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John L. Hoogland
Appalachian Evironmental Laboratory, University of Maryland - Frostburg

Diane Kay Angell
Brown University, Providence, RI.

James G. Daley
Appalachian Environmental Laboratory, University of Maryland, Frostburg, MD

Matthew C. Radcliffe
Appalachian Environmental Laboratory, University of Maryland, Frostburg, MD

Demography and Population Dynamics of Prairie Dogs[1]

John L. Hoogland[2], Diane K. Angell[3], James G. Daley[4], and Matthew C. Radcliffe[4]

Abstract.--For the last 14 years, we have been studying the sociobiology, demography, and population dynamics of black-tailed prairie dogs (Cynomys ludovicianus) in Wind Cave National Park, South Dakota. Our study colony covers 6.6 hectares (16 acres) and has not expanded during the period of research; in late spring of each year the colony contains a mean ± SD of 133 ± 29 adults and yearlings and 81 ± 33 juveniles. We have discovered four surprising aspects of the demography and populations dynamics of prairie dogs. (1) Mortality during the first year is approximately 50% for both sexes. Those males that survive the first year can live as long as 5 years, and females that survive the first year can live as long as 7 years. (2) Litter size ranges from 1 to 6, the mean ± SD is 3.05 ± 1.08, and the mode is 3. (3) Although individuals of both sexes usually defer first breeding until the second year, 9% of females and 3% of males first produce offspring as yearlings. (4) Infanticide is the major source of juvenile mortality, accounting for the partial or total demise of 51% of all litters born. In the most common type of infanticide, lactating females kill the unweaned offspring of their sisters and daughters.

INTRODUCTION

Black-tailed prairie dogs (Cynomys ludovicianus) are large (600-1200 grams), diurnal, colonial, harem-polygynous rodents of the squirrel family (Sciuridae) (King 1955; Koford 1958; Smith 1958; Tileston and Lechleitner 1966; Foltz and Hoogland 1981). At Wind Cave National Park, Hot Springs, South Dakota, prairie dogs breed in February and March, and juveniles first emerge from their natal burrows in May and June (King 1955; Hoogland and Foltz 1982). Colony residents live in contiguous family groups called coteries (King 1955), which typically contain one adult (≥ 2 years old) male, 3-4 adult females, and several yearling and juvenile offspring. Coterie members restrict all foraging and other activities to a clearly defined, vigorously defended coterie territory. Litter size, juvenile growth rate, survivorship during the first year, age of first reproduction, and pregnancy rate all seem to be affected by the availability of food (Garrett et al. 1982). Estrous females usually copulate exclusively with the adult male in the home coterie (Hoogland and Foltz 1982), and inbreeding is rare (Hoogland 1982a; Foltz and Hoogland 1983). Females within a colony synchronize their breeding, and synchronization within coteries is also evident (Hoogland 1981a). The mean ± SD gestation period for prairie dogs is 34.8 ± 0.7 days (N = 32; range = 34-37), and the mean ± SD time between parturition and the first emergence of weaned juveniles is 43.4 ± 3.5 days (N = 17; range = 38-50) (Hoogland 1985a).

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[2]John L. Hoogland is Assistant Professor of Wildlife Biology, Appalachian Environmental Laboratory, The University of Maryland, Frostburg, MD.

[3]Diane K. Angell is a graduate student in the Department of Biology, Brown University, Providence, RI.

[4]James G. Daley and Matthew C. Radcliffe are graduate students at the Appalachian Environmental Laboratory, The University of Maryland, Frostburg, MD.

Disadvantages of coloniality for individual prairie dogs include increased aggression and increased ectoparasitism by fleas and lice (Hoogland 1979a). To offset these costs, there may be only one benefit of prairie dog coloniality: increased protection from predators such as coyotes (Canis latrans), badgers (Taxidea taxus), bobcats (Lynx rufus), golden eagles (Aquila chrysaetos), prairie falcons (Falco mexicanus), and various buteo hawks (Buteo spp.) (King 1955; Hoogland 1981a). Prairie dogs in large colonies not only detect predators more quickly than do dogs in smaller colonies, but also spend less time scanning for predators (Hoogland 1979b, 1981a). The dense coloniality of prairie dogs which has evolved in response to most predators has evidently left the dogs especially vulnerable to another predator: the black-footed ferret (Mustela nigripes) (Hoogland 1981a, 1982b). Ferrets do not prey heavily on prairie dogs now since the ferrets are so rare, but may have been important in regulating prairie dog numbers for most of the prairie dogs' evolutionary history (Hoogland 1982b).

Nepotism, the preferential treatment of genetic relatives (Alexander 1974; Sherman 1980), is pronounced among prairie dogs. For example, individuals are less likely to fight with, and more likely to interact amicably with, kin than with nonkin (Hoogland 1981b; Hoogland 1986). Further, prairie dogs with living kin within earshot are more likely to give an alarm call in response to a predator than are dogs without such kin (Hoogland 1983a).

Here we report our findings that are relevant to the demography and population dynamics of prairie dogs.

METHODS

Our study colony, inhabited for at least the last 35 years and possibly much longer, is approximately 500 meters x 130 meters (6.6 hectares). Most of this colony is surrounded by trees, but there is room for potential expansion at the south end. The colony is gridded into 15.2 m x 15.2 m squares with garden stakes, and burrows are marked with Ritchey Cattle Eartags mounted on clothesline wire (Hoogland 1977). The nearest other colony to the study colony is approximately 0.7 kilometers away.

For permanent identification, prairie dogs are marked in the ear with numbered National Band and Tag Fingerling Tags (Hoogland 1979a). Each eartag usually remains with the dog until its death, but tags are sometimes lost during vicious fights. For this reason, one numbered tag is placed in each ear; since 1975, only five dogs, including all four offspring from one litter, have lost both eartags. Using prairie dogs of known age for comparison, we have recently devised a method for placing individual dogs of unknown age into one of three age classes (Hoogland and Hutter 1987). Through eartagging, observation, and an electrophoretic analysis of blood samples, maternal, sibling, and putative paternal genetic relationships have been determined for all young weaned at the study colony since 1975 (968 young from 317 litters) (Foltz and Hoogland 1981; Hoogland and Foltz 1982; Hoogland 1986).

For visual identification from a distance, we use Nyanzol-D fur dye from J. Belmar Inc (King 1955; Hoogland 1979a). Males are marked with numbers under 50, and females are marked either with numbers above 50 or with gross markers such as stripes and blotches. Dogs marked with Nyanzol-D can be identified with binoculars from distances over 300 meters.

Observations are made from three 5-meter high observation towers positioned at the periphery of the study colony. From before the first copulation in mid-February until the last juvenile has been eartagged and colormarked in June, all three towers are manned from early in the morning before any dogs emerge until late in the afternoon when all dogs have immerged for the night.

RESULTS

Variation in population size.--The number of adults and yearlings in April at the study colony has ranged from a low of 92 in 1985 to a high of 216 in 1975, with a mean $\pm$ SD of 132.5 $\pm$ 29.3. The number of weaned juveniles has ranged from a low of 4 in 1975 to a high of 133 in 1986, with a mean $\pm$ SD of 80.7 $\pm$ 33.0. As expected, the number of weaned juveniles seems to vary inversely with the number of adults and yearlings. In other words, prairie dogs at the study colony typically produce more offspring when colony size (the number of adults and yearlings) is low, and fewer offspring when colony size is high (Hoogland, in preparation). Within a coterie, the number of weaned offspring also varies inversely with the number of adults and yearlings (Hoogland 1981b).

Variation in physical area of colony.--Even though the number of prairie dogs foraging aboveground at the study colony has ranged from 92 in April of 1985 to 252 in May of 1981, the physical area occupied by the dogs has remained EXACTLY THE SAME for fourteen consecutive years. Further, despite dramatic fluctuations in the number of dogs within a coterie, most of the coterie territories at the study colony have remained exactly the same for fourteen consecutive years. Increases in the size of the home coterie territory usually occur only after expansion into an adjacent coterie territory in which all the females have disappeared.

Variation in number of burrow entrances.--When we mapped the study colony in May of 1975, there were 1,591 burrow entrances (Hoogland 1977). While the prairie dogs typically excavate several new burrow systems each year, others disappear from lack of use. The result is that the number of burrow entrances has remained remarkably constant, varying by fewer than 10 entrances from one year to the next (Hoogland, unpublished).

Longevity.--For males at the study colony, survivorship during the first year has ranged from 13/36 = 36% in 1984 to 34/43 = 79% in 1980, with a mean ± SD of 51% ± 16%. Males that survive the first year commonly live to be 3 or 4. Only 9 males have lived as long as 5 years.

For females at the study colony, survivorship during the first year has ranged from 13/41 = 32% in 1978 to 27/39 = 69% in 1980, with a mean ± SD of 56% ± 13%. Females that survive the first year commonly live to be 4, 5, or even 6. Only 12 females have lived as long as 7 years.

Age of first reproduction.--In general, individuals of both sexes do not first reproduce until February-March of the second year (King 1955; Hoogland and Foltz 1982). Although approximately 40% of females first copulate as yearlings, only 20 /213 = 9% of yearling females have successfully weaned a litter. Many females do not first wean a litter until 3 or 4 years old. Mainly because of infanticide (see below), the mean ± SD percentage of adult females that weans a litter each year is only 47% ± 14% (range = 30% in 1976 to 73% in 1986). Only 7/216 = 3% of yearling males have successfully sired offspring.

Litter size.--Litter size at first juvenile emergence among prairie dogs at the study colony ranges from 1 to 6, with a mean ± SD of 3.05 ± 1.08 (N = 311 litters); we have no information about litter size at birth. The most common litter sizes at first juvenile emergence are 2 (19%), 3 (38%), and 4 (26%). As predicted from ecological theory (Williams 1957; Sherman and Morton 1984), the relationship between female age and litter size at first juvenile emergence is curvilinear: litter sizes of 3- and 4-year old females are larger than litter sizes of younger and older females (Hoogland, in preparation). The relationship between male reproductive success and age may also be curvilinear.

Variation in sex ratio at weaning.--For all young weaned at the study colony each year, the percent of males has varied from 31/74 = 42% in 1985 to 55/93 = 59% in 1983, with a mean + SD of 53% + 6%. We have no information about the sex ratio at birth.

Dispersal and immigration.--In general, prairie dog females at our study colony remain in the natal coterie territory for their entire lifetimes (Hoogland 1982a; see also Garrett 1982). Those rare females that do disperse usually leave the study colony entirely. Only 3 females have successfully transferred from the natal coterie into another coterie within the study colony. Since 1975, only 5 females have immigrated into the study colony from somewhere on the outside and then weaned offspring. None of these females was recruited into an established coterie territory. Three of these immigrants lived at the periphery of the study colony, and the other two evicted females from established coterie territories and then moved into these vacated territories.

Yearling males at the study colony typically disperse from the natal coterie territory approximately 12-14 months after weaning (Hoogland 1982a; see also Garrett 1982). These young males sometimes disperse to other coteries within the study colony, but other times leave the study colony entirely in search of another colony. Occasionally males remain in the natal coterie territory for a second year: almost invariably, these males delay sexual maturity until the third year. Although the peak of dispersal by yearling males occurs in May, June and July, a second peak occurs in February, just before the onset of the breeding season. Older males also disperse after one or two years in the same coterie, probably to avoid inbreeding with their daughters (Hoogland 1982a). Whereas younger males disperse both intra- and inter- colonially, older males seem to restrict almost all of their movements to the study colony, and most of these older males disperse to adjacent coteries. Since 1975, only 14 males have immigrated into the study colony from somewhere on the outside and successfully sired offspring there.

Infanticide.--Infanticide, the killing of juvenile conspecifics (Sherman 1981; Hausfater and Hrdy 1984), is the major source of preweaning and postweaning juvenile mortality at the study colony, accounting for the total or partial demise of 51% of all litters born. Infanticide occurs in four different contexts (Hoogland 1985a, in preparation), as summarized below.

In Type I infanticide, female immigrants from somehere on the outside move into an established coterie territory in late spring or early summer, evict the resident females there, and then kill the recently weaned offspring. This is the rarest type of infanticide, mainly because female immigrants are so rare, and accounts for the elimination of 1% of all litters born.

In Type II infanticide, females abandon their offspring shortly after parturition and allow other coterie members to kill and cannibalize them. The details and possible reasons are poorly understood for Type II infanticide, which accounts for the elimination of 13% of all litters born.

As noted above, most dispersals by young males occur in May and June, just before or just after the weaning of juveniles. When a yearling male is successful in entering a new coterie, all the unweaned or weaned juveniles typically disappear within a few days. Male invaders presumably kill the juveniles that disappear (Type III infanticide): maimed carcasses were found aboveground after six invasions, and actual killings were observed twice. Type III infanticide accounts for the total or partial elimination of 7% of all litters born.

Type IV infanticide is the most extraordinary, since it involves the killing by lactating females of the offspring of close kin (mother, daughter, sister, aunt, niece, etc.) within the home coterie. Type IV infanticide is also the most common, accounting for the total or partial elimination of 30% of all litters born. Lactating females may kill

and cannibalize nondescendant juvenile kin in order to obtain sustenance necessary for the weaning of their own litters, or they may kill to remove future competitors from themselves and their offspring. Type IV and other types of infanticide observed at the study colony do not result merely from possible overcrowding, since infanticides were also observed at two other colonies at Wind Cave, both of which were young and expanding.

DISCUSSION

Here we have summarized those findings of our study that pertain to the demography and population dynamics of black-tailed prairie dogs at Wind Cave National Park, South Dakota. These findings have direct relevance to those situations in which management and control of prairie dogs might be considered necessary. To further investigate management of prairie dogs, one of us (Radcliffe) has initiated research to determine how quickly prairie dog colonies return to initial size after an artificial reduction of 90%. Another of us (Daley) has begun to examine the effects of colony size and artificial reduction on genetic variation within and between prairie dog colonies. All of us are continuing to investigate infanticide: if we can better understand why prairie dogs regularly kill 51% of all offspring born and those conditions which encourage such infanticide, then perhaps it will be possible to devise effective methods of management which capitalize on infanticide and which do not require shooting or poisoning.

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