

**LINKAGES AMONG LIFE-HISTORY COMPONENTS THROUGH TIME:  
 CARRYOVER EFFECTS ON THE DEMOGRAPHY OF A SHORT-LIVED  
 POLYCARPIC PLANT<sup>1</sup>**

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- *Premise of the study:* Current reproduction in polycarpic plants may be affected by a wide variety of factors, including carryover or “historical” effects derived from environments experienced early in life and from previous investments in organ preformation or other life functions, such as growth or reproduction. Historical effects as determinants of plant reproductive success in a specific season have received considerably less attention than events during the current reproductive episode, especially for short-lived plants.
- *Methods:* We used structural equation modeling to assess direct and indirect relations between past reproduction and both subsequent reproduction and growth in *Helianthemum squamatum*, a short-lived polycarpic plant. Additionally, we explored the effects of current reproduction on future survival (binomial variable) by using logistic regression.
- *Key results:* Historical effects derived from previous growth positively affected current reproduction, suggesting the existence of a reproductive hierarchy in the population, in which some individuals are consistently better growers and seeders. The lack of effects of current reproduction on future reproduction, together with the existence of a negative effect on future survival, suggests that to invest maximally in reproduction at the expense of a short life span may be the optimal strategy for *H. squamatum*, a species inhabiting very unpredictable ecosystems.
- *Conclusions:* Historical effects derived from past investments in growth or reproduction may have important consequences for current plant performance and may play an essential role in shaping life histories.

**Key words:** Cistaceae; *Helianthemum squamatum*; Mediterranean; reproductive hierarchy; reproductive lifetime; semiarid; structural equation modeling.

Several factors may contribute to plant reproductive success in a given season. These include extrinsic factors, such as climatic conditions during flowering and fruiting (Bergman et al., 1996; Kudo et al., 2004), pollen limitation (Ashman et al., 2004), pollen quality (Byers, 1995), and seed predation (Louda, 1983), and intrinsic factors, such as genotype (Kärkkäinen et al., 1999), plant resources (Stephenson, 1981; Susko and Lovett-Doust, 1999), floral display (Schemske, 1980; Nielsen et al., 2002), and reproductive phenology (Mahoro, 2002), as well as interactions between all these factors (Herrera, 1991; Ehrlén, 2002). Furthermore, current plant reproductive success can depend on carryover or “historical” effects (Geber et al., 1997; Ehrlén, 2000). For example, plant performance in a given season can be the result of past environmental conditions at several time scales (Crone, 1997; Rose et al., 1998), organ preformation

(Geber et al., 1997; Worley and Harder, 1999), and resource depletion due to past reproductive or vegetative investments (Piñero et al., 1982; Primack and Hall, 1990).

Historical effects as determinants of plant reproductive success in a specific season have received considerably less attention than events during the current reproductive episode. Emphasized have been the negative effects on plant performance associated with allocation of resources to past reproduction, referred to as the “cost of reproduction” (Obeso, 2002, and references therein). Those negative historical effects derived from past reproductive events are assumed to affect current reproduction indirectly through their effect on current plant resource status (Kozłowski, 1991). However, positive correlations between past reproduction and current plant performance also have been reported (Pitelka et al., 1985; Rose et al., 1998; Lázaro et al., 2006), suggesting that certain individuals consistently set more seeds than others. Reproductive hierarchies, in which a few individuals are exceptionally fecund and the rest produce relatively small quantities of fruits, are generally derived from size hierarchies (Pfister and Stevens, 2002). Size—and fecundity—hierarchies may be caused by factors such as differences in age or growth rate (Herrera, 1991), genetic variation (Herrera and Bazaga, 2009), heterogeneity of resources (Sugiyama and Bazzaz, 1998), competition, or differential herbivory (Gange and Brown, 1989). Because of differences in “individual quality,” some individuals have more resources to allocate to all aspects of their life history (Reznick et al., 2000). From a scaled-up demographic perspective, we can assess how the establishment of reproductive hierarchies in populations, and the persistence of such hierarchies across

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reproductive episodes, may contribute to positive historical effects that have important ecologic and evolutionary implications (Wiener and Solbrig, 1984).

Positive historical effects in the form of reproductive hierarchies also have important practical implications because they enable the extrapolation of lifetime fitness from short-term fitness studies. However, detection of historical effects, and their signs, may depend on the temporal scale considered. For instance, reproduction can be negatively related to growth or reproduction in the previous year but positively related to growth or reproduction that occurred several years ago (Silvertown and Dodd, 1999; Koenig and Knops, 2000). These apparently contradictory responses suggest that determining the lifetime reproductive success of a plant requires consideration of the positive and negative historical effects and their relative magnitude. Such a task can be daunting in the study of long-lived plants (e.g., tree species), but it can be tackled more easily for short-lived plants. Unfortunately, most studies reporting historical effects on reproductive success have focused on long-lived plants, either herbaceous (Geber et al., 1997; Ehrlén, 2000) or woody (Silvertown and Dodd, 1999) perennials. In fact, historical effects may be easier to detect in short-lived perennials because influences on plant performance early in life usually fade with time (Roach and Wulff, 1987; however, see Zuidema et al., 2009).

In this study, we examined the extent to which current individual plant performance is affected by the history of reproduction and growth in a short-lived polycarpic chamaephyte, *Helianthemum squamatum*. Experimental evidence exists of short-term effects of current reproduction on next-year survival in this species (Aragón et al., 2009). To assess direct and indirect relations between past and subsequent reproduction and growth, we used structural equation modeling (SEM), an extension of regression and path analysis. Structural equation modeling can be used to model multivariate relations and to test multivariate hypotheses (Shipley, 2002), and its application to address biological queries has gained strength in recent years (Iriando et al., 2003; Giménez-Benavides et al., 2007). The technique requires the proposal of a complete set of aprioristic causal relations among predictors. Thus, we hypothesized that current reproduction is controlled by plant size, growth, and reproduction in the previous years, not only in the current or in the immediately previous year. The use of SEM allowed us to disentangle the effects of plant size and of other unexplained causes of variation from the relation between current reproduction and subsequent growth and reproduction per se. Additionally, we explored the effects of current reproduction on future survival. Because of the nature of the variable “survival” (binomial) and the difficulties it would pose in our SEM calculations (related to the need for a significantly larger data set to deal with nonnormal variables [Grace, 2006]), we analyzed this relation by using logistic regressions.

## MATERIALS AND METHODS

**Species and study area**—*Helianthemum squamatum* (L.) Dum. Cours. (Cistaceae) is a perennial nonclonal subshrub (10–40 cm) that is distributed mainly in the southern half of the Iberian Peninsula (with an additional locality in northern Algeria). It grows only in gypsum soils and is a diagnostic species of Iberian gypsum vegetation (Palacio et al., 2007). The species' life span ranges from 4 to 6 yr (Caballero, 2006), and reproduction usually begins after the first year (C.F. Aragón, unpublished data). The reproductive phase occurs

during late spring and summer, from May to August (Aragón et al., 2007), and no flower preformation occurs (S. Palacio, IPE-CSIC, Spain, personal communication). Flowers are hermaphroditic and arranged in dense scorpioid cymes at the tip of new branches. Fruits are small capsules (3 mm in diameter) generally bearing 1–7 seeds, with an average of 1.7 viable seeds per fruit (Aragón et al., 2007). *Helianthemum squamatum* shows an extremely high fecundity under a wide variety of environmental conditions (Aragón et al., 2007). The growing phase extends throughout winter and early spring and does not overlap with the reproductive phase. In this sense, *H. squamatum* can be considered a “phenophase sequencer” (Castro-Díez and Montserrat-Martí, 1998). Herbivory levels are very low and do not significantly influence growth, survival, or reproduction (Aragón, personal observation).

We conducted the study in southeast Madrid, central Spain (40°08'N, 3°26'W, 673 m altitude), in a semiarid Mediterranean gypsum landscape. For further details of the study area, see Aragón et al. (2007, 2008).

**Data collection**—The initial set of plants included 465 adult (reproductive) individuals, marked in 2002 before the reproductive season. During 3 consecutive years (2002, 2003, and 2004), plants were monitored, and size and fecundity were estimated. Plant size was estimated as a function of plant height ( $h$ ), maximum diameter ( $M$ ), and perpendicular length ( $m$ ), which were measured directly on the plants before flowering (mid May). Then, plant size was calculated as an approximation to the volume of an ellipsoid ( $2/3 \cdot \pi h M m$ ). This estimate of plant size is closely correlated to the reproductive variables considered and has proved useful in other studies with the same species (Aragón et al., 2007, 2008). Fecundity was estimated as the mean number of flowers per plant, which is strongly correlated to the total number of seeds yielded per plant (Aragón et al., 2007). We counted the total number of inflorescences per plant in the field and randomly selected 10 inflorescences from each. The mean numbers of flowers per inflorescence and per plant were calculated. Plant survival was recorded in 2003 and 2004 before the beginning of flowering (mid May). Vegetative growth rate was calculated for each period (2002–2003 and 2003–2004) as the difference between the final and initial sizes divided by the initial size (Eckhart et al., 2004).

**Data analysis**—We used SEM to analyze the effects of past reproductive and growth events on current plant reproduction in *H. squamatum*. The structure of the hypothesized relation between reproduction and growth is shown in Fig. 1A. The construction of these paths was based on the assumption that carryover effects derived from past reproductive or growth events exist and may affect current reproduction (Ehrlén, 2000). We considered plant size at the beginning of the study (2002) to be the first driving variable, since plant size is a widely accepted surrogate of plant resource status, and plant fecundity and growth are often highly size dependent (Herrera, 1991). By including the initial plant size and the growth that occurred before and after each reproductive event, we were able to disentangle the potential positive effects of prior size on reproduction from the potential negative effects of reproduction on subsequent growth. This approach also allowed us to distinguish the effect of unexplained causes of variation from the potential causal relation between current reproduction and future growth and reproduction.

Standardized path coefficients were estimated with the maximum-likelihood method, which is recommended for relatively reduced sample sizes (only 96 of the initial set of 465 plants survived until the end of the field monitoring; see Results). The degree of fit between the observed and expected covariance structures was assessed by a chi-square goodness-of-fit test; a significant result indicates the model does not fit the data. We also evaluated the fit of the model to the data by means of Bentler's comparative fit index (CFI), Bentler and Bonett's normed fit index (NFI), and the goodness of fit index (GFI), which are often used in SEM (Iriando et al., 2003). Values of CFI, NFI, and GFI range between 0 and 1, and values greater than 0.9 indicate an acceptable fit of the model to the data. Before analysis, all the variables were transformed to improve normality according to Zar (1999). Analyses were performed using the CALIS procedure of SAS statistical software (SAS Institute, 1990).

Additionally, the relation between reproductive output in one season and the probability of survival in the following years was evaluated with generalized linear models (GLMs; McCullagh and Nelder, 1989), as implemented by the GENMOD procedure of SAS. Survival was modeled assuming a binomial distribution (link function: logit). We modeled (1) the probability of survival in 2003, including the number of flowers produced in 2002 as our explanatory variable and plant size as a covariate, and (2) the probability of survival in 2004, including the number of flowers produced in both 2002 and 2003 as explanatory variables and plant size in both years as covariates.

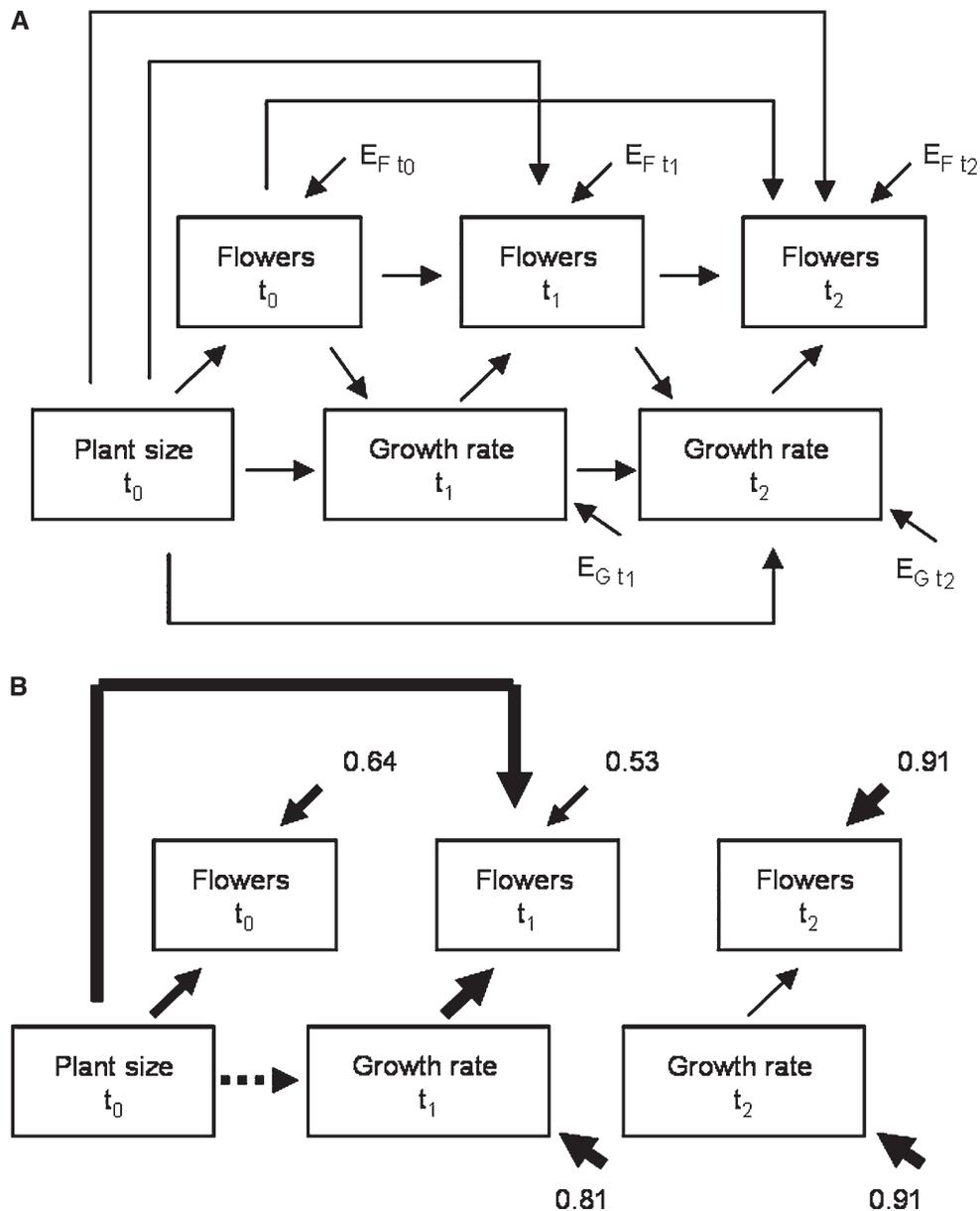


Fig. 1. Structural equation models of *Helianthemum squamatum*. (A) Hypothesized structural equation model of the relation between reproduction and growth during the reproductive lifetime of *H. squamatum* ( $t_i$  = time in years). One-headed arrows represent causal relations. Residual error variables ( $E_i$ ) represent the effects of unexplained causes of variation. (B) Structural equation model derived from the model in (A). Solid and dashed arrows indicate positive and negative effects, respectively. Numbers are the standardized path coefficients. Arrow widths are proportional to the standardized path coefficients. Nonsignificant paths ( $P > 0.05$ ) are not shown. The effects of unexplained causes are represented as external arrows to each response variable. Fit statistics for the model:  $\chi^2 = 5.671$ ,  $df = 3$ ,  $P = 0.129$ ; comparative fit index = 0.99; normed fit index = 0.98; goodness-of-fit index = 0.98.

## RESULTS

Only 96 plants (21%) from the initial set survived to 2004 and could be included in the SEM. All 96 plants flowered and set fruits every year. However, average flower production fluctuated among years (mean  $\pm$  SD: 258.9  $\pm$  408.5, 2002; 620.2  $\pm$  848.5, 2003; 238.5  $\pm$  392.3, 2004). The size frequency distribution in all years was skewed toward small individuals (Fig. 2). Smaller-size categories produced fewer flowers on average and contributed a smaller proportion of the population's total production of flowers compared with the larger-size categories (Fig. 2).

The hypothesized model provided a good fit to the data, as indicated by the nonsignificant results of the chi-square test ( $\chi^2 = 5.671$ ;  $df = 3$ ;  $P = 0.129$ ). This result was confirmed by indices of fit higher than 0.90 (CFI = 0.99; NFI = 0.98; GFI = 0.98). The main effects were driven by the initial plant size, which positively affected the number of flowers produced in the first and the second year, and it had a negative effect on the vegetative growth rate from 2002 to 2003 (Fig. 1B). On the other hand, a significant positive path existed from vegetative growth rate in both periods (from 2002 to 2003 and from 2003 to 2004) to number of flowers produced in 2003 and 2004, respectively

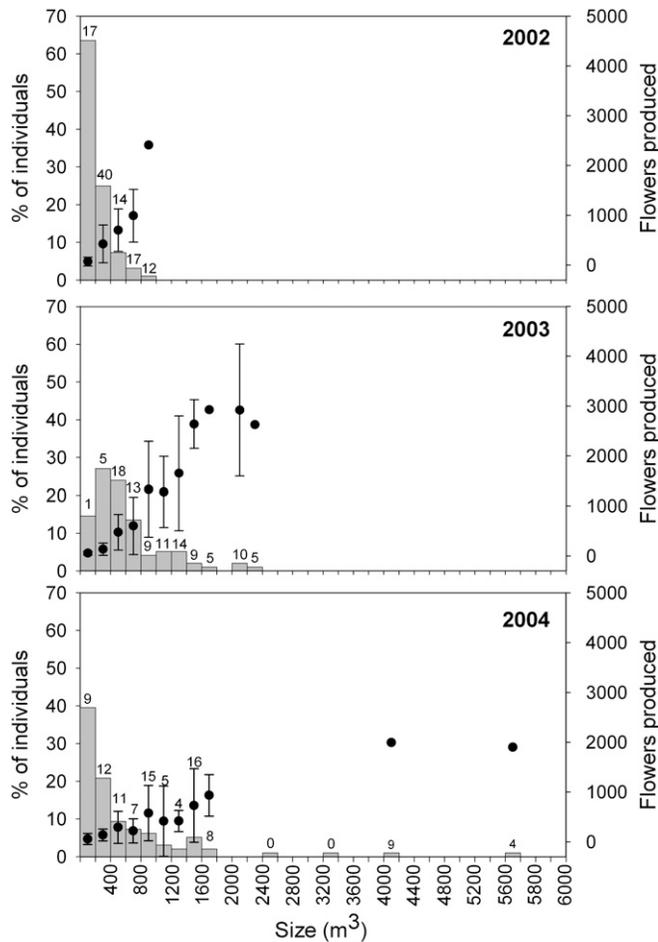


Fig. 2. Size frequency distribution (bars) of *Helianthemum squamatum* plants included in the structural equation model ( $N = 96$ ) and average number of flowers produced by each size category (data points, mean  $\pm$  SD) in 2002, 2003, and 2004. Numbers shown at the top of each bar indicate the percentage of flowers produced by the individuals included in that size category relative to the total number of flowers produced by all individuals in that year

(Fig. 1B). No significant causal relations were found from current flower production to future flower production or future growth rate (Fig. 1B).

Percentages of survival were 48% and 43% for 2003 and 2004, respectively. The probability of survival was not size dependent in any of the models (Table 1). Previous-year flower production was not a significant predictor of the probability of survival in 2003, but it had a significant positive effect on survival in 2004. In contrast, the probability of survival in 2004 was negatively affected by the number of flowers produced 2 yr before (Table 1, Fig. 3).

DISCUSSION

Current reproduction in polycarpic plants may be affected by historical effects derived from previous investments in other life functions, such as growth or reproduction (Stearns, 1992), or from environments experienced early in life (González-Astorga and Núñez-Farfán, 2000). In this study, both positive

TABLE 1. Generalized linear models for the probability of survival of *Helianthemum squamatum* in 2003 and 2004.

Explanatory variables	Probability of survival					
	2003			2004		
	$\beta$	$\chi^2$	$P$	$\beta$	$\chi^2$	$P$
2002						
Plant size	0.0010	1.79	0.1812	0.0015	2.14	0.1432
Flowers	-0.0001	2.81	0.0934	-0.0013	7.26	<b>0.0071</b>
2003						
Plant size	—	—	—	-0.0011	2.15	0.1428
Flowers	—	—	—	0.0012	10.88	<b>0.0010</b>
Intercept	-0.0187			-0.1764		

Note: The model of 2003 ( $N = 465$  plants) includes the production of flowers and plant size in the previous year. The model of 2004 ( $N = 222$  plants) includes the production of flowers and plant size in the 2 previous years. The probability of survival was modeled assuming a binomial error distribution (link function: logit). Data represent the parameters of the logistic model ( $\beta$  and intercept), the value of the chi-square statistic ( $\chi^2$ ), and the associated  $P$  value. Significant  $P$  values ( $<0.05$ ) are shown in boldface type.

and negative historical effects existed for several demographic parameters of *H. squamatum*.

We found that previous reproductive events did not influence current reproduction, indicating no presence of historical effects associated with previous reproduction. However, a positive relation was found between flower production in a given year and the previous growth event. In addition, plant size in 2002 positively influenced flower production in 2003. This positive relation between current reproduction and previous growth suggests that some individuals were always better growers and seeders, which is in agreement with the fecundity hierarchy detected. Although we cannot rule out the possibility that age heterogeneity has some uncontrolled effect in our results (for instance, we cannot assure that our plants formed an even-aged cohort), our finding of a significant signal indicates that this potential effect is not enough to mask the tight relation detected

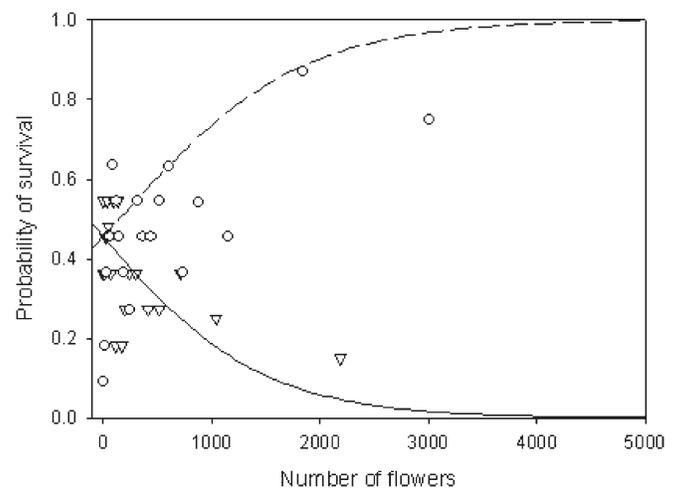


Fig. 3. Survival probability of *Helianthemum squamatum* in 2004 dependent on the production of flowers in the previous years (2002, solid line, and 2003, dashed line). The logistic curves reflect the parameters ( $\beta$  and intercept) of the logistic regression shown in Table 1. Symbols (triangles for 2002 and circles for 2003) represent the mean production of flowers and the associated probability of survival calculated in subsamples of 11 plants.

between reproduction and growth. The ecologic and evolutionary implications of size hierarchies in plant populations are considerable because they result in reproductive hierarchies (Pfister and Stevens, 2002), in which a large proportion of a plant population's genes may be descended from a very small number of individuals in previous generations. Size and reproductive hierarchies can be the result of environmental effects (Gange and Brown, 1989) but also of genetic variation (Herrera and Bazaga, 2009) or of maternal effects (Lacey et al., 2003). Although we lack information on the factors causing size and reproductive hierarchies in *H. squamatum*, we suggest that environmental factors are likely. We advance the hypothesis that the reasons for positive historical effects could be different for short- and long-lived plants, with decreasing influence of environmental effects in the latter because of a longer time for environmental effects to dilute, compared with genetic influences. Many studies have found a strong environmental dependence of survival or early success in short-lived species (e.g., Narita, 1998). For long-lived plants, mixed evidence is available. Herrera and Bazaga (2009) found genetically based fecundity hierarchies, whereas Herrera and Jovani (2010) reported environmentally based fecundity hierarchies.

A lack of negative effects of previous reproduction on future growth or fecundity often has been attributed to the effect of confounding variables (Reznick et al., 2000; Knops et al., 2007). Nevertheless, the strength of our study relies on the use of a versatile and integrative statistical approach that accounts for the direct and also indirect contribution of potential confounding effects. Furthermore, it has been strongly recommended that the results from path analysis approaches be supported with experimental verification of the cause-and-effect pathways (Sinervo and DeNardo, 1996). To this regard, our results are consistent with those obtained from an experimental manipulation in the same study system (Aragón et al., 2009). In Aragón et al. (2009), we found that the survival probability in *H. squamatum* was significantly higher in plants that had been prevented from flowering (experimental flower-buds removal) compared with a control group of flowering plants.

We found a transition from a positive to a negative relation between flower production and the probability of survival when we increased the temporal scale (1 vs. 2 previous yr), suggesting that historical effects derived from past reproduction influence survival in *H. squamatum*. The mechanisms underlying this pattern likely are related to the so-called cost of reproduction (Obeso, 2002), since experimental evidence of survival costs of reproduction has been shown in this species (Aragón et al., 2009), as we mentioned previously.

The existence of a negative effect of current reproduction on future survival, together with the lack of an effect on future reproduction, suggests that reproduction might be a priority in resource allocation at the expense of survival in *H. squamatum*. The optimal compromise between the investment in current reproduction and in future survival is thought to determine the direction of selection on life span (Stearns, 1992). Whereas resources invested in current reproduction contribute directly to fitness, the benefits from all other investments will be achieved only if the organism survives. Thus, investing maximally in reproduction at the expense of a short life may be the optimal strategy for *H. squamatum*, a species that inhabits very unpredictable ecosystems (Aragón, et al., 2007) and experiences high rates of extrinsic mortality. Elevated mortality due to external causes may shift the optimal compromise toward shorter life spans (Stearns, 1992). The maintenance of a high reproductive

investment across a wide span of environmental conditions (Aragón et al., 2007), which affects future survival, likely contributes to the short life cycle of *H. squamatum*, rather unusual for a perennial species in a semiarid environment (Agami, 1987; Cody, 2000). In semiarid and arid climates, characterized by a high environmental stochasticity (Sher et al., 2004; Aragón et al., 2007), the persistence of perennial plants usually relies on their longevity (García and Zamora, 2003) because the effort invested in the establishment of new individuals seems to be great. In this sense, *H. squamatum* is considered a perennial plant with almost weedy characteristics (Aragón et al., 2009; Quintana-Ascencio et al., 2009).

The overall conclusions to be drawn from this study are that (1) there were historical effects in a short-lived plant, (2) some of these historical effects were positive, suggesting the influence of genetic, maternal, or environmental effects, and (3) some of these historical effects were negative, suggesting, with the support of previous empirical evidence, the existence of costs of reproduction. Historical effects may have important consequences in current plant performance and can play an essential role in shaping life histories. Their existence underlines the need for multiyear studies, even in short-lived plants. In addition, future research should address whether the underlying causes of historical effects differ for short- and long-lived plants.

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