

# Decomposing the variation in population growth into contributions from multiple demographic rates

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## Summary

1. The decomposition of variation in population growth into the relative contributions from different demographic rates has multiple uses in population, conservation and evolutionary biology. Recent research has favoured methods based on matrix models termed 'life-table-response experiments' or more generally 'the retrospective matrix method', which provide an approximation of a complete demographic decomposition. The performance of the approximation has not been assessed.

2. We compare the performance of the retrospective matrix method to a complete decomposition for two bighorn sheep populations and one red deer population.

3. Different demographic rates make markedly different contributions to variation in growth rate between populations, because each population is subject to different types of environmental variation.

4. The most influential demographic rates identified from decomposing observed variation in population growth are often not those showing the highest elasticity. Consequently, those demographic rates most strongly associated with deterministic population growth are not necessarily strongly associated with temporal variation in population growth.

5. The retrospective matrix method provides a good approximation of the demographic rate associated most strongly with variation in population growth. However, failure to incorporate the contribution of covariation between demographic rates when decomposing variation in population growth can lead to spurious conclusions.

*Key-words:* bighorn sheep, critical life history stage, demographic variation, elasticity, red deer, retrospective matrix method, vital rates.

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## Introduction

Ecologists are interested in the relative contribution of different demographic rates to variation in population growth, because knowledge of these contributions is required to inform wildlife-management strategies (Caswell, Fujiwara & Brault 1999) and to explore selection on life-history traits (Benton, Grant & Clutton-Brock 1995; Saether & Bakke 2000; van Tienderen 2000). For example, to halt a decline in population size, an obvious first step is to identify the demographic cause of the

decline. Several methods to identify the relative contributions of demographic rates to variation in population growth have been developed (Varley & Gradwell 1960; Brown & Alexander 1991; Brault & Caswell 1993; Horvitz, Schemske & Caswell 1997; Sibly & Smith 1997) and have been used widely for ungulates (Brown *et al.* 1993; Coulson *et al.* 1999; Albon *et al.* 2000; Gaillard *et al.* 2000), birds (Erikstad *et al.* 1998; Saether & Bakke 2000; Wisdom, Mills & Doak 2000), reptiles (Mills, Doak & Wisdom 1999; Caswell 2001), small mammals (Dobson & Oli 2001) and marine mammals (Brault & Caswell 1993). Reviews of this literature have led to proposed generalizations (outlined later) about the associations between demographic rates and variation in population growth. These generalizations,

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however, are speculative because (i) comparisons of the various methods have not been made, (ii) most research has ignored the contribution of the covariation between demographic rates on variation in population growth and (iii) there are few comparisons between multiple populations of the same species living in contrasting environments.

The first method developed to decompose the variation in population growth into the relative contributions of different demographic rates was  $k$ -value analysis (Varley & Gradwell 1960). This involves regressing  $k$ -values describing state-specific per generation mortality and recruitment rates against the sum of the  $k$ -values.  $K$ -value analysis was used widely until Manly (1990) and Royama (1996) highlighted several problems with the method. At this point, ecologists began using approaches developed in demography (e.g. Tuljapurkar 1982; Lande 1988) or developed their own approaches (e.g. Sibly & Smith 1997). The most accurate of these methods is structured accounting of the variance of demographic change (SDA, Brown & Alexander 1991), which provides a complete account of causes of variation in a time series of per capita change  $[(N_{t+1} - N_t)/N_t]$  where  $N_t$  is population size in year  $t$ . Because it requires perfect demographic knowledge of a population, however, the method has been rarely applied.

Another method based on matrix models (Caswell 2001) has been applied widely by researchers interested in stochastic demography. Following Caswell's (2000) definitions, we call this approach the retrospective matrix method. It provides an asymptotic first-order linear approximation of a complete decomposition of variation in the natural rate of increase  $(N_{t+1}/N_t)$  (Lande 1988; Brault & Caswell 1993; Horvitz *et al.* 1997; Gaillard *et al.* 2000). The approximation is asymptotic because it is based on elasticities (or sensitivities) of the dominant eigenvalue ( $\lambda$ ) to elements of a deterministic matrix: the method assumes that temporal fluctuations in the demographic structure of the population do not have a substantial impact on variation in a time-series of  $N_{t+1}/N_t$ . In contrast, SDA incorporates any influence of demographic fluctuations on variation in the per capita change  $[(N_{t+1} - N_t)/N_t = N_{t+1}/N_t - 1]$ . The natural rate of increase  $(N_{t+1}/N_t)$  and per capita change  $(N_{t+1}/N_t - 1)$  are quantities with different means (1 and 0, respectively) but equivalent variances. Consequently, the decomposition provided by the retrospective matrix method can be compared with the decomposition provided by SDA. Having made the distinction between the two quantities for brevity we will refer to both  $N_{t+1}/N_t$  and  $N_{t+1}/N_t - 1$  as population growth and the asymptotic approximation of  $N_{t+1}/N_t$  as  $\lambda$ .

The retrospective matrix method differs from the prospective matrix method, which determines the functional dependence of deterministic population growth on a demographic rate. Specifically, the prospective matrix method determines how much  $\lambda$  would change if a change in a demographic rate were to occur, while the retrospective matrix method extends the prospective

matrix method to approximate a decomposition of variation in population growth by incorporating variation in demographic rates.

Research developing the retrospective matrix method was initiated by Tuljapurkar (1982), who provided the first analytical approximation of a link between demographic rates and variation in population growth, by decomposing the dominant Lyapunov exponent of population growth [specifically  $\ln(\lambda)$ ]. Lande (1988) and Brault & Caswell (1993) introduced the now widely used decomposition of variance in population growth which was subsequently made popular by, among others, Horvitz *et al.* (1997), Saether & Bakke (2000) and Gaillard *et al.* (2000). As far as we are aware there have been no comparisons of the performance of the first-order linear approximations of the decomposition of variance in population growth provided by the retrospective matrix method with the complete decomposition provided by the SDA method.

Most applications of the retrospective matrix method have been based on a yearly description of the life cycle, and have reported contribution to age- or stage-specific demographic rates to variation in population growth. In contrast, most applications of the SDA approach have reported results from a seasonal description of the life cycle and have reported contributions of age-classes, or of demographic rates to variation in population growth. Both the retrospective matrix method and SDA can be applied to seasonal and non-seasonal descriptions of the life cycle, and both methods allow variance decompositions to be reported across age classes, across demographic rates or across class-specific demographic rates. We report decompositions that are comparable to previous publications using both approaches. As the retrospective matrix method has been applied mainly to non-seasonal descriptions of life cycles and has been applied more widely than SDA we compare the two approaches with a non-seasonal description of the life cycle.

Here we present the first comparison between the SDA and the retrospective matrix method using detailed individual-based life-history data from two populations of bighorn sheep (*Ovis canadensis*, Shaw) in Alberta, Canada (Jorgenson *et al.* 1997; Festa-Bianchet & Jorgenson 1998) and a population of red deer on Rum, Scotland (Clutton-Brock, Guinness & Albon 1982; Coulson *et al.* 2003b). First we present a complete decomposition of variation in population growth for the bighorn sheep populations using SDA and a seasonal description of the life cycle. These results can be compared with previous publications using SDA, including application of the approach to the red deer data (Albon *et al.* 2000). Next, we use SDA to provide results from a non-seasonal description of the life cycle that are compared with results from the retrospective matrix method. We report results that (i) support Royama's (1992) observation that results depend on the description of the life cycle used, (ii) show that for ungulate populations the retrospective matrix method

provides an acceptable approximation of the complete decomposition of population growth provided by SDA, (iii) report that in all populations examined covariation between demographic rates contributed substantially to variation in population growth and (iv) suggest that cross-population generalizations concerning the association between demographic rates and variation in population growth may be unwarranted if covariation between demographic rates is strongly associated with variation in population growth. Finally we caution against the unfettered use of prospective and retrospective matrix methods for conservation.

## Methods

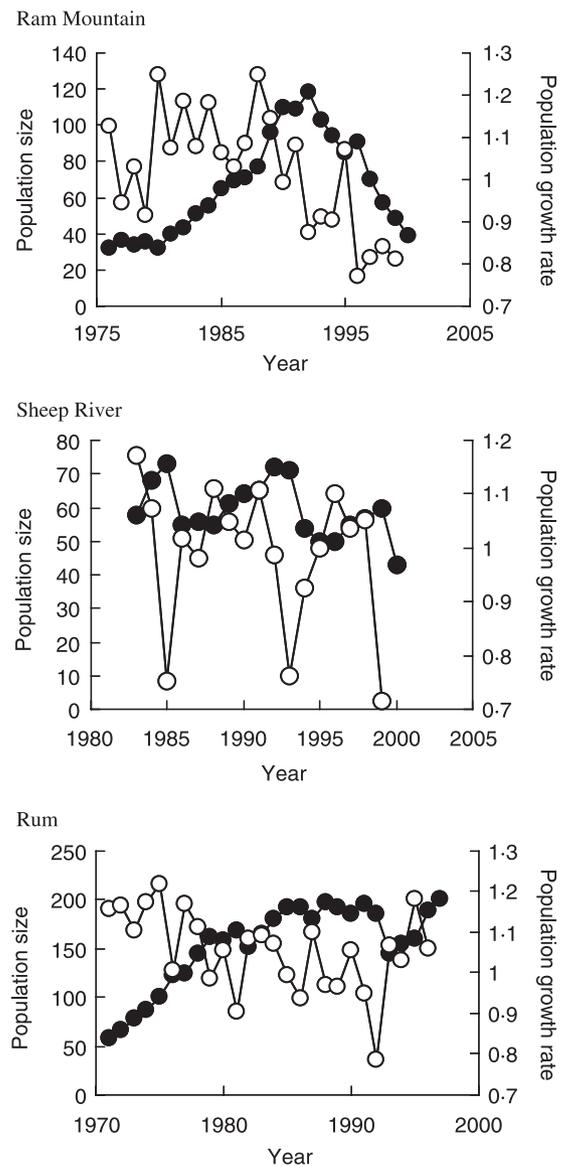
### STUDY SYSTEMS

Each study followed a similar data-collection protocol, where individuals are captured within a few days (red deer) to a few months (bighorn sheep) of birth, tagged, weighed and then monitored throughout life with death dates and breeding attempts recorded. Over 95% of yearling and adult females were individually recognizable in all populations each year. Genotyping and behavioural observation identify mother–young relationships. Yearly resighting probabilities are > 99% for females and > 95% for males in all populations, and population size and age and sex structure are known exactly. Further details of study areas and data collection methods are published elsewhere (Jorgenson *et al.* 1997; Festa-Bianchet, Gaillard & Jorgenson 1998a; for bighorn sheep; Clutton-Brock *et al.* 1982; Clutton-Brock & Coulson 2002 for red deer).

Bighorn sheep ewes at Ram Mountain were experimentally transplanted to another population from 1972 to 1980; complete data on population size and composition exist from 1976 to the present. An average of 2.6 (range 0–6) mature rams each year was shot by hunters between 1976 and 1997. In 1997, 14 more ewes were removed as part of an experimental manipulation and mortality was affected by a subsequent substantial increase in cougar predation, so we chose to concentrate on detailed data up to the summer of 1997 only. Consequently, the Ram Mountain data set consists of yearly population composition and demographic rates for the years 1976–96. Ewes transplanted in 1976–80 ( $n = 39$ ) or that died in trapping accidents ( $n = 3$ ) were excluded from the analyses. Between 1976 and 1987 the population increased in size ('increase period'); between 1988 and 1996 the population showed no persistent temporal trend ('no trend period') (Fig. 1). We analyse data for all years (1976–96) and for the 'increase' and 'no trend' periods separately.

We used detailed data on the bighorn sheep population at Sheep River from 1983 to 2000. Over this period the population showed no persistent temporal trend (Fig. 1) so we only consider the data set as a whole.

The red deer population living in the North Block of Rum was released from culling in 1972, increased



**Fig. 1.** Time-series of counts (solid symbols) and population growth ( $N_{t+1}/N_t$ ; open symbols) for the female component (yearlings and adults) of the population for the bighorn sheep populations at Ram Mountain and Sheep River and for the red deer population in the North Block of Rum.

during the 1970s and has been comparatively stable since the early 1980s. Albon *et al.* (2000) applied the SDA approach to data from this population for the years 1971–97, and for comparison with these results we consider the same data set. We consider an 'increase period' from 1971 to 1981 and a 'no trend period' when the population was fluctuating around ecological carrying capacity (1982–97), as well as considering the data set as a whole.

For both bighorn sheep populations we considered three age classes – yearlings, adults (aged between 2 and 7) and older adults (Loison *et al.* 1999). The year ran from 1 May in year  $t$  to 30 April in year  $t + 1$ , with all births assumed to happen on 1 May (Festa-Bianchet 1988a). For red deer we considered yearlings, adults

(aged between two and 10) and older adults. The onset of survival senescence is at about 8 years for bighorn sheep (Loison *et al.* 1999) and about 11 years for red deer (Benton *et al.* 1995). We consider only the female components of our study populations.

#### SDA APPROACH

We used structured accounting of the variance of demographic change (SDA) to produce an exact decomposition of the variation in population growth for each study and subset of years defined above. Full methodological details of SDA have been published elsewhere (Brown & Alexander 1991) and the method has been implemented for large vertebrate data sets (Brown *et al.* 1993; Coulson *et al.* 1999; Albon *et al.* 2000). Below we give a verbal account of the philosophy underlying SDA.

If complete demographic information is known it is possible to decompose the variation in population growth over a period of time into contributions from age-specific demographic rates, fluctuations in the age-structure and covariation between the demographic rates. To do this an equation that describes the population dynamics needs to be formulated. We first consider an equation incorporating seasonal variation in survival rates to allow comparison with previous applications of the SDA approach. When this equation is parameterized and observed initial conditions set, it will produce the observed change in population size between two time steps. For example, eqn 1 describes the population growth in population size between years  $i$  and  $i + 1$  ( $\delta N = (N_{i+1} - N_i)/N_i$ ) caused by age-specific birth and death processes in a seasonal environment as used by Coulson *et al.* (1999) and Albon *et al.* (2000)

$$\delta N_i = \sum_{j=1}^n (a_j b_j s_j t_j - a_j (1 - S_j T_j)) \quad \text{eqn 1}$$

This equation can be rewritten as:

$$\delta N_i = \sum_{j=1}^n (a_j b_j s_j t_j - a_j + a_j S_j T_j) \quad \text{eqn 2}$$

where  $n$  is the total number of age/stage groups,  $a_j$  is the proportion of the population in age group  $j$ ,  $b_j$  is the birth rate of individuals in age groups  $j$ ,  $s_j$  and  $t_j$  are, respectively, the summer and winter survival rates of offspring born to individuals in group  $j$ ,  $S_j$  and  $T_j$  are, respectively, the summer and winter survival rate of individuals in group  $j$ . Summer survival was measured from 1 May to 1 October, and winter survival was measured from 1 October to 1 May in the following year. Note that in this formulation recruits to the population are described as the product of age-specific birth rate, summer survival rate and winter survival rate for each age class (yearlings, prime aged adults and older adults).

Over  $i$  years, there will be  $i^{-1}$  values of  $\delta N$ . Because all animals in each population were individually marked and closely monitored, each  $\delta N$  is known exactly, as is

the value of each of the parameters that determine each  $\delta N_i$ . SDA then decomposes the variation in population growth [specifically  $\text{var}(\delta N)$ ] into contributions from the variation of each age-class specific demographic rate and all the covariations between model parameters. The method produces a structured demographic account that is the variance in the relative change in size of the whole population expressed as a sum over age classes and/or demographic rates, each expressed in terms of products of elements such as birth rate, offspring and adult survival rates (Brown *et al.* 1991). The account can be presented in a variety of ways. In the results section we initially follow the protocol of Brown & Alexander (1991) by providing two accounts. First we present the contribution of variation in demographic rates to variation in population growth. In other words  $\text{var}(\delta N_i)$  is described by contributions from variation in the age-structure ( $a$ ), in the birth rate ( $b$ ), in offspring summer survival ( $s$ ), in offspring winter survival ( $t$ ), in adult summer survival ( $S$ ), in adult winter survival ( $T$ ) and all the covariances between these demographic rates. This decomposition does not distinguish between demographic rates of specific age classes – for example, the account reports the contribution of variation in the birth rate pooled across yearlings, prime-aged adults and older adults rather than contributions from each age class. The second account reports the contribution of variation in demographic rates pooled for each age class and covariation between pooled demographic rates between age-classes. For example, this account reports that variation in demographic rates in age-class  $x$  explained  $y\%$  of variation in  $\text{var}(\delta N)$ . Results from this decomposition are comparable with previous publications using the SDA method and a seasonal description of the life cycle (Brown & Alexander 1991; Coulson *et al.* 1999; Albon *et al.* 2000).

To make our results comparable with the retrospective matrix method described below, however, we simplify eqn 1 to remove the seasonal components and estimate annual survival rates, re-run the analyses and then report the account in a third way. We do this by re-running the SDA analysis on a non-seasonal (yearly) description of variation in population growth using the following demographic rates:

- recruitment rate of prime-aged adult females (AR): the number of daughters aged 1 year that enter the population at the beginning of year  $t + 1$  per prime-aged adult female in the population at the beginning of year  $t$ .
- recruitment rate of older adult females (SR): the number of daughters aged 1 year that enter the population at the beginning of year  $t + 1$  per older adult female in the population at the beginning of year  $t$ .
- yearling survival (YS): the proportion of females aged one year at the beginning of year  $t$  that survive to the beginning of year  $t + 1$ .
- adult survival (AS): the proportion of adult females that survived from the beginning of year  $t$  to the beginning of year  $t + 1$ .

• older adult survival (SS): the proportion of older females that survived from the beginning of year  $t$  to the beginning of year  $t + 1$ .

This third account reports the contribution of variation in  $AR$ ,  $SR$ ,  $YS$ ,  $AS$  and  $SS$  and their covariances. For brevity, we did not report various other terms that include variation and covariation involving age-structure,  $a$ .

#### RETROSPECTIVE MATRIX METHOD

For each of the five demographic rates described above we estimated means and variances over the time periods being considered. We used the mean values to construct a prebreeding census Leslie matrix model (Caswell 2001), e.g.

$$T = \begin{pmatrix} 0 & 0 & AR & \cdots & SR \\ YS & 0 & 0 & \cdots & 0 \\ & AS & 0 & \cdots & 0 \\ & & AS & \cdots & 0 \\ & & & \ddots & SS \end{pmatrix} \quad \text{eqn 3}$$

for red deer.

From this matrix we analytically estimated elasticities of  $\lambda$  (i.e. change in  $\lambda$  resulting from a proportional change in a demographic rate) for each demographic rate independently (see Caswell 2001 for further details). For  $AS$  and  $AR$  we summed the appropriate age-specific elasticities to generate a single value for each age-class-specific demographic rate. Matrix algebra was performed in MATLAB (version 6.1).

The approximation of the association between variation in a demographic rate and variation in population growth is estimated by multiplying the square of the elasticity by the square of the CV of the associated demographic rate. Identical results can be obtained by using the square of the sensitivity of a demographic rate multiplied by the variance in that demographic rate (e.g. Horvitz *et al.* 1997; Gaillard & Yoccoz 2003).

The approximation of the association between the covariation between two demographic rates ( $VR_1$  and  $VR_2$ ) and variation in population growth can be estimated by  $e_1 * CV_1 * e_2 * CV_2 * \text{cor}(VR_1, VR_2)$  where  $e_i$  is the elasticity of  $VR_i$ ,  $CV_i$  is the coefficient of variation of  $VR_i$ , and  $\text{cor}(VR_1, VR_2)$  is the parametric correlation between  $VR_1$  and  $VR_2$ .

#### COMPARISONS BETWEEN THE SDA AND THE RETROSPECTIVE MATRIX METHODS

There are two important differences between the SDA approach and the retrospective matrix method. First, the retrospective matrix method assumes that the population age structure is at equilibrium, while the SDA approach does not. Second, the retrospective matrix method provides an asymptotic linear approximation of the decomposition of variation in population growth, while the SDA approach provides an exact decomposition of variation in population growth. If variation

in population growth is small, then we would expect the first order linear approximation to work well and the population to remain relatively close to its equilibrium age structure. Any lack of fit of a correlation between estimates from the SDA method and estimates from the retrospective matrix method will provide an idea of the effects of variation in age structure and covariation between age-structure and demographic rates upon variation in population growth. We describe the similarity between the approaches using  $r^2$  values from parametric regression fits and  $\rho$ -values from non-parametric regression fits between the contributions of the SDA and retrospective analyses.

## Results

#### INTERPRETING SDA RESULTS

Using our population model we report the contributions of the recruitment component ( $a_j b_j s_j t_j$ ), the mortality component ( $a_j T_j$ ), the covariation between recruitment and mortality and all components combined ('performance' *sensu* Brown & Alexander 1991). We do this across all age classes (the top row of tables in Table 1) for the birth rate, summer offspring survival, winter offspring survival and mortality pooled across yearlings, adults and older adults, and by age class (the second row of tables in Table 1) pooled across demographic rates. This decomposition cannot be compared directly with the retrospective matrix method as applied here, but allows comparison with the published work of Brown *et al.* (1993), Albon *et al.* (2000) and Coulson *et al.* (1999).

To illustrate how to interpret these results we provide a specific description of Table 1. At Ram Mountain the variation in birth rate across all age classes contributed 9.2% to the variation in population growth and the covariation between the birth rate and adult survival contributed 1.8% (first row of tables). The age class column reports how much variation in population growth is explained by variation in the age structure over the time period considered. For example, covariation between the age structure and the birth rate explained -3.7% of variation in population growth at Ram Mountain. A negative percentage represents a pairwise covariation between age-structure variation and birth rate variation that decreases variation in population growth. When we consider the contribution of different age classes (second row of tables) we can see that yearlings contributed 3.7% to the variation in growth, entirely via the mortality component (value of 3.7 in the mortality part in the second row of Table 1), because yearlings do not reproduce. The covariation between adult and older adult mortality contributed 0.2% and mortality across all age classes contributed a total of 12.3% to variation in per capita growth. The correlation coefficient between yearling and prime adult mortality was 0.4 (third row of tables). The values in the above paragraph are highlighted with cell borders in Table 1.

**Table 1.** Results from a decomposition of variation of per capita change for two bighorn sheep populations using a structured demographic account (SDA). The first row of tables reports the contributions of each demographic rate across all ages. The central diagonal represents the contribution of each demographic rate; off-diagonals in the upper right-hand corner of the top row of matrices represent the pairwise covariation between demographic rates and off-diagonals in the lower left-hand corner of the matrices represent the simultaneous independent variation in each pair of demographic rates (see Brown & Alexander 1991). Values represent mean percentage contributions from 1000 bootstraps, and values in the shaded cells give the bootstrap standard errors. Only two-way covariances are reported. The second row of tables reports the contribution of different age-classes across demographic rates and decomposed into the contributions from recruitment, mortality and their covariation. Again, values represent percentage contributions. The third (and final) row of tables reports correlation coefficients between the age-specific demographic rates for performance, recruitment, mortality and their covariation. Boxed values are referred to in the text

	Ram Mountain 1976–1996					Sheep River 1976–1996				
	Age structure	Birth rate	Lamb summer survival	Lamb winter survival	Adult survival	Age structure	Birth rate	Lamb summer survival	Lamb winter survival	Adult survival
Age structure	<b>3.5</b>	-3.7	-0.3	-0.3	-0.7	<b>0.5</b>	0.3	-0.1	-0.1	-0.6
	1.10	2.82	2.30	3.37	5.67	0.15	0.46	0.75	1.57	2.90
Birth rate	0.5	<b>9.2</b>	2.6	0.7	1.8	0.1	<b>1.7</b>	1.2	-0.3	2.0
	0.13	3.02	3.43	4.78	4.94	0.02	0.49	1.13	2.11	3.22
Lamb summer survival	0.3	0.4	<b>8.0</b>	3.2	13.0	0.1	0.1	<b>4.1</b>	-2.6	10.0
	0.07	0.11	1.29	0.54	2.05	0.03	0.01	0.32	0.21	0.69
Lamb winter survival	0.8	1.1	0.6	<b>21.2</b>	17.5	0.3	0.4	0.6	<b>13.9</b>	34.9
	0.23	0.28	0.10	3.41	3.00	0.10	0.04	0.05	1.04	2.41
Adult survival	1.9	0.0	0.0	0.0	<b>15.3</b>	1.2	0.0	0.0	0.0	<b>44.0</b>
	0.47	0.00	0.00	0.00	2.64	0.24	0.00	0.00	0.00	3.08

	Performance				Performance			
	Yearlings	2–7 years	> 7 years	Total	Yearlings	2–7 years	> 7 years	Total
Yearlings	<b>3.7</b>				2.8			
2–7 years	11.4	<b>47.5</b>			4.8	<b>35.5</b>		
> 7 years	0.2	21.8	<b>15.3</b>	<b>100</b>	5.1	32.9	<b>18.9</b>	<b>100</b>
	Recruitment				Recruitment			
Yearlings								
2–7 years		<b>42.5</b>				<b>10.7</b>		
> 7 years		5.4	<b>7.6</b>	<b>55.5</b>		2.5	<b>10.8</b>	<b>23.9</b>
	Mortality				Mortality			
Yearlings	<b>3.7</b>				2.8			
2–7 years	-2.0	<b>4.0</b>			1.0	<b>17.7</b>		
> 7 years	1.6	<b>0.2</b>	<b>4.7</b>	<b>12.3</b>	4.5	6.0	<b>12.5</b>	<b>44.5</b>
	Recruitment mortality				Recruitment mortality			
Yearlings								
2–7 years	13.5	0.9	19.1		3.8	7.1	8.0	
> 7 years	-1.4	-2.9	3.0	<b>32.2</b>	0.7	16.4	-4.4	<b>31.6</b>

	Performance			Performance		
	Yearlings	2–7 years	> 7 years	Yearlings	2–7 years	> 7 years
Yearlings	<b>1</b>			<b>1</b>		
2–7 years	0.4	<b>1</b>		0.2	<b>1</b>	
> 7 years	0.0	0.4	<b>1</b>	0.4	0.6	<b>1</b>
	Recruitment			Recruitment		
Yearlings						
2–7 years		<b>1</b>			<b>1</b>	
> 7 years		0.0	<b>1</b>		0.1	<b>1</b>
	Mortality			Mortality		
Yearlings	<b>1</b>			<b>1</b>		
2–7 years	<b>0.4</b>	<b>1</b>		0.1	<b>1</b>	
> 7 years	0.0	0.2	<b>1</b>	0.4	0.2	<b>1</b>
	Recruitment mortality			Recruitment mortality		
Yearlings						
2–7 years	0.5	0.0	0.7	0.351	0.257	0.347
> 7 years	-0.1	-0.3	0.3	0.061	0.595	-0.191

COMPARISON BETWEEN POPULATIONS  
WITHIN SPECIES

Results differed between the Ram Mountain and Sheep River populations (Table 1), demonstrating that variation in growth in two populations of the same species can be affected in different ways by variation in demographic rates, even though they exhibited similar variation in population growth (Sheep River  $\text{var}(\delta N_t) = 0.015$ , Ram Mountain  $\text{var}(\delta N_t) = 0.012$ ). At Ram Mountain the direct contribution of mortality pooled across yearlings, prime adults and older adults explained 15.3% of the variation in population growth compared to 44% at Sheep River. Lamb winter survival, explained 21.2% and 13.9% of the variance in the two populations. The contributions of covariation between demographic rates to variation in population growth were similar and substantial (32.2% at Ram Mountain a 31.6% at Sheep River). The contribution of individual covariances, however, did vary between the two studies. For example, the covariation between lamb winter survival and adult survival was larger at Sheep River (34.9% vs. 17.5% at Ram Mountain).

All the results reported above suggest a striking difference between the two populations, but are the differences significant? As well as the estimated contributions of each demographic rate to variation in population growth, Table 1 reports standard errors from 1000 bootstraps of the data. If statistical significance is assessed by comparing the means  $\pm 1.96$  times the bootstrap standard errors the differences reported above are statistically significant.

COMPARISONS BETWEEN POPULATIONS IN  
'INCREASE' AND 'NO TREND' PERIODS

Bighorn sheep on Ram Mountain and red deer on Rum show similar patterns of variation in direct contributions of demographic rates to variation in population growth during their respective increase periods (Fig. 2). A linear regression between the direct contributions for each population was highly significant ( $F_{1,30} = 24.11$ ,  $P = 0.016$ ,  $r^2 > 0.5$ ). For both populations the birth rate was the dominant demographic rate explaining 38.6% and 29.9% of the variation for bighorn sheep and red deer, respectively; the second most dominant demographic rate was survival pooled across yearlings, prime aged adults and older adults: it explained 22.3% and 28.1%, respectively. Differences between these two populations arose when the impact of covariation between demographic rates was explored; the most important covariation for bighorn sheep was between lamb summer survival and survival pooled across yearlings, prime aged adults and older adults (17.9%), while for red deer it was between birth rate and pooled survival (22.6%). A linear regression comparing all contributions (both direct and from the covariances) between the populations was significant ( $F_{1,16} = 6.27$ ,  $P = 0.026$ ,  $r^2 = 0.33$ ; Fig. 2). For both populations the prime-aged

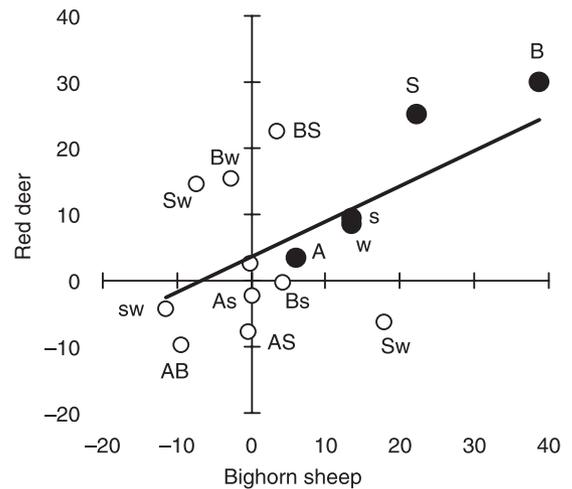
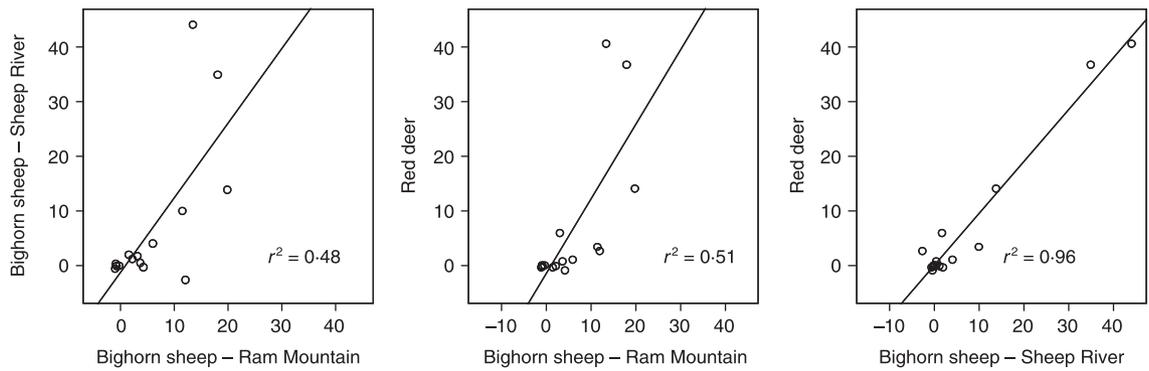


Fig. 2. Scatter plot of the relationship between the contributions of demographic rates to population growth for the red deer population and the bighorn sheep population at Ram Mountain during their increase phases. Values on the axes represent percentage contribution to demographic rates. A = age group, B = birth rate, S = adult survival, s = offspring summer survival, w = offspring winter survival and two letter combinations of these demographic rates represent pairwise simultaneous covariation between the demographic rates.

adult class dominated the account explaining 50.7% of the variation for bighorn sheep and 54.7% of the variation for red deer. Note that demographic rates are pooled across age classes for this comparison.

There was very good agreement in the direct contribution of demographic rates and covariation between demographic rates to variation in growth between the red deer population during the 'no trend' period and the Sheep River bighorn sheep population (Fig. 3:  $F_{1,13} = 281.5$ ,  $P \sim 0$ ,  $r^2 = 0.98$ ). In both populations pooled survival was the dominant demographic rate (bighorn sheep 44%, red deer 40.6%) followed by juvenile winter survival (bighorn sheep 13.9%, red deer 14.1%). The most important covariation was between adult survival and juvenile winter survival (bighorn sheep 34.9%, red deer 40.6%).

The bighorn sheep population at Ram Mountain during the 'no trend' period differed substantially from either the bighorn sheep population at Sheep River or the 'no trend' period for the red deer population in two contributions (Fig. 3). The contribution of pooled survival and the covariation between pooled survival and juvenile winter survival contributed only 13.47% and 18.05%, respectively, at Sheep River, so were approximately half as important as the covariation in the other two study systems. This suggests that the difference between the two bighorn sheep populations is not simply a result of the different population trajectories. In addition, the dominant demographic rate at Sheep River was lamb winter survival (19.9%) compared to survival pooled across yearlings, prime aged adults and older adults at Ram Mountain and on Rum. Finally, there was a substantial contribution of the covariation between juvenile summer survival and juvenile winter



**Fig. 3.** Scatter plots of the relationships between the contributions of demographic rates to population growth for the red deer population and the two bighorn sheep populations for the no trend periods. Values represent percentage contributions. Fitted lines represent regression fits – all of which are significant (Sheep River vs. Ram Mountain  $F_{1,13} = 11.94$ ,  $r = 0.004$ ; Ram Mountain vs. red deer  $F_{1,13} = 13.4$ ,  $P = 0.0028$  and Sheep River vs. red deer  $F_{1,13} = 281.5$ ,  $P \sim 0$ ).

**Table 2.** Results from the simplified SDA approach. Values on the diagonal represent the percentage contribution of each demographic rate to variation in population growth and values below the main diagonal represent the pairwise covariation between demographic rates. We report only contributions of the terms that provide comparisons with the retrospective matrix method

	Increase					No trend					All years				
<b>Red deer</b>															
Adult recruitment	27.1	25.5	3.9	0.7	1.2	8.4	4.6	3.0	3.3	5.6	15.3	13.9	3.3	3.3	7.2
Older adult recruitment		18.5	13.8	3.3	3.1		9.5	4.2	2.3	14.5		13.8	7.0	3.8	11.2
Yearling survival			11.4	-0.5	-4.4			2.7	2.8	10.3			4.4	1.9	3.4
Adult survival				4.7	7.6				1.9	5.7				2.7	6.4
Older adult survival					9.3					17.6					11.9
<b>Bighorn sheep, Ram Mountain</b>															
Adult recruitment	49.3	-0.8	27.1	2.0	5.8	23.0	33.4	10.8	-1.6	15.0	37.5	13.9	21.1	3.9	11.0
Older adult recruitment		6.3	-6.1	-5.7	-5.6		22.8	8.5	-5.7	15.0		10.6	2.6	-4.6	3.0
Yearling survival			21.6	-28.2	-0.8			6.5	-1.4	5.6			8.7	-2.4	3.4
Adult survival				23.6	-10.0				4.5	-4.4				6.1	-0.9
Older adult survival					22.5					7.2					5.4
<b>Bighorn sheep, Sheep River</b>															
Adult recruitment	0.5	6.3	3.5	6.8	4.6										
Older adult recruitment		7.8	1.2	13.2	3.6										
Yearling survival			3.2	0.5	3.3										
Adult survival				16.5	9.6										
Older adult survival					11.4										

survival (12.1%) at Sheep River that was not observed in either of the other studies. However, if we except the two markedly lower contributions of covariation between pooled survival and juvenile winter survival and of pooled survival observed at Ram Mountain, the contributions across studies were well correlated (Fig. 3).

We next report a demographic account to produce estimates of the contribution of age-specific demographic rates to variation in population growth that are comparable with results from the retrospective matrix method reported in Table 2. Table 2 reports the contribution of age-specific recruitment and survival rates on variation in population growth but does not show the contribution of age-structure variation or covariation with demographic rates.

COMPARISON BETWEEN METHODS

Means and variances of demographic rates that were used to compare the SDA method run on a yearly basis and the retrospective matrix method are displayed in Table 4. Parametric and non-parametric linear regressions between the SDA contributions and contributions from the retrospective matrix method are all significant (Table 5) and, with the exception of red deer at high density ( $r^2 = 0.46$ ,  $\rho < 0.05$ ), all had  $r^2$  values greater than 0.7. Examination of the residuals revealed no consistent patterns of positive or negative residuals between methods. The retrospective matrix method identified the same important contributions of demographic rate covariation as the SDA method. Covariation between demographic rates explained between 1/

**Table 3.** Comparison between the impact of the recruitment and mortality components and their covariances between the full and the simplified SDA approaches

	Bighorn sheep, Ram Mountain		Red deer			
	Simple	Full	Simple	Full		
Increase period						
Recruitment	54.8	52.1	71.1	51.2		
Mortality	28.8	28.1	27.7	27.6		
Covariation	17.4	13.8	26.0	21.2		
	Bighorn sheep, Ram Mountain		Bighorn sheep, Sheep River		Red deer	
	Simple	Full	Simple	Full	Simple	Full
No trend period						
Recruitment	79.2	49.4	14.6	18.5	22.5	23.4
Mortality	18.0	16.2	44.6	44.0	41.0	41.0
Covariation	42.0	31.1	32.9	46.9	31.9	39.8

**Table 4.** Means and variances for the five demographic rates used for the retrospective matrix analysis by study and period

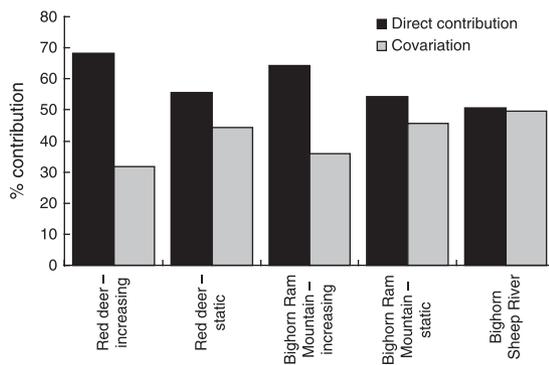
Demographic rate	Red deer		Bighorn sheep (Ram Mountain)		Bighorn sheep (Sheep River)	
	Mean	Variance	Mean	Variance	Mean	Variance
	1971–1997		1976–1997		1983–2000	
AR	0.1729	0.0037	0.2005	0.0117	0.1317	0.0045
SR	0.2111	0.0069	0.2459	0.0316	0.1593	0.0121
YS	0.9230	0.0038	0.7718	0.0403	0.8795	0.0274
AS	0.9550	0.0009	0.9403	0.0017	0.9029	0.0081
SS	0.8862	0.0075	0.8374	0.0155	0.7890	0.0173
	1971–1980		1976–1987			
AR	0.2044	0.0032	0.2554	0.0068		
SR	0.2614	0.0066	0.2390	0.0183		
YS	0.9327	0.0037	0.8462	0.0197		
AS	0.9721	0.0005	0.9485	0.0020		
SS	0.9124	0.0034	0.8499	0.0187		
	1980–1997		1988–1997			
AR	0.1546	0.0032	0.1457	0.0113		
SR	0.1815	0.0050	0.2529	0.0492		
YS	0.9173	0.0039	0.6974	0.0540		
AS	0.9449	0.0008	0.9321	0.0015		
SS	0.8708	0.0095	0.8250	0.0141		

**Table 5.** Summary of parametric and non-parametric regressions between results from the SDA analysis and the retrospective matrix methods for bighorn sheep and red deer

Data set	$F_{(1,13)}$	$r^2$	$P$ -value	rho	$P$ -value
Red deer – low density	34.2810	0.7250	<0.0001	0.918	<0.0001
Red deer – high density	11.1020	0.4610	0.0054	0.7320	0.0062
Red deer – all years	12.0800	0.4816	0.0041	0.729	0.0065
Bighorn sheep, Ram Mountain: low density	80.8010	0.8610	<0.0001	0.925	0.0005
Bighorn sheep, Ram Mountain: high density	25.2490	0.6600	0.0002	0.8880	0.0009
Bighorn sheep, Ram Mountain: all years	36.4500	0.7344	<0.0001	0.889	0.0009
Bighorn sheep, Sheep River: all years	39.4170	0.7520	0.0001	0.862	0.0012

3 and 1/2 of the variation in population growth (Fig. 4). Survival of prime-aged females had the highest elasticities of  $\lambda$  in all five case studies. However, the demographic rate showing the largest contribution (excluding

covariation between demographic rates) to variation in  $\lambda$  differed among case studies: recruitment by prime-aged females was the critical demographic rate in red deer and bighorn sheep at Ram Mountain during the



**Fig. 4.** The relative contribution of direct effects and covariation between demographic rates on variation in population growth for each species and period from the retrospective matrix method. Values have been transformed to percentages to aid comparison between analyses.

‘increase’ period as well as in bighorn sheep at Ram Mountain during the ‘no trend’ period (along with recruitment by older females in that latter case), whereas variation in the survival of old females and in the prime-aged survival accounted for most changes in red deer during the ‘no trend’ period and in bighorn sheep at Sheep River, respectively (Table 2).

## Discussion

Our analyses produced five important results. First, populations of the same species living in different environments can have contrasting associations between variation in demographic rates and variation in population growth. Second, demographic rates with the highest elasticities of  $\lambda$  are not often those showing the largest contributions to variation in population growth. Third, there is little evidence that either of the previous generalizations (Gaillard *et al.* 2000; Coulson & Hudson 2003) is supported. Fourth, any decomposition of variation in population growth should consider covariation between demographic rates. Finally, the retrospective matrix method provides a satisfactory decomposition under the majority of circumstances we investigated.

The proximate reason for the contrasting results between the two bighorn sheep populations is their difference in variation around demographic rates. For large mammals, adult survival will invariably have the largest potential impact (elasticity) as adult survival rates are high and the majority of animals within a population are adults (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000). The contribution of a demographic rate to variation in population growth, however, is also dependent on its temporal variation. Because adult survival at Sheep River was high but variable it accounted for three times as much variation in population growth compared to Ram Mountain, where adult survival rates were high and constant. The ultimate reason for the contrasting results is differences in the ecological processes that generate variation in

population growth [pneumonia and predation at Sheep River (Festa-Bianchet 1988b; Jorgenson *et al.* 1997; Ross *et al.* 1997) and density-dependence at Ram Mountain (Festa-Bianchet & Jorgenson 1998; Festa-Bianchet *et al.* 1998a; Festa-Bianchet, Gaillard & Côté 2003)].

The large diversity of ecological processes that affect populations of large vertebrates generates different demographic responses that potentially allow all life-history stages to play a substantial role in contributing to distributions of population growth characterized from a time series. As Gaillard *et al.* (2000) and Caswell (2000) observed, prospective and retrospective matrix methods can identify different demographic rates influencing different moments of a distribution of population growth. Although this result is not surprising – there is no a priori expectation for a demographic rate to be strongly associated with both the mean (the prospective matrix method) and the variance (the retrospective matrix method) of a time-series of population growth – some conservation managers may consider the prospective and retrospective matrix methods as addressing the same question (see Caswell 2000 for an excellent discussion of the two methods).

Our two SDA analyses also provide support for Royama’s (1992) observation that the way the life history is described can influence the interpretation of an analysis of population dynamics. The different ways of reporting the SDA analyses also demonstrate there are various ways to report a decomposition of variation in population growth. Retrospective matrix methods typically report contributions of age-specific demographic rates measured on an annual scale. However, there are circumstances – for example, estimating the role of recruitment or survival across age-classes to variation in population growth – when it could also be illuminating to report the contribution of age-classes across demographic rates, or the contribution of demographic rates across age-classes. This can be achieved using the retrospective matrix method by summing contributions across rates or classes. Recently Lande, Engen & Saether (2003) showed how to decompose variation in population growth into contributions from density-dependence, environmental and demographic stochasticity. It may prove useful to combine the various decomposition methods available to estimate the contribution of different ecological processes within and between age-classes and demographic rates.

With detailed data on three populations we can only make a limited number of comparisons. Our results, however, do not completely support either of two previously suggested generalizations. First, although the dominant demographic rate contributing to variation in population growth in increasing populations of both red deer and bighorn sheep was adult recruitment as proposed by Coulson & Hudson (2003), results from Ram Mountain in the ‘no trend’ period do not support their argument that prime-aged and older adult survival are the dominant demographic rates in static

populations; in this population during the 'no trend' period, recruitment of yearlings by prime-aged and older adults was the dominant demographic rate. Second, results from Sheep River and Rum (see also Albon *et al.* 2000) demonstrate that the contribution of variation in juvenile survival to variation in population growth is not necessarily dominant as reported by Gaillard *et al.* (2000). The generalizations proposed by Gaillard *et al.* (2000) and Coulson & Hudson (2003) were based on studies that ignored covariation between demographic rates. Before any new generalizations can be proposed further studies examining the association between demographic rate covariation and variation in population growth are required. The probable reason for the differences between the results reported here and the results reported by Gaillard *et al.* (2000) for the same populations is that Gaillard *et al.* (2000) did not incorporate demographic rate covariation into their analyses.

The result that covariation between demographic rates provides a substantial contribution to variation in population growth is unsurprising from a life-history perspective. This is because life-history variation – including cohort effects – generates variation in demographic rates that can be correlated (Benton & Grant 1999b, 2000; Beckerman *et al.* 2002; Beckerman *et al.* 2003). Genetic constraints (Lande 1982) and environmental variation (Coulson *et al.* 2004) can generate both life-history variation and covariation in demographic rates. For example, an environmentally favourable year may lead to elevated survival and fecundity leading to no detectable survival costs to reproduction. In contrast, an environmentally challenging year may generate a survival cost of reproduction (Marrow *et al.* 1996; Tavecchia *et al.* 2005). Across a series of good and bad years this will generate covariation between survival and fecundity rates that could impact on variation in population growth. Given that environments and limiting factors differ between populations of the same species it is also unsurprising that different populations exhibit different associations between the covariation in demographic rates and variation in population growth. A critical question for ecologists concerns how these differences manifest themselves between populations and species.

Failure to ignore the contribution of covariation between demographic rates on variation in population growth can lead to misleading conclusions, with important implications for applied ecology. Conservation biologists, for example, are often interested in devising strategies that target demographic rates that contribute most to variation in population growth. Considering only the direct effects each demographic rate has on variation in population growth could lead to flawed conservation strategies if demographic rates covary and impact on population dynamics. Although previous analyses using the SDA method reported substantial contributions of demographic rate covariation (Brown *et al.* 1993; Coulson *et al.* 1999; Albon *et al.*

2000) few retrospective analyses considered such contributions (but see Dobson & Oli 2001). Part of the reason could be that few demographic studies report demographic rate covariation (Wisdom *et al.* 2000). We found that demographic rate covariation can explain between one-third and one-half of the variation in population growth. When using the retrospective matrix method we estimated only the contribution of second order covariances. We did not consider higher-order covariances, as the SDA method has never found these to be important for large mammals (Brown *et al.* 1993; Coulson *et al.* 1999; Albon *et al.* 2000). Although we are now hesitant to propose generalities, it is noticeable that the contribution of demographic rate covariation to variation in population growth is greatest in those populations that show no temporal trend. As successful population management and conservation can depend on the accurate decomposition of variation in population growth, we recommend that future application of the retrospective matrix method should consider demographic rate covariation.

The retrospective matrix method is a first-order linear approximation of the decomposition of variation in population growth (Horvitz *et al.* 1997; Caswell 2001). Although the approximation ignores fluctuations in age structure, our analyses suggest that the retrospective matrix method generally performs well for ungulate life histories. Given that the retrospective matrix method does not require the complete demographic information necessary for a complete decomposition of variation in population growth, this result is reassuring. There are, however, cases when the retrospective matrix method does not perform particularly well. For example, in the red deer population at high density the  $r^2$  value between the SDA contributions and the retrospective contributions is only 0.46. We do not know under what circumstances the performance of the retrospective approximation becomes unsatisfactory – although it should be noted that the red deer population experienced a long-term age-structure transient following release from culling, which generated marked age-structure effects on the population dynamics (Coulson *et al.* 2004). The non-parametric correlations are considerably higher than the parametric correlations for red deer, suggesting that although the retrospective matrix method does not always generate particularly accurate estimates of demographic rates contributions, it does tend to rank contributions in the correct order. In general, we consider the retrospective matrix method a very useful method for decomposing variation in population growth.

The many applications of understanding the association between demographic rates and population growth range from management to understanding evolutionary processes (Grant 1997; Benton & Grant 1999a; Caswell 2001), and any generalizations could prove useful. Our results, however, suggest that the relationship between variation in a demographic rate and variation in population growth is complex.

Because both the mean value (and hence its potential effect on changes in population growth) and the temporal variation in a demographic rate determine its contribution to fluctuations in population size it appears that the source of environmental variation in demographic rates is as, or perhaps even more, important than population trajectory or distance from carrying capacity. An understanding of variation in population growth is therefore likely to require an understanding of the sources of variation in multiple demographic rates. We now require a detailed investigation of the effects of life-history variation and environmental variation on variation in population growth across taxa.

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