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Population dynamics of the cactus *Mammillaria gaumeri*: an integral projection model approach

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Abstract The Cactaceae family in Mexico is particularly important because members of this family exhibit a high degree of endemism. Unfortunately, many species of the Cactaceae are threatened or endangered. We employed an integral projection model for studies of the population dynamics of *Mammillaria gaumeri*, an endemic cactus of the Yucatán characterized by a small population size. The integral projection model provides estimates of the asymptotic growth rate, stable size distribution, reproductive values, and sensitivities and elasticities of the growth rate to changes in vital rates. Nine locations of this species were studied along the Yucatan coast over a 9-year period. Individuals were classified by plant volume. Most population growth rate (λ) values were below unity. The highest elasticity values corresponded to the survival of intermediate size individuals. The percentage of germination in the field was low, and consequently, fecundity values were also low. Reproductive values were observed to increase with plant volume. The stable size distribution of *M. gaumeri* was skewed toward small individuals. For all years, the kernel showed that individual survival determined the population growth rate.

Introduction

The Cactaceae family in Mexico is particularly important because it comprises >900 species (37% of all known species; Guzmán et al. 2003) and exhibits a high degree of endemism (84% are endemic; Bravo-Hollis and Sánchez-Mejorada 1978, 1991; Arias-Montes 1993; Hernández and Godínez-Álvarez 1994). Unfortunately, many species of the Cactaceae are threatened or endangered (sensu Rabinowitz 1981). Additionally, many cacti are highly susceptible to environmental perturbations. Their limited distributions and specialized habitats make them prone to extinction caused by habitat destruction and land-use changes (Hernández and Godínez-Álvarez 1994; Esparza-Olguín et al. 2002; Godínez-Álvarez et al. 2003). Because of their low individual growth rates and highly vulnerable early stages of development, these species seem to be particularly sensitive to disturbances (Hernández and Godínez-Álvarez 1994; Hernández and Bárcenas 1995, 1996; Esparza-Olguín et al. 2002).

In addition to these ecological traits, cacti can be negatively affected by human activities, such as illegal harvesting for national and international trade, which is an increasing pressure on many cactus populations. Finally, their habitats are located in rural regions with severe economic problems, where the pressure of increasing human populations on land-use changes toward farming and cattle ranching is particularly strong (Boyle and Anderson 2002; Arias et al. 2005; Carrillo-Ángeles et al. 2005; Valverde and Zavala-Hurtado 2006).

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Although efforts are being made by Mexican private and government organizations to protect some of these species (Godínez-Álvarez et al. 1999; Méndez et al. 2004; Valverde and Zavala-Hurtado 2006; Mandujano et al. 2007), many cacti continue to be vulnerable. Conservation and management plans are almost non-existent because of the lack of information concerning their population biology (Anderson et al. 1994; Hernández and Godínez-Álvarez 1994; Hunt 1999; Contreras and Valverde 2002; Godínez-Álvarez et al. 2003; Valverde et al. 2004). Studies on the population ecology of cacti are urgently needed to provide the necessary tools to evaluate the current status of existing populations, detect vulnerable stages in species' life cycles, assess population viability under different ecological scenarios, and design conservation and management plans (e.g., Martínez-Avalos et al. 1993; Valverde et al. 2004).

Integral projection models are extensions of matrix models that yield similar outputs (i.e., population growth, sensitivity, elasticity), but use continuous relations of vital rates (growth, survival, reproduction) versus size (or age) as inputs instead of category-specific values to calculate vital rates (Easterling et al. 2000; Ellner and Rees 2006). We studied the rare globular cactus *Mammillaria gaumeri* (Britton & Rose) Orcutt, using this approach. This species occurs only in northern Yucatán coastal dune scrublands and tropical dry deciduous forests (Durán et al. 1998).

Mammillaria gaumeri is particularly vulnerable to environmental variation and land-use changes because of its narrow geographic range, high habitat specificity and low population numbers. It is listed as being threatened in the Protection of Natural Resources Document of the Mexican Government (SEMARNAT 2010) and considered vulnerable in the system of the International Union for Conservation of Nature and Natural Resources (IUCN 1985). We conducted a demographic study to examine the dynamics of this rare species as a fundamental step toward the development of management and conservation programs. We analyzed the population dynamics of *M. gaumeri* over a 9-year period. We used integral projection models to evaluate its demographic performance and identify the size stages that contribute most to the population growth rate. The objective of this study was to evaluate the demographic patterns of *M. gaumeri* using an integral projection model.

Materials and methods

Study species

Mammillaria gaumeri is a globular cactus with a green to gray-green coloration, exhibiting one to several cylindrical stems forming large clusters. It is a perennial plant of slow growth. Flowering occurs from December to May, and it is pollinated by bees. The flowers open at midday and remain open until sundown. Fruiting occurs from June to December, increasing in September. Each fruit contains between 4 and 130 seeds (Bravo-Hollis and Sánchez-Mejorada 1991); these are predated by ants (M. Ferrer, personal observation). The survival of seedlings depends largely on the presence of nurse plants and is affected by the severity of the annual drought period (Leirana-Alcocer and Parra-Tabla 1999; Cervera et al. 2006). Field observations indicate that recruitment of new individuals is scarce. We do not have evidence of the occurrence of a seed bank (M. Ferrer, personal observation). *Mammillaria gaumeri* grows only along the northern Yucatan coast (Durán et al. 1998).

Study area

Our demographic analysis of *M. gaumeri* was carried out on the northern coast of the Yucatán Peninsula, Mexico. Study sites were located between 20°31′N and 21°17′N and 90°27′W and 87°40′W. The climate is semiarid, with an average mean annual temperature of 26°C, a maximum temperature of 45°C, and a minimum of 10°C (Thien et al. 1982). The region receives average annual precipitation of <700 mm, most of which falls between June and October, with some isolated precipitation (20–60 mm) falling between November and February, in association with strong winds (>80 km/h) and relatively low temperatures (<22°C) (SARH 1988). A marked dry season occurs from March to May (Orellana et al. 1999).

Field methods

We sampled nine populations of *M. gaumeri* that encompass its entire known range of distribution in the Yucatan Peninsula. Seven sites were located in coastal dune scrublands, and two sites were in tropical dry deciduous forests. At each site, three 100 m^2 permanent observation plots were established. Beginning in September 1999, all *M. gaumeri* plants within the plots were located, tagged, mapped, and monitored for 9 years (1999–2008). We initially marked 778 individuals across the nine sites, which were then monitored during the study. The diameter and length of each plant were measured with calipers and used to calculate plant volume (assuming that each plant is a circular cylinder). Plant volume was found to be the variable that best explained survival (logistic regression, $P < 0.05$). When a plant presented several ramets, the length and diameter of each ramet was measured separately, and we calculated the volume for each stem. We then added them together to give a measure of total plant volume. Plants were measured during the summer in each

year. Data from the nine populations were pooled for analysis.

To estimate fertility (average number of seedlings produced by an individual), we evaluated fruit production and seed germination of *M. gaumeri*. During the reproductive season in every year, we recorded the number of mature fruits produced per plant. Additionally, random samples of fruit ($n = 95$) were collected outside of the study sites to obtain an estimate of the mean number of seeds produced per fruit and to perform germination experiments. These experiments were carried out under controlled conditions (growth chambers) to test seed viability, and under field conditions to obtain estimates of seed germination under natural conditions.

We carried out field experiments to obtain estimates of germination, seedling survivorship and growth. We obtained these estimates experimentally because there was an insufficient number of seedlings that could be followed directly in the field to determine the fate and size of the seedlings for each year studied. These experiments were conducted at three sites, two of which were located in coastal dune scrublands, while the other was in a tropical dry deciduous forest. Seeds were sown at the beginning of the rainy season in September 2005, 2006, and 2007. At each site, we selected four shrubs as nurse plants for *M. gaumeri* seedlings as well as bare areas with no vegetation. The species selected as nurse plants in the dune scrubland were *Agave angustifolia* Haw, *Bravaisia berlandieriana* (Nees) T.F. Daniel, *Pithecellobium keyense* Britton and *Caesalpinia vesicaria* L., and in the tropical dry deciduous forest they were *Acacia gaumeri* S.F. Blake, *Acacia pringlei* Rose, *Gymnopodium floribundum* Rolfe and *Caesalpinia gaumeri* Greenm. Thirty boxes, holding 20 seeds each, were placed on the ground. Half of the seed plots (15) were protected from predators with wire mesh cages ($15 \times 15 \times 10$ cm) that were partially buried in the soil. To exclude ants from the protected plots, chlordane was applied to the soil on the periphery of each plot every week. Of these 15 seed plots, three cages were placed in completely open conditions (full sunlight), while three cages were placed under the cover of the different "nurse plants" that were chosen for each site. The other half of the seed plots were sown without protection, and no insecticide was applied. We deployed three seed plots for each nurse plant and three in completely open conditions.

We used data from these observations together with the information on seed production to calculate fertility (fertility = number of seeds per plant × seed germination probability) in the subsequent analyses. We only considered fecundity as seedlings because this species does not form a long-term seed bank. To estimate seedling survival, we followed the seedlings germinated during the

germination experiments. Seedling survival was monitored monthly for 1 year.

Data analysis

Population dynamics: the integral projection model

An integral projection model describes how a population structured by a continuous individual-level state variable changes in discrete time intervals (Easterling et al. 2000). In the integral projection model, the state of the population is described by the size distribution $n(y, t)$.

Formally, $n(y, t)$ is the probability density of individual size y at time t, defined by the property that the number of individuals between sizes y and $y + dy$ at time t is given by $n(y, t)dy$, with relative error that goes to zero as dy decreases to zero. Individuals in the population may grow, survive, and produce new individuals in each time step. Let $p(x, y)dy$ represent the probability that an individual of size x at time t is alive and in the size interval $(y, y + dy)$ at time $t + 1$. Finally, $f(x, y)dy$ is defined as the number of new seedlings at time $t + 1$ in the size interval $(y, y + dy)$ per size x individual alive at time t. The integral projection model for the number of individuals of size y at time $t + 1$ is then

$$n(y, t+1) = \int_\Omega [p(x, y) + f(x, y)]n(x, t)dx$$
$$= \int_\Omega k(y, x)n(x, t)dx$$

with the integration being carried out over the set of all possible sizes Ω. The function $k(y, x) = p(x, y) + f(x, y)$ is called the kernel, which is a nonnegative surface representing all possible transitions from size x to size y, including births and is analogous to the projection matrix A containing nonzero values for survival, growth and fecundity. The function $p(x, y)$ incorporates both growth and survival. It corresponds to the survival and growth entries in a Lefkovitch (1965) matrix, and it can account for individuals that grow larger or smaller. It is important to note that $\int p(x, y)dy$ will typically be less than one, even though $p(x, y)$ is defined as a probability, because not all individuals survive from time t to time $t + 1$. The fecundity entries in a matrix model are typically along the top row of the matrix, representing the contributions of each age class to the stage class containing newborns (e.g., the smallest size class). The analog for the integral model would be a function $f(x, y)$ that is positive for large x (parents) and small y (offspring) and is zero in other cases (Easterling et al. 2000). The integral projection model has a dominant eigenvalue λ that represents the population's

asymptotic growth rate under biological assumptions that are no more restrictive than those required in the matrix model. Corresponding to λ are the dominant right and left eigenvectors $w(x)$ and $v(x)$, and as in the matrix model, these give the stable size distribution and size-specific reproductive values respectively. However, in the integral model these "eigenvectors" are functions of the continuous variable individual size (x).

Because the fecundities and survivorship in the integral projection model are represented by a surface rather than a matrix, sensitivity analysis for the model involves determining the sensitivity of the dominant eigenvalue to changes in the survivorship/fecundity surface $k(y, x)$ over a small region centered over each point (y, x). In the integral projection model, sensitivity describes the change in λ resulting from a change in demographic parameters affecting only individuals of a particular size. In the matrix model, sensitivity describes the total effect of a parameter change applied to all individuals in a size class. Because an individual may remain in the same size class for more than a year, individuals may see the parameter change more than once. With this definition, the sensitivity and elasticity formulas are

$$s(z_1, z_2) = \frac{\delta\lambda}{\delta\lambda(z_1, z_2)} = \frac{v(z_1)w(z_2)}{[w, v]}$$

where $s(z_1, z_2)$ is the sensitivity of λ to a small change in the $k(y, x)$ values near (z_1, z_2) and $[w, v] = \int w(x)v(x)dx$ (Easterling 1998). The corresponding elasticity estimates are therefore given by

$$e(z_1, z_2) = \frac{k(z_1, z_2)}{\lambda} \times \frac{v(z_1)w(z_2)}{[w, v]}$$

The elasticity function integrates to unity (i.e., $\iint e(z_1, z_2) dz_1 dz_2 = 1$), corresponding to the elasticities summing to unity in the matrix projection model (Easterling 1998).

Estimating the kernel

For estimating the kernel $k(y, x)$ for *M. gaumeri*, it was necessary to separately estimate the survival transitions $p(x, y)$ and the fecundity $f(x, y)$. The information used was as follows: the size (plant volume) of each individual at time t; whether or not the individual survived to time $t + 1$; the size (plant volume) of surviving individuals at time $t + 1$; and the number of offspring produced by each individual at time t. To determine the kernel's components, we first fitted linear terms for each function and then tested it against nonlinear alternatives: quadratic and cubic terms and B-splines. Models were fitted using the R program (R Development Core Team 2009), and the significance of nonlinear terms was tested using an ANOVA function with a χ^2 test statistic (Hastie and Pregibon 1992).

The growth and survival function $p(x, y)$ was estimated by dividing it into separate growth and survival components. Survival and growth were separated by presenting $p(x, y)$ in the form $p(x, y) = s(x)g(x, y)$, where $s(x)$ is the survival probability of a size-x individual, and $g(x, y)$ is the probability of a size-x individual growing to be size y. Because any individual that survives must be some size in the next year, we must have $\int g(x, y)dy = 1$. For all years, the survival function $s(x)$ was estimated by logistic regression of survival on size x (Fig. 1a). The best fitted linear model was of the form $\log(s(x)/(1 - s(x))) = a + bx$ and the nonlinear terms were not significant ($P > 0.1$) in any year. The survival parameters indicated a positive association of *M. gaumeri* survival with the volume of individuals (Fig. 1a).

To fit the growth function $g(x, y)$, we first plotted the relationship between individual sizes (plant volume) at time t and time $t + 1$ (Fig. 1b). A linear model appeared to be adequate for describing the relationship between size at time t and mean size at time $t + 1$ ($P < 0.05$). The residuals from this linear model, which represent the random component of individual growth trajectories, conformed reasonably well to a normal distribution (Fig. 1c). However, the variance in size at time $t + 1$ may also be affected by size at time t. Residual variance is equal to the mean square of the residuals, so we can estimate the size dependence of the variance by plotting the squared residuals versus size (Fig. 1d). Again, a linear model was adequate. The growth function indicated low growth in all years. The fecundity function $f(x, y)$ was estimated from the data in a similar way. Fecundity was split into $f(x, y) = f_1(x) f_2(x, y)$, where the function $f_1(x)$ is the mean number of offspring from a size-x individual, while $f_2(x, y)$ is the probability distribution of offspring size y for an adult of size x, which has $\int f_2(x, y)dy = 1$. In this case, the term "adult" refers to any individual large enough to reproduce (individuals >100 cm^3 volume). The mean number of offspring was fitted by a Poisson linear regression on adult size and the linear terms were the best alternative ($P < 0.05$ for all years, Fig. 2). General linear models with Poisson errors properly deal with the error structure of count data (Crawley 2007). The fecundity was low in all years, which was explained by the low germination probability. Note that a small portion of individuals were reproductive, as shown in Fig. 2. However, in the periods 2002–2003 and 2004–2005, we obtained a high number of offspring with a maximum value of 35 seedlings (Fig. 2d, f). One can view the fecundity data (Fig. 2a) as follows: plants of size x have some probability of having 0, 1, 2, 3… or 7 offspring, and these probabilities vary with size x. The mean number of offspring for a size-x plant is:

$$\begin{aligned} f_1(x) = &\Pr(n = 0, x) \times 0 + \Pr(n = 1, x) \times 1 \\ &+ \Pr(n = 2, x) \times 2 + \ldots \Pr(n = 7, x) \times 7 \end{aligned}$$
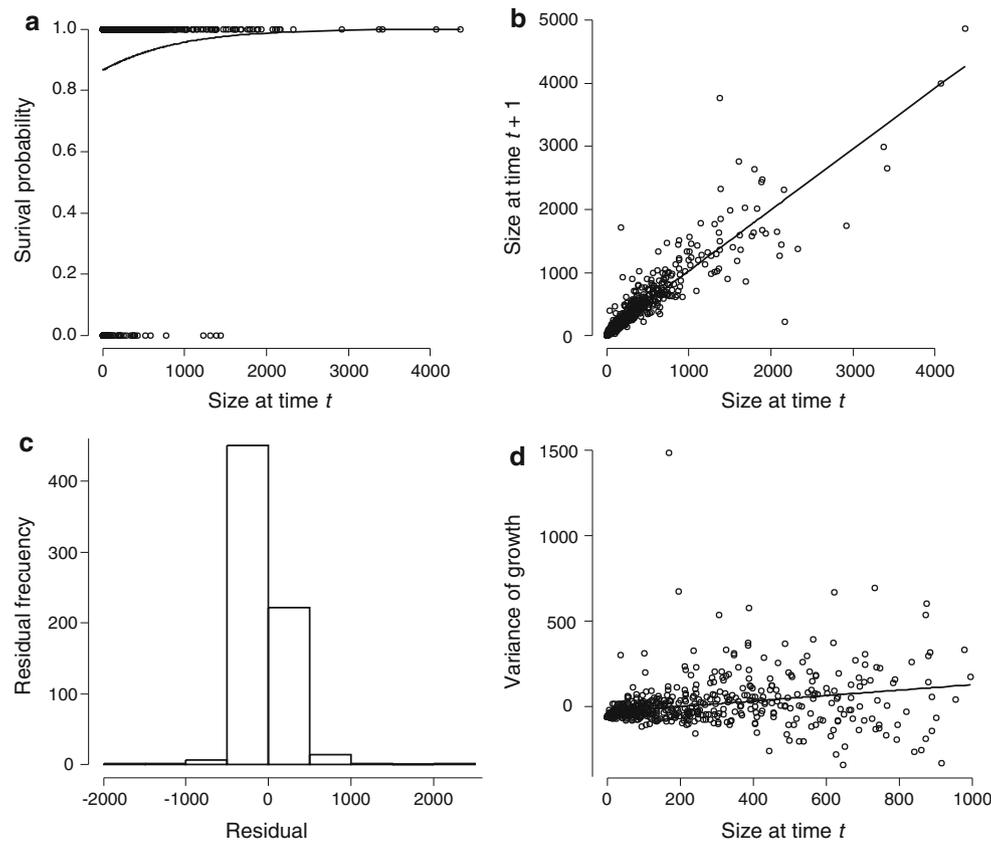
Fig. 1 Fitting of survival and growth functions to the *M. gaumeri* 1999 data. **a** The survival data are plotted (0, death; 1, survival) as a function of individual size x (plant volume in cm^3), along with a logistic regression fitted to the data. The fitted curve is $\log(s/(1-s)) = 1.86 + 0.0012x$ ($P < 0.05$). **b** The data on year-to-year changes in size, along with the linear regression fit for mean size at year $t + 1$ as a function of size in year t. The fitted line is $y = 61.8 + 0.96x$ ($P < 0.05$). **c** *Histogram* of residuals from the linear model in *panel*. **d** Squared growth residuals as a function of individual size, along with the linear regression fit for the mean squared residuals, which are the variance of size in year $t + 1$, given the size in year t. The figures represent data grouped by annual periods for the nine study sites. The y-axis scales are different among the *panels*

The model of data in Fig. 2 does not appear to be linear, because each data point corresponds to one of the terms on the right-hand side of this equation (i.e., an actual discrete number of offspring). The linear regression line is an estimate of the expected total contribution from each term to the offspring production in a given year, which is the quantity that enters into the model. Note that when estimating the per capita fecundity f_1, all individuals that are alive at the start of the time step must be included, even if they die between times t and $t + 1$. Just as the survival function $s(x)$ should be fitted to remain between zero and one, f_1 should be fitted so that the number of offspring remains nonnegative for all adult sizes.

Although integral projection models define size-related vital rates in a continuous fashion and do not define size classes, the implementation of these models requires calculating the integrals, which is most practically conducted by applying fine categorization. The integration must run over all possible sizes, not just those observed in the data. We set the limits of integration based on the variance of

growth (described extensively in Easterling et al. 2000). The lower limit of integration was set at the minimum observed size $x_{\min}$ minus three standard deviations of the growth increment at $x_{\min}$, and the upper limit was set at the maximum observed size $x_{\max}$ plus three standard deviations of the growth increment at $x_{\max}$. Finally, for the analyses, we used the script written by Easterling et al. (2000) for the R program (R Development Core Team 2009) and determined the population growth (λ), the stable size-class distribution (w), the reproductive value (v), the sensibility and elasticity analyses, and the kernel.

Results

Density, germination and seedling survival

In an area of 2,700 m^2, we found 778 individuals of *M. gaumeri* in 1999 (density: 0.29 individuals/m^2). The abundance varied from 9 to 307 plants among sites

Fig. 2 Number of offspring as a function of individual size x (plant volume in cm^3), along with the linear regression for the mean number of offspring for **a** 1999–2000, **b** 2000–2001, **c** 2001–2002, **d** 2002–2003, **e** 2003–2004, **f** 2004–2005. The y-axis scales are different among the *panels*
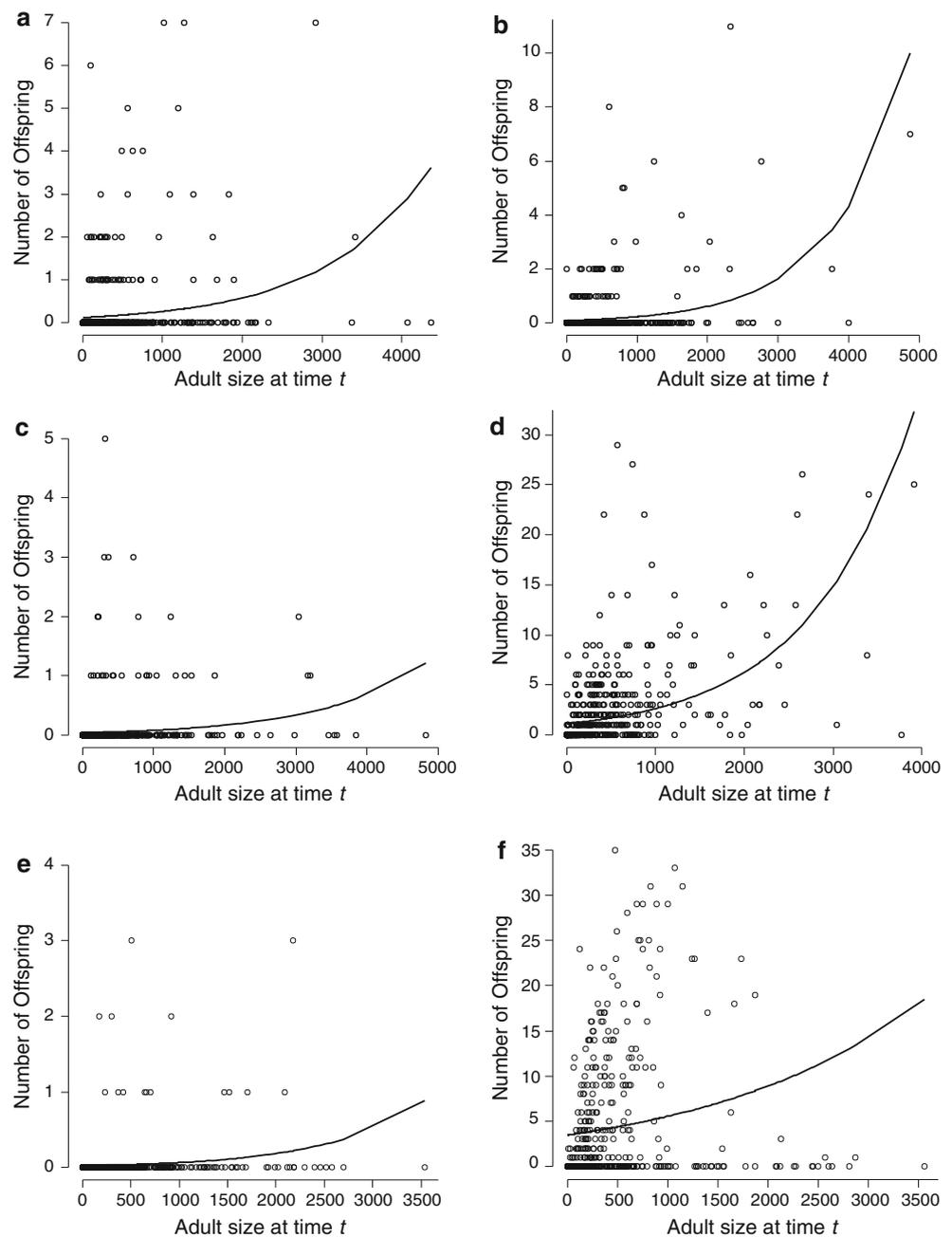
throughout its distribution range. In the 2007 census, we found 419 plants with a density of 0.16 individuals/m^2, and in 2008, the final census, we found 663 plants (0.24 individuals/m^2).

In the germination experiments during 2005 and 2006 (600 seeds sown, 300 in shade and 300 in open conditions), we did not observe a single germinating seed after 1 year; in 2007, only four seeds out of 300 germinated (in the shade and protected treatment). We did not observe germination in the open sites treatment in any year. The average number of seeds per fruit was 72 ± 28 ($n = 95$).

The low number of seeds germinated for each treatment did not allow further statistical analysis of these results. Because no field data were available for seed germination, an estimate (i.e., $0.01 = 1\%$) had to be incorporated into the calculation of the fecundity, reflecting a low germination probability. This was also the case for seedling survival, as no seedling survival was observed, and a low value was incorporated (0.001) assuming that only one seedling out of 1,000 becomes established. These values were used in demographic studies of other species of the genus *Mammillaria* for which no seed germination and

Table 1 Lambda values (λ) for the period 1999–2008 for all populations of *M. gaumeri*

Period	Growth rate (λ)
1999–2000	0.9790
2000–2001	1.4893
2001–2002	0.8302
2002–2003	0.8471
2003–2004	0.9411
2004–2005	0.8873
2005–2006	0.8544
2006–2007	0.9001
2007–2008	1.2505

seedling survival were observed in the field (Contreras and Valverde 2002; Valverde et al. 2004). In the growth chamber, we obtained average seed germination rates of 70–88% within the first 22 days; no further germination was recorded after this duration.

Growth rate (λ), stable size distribution and reproductive value

The population growth rate (λ) was under unity for almost all periods, with the exception of 2000–2001 and 2007–2008, for which we found population growth rates above unity (Table 1; range 0.8302–1.4893). The stable

Fig. 3 Stable size distribution for the integral projection model fitted to the *M. gaumeri* data and the histogram distribution of plant sizes (plant volume in cm^3) in the *M. gaumeri* dataset. **a** 1999–2000, **b** 2000–2001, **c** 2001–2002, **d** 2002–2003, **e** 2003–2004, **f** 2004–2005. The *y*-axis scales are different among the *panels*
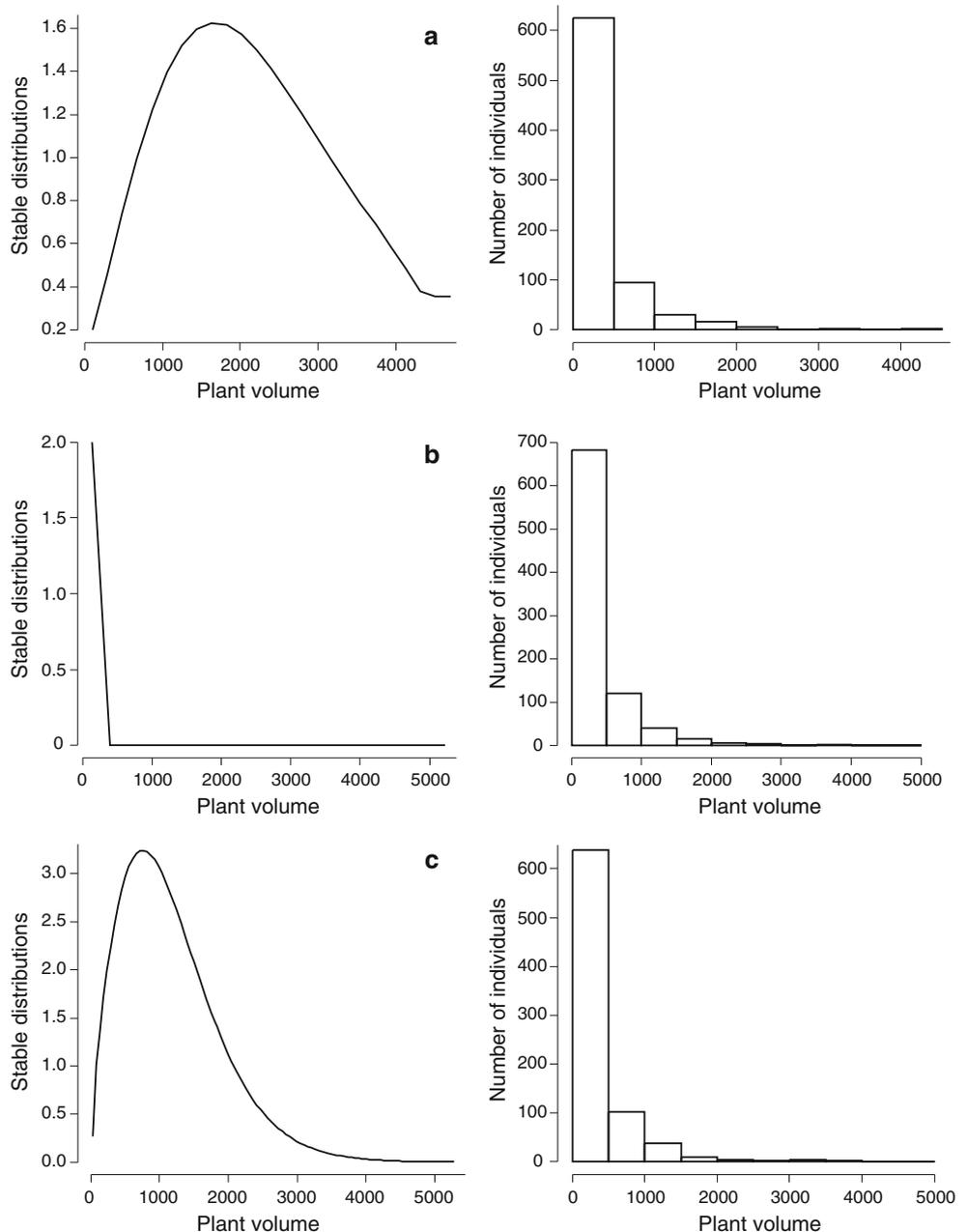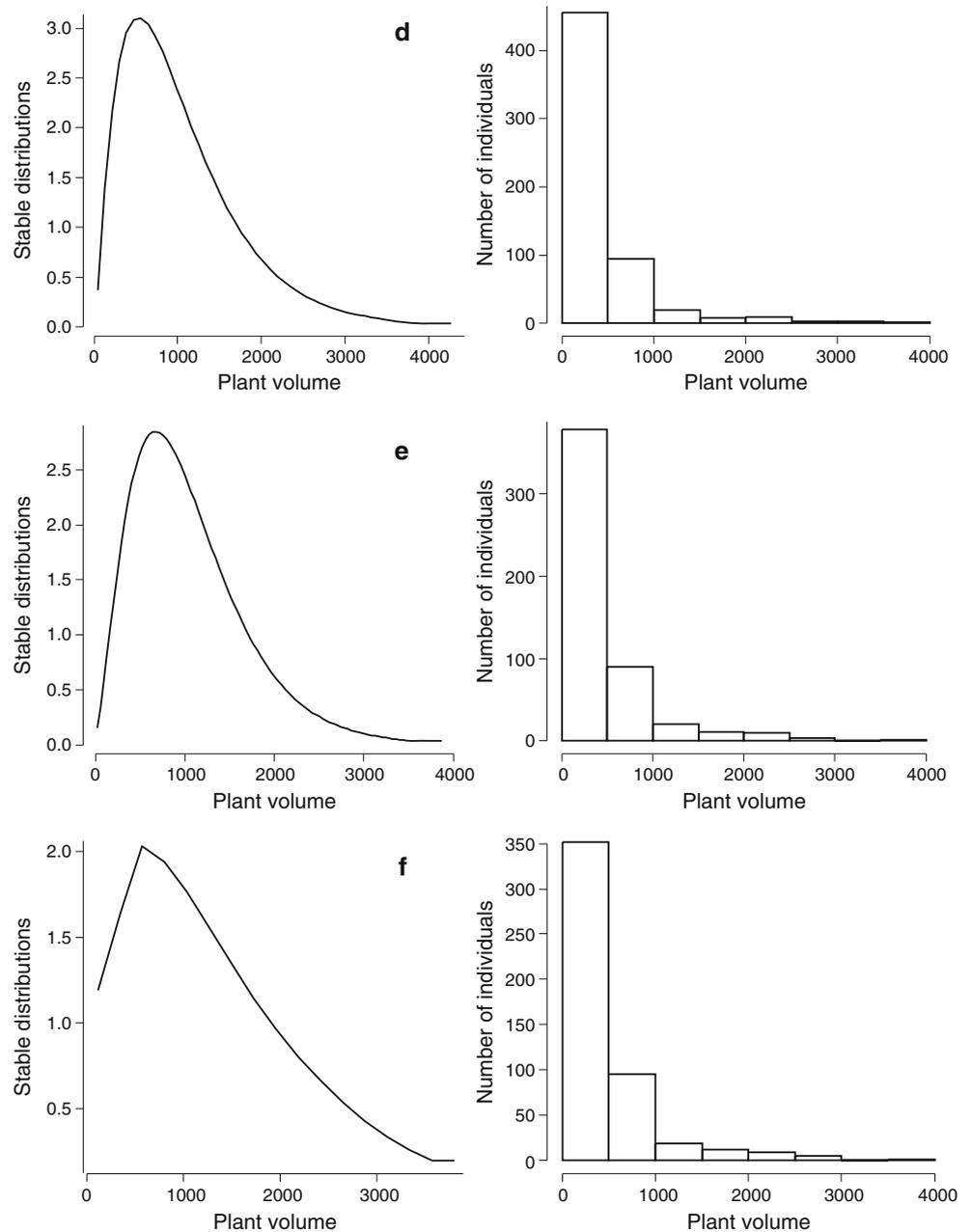
Fig. 3 continued

size distribution was skewed heavily towards smaller sizes (Fig. 3). Stable size distribution in the early years (1999–2000, 2000–2002, 2002–2003, 2003–2004, 2004–2005) indicated that under deterministic conditions many populations could include larger numbers of individuals with a volume of 500–2000 cm^3 (Fig. 3a, c–f). However, the stable size distribution was different from the observed size histogram-distribution in the data used to fit the model. The reproductive value curve, in all years, shows that reproductive value increased with plant volume, reflecting the fact that larger plants have higher fecundity. We present only 6 years as examples (Fig. 4).

Sensitivity, elasticity and the kernel

The sensitivity values increased with plant volume, and the elasticity values were high along the ridges representing the survival of intermediate size individuals. We presented the sensitivity and elasticity values for three periods because the pattern was similar for all years (Fig. 5).

The kernel [$k(y, x)$] represents the summation of all of the investigated parameters of *M. gaumeri* (survival, growth and fecundity) for each individual. The surface was almost smooth and near zero over the majority of their extension, except for the ridge running near the diagonal (or the central region) of the

Fig. 4 Relative reproductive
value for the integral projection
model of the *M. gaumeri* dataset
(plant volume in cm^3):
a 1999–2000, b 2001–2002,
c 2002–2003, d 2003–2004,
e 2005–2006, f 2006–2007. The
y-axis scales are different
among the *panels*
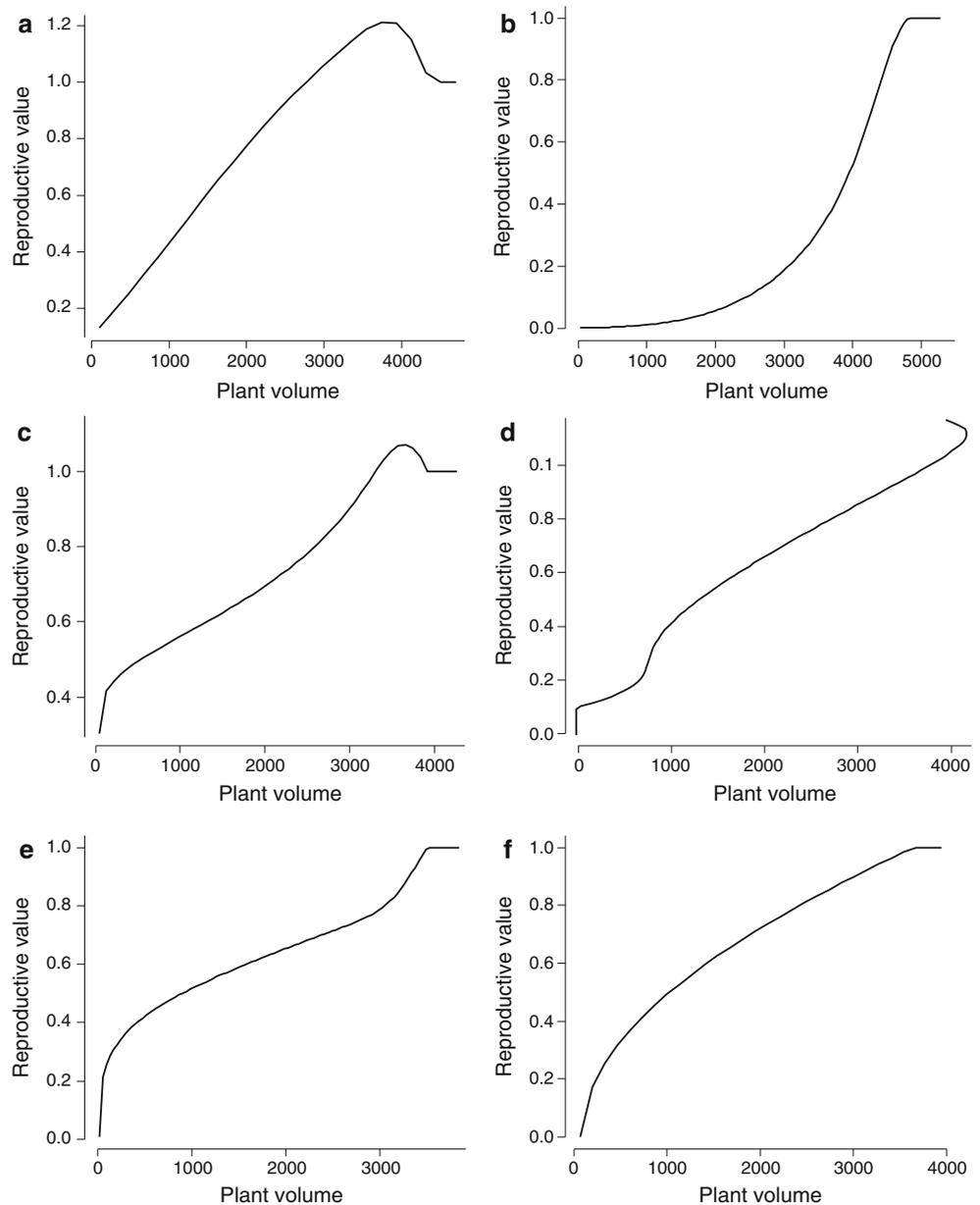
kernel, which was dominated by the survival function representing individuals who survive to the next year without changing much in size (stasis) (Fig. 6). The kernel [*k*(*y*, *x*)] resembles a Lefkovitch (1965) matrix for a size-structured population: the smaller values in the top row represent newborns, all of which enter the smallest size class, and the ridge of large values near the diagonal represents survival with a possible transition to a neighboring size class. Similar tendencies were observed in all years, so we present only 6 years (Fig. 6).

Discussion

The nine investigated localities of *M. gaumeri* were characterized by low population densities. These results are

within the range of densities reported for other *Mammillaria* species. Ramos-López (2007) reported a *Mammillaria dixanthocentron* maximum density of 1.04 individuals/m^2 in the Cuicatlán Valley, Oaxaca; while Peters and Martorell (2001) found a density of 0.26 individuals/m^2 for the same species in the Tehuacan Valley. Valverde et al. (2004) reported densities of 0.06 individuals/m^2 for *Mammillaria magnimamma*, while for *Mammillaria crucigera* Contreras and Valverde (2002) reported densities of 1.0 individuals/m^2.

The observed decreasing densities may be caused by the characteristics of the species and the occurrence of different disturbance events, as suggested by Olmsted and Álvarez-Buylla (1995) for other Cactaceae. In the case of *M. gaumeri*, the recurring presence of hurricanes is a
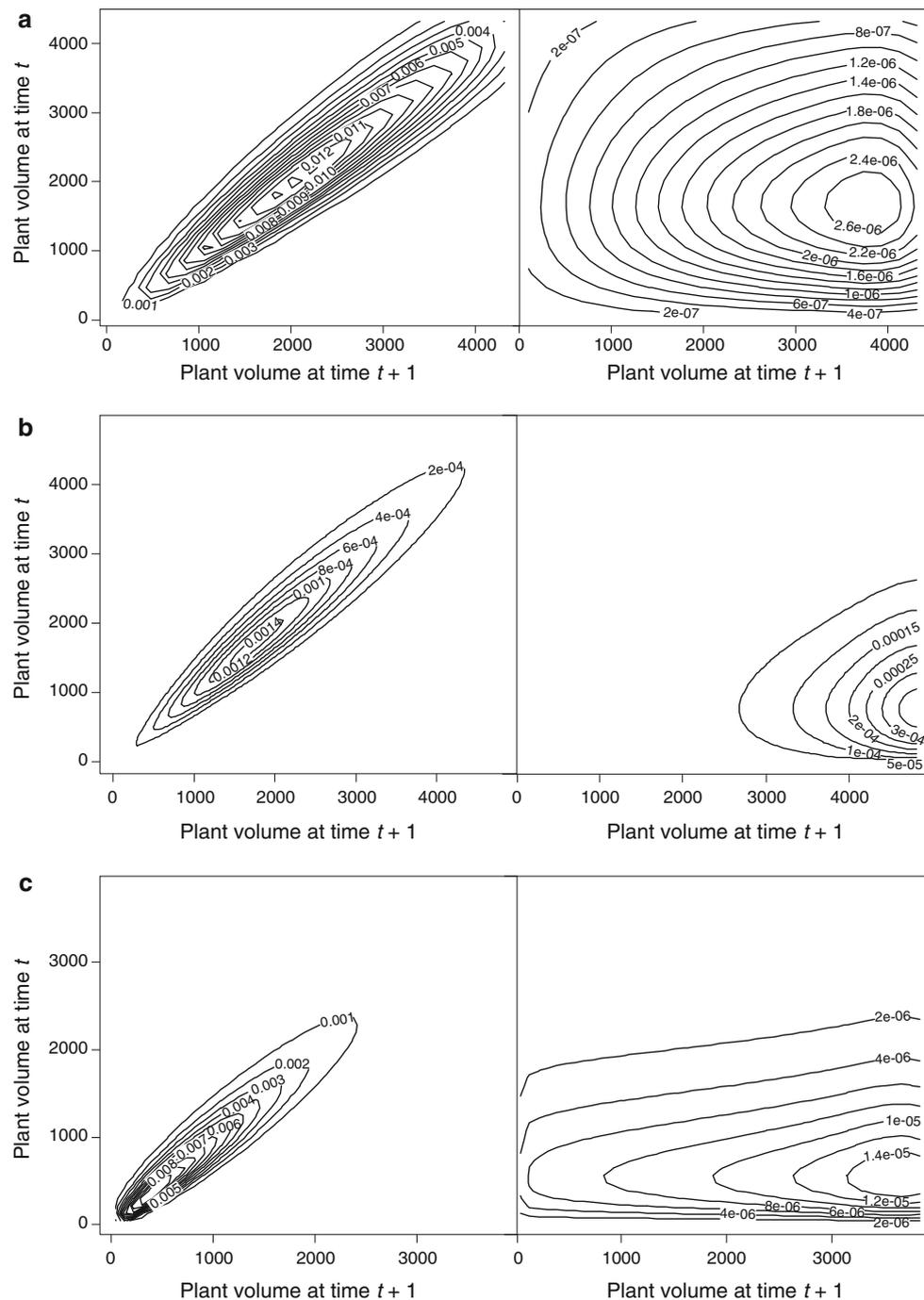
Fig. 5 Elasticity and sensitivity surface for the integral projection model fitted to the *M. gaumeri* data. **a** 1999–2000, **b** 2001–2002, **c** 2002–2003. The *y*-axis scales are different among the *panels*

phenomenon that has strongly impacted several of its locations; for example, floods caused by Isidore in 2002 resulted in the death of a large percentage of individuals at some sites. Moreover, the endangered status of *M. gaumeri* is primarily caused by anthropogenic disturbances, such as urbanization, road construction, cattle ranch management, and agriculture, which are changing the composition of the

vegetation and fragmenting its already restricted habitat (Durán et al. 1998). The results of this study indicated that the localities where *M. gaumeri* was found presented low population densities and were mainly composed of adults (individuals >100 cm^3 volume), whereas no seedlings were found at most of the investigated sites. In Yucatan, only nine populations of *M. gaumeri* currently remain, and in

Fig. 6 The fitted kernel for *M. gaumeri* and its components: the survival and fecundity function. **a** 1999–2000, **b** 2000–2001, **c** 2001–2002, **d** 2002–2003, **e** 2003–2004, **f** 2004–2005
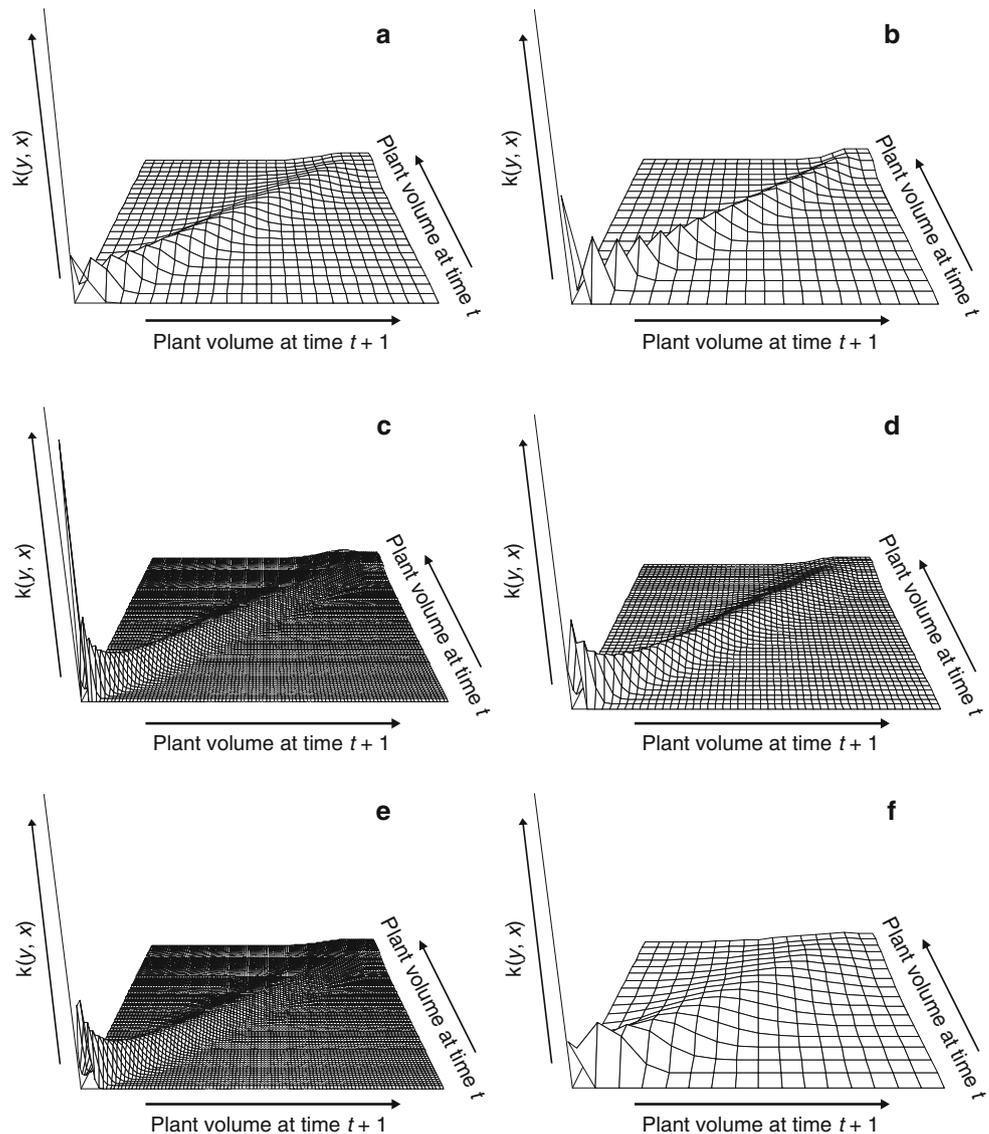
recent years, the locality where this species was most abundant was destroyed, thus resulting in the need to take serious steps to preserve it.

Unexpectedly, we obtained a good germination percentage under controlled conditions (88%). These results are similar to those of other studies on the germination of this species of cacti. For example, *M. crucigera*, *M. magnimamma* and *Neobuxbaumia macrocephala* exhibit higher germination under controlled conditions (>90%) than in the field (Ruedas et al. 2000; Contreras and Valverde 2002; Esparza-Olguín et al. 2002). However, the germination rates observed in the field experiments were very low (1%), and in some years, we did not observe any germination in the field experiments. Similar results have been previously reported for *M. magnimamma* (Contreras and Valverde 2002).

Even though germination of *M. gaumeri* was found to occur, the seedlings in most cases did not survive the first year of life. López-Haas (2007) reported a 4.8% germination rate for this species in the field, but after 1 year, the seedlings' survival probability was only 0.016 (1.6%). Additionally, Cervera et al. (2006) reported a 92% germination rate for *M. gaumeri* in the field, with a mortality of 100%. Seedlings of *Strombocactus disciformis* (DC.) Britton & Rose and *Turbinicarpus pseudomacrochele* (Backeb.) Buxb. & Backeb. were observed to survive in the field for only 20 and 150 days, respectively (Álvarez et al. 2004). The results of our germination experiments and the high mortality of seedlings found in the field clearly indicate that these life cycle stages represent a dramatic bottleneck in the population dynamics of this species.

The stable size distribution obtained in the model was comprised mostly of small individuals (young adults) and was different from the population structure found in the field. This pattern can also be seen in the majority of

studies involving cactus species associated with low recruitment and high elasticities for survival (Godínez-Álvarez et al. 1999; Esparza-Olguín et al. 2002; Jiménez-Sierra et al. 2007).We found a low frequency of individuals in the smaller size categories and the largest size category, possibly indicating low recruitment of this species in the former category and extraction of adults in the latter case. The growth rates were low for all size classes showing particularly high survival of individuals, which is consistent with trends found among the Cactaceae and for other long-lived species (Godínez-Álvarez et al. 1999; Rosas and Mandujano 2002; Mandujano et al. 2007).

The population growth rate of *M. gaumeri* was below unity. Lower lambdas during some years can be attributed to the high mortality of individuals in those years. For example, in the period 2001–2002, several locations experienced a high mortality of plants because of floods caused by Hurricane Isidore and as a result of the fragmentation of coastal vegetation and the looting of individuals. In the following years, the population was maintained with values below unity, until the last evaluation period (2007–2008) when the growth rate was greater than one. This increase in population growth rate was probably caused by recruitment that occurred in 2008, an event that had not been presented since 2000.

According to the obtained elasticity values, the population dynamics *of M. gaumeri* depend strongly on the retention or survival of individuals. For this reason, conservation efforts for this species should consider the protection and survival of individuals as a focal point. This same pattern has also been reported in other demographic studies of cacti and for long-lived species in general (Silvertown et al. 1993; Godínez-Álvarez et al. 2003).

Integral projection modeling offers benefits over classic matrix modeling. The classic matrix model entries represent mean vital rates for individuals within the class. Even if size class boundaries represent natural biological delimiters (such as size at first reproduction), information is lost when individuals of different sizes are grouped into a class and treated as if they were identical. Growth variation can be incorporated to distinguish between groups of individuals with fast growth, slow growth and those that shrink in size (Salguero-Gómez and Casper 2010), but this does not include variation between all individuals. Moreover, growth variation among individuals may strongly influence the dynamics and growth rates of populations, especially for long-lived species (Zuidema et al. 2010). Population growth rates λ and elasticities of matrix models are sensitive to variation in the number of categories (Enright et al. 1995; Ramula and Lehtilä 2005). Integral Projection Models provide solutions for both of the above-mentioned problems. These models are extensions of matrix models that yield similar outputs, but use continuous relations of vital rates (growth, survival, reproduction) versus size (or age) as inputs, instead of category-specific values (Easterling et al. 2000; Ellner and Rees 2006). So far, integral projection models have rarely been used for long-lived species and species with a small population size (Metcalf et al. 2009) despite their potential to be used for these species groups. Therefore, the application of this model presents new alternatives for studies of the population dynamics of plants. However, we should mention that our current approach is deterministic and does not evaluate the stochastic growth rate.

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