Growth and Life-History Changes in Gunnison's Prairie Dogs after a Plague Epizootic

Author(s): Jack F. Cully, Jr.


Published by: American Society of Mammalogists


Accessed: 27/05/2011 12:18

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at [http://www.jstor.org/page/info/about/policies/terms.jsp](http://www.jstor.org/page/info/about/policies/terms.jsp). JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at [http://www.jstor.org/action/showPublisher?publisherCode=asm](http://www.jstor.org/action/showPublisher?publisherCode=asm).

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.
GROWTH AND LIFE-HISTORY CHANGES IN GUNNISON’S PRAIRIE DOGS AFTER A PLAGUE EPIZOOTIC

JACK F. CULLY, JR.

Kansas Cooperative Fish and Wildlife Research Unit, 204 Leasure Hall, Kansas State University, Manhattan, KS 66506-3501

I measured rates of growth of individual Gunnison’s prairie dogs (*Cynomys gunnisoni*) at three towns in the Moreno Valley, New Mexico; at an established prairie dog town (site 1) prior to a plague (*Yersinia pestis*) epizootic and at two towns reestablished after the epizootic (sites 2 and 3). Populations declined by >99% during the epizootic. After the epizootic, adults had greater mass, and juveniles grew faster than before. At sites 2 and 3, juveniles had high interyear survival (39%), whereas at site 1, prior to plague, survival of juveniles was 17%. At sites 2 and 3, yearlings bred, whereas they did not at site 1. Mean litter size near the end of lactation was 1.5 at site 1 and 5.0 at sites 2 and 3. Application of observed demographic parameters to Leslie-matrix analysis indicated that projected size of population was declining ($\lambda = 0.829$) at site 1 and was tripling annually ($\lambda = 2.905$) at sites 2 and 3. The difference in $\lambda$ was mostly due to increased survivorship of juveniles and reproduction at an earlier age in the new towns.

Key words: *Cynomys gunnisoni*, prairie dogs, life-history, demography, growth, Leslie matrix

Life-history traits vary among species and populations of ground squirrels (Armitage, 1981; Dobson, 1992; Dobson and Kjelgaard, 1985a, 1985b; Dobson and Murie, 1987; Dobson et al., 1986; Wiggett and Boag, 1993), prairie dogs (Garrett et al., 1982; Hoogland, 1995; Menkens and Anderson, 1989; Rayor, 1985), and marmots (Armitage and Downhower, 1974; Barash, 1989). Many authors believe that life-history attributes of a species vary with the variability of food resources, although other factors such as predation or disease may also contribute (Barnes, 1982; Connell, 1975; Hestbeck, 1986, 1987; Mihok et al., 1985; Nielson and Morris, 1964; Paine and Levin, 1981). Where populations vary due to unpredictable extrinsic factors, rate of growth per generation may vary greatly as constraints associated with limitations of food are periodically removed (Stearns, 1992).

A plague (*Yersinia pestis*) epizootic in Gunnison’s prairie dogs (*Cynomys gunnisoni*) occurred in the Moreno Valley in northcentral New Mexico during winter 1984 to summer 1986. The epizootic killed >99% of the prairie dogs (Cully, 1989, 1993). Formerly extensive colonies of prairie dogs were extirpated as the epizootic passed, leaving few survivors.

I compared changes in mass and individual rates of growth of Gunnison’s prairie dogs at an established colony at high population density prior to the plague epizootic with nearby, but newly established, colonies in the same or similar habitat following the epizootic. Although density of prairie dogs changed dramatically following the plague epizootic, this study was not designed to link density per se with the altered life-history parameters. Rather, the emphasis was on the link of rates of growth in body mass to changes in life-history characteristics (time to maturity, survivorship, fecundity). Although reductions in density are a possible cause for the increased growth reported below, other factors associated with climate, location, or social behavior may also be causal.
STUDY AREA

The study area was in the Moreno Valley, Colfax Co., New Mexico, in the Sangre de Cristo Mountains, 36°32'N, 105°16'W, at an elevation of 2,500–2,560 m. The grasslands cover an area ca. 5 by 20 km. The grasslands and shrub-grasslands on the sides and tops of ridges were preferred by Gunnison’s prairie dogs, and the three study areas occurred in this habitat. Wet meadows, where prairie dogs did not dig burrows, occur along permanent streams. The climate of the Moreno Valley is characterized by cold, dry winters and cool, relatively wet, summers. During this study, annual precipitation varied from 36 to 50 cm (weather records for Eagle Nest, NM). The annual mean temperature was 4.2°C. Mean monthly temperatures ranged from -5°C in January to 18°C in July.

At the beginning of the study in October 1984, prairie dogs were abundant in appropriate habitat in the Moreno Valley. In October 1984, prior to the onset of plague, I located the study area at site 1 within a large prairie dog colony in the middle section of the valley adjacent to Eagle Nest Lake, 5 km south of the town of Eagle Nest. Site 1 was surrounded by territories of other prairie dogs.

By 1984, a plague epizootic was underway among prairie dogs in the Moreno Valley. The epizootic moved from north to south between December 1984 and August 1987, killing >99% of the prairie dogs in the valley. During 1985, plague extirpated prairie dogs at my study site, site 1 (Cully, 1989, 1993).

When plague struck, individual surviving prairie dogs remained widely dispersed. In the following breeding season, however, they aggregated into new colonies. These new colonies initially were small and at low densities; and were surrounded by habitat available for expansion of colonies as the populations grew. In spring 1986, I discovered a small population in the northern one-third of the valley, 5 km north of site 1 and 2 km west of Eagle Nest and established a second study area (site 2) there in April 1986. I found a third colony and located another study area in the middle-third of the valley at the south entrance to Eagle Nest Lake (site 3), 2 km south of site 1 in spring 1987. All three study sites were grazed by cattle.

MATERIALS AND METHODS

I determined the schedule of emergence each winter by visiting the study areas at 2-week intervals, beginning in mid-February. I trapped prairie dogs at site 1 during October and November 1984 and from April to October 1985, at ca. 2-week intervals to measure body mass; Gunnison’s prairie dogs hibernated between November and March. At site 2, I trapped at ca. 2-week intervals from early April to late October 1986, and from May to October 1987. At site 3, I trapped similarly from May to October 1987.

In October 1984, I marked the study area at site 1 with wire flags set at 20-m intervals over a 4-ha area to serve as a guide during trapping. In autumn 1984, trapping was concentrated in a 1.5-ha area at the southeast corner of the grid. During 1985, prairie dogs on the marked grid and the adjacent 2 ha were trapped at site 1. At sites 2 and 3, 2-ha grids of stakes were placed in a rectangle, 100 by 200 m, at the center of the prairie dog distributions in summer 1987. Trapping effort was concentrated in the marked areas, but at both sites some animals were trapped off the marked grids.

I measured vegetation at sites 2 and 3 in June 1985, and at site 1 in November 1984 and June 1988, because vegetative differences between sites could contribute to differences in body mass. I quantified cover of foliage, categorized as grasses, shrubs, and other (mostly herbaceous perennials), with the line-intercept method (Canfield, 1941). At site 1, I measured cover along alternate 10-m segments of a 100-m tape laid perpendicular to the east edge of the study area, so that a distance of 50 m was measured along the line. Three parallel lines were measured for a total of 150 m in 1984, and one line was measured in 1988. At sites 2 and 3, I selected 15 grid-marker stakes by row and column number using a random-number generator. The selected stakes were the center points for 10-m sample lines set perpendicular to my direction of travel.

I trapped prairie dogs in single-door, folding, Tomahawk live traps (14 by 14 by 40 cm) baited with rolled oats, in order to mark and weigh individuals and to estimate the numbers present. As many as 50 traps were placed in groups of five or six around burrow clusters. During a trap session of 3–5 days, the traps were moved among burrow clusters when unmarked individuals no longer entered traps. Prairie dogs were
weighed to the nearest 1.0 g, marked by toe clipping or with an aluminum fingerling tag in the ear that was uniquely numbered. They were identified to sex and age class. The classes were juvenile, yearling (if known), and adult (juvenile <8 months, yearling 8–20 months, and adult >8 months, unless I knew they were yearlings). Newly emerged juvenile prairie dogs were distinguished by gray pelage and were small (<400 g at first capture). By late July they had molted and their coats had adult color. Prairie dogs also were individually marked on their fur with commercial hair dye and released at the point of capture. Traps were baited early in the morning, usually within 1 h after the first animals emerged from burrows, and checked frequently during the day. I weighed 69 adult males 129 times, 106 adult females 224 times, 121 juvenile males 218 times, and 108 juvenile females 188 times at the three sites. Based on visual observations of dye marks on animals within the marked study areas, it appeared that I caught and marked ≥90% of the prairie dogs resident on the grids. Population density at the three study sites was estimated as the total number of animals caught or counted at one time on marked grids (Krebs, 1966), divided by size of the area trapped. Because animals may have moved from surrounding clans to enter traps, it is possible that densities at site 1 were inflated by neighboring animals entering traps. I believe the size of the area trapped at site 1 during 1995 (6 ha) was large enough to minimize that bias. In 1994, when only 1.5 ha were trapped, edge effects could have been a small factor. I watched the marked prairie dogs fairly closely, however, and rarely saw marked animals more than a few meters beyond the areas trapped. At site 2, the highest density was recorded from visual counts, so trap bias was not a factor. I calculated individual growth rates of juveniles to determine if they could explain either changes in time to maturity or in survivorship. Growth rates are the difference in body mass from first capture to last capture in a year, divided by the number of days between captures. I calculated growth rates only when the time between first and last capture was ≥10 days. I calculated growth rates of individuals were compared between areas with analysis of variance (ANOVA). To further assess growth rates within populations, mass was regressed against number of days after emergence for each group. Because some animals had multiple captures, I calculated mean body mass and mean time since emergence for each individual. Differences between populations in rate of growth were tested by comparing regression slopes from the three sites. The ANOVA of individual growth rates provides an additional test of the significance of the differences in growth rate. Emergence dates varied among years and occurred over a 2–3 week period within years. In years when emergence was late, comparison of body mass using calendar dates biases the data such that late-emerging animals will have less mass on a given calendar date than animals that have had a longer
period to forage because they emerged earlier. Mean date of emergence was estimated as about the mid-point between the first and last known emergence. Although individual dates of emergence varied within years by as much as 3 weeks, using time since the mean date of emergence during a given year reduced the interyear bias. Comparisons of growth rate per se, estimated by the slope of the regression, were not affected by variance in date of emergence. The intercept, which estimates mass at emergence, is affected by that variance.

Differences in mass may explain differences in survivorship or fecundity. For each sex-age class, I compared body mass among sites by standardizing each mass to the time since the mean date of emergence (120 day for adults, 60 days for juveniles). Daily growth for the size age-class at a site (e.g., 3.08 g/day for adult males at site 2) was used to standardize mass. I then calculated the mean standardized mass for each individual. Mean masses of individuals were then compared among sites so that each animal was represented one time in the ANOVA. Because mass of adult females did not show significant change in mass with time since mean emergence, masses of adult females were not standardized. Data from sites 2 and 3 were pooled for these analyses because both represent post-plague towns and because samples were small at site 3.

Leslie-matrix analysis was used to identify the importance of the different demographic parameters for population growth (Caswell, 1989). Extrapolating rates of population growth from a Leslie matrix requires assumptions that the estimates of survival and fecundity are correlated with age, population growth is density independent over the length of the projection (1 year in this case), and that the population is at a stable age distribution (Caswell, 1989). The first two assumptions were probably adequately met by these populations, but there were no data from this study on age structure. However, following plague epizootics it is unlikely that the populations were at a stable age distribution. Data for the life table were based on females only. I assumed for these analyses that annual survivorship of adults (set at 0.5, based on the limited data from site 2) was similar among sites in the Moreno Valley. The analyses treat emigration as death. Successful emigration among yearlings could cause significant increases in $\lambda$, the rate of population growth. If survivorship is higher for heavier prairie dogs, as it is for juveniles and has been reported for juvenile (but not adult) Columbian ground squirrels (Spermophilus columbianus—Murie and Boag, 1984), the calculated differences in $\lambda$ among sites may be too low.

I used the values of fecundity and survivorship derived from the three sites as presented below. The rate of population growth, $\lambda$, is estimated as the dominant eigenvalue of the Leslie matrix (Caswell, 1989). Mathcad 3.1 for Windows (Mathsoft, 1992) was used to calculate $\lambda$. The relative sensitivity of population growth to changes in age-specific survival and fecundity were calculated as elasticity (Caswell, 1989; Stearns, 1992). Elasticity, $e_{ij} = \frac{\partial \log \text{X}}{\partial \log a_{ij}}$, "gives the proportional change in $\lambda$ resulting from a proportional change in $a_{ij}$" (Caswell, 1989: 132). See Caswell (1989) for details of calculation.

RESULTS

Vegetation varied from site to site (Fig. 1). Grass cover was higher early in the growing season at sites 3 and 1 in June 1988 than it was at the end of the growing season at site 1 in November 1984. Shrub cover was higher at site 1 in 1984 (23%) and 1988 (22%) than at sites 3 (10%) or 2 (9%) in 1988. Grass cover was higher at both site 1 (29 and 45% in 1984 and 1988) and 3 (52%) than at site 2 (23%), but other vegetation was more abundant at site 2 (7%) than at the other two sites (4% each). The most impressive difference in grass cover was between years at site 1, with an increase from 29 to 45%.

Most adults emerged during March in 1985 and 1986, so I used a mean date of emergence of 15 March for the regression analyses used to calculate growth rates for those years. In 1987, heavy snow cover persisted until April and resulted in most prairie dogs not emerging until ca. 15 April, the date used to estimate mean emergence for that year.

Mean date of emergence for juveniles at site 1 was ca. 15 June 1985. Given the similarity of weather in spring 1984, I assumed
that natal emergence occurred at the same time in 1984. At site 2 in 1986, all juveniles emerged 1–15 June, so the mean date of emergence was ca. 8 June 1986. At both sites 2 and 3 in 1987, juveniles emerged 15 June–8 July, so I used a mean date of emergence of 25 June.

Individual gain in weight among adult males with multiple captures was greater at sites 2 and 3 (3.08 g/day, n = 11) than at site 1 (1.42 g/day, n = 19, F = 6.02, P < 0.05). Regression of body mass against time since mean emergence was significant for both site 1 and sites 2 and 3 pooled (Table 1). Mass of males was standardized to 120 days time since mean emergence. It differed between site 1 (745 g, n = 54) and the other two sites, site 2 (1,003 g, n = 13) and site 3 (1,160 g, n = 2), pooled (F = 17.0, d.f. = 1,67, P < 0.001).

Individual growth rates of adult females were −0.21 g/day at site 1 (n = 26) and 1.28 g/day at sites 2 and 3 pooled (n = 33), but they did not differ significantly (F = 3.39). The regression slopes for adult females were not significantly different from zero (Table 1). Mean mass of adult females differed between site 1 (606 g, n = 67) and the pooled masses at sites 2 (699 g, n = 35) and 3 (672 g, n = 4; F = 29.6, d.f. = 1,104, P < 0.001). Variance in mass of females during the course of the reproductive cycle (increase during pregnancy, decrease during lactation, and increase again leading to emergence) makes linear regression of mass of adult females against time since mean emergence of questionable value.

Masses of juvenile males and females at all three sites were similar within 10 days of mean date of emergence (F = 3.08, d.f. = 1,65, 0.10 > P > 0.05). At site 1, 12 juveniles weighed 116–198 g. At site 2 in 1986, at first capture 15–18 June 1986, mass of 16 young ranged from 148 to 330 g. Juveniles caught at site 3 (n = 11) weighed 124–260 g. Emergence of juveniles at site 2 was later and less synchronized in 1987, when mass of 28 juveniles on first capture was 100–373 g between 30 June and 5 July.

The regression of mass against time since mean emergence did not indicate that ju-
TABLE 1.—Regression of mean body mass of individual Gunnison’s prairie dogs against individual mean time since emergence from natal burrows (juveniles) or hibernation burrows (adults) at sites 1 or 2 and 3 pooled in the Moreno Valley, New Mexico. See text for emergence dates. The intercept estimates the emergence weight, and the slope describes daily gain of mass in grams.

<table>
<thead>
<tr>
<th>Age and sex class</th>
<th>Intercept</th>
<th>Slope</th>
<th>$R^2$</th>
<th>n</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Juvenile males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 1</td>
<td>199</td>
<td>2.7</td>
<td>0.86</td>
<td>42</td>
<td>507.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sites 2 and 3</td>
<td>165</td>
<td>6.6</td>
<td>0.89</td>
<td>79</td>
<td>656.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Test for equal slopes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>507.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Juvenile females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 1</td>
<td>246</td>
<td>2.0</td>
<td>0.60</td>
<td>31</td>
<td>46.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sites 2 and 3</td>
<td>185</td>
<td>4.9</td>
<td>0.78</td>
<td>77</td>
<td>265.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Test for equal slopes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>97.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Adult males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 1</td>
<td>572</td>
<td>1.4</td>
<td>0.45</td>
<td>54</td>
<td>42.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sites 2 and 3</td>
<td>802</td>
<td>1.5</td>
<td>0.54</td>
<td>13</td>
<td>12.7</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td>Test for equal slopes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.2</td>
<td>ns</td>
</tr>
<tr>
<td><strong>Adult females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 1</td>
<td>565</td>
<td>0.0</td>
<td>0.67</td>
<td>67</td>
<td>3.9</td>
<td>ns</td>
</tr>
<tr>
<td>Sites 2 and 3</td>
<td>654</td>
<td>0.0</td>
<td>0.39</td>
<td>39</td>
<td>3.9</td>
<td>ns</td>
</tr>
</tbody>
</table>

Juvenile males grew significantly faster than juvenile females (Table 1). However, for those animals with multiple captures, males grew faster (6.3 g/day, $n = 35$) than females (5.3 g/day, $n = 40$) at sites 2 and 3 pooled ($F = 4.99$, $d.f. = 1.73$, $P < 0.05$). At site 1, growth did not differ between sexes. Growth rates of juveniles were significantly faster at sites 2 and 3 than at site 1 for both males ($F = 4.23$, $d.f. = 1.42$, $P < 0.05$) and females ($F = 3.78$, $d.f. = 1.45$, $P < 0.05$). At site 1 in October, mass of juvenile males averaged 63% of the mass of adult males, and juvenile females averaged 66% of the mass of adult females. At site 2 in October, mass of juvenile males was 81% of mass of adult males at their last capture before emergence. Juvenile females at site 2 in October had 95% of the mass of adult females prior to hibernation in September.

Reproductive output for males is not known. At site 2, the young-of-the-year had attained mass of adults, so age of females that were present in April 1986 could not be determined on the basis of body mass. All females there became pregnant and raised litters, as did all females at site 3. Litter size, at emergence from the natal burrows, at site 2 averaged 5.1 young per female in 1986 ($n = 6$ females), and 5.0 at both sites 2 ($n = 11$ females) and 3 ($n = 2$ females) in 1987. At site 1 in 1985, 24 adult females were present at the 4-ha core where I trapped most extensively. Of those females, 11 had enlarged nipples in late May and early June, indicating reproductive status; the remaining 13 appeared to be nonreproductive. Thirty-five young emerged in 1985. Mean reproductive rate was 1.5 young/female, or 3.7/reproductive female, at site 1.

At site 2 in 1987, 16 of 27 adult females captured had been marked in 1986. Of these 16, 10 were yearlings, and all reproduced. In 1985 at site 1, none of the four surviving females that I identified as juveniles in 1984 bred in 1985; furthermore, none of the six small females (<550 g) without previous capture records, that were tentatively identified as yearlings in 1985, were pregnant. Whereas all the known yearlings at site 2 bred, few or none did at site 1.

Survivorship of juveniles was higher at sites 2 and 3 than at site 1 ($\chi^2 = 5.5$, $P =$
TABLE 2.—Populations of Gunnison’s prairie dogs at sites 1 and 2 during and after the plague epizootic in the Moreno Valley, New Mexico. The number of prairie dogs includes adults and juveniles. Size refers to the size of the area trapped.

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Size (ha)</th>
<th>Number/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 1</td>
<td>October 1984</td>
<td>1.5</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>July 1985</td>
<td>6.0</td>
<td>137</td>
</tr>
<tr>
<td>Site 2</td>
<td>April 1986</td>
<td>2.0</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>October 1986</td>
<td>4.0</td>
<td>75</td>
</tr>
<tr>
<td></td>
<td>July 1987</td>
<td>3.0</td>
<td>117</td>
</tr>
<tr>
<td></td>
<td>July 1988</td>
<td>2.0</td>
<td>180</td>
</tr>
<tr>
<td></td>
<td>September 1988</td>
<td>2.0</td>
<td>0</td>
</tr>
</tbody>
</table>

0.019, d.f. = 1). During spring 1985, I recovered six of 35 prairie dogs marked as juveniles at site 1 in 1984, for a survival (minus emigration) rate of 17%. I marked 54 juveniles at site 2 in 1986, and recaptured or identified the dye marks on 22 in 1987, for a survival rate (minus emigration) of 39%. Two of five adult males (40%) and six of 12 adult females (50%) marked at site 2 in 1986 were still present in 1987. During April and May 1987, I either captured or identified by their dye marks 32 prairie dogs at the eastern one-half of that town; eight of these were immigrants. I counted ≥15 additional prairie dogs on the western one-half. Assuming that 75% of those were marked in 1986, survivorship of individuals at the town was 48% (36 of 75). Thirteen adult prairie dogs captured at site 2 in 1987 were unmarked immigrants.

Sites 2 and 3 were established by small local populations that initially were surrounded by unoccupied habitat (Table 2). When it was established in April 1986, site 2 consisted of 17 prairie dogs on an area of ca. 2 ha (9/ha). When prairie dogs entered hibernation in October, the population occupied ca. 4 ha. In July, after the juveniles emerged from their natal burrows, six of 10 adult females and two of four adult males moved to the periphery of the town, leaving the juveniles with the original burrows. In September, territorial calling was accompanied by additional expansion as males moved to the edges of the town. In spring 1987, there was again territorial calling among males, which was accompanied by further expansion of the colony. By the end of the 1987 breeding season, the colony had expanded to an area of ca. 8 ha. After natal emergence in June 1988, the colony covered ca. 15 ha. During July–September, the population at site 2 crashed to 0 at the grid. Plague-positive fleas were collected from burrows in September, indicating that a second plague epizootic was responsible.

Rates of age-specific survivorship and fecundity differed between site 1 and site 2 (Table 3). Yearlings bred at site 2, but did not at site 1. Survival over the 1st winter was higher at site 2, as was fecundity. The total captures pooled for all three areas indicated a 1:1 sex ratio for juveniles ($\chi^2 = 2.06, P > 0.05$), but a biased sex ratio for adults ($\chi^2 = 4.06, P < 0.05, d.f. = 1$), with females outnumbering males 3:2. I assumed that survivorship of adults (set at 0.5, based on the limited data from site 2) was similar between sites. The Leslie-matrix analysis for site 1 yielded $\lambda = 0.829$; at site 2, $\lambda =$
FIG. 2.—Elasticities of entries in the life table of Gunnison’s prairie dog in, a) the growing population at sites 2 and 3, and b) the declining population at site 1. Elasticities describe the proportional change in λ with a proportional change in cell a_0j of the Leslie matrix. The circles in the life-cycle graph (Caswell, 1989) represent age classes. Arrows between circles represent the transitions between ages. Arrows between age classes and age 0 represent reproduction. The numbers next to arrows are elasticities, which sum to 1.0 in each graph. Large values for elasticity indicate that changes in those cells, e.g., fecundity of yearlings in graph a or first-year survivorship in graph b, will have the largest effects on λ.

In the sensitivity analyses, the most important factors accounting for the differences in λ, were age at first reproduction, and survivorship over 1st winter at sites 2 and 3, and annual survival to age 3 at site 1 (Fig. 2).

**DISCUSSION**

Life history characteristics of Gunnison’s prairie dogs in the Moreno Valley changed among colonies living in similar habitats following population changes attributable to plague. Individual growth of juveniles was faster at the post-plague colonies, with the result that juveniles there entered hibernation at higher body mass. The higher body mass of hibernating juveniles resulted in enhanced survivorship. In addition, presumably because of the larger size, yearling prairie dogs bred at the post-plague sites,
whereas they did not at the pre-plague site. Finally, fecundity of females was higher at the post-plague sites. The result of these differences was that $\lambda$, the projected population growth rate, at the post-plague sites was $>3 \times$ as great as at the pre-plague site. Observations on population change at sites 1 and 2 were similar to the rates of growth calculated by the analyses of life tables.

Is it possible that plague could have been responsible for 13 females (out of 24) at site 1 not producing litters? I do not believe plague was a factor, because the 11 females identified as reproductive were identified on the basis of enlarged nipples, whereas the others had small nipples, and therefore were assumed to be nonreproductive in 1985. Also, because plague is so highly virulent and transmission so effective (Cully, 1989, 1993), it is unlikely that there would be any survivors in family groups that acquired plague.

The changes in life history occurred in the absence of striking differences in the composition of vegetation or in weather. All four sex-age classes attained greater body mass at the post-plague sites than at the pre-plague site. There were differences in vegetation among the three colonies, but the variation did not correspond to individual rates of growth at the colonies. Grass cover and total plant cover were similar at sites 1 (1984) and 2 (1988), but higher at sites 1 and 3 in 1988, whereas body mass and growth differed greatly between those sites. Growth of juveniles and body mass of adults were higher at site 2 (low cover) and 3 (high cover) than they were at site 1 (low cover). Thus, plant cover per se did not account for differences in growth of juveniles and mass of adults.

Other attributes of the vegetation, which were not measured, may have correlated with growth of prairie dogs. For example, with reduced exploitation the most nutritious species of plants may have had more abundant palatable tissue, which would lead to faster growth later into the season. There was an increase in grass cover at site 1 from 1984 to 1988. This increase indicates that grass was not harvested as intensely following the plague as before, and therefore that a larger quantity of nutritious forage should have been present. Grass cover was similar at sites 3 and 1 in 1988. Grass cover was lower at site 2, but I do not know if it changed from before the plague.

In other studies of Gunnison's prairie dogs (Rayor, 1985) and black-tailed prairie dogs (Cynomys ludovicianus—Garrett et al., 1982), growth rates of juveniles varied with the availability or quality of forage. In Colorado, Rayor (1985) found the average growth rate of juvenile males was 6.7 g/day and that of juvenile females was 5.4 g/day at one site, a rate slightly higher than I found at site 1. At another, higher-quality site, Rayor (1985) reported growth rates for juvenile males of 8.2 g/day and for juvenile females of 7.1 g/day, compared to 6.3 g/day for males and 5.3 g/day for females at my sites 2 and 3.

Mean size of litters at emergence from natal burrows of female Gunnison's prairie dog in central Colorado were 5.3 young (at Blue Mesa) and 6.6 young (at Quartz Creek). At the former site, 32 of 93 females weaned litters, and at the latter site 8 of 15 females weaned litters (Rayor, 1985). Thus, reproduction per female was 1.8 and 3.5, respectively. These figures are comparable to those at site 1 (1.5 young/female) in the Moreno Valley, but are lower than those at sites 2 and 3 (5.0 young/female).

Age at first reproduction decreased and fecundity rates increased in the Moreno Valley following plague. Black-tailed prairie dogs usually reproduce first at the end of their 2nd year (Hoogland, 1995). C. gunnisoni in Colorado (Rayor, 1985), and C. ludovicianus (Garrett et al., 1982) show increases in fecundity with increased growth rates. Black-tailed prairie dogs at a new colony also recruit younger animals into the reproductive population. This was presumably because fresh habitat at the edge of the colony provided unlimited food, which contributed to faster growth.
Published data are not available on survivorship of adult *C. gunnisoni*, exclusive of the effects of plague. Among white-tailed prairie dogs, annual survivorship of adults varies from 0.09 to 0.70 among males, and 0.20–0.63 among females (Menkens and Anderson, 1989). Among black-tailed prairie dogs, survivorship of adults follows a curvilinear pattern, with the highest value in year 2, followed by slow declines (Hoogland, 1995). Hoogland (1995) found higher survivorship in black-tailed prairie dogs than I observed in this study, with the highest value being 0.69 for 2-year-old females.

Life-history patterns in ground squirrels are plastic (Armitage, 1981; Dobson, 1992; Dobson and Kjelgaard, 1985a, 1985b; Dobson and Murie, 1987; Menkens and Anderson, 1989; Rayor, 1985; Zammuto, 1987; Zammuto and Millar, 1985; Zammuto and Sherman, 1986). In an experiment where food supplements were provided to Columbian ground squirrels, growth and survivorship of juveniles increased, but survivorship of adults was unchanged (Dobson and Kjelgaard, 1985a, 1985b). Among adults, the extra energy was believed to be allocated to increased reproduction (Dobson et al., 1986). Similar patterns are reported for black-tailed, white-tailed (*Cynomys leucurus*), and Gunnison’s prairie dogs, where the availability of resources probably varied as well (Garrett et al., 1982; Menkens and Anderson, 1989; Rayor, 1985).

The colonies of *C. gunnisoni* that I observed immediately after their establishment at site 2 in 1986 and at site 3 in 1987 were small and at lower population density than site 1 was in 1984. However, after 2 years of population growth the density at site 2, after emergence of juveniles in 1987, was higher (39/ha) than at site 1 in 1984 (29/ha) or 1985 (23/ha). The population density at site 2 increased to 90/ha after emergence of juveniles in July 1988. At that time, however, another plague epizootic ensued and the population crashed.

Analysis of life tables illustrates the importance of individual life-history traits to *λ*, the rate of population growth. Using the parameters for site 1 (Table 3), *λ* = 0.829, while the parameters at site 2 yield *λ* = 2.905. The estimates of *λ* from the life-table analyses are similar to the changes in population density that were observed after emergence of juveniles at site 1 and site 2 (Table 2). At site 2, the area of the colony was expanding at the same time that density was increasing, so the total population was growing faster than the density figures alone suggest. In the most thorough study to date of black-tailed prairie dogs, Hoogland (1995) calculated the reproductive output (*R₀*) of males and females in the population over 15 years. Among females, *R₀* = 1.847, and among males, *R₀* = 2.148. Using Hoogland’s (1995) values a stable population will have *R₀* = 2.0 (Hoogland calculated *R₀* based on the numbers of offspring of both sexes because the sex ratio of juveniles was not 1:1 as it was in my study).

The life-history parameters of Gunnison’s prairie dogs do not affect *λ* equally. Elasticities (Fig. 2) indicate the relative importance to *λ* of changes in specific attributes of the life table. Elasticities are dependent on the values of all cells in the Leslie matrix, and so are different between the growing populations at sites 2 and 3 and the declining population at site 1. At the growing populations, reproduction of yearlings has the highest value, meaning that changes in reproduction of yearlings will have the greatest effect on *λ*. In the declining population, survivorship values to age 3 years have the highest elasticities. Because yearling females at site 1 did not breed, elasticity cannot be calculated for that cell. However, if yearling females there did breed, even using the conservative value for reproduction seen among adults at site 1, *λ* would increase by 248% to 2.052. In terms of impact on projected growth rate, this is much greater than the change attributed to increased fecundity among adults or increased survivorship of adults. These re-
results match theoretical expectations (Stearns, 1992) that $\lambda$ is most sensitive to age at first reproduction in growing populations, whereas increased survivorship of adults is most important in more stable populations. If survivorship of adults during years 2–5 were raised to 0.8 in the Leslie matrix, a higher value than has been reported for prairie dogs, $\lambda$ would only increase to 0.977.

Given that greater body mass at the beginning of hibernation resulted in higher survivorship of juveniles, higher fecundity, and faster attainment of reproductive maturity, it is clear that the differences in growth rate of populations resulted from differences in the ability of juveniles to grow rapidly during their 1st year. The increase in growth rate of juvenile prairie dogs at sites 2 and 3 had pronounced effects on life-history parameters that, in combination, resulted in more than tripling the population growth rate.

ACKNOWLEDGMENTS

I thank the landowners of the Moreno Valley on whose land this work took place. I am particularly indebted to the late W. Gallagher and his family for allowing prairie dogs to persist on their ranch and for providing me with a place to live in the Moreno Valley and to Mr. and Mrs. L. Davis for giving me permission to work on their C/S Ranch adjacent to Eagle Nest Lake. F. S. Dobson, J. L. Hoogland, P. S. Gipson, J. O. Murie, L. S. Rayor, and an anonymous reviewer made many helpful suggestions on an earlier manuscript, and I thank them for their help. M. Hohman assisted with field work. Funding for this work was provided by the New Mexico Department of Game and Fish. I am indebted to J. P. Hubbard, G. L. Graham, and the New Mexico Share With Wildlife Committee.

LITERATURE CITED


Associate Editor was Barbara H. Blake.