The Demography of a Small Population of Yellow Columbines in the Organ Mountains

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Abstract: Yellow-flowered columbines (*Aquilegia chrysantha* Gray) are usually found in small, isolated populations near streams and pools in mountain ranges throughout the southwestern United States. To study the long-term dynamics of these populations, which are vulnerable to extinction, we have monitored the demography of a population in Fillmore Canyon in the Organ Mountains of southern New Mexico. Annual estimates of growth, survival, and reproduction were recorded for 2,152 individuals in 15 one-meter square plots for 6 years. We estimated a seed bank survival rate from experimental plots and constructed annual size-structured transition matrices to determine population growth rates. Annual growth rates varied widely between 0.46 and 1.72 and were strongly correlated with spring precipitation. We calculated a weighted mean matrix, based on the historical frequency of spring rainfall events, resulting in a population growth rate of 1.02. The relationship between population growth rate and precipitation was used to calculate a mean growth rate from 75 years of recorded climate data and to project future growth rates under different climate conditions. These methods provide both an additional approach to modeling population persistence and a clearer understanding of the likelihood of extinction for a species dependent on mesic habitat in Fillmore Canyon.

Demographic studies often model the likelihood of population persistence based on empirical data collected from the entire life cycle of individuals and projections of population growth rate, size, or structure (Menges 2000). These projection models generally rely on a few years of data that may not adequately represent the species' population dynamics or environmental conditions (Menges 2000, Bierzychudek 1999, Damman and Cain 1998). Long-term studies have typically found considerable variation in demographic rates over time (Oostermeijer et al. 1996, Horvitz and Schemske 1995). Short-term studies, such as Beirzychudek's (1982) study of jack-in-the-pulpits, often fail to accurately project changes in population size. After revisiting her two study populations 15 years later, Beirzychudek has suggested (1999) that one possible limitation of her projection model was the limited time available to accurately capture the complete range of year-to-year environmental variability.

The feasibility of a long-term plant demography study is a concern for land managers who need to budget, plan, and justify rare plant studies. In combining demographic and rainfall data collected from a small population of *Aquilegia chrysantha* Gray (yellow columbines) in the Organ Mountains of New Mexico, we focused on reconciling some of the problems inherent in projection models that rely on just a few years of data.

Precipitation in the Southwest is quite variable. Regional correlations in precipitation are implicated in cycles of tree dynamics and shrub invasions of grasslands (Swetnam and Betancourt 1998), and at smaller scales with plant cover, seedling establishment, and primary productivity (Ernest et al. 2000, Bowers 1997, Sala et al. 1988, Beatley 1974). Population growth rates of this particular columbine population varied widely between years and were also correlated with spring precipitation. Therefore, we used a 75-year precipitation record to calculate a weighted mean matrix based on the frequency of "good" and "bad" rainfall years encountered in the present study and to check how well the past six rainfall events represent the possible range of environmental variation at our study site. We also utilized the relationship between population growth rate and precipitation to calculate a mean and median growth rate from 75 years of recorded climate data and to predict future growth rates under different climate conditions. Finally, we discuss the methods used to monitor the demography of *Aquilegia chrysantha*, a plant with a complex life history that includes dormant seeds and dormant plants.

Methods

Aquilegia chrysantha Gray (yellow columbine) is a perennial herb restricted to mesic habitats near streams, pools, and cliffs in mountain ranges

throughout the southwestern United States and Mexico. Charles Wright first collected the species in 1852 in "wet springy soil, ravines in the Organ Mountains" (Wooton and Standley 1915, Shaw 1987). Based on Wright's plant list (Shaw 1987) and a detailed description of the area by John C. Bartlett (1854) a few months later, the holotype population is probably at or near the springs in Fillmore Canyon where our study site is located.

The Organ Mountains of south-central New Mexico form a relatively small, isolated mountain range with mesic canyons that are characterized by a large number of rare and endemic plant species (Debruin 1996). A population of yellow columbines in Fillmore Canyon, which drains the central-western slope of the Organ Mountains, was censused annually beginning in April of 1995. The study site is at the springs on a north-facing outcrop of limestone at 1890 m elevation. During periods of normal late summer and winter precipitation, water seeps continuously down the moss-covered slope.

New growth of yellow columbines occurs primarily in the spring, although flowering will continue late into the monsoon season. The yellow flowers are protandrous and self-compatible, with five long petal spurs filled with nectar. The pollinators are primarily short-tongue hawkmoths (Miller 1985). The fruits have five follicles that dehisce apically, and the small black seeds lack any specialized adaptations for dispersal. One flowering stalk develops from a single rosette with four to six leaves. The following season, rosettes that produced a flowering stalk have died, and usually another rosette develops on the caudex directly below the old rosette. Older plants produce a branching, woody caudex with one to several rosettes. In dry years, the caudex can serve as an organ of dormancy, and no rosettes will develop.

Field Sampling

Two types of 1 m^2 plots were established in Fillmore Canyon in April of 1995 (Figure 1). One set of 15 plots was used to monitor the demography of *A. chrysantha* individuals. Another set of 10 plots was established to monitor the emergence of seedlings from the seed bank by removing immature fruit from plants both on and within 1 m of each plot during the first three seasons.

To select the study plots, a grid of 1 m^2 was mapped on a 30 x 10 m area of columbine plants on the north-facing slope. Eighteen transects were placed upon this grid, and 15 plots were chosen at random to monitor the demography of columbine individuals. Another 10 random plots were se-

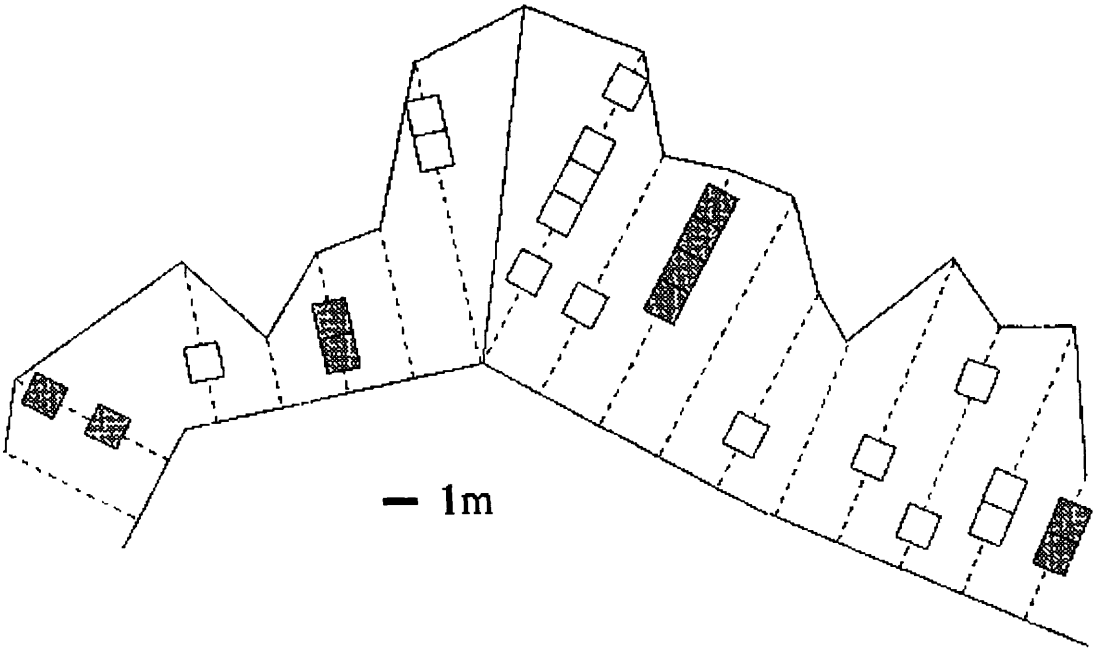

Figure 1. Map of the Fillmore Canyon population. Experimental seed rain removal plots are indicated by shaded boxes and demography plots are indicated by white boxes.

lected for the seed rain exclusion experiment, subject to the constraint that they did not fall within 2 m of the demography plots. This was intended to prevent seed movement into these plots and to minimize the effect of fruit removal on the 15 demography plots. Plot corners were marked with rebar and numbered with an aluminum tag; the dimensions of the demography plots were measured and detailed maps were made.

To obtain estimates of survival, growth, and reproduction, we conducted a complete census of each plot annually in May just before plants started producing flowers (Figure 2). The fates of individual plants were determined by relocating mapped and tagged plants in the next growing season. Large plants were marked by attaching aluminum or laminated tags around the base of the caudex with insulated telephone wire. Seedlings and small plants were marked with very small laminated tags placed on a colored plastic cocktail sword. Detailed maps of tagged plants were made in the field and later digitized to help relocate plants in subsequent years. This year, only 18 of 765 tags from the previous year were not found; in previous years the percentage of lost tags ranged from 10.9 to 24.3 percent. Individuals missing tags were identified from locations on digitized maps.

We measured two indices of plant size; total number of leaves and total number of rosettes. Because a rosette can produce a single flowering stalk, we used the number of rosettes to define size classes. Before 1998, rosette numbers were not counted, so for those early years we divided size classes into leaf number intervals based on the relationship between rosette number and leaf number (corresponding to leaf number intervals of 1–5, 6–11, 12–17, 18–23, >23 leaves). Additional size classes recognized in the life cycle of a columbine include dormant plants, seeds in the seed bank, and new recruits (plants that have germinated in the fall or spring before the annual census).

To estimate reproduction, we counted inflorescences, buds, flowers, immature fruits, and mature fruits periodically (about every 3 weeks) until the end of the summer monsoons. Mature fruits were marked with a small piece of wire, and the total number of fruits that dehisced throughout a season was used as a measure of total fruit set. Seed production per plant was estimated from seed counts of fruits collected nearby in 1995 and 1999. Note that since the size of plants was determined just prior to flowering, values for fertility in a prebreeding census also include the probability of seeds surviving to the next census (Caswell 2001).

A difficult transition to assess is the survival rate of seeds within the seed bank from year to year, because one can estimate seed fate probabilities only by experimental manipulation. We used data from the seed rain removal plots to estimate this survival rate (Strand 1997). The number of seedlings recruited into these plots, St, was measured by direct counts in each of 3 years (1995–1997). We assumed a model of geometric decay in the size of each seed bank cohort in which seeds are lost to germination at a constant rate or survive until the next year at a constant rate. The germination rate, g, was estimated as the ratio of the average number of seedlings m^{-2} that germinated from the first year's seed rain to the total seed rain m^{-2} (Figure 3). We assumed that g does not vary among plots or in time (but see Horvitz and Schemske 1995 who estimated different germination rates in "good" and "bad" years). We used the estimate of g in the following model to estimate the survivorship of seeds in the seed bank, s, and the number of seeds in the seed bank, No, from the emergence of seeds in the experimental seed rain plots, St, in a given year, t:

$$S_t = N_o [s (1-g)]^t g$$

Finally, we also assumed that g does not vary between newly produced seeds or seeds in the seed bank (both are found on the surface of the limestone in cracks or moss). This assumption was needed to estimate the relative contributions of seeds from flowering plants and seeds in the seed bank to new recruits the following year in the construction of transition matrices.

Daily rainfall data were collected and summed 6 months prior to the annual census (Dec-May) from a remote automated weather station at Dripping Springs established in 1994 (Lat 32° 19' 24" N, Long 106° 35' 12" W, elevation 1881 m) and from a cooperator network station at the Jornada Experimental Range established in 1926 (Lat 32° 31' 17 N, Long 106° 47' 50" W, elevation 1359 m).

Transition Matrix Model

We used a stage-based projection matrix model (Leftovitch 1965). The form of the model is $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$ where $\mathbf{n}(t)$ is a vector of all the individuals in the population at time t classified by stage, $\mathbf{n}(t+1)$ is the vector of the population at the next census, and $\mathbf{A}$ is a matrix of transition probabilities between different stages from time t to t + 1. When the matrix $\mathbf{A}$ is multiplied by $\mathbf{n}(t)$ and

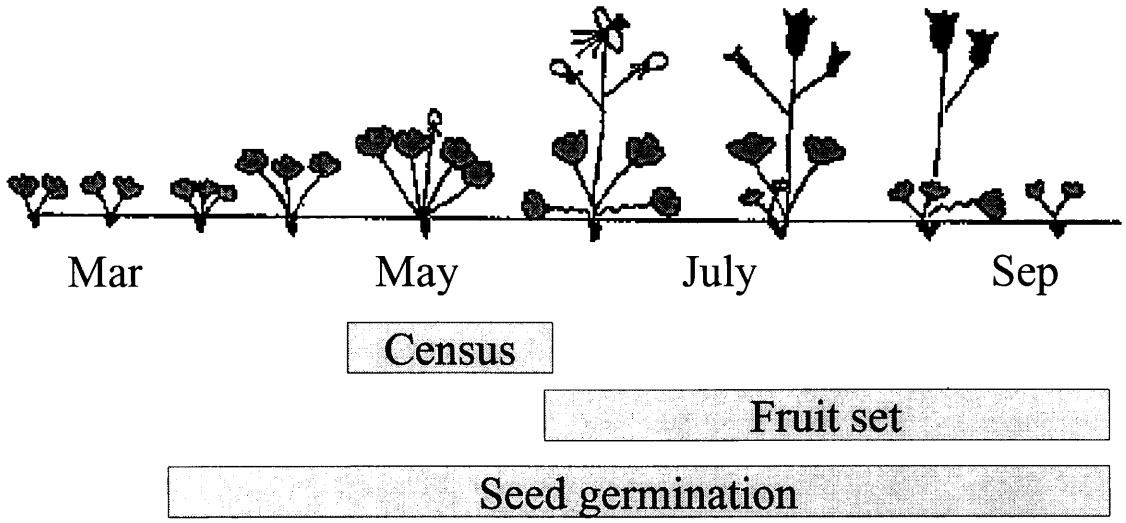

Figure 2. Diagram of *Aquilegia chrysantha* phenology and timing of the annual census, fruit set, and seed germination. Mature fruits are marked and counted about every 3 weeks until the end of fruit set.

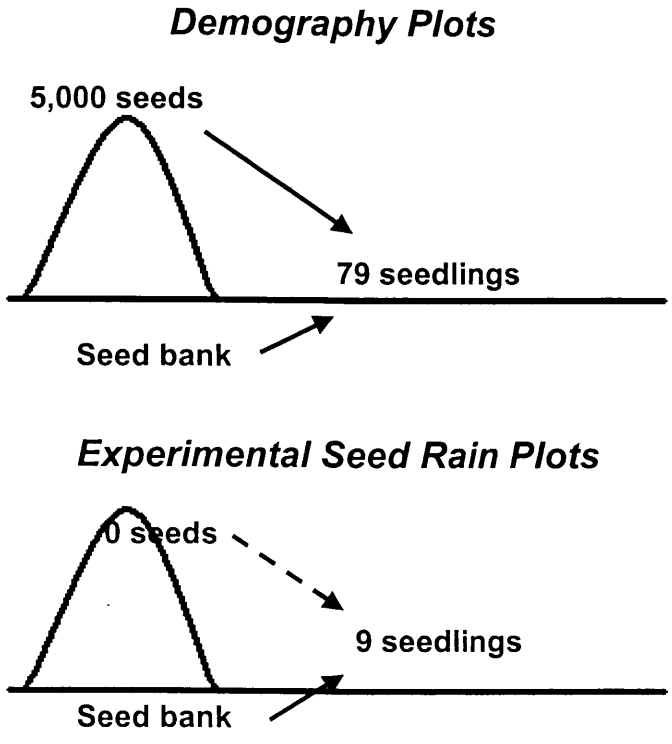

Figure 3. Diagram of the seed germination experiment in 1995. By eliminating the production of seeds falling into the seed rain plots, we estimated the relative contributions of both the seed bank and seeds released from fruits to new recruits. The germination rate is (79 – 9)/5000 = 0.014. Assuming an equal germination rate, the initial seed bank size is 9/0.014 = 9645 seeds.

subsequent products a number of times, eventually the population converges to a stable stage distribution at which time each stage is changing by a factor of λ (lambda) each time period. Lambda, or the population growth rate, quantifies the change in number of individuals through time. When $\lambda > 1$, a population is projected to increase over time; when $\lambda < 1$, a population is projected to decline.

We constructed annual, mean, and product matrices and calculated the dominant eigenvalue corresponding to the population growth rate (Caswell 2001). A weighted mean matrix was also constructed by weighting the total frequency of annual matrices in above-average rainfall years at 0.5, and those occurring in below-average rainfall years at 0.5. Annual growth rates were regressed on spring precipitation, and the resulting regression equation was used to estimate annual population growth rates from 75 years of recorded climate data. All matrix algebra was done using Numeric Python, a module of the programming language Python that we use to manipulate matrices and to generate queries to a large demography database (Python version 2.0 available at www.python.org). The regression analyses were generated using SAS/STAT software (SAS 1999).

Results and Discussion

We followed the fates of 2,152 plants in Fillmore Canyon over the last 6 years. The number of individuals within each size class varied considerably throughout the 6 years (Table 1). Flowering plants produced 577 mature fruits in 1995, followed by 252, 16, 314, and 313 mature fruits during the years 1996–1999 respectively. On average, fruits collected outside of the plots in 1995 produced 130 seeds (95% confidence interval is 110–150 seeds, Strand 1997) and 141 seeds in 1999 (n = 10, s = 54). The seed germination rate was estimated at 1.4 percent (see Figure 3). Combined with direct counts of the number of seedlings recruited into the seed rain removal plots (9, 3.6, and 0.6 recruits in 1995–1997), the seed bank decay model estimated a 12.6 percent seed survival rate and initial seed bank size of 13,100 seeds ($R^2 = 0.82$, Strand 1997).

The mean spring precipitation over the last 75 years at the Jornada Experimental Range was 6.33 cm (CV = 64%). During this study, average rainfall (6.50 cm) was recorded in spring of 1998, below-average rainfall (2.06, 2.51, and 3.43 cm) in the spring of 2000, 1996, and 1999 respectively, and above-average rainfall (9.75 cm) in the spring of 1997. Also, 78 percent of recorded observations at the Jornada weather station are within the range of conditions experienced in the last 6 years (Figure 4). However, of the 14 spring rainfall events outside this range, 10 were more extreme, and these high rainfall years may be very important for plant demography (e.g., Bowers 1997).

Population growth rates calculated from annual transition matrices varied between 0.46 and 1.72 (Table 2). Both the mean and product matrices project a population growth rate of less than one, whereas the population growth rate calculated from the weighted mean matrix was 1.02, indicating a relatively stable population. However, increasing the frequency of below-average rainfall years occurring in the weighted mean matrix to 54 percent results in a population growth rate of 1.00. Therefore, a long series of years with below-average rainfall would likely increase the risk of extinction in this small population.

The regression equation (growth rate = 0.132 precipitation + 0.331) describing the relationship between population growth rate and spring precipitation was significant (p = 0.036, Figure 5), providing further support that this population is sensitive to changes in rainfall conditions. To provide a potential long-term demography data

Table 1. Vectors of the size class distributions for *Aquilegia chrysantha* from 1995 to 2000 at Fillmore Canyon. Seeds in the seed bank were estimated from a 12 percent survival of the seed bank plus the relative contributions of seeds produced by flowering plants in the preceding year.

Size Class	1995	1996	1997	1998	1999	2000
Seed bank	9645	10684	5474	952	5263	5790
Recruit	79	15	555	394	315	9
1 rosette	360	223	75	137	220	115
2 rosettes	149	79	77	79	66	56
3 rosettes	47	29	37	37	38	34
4 rosettes	26	8	23	26	20	18
5+ rosettes	19	2	22	21	42	21
Dormant	0	41	5	0	3	83

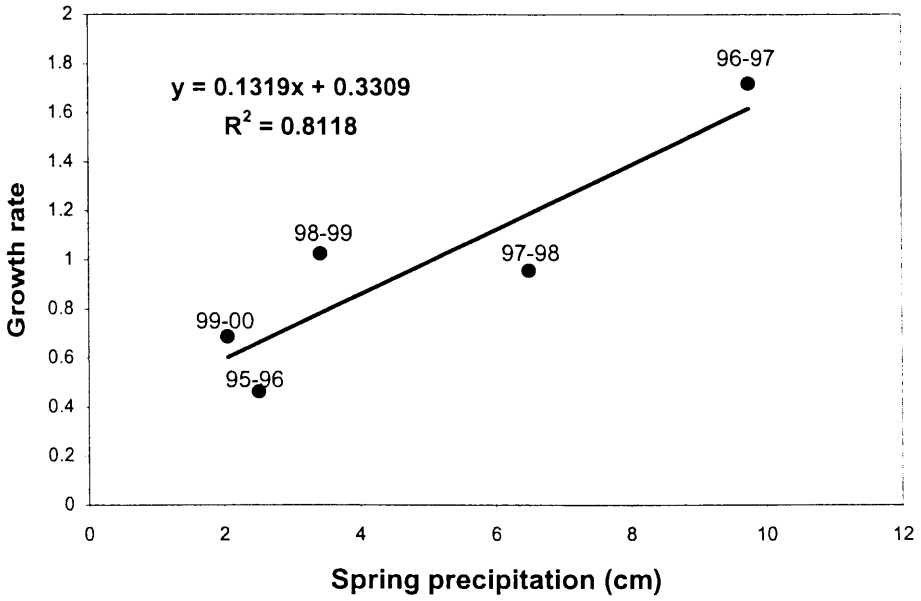

Figure 4. The relationship between spring precipitation and population growth rate at Fillmore Canyon.

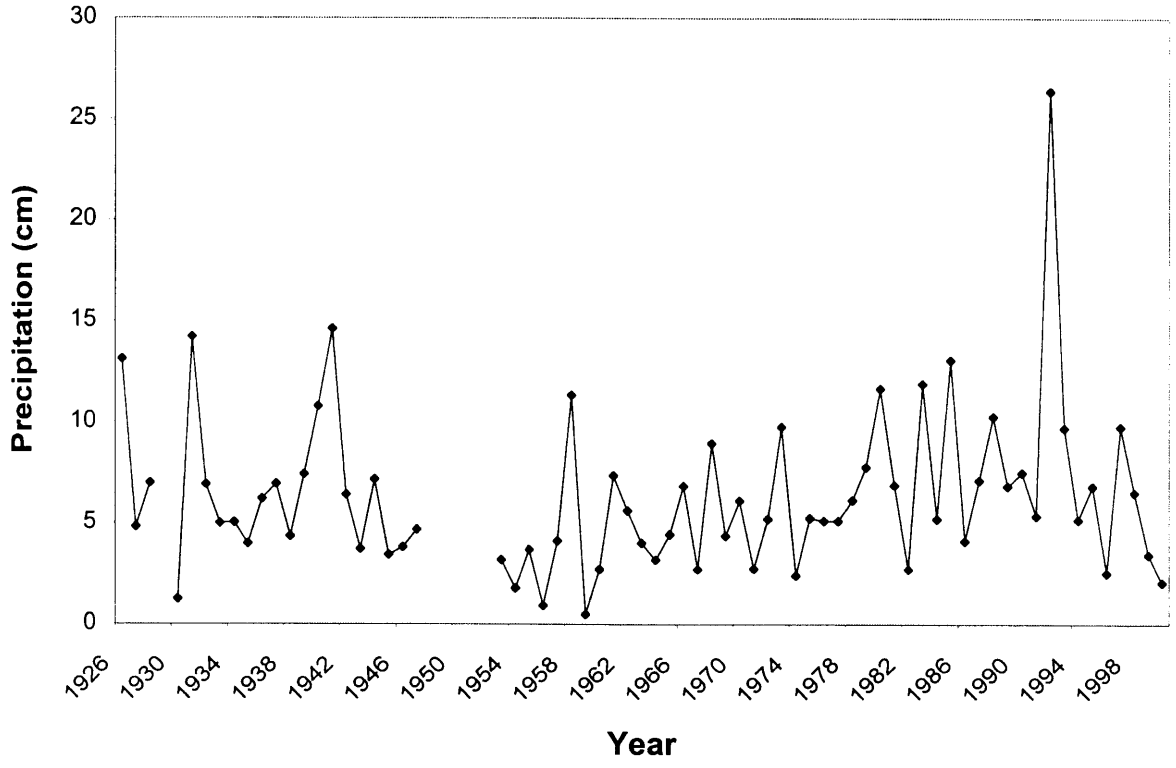

Figure 5. Spring precipitation (Dec-May) at the Jornada Experimental Range. The last six points on the graph represent the time span of the current study.

Table 2. Annual population growth rates for *Aquilegia chrysantha* from annual matrices, plus the growth rate calculated from the mean, weighted mean, and product matrix.

Transition matrix	Growth rate
1995–1996	0.464
1996–1997	1.720
1997–1998	0.957
1998–1999	1.025
1999–2000	0.688
Mean	0.963
Weighted mean	1.023
Product	0.541

set, we used the historical spring precipitation records and the regression equation above to estimate annual population growth rates at Fillmore Canyon since 1926. The distribution of these estimated growth rates is shown in Figure 6. The median growth rate of this 75-year period is 1.02 and the geometric and arithmetic means are 1.07 and 1.18 respectively, indicating a relatively stable to increasing population.

We also used the relationship between population growth rate and spring precipitation to check the effect on columbine population growth rate of weather forecasts predicting rainfall at 75 percent of normal in the Southwest for the next 30 years. As an initial approach, we multiplied the historical climate records by 0.75 and calculated new growth rates using the regression equation. The median growth rate of this new distribution is 0.85 and a geometric and arithmetic means are 0.89 and 0.96 respectively, indicating a declining population.

Finally, stochastic modeling of environmental variation typically involves calculation of annual transition matrices, which are assumed to occur independently, with equal probability, and to represent environmental conditions at a study site (Bierzychudek 1982, Menges 1990, Dammon and Cain 1998). Then, models of the distribution of population growth rates over a given time period or time to extinction (persistence times) are calculated by randomly sampling from the set of annual matrices. We plan to investigate the effects of assigning equal probability to annual matrices in typical stochastic models, and how unequal weighting of the matrices based on historical precipitation records would affect the outcome of persistence times. This approach was first used by

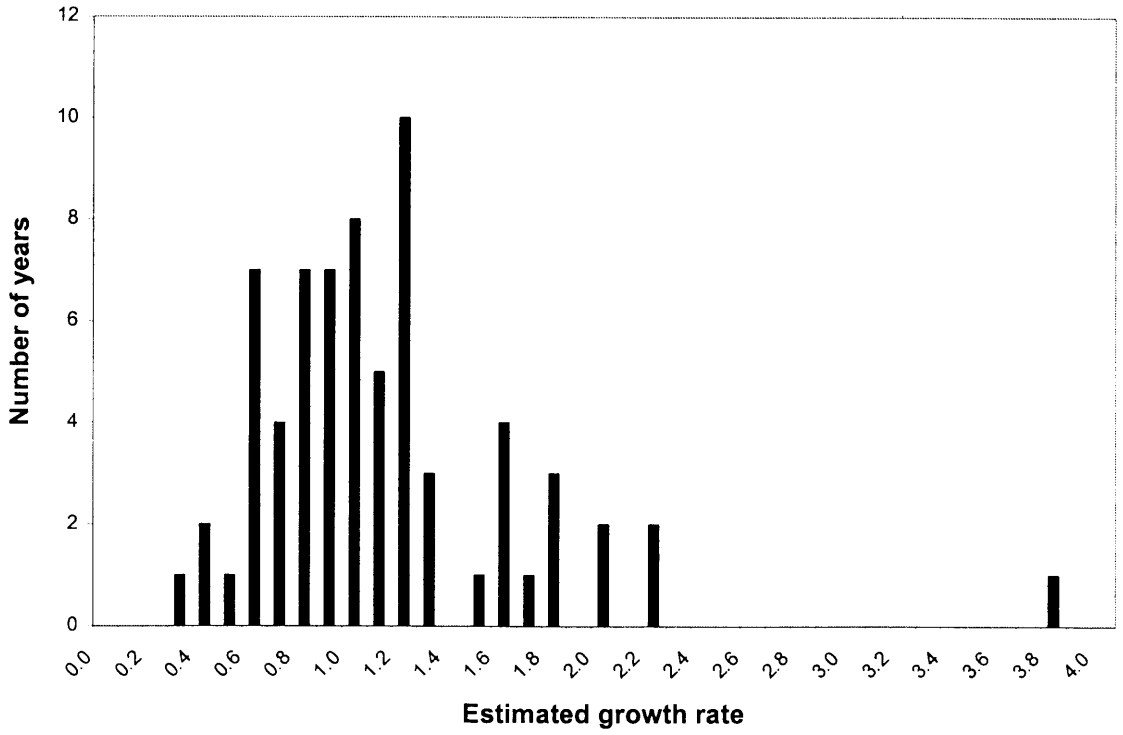

Figure 6. The distribution of annual population growth rates estimated at Fillmore Canyon since 1926. The median growth rate is 1.02 and the geometric mean is 1.07.

Aberg (1992), who modeled the stochastic growth rate of an intertidal seaweed based on frequencies taken from historical records of the amount of ice cover. These methods are particularly suited to plants in arid environments, where there is a correlation between the amount of rainfall and vital rates. Given a long-term record of precipitation and a few years of demographic data, the frequency of rainfall events can be used as the stochastic process to generate the sequence of matrices in a stochastic model.

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