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Lognormal distribution of individual lifetime fecundity: insights from a 23-year study

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Abstract. Individual variance in lifetime fecundity within populations is a life-history parameter of crucial evolutionary and ecological significance. However, knowledge of its magnitude and underlying mechanisms in natural populations is biased toward short-lived taxa. This paper summarizes results of a 23-year study on a population of the Mediterranean shrub *Lavandula latifolia*. We document the within-population pattern of individual variation in instantaneous and lifetime fecundity (as estimated by inflorescence production) and explore the mechanisms producing the lognormal distribution of individual fecundities by means of an individual-based simulation model. Throughout the study period, a few individuals consistently produced most inflorescences while the majority of plants exhibited moderate-to-low fecundities. The shape of yearly distributions of annual fecundities varied little across years, and most annual fecundity distributions did not depart significantly from a lognormal. The distribution of individual lifetime fecundity did not depart from lognormality. Despite the simplicity of the premises of our simulation model, it was remarkably successful at predicting the shapes of fecundity distributions and the early establishment of a persistent fecundity hierarchy. The agreement between model results and empirical data supports the view that multiplicative interactions of randomly varying environmental effects can play a central role in determining individual variation in lifetime fecundity in *L. latifolia*, and suggests that environmental stochasticity can be decisive in the genesis of strong fecundity hierarchies in long-lived plants.

Key words: *demography; fecundity hierarchy;* Lavandula latifolia; *lognormal distribution; multiplicative random effects; plant senescence; simulation model.*

Introduction

Variance in individual lifetime fecundity (defined as the total number of zygotes produced by a sexually reproducing individual over its whole lifetime) is a life-history parameter with crucial evolutionary, genetic, and ecological implications: (1) it provides the raw material for natural selection, condition the evolutionary trajectory of populations, and affect the "opportunity for selection" of fitness-related traits (Brodie et al. 1995); (2) by reducing the effective size of populations, it may decrease the genetic diversity of populations, enhancing the importance of genetic drift as an agent of genetic structuring (Barrowclough and Rockwell 1993, Dodd and Silvertown 2000); and (3) from an ecological viewpoint, it may decisively influence patterns of population recruitment and dispersal, and shape the temporal dynamics, demographic structure, and persistence of populations (Harper 1977, Clutton-Brock 1988, Newton 1989).

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Our knowledge of the magnitude of the variance in individual lifetime fecundity occurring in natural populations, the shape of within-population distributions of lifetime fecundities, and the proximate mechanisms giving rise to them, is imperfect and biased toward certain organisms and causal processes. While there is extensive information on lifetime fecundity variability for many species of animals from diverse taxonomic groups and life styles (Clutton-Brock 1988, Newton 1989), similar information is scarce for natural plant populations, being generally based on indirect estimates of fecundity and referring almost exclusively to annuals and monocarpic perennials. In addition, research has mostly focused on experimental monospecific populations grown at high densities, using individual size as a surrogate for fecundity (Solbrig and Solbrig 1984, Weiner and Solbrig 1984, Waller 1985, Weiner 1985, Weiner et al. 2001, Pfister and Steven 2002). Relatively few investigations have examined individual differences in fecundity in polycarpic perennials, and these have often covered only a fraction of the life span of individual plants and/or have relied on size differences to infer fecundity variation (Cook and Lyons 1983, Scheiner 1987, Bullock 1989, Herrera 1991, Dodd and Silvertown 2000). In fact, we were unable to locate any

report describing the magnitude of variance and the shape of the distribution of individual lifetime fecundity for any long-lived polycarpic plant, based on data obtained along the complete life span of individual plants growing under natural conditions. For annual plants, (asymmetric) competition has been often argued as the main mechanism shaping the distribution of individual lifetime fecundity (Weiner et al. 2001, Laird and Aarssen 2005), yet other factors could also be involved in the case of long-lived plants, such as cumulative stochastic effects (e.g., accidents, biotic and abiotic environmental fluctuations) faced by individuals over their lifetimes.

This paper summarizes results of a 23-year study on a population of the Mediterranean shrub *Lavandula latifolia*, and it provides possibly the first analysis of within-population variation in lifetime fecundity for a long-lived plant. Lifetime fecundities were found to conform to a lognormal, a distribution known to arise from the multiplicative rather than additive combination of independent factors (Aitchison and Brown 1969, May 1975, Limpert et al. 2001). We thus explored the potential significance for lifetime fecundity of independent multiplicative phenomena, and more specifically of the multiplicative amplification of environmental stochasticity imposed on future fecundity by the regularly dichotomous, dichasial branching pattern of *L. latifolia*. An individual-based model is formulated that, despite incorporating only a reduced set of simple premises and parameters, predicts the shape of lifetime (i.e., cumulative over the entire life span) and instantaneous (i.e., on a single reproductive episode) distributions of individual fecundity. This result illustrates the potential of environmental stochasticity for conditioning patterns of individual lifetime fecundities in some long-lived plants.

Methods

Study plant.—*Lavandula latifolia* Med. is a low, dome-shaped evergreen shrub characteristic of clearings and undergrowth in mid-elevation mixed woodlands of the eastern Iberian Peninsula, producing long-stalked inflorescences in early summer (Fig. A1). Flowers are hermaphrodite and insect pollinated. The species reproduces exclusively by seed. Seeds are short-lived, becoming inviable after 2–3 years in the soil. Seedlings emerge in spring, and mortality is very high during the first few subsequent summers, <6% remaining alive six years past emergence (Herrera 2000*a*). Spatiotemporal environmental stochasticity seems to play an important role on the fecundity of this plant. For example, growth and inflorescence production are reduced in years with lower-than-average spring rainfall, very small-scale variations in soil texture and nutrient concentration have significant effects on seedling emergence and juvenile survival, and accidental events like stone falls or trampling by large mammals condition future reproduction (Herrera 2002; C. M. Herrera, *personal observations*). The branching pattern is dichasial, regularly dichotomous, and resembles Leeuwenberg's development model (Hallé et al. 1978). Each spring, opposite axillary buds under the apical one grow more or less symmetrically following the developmental arrest of the apical bud, eventually resulting into a fork-like division. Under optimal growth conditions, and if undisturbed by some damaging agent, this dichotomous branching pattern eventually leads to the dome-shaped growth habit characteristic of the species. Inflorescences are usually produced at the tip of stems produced during the previous year's growth before they enter into arrested development. This leads to an architecturally mediated relationship between the number of inflorescences produced by a shrub at a given season and the total number of active growing tips in the previous season (termed "modules" in the terminology of our model; see below and Appendix B), and a close correlation between yearly inflorescence production and current leaf biomass of individual plants (Herrera 1991).

Field methods.—This study was conducted between 1986 and 2008 in the Sierra de Cazorla, Jaén province (southeastern Spain). A permanent 200-m^2 plot was established in 1986 at the "Aguaderillos-2" site of Herrera (1988, 1991), in an open mixed forest of *Pinus nigra* and *Quercus ilex* with a understory dominated by *Lavandula latifolia*. To promote the natural establishment of an even-aged population for long-term monitoring, all *L. latifolia* plants growing within the plot, including first-year seedlings, were removed by hand in July 1986. Particular care was taken to minimize disturbances of the upper soil layer. The plot was thoroughly screened on several occasions until all plants were removed. Surveys were later performed on August 1989 and October 1990, and all *L. latifolia* juveniles >1 year old ($N = 214$ plants) were individually tagged (Fig. A2). This marked population was thus a nearly even-aged cohort originating from seedlings emerged in 1987 or 1988. Marked plants were monitored at the end of every flowering season until 2008 (Fig. A3). On each occasion, the status (live or dead) and number of inflorescences produced during the current year were recorded for every plant. During the second half of the study, most marked plants (67.3%) exhibited signs of senescence in the form of partial growth cessation, decreased amount of foliage, and progressive death of branches (Fig. A4). In these cases, the extent of senescence symptoms (percent total leaf biomass reduction) was estimated as the proportion of a plant's vertical projection consisting of dead branches. Out of the 214 plants initially marked, those that lost their tags ($N = 7$) or died without ever flowering ($N = 28$) during the 1989–2008 monitoring period were excluded from the analyses. All plants remaining alive in 2008 ($N = 66$) had flowered at least once during the study period.

Direct counts of the number of flowers or ripe seeds annually produced by each marked plant were impractical because of the extended flowering and seed maturation period of this species and the destructive

sampling required to accurately estimating seed production (Herrera 1991). In addition, seed counts would have provided an assessment of the maternal component of fecundity, but the paternal component (i.e., number of seeds sired) would have been missed anyway. Therefore, here we use lifetime inflorescence production as a proxy for plant lifetime fecundity (i.e., male plus female components), since at the study site yearly inflorescence production by individual *L. latifolia* plants is closely correlated with both the number of seeds produced and the number of pollen grains dispersed, the latter being a useful comparative estimate of paternal reproductive success (Herrera 1991, 2001; C. M. Herrera, *unpublished data*). Inflorescences persist on plants for several months after the end of the flowering period, thus counts at the end of the flowering season provide a reliable measure of annual fecundity.

Statistical analyses and simulation model.—The composite hypothesis of lognormality of lifetime fecundity distributions was tested by applying the Lilliefors normality test to log-transformed fecundity data (Limpert et al. 2001). Yearly distributions of annual fecundities were also tested for lognormality with the Lilliefors test, and in this case significance levels were Bonferroni-corrected to account for the multiplicity of tests. Computations were done with the *lillie.test* function of the nortest package for the R computing environment (R Development Core Team 2008). Fecundity histograms on logarithmic scales were constructed using multiplicative bins of the form $[X^n, X^{n+1} - 1]$, as described by Jovani et al. (2008), with $X = 2$ and $n = 0, 1, 2, 3, \ldots$, i.e., bins were [1,1], [2,3], [4,7], [8,15], ...

An individual-based stochastic model was developed to explore the potential of the multiplicative growth (dichasial, dichotomous branching) of *L. latifolia* plants, acting in concert with spatiotemporal stochastic environmental variation, to shape the instantaneous and lifetime frequency distributions of individual fecundities. See Appendix B for a description of the simulation model following the ODD protocol (Grimm and Railsback 2005, Grimm et al. 2006). The model was implemented in NetLogo 4.0 (Wilensky 1999) and the code is available in the Supplement. In brief, the complete life of 1000 plants born with Nmodules = 1 was simulated with yearly time steps following current knowledge on *L. latifolia*. Environmental stochasticity (simulated as a pseudorandom number uniformly distributed between 0.6 and 1) influences both the production of Nmodules and their conversion to Ninflorescences. Because of dichotomous branching, each plant can produce at year t from zero to $2 \times \text{Nmodules}_{t-1}$, and eventually produce from zero to Ninflorescences = Nmodules according to prevailing environmental conditions. Long-term demographic observations conducted at the study site between 1982 and 2008 have shown that *L. latifolia* plants only exceptionally live more than 32 years (C. M. Herrera, *unpublished data*). Furthermore, as noted above, most plants exhibited clear signs of senescence during the years immediately preceding death. Since the specific shape of the senescence function is unknown, we conservatively applied a linear senescence rate on growth and reproduction. Overall, each year, Nmodules and Ninflorescences were updated (rounded to the nearest integer and recorded as the model output) for each plant as follows:

$$\text{Nmodules}_t = 2 \times \text{Nmodules}_{t-1} \times (1 - [t/32]) \times \text{environmental stochasticity}$$

$$\text{Ninflorescences}_t = \text{Nmodules}_t \times \text{environmental stochasticity}$$

Ninflorescences_t figures were then used to obtain instantaneous and lifetime frequency distributions of individual fecundities of simulated plants.

Results

Longitudinal fecundity patterns.—With increasing age, inflorescence production by *L. latifolia* individuals first tended to increase up to reaching a maximum, then remained fairly stable for a few years, and finally declined steadily until the plant's death (Fig. 1). Fecundity decline late in life and eventual death were significantly associated with visible senescence symptoms. In the subset of plants that survived past 1999, those that died before 2008 had experienced a greater percent biomass reduction (mean ± SE = 45.3% ± 4.0%, $N = 93$) than those that did not (30.2% ± 3.6%, $N = 66$; $P = 0.016$, Wilcoxon rank-sum test). Although the lifetime course of fecundity was similar for most plants, the maximum fecundity attained varied widely between individuals. While a majority of plants never trespassed a moderate-to-low fecundity threshold, a minority of individuals consistently produced large numbers of inflorescences for most of the study period (e.g., red and green trajectories in Fig. 1). The lifetime fecundity trajectories of simulated plants closely matched those of plants with lifetime data (Fig. 1), mirroring the early establishment of a persistent fecundity hierarchy and the shape of individual lifetime patterns, and similarity with real plants included the broad individual variation in maximum fecundity.

Instantaneous fecundity distributions.—Frequency distributions of annual fecundity of individual plants for each year in the interval 1990–2008 are shown in Fig. 2. Over the years, the modal fecundity class on a logarithmic scale first shifted upwards as most individual plants grew and turned more fecund with increasing age (mainly over 1990–1996), then stabilized (1997–2003), and eventually shifted downward (2004–2008) as many plants entered senescence and eventually died (Fig. A4). Despite these shifts in central trend, however, the shape of the frequency distributions varied remarkably little across years, 14 out of the 19 annual fecundity distributions not departing significantly from a log-

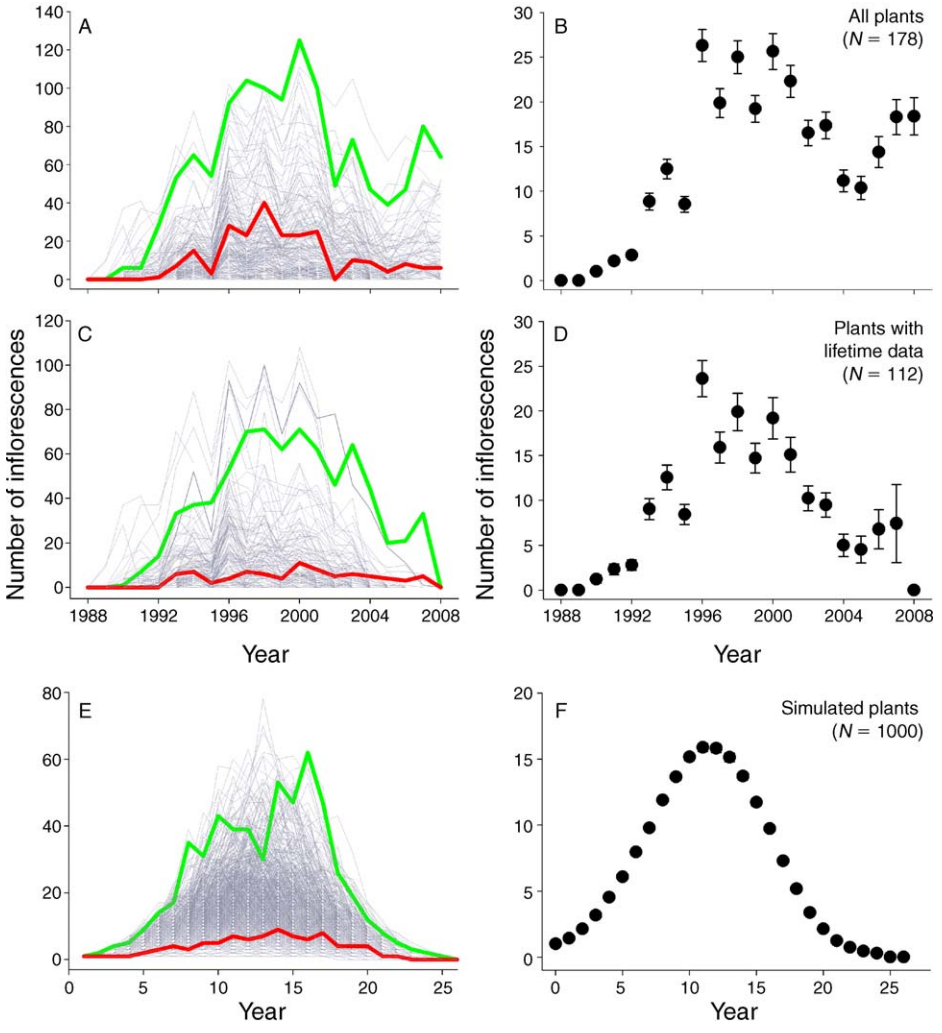

FIG. 1. Long-term variation in the number of inflorescences produced annually by marked *Lavandula latifolia* individuals during the study period, separately for (A, B) the whole set of monitored plants and (C, D) the subset of individuals that died during the study period, for which the temporal variation in annual fecundity shown depicts their lifetime fecundity histories. Panels (E) and (F) depict the results for simulated plants. In panels (A), (C), and (E), each line corresponds to a different plant. Red and green lines represent arbitrarily selected individuals chosen to illustrate the course of fecundity in representative low- and high-fecundity plants, respectively. Panels (B), (D), and (F) show annual means ± SE.

normal (Fig. 2). Annual frequency distributions of yearly fecundities for simulated plants are shown in Appendix C, and were remarkably similar to the empirical ones depicted in Fig. 2. Annual fecundity distributions on a logarithmic scale had a normal appearance over most of the simulated time interval, and their central trend first shifted upwards during the earlier years, and then downwards in later years, as denoted by shifts in the modal fecundity class.

Lifetime patterns.—The cumulative fecundity of marked plants ranged between 2 and 1226 inflorescences (median = 155, mean ± SE = 222.3 ± 17.3), thus spanning three orders of magnitude. On a linear scale, the frequency distribution of individual fecundity was strongly skewed to the right, with a majority of plants (60% of total) producing <200 inflorescences and only a few individuals (9%) producing >600 inflorescences (Fig. 3). The cumulative fecundity distribution was even more strongly skewed for the subset of $N = 112$ plants that died in the course of the study, i.e., those individuals for which the cumulative fecundity over 1989–2008 corresponds to their lifetime fecundity. Among these plants, lifetime fecundity ranged between 2 and 871 inflorescences (median = 93, mean ± SE = 148.5 ± 16.3), 80% of plants produced <200 inflorescences, and only 5% produced >600 inflorescences (Fig. 3).

Distributions of individual fecundity become fairly symmetrical and attain a distinct appearance of normality when plotted on a logarithmic scale, particularly

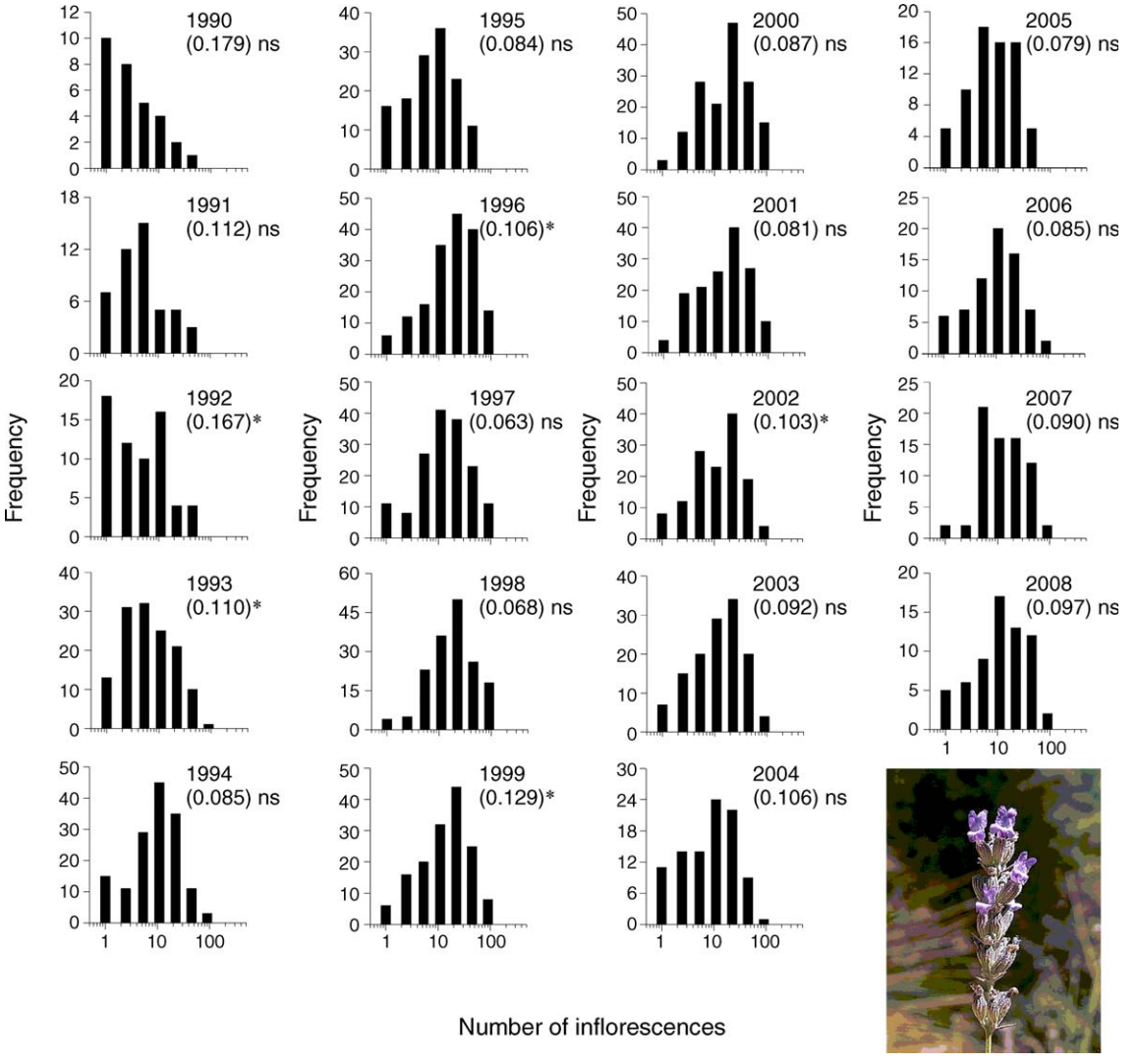

FIG. 2. Yearly frequency distributions of annual fecundity (inflorescences produced per year) of marked plants in the period 1990–2008. Very few plants flowered in 1989, and the distribution for that year is omitted. The corresponding frequency distributions for simulated plants are shown in Appendix C. Figures in parentheses are the *D* statistic from a Lilliefors test of normality of the log-transformed fecundity distribution. Significance is indicated by asterisks. The inset at the bottom right shows the distal portion of a *Lavandula latifolia* inflorescence.

* Significant ($P < 0.05$) departure from lognormal; ns, not departing significantly from lognormal.

the distribution corresponding to the plants with lifetime data (Fig. 3). The distribution of log-transformed fecundity data for the whole set of marked plants departs significantly from normality ($P = 0.009$, Lilliefors test), while the hypothesis of normality could not be rejected for the distribution of log-transformed lifetime fecundities ($P = 0.12$). This result suggests that lifetime fecundity is lognormally distributed in the set of *L. latifolia* plants studied. In close coincidence with the distributions for empirical data, lifetime fecundity distributions of simulated plants are also characterized by strong right skew when plotted on a linear scale, and by symmetrical and normal appearance when plotted on a logarithmic scale (Fig. 3).

DISCUSSION

Significance of long-term longitudinal studies.—Few long-term longitudinal studies similar to the present one have been conducted on long-lived polycarpic plants, and these generally encompassed only part of individual life spans (see references in the *Introduction*). Individual-based longitudinal studies encompassing complete life spans, however, are uniquely suited to (1) gain insights on when and how fecundity hierarchies, a "universal characteristic of all populations of plants" (Solbrig and Solbrig 1984), become established in natural plant populations; (2) contribute to the current debate on aging and senescence in perennial plants (Munné-Bosch

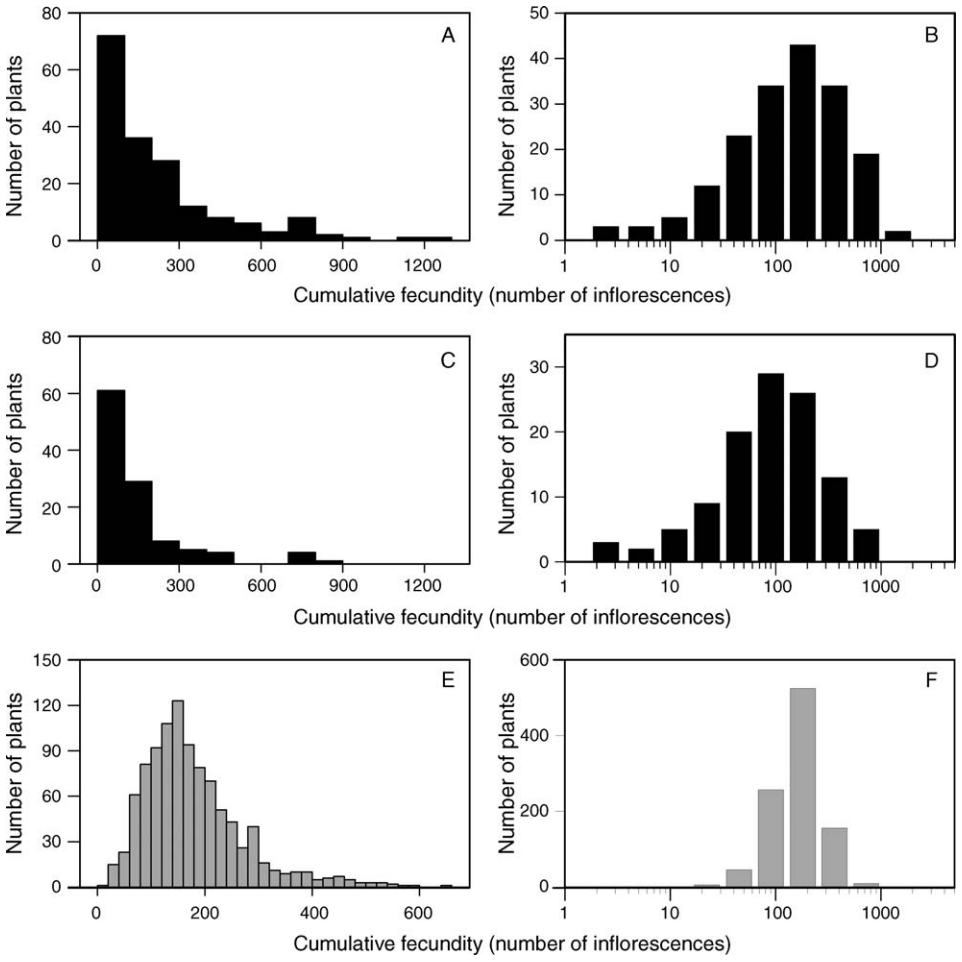

FIG. 3. Frequency distributions of cumulative fecundity (number of inflorescences) of *Lavandula latifolia* plants over the 1989–2008 study period (black bars), plotted on (A, C) linear and (B, D) logarithmic scales. Separate histograms are shown for (A, B) the whole set of monitored plants and (C, D) the subset of individuals that died during the study period. For these latter, distributions of cumulative fecundities stand for the distributions of their lifetime fecundities. Panels (E) and (F) show the frequency distributions of lifetime fecundities for simulated plants obtained from the individual-based stochastic model. Sample sizes are as in Fig. 1.

2007); and (3) elucidate the importance of genetic differences as causal agents of fecundity hierarchies (Herrera and Bazaga 2009). As genetic information for our study plants is not yet available, we will consider exclusively aspects 1 and 2.

In the present study, annual fecundity (indirectly estimated by inflorescence production) from emergence to death was obtained for more than one hundred individual plants. In this set of plants, individual lifetime fecundity trajectories had a similarly inverted U-shape pattern, but the sustained maximum fecundity achieved (at mid-age) varied widely among individual plants. These differences in annual fecundity became established early in the life of individuals and then persisted essentially unaltered until their death (Fig. 1). In other words, *L. latifolia* individuals that ranked high in the fecundity hierarchy early on, remained on that dominant position for the rest of their lives, and vice versa. Although incomplete, patterns are similar in the group of plants remaining alive in 2008. Our results were obtained from an even-aged population, but similar patterns of age-specific annual fecundity have been also observed in natural, uneven-aged *L. latifolia* populations monitored between 1986 and 2008 at the study locality (C. M. Herrera, *unpublished data*). The large proportion of individual variance in instantaneous fecundity that remains unexplained in these natural populations after statistically accounting for age heterogeneity (Herrera 1991; C. M. Herrera, *unpublished data*) are most likely due to individual variation in age-specific fecundity similar to that documented in this study.

Senescence can be defined as the progressive reduction in age-specific survival and fecundity taking place in individuals of sufficiently advanced age (Munné-Bosch 2007). In addition to experiencing a reduction in annual per capita fecundity during the years immediately

preceding death (Fig. 1), ageing *L. latifolia* plants experienced also a reduction in age-specific survivorship. The study population followed a Type I curve, with yearly mortality rate remaining uniformly low until 2002 (mean = 0.027 yr^{-1}; range = 0.006–0.063 yr^{-1}) and increasing abruptly beyond that year (mean = 0.122 yr^{-1}; range = 0.027–0.265 yr^{-1}; data not shown). Our results thus provide one of the few documented instances of senescence for a polycarpic perennial (Munné-Bosch 2007).

Logarithmic look on fecundity distributions.—Lifetime fecundities of *L. latifolia* plants were extremely variable, spanning three orders of magnitude. Furthermore, the frequency distribution of lifetime fecundities was strongly skewed to the right, the population being made up of a few exceptionally fecund individuals and a majority of plants producing a small number of inflorescences each one, thus exemplifying a typical "fecundity hierarchy" (Solbrig and Solbrig 1984). We were unable to find comparable data in the literature based on complete life spans, but the limited information available suggests that both extensive variability and strongly right-skewed distributions of lifetime fecundity are probably two characteristics of most populations of iteroparous perennials (Cook and Lyons 1983, Scheiner 1987, Bullock 1989, Herrera and Bazaga 2009). Interestingly, perennials apparently do not differ much in these respects from annuals, which have been long known to possess very high levels of individual variation and right-skewed distributions of lifetime fecundity (Salisbury 1942).

In *L. latifolia*, annual and lifetime fecundity distributions were satisfactorily described by lognormal distributions. Considerable effort has been devoted to developing methods to measure and describe the long-tailed, right-skewed fecundity distributions of plant populations (Weiner and Solbrig 1984, Damgaard and Weiner 2000, Pfister and Stevens 2002), but the topic does not seem to have been addressed before by explicitly adopting the "logarithmic point of view" (Jovani et al. 2008) used here (but see Damgaard and Weiner 2000). It is not possible to know with which frequency other heavily right-skewed fecundity distributions are also lognormal. However, preliminary analyses of fecundity distributions found in plant and animal ecology literature suggest that lognormality could be a widespread feature of lifetime fecundity distributions in plants and animals (C. M. Herrera and R. Jovani, *unpublished data*), which would add another example of lognormal distributions in ecological systems (see e.g., May 1975, Bak and Meesters 1998, Limpert et al. 2001, Jovani et al. 2008, for other examples). Apart from this, and more importantly, adopting a logarithmic point of view will bring the benefit of opening new analytical pathways for dissecting and comparing patterns of variability in fecundity, and allowing for the exploration of hypotheses on the mechanisms causing such widespread variability, as discussed briefly below. Limpert et al. (2001) presented a thorough review of lognormal distributions in natural systems, and argued extensively for the insights that can be gained by incorporating the lognormal distribution and its associated logarithmic perspective to the biologist's statistical toolbox (see also Bak and Meesters 1998, Jovani et al. 2008, for thoroughly worked out examples).

Fecundity distributions have been traditionally depicted using common histograms on linear scales (Salisbury 1942, Solbrig and Solbrig 1984, Weiner 1985, Scheiner 1987, Clutton-Brock 1988, Newton 1989; among many others). This method is relatively insensitive to long-tailed distributions and important information can remain hidden in the first few bins. In contrast, histograms using logarithmic binning expand the information condensed into the first few bins of common histograms while at the same time condenses the scattered information in its large bins (compare, e.g., left and right columns in Fig. 3). As illustrated by Bak and Meesters (1998) and Jovani et al. (2008), logarithmic binning can reveal unrecognized structure in long-tailed distributions that is of great ecological significance. Furthermore, as discussed in detail by Limpert et al. (2001), the multiplicative or geometric standard deviation of lognormally distributed data (σ^*, defined as the antilogarithm of the standard deviation of log-transformed data) provides a unitless, scale-free measurement of variability equivalent to the widely used coefficient of variation (CV = SD/mean) of normally distributed data, and can also be used for obtaining parametric confidence intervals (see also Aitchison and Brown 1969). These tools have a distinct potential for comparative studies of variability in individual fecundity among populations, species or life histories. Given the manifold implications of individual variation in fecundity outlined in the Introduction, such comparative analyses are bound to contribute fresh insights on important aspects of the ecology and evolution of plant and animal populations.

In addition to its methodological potential, the application of a logarithmic point of view to the study of fecundity hierarchies also provides opportunities for an improved understanding of their causal mechanisms through the formulation of specific hypotheses and models. In contrast to the normal or Gaussian distribution that arises from the additive combination of a series of independent effects, the lognormal distribution arises when such effects combine multiplicatively. The lognormal distribution can be framed in terms of the multiplicative version of the central limit theorem, whereby the product of many independent, identically distributed, positive random variable has approximately a lognormal distribution. The product of independent lognormal quantities also follows a lognormal distribution (Limpert et al. 2001). Recognition of the lognormality of a distribution can thus motivate hypotheses about possible multiplicative processes underlying it, and allow for the formulation of

theoretical models explicitly aimed at exploring such hypotheses. This strategy has been successfully applied, for example, in physical sciences to understand the origin of lognormally distributed variability in nanoparticle size (Kiss et al. 1999, Espiau de Lamaëstre and Bernas 2006), and it is also the approach we used in this paper. After finding that lifetime fecundity of *L. latifolia* individuals was lognormally distributed, we hypothesized that such distribution was the outcome of multiplicative processes acting on individuals over their life spans, and the individual-based simulation model was thus formulated on this premise. In the model, random environmental stochasticity influences *multiplicatively* both the production of Nmodules and their conversion to Ninflorescences. This "environmental stochasticity" can include variation in some abiotic (e.g., water stress) or biotic (e.g., herbivores) components of the environment influential on plants, or in some additive or multiplicative combination of several of such components. Instances of multiplicative effects of biotic interactions on individual plant fecundity, such as those involving pollinators and herbivores, are being increasingly reported (Herrera 2000*b*, Herrera et al. 2002, Gómez 2005). Stochastic variation over the years of the joint effect on plant fecundity of two or more biotic interactions that combine multiplicatively would provide a nice example of the type of environmental effect that is contemplated by our simulation model. Despite its simplicity and the small number of parameters involved, the model was remarkably successful at predicting the shapes of both yearly (instantaneous) and lifetime (cumulative) fecundity distributions. An important prediction of the model that was corroborated by the data is that, even though stochastic effects on fecundity act throughout the individuals' lifetimes, their impact on lifetime fecundity was time-dependent, being disproportionately high when they operated at the earliest stages of population establishment, as shown by the long-term persistence of the fecundity hierarchy arising in the first few years of the study. These findings suggest that environmental stochasticity early in life plays a decisive role in the genesis of lifetime fecundity hierarchies in *L. latifolia*, which rises an intriguing parallel with the long-lasting fitness and performance consequences of factors experienced by vertebrates early in life (Lindström 1999, Metcalfe and Monaghan 2001).

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APPENDIX A

Photographs of *Lavandula latifolia* plants and the study plot (*Ecological Archives* E091-031-A1).

APPENDIX B

Description of the individual-based stochastic model used to simulate frequency distributions of instantaneous and lifetime fecundities (*Ecological Archives* E091-031-A2).

APPENDIX C

Yearly frequency distributions of annual fecundity (number of inflorescences produced each year) of simulated plants over a 23-year period (*Ecological Archives* E091-031-A3).

SUPPLEMENT

NetLogo program code used to simulate yearly and lifetime fecundity distributions of individual plants (*Ecological Archives* E091-031-S1.