  is the magnitude of the proportional change in the vital rate, note that  $Pr(\Delta N(T)/N(T) \geq \alpha) = Pr(M(T) \geq \alpha/\epsilon)$  and

$$Pr(M(T) \geq \alpha/\epsilon) = 1 - \Phi\left(\frac{\alpha/\epsilon - T E_S}{\sqrt{T}\sigma_e}\right). \tag{7}$$

Here  $\Phi(\cdot)$  denotes the cumulative distribution function of the standard normal distribution.

- An important consequence of result (II) is that the response of population size to perturbation of a vital rate depends not just on the elasticity of the long-term growth rate but also on the variance (in fact, on the distribution of  $M(T)$ ) of the change in population size. Hence, a vital rate having a larger elasticity of the long-term growth rate  $\lambda_S$ , if perturbed, produces a larger mean proportional change in population size as compared to a vital rate with a smaller elasticity of long-term growth

**Fig. 1** **a** Elasticity ( $E_{(3,1)}^S$ ) of population growth rate  $\lambda_S$  for *C. pepo* with respect to matrix element  $A_{(3,1)}(t)$  as computed from the proportional changes in total population size. Results from two independent simulations, each from  $t = 1$  to  $t = 300$ , are shown. **b** Histogram of the elasticity of population size resulting from perturbation of  $A_{(3,1)}(t)$ . **c** Mean of the elasticity of population size as a function of time. **d** Standard error of the elasticity of population size as a function of time. Results are from 500 simulations where each simulation is of 10,000 time steps



rate. But the probability that the change in population size is bigger than a specific target value may be larger when the vital rate with smaller elasticity of  $\lambda_S$  is perturbed (Figs. 4b and 5b). This is because the probability of such an event also depends (see Eq. 7) on the variance of the percentage change in population size.

- While the mean  $E_S$  of the normal distribution for  $M(T)/T$  is the elasticity of  $\lambda_S$  (long-term growth rate of the original population), the variance  $\sigma_e^2$  is *not* the elasticity of the long-term variance of the original population. Rather, it is the variance of the elasticity of the population size with respect to the vital rate and can be estimated from demographic data as described in Haridas et al. (2009).
- Note that if elasticities of two vital rates are equal (as is the case with some vital rates in certain life-histories; see Claessen 2005), then the vital rates produce exactly the same long-term proportional changes in population size. Therefore, the long-term variance in  $M(T)$  will be the same for both vital rates.
- The *sensitivity* of population size (absolute change in population size) with respect to perturbations of a vital rate  $A_{(i,j)}(t)$ ,  $t = 1, \dots, T$  is given by  $\Delta N(T)/\Delta A_{(i,j)}(T)$  which is equal to the product of the elasticity of population size  $M(T)$  and  $N(T)/A_{(i,j)}(T)$ . Hence, the distribution of sensitivity depends upon distribution of the vital rate

and, in general, the sensitivity has to be evaluated numerically.

### Change in expected population size

An associated quantity of interest is the change in the expected population size  $E(N(t))$ . The proportional change in expected population size is given by  $\Delta E(N(t))/E(N(t))$ . Hence, the elasticity of the expected population size is different from the expected value of the elasticity of population size (which is  $\approx t E_S$ , as derived above). When vital rates are serially independent and identically distributed over years, we know (Cohen 1977) that  $\log(E(N(t)))$  grows at a rate given by  $t \log \lambda_0$ , where  $\lambda_0$  is the largest eigenvalue of the average matrix  $E(\mathbf{A}_t)$ . This means that the elasticity of the expected population size  $E(N(t))$  to a vital rate  $A_{(i,j)}(t)$  is  $\approx t e_{\mu_{(i,j)}}$ , where  $e_{\mu_{(i,j)}}$  is the classical deterministic elasticity of  $\lambda_0$  to the mean  $\mu_{(i,j)}$  of the vital rate  $A_{(i,j)}(t)$ . In general, no comparison is possible between the two except to say that they will be similar in magnitude when temporal variation is small. When vital rates are serially correlated,  $\log(E(N(t)))$  grows at a rate given by  $t \log \mu$ , which could be different from  $t \log \lambda_0$  (Cohen 1977; Tuljapurkar 1990). In this case, one needs to calculate elasticities of  $\log \mu$ , which can be evaluated exactly when vital rates vary according to a Markov chain (Tuljapurkar et al. 2003).

### Illustration: two examples

We use demographic data from two plant species to illustrate our analytical results. The purpose of these examples is mainly to explain the results rather than to understand specific biological details of these species.

#### Example 1 Wild squash, *C. pepo*

In our first example, we consider a stochastic matrix model for the population dynamics of *C. pepo* (wild squash), a monoecious annual species native to south-central USA and northern Mexico (Wilson 1993). Experimental populations were established in an abandoned farm field in Mississippi, and germination, seedling survival, and gourd production were monitored to derive demographic transition matrices. We used three life-history stages: dormant gourds, dormant seeds in the seed bank, and adult plants. A more detailed description on the experiments and data analysis to estimate the transition rates between these life-history stages can be found in Prendeville (2010). In 2006, precipitation was below average causing large reduction in recruitment while 2007 was a normal year. The corresponding transition matrices are

$$\mathbf{A1} = \left( \begin{array}{c|ccc} 2006 & \text{Gourds} & \text{Seeds} & \text{Adults} \\ \hline \text{Gourds} & 0.047 & 0.00 & 0.075 \\ \text{Seeds} & 0.044 & 0.036 & 0.087 \\ \text{Adults} & 0.12 & 0.033 & 0.477 \end{array} \right)$$

and

$$\mathbf{A2} = \left( \begin{array}{c|ccc} 2007 & \text{Gourds} & \text{Seeds} & \text{Adults} \\ \hline \text{Gourds} & 0.047 & 0.00 & 0.36 \\ \text{Seeds} & 0.045 & 0.025 & 0.73 \\ \text{Adults} & 0.37 & 0.069 & 4.09 \end{array} \right).$$

To construct the stochastic model, we assumed that matrix **A1** occurs with probability 0.33 and matrix **A2** occurs with probability 0.67. Information on the frequency of good and bad years is not available, so our choice of these frequencies was made on two criteria: First, it makes sure that long-term growth rate  $\lambda_S$  is  $> 1$  (population size is increasing over time). Secondly, for computational purposes, we wanted populations to grow sufficiently slow to prevent an overflow of population sizes. We first used Eq. 1 to simulate 500 population trajectories each of length 10,000 time steps, starting with one individual in each stage and using

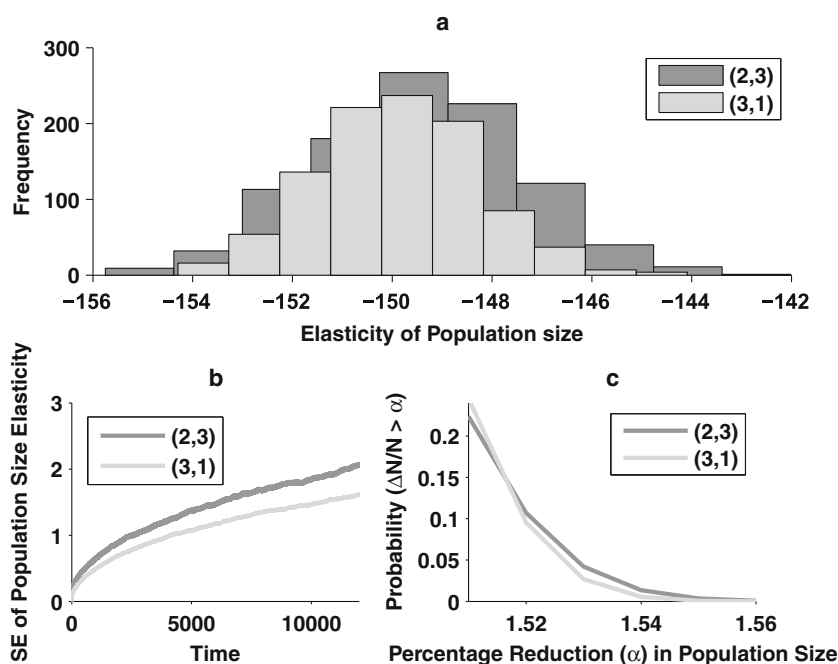
projection matrices **A1** and **A2**. Simulations were then repeated with each  $A_{(i,j)}(t)$  now replaced by  $A_{(i,j)}(t) + \epsilon A_{(i,j)}(t)$ , where  $\epsilon = 0.0001$ . The parameter  $\epsilon$  denotes the small proportional increase in the value of  $A_{(i,j)}(t)$ . Note that this change produces a proportional increase (of magnitude  $\epsilon$ ) in the mean and variance of  $A_{(i,j)}(t)$  without changing its coefficient of variation. We calculated  $\frac{\Delta N(t)/N(t)}{\epsilon}$  for 10,000 time steps for each of 500 simulations. As predicted by result (I), these ratios (after dividing by  $t$ ) converged to the elasticity of  $\lambda_S$  with respect to  $A_{(i,j)}(t)$  (Fig. 1a, showing convergence for  $A_{(3,1)}(t)$ , transition rate from adult stage to gourd stage). In addition, by generating age structure vectors and reproductive value vectors, we used methods in Tuljapurkar et al. (2003) to confirm the value of  $E_{(3,1)}^S (= 0.025)$ . The elasticity of population size had a normal distribution (Fig. 1b) whose mean ( $= t E_{(3,1)}^S$ ) increases linearly with time  $t$  (Fig. 1c), while the standard error scales as  $\sqrt{t}$  (Fig. 1d), in agreement with result (II).

To illustrate how increasing the variance in a vital rate affects population size, we replaced  $A_{(3,1)}(t)$  by  $A_{(3,1)}(t) + \epsilon (A_{(3,1)}(t) - \mu_{(3,1)})$  and proceeded as before. Note that this change produces a proportional increase (of magnitude  $\epsilon$ ) in the variance of  $A_{(3,1)}(t)$  without changing its mean. Increasing the variance decreased long-term population size, and consequently, elasticities of population size and that of  $\lambda_S (E_{(3,1)}^{S\sigma})$  were both negative (Fig. 2a). Increasing the variance in matrix element  $A_{(2,3)}(t)$  (representing transition from “adults” to “seeds”) produced similar but relatively smaller effects (in magnitude), as compared to  $E_{(3,1)}^{S\sigma}$  (Fig. 2a). Variance in elasticity of population size was larger when variance in  $A_{(2,3)}(t)$  was increased as compared to increased variance in  $A_{(3,1)}(t)$  (Fig. 2b).

To check the validity of the normal approximation in result (II), we perturbed the variance in  $A_{(3,1)}(t)$  and  $A_{(2,3)}(t)$  and calculated probabilities of reduction in population size using the normal approximation and compared it with simulations. Figure 3 illustrates that the normal approximation (see Eq. 7) works well even for short-term predictions. The relatively lower accuracy for the approximation for very short time periods (like  $t = 10$ , Fig. 3) is due to strong transient effects.

Further, we used the normal distribution in result (II) to compare the effects of increasing variance of  $A_{(3,1)}(t)$  with that of  $A_{(2,3)}(t)$  by calculating the probabilities  $\text{Prob}(\frac{\Delta N(t)}{N(t)} > \alpha)$  (Fig. 2c). Interestingly, larger reductions in total size were more likely when the variance in  $A_{(2,3)}(t)$  was increased in comparison to increased variance in  $A_{(3,1)}(t)$ , even though the variance elasticity of  $A_{(2,3)}(t)$  was smaller (in magnitude) than

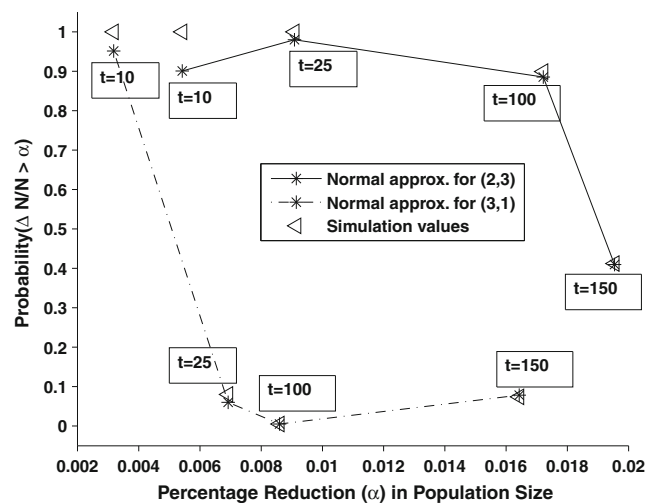
**Fig. 2** **a** Histograms of the elasticities of population size at  $t = 12,000$  for *C. pepo* due to increasing variance in the rate  $A_{(3,1)}(t)$  (light) and  $A_{(2,3)}(t)$  (dark). **b** Standard error of the elasticity of population size as a function of time. **c** Probability (y-axis) that the reduction in total size is more than a fixed percentage  $\alpha$  (x-axis) when increasing the variance in  $A_{(2,3)}(t)$  (dark) and  $A_{(3,1)}(t)$  (light). Results are from 500 simulations where each simulation is of 12,000 time steps



that of  $A_{(3,1)}(t)$  (Fig. 2a, c). This feature is further illustrated in the next example.

#### Example 2 *F. procumbens*

Bengtsson (1993) studied the population dynamics of *F. procumbens*, a perennial woody shrub species

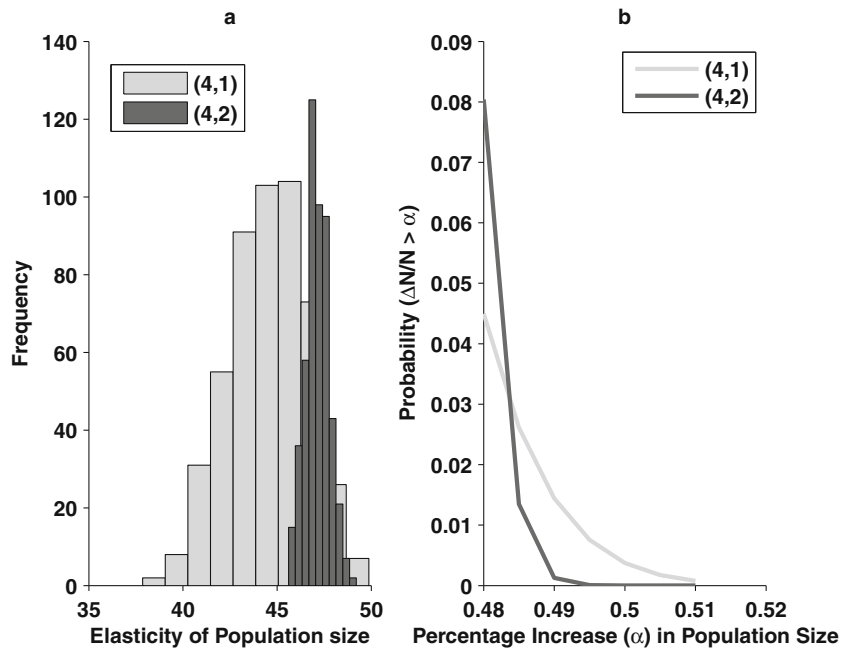


**Fig. 3** Probability (y-axis) that the reduction in total size is more than a fixed percentage  $\alpha$  (x-axis) when increasing the variance in  $A_{(2,3)}(t)$  and  $A_{(3,1)}(t)$  for *C. pepo*. Shown are values obtained from the normal approximation (Eq. 7) as well as from simulations

found in the baltic island of Öland. The population model consisted of six life-history stages: seedlings, juveniles with  $\leq 2$  shoots/branches, juveniles with  $> 2$  shoots/branches, adults reproducing  $\leq 3$  fruits produced, adults reproducing  $> 3$  fruits produced, and non-reproductive adults. Bengtsson (1993) reported demographic projection matrices for 6 years (1985–1986 to 1990–1991; Table 7, Bengtsson 1993). To incorporate the effects of environmental variation on demographic rates, we assumed that each matrix occurs equally likely (with probability = 1/6) every year. Simulations were done exactly as in the previous example.

First, we verified that the normal approximation does well as in the previous example (not shown). When the vital rate  $A_{(4,1)}(t)$  (transition rate from seedling stage to adults reproducing  $\leq 3$  fruits) was perturbed, so that its mean and variance increased by the same percentage, population size increased (Fig. 4a, light). We observed a similar effect when vital rate  $A_{(4,2)}(t)$  (transition rate from juveniles with  $\leq 2$  shoots to adults reproducing  $\leq 3$  fruits) was perturbed (Fig. 4a, dark), but the mean of this change was larger than corresponding mean after perturbing  $A_{(4,1)}(t)$ . However, a larger percentage change in total population size was more probable when  $A_{(4,1)}(t)$  was perturbed (Fig. 4b, where probabilities are calculated at  $t = 10,000$ ). Population size decreased when the variance of  $A_{(4,6)}(t)$  was increased keeping its mean unchanged (Fig. 5a). We compared this effect with that of increasing the variance of  $A_{(3,1)}(t)$ . Two features are noticeable: Firstly, though

**Fig. 4** **a** Histograms of the elasticities of population size at  $t = 10,000$  for *F. procumbens* due to increasing vital rates  $A_{(4,1)}(t)$  (light) and  $A_{(4,2)}(t)$  (dark). **b** Probability (y-axis) that the proportional increase in total population size is more than a fixed percentage  $\alpha$  (x-axis) when perturbing  $A_{(4,1)}(t)$  (light) and  $A_{(4,2)}(t)$  (dark). Results are from 500 simulations where each simulation is of 10,000 time steps



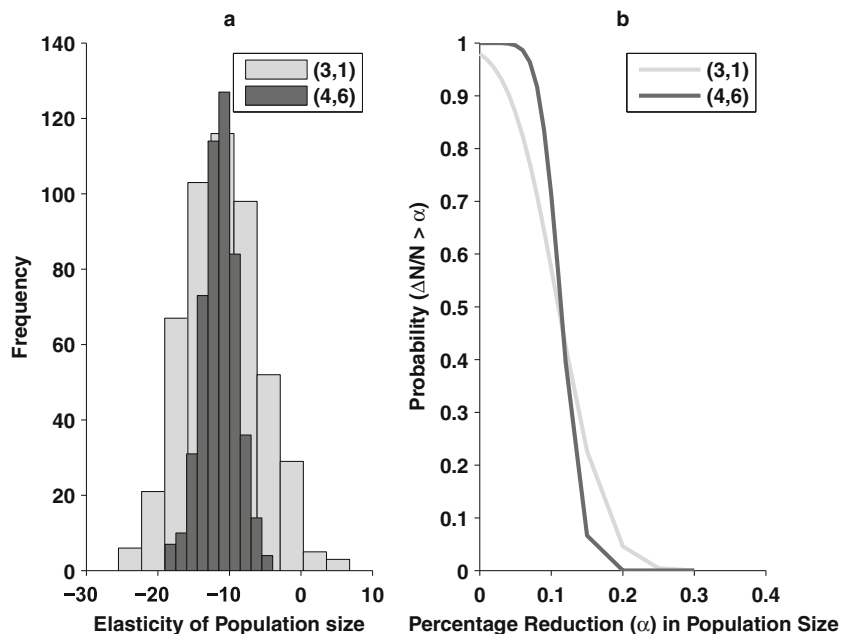
the elasticity of  $\lambda_S$  with respect to variance of  $A_{(3,1)}(t)$  was negative (which means that  $\lambda_S$  is reduced when variance is increased), there was a non-zero probability that population size increased due to increasing variance (Fig. 5a, light histogram, when  $t = 40,000$ ). Secondly, the probability of low to moderate percentage decrease in population size was larger when variance in  $A_{(4,6)}(t)$  was increased while higher reduction was more likely when variance in  $A_{(3,1)}(t)$  was increased (Fig. 5b). Hence, even though the elasticity  $E_{(4,6)}^{S\sigma}$  of  $\lambda_S$  was larger in magnitude than  $E_{(3,1)}^{S\sigma}$ , we see that

perturbing variance of  $A_{(3,1)}(t)$  was more likely to result in large percentage reduction in population size.

**Discussion**

It is of fundamental importance in ecology and evolution to understand fluctuations in population size caused by changes in vital rates. In the absence of density dependence, we show that the proportional change in population size resulting from a small proportional

**Fig. 5** **a** Histograms of the elasticities of population size at  $t = 40,000$  for *F. procumbens* due to increasing the variance in vital rates  $A_{(3,1)}(t)$  (light) and  $A_{(4,6)}(t)$  (dark). **b** Probability (y-axis) that the proportional reduction in population size is more than a fixed percentage  $\alpha$  (x-axis) when increasing the variance in  $A_{(4,6)}(t)$  (dark) and  $A_{(3,1)}(t)$  (light). Results are from 500 simulations where each simulation is of 40,000 time steps



change in a vital rate has a long-term normal distribution. The mean of this distribution grows linearly with time at a rate given by the elasticity of the long-term stochastic growth rate  $\lambda_S$  with respect to the vital rate. Observe that, in deterministic environments, the elasticity of the population growth rate alone determines the response of population size to changes in vital rates. The normal approximation provides a tool to estimate the probability of a percentage increase/decrease in total population size due to changes in a vital rate. In our examples, we show that the normal approximation works well for relatively short time intervals (15–25 years) making it a valuable tool for short-term predictions on the fluctuations of population size.

Our results show that the response of population size to perturbations depends not only on the change in long-term population growth rate but also on the variance in this response. In the two examples analyzed, we showed that perturbing a vital rate with lower elasticity of the long-term growth rate  $\lambda_S$  is often more likely to produce a given percentage change in the population size as compared to perturbing a vital rate with a larger elasticity of  $\lambda_S$ . We also showed (in *F. procumbens*) that perturbing a vital rate can increase population size for several years (beyond the transient stage) even though it reduces the long-term population growth rate  $\lambda_S$ . Our analysis shows the role of variation in change in population size in determining if population size increases/decreases due to changes in vital rates. Note that this variance depends upon the variance of annual elasticities as well as their serial autocorrelations (Eq. 6). It will also be of interest to know how the current variance in population size ( $\sigma^2$ ) affects variance in change of population size ( $\sigma_e^2$ ).

In evolutionary genetics, long-term population growth rate is used as the geometric mean fitness measure: At a diploid locus, the long-term population growth rate of a rare heterozygote determines whether it can successfully “invade” a large population in a fluctuating environment, and a polymorphism of two alleles can be maintained if the long-term growth rate of the heterozygote exceeds that of either homozygote (Gillespie 1973). Our results suggest that conditions for fixation and polymorphism should also include the variance in change in gene frequencies in addition to the long-term growth rate. Such variance effects would be especially important in short-term changes and also in autocorrelated environments (Vasseur and Yodzis 2004), which can exacerbate variation in population growth rates and sizes.

Our results have implications for population management in varying environments. We show that predictions on the effects of vital rate perturbations on

the change in population size based on elasticities of long-term growth rate alone might be erroneous since change in population size also depends on the variance. Management actions aim to target population parameters, and in order to choose the most effective management strategy, it is critical to know how population size responds to perturbing particular vital rates. In particular, a manager may want to know how likely a particular management action will cause the population size to exceed or to remain below a target value. One could readily estimate these probabilities using the normal approximation we derived here.

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