VITALLY IMPORTANT: THE ROLE OF DEMOGRAPHY IN ASSESSING THE CURRENT AND FUTURE STATUS OF BLACK-TAILED PRAIRIE DOGS

BY

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ABSTRACT

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Black-tailed prairie dogs have declined across their range by an estimated 98% in the last 100 years as the result of habitat loss, disease and human persecution. Commonly regarded as a keystone species, they represent a unique conservation dilemma because of their importance to other species, (e.g. the black-footed ferret-*Mustela nigripes*), while having the general reputation as an agricultural pest.

Conservation of black-tailed prairie dogs largely involves documenting their status by estimating occupied habitat throughout their range, or attempting to expand prairie dogs into areas where they were historically present. Both of these aspects of prairie dog conservation lack information about vital rates that are important to assessing and managing the species.

In 2004, black-tailed prairie dogs were removed from the candidate list for protection under the Endangered Species Act because it was concluded that threats to the species were exaggerated. This decision was based on indices which are potentially biased and unreliable. I studied three colonies of black-tailed prairie dogs over the course of three years testing mark-resight methods against other approaches. I found that mark-resight outperforms other approaches for estimating population size in addition to providing valuable demographic data. I concluded that resource agencies should employ a multi-faceted approach to monitor prairie dogs that should be augmented with demographic data from the colony level.

Prairie dog conservation plans estimate that the greatest potential habitat for black-tailed prairie dogs occurs within desert grassland. The extent of this habitat is considerable (42% of total habitat; > 40,000,000 ha), but conservation plans have failed to explore the differences that climate exerts on vital rates of prairie dogs in desert grasslands. These regions are the driest portion of the black-tailed prairie dog's range and this creates a circumstance that may hinder prairie dog population growth. I studied six reintroduced colonies of black-tailed prairie dogs for three years using mark-recapture/resight techniques to elucidate patterns of survival and reproduction. I documented rapid declines in monthly survival that coincide with loss of adult body mass and a year of extreme below-average precipitation. Vital rates were linked to body mass and resource limitation. I conclude that further exploration of climate and resource limitation is vital to understanding and conserving populations of black-tailed prairie dogs in desert grasslands.

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CHAPTER I

WAS THE REMOVAL OF THE BLACK-TAILED PRAIRIE DOG FROM THE CANDIDATE SPECIES LIST JUSTIFIED?

Abstract:

Black-tailed prairie dogs (*Cynomys ludovicianus)* were originally considered for listing under the U.S. Endangered Species Act, but were removed from the candidate species list in 2004 after the U.S. Fish and Wildlife Service concluded that the area they occupied was greater than previously estimated and that threats to the species were exaggerated. This decision was based largely on remotely sensed estimates of occupied habitat – an index of abundance. Indices often are biased rendering them unreliable for monitoring populations. I introduce a novel application of mark-resight to estimate prairie dog demographic parameters and show that mark-resight outperforms other approaches. Estimates of prairie dog density from 3 colonies over a 3-year period varied considerably (1.3 to 28.3 prairie dogs/ha) and, when applied to the area potentially occupied by prairie dogs in the United States (745,400 ha), yielded a range-wide abundance of < 1 million to > 21 million prairie dogs. Exclusive use of indices and/or estimates of prairie dog density from a limited portion of their range may result in inaccurate estimates of range-wide abundance, and may adversely affect conservation decisions. Resource agencies should consider a multifaceted approach to prairie dog conservation that includes: 1) an assessment of

range-wide occupancy coupled with, 2) a determination of colony extinction dynamics at the regional level that is, 3) augmented with demographic data at the colony level. Until such data are available, the status of the black-tailed prairie dog is really unknown.

Introduction

Effective management of prairie dogs (*Cynomys* spp.*)* has become necessary owing to declines in all five species, the listing of two species (Utah prairie dog, *C. parvidens* and Mexican prairie dog, *C. mexicanus*) under the U.S. Endangered Species Act (hereafter, ESA), and the need to identify suitable habitat for reintroducing the endangered black-footed ferret (*Mustela nigripes*) (USFWS, 1970, 1984**,** 2000, 2004; Miller et al., 1996). Viable populations of Cynomys, a genus endemic to North America are necessary for recovering black-footed ferrets because of the obligate nature of their predator-prey relationship. Black-tailed prairie dogs (*C. ludovicianus)* occurred over an area of ~ 160 million ha but have declined across most of their historic range (Miller et al., 1996; Proctor et al., 2006). They were considered for listing under the ESA but were recently removed from the candidate species list in 2004 after the U.S. Fish and Wildlife Service (USFWS) reevaluated their status and concluded that the area they occupied was greater than previously estimated and that threats to the species were not as serious as once believed (USFWS, 2000, 2004; Manes, 2006).

Recent range-wide estimates of black-tailed prairie dog abundance were based primarily on remotely sensed estimates of "occupied habitat" (745 400 ha in the United States; 766 000 ha in North America including southern Canada and northern Mexico) rather than numbers of individuals because of the associated effort and cost of estimating population size over such a large spatial scale (Dalsted et al., 1981; Sidle et al., 2001, 2002; USFWS, 2004; White et al., 2005; Manes 2006). Although remote sensing is probably the only approach available to assess abundance across the continent, a remote estimate of habitat occupied by prairie dogs is nonetheless simply based on the presence or absence of prairie dog burrows. These indices cannot be used to enumerate prairie dogs nor can they be used to distinguish a truly occupied colony from one that was extirpated or that has experienced a precipitous decline (Biggins et al., 2006). Indices are notoriously problematic (Anderson, 2001, 2003) and remote approaches fail to take into account differences in density throughout a colony, a complex or a species range (White et al., 2005).

In their recent decision to remove the black-tailed prairie dog from the candidate species list, the USFWS used an average density of 24.71 prairie dogs/ha to estimate total abundance (18,420,000 individuals); however, they noted that prairie dog densities can vary from 5 – 45 prairie dogs/ha, and were unclear as to how those estimates were derived and whether they were representative of the species density across its entire range (USFWS, 2004).

Estimating vital rates, such as survival and reproduction, that influence demography, are important for conserving vertebrate species (Morris and Doak,

2002) but are lacking in current prairie dog conservation plans and in the recent USFWS reanalysis. Habitat loss and plague (*Yersinia pestis)* are considered the main causes of decline in prairie dogs (Menkens and Anderson, 1991; Cully et al., 1997; Cully and Williams, 2001). Prairie dog populations also fluctuate in response to habitat quality (Rayor, 1985), colony age (Garrett et al., 1982); and the persistence of colonies is influenced by their size and connectivity (Lomolino and Smith, 2001; Lomolino et al., 2003). In sum, the processes influencing prairie dog populations are poorly understood.

Here I advocate an approach that incorporates mark-resight to estimate prairie dog population size and vital rates. I compare the utility of mark-resight to other approaches, address current threats and discuss the conservation issues related to the black-tailed prairie dog. I conclude with a plea for adopting a multifaceted approach to more accurately assess their status that includes: 1) range-wide estimates of occupied habitat derived from remote sensing that are 2) verified on a regional level by observing or estimating whether colonies are truly occupied and 3) incorporating estimates of demographic parameters using mark-resight that can be used to model demography and estimate range-wide abundance.

Methods

Study Site and Study Populations

My study was conducted on the Armendaris Ranch, Engle, Sierra County, NM. The Armendaris Ranch, owned by Turner Enterprises, is a working bison (*Bison*

bison) ranch dedicated to wildlife conservation. Located at the northern end of the Chihuahuan Desert the ranch contains desert grasslands dominated by perennial grasses including alkali sacaton (*Sporobolus airoides*), burrograss (*Scleropogon brevifolius)* and tobosa (*Pleuraphis mutica)*.

A total of 19 prairie dog colonies have been established on the ranch in an effort to reestablish the species (Truett and Savage, 1998). I studied the three oldest and largest colonies on the ranch: 1) Deep Well Colony (DWC) established in 1999 and currently 9 ha in size (2005); 2) Red Lake Colony (RLC) established in 1998 and currently 11.75 ha; and 3) S-Curve Colony (SCC) established in 1999 and currently 6 ha. From January 2003 through October 2005, I estimated population size and survival from 33 mark-recapture and 29 resight sessions. Sessions were conducted such that estimates could be made prior to (pre-birth) and after (post-birth) the emergence of juveniles. Colonies were 3-6 km apart. Topography was flat (slopes < 5%) and vegetation height low creating few features to hinder observation of prairie dogs.

These three colonies have a known history with specific dates of reintroduction, number of animals reintroduced, and documented expansion (Northcott, 2004). The small size of the colonies helped to accurately delineate colony area and make our estimates of density more precise. Their relative isolation reduced the influence of dispersal, ensuring geographic closure and enabling more accurate population estimates (Hoogland, 1995).

Capture and Marking

A sufficient number of medium-sized box traps (61 cm x 18 cm x 20 cm steel-mesh live traps, Wildlife Control Supplies, Simsbury, CT) was used such that any single prairie dog had access to multiple traps (2-3 traps per burrow). Changes in population size caused us to alter my trap allocations to colonies. The average number of traps used at DWC, RLC and SCC was 108 (SD = 21.6), 177 (SD = 41.1) and 123 (SD = 46.5) traps, respectively, and at no time were fewer than 75 or greater than 238 traps used at any colony. Traps were pre-baited for one week before being set. Captured animals were uniquely marked using a subcutaneous passive integrated transponder (TX1440ST, Biomark, Boise, ID) and externally marked with a unique alphanumeric code using Nyanzol-D dye (Albanil Dyestuff Manufacturers, Jersey City, NJ), that remains visible until they molt (King, 1955). Prairie dogs were trapped for several consecutive days until greater than 50% of the colony was marked prior to initiating mark-resight sampling sessions. All capture and handling methods followed guidelines of the Institutional Animal Care and Use Committee (NMSU Permit No. 2002 - 06).

Resight Scans

Scans were performed from an elevated position (3 m) using a 20-60x spotting scope. Scans began and ended at predetermined points located off colony and were conducted in the morning (0700 - 1000 hrs) and/or evening (1600 - 1900 hrs) to minimize heat mirage and maximize the number of individual animals that could be observed. Marked animals were identified and unmarked animals were simply counted. Resight sampling was based on the robust design (Pollock, 1982). Trapping sessions were divided into periods in which the population was assumed closed from births, deaths, immigration and emigration. These periods consisted of 2-6 individual scans (secondary periods) and comprised a single primary period for which the interval between primary periods was assumed to be open.

Population Estimates

The timing of scans, relative to periods when marks were applied, could not always allow for the assumption of a closed population. Despite this violation, an unbiased estimate of initial population size is possible with the Lincoln-Petersen estimator (Seber, 1982). I used the unbiased Lincoln-Petersen estimator proposed by Chapman (1951) to estimate initial population size from each scan:

$$\hat{N} = \{(M + 1) * (n + 1) / (m + 1)\} - 1$$

Where M = number of marked animals in the population

n = total number of animals seen during scan

m = number of marked animals seen during scan

The mean of all scans was used to estimate initial population size for a colony, which was defined as the first primary period following the initial marking session within each season; this corresponded to a time frame when marks would not have been lost via molting. The minimum number of animals known alive (MNKA) was determined by adding the total number of marked animals to the maximum number of unmarked animals observed during this or subsequent primary periods. I made estimates of the MNKA for subsequent primary periods by positively identifying that a marked animal was alive either during that period or any following period and adding the number of marked animals to the maximum number of unmarked animals observed during the particular primary period.

The Chapman estimator is potentially biased when a small percentage of the population is marked, when the probability of sighting an individual is low or when individual heterogeneity in sighting probability exists (White and Garrott, 1990; White and Shenk, 2001). I assumed *a priori* that the Chapman estimator would perform less satisfactory compared to other estimators and would therefore serve as a minimum standard for comparison to other methods, such as mark-recapture. To evaluate this potential bias, I compared population estimates from the Chapman estimator with those made using the Joint Hypergeometric estimator (JHE) and Bowden's estimator as found in program NOREMARK (White, 1996). Data from all scans were used to estimate initial population size with the JHE, but I used only data from those scans that occurred when the population was assumed closed when using Bowden's estimator.

Mark-recapture population estimates were derived using program MARK (White and Burnham, 1999). The Chapman estimator was used when only two trapping occasions were conducted whereas the model selection procedure embodied in MARK was used to select an estimator when three or more trapping occasions were conducted.

The Severson and Plumb (1998; hereafter S and P formula) regression formula was applied to the maximum above ground counts (MAGC) to estimate population size as:

$$\hat{N} = (MAGC - 3.04) / (0.4).$$

Estimates for a primary period utilized the MAGC for that respective time period only.

Using the binomial distribution I tested the null hypothesis that a particular method produced estimates that were above the MNKA 90% of the time. The null hypothesis was rejected if $p \leq 0.05$.

Reduced Effort with Mark-Resight

I assumed that marking more animals at a colony would produce better estimates of population size and then assessed how the accuracy and precision of the estimates changed by marking a reduced percentage of the population. I also used simulations to compare and corroborate inferences drawn from my empirical data.

Population estimates were made with approximately 5%, 10%, 25%, 50% and >60% of the population marked; actual percentages varied depending on the number of marked animals at a particular colony. The estimates of initial population size were assumed unbiased and for this reason I assessed the reduction in marking effort with only these estimates (17 session). I could not estimate population size with a reduced number of individuals marked for five of the 17 sessions, because marks were being lost as a consequence of the molt and I could not confidently identify all individuals. For each level of marking effort, I used 10 random samples of individuals to estimate mean population size and the Coefficient of Variation (CV). In cases where I had an insufficient number of marked animals to create 10 different samples (i.e., the same group of animals was chosen more than once), I used five random samples.

Estimates produced with the highest number of marked animals were considered the “best”. The optimal estimates were compared to those made with a reduced percentage of the population marked by calculating the percent deviation and the CV and examining both for a relationship with the percent of the colony marked using non-linear regression. Finally, I tested the null hypothesis that 90% of the estimates made at a particular level of marking effort would be above the MNKA using the binomial distribution**.**

A potential flaw with this approach was that I did not know the actual population size and thus how accurate our population estimates were based on a reduced percentage of the population marked. To evaluate this potential bias, I simulated scans for varying levels of marking effort with a known population size and sampling distribution. Simulations were constructed using a random number function (RAND) based on the hypergeometric distribution in SAS (Statistical Application

Software, Cary, NC). This function creates a random value with a probability distribution defined by the following parameters:

N = population size

R = the number of marked animals in a population

n = total number of animals seen on a scan (marked + unmarked).

I simulated two distributions, one for the number of marked animals seen and another for the number of unmarked animals seen. To simulate a single scan I drew a random value from each of these distributions. Each simulated scan was parameterized such that our empirical estimates of initial population size were used as the parameter "N", and the average number of animals seen during a season was used as the parameter "n". The value for "R" changed depending on the percentage of the simulated population that was marked (i.e., if $N = 100$ and 10% of the population were marked, $R = 10$). Scans were simulated with 5%, 10%, 25%, 50%, 75%, and 90% of the population marked. I estimated mean population size with the Chapman estimator. Estimates were made with 2, 10, 50, and 100 scans to gauge how estimates changed with increasing sampling effort. I used non-linear regression to examine the relationship between percent deviation and CV with respect to the percentage of the population marked, and I tested for mean differences in deviation and CV with respect to number of scans using a Kruskal-Wallis ranked ANOVA. I also examined the number of times estimates made with a reduced percentage of the population marked were above the MNKA based on 10 scans using the binomial test.

Simulations were used to infer how precision (CV) changed in response to marking effort and sighting probability. I simulated 100 estimates of population size for each level of marking effort (see above) using sighting probabilities of 0.2 to 0.8. A population size of 100 individuals and 10 scans were used for each population estimate.

Apparent Survival

Survival estimates were made with program MARK (White and Burnham, 1999) using three distinct yet related datasets: mark-resight, mark-recapture, and the combined data. This latter dataset was considered the “optimal” dataset because knowledge of an individual’s presence within any colony was derived from two independent approaches that together maximized the opportunity for detecting an individual animal.

Secondary periods were collapsed to produce an encounter history that could be used in the “recaptures only” option in MARK. Survival analyses were kept simple: I used time, sex, and combinations of those factors to model survival. Global models were tested using the parametric bootstrap goodness of fit test within MARK (100 simulations with random number seed = null). I used the Quasi-Akaike’s Information Criterion-corrected ($QAIC_c$) to select the most appropriate model (Burnham and Anderson, 1998). Apparent survival (Φ) was estimated as a monthly rate. I determined survival for three different seasonal periods, spring (January –

May), summer (May – September) and winter (October - December), by raising the monthly survival rate to the power of time in months.

Reproduction

Reproductive rates were estimated through mark-resight by counting the number of pups first emerging from a particular burrow coupled with identifying the individual adult female using the burrow. Scans were performed multiple times a day from the time juveniles first emerged until juveniles mixed rendering counts of litter size unreliable. The maximum number of pups per female was used to estimate fertility. The total number of litters counted was used as an estimate of the number of reproductively successful females.

Reproductive rates were estimated from mark-recapture sessions conducted within one month after initial emergence. Adult females were deemed to have successfully reproduced if they were noticeably lactating (e.g., swollen teats). Pups trapped together or at the same burrow were considered part of the same litter and lactating females trapped with pups or at the same burrow were considered the mother of that litter. The maximum number of pups associated with a female or burrow was considered the number of young produced by that female. I compared the mean estimates of both reproductive parameters derived from the mark-resight and mark-recapture datasets using a paired t-test.

Results

Population Estimates

Populations underwent a decline at all three colonies from 2003 to 2004 (Figure 1). The DWC declined from 35 animals to 16 (54.3% decline), RLC dropped from 91 to 76 animals (16.5%) whereas SCC experienced a large decline (90.7%) falling from an estimated pre-birth population size of 86 in 2003, to a pre-birth estimate of 8 animals in 2004 (Table 1). In fact, after marking 8 animals in early 2004 I never observed an unmarked animal until after the birth pulse. Population size at all three colonies remained stable or increased from 2004 to 2005.

Estimates of population size made with the Chapman's, JHE, and Bowden's estimators were similar (Table 1). Generally, the Chapman estimator yielded estimates and larger confidence intervals than those derived with either the JHE or Bowden's estimator (Table 1). In subsequent comparisons with other approaches, I "handicapped" the resight approach by using the Chapman's estimator.

Estimates of initial population size were less biased using mark-resight than other approaches. Population estimates made with Chapman's estimator were above the population threshold (MKNA) in all but one instance (5.9%; Figure 1) and could not be rejected as estimating population size above this threshold for 90% of the primary periods ($p = 0.23$, n = 29). In contrast, mark-recapture underestimated initial population size 9 of 17 times (52.9%) which was significantly different from our null hypothesis of being above the MNKA 90% of the time across all primary periods ($p <$

0.01, n = 33). The maximum above ground count (MAGC) was never above the MNKA and estimates made using the S and P formula fell below the MNKA on 6 of 17 (35.3%) occasions, which again was significantly different from our null hypothesis across all primary periods ($p < 0.01$, n = 29).

Reduced Effort with Mark-resight

As the percentage of the population marked increased, the percent deviation between estimates declined ($r^2 = 0.12$, $F_{1,61} = 4.07$, $p = 0.02$) indicating that as more animals were marked the accuracy of the population estimate improved. There was a declining trend in the size of the CV with an increase in the percentage of the population marked but this trend was not significant ($r^2 = 0.05$, $F_{1,61} = 1.44$, $p = 0.24$). Finally, as the percentage of the colony marked increased, there was a greater likelihood that subsequent population estimates were greater than the MNKA (Table 2).

The simulated data mirrored trends in the empirical data. The percent deviation was negatively correlated with the percentage of the population marked (r^2 was 0.40, 0.37, 0.43 and 0.40 when estimates were made using 2, 10, 50 or 100 scans, respectively, $F_{1, 70} = 21.2$ to 26.9, $p < 0.01$ for all), indicating that as a greater percentage of the population was marked, the more accurate the population estimate became regardless of the number of scans employed. Similarly, the CV was

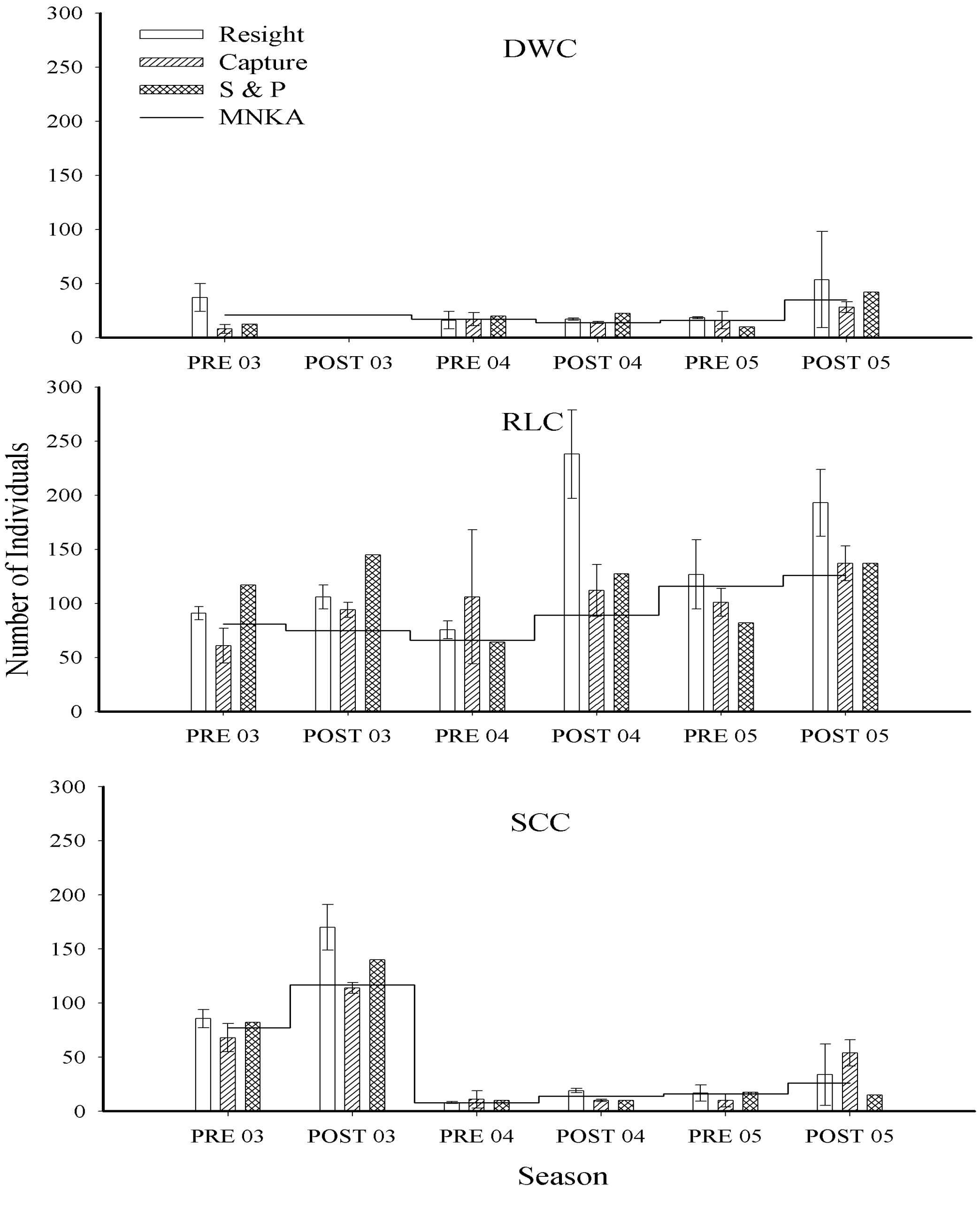

Figure 1. Estimates of population size at three reintroduced colonies of black-tailed prairie dogs (DWC, RLC, SCC) using mark-resight (Resight), mark-recapture (Capture), both with 95% confidence intervals shown, and the Severson and Plumb formula (S & P) compared to the minimum number of animals known alive (MNKA) in the pre and post-birth periods of 2003, 2004 and 2005.

Table 1. Comparison of black-tailed prairie dog population estimates using the Chapman, Bowden's, and Joint Hypergeomtric Estimators (JHE) at three colonies, pre and post-birth pulse, from 2003 to 2005 (95% Confidence Intervals in parentheses).

Colony	Time	Chapman		Bowden's		JHE	
DWC	PRE 03	37	(24 – 50)	---[a]		44	(30 – 78)
	PRE 04	16	(8 – 24)	13	(10 – 18)	24	(19 – 38)
	POST 04	17	(16 – 18)	---[a]		18	(18 – 19)
	PRE 05	18	(17 – 19)	17	(15 – 19)	19	(19 – 20)
	POST 05	54	(9 – 98)	61	(37 – 101)	65	(45 – 119)
RLC	PRE 03	91	(84 – 97)	117	(84 – 165)	91	(88 – 94)
	POST 03	106	(95 – 118)	110	(80 – 140)	110	(103 – 119)
	PRE 04	76	(67 – 84)	68	(60 – 78)	75	(71 – 80)
	POST 04	238	(230 – 248)	248	(175 – 248)	249	(194 – 320)
	PRE 05	127	(95 – 159)	111	(93 – 132)	141	(130 – 154)
	POST 05	193	(162 – 230)	202	(174 – 243)	195	(168 – 235)
SCC	PRE 03	86	(77 – 94)	94	(57 – 153)	82	(80 – 85)
	POST 03	170	(149 – 194)	194	(153 – 247)	173	(190 – 246)
	PRE 04	8	(8 – 8)	8	(8 – 9)	8	(8 – 8)
	POST 04	19	(17 – 22)	---[a]		19	(15 – 27)
	PRE 05	17	(9 – 24)	17	(14 – 20)	17	(16 – 22)
	POST 05	34	(5 – 62)	43	(25 – 76)	42	(30 – 75)

[a] Estimates could not be made with Bowden's estimator because individual records of sighted animals were not kept.

negatively correlated with the percentage of individuals marked (r^2 ranged from 0.15 to 0.35 for all four scan sample sizes, $F_{1,70} = 7.0$ to 20.2, $p < 0.01$). The number of scans used to make estimates did not significantly affect either the percent deviation ($\chi_{kw}^2 = 6.03$, DF = 3, $p = 0.11$) or the CV ($\chi_{kw}^2 = 6.75$, DF = 3, $p = 0.08$), but there was a trend for precision to improve as the number of scans increased.

For the simulated data, estimates of population size were above the MNKA 75% of the time when greater than 50% of the population was marked (Table 2). When 25% of the population was marked estimates were above the MNKA at least 66% of the time. Because of numerous tests, the Type I error rate was inflated so I used a Bonferroni adjustment (0.05/11) which suggested that even when only 25% of the population was marked I could not reject the null hypothesis that 90% of our population estimates would be above the MNKA.

Simulations indicated that both accuracy increased with both marking effort and sighting probability with marking effort having a greater influence (Figure 2). This relationship was non-linear, however, as accuracy approached an asymptote with greater marking effort (Fig 2).

Survival

Mark-resight, mark-recapture, and a combination of both techniques identified similar factors influencing survival at all three colonies (Table 3). Survival rates were affected chiefly by time at DWC and SCC with no sex or interaction effects detected.

Conversely, there was strong support for a sex affect on survival at the RLC but not for time (Table 3).

Table 2. A comparison of the number of population estimates and the proportion of times the estimates were above the minimum number of animals known alive (MNKA) at five different levels of marking effort for a random subset of marked individuals (Random) and six levels of marking effort for a simulated population (Simulated). Significance values (*p*-value) are based on a binomial distribution where the null hypothesis is equivalent to 90% of the estimates being above the MNKA.

Test	Percent of the Colony Marked	Number of estimates Above MNKA	Proportion of estimates above MNKA	*p*-value
Random	5	1	0.09	< 0.01
	10	4	0.33	< 0.01
	25	8	0.66	0.03[a]
	50	12	1.00	1.00
	≥ 60	8	1.00	1.00[b]
Simulated	5	4	0.36	< 0.01
	10	4	0.33	< 0.01
	25	8	0.66	0.03[a]
	50	9	0.75	0.11
	75	10	0.83	0.34
	90	11	0.92	0.71

[a] Not significant with a Bonferroni correction (0.05/11).

[b] Sample size is reduced to eight because $\geq$60% of population was not marked in four cases.

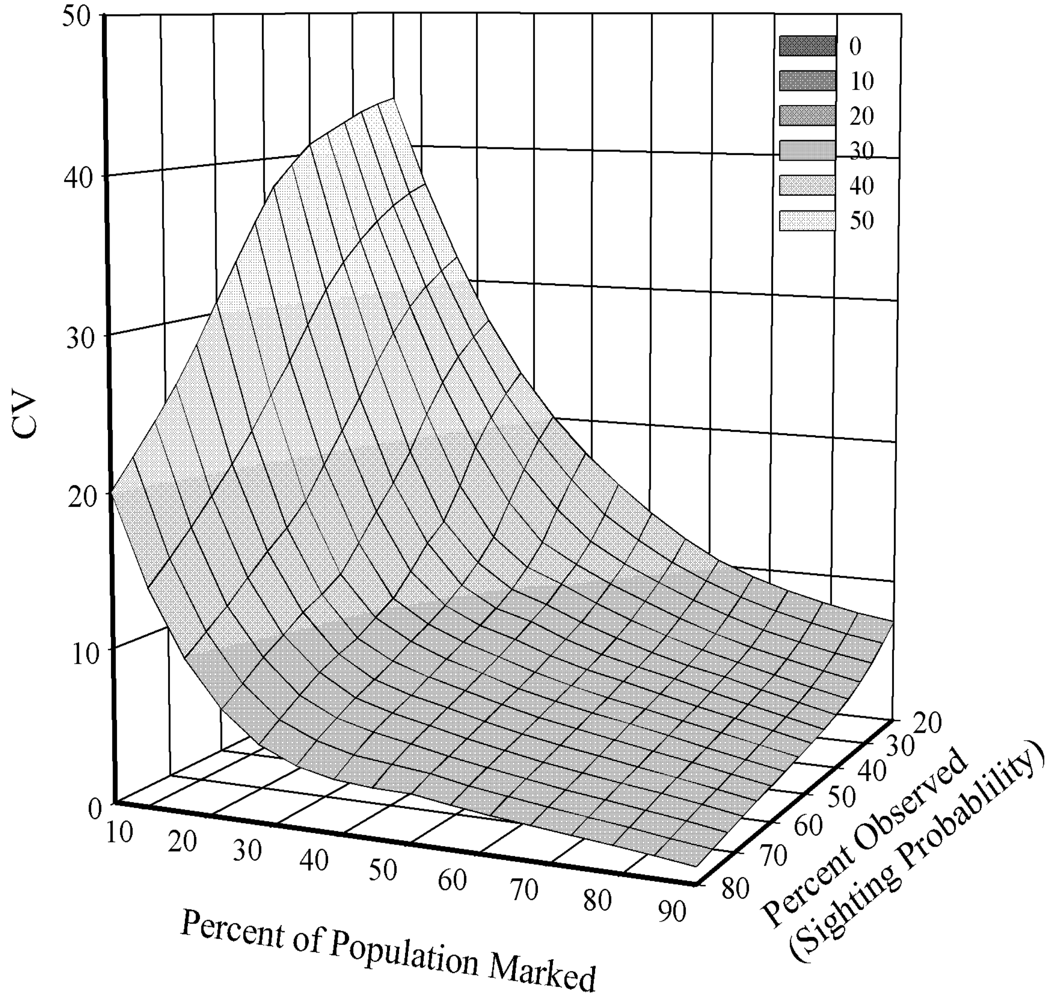

Figure 2. The response of precision (CV) to changes in the percentage of a population marked and the average sighting probability (per scan) based on simulated data; population size was 100 individuals and scan effort was held constant (10 scans).

Table 3. The first and second best models selected using QAICc (with model weight shown) explaining black-tailed prairie dog survival (Φ) and capture probability (*p*) for three colonies from January 2003 through May 2005 using mark-resight (Resight), mark-recapture (Capture) and both datasets combined (ALL).

Colony	Data	1st Model	QAICc Weight	2nd model	QAICc weight
DWC	Resight	Φ(time) *p*(time)	0.47	Φ(sex) *p* (time)	0.33
	Capture	Φ(time) *p*(time)	0.97	Φ(constant) *p*(time)	0.02
	All	Φ(time) *p*(time)	0.78	Φ(sex) *p*(time)	0.12
RLC	Resight	Φ(sex) *p*(sex*time)	0.99	Φ(constant) *p*(time)	<0.01
	Capture	Φ(sex) *p*(time)	0.42	Φ(sex) *p*(sex*time)	0.36
	All	Φ(sex) *p*(sex*time)	0.89	Φ(constant) *p*(sex*time)	0.10
SCC	Resight	Φ(time) *p*(time)	0.87	Φ(constant) *p*(time)	0.02
	Capture	Φ(time) *p*(time)	0.99	Φ(time) *p*(sex*time)	<0.01
	All	Φ(time) *p*(time)	0.99	Φ(time) *p*(sex*time)	<0.01

Estimates made with the combined dataset tended to have the lowest variance, and both mark-resight and mark-recapture produced estimates that were at times inconsistent with the combined dataset, but, in general, the patterns in survival were similar (Figure 3). The inconsistency among datasets may have been a result of either the number of encounter histories used to derive the estimate (highest for mark-recapture and the combined dataset), or because the combined dataset had a more accurate description of encounter history for each individual.

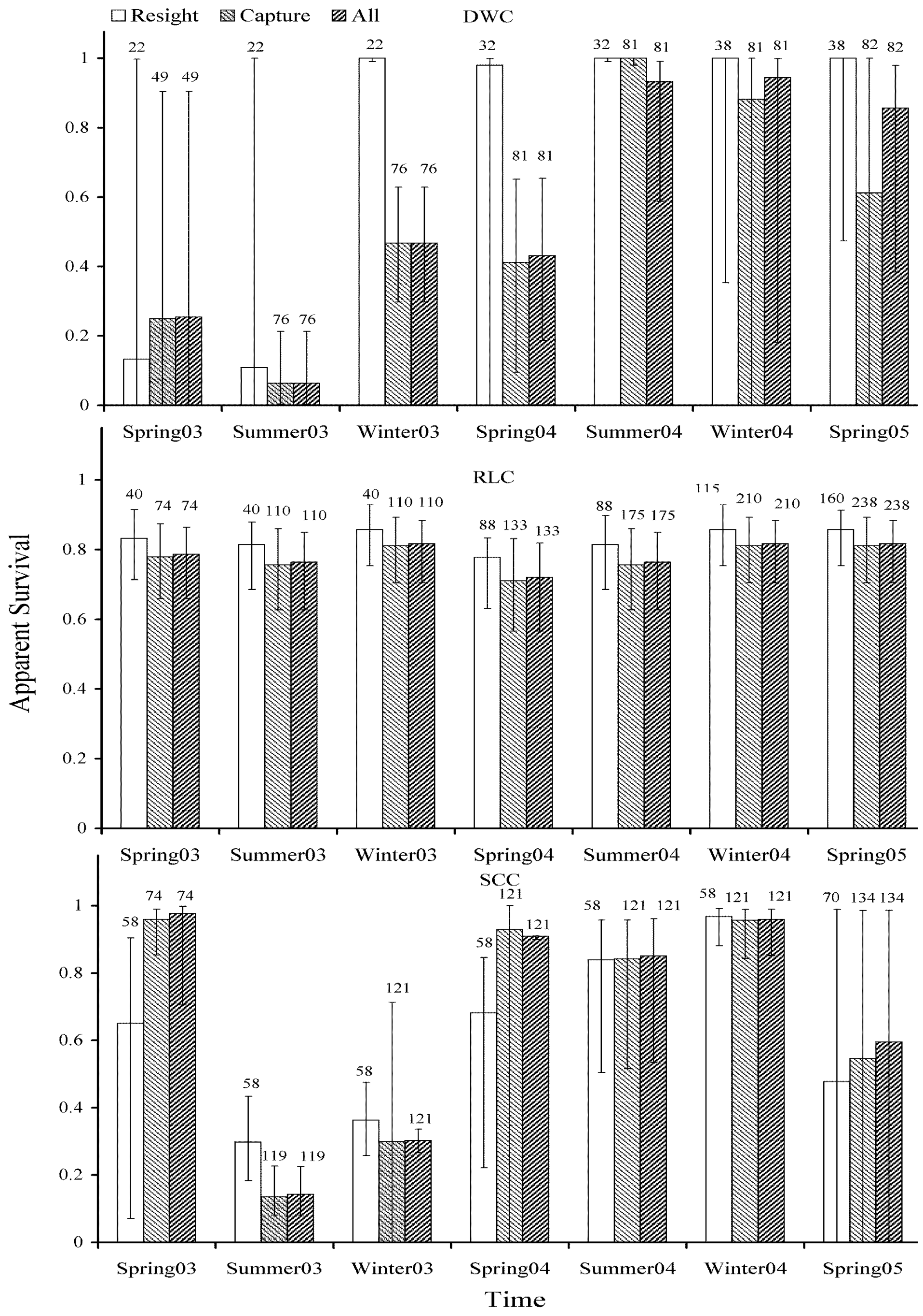

Figure 3. Seasonal survival of adult black-tailed prairie dogs from January 2003 through May 2005 at three reintroduced colonies (DWC, RLC, SCC) using mark-resight (Resight), mark-recapture (Capture), and a combination of both datasets (All) with 95% confidence intervals shown (sample sizes shown above the estimates).

Reproduction

The average number of reproductively successful females estimated with mark-resight (across all colonies and years) was 17.1 (SD = 14.8, n = 8) and was not significantly different ($t = -1.4$, DF = 7, $p = 0.10$) from that estimated directly from the mark-recapture data (mean =18.6, SD = 16.5, n = 8; Figure 4). Estimates of litter size (mean = 3.3 pups/litter, SD = 1.6) derived from mark-resight were significantly higher ($t = 4.7$, DF = 7, $p < 0.01$,) than those estimated with mark-recapture, however (mean = 1.1 pups/litter, SD = 0.70).

Comparative Effort

A total of 21,135 trap days yielded 2,838 captures of 549 individuals across all colonies. Average estimated capture rate ($\bar{p}$) was 0.40 (SD = 0.17, range = 0.13 - 0.80) and fell below 0.20 on only 2 of 33 primary periods. On average, it took 28.7 trap days (SD = 15.8) to capture an individual. Total time spent setting traps was 452.4 hours with a single person averaging 45 traps set per hour (SD = 18).

The total time spent trapping for the purposes of externally marking animals was 373.8 hours. The average estimated probability of capture from sighting an animal was slightly lower than from trapping rate (mean $\bar{p} = 0.34$, SD = 0.17, range = 0.01 - 0.63) and fell below 0.20 on only 3 of 29 primary periods. Sighting probability was based only on the marked population and varied significantly across years ($\chi_{kw}^2 = 12.17$, DF = 2, $p < 0.01$). Total time spent scanning was 36 hours with 132 scans (mean = 16 min/scan, SD = 10) conducted.

Total time observing colonies to estimate reproduction was 44 days across all years except for the DWC during 2003, which was not assessed. On average 5.5 days (SD = 2.13, n = 8) were spent observing a colony to estimate reproduction. A total of 49 days (5 117 trap days) was spent trapping to estimate reproduction with an average annual effort per colony of 5.4 days (SD = 3.5); however, it should be noted that I could scan every colony on a single day, whereas I could only trap a single colony on a given day due to limitations in time, personnel and number of traps (n = 250).

Discussion

Historic declines in the black-tailed prairie dog prompted state resource agencies to develop monitoring programs to aid recovery (e.g., Luce et al., 2006). Yet the recent decision by the USFWS to remove the black-tailed prairie dog from the candidate species list has left resource agencies with a potential quandary regarding their future conservation (Sidle et al., 2006). If the black-tailed prairie dog is no longer considered a species of concern, are resource agencies obligated to consider potential impacts and develop strategies for conservation? This is an important question especially in light of the important role prairie dogs play in grassland ecosystems and the fact that their presence influences already listed species, including the critically endangered black-footed ferret, an obligate prairie dog predator (Miller et al., 1996; Stapp, 1998; Kotliar et al., 1999).

The removal of the black-tailed prairie dog from the candidate species list was based on a reappraisal of occupied habitat determined by remotely sensing burrows coupled with an average density of 24.71 prairie dogs/ha (USFWS, 2004). My estimates of density averaged 8.4 prairie dogs/ha (SD = 7.6) and varied from a low of 1.3 to a high of 28.3 (Table 1). Applying this range of density estimates to the estimated area occupied in the U.S. (745 400 ha) yields a range-wide abundance that varies from < 1 million to > 21 million prairie dogs. Estimates of prairie dog density on single wards using mark-resight and direct enumeration in South Dakota yielded an average of 21.7 (SD = 11.0) and 18.6 (SD = 2.2) prairie dogs/ha in the Black Hills and Wind Cave National Park, respectively (King, 1955; Hoogland, 1995). Clearly, prairie dog populations can fluctuate greatly, even over small spatial and temporal scales, and vary considerably in density across their range. Applying a single, potentially high estimate of density may have led to a gross overestimate of the total number of black-tailed prairie dogs currently inhabiting the U.S. This potential error points to the need for a sampling design that will more accurately estimate abundance throughout the species' range.

The Dynamics of Prairie dog Metapopulations

The recent USFWS reassessment of the black-tailed prairie dog used the presence of burrows to determine “occupied habitat” (USFWS, 2004), however, it was not apparent if attempts were made to assess whether prairie dogs were present on those colonies. A line-intercept approach employing low-level aerial flight was used to assess occupied habitat across four states (Nebraska, North Dakota, South Dakota and Wyoming) that contained active prairie dog colonies (Sidle et al., 2001). Active colonies were identified using a suite of colony characteristics including observing prairie dogs. Nearly 3 million ha of prairie dog colonies existed but, on average, 19.1% of all colonies did not harbor prairie dogs (Sidle et al., 2001), that is, nearly one-fifth of all colonies were unoccupied.

Colony persistence is influenced by many factors and this dynamic has changed with the introduction of plague. In Oklahoma, colony persistence was originally positively related to colony size and negatively related to colony isolation, a pattern that reversed in the late 1980s and 1990s when colony persistence became positively related to colony isolation as a consequence of plague outbreaks (Lomolino and Smith, 2001; Lomolino et al., 2003). Further, town persistence over the entire study was extremely low; only 5 (2%) of the original 281 towns mapped in 1967 were still active in 1999.

In the Pawnee National Grasslands of northern Colorado, plague outbreaks were linked to El Niño events; from 18-68% of all colonies went extinct and 75% (47 of 63) of all recorded extinctions over a 21-year period were associated with an El Niño (Stapp et al., 2004). Unlike the findings in Oklahoma, there was no relationship between colony isolation and extinction risk. Despite numerous extinction events, colonies were recolonized and by the end of the study, overall colony area had increased to 416 ha distributed among ~ 27 colonies (Stapp et al., 2004). Such long-term datasets, like this one amassed by the USDA Forest Service, are needed to further our understanding of plague dynamics and evaluate the risk of colony extinction across the range of the black-tailed prairie dog. The recent change in species status could hamper such efforts (Sidle et al., 2006).

The Efficacy of Mark-Resight as a Monitoring Method

Estimating prairie dog abundance is a matter of scale: What works at the landscape level is not appropriate at the population level and vice versa. I suggest that a sound monitoring program for prairie dogs requires at least three pertinent scales of assessment: 1) range-wide estimates of potentially occupied habitat coupled with 2) regional, landscape-scale assessments of colony occupancy, persistence and extinction dynamics, which are augmented by 3) population scale assessments of demographic processes that can be used to estimate range-wide abundance, model population dynamics and infer causal factors.

Mark-resight has the potential to provide unbiased estimates of population size and vital rates (Seber, 1982; Williams et al., 2001). Other methods were inferior because the information they provided was either biased, incomplete, or more time consuming. Estimates of survival and reproduction could only be achieved with mark-resight and mark-recapture though they were not equivalent because mark-recapture was more time consuming and estimates of reproduction were biased low.

Most monitoring programs incorporate estimates of habitat occupied by prairie dogs based on the presence and condition of burrows, or employ population indices to track population size (Biggins et al., 2006). Active burrow indices may be useful to track large changes in population size (Biggins and Kosoy, 2001), but they can be highly biased and also may miss population declines as burrow presence may not reflect population change (Hoogland, 1995; Anderson, 2001, 2003; Biggins et al., 2006). Burrow indices also perform poorly in comparison to aboveground counts (Severson and Plumb, 1998).

Western state resource agencies have developed management plans for black-tailed prairie dogs. Several of these plans recommend the use of aerial surveys or remote sensing to estimate occupied habitat, but only five state agencies ground truth to ensure that colonies are active and only three state agencies mention the need for detecting population change. They do not suggest how populations should be monitored, however. None of the state plans outline approaches to estimate density (Knowles, 1999; CDNR, 2000; NDGF, 2001; NMBTPDWG, 2001; KBTPDWG, 2002; Luce, 2003; TBTPDWG, 2004; WGFD, 2004; Cooper and Gabriel, 2005).

Mark-resight can be used with indices or other approaches to correct bias, increase precision or increase sample size (Burnham and Overton, 1979; Nichols et al., 1981; Eberhardt and Simmons, 1987; McClintock, 2004). Additionally, there is a threshold of marking effort after which the accuracy of estimates improves little, so not all animals need be marked (Figure 2). The MAGC was significantly correlated with our population estimates over all years ($r^2 = 0.82$, $F_{1,16} = 73.2$, $p < 0.01$). However, detection probability varied annually. Thus, the index should be corrected annually and once adjusted the MAGC could be used to sample random plots representative of a larger colony or complex where population estimates are not attempted. When coupled with range-wide estimates of occupied habitat and regional assessments of colony occupancy, either directly or indirectly (MacKenzie et al., 2003), mark-resight could be a cost-effective management tool.

Conservation Implications

Techniques to monitor prairie dogs were largely developed to facilitate black-footed ferret reintroduction and recovery (Fagerstone and Biggins, 1986; Biggins et al., 1993). Yet, in their recent determination regarding the black-tailed prairie dog, the USFWS (2004) placed little emphasis on the preservation of associated species in jeopardy in particular the black-footed ferret. The interactions between black-tailed prairie dogs, black-footed ferrets and plague are not well understood, but are key to the conservation of these linked vertebrates (Antolin et al., 2002). Moreover, plague has recently been found near the Conata Basin of South Dakota, where the largest and most viable reintroduced population of black-footed ferrets exists (T. Livieri, pers. comm.). It is widely recognized that prairie dogs themselves are in jeopardy: two species are listed under the ESA and the black-tailed prairie dog has been reduced over a significant portion of its range as a result of habitat conversion to agriculture, urban expansion, past government-sponsored eradication programs, introduced plague and recreational shooting. In fragmented landscapes on the front range of Colorado, aboveground counts yielded densities from 32 to 122 prairie dogs/ha, which were considered abnormally high with the potential for negative demographic consequences (Johnson and Collinge, 2004). Urban expansion in Colorado is projected to reduce the area occupied by black-tailed prairie dogs, whereas all other states are attempting to increase the area occupied (Luce et al., 2006). Finally, the black-tailed prairie dog has been extirpated in Arizona. The recent change in federal status may hamper conservation efforts.

I have outlined a multifaceted approach incorporating mark-resight that provides accurate estimates of population size and vital rates which together contribute to a more effective monitoring of prairie dog populations. Most state resource agencies already employ a method to estimate area occupied and some determine the percentage of habitat that is actually occupied, but density estimates across the range of the species are lacking. Until such estimates are available and comprehensive monitoring approaches adopted, the status of the black-tailed prairie dog is truly unknown.

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CHAPTER II

UPS AND DOWNS: BLACK-TAILED PRAIRIE DOG POPULATIONS FLUCTUATE IN RESPONSE TO RESOURCE LIMITATION IN DESERT GRASSLANDS

Abstract

Black-tailed prairie dogs (*Cynomys ludovicianus*) historically lived in a geographically large region with diverse climates and vegetation. In the last 100 years prairie dogs have been extirpated from as much as 98% of this range. Large tracts of this historic range occur within desert grasslands making this habitat a potentially important region for future conservation of black-tailed prairie dogs. Desert grasslands are at the southern extent of the prairie dog's range and receive the least amount of annual precipitation compared to more northern regions. Differences in amount and timing of precipitation may limit resources during crucial periods of their life cycle. Resource limitation has been shown to negatively influence prairie dogs and other ground squirrel species. Yet, to date little is known about survival and reproduction of prairie dogs in desert ecosystems. I hypothesize that black-tailed prairie dog populations will be strongly influenced by resource abundance. Using mark-capture and mark-resight techniques I collected data from 2,986 captures of 577 individual prairie dogs over the course of three years at six colonies on the Armendaris Ranch, New Mexico (located in the Northern Chihuahuan Desert). I describe low rates of adult monthly survival (0.70 – 0.83) and a rapid loss in adult body mass ($\bar{x}$ = 214 grams, SE = 21, n = 94) at two prairie dog colonies that occur

during a year when precipitation was 43% below the 100-year average. Population sizes declined 18 – 91% ($\bar{x} = 64\%$, SE = 11) during this period at six colonies; in addition the lowest rates of juvenile survival were observed during this part of the study. Adult body mass is linked to reproductive activity, litter size and date of juvenile emergence. Low female body mass caused animals to forego reproduction in at least one colony. Prairie dog body mass changed seasonally and crested in the early fall with peak vegetation growth and monsoonal rains. I conclude that prairie dog populations are influenced by resource limitation in desert grasslands and may be at greater risk of rapid population declines during periods of extended drought. This characteristic of desert grassland systems may make colonies more prone to extinction than those located in more northern latitudes. I suggest this relationship be further explored along with the implications for the future conservation and restoration of black-tailed prairie dogs in desert grasslands.

Introduction

The historic range of the black-tailed tailed prairie dog (*Cynomys ludovicianus)* is vast, reaching from northern Mexico to the southern edge of Canada and from the eastern edge of the Rocky Mountains through most of the Great Plains (Hoogland, 1995). The extent of this range is proportionate to the important role prairie dogs play in the habitats they occupy (Miller, 1994; Miller et al.. 1996; Kotliar, 2000; Kotliar, 2006; Knowles et al., 1982).

The prairie dog range is generally categorized into three diverse vegetation zones with variable precipitation regimes (Detling, 2006). Of these vegetation zones the desert grasslands have the lowest annual mean precipitation (200-300 mm) and are more prone to periods of drought than any other region (Detling, 2006). Desert grassland habitats receive the majority of their precipitation from July through October in the form of monsoonal rains (Comrie and Glenn, 1998). This is in marked contrast to the other two zones which receive peak precipitation in spring and summer months. Areas within the range of the black-tailed prairie dog that contain desert grasslands include the American Southwest (Arizona, New Mexico and Texas) and Mexico; historically these regions contained large tracts of prairie dog habitat.

Desert grasslands may be more significant now for conserving prairie dogs than they were historically because of the decline in prairie dog habitat (Miller et al., 1996; Cully and Williams, 2001, Proctor et al. 2006). Black-tailed prairie dogs have been reduced to such an extent that they were considered candidates for protection under the Federal Endangered Species Act (USFWS, 2000) and were the subject of an extensive multi-state conservation plan (Luce et al., 2006). This conservation plan identified potential habitat, key focal habitat, and goals for prairie dog expansion and management activities. Current management goals would expand the occupied habitat of prairie dogs in Arizona, New Mexico and Texas from 16% (104,085 ha) of the 2003 total occupied habitat to 22% (155,866 ha) of the total by 2011. Current plans would decrease the habitat in Colorado from 40% (255,596 ha) of the 2003 total to 15% (103,588) of the 2011 total (Luce et al. 2006). Arizona, New Mexico, Texas, and

Mexico represent 42% of the total potential habitat and New Mexico and Texas are estimated to have the highest percent of potential habitat of all states (16% and 23%, respectively; Proctor et al., 2006). Though these areas represent a potential boon for prairie dog conservation, the long-term viability of prairie dogs in desert grasslands remains unknown. Further, the only potential means of expanding prairie dogs into some proposed areas is through translocations from one area to another. Translocations are expensive endeavors that sometimes fail (~ 10% failure rate) and few studies have evaluated the long-term efficacy of reintroducing colonies by monitoring their demography and persistence (Truett and Savage, 1998; Truett et al., 2001; Long et al., 2006; Dullum et al., 2005).

Current knowledge of black-tailed prairie dog population dynamics is restricted to the northern, more mesic parts of their range (King, 1955; Knowles, 1987; Hoogland, 1995, 2006). The most extensive work on population dynamics emanates from a 16-year behavioral study conducted by J.L. Hoogland at one colony in Wind Cave National Park, South Dakota (Hoogland, 1995). In conjunction with subsequent work on two other species (Gunnison's prairie dog, *C. gunnisoni* and Utah prairie dogs, *C. parvidens*) Hoogland (2001) concluded that all three species reproduce slowly as a result of: 1) low yearling survival, 2) low yearling reproductive success, and 3) a poor probability of weaning litters. Hoogland found that annual adult survival was less than 60% for all three species. Only 35% of yearling female black-tailed prairie dogs successfully reproduced compared to 100% of yearlings from the other two species. The probability of weaning a litter was 43% for black-tailed prairie dogs, 82% for Gunnison's and 67% for Utah prairie dogs. Female black-tailed prairie dogs produce only one litter of pups per year and average litter size is relatively small (3.08 pups, SD = 1.06; Hoogland, 1995). These findings suggest considerable variation in vital rates with respect to location and species. Given that data were collected for black-tailed prairie dogs in Wind Cave National Park, South Dakota, and in Arizona and Utah for Gunnison's and Utah prairie dogs, respectively, it becomes difficult to attribute observed differences in these vital rates to species, climate, random variation or a combination of these factors.

Vital rates for prairie dogs and other ground-dwelling squirrels show responses to changes in resource quality and quantity (Rayor, 1985; Knowles, 1987; Hoogland, 1995; Bennett, 1999). In some situations, responses to resource deficiencies can be so severe as to cause population collapse (Van Horne et al., 1997). Therefore, prairie dogs living in regions that may have limited resources due to limited precipitation or poor habitat quality may have reduced survival and reproduction and poor long-term viability.

The black-tailed prairie dog life cycle adds another layer of complexity to this scenario. Prairie dogs produce young in late spring. In northern climates the rigors of mating, lactation, and juvenile development coincide with peak precipitation and primary production (Hoogland, 2006). In desert grasslands, prairie dogs are forced to endure this taxing part of their life cycle several months prior to peak precipitation and primary production (Figure 1). Desert rainfall patterns also are highly variable, both temporally and spatially, and this variation can create a high degree of heterogeneity in vegetation, both in quality and quantity (Noy-Meir, 1973; Whitford, 2002; Asner and Heidebrecht, 2005).

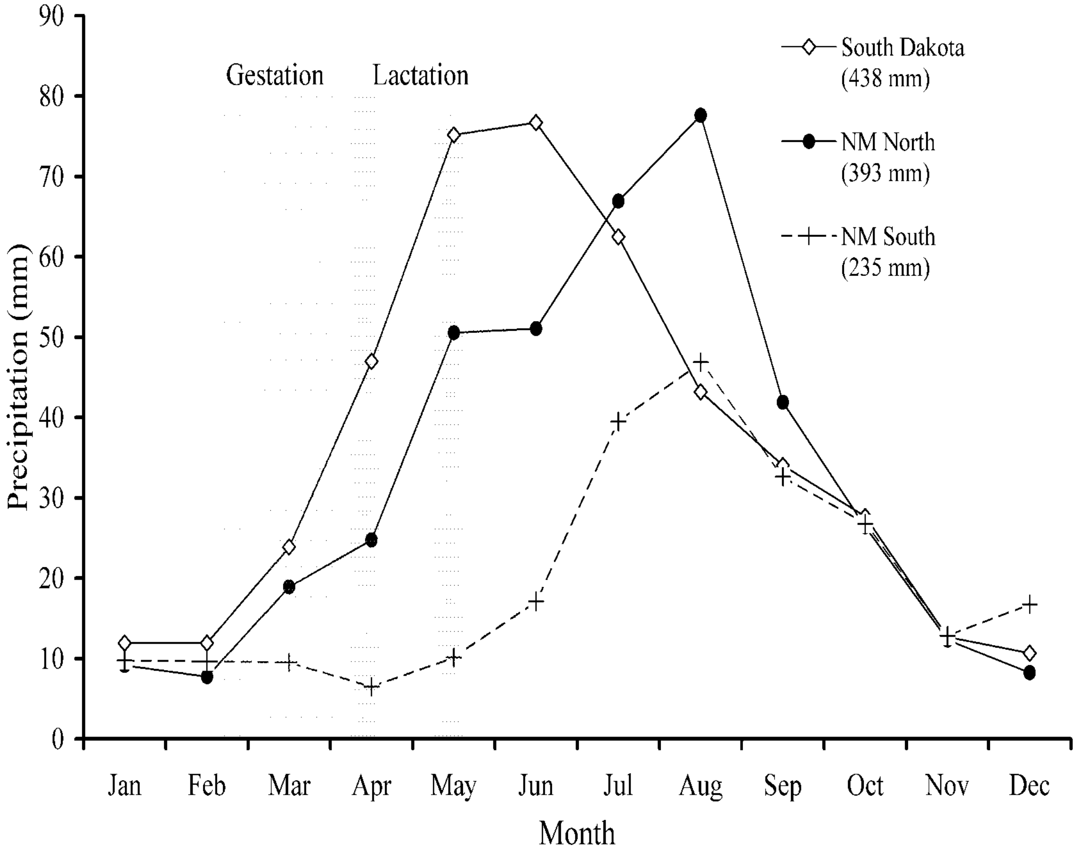


Figure 1. Average monthly precipitation for three regions (average annual precipitation in parentheses): Bosque Del Apache, NM (NM South), Maxwell, NM (NM North) and Hot Springs, SD (South Dakota; shaded bars represent the periods when black-tailed prairie dogs are breeding/pregnant (Gestation) and when females are nursing juveniles (Lactation).

This variation can create a situation where prairie dog populations may experience long periods without precipitation and accompanying plant growth. These factors lead to the possibility that prairie dog populations in desert grasslands may have more variable and possibly depressed vital rates compared to populations in more northern climates.

I hypothesized that black-tailed prairie dog populations in desert grasslands will be limited by the abundance or timing of resources. I predict that prairie dogs will experience their lowest rates of adult and juvenile survival during the summer months before monsoonal precipitation when resources should be most limited. Second, I predict that individuals in better body condition (higher body mass) will have higher rates of survival and reproduction.

Body mass and changes in body mass have been shown to reflect resource availability or the ability of individuals to acquire those resources from the environment (Dobson, 1992; Hoogland, 1995; Bennett, 1999; Dobson et al., 1999; Woods and Armitage, 2003). Using body mass as a proxy for resource abundance, I examined how and if resource limitation influences survival, reproduction and population growth of black-tailed prairie dogs in desert grassland ecosystems.

Field Methods

Study Site and Study Populations

I conducted research on the Armendaris Ranch, Engle, Sierra County, NM. Located at the northern end of the Chihuahuan Desert, the ranch is dominated by desert grasslands with perennial grasses including alkali sacaton (*Sporobolus airoides*), burrograss (*Scleropogon brevifolius)* and tobosa (*Pleuraphis mutica)*.

Abundant forbs such as spurge (*Chamaesyce* spp.), hogpotato (*Hoffmanseggia* spp.) and spectacle pod (*Dimorphocarpa wislizenii*) were present throughout the ranch. Mesquite (*Prosopis gladulosa*) and creosote (*Larrea tridentate)* were common shrubs but were rarely encountered on prairie dog colonies.

The Armendaris Ranch provided a unique opportunity to evaluate black-tailed prairie dog population dynamics in desert grasslands. The Armendaris Ranch, owned by Turner Enterprises, is dedicated to the conservation of threatened and endangered species. Over the last ten years, 19 black-tailed prairie dog colonies have been established through reintroduction (Truett and Savage 1998, Hendrie 2004). I began studying three of these colonies in January 2003, they were (with initial number of reintroduced individuals): Deep Well Colony (DWC) established in 1999 (N = 56), Red Lake Colony (RLC) established in 1998 (N = 66) and S-Curve Colony (SCC) established in 1999 (N = 59). In March 2004, I expanded my study to include three smaller colonies. These were: Burrograss East (BGE) established in August 2001 (N = 51), Burrograss West (BGW) established in September 2001 (N = 35) and Tire Drinker Colony (TDC) established in September 2000 (N = 53). The two Burrograss colonies (BG) were nearest to one another (1 km apart) and were the furthest away from all other colonies (13-20 km). Deep Well Colony, RLC, SCC, and TDC were 3-6 km from one another. The ranch is closed to the majority of the public and there is no recreational shooting or poisoning of prairie dogs.

Capture and Resight

Trapping and resight sampling were based on the robust design (Pollock, 1982). Two to 12 scans or secondary periods comprised a single primary period. The populations were assumed to be closed within a primary period but open (births, deaths, etc) between them. Trapping occurred a minimum of two times during the spring (January – April), once during lactation (May – June), and once during the fall (September – November). I did not sample at DWC during the fall of 2003 or at SCC and TDC during the fall of 2004. Resight scans were done 3-20 times on colonies during the spring time period to provide survival data for periods when I did not trap.

Multiple numbers of medium-sized box traps (61 cm x 18 cm x 20 cm steel-mesh live traps, Wildlife Control Supplies, Simsbury, CT) were used to capture prairie dogs (2-3 traps per active burrow). I altered the number of traps used at each colony over time because populations changed in size. The average number of traps used at DWC, RLC, SCC, BGE, BGW and TDC was 108 (SD = 21.6), 177 (SD = 41.1), 123 (SD = 46.5), 27 (SD = 4.6), 66 (SD = 17.9) and 50 (SD = 14.5), respectively. Traps were pre-baited for one week before being set.

Captured animals were uniquely marked using a subcutaneous passive integrated transponder (TX1440ST, Biomark, Boise, ID) and externally marked with a unique alphanumeric code using Nyanzol-D dye (Albanil Dyestuff Manufacturers, Jersey City, NJ), which remains visible until they molt (King, 1955). Individuals were weighed to the nearest 10 g the first time they were trapped during a primary occasion. Females were classified as reproductively active if they were noticeably lactating (e.g., swollen teats) or if they were obviously pregnant at the time of capture. Males were reproductively active if their testes were noticeably descended (Hoogland, 1995). All capture and handling methods followed guidelines of the Institutional Animal Care and Use Committee (NMSU Permit No. 2002 - 06).

Scans were performed from an elevated position (3 m) using a 20 - 60x spotting scope. Scans began and ended at predetermined points located off colony and were conducted in the morning (0700 - 1000 hrs) and/or evening (1600 - 1900 hrs) to minimize heat mirage and maximize the number of individual animals that could be observed. Marked animals were identified and unmarked animals were simply counted.

Reproduction

At the end of April all colonies were observed multiple times per day to document the date young of year animals (YOY) first emerged and to estimate mean number of young per litter. Young per litter was estimated by counting the number of pups first emerging from a particular burrow. Adult females known to use a burrow (females rear young in a maternity burrow exclusive to other females; Hoogland 1995) were assigned maternity of an emergent litter. Subsequent to first emergence, I continued to observe colonies multiple times a day until juveniles from adjacent litters mixed rendering counts of litter size unreliable. The maximum number of pups per female was used to estimate fertility. Within one month after first emergence I trapped colonies in an attempt to capture and tag juveniles as well as to identify mothers that I had failed to trap on prior occasions and to record female weights.

Vegetation

I used the point-intercept method to assess vegetation on all six colonies. I sampled vegetation once per colony during the spring and fall of 2004 and 2005. Spring sampling occurred during May of each year; fall sampling occurred in the last week of September or during October. For each colony I randomly selected 10 to 25, 20 m transects with a constant bearing of 275°. Number of transects varied depending on the size of the colony being sampled (larger colonies = more transects). At BGE, BGW and TDC (area < 2.2 ha) I sampled 10 transects; at DWC (area = 4.4 ha), RLC (area =11.1 ha) and SCC (area = 10.1 ha) I sampled a minimum of 20 transects for each colony except for DWC fall 2004 = 15 and RLC fall 2005 = 25. For each transect I recorded the vegetation component at 200 points (1 point every 10 cm). Vegetation was categorized as grass, forbs, litter (any non-living organic matter), and bare ground.

Analysis

Body Mass

I used proc GLM Statistical Application Software (SAS; Cary, NC) to test for differences in the response of individual body mass based on the predictor variables: sex, colony, year, month, and interactions of those factors including the global model which contained all terms. Mean body mass was used for animals that were captured more than once during any month. Because juvenile animals weigh less than adults, I placed YOY animals into a separate group and analyzed both separately. I considered YOY animals as a cohort, rather than individuals, and included them in the analysis with adults only when the mean body mass of the cohort was within one standard deviation of the adults. This was done by colony and sex to take into account differences that may have existed based on those attributes. Post-hoc tests were performed only if statistically significant differences were found for the overall test and for the specific group effect. Fisher's LSD was used for all post-hoc comparisons because of its increased power relative to other tests (Zar, 1999: 209). In some cases post-hoc analysis for particular comparisons was complicated by differences in the time of trapping events between years and colonies. This created the appearance of time differences when there may have been differences in body mass owing to colony effects or vice versa. In cases where this was likely, I eliminated data that were not comparable and performed another analysis on the reduced data set to ensure appropriate inferences were made.

Comparisons of body mass for YOY animals were difficult because the time of initial capture relative to emergence was not the same for colony or year. Therefore, I performed a two-way analysis of variance (ANOVA) on the response of body mass (at first capture) to sex and year. Differences in year were assumed to reflect relative development (length of time after birth) rather than a comparable difference in condition of juveniles after emergence. I also tested for differences in body mass during the fall but the 2003 year was eliminated from this group because of a lack of YOY animals captured during this period. These analyses were done using proc GLM and Fisher's LSD was used as the post-hoc test only when a statistically significant overall effect was found. All means are reported ± standard error unless specified otherwise.

Reproduction

I analyzed litter size (pups per litter) with a Kruskal-Wallis ranked ANOVA for year and colony effects separately as these data were both non-normal and heteroscedastic. The addition of colonies in 2004 (BGE, BGW and TDC) possibly confounded the influence of year, therefore, I analyzed a subset of the data in which only RLC and SCC were included. I used Spearman's ranked correlation to assess relationships between litter size at first juvenile emergence and maternal body mass during the previous autumn, spring and during lactation across all years. I modeled the probability of being reproductively active (for males and females) based on the predictor variables: body mass (during the previous fall, spring and lactation periods) and year using logistic regression. To determine what relationship body mass had on the timing of reproduction, I used Spearman's ranked correlation to assess if mean body mass of active females during the spring and lactation periods was correlated with the number of days to first juvenile emergence (days after May 1st of each year) at each colony.

Survival

I used program MARK for all survival analyses (White and Burnham, 1999) using the Huggins Robust design with full heterogeneity for closed captures option. This option employs the customary robust design open population models to estimate survival and dispersal in conjunction with closed population models developed to estimate population size (Huggins, 1989, 1991). Time periods when the population is open contain three parameters: survival (S), emigration (γ'') and immigration ($\acute{\gamma}$), in addition to the three parameters used for closed population periods: a mixture variable π, capture probability (p), and recapture rate (c). Parameter π is a means to estimate individual heterogeneity in capture histories and was set to the default value of 2 (Pledger, 2000). Estimates of survival, in addition to other parameters, were taken from models having the smallest Akaike's Information Criterion-corrected (AIC_c) (Burnham and Andersen, 1998).

I performed a general analysis using both mark-recapture and mark-resight from all primary periods throughout the study (Chapter 1). All colonies were analyzed separately except for the BGE and BGW colonies which were combined due to their proximity to one another and the congruity with which they were trapped. Individuals were placed into groups based on their sex and their age class for a maximum of eight possible groups, though only RLC and SCC contained all groups. For each analysis I constructed models using combinations of time, sex, age and location (for BGE and BGW only) and interactions between these variables. Though Huggins closed population models differ in their derivation of population estimates they are structurally similar to the models described by Otis et al. (1978). Therefore, I followed these eight models when testing closed capture models. Estimates were allowed to vary from one primary period to the next. Appropriate closed session models were then judged based on which one produced the lowest AIC_c in conjunction with the open population estimates.

To explore the influence of body mass on rates of survival, I conducted a second more complex series of analyses on DWC, RLC, and SCC because sample sizes were suitably large. I used data from only the lactation and fall time periods, which served to reduce the number of time dependent parameters while making the data less cumbersome to model. Using these time periods reduced overall sample size minimally (529 encounter histories in the first analysis to 499 in the second). I examined survival in an individual covariate approach where the body mass of an individual during the lactation period and fall season was used to model the probability of survival. Individual covariates were tested in conjunction with different combinations of time, sex and age as well as interactions between those factors. For periods in which individuals were not captured and hence had no covariate, the mean body mass from an individual's group was used.

Vegetation

For each transect the percent grass, forbs, litter and bare ground were determined. The mean percentages across transects for each colony and time were analyzed with Proc MIXED in SAS. I treated each colony as a sample unit in a repeated measures approach, using the mean value from each colony (24 means = 6 colonies * 4 time periods for each component), and analyzed each vegetative component separately. The null hypothesis was that there would be no difference between any of the four periods (spring 2004, fall 2004, spring 2005 and fall 2005). Contrasts were used to test for differences in year, season and interactions between year and season if an overall time difference was detected. The Tukey-Kramer multiple comparison test was used on the Least Squares means (LS means) to detect differences between groups that had an overall significant result (Zar 1999: 209).

Results

Body Mass

Test of the global model revealed a change in body mass due to a difference in at least one predictor variable or interaction between those variables ($F_{116,\ 1098} = 9.50$, $p < 0.01$; Table 1). Adult female body mass averaged 907.58 g ± 6.21 (n = 714) compared to an average male body mass of 968.67 g ±7.92 (n = 501). Interactions with sex and time (year and month) reflected changes in the relationship of body mass between females and males that largely took place during the spring when males often weighed less than females and just after the lactation period when females weighed less than males (Figure 2). Female body mass usually followed a similar pattern during the year with body mass being lightest during the lactation period (May and June). Males tended to be lighter in the spring (March) when they are actively breeding and competing for mates. Post-hoc tests indicate that the body mass in the months of March ($\bar{x}$ = 882.07 g ± 12.80, n = 199), May ($\bar{x}$ = 896.14 g ± 7.33, n = 317) and June ($\bar{x}$ = 875.01 g ± 10.33, n = 207) were significantly lighter from all other months when sex is ignored. Body mass during the fall months of September ($\bar{x}$ = 988.84 g ± 15.59, n = 85) and October ($\bar{x}$ = 1029.38 g ± 15.02, n = 140) were significantly higher than other months except for February. November 2004 had the highest average body mass of any time period ($\bar{x}$ = 1325.72 g ± 43.51, n = 15) throughout the study but this was from a single sample (DWC during the fall of 2004). Overall, body mass during the fall of 2004 was considerably higher than during the fall of 2003 (Figure 2).

Table 1. The results of the global model testing for effects and interactions on adult body mass. Only those variables with a *p*-value < 0.05 are shown. In addition the completely interactive term is presented though it was not significant. For the overall model DF = 116, Error DF = 1098.

Source	DF	*F*	*p*-value
Sex	1	33.37	< 0.001
Year	2	18.87	< 0.001
Month	9	22.44	< 0.001
Colony	5	7.91	< 0.001
Sex*Year	2	4.87	0.008
Sex*Month	9	2.75	0.004
Year*Month	8	9.46	< 0.001
Colony*Year	4	7.11	< 0.001
Colony*Month	20	1.72	0.026
Colony*Sex*Year*Month	26	1.08	0.355

Monthly patterns were not always consistent from year to year, which was reflected by the interaction between month and year (Table 1). For example, when the spring months were analyzed separately a significant difference in both month and year ($F_{10,403} = 24.69$, $p < 0.01$, n = 414) was detected; mean body mass for both sexes during the spring months was significantly lighter in 2004 ($\bar{x}$ = 808.33 g ± 16.74, n = 132; Figure 2). Despite the interactions with month, animals tended to be heavier in 2005 ($\bar{x}$ = 960.71 g ± 8.00, n = 383) than in 2004 ($\bar{x}$ = 898.27 ± 9.76, n = 381).

Differences in colony were also evident; when all data were combined, animals at DWC tended to weigh more than animals anywhere else ($\bar{x}$ = 1056.22 g ± 18.11, n = 146). Of the three largest colonies, animals at RLC generally were the lightest ($\bar{x}$ = 907 g ± 5.95, n = 759) though not statistically different from animals at SCC ($\bar{x}$ = 951 g ± 8.98 grams, n = 239). Differences were also detected for the smaller colonies but these were difficult to interpret as they may have arisen from differences in sample size.

Body mass at the colony level also is highly dynamic. For example, in the spring of 2004 animals at DWC weighed an average of 652.27 g ±78.71 (n = 11), the lowest mean weight observed during the study. By the fall, animals at DWC increased their mass by 103% and averaged 1325.70 g ± 43.45 (n = 15) which was over 300 g heavier than the next highest mean mass recorded for animals at RLC.

Analysis of body mass for YOY animals following emergence revealed a statistical difference in body mass based on at least one predictor variable ($F_{5,220}$ = 60.41, $p < 0.01$, n = 226), but this effect was largely attributable to year only ($F_{2,220}$

$= 148.53$ $p < 0.01$, n = 226). Young of year body mass at time of first capture in 2005 was higher ($\bar{x}$ = 437.82 g ± 16.76 n = 78) than for either 2004 ($\bar{x}$ = 161.71 g ± 5.54, n = 53) or 2003 ($\bar{x}$ = 191.43 g ± 9.06, n = 95; Figure 3). Body mass for YOY animals during the fall of their first year was significantly affected by sex

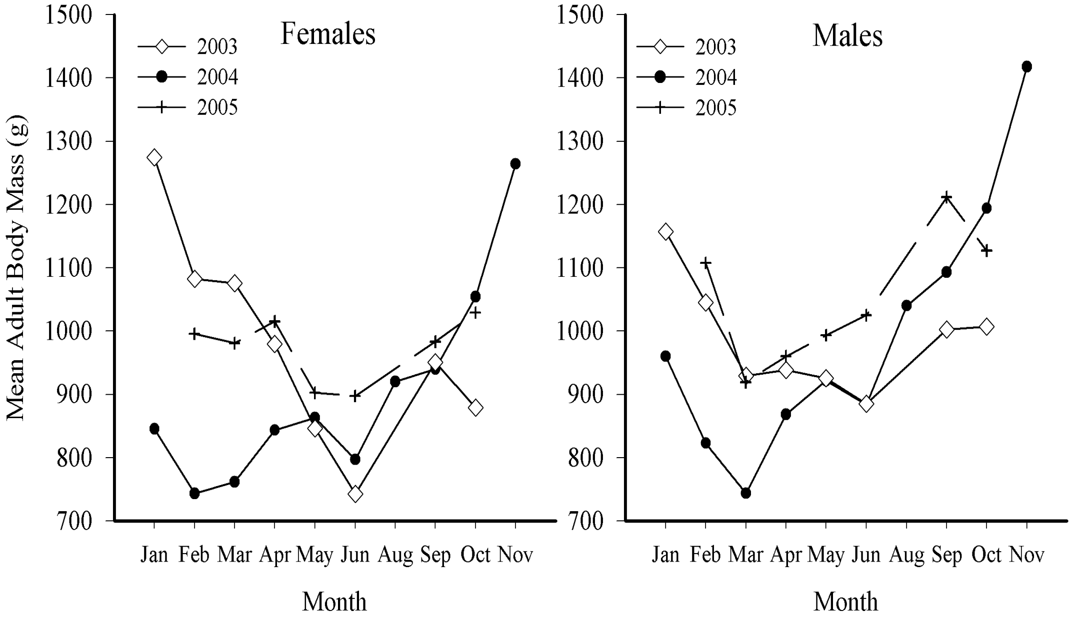


Figure 2. Mean adult body mass across colonies from January through October (November 2004 represents DWC only) by year for females and males.

($F_{1,90} = 5.29$, $p = 0.02$, n = 104) and colony ($F_{5,90} = 11.52$, $p < 0.01$, n = 104), but year differences were not seen between 2004 and 2005 ($F_{2,90} = 25.90$, $p = 0.19$, n =104). During the fall, male YOY animals weighed an average of 827.10 g ± 18.07 (n = 54) while females weighed an average of 757.75 g ± 15.75 (n = 49; Figure 3).

Reproduction

Mean litter size across all years and colonies was 3.30 ± 0.12 pups/litter (n = 161) and average date of emergence was May 18th ± 2.99 days (n = 14). Litter size differed between years ($\chi_{kw}^2 = 8.98$, DF = 2, $p = 0.01$) when all colonies were analyzed together. I could not detect this temporal difference when I included only RLC and SCC ($\chi_{kw}^2 = 5.15$, DF = 2, $p = 0.08$); both colonies had larger litter sizes on average in 2004 and 2005 (Table 2).

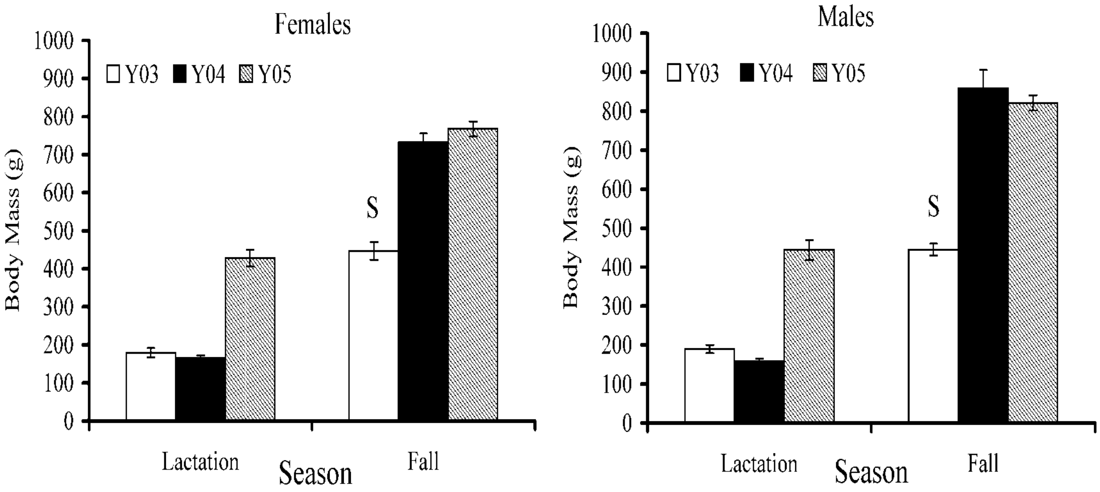


Figure 3. Mean body mass of young of year animals born in 2003 (Y03), 2004 (Y04) and 2005 (Y05), by sex, during the time period following their initial emergence (Lactation) and during the fall of their first year (S during the fall for the Y03 class signifies estimated body mass for YOY animals during the following spring as no estimates were available during the fall- not included in analysis).

The influence of colony on litter size was marginally significant ($\chi_{kw}^2 = 10.82$, DF = 5, $p = 0.06$). Litter size varied little at the RLC through the course of the study, though there were progressively larger numbers of total pups and an increase in number of litters in 2005. Other colonies exhibited greater degrees of variation, the DWC produced no emergent young in 2004 but produced 4.66 pups per litter in 2005 (Table 2). The number of juveniles produced relative to the entire female population of a colony increased with year (2003 being the lowest and 2005 highest; Table 2). There was no statistically detectable difference in the mean number of juveniles per female across years or colony.

There was a positive correlation between litter size and maternal body mass from both the previous autumn ($r_s = 0.38$, $p < 0.01$, n = 47) and during lactation ($r_s = 0.32$, $p < 0.01$, n = 119). Maternal body mass during March was not correlated to the number of emergent young ($r_s = 0.15$, $p = 0.21$, n = 65), however. Nevertheless, I rejected the null hypothesis that March body mass and time (year) had no relationship to female reproductive activity ($\chi^2 = 49.35$, DF = 3, $p < 0.01$, n = 130). Females still had a higher probability of being reproductively active as March body mass increased ($\beta = 17.91 \pm 8.34$, $\chi^2_{\text{Wald}} = 4.61$, $p = 0.03$), year effects were detected ($\beta = 6.05 \pm 3.06$, $\chi^2_{\text{Wald}} = 3.91$, $p = 0.05$) in addition to a year by body mass interaction ($\beta = -0.01 \pm 0.004$, $\chi^2_{\text{Wald}} = 4.60$, $p = 0.03$; Figure 4).

These estimates of individual success corroborate the general pattern seen at the colony level. In 2003, females had an average March body mass of 1076 g ± 23.80 (n = 89) which corresponded to the highest percentage of animals being active (81%) for all years. This was higher than the corresponding values in 2004 (March body mass = 737 g ± 27.3, n = 72) when 65% of females were active or in 2005 (877 g ± 25.3, n = 113) when 71% were active. A relationship between female reproductive status and body mass from either the previous autumn ($\chi^2 = 1.28$, DF = 3, $p = 0.73$, n = 60) or during lactation could not be established ($\chi^2 = 1.97$, DF = 3, $p = 0.58$, n = 225).

There was a negative correlation between mean female body mass during March and the number of days until first juvenile emergence at all colonies ($r_s = -0.85$, $p < 0.01$, n = 14). Data from DWC in 2004 were omitted from this analysis because no emergent young were observed. This is an important result nonetheless, because this colony had the lowest mean female body mass for the spring of any year and was the only example of a colony that did not produce emergent young.

The global models for logistic regressions of male reproductive activity (testes descended) showed an overall affect due to the previous autumn's body mass ($\chi^2 = 8.64$, DF = 3, $p = 0.03$, n = 57), March body mass ($\chi^2 = 12.17$, DF = 3, $p < 0.01$, n = 97) and for body mass during the lactation period ($\chi^2 = 252.52$, DF = 3, $p < 0.01$, n = 182). These results were clouded, however, because neither body mass nor year were found to be individually significant. This is potentially due to the way that individual components are tested with the Wald Chi-square in logistic regression (see Menard 1995: 39), therefore I performed a second set of tests where I modeled male reproductive status for each time period without time effects and compared these to the competing model that incorporated year. Models containing a body mass term were not significant and had a larger AIC (see Burnham and Andersen, 1998) than competing models with only year terms. A final analysis of male reproductive status incorporating only a year effect was significant ($\chi^2 = 15.66$, DF = 1, $p < 0.01$

Table 2. Estimates of litter size (Mean Young/Litter ± SE), YOY per adult female (YOY/Fem), the minimum number of emergent young (Minimum Produced), number of litters produced (Litters) and the time till juveniles were first observed (Days After May 1), at three colonies in 2003 (DWC, RLC and SCC) and six colonies in 2004 and 2005 (BGE, BGW, DWC, RLC, SCC and TDC).

Year	Colony	Mean Young/Litter	YOY/Fem	Minimum Produced	Litters	Days After May 1
2003	DWC	---[a]	1.60[a]	24[a]	---[a]	5[b]
	RLC	2.92 (0.23)	1.78	82	28	14
	SCC	2.86 (0.27)	2.04	92	38	5
2004	BGE	5.00 (-----)	2.50	5	1	27
	BGW	5.00 (-----)	1.00	5	1	34
	DWC		No Juveniles Emerged			
	RLC	3.41 (0.24)	2.71	92	27	24
	SCC	4.50 (0.50)	4.50	9	2	33
	TDC	4.50 (0.50)	4.50	9	2	32
2005	BGE	2.00 (-----)	1.00	2	1	24
	BGW	3.50 (0.50)	3.50	7	2	13
	DWC	5.00 (0.37)	4.29	30	6	4
	RLC	3.08 (0.19)	1.73	114	37	8
	SCC	5.00 (0.78)	5.83	35	7	9
	TDC	3.75 (0.53)	7.50	30	8	11

[a] Estimates of juvenile production only available from trap data.

[b] Date after May 1 reflects earliest known occurrence of juveniles.

n = 199). So it appears that conditions in a given year, whatever they might be, influence male reproductive activity more than male body mass does.

Survival

Survival results were generated from 2,986 captures of 577 individuals during 23,313 total trap nights. DWC, RLC and SCC combined accounted for 95% of all captures and RLC alone accounted for 54% of the total captures through the entire study.

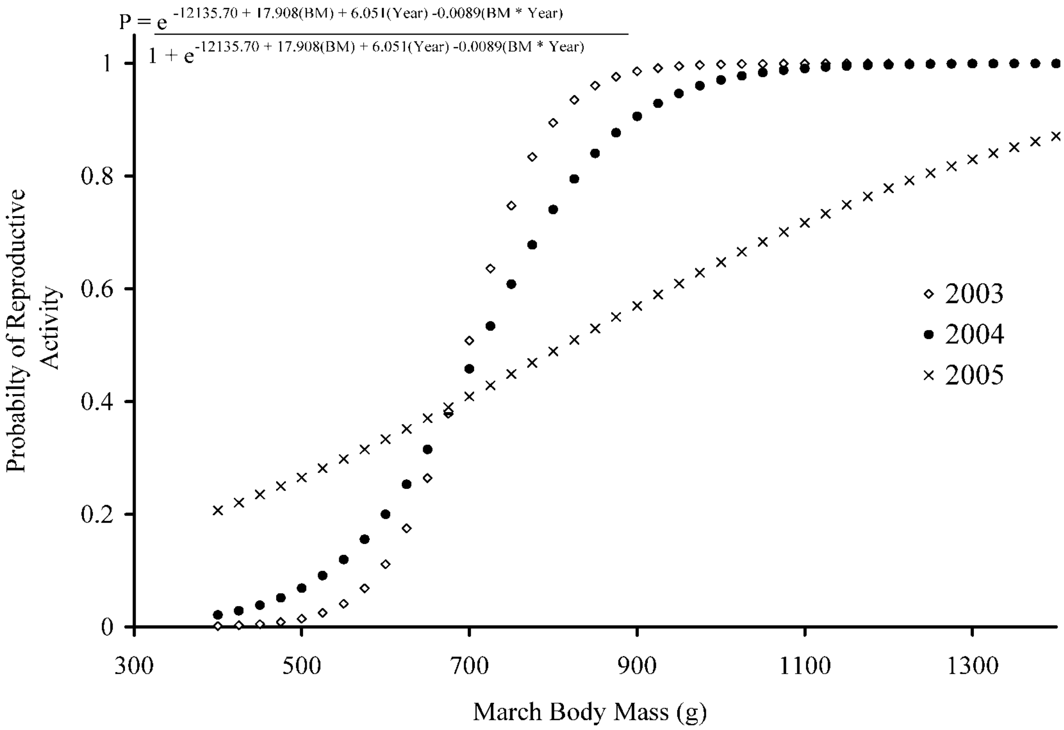


Figure 4. Estimate of the probability of females being reproductively active as a function of March body mass and year as defined by back transformed linear model (Beta values extend to 3 significant digits in model estimates for purposes of accuracy).

Likewise, the greatest numbers of individuals in all age classes were captured at RLC followed by SCC and DWC (Table 3). I performed 162 individual mark-resight scans across colonies with more scans being conducted at the three larger colonies: DWC

(33 scans), RLC (60 scans) and SCC (39 scans). Total numbers of newly captured animals changed little from year to year at RLC, though this contribution changed by age class, whereas both DWC and SCC had relatively high proportions of their total animals captured in 2003 and virtually no new animals captured in 2004 (Table 3). The total number of animals captured at either of the BG colonies or TDC was meager compared to the larger colonies though they were comparable in numbers of animals to both DWC and SCC following 2003 after major population crashes had occurred at these latter two colonies (Chapter 1).

Probability of initial capture for all primary periods was 0.35 ± 0.03 (n = 53) though it varied considerably through time and with colony. Rates of capture were not found to be different between BGE and BGW but were higher on average than all other colonies ($\bar{x}$ = 0.48 ± 0.09, n = 6), followed by SCC ($\bar{x}$ = 0.43 ± 0.06, n = 12), DWC ($\bar{x}$ = 0.35 ± 0.07, n = 10), RLC ($\bar{x}$ = 0.32 ± 0.02, n = 20) and finally TDC ($\bar{x}$ = 0.15 ± 0.11, n = 5). Capture rates were usually lowest the first time a colony was trapped ($\bar{x}$ = 0.18 ± 0.43, n = 5) but rose in subsequent periods and eventually leveled off. Only RLC and TDC had models indicating a behavioral response from animals although time influences may represent a behavioral response (Table 4; see closed population parts of models-M).

Adult survival was variable both within and among colonies particularly for DWC and SCC where adult survival estimates changed fairly dramatically through time (Figure 5). During the lactation phase of 2003, monthly survival decreased to 0.83 ± 0.07 at DWC and to 0.70 ± 0.037 at SCC from rates that ranged from 0.96 –

1.00 in the preceding months (Figure 5). Following these declines, monthly survival at DWC increased to 0.89 ± 0.07 during the spring months of 2004 and then never fell below 0.90 throughout the remainder of the study. SCC also experienced relatively low monthly survival for the remainder of 2003 (0.82 ± 0.06), but then survival rates increased above 0.94 for the remainder of the study (Figure 5). Despite the strong time effect at these two colonies, survival rates at RLC remained relatively constant and there was little support for a time effect on survival (Table 4). Adult survival was found to differ between sexes at RLC with females having a higher monthly survival rate (0.97 ± 0.01) than males (0.95 ±0.01). Monthly survival at the smaller colonies mirrored the results found at RLC with BG and TDC showing differences between the sexes that were biased high toward females (BG: females = 0.92 ± 0.03, males = 0.85 ± 0.06; TDC: females = 0.99 ± 0.02, males = 0.97 ± 0.03). The second most supported model at TDC was essentially tied ($AIC_c \leq 2$; Burnham and Anderson, 1998) with the first model and suggested an overall difference in survival based on age class but not sex: estimates for adults = 0.97 ± 0.21, Y04 = 1.0 ± 0.01 and Y05 = 0.80 ± 0.16.

Juvenile survival was more variable than adult survival. Juvenile monthly survival at DWC (0.02 ± 0.18) and SCC (0.025 ± 0.01) were near zero in 2003. In addition, of the 69 juveniles marked at these two colonies in 2003 not a single one was ever captured again after June 2003. Juveniles at RLC also experienced lower rates of monthly survival (0.71 ± 0.06) in 2003 relative to adults or to juvenile cohorts in subsequent years (Figure 5). Monthly juvenile survival averaged 0.90 (SD = 0.09) in 2005 among these three colonies. All models for juvenile survival suggest that for the first 6-8 months after emergence, juveniles have non-sex biased survival rates that are lower than adults at their respective colonies. Following this period, however,

Table 3. The total number of animals captured (N), the number of females and males in each age class, and the number of animals in each age class captured for the first time (Adult = animals born prior to 2003 or unknown birth year, Y03, Y04 and Y05 = animals born in 2003, 2004 and 2005, respectively).

					Number of animals captured for 1st time by year			
Colony	N	Age Class	Females	Males	Prior to 2003	2003	2004	2005
BGE	10	Adult	3	3			6	
		Y04	4	---			4	
BGW	10	Adult	3	4			7	
		Y05	2	1				3
DWC	90	Adult	26	21	8	24	11[a]	4
		Y03	8	18		24	1	1[a]
		Y04	---	1				1[a]
		Y05	7	9				16
RLC	281	Adult	54	46	24	67	7	5
		Y03	18	19		26	11	
		Y04	46	36			63	17
		Y05	27	35				61[b]
SCC	158	Adult	43	34	24	53		1
		Y03	18	28		45		
		Y04	7	2				9
		Y05	15	11				26
TDC	33	Adult	3	2			5[c]	
		Y04	7	1				8
		Y05	10	10				20
Totals	582(577)		301	281	56	239	115	172

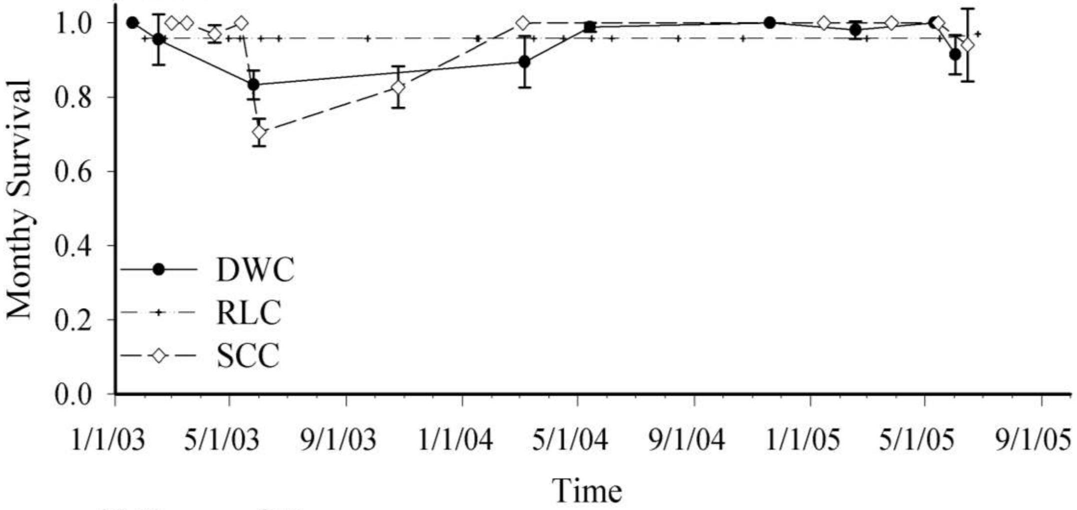
Note. Number of animals (in parentheses) refers to the number of individuals marked but animals that dispersed and trapped at other sites were considered a "new" animal.

[a] Indicates animals originally marked at RLC but later trapped at DWC (n = 3).

[b] One female originally marked at SCC during June of 2005 dispersed to RLC.

[c] One female originally marked at SCC during February of 2002 dispersed to TDC.

a) Adults



b) Young of Year

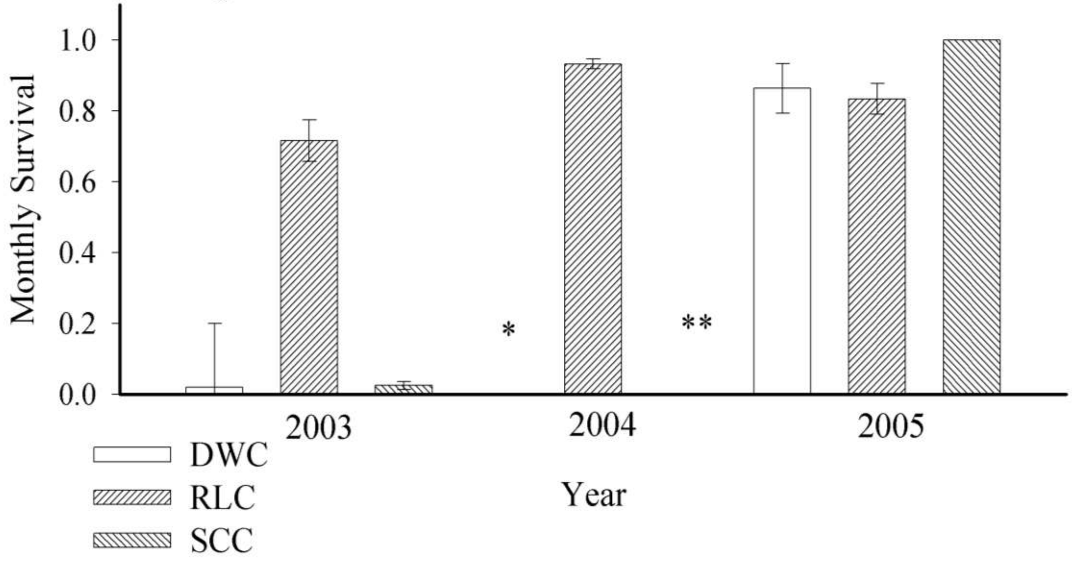


Figure 5. (a) Estimates of monthly survival (± SE) through time for adults at DWC, RLC, and SCC. Estimates for RLC were constant through the study with differences in sex, it is shown here as a mean value between sexes (females = 0.970 ± 0.006; males = 0.946 ± .009). (b) Estimates of monthly survival (± SE) for young of year animals by colony for the first six months after emergence * = No juveniles emerged at DWC in 2004, ** = Juveniles emerged but were not captured at SCC in 2004.

Table 4. A list of ten competing models for each analysis of survival by colony (BGE and BGW combined). For each model the model selection criterion (AIC_c), the difference between each model and the most supported model (Delta AIC_c), the relative support given to a model (AIC_c Weights), the model likelihood, number of estimated parameters (Num. Par), and the deviance (Deviance) is given. Large case letters under Model Names refers to the parameters, S = Survival, γ'' = Emigration, γ' = Immigration, M = Closed capture model, the symbol in parentheses describes the parameterization for each parameter (see legend at the bottom of table).

Colony	Model Name (description)	AIC_c	Delta AIC_c	AIC_c Weights	Model Likelihood	Num. Par	Deviance[a]
BG	S(s) γ"(.) γ'(.) M(t)	272.92	0.00	0.29	1.00	22	183.38
	S(s) γ"(.) γ'(.) M(h)	273.91	0.99	0.18	0.60	9	229.76
	S(site) γ"(.) γ'(.) M(t)	274.69	1.77	0.12	0.41	22	185.15
	{S(s) γ"(site) γ'(.) M(t)	276.36	3.44	0.053	0.17	23	182.22
	{S(s) γ"(s) γ'(.) M(t)	276.88	3.96	0.041	0.13	23	182.73
	{S(s) γ"(.) γ'(s) M(t)	276.88	3.97	0.041	0.14	23	182.74
	{S(s) γ"(.) γ'(site) M(t)	277.52	4.60	0.03	0.10	23	183.38
	{S(s*site) γ"(.) γ'(.) M(tb)	278.95	6.03	0.01	0.05	11	229.18
	{S(s*site) γ"(.) γ'(.) M(t)	281.75	8.83	0.01	0.01	24	182.80
	{S(t*s) γ"(.) γ'(.) M(t)	303.84	30.93	0.00	0.00	29	177.01
DWC	S[ad(t)/y03(.)/y05(.)] γ"(.) γ'(g) 0M(t)	1101.23	0.00	0.72	1.00	53	1005.88
	S[ad(t)/yoy(age)] γ"(.) γ'(g) M(t)	1103.94	2.71	0.18	0.25	54	1005.53
	S[ad(t)/y03(rec)/yoy05(.) γ"(.) γ'(g) M(t)	1106.11	4.88	0.06	0.08	54	1007.70
	S[ad(t)/yoy(.)] γ"(.) γ'(s*ac) M(null)	1107.31	6.08	0.03	0.04	22	1095.07
	S(ac*t) γ"(.) γ'(s*ac) M(null)	1109.69	8.45	0.01	0.01	23	1095.07
	S(ac*t) γ"(.) γ'(s*ac) M(b)	1111.60	10.35	0.01	0.01	32	1074.78
	S(ac) γ"(t) γ'(.) M(tb)	1114.15	12.92	0.00	0.00	33	1074.78
	S(t) γ"(.) γ'(.) M(h)	1114.16	12.93	0.00	0.00	20	1106.60

Table 4 Cont.

Colony	Model Name (description)	AIC_c	Delta AIC_c	AIC_c Weights	Model Likelihood	Num. Par	Deviance[a]
DWC	S[ad(t)/y03(.)./y05(.)] γ"(.) γ'(.) M(h)	1117.37	16.13	0.00	0.00	32	1080.56
	S[ad(t)/yoy(.)]γ"(t) γ'(.) M(t)	1128.95	27.72	0.00	0.00	62	1005.08
RLC	S[(ad(s)/y03(rec)/y04(rec)/y05(rec)]γ"(s*ac) γ'(t) M(tb)	8857.57	0.00	0.99	1.00	213	11186.46
	S(s*ac) γ"(s*ac) γ'(t) M(tb)	8867.50	9.93	0.01	0.01	214	11193.93
	S[ads(s)/yoy(.)] γ"(s*ac) γ'(t) M(tb)	8878.41	20.84	0.00	0.00	213	11207.30
	S[ad(s)/yoy(.)] γ"(s*ac) γ'(t) M(tb)	8879.78	22.20	0.00	0.00	214	11206.21
	S[ad(s)/yoy(rec)]) γ"(s*ac) γ'(t) M(t)	8886.95	29.38	0.00	0.00	134	11402.40
	S(s*ac) γ"(s*ac) γ'(t) M(t)	8900.38	42.80	0.00	0.00	136	11411.28
	S(t) γ"(s*ac) γ'(t) M(tb)	8903.39	45.82	0.00	0.00	227	11197.65
	S(s*ac) γ"(s*ac) γ'(t) M(b)	9086.99	229.42	0.00	0.00	135	11600.17
	S(s) γ"(s*ac) γ'(t) M(null)	9373.11	515.53	0.00	0.00	68	12033.75
	S[ads(s*t)/y03(.)/y04(.)/y05(.)] γ"(g) γ'(t) M(null)	9408.62	551.05	0.00	0.00	106	11986.79
SCC	S[ads(t)/y03(rec)/y05(rec)] γ"(t) γ'(s*ac *t) M(t)	2525.18	0.00	1.00	1.00	30	3084.93
	S(t) γ"(t) γ'(s*ac*t) M(t)	2581.73	56.56	0.00	0.00	44	3110.54
	S(t) γ"(t) γ'(t) M(t)	2599.81	74.63	0.00	0.00	44	3128.61
	S(t) γ"(t) γ'(s*ac) M(t)	2624.94	99.76	0.00	0.00	54	3130.89
	S(t) γ"(t) γ'(s*ac *t) M(null)	2634.99	109.81	0.00	0.00	66	3112.66
	S[ads(t)/y03(rec)/y05(rec)] γ"(.) γ'(.) M(t)	2645.92	120.75	0.00	0.00	66	3123.60

Table 4. Cont.

Colony	Model Name (description)	AIC_c	Delta AIC_c	AIC_c Weights	Model Likelihood	Num. Par	Deviance[a]
SCC	S(t) γ''(t) γ'(.) M(t)	2669.27	144.09	0.00	0.00	70	3137.31
	S(t) γ''(t) γ'(s*ac*t) M(tb)	2769.06	243.88	0.00	0.00	143	3039.44
	S[ads(t)/y03(rec)/y05(rec)] γ''(t) γ'(s*ac *t) M(h)	2894.76	369.58	0.00	0.00	47	3416.77
	S[ads(t)yoy(.)] γ''(t) γ'(s*ac*t) M(null)	2916.42	391.24	0.00	0.00	75	3372.24
TDC	S(s) γ''(.) γ'(.) M(b)	314.52	0.00	0.40	1.00	13	258.77
	S[ad(.)/y04(.)/y05(.)] γ''(.) γ'(.) M(b)	315.39	0.87	0.26	0.65	14	256.69
	S[ad(s)/y04(.)/y05(.)] γ''(.) γ'(.) M(b)	318.24	3.72	0.06	0.16	15	256.50
	S([ad(.)/y04(.)/y05(.)]γ''(.) γ'(.) M(h)	318.99	4.47	0.04	0.11	10	271.57
	S[ad(.)/y04(.)/y05(.)]γ''(s) γ'(.) M(null)	320.04	5.53	0.03	0.06	11	269.93
	S(s) γ''(.) γ'(.) M(h)	320.36	5.84	0.02	0.05	9	275.55
	S[ad(s)/y04(s)/y05(.)] γ''(.) γ'(.) M(t)	331.60	17.08	0.00	0.00	24	237.55
	S[ad(t)/yoy(s)] γ''(.) γ'(.) M(b)	338.66	24.14	0.00	0.00	21	256.49
	{S(ad*s/04*sex/05same) γ''(.) γ'(.) M(t)	331.60	17.08	0.00	0.00	24	237.55

Note. Model codes, s = sex, ac = age class, t = time, yoy = all juvenile age classes combined (no difference in estimates), y03 = young of year from 2003, y04 = young of year from 2004, y05 = young of year from 2005, rec = 'recruitment' animals are analyzed separately from adults until the spring of the following year at which time they become part of the adult cohort, / = separates groups that are estimated separately, * = interactions between groups or effects. Closed model coding follows (Otis et al. 1978) where null = no difference between probability of initial capture or recapture, t = capture probability varies with time, b = difference in probability of initial capture and recapture, h = heterogeneity; all animals have a different probability of capture, tb = initial capture and recapture probabilities vary with time, th = individual have different probabilities of capture that vary with time, bh = individual have different probabilities of initial capture and recapture, tbh = all individuals have a different probability of initial capture and recapture which vary with time.
[a]Deviance = -2log(Likelihood) of the tested model – 2log(Likelihood) of the saturated model (where the saturated model is defined as the model where the number of parameters equals sample size).

juveniles were indistinguishable from adults in their survival patterns; it is at this time that juveniles effectively reach adult body mass. These patterns in adult and juvenile survival indicate that survival differs with age and that there was an important decline in juvenile and adult survival in 2003.

Estimates of survival during the lactation and fall periods matched very closely those derived from the more complete data sets. At RLC and DWC, I found no affect of body mass on survival. Conversely, estimates from both the lactation period and fall 2003 suggest a positive relationship between body mass and monthly survival for SCC (AIC_c weight = 0.44, model likelihood = 1.00; Figure 6). Animals had a reduced probability of survival during lactation compared to the fall and animals in the fall appeared to reach a threshold body mass of around 1000 grams after which they approached a survival rate of 1.0. Age effects were strong, differences based on sex were once again not apparent, and juvenile body mass was not found to be an important covariate influencing survival for this colony at any time. Estimates of survival for a specific body mass were derived with the linear model (back converted from logit link) for lactation in 2003,

$$S = \frac{e^{25.64 + 0.96(\text{age}) - 27.76(\text{time}) + 0.0012(\text{body mass}) + 0.0012(\text{time} * \text{body mass})}}{1 + e^{25.64 + 0.96(\text{age}) - 27.76(\text{time}) + 0.0012(\text{body mass}) + 0.0012(\text{time} * \text{body mass})}}$$

and for the fall of 2003,

$$S = \frac{e^{25.63 + 0.96(\text{age}) - 32.11(\text{time}) + 0.0045(\text{body mass}) + 0.0045(\text{time} * \text{body mass})}}{1 + e^{25.63 + 0.96(\text{age}) - 32.11(\text{time}) + 0.0045(\text{body mass}) + 0.0045(\text{time} * \text{body mass})}}$$

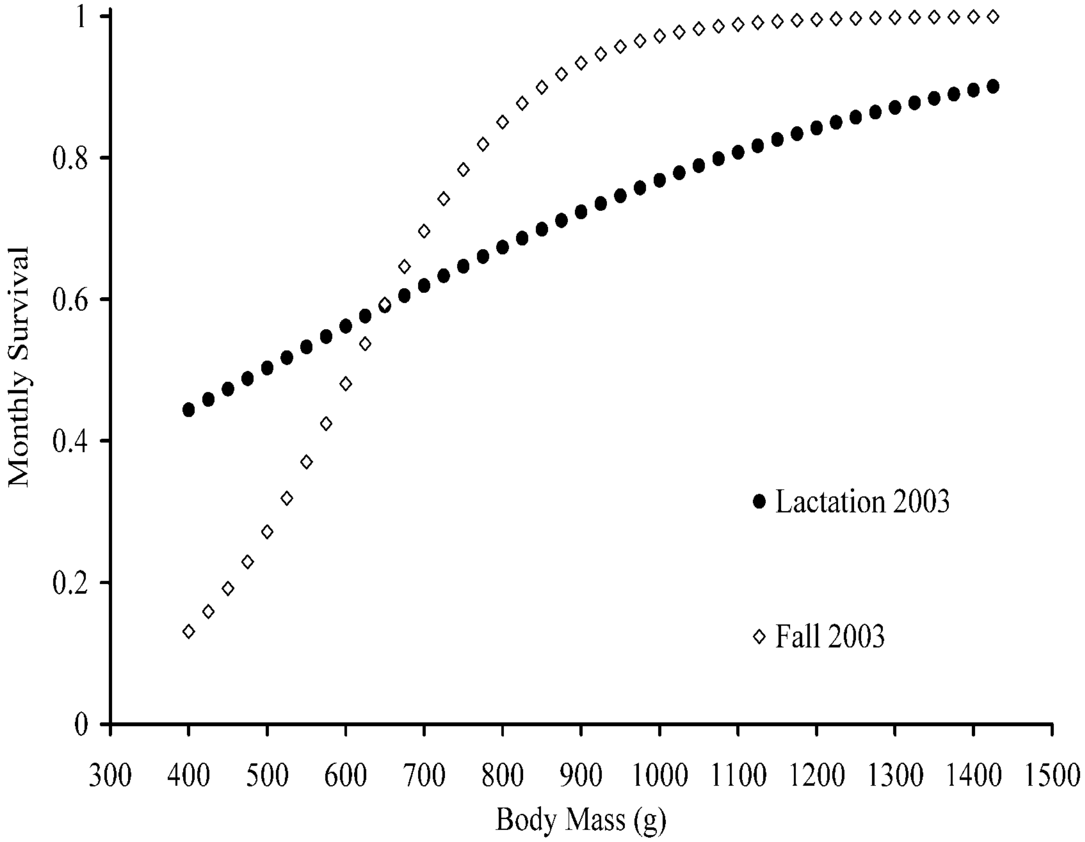


Figure 6. Estimated relationship between individual body mass and monthly survival of adult black-tailed prairie dogs at SCC during 2003 (mean body mass during lactation = 869 g, fall = 876 g).

Vegetation

Statistically detectable differences in vegetation were only found for bare ground and litter (Table 5). Contrasts found a seasonal ($F = 51.58$, DF = 1, $p < 0.01$) and year influence ($F = 5.95$, DF = 1, $p = 0.03$) for bare ground, while detecting an interaction between season and year (F = 6.05, DF = 1, $p = 0.03$) and a year effect (F = 11.66, DF = 1, $p < 0.01$) for the litter component. The percentage of grass and forbs were lowest in the spring of 2004 and highest in the fall of 2004. Spring of 2004 also had the highest percentage of bare ground compared to any other period. Fall of both years had a higher percentage of grass and forbs while having smaller percentages of bare ground (Table 5). Litter seemed to follow the general trends of grass and forbs except in the fall of 2005 when it was lower than during any of the other time periods and was statistically different from the fall 2004 and spring 2005.

Discussion

Vital rates of black-tailed prairie dogs are dynamic in desert grasslands. Prairie dogs in these environments experience large temporal and spatial variation in both their rates of survival and reproduction. This heterogeneity in vital rates appears responsible for large scale declines in population size in two of the three intensively studied colonies during relatively short periods of time; vital rates in other colonies remained relatively stable. I further observed that all females at a particular colony (DWC) completely failed to reproduce in one year while other colonies produced large numbers of juveniles. Finally, individual rates of reproduction were linked directly to female body mass while large scale population declines coincided with precipitous declines in body mass during one particular year (2003). Body mass was highly dynamic throughout the study, but not without a discernable pattern. Both females and males appear to gain mass in the fall after the monsoonal showers. Individuals of both sexes lose mass during time periods that are energetically taxing. In all years, females lost mass during May and June coinciding with lactation.

Table 5. Changes in the mean percent cover of four vegetative components across six prairie dog colonies during the spring and fall of 2004 and 2005. An ANOVA was used to test the null hypothesis of no difference in mean percent cover with time (for all *F*-values: DF = 3, 15, n = 24).

				Overall Test	
Component	Time	Mean Percent (± SE)	LS Means Difference	*F*	*p*-value
Bare Ground	Spring 04	70 (2.3)	A	179.91	< 0.01
	Fall 04	43 (4.8)	A B		
	Spring 05	69 (2.3)	B C		
	Fall 05	59 (4.3)	C		
Litter	Spring 04	17 (2.5)		4.93	0.01
	Fall 04	25 (3.6)	A B		
	Spring 05	12 (2.0)	A		
	Fall 05	8 (2.5)	B		
Grass	Spring 04	11 (3.7)		1.09	0.38
	Fall 04	19 (3.7)			
	Spring 05	11 (3.7)			
	Fall 05	15 (3.8)			
Forbs	Spring 04	1 (0.1)		3.14	0.06
	Fall 04	13 (6.0			
	Spring 05	7 (2.0)			
	Fall 05	11 (5.0)			

Note. Values with the same letters are significantly different from one another ($\alpha = 0.05$) using Tukey-Kramer post-hoc tests.

Males lost a significant proportion of body mass during the early spring when they are actively engaged in intraspecific competition for mates. For female and males alike, 2003 represented a year of extreme weight loss. Individuals of both sexes were relatively heavy in the early spring but subsequently dropped large amounts of body mass toward the end of spring and during the summer. Females in 2003 lost an average of 256 g (SD = 58, n =3; averaged across colony) between February and May (Figure 2). The size of this decline was never seen again in the two subsequent years and indicates that the factors influencing body mass were particularly harsh during the late spring and early summer of 2003.

Conditions during 2003 continued to influence individual body mass during the fall of that year. Though body mass increased for both sexes during each year of the study, animals weighed less during fall of 2003 than they did in either 2004 or 2005. This inability to regain body mass in the fall relates to conditions in the spring of 2004. Individuals of both sexes during the months of February and March were consistently lighter during 2004 than during any other year (Figure 2). Average body mass across sex and colony during February of 2003 and 2005 was 1062 g (SD = 172.89, n = 43) and 1044 (SD = 193.21, n = 30) respectively, but was only 793 g (SD = 117.83, n = 27) during February of 2004. Animals at DWC, the colony that crashed in 2004, showed large differences in body mass between years during the month of February. During 2003 and 2005 animals at DWC had average body masses above 1200 grams ($\bar{x}$ = 1209.42, SD = 144.70, n = 31) but during 2004 had an average body mass of only 652.27 grams (SD = 78.72, n = 11).

Juvenile body mass varied considerably, following the pattern observed in the adults. Young of year animals weighed less during the period after emergence in 2003 and 2004 compared to animals in 2005 (Figure 3). Juveniles born in 2003 gained less mass during their first fall (Figure 3). Young of year animals from 2004 appeared to compensate for their relatively light mass following emergence and by their first fall averaged more than 700 grams (Figure 3). The patterns of body mass change in juveniles followed the temporal pattern I saw in adults where animals were lighter during the summer of 2003 and the spring of 2004 but gained mass in the fall of 2004. Animals in 2005 appeared to fair better throughout the year. For both age classes the patterns of body mass change are concordant, appear to track changes in precipitation and influence population growth through their affect on survival and, more importantly, reproduction.

Body mass and its influence on reproduction

For all years there was a relationship between the probability of a female becoming sexually active and her March body mass (Figure 4). The higher a female's March body mass was the more likely she was to become sexually active (exhibit signs of lactation). There also appeared to be a threshold body mass below which the probability of females reproducing was reduced particularly in 2003 and 2004. Females below 700 grams had less than a 20% chance of reproducing in 2003 and 2004 (Figure 4). As an example all females at DWC in 2004 had body masses below 650 grams and no individual successfully reproduced. Therefore, the conditions of 2003 and early 2004 seemed to have negatively influenced female reproduction and ultimately population growth. In addition, the negative influence of poor body condition in 2003 may have influenced the late emergence of juveniles at all colonies in 2004. Lastly, large females that became pregnant have larger litters. These factors are important to population growth because larger animals will result in populations with more breeding females that produce more juveniles per female.

Body mass and survival

Though the link between reproduction and body mass appeared strong, the relationship between body mass and survival was not as well supported by the data. There was an association between survival and body mass at SCC during the interval following lactation in 2003. This time period coincided with the lowest rates of adult survival observed during the study; however, this was the only colony where I could detect this relationship. Following the fall of 2003 and the spring of 2004, adult monthly survival was > 0.90 for all colonies. Similarly, I could not establish a relationship between body mass and juvenile survival for any particular interval, but juveniles marked in 2003, at either DWC or SCC, were never recaptured again and at the RLC, only 2 of the 26 YOY animals originally trapped in 2003 were encountered again. In the fall, juveniles weighed significantly less in 2003 than in either 2004 or 2005 (Figure 3). Although the mechanism behind the low juvenile survival observed for the 2003 cohort is not known, the low body masses observed suggests that resource limitation may have resulted in poor body condition which could have adversely impacted survival directly, through starvation, or indirectly by lowering disease resistance or making prairie dogs more susceptible to predation.

Low rates of survival for both adults and juveniles coincided with periods when prairie dogs experienced large declines in body mass. Population sizes also fell at all colonies following the lactation period of 2003, most dramatically at SCC where the population size was estimated at 85 animals (95 % CI = 77 – 94) prior to emergence of young but fell to 8 individuals (CI = 8 – 9) by the following January (see Chapter 1). Similarly, the populations at DWC and RLC fell from an estimated 37 (CI = 24 – 50) and 91 (CI = 84 – 97) animals prior to emergence to 16 (CI = 10 - 18) and 76 (CI = 67 – 84) animals, respectively, by the next spring.

There is additional evidence that these population declines were not limited to DWC, RLC and SCC but rather occurred at many prairie dog populations throughout the ranch. During the summer of 2003, BGE, BGW and TDC had a minimum of 20, 29, and 18 animals, respectively (Hendrie 2004). Despite 950 total trap nights, I was only able to document 6, 7 and 5 animals at BGE, BGW and TDC, by the spring of 2004. Though there is the possibility that animals simply went undetected during these trapping sessions, it is unlikely that the populations were much larger than this because in over 15 observations of each colony I never observed more animals than could be verified with trapping. In total, rates of survival and population growth indicated that during 2003 conditions were sufficiently different from subsequent years to cause dramatic population crashes and overall population decline.

A common factor that all prairie dog colonies faced during 2003 was an extreme drought throughout the region. Average precipitation from five weather stations located near (Bosque Del Apache, Truth or Consequences and Elephant

Butte; WRCC) and on the ranch (Engle and Casa Grande; Traphagen 2005, unpublished data) reveal that the total rainfall during 2003 was only 129 mm (43% below average). Precipitation during 2004 was 265 mm (17% above average) and for 2005 was 204 mm (11% below average).

Resource limitation and other causes of population decline in ground-dwelling squirrels

Throughout the majority of their range precipitous declines in prairie dog populations are usually attributed to sylvatic plague (*Yersina pestis*) (Biggins and Kosoy, 2001a; Biggins and Kosoy, 2001b; Cully and Williams, 2001). In black-tailed prairie dogs, plague often completely decimates a colony with survival rates approaching zero and all cohorts of the population affected relatively equally with no age or sex bias (Menkens and Anderson, 1991; Cully and Williams, 2001). As of 2003 only two instances of human and feline plague had been confirmed in either Socorro or Sierra County (the ranch lies within both; NMDH 2006). The Armendaris Ranch has been opportunistically sampled by testing culled coyotes (*Canis latrans*) since 1994 (~ 30 samples) and there has never been a plague titer high enough to confirm plague exposure within the population (Tom Waddell, pers. comm.). Though I cannot rule out the possibility that plague affected my study colonies, the population declines observed in 2003 were not consistent with a plague outbreak. First, although all colonies experienced population declines, none went extinct. Second, colonies were very close together ($\leq$ 6 km) and at least 1 colony (RLC) did not decline as much as the others. If plague had occurred, I would have expected all colonies to decline by a similar and significant percentage (> 90%). Finally, plague has a very low prevalence in the region. If plague were not the cause of the observed declines it is an important finding because it suggests an alternate mechanism, namely resource limitation, whereby prairie dog populations can decline rapidly.

Van Horne et al. (1997) found that during a severe drought persistence of adult Townsend's ground squirrels (*Spermophilus townsendii*), while low, was still higher than that of juveniles, which was near zero. These results mirrored my observations in 2003 when high juvenile and adult mortality occurred during the severe drought. Though the relationship between rodent population growth and rainfall is often non-linear and complex there is still a fundamental relationship (Brown and Ernest, 2002).

Primary production in desert ecosystems is controlled largely by precipitation (Noy-Meir, 1973; Knapp and Smith, 2001). Each mm of rain produces only 4 kg of above ground dry matter per ha/year in arid lands (Le Houerou 1988) and even drought resistant grasses can be negatively influenced by low precipitation (Fernandez, 1999). Given the relatively small amount of precipitation during 2003, the large declines in body mass and the population declines at six prairie dog colonies it is difficult to believe that these factors are unrelated or simply coincidental. Further, it suggests that the high mortality of all juveniles and adults in two colonies were also related to resource abundance and precipitation.

The possibility also exists that factors other than resource limitation can explain the declines in 2003. Declines could have resulted from dispersal or predation. Dispersal between colonies does not appear high on the ranch. Of the 577 animals marked I can confirm only five that successfully dispersed among the colonies, which indicates that animals did not simply emigrate to other sites (Table 3). I did not quantify rates of predation though I did witness predation events. On three separate occasions I witnessed ravens kill and consume juvenile prairie dogs on RLC. In addition, an entire litter of pups was killed by a single raven at BGW (M. Hendrie, pers. comm.). During the spring and summer of 2003, ravens (*Corvus* spp.) were numerous on the ranch and at times I observed > 30 on RLC and SCC at once. In subsequent years ravens were far less common on the ranch, and I seldom saw more than 3 ravens on any colony at a time. Therefore, predation was likely partly responsible for declines during 2003, but raven predation would have been restricted to YOY and cannot explain the reduction in adult survival or reproduction.

Predation, however, may not be independent of resource limitation. Animals in poor body condition have been shown to alter their foraging habits thereby increasing predation risk (Bachman, 1993; Wirsing and Murray, 2002). Survival rates that vary with body mass (Figure 5) potentially support either model for survival declines at SCC (predation/starvation), and although predation could have been a proximate mechanism leading to population declines, resource limitation would still have been the ultimate cause if prairie dogs altered foraging activity and thereby increased predation risk.

Hoogland (2006) outlined several important factors related to black-tailed prairie dog demography. Of these factors he listed over-winter mortality as a critical period for prairie dogs because of resource limitation and harsh winter conditions. Other animals living in harsh northern regions appear to be affected by over-winter mortality in a similar fashion (Hubbs and Boonstra, 1997; Karels et al, 2000; Patapov et al, 2004; Hodges et al., 2006). My study suggests that winter survival, even in the worst years, was relatively high in desert grasslands and that the period following reproduction may be more crucial to prairie dog survival in areas where animals experience the most extreme conditions during the summer, as they do in desert grasslands (Figure 1).

Of equal importance in desert grasslands is the reproductive status of individuals and ultimately populations. Hoogland (1995) demonstrated that increased body mass resulted in increased litter size in black-tailed prairie dogs. Other studies on prairie dogs have found a direct link between resource abundance and reproduction (Hoogland and Garret, 1982; Rayor, 1985). This study supports that pattern, but also demonstrates that a single bad year or period may influence prairie dog populations in subsequent years (DWC 2004). If rates of survival are low and are coincident with or followed by poor reproduction the population may actually reduce its ability to propagate as older females become senescent (Hoogland 1995).

Conclusions

I have demonstrated that prairie dog vital rates are dynamic in desert grasslands and that large-scale population crashes can occur in short periods of time. Body mass is also highly variable and influences both the probability that a female will become reproductively active as well as the number of young she produces. There is also some support linking declines in survival to declines in body mass. More importantly, I have demonstrated that reproduction, survival and population declines are coincident with a period of extreme drought. Though, these results are not conclusive, they do support the premise that resource limitation is an important determinant of prairie dog population dynamics and that more research in this area is needed.

In sum, the way that precipitation, climate and vegetation alter prairie dog populations in desert grasslands are still largely unknown, but this study suggests the possibility of very real threats to long-term persistence of prairie dogs related to resource variability and limitation. Ultimately, there is a need to evaluate the conditions under which black-tailed prairie dogs can exist and expand; failure to address these issues may result in failures to expand and conserve prairie dogs within desert grasslands.

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