

## AN EXTENDED FLOWERING AND FRUITING SEASON HAS FEW DEMOGRAPHIC EFFECTS IN A MEDITERRANEAN PERENNIAL HERB

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**Abstract.** The Mediterranean perennial herb *Lobularia maritima* shows an exceptionally extended flowering and fruiting that lasts for 10 months, from early September to late June. We hypothesized that such an extended phenology may be a flexible mechanism that enhances population persistence in variable Mediterranean environments, as fecundity in one part of the season could compensate for reproductive failure in another part of the season. We predicted that (1) fecundities throughout the year would significantly contribute to mean population growth rate  $\lambda$ , (2) negative covariances among fecundities in different periods of the year would reduce variance in population growth rate, and (3) extended flowering and fruiting would enhance long-term stochastic population growth rates. We used a periodic matrix model to describe the demography of a *L. maritima* population over five years, in which each year was divided into six periods of two months each.

Population growth rates varied from a low of 0.25 to a high of 4.81 over the five years of study. Periodic elasticity analyses revealed that fecundities in the first two periods of the year, i.e., the autumn periods, were the major determinants of population growth in most of the years, rather than fecundities over the whole flowering and fruiting season. Variation in the autumn fecundities also made the largest contribution to the observed variance in  $\lambda$ . Hence, unlike earlier generalizations, highly variable parameters also had relatively high elasticities. As predicted, negative covariances appeared between the fecundities, but only between those of the two autumn periods. These negative covariances were interpreted as a flexible mechanism to tailor the onset of reproduction to the start of the autumn rains, thereby reducing the variance in  $\lambda$ . We used stochastic matrix models to investigate the effect of different reproductive strategies on stochastic population growth rate. We created hypothetical populations with either an even distribution of fecundity throughout the year or with concentrated flowering and fruiting in autumn or in spring. Stochastic population growth rates were high if a major part of the reproduction remained in autumn. A hypothetically even distribution of fecundities over the entire flowering season increased both the mean and the variance in  $\lambda$ , with little overall effect on stochastic population growth rate.

All together, our results indicate that a reproductive failure of *L. maritima* in autumn cannot be compensated for by reproduction in winter and spring. The extended flowering and fruiting season thus has very little effect on the population dynamics of the species. Alternative explanations for the unusual phenology of *L. maritima* in the Mediterranean environment are discussed.

**Key words:** elasticity analysis; extended flowering and fruiting; *Lobularia maritima*; Mediterranean environments; periodic matrix model; population growth rate; stochastic simulations; temporal variation; variance decomposition analysis.

### INTRODUCTION

The Mediterranean climate is characterized by the large seasonal differences in environmental conditions, with mild or cold winters and hot dry summers (Aschmann 1973, Mooney et al. 1974, Orshan 1983, Dafni and O'Toole 1994). Many Mediterranean perennial plant species concentrate their flowering in particular

seasons of the year, such as spring (Herrera 1992, Proctor et al. 1996:389) or autumn (Mooney et al. 1974, Kummerow 1983, Herrera 1986). However, a few plant species can extend their flowering to much longer periods. This is the case of the crucifer *Lobularia maritima* (L.) Desv., a polycarpic perennial herb that shows an unusually extended flowering and fruiting season that lasts for 10 mo (Bosch et al. 1997, Picó and Retana 2000). This is a very rare phenology and only 2% of the perennial crucifers in the western Mediterranean basin (i.e., *Sisymbrium irio* L., *Diploaxis viminea* (L.) DC., and *L. maritima*) show a flowering season that

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last for more than eight months (Bolòs et al. 1993). In this paper we investigate the population dynamical consequences of this exceptional phenological pattern.

Within Mediterranean seasons, climatic events such as the length of the summer drought or episodic rains in different parts of the year can be highly unpredictable (Herrera 1988). Plant species living in highly stochastic environments show mechanisms that enhance population persistence over time. For instance, iteroparity (Goodman 1984, Orzack and Tuljapurkar 1989, Charlesworth 1994), some degree of reproductive delay (Tuljapurkar 1990, Orzack 1997), and delayed germination (Cohen 1966, Venable and Lawlor 1980, Brown and Venable 1986, Klinkhamer et al. 1987) appear to be advantageous life history strategies. These mechanisms buffer the negative effects of environmental variability on population persistence (Tuljapurkar and Orzack 1980, Doak et al. 1994, Menges 1997, Sæther et al. 1998, Caswell 2001). For example, long-lived seed banks permit population survival in poor years, since seeds buried in the soil keep the ability to germinate when environmental conditions become more favorable (Kalisz and McPeck 1992). It has been suggested that one of the advantages of an extended flowering season is that successful flowering and fruiting in one part of the year may compensate for reproductive failure in another part of the year (Bawa 1983). If the favorability of the seasons varies greatly between the years, as occurs in Mediterranean environments, prolonged flowering and fruiting of *L. maritima* may allow the population to flexibly adjust to this temporal variability, buffering its effect on fecundity. We thus hypothesize that the unusual phenological pattern of *L. maritima* acts as a mechanism that buffers variation in population growth rate and enhances long-term population performance.

Based on this hypothesis, we investigate three predictions. First, we predict that fecundity in different parts of the year contributes significantly to population growth rate, and because of the annual variability in the climatic conditions, these contributions show a large variation from year to year. We apply a periodic matrix-transition model for *L. maritima* in which the annual transition was divided into six periods of 2 mo each. In five out of six periods the plants flowered and fruited. Contributions of demographic parameters in each of five different years were quantified by elasticities for the periodic transitions, using the equations of Caswell and Trevisan (1994).

Second, we compute the contributions of the variation in demographic parameters in different periods to the observed variance in population growth rate over the 5 yr of study. An extension of the variance decomposition analysis of Brault and Caswell (1993) takes into account the variance in, and covariance among, the demographic parameters both within and among periods. We expect to find important negative covariances between fecundity and/or other demographic pa-

rameters among periods that reflect the flexibility of *L. maritima* to adjust to environmental variability.

Finally, we predict that extended flowering and fruiting of *L. maritima* contributes significantly to population persistence in the variable Mediterranean environment. We used stochastic matrix models to investigate the effect of different reproductive strategies on stochastic population growth rate, a measure of long-term population performance. We compute the stochastic population growth rate for the observed population of study, and for hypothetical populations with either an even distribution of fecundity throughout the year or with concentrated flowering and fruiting in autumn or in spring. We expect to find lower stochastic population growth rates for populations with concentrated phenological patterns, as these populations cannot buffer environmental variation by extended flowering and fruiting.

## MATERIALS AND METHODS

### *The plant species*

The short-lived crucifer *Lobularia maritima* (L.) Desv., sweet alyssum, is a Mediterranean polycarpic herb whose range includes all of the Mediterranean basin, growing in dunes and coastal scrublands (Bolòs et al. 1993). Reproductive plants of this autogamous species form a basal rosette of racemose flowering stalks, with flowering and fruiting that last for 10 mo, from early September to late June (Bosch et al. 1997, Picó and Retana 2000). Flowers are hermaphrodite and insect pollinated, mainly by syrphids (Bosch et al. 1997) although some ant species may also act as effective pollinators (Gómez 2000). The period of time from anthesis to fruit ripening and seed dispersal varies between 15 d (in autumn and spring) and 60 d (in winter). Fruits are siliqua (2–3.5 mm length) containing two seeds (1–2 mm length) that do not show any obvious primary dispersal mechanism and are dispersed passively by gravity.

### *Partitioning of the year in periods*

Given the extended flowering and fruiting season of *L. maritima* and the seasonal differences in climatic conditions throughout the year, each of the years of this study was divided into six periods. Each of the periods lasted for 2 mo and were denoted by the first of the two months, i.e., September, November, January, March, May, and July. The September period included data from September and October, the November period included data from November and December, and so on. Each of these periods clearly differed in climatic conditions, such as mean temperature ( $N = 28$ ,  $F_{5,162} = 816.8$ ,  $P < 0.0001$ ; one-way ANOVA) and total precipitation ( $N = 28$ ,  $df = 5$ ,  $F_{5,162} = 3.4$ ,  $P = 0.006$ ; one-way ANOVA). ANOVAs are based on climatic data from the Fabra Meteorological Station, located 2 km from the study site, over the last 28 yr.

### Population sampling and model parameterization

The *L. maritima* population studied was located in a coastal scrubland at the Collserola Park, a protected area near Barcelona, in northeast Spain (see Picó and Retana 2000 for a detailed site description), and monitored during 5 yr, from 1993 to 1998. Six censuses per year were carried out. Three life history stages were distinguished for *L. maritima*: seeds, seedlings, and adults, the latter divided into three size classes.

Basically, all the demographic parameters were estimated from 12 (eight in 1994–1995)  $1 \times 1$  m<sup>2</sup> plots, separated from each other by 3–30 m, and haphazardly placed at the study site (~1000 m<sup>2</sup> area). Given the low density of plants in some plots, the sample size was increased by tagging additional plants outside the plots. Data from all plots were pooled and treated as one unit of observation. At the beginning of each flowering season, i.e., in September, we censused and mapped 116–583 *L. maritima* individuals in each year. Because *L. maritima* plants consist of a rosette of flowering stalks each with few tiny leaves, and because neither vegetative branches nor a basal rosette of leaves exist in this plant species, the number of flowering stalks was used as a measure of plant size. We used the Moloney (1986) algorithm to delimit size classes of adults based on the maximum number of flowering stalks produced throughout the whole flowering and fruiting season. The resulting size classes were identified as small (from 1 to 25 flowering stalks), medium (from 26 to 40 flowering stalks), and large (>40 flowering stalks). The fate of adults was recorded in each census, obtaining the stasis, growth, and retrogression periodic transitions. The fate of seedlings that emerged in the demographic plots was also recorded in each of the censuses, obtaining the proportion of seedlings that survived and the proportion that established as adults of any size class in each of the periods.

Fecundity had two components and was estimated as the mean number of seeds and seedlings produced per plant of a given size class at a given period in each year. To estimate seed production, the number of fruits produced per plant was multiplied by the estimated number of seeds per fruit. Losses due to flower abortion and fruit predation by ants were taken into account to estimate the final number of seeds. See Picó and Retana (2000) for a detailed description of the experiments carried out to estimate fruit production rate, the number of seeds per fruit, flower abortion rate, and seed predation rate.

Because seeds could germinate within the same period in which they were produced and dispersed, the mean number of seedlings produced per plant of each size class was also estimated for each period of the year. This number was computed by multiplying mean number of seeds produced per plant and size class, first, by the seed survival rate in the soil seed bank, i.e., those that escaped from postdispersal seed predation

(see Picó and Retana 2000 for a description of the seed survival rate estimation), and second, by the seed germination rate. Seed germination rate in a given period  $h$  was estimated as the ratio of the number of new seedlings that emerged in the period  $h$  and the number of seeds that dispersed and survived in the soil in the period  $h - 1$ . We used the mean of all demographic plots monitored in each period. Our long-term experiments on seed viability did not show any significant loss of seed viability after one year ( $N = 5$ ,  $F_{1,8} = 0.08$ ,  $P = 0.8$ ; one-way ANOVA), and it was assumed that all surviving seeds in the soil remained capable of germinating throughout the year.

Some of the studies and experiments performed to estimate demographic parameters or components of these demographic parameters were not carried out in every year of the 5 yr of study. For instance, during the first year, growth, survival, and fecundity of adults were monitored in each period but it was the only year in which survival and establishment of seedlings were not recorded. Table 1 gives a summary of the significant linear relationships that some transitions showed with climatic variables and that were used to estimate their values in the missing years. Mean values were used for other missing transitions or components of these transitions (see Table 1) when no significant relationship with climatic variables was found. Seed survival in the soil was estimated in all periods but for the 1994–1995 year only. This factor can show a great temporal variation because it is determined by the foraging activity of ants of the genus *Messor* (Picó and Retana 2000). For September, May, and July periods, when the maximum seasonal activity of *Messor* ants occurred (Cerdá and Retana 1994), the estimated seed survival rate for each of these periods was used for all years. For the remaining periods, i.e., November, January, and March, when ant activity was lower and more unpredictable, the mean of the six periodic values of seed survival rate was used for all years to integrate such variability. As a result of the partitioning of each study year in six periods, a total of 415 periodic transition elements were quantified, but only 34 of them were estimated by the methods explained above.

### Periodic matrix model and elasticity analysis

A total of 30 matrices (6 periods  $\times$  5 yr) were constructed from the demographic field data. The model used in this analysis is a periodic matrix model (Caswell and Trevisan 1994, Caswell 2001). Each year is composed of  $m$  periods ( $m = 6$  periods of 2 mo each in this study) with the population projection matrices for each period of a given year denoted as  $\mathbf{B}^{(1)}, \dots, \mathbf{B}^{(m)}$ . According to Caswell (2001), the dynamics of the population over the whole cycle are described by a periodic matrix product:

$$\mathbf{n}(t + m) = [\mathbf{B}^{(m)}\mathbf{B}^{(m-1)} \dots \mathbf{B}^{(1)}]\mathbf{n}(t) \quad (1)$$

$$= \mathbf{A}^{(1)}\mathbf{n}(t). \quad (2)$$

TABLE 1. Transitions or components of transitions estimated in the missing year(s).

Transition or component of transition	Number of years (periods)	Estimation	Statistics				
			<i>N</i>	<i>R</i> <sup>2</sup>	<i>F</i> (df)	<i>P</i>	Range
Seedling survival	4 (4)	linear regression with TPP <sup>†</sup>	16	0.29	7.18 (1, 15)	0.015	
Seed germination	4 (5)	linear regression with MTP <sup>‡</sup>	20	0.35	13.82 (1, 19)	0.001	
Seed establishment (September)	4 (1)	mean value					0.00–0.08
Seedling establishment (November)	4 (1)	mean value					0.01–0.20
Seedling establishment (July)	4 (1)	mean value					0.09–0.37
No. of seeds per fruit	1 (5)	mean value					1.24–1.78
Fruit set <sup>§</sup>	3 (5)	mean value					0.67–0.99
Seed predation rate	3 (5)	mean value					0.01–0.11
Seed survival in the soil	1 (6)	mean value					0.04–0.12

Notes: The range of mean values per period obtained in all sampling periods is given. In the case of linear regressions between transitions and climatic variables, the corresponding statistics are indicated. Abbreviations: TPP, total precipitation recorded in the previous period; MTP, mean temperature recorded the previous period.

<sup>†</sup> Seedling survival = 1.68 – 0.53 (TPP).

<sup>‡</sup> Seed germination = –0.03 + 0.59 (MTP).

<sup>§</sup> Fruit set = 1 – (flower abortion rate). Both fruit set and seed predation rate were used to estimate the number of fruits produced per plant. All these components were estimated with the same experiment (for details, see Picó and Retana [2000]).

The matrix product  $\mathbf{A}^{(1)}$  projects the population through the whole year. The superscripts on  $\mathbf{B}$  and  $\mathbf{A}$  indicate the period at which the population projection starts. In the case of *L. maritima*,  $\mathbf{B}^{(1)}$  projects the population from 1 September to 31 October,  $\mathbf{B}^{(2)}$  from 1 November to 31 December, and so on. The periodic matrix product  $\mathbf{A}^{(1)}$  projects from 1 September to 31 August of the next year,  $\mathbf{A}^{(2)}$  from 1 November to 31 October, and so on. For a given year, the matrices  $\mathbf{A}^{(1)}, \mathbf{A}^{(2)}, \dots, \mathbf{A}^{(m)}$  may differ greatly in form, because they start in different periods of the year although they all yield the same population growth rate  $\lambda$  (Caswell and Trevisan 1994, Caswell 2001).

The sensitivity of demographic parameters ( $s_{ij} = \partial\lambda / \partial a_{ij}$ ) measures the impact on  $\lambda$  of small changes in the matrix entries (Caswell 2001). Elasticity ( $e_{ij} = s_{ij} \times a_{ij} / \lambda$ ) is a measure of the proportional change in  $\lambda$  in response to a small proportional change in the value of a matrix element (de Kroon et al. 1986, 2000, Caswell 2001). Caswell and Trevisan (1994) demonstrated that the sensitivity of  $\lambda$  to changes in the periodic matrix entries in a given period  $h$  is given by

$$\mathbf{S}_B^{(h)} = [\mathbf{B}^{(h-1)} \mathbf{B}^{(h-2)} \dots \mathbf{B}^{(1)} \mathbf{B}^{(m)} \mathbf{B}^{(m-1)} \dots \mathbf{B}^{(h+1)}]^T \mathbf{S}_A^{(h)} \quad (3)$$

where  $\mathbf{S}_B^{(h)}$  is the sensitivity matrix of the periodic matrix  $\mathbf{B}^{(h)}$ , and  $\mathbf{S}_A^{(h)}$  is the sensitivity matrix of the annual matrix  $\mathbf{A}^{(h)}$ , both evaluated at the period  $h$ . The superscript T denotes the matrix transpose. The elasticity matrix,  $\mathbf{E}_B^{(h)}$ , of the periodic matrix  $\mathbf{B}^{(h)}$  in the period  $h$  is obtained as

$$\mathbf{E}_B^{(h)} = 1/\lambda \mathbf{B}^{(h)} * \mathbf{S}_B^{(h)} \quad (4)$$

where the symbol (\*) indicates a matrix product, element by element. Elasticities sum to one (de Kroon et al. 1986) and may be interpreted as the relative contribution of a matrix element to  $\lambda$  (de Kroon et al. 1986,

2000). Elasticities of each of the periodic matrices also sum to one, and  $\lambda$  may be decomposed into contributions made by each of the periodic matrix elements as given by their elasticities.

#### Decomposition of the variance in $\lambda$

As a result of the application of the matrix model on the present 5-yr data set, we obtained a set of five growth rates  $\lambda_1, \dots, \lambda_5$  from which we calculated the variance in  $\lambda$ , denoted as  $V(\lambda)$  hereafter, for the *L. maritima* population. Variance decomposition analyses estimate the contributions of the observed variance in the demographic parameters to the observed variance in  $\lambda$  (Caswell 2000, 2001). We decomposed the observed  $V(\lambda)$  into contributions from the variability in the demographic parameters over the study years, based on a random design (Brault and Caswell 1993, Horvitz et al. 1997, Caswell 2000, 2001). Following Caswell (2000, 2001), the first-order approximation to  $V(\lambda)$  is given by

$$V(\lambda) \approx \sum_{ij} V(a_{ij}) s_{ij}^2 + \sum_{ij \neq kl} \text{Cov}(a_{ij}, a_{kl}) s_{ij} s_{kl} \quad (5)$$

where  $V(a_{ij})$  is the variance in the  $ij$ th demographic parameters,  $\text{Cov}(a_{ij}, a_{kl})$  denotes the covariance between the  $ij$ th and  $kl$ th demographic parameters, and  $s_{ij}$  and  $s_{kl}$  are the sensitivities of the  $ij$ th and  $kl$ th demographic parameters, respectively, evaluated at the mean matrix, consisting of mean transition probabilities of all matrices over which  $V(\lambda)$  is computed. Note that the variability in the demographic parameters is expressed not only as the variance but also as the covariance among them. Taking into account such covariances is of paramount importance since the demographic parameters do not vary independently (van Tienderen 1995, Horvitz et al. 1997, Caswell 2000).

In a periodic system as the model of *L. maritima*, a given demographic parameter can contribute to  $V(\lambda)$  because of its variance among years, because of its covariance with demographic parameters within the same period, and because of its covariance with demographic parameters of other periods. Thus, a third component of variability in demographic parameters must be considered, i.e., the covariance among demographic parameters among periods. We extended Eq. 5 to a periodic system to quantify the contributions to  $V(\lambda)$  of these three components and for each demographic parameter in each period of the year. Thus, the proportion of  $V(\lambda)$  explained by variation in parameters of the period  $h$  ( $h = 6$  periods in this study) can be decomposed as

$$V(\lambda)^h \approx \sum_{ij} V(a_{ij}^h)(s_{ij}^h)^2 + \sum_{ij \neq kl} \text{Cov}(a_{ij}^h, a_{kl}^h)s_{ij}^h s_{kl}^h + \sum_{ij} \sum_{kl} \text{Cov}(a_{ij}^h, a_{kl}^s)s_{ij}^h s_{kl}^s \quad \text{with } h \neq s \quad (6)$$

where  $V(a_{ij}^h)$  is the variance of the  $ij$ th element in the period  $h$ ,  $\text{Cov}(a_{ij}^h, a_{kl}^h)$  is the covariance between the  $ij$ th and the  $kl$ th element in the period  $h$ ,  $\text{Cov}(a_{ij}^h, a_{kl}^s)$  is the covariance between the  $ij$ th element in the period  $h$  and the  $kl$ th element in the period  $s$ ,  $s_{ij}^h$  and  $s_{kl}^h$  are the periodic sensitivities of the  $ij$ th and the  $kl$ th element in the matrix of the period  $h$ , respectively, and  $s_{kl}^s$  is the periodic sensitivity of the  $kl$ th element in the matrix of the period  $s$ . The variance-covariance structure of the periodic demographic parameters were computed directly from the data on periodic matrices  $\mathbf{B}^{(h)}$ . The periodic sensitivities in each period  $h$  were obtained by using the computation of periodic sensitivities given in Eq. 3 evaluated at the mean periodic matrices.

Because Eq. 6 gives the proportion of  $V(\lambda)$  explained by variation in parameters in only one period of the year, it follows that the sum of all periodic contributions  $V(\lambda)^h$  must approximate the observed  $V(\lambda)$ :

$$V(\lambda) \approx \sum_h V(\lambda)^h. \quad (7)$$

Note that the periodic contributions to  $V(\lambda)$  in Eq. 6 depend on the covariances among pairs of demographic parameters (within and among periods). In order to obtain the total contributions to  $V(\lambda)$  from each single demographic parameter in each period, total contributions  $\chi_{ij}$  to  $V(\lambda)$  were computed by using the covariance method (Horvitz et al. 1997) in which the contribution made by the  $ij$ ,  $kl$ th pair is divided by two and each half assigned to the  $ij$ th and  $kl$ th demographic parameter, respectively. It is possible in this way to evaluate whether a high contribution to  $V(\lambda)$  from a given demographic parameter in a given period is due to its high variation, its high covariation with other demographic parameters within the same period, and/or its high covariation with demographic parameters of other periods.

### Stochastic simulations

Stochastic simulations were carried out with annual projection matrices (i.e., populations were projected from the beginning of September of year  $t$  to the end of August of year  $t + 1$ ). We obtained five annual matrices by multiplying the six periodic matrices per year (using Eqs. 1–2). At each time step of the simulations, one matrix from a pool of five annual matrices was sampled with equal probability. We estimated the stochastic population growth rate  $\ln \lambda_s$  numerically where  $\ln \lambda_s$  can be computed by averaging a number of one step estimates of  $\ln \lambda_s$  over  $T$  time units (Heyde and Cohen 1985, Cohen 1986, Caswell 2001). Thus,

$$\ln \lambda_s(i) = \ln N(i + 1) - \ln N(i) \quad (8)$$

$$\ln \lambda_s = \sum_i \ln \lambda_s(i) / (T - 1). \quad (9)$$

To estimate  $\ln \lambda_s$ , an initial vector of 100 individuals, distributed as small rosettes in September, was projected over a 1500-yr stochastic sample path, and only the last 1000 yr were used to estimate  $\ln \lambda_s$  to avoid the transient behavior of the model. The 95% confidence intervals of  $\ln \lambda_s$  are given by  $\pm 1.96 (V[\ln \lambda_s(i)]/T)^{1/2}$  where  $V[\ln \lambda_s(i)]$  is the variance of  $\ln \lambda_s(i)$  (Heyde and Cohen 1985).

To test the effect of different flowering and fruiting patterns on  $\ln \lambda_s$ , we modified the observed sets of periodic matrices by reallocating seeds and seedlings produced between the periods of the year. For each of the 5 yr of study, fecundities were reallocated resulting in a hypothetical set of five new annual matrices. Three of these sets of matrices were obtained as follows: (1) a population with an even distribution of fecundities among the first five periods of the year, i.e., the seed and seedling productions were the same for each of the September, November, January, March, and May periods, (2) a population with fecundities of January, March, and May periods (i.e., the second half of the season) reallocated to the September and November periods (i.e., the first half of the season), and (3) a population with fecundity of the first half of the season reallocated to the second half of the season. When fecundities from particular periods were reallocated to other periods, seeds and seedlings were equally distributed among the other periods. Redistributions of fecundity among periods were carried out in such a way that (1) the total number of seeds and seedlings produced per year remained unchanged, and (2) the proportional fecundities of different size classes in each period of the year was unaltered. We calculated  $\ln \lambda_s$  for the observed population and for each of the three hypothetical fecundity schedules by using Eqs. 8–9.

## RESULTS

### Periodic life cycle graphs

A graphical representation of the five-stage, size-structured life cycle of *L. maritima* for each period of

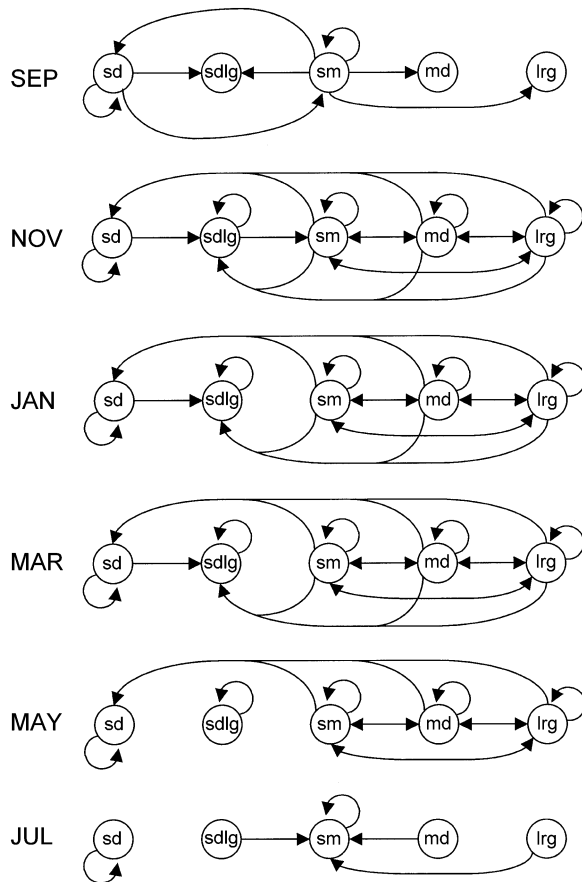


FIG. 1. Life-cycle graphs of *L. maritima* for each of the six periods of the year. Nodes correspond to plant stages, and arcs represent the transitions between stages. Stages are seeds (sd), seedlings (sdlg), and small (sm), medium (md), and large (lrg) adult plants. Period names are September (SEP), November (NOV), January (JAN), March (MAR), May (MAY), and July (JUL). Each period includes two months and is denoted by the first of the two months.

the year is shown in Fig. 1. Each periodic life-cycle graph in Fig. 1 corresponds to one periodic projection matrix. The onset of the flowering and fruiting season of *L. maritima* occurred in the September period when only few seeds in the soil and small adults were present. Seeds in the soil germinated and some seedlings established whereas small adults grew in size producing several flowering stalks. In the November period, many individuals reached the largest size class showing high seed and seedling production rates (Table 2). During January and March periods, in general, adults decreased in size and fecundities were much lower than in autumn (Table 2). Given the continuous production of seedlings and their high survival rates in all periods of the season, a seedling bank was created and consolidated throughout the season. In the May period, almost all individuals reduced in size to the smallest category and no germination event was recorded. During the July period, the few adults remaining lost all

flowering stalks and all seedlings produced during the season established as small adults or died.

#### *Population growth rates and temporal variation in periodic transitions*

During this 5-yr study, the *L. maritima* population varied greatly in population growth rate  $\lambda$ , ranging from a low of 0.25 to a high of 4.81 ( $\lambda$  of mean periodic matrices = 2.31). During the first 4 yr, the population was increasing but it declined during the last year of study. Mean periodic transitions are shown in Table 2 with their coefficients of variation (cv) that measure their among-year variability. The highest values for fecundity and growth transitions occurred in the September and November periods. In January, March, and May periods fecundity decreased and stasis and retrogression transitions increased concomitantly. Seedling survival was high throughout the year, and the highest mortality rates of both seedlings and adults were recorded in the July period in all study years. Seeds survived in the soil although high seed predation rates produced severe losses throughout the year. Many periodic transitions showed coefficients of variation over 100% in many periods, with fecundity and growth as the most variable transitions among years and seedling survival and stasis of small adults as the least variable (Table 2).

#### *Elasticity analysis*

Mean periodic elasticities (Table 2) revealed that, on average, seedling production showed high contributions to mean  $\lambda$  in the September and November periods. Seedling survival in each period of the year and seedling establishment in the July period also showed very high mean elasticities, as well as survival of small adults in almost all periods. The elasticity patterns for each of the 5 yr of study are summarized in Fig. 2. In the first 4 yr, seedling production at the beginning of the flowering season (in September or November, and more rarely in January), the survival of such seedlings throughout the year, and their final establishment as small adults in July, together represent the demographic pathway (sensu van Groenendael et al. 1994) that made the largest contribution to  $\lambda$  throughout the year. Survival of adults in each period of the year represents the second most important pathway. We refer to these sequences of transitions as the "seedling pathway" and the "adult pathway," respectively. A third "seed pathway," which included seed production, seed germination, and seed survival in the soil, generally made a small contribution to  $\lambda$ . Seed production obtained relatively high elasticities, although smaller than those of seedling production and adult survival, and only during the first two periods in some of the years (see Fig. 2). In none of the years of study were elasticities of seed and seedling production high in January, March, and May periods (except seedling production in the January period in the 1993–1994 year). In the first 4 yr,  $\lambda$  was

always positive (see Fig. 2). During the last year only did the seedling pathway barely contribute to  $\lambda$  and the adult pathway accumulated almost all of the total elasticity, corresponding with a highly negative population growth rate ( $\lambda = 0.25$ ).

There was a significant negative relationship between mean elasticity and among-year variability (i.e., cv) in periodic demographic parameters (Fig. 3). All four seedling survival transitions plus seedling establishment in July, were the parameters with the highest elasticity and among the least variable. Also some of the adult survival transitions had high elasticities and low cvs. The reverse was true for seed and seedling production. These parameters were among the most variable, but some of them, i.e., seedling production in the September and November periods, also had high mean elasticity values (Fig. 3).

#### *Decomposition of the variance in $\lambda$*

Contributions to the variance in  $\lambda$ ,  $V(\lambda)$ , over the 5 yr of study by the variances and covariances of all periodic matrix elements summed to 2.99, which can be considered a good approximation to the observed  $V(\lambda) = 3.16$ . Major contributions to  $V(\lambda)$  were made only in the September, November, and July periods (Table 3). Most of  $V(\lambda)$  is explained by the variance in matrix entries (sum of contributions = 2.10) although contributions to  $V(\lambda)$  from the covariance within periods were also significant (sum of contributions = 0.83). Contributions from covariances among periods summed to only 0.06 because positive and negative covariance contributions cancelled out.

Transitions involved in the decomposition of  $V(\lambda)$  are shown in Fig. 4. The variance in seedling production in the September and November periods made the largest contribution to  $V(\lambda)$ . The contribution of the variance in adult survival in the September period was also large. Important and positive contributions to  $V(\lambda)$  were made by the covariance of seedling production with other transitions within both the September and November periods. In each of these periods, seedling production strongly positively covaried with seed production, resulting in a relatively large contribution to  $V(\lambda)$  by the covariation of these two fecundity parameters (results not shown). Note that contributions to  $V(\lambda)$  from the other periods were negligible except for the July period in which the variance in seedling establishment and adult survival slightly contributed to  $V(\lambda)$ .

Contributions from the third component in Eq. 6, i.e., contributions to  $V(\lambda)$  from the covariance among periods, were large in the September period (Fig. 4). Particularly striking was the negative covariance of seedling production in September with transitions in other periods. Further analyses indicated that seedling production in September strongly negatively covaried with seedling production in November (contribution to  $V(\lambda) = -0.36$ ; results not shown). This negative co-

variance did not appear in the November period in Fig. 4 because this negative covariance was cancelled out by a positive covariance of similar magnitude between seedling production in November and seedling establishment (contribution to  $V(\lambda) = 0.27$ ; results not shown) and adult survival (contribution to  $V(\lambda) = 0.20$ ; results not shown) in July. No other notable contributions to  $V(\lambda)$  from the covariances among periods appeared in our analysis.

#### *Stochastic simulations*

Reallocation of fecundities among periods to create new sets of annual matrices led to changes in their annual  $\lambda$ 's (Table 4). Growth rate of the population in which fecundity of the second half was reallocated to the first half of the season differed little from those of the observed population. Greater changes appeared for the simulated population with fecundity of the first half reallocated to the second half of the season. In particular,  $\lambda$  of the 1994–1995 year overwhelmingly increased nearly  $3.5\times$  whereas  $\lambda$  of 1995–1996 and 1996–1997 years decreased sharply. The simulated population with even distribution of fecundities among periods showed a twofold increase in  $\lambda$  in the 1994–1995 year but smaller changes in  $\lambda$  for the other years. Such changes in  $\lambda$  can be explained by the magnitude of the reproductive output in a given year in conjunction with the differential fate of seeds and seedlings between the first and second half of the season. For example, for the 1994–1995 year with high reproduction, reallocating fecundity to the second half of the season led to an increase in  $\lambda$  as a result of increasing the number of surviving seedlings. A similar shift in  $\lambda$  did not occur for other years, because seedling establishment in these years was disproportionately lower in the second half compared to the first half of the season. As a result of these changes in  $\lambda$  for each of the years, both mean  $\lambda_s$  and the variance in  $\lambda$  increased in the simulations in which first half season fecundity was reallocated, and fecundities were evenly distributed (Table 4).

The population with fecundity of the second half reallocated to the first half of the season yielded a stochastic population growth rate  $\ln \lambda_s$  that was indistinguishable from that of the observed population (Table 4). While the mean deterministic  $\lambda$  of the five years simulated was much higher for the population in which fecundity of the first half of the season was reallocated to the second half, the  $\ln \lambda_s$  was significantly lower than  $\ln \lambda_s$  of the observed population. Finally, the population with even distribution of fecundities among periods showed the highest  $\ln \lambda_s$  although it was not significantly different from  $\ln \lambda_s$  of the observed population.

## DISCUSSION

### *Population growth rates and elasticity analysis*

We investigated the demographic implications of a unusual phenology in Mediterranean environments, in

TABLE 2. Mean transitions, coefficients of variation (CV = SD/mean × 100), and elasticities (in %) of mean periodic matrix entries.

Time $t + 1$ (by period and stage)	Mean transitions, at time $t$ by stage					CV at time $t$ by stage				
	sd	sdlg	sm	md	lrg	sd	sdlg	sm	md	lrg
<b>SEP</b>										
sd	0.043	...	45.55	...	...	...	...	<b>111.6</b>	...	...
sdlg	0.057	...	2.96	...	...	77.4	...	78.7	...	...
sm	0.023	...	0.537	...	...	<b>149.7</b>	...	60.3	...	...
md	...	...	0.162	...	...	...	...	<u>21.5</u>	...	...
lrg	...	...	0.406	...	...	...	...	<u>48.6</u>	...	...
<b>NOV</b>										
sd	0.118	...	12.70	38.26	177.68	...	...	<b>214.5</b>	<b>139.7</b>	<b>139.5</b>
sdlg	0.014	0.878	0.29	0.89	4.53	82.9	<u>13.6</u>	<b>457.4</b>	<b>193.1</b>	<b>151.8</b>
sm	...	0.086	0.687	0.396	0.166	...	<u>96.3</u>	<u>26.4</u>	91.5	108.3
md	...	...	0.164	0.263	0.121	...	...	89.4	95.1	37.9
lrg	...	...	0.154	0.342	0.699	...	...	94.7	<b>130.9</b>	31.7
<b>JAN</b>										
sd	0.118	...	6.37	22.91	83.21	...	...	65.7	57.5	68.8
sdlg	0.010	0.981	0.05	0.18	0.67	74.1	<u>2.7</u>	<b>142.9</b>	73.2	79.1
sm	...	...	0.947	0.754	0.214	...	...	6.6	36.7	<b>118.6</b>
md	...	...	0.025	0.180	0.339	...	...	<b>102.3</b>	<b>161.0</b>	20.2
lrg	...	...	...	0.083	0.446	...	...	...	<b>200.0</b>	52.9
<b>MAR</b>										
sd	0.118	...	3.03	9.44	24.70	...	...	<b>198.8</b>	<b>186.6</b>	<b>105.9</b>
sdlg	0.002	0.937	0.01	0.04	0.22	<b>122.7</b>	<u>5.9</u>	<b>447.2</b>	<b>143.1</b>	<b>114.3</b>
sm	...	...	0.896	0.714	0.226	...	...	<u>12.2</u>	29.6	84.9
md	...	...	0.037	0.206	0.125	...	...	<b>161.7</b>	97.3	<b>117.8</b>
lrg	...	...	0.011	0.028	0.542	...	...	<b>200.0</b>	<b>200.0</b>	68.9
<b>MAY</b>										
sd	0.065	...	0.32	0.18	3.75	...	...	<b>211.9</b>	<b>179.8</b>	<b>106.7</b>
sdlg	...	0.952	...	...	...	...	<u>7.8</u>	...	...	...
sm	...	...	0.917	0.650	0.550	...	...	5.9	72.7	80.6
md	...	...	0.024	0.225	0.200	...	...	<b>138.7</b>	<b>116.9</b>	<b>141.4</b>
lrg	...	...	...	...	0.250	...	...	...	...	<b>200.0</b>
<b>JUL</b>										
sd	0.065	...	...	...	...	...	...	...	...	...
sdlg	...	...	...	...	...	...	...	...	...	...
sm	...	0.293	0.474	0.417	0.500	...	<u>18.6</u>	61.9	<u>28.3</u>	<b>141.4</b>
md	...	...	...	...	...	...	...	...	...	...
lrg	...	...	...	...	...	...	...	...	...	...

Notes: For each period, values of the coefficient of variation over 100% are shown in boldface, and the two least variable parameters are underlined. In the elasticity matrix, elasticities over 10% are in boldface. Nonexistent transitions are represented by ellipses. Period and stage names are as in Fig. 1.

which the short-lived perennial plant *Lobularia maritima* exhibits a flowering and fruiting season that lasts for 10 mo. We hypothesized that this extended phenology can act as a mechanism to enhance population persistence in the variable Mediterranean environment. Elasticity analysis showed, in contrast to our predictions, that only fecundity in autumn contributed significantly to population growth rate. Fecundity elasticities in winter and spring were negligible, despite the continuous production of seeds and seedlings throughout the season. When environmental conditions were too unfavorable to allow massive seedling recruitment in any of the autumn periods, as occurred in the last year of our study, fecundity and recruitment in winter and spring were not able to buffer the reproductive failure in autumn.

Population growth rates of *L. maritima* were highly

variable over the 5 yr of study. A seedling pathway, comprising seedling production in autumn, seedling survival during winter and spring, and seedling establishment in summer, made the largest contribution to  $\lambda$  in years with positive growth rates (Fig. 2). In one particularly poor year, the importance of the seedling pathway dramatically decreased and the adult survival throughout the year accumulated nearly all the elasticity in  $\lambda$ . These results accord with those of an increasing number of studies showing that high growth rates may only be obtained when high fecundity rates occur (Silvertown et al. 1993, 1996, Oostermeijer et al. 1996, Fiedler et al. 1997, de Kroon et al. 2000).

Another general pattern exhibited by *L. maritima* is that those life history traits with a greater importance for population growth (i.e., high elasticities) showed the lowest levels of temporal variation, as shown by

TABLE 2. Extended.

Mean elasticities at time <i>t</i> by stage				
sd	sdlg	sm	md	lrg
0.01	...	7.88	...	...
0.03	...	<b>33.48</b>	...	...
0.03	...	<b>13.56</b>	...	...
...	...	5.99	...	...
...	...	<b>39.03</b>	...	...
0.61	...	0.77	0.71	8.21
7.25	<b>28.76</b>	1.73	1.62	<b>20.34</b>
...	4.65	6.80	1.19	1.24
...	...	1.88	0.92	1.04
...	...	2.38	1.62	8.17
0.27	...	0.12	0.11	0.89
9.94	<b>59.95</b>	0.43	0.37	3.16
...	...	<b>13.01</b>	2.50	1.63
...	...	0.34	0.60	2.60
...	...	...	0.31	3.78
0.01	...	0.01	0.01	0.01
1.39	<b>73.69</b>	0.11	0.09	0.54
...	...	<b>16.22</b>	2.65	0.89
...	...	0.60	0.69	0.44
...	...	0.22	0.11	2.55
0.04	...	0.01	0.01	0.02
...	<b>75.94</b>	...	...	...
...	...	<b>19.28</b>	1.32	1.43
...	...	0.45	0.40	0.46
...	...	...	...	0.69
0.07	...	...	...	...
...	...	...	...	...
...	<b>75.63</b>	<b>21.96</b>	1.65	0.69
...	...	...	...	...
...	...	...	...	...

many other life histories including several taxa (Ehrlén and van Groenendael 1998, Pfister 1998, de Kroon et al. 2000, Sæther and Bakke 2000, Wisdom et al. 2000). Demographic parameters comprising the seedling and adult pathways showed the highest elasticities and low levels of temporal variation. However, some transitions, i.e., seedling production in the September and November periods, exhibited both a high elasticity and a relatively high temporal variation (see Fig. 3), modifying therefore the general trend found by Pfister (1998). From an evolutionary point of view, variability in the onset of the seedling pathway might have been an advantageous trait since, basically, population growth of *L. maritima* depends on the fate of seedlings produced early or late in the autumn. We suggest that the variance/covariance structure in seedling production in the September and November periods can explain this result, given that not only the mean but also the variance in, and covariance among, traits can affect

life history evolution (Real and Ellner 1992, Sasaki and Ellner 1997).

#### Variance decomposition analysis

We predicted that *L. maritima* would exhibit negative covariances between fecundities of different periods of the year. The demographic importance of negative covariances between demographic parameters is that they reduce the temporal variation in population growth rate (cf. Horvitz et al. 1997), and decreasing variation in population growth rate leads to increasing population persistence (Tuljapurkar and Orzack 1980). Such negative covariances were indeed found, but only for seedling production in September that strongly negatively covaried with seedling production in November. This negative relationship can be explained by the variability in the precipitation regime. The peak of precipitation can occur either in the September period or in the November period. In 22 out of a total of 28 yr, >60% of the total precipitation recorded in the two autumn periods fell either in the September period or in the November period (F. X. Picó, unpublished data). As a result, the bulk of seed production and recruitment occurred either in September or in November, but rarely in both periods in the same year. We conclude that, during the autumn periods, the life history of *L. maritima* is flexible enough to tailor the onset of reproduction to the onset of the rainy season, buffering the effects of environmental variability in autumn on fecundity. Similar negative covariances were lacking between the autumn and the winter/spring periods indicating that a similar reproductive compensation cannot occur between more separate periods within the flowering and fruiting season of *L. maritima*. Although there is a second peak of precipitation in spring, the amount of precipitation is always lower and not so concentrated as the peak of precipitation in autumn. Moreover, due to the unpredictability of the environment, i.e., a dry autumn is not necessarily followed by a wet spring, fecundity in spring cannot compensate the reproductive failure occurred in autumn.

Another explanation why *L. maritima* plants are unable to peak fecundity in spring may be that reproduction is costly. Consistent with such costs, in all 5 yr of study, the reproductive output of individual *L. maritima* plants, estimated as the maximum number of flowering stalks borne per plant, was significantly lower in spring than in autumn ( $N > 19$ ,  $t > 3.1$ ,  $P < 0.005$ ; pairwise comparisons separately for each of 5 yr). However, because of the interaction with the precipitation regime, it is not possible to relate this trend directly to the costs of reproduction. Other observations suggest that the costs of reproduction are very low in *L. maritima*. For example, the maximum reproductive output in a given year was not significantly related to plant survival after the summer ( $N = 155$ ,  $R^2 = 0.025$ ,  $\chi^2 = 2.76$ ,  $P = 0.096$ ; logistic regression),

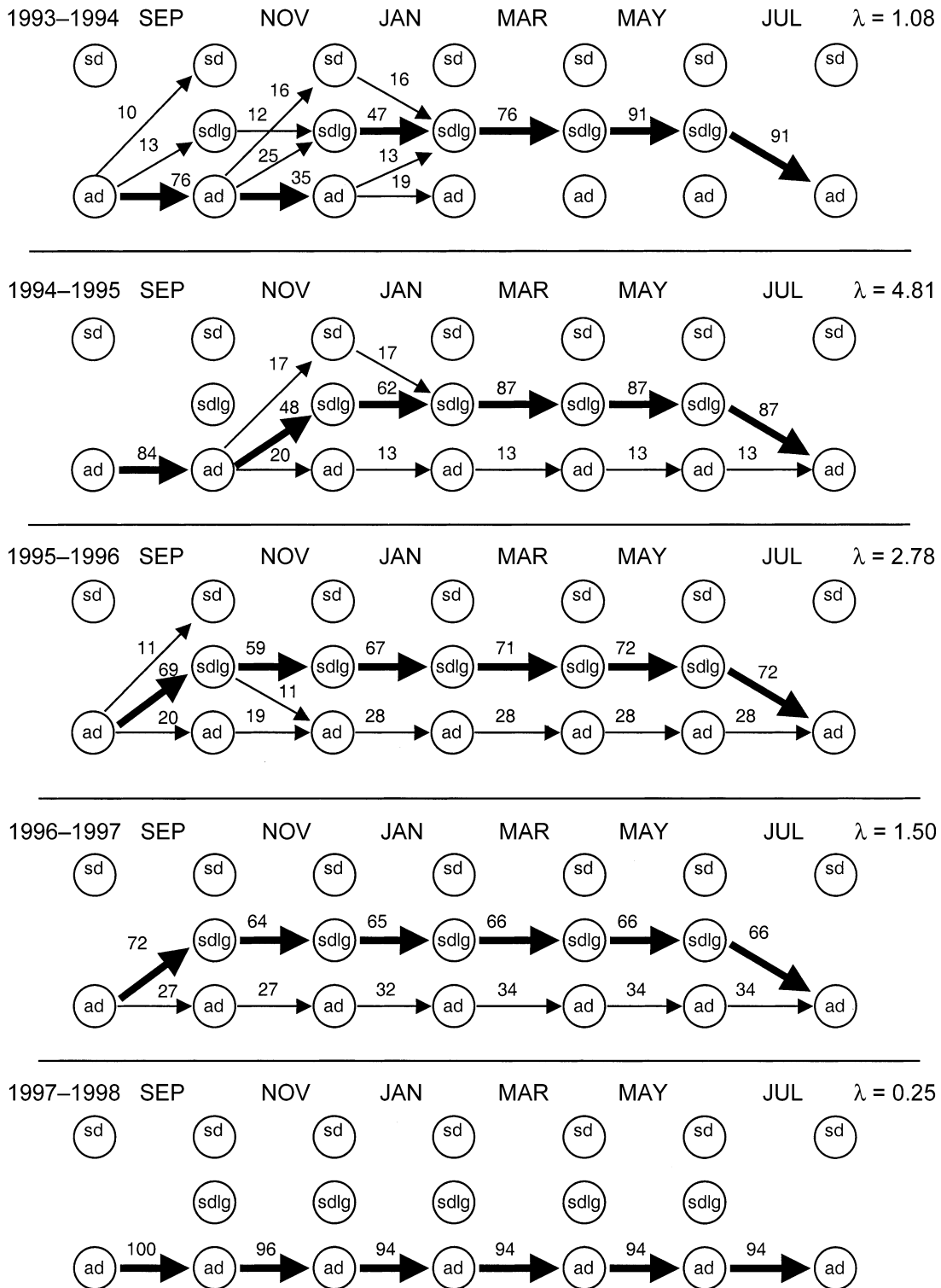


FIG. 2. Periodic elasticity values for each of the five years in which the *L. maritima* population was studied. Stages are seeds (sd), seedlings (sdlg), and adult plants (ad) in which small, medium, and large adults are merged. The numbers adjacent to the arcs are the corresponding periodic elasticities (%). Elasticities <10% are not shown. Thicker arrows indicate the transition with the largest elasticity in a given period of the season. Together they comprise the main life-history pathway that contributes to the population growth rate throughout the year. Population growth rates ( $\lambda$ ) for each year are also given. Period names are as in Fig. 1.

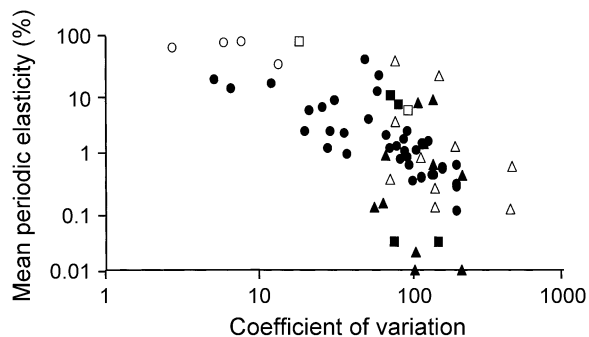


FIG. 3. Significant log-log linear regression ( $N = 69$ ,  $R^2 = 0.42$ ,  $F_{1,68} = 47.6$ ,  $P < 0.0001$ ) between the coefficient of variation and elasticity for each mean periodic demographic parameter. Basic data are given in Table 2. Demographic parameters were grouped into six categories that are related to the three main life-history pathways as identified in Fig. 2. Seed production (solid triangles) and seed fate (solid quadrats), which includes contributions from seed germination and seed survival in the soil, form the "seed pathway." Seedling production (open triangles), seedling survival (open circles), and seedling establishment (open quadrats), form the "seedling pathway." Adult survival (solid circles), which includes survival, growth, and retrogression of all adult stages, forms the "adult pathway."

suggesting that there was no trade-off between reproduction and survival.

#### Stochastic simulations

Through population explosions, due to massive recruitment, in exceptionally favorable years, *L. maritima* was able to cope with the high environmental variance occurring in its environment, as shown by the positive stochastic population growth rate (Table 4). Simulated populations with different fecundity schedules showed that flowering and fruiting in autumn were critical to maintain high stochastic population growth rates, because a reallocation of fecundity to the second half of the season, i.e., winter and spring periods, resulted in a significant lower stochastic population growth rate. In contrast to our expectations, population persistence is enhanced by very high fecundities in autumn rather than by the length of the flowering and fruiting season itself (Table 4). In this sense, the short-lived perennial *L. maritima* acts as an annual plant with a seed bank, which buffer environmental variation by

replenishing the seed bank (the seedling bank in the case of *L. maritima*) through population explosions in favorable years (Kalisz and McPeck 1992).

Spreading reproduction evenly within a season produced a marked increase in the variance in mean and the variance in population growth rate, because the fecundity schedule in autumn was dramatically altered. Interestingly, the net effect of such increase for the simulated *L. maritima* population on its long-term stochastic growth rate only was slightly positive. The negative effect of increasing variance, as predicted by theory (Tuljapurkar and Orzack 1980), was apparently compensated for by the higher mean population growth rate. When such variance became greater, as for the simulated population with fecundities of the first half reallocated to the second half of the season, the subsequent stochastic population growth rate decreased significantly. However, stochastic population growth rate remained positive. Here the higher population growth rate could no longer compensate for the negative effects of variation in stochastic growth rate. These results therefore also indicate that rare and exceptionally favorable years may allow for population persistence although in most years the population is in decline. This scenario has been suggested by Eriksson (1996) and recently by Higgins et al. (2000), who showed that life histories with erratic massive recruitment and potential to store reproductive capacity might be able to endure long series of poor years.

#### Final considerations

We hypothesized that the extended flowering and fruiting of *L. maritima* would represent a mechanism to enhance population persistence in the Mediterranean variable environment. However, only fecundity during the first two periods of the season (i.e., four months) significantly contributed to the species' population dynamics and therefore to the long-term persistence of the species. Why then does *L. maritima* show such extended flowering and fruiting? Low costs of reproduction, as suggested above, could induce the plant to produce flowers, fruits, and seeds during several months even when the extended reproduction is demographically meaningless. Moreover, flowering seems morphologically inevitable in *L. maritima*, i.e., the plant is simply a rosette of reproductive stalks and

TABLE 3. Total contributions to the variance in  $\lambda$ ,  $V(\lambda)$ , for the *L. maritima* population monitored from 1993 to 1998.

Variance component	Period						Total
	SEP	NOV	JAN	MAR	MAY	JUL	
Variance	0.996	0.823	0.040	0.018	0.020	0.207	2.104
Covariance within periods	0.192	0.580	-0.001	-0.003	-0.004	0.064	0.829
Covariance among periods	-0.402	-0.018	-0.005	0.022	0.073	0.387	0.057
Total	0.786	1.385	0.034	0.037	0.089	0.658	2.990

Notes: For each period, contributions to  $V(\lambda)$  come from three different components (see Eq. 6): (1) from the variance in transitions, (2) from the covariance among transitions of the same period, and (3) from the covariance among transitions of different periods. Period names are as in Fig. 1.

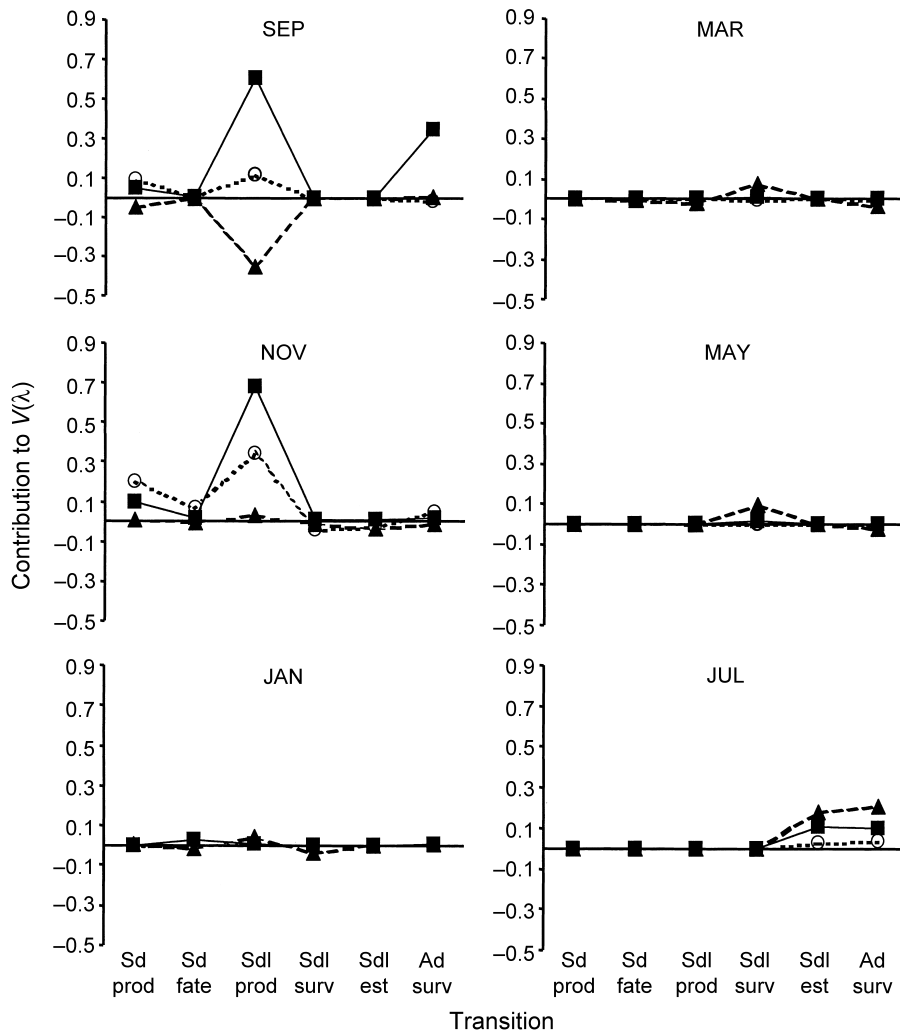


FIG. 4. Total contributions to the variance in  $\lambda$ ,  $V(\lambda)$ , from transitions in each period of the year. Total contributions to  $V(\lambda)$  are made by three components (Eq. 6): the variance in transitions (solid squares), the covariance among transitions of the same period (open circles), and the covariance among transitions of different periods (solid triangles). Contributions to  $V(\lambda)$  are grouped in the same six categories as in Fig. 3. Abbreviations: Sd prod, seed production; Sd fate, seed fate; Sdl prod, seedling production; Sdl surv, seedling survival; Sdl est, seedling establishment; Ad surv, adult survival. Period names are as in Fig. 1.

TABLE 4. Deterministic population growth rates ( $\lambda$ ) for each year of study, deterministic mean  $\lambda \pm 1$  SE, and stochastic population growth rates  $\ln \lambda_s \pm 95\%$  CI for the *L. maritima* population of study for four different sets of simulations: (1) the observed set of periodic matrices, (2) with fecundity (i.e., seed and seedling production) of the January, March, and May periods (i.e., the second half of the season) evenly reallocated to the September and November periods (i.e., the first half of the season), (3) with fecundity of the first half evenly reallocated to the second half of the season, and (4) with fecundity evenly distributed over periods excluding the summer period.

Simulation	$\lambda$					Mean $\lambda \pm 1$ SE	$\ln \lambda_s \pm 95$ CI
	(1993–1994)	(1994–1995)	(1995–1996)	(1996–1997)	(1997–1998)		
Observed matrices	1.08	4.81	2.78	1.50	0.25	$2.09 \pm 0.887$	$0.322 \pm 0.062$
Second half reallocated	1.66	4.92	1.96	1.13	0.27	$1.99 \pm 0.879$	$0.263 \pm 0.058$
First half reallocated	1.00	16.54	0.64	0.63	0.24	$3.81 \pm 3.561$	$0.121 \pm 0.087$
Even distribution	1.28	10.64	1.41	0.97	0.27	$2.91 \pm 2.172$	$0.355 \pm 0.074$

plant growth can only occur by increasing the number of such stalks. In addition, some of the woody species of the Mediterranean flora also show unusual fruiting patterns, e.g., *Osyris quadripartita* Salzm. (Herrera 1988). These have been attributed to the origin of these woody species as tropical relicts, having changed little since the initiation of the Mediterranean conditions in the Pliocene (Herrera 1988 and references therein). In fact, there is strong evidence that flowering phenologies of plant species are strongly affected by phylogenetic constraints (Kochmer and Handel 1986), factor that could also apply to *L. maritima*, perhaps in conjunction with morphological constraints and low costs of reproduction.

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#### LITERATURE CITED

- Aschmann, H. 1973. Distribution and peculiarity of Mediterranean ecosystems. Pages 121–142 in F. di Castri and H. A. Mooney, editors. Mediterranean-type ecosystems. Origin and structure. Springer-Verlag, Berlin, Germany.
- Bawa, K. S. 1983. Patterns of flowering in tropical plants. Pages 394–410 in C. E. Jones and R. J. Little, editors. A handbook of experimental pollination ecology. Van Nostrand, New York, New York, USA.
- Bolòs, O., J. Vigo, R. Masalles, and J. Ninot. 1993. Flora dels Països Catalans. Editorial Barcino, Barcelona, Spain.
- Bosch, J., J. Retana, and X. Cerdà. 1997. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* **109**: 583–591.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* **74**:1444–1454.
- Brown, J. S., and D. L. Venable. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. *American Naturalist* **127**:31–47.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81**: 619–627.
- Caswell, H. 2001. Matrix population models. Construction, analysis and interpretation. Second edition. Sinauer, Sunderland, Massachusetts, USA.
- Caswell, H., and M. C. Trevisan. 1994. Sensitivity analysis of periodic matrix models. *Ecology* **75**:1299–1303.
- Cerdà, X., and J. Retana. 1994. Food exploitation patterns of two sympatric seed-harvesting ants *Messor bouvieri* (Bond.) and *Messor capitatus* (Latr.) (Hym., Formicidae) from Spain. *Journal of Applied Entomology* **117**:268–277.
- Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge, UK.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* **12**: 119–129.
- Cohen, J. E. 1986. Population forecast and confidence intervals for Sweden: a comparison of model-based and empirical approaches. *Demography* **23**:105–126.
- Dafni, A., and C. O'Toole. 1994. Pollination syndromes in the Mediterranean: generalisations and peculiarities. Pages 125–135 in M. Arianoutsou and R. H. Groves, editors. Plant–animal interactions in mediterranean-type ecosystems. Kluwer Academic, Dordrecht, The Netherlands.
- de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**:1427–1431.
- de Kroon, H., J. van Groenendael, and J. Ehrlén. 2000. Elasticities: a review of methods and model limitations. *Ecology* **81**:607–618.
- Doak, P., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. *Ecological Applications* **4**:446–460.
- Ehrlén, J., and J. van Groenendael. 1998. Direct perturbation analysis for better conservation. *Conservation Biology* **12**: 470–474.
- Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source–sink, and metapopulations. *Oikos* **77**:248–258.
- Fiedler, P. L., B. E. Knapp, and N. Fredricks. 1997. Rare plant demography: lessons from the Mariposa Lilly (*Calochortus*: Liliaceae). Pages 28–48 in P. L. Fiedler and P. M. Kareiva, editors. Conservation biology: for the coming decade. Chapman and Hall, New York, New York, USA.
- Gómez, J. M. 2000. Effectiveness of ants as pollinators of *Lobularia maritima*: effects on main sequential fitness components of the host plant. *Oecologia* **122**:90–97.
- Goodman, D. 1984. Risk spreading as an adaptive strategy in iteroparous life histories. *Theoretical Population Biology* **25**:1–20.
- Herrera, C. M. 1988. The fruiting ecology of *Osyris quadripartita*: individual variation and evolutionary potential. *Ecology* **69**:233–249.
- Herrera, C. M. 1992. Individual flowering time and maternal fecundity in a summer-flowering Mediterranean shrub: making the right prediction for the wrong season. *Acta Oecologica* **13**:13–24.
- Herrera, J. 1986. Flowering and fruiting phenology in the coastal shrublands of Doñana, south Spain. *Vegetatio* **68**: 91–98.
- Heyde, C. C., and J. E. Cohen. 1985. Confidence intervals for demographic projections based on products of random matrices. *Theoretical Population Biology* **27**:120–153.
- Higgins, S. I., S. T. A. Pickett, and W. J. Bond. 2000. Predicting extinction risks for plants: environmental stochasticity can save declining populations. *Trends in Ecology and Evolution* **15**:516–520.
- Horvitz, C. C., D. W. Schemske, and H. Caswell. 1997. The relative “importance” of life-history stages to population growth: prospective and retrospective analyses. Pages 247–271 in S. Tuljapurkar and H. Caswell, editors. Structured population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York, USA.
- Kalisz, S., and M. A. McPeck. 1992. Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology* **73**:1082–1093.
- Klinkhamer, P. G. L., T. J. de Jong, J. A. J. Metz, and J. Val. 1987. Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theoretical Population Biology* **32**:127–156.
- Kochmer, J. P., and S. N. Handel. 1986. Constraints and competition in the evolution of flowering phenology. *Ecological Monographs* **56**:303–325.
- Kummerow, J. 1983. Comparative phenology of Mediterranean-type plant communities. Pages 300–317 in F. J. Kruger, D. T. Mitchell, and J. U. M. Jarvis, editors. Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin, Germany.
- Menges, E. S. 1997. Evaluating extinction risks in plant populations. Pages 49–65 in P. L. Fiedler and P. M. Kareiva,

- editors. Conservation biology for the coming decade. Chapman and Hall, New York, New York, USA.
- Moloney, K. A. 1986. A generalized algorithm for determining category size. *Oecologia* **69**:176–180.
- Mooney, H. A., D. J. Parsons, and J. Kummerow. 1974. Plant development in Mediterranean climates. Pages 255–267 in H. Lieth, editor. Phenology and seasonality modeling. Springer-Verlag, Berlin, Germany.
- Oostermeijer, J. G. B., M. L. Brugman, E. R. de Boer, and H. C. M. den Nijs. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology* **84**:153–166.
- Orshan, G. 1983. Approaches to the definition of Mediterranean growth forms. Pages 282–299 in F. J. Kruger, D. T. Mitchell, and J. U. M. Jarvis, editors. Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, Berlin, Germany.
- Orzack, S. H. 1997. Life history evolution and extinction. Pages 273–302 in S. Tuljapurkar and H. Caswell, editors. Structured population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York, USA.
- Orzack, S. H., and S. D. Tuljapurkar. 1989. Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *American Naturalist* **133**:901–923.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences (USA)* **95**:213–218.
- Picó, F. X., and J. Retana. 2000. Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb. *Oikos* **89**:485–492.
- Proctor, M., P. Yeo, and A. Lack. 1996. The natural history of pollination. Timber, Portland, Oregon, USA.
- Real, L. A., and S. Ellner. 1992. Life history evolution in stochastic environments: a graphical mean-variance approach. *Ecology* **73**:1227–1236.
- Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642–653.
- Sæther, B.-E., S. Engen, A. Islam, R. McCleery, and C. Perrins. 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *American Naturalist* **151**:441–450.
- Sasaki, A., and S. Ellner. 1997. Quantitative genetic variance maintained by fluctuating selection with overlapping generations: variance components and covariances. *Evolution* **51**:682–696.
- Silvertown, J., M. Franco, and E. S. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* **10**:591–597.
- Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparing plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* **81**:465–476.
- Tuljapurkar, S. D. 1990. Delayed reproduction and fitness in variable environments. *Proceedings of the National Academy of Sciences (USA)* **87**:1139–1143.
- Tuljapurkar, S. D., and S. H. Orzack. 1980. Population-dynamics in variable environments. I. Long-run growth-rates and extinction. *Theoretical Population Biology* **18**:314–342.
- van Groenendael, J., H. de Kroon, S. Kalisz, and S. Tuljapurkar. 1994. Loop analysis: evaluating life history pathways in population projection matrices. *Ecology* **75**:2410–2415.
- van Tienderen, P. H. 1995. Life cycle trade-offs in matrix population models. *Ecology* **76**:2482–2489.
- Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* **46**:272–282.
- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* **81**:628–641.