

## Notes and Comments

### Habitat Dependence and Correlations between Elasticities of Long-Term Growth Rates

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**ABSTRACT:** In population biology, elasticity is a measure of the importance of a demographic rate on population growth. A relatively small amount of stochasticity can substantially impact the dynamics of a population whose growth is a function of deterministic and stochastic processes. Analyses of natural populations frequently neglect the latter. Even in a population that fluctuates substantially with time, the results of a deterministic perturbation analysis correlated strongly with results of a perturbation analysis of the long-run stochastic growth rate. Population growth was, however, not uniformly sensitive to demographic rates across different environmental conditions. The overall correlation between deterministic and stochastic perturbation analysis may be high, but environmental variability can dramatically alter the contributions of demographic rates in different environmental conditions. This potentially informative detail is neglected by deterministic analysis, yet it highlights one difficulty when extrapolating results from long-term analysis to shorter-term environmental change.

*Keywords:* demography, Markov chain, sensitivity, Soay sheep, St. Kilda, vital rate.

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If individuals of different stages or ages are affected by their environment in different ways (Leirs et al. 1997;

Coulson et al. 2001), then matrix models are a flexible tool to examine the link between demographic rates and population dynamics (Caswell 2001). The relative importance of these different classes and rates can be investigated using perturbation analysis, that is, some measure of sensitivity or elasticity that aims to identify the importance of demographic rates on some measure of population performance (Caswell 2001). Analysis of the asymptotic population growth rate  $\lambda_0$  predicts the eventual behavior of a system described by some model. Analysis of  $\lambda_0$  with and without observed variation in demographic rates can produce contrasting results (Coulson et al. 2005; Ezard et al. 2006). Therefore, potential appears to exist for stochastic models to quantify how demographic rates determine population growth more accurately.

Deterministic and stochastic processes affect survival and recruitment, and these conjointly determine population growth (Bjornstad and Grenfell 2001; Lande et al. 2003). Furthermore, the dynamic consequences of stochasticity depend on the population structure: populations of different stage or age structure but of similar size and environments can exhibit contrasting short-term dynamics (Benton et al. 2001). Despite the important role of stochasticity in population dynamics, perturbation analyses performed on natural populations frequently assume density-independent growth, a stable age distribution, and a constant environment (Caswell 2001); that is, they are deterministic. Given the considerable interest in population dynamics in variable environments, recent research (Tuljapurkar et al. 2003; Haridas and Tuljapurkar 2005; Horvitz et al. 2005; Morris et al. 2006; Tuljapurkar and Haridas 2006) has relaxed Tuljapurkar's (1982) small-noise approximation, which permits demographic rates to vary only by small amounts. This suite of work uses sequences of discrete habitat states—generated using Markov chains—to model environmental change. It has produced a comprehensive array of quantities that describe diverse aspects of the long-run stochastic growth rate  $\lambda_s$ . The influence on  $\lambda_s$  of a change in the distribution of some matrix element  $a_{ij}$  (often a demographic or vital rate;

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Caswell 2001)—the elasticity of  $\lambda_s$  to  $a_{ij}$ —is frequently considered to be the analog of the deterministic elasticity of  $\lambda_0$  to  $a_{ij}$ . Increasing  $a_{ij}$  by a small amount in the stochastic case perturbs the mean and variance of  $a_{ij}$  (denoted here as  $\mu_{ij}$  and  $\sigma_{ij}$ , respectively) such that the coefficient of variation of  $a_{ij}$  remains constant. In the deterministic case, however, only  $\mu_{ij}$  is perturbed (Tuljapurkar et al. 2003). Acknowledging that simultaneous perturbations to  $\mu_{ij}$  and  $\sigma_{ij}$  are difficult to interpret in natural populations, Tuljapurkar et al. (2003) partitioned the stochastic elasticity of  $\lambda_s$  to  $a_{ij}$  into contributions from  $\mu_{ij}$  and  $\sigma_{ij}$ . Such a partition treats all environmental conditions as equal, whereas there is no guarantee that the importance of certain processes in one habitat state will persist in another (Horvitz et al. 2005). The calculation of elasticities of  $\lambda_s$  to  $\mu_{ij}$  and  $\sigma_{ij}$  is more challenging than the calculation of the elasticity of  $\lambda_0$  to  $a_{ij}$ . It has also been argued that, for many systems,  $a_{ij}$  and  $\mu_{ij}$  will be similar when  $\sigma_{ij}$  is small. This theory has been demonstrated on an understory shrub population in a sequential, disturbance-prone system (see Tuljapurkar et al. 2003). Does analysis of  $\lambda_s$  provide insight, which is unobtainable from analysis of  $\lambda_0$ , into determinants of population growth in disparate systems influenced by stochastic processes?

Soay sheep (*Ovis aries*) are the only vertebrate herbivores on the island of Hirta in the St. Kilda archipelago (Scotland; Clutton-Brock and Pemberton 2004). The dynamics of this population are characterized by overcompensatory density dependence (Clutton-Brock et al. 1997), yet they are known to be influenced by stochastic processes. Food limitation is the primary cause of winter mortality (Crawley et al. 2004), although winter weather and age and sex structure also contribute significantly (Coulson et al. 2001). This contradicts the assumptions of deterministic analysis. This note addresses three principle questions. (1) Does use of  $\lambda_s$ , rather than  $\lambda_0$ , qualitatively alter predictions of the key demographic rate for population growth? (2) Is the relative importance of demographic rates consistent for perturbations to  $\mu_{ij}$  and  $\sigma_{ij}$ ? (3) How does the relative importance of demographic rates vary between habitat states?

## Methods

### Study Population

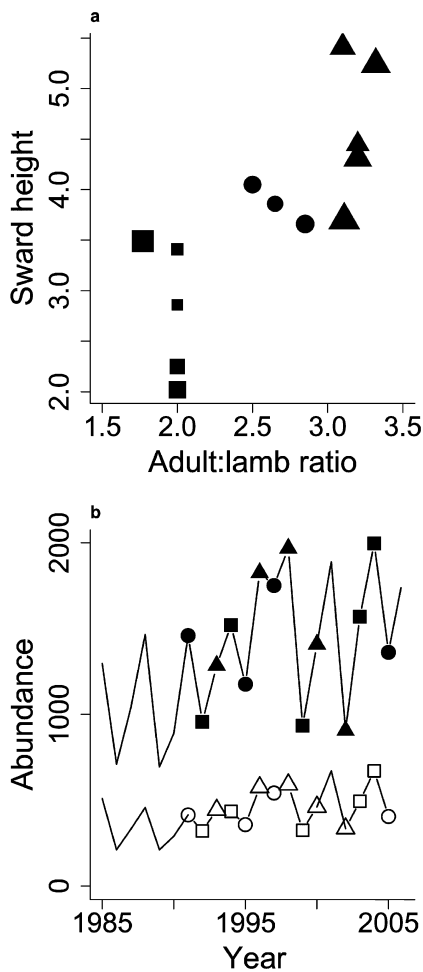
Individual-based data have been collected under an identical protocol since 1985 from the population of Soay sheep living in Village Bay on Hirta (57°49' N 8°34' W) in the St. Kilda archipelago. Three trips are made annually to collect data: during the birth pulse (late March–early May), to perform an annual catch (August), and during the rut (October–November). Full details of the data collection

protocol and population history are available in Clutton-Brock and Pemberton (2004). Population size is defined here as the number of sheep alive on August 1 each year.

### Population Model and the Markov Chain

Demographic and environmental data were available from 1991 to 2006 inclusive (except for 2001, because of an outbreak of foot-and-mouth disease on the mainland). Only females were considered, for which the most parsimonious age structure has four age classes (Catchpole et al. 2000): lambs (*L*), yearlings (*Y*), prime-aged individuals (2–6 years old; *P*), and older individuals (>6 years old; *O*). A postbreeding Leslie matrix (Caswell 2001) **A** was constructed with eight age classes (for the matrix and the lifecycle graph, see the appendix). The population model is  $\mathbf{p}(t) = \mathbf{A}(t)\mathbf{p}(t-1)$ , where  $\mathbf{p}(t)$  is the population vector at time *t* and  $\mathbf{A}(t)$  a transition matrix at time *t* chosen according to the probabilities defined by a Markov chain.

The Markov chain of habitat states (Tuljapurkar et al. 2003) was generated using mean sward height in March, mean station-based North Atlantic oscillation (NAO; Hurrell 1995) between December and March, and adult : lamb ratio. Sward height is a measure of vegetation and is dependent not only on the number of sheep but also on plant biomass over each growing season (Crawley et al. 2004; Jones et al. 2006). NAO is a broad proxy for weather conditions, with higher values indicating more winter storms and harsher conditions in northern Scotland. Lamb survival is most strongly influenced by weather throughout the winter, whereas other female age classes are most influenced by conditions at the end of winter (Coulson et al. 2001). Adult : lamb ratio approximates the population structure, which can fluctuate independently of total abundance and which significantly affects population growth (Coulson et al. 2001). Tree regression, which generates discrete classes of explanatory variables (Venables and Ripley 1999), indicated that sward height should be split at ~3.5 (range, 2.02–5.24) and that the adult : lamb ratio should be split at approximately 3.0 (range, 1.77–3.32). In an additive model containing all terms, NAO was consistently subdominant, except for a small change in fecundity of prime-aged individuals. This rate is relatively invariant to environmental change when compared with other demographic rates (Coulson et al. 2001) and was thus disregarded. Two classes were adopted for each of sward height and adult : lamb ratio, thus producing four habitat states when combined. No years were classified as low sward and low adult : lamb ratio, which left three habitat states (fig. 1). There were five years in state 1 (low sward height; lowest-quality habitat with  $\lambda_0$  for the mean matrix of all years in that habitat, 0.91), three in intermediate state 2 (high sward and low adult : lamb ratio;  $\lambda_0$  of mean



**Figure 1:** *a*, The three habitat states (squares, habitat state 1, the lowest-quality state; circles, state 2; triangles, state 3, the highest-quality state) with symbol size proportional to  $\lambda_0$  in the observed year. *b*, The time series from 1985 to 2006 of abundance of Soay sheep for Hirta (filled symbols) and the Village Bay study population (open symbols). Data used in this study were collected between 1991 and 2006; annual population growth varied from 0.61 to 1.34 over these years.

matrix, 0.99), and five in the highest-quality habitat state 3 (high sward and high adult : lamb ratio;  $\lambda_0$  of mean matrix, 1.22).

The habitat transition probabilities were obtained using observed rates of transition after defining the three habitat states (fig. 1*a*; for habitat transition matrix  $\mathbf{H}$ , see appendix). The habitat state at time  $t + 1$  is probabilistically dependent on the habitat state at time  $t$ . The process was iterated to generate one Markov chain of length 100,000 (with an initial transient of length 10,000 discarded). The sequence determined the habitat state that the population experienced at each time step. Feedback between population growth, demographic rates, and environmental var-

iables in the sequence of habitat states is extrapolated from the feedback observed within the study period (see fig. 1*b*). Each  $\mathbf{A}(t)$  was obtained in the following manner: (1) the habitat state at time  $t$  was obtained from the Markov chain; (2) a year was randomly selected in which the population was in that habitat state (see fig. 1); (3)  $\mathbf{A}(t)$  was filled using the observed demographic rates for that year. These processes generated a transition matrix at each time, which was stored with associated vectors of population structure and reproductive value for perturbation analysis (Tuljapurkar et al. 2003). Note that simulated, not asymptotic, sequences of population structure and reproductive value were stored; that is, the population structure does not converge to the stable-age distribution.

#### Perturbation Analysis

Elasticities of asymptotic growth  $\lambda_0$  to a matrix element  $a_{ij}$  (here, a demographic rate) are the proportional change in  $\lambda_0$  from a proportional change in  $\mu_{ij}$  (mean  $a_{ij}$ ) over all 100,000 time steps. This quantity was calculated and is denoted  $E_{ij}^D$ .

The long-run stochastic growth rate  $\lambda_s$  was calculated over all 100,000 time steps and is defined as  $\log(\lambda_s) = \lim_{t \rightarrow \infty} (1/t) \log[\mathbf{p}(t)/\mathbf{p}(0)]$ . The stochastic elasticity (denoted  $E_{ij}^{S\lambda}$ ) of  $\lambda_s$  with respect to element  $a_{ij}$  is the proportional change in  $\lambda_s$  for a proportional change in  $a_{ij}$ , such that the coefficient of variation of  $a_{ij}$  does not change (Tuljapurkar et al. 2003). The elasticity of  $\lambda_s$  with respect to  $\mu_{ij}$  (denoted  $E_{ij}^{S\mu}$ ) is the proportional change in  $\lambda_s$  for a proportional change in  $\mu_{ij}$ , which is the same perturbation as in  $E_{ij}^D$ , but to  $\lambda_s$ , not  $\lambda_0$  (Tuljapurkar et al. 2003). The elasticity of  $\lambda_s$  with respect to variation in  $a_{ij}$  ( $\sigma_{ij}$ , denoted  $E_{ij}^{S\sigma}$ ) is the proportional change in  $\lambda_s$  for a proportional change in  $\sigma_{ij}$  (Tuljapurkar et al. 2003).

These quantities perturb every matrix in the simulated sequence and do not consider habitat dependence, whereas the habitat-stage elasticity (denoted  $E_{ij\beta}$ ) of  $\lambda_s$  with respect to  $a_{ij}$  and habitat state  $\beta$  does. The quantity  $E_{ij\beta}$  is the proportional change in  $\lambda_s$  for a proportional change in  $a_{ij}$  if and only if the environment is in habitat state  $\beta$  (Horvitz et al. 2005). This quantity is, in part, dependent on the frequency of the habitat state in the Markov chain (Horvitz et al. 2005). It is therefore presented as the contribution of each  $a_{ij}$  to  $E_{ij\beta}$  ( $E_{ij\beta} / \sum E_{ij\beta}$ ; Horvitz et al. 2005).

Calculations were performed in R, version 2.6.0 (R Development Core Team 2007). Tree regression employed the tree package (ver. 1.0–1.25; Venables and Ripley 1999). Source code to calculate the elasticities described above is available on request from T. H. G. Ezard. After calculation, elasticities were summed to quantify the impact on the values of  $\lambda_s$  or  $\lambda_0$  of each rate per age class.

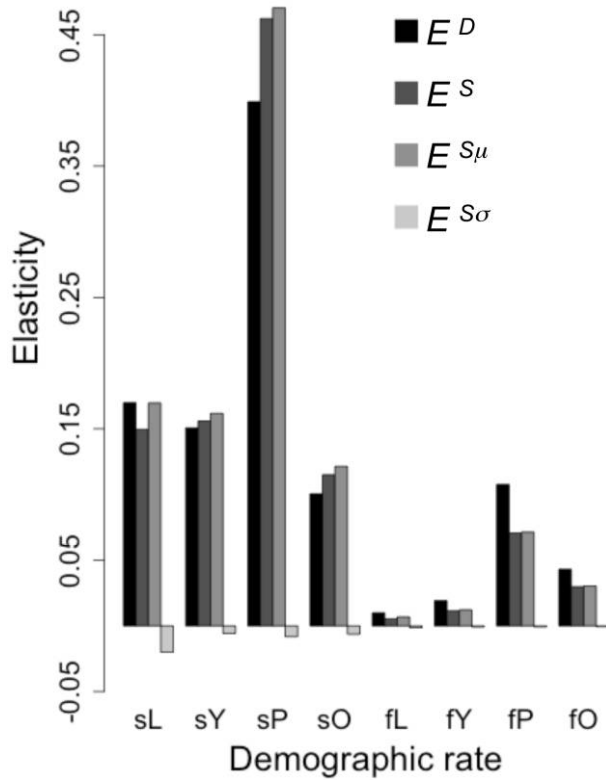


Figure 2: Elasticities of asymptotic growth to matrix elements  $a_{ij}$  ( $E_{ij}^D$ ) and of long-run stochastic growth to  $a_{ij}$  ( $E_{ij}^S$ ), to overall mean  $a_{ij}$  ( $E_{ij}^{S\mu}$ ), and to overall variation in  $a_{ij}$  ( $E_{ij}^{S\sigma}$ ). Values of  $E_{ij}^D$  were strongly correlated with  $E_{ij}^S$  ( $r = 0.924$ ) and  $E_{ij}^{S\mu}$  ( $r = 0.923$ ), as were values of  $E_{ij}^S$  and  $E_{ij}^{S\mu}$  ( $r = 0.998$ ). Values of  $E_{ij}^{S\sigma}$  were not strongly correlated with values of either  $E_{ij}^D$ ,  $E_{ij}^S$  or  $E_{ij}^{S\mu}$  ( $r = -0.223$ ,  $r = -0.223$ , and  $r = -0.290$ , respectively). The eight demographic rates are composites of survival (s), fecundity (f), lambs (L), yearlings (Y), prime-aged individuals (P), and oldest individuals (O).

Results

The values of  $\lambda_s$  and  $\lambda_o$  were 1.037 and 1.062, respectively. Even in a dynamic system that is rarely at mean population size (fig. 1b),  $E_{ij}^D$  (deterministic elasticities of  $\lambda_o$  to  $a_{ij}$ ) were highly correlated with  $E_{ij}^S$  (stochastic elasticities of  $\lambda_s$  to  $a_{ij}$ ) and  $E_{ij}^{S\mu}$  (elasticities of  $\lambda_s$  to  $\mu_{ij}$ ; fig. 2). Values of  $E_{ij}^D$ ,  $E_{ij}^S$  and  $E_{ij}^{S\mu}$  were not strongly correlated with  $E_{ij}^{S\sigma}$  (elasticities of  $\lambda_s$  to  $\sigma_{ij}$ ; fig. 2).

Contributions to habitat-stage elasticities of  $\lambda_s$  differed across different habitat states, although the overall contribution of survival was relatively constant at  $\sim 0.8$  (fig. 3). Survival of prime-aged individuals made the largest contribution to  $\lambda_s$  in all habitat states, which is consistent with expectations in the deterministic case. Age-class contributions of survival and fecundity differed: lamb survival contributed 0.122 in the lowest-quality habitat but 0.203

in the highest. Survival of oldest individuals contributed 0.198 in the lowest-quality habitat but 0.104 in the highest (fig. 3). Yearlings (0.162 with survival and fecundity pooled) made their greatest contribution in the lowest-quality habitat, whereas lambs contributed most to  $\lambda_s$  in the highest-quality habitat (0.225 when pooled).

Discussion

Stochasticity has long been recognized by ecologists as playing a pivotal role in population dynamics (Andre-

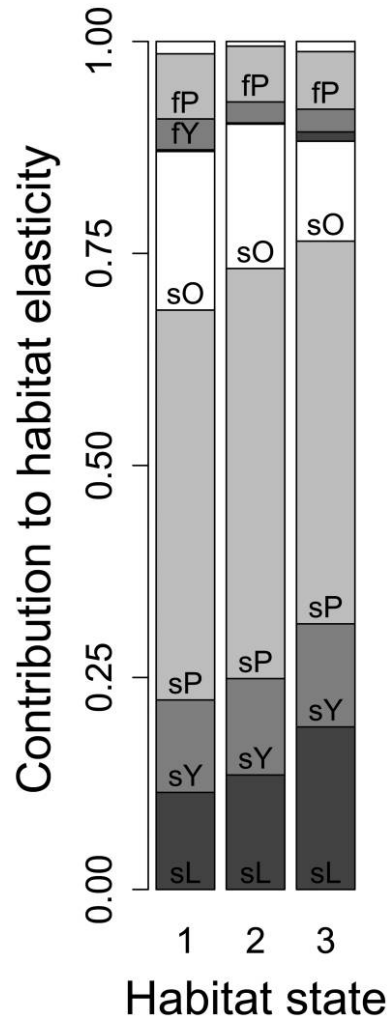


Figure 3: Contribution to habitat elasticity  $E_{ij}^D / \sum E_{ij}^D$  of each demographic rate per age class. The eight demographic rate codes are composites of survival (s), fecundity (f), lambs (L; black), yearlings (Y; dark gray), prime-aged individuals (P; light gray), and oldest individuals (O; white). The demographic rate is indicated by letters only if the contribution is  $>3\%$ . Shading is such that the stacked elasticities are (from bottom to top) in the order sL, sY, sP, sO, fL, fY, fP, and fO.

wartha and Birch 1954). The food-limited Soay sheep population on Hirta experiences irregular yet frequent crashes in population size (Clutton-Brock and Pemberton 2004; see also fig. 1*b*). Even in a population that fluctuates dramatically in size and whose annual growth is poorly described by mean population growth, values for  $E_{ij}^D$ ,  $E_{ij}^S$ , and  $E_{ij}^{SM}$  were all strongly correlated (fig. 2). However, the age classes contributed variably to  $\lambda_s$  across different habitat states (fig. 3), which suggests that one quantity may be insufficient to describe how demographic rates contribute to the growth of populations exposed to variable environments.

The impact of environmental stochasticity of another ungulate population on a Hebridean island was negligible: sensitivity calculations in deterministic and stochastic environments differed by  $\sim 1\%$  (Benton et al. 1995). Despite shorter generation times (Clutton-Brock and Pemberton 2004), an extreme example of variation in population dynamics for this life history (Clutton-Brock et al. 1997), and relaxation of the small-noise approximation (see Tuljapurkar 1982) for variation in demographic rates, predictions made using density-independent methods were not qualitatively altered for the Soay sheep population considered in our study. Is this because of the high similarity between  $\lambda_s$  and  $\lambda_0$ ? Benton et al. (1995) found an even greater similarity ( $\lambda_0 = 1.060$ ,  $\lambda_s = 1.058$  when calculated assuming small noise) between these growth rates. Lande et al. (2003, p. 164) cite Bro et al. (2000) as an example when correlations between  $\lambda_s$  and  $\lambda_0$  are lower. However, Bro et al. (2000) use 250 time steps, not 100,000 as was used in our study and elsewhere (e.g., Tuljapurkar et al. 2003). Whether strong correlations between  $\lambda_s$  and  $\lambda_0$ , as well as between  $E_{ij}^D$ ,  $E_{ij}^S$ , and  $E_{ij}^{SM}$ , persist across diverse life histories and shorter time series remains to be seen (see Benton and Grant 1996).

Transient analysis (Caswell 2007; Haridas and Tuljapurkar 2007; Townley et al. 2007) may be more appropriate for short-term applications, especially for long-lived species (Koons et al. 2005). In this study, the relative importance of demographic rates differed across different habitat states (fig. 3). The dominant demographic rate for short-term population persistence likely depends on the initial habitat state and the habitat states that succeed it. The Markov chain consisted of three discrete habitat states (fig. 1*b*). Values of  $\lambda_s$  were differentially sensitive to events in different habitat states (fig. 3): the youngest individuals are most sensitive to harsh conditions (hence their lowest contribution to habitat-stage elasticity in the lowest-quality habitat), whereas older individuals are simultaneously more capable (fig. 3). Elasticity analysis of, for example, 5 years of data might struggle to “correctly” identify the optimal rate for management action (Heppell et al. 2000) if the frequency of and transition probabilities between

habitat states are unrepresentative of the range a population experiences over longer periods.

Sensitivities are transformed elasticities (Caswell 2001, p. 295). Both elasticities and sensitivities can be interpreted as weights in evolutionary calculations (Lande 1982; van Tienderen 2000). Altwegg et al. (2007) found a high correlation between sensitivities of  $\lambda_s$  to  $\mu_{ij}$  and sensitivities of  $\lambda_0$  to  $a_{ij}$ . The relative importance of stochastic variables changes from year to year, however, such that the dominant demographic rate for population growth is also variable (Coulson et al. 2003). The habitat-stage elasticities (fig. 3) indicate that perturbing demographic rates by the same amount across all years ignores these dynamic patterns in demographic rate dominance. Lande (2007) argued synonymously that for a genotype or phenotype,  $\lambda_s$  is not a valid measure of fitness in a fluctuating environment. Elasticities can change markedly from one year to the next. Use of long-term measures of population growth—deterministic or stochastic—neglects these dynamic patterns, which can be revealed by, for example, partitioning the environment into groups of similar state.

The models presented here directly link herbivores to their food source. The high correlation observed between  $E_{ij}^S$  and  $E_{ij}^D$  is consistent with earlier work on ungulate populations (Benton et al. 1995), but the partitioning of  $E_{ij}^S$  into habitat-dependent contributions (Horvitz et al. 2005) suggests that long-term analysis will not always yield optimal results for populations in variable environments. Although deterministic analyses may appear to be superficially acceptable, they may neglect informative detail as to how populations respond to inevitable stochasticity in their environments.

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### APPENDIX

#### Population Model and Markov Chain

Further detail on how the transition matrices  $\mathbf{A}(t)$  and habitat transition matrix  $\mathbf{H}$  were constructed.

Matrix Population Model

Four age classes have been identified as the most parsimonious age structure for female Soay sheep (Catchpole et al. 2000): lambs (*L*), yearlings (*Y*), prime-aged individuals (2–6 years old; *P*), and older individuals (>6 years old; *O*). A postbreeding Leslie matrix model (Caswell 2001) **A** was constructed with eight age classes where sub-diagonal elements are survival rates (*s*; from August to August) and top row elements are fecundity rates (*f*; lambs that survive to the August in year *t* + 1, born from individuals that survive from August in year *t* until the birth pulse in year *t* + 1):

$$\mathbf{A} = \begin{bmatrix} fL & fY & fP & fP & fP & fP & fP & fO \\ sL & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP & sO \end{bmatrix}$$

The corresponding life cycle graph (with matrix elements given as [row, column] next to each age-age transition) is in figure A1.

Environmental Stochasticity

Tree regression generates discrete classes of the three explanatory variables (Venables and Ripley 1999). In an additive model containing sward height, North Atlantic oscillation (NAO), and adult : lamb ratio, NAO was consistently subdominant except for a small change in *fP* that has previously been shown to be invariant to environmental change (Coulson et al. 2001). Results indicated that sward height should be split at ~3.5 (range, 2.02–5.24) and that adult : lamb ratio should be split at ~3 (range, 1.77–3.32). Two classes were adopted for sward height and adult : lamb ratio, thus producing four habitat states when combined. No years were classified as low sward and low adult : lamb ratio, which left three habitat states (fig. 1A) to construct the Markov chain. The habitat transition matrix **H** was, therefore, of size 3 × 3:

$$\mathbf{H} = \begin{bmatrix} 0.2 & 0 & 0.75 \\ 0.4 & 0 & 0.25 \\ 0.4 & 1 & 0 \end{bmatrix}$$

For example, 5 years were in habitat state 1 (denoted by squares in fig. 1). The subsequent habitat state is 1 in 1992, 2 in 1994, 3 in 1998, 2 in 2003, and 3 in 2004. The state at time *t* is the column number, and the state at time

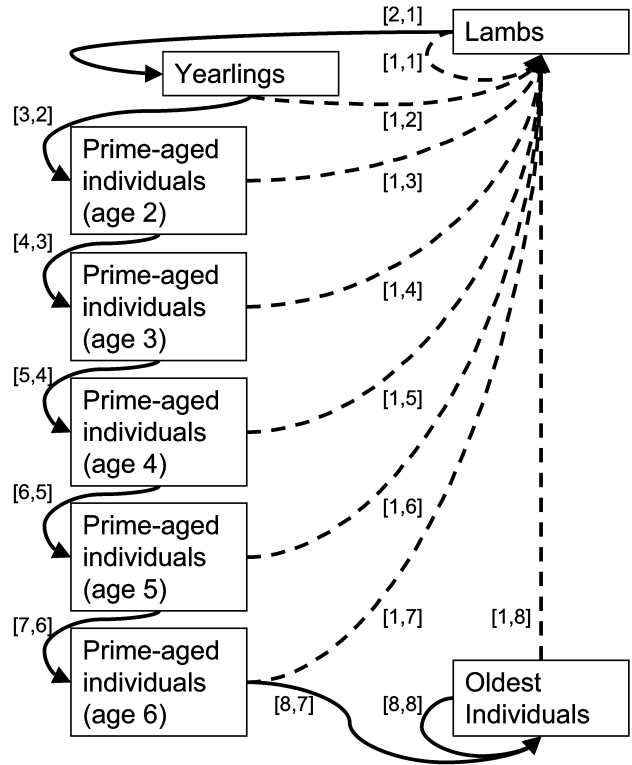


Figure A1: Life-cycle graph for the postbreeding Leslie matrix model **A**. Solid lines are survival; dashed lines are fecundity. Values in square brackets are matrix elements: [row, column].

*t* + 1 is the row number. For example, the transition probability from state 1 to state 2 is 0.4 (cell [1,2] in **H**).

Autocorrelation in the habitat-state sequences experienced by populations can influence  $\lambda_s$  (at least) as much as variability between these states (Tuljapurkar and Haridas 2006). The autocorrelation in the Markov chain can be determined from its subdominant eigenvalue (Tuljapurkar 1990), which can explain potentially as much variation as differences between the states themselves (Tuljapurkar and Haridas 2006). In this instance, autocorrelation was relatively low ( $-0.4 + 0.3i$ ; absolute value, 0.5), certainly more so than in Tuljapurkar et al.’s (2003) and Tuljapurkar and Haridas’s (2006) examples, where in the least correlated state it is 0.813 and the historical environmental autocorrelation is 0.890.

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