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The effects of serotiny and rainfall-cued dispersal on fitness: bet-hedging in the threatened cactus *Mammillaria pectinifera*

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Abstract Serotiny—the retention of seeds in the mother plant for over a year—in unpredictable environments may increase the probability that at least some seeds are dispersed during favorable periods. Propagules may be expelled when environmental cues announcing favorable conditions occur, or be gradually released into the environment. This could be a bet-hedging strategy increasing the long-term fitness by reducing interannual variability in reproduction. However, the impact of seed retention on the population dynamics of serotinous species and its contribution to fitness has been barely explored under field conditions. We assessed these issues in the threatened *Mammillaria pectinifera*, a small globose cactus that gets established only in exceptionally rainy years. This species expels some seeds actively during unusually rainy periods, while dispersing others passively over several years. Dynamics of the seeds in the mother plant over two very contrasting years in terms of precipitation was incorporated into a stochastic matrix model. Seed retention was found to increase significantly the probability that some of the seeds retained in any given year are dispersed within a subsequent rainy period. Active seed-expulsion raises this

probability even further. As expected in bet hedgers, seed retention increased fitness in the presence of temporal variability. Active fruit expulsion did not affect fitness, but reduced demographic stochasticity. The incomplete serotiny and fruit expulsion observed is the evolutionary outcome expected for the environment and life-history attributes of the species.

Keywords Bradyspory · El Niño-La Niña · Environmental stochasticity · Hygrochasy · Seed bank · Stochastic population models

Introduction

Dispersal, germination, and establishment constitute the most vulnerable stages in the life cycle of plants because seedlings have limited mechanisms to face unfavorable conditions (Harper 1977; Angevine and Chabot 1979; Solbrig 1980). In cacti, germination and establishment are usually very low. Only in exceptional years are the environmental conditions appropriate for successful establishment to take place (Godínez-Álvarez et al. 2003). It is a well-known fact that reproduction of desert plants occurs mostly during occasional humid years. In this regard, the El Niño–La Niña cycle has received increasing attention (Holmgren et al. 2001).

It has been suggested that retaining seeds in the mother plant for at least enough time for the next cohort of seeds to ripen (usually more than 1 year; Lamont and Enright 2000), a phenomenon known as serotiny, may confer adaptive advantages in environments where the opportunities to establish are infrequent and unpredictable. Two mechanisms may be involved. In some plants, seeds are released when an environmental cue such as rainfall or fire

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indicates that appropriate conditions are present. Other species release their seeds gradually, thus increasing the chances of finding an appropriate time window for their establishment (Cohen 1966; Venable and Lawlor 1980). This seems of especial importance in drylands, where rainfall is highly unpredictable and seed retention has evolved in several plant families (Went 1949; Beatley 1974; Ellner and Schmid 1981; Kamenetsky and Gutterman 1994; van Oudtshoorn and van Rooyen 1999). Bet-hedging is expected to operate in nature if the long-term fitness (i.e., the geometric mean of annual fitness values) is maximized, even if there is a reduction in the (arithmetic) mean annual fitness. This is frequently achieved by means of a reduction in the interannual variability in fitness (Tuljapurkar 1982; Stearns 1992).

Some species of globose cacti in the genus *Mammillaria* (Cactaceae) show both gradual and cued dispersal of their seeds. Most of their fruits are retained inside the succulent stem, releasing their seeds spontaneously over several years. A larger fraction of the seeds are retained in more unpredictable environments (Rodríguez-Ortega and Franco 2001; Rodríguez-Ortega et al. 2006). In the serotinous *Mammillaria pectinifera* F.A.C. Weber, some fruits are expelled when intense early rainfall occurs, an environmental cue that indicates the onset of a rainy season with a highly increased chance of successful establishment (Peters et al. 2009). Both mechanisms seem to ensure that at least a fraction of the seeds produced in a given year may germinate during wet pulses, when conditions for establishment and survival are more adequate (Noy-Meir 1973; Gutterman 1995; van Oudtshoorn and van Rooyen 1999). However, the impacts of serotiny and cued dispersal on fitness over the whole life cycle have been assessed very rarely, and all of the information available concerns species in fire-prone environments (Enright et al. 1998a, b).

In this paper, we assess the adaptive value of serotiny and cued seed dispersal in the threatened species *Mammillaria pectinifera*. To do so, we estimated the fitness of individuals that have both traits, and compared it to that of individuals that are not serotinous, or that are unable to expel their fruits in favorable years. Because the adaptive value of serotiny may be related to bet-hedging in an unpredictable environment, we estimated fitness by means of the geometric mean of population growth rates (λ_s) using a model in which environmental conditions changed randomly (Tuljapurkar 1982; Caswell 2001): If bet-hedging occurs, we expected serotinous individuals to have a larger λ_s and lower variance of annual growth rates compared to non-serotinous individuals. We expected cued dispersal to further increase λ_s values, and that the fraction of fruits expelled in favorable years would be near to an optimum, as suggested by Cohen's (1966) model.

Material and methods

Description of the study site and species

Mammillaria pectinifera is a globose cactus, 3–4 cm in diameter. The flowers open in circular crowns around the apex. Flowering occurs in December–January, and seeds ripen in April. The fruit is whitish berry that, when retained, gradually releases seeds over a period up to 7–8 years, but not in the year it is produced. Fruits may also be expelled in the year that it is produced in the presence of intense early rainfall. Seeds retained in the mother plant do not lose viability (Peters et al. 2009). Due to its restricted distribution, destruction of its habitat, and to looting, the species is considered as being threatened and is included in CITES Appendix I (Semarnat 2002; Martorell and Peters 2005; Valverde and Zavala-Hurtado 2006).

The species is endemic to the Tehuacán Valley, State of Puebla, Mexico, receiving 400–600 mm of annual precipitation. Because bet-hedging strategies are associated to interannual variations, a measure of precipitation unpredictability is required. A gamma distribution fitted by maximum likelihood to historical data from the closest weather station (Tehuacán). The coefficient of variation in annual rainfall for the study site, estimated as the reciprocal of the square root of the shape parameter α of the gamma distribution, was found to be 0.37. This figure corresponds to the lower limits of unpredictability found in other deserts (Mosiño-Alemán and García 1981; Abdullah and Al-Mazroui 1998).

Demographic data

The area under study was delimited by a 238-m² polygon. Eighty-one individuals (plus seedlings that were recruited through the study period) were marked therein. The sample was small because marks are known to make cacti conspicuous to looters and the species is threatened. Individuals of all sizes were chosen so as to estimate more precisely the plant's vital rates, which are known to depend on size (Caswell 2001). The observed size structure in the field was estimated by randomly sampling 25 squares of 1 m². Size was measured as the plant diameter. Mortality causes were recorded. The records on growth, fecundity, and mortality were taken from June 1997 (the start of the summer monsoon season) to May 1999 (the end of the post-monsoon winter–spring drought). The number of seedlings recruited was registered at the end of each annual period in 55 1-m² quadrats chosen at random. We counted the seeds retained inside a total of 237 fruits of known age (estimated from stem-rings that correspond to annual flowering seasons) in 20 different-sized adult plants.

Demographic model

The individuals registered were grouped into five categories based on their diameter: (1) 3–5 mm; (2) 6–9 mm; (3) 10–18 mm; (4) 19–29 mm; and (5) ≥ 30 mm. Individual-plant growth rates were used to estimate transition probabilities. The probabilities of dispersal and retention of seeds were estimated from the numbers of seeds found in fruits having different ages (see Appendix for methodological details). Dispersal was found to depend on the age of the fruit and the size of the mother plant, so seven more categories were incorporated to the demographic model in order to describe in detail the seed bank dynamics (Fig. 1). Size-specific fecundity was calculated assuming that seedlings derive from the different reproductive categories proportionally to the number of seeds released by plants in each category (Menges 1990). Using all the previous information, transition matrices for the 1997–1998 and 1998–1999 periods were built (see Appendix).

The first year of our study (June 1997–May 1998) coincided with an El Niño event, while the second year (June 1998–May 1999) corresponded to La Niña conditions. Because the warm Pacific waters that characterize El Niño tend to lessen the intensity of the summer monsoon (Holmgren et al. 2001), precipitation during the first year (267 mm) was lower than the 36-year average (424 mm), while during the second year, rainfall (817 mm) almost doubled the mean.

To analyze the role of seed retention in relation to this highly unpredictable temporal variability we used stochastic matrices (Tuljapurkar 1999). This requires that one of the matrices is randomly chosen in each iteration with a

given probability. To estimate this probability, the average precipitation of the two study years (542 mm) was calculated, and we assumed that the matrix for 1997–1998 was representative of years having an annual rainfall below this figure, and that the matrix for 1998–1999 was typical of rainier years. Only 8 out of the 36 recorded years had a precipitation higher than 542 mm. Thus, the probability of occurrence of a rainy year was estimated as 0.222. When running the Monte Carlo simulation, the 1998–1999 transition matrix was selected with that probability; otherwise the matrix for the drier 1997–1998 period was used. The model was iterated 5,000 times. The annual population growth rates, λ , of the last 4,500 iterations were recorded, discarding the first 500 in order to allow the model to reach its stable distribution of population structures (Caswell 2001). The geometric (λ_s) and arithmetic ($\bar{\lambda}$) means, and the standard deviation of these λ values was estimated. The whole procedure was repeated 500 times and the resulting statistics averaged to achieve greater precision.

In order to estimate the adaptive value of serotiny and cued dispersal, we used λ_s as a measure of fitness (Tuljapurkar 1982; Caswell 2001). Simulations were performed for populations that had seed retention and active fruit dispersal, populations where all the fruits were retained (no active dispersal), and populations where all the fruits were expelled in the year they were produced (no seed bank on the mother plant). The proportion of fruits actively expelled in the wet year was modified in another set of models in order to assess if the observed fraction was optimal.

Results

All plants in the size categories 4 and 5 and one plant in the third one were reproductive. Transition, permanence, observed fecundity, and dynamics regarding the seed bank resulted in a complex life cycle (Fig. 1). In the seed bank, the number of remaining seeds per fruit decreased as the fruit aged ($\chi^2 = 26.85, P < 0.0001, df = 1$; see Appendix for statistical details). Seeds in fruits from category 4 plants had a higher rate of decrease in numbers ($\chi^2 = 38.45, P < 0.0001, df = 1$), so the estimated dispersion rates were higher in this category. Seeds older than 3 years were rare in category 4 plants, while in category 5, we found very few seeds older than 4 years (Fig. 2). Hence, seeds older than these topmost ages were not included in the matrix model (Fig. 1).

The plants grew at different rates depending on their initial size ($F = 9.04, P = 0.0031, df = 1$), with maximum growth occurring in plants around 25 mm in diameter (Fig. 3). On average, growth was significantly higher during the second, rainier year ($F = 27.76, P < 0.0001, df = 1$). Mortality was also higher in the second year due

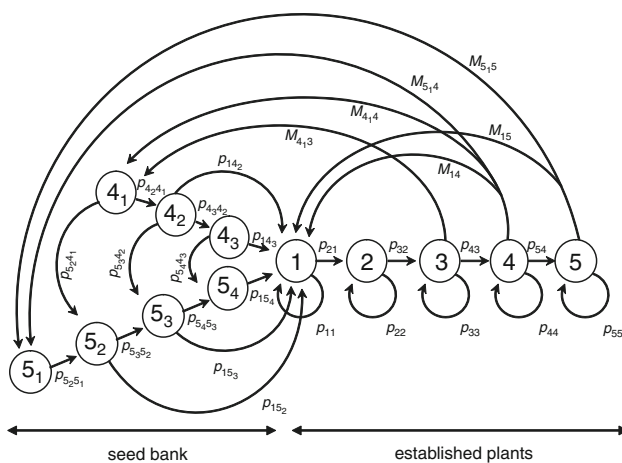


Fig. 1 Life cycle of *Mammillaria pectinifera*. p represents transitions and M fecundity. Adult plants in categories 4 and 5 retain a seed bank within their stems. Seed category names are composed of the mother-plant category and the age of the seed indicated by subscript numbers. Note that seeds are not released from the fruit in the year in which they are produced unless the whole fruit is expelled

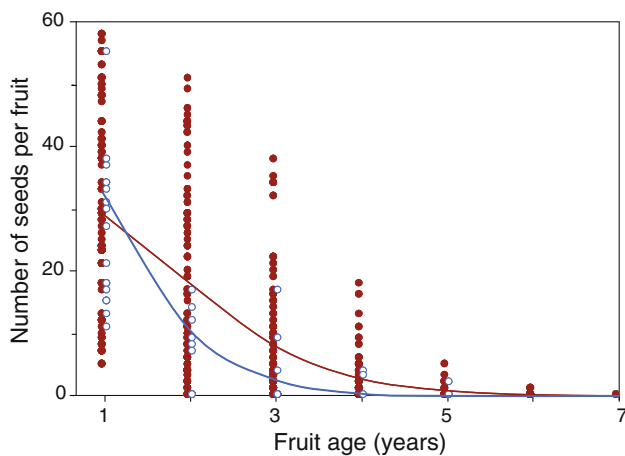


Fig. 2 Number of seeds in fruits of different age found on mother plants of category 4 (open circles, thick line) and category 5 (closed circles, thin line). $R^2 = 65.1\%$

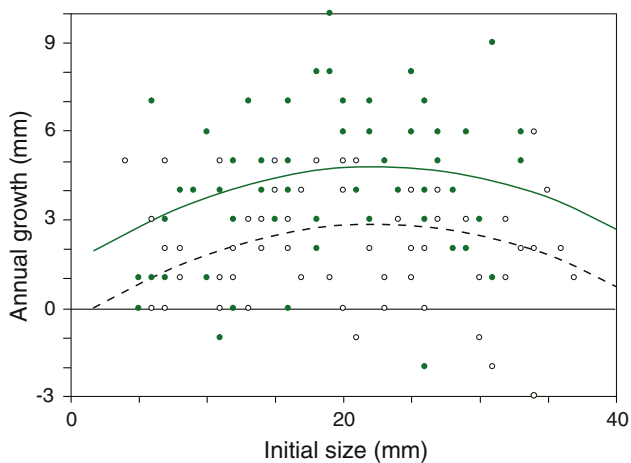


Fig. 3 Annual growth of different-sized plants in 1997–1998 (open circles) and 1998–1999 (closed circles). $R^2 = 23.8\%$

to an outbreak of beetles that ate the plants (9 vs 19% in the first and second years, respectively). The estimated probability that a seed gets established was low overall, but much larger during the rainy year (0.0010 for 1997–1998, 0.0440 for 1998–1999).

The projection matrices (1997–1998 and 1998–1999, Table 1) were iterated separately. The λ values for the two study years suggest that the population is decreasing (0.985 and 0.977, respectively). However, a model for the second year that did not include the mortality caused by beetles resulted in a λ value of 1.038. Using the classification of vital rates proposed by Silvertown et al. (1993), and summing the elasticities accordingly, the λ for both study years was more sensitive to changes in stasis than to changes in any other parameter, especially in the dry year. Growth displayed an intermediate impact on λ , while fecundity, seed bank, and fruit expulsion had a low sensitivity (Table 2).

The λ values obtained from the stochastic model project below-replacement growth rates for randomized mixtures of the two matrices ($\lambda_s = 0.983$, $\bar{\lambda} = 0.984$, $s = 0.029$; where s is the standard deviation of annual λ values), but nearly reached equilibrium even after eliminating the mortality caused by beetles ($\lambda_s = 0.996$). An even smaller λ_s was obtained when simulating plants that always expel all their fruits, that is, cacti without a maternal seed bank. These showed a very large variability in λ values, and a slightly larger $\bar{\lambda}$ than serotinous individuals ($\lambda_s = 0.969$, $\bar{\lambda} = 0.988$, $s = 0.213$).

Estimated λ values for hypothetical plants that never actively expel their fruits were quite similar to those that correspond to matrices that do expel some of them ($\lambda_s = 0.981$, $\bar{\lambda} = 0.984$, $s = 0.070$). This negligible effect of cued dispersal on fitness held even if beetle predation is removed from the model ($\lambda_s = 0.993$ compared to 0.996). However, the standard deviation of λ among years was higher for the randomized matrices lacking active fruit expulsion than for the original matrices. The observed levels of fruit expulsion were not optimal, as a complete release of newly produced seeds into the environment during the rainy years would result in the largest fitness but also the greatest variability among years ($\lambda_s = 0.989$, $\bar{\lambda} = 1.044$, $s = 0.314$). Nevertheless, the minimum variance was about its lowest near the observed expulsion rate (Fig. 4).

Discussion

Seed dispersal and environmental variability

Serotiny acts as an effective bet-hedging strategy in *M. pectinifera*. As expected, the presence of the seed bank increased λ_s in the presence of temporal variability compared to a hypothetical species that expels all its fruits. This is clearly the result of a reduction in the interannual variability in fitness (Tuljapurkar 1999; Caswell 2001), as there was a sevenfold decrease in the standard deviation in λ . This may explain why in a previous work that did not account for climatic variability no changes in fitness were detected after changing the proportion of seeds retained (Valverde and Zavala-Hurtado 2006).

Contrary to what would be expected to happen in bet-hedging species, serotiny had no cost in terms of annual λ values (Tuljapurkar 1982; Caswell 2001), as $\bar{\lambda}$ was only slightly reduced by seed retention compared to the hypothetical non-serotinous individuals. As occurs in other *Mammillaria* (Rodríguez-Ortega et al. 2006), retained seeds in our species kept a high viability (Peters et al. 2009), which would reduce the demographic costs of delaying germination, i.e., the death of seeds before they

Table 1 Transition matrices for 1997–1998 and 1998–1999

	4 ₁	4 ₂	4 ₃	5 ₁	5 ₂	5 ₃	5 ₄	1	2	3	4	5
1997–1998												
4 ₁										3.68454	46.41607	
4 ₂	0.73182											
4 ₃		0.23897										
5 ₁											14.74393	91.09000
5 ₂	0.23246			0.87500								
5 ₃		0.07591			0.54192							
5 ₄						0.38519						
1	0.00004	0.00071	0.00104	0.00013	0.00048	0.00064	0.00440	0.83333				
2								0.16667	0.68182			
3									0.22727	0.73043		
4										0.18261	0.72321	
5											0.24107	0.87500
1998–1999												
4 ₁										3.22397	36.67977	
4 ₂	0.70315											
4 ₃		0.22961										
5 ₁											13.62205	92.64129
5 ₂	0.26113			0.85714								
5 ₃		0.08527			0.61934							
5 ₄						0.61934						
1	0.00082	0.00323	0.00440	0.00063	0.00206	0.00274	0.00440	0.37500			0.04915	0.12687
2								0.37500	0.35000			
3									0.35000	0.56413		
4										0.28202	0.54169	
5											0.27081	0.85714

Gutter names correspond to those shown in Fig. 1

Table 2 Elasticity values for the three main demographic processes and for selected sets of vital rates regarding seed fate

	1997–1998 (drought)	1998–1999 (rainy)
Stasis	0.715	0.577
Reproduction	0.036	0.060
Growth	0.249	0.363
Seed bank (survival)	0.074	0.083
Seed bank (germination)	0.036	0.050
New seeds expulsion and germination	0	0.011

Elasticities were estimated from deterministic models for the two study years separately. Note that the first three rows encompass all the matrix elements, while only a few of them are reported in the last rows. Those elements were considered twice, so the columns do not add to unity. The last row corresponds to seeds actively expelled altogether with newly produced fruits

even germinate (Stearns 1992; Enright et al. 1998a; Battisti et al. 2003). We believe that only a small fraction of the seeds are released belowground where they cannot

germinate (see Appendix), but if we are wrong this could actually represent a considerable cost that we are not acknowledging. Also, seeds of *Mammillaria* are not stored in costly structures such as fire-resistant cones, which indirectly reduce fitness (Enright et al. 1998a). Such a “serotiny for free” scenario is probably one of the drivers behind the evolution of seed retention in the genus. Additionally, seed retention may give *M. pectinifera* protection over granivores, mainly ants that actively collect seeds in the study area. If seeds were dispersed when they mature, they would do so from March to April, right in the middle of the dry season, when ants feed the most. Thus, fruit retention may reduce consumption by ants until the rainy season starts and ant activity decreases considerably (Guterman 1994).

The release of seeds into the environment during opportunity windows may be especially important in a taxonomic group where mortality during the first stages of the life-cycle is very high (Godínez-Álvarez et al. 2003). From the probability of observing a rainy year as estimated in this study (0.222), it may be calculated that the

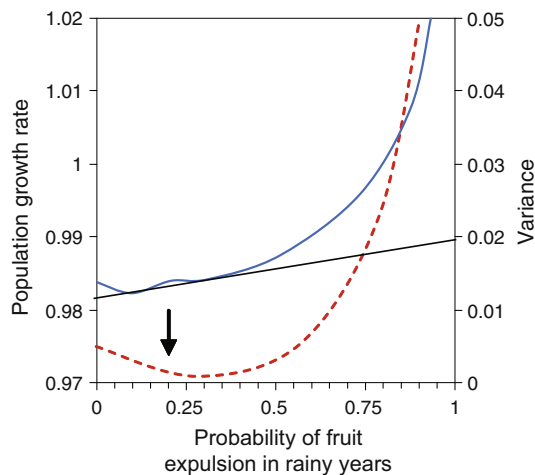


Fig. 4 Effect of different fruit expulsion probabilities during rainy years on the population growth rate. *Thick light line* long-term population growth rate (λ_s). *Thin black line* average annual population growth rate ($\bar{\lambda}$). *Dashed line* variance in annual population growth rates. *Arrow* observed expulsion probability

probability that at least some of the seeds retained in any given year are dispersed in a rainy period within the ensuing 4 years is $1 - (1 - 0.222)^4 = 0.634$. Considering the fruit expulsion rate found in the field in rainy years ($\sim 20\%$; see Appendix), this probability increases up to 0.707. Expelling fruits during rainy periods would seem advantageous because the estimated probability of establishment was much higher then (see also Peters et al. 2009).

Despite this, the inclusion of fruit expulsion in the projection matrices had a negligible effect on fitness. Our model estimated that active dispersal caused an increase in λ_s of only 0.002. This is in agreement with the low elasticity values estimated for fruit expulsion, which indicate that it would not affect fitness. The extremely low impact that cued dispersal had on fitness may yet cause evolutionary change over very long time periods (Hartl and Clark 2007).

However, the active expulsion of fruits may serve for purposes other than increasing the number of seeds expelled on favorable years. Ejecting the fruits at the beginning of the rainy season would allow seedlings to make the most of it (Gutterman 1972), to establish before other plants do, providing them with a competitive edge (Tielbörger and Prasse 2009), or to germinate rapidly and avoid predation (Venable and Brown 1988; Narita and Wada 1998). These processes would affect the establishment probability of seeds that are expelled with the fruit or that are dispersed from the seed bank. As we assumed equal probabilities for all the seeds regardless of their origin, the model is incapable of assessing the adaptive value that fruit expulsion would have under these alternative hypotheses.

It must be noted that cued dispersal reduced the interannual variance in λ . In the long term, λ_s is expected to be

highly affected by extremely adverse years (Stearns 1992), so the strategy of expelling some fruits and retaining others seems to confer lower risks of wide drifts, and to decrease the probability of disappearance (i.e., zero fitness). In the models for which we augmented the fraction of fruits expelled in rainy years, there was an inordinate increase in interannual variability, so large that even the correlated boost in $\bar{\lambda}$ was incapable of substantially affecting the long-term λ_s . Large demographic stochasticity increases the probability of population extinction (Gilpin and Soulé 1986), and may play a role in keeping expulsion probabilities well below their optimum in terms of fitness but close to the lowest possible interannual variability. Given the short duration of our study, we may not have observed enough variability to achieve a more realistic estimation of the impact of reduced stochasticity caused by cued dispersal.

Nevertheless, there are reasons to expect that not all the fruits are expelled in rainy years, which would be optimal given our model. In a theoretical approach developed for seed banks, a small chance of successful establishment even during the favorable years (as it occurs in our species) would be expected to preclude the full germination of newly-produced seeds, especially if their viability is not compromised by delayed germination (Cohen 1966). Also, if seedlings are able get established in adverse years, as occurs in *M. pectinifera*, a mixed strategy in which only part of the seeds are expelled during opportunity windows and others are stored is expected to evolve in serotinous species (Enright et al. 1998a, b). Evolutionary trade-offs may also be involved: a more sensitive mechanism that allows for a complete fruit expulsion in rainy years may also cause some expulsion with less rainfall, leading to seed release in adverse periods (Williams 1966). Actually, the complete expulsion of fruits in *M. pectinifera* only occurs under extremely large amounts of irrigation (Peters et al. 2009).

The only other measurement of the impact of serotiny on fitness over the whole life cycle known to us (Enright et al. 1998a, b) also found an increase in the long-term growth rate of serotinous populations compared to hypothetical populations lacking seed retention, but that increase was potentially much larger (from 1.02 to 1.11) than observed in *M. pectinifera*. In Enright et al.'s system, seeds only established after the occurrence of fire, and do so very successfully. In contrast, we observed recruitment even in the dry year, and an overall low success even during La Niña. The more contrasting establishment patterns observed in the fire-prone environment are likely to translate into higher increases in fitness related to serotiny.

Differences in the environmental variability regime may also affect the adaptive value of serotiny. Our study site is relatively predictable compared to other arid zones (Mosiño-Alemán and García 1981; Abdullah and Al-Mazroui 1998).

The fact that even under these conditions we found evidence for bet-hedging suggests that in dryer, more variable deserts (Günster 1992; Gutterman 1994; Kamenetsky and Gutterman 1994; van Oudtshoorn and van Rooyen 1999) serotiny may also have evolved as a mechanism for spreading risks over time. In some communities, recruitment opportunities occur rarely, such as wildfires in coniferous forests and sclerophyllous scrubs (Lamont and Enright 2000; Enright et al. 1998a, b). An early fire reduces seedling establishment because time is insufficient to build a large aerial bank, but a long period without fire may result in the death of all the individuals in the population before they can reproduce (Enright et al. 1998a, b). Both kinds of events thus reduce fitness compared to fires occurring at intermediate intervals. In contrast, desert perennials are usually long-lived, and certainly experience several ENSO cycles over their lifetime. This may reduce the overall variance in λ , as we observed in *M. pectinifera* when serotiny was considered.

Population growth

Under current field conditions, the values of the stochastic population growth rate λ_s for both study years suggest that the population may be decreasing. This is in agreement with previous results for the species, which, nevertheless, suggest a much more drastic estimation of the rate of population reduction due to another beetle outbreak ($\lambda = 0.743$; Valverde and Zavala-Hurtado 2006).

It is widely accepted that the regulating factor of most processes in arid lands is water (Noy-Meir 1973). We would expect that the observed differences among years in population growth rates would be related to the noticeable differences in rainfall. This, however, was not the case. The higher precipitation during the second year presumably affected fecundity—5.5 more plants were recruited into the population—and growth, which nearly doubled the rates recorded in the first year. However, since the elasticities of fecundity and growth are small, these differences seemingly had a small impact on λ . The highest elasticity was recorded in stasis, so the high mortality observed in 1998–1999 (nearly 1 out of every 5 plants died due to the beetle outbreak) seems to be responsible for the reduction in λ during that period. Outbreaks do not seem to be associated with high rainfall, as Valverde and Zavala-Hurtado (2006) report a high beetle incidence in a climatically typical year. The $\lambda = 1.038$ estimated for this year after removing the effect of predation is probably a more accurate reflection of the prevailing population dynamics in rainy years.

It must be noted that the two demographic studies available for *M. pectinifera* (Valverde and Zavala-Hurtado 2006; and this study) have been conducted in heavily

disturbed sites. Many other populations of this species occur in areas where anthropic activities are less intense, and where this globose cactus can be expected to increase its numbers (Martorell and Peters 2009). Our model suggests that only if beetles are completely eradicated may the population persist in the long term. It is unclear whether these high predation rates have developed recently as an indirect result from anthropogenic influence, but it is known to facilitate insect and pathogen outbreaks in temperate systems (Manion 1981; Koltunov and Andreeva 1999; Marçais and Bréda 2006; Hartmann and Messier 2008). However, the fact that the two demographic studies available report heavy predation with substantial (and sometimes catastrophic) consequences for population growth, calls for a more detailed study of the predator–prey dynamics in this system.

Concluding remarks

Mammillaria pectinifera has two seed dispersal mechanisms: (1) passive dispersal of seeds retained in the bank, and (2) active expulsion of newly produced fruits. This cactus seems to be combining both strategies in order to increase the chance that some of its seeds are released in favorable periods. Serotiny is a bet-hedging strategy that increases fitness by augmenting the long-term population growth rate and reducing demographic stochasticity, which is further diminished by active dispersal. However, these sophisticated dispersal mechanisms are not capable of maintaining a viable population in the presence of pulses of intense predation by beetles. Predation certainly has not had such a large impact in the past, or *M. pectinifera* would be extinct by now. The role of human impacts in either increasing predation or reducing the tolerance of cacti to it needs to be urgently assessed.

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Appendix: Demographic model

Mortality, permanence, and transition of established plants

Because of the slow growth rates of cacti and of our small sample, we expected to observe very few transitions among size categories, so these probabilities were estimated from the individual's growth rate. To do so, annual growth was regressed on the initial diameter. Polynomial models

appropriately describe cactus growth (E. Ezcurra, unpublished data), so quadratic and cubic terms were tested. This regression allows us to estimate the diameter that a plant observed at time t will have at times $t + 1$, $t + 2$, and so on. The number of years τ_i that the smallest plant in a category i needs to transit to category $i + 1$ was thus calculated. The probability p_i of observing a plant in the year it finally transits to the next category is

$$p_i = \frac{1}{\tau_i} \tag{1}$$

Which, of course, only applies if the plant survives. If q_i is the observed mortality rate of category i , then the probability $p_{(i+1)i}$ of any plant of surviving and transiting to the next category is:

$$p_{(i+1)i} = p_i(1 - q_i) \tag{2}$$

Equivalently, the probability of permanence p_{ii} is

$$p_{ii} = (1 - p_i)(1 - q_i) = 1 - q_i - p_{(i+1)i} \tag{3}$$

The largest plant observed in the field was considered to have the maximum size M . *pectinifera* may reach before dying. Transition would then mean death, so $q_5 = p_5$.

Seed bank dynamics

The number of retained seeds was regressed on the age of the fruit by means of a log-linear model in GLIM 4.0 comparing adults of different size classes. The probability that a seed is dispersed on a given year was defined as:

$$d_{ij} = \frac{v_{ij} - v_{i(j+1)}}{v_{ij}} \tag{4}$$

where v_{ij} = average number of seeds per fruit of age j in a category i plant. That is, we assumed that all the missing seeds between fruits of different ages had dispersed.

When fruits become buried by the growth of the mother-plant’s stem, seeds could be released deep belowground where they would be unable to germinate. It is difficult to measure this, but it may have only a minor effect on our estimations of fitness. First, during the rainy season, water absorption causes a large portion of the stem to protrude from the ground, exposing about three annual rings of fruits—nearly the same number of years for which seed bank dynamics was modeled. Second, in another species in which fruits do not undergo these exposure-burial cycles, buried fruits are not able to release seeds (Santini 2007). This suggests that seeds from old fruits in *M. pectinifera* are only released when they become exposed, thus near the soil surface.

If the mother plant dies, its tissues decay and all the seeds in the bank are released. A small fraction of the fruits are actively expelled from the mother plant in the same

season it is produced. The fraction e_i was calculated as the ratio of expelled to produced fruits in category i . No fruits were expelled in the first year, and during the second, the values were $e_4 = 0.182$ and $e_5 = 0.238$.

Seeds in the bank do not lose their viability (Peters et al. 2009). It is important to categorize seeds in terms of the plant that contains them, because the dynamics of the seed bank changes depending on the size of the mother plant (see “Results”). If seeds are retained, they undergo the same transitions experienced by the mother. Because they were also categorized by means of their age, they must either transit to the next category after 1 year or disperse. If $p_{c(a+1)b_a}$ is the probability that a seed having age a remains in a mother plant that transits from category b to category c , then

$$p_{i(j+1)j} = (1 - d_{ij})p_{ii} \tag{5}$$

$$p_{(i+1)(j+1)j} = (1 - d_{ij})p_{(i+1)i} \tag{6}$$

Seeds do not disperse during the year they are produced unless the fruit is expelled (in which case we assumed that all the seeds in it are immediately released), so all of them enter the seed bank of the mother plant. That is:

$$M_{i,i} = m_i(1 - e_i)p_{ii} \tag{7}$$

$$M_{(i+1),i} = m_i(1 - e_i)p_{(i+1)i} \tag{8}$$

where m_i is the average number of seeds produced by a size i plant. Equations 5 and 7 correspond to seeds staying in or entering the seed bank of a cactus that does not transit to the next size category in that year, while Eqs. 6 and 8 apply to cacti that do so.

Establishment

We assumed that viable seeds have the same chance of getting established once they are released to the environment regardless of their previous history (whether they come from the seed bank or from an expelled fresh fruit, and independently of their age). Due to the intensity of granivory in drylands it was assumed that seeds either germinate in the year they are dispersed or die, so no seed bank develops in the soil (Rojas-Ar echiga and Batis 2001).

We estimated the probability that an individual dispersed seed gets established, p_e , as:

$$p_e = \frac{n_0}{\sum_i n_i(z_{p_i} + z_{a_i} + z_{d_i})} \tag{9}$$

where n_i is the number of individuals in category i in the whole study area, with n_0 being the observed number of seedlings that became established during the study year. z_i refers to the number of seeds dispersed by an individual of size i , which may come by passive (z_{p_i}) or active (z_{a_i}) dispersal, or from dead mother plants (z_{d_i}). These numbers were estimated as:

$$z_{p_i} = (1 - q_i) \sum_j v_{ij} f_{ij} d_{ij} \quad (10)$$

$$z_{a_i} = (1 - q_i) e_i m_i \quad (11)$$

$$z_{d_i} = q_i \left(\sum_j v_{ij} f_{ij} + m_i \right) \quad (12)$$

where f_{ij} is the average number of fruits of age j found in a size i mother plant, and m_i is the average number of seeds produced by a size i plant. Equation 12 considers the seeds in the bank as well as those that are produced in the same year that the mother plant dies, and therefore do not enter its seed bank. For the calculation of Eqs. 10–12 only the observed q_i were used, and not the equivalence $q_5 = p_5$, in order to accurately estimate the number of seeds dispersed in the study years.

If seedlings come from expelled fresh fruits they were considered as a form of fecundity and calculated as:

$$M_{1i} = m_i e_i p_e$$

Transitions from seeds in the bank to seedlings were estimated as:

$$p_{1ij} = ((1 - q_i) d_{ij} + q_i) p_e.$$

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