BRIEF COMMUNICATION

Life span correlates with population dynamics in perennial herbaceous plants[1]

María B. García,[2,6] F. Xavier Picó,[3,4] and Johan Ehrlén[5]

[2]Instituto Pirenaico de Ecología, CSIC, Apdo. 202, Zaragoza, Spain; [3]Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Universitat Autònoma de Barcelona 08193 Bellaterra (Barcelona), Spain; [4]Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n 41013 Seville, Spain; and [5]Department of Botany, University of Stockholm, Stockholm 10691, Sweden

Survival and fecundity are basic components of demography and therefore have a strong influence on population dynamics. These two key parameters and their relationship are crucial to understand the evolution of life histories. It remains, however, to be empirically established how life span, fecundity, and population dynamics are linked in different organism groups. We conducted a comparative study based on demographic data sets of 55 populations of 23 perennial herbs for which structured demographic models and among-year natural variation in demographic attributes were available. Life span (from 4 to 128 yr old), estimated by using an algorithm, was inversely correlated with the deviance of the population growth rate from equilibrium as well as with among-year population fluctuations. Temporal variability was greater for short-lived species than for the long-lived ones because fecundity was more variable than survival and relatively more important for population dynamics for the short-lived species. The relationship between life span and population stability suggests that selection for longevity may have played an important role in the life history evolution of plants because of its ability to buffer temporal fluctuations in population size.

Key words: demography; elasticity; life-cycle components; life history evolution; matrix models; perennial herbs; population growth rate; temporal variability.

Life span is a central aspect of life history diversification, and plants have the largest variation and the absolute record in longevity of all organisms: from a few weeks to thousands of years. Life span depends on the organism's survival schedule and is often associated with fecundity (Franco and Silvertown, 1996). The combination of these two complementary fitness components (survival and fecundity) constitutes the basis for understanding the evolution of life histories (Roff, 1992; Stearns, 1992).

The theory of *r*- and *K*-selection, originally coined in a demographic context to describe different density-dependent types of selection, predicts that life histories can evolve toward short or long life spans as a result of variation in ecological factors such as resource availability (Reznick et al., 2002). Resource limitations impose trade-offs between different fitness components (e.g., reproductive effort vs. individual growth rate) that are expected to translate into different demographic patterns. For example, as life span increases, the importance of fecundity for overall population dynamics is progressively replaced by that of survival (e.g., Franco and Silvertown, 1996; Forbis and Doak, 2004). Accordingly, life history variation has been placed along a slow–fast continuum, with low reproductive rate, slow development, and long life span at the slow end (Charnov, 1991; Heppell et al., 2000; Ricklefs and Wikelski, 2002). Given that survival and fecundity are the two basic components of demography, a strong correlation between life span and population dynamics is intuitively expected. Previous

studies have not found such relationship in plants (Franco and Silvertown, 1996, 2004), however, and it remains to be empirically established how life span and population dynamics are linked in different organism groups.

The aim of this study was to explore the relationship between life span and population growth rate (λ), temporal variation in population size, and the relative importance and variability of survival and fecundity. To this end, we used available demographic studies of perennial herbs spread over a long life span gradient that included among-year variation data. Matrix population models were used to compute population growth rate (λ; Caswell, 2001), life span (Cochran and Ellner, 1992), and the demographic importance of survival and fecundity for population growth rates (elasticity, de Kroon et al., 1986). We addressed the following questions: (1) Is a longer life span correlated with more stable population dynamics? (2) If so, to what extent are fecundity and survival, and their respective variances, responsible for this relationship?

MATERIALS AND METHODS

The plant database—We gathered data from plant demographic studies of perennial herbs published up to 2006, based on either size or stage-structured matrix models (a projection matrix summarizes transitions of individuals arranged into classes over the entire life cycle: fecundity, stasis, growth, and retrogression). We only used studies encompassing at least three 1-yr transition intervals and where temporal variation was due to fluctuations in environmental conditions and not to perturbations such as fire or experimental treatments like clipping. Overall, 55 populations of 23 herbaceous species included in the study represented 14 families and different habitats, although they were predominantly from temperate areas of the northern hemisphere (Table 1). Species represented by single and multiple populations were evenly distributed over the longevity gradient.

Life span—Life span was estimated using the algorithm reported in Cochran and Ellner (1992) as the maximum value of "conditional total life span,"

TABLE 1. Information for each of the 23 species studied: family, main habitat, number of populations (Pops.) and years (i.e., matrices) included, matrix dimension (Dim.), presence of seed bank, and the main parameters computed, such as deviance of λ from unity, temporal variance (Temp. var.), and estimated life span across populations.

Species	Family	Habitat	Pops.	Years	Dim.	Seed class	Deviance λ	Temp. var.	Life span	Reference
Actaea spicata	Ranunculaceae	Forest	2	6	6	Yes	0.0469	0.1342	16.4	Fröborg and Eriksson, 2003
Agrimonia eupatoria	Rosaceae	Open sites	2	5	4	No	0.0385	0.0080	53.7	Kiviniemi, 2002
Astragalus tyghensis	Fabaceae	Forest	5	9	5	No	0.0641	0.2181	12.4	Kaye and Pyke, 2003
Borderea chouardii	Dioscoreaceae	Rupicolous	1	7	6	Yes	0.0005	0.0002	127.7	García, 2003
Calathea ovadensis	Marantaceae	Forest	4	4	8	Yes	0.0261	0.8209	21.0	Horvitz and Schemske, 1995
Cimicifuga elata	Ranunculaceae	Forest	3	3–5	5	No	0.0544	0.0320	18.2	Kaye and Pyke, 2003
Daucus carota	Apiaceae	Open sites	1	3	3	No	0.8150	4.8300	4.6	Verkaar and Schenkeveld,
Geum rivale	Rosaceae	Wetlands	1	3	5	No	0.0012	0.0073	37.9	Kiviniemi, 2002
Kosteletzkya pentacarpos	Malvaceae	Wetlands	1	8	3	No	0.0884	0.2295	92.0	Pino et al., 2007
Lathyrus vernus	Fabaceae	Forest	2	3	7	Yes	0.0285	0.0044	66.8	Ehrlén, 1995
Lobularia maritima	Cruciferae	Shrublands	1	5	3	Yes	0.4790	4.6000	3.9	Picó et al., 2002
Lomatium bradshawii	Apiaceae	Wetlands	1	7	5	No	0.1694	0.0484	8.5	Kaye and Pyke, 2003
Lomatium cookii	Apiaceae	Wetlands	2	5	5	No	0.1048	0.0884	13.6	Kaye and Pyke, 2003
Mimulus cardinalis	Phrymaceae	Wetlands	4	3	4	Yes	0.3247	0.0060	6.2	Angert, 2006
Mimulus lewisii	Phrymaceae	Wetlands	4	3	4	Yes	0.1809	0.0040	13.0	Angert, 2006
Petrocoptis pseudoviscosa	Caryophyllaceae	Rupicolous	3	4–5	5	Yes	0.0207	0.0042	45.3	García, 2008
Plantago media	Plantaginaceae	Grasslands	2	4	5	No	0.0950	0.0391	28.5	Eriksson and Eriksson, 2000
Potentilla anserina	Rosaceae	Grasslands	1	3	6	No	0.1290	0.0218	10.3	Eriksson, 1988
Primula farinosa	Primulaceae	Wetlands	5	3	4	No	0.0725	0.0172	17.4	Lindborg and Ehrlén, 2002
Primula veris	Primulaceae	Grasslands	1	3	6	Yes	0.0859	0.0229	32.0	Lehtilä et al., 2006
Ramonda myconi	Gesneriaceae	Rupicolous	3	3–5	5	No	0.0237	0.0450	47.8	Picó and Riba, 2002
Scabiosa columbaria	Dipsacaceae	Grasslands	1	3	3	No	0.2062	0.8059	9.5	Verkaar and Schenkeveld, 1984
Succisa pratensis	Dipsacaceae	Grasslands	5	3	5	Yes	0.1274	0.3893	19.3	Herbén et al., 2006

or mean age at death, conditional on reaching a given stage, minus one. This time-invariant method is suitable for situations where environmental variability is not driven by strong stochastic disturbances (Tuljapurkar and Horvitz, 2006), a common situation in this study. To reduce the influence of each particular year's survival pattern, life span was estimated from the mean matrix over years for each population. If studies provided data for more than one population, we averaged values across populations to derive one specific value.

Life span is not a fixed, specific value but depends on mortality rates that vary over space and time. Our estimates of life span thus include a sampling error. We are, however, confident that they are properly ranked across species. First, our estimates for the shortest-lived and longest-lived species agreed well with our own estimates from monitoring (Picó et al., 2002) and real-age recordings (García, 2003). In addition, Ehrlén and Lehtilä (2002) found in a larger database that such estimates agreed well with estimates derived from other sources. Moreover, we computed specific life spans in this study from matrices that averaged at least three different years (4.5 ± 1.8 matrices per population, mean ± SD), and often from different populations under natural conditions, which should reduce the effect of extreme environmental conditions.

Population growth rates and temporal variability—Because we dealt with a sequence of n years (n matrices: A_1 to A_n) for each population, the deterministic population growth rate (λ) was computed from the resulting matrix for each temporal series as $(A_n \cdot A_{n-1} \cdot \ldots \cdot A_1)^{1/n}$. Each series represents a real sequence of matrices, a more realistic situation than the mean matrix or the average of deterministic yearly λ values. Deviance of the resulting λ from unity was used to explore how far the population dynamics was from equilibrium. The deviance was calculated as the absolute value of $1 - \lambda$ for each population. For exploring population trends at the specific level when more than one population is involved, mean deviance is more informative than mean λ because the average for increasing and decreasing populations could result in λ values close to equilibrium.

Temporal variance in λ was calculated from simulations rather than using the analytical variance of yearly deterministic (stationary) λ because the former was considered more relevant to the actual dynamics of populations. An initial population vector containing thousands of individuals in each class (to avoid extinctions) was consecutively multiplied by a matrix randomly selected from the particular set of matrices from the population. The resulting population size (N_i) after each multiplication ($t = 10\,000$ iterations with the first 1000 values

discarded to eliminate transient effects) was used to calculate the N_{t+1}/N_t ratios whose variance was computed as an estimate of fluctuation in population size. The seed bank was included in the simulations when this class was part of the matrices (10 species, see Table 1), but seeds were excluded to calculate N_i. Thus, temporal variance in λ was always computed taking only into account the number of aboveground plants. Again, temporal variability was averaged across populations if more than one was available per species. The statistical significance of the relationships between life span and deviance of λ from unity, and variance in λ were tested by linear regression models.

Importance and variability of life history components—Elasticity is defined as the proportional change in λ resulting from a proportional change in a matrix element, and may be interpreted as the contribution of a matrix element to λ (de Kroon et al., 1986; Caswell, 2001). The sum of elasticities of all matrix elements is one, allowing comparisons of single or grouped elasticities. To examine how the relative importance of survival and fecundity are related to life span, we computed elasticities for matrix elements and summed the transitions representing survival (growth, stasis, and retrogression) and fecundity (seed and/or seedling production). Given that elasticity values may change with matrix dimensionality (Ramula and Lehtilä, 2005), we also checked if matrix size was correlated with life span.

We computed the among-year variance in survival and fecundity to explore to what extent the pattern of variability in λ was influenced by variation in these two demographic components. Because the published information that was the basis for our analyses was arranged into matrices, fecundity and survival could only be examined within particular classes of sizes or stages. For this reason, we focused on the class with the highest fecundity and survival in each population. The coefficient of variation (CV) for fecundity was computed from seedling production (when it was provided by the matrix), or from the product of number of seeds and proportion of seeds germinating (for species including a seed bank class). Temporal variation in survival was computed in terms of "relativized CV" (CV/CV_{max}), following the procedure suggested by Morris and Doak (2004). This method takes into account that when vital rates are constrained from zero-to-one following a beta distribution, CV decreases as the mean approaches the upper or lower limit of this range. The variability in fecundity and survival was averaged across populations if more than one was available. A paired t test was then performed to compare the variability of both components within species, and linear regression was used to examine the relationship between life span and the CVs of fecundity and survival.

RESULTS

Estimated life spans ranged from 4 years in *Lobularia maritima* to 128 in *Borderea chouardii*, with a median of 17 years (Table 1). Neither matrix dimension ($P = 0.35$) nor the duration of the study ($P = 0.10$) were correlated with life span so that these two parameters did not bias our results. Population growth rates (λ) ranged between 0.523 (decreasing dynamics) and 1.815 (increasing dynamics). Overall, λ values were closer to unity in long-lived plants, whereas short-lived plants had a wider range of λ values including decreasing and increasing population dynamics (Fig. 1). Deviance of λ from unity significantly decreased with increasing life span (Fig. 2; $r = -0.76$, $R^2 = 0.57$; $F = 27.9$; $P < 0.0001$).

Temporal variance in λ was also significantly negatively correlated with life span (Fig. 2; $r = -0.60$, $R^2 = 0.36$, $F = 12.1$, $P = 0.0022$). Temporal variation in fecundity was, on average, three times larger than variation in survival (paired t test, $t = 7.80$, $P < 0.0001$, $N = 23$), and significantly decreased with increasing life span (Fig. 3; $r = -0.53$, $R^2 = 0.32$, $F = 10.65$, $P = 0.004$). Temporal variation in survival, on the contrary, was not correlated with life span (Fig. 3; $P = 0.11$). The elasticity of survival was higher than 90% in plants with life span estimates greater than 15 years (Fig. 4), and the two variables were positively significantly correlated ($r = 0.75$, $R^2 = 0.56$, $F = 27.2$, $P < 0.0001$; age was log transformed). In contrast, and because the elasticity of survival and fecundity sum to one, the opposite pattern was observed for fecundity: it drastically decreased from 40% to less than 10% in plants with life span estimates over 15 years. Thus, the observed higher temporal fluctuations in λ in short-lived plants were the result of a higher variability in fecundity than in survival and a higher relative importance of fecundity to overall demographic performance.

DISCUSSION

Life span is an important life history trait that is often unknown for herbaceous plants (but see Bender et al., 2000; Ehrlén and Lehtilä, 2002). In this study we incorporated a wide range of life spans for herbaceous perennials and were able to demonstrate a clear negative relationship between life span and deviance of population growth rate from equilibrium and temporal variance in population growth rate. Although these patterns seem intuitive, they have not been demonstrated previously;
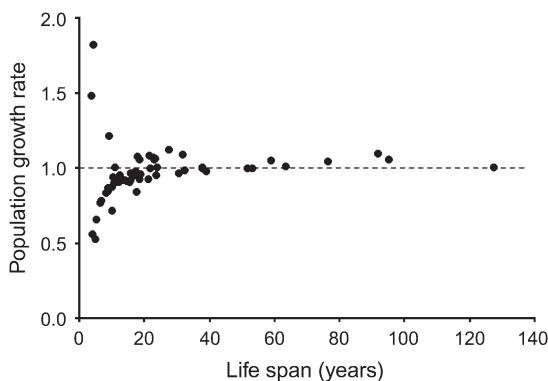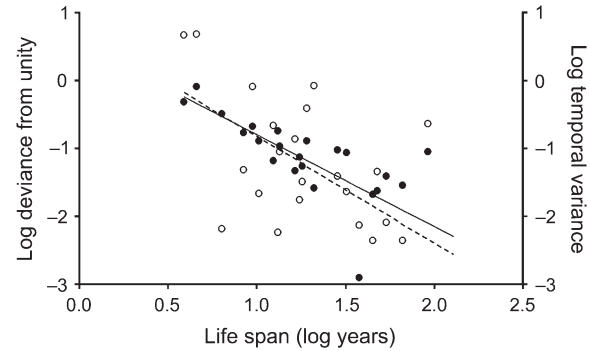

Fig. 2. Relationship between life span, deviance of population growth rate from unity (filled circles), and temporal variance in population growth rate (open circles) for 23 perennial herbs.

earlier studies failed to establish such relationships between life span and population dynamics (Franco and Silvertown, 1996, 2004; Ehrlén and Lehtilä, 2002). The reason for a lack of correlation may be associated with smaller sample sizes, smaller range of life spans, and the consideration of different life forms in the same analysis. Population sizes of species with short life spans were more variable among years than those of species with longer life spans. This pattern was the result of a higher temporal variability in fecundity than in survival (also reported in Franco and Silvertown, 2004) and a higher elasticity of fecundity in short-lived species.

Short-lived herbs, such as *Daucus carota* or *Lobularia maritima*, occur in open, disturbed areas often colonized by more competitive species after a few years. Fast life cycles and high fecundity schedules are efficient mechanisms to replenish the seed bank or disperse and efficiently exploit newly opened habitats. Because short-lived herbs have large temporal population fluctuations, they will be more prone to local extinctions (Tuljapurkar and Orzack, 1980; Menges, 1997) unless longevity is assured through seed bank (Eriksson, 1996; Ehrlén and Lehtilä, 2002). In contrast, long-lived plants, such as *Borderea chouardii, Ramonda myconi, or Lathyrus vernus*, occur in environments where not only competition for resources is strong (e.g., mature forests), but also more generally where few safe-sites for recruitment are available (e.g., rocky places). High survival of

Fig. 1. Relationship between deterministic population growth rate and life span for 55 populations grouped in 23 species.
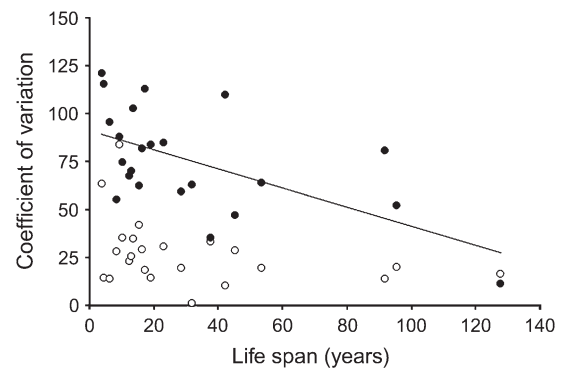

Fig. 3. Relationship between life span and coefficient of variation of survival (open circles) and fecundity (filled circles) of the class with the highest contribution to both components for 23 perennial herbs. The significant regression line corresponding to the fecundity component is depicted.
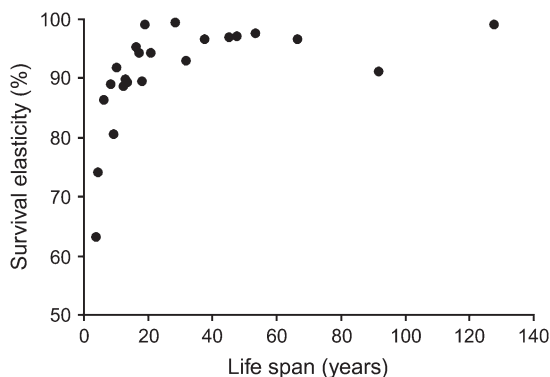
Fig. 4. Relationship between elasticity of the survival component and life span for 23 perennial herbs. The elasticity of fecundity is the reciprocal of that of survival so that both percent elasticity values sum to 100.

established individuals translates into a reduced dependence from fecundity and thus a higher probability of local persistence regardless of environmental variability. Longevity has been claimed as an important life history trait for the persistence of populations at harsh or extreme environments or under frequent long periods of adverse conditions (Eriksson, 1996; Larson et al., 1999; García and Zamora, 2003; Forbis and Doak, 2004; Arx et al., 2006). A long life span would therefore be a good strategy to avoid local extinctions caused by scarce and unpredictable recruitment as well as large population fluctuations.

We looked for demographic patterns along a wide range of life spans within a group of plants of similar life form. Our results supported the expected positive relationship between life span and stable population dynamics. This pattern is due to the fact that both temporal variability in fecundity and relative importance of population growth rate to fecundity are higher in short-lived than in long-lived herbs. The relationship between life span and population stability suggests that longevity may have evolved to mitigate the effects of variable and unpredictable environments. Living longer, thus, may be an adaptive strategy to persist in difficult ecological scenarios.

LITERATURE CITED

Angert, A. L. 2006. Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. levisii*). *Ecology* 87: 2014–2025.

Arx, G. von, P. J. Edwards, and H. Dietz. 2006. Evidence for life history changes in high-altitude populations of three perennial forbs. *Ecology* 87: 665–674.

Bender, M. H., J. M. Baskin, and C. C. Baskin. 2000. Age of maturity and life span in herbaceous, polycarpic perennials. *Botanical Review* 66: 311–349.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation. Sinauer, Sunderland, Massachusetts, USA.

Charnov, E. L. 1991. Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences, USA* 88: 1134–1137.

Cochran, M. E., and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs* 62: 345–364.

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.

Ehrlén, J. 1995. Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. *Journal of Ecology* 83: 297–308.

Ehrlén, J., and K. Lehtilä. 2002. How perennial are perennial plants? *Oikos* 98: 308–322.

Eriksson, Å., and O. Eriksson. 2000. Population dynamics of the perennial *Plantago media* in semi-natural grasslands. *Journal of Vegetation Science* 11: 245–252.

Eriksson, O. 1988. Ramet behaviour and population growth in the clonal herb *Potentilla anserina*. *Journal of Ecology* 76: 522–536.

Eriksson, O. 1996. Regional dynamics of plants: A review of evidence for remnant, source–sink and metapopulations. *Oikos* 77: 248–258.

Forbis, T. A., and D. F. Doak. 2004. Seedling establishment and life history trade-offs in alpine plants. *American Journal of Botany* 91: 1147–1153.

Franco, M., and J. Silvertown. 1996. Life history variation in plants: An exploration of the fast–slow continuum hypothesis. *Philosophical Transactions of the Royal Society, London, B, Biological Sciences* 351: 1341–1348.

Franco, M., and J. Silvertown. 2004. A comparative demography of plants based upon elasticities of vital rates. *Ecology* 85: 531–538.

Fröborg, H., and O. Eriksson. 2003. Predispersal seed predation and population dynamics in the perennial understorey herb *Actaea spicata*. *Canadian Journal of Botany* 81: 1058–1069.

García, D., and R. Zamora. 2003. Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. *Journal of Vegetation Science* 14: 921–926.

García, M. B. 2003. Demographic viability of a relict population of the critically endangered plant *Borderea chouardii*. *Conservation Biology* 17: 1672–1680.

García, M. B. 2008. Life history and population size variability in a relict plant. Different routes towards long-term persistence. *Diversity and Distributions* 14: 106–113.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology* 81: 654–665.

Herbén, T., Z. Münzbergová, M. Mildén, J. Ehrlén, S. A. O. Cousins, and O. Eriksson. 2006. Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: Linking dynamical modelling with historical maps. *Journal of Ecology* 94: 131–143.

Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: Projection matrix analysis. *Ecological Monographs* 65: 155–192.

Kaye, T. N., and D. A. Pyke. 2003. The effect of stochastic technique on estimates of population viability from transition matrix models. *Ecology* 84: 1464–1476.

Kiviniemi, K. 2002. Population dynamics of *Agrimonia eupatoria* and *Geum rivale*, two perennial grassland species. *Plant Ecology* 159: 153–169.

Larson, D. W., U. Matthes, J. A. Gerrath, J. M. Gerrath, J. C. Nekola, G. L. Walkers, S. Porembski, A. Charlton, and N. W. K. Larson. 1999. Ancient stunted trees on cliffs. *Nature* 398: 382–383.

Lehtilä, K., K. Syrjänen, R. Leimu, M. B. García, and J. Ehrlén. 2006. Habitat change and demography of *Primula veris*: Identification of management targets. *Conservation Biology* 20: 833–843.

Lindborg, R., and J. Ehrlén. 2002. Evaluating the extinction risk of a perennial herb: Demographic data versus historical records. *Conservation Biology* 16: 683–690.

Menges, E. S. 1997. Evaluating extinction risks in plant populations. *In* P. L. Fiedler and P. M. Kareiva [eds.], Conservation biology for the coming decade, 49–65. Chapman and Hall, New York, New York, USA.

Morris, W. F., and D. F. Doak. 2004. Buffering of life histories against environmental stochasticity: Accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *The American Naturalist* 163: 579–590.

Picó, F. X., H. de Kroon, and J. Retana. 2002. An extended flowering and fruiting season has few demographic effects in a Mediterranean perennial herb. *Ecology* 83: 1991–2004.

Picó, F. X., AND M. Riba. 2002. Regional-scale demography of *Ramonda myconi*: Remnant population dynamics in a preglacial relict species. *Plant Ecology* 161: 1–13.

Pino, J., F. X. Picó, AND E. de Roa. 2007. Population dynamics of the rare plant *Kosteletzkya pentacarpos* (Malvaceae): A nine-year study. *Botanical Journal of the Linnean Society* 153: 455–462.

Ramula, S., AND K. Lehtilä. 2005. Matrix dimensionality in demographic analyses of plants: When to use smaller matrices? *Oikos* 111: 563–573.

Reznick, D. K., M. J. Bryant, AND F. Bashey. 2002. *r*- and *K*-selection revisited: The role of population regulation in life-history evolution. *Ecology* 83: 1509–1520.

Ricklefs, R. E., AND M. Wikelski. 2002. The physiology/life-history nexus. *Trends in Ecology & Evolution* 17: 462–468.

Roff, D. A. 1992. The evolution of life histories. Theory and analysis. Chapman and Hall, New York, New York, USA.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.

Tuljapurkar, S. D., AND C. C. Horvitz. 2006. From stage to age in variable environments: Life expectancy and survivorship. *Ecology* 87: 1497–1509.

Tuljapurkar, S. D., AND S. H. Orzack. 1980. Population dynamics in variable environment I. Long-run growth rates and extinction. *Theoretical Population Biology* 18: 314–342.

Verkaar, H. J., AND A. J. Schenkeveld. 1984. On the ecology of short-lived forbs in chalk grasslands: life-history characteristics. *The New Phytologist* 98: 659–672.