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Population Viability Analysis of the Utah Prairie Dog



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Introduction

Utah prairie dogs (*Cynomys parvidens*) are sciuromorph rodents endemic to semi-arid grasslands in southwestern Utah. An estimated 95,000 individuals existed in 1920 (McDonald 1993). By the 1960s, however, the species' numbers had been severely reduced by anthropogenic habitat changes, poisoning, plague and drought (USFWS 1991). Populations were restricted to a fraction of the species' former range (Fig. 1). Collier and Spillett (1975) identified poisoning, combined with climatic and vegetational conditions, as responsible for reducing the area inhabited by Utah prairie dogs from approximately 92,000 acres (37,232 ha) in 1920 to a mere 2,400 acres (971 ha) in 1971. In an attempt to forestall imminent extinction, the species was listed as Endangered under the U.S. Endangered Species Act in June 1973. Numbers increased following protection, particularly on private lands (Fig. 2), and the Utah prairie dog was downlisted to Threatened status in May 1984.

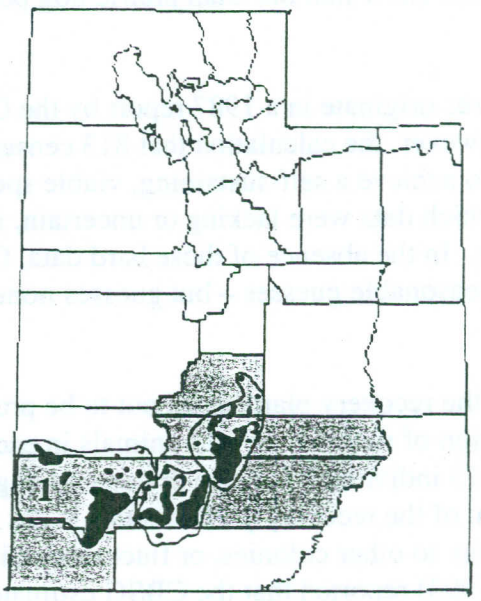


Figure 1. Present distribution (solid black) and past occurrence (outlined) of Utah prairie dogs. 1 = West Desert; 2 = Paunsaugunt; 3 = Awapa Plateau. Shaded counties have significant presence of Utah prairie dogs (derived from maps in Messmer et al. 1998 and NPWRC 2000).

A long-term recovery plan, aimed at securing the future of the Utah prairie dog, was formally adopted by the U.S. Fish and Wildlife Service in 1991 (USFWS 1991). The general goal of the Utah prairie dog recovery plan is the maintenance of the species as a "self-sustaining, viable unit" with retention of genetic diversity. Based on the 1987 recommendations of the World Conservation Union's Captive Breeding Specialist Group (currently Conservation Breeding Specialist group, CBSG), the concrete objectives are to retain 90 percent of the genetic diversity of the species for 200 years. To achieve this, the recovery plan sets the specific target of establishing and maintaining one population each on public lands in the West Desert, Paunsaugunt Area and Awapa Plateau of Utah, each with a minimum of 813 adults in the annual spring census, with animals transferred between populations for gene exchange and managed intensively.

Because of conflicts between prairie dogs and agriculturists and land developers, the U.S. Fish and Wildlife Service has attempted to establish new Utah prairie dog populations by transplantation onto public lands within the historical range of the species, where they may be managed more easily without regard to private landowners' demands. Considerable expense and effort has been invested in these transplantations. The majority of Utah prairie dogs remain on private lands, however (Fig. 3). In all three recovery areas (Awapa, Paunsaugunt and West Desert), most increases in prairie dog numbers during the past twenty years have occurred on private, not public lands (Fig. 4). Recent Spring census results show that the Utah prairie dog population continues to fluctuate over time.

Recovery plan target figures originate in a 1987 report by the Captive Breeding Specialist Group (CBSG 1987). However, the calculation that 813 censused adults in three populations are required to achieve a self-sustaining, viable species is sensitive to a number of variables for which data were lacking or uncertain, including the ratio of breeding males to females. In the absence of those hard data, CBSG workshop participants had to make reasonable guesses – but guesses nonetheless – about the value of many variables.

Moreover, key aspects of the recovery plan turned out to be problematic. Left unanswered was the question of whether the 813 animals in each recovery area should be located in one colony of 813 individuals, or else divided amongst several smaller colonies. Another criticism of the recovery plan was that it did not take into consideration the proximity of each colony to other colonies, or fluctuations in local numbers (O'Neill et al. 1999). McDonald (1993) reported that the CBSG estimate seems to assume, unrealistically, that all animals are connected and interbreeding. Although the existing recovery plan did speculate that Utah prairie dogs might persist as a viable metapopulation (in which local populations could go extinct but be recolonized from other areas), the analysis on which its targets were based did not incorporate metapopulation dynamics into its calculations of minimum population size (UPDRIT 1997). Ritchie (1995; cited in O'Neill et al. 1999) called for a revision of the recovery goals to incorporate metapopulation theory as it relates to Utah prairie dog population dynamics.

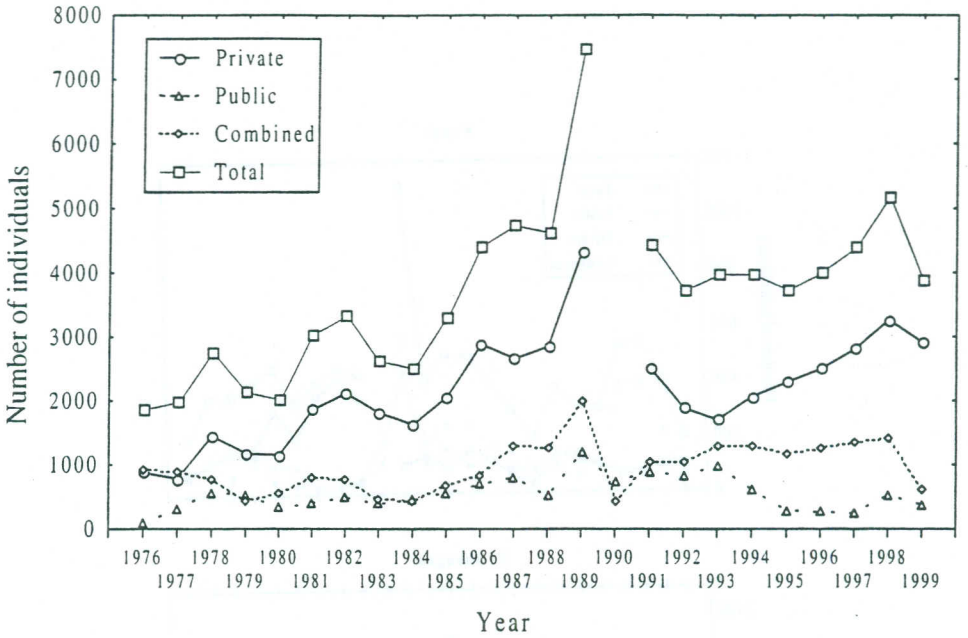


Figure 2. Numbers of Utah prairie dogs counted in Spring censuses from 1976 to 1999, categorized by current ownership of land on which their complexes are found. There was no Spring census on private land in 1990. Complexes on combined-ownership land have some of their constituent colonies on private land and some on public land.

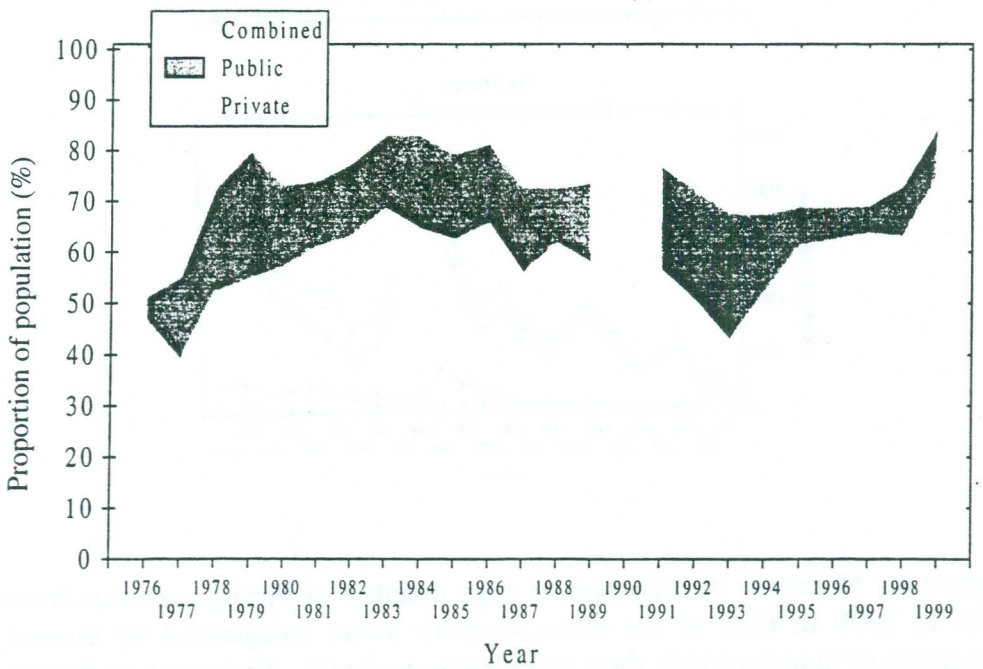


Figure 3. Proportion of Utah prairie dog population on public, private and combined-ownership land from 1976 to 1999.

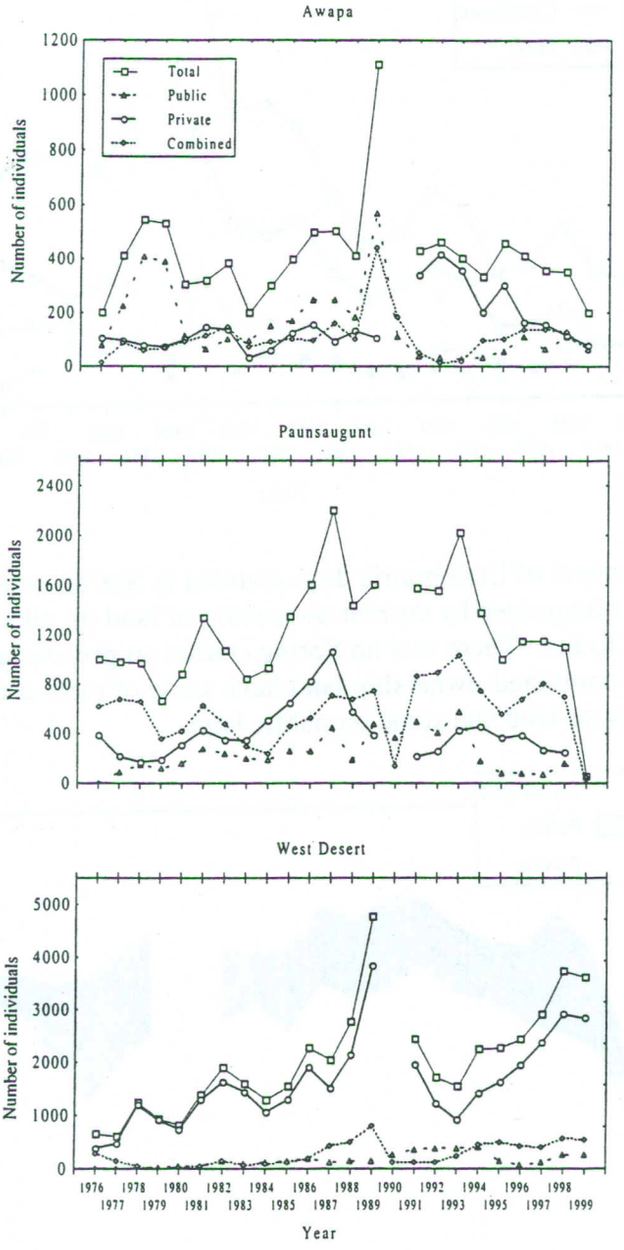


Figure 4. Numbers of Utah prairie dogs counted in Spring censuses from 1976 to 1999 in each of the three recovery areas, categorized by current ownership of land on which their complexes are found. There was no Spring census on private land in 1990.

To address these concerns, we have conducted a population viability analysis (PVA) for the Utah prairie dog. In broad terms, PVAs forecast the fate of a given population and allow one to contrast the relative merit of a portfolio of possible management alternatives (Boyce 1992; Possingham et al. 1993). Using available information on the demography and population structure of the Utah prairie dog, we assess the interaction between stochasticity, habitat destruction, catastrophes, and natural recolonization by dispersing individuals. We also carry out a separate set of simulations to evaluate the CBSG's recommendation of achieving a minimum population size of 813 individuals in order to retain 90 percent of the genetic diversity of the species for 200 years. Finally, we point to possible directions for future research.

Definitions

Throughout this report we follow the spatial definitions of Utah prairie dog groupings given in USFWS (1991; p. vii):

"Colonies are groups of animals with associated mounds, burrows, and food resources that are within calling distance. ...

Complexes are groups of colonies that are within 2 miles (3.2 kilometers) of each other, not separated by geographical barriers, ...

Populations are groups of complexes within a geographic area that are not separated by geographical barriers but are generally separated by distances greater than 2 miles (3.2 kilometers)."

The Utah Division of Wildlife Resources provided us with numerical and letter designations for individual complexes and colonies, respectively. We focus our analyses on individual colonies thus assigned.

Methods

Maintenance of Genetic Diversity

There is currently no clear indication of what population size would be required to preserve biologically meaningful genetic variability in Utah prairie dogs. Existing data suggest that genetic variability in this species is extremely low, with an electrophoresis study that examined 32 gene loci finding only 1 that was polymorphic (Chesser 1984). Because many existing Utah prairie dog colonies are spaced too far apart to permit natural exchange of individuals, the metapopulation is fragmented and does not represent the single breeding unit which seems to have been envisaged by the CBSG in their calculations of viable population size (CBSG 1987).

One of the explicit targets of the action plan is the establishment of three populations of Utah prairie dogs, such that each one retains 90 percent of the genetic diversity of the population for 200 years. An initial assessment carried out by Captive Breeding Specialist Group (CBSG, currently Conservation Breeding Specialist Group) of the Species Survival Commission, World Conservation Union, suggested that such a target could be achieved by assuring a minimum population of 813 adults in the annual spring census, maintained by long-term management, including transfer of individuals for genetic purposes.

At the time of the CBSG assessment, most of the population viability analysis (PVA) tools currently available did not exist (for reviews and recent applications of these methods see Beissinger and Westphal 1998; Boyce 1992; Brook et al. 2000; Possingham et al. 1993). One such tool, the software program VORTEX (Lacy 1993) allows users to measure loss of genetic variability while forecasting a population's extinction risk. To do this, at the beginning of the simulation the program assigns to each individual a pair of unique alleles. These alleles are inherited by the offspring following a traditional Mendelian segregation and are lost from the population as any individual with a unique allele dies. At the end of the simulation, the program provides a measure of remnant heterozygosity, as the percentage of individuals of the population whose set of alleles is heterozygous. Thus, in order to test the likelihood of meeting the "90% genetic diversity" maintenance required by the action plan, we use VORTEX to estimate the population size at which they retain 90% of the heterozygosity after 200 years of simulation.

The basic population parameters that we use are identical to those used for the *Population Trajectory* section of this analysis (see below). In all cases, we ran the simulations for 200 years and repeated each scenario 1000 times. To assess the effect of population size, we explored initial abundances that covered the range (0, 10, 50, 100, 150, ... 1000). In each simulation scenario, carrying capacity was set to the same value of the initial population size in order to mimic management actions aimed at maintaining a constant population size.

Two aspects of UPD life history make it particularly prone to loss of genetic variability: their polygamous reproductive system, and their propensity to experience catastrophic

population declines due to plague or other factors. A polygamous reproductive system leads to rapid genetic loss because a relatively small proportion of all available males actually breed each year. Therefore the genetic makeup of the subsequent generation does not include the alleles from the males that did not breed, and may be permanently lost from the population unless they successfully breed in the following years. Catastrophes also lead to rapid genetic loss, as they repeatedly lead populations through bottlenecks, eliminating all but few individuals. As the population recovers from such bottlenecks, its genetic makeup will include only the alleles of the individuals that survived.

Therefore, we focus the sensitivity analysis of our simulations on the degree of polygamy and the severity of catastrophes. First, we considered catastrophes that occurred on average every 20 years ($p = 0.05$) and whose effect was extremely severe, eliminating 95% of all individuals of the affected population. We then compared the effect of reducing the severity of catastrophes by exploring other catastrophes which, though equally frequent, eliminate either 50% or 10% of individuals. This allows us to consider the possibility that the entire population does not function as a single block, but rather as a loosely connected set of subpopulations that regularly exchange individuals. Finally, using as a reference the intermediate level of catastrophe severity (50% impact on survival) we explored three degrees of polygamy: 20% of males control all females, 50% of males control all females, and 80% of males have access to females.

Population Trajectories

To analyze the possible population trajectories of the Utah prairie dog, we constructed stage-structured, spatially-explicit metapopulation models with the population viability analysis software package RAMAS (Akçakaya 1998). Using the module RAMAS Metapop, we ran simulations with these models to predict the risk and time course of species extinction, expected metapopulation abundance and its variation and spatial distribution.

A recent test, in which historical trends in real populations were compared with predictions of different PVA software packages, demonstrated that RAMAS makes highly accurate predictions of population size. RAMAS performed as well as did VORTEX, and made more accurate predictions (though not significantly so) than the other software packages examined in the test (Brook et al. 2000).

RAMAS takes as input both demographic variables (population size, survival rates, fecundities, the presence, absence and nature of density-dependence, etc.) and spatial data (location of subpopulations). As is common practice in population viability analysis, we modeled only females (Caughley 1977; Caswell 1989). We parameterized our models as follows:

Demographic data

Demographic variables have a large effect on the dynamics of any population (Lande 1988, Lande 1993), so must be incorporated into any rigorous population viability analysis. Essential variables are the initial numbers of individuals to begin the simulation, survival rate, S_x, defined as the proportion of x-year old individuals that survive to be $x + 1$ years old, one time step later, and the fecundity rate, F_x, which is the average number, per individual of age x alive at a given time step, of offspring censused at the next time step.

Initial abundance

The Utah Division of Wildlife Resources supplied us with their annual censuses of Utah prairie dogs. Censuses are carried out in the spring, before juveniles emerge above ground, so that only adult animals are counted (O'Neill et al. 1999).

We set the initial abundances for each population in our simulations to the individual colony values in the 1998 population counts. We chose this year on the basis of it offering more comprehensive coverage of prairie dog colonies than the count data available to us from the 1999 spring census, while still being recent and thus representative of current Utah prairie dog numbers.

Because we modeled females only, we had to adjust count data to exclude males. Mackley (1988) found the adult female to adult male sex ratio for Utah prairie dogs in John's Valley from 1985 to 1987 to be 1.79 ± 0.16, yielding 0.64 as the average proportion of individuals in the adult population that were female. This value agrees well with the average proportion of 0.63 observed by Wright-Smith (1978), who reported adult male to adult female ratios of 0.56 and 0.43 in 1975 and 1976, respectively, for a site near Bryce Canyon National Park, and an adult male/adult female ratio of 0.80 for another site 24 km away in 1976 (average male/female ratio of 0.60 = average female/male ratio of 1.68). As the mean of the proportions from Mackley's (1988) and Wright-Smith's (1978) studies rounds to 0.64, we estimated the numbers of females in each colony by multiplying counts by this value. Fractional prairie dogs are meaningless, so whenever the estimated number of females was not a whole number, we rounded up to the nearest integer.

Crocker-Bedford (unpubl. manuscript) found that only 40 – 60% of adult Utah prairie dogs are above ground at a given time during daylight hours, indicating that censuses may underestimate the true numbers of individuals. McDonald (1993) reports three regression formulae derived from data on the number of prairie dogs counted visually versus the number captured, all of which were significant at $\alpha = 0.0001$. For a subset of our simulations, we examined the effect of compensating for possible underestimation of true prairie dog numbers in the annual census, using these formulae:

$$(1) \qquad N_{corr} = \begin{cases} 1.403 N_{census} & \text{when } 1 \le N_{census} \le 8 \\ 1.583\, N_{census} & \text{when } 9 \le N_{census} \le 30 \\ 1.682\, N_{census} & \text{when } N_{census} > 30 \end{cases},$$

where N_{census} is the number of prairie dogs counted, and N_{corr} is the estimated "true" number of prairie dogs. We applied these formulae to the estimated number of females calculated from census data, rounding up to whole numbers.

Survival rates

The most comprehensive information available to us at the time of writing is contained in Hoogland (in review), which provides survival rates for wild Utah prairie dogs in Bryce Canyon National Park, for each year-class from juveniles to four-year-olds (Table 1). Because Hoogland's ongoing Utah prairie dog study began in 1995, survival rates from the fourth to fifth year were not available at the time of our writing.

Table 1. Survival rates for female Utah prairie dogs (data from Figure 1c in Hoogland, in review). x is age; l_x is the proportion of the original individuals present at time 0 that is still alive at age x; q_x is the mortality rate during the interval of x to $x + 1$; and $S_x = 1 - q_x$, and is survival rate during the interval of x to $x + 1$.

x (years)	l_x	q_x	S_x
0	1	0.529	0.471
1	0.471	0.320	0.680
2	0.320	0.310	0.690
3	0.221	0.167	0.833
4	0.184		

We plan to extend this table when data for survival to age 5, S_4, becomes available from Hoogland's study. However, we do not predict that substantive changes in our results will emerge when we include S_4 in simulations, because only a small proportion of females are expected to live this long, so their effect on population trajectories should be minimal. For example, approximately 1 % of female Gunnison's prairie dogs, *Cynomys gunnisoni*, survive to their fifth year. Longevity is greater in black-tailed prairie dogs, *C. ludovicianus*, but less than 14 % of females survive to age 5 (Hoogland, in review). We expect survival values for Utah prairie dogs to be more similar to those for Gunnison's prairie dogs, which are closer relatives than are black-tailed prairie dogs (Pizzimenti 1975).

Fecundity

Utah prairie dogs breed just once per year, from mid-March to early April, and young are born after a 30-day gestation, remaining below ground for an additional 5 to 7 weeks, thus emerging in mid- to late May (Wright-Smith, 1978). Females bear a single litter a year. Typically, all females breed in their first year of life, unlike in black-tailed prairie dogs (Hoogland, in review).

Utah prairie dogs display a range of litter sizes. Pizzimenti and Collier (1975) obtained litter sizes ranging from 3 - 6, with a mean of 4.8, in four females that gave birth in captivity. Hurst et al. (1976) reported a mean litter size of about 5.5, varying from 3 - 8 for females in Bryce Canyon National Park. Wright-Smith (1978) reported litter size varying from 1 - 6 at a site near Bryce Canyon National Park, with means of 3.9 in 1975 and 2.8 in 1976. Ten litters of captive Utah prairie dogs at the National Zoological Park in Washington, D.C., ranged from 2 - 4 pups per litter, with a mean of 3.4 (Harold Egoscue, pers. comm., reported in USFWS 1991). Mackley (1988) calculated a mean litter size of 3.64, with annual means ranging from 3.45 - 3.86, in John's Valley from 1985 to 1987, based on the number of juveniles observed aboveground to the number of adult females. These estimates agree broadly with results obtained by Hoogland (in review) from wild Utah prairie dogs in Bryce Canyon National Park from 1995-1999, which give a litter size range of 1 – 7, with a mean of 3.88.

None of these sources, however, provide age-specific fecundity rates for Utah prairie dogs. To calculate our values of fecundity, therefore, we used the average litter size, m, presented for adult Utah prairie dogs in Hoogland (in review): 3.88. We chose Hoogland's data because they are derived from a wild population and because we judged that his method of surrounding nursery burrows with traps soon after juveniles emerged would minimize underestimation of litter size due to post-emergence juvenile mortality.

Because fecundity, F_x refers to the average number of offspring at time t produced by individuals who were x years old at time $t - 1$, it is not simply equivalent to age-specific litter size, m_x. This is because, for the present situation in which annual censuses are carried out shortly before young have been produced, the youngest individuals censused (age 0) were born after the *previous* year's census, and are thus nearly, but not quite one year old. Consequently, the number of these individuals is equal to the number born last year times their survival rate in the intervening year, S_0 (Akçakaya 1998). Furthermore, as we are modeling females only, litter size must be multiplied by the proportion of newborns that are female; in this case, 0.5 (McDonald 1993). In the present case, therefore, the fecundity for all age classes is,

$$F_x = S_o \times 3.88 \times 0.5 = 0.913 \ .$$

Because female Utah prairie dogs breed in their first year, the above fecundity value applies to F_0. Note that because the spring census is carried out before young emerge, F_0 is the fecundity of females almost, but not quite one year old, *not* the fecundity of newborns.

Leslie matrix

Modeling the future trajectory of an age-structured population is achieved by multiplying the numbers of current individuals in different age classes by the appropriate vital rates. In the case of Utah prairie dogs, for which censuses are carried out before reproduction has occurred, the individuals in age class 0 at time t are the surviving young born the previous year, $t - 1$, so the number of individuals in age class 0 at time t, $N_0(t)$, is equal to the sum of the number of individuals in each age class at time $t - 1$, $N_x(t - 1)$, multiplied by the average number of offspring born to mothers in each age class at time t – 1, m_x, multiplied by the survival rate of these offspring from $t - 1$ to t, S_0; i.e.,

$$N_0(t) = N_0(t-1)\, m_0S_0 + N_1(t-1)m_1S_0 + N_2(t-1)m_2S_0 + N_3(t-1)m_3S_0 \ldots$$

The number of individuals in age class 1 at time t, $N_1(t)$, depends only on the number of individuals in age class 0 at time $t - 1$, $N_0(t - 1)$, multiplied by the survival rate of these individuals from $t - 1$ to t, S_1. In general, for x greater than 0,

$$N_x(t) = N_{x-1}(t-1)S_x \,.$$

For our population trajectory simulations, we specified values of the survival and fecundity in the form of a Leslie matrix (Leslie 1945; see, e.g., Caswell 1989, McDonald and Caswell 1993). The Leslie matrix is a way to express age-specific vital rates in a form convenient for computer manipulation using the rules of matrix algebra. If no Utah prairie dogs survived to their fifth year, their Leslie matrix would be of the form,

$$L = \begin{bmatrix} m_0S_0 & m_1S_0 & m_2S_0 & m_3S_0 \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_3 & 0 \end{bmatrix} .$$

This matrix is multiplied by the current age-structured population such that each $N_x(t)$ is the sum of all products of the n^{th} element in the same row of the Leslie matrix times the n^{th} element in the vector of counts at $t - 1$:

$$\begin{bmatrix} N_0(t \\ N_1(t \\ N_2(t \\ N_3(t \end{bmatrix} = \begin{bmatrix} m_0S_0 & m_1S_0 & m_2S_0 & m_3S_0 \\ S_1 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 \\ 0 & 0 & S_3 & 0 \end{bmatrix} \times \begin{bmatrix} N_0(t-1) \\ N_1(t-1) \\ N_2(t-1) \\ N_3(t-1) \end{bmatrix} .$$

Note that zeros are appropriately placed in the Leslie matrix so that surviving individuals in one age class can only move forward to the next age class, and not skip age classes,

remain in the same age class or go backwards. For example, the number of individuals in age class 2 at time t depends only on the survival of individuals in age class 1 at $t-1$, as can be seen by expanding the matrix-vector multiplication:

$$N_2(t) = 0 \times N_0(t-1) + S_2 \times N_1(t-1) + 0 \times N_2(t-1) + 0 \times N_3(t-1)$$

$$= S_2 N_1(t-1) .$$

Applying the values we derived above for S_x and F_x yields the following Leslie matrix for Utah prairie dogs, which we entered into RAMAS Metapop's stage matrix:

$$L = \begin{bmatrix} 0.913 & 0.913 & 0.913 & 0.913 \\ 0.680 & 0 & 0 & 0 \\ 0 & 0.690 & 0 & 0 \\ 0 & 0 & 0.833 & 0 \end{bmatrix} .$$

This Leslie matrix does not extend past age 4, because, as explained above, survival to age 5 was not available from Hoogland (in review). However, we predict that addition of the fifth age class (one extra row and column) to the matrix would make no substantive difference to our results or conclusions, because we expect only a small proportion of Utah prairie dog females to live longer than 4 years. In the Gunnison's prairie dog, a species in the same subgenus as Utah prairie dogs (*Leucocrossuromys*; Pizzimenti 1975), only 1 % of females survive to their fifth year (Hoogland, in review). If Utah prairie dog longevity is similar, the effect of so few additional individuals on population trajectories would be negligible.

Density dependence

To account for the fact that resources for Utah prairie dogs are limited, and thus rates of population growth should decrease with population density, we incorporated a simple form of density dependence into our simulations. Growth was exponential until a ceiling was reached (density dependence type "Ceiling" in RAMAS Metapop). This ceiling, or carrying capacity, K, was determined separately for each colony, using the highest population size attained by each colony during the available years of censuses. In the absence of a detailed knowledge of the resources available at each colony site and the requirements of the prairie dogs, this is the safest estimate of carrying capacity. In essence, we modeled whether or not Utah prairie dogs would persist if each colony does as well as it has ever done so far.

For simulations in which we compensated for possible census underestimation by adjusting colony numbers using Equation 1, above, we also adjusted K accordingly.

Demographic stochasticity

Demographic stochasticity was included in the calculation of population growth. RAMAS samples the number of survivors and emigrants from a binomial distribution, and the number of juveniles from a Poisson distribution.

Spatial data

The Utah Division of Wildlife Resources furnished us with spatial data for virtually all Utah prairie dog colonies. Boundaries of prairie dog colonies in the West Desert recovery area were supplied as ArcView/ArcInfo files, while the Northernmost, Southernmost, Easternmost and Westernmost points of Awapa Plateau and Paunsaugunt recovery area colonies were given in UTM-coordinates. We calculated the central point of all colonies for entry into RAMAS Metapop as colony location coordinates. Because UTM-coordinates are in units of meters, it was simple to use them when calculating dispersal rates (see below).

All colonies that had an initial abundance greater than zero for the 1998 count were entered into the analysis as separate populations. The West Desert recovery area had 182 active colonies in 1998, exceeding by 22 the maximum number of individual populations that RAMAS Metapop can include. Since many West Desert colonies are close to one another, we were able to combine colonies that were less than 350 m apart, measured from center to center, thereby reducing the number of individual populations to 156. These inter-colony distances all fall within the range of diameters of female Utah prairie dog home areas (see Table 2 below), so lumping colonies 350 m or less apart is biologically reasonable.

Dispersal

Dispersal is defined as movement of organisms from one population to another, and dispersal rates are the proportions of individuals dispersing per time step from one population to another. Mackley (1988) reported a dispersal rate in Utah prairie dogs of 12.1 %; 78 of 646 identifiable individuals were recaptured at plots distant from their initial capture plot within his John's Valley study site.

Most migration in prairie dogs is accounted for by movements of juveniles. Of the 78 migrants that Mackley (1988) encountered, 67 (86 %) were juveniles. Adult Utah prairie dogs are relatively sedentary. Home ranges tend to be elongate, with males' home areas being longer and larger than those of females (Table 2). In a study of home ranges in a colony in Bryce Canyon, Crocker-Bedford and Spillett (1977) observed prairie dogs traveling 100 - 300 m from their home burrows to feeding areas.

Table 2. Home range sizes of adult Utah prairie dogs. Data are from Crocker-Bedford and Spillett (1977).

Sex	Length of longest axis (range, m)	Area (range, ha)	*N*
Males	370-630	2.8-8.2	3
Females	220-350	1.2-4.5	7

Turning to true dispersal, rather than movement within a home range, Mackley (1988) reported that the average distance moved by known individuals in John's Valley was 0.27 km for adult males and 0.68 km for adult females. However, as the maximum distance between any two study plots that Mackley (1988) sampled was only 1.76 km, he points out that his results may underestimate true dispersal.

We generated dispersal matrices that gave the proportion of individuals in each population that move to other populations, as calculated by the dispersal-distance function,

$$m_{ij} = a \times \exp \frac{-D_{ij}^{c}}{b} \qquad \text{if } D_{ij} \le D_{max}$$

$$m_{ij} = 0 \qquad \text{if } D_{ij} > D_{max} \quad ,$$

where m_{ij} is the dispersal rate between the i^{th} and j^{th} populations, D_{ij} is the distance between the two populations, D_{max} is the maximum dispersal distance of the prairie dogs, and a, b, and c are the function parameters.

We parameterized this dispersal-distance function for Utah prairie dogs by fitting an exponential equation to data for prairie dog movements in John's Valley from 1985 to 1987 (data taken from Fig. 2 of Mackley 1988; see our Fig. 5):

$$m = 0.033 \times \exp(-1.522 \times D) \, ,$$

where D is in km. This equation was fit using STATISTICA, with m entered as the proportions of all individuals captured during Mackley's (1988) study that were recaptured at distance D from the initial capture location.

As Figure 5 demonstrates, Utah prairie dog dispersal is predicted to be negligible across distances of 5 km, so we set $D_{max} = 5$ km. Although this prediction is based on extrapolating the curve beyond the range of data points, this was also the maximum straight-line distance traveled by black-tailed prairie dog dispersers in a study by Garrett and Franklin (1988).

Through RAMAS' relative dispersal variable, we were able to include age-specific dispersal. This variable gives the dispersal rate for each age class relative to the total dispersal rate specified in the dispersal matrix. Based on Mackley's (1988, Table 2) data on the proportions of his study population in each age class and the proportions of migrants in different age classes, we assigned a relative dispersal of 1.0 to juveniles, and 0.44 to adults in all other age classes (Table 3).

Reducing the relative dispersal rate for adults below 1.0 decreases the overall dispersal rate below the rate specified in the dispersal-distance function, so we adjusted the dispersal-distance function by multiplying a by 1.18, which is the ratio of the overall dispersal rate calculated from Mackley's (1988) data (12.07 %) to the overall dispersal rate yielded by incorporation of the relative dispersal variable (10.24 %). This yields the adjusted dispersal-distance function,

$$m = 0.04 \times \exp(-1.522 \times D).$$

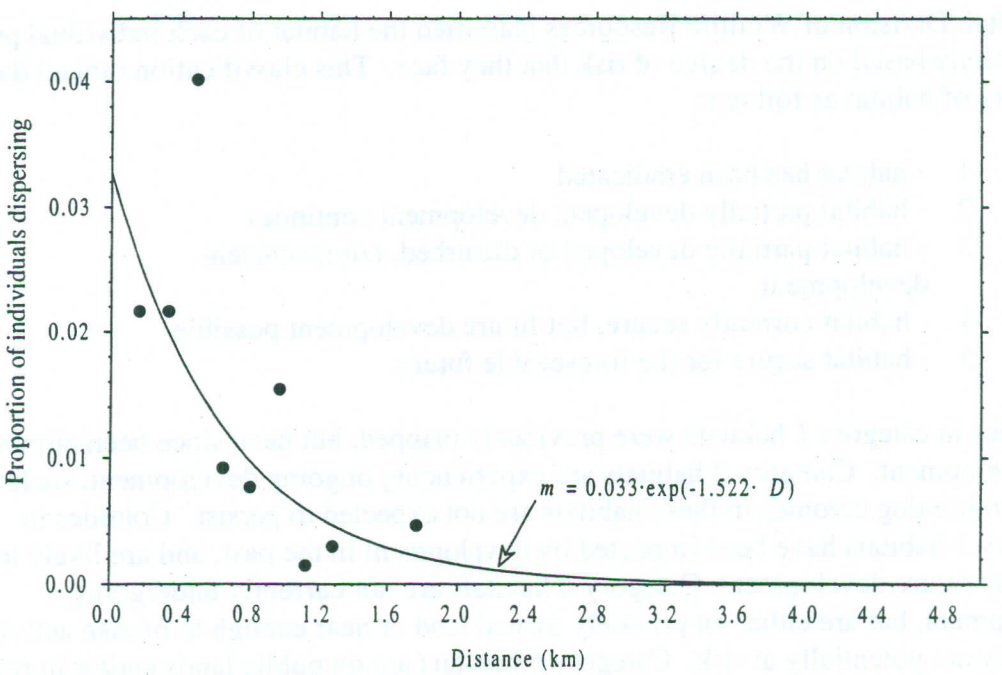


Figure 5. Dispersal distance function for Utah prairie dogs. Curve is fit to data from Figure 2 in Mackley (1988).

Table 3. Derivation of relative dispersal rate. Data are from Mackley (1988).

	Juveniles	Adults
N (1986 cohort)	164	61
Proportion (1986 cohort)	0.729	0.271
× 646 individuals captured 1985-87	470.9	175.1
Migrants 1985-87	67	11
Dispersal rate	14.23	6.28
Relative dispersal rate	1	0.44

In our simulations, Utah prairie dogs do not establish new colonies. Modeling this possibility would require detailed, spatially explicit data that indicate what locations are available and suitable for new colonization.

Habitat security

The Utah Division of Wildlife Resources classified the habitat of each individual prairie dog colony based on the degree of risk that they face. This classification ranked the security of habitat as follows:

1 - habitat has been eradicated
2 - habitat partially developed, development continues
3 - habitat partially developed or disturbed, but no current development
4 - habitat currently secure, but future development possible
5 - habitat secure for the foreseeable future.

Colonies in category 1 habitats were previously mapped, but have since been eliminated by development. Category 2 habitats are experiencing ongoing development, such that Utah prairie dog colonies in these habitats are not expected to persist. Colonies in category 3 habitats have been impacted by development in the past, and are likely to be again by future development. Category 4 habitats are not currently undergoing development, but are either on privately owned land or near enough to human activities that they are potentially at risk. Category 5 habitats are on public lands and/or in remote locations so far from human population centers and activities that they are unlikely to be threatened by humans. While it is not possible to place a precise time frame on the security of prairie dog colonies in category 5 habitats, they are expected to be safe from development and other human pressures for at least the next 20 years, and likely much longer (Keith Day, pers. comm.).

To simulate the effect of progressive human encroachment on Utah prairie dog habitat, we conducted a subset of simulations on only land classified as secure for the foreseeable future (category 5).

Catastrophes

Predicting population crashes in Utah prairie dog colonies and colonies is not yet possible. Although one can calculate the rate at which numbers have crashed in the past, constructing a model to predict the occurrence of future crashes would require an understanding of the variables driving past crashes. Unfortunately, such knowledge remains elusive. For example, the reasons are unknown for drastic crashes in the Buckskin Colony, from 199 adults censused in 1994 to zero in 1995, and in the Gooseberry Colony from 242 in 1993 to 7 in 1995 (McDonald 1996).

Collier and Spillett (1975) named climate as the single most important factor influencing Utah prairie dog populations, and listed several historical cases in which population numbers crashed following droughts. The authors hypothesized that drought is doubly harsh on Utah prairie dogs, forcing them to spend more time aestivating and less time foraging because of extreme summer heat, at the same time that it reduces vegetation cover and quality, leaving less vegetation and vegetative moisture (Utah prairie dog's main source of water; Collier 1975).

Sylvatic plague (*Yersinia pestis*) is also considered to be a major threat to Utah prairie dog populations. Plague was reported to have significantly reduced populations in 1937, although the extent of the reduction is indicated only by the reduction of the poisoning effort deemed necessary to control prairie dog numbers that year, because populations were not censused at that time (USFWS 1991). Plague may also have been a major factor in the eradication of several colonies in the Cedar-Parowan Valley area in 1990 (M. Coffeen pers. comm., reported in USFWS 1991). Plague was documented in Bryce Canyon National Park in 1983, where fleas and serum taken from terminally-ill prairie dogs tested positive for *Yersinia pestis* (Coffeen and Pederson 1989). Plague was also confirmed as the cause of die-offs in the Bryce Canyon/Ruby's Inn and East Creek colonies from a combined total of 285 in 1994 to 38 in 1995 (McDonald 1996).

The dynamics of sylvatic plague are not well understood in any prairie dog species. In a recent study on the closely-related white-tailed prairie dog (*C. leucurus*), Anderson and Williams (1997) concluded that predicting plague movements is not yet possible, and that the role of other mammals in the maintenance of plague in prairie dogs remains unclear. We currently lack data for Utah prairie dogs that would allow rigorous modeling of plague dynamics in this species.

Clearly, we do not understand fully the mechanisms driving catastrophic declines in Utah prairie dog populations. Nevertheless, it is possible to calculate the *rate* of catastrophes, based on past occurrences. Catastrophe rate may be estimated by deriving λ (lambda), the change in population size, N, from one year to the next, where

$$\lambda = \frac{N_{t+1}}{N_t} .$$

A λ of 1 would indicate a stable population; greater than 1, population growth; less than 1, population decline; and 0, population extinction.

Based on an analysis of trends since 1976, Mark Ritchie showed that a given Utah prairie dog complex is likely to go extinct within 20 years (cited in UDPRIT 1997), corresponding to an annual catastrophe rate of 0.05. Note, however, that this result applies to complexes, and not individual colonies within complexes, which is the level of our current analysis.

To determine how frequently Utah prairie dog colonies have suffered catastrophes in the past, we calculated λ for all individual colonies that were not identified as being transplant colonies, for all years from 1976 to 1999. Data for the year 1990 were excluded, because colonies on private lands were not censused that year. As a result, λ for 1989 is the rate of population change from 1989 to 1991. λ was calculated only for years in which $N_t \neq 0$, to avoid division by 0.

The distribution of values of λ for all Utah prairie dog colonies from 1976 to 1999 displays a large class of zero λ (Fig. 6), indicating catastrophic population crashes. Occurrences of $\lambda = 0$ represent 24.5% of cases, corresponding to a catastrophe rate of once every 4 years. This value may be an over-estimate of the true colony extinction rate, however, because it does not distinguish between large colonies that crashed precipitously and small colonies in which loss of just a few individuals would yield very low λ. It also does not take into account the fact that some prairie dogs may have gone unobserved in certain colonies in certain years, resulting in false zero counts.

To observe the effects of different possible colony-level catastrophe rates, we ran separate simulations with catastrophe rates of 0.05 (as calculated for complexes; see UDPRIT 1997), 0.25 (as derived for colonies; our study) and 0.15 (an intermediate value). Simulated catastrophes result in 100 % mortality in the affected colony.

In our models we assumed that catastrophes occur only locally and that there is no correlation among populations, as might be true of plague. As Figure 7 shows, there was clustering of low λ in and around certain years, meaning that several complexes and individual colonies in those years were experiencing catastrophic declines. However, these clusterings may contain artifacts of the censusing methods. For example, although we excluded zero λ values in 1990 on private land to account for the absence of censusing on private lands that year, we note a strong peak in very low λ in complexes on other lands at that time. Spatial and temporal correlations in catastrophic events should be explored in future work, but for now we remain conservative and leave catastrophe rate uncorrelated among colonies.

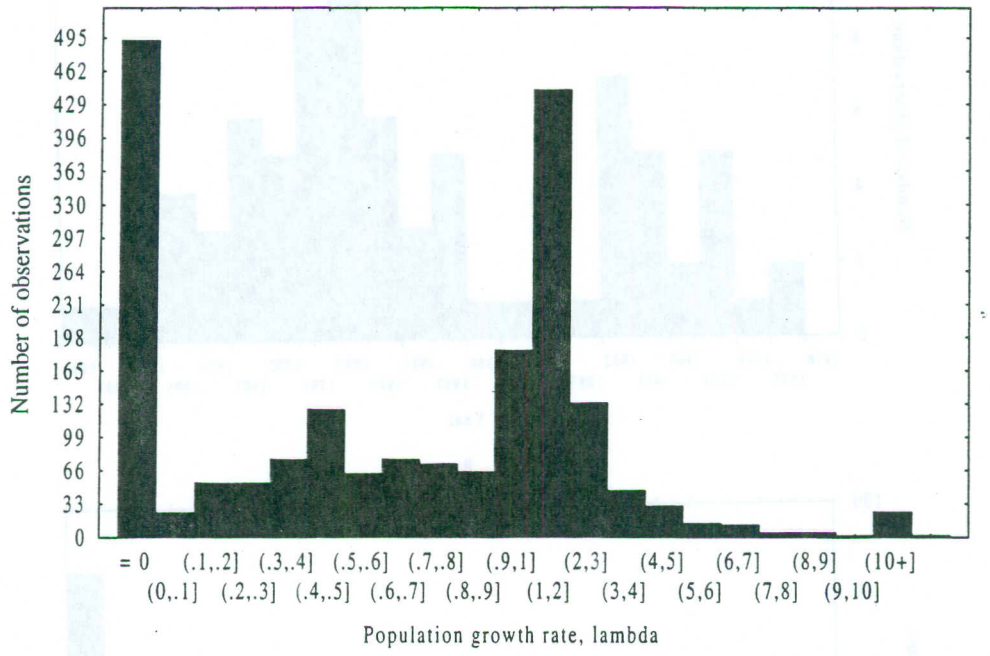


Figure 6. Frequency histogram of Utah prairie dog colony growth rates (lambda, λ) from one year to the next. Each bar represents the number of non-transplant colonies for which a particular λ was observed, based on Spring counts from 1976 to 1999.

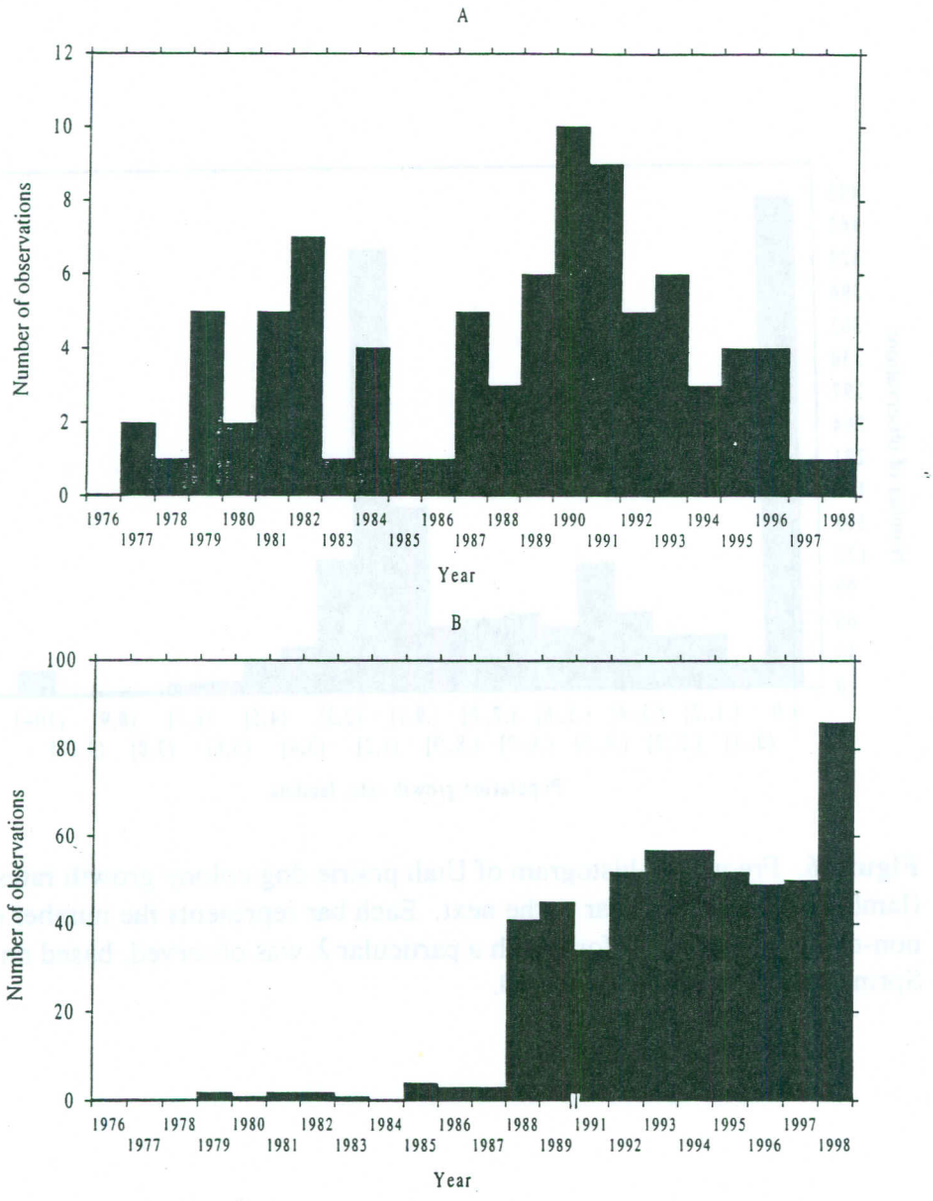


Figure 7. Frequency histogram of population crashes in Utah prairie dog complexes (A) and colonies (B). For complexes (A), each bar represents the number of complexes for which $0 \leq \lambda < 0.1$ from the current to the next year, based on Spring counts from 1976 to 1999. There were no occurrences of $0 \leq \lambda < 0.1$ in A from 1976 to 1977, because only a few complexes were surveyed in 1976, the first year of rigorous censusing. For colonies (B), each bar represents the number of non-transplant colonies for which $\lambda = 0$ from the current to the next year. Counts for 1990 are excluded in B, so λ for 1989 is the growth rate from 1989 to 1991. The higher number of occurrences of $\lambda = 0$ after 1988 reflects the increase in reporting censuses at the colony level, rather than the complex level. 1998 is the last year for which λ can be calculated because 1999 was the last year for which count data are available.

Summary of simulation scenarios

We performed population trajectory simulations at the combinations of catastrophe rate and initial abundance identified by an "X" in the following list:

Colony-level catastrophe rate	1998 census, all colonies	Adjusted 1998 census, all colonies	Adjusted 1998 census, security category 5 colonies only
0.05	X		
0.15	X	X	X
0.25	X	X	X

All simulations were repeated 1000 times, and we set the simulations to project 200 years into the future.

Results

Maintenance of Genetic Diversity

Figure 8 exhibits the impact of catastrophes with a different degree of severity. In general, as initial population size increases, the amount of genetic variation retained increases as well. The increase is not linear, however. At small population sizes (0-300 individuals), final observed heterozygosity (%H) increases sharply with population size, but the rate of increase gradually declines with further population increases. At approximately 800-900 individuals, and at low or intermediate degrees of catastrophe severity, the rate of increase of %H stabilizes at about 80%. Further increases in %H require increasingly larger initial population sizes. At high levels of catastrophe severity, even large population sizes are unable to retain large %H. These results suggest that independently of catastrophe severity, in order to meet the stated goal of retaining "90 percent of the genetic diversity of the population for 200 years," would require populations whose total size is significantly larger than 1000 individuals.

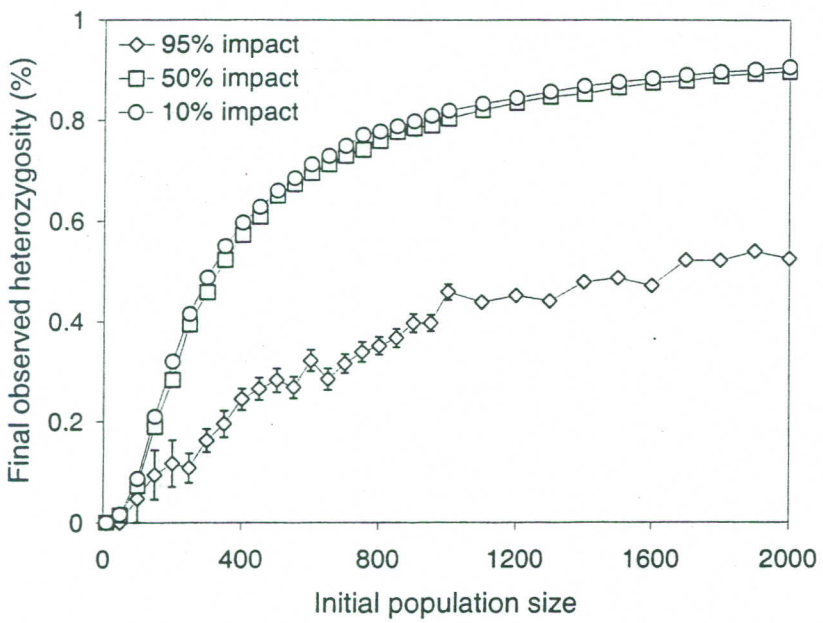


Figure 8. Proportion of genetic diversity retained, as a function of catastrophes of different intensity.

A similar, but much more drastic pattern characterizes extinction risk (Fig. 9). At low and intermediate levels of catastrophe severity, populations are almost certain to persist 200 years, once reaching an initial population size of 100 individuals or so. Likelihood of survival at high levels of catastrophe intensity is very low.

The previous simulations assumed that only 20% of males participate in reproductions. But what happens if this is an underestimate? Figure 10 shows that an increase in the

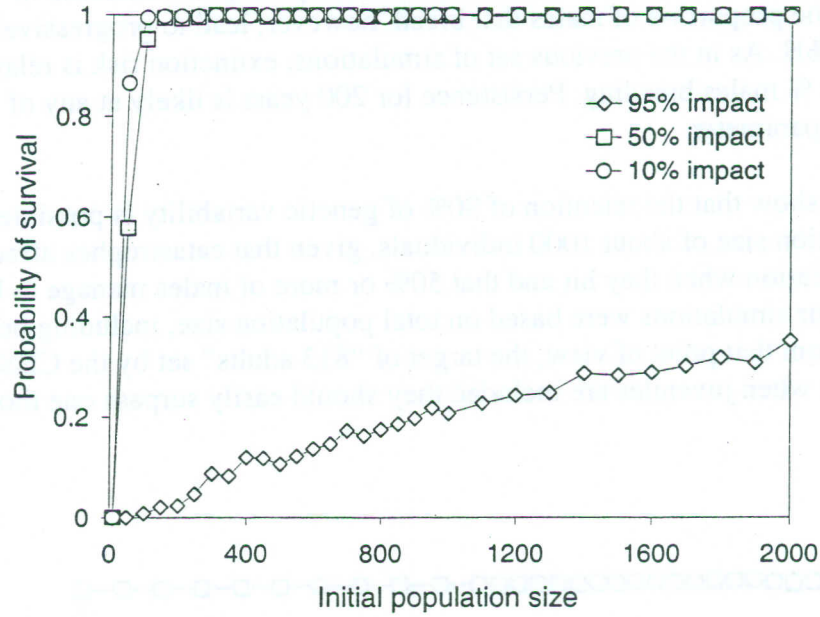


Figure 9. Likelihood of survival of the simulated population, as a function of catastrophes of different intensity.

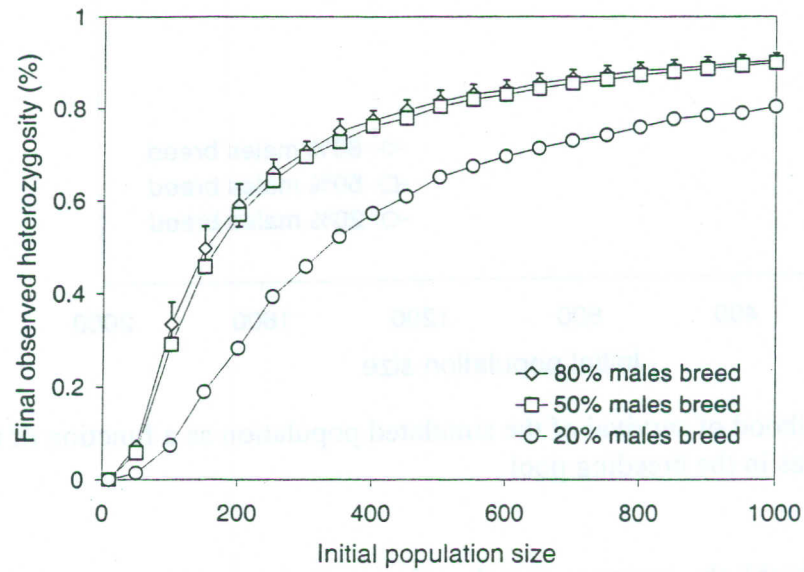


Figure 10. Proportion of genetic diversity retained, as a function of proportion of males in the breeding pool.

proportion of breeders from 20% to 50% results in a perceptible increase in %H. Further increases in the proportion of males that breed, however, lead to progressively smaller increases in %H. As in the previous set of simulations, extinction risk is relatively insensitive to % males breeding. Persistence for 200 years is likely at any of the explored levels of this parameter.

These results show that the retention of 90% of genetic variability is possible for an initial population size of about 1000 individuals, given that catastrophes affect 50% or less of a population when they hit and that 50% or more of males manage to breed any given year. Our simulations were based on total population size, including both juveniles and adults. From that point of view, the target of "813 adults" set by the CBSG seems reasonable, as when juveniles are included they should easily surpass one thousand individuals.

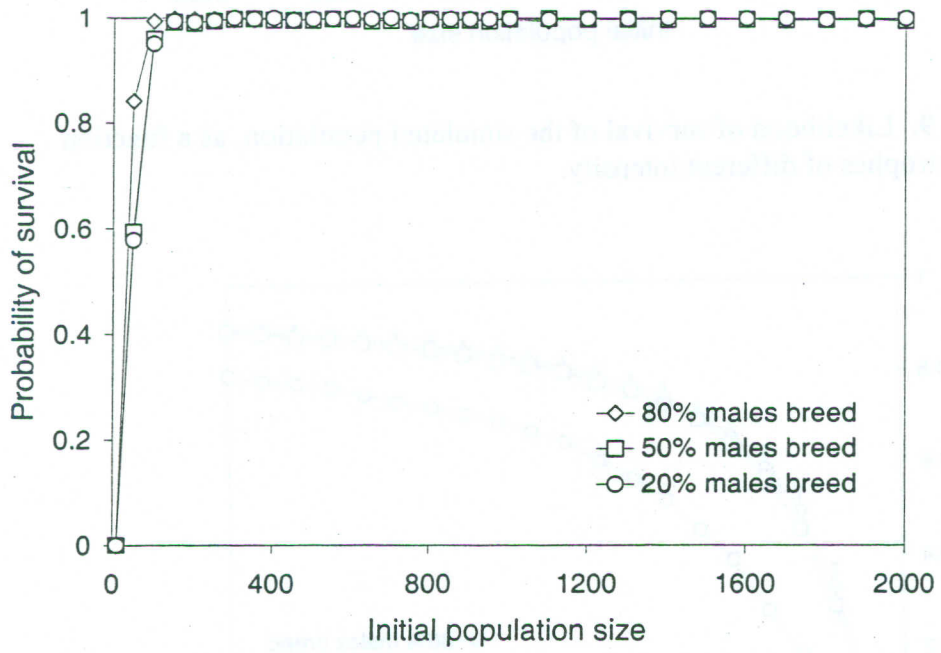


Figure 11. Likelihood of survival of the simulated population as a function of the proportion of males in the breeding pool.

It is important to highlight, however, that though our results provide support for the stated target, our analysis is based on a series of assumptions that need to be verified with field data. Given the available information, it seems reasonable to assume that the severity of catastrophes is on the order of 50% or less (i.e., this means that at most 50% of all the population in a recovery area is wiped out by a single catastrophic event). We are not certain whether a 50% degree is adequate, however. As is shown in Fig. 10, this could clearly affect %H. We strongly encourage the collection of field data that allow evaluation of the assumptions of our analysis.

Population Trajectories

Our simulations demonstrate that Utah prairie dogs are not declining deterministically; in other words, in the absence of plague epidemics and other catastrophes, their intrinsic survival and fecundity rates should allow their populations to persist in the long term. This can be seen in the top row of Figure 12, in which catastrophes are set to the low rate of 0.05, equivalent to a per-colony occurrence of once every twenty years. With this low a rate of catastrophic population crashes, survival and fecundity rates are favorable enough to cause the Utah prairie dog metapopulation size to increase to the summed carrying capacity of its constituent colonies. Under these conditions, each recovery area's population displays an initial steep increase in size, followed by a minor decline before leveling off. This is attributable to the fact that initially catastrophes wipe out few or no colonies, but as time steps proceed, some colonies are wiped out and are not recolonized. When the catastrophe rate is low, however, few colonies suffer catastrophic decline. For all three recovery areas, such conditions (low catastrophe rates) lead to predictions that the Utah prairie dog metapopulation is not threatened with extinction within the next 200 years.

Although these simulations with low catastrophe rates do not predict extinction of Utah prairie dogs in any of the three recovery areas, simulations indicate that the number of individual colonies inhabited by prairie dogs will decline over time (Figure 13, top row). This is because several colonies are farther from other colonies than the maximum dispersal distance of Utah prairie dogs, here set at 5 km (Fig. 14). When these colonies are wiped out by catastrophes, they are too far away from sources of dispersers to be recolonized by natural dispersal.

As explained above, the catastrophe rate of 0.05 is based on historical λ values for Utah prairie dog complexes, not colonies. Because our analysis focuses on colonies, which are expected to exhibit proportionally greater volatility than complexes, this value is undoubtedly an underestimate of the true colony catastrophe rate. In the middle and bottom rows of Figures 12 and 13, we depict the effect of increasing the catastrophe rate to 0.15 and 0.25. The latter value, though high, is based on the historical record of colony censuses, so we expect the true value to be closer to 0.25 or the intermediate 0.15 than to 0.05.

Under these more realistic conditions, the Awapa Plateau recovery area exhibits a small probability of going extinct during the next 200 years if catastrophes occur every 6-7 years, but a high probability of extinction if catastrophes occur every 4 years (catastrophe rates of 0.15 and 0.25, respectively; Figs. 15 and 16). The reason for the population declines at these higher catastrophe rates, shown in the middle and bottom rows of Figure 12, is that individual colonies are wiped out faster than natural dispersers can recolonize them. This is evidenced by the decline in numbers of active colonies on the Awapa Plateau seen in the middle and bottom rows of Figure 13.

The critical importance of inter-colony distance is demonstrated by the fact that, unlike the Awapa Plateau, the Paunsaugunt and West Desert recovery areas are not predicted to

go extinct in the next 200 years when the catastrophe rate is 0.15 (Fig. 12, middle row). A higher proportion of colonies are close to one another in the Paunsaugunt and West Desert recovery areas than in the Awapa Plateau (Fig. 14). Because dispersal rate increases with decreasing inter-colony distance (see Fig. 5), dispersers are able to restock colonies that have been wiped out by catastrophes at a higher rate in the West Desert and Paunsaugunt than in the Awapa Plateau.

The West Desert recovery area has enough prairie dog colonies close enough together to run only a negligible risk of extinction even when the catastrophe rate is 0.25 (though at greatly reduced abundance; Figs. 12 and 16). The proportion of Paunsaugunt colonies that are close to one another is lower than in the West Desert (Fig. 14), so when the catastrophe rate is 0.25, Paunsaugunt colonies go extinct at a much higher rate than their recolonization rate, leading to a high probability of extinction for the recovery area (Fig. 16).

To account for the possibility that predictions of high risks of extinction at high catastrophe rates could be influenced by underestimation of true Utah prairie dog abundance in the annual visual census, we repeated simulations with adjusted initial abundances, for catastrophe rates of 0.15 and 0.25. Applying the corrections in Equation 1 (see *Methods*) to the 1998 census results in improved performance of all simulated recovery area populations, with no predicted risk of extinction for any of the three when the catastrophe rate is 0.15 (Fig. 17). This improvement occurs even though the spatial arrangement of colonies is unchanged, because multiplying the same dispersal rate by a higher number of individuals results in a higher number of dispersers able to recolonize eradicated colonies. Consequently, the decline in numbers of active colonies is less steep when initial abundance is adjusted to correct for underestimation in visual censusing (Fig. 18).

Adjusting the initial abundance to correct for underestimation in census counts also enables the West Desert colonies to persist without risk of extinction even when the catastrophe rate is 0.25, though this catastrophe rate is too high for natural dispersal to overcome in both other recovery areas, in which prairie dogs are still expected to die out within 200 years (Figs. 17 - 19).

A crucial determinant of long-term persistence of Utah prairie dogs is the security of their habitat. To model the effect of future loss of prairie dog habitat to human activity, we repeated the simulations for catastrophe rates of 0.15 and 0.25 using adjusted initial abundances, this time including only those colonies that exist on habitat listed by the UDWR as being secure for the foreseeable future. Because only 2 of 61 Awapa Plateau prairie dog colonies active in 1998 were not on land secure for the foreseeable future, excluding these made no significant difference to the performance of Awapa Plateau prairie dog colonies (compare Figs. 17 and 20; 18 and 21). However, incorporating potential habitat loss in this way results in significant increases in the likelihood of extinction for the Paunsaugunt and West Desert Utah prairie dog populations (Figs. 22 and 23). The most striking effect of potential habitat loss was seen in West Desert colonies, which to this point in our simulations had been the most robust. Fully 122 of

182 active West Desert prairie dog colonies are located on land with varying degrees of present or possible future human-related disturbance (Fig. 24). Eliminating these colonies from the simulations leads to the conclusion that the West Desert recovery area is the most seriously threatened with extinction of the three when probable risk to habitat is considered (Figs. 22 and 23).

Figure 12 (following page). Predicted changes in numbers of female Utah prairie dogs in the three recovery areas, with three different colony-level catastrophe rates. Solid lines give average of 1000 simulations; dashed lines give ± 1 standard deviation; dotted lines give maximum and minimum. Initial abundance is based on uncorrected census values.

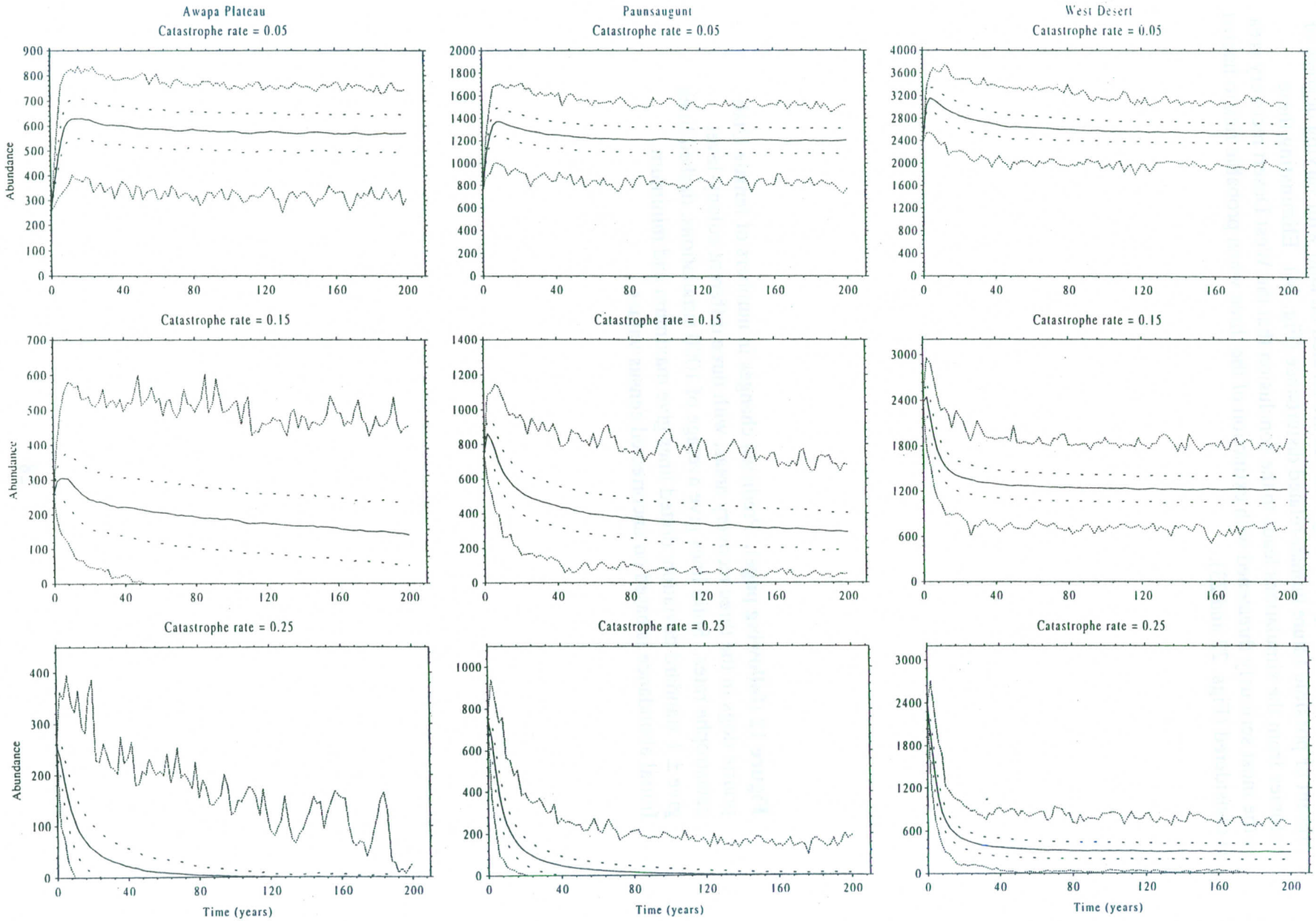
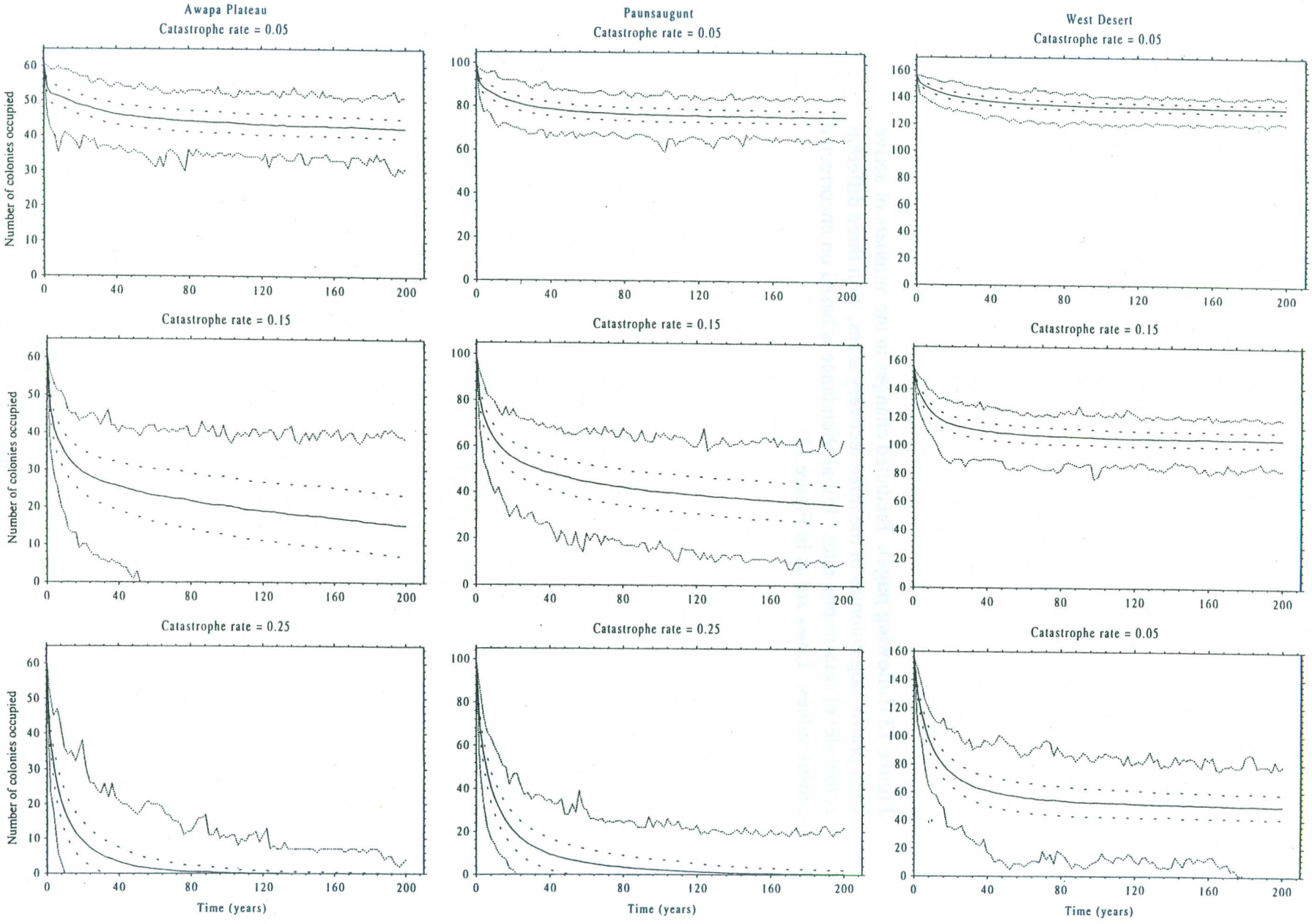

Awapa Plateau
Catastrophe rate = 0.05
Paunsaugunt
Catastrophe rate = 0.05
West Desert
Catastrophe rate = 0.05
Catastrophe rate = 0.15
Catastrophe rate = 0.15
Catastrophe rate = 0.15
Catastrophe rate = 0.25
Catastrophe rate = 0.25
Catastrophe rate = 0.25
Abundance
Time (years)

Figure 13 (following page). Predicted changes in the numbers of active Utah prairie dog colonies in the three recovery areas, with three different colony-level catastrophe rates. Initial abundance is based on uncorrected census values. Lines are as in Figure 12.


Awapa Plateau
Catastrophe rate = 0.05
Paunsaugunt
Catastrophe rate = 0.05
West Desert
Catastrophe rate = 0.05
Catastrophe rate = 0.15
Catastrophe rate = 0.15
Catastrophe rate = 0.15
Catastrophe rate = 0.25
Catastrophe rate = 0.25
Catastrophe rate = 0.05
Number of colonies occupied
Time (years)

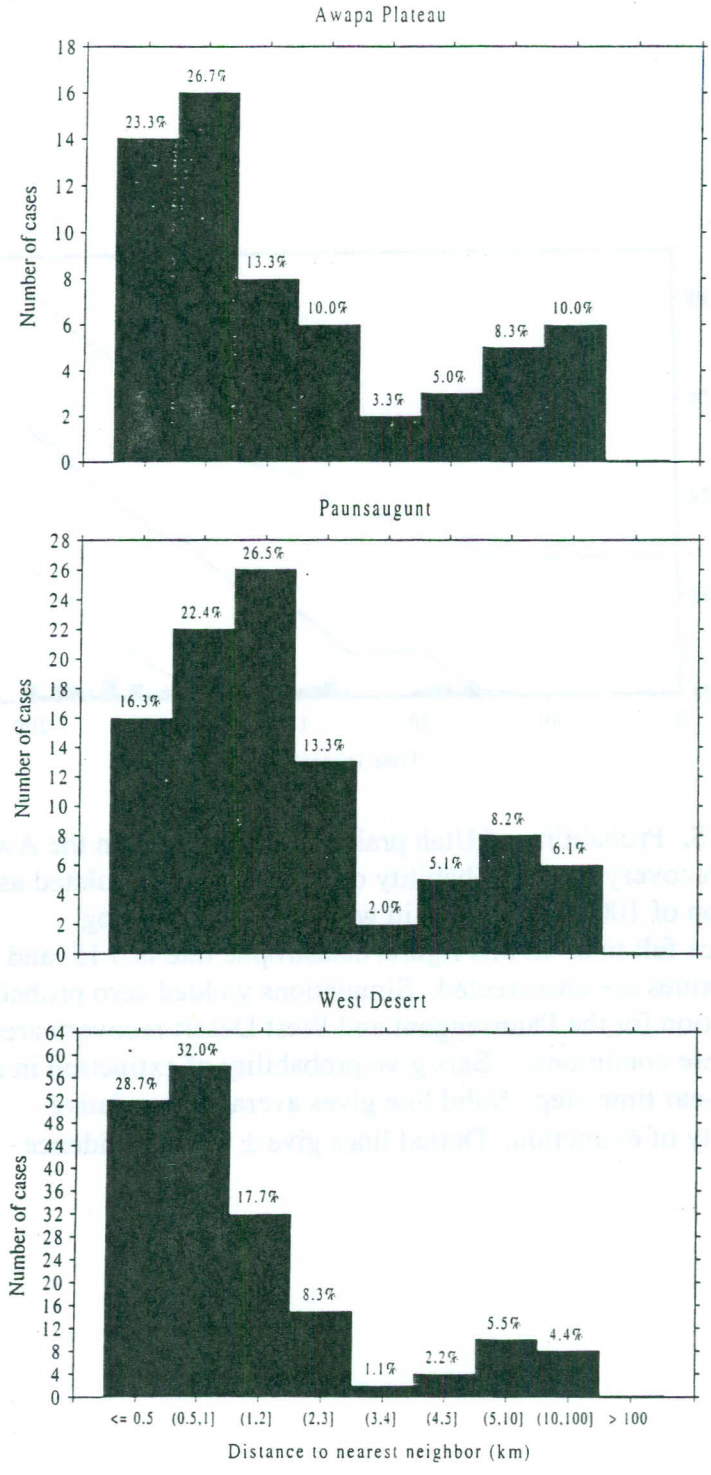


Figure 14. Frequency histogram of center-to-center distances from each prairie dog colony to its nearest neighbor.

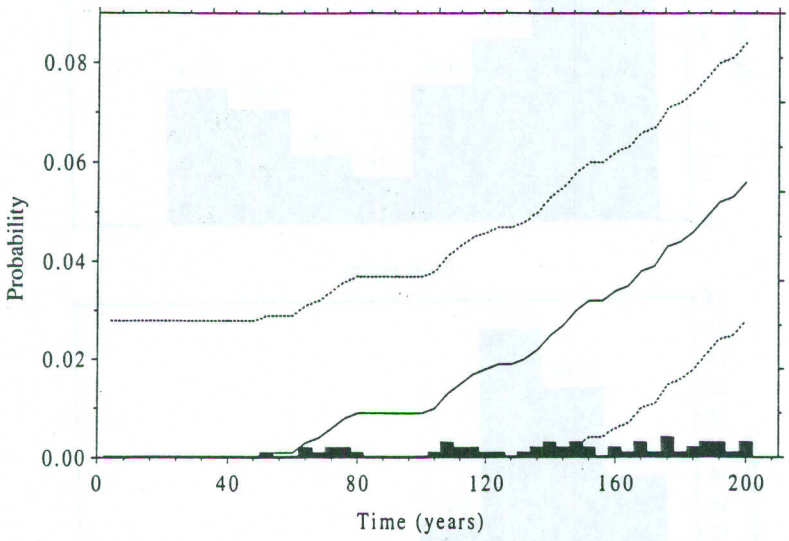


Figure 15. Probability of Utah prairie dog extinction in the Awapa Plateau recovery area. Probability of extinction is calculated as the proportion of 1000 simulations in which Utah prairie dog abundance fell to 0. In this figure, catastrophe rate is 0.15, and census values are uncorrected. Simulations yielded zero probability of extinction for the Paunsaugunt and West Desert recovery areas under these conditions. Bars give probability of extinction in a given 4-year time-step. Solid line gives average cumulative probability of extinction. Dotted lines give ± 95% confidence interval.

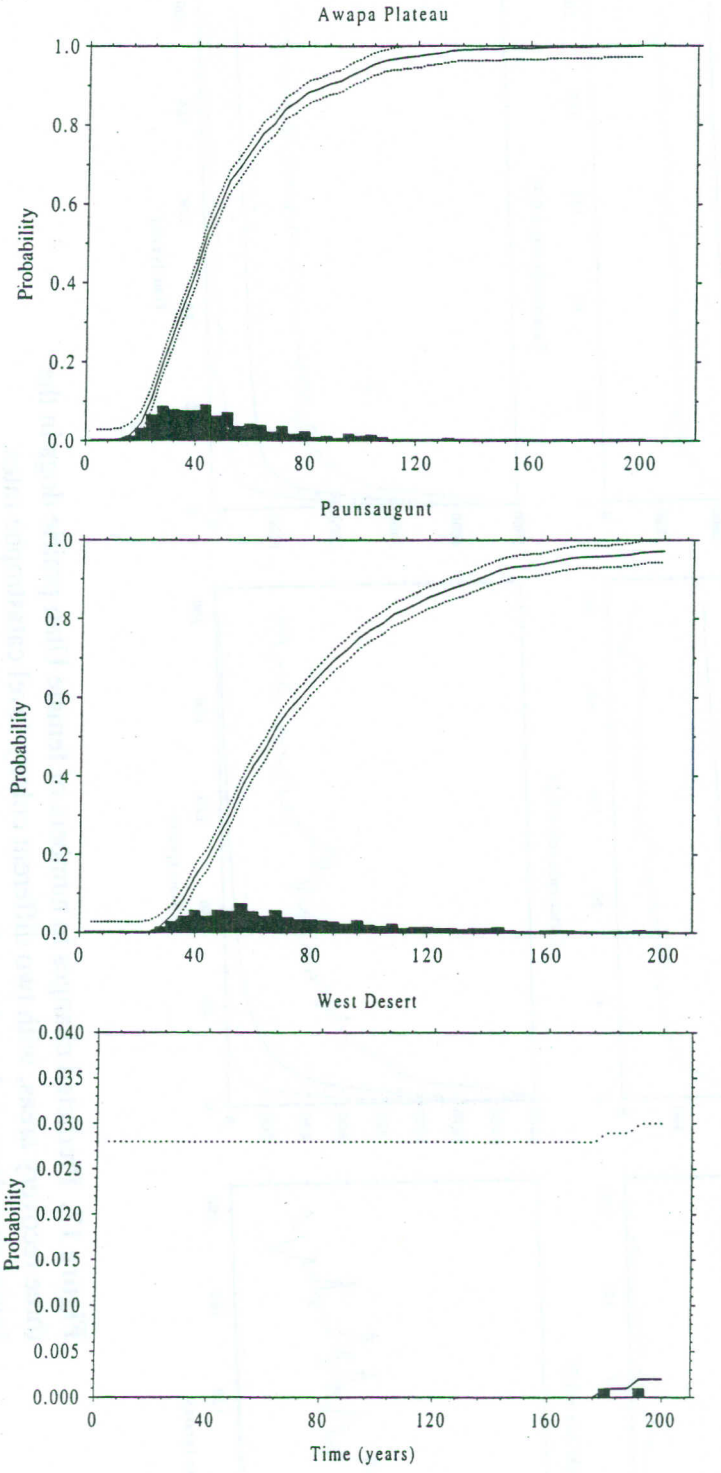


Figure 16. Probability of extinction in Utah prairie dog recovery areas, based on 1000 simulations with a catastrophe rate of 0.25, using uncorrected census values. Bars and lines are as in Figure 15.

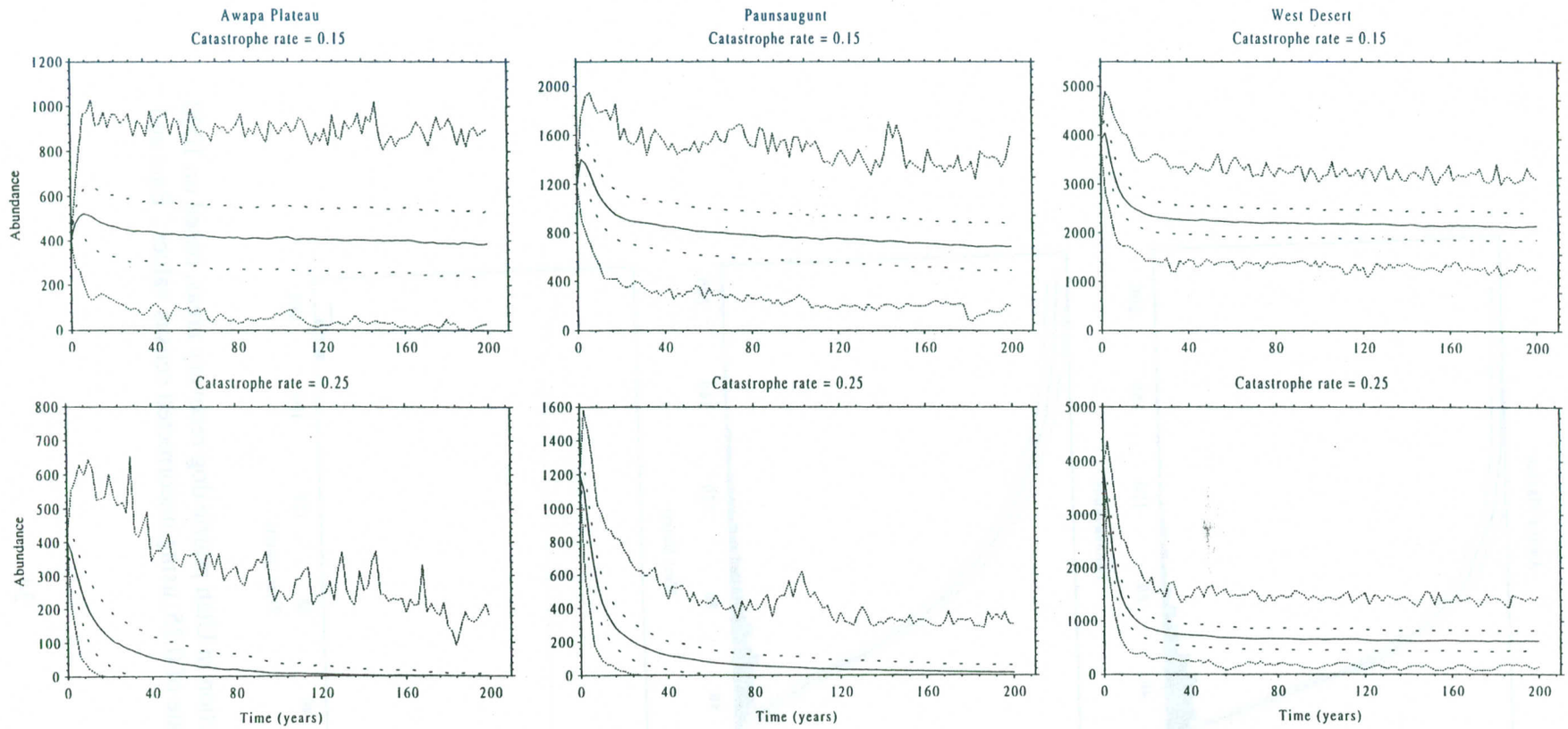


Figure 17. Predicted changes in numbers of female Utah prairie dogs in the three recovery areas, with two different colony-level catastrophe rates. Initial abundance is based on adjusted census values. Lines are as in Figure 12.

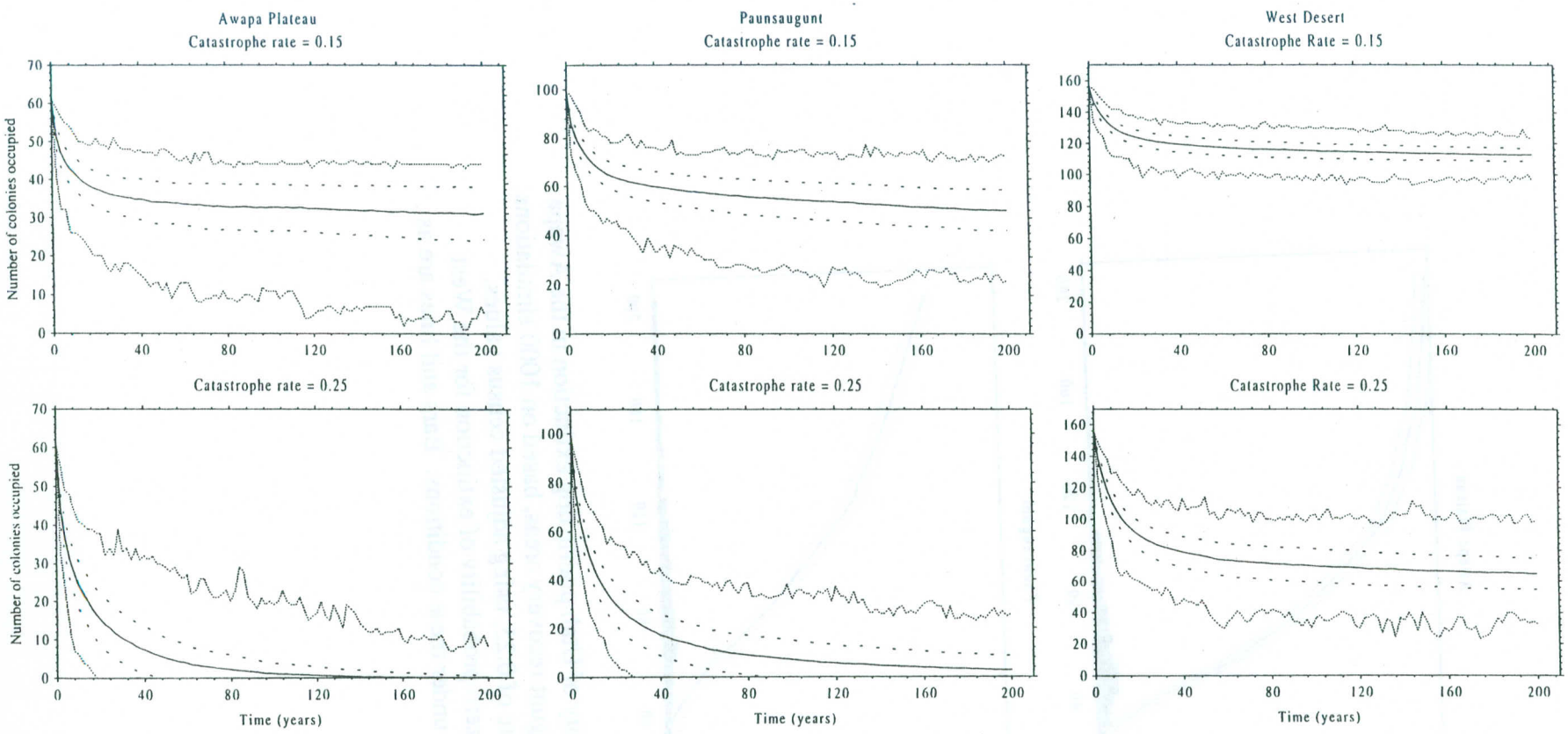


Figure 18. Predicted changes in the numbers of active Utah prairie dog colonies in the three recovery areas, with two different colony-level catastrophe rates. Initial abundance is based on adjusted census values. Lines are as in Figure 12.

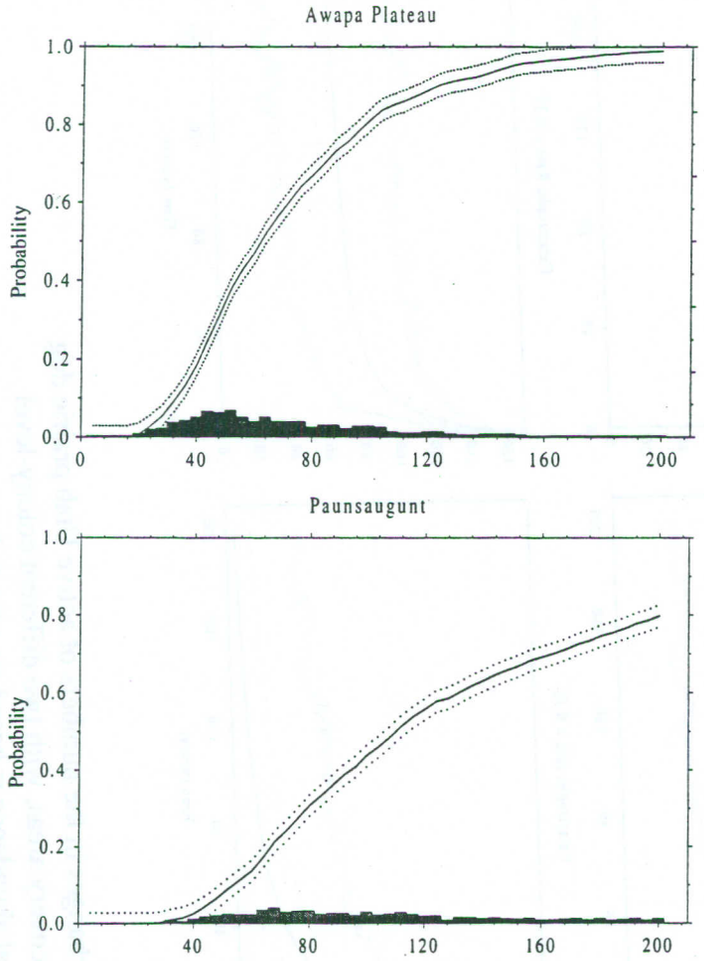


Figure 19. Probability of Utah prairie dog extinction in the Awapa Plateau and Paunsaugunt recovery areas, based on 1000 simulations with a catastrophe rate of 0.25, using adjusted census values. Simulations yielded zero probability of extinction for the West Desert recovery area under these conditions. Bars and lines are as in Figure 15.

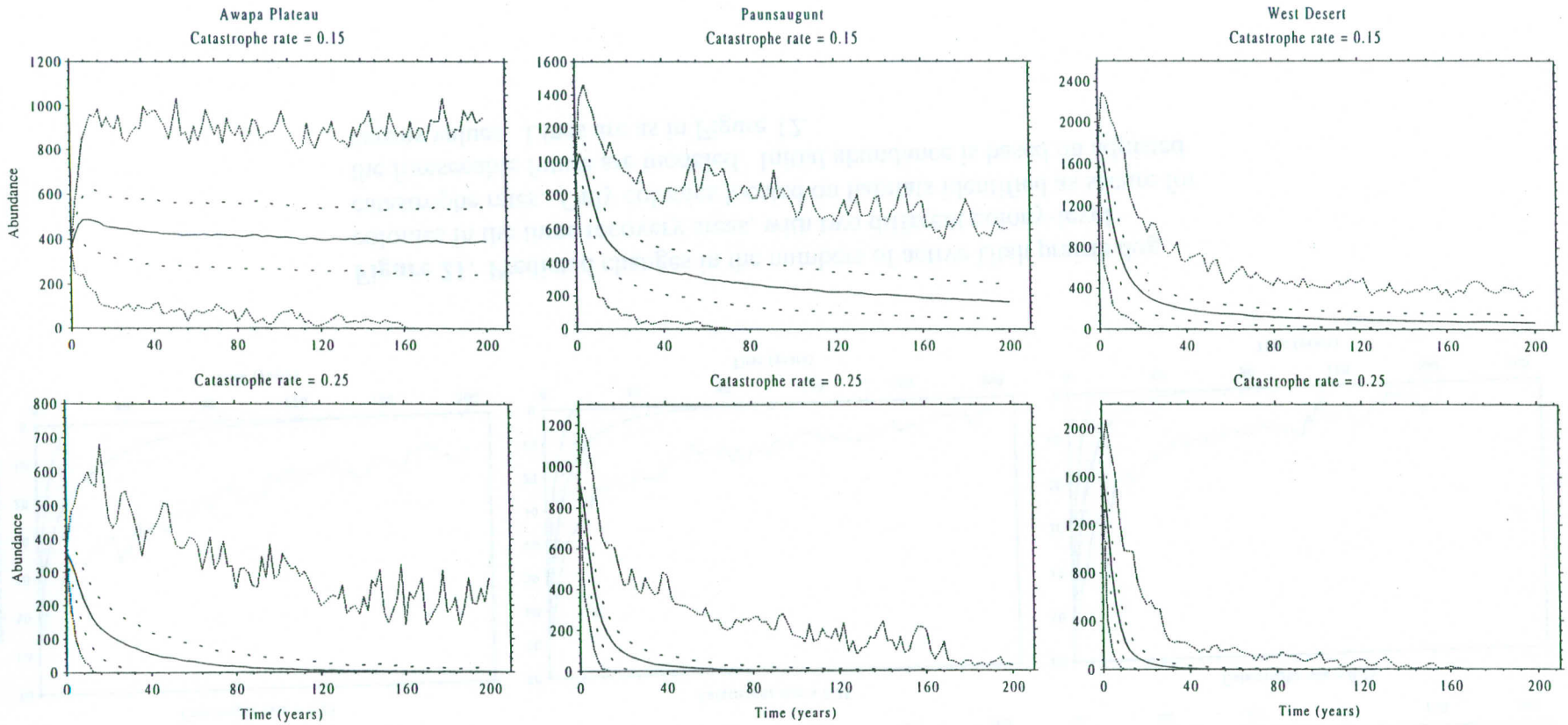


Figure 20. Predicted changes in numbers of female Utah prairie dogs in the three recovery areas, with two different colony-level catastrophe rates. Only colonies located on habitats identified as secure for the foreseeable future are modeled. Initial abundance is based on adjusted census values. Lines are as in Figure 12.

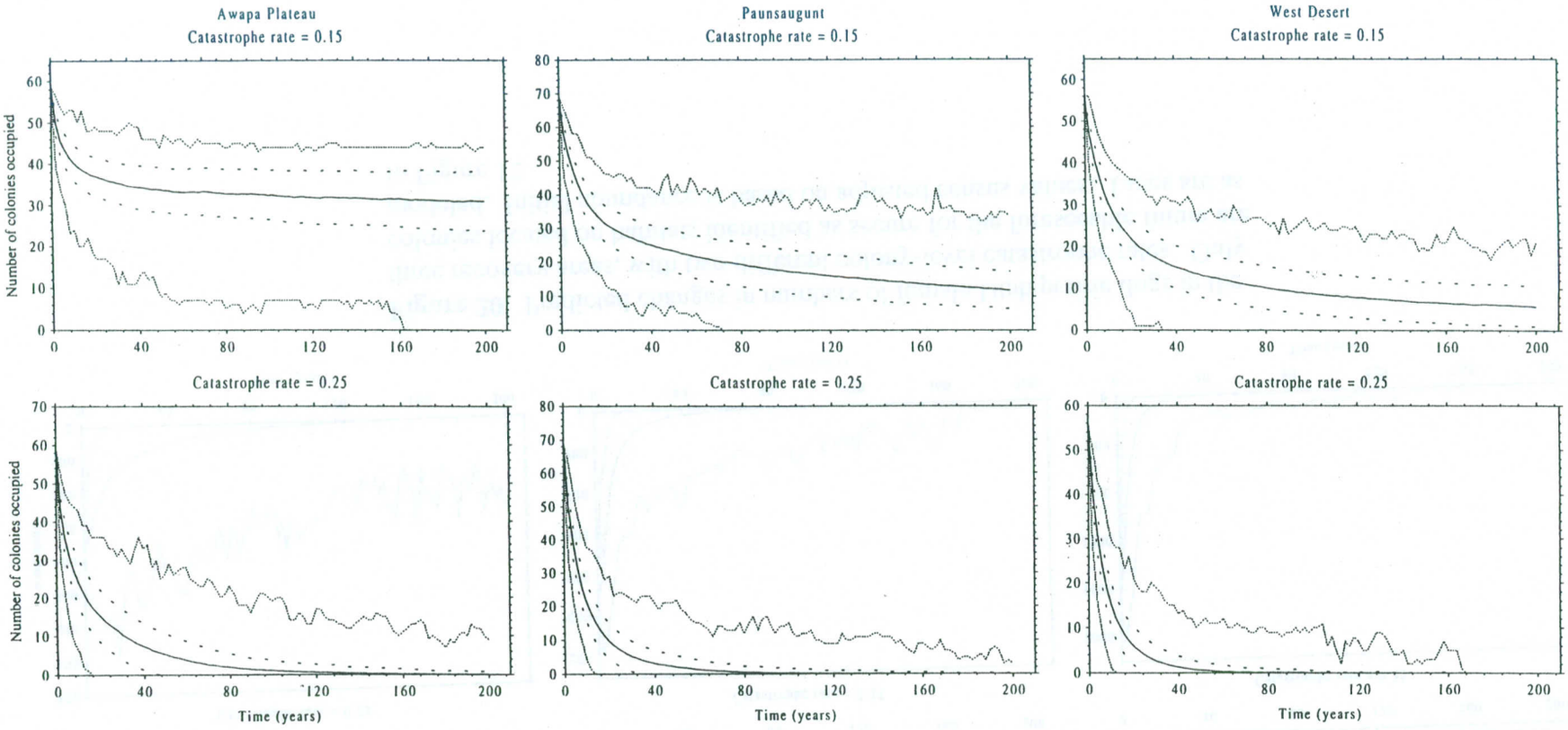


Figure 21. Predicted changes in the numbers of active Utah prairie dog colonies in the three recovery areas, with two different colony-level catastrophe rates. Only colonies located on habitats identified as secure for the foreseeable future are modeled. Initial abundance is based on adjusted census values. Lines are as in Figure 12.

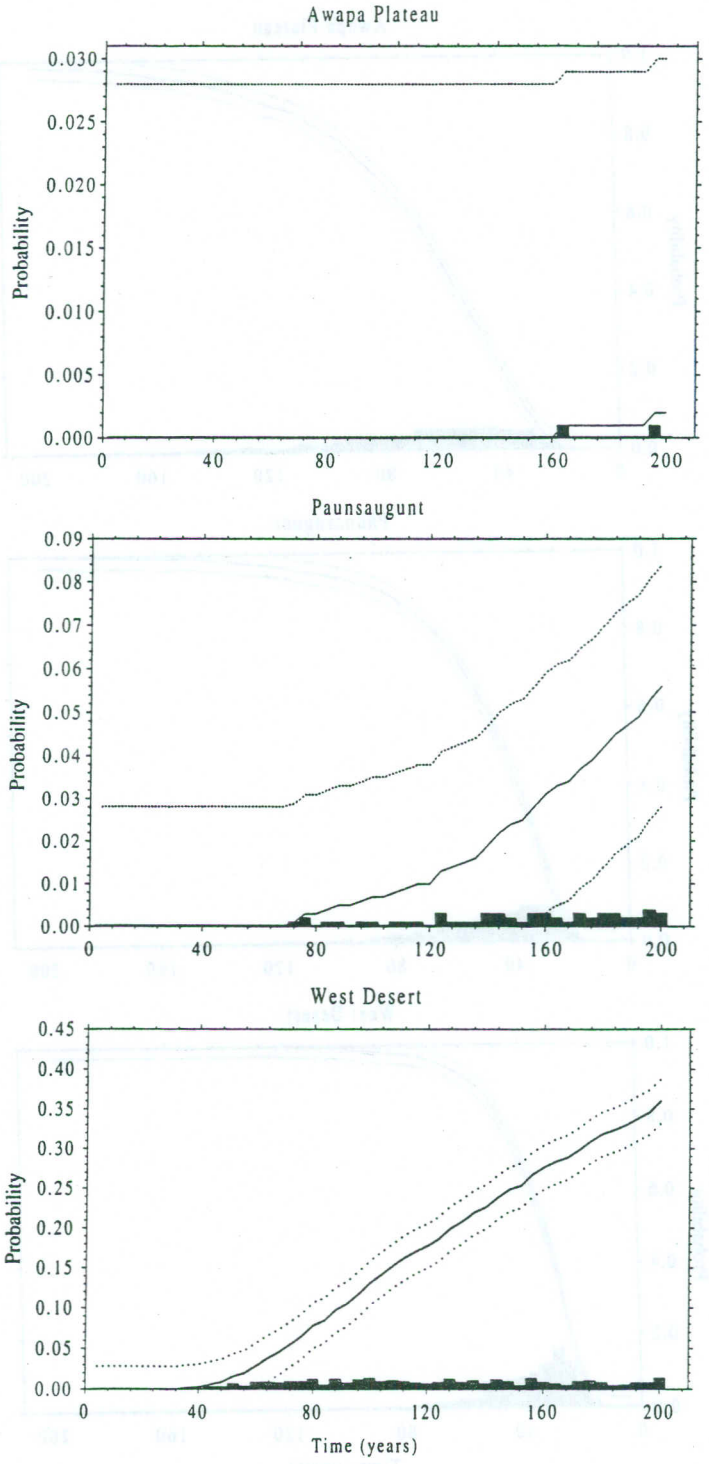


Figure 22. Probability of extinction in Utah prairie dog recovery areas, based on 1000 simulations with a catastrophe rate of 0.15, using adjusted census values and modeling only colonies on habitats identified as secure for the foreseeable future. Bars and lines are as in Figure 15.

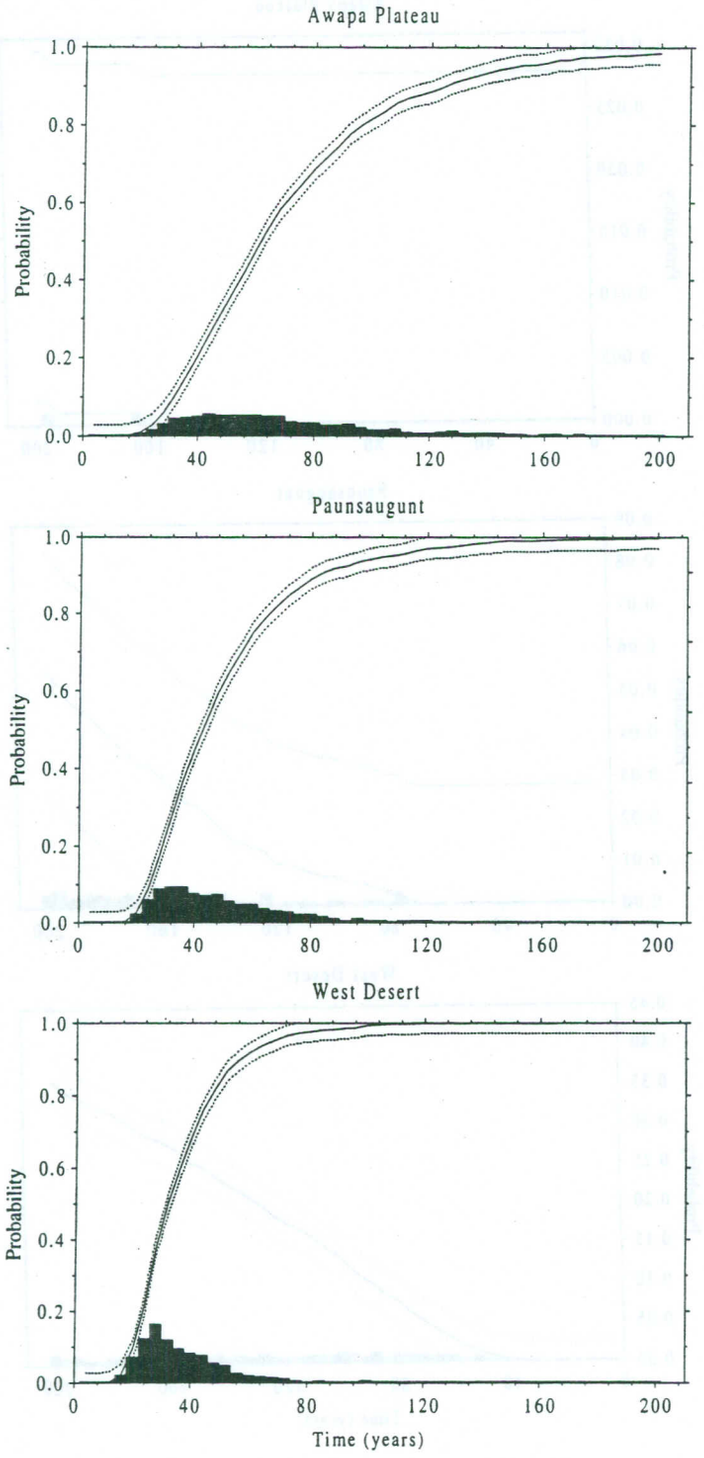


Figure 23. Probability of extinction in Utah prairie dog recovery areas, based on 1000 simulations with a catastrophe rate of 0.25, using adjusted census values and modeling only colonies on habitats identified as secure for the foreseeable future. Bars and lines are as in Figure 15.

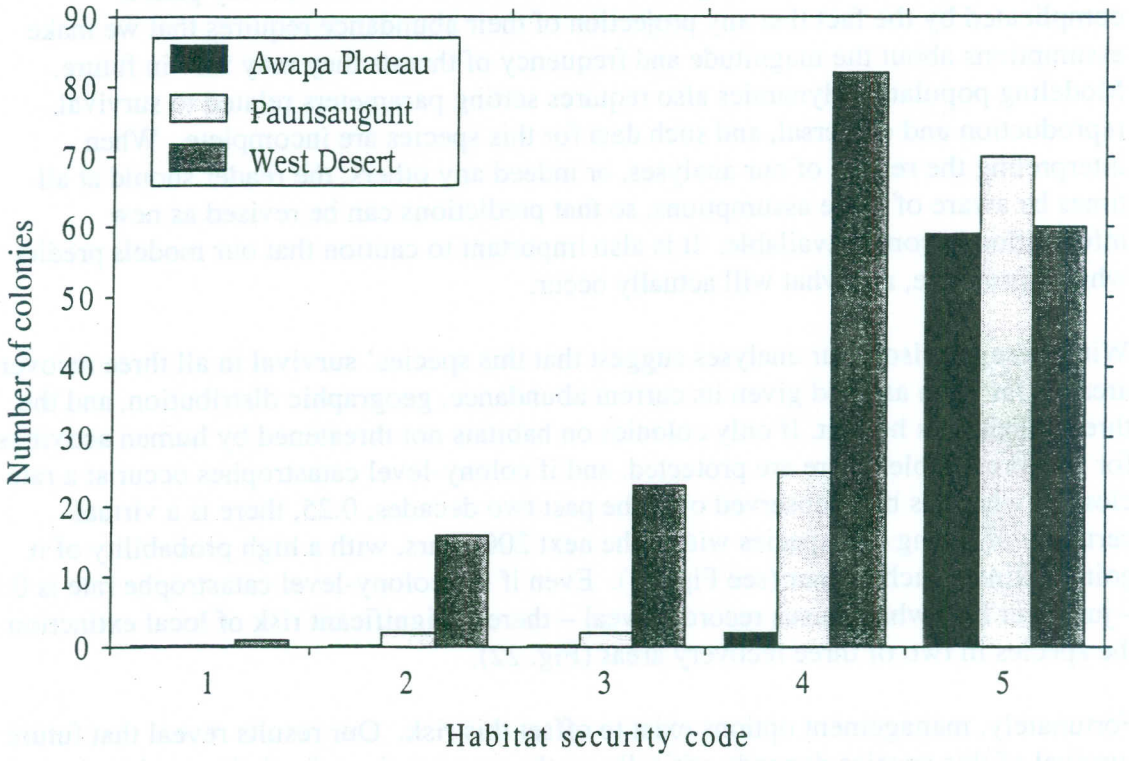


Figure 24. Threat to prairie dog colony habitat. Habitat security codes are as defined above in *Methods*, with 1 being most threatened and 5 least threatened.

Discussion

Management of Utah prairie dogs to meet the mandate of the recovery plan is complicated by the fact that any projection of their abundance requires that we make assumptions about the magnitude and frequency of threats they may face in future. Modeling population dynamics also requires setting parameters related to survival, reproduction and dispersal, and such data for this species are incomplete. When interpreting the results of our analyses, or indeed any others, the reader should at all times be aware of these assumptions, so that predictions can be revised as new information becomes available. It is also important to caution that our models predict what is probable, not what will actually occur.

With these provisos, our analyses suggest that this species' survival in all three recovery areas is far from assured given its current abundance, geographic distribution, and the threats facing its habitat. If only colonies on habitats not threatened by human activities for the foreseeable future are protected, and if colony-level catastrophes occur at a rate close to what has been observed over the past two decades, 0.25, there is a virtual certainty of losing this species within the next 200 years, with a high probability of it going extinct much sooner (see Fig. 23). Even if the colony-level catastrophe rate is 0.15 – just over half what census records reveal – there is significant risk of local extinction of the species in two of three recovery areas (Fig. 22).

Fortunately, management options exist to offset this risk. Our results reveal that future survival of this species depends critically on the preservation of existing prairie dog colonies, so immediate steps should be taken to preserve the suitability of habitat that currently supports Utah prairie dogs. Our most urgent recommendation is based on the alarming susceptibility to potential habitat destruction of the most successful recovery area population, in the West Desert (Fig. 24). As many West Desert colonies are on private land, obtaining the cooperation of private landowners and developers in preserving prairie dogs is most critical in the West Desert recovery area.

If existing prairie dog habitat in the West Desert recovery area can be protected, our simulations suggest that colonies there are sufficiently dense to permit natural recolonization following catastrophic events like plague and drought and to prevent extinction (Figs. 14, 17 and 18). However, we note with concern that even if all existing colonies in the Paunsaugunt and Awapa Plateau recovery areas are protected from human activity, these two recovery areas are still at risk of extinction, given realistic estimates of colony-level catastrophe rates (Figs. 17 - 19). This is because colonies are too sparsely distributed there for natural dispersal to restock colonies that have been wiped out (Fig. 14). Successful establishment of new Utah prairie dog colonies close enough to existing colonies to allow movement of colonists is critical to ensure the species' persistence in those areas.

An important determinant of future Utah prairie dog success is the distance between colonies, which dictates prairie dogs' ability to recolonize areas that have suffered

catastrophic losses. Reducing inter-colony distances could be achieved by placement of new transplant colonies between existing colonies, to provide additional sources of dispersers. Increased transmission of disease, particularly plague, is a concern when locating new colonies. We lack precise information about the optimal inter-colony distance that maximizes prairie dog exchange without increasing the risk of plague transmission, but placement of new colonies within approximately 2.5 km of others would allow for a degree of prairie dog dispersal (Fig. 5) without necessarily increasing the spread of plague (Jack Cully, pers. comm.).

Alternatively or concurrently, managers could reintroduce prairie dogs into sites where colonies have died out, as is current practice. The latter approach requires that colonies continue to be monitored annually, so that catastrophes can be detected and colonies restocked.

A larger Utah prairie dog population provides a greater number of dispersers that can resupply eradicated colonies naturally. Because even large colonies can be wiped out by catastrophes, however, simply increasing numbers of prairie dog individuals at each colony should not be the primary management goal. Increasing the number of distinct colonies offers a better guarantee of long-term survival.

We have not considered the existing physical barriers that could impair prairie dog dispersal (e.g., roads). This issue needs to be addressed when situating new transplant colonies, and should be incorporated into any environmental impact assessments for development in Utah prairie dog areas.

Another way to decrease extinction risk is to decrease the rate of catastrophes. Ritchie (1998, 1999) revealed a strong negative correlation between the frequency with which colonies crashed to low levels and plant diversity (i.e., prairie dog numbers crashed more when plant diversity was low). Managing existing prairie dog habitats for high plant diversity, and situating translocated colonies at high-diversity sites, could reduce the frequency with which colonies suffer catastrophic declines.

Our results suggest that different management priorities should be assigned to Utah prairie dogs in the three recovery areas. As shown in Figure 24, prairie dog habitat is at greater risk of development in the Paunsaugunt than the Awapa Plateau, and in the West Desert than in either of these recovery areas. Efforts to protect prairie dog habitat should, therefore, be undertaken most urgently in the West Desert, followed by Paunsaugunt and then the Awapa Plateau.

Conversely, the order of priority for establishing new transplant colonies should be the reverse of the ranking for habitat protection. The Awapa Plateau currently has the fewest and most sparsely distributed colonies (Fig. 14), so once existing prairie dog habitat is protected in all three recovery areas, prairie dogs in the Awapa Plateau still face the greatest risk of extinction (Figs. 17 – 19). The West Desert has the most favorable distribution of colonies, and the lowest extinction risk if these are protected; corresponding values for Paunsaugunt fall in between those for the West Desert and

Awapa Plateau (Figs. 14, 17 – 19). Efforts to establish new transplant colonies should, therefore, focus on the Awapa Plateau, followed by Paunsaugunt and the West Desert.

An assumption of the matrix approach we have used in our simulations is that individuals of the same age are likely to have the same survival and fecundity rates, and that population structure is stable and stationary. Menkens and Anderson (1989), however, found considerable variation among six white-tailed prairie dog (*Cynomys leucurus*) towns in Wyoming within years, and within towns among years, in reproductive rates and the percentage of females that bred. Population densities and annual survival rates also fluctuated in time and space. Menkens and Anderson (1989) cautioned that the assumptions made in life table models that age distributions are stable or stationary are not met in white-tailed prairie dogs, and probably not in other ground squirrel species.

This caution is undoubtedly applicable to *C. parvidens*, which is closely related to *C. leucurus*. For example, Mackley (1988) reported that 96 - 98 % of adult females brought a litter above ground each year from 1985 to 1987 in his study site in John's Valley. This stands in marked contrast with values for Utah prairie dogs in Bryce Canyon National Park in 1993, when only 25 % of females succeeded in bringing a litter above ground, possibly due to burrow flooding following high snowfall the previous winter and spring (Hoogland pers. comm., cited in McDonald 1995).

To arrive at increasingly realistic predictions of future Utah prairie dog abundance, therefore, we require rigorous measurements of survival and fecundity rates for different age classes of this species, as John Hoogland has carried out for black-tailed and Gunnison's prairie dogs (Hoogland 1995; in review) and as he is currently carrying out for Utah prairie dogs (John Hoogland, pers. comm.). A better understanding of the range of these values that is realistic for Utah prairie dogs will allow construction of simulation models that incorporate variability in life history parameters.

We also need a better understanding of plague dynamics in this species; in particular, we require knowledge of what range of population densities predisposes a colony to a plague outbreak, so that optimal colony size can be determined. Also important to determine is the role of other mammal species in harboring plague between outbreaks in prairie dogs (Anderson and Williams 1997; Cully et al. 1997)

Finally, more research should be undertaken to account for the difference in past success of Utah prairie dogs in different colonies, especially on private versus on public lands. A mechanistic understanding of this difference would point out habitat features that are important to replicate – and to avoid – when managing for prairie dogs.

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ENVIRONMENTAL DEFENSE
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July 17, 2000

To: Ted Owens, Keith Day, Becky Bonebrake, Teresa Bonzo, Kate Grandison, John Hoogland, Mark Ritchie, Michael Soulé

From: David Wilcove DW

Re: Utah Prairie Dog PVA

Enclosed please find the final report of the Princeton team. We welcome your comments and suggestions. You should also feel free to contact the authors directly. Their email addresses are as follows:



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Robert Bonnie and I are very grateful to all of you for your assistance with this project.

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ENVIRONMENTAL DEFENSE
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MEMORANDUM

TO: Ted Owens, Keith Day, Becky Bonebrake, Teresa Bonzo, Kate Grandison, John Hoogland, Mark Ritchie, Michael Soulé

FROM: David Wilcove DW

DATE: July 20, 2000

RE: Corrections to *Population Viability Analysis of the Utah Prairie Dog*

Attached are three pages with corrections for the *Population Viability Analysis of the Utah Prairie Dog*, which was mailed to you earlier this week. Please note that these changes do not affect the major conclusions of the report.

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Princeton, New Jersey 08544-1003

19 July 2000

Dr. David Wilcove
Senior Ecologist
Environmental Defense
1875 Connecticut Ave., NW
Washington DC 20009

Dear David,

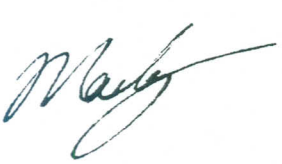
Enclosed are three corrected pages for the *Population Viability Analysis of the Utah Prairie Dog*. Carrying over from a database error that affected the draft version of the report, the 1999 Paunsaugunt census did not appear correctly in the middle panel of what is now Figure 4 on p. 5 in the final report we sent you. This results in a spurious population crash in 1999 in the Paunsaugunt recovery area. The same error affects the 1999 total counts and proportions in Figures 2 and 3 on p. 4. The enclosed pages 4 and 5 correct the error in the Paunsaugunt count so that these three Figures give the true 1999 census values.

I regret that none of us discovered this mistake sooner. The reason it escaped notice is likely that Figures 2 – 4 give only the historical trends in Utah prairie dog numbers, and do not enter into the population viability analysis *per se*. None of the text of the report is affected by this error. Our simulations are also unaffected because we used the 1998 census, not the 1999 census, as initial abundance in all simulations. Even if we had used the 1999 census, the simulations use colony counts, not the complex counts in which the error originated, so would have been unaffected. None of our results or conclusions is affected in any way by this error or its correction.

I am also taking this opportunity to send you a copy of p. 17 on which I have corrected column width problems in Table 3 (the "s" in "Juveniles" split to a second row in the final report), and in the list of habitat security rankings (for category 3, the word "development" split to a second row in the final report). These changes are purely cosmetic.

I apologise for these errors, and hope that the enclosed corrections will forestall any criticism of the report that might have resulted from other readers finding them first.

Best wishes,



W. Mark Roberts

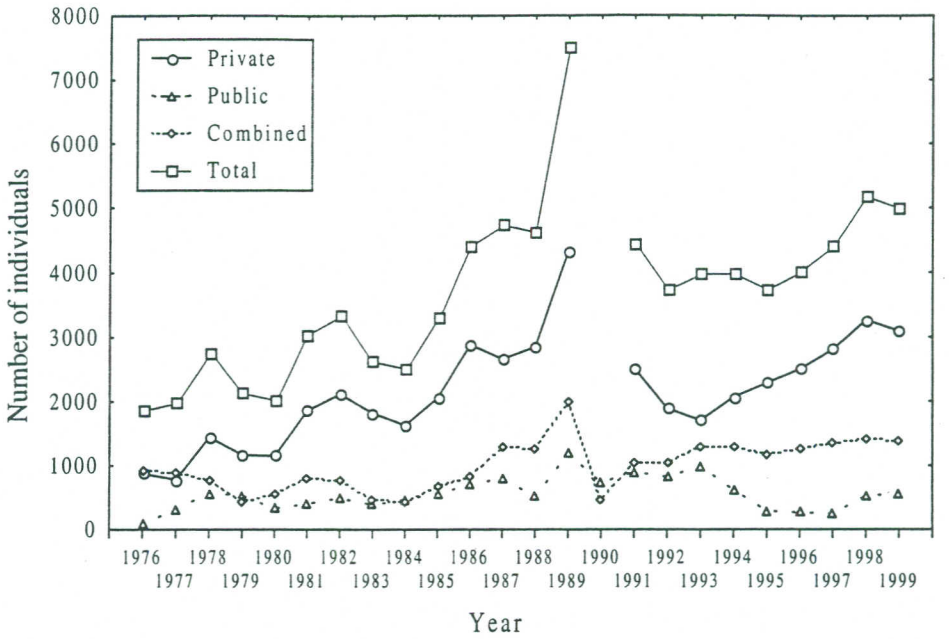


Figure 2. Numbers of Utah prairie dogs counted in Spring censuses from 1976 to 1999, categorized by current ownership of land on which their complexes are found. There was no Spring census on private land in 1990. Complexes on combined-ownership land have some of their constituent colonies on private land and some on public land.

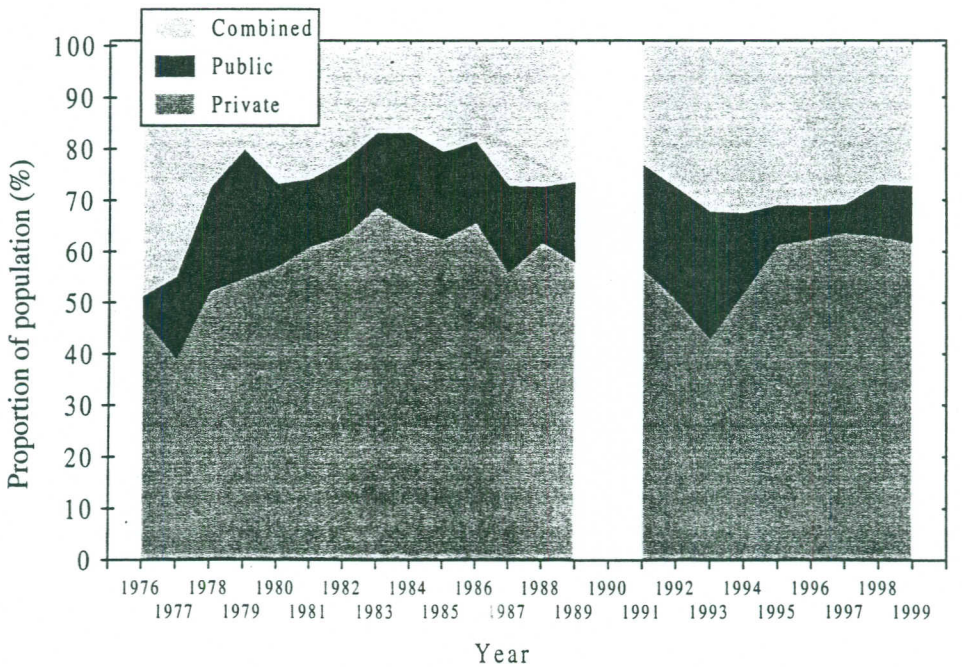


Figure 3. Proportion of Utah prairie dog population on public, private and combined-ownership land from 1976 to 1999.

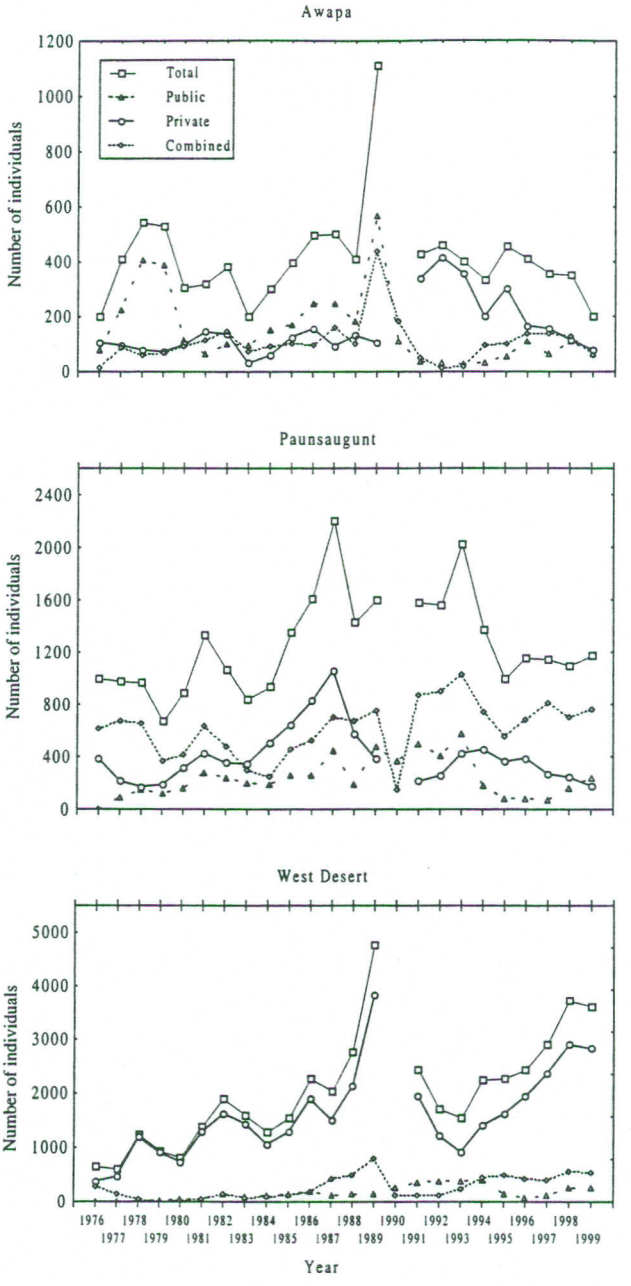


Figure 4. Numbers of Utah prairie dogs counted in Spring censuses from 1976 to 1999 in each of the three recovery areas, categorized by current ownership of land on which their complexes are found. There was no Spring census on private land in 1990.



Table 3. Derivation of relative dispersal rate. Data are from Mackley (1988).

	Juveniles	Adults
N (1986 cohort)	164	61
Proportion (1986 cohort)	0.729	0.271
× 646 individuals captured 1985-87	470.9	175.1
Migrants 1985-87	67	11
Dispersal rate	14.23	6.28
Relative dispersal rate	1	0.44

In our simulations, Utah prairie dogs do not establish new colonies. Modeling this possibility would require detailed, spatially explicit data that indicate what locations are available and suitable for new colonization.

Habitat security

The Utah Division of Wildlife Resources classified the habitat of each individual prairie dog colony based on the degree of risk that they face. This classification ranked the security of habitat as follows:

1 - habitat has been eradicated
2 - habitat partially developed, development continues
3 - habitat partially developed or disturbed, but no current development
4 - habitat currently secure, but future development possible
5 - habitat secure for the foreseeable future.

Colonies in category 1 habitats were previously mapped, but have since been eliminated by development. Category 2 habitats are experiencing ongoing development, such that Utah prairie dog colonies in these habitats are not expected to persist. Colonies in category 3 habitats have been impacted by development in the past, and are likely to be again by future development. Category 4 habitats are not currently undergoing development, but are either on privately owned land or near enough to human activities that they are potentially at risk. Category 5 habitats are on public lands and/or in remote locations so far from human population centers and activities that they are unlikely to be threatened by humans. While it is not possible to place a precise time frame on the security of prairie dog colonies in category 5 habitats, they are expected to be safe from development and other human pressures for at least the next 20 years, and likely much longer (Keith Day, pers. comm.).