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Doak, Daniel F
Morris, William F
Pfister, Cathy
[et al.](#)

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Correctly Estimating How Environmental Stochasticity Influences Fitness and Population Growth

Daniel F. Doak,^{1,*} William F. Morris,^{2,†} Cathy Pfister,^{3,‡} Bruce E. Kendall,^{4,§} and Emilio M. Bruna^{5,||}

1. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064;

2. Biology Department, Duke University, Durham, North Carolina 27708;

3. Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637;

4. Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, California 93106;

5. Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611

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ABSTRACT: Increased temporal variance in life-history traits is generally predicted to decrease individual fitness and population growth. We show that a widely used result of stochastic sensitivity analysis that bolsters this generality is flawed because it ignores the effects of correlations between vital rates. Considering the effects of these correlations (although ignoring autocorrelations), we show that the apparently simple relationship between vital rate variance and fitness can be considerably more complex than previously thought. In particular, the previously estimated negative sensitivities of fitness or population growth to variance in a vital rate can be either enhanced by positive correlations between rates or reversed by negative correlations, even to the point that variability in a rate can increase fitness or population growth. We apply this new sensitivity calculation to data from the desert tortoise and discuss its interpretation in light of the factors generating vital rate correlations.

Keywords: stochasticity, matrix models, sensitivity, elasticity.

* Corresponding author; e-mail: doak@biology.ucsc.edu.

† E-mail: wfmorris@duke.edu.

‡ E-mail: cpfister@uchicago.edu.

§ E-mail: kendall@bren.ucsb.edu.

|| E-mail: brunae@wec.ufl.edu.

The constellation of effects that variable environments have on individual fitness and population growth is a major focus of both life-history analysis and demography (Cole 1954; Cohen 1966, 1968; Lewontin and Cohen 1969; Schaffer 1974; Tuljapurkar and Orzack 1980; Ellner 1985*a*, 1985*b*, 1987; Lande and Orzack 1988; Orzack 1993). For instance, many general theories of life-history evolution rely on some consideration of the effects of temporal variability (Gillespie 1977; Seger and Brockman 1987; Stearns 1992; Hairston and Bohonak 1998). Similarly, it is increasingly recognized that the failure to consider environmental stochasticity in demographic analyses can result in less precise and frequently biased results (Tuljapurkar 1990; Caswell 2001; Fieberg and Ellner 2001; Doak et al., forthcoming).

A long tradition of theoretical work has predicted that temporal variation in the components of individual performance is important in shaping population dynamics and life-history patterns. However, careful empirical analysis of the effects of stochasticity has been far less common, in part because of difficulties in using the types of data most commonly and readily collected to test these predictions. The exception to this mismatch is the use of demographic data and models to link empirical estimates of variance and correlation among life-history traits with the effects of stochasticity on population performance and fitness (Boyce and Perrins 1987; Kalisz and McPeck 1993; Liou et al. 1993; Philippi 1993*a*, 1993*b*; Pfister 1998; Menu et al. 2000; Menu and Desouhant 2002). A key generality to emerge from stochastic demography is that temporal variation in growth, survival, and other vital rates will negatively influence population growth and fitness. In particular, variation in the vital rates to which population growth is most sensitive will disproportionately decrease stochastic growth, and thus there should be strong selection against variation in these rates. The pleasantly intuitive nature of this result and the ability to test it with empirical data (e.g., Pfister 1998) have made this one of the most influential and widely understood results of stochastic demography.

Our goal here is threefold. First, we show that past

calculations of the sensitivities of population growth to the variability of vital rate values do not properly account for correlations among vital rates, and we derive the correct expression for these sensitivities. Second, we explain the biological importance of using this corrected formula. Briefly, when most correlations between vital rates are positive, the negative effects of variation in a rate can be substantially higher than previously estimated. Conversely, negative correlations can result in selection for higher variability in some rates, contrary to the results of past analyses. To our knowledge, this prediction, which runs counter to the predictions of the bet-hedging theory and other stochastic analyses, has not been explicitly made before. Finally, we provide an example to show that corrected estimates of sensitivity can differ substantially from those previously estimated. In particular, we show that positive sensitivities for variability in some vital rates can arise from real demographic patterns. For these discussions to make sense, we must first briefly review the generalities that have emerged from demographic matrix models about the consequences of stochastic variation in life-history traits.

Background

The starting point for analytical explorations of stochastic demography is Tuljapurkar's (1990) approximation for the stochastic log growth rate, $\log \lambda_s$. While Tuljapurkar's full approximation includes the effects of between-year correlations in matrix elements, we use the simpler version of his formula that omits this complication:

$$\log \lambda_s \approx \log \bar{\lambda}_1 - \frac{1}{2} \left(\frac{\tau^2}{\bar{\lambda}_1^2} \right),$$

$$\text{where } \tau^2 = \sum_{k=1}^s \sum_{l=1}^s \sum_{m=1}^s \sum_{n=1}^s \text{Cov}(e_{k,l}, e_{m,n}) \bar{S}_{e_{k,l}} \bar{S}_{e_{m,n}}. \quad (1)$$

Here, $\bar{\lambda}_1$ is the dominant eigenvalue of the mean matrix $\bar{\mathbf{A}}$, obtained by averaging each of the elements across all estimated annual projection matrices and weighting each by the frequency at which it is expected to occur. The approximate variance of the annual population growth rate caused by variation in the matrix elements, τ^2 , is a summation across all pairs of matrix elements ($e_{k,l}$ and $e_{m,n}$) of the covariances between the elements, $\text{Cov}(e_{k,l}, e_{m,n})$, multiplied by the sensitivities of $\bar{\lambda}_1$ to each of those elements, $\bar{S}_{e_{k,l}} \bar{S}_{e_{m,n}}$ (where the indexes k, l, m , and n refer to rows and columns of the population matrix). A sensitivity value such as $\bar{S}_{e_{k,l}}$ is the partial derivative of $\bar{\lambda}_1$ with respect to matrix element $e_{k,l}$ evaluated at its mean value: $\partial \bar{\lambda}_1 / \partial e_{k,l} |_{e_{k,l} = \bar{e}_{k,l}}$. Remember that $\text{Cov}(e_{k,l}, e_{k,l})$ is the variance of $e_{k,l}$ so that τ^2 includes both the variances and

covariances of the matrix elements. Analyses based on Tuljapurkar's approximation rest on the assumption that variation in matrix elements is relatively small, yet in general this small-noise approximation has proven quite robust (Fieberg and Ellner 2001; Doak et al., forthcoming).

One can arrive at the general result that variability in annual population growth reduces fitness by examining equation (1): $\log \lambda_s$ is approximately equal to the log deterministic growth rate, decreased by the variability term $-\tau^2/2\bar{\lambda}_1^2$. However, the more interesting question is how variation in a particular matrix element influences fitness. The terms in τ^2 with $k, l = m, n$ are simply $\text{Var}(e_{k,l}) \bar{S}_{e_{k,l}}^2$ so that the negative effect on $\log \lambda_s$ of variance in $e_{k,l}$ is weighted by the square of its deterministic sensitivity value. Thus, selection against variation in matrix elements will be highest for those elements with the highest sensitivity values.

This prediction is illustrated more completely by taking the derivative of equation (1) with respect to a particular covariance or variance term and approximating the sensitivity of $\log \lambda_s$ to changes in that variance or covariance (Caswell 2001). As with deterministic sensitivities, these stochastic sensitivities are widely interpreted as measures of the force of selection acting on elements of the life history (Caswell 2001). The vast majority of the terms in τ^2 do not include any particular covariance term, so the resulting stochastic sensitivity values are quite simple:

$$\frac{\partial \log \lambda_s}{\partial \text{Var}(e_{k,l})} \approx -\frac{1}{2\bar{\lambda}_1^2} (\bar{S}_{e_{k,l}})^2, \quad (2a)$$

$$\frac{\partial \log \lambda_s}{\partial \text{Cov}(e_{k,l}, e_{m,n})} \approx -\frac{1}{\bar{\lambda}_1^2} \bar{S}_{e_{k,l}} \bar{S}_{e_{m,n}}. \quad (2b)$$

Note that in these approximations, the sensitivity of stochastic growth to a variance or covariance term is a function only of the deterministic growth rate of the mean matrix and the deterministic sensitivity values of the mean matrix elements for the variance or covariance being considered.

Because sensitivities to matrix elements are always positive, the estimated sensitivities of $\log \lambda_s$ to variances and covariances are always negative (eqq. [2]). Equation (2a) is the basis for the generality that those matrix elements (and more important, the life-history traits they represent) that have higher sensitivity values should be under the strongest selection for low variance. In support of this prediction, Pfister (1998) found a negative correlation between the variances of matrix elements and their sensitivities across a range of species (the same pattern held for coefficients of variation and elasticities, which are rescaled sensitivity values; but see Morris and Doak 2004). Equation (2b) also implies that selection should favor more

negative covariances between stochastically varying matrix elements (Orzack and Tuljapurkar 1989).

A Complication in Analyzing Variance-Importance Trade-Offs

As we noted above, the standard stochastic sensitivity results rely on the assumption that only the terms of τ^2 that contain a particular variance and covariance term will influence the sensitivity value for that term. Implicitly, this is an assumption that the variance and covariance terms contained in τ^2 are independent of one another. In fact, this is wrong. One way to see this is to express the covariance of two rates in terms of their correlation and standard deviations: $\text{Cov}(e_{k,l}, e_{m,n}) = \text{Corr}(e_{k,l}, e_{m,n})\sigma_{e_{k,l}}\sigma_{e_{m,n}}$. A change in the covariance of these two rates can result from either a change in their correlation, a change in the standard deviation of $e_{k,l}$ or a change in the standard deviation of $e_{m,n}$. Conversely, a change in a standard deviation or variance of a matrix element must create changes in the covariances of that rate with all other rates, unless the correlations between these rates are also to change. This means that the simple sensitivity and elasticity expressions usually shown for variances and covariances in equations (2) (e.g., eqq. [14.110] and [14.111] in Caswell 2001 and eq. [9.15] in Morris and Doak 2002) are incorrect.

To derive better estimates of these sensitivities and elasticities, it helps to recast the problem in terms of correlations and standard deviations, thereby separating variance from correlation at the onset. While we are at it, it also makes for more biologically informative results to express Tuljapurkar's expression for τ^2 in terms of the vital rates (e.g., survival, growth, and fecundity values) that underlie the matrix elements rather than the matrix elements themselves:

$$\tau^2 = \sum_i \sum_j \rho_{v_i v_j} \sigma_{v_i} \sigma_{v_j} \bar{S}_{v_i} \bar{S}_{v_j}, \quad (3)$$

where the summations across i and j now refer to vital rates v_i and v_j , \bar{S}_{v_i} is the sensitivity of λ_1 to changes in the mean of vital rate i , σ_{v_i} is the standard deviation of vital rate i , and $\rho_{v_i v_j}$ is the correlation between rates v_i and v_j . With this reexpression, we see that the contribution of the variability of v_i to τ^2 is $\sigma_{v_i}^2 \bar{S}_{v_i}^2 + \sigma_{v_i} \bar{S}_{v_i} \sum_{j \neq i} \rho_{v_i v_j} \sigma_{v_j} \bar{S}_{v_j}$. In other words, the influence of variability in v_i is determined not only by its own sensitivity but also by the sensitivity and variability of all other vital rates to which it is correlated.

To see how these correlations can mediate selection on variability in vital rates, it helps to consider the sensitivities of $\log \lambda_s$ to standard deviations and correlations in vital rates:

$$\frac{\partial(\log \lambda_s)}{\partial \sigma_{v_i}} \approx \frac{-1}{\lambda_1^2} \sum_j \bar{S}_{v_i} \bar{S}_{v_j} \rho_{v_i v_j} \sigma_{v_j}, \quad (4a)$$

$$\frac{\partial(\log \lambda_s)}{\partial \rho_{v_i v_j}} \approx \frac{-1}{\lambda_1^2} \bar{S}_{v_i} \bar{S}_{v_j} \sigma_{v_i} \sigma_{v_j}. \quad (4b)$$

The key difference between the expression for $\partial(\log \lambda_s)/\partial \sigma_{v_i}$ in equation (4a) and that for $\partial \log \lambda_s / \partial \text{Var}(e_{k,l})$ in equation (2a) is that the summation on the right-hand side of equation (4a) includes the standard deviations of all vital rates that are correlated with v_i . Rewriting equation (4a) to separate these standard deviations from that of the target vital rate, v_i , yields

$$\frac{\partial(\log \lambda_s)}{\partial \sigma_{v_i}} \approx \frac{-1}{\lambda_1^2} \left(\bar{S}_{v_i}^2 \sigma_{v_i} + \sum_{j \neq i} \bar{S}_{v_i} \bar{S}_{v_j} \sigma_{v_j} \rho_{v_i v_j} \right). \quad (5)$$

A simple transformation can also be used to yield the elasticities of λ_s (not $\log \lambda_s$ as above) to variance and correlation $E_{\sigma_{v_i}}$ and $E_{\rho_{v_i v_j}}$:

$$E_{\sigma_{v_i}} \approx \frac{-\sigma_{v_i} S_{v_i}}{\lambda_1^2} \left(\bar{S}_{v_i} \sigma_{v_i} + \sum_{j \neq i} \bar{S}_{v_j} \rho_{v_i v_j} \sigma_{v_j} \right), \quad (6a)$$

$$E_{\rho_{v_i v_j}} \approx \frac{-\rho_{v_i v_j} \bar{S}_{v_i} \bar{S}_{v_j}}{\lambda_1^2} \sigma_{v_i} \sigma_{v_j}. \quad (6b)$$

The expression in the parentheses of equation (5) shows that it is possible for strong correlations with other vital rates to substantially influence the overall sensitivity of λ_s to variation in a vital rate. Consider the situation in which all \bar{S}_{v_i} values are positive. When considered alone, variance in each vital rate will negatively influence stochastic growth. In this case, negative correlations between v_i and other rates will lead to a positive elasticity for variance if $-\sum_{j \neq i} \bar{S}_{v_j} \rho_{v_i v_j} \sigma_{v_j} > \bar{S}_{v_i} \sigma_{v_i}$. In words, if v_i is sufficiently negatively correlated with vital rates that have sufficiently high variances and sensitivities, then selection can favor higher variance in that rate, even if variance in v_i would appear maladaptive if considered alone.

It is important to remember that unlike the sensitivities of matrix elements, deterministic sensitivities of vital rate means are not necessarily positive. Vital rates such as the probability of shrinking into a smaller size class (for plants and some invertebrates) or transitioning to postbreeding stages (observed in many animals) will usually have negative sensitivity and elasticity values. The same is true of the probabilities of death that arise from particular causes, which, especially in management contexts, are often included in matrices as mortality rather than survival probabilities. For rates such as these, strong positive correlations with vital rates having positive deterministic sen-

sitivities may reverse the sign of otherwise positive variance elasticity and sensitivity values, leading to selection for low variance. To illustrate the possible effects of correlations on variance sensitivity values, consider the effect of just one correlated vital rate j on the sensitivity to variance in rate i . This effect is determined by a single term in the summation in equation (5), $\bar{S}_{v_i} \bar{S}_{v_j} \sigma_{v_i v_j} \rho_{v_i v_j}$, the sign of which will vary with the combined signs of both deterministic sensitivity values and the correlation between the two rates (table 1).

A clear understanding of the forces generating these results is important to avoid their misinterpretation. In particular, the possible benefit of increased variance in a life-history trait shown by these sensitivity results is not due to a life-history trade-off, in any usual sense of the term. A trade-off would imply that increased variability in one vital rate would lead to an increased mean or decreased variability in another rate, thereby benefiting fitness. Such allocation trade-offs are likely in many contexts and, with enough data to estimate their parameters, can be incorporated into matrix models fairly easily (e.g., van Tienderen 1995). This type of trade-off can be one source of the negative correlations between vital rates that we might observe and use as parameters in a stochastic demography model. However, the trade-offs themselves are not included in the analysis we explore here, which assumes that changes in one vital rate variance can occur independently of any other variance or mean. Rather, the effects of correlations that we show result from the ability of variation in negatively correlated rates to counteract each other's effects. This reduces τ^2 , the overall variability in annual growth or performance, from year to year. If increased variance in one vital rate will offset the variation in τ^2 caused by others, this variation will be favored. While Tuljapurkar's approximation and hence our analyses do not fully account for the complexities of real structured population growth (Tuljapurkar 1990; Caswell 2001), simulations we have conducted confirm that variability in vital rates can indeed result in higher population growth rates.

Does This Correction Make a Difference?

To show how the corrected formula for variance sensitivities (eq. [5]) can alter the conclusions of a stochastic sensitivity analysis, we used information for the desert tortoise, a widely used example of a stochastic matrix model (Doak et al. 1994; Caswell 2001; Morris and Doak 2002). In particular, we contrasted the results of equation (5) with predictions that ignore all correlated vital rate effects (i.e., setting the summation on the right-hand side of eq. [5] to 0; this is the equivalent of eq. [2a] for covariances between mean matrix elements). The corrected sensitivity values differ sharply from the uncorrected ones,

Table 1: Effect of correlations between vital rates on the sensitivity of stochastic growth rate to vital rate variation

Correlation between the two vital rates	Deterministic sensitivities of a pair of vital rates		
	Both positive	One positive, one negative	Both negative
Positive	–	+	–
Negative	+	–	+

Note: The sign of the correlation between two rates ($\rho_{v_i v_j}$) combines with the signs of their deterministic sensitivity values (\bar{S}_{v_i} and \bar{S}_{v_j}) to determine whether stochasticity sensitivity will be increased (plus sign) or decreased (minus sign).

increasing by up to 97-fold in magnitude and, in four out of 11 cases, changing from negative to positive (fig. 1A). For most variances, the contribution to the entire corrected sensitivity value from indirect effects of correlated rates was nearly as high or even higher than that of the direct effects (fig. 1B).

Examination of particular vital rates makes it clear why some sensitivities change so dramatically. When including correlation effects, the sensitivity of growth to the standard deviation in survival of class 4 tortoises, σ_{s_4} , becomes far more negative. This is because the survivorship of class 4 tortoises, s_4 , is positively correlated with all of the other survival rates except that of the largest tortoises, to which λ_s is least sensitive (fig. 2A). While growth rates show a mix of positive and negative correlations, they have much lower sensitivity values than do the survival rates to which s_4 is consistently positively correlated. Thus, the negative effect on λ_s of increasing σ_{s_4} would be greater than otherwise predicted because s_4 varies in concert with these other survival rates. In contrast, the sensitivity to variability in size class 2 tortoises, σ_{g_2} , goes from near 0 to positive when considering indirect effects. This is because g_2 is negatively correlated with all of the survival rates except that of the largest size class (fig. 2B). In other words, σ_{g_2} helps to balance the variance in these other vital rates, thereby reducing their effects on λ_s . Other vital rates, such as g_6 , have low or mixed correlations with the influential survival rates. Their variance sensitivities are therefore little changed by including correlated effects (fig. 2C). Overall, the use of our new formulation substantially changes the picture that emerges from a stochastic sensitivity analysis of variance terms and shows that predictions of selection for higher variability can emerge from real life-history patterns.

Conclusions

Matrix models have become one of the most commonly used quantitative tools in ecology, with applications rang-

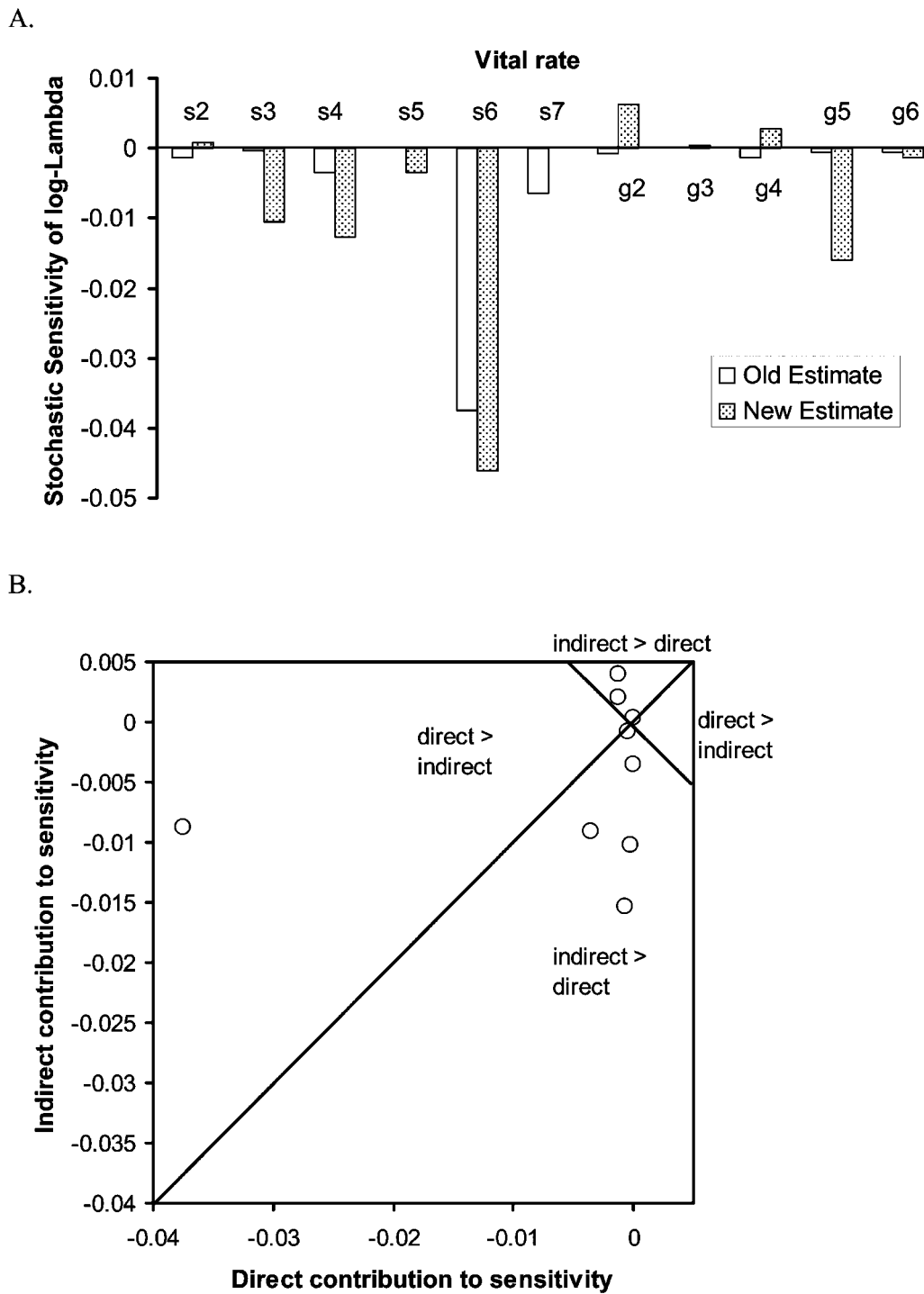


Figure 1: Results of old and revised sensitivity analyses for the desert tortoise. *A*, Sensitivity of $\log \lambda_s$ to the standard deviations of survival and growth rates for the desert tortoise. Old estimates do not account for correlations between vital rates, while new estimates use equation (5) to include these effects. Rates are for stages 2–7 for survival (s_2 – s_7) and stages 2–6 for growth (g_2 – g_6). *B*, Direct contribution to each stochastic sensitivity value is plotted against the indirect contribution due to correlations with other rates. Labels indicate regions where the magnitude of the direct contribution is greater than that of indirect contributions or visa versa. See Doak et al. (1994) for underlying data and definitions of vital rates.

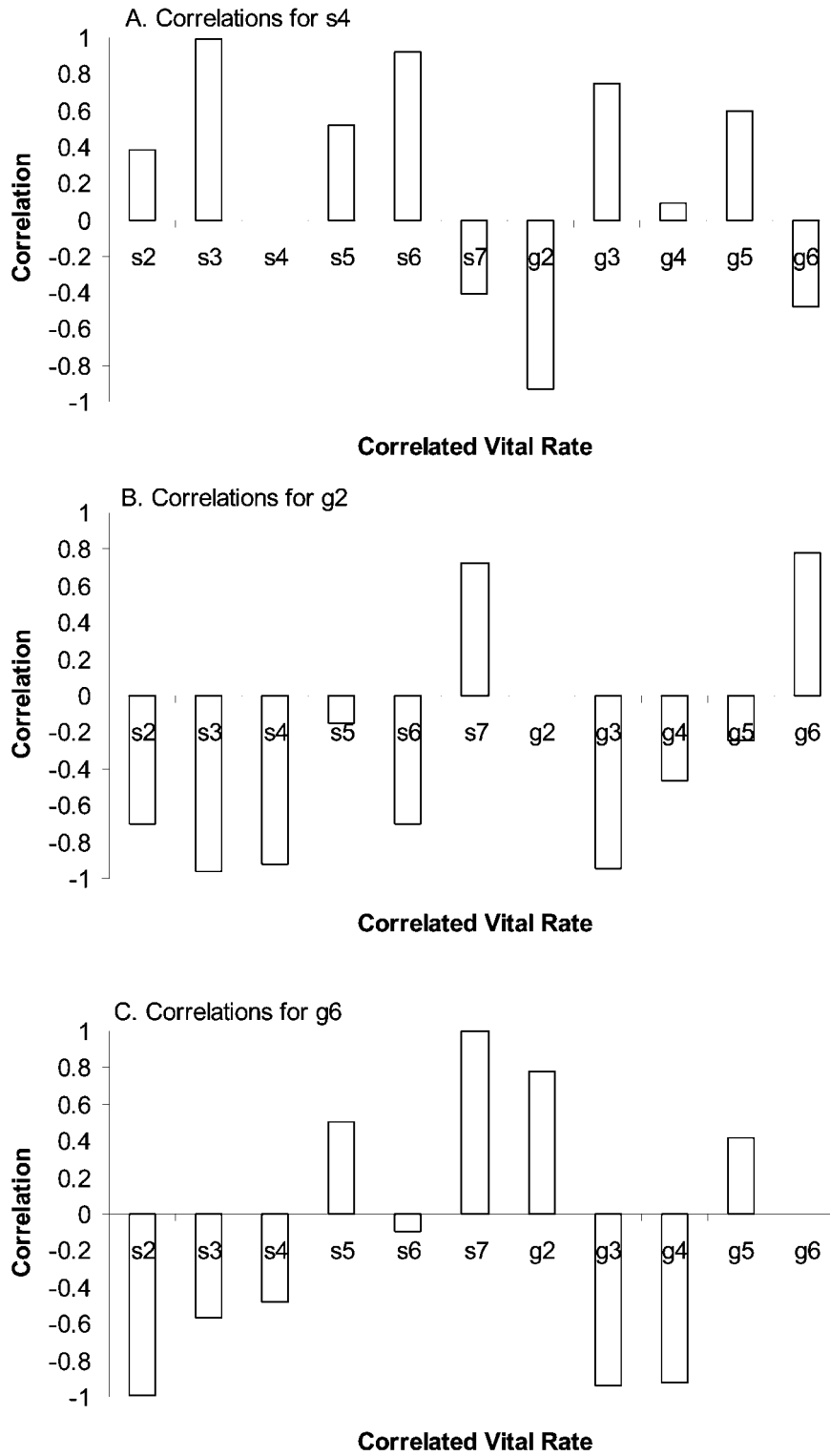


Figure 2: Examples of correlations between vital rates for the desert tortoise. Each graph shows estimated correlations with other survival and growth rates (no estimates of fecundities were available with which to make correlation estimates; Doak et al 1994). Correlations are shown for A, *s4*; B, *g2*; and C, *g6*.

ing from the management of populations to the search for life-history patterns. A major use of matrix models is sensitivity analysis, which provides a way to predict the fitness consequences of changes in different vital rates and the efficacy of management actions. We show here that a broad generality of stochastic matrix models—that increased variance in vital rates is never favored—is a substantial oversimplification. In particular, negative correlations in the variance of different vital rates can drastically change the sensitivity of stochastic population growth to vital rate variation, even leading to higher population growth rates with increased variability of some vital rates.

In a similar but distinct vein, Tuljapurkar (1990, pp. 82–83) provides an example of synergistic effects of matrices on population growth. Also, Tuljapurkar et al. (2003) found cases in which increasing the variability of matrix elements predicted increased population growth rate. However, in neither case have previous researchers noted the general ability of sensitivity analysis to predict selection for variation and the importance of correlation structures in generating these results. We caution that the corrected sensitivities and elasticities we present in equations (4)–(6) inherit from Tuljapurkar's approximation (eq. [1]) the assumptions that the environment is uncorrelated from year to year and that environmental variability is not excessive. When either assumption is seriously violated, sensitivities of the population growth rate to vital rate variability could also be computed by perturbation methods described by Tuljapurkar (1990) and Tuljapurkar et al. (2003).

Overall, our results demonstrate that vital rate variation can have stronger and more varied effects on fitness and population growth than have been previously shown, opening the door to more informative analyses and applications of demographic models. We do not expect that our revised sensitivity expressions will always result in substantial changes in estimated sensitivities. However, when individuals of different stages live in close proximity, many vital rates are expected to have substantial correlations from the effects of shared environmental drivers. These correlations, which can be positive or negative, will have significant effects in sensitivity analyses. This is especially true for the estimation of the sensitivity of population growth or fitness to variation in traits.

Because of the importance of correlations in determining sensitivity values, our results emphasize the need for empirical studies to estimate correlation patterns as accurately as possible and to consider these estimates when making demographic predictions. In many cases, correlations are not considered in demographic analyses because they can be only poorly estimated (Fieberg and Ellner 2001). Furthermore, almost all estimates of correlations are biased toward 0, so we routinely underestimate

the strength of their effects (Doak et al., forthcoming). While many of the problems of accurately estimating variation and correlation in vital rates cannot be easily solved, our results show the importance of these parameters for an accurate understanding of demographic and evolutionary predictions and therefore the need to judiciously use this information in future analyses.

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