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Unstructured individual variation and demographic stochasticity

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Abstract

Demographic stochasticity increases the variance in the growth rate of small populations, and is an important factor to consider when predicting the fates of such populations. Unfortunately, the concept has been treated inconsistently. It is often defined verbally as representing chance variation among individuals in both traits (such as survival probability) and fates (such as whether the individual survived or not). In practice it is modeled as variation in fates only, with all individuals having identical underlying traits. In previous work we demonstrated that structured (but unmodeled) individual variability in survival traits can reduce the variance in population survivorship associated with demographic stochasticity, but that unstructured random variability in survival traits has no such effect. We implicitly generalized the latter result to fecundity, without offering proof. Robert et al. (2003) have demonstrated, using simulations, that unstructured individual variability in fecundity traits can increase the extinction risk of a small population when demographic stochasticity in fecundity is modeled as following a Poisson distribution. In this paper we extend our earlier theory to correct our mistaken speculations and analytically show the source of Robert et al.'s results. We also provide general predictions about the circumstances under which both structured and unstructured individual trait variation should either increase or decrease the magnitude of demographic stochasticity in the population.

The term *demographic stochasticity* is plagued by vague and contradictory definitions. It appears to have been coined by Robert May, who used it to describe the “stochastic features [that arise] because the population variable is fundamentally a discrete one” (May 1973: 33). This is picked up by influential papers (e.g., “chance events in the survival and reproductive success of a finite number of individuals;” Shaffer [1981: 131]) and textbooks (e.g., “individuals do not usually produce the average number of offspring, but rather, may have

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no offspring, fewer than the average, or more than the average;” Primack [2000: 132]) in conservation biology. These definitions do not clearly distinguish between variation in individual *traits* and variation in individual *fates*. Indeed, a major ecology textbook explicitly includes both in the definition: “random variations in the number of individuals that are born male or female, or in the number that happen to die or reproduce in a given year or in the quality (genotypic/phenotypic) of the individuals” (Begon et al. 1996: 927). In contrast, theoretical ecologists (e.g., Roughgarden 1975) rapidly linked the concept to existing statistical models of variation in the fate of individuals all sharing the same demographic traits. The latter definition, assuming that all individuals share the same traits, has been used in all quantitative applications in conservation biology.

Is trait variation important? We have shown that structured variation among individuals in their mortality risk can reduce the population-level variance associated with demographic stochasticity, suggesting that such structure might reduce extinction risk (Kendall & Fox 2002). By *structure* we mean that an individual’s demographic trait is not independent of the traits of the other individuals in the population, or of the identity of the individual. This can be because there are correlations among individuals at a given time (e.g., first-hatched chicks have higher survival than last-hatched chicks; “demographic covariance” sensu Engen et al. 1998) or within individuals across time (e.g., some individuals are healthier throughout their lives; “individual heterogeneity” sensu Conner & White 1999). Kendall & Fox (2002) also show that *unstructured* variation in survival probabilities (i.e., each individual draws its trait at random, independently of all the other individuals) would have no effect on the overall demographic variance (see Fox and Kendall [2002] for a more general proof).

In Kendall & Fox (2002) we did not explicitly claim that the second result (no effect of unstructured variation) extended to demographic processes other than survival. But we certainly believed that it did. This led to some sloppy claims, such as “... under the Poisson assumption, variation among individuals has no effect on demographic variance” (Kendall & Fox 2002: 113), which was really only justified for structured individual variation. However, in Fox & Kendall (2002: 1931) we did claim (without proof) that the result extended to fecundity.

Robert et al. (2003) analyzed a simulation model with two stage classes, demographic stochasticity (binomially distributed survival, Poisson-distributed fecundity) and unstructured variation in survival, fecundity, or both. They found that survival variation alone had no effect on the extinction risk, confirming our results. However, unstructured variation in fecundity increased the extinction risk. This was particularly surprising to us because we had also shown (Fox & Kendall 2002) that structured variation in Poisson-distributed fecundity should have no effect on the demographic variance.

This result showed that our generalization was wrong and that we had missed something important in the development of our theory. So, we sharpened our pencils, went back to work, and found that unstructured individual variation in fecundity (or in survival under a model other than the binomial) can have an effect on the demographic variance.

Before discussing our results, we need to define a variety of subtly different variances.

Variance in trait, $\text{var}(m)$: variance among individuals in m , the trait that underlies demographic performance (e.g., expected fecundity or survival probability; p in our earlier work).

Variance in individual fate, $\text{var}(f)$: variance associated with the uncertainty in f , an individual's fate (S in our earlier work). This uncertainty stems from both conventional demographic stochasticity and the unpredictability of the individual's trait.

Variance in population fate, $\text{var}(F)$: variance in F , the number of offspring or survivors for the entire population. If traits and fates are uncorrelated among individuals, then in a population of size N , $\text{var}(F) = N\text{var}(f)$.

Demographic variance, $V_D(m)$: variance in individual fate associated with conventional demographic stochasticity, given trait value m . For binomial survival, $V_D(m) = m(1 - m)$, and for Poisson-distributed fecundity, $V_D(m) = m$.

Demographic variance associated with the mean trait, $V_D(E[m])$: variance in individual fate associated with conventional demographic stochasticity, given the expected trait value for the entire population ($E[m]$). If all individuals had identical traits, then $\text{var}(f) = V_D(E[m])$ for all individuals and $\text{var}(F) = NV_D(E[m])$ for the population. We are looking for departures from this as a consequence of trait variation.

Our general result (see Appendix for derivation) is that the population-level demographic variance is related to the among-individual trait variance by

$$\text{var}(F) = N \left(V_D(E[m]) + \left[\frac{V_D''(E[m])}{2!} + 1 \right] \text{var}(m) + \frac{V_D'''(E[m])}{3!} \text{skw}(m) + \dots \right). \quad (1)$$

The primes refer to differentiation with respect to m , and $\text{skw}(m)$ is the skew of the trait distribution. The extension of the series involves successively higher-order derivatives of V_D and central moments of m .

This bears a striking resemblance to our previous result for structured individual variation (Fox & Kendall 2002):

$$\text{var}(F) = N \left(V_D(E[m]) + \frac{V_D''(E[m])}{2!} \text{var}(m) + \frac{V_D'''(E[m])}{3!} \text{skw}(m) + \dots \right). \quad (2)$$

The only difference is the $+1$ in the coefficient of $\text{var}(m)$, which is a mathematical (and nonintuitive) consequence of whether or not each individual's trait is predictable, as detailed in the appendix. This difference turns out to be crucial. For binomially distributed survival, $V_D'' = -2$, so the second term in the sum is zero, and because all higher-order derivatives are zero, there is no effect of

unstructured individual variability, confirming our prior results. However, for Poisson distributed fecundity, $V_D'' = 0$, so unstructured variation *increases* the population-level demographic variance:

$$\text{var}(F) = N [V_D(E[m]) + \text{var}(m)] . \quad (3)$$

Structured variation in Poisson-distributed fecundity has no effect on $\text{var}(F)$.

The Poisson distribution will not always be a biologically appropriate model for demographic stochasticity in fecundity. Other models will have different values of V_D'' . This term may even depend on $E[m]$. In anticipation of more plausible models, we can make the following generalizations:

- If $V_D''(E[m]) > 0$, then both structured and unstructured individual variation will *increase* the magnitude of demographic stochasticity, with negative effects on population persistence.
- If $V_D''(E[m]) < -2$, then both structured and unstructured individual variation will *decrease* the magnitude of demographic stochasticity, with positive effects on population persistence.
- If $-2 < V_D''(E[m]) < 0$, then structured and unstructured individual variation will have *opposite* effects on the magnitude of demographic stochasticity, with structured variation decreasing it and unstructured variation increasing it.
- Under all circumstances, unstructured individual variation will be more detrimental or less beneficial than structured variation.

So far we have only considered two extremes: the among-individual variation is either completely random or completely determined. Many sources of individual variation are likely to be intermediate, with partially correlated random variation. We suspect that the effects of partially structured variation will be intermediate between the cases examined here, but this is an important area for theoretical development.

We were clearly too sanguine in our earlier assessments of the benefits of individual variation in demographic traits. The results reported by Robert et al. (2003), together with the theory developed in this paper, make it clear that accurate population viability assessments will require both a biologically defensible model for demographic stochasticity in fecundity (which the Poisson distribution is not) and reasonable estimates of the structure and magnitude of individual variation in demographic traits. Only then will we be able to accurately estimate the magnitude of demographic stochasticity and its associated threat to the persistence of small populations.

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Appendix

Here we present the mathematical derivation of the effect of unstructured individual variation on the variance of population fate (Eq. 1). Assume each individual draws its trait from a probability distribution $p(m)$, with mean $E[m]$ and variance $\text{var}(m)$. The unstructured model means that each individual draws from the same distribution and that the draws are independent of one another. Thus, we need to consider two uncorrelated random processes: the drawing of the trait and the drawing of the fate conditioned on that trait, denoted $\text{Pr}[f|m]$. The demographic variance is formally defined as

$$V_D(m) = \sum_f (f - m)^2 \text{Pr}[f|m], \quad (\text{A.1})$$

where $\sum_f$ is the sum over all possible fates.

The probability that a given individual has a particular fate f is found by integrating Eq. A.1 over all possible fates:

$$\text{Pr}[f] = \int \text{Pr}[f|m] p(m) dm. \quad (\text{A.2})$$

The expected fate of the individual is $E[m]$. The variance in possible fates is

$$\text{var}(f) = \sum_f [(f - E[m])^2 \text{Pr}[f]] \quad (\text{A.3})$$

$$= \sum_f \left[(f - E[m])^2 \int \text{Pr}[f|m] p(m) dm \right] \quad (\text{A.4})$$

$$= \sum_f \left[\int (f - E[m])^2 \text{Pr}[f|m] p(m) dm \right] \quad (\text{A.5})$$

$$= \sum_f \left[\int [(f - m) + (m - E[m])]^2 \text{Pr}[f|m] p(m) dm \right] \quad (\text{A.6})$$

$$\begin{aligned} &= \int \sum_f [(f - m)^2 \text{Pr}[f|m]] p(m) dm \\ &+ 2 \int (m - E[m]) \sum_f [(f - m) \text{Pr}[f|m]] p(m) dm \\ &+ \int (m - E[m])^2 \sum_f (\text{Pr}[f|m]) p(m) dm. \end{aligned} \quad (\text{A.7})$$

The three sums in Eq. A.7 are respectively $V_D(m)$, zero, and one, so the variance in fates for the population is

$$\text{var}(f) = \int V_D(m) p(m) dm + \int (m - E[m])^2 p(m) dm \quad (\text{A.8})$$

$$= E[V_D(m)] + \text{var}(m). \quad (\text{A.9})$$

Unless V_D is linear, $E[V_D(m)] \neq V_D(E[m])$. Rather, it is given by

$$E[V_D(m)] = \int V_D(m)p(m)dm. \quad (\text{A.10})$$

To obtain general results, we replace $V_D(m)$ by its Taylor expansion around $E[m]$:

$$\begin{aligned} V_D(m) = V_D(E[m]) + V'_D(E[m])(m - E[m]) + \frac{V''_D(E[m])}{2!}(m - E[m])^2 \\ + \frac{V'''_D(E[m])}{3!}(m - E[m])^3 + \dots \end{aligned} \quad (\text{A.11})$$

Substituting this into Eq. A.10 and then simplifying gives

$$E[V_D(m)] = V_D(E[m]) + \frac{V''_D(E[m])}{2!}\text{var}(m) + \frac{V'''_D(E[m])}{3!}\text{skw}(m) + \dots \quad (\text{A.12})$$

Finally, substituting this expression into Eq. A.9 finally gives

$$\text{var}(f) = V_D(E[m]) + \left[\frac{V_D(E[m])}{2!} + 1 \right] \text{var}(m) + \frac{V'''_D(E[m])}{3!}\text{skw}(m) + \dots \quad (\text{A.13})$$

The population-level demographic variance is simply the population size times the individual-level demographic variance, giving rise to Eq. 1.