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Contributions of Covariance: Decomposing the components of stochastic population growth in *Cypripedium calceolus*

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Abstract

Although correlations between vital rates can have important effects on evolution and demography, few studies have investigated their effects on population dynamics. Here, we extend Life Table Response Experiments (LTREs) to variable environments, showing how to quantify contributions made by: (1) mean vital rates, (2) variability driven by environmental fluctuations, (3) correlations implying demographic tradeoffs and reflecting stage transition synchrony and (4) elasticities reflecting local selection pressures. Applying our methods to the Lady's Slipper orchid *Cypripedium calceolus*, we found that mean rates accounted for 77.1% of all effects on the stochastic growth rate, variability accounted for 12.6%, elasticities 6.6% and correlations 3.7%. Stochastic effects accounted for 17.6%, 15.3% and 35.9% of the total in our three populations. Larger elasticities to transitions between dormancy states and stronger correlations between emergence and survival suggest that one population was under greater pressure to remain active while the other two showed survival payoffs for dormancy in poor years. Strong negative correlations between dormancy, emergence and stasis balanced opposing contributions, resulting in near-stationarity in two populations. These new methods provide an additional tool for researchers investigating stochastic population dynamics and should be useful for a broad range of applications in basic ecology and conservation biology.

Keywords

Covariance; Stochastic Population Growth; Life Table Response Experiment (LTRE); Correlation; Elasticity

Introduction

Natural populations experience fluctuations in environmental conditions which, in turn, produce fluctuations in the vital rates that drive population dynamics. Furthermore, vital rates are often correlated, with some rates increasing or decreasing simultaneously and others diverging. These correlations can have important effects on both evolution (Lande and Arnold 1983) and demography (van Noordwijk and de Jong 1986). Correlations between vital rates illustrate the relative synchrony of different stage transitions and they often reveal fundamental life history tradeoffs imposed by physiological or environmental

constraints. Although vital rate correlations may also be genetically based (e.g., Cheverud 1988; Endels et al. 2007), these are often difficult to distinguish from the phenotypic correlations (Roff 1995) reflecting covariance of demographic rates and responses to environmental drivers that are latent in our models (Cheverud 1988; Nicolè et al. 2011).

Correlations between vital rates can be either negative or positive. Negative correlations may reflect zero-sum physiological constraints on life histories, like those placed on individuals allocating finite resources to one life cycle pathway as opposed to another (e.g., spending energy on growth that could be used for reproduction). Negative correlations may also highlight differences in the environmental cues for development and reproduction, as when growth is favored under some conditions and reproduction under others. For instance, negative correlations between fertility and survival probabilities of a given stage or age class may describe a cost of reproduction or indicate differences in the conditions favoring survival vs. reproduction (e.g., Jongejans and de Kroon 2005).

Positive correlations between vital rates, on the other hand, may indicate commonality in the environmental conditions favoring particular transitions. For survival transitions, rates may increase or decrease together because of similarity in the sources of mortality or in the conditions favoring growth, while positive correlations between fertility and survival may indicate that individuals are tracking their reproductive potential and are staying within the physiological constraints placed on them by their own nutritional status or by local environmental conditions (e.g., Descamps et al. 2006, Jongejans et al. 2010). For instance, healthy individuals, or those living in favorable habitats, may be able to reproduce at higher levels without survival costs while those with fewer resources avoid the survival costs by limiting reproduction (e.g., Law 1979, Pyle et al. 1999). Thus fertility and survival go up and down together as individuals respond to changing environmental conditions.

Between populations, vital rates often differ greatly due to local adaptation or due to differences in the habitat conditions driving vital rates (Jongejans and de Kroon 2005). The degree to which vital rates vary and the correlations between vital rates are also expected to differ between some populations and these differences may be apparent when comparing the covariance structures of vital rates estimated for distinct populations. Because vital rate correlations can have large effects on populations (Wisdom et al. 2000), differences in the strength (or sign) of correlations may drive population growth rates apart. Phenotypic correlations are likely to reflect important processes driving population dynamics, so understanding these correlations provides us with valuable information about the ecological and selective contexts within which populations persist or decline. Understanding correlations also enables managers to more effectively target interventions that leverage positive correlations to produce synergies among management effects while avoiding undesirable indirect effects that correlations may indicate.

For instance, if there is a higher survival cost of reproduction in harsh environments, a stronger negative correlation between survival and reproduction can be expected in marginal populations, resulting in low population growth rates in poor habitats. Quantifying the effects of these differences can tell us which particular tradeoffs are important for population dynamics. These differences may be due to population genetics reflecting adaptation to local selection pressures, or they may be due to habitat conditions that buffer or magnify the effects of environmental variability. In either case, knowing that the survival costs of reproduction are higher in certain populations may suggest that some populations would benefit from transplanted individuals born in populations with lower costs of reproduction.

Despite their recognized importance, few studies have directly investigated the effects of vital rate correlations on the demography of plant and animal species. Indirect elasticities

(van Tienderen 1995) can estimate the potential effect of correlations on population growth rates (e.g., Saether and Bakke 2000) but no one has used these to decompose observed population-level differences. In population biology and evolutionary ecology, Life Table Response Experiments (LTREs) are a common method for comparing the population-level effects of differences in vital rates and these have traditionally relied solely on mean vital rates (Caswell 2001). Recent stochastic LTREs quantify the effects of variability in vital rates (Davison et al. 2010) or distinguish the effects of vital rate responses from those of local habitat dynamics (Caswell 2010), but none of these techniques access the effects of correlations between vital rates or address differences in vital rate elasticities.

In this paper, we develop Stochastic Life Table Response Experiment (SLTRE) methods for decomposing differences in population growth rates into contributions from (1) mean vital rates, (2) variability of vital rates, (3) correlations between vital rates and (4) elasticities of vital rates. Mean vital rates describe average performance, variability in vital rates describes responses to fluctuating environments and correlations may indicate tradeoffs or synchrony of stage transitions (Boyce et al. 2006), while vital rate elasticities reflect local selection pressures (Benton and Grant 1996, 1999).

We apply a singular value decomposition developed by Kitagawa (1955) to the small noise approximation of the stochastic growth rate (Tuljapurkar 1990) in order to rank the importance of covariance elements as drivers of observed population dynamics. Our methods identify which statistical factors contribute to differences in population growth rates and allow us to interpret these differences in terms of the forces (e.g., environmental variability, phenotypic trade-offs, etc.) that shape variance and correlations among vital rates. We begin by describing the decomposition method, which is somewhat tedious but straightforward. We then illustrate this new method using empirical data on the Lady's Slipper orchid *Cypripedium calceolus*

In particular, our objectives are to: (1) disentangle the contributions of means, variances, correlations and elasticities of vital rates to stochastic population growth rates; (2) quantify the effects of phenotypic tradeoffs implied by the correlation structure of vital rates; (3) understand how variability in these tradeoffs drives observed population dynamics; and (4) show how differences in local selection pressures can drive population growth rates. This allows us to interpret vital rate correlations and elasticities in meaningful biological terms and relate them to environmental factors.

Small noise decomposition of stochastic contributions

When demographic rates vary with time, population growth is described by a stochastic growth rate (Cohen 1977; Tuljapurkar and Orzack 1980). For a stage-structured population with N stages (labeled i, j) an annual projection matrix $\mathbf{A}$ ($\mathbf{A}(t) = \{a_{ij}(t)\}$) describes the number of stage i individuals contributed to the population in year $t+1$ by one stage j individual in year t ; we observe rates over the years $t = 1, 2, \dots, T$. When fluctuating vital rates (e.g., survival and fertility) alter the matrix elements a_{ij} , this drives fluctuations in annual population growth rates described by the dominant eigenvalues ($\lambda(t)$) of the projection matrices $\mathbf{A}(t)$. In this case, long term population growth is described by the stochastic growth rate ($\lambda = \log \lambda$) and is often well approximated by the small noise approximation (Tuljapurkar 1990).

The dominant eigenvalue (λ) and the intrinsic growth rate ($r = \log \lambda$) of the mean projection matrix $\mathbf{B}$ ($\mathbf{B} = \{\mu_{ij}\}$) depend on mean rates μ_{ij} (where $\mu_{ij} = E_t\{a_{ij}(t)\}$) and E_t is the expectation over T years). For each pair of elements ij and kl , we can also compute

sensitivities s_{ij} and s_{kl} , elasticities e_{ij} and e_{kl} , standard deviations σ_{ij} and σ_{kl} , coefficients of variation c_{ij} and c_{kl} , and the correlation coefficient $\rho_{ij,kl}$.

For population m the small noise approximation can be written in terms of elasticities (e_{ij} , e_{kl}) and the scaled covariance ($c_{ij}c_{kl}\rho_{ij,kl}$) of the matrix elements a_{ij} , a_{kl} (Caswell 2001: 399):

$$a^{(m)} = \log \lambda_s^{(m)} \approx r^{(m)} - \frac{1}{2} \sum_{i,j} \sum_{k,l} \{e_{ij}e_{kl}c_{ij}c_{kl}\rho_{ij,kl}\}^{(m)}. \quad (1)$$

To compare a given set of populations, we examine the difference between the stochastic growth rates $a^{(m)}$ of each population m and $a^{(R)}$ computed for a reference population R , which may be an experimental control or, commonly, the mean across populations (Caswell 2001). We follow Davison et al. (2010) and reference to the average across populations,

where $a_{ij}^{(R)}(t) = E_m \{a_{ij}^{(m)}(t)\}$ and $\mu_{ij}^{(R)} = E_t \{a_{ij}^{(R)}(t)\}$.

We work with the lower-level parameters determining matrix elements (Caswell 2001: 232) and in the remainder of this paper we will refer to them simply as the vital rates, which include fertility rates f_j (in our example first row off-diagonal matrix elements), stage-specific survival probabilities p_j and survival-conditioned stage transition rates t_{ij} . For non-

fertility elements $a_{ij} = p_j t_{ij}$ and the survival-conditioned transition matrix is $\mathbf{T} = \left\{ t_{ij} = \frac{a_{ij}}{p_j} \right\}$,

where $\sum_j t_{ij} = 1$. We stack these vital rates to form a vector x_k ($x_k = \{f_j, t_{ij}, p_j\}$) containing vital rates for population m in year t . We then compute means (μ_k), elasticities (e_k), coefficients of variation (c_k), and pairwise correlations (ρ_{kl}) of these lower-level vital rates. Note that elasticities to lower-level parameters do not necessarily sum to 1 (Caswell 2001).

The difference () between the stochastic growth rates of each population m and population R is

$$\begin{aligned} (a^{(m)} - a^{(R)}) &\approx (r^{(m)} - r^{(R)}) - \frac{1}{2} \left(\sum_{k,l} \{e_k e_l c_k c_l \rho_{kl}\}^{(m)} - \sum_{k,l} \{e_k e_l c_k c_l \rho_{kl}\}^{(R)} \right) \\ &\approx \Delta r - \frac{1}{2} \Delta \left(\sum_{k,l} \{e_k e_l c_k c_l \rho_{kl}\} \right). \end{aligned} \quad (2)$$

Singular Value Decomposition

The last term on the right in equation (2) contains pairwise products of the elasticities (e_k, e_l) and coefficients of variation (c_k, c_l) and pairwise correlations (ρ_{kl}). To isolate the effect of differences in each, we apply the singular value decomposition for a sum of products developed by Kitagawa (1955). Suppose that population A is characterized by parameters ($X_1^{(A)}, X_2^{(A)}$) and ($Y_1^{(A)}, Y_2^{(A)}$) and population B by ($X_1^{(B)}, X_2^{(B)}$) and ($Y_1^{(B)}, Y_2^{(B)}$). We are

interested in the difference between $Z^{(A)} = \sum_i X_i^{(A)} Y_i^{(A)}$ and $Z^{(B)} = \sum_i X_i^{(B)} Y_i^{(B)}$. Using averages ($\bar{X}_i = 0.5(X_i^{(A)} + X_i^{(B)})$) and differences $\Delta X_i = X_i^{(A)} - X_i^{(B)}$, the Kitagawa decomposition states that

$$Z^{(A)} - Z^{(B)} \sum_i X_i^{(A)} Y_i^{(A)} - \sum_i X_i^{(B)} Y_i^{(B)} = \sum_i \bar{X}_i (\Delta Y_i) + \sum_i \bar{Y}_i (\Delta X_i). \quad (3)$$

The first summed term isolates the effect of differences in the Y_i because each X_i is held constant at its mean value; the second summed term isolates the effect of differences in the X_i . In our application the X_i and Y_i are the factors in the small noise approximation, representing the pairs of either elasticities ($e_k e_l$) or coefficients of variation ($c_k c_l$), or the correlation coefficients (ρ_{kl}). The differences (ΔX) are calculated between, and the averages ($\bar{X}$) are calculated across, each pair of vital rates in each target population (m) relative to the corresponding pair in the reference population (R). For instance, for elasticity elements (e_k, e_l), $\Delta\{e_k e_l\} = e_k e_l^{(m)} - e_k e_l^{(R)}$ and $\bar{e}_k \bar{e}_l = 0.5(e_k e_l^{(m)} + e_k e_l^{(R)})$.

We iterate the decomposition twice in order to compute the contributions of each pair ($e_k e_l$, $c_k c_l$ and ρ_{kl}) (see Appendix A for intermediate steps):

$$\Delta \sum_{k,l} \{e_k e_l c_k c_l \rho_{kl}\} = \sum_{k,l} (\bar{c}_k \bar{c}_l \bar{\rho}_{kl} \Delta\{e_k e_l\}) + \sum_{k,l} (\bar{e}_k \bar{e}_l \bar{\rho}_{kl} \Delta\{c_k c_l\}) + \sum_{k,l} (\bar{e}_k \bar{e}_l \bar{c}_k \bar{c}_l \Delta\{\rho_{kl}\}). \quad (4)$$

Taken individually, these sums are contributions that represent the “pure” effects of differences in elasticities, in variability and in correlations, respectively. For the difference in intrinsic growth rates (r) we use deterministic LTRE (Caswell 2001) with a transformation to predict the change in $r = \log \lambda$ instead of the change in λ (see Appendix B):

$$\Delta r = r^{(m)} - r^{(R)} = \sum_k \left(\frac{\Delta \mu_k^{(m)}}{\mu_k^{(R)}} \right) e_k^{(R)}. \quad (5)$$

Putting it all together,

$$\Delta a = a^{(m)} - a^{(R)} \approx (r^{(m)} - r^{(R)}) - \frac{1}{2} \left(\sum_{k,l} \{e_k e_l c_k c_l \rho_{kl}\}^{(m)} - \sum_{k,l} \{e_k e_l c_k c_l \rho_{kl}\}^{(R)} \right) \quad (6)$$

$$\approx \left(\sum_k \left(\frac{\Delta \mu_k^{(m)}}{\mu_k^{(R)}} \right) e_k^{(R)} \right) - \frac{1}{2} \left(\sum_{k,l} (\bar{c}_k \bar{c}_l \bar{\rho}_{kl} \Delta\{e_k e_l\}) + \sum_{k,l} \bar{e}_k \bar{e}_l \bar{\rho}_{kl} \Delta\{c_k c_l\} + \sum_{k,l} \bar{e}_k \bar{e}_l \bar{c}_k \bar{c}_l \Delta\{\rho_{kl}\} \right). \quad (7)$$

We denote the contributions C_k^μ , C_{kl}^e , C_{kl}^c and C_{kl}^ρ , where the superscript indicates one of four contributions: means (μ_k), elasticities ($e_k e_l$), variability ($c_k c_l$) or correlations (ρ_{kl}) of a particular vital rate (x_k) or pair of vital rates (x_k, x_l). For clarity we label the contribution of differential variability C even though we are computing contributions of coefficients of variation ($c_k = CV_k = s_k / \mu_k$) instead of those of standard deviations (s_k) directly. At the

population level, $(\sum_k C_k^{\varphi(m)})$ estimates the net contribution in population m made by

differences in the statistic ($= \mu, e, c, \text{ or } \rho$) and $(\sum_k |C_k^{\varphi(m)}|)$ estimates the total effect of

that vital rate (counting both positive and negative effects). Likewise, $(\sum_\varphi C_k^{\varphi(m)})$ estimates

the net contribution of the vital rate x_k and $\left(\sum_{\varphi} |C_k^{\varphi(m)}|\right)$ estimates the total effect of on the stochastic growth rate. In Appendix C, we provide definitions of each type of stochastic contribution, as well as the conditions under which they will increase the stochastic growth rate (i.e., $C_k^{\varphi} > 0$). Appendix D contains a simple numerical example showing how to calculate these stochastic contributions and Appendix E contains MATLAB code for calculating stochastic contributions from population projection matrix elements.

Within-stage vs. between stage correlations

Within-stage correlations are those computed among transitions out of a given stage (i.e., those within the same column of a projection matrix). For a given population, these are calculated across the time frame of a study and may indicate tradeoffs due to physiological costs of reproduction or growth during the period of observation. For instance, a contribution of the correlation between young adult fertility and survival probabilities may indicate differences in the survival cost of reproduction for that stage class. These correlations may also indicate differences in the conditions favoring fertility and survival, or they may reflect the algebraic structure of our models necessitated by zero-sum constraints on alternative survival transitions such as stasis vs. growth.

Between-stage correlations describe the relative synchrony of stage transitions and they reflect the effects of common environments on different life cycle stages (e.g., whether environmental conditions that are favorable for growth or fertility of one stage class are also favorable for other stages in the life cycle). If, for example, we identify a contribution of the correlation between juvenile and adult survival, we conclude that the distribution of relative risks experienced by individuals of these stages differs between populations. In this case, it may be that a drought year reduces both juvenile and adult survival in one population while in another population adults are buffered against mortality by deeper soils or greater water availability. We pay particular attention to between-stage correlations that describe the relative synchrony of similar life cycle transitions (Silvertown et al. 1992; Silvertown et al. 1993). For instance, contributions of the correlations between growth probabilities of different stages describe the effects of population-level differences in the conditions favoring growth.

Differences in vital rate correlations can result from the combined effects of local environmental differences and of different responses to “shared” environments. Spatially distinct populations may be close enough to experience the same weather and yet differ in habitat characteristics such as soil structure or nutrient availability. These differences may influence populations responses to a common temporal weather sequence and may alter the degree, or even the sign, of correlations between vital rates.

Decomposition of *Cypripedium calceolus* stochastic growth rates

In this section we examine the role vital rate covariances play in driving the population dynamics of *Cypripedium calceolus* (Lady’s Slipper orchid), a long-lived perennial orchid growing in shady woodlands on calcareous soils (Cribb 1997). The species has protected conservation status across Europe (Kull 1999). Because previous research (Nicolè et al. 2005) found that dormancy transitions explained 40% of the variance in deterministic population growth rates, we pay particular attention to the effects of tradeoffs between dormancy and survival or growth.

Three natural populations of this boreal geophyte grow in Biebrza National Park, northeast Poland, the largest protected swamp in western Europe. Populations were surveyed on three

mineral islands in the Biebrza River: Zabudnik (ZAB), an oak-hornbeam forest; Pogorzaly (POG), an oak-linden-hornbeam forest; and Oparzelisko (OPA), a 15–20 year-old birch forest (Brzosko 2002; Brzosko et al. 2002; Nicolè et al. 2005). Eight annual surveys yielded seven transition matrices for each population. The life cycle is divided into 10 stages representing a seed bank with stasis, three underground protocorm stages (described by annual protocorm survival probabilities) and three size classes (juveniles, young clumps and adult clumps)(see fig. 1 for life cycle diagram). We note that survival of seeds and protocorms were not observed at each stage; because juveniles take four years from germination to emerge, seed-to-juvenile survival was estimated as the ratio of newly-emerged juveniles to seeds produced four years earlier (see Nicolè et al. 2005 for more details).

Each size class has dormant and active above-ground phases, yielding six stages beyond protocorm that do not transition back to protocorm but may transition between one another through growth and changes in dormancy status (there is no retrogression). Above-ground (active) stages may grow or remain in their class as well as enter dormant below-ground stages of the same size (i.e., dormant juveniles, dormant young clumps and dormant adult clumps); dormant stages may remain dormant or emerge but may not grow while in dormancy. There are two fertility rates, with active adult clumps producing far more seeds than active young clumps.

Correlations in the *Cypripedium calceolus* reference population

The complex life history of *C. calceolus* presents an interesting correlation pattern that highlights the potential for important reproductive and developmental tradeoffs as well as illustrating mathematical constraints on correlations due to the summing to unity of survival-conditioned stasis and growth transitions (see fig. 2 for a graph illustrating the correlation structure of the reference population (R)). Note: because we use time-averaged rates for fertilities (F_6 , F_7), seed bank stasis (S_I), and germination (G_I), we cannot compute covariances or stochastic contributions for these rates. Because we apply a set of common protocorm survival estimates (P_2 , P_3 , P_4) to each population we cannot estimate any contributions for these rates. Also, because we do not have separate survival estimates for dormant and above-ground stages, we compute correlations with juvenile survival $P_j = P_5 = P_8$, young clump survival $P_y = P_6 = P_9$, and adult survival $P_a = P_7 = P_{10}$. Correlations between emergence and stasis were perfectly negative ($(A_j, S_j) = -1$) since dormant individuals that survived could not grow but could only emerge or remain dormant, as were correlations between dormancy and stasis of adult clumps ($(D_{10}, S_{10}) = -1$) since adults could only go dormant or remain active in the same class.

Survival Correlations—Although juvenile and young clump survival probabilities (P_j, P_y) were strongly correlated in the reference population (R), neither was correlated with adult survival (P_a). This indicates similar sources of mortality for juvenile and young clumps that differ from the risks faced by adults. A strong negative correlation between stasis and survival of dormant juveniles (S_j, P_j), mirrored by a strong positive correlation between juvenile emergence and survival (A_j, P_j), suggests that juveniles pay a survival cost of dormancy. In contrast, a negative correlation (S_7, P_a) suggests that active adults appear to pay a small survival cost of stasis, while the moderate positive correlation between adult survival and dormancy transitions (P_a, D_7) suggests that adult dormancy may be a survival mechanism under poor environmental conditions or physiological stress. This difference is likely due to the undeveloped rhizome structures of juveniles, which lack the nutrient reserves that allow adults to survive dormancy. The strong positive correlation between young clump growth and survival (G_6, P_y) supports the intuition that, at least for this stage, similar conditions favor both survival and growth.

Different stages tend to emerge from dormancy in the same years but juveniles experience reduced mortality when they emerge while young and adult clumps do not; this suggests that dormant juveniles must emerge soon or they will suffer increased mortality. Larger individuals may have enough nutrients stored in their roots to hedge their bets and remain dormant through one or more seasons. The strong positive correlation between adult emergence and juvenile survival ($A_{JO}P_J$) suggests that adults may wait to emerge until conditions are favorable enough that even juveniles are likely to survive.

Stasis and growth correlations—For both above- and below-ground stages, stasis probabilities were positively correlated with one another and this pattern was replicated in dormancy-dormancy correlations and in emergence-emergence correlations. Furthermore, there was little growth observed, so above-ground stasis correlations closely mirrored same-stage dormancy transitions, while below-ground stasis correlations exactly mirrored those of emergence transitions. For juveniles and young clumps, negative dormancy-growth correlations confirm the intuitive expectation that years in which juveniles and young clumps went dormant were also poor years for growth into larger size classes. The correlations between dormancy transitions (D_JD_a and D_JD_y) of mature and immature individuals was much weaker than that between young and adult clumps (D_yD_a), highlighting stage-specific differences in the opportunity for growth. This is also evidenced by the negative correlation between juvenile dormancy and growth (D_JG_J), which is much stronger than that among young clumps (D_yG_y). This suggests that in years that are poor for juveniles, there is little growth and many juveniles become dormant, but that young clumps are more able to remain active in years unfavorable for growth. Taken together, these differences indicate that young and adult clumps are less susceptible to poor environments than juveniles, being more likely to grow and less likely to go dormant under similar conditions.

Stochastic contributions of vital rates for *Cypripedium calceolus*

Previous research (Nicolè et al. 2005) found that adult survival had the highest deterministic elasticity, while growth and fertility had much lower elasticities; the adult stage, and especially adult dormancy transitions, made the largest contributions to the variance in deterministic growth rates of these three populations.

In our analysis, the largest contributions were made by adult stasis (S_J) and dormancy transitions (D_J), with smaller contributions from dormant adult stasis (S_{JO}) and emergence (A_{JO}) and adult survival (P_a), though their rankings differed between populations (see fig. 3). Because these contributions describe the effects of rates with strong (or perfect) negative correlations, these contributions came in conjugate pairs, meaning they appear as mirror images of each with roughly equal magnitudes but opposite signs. Because stochastic contributions made by each vital rate may contain both positive and negative components,

we distinguish the effects of vital rates $\left(\sum_{\varphi} |C_k^{\varphi}|\right)$ from ‘contributions’, which are the net effects after cancelling of positive and negative components.

On ZAB and POG positive contributions of active adult stasis (S_J) offset negative contributions of adult dormancy transitions (D_J), while on OPA these same vital rates made the largest contributions but in opposite directions. On ZAB there were also fairly large negative contributions of adult emergence (A_{JO}) offset by positive contributions of dormant adult stasis (S_{JO}). Adult survival (P_a) made positive contributions on ZAB and smaller positive contributions on POG but negative contributions on OPA. On OPA there were also negative contributions from very low growth rates of young clumps (G_{θ}) and there were smaller negative contributions from dormant adult stasis (S_{JO}) and positive contributions of

adult emergence (A_{IO}). The result was near-stationary population growth rates on ZAB ($a = -0.0046$) and POG ($a = -0.0019$), but a negative stochastic growth rate on OPA ($a = -0.0175$).

Overall, mean vital rates (u_k) made the largest contributions, but there were important stochastic contributions on all three islands (see Table 1). In terms of the summed effect of all contributions (counting both positive and negative contributions), mean rates made up 82.5% of the total effect on the stochastic growth rate on ZAB, 84.6% on POG and 64.2% on OPA (see rightmost panels in fig. 3). Differences in elasticities made up 3.0% on ZAB, 5.5% on POG and 11.3% on OPA; differential variability made up 10.6% on ZAB, 6.9% on POG and 20.3% on OPA; and differences in vital rate correlations made up 4.0% on ZAB, 2.9% on POG and 4.3% on OPA.

On ZAB, there were five vital rates that made up at least 5% of the total combined effect on the stochastic growth rate on that island, and the combined effect of stochastic elements (μ_k , c_k and ρ_{kl}) accounted for more than 10% of the total effect from four of these vital rates (see Table 1). The greatest overall effect (26.6% of the total) came from adult stasis (S_7) and stochastic effects accounted for 21.6% of that contribution. Adult dormancy (D_7) accounted for 26.0% of the total effect on the population growth rate and 19.7% of that was due to differences other than the mean. Variability (c_k) had the largest stochastic effect in each of the five vital rates making the largest overall contributions on ZAB. For two of these five vital rates (S_7 and D_7), elasticity (e_k) had the second largest effect while correlations (ρ_{kl}) with the other three vital rates (A_{IO} , S_{IO} and P_a) had larger effects than their elasticities.

On POG, two vital rates (S_7 and D_7) together made up 72.4% of the total effect on the stochastic growth rate (a) and adult survival (P_a) accounted for 5.7% of the total effect on a . Stochastic contributions accounted for 10.9% of the total effect of adult stasis, 10.3% of the effect of adult dormancy transitions and 13.3% of the effect of adult survival. Variability had the largest stochastic effect for adult stasis (7.1% of the total for that rate) and for adult survival (6.0%), but elasticity had the largest stochastic effect for adult dormancy (6.0% of its total effect).

On OPA, the ranking of the vital rates with the largest effects was the same as on POG, but dormant adult stasis (S_{IO}) and emergence (A_{IO}) also accounted for at least 5% of the effect on the stochastic growth rate of OPA. The contribution of low mean growth probabilities (G_0) made by young clumps was larger than the net contributions of adult stasis or emergence, but this accounted for less than 5% of the combined effects of all contributions. The smaller net contributions of adult stasis and emergence were due to balancing of positive and negative stochastic effects within each rate. The effects of stochasticity were the highest in this population, accounting for more than 35.9% of the total effect on a . Among the most important vital rates, stochastic effects accounted for more than 30% of the total made by two (S_7 and D_7), more than 70% made by two others (S_{IO} and A_{IO}) and almost 20% of the effect of adult survival (P_a). In this population, vital rate variability (c_k) had the largest stochastic effects and had larger effects than the means for dormant adult stasis (S_{IO}) and emergence (A_{IO}). Elasticities (e_k) and correlations (ρ_{kl}) also had larger effects on OPA than on ZAB or POG. Elasticity accounted for more than 20% of the total effects of dormant adult stasis (S_{IO}) and of emergence (A_{IO}) and over 10% of the total effect of adult dormancy transitions (D_7), while correlations accounted for almost 15% of the total effects of dormant adult stasis (S_{IO}) and of emergence (A_{IO}).

Discussion

On the whole, the stochastic population dynamics of *C. calceolus* growing on these three islands were driven much more by emergence and dormancy transitions than by growth and survival, confirming previous findings (Nicolè et al. 2005). Although mean rates were the largest overall drivers of population growth rates, stochastic elements made up substantial portions of the most important contributions, with variability in vital rates playing the largest role. Correlations and elasticities were also important for population dynamics, especially on OPA, where stochastic effects were the strongest. For dormant adults in this population, survival (P_a) was positively correlated with emergence and negatively correlated with stasis, whereas these correlations were much weaker in the other two populations. This implies that there was a greater cost of dormancy in this population and individuals that stayed dormant were more likely to die. There was also a strong (positive) correlation between survival of young and adult clumps that was not present in the other populations, implying that larger size did not buffer plants from the mortality facing smaller individuals. This, together with the very low growth probabilities of young clumps and the overall larger effect of variability in vital rates, helps explain why this population was doing poorly relative to the other two.

Our methods identify important correlations between vital rates and provide quantitative insights into the effects of tradeoffs and constraints facing populations in variable environments. We found that variability in vital rates was an important driver of population dynamics. We also found that, in one of these populations, contributions of elasticities and vital rate correlations indicate that local selection pressures and differences in the tradeoffs associated with dormancy may differ; this helps explain why one of these populations is faring worse than the others. As our example shows, the signs and magnitudes of stochastic contributions highlight differences in the tradeoffs and constraints populations face and provide valuable insights for managers attempting to conserve populations of concern.

Examining the effects of coefficients of variation instead of variances increased the relevance of comparisons of fertility contributions with those of rates describing survival transitions, which are necessarily constrained between 0 and 1. Also, by separating the effects of survival from those of growth and dormancy transitions we avoid some of the spurious correlations (Morris and Doak 2004) among matrix elements describing survival transitions, but the strict either-or nature of emergence vs. stasis made the conjugate pairing between contributions of these rates inevitable since they go up or down by the same values.

Correlations between survival and retrogressive stage transitions (e.g., dormancy or shrinkage) may be evidence of demographic buffering against the mortality effects of particular environments or seasons (Salguero-Gomez et al. 2010). The reference population vital rates (calculated from rates averaged across populations) exhibit a moderate positive correlation between adult survival and dormancy transitions, so we expected that adult dormancy might be such a buffer for *C. calceolus*. However, correlations with adult dormancy differed between populations, suggesting that the correlations in the reference population may overestimate the survival payoff to dormancy (at least on OPA).

Our new methods for decomposing differences in stochastic growth rates has been applied in other study systems (e.g., Jacquemyn et al. 2012) and may be helpful for a broad range of research on populations in varying environments. Understanding correlation patterns can be especially relevant in applied or conservation work where prioritization of management interventions relies on estimates of the relative “importance” of demographic rates, which may depend on the degree these rates vary and on tradeoffs associated with particular transitions. With this in mind, Wisdom et al. (2000) caution managers to consider the potential for unintended consequences of actions affecting correlated rates. For instance,

costs of reproduction described by negative correlations could lead to low survival if interventions increase fertility or individual growth rates to levels unsustainable under physiological or environmental constraints. It is important to note, however, that just as phenotypic correlations may differ between populations, correlations may also change over time. Therefore, we must analyze them with the understanding that, even if we are correct in our biological interpretations of them, these correlation estimates can only reflect relationships within the limited time frame of our study. They may nevertheless provide useful information that we would miss if we overlooked them and examined only mean rates or even just variance over time.

Until recently (Tuljapurkar et al. 2003) prospective analysis using elasticities relied on mean rates to rank the importance of vital rates but overlooked the role of temporal variability. With notable exceptions (e.g., van Tienderen 1995, Benton and Grant 1999) they do not address correlations between vital rates. Also, because elasticities may vary between spatially distinct populations, or even across the time frame of a single study, differences in local elasticities may also drive population growth rates apart. The methods we present allow an exact retrospective decomposition of the effects of elasticities, vital rate variability and correlations on observed population dynamics. By quantifying their effects, we provide an additional tool for researchers investigating population dynamics that should be highly useful for applications in basic ecology and conservation biology.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Life cycle diagram of *Cypripedium calceolus* divided into 10 demographic stage classes: There are seven underground (pre-emergent or dormant) stages and three active, above-ground stages. Arrows indicate stage transitions: growth (G), stasis (S), dormancy (D) and fertility (F).

Figure 2.

Correlation structure of *Cypripedium calceolus* survival-conditioned vital rates, computed for the reference population (R). The size of each dot represents the magnitude and the color indicates the sign of correlation; crosses highlight within-stage correlations. Rates are grouped by life cycle component: stasis (S), growth (G), transitions into dormancy (D), activity/emergence (A) and survival (P); the associated numbers indicate life cycle stages beyond protocorm (5. juveniles, 6. young clumps, 7. adult clumps, 8. dormant juveniles, 9. dormant young clumps, 10. dormant adults). Note: we use common survival probabilities for dormant vs. above-ground stages, so we compute correlations with $P_{juvenile}$ (P_j), P_{young} (P_y) and P_{adult} (P_a).

Figure 3.

For three populations (ZAB, POG and OPA) of *Cypripedium calceolus* contributions to the stochastic growth rate are summed across all pairings with each demographic vital rate. Vital rates are grouped by life cycle transition type (fertility (*F*), stasis (*S*), growth (*G*), dormancy (*D*), activity/emergence (*A*) and survival (*P*)). Positive and negative contributions are summed separately and the narrow white bars indicate the net contribution of each vital rate. Stacked bars distinguish contributions of mean vital rates, vital rate elasticities, vital rate variability and correlations between vital rates. The panels on the right show the summed contributions across all vital rates in each population. Note: the summed contributions do not predict the stochastic growth rates $a^{(m)} = \log \lambda_s^{(m)}$ but rather the deviation from $a^{(R)} = \log \lambda_s^{(R)} = 0.0071$.

For three populations (ZAB, POG and OPA) of *Cypridium calceolus*, the relative magnitudes of contributions are shown for each vital rate making up at least 5% of the combined magnitude of effects for that population. Total effects are given as a percent of the combined magnitude of all effects on the stochastic growth rate of that population. Effects of means (μ_i), elasticities (e_k), variability (c_k) and correlations (ρ) are given as percentages of the total combined effect for that rate. The last column shows the percentage of the total effect of each vital rate stemming from stochastic effects (e_k , c_k and ρ).

Table 1

Population	Vital Rate	Combined effect (% of total for that rate)					Stochastic Effects
		Total (%)	μ_i	e_i	c_i	ρ_j	
ZAB	All Rates	100	82.5	3	10.6	4.0	17.6
	S_7	26.6	78.4	2.8	16.3	2.5	21.6
	D_7	26.0	80.3	4.6	12.5	2.6	19.7
	A_{10}	13.1	83.9	1.6	9.4	5.1	16.1
	S_{10}	12.7	86.2	1.5	7.2	5.1	13.8
	P_a	9.6	92.5	1.1	3.7	2.7	7.5
POG	All Rates	100	84.6	5.5	6.9	2.9	15.3
	S_7	36.4	89.2	2.4	7.1	1.4	10.9
	D_7	36.0	89.8	6.0	2.7	1.6	10.3
	P_a	5.7	86.7	3.2	6.0	4.1	13.3
OPA	All Rates	100	64.2	11.3	20.3	4.3	35.85
	S_7	37.5	67.8	6.1	23.2	2.8	32.1
	D_7	36.7	69.2	13.7	14.5	2.6	30.8
	P_a	7.2	80.2	3.8	14.5	1.5	19.8
	S_{10}	6.9	29.1	20.4	35.7	14.8	70.9
	A_{10}	6.9	29.1	22.6	33.7	14.6	70.9