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Demographic Differences Between an Old and a New Colony of Black-tailed Prairie Dogs (*Cynomys ludovicianus*)¹

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ABSTRACT: Two colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) in Wind Cave National Park, South Dakota, were compared during 1979 and 1980 to investigate the effects of (1) the age of the population and (2) the availability of resources on specific demographic parameters. The younger colony was surrounded by, and expanding into, unused available habitat. The older colony had little available habitat for expansion. At the younger colony (1) there was a greater proportion of successful pregnancies; (2) the litters were larger; (3) the juveniles grew faster; (4) yearlings were more likely to reproduce; (5) survivorship of adults and juveniles was greater, and (6) the density was more than 2X that of the older colony. Individuals at the younger colony showed a distinct feeding preference for vegetation growing at the colony periphery. Because this peripheral vegetation had only recently been modified from surplus habitat, we hypothesize that surplus habitat available to the younger colony accounted for the observed demographic differences.

INTRODUCTION

The demographic properties of a growing population vary with population size and environmental modification that may accompany population growth. Wilson (1975) points out that each population has an "optimum environment" where the intrinsic rate of increase (r) reaches its maximum value because of abundant food and space. However, because b (average birth rate per individual) and d (average death rate per individual) may be affected by increasing density and competition associated with population growth, exponential growth is reduced to logistic growth, and the population stabilizes when b equals d (K) (Chitty, 1967; Krebs, 1964; Lack, 1954; Lidicker, 1965.) The position of a population on its respective growth curve depends upon several factors, including the length of time the population has existed and the abundance of available resources. These factors may determine the degree of resource exhaustion and the level of competition for those resources.

These arguments suggest that a newly founded population may be characterized by high fecundity and survivorship, and even though the initial number of individuals is small, the population density may reach high levels (Krebs, 1966; Krebs *et al.*, 1969; Lidicker, 1965, 1973; Lack, 1954; MacArthur, 1962). As time passes and population size increases, resource shortages and mutual interference may cause a decline in population growth and density (Chitty, 1967; Christian, 1955, 1961; Krebs, 1964). To this point, all relevant data have come from laboratory studies, manipulation of wild populations and historical accounts of a single population over long periods of time. To our knowledge, there has been no study involving a comparison at the same time and in the same area of an old and a new natural population.

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The black-tailed prairie dog (*Cynomys ludovicianus*) is a large, colonial ground squirrel (Sciuridae) of the North American shortgrass plains. Colonies of prairie dogs are restricted by tall vegetation and topographic barriers (King, 1955; Koford, 1958). Colonies are subdivided into cooperative family units called *coterie*s (King, 1955). A *coterie* typically contains one adult male, 3-4 adult females and several yearlings and juveniles of both sexes (King, 1955; Hoogland, 1981a). Members of a *coterie* generally restrict their activities within a well-defined *coterie territory*, which they defend from members of other *coterie*s.

In northern latitudes, male and female prairie dogs generally do not breed until 2 years old; breeding occurs during late February and throughout March, gestation is about 34 days, infants remain underground for an additional 5-6 weeks, and weaned juveniles emerge from their natal burrows in May and early June (King, 1955; Hoogland, 1977, 1982). Females usually remain in their natal *coterie*s for their entire lives, whereas males usually spend their 1st year in their natal *coterie* and disperse during their 2nd year (Hoogland, 1981a).

Hoogland (1981a) noted survivorship of prairie dogs of both sexes was approximately 50% during their 1st year. After the 1st year chances of survival increase. King (1955) found an annual loss of 30% over a 2-year period (all age classes including juveniles).

Prairie dogs are almost entirely herbivorous and prefer graminoids over forbs (Hansen and Gold, 1977; Kelso, 1939; Koford, 1958; Smith, 1958; Summers and Linder, 1978; Wydeven, 1979). Burrowing and grazing by prairie dogs influence the soil and vegetation. Due to vegetative changes that prairie dogs cause in their environment, *vegetation zones* in roughly concentric rings may be produced on prairie dog colonies (Bonham and Lerwick, 1976; Hansen and Gold, 1977; King, 1955; Osborn and Allan, 1949). Intensive grazing results in depletion of grass in the middle of the colony; forbs subsequently invade the disturbed area and become dominant.

The purpose of this study was to compare specific demographic parameters in two colonies of prairie dogs. One colony was relatively young and expanding rapidly into favorable habitat, while the other was relatively old and had little available habitat for expansion. If logistic theory is applicable to these two naturally occurring populations, there should be marked differences in reproduction, development and maturation of juveniles, and survivorship. Because of abundant resources (food and space) (1) females of the younger colony should reproduce more successfully; (2) juveniles born at the younger colony should grow and develop faster and, consequently, reproduce sooner (*see* Cole and Batzli, 1978, 1979; Krebs, 1966; Lack, 1954); (3) individuals of the younger colony should survive better and (4) the younger colony should support a greater density of individuals compared with that of the older colony.

METHODS AND MATERIALS

Definitions.—In this paper, we define a *colony* as the physical area inhabited by prairie dogs, which is characterized by burrow mounds and modified vegetation. The *population* refers to the prairie dogs inhabiting the colony. *Demographic properties* are those characteristics that describe the growth or decline of a population—for example, reproduction, dispersal, survivorship, mortality, natality. *Dispersal* is defined as the movement of an individual away from its natal site. We were unable to discriminate between death and emigration from the colony. *Survivorship* refers to the number of individuals that remained in a particular colony from one time to another.

Procedures.—To obtain accurate information on reproduction and life histories, all prairie dogs at both study colonies were captured and marked with eartags and fur dye. Procedures used for live trapping, handling, and marking prairie dogs for observation are outlined elsewhere (Hoogland, 1977, 1979). Behavioral data were obtained from both colonies by observing the prairie dogs from observation towers. Breeding behavior of both study colonies was observed in 1980, but because research at the younger colony did not begin until May 1979, a comparison of reproduction in 1979

could not be made. Data could not be compared in 1981 because a synthetic estrogen was administered to the younger colony as part of another study.

A female prairie dog was considered pregnant if she was observed to copulate (Hoogland, 1982) or she (1) defended a nest burrow against other coterie members, and (2) frequently carried nest material into the defended burrow (King, 1955). A pregnancy *defection* was counted if, after exhibiting the above behaviors, a female began allowing other coterie members the use of her nest burrow and she did not wean a litter.

A yearling male was considered to be a breeding male if he dispersed from his natal coterie prior to the breeding season and was dominant over any other male that may have shared his newly acquired territory with him (King, 1955). Such individuals probably sired most of the offspring within that coterie during that breeding season (Foltz and Hoogland, 1981).

Feeding preference was calculated by dividing percent utilization by percent availability (Petrides, 1975). Percent utilization was determined by recording locations of all feeding prairie dogs at hourly intervals. Percent availability was determined by mapping and measuring the surface area of colony vegetation types. Data on feeding preferences were only available for the younger colony.

Standing-crop biomass was compared during the last week of June 1980. A transect was laid across the length of each study colony, and 40 0.1-m² plots were placed at 10-m intervals (Daubenmire, 1959). Vegetation in each plot was clipped to within 1 cm of the ground, air-dried for 72 hr, and weighed to the nearest 0.1 g. This did not include the unmodified vegetation surrounding the younger colony. We did not quantify individual plant species; rather, vegetation was grouped as graminoids, forbs and standing dead.

Flea counts were made between 0900 and 1500 hr on 2 and 3 November 1981. Fleas were collected from burrow entrances of both colonies following the procedure outlined by Hoogland (1979), who found that flea counts from burrow entrances positively correlate with counts from the animals themselves.

Results are based on data obtained from 15 May to 21 June 1979, 28 February to 13 June 1980, 19 to 31 October 1980 and 2 to 3 November 1981.

The study colonies.—The two study colonies were located in Wind Cave National Park, Hot Springs, South Dakota. The area is rolling mixed-grass prairie with coniferous forest on slopes and ridge tops (*see* King, 1955). Both study colonies were protected from shooting, poisoning and other human disturbance during the period of study.

The Rankin Ridge (RR) colony occupied a 6.6-ha valley located 15 km N of Hot Springs in sec. 14, T. 5 S., R. 5 E. The elevation at this site is approximately 1500 m. The soil is a deep dark-colored loam. The RR colony was established prior to the early 1950s (Cole, 1958). Pure stands of ponderosa pine (*Pinus ponderosa*) on steep slopes surround most of the colony. A small part of RR also is bordered by a dense growth of bluestem (*Andropogon* spp.). There has been no colony expansion since research began at Rankin Ridge in 1974.

The Wind Cave Canyon (WCC) colony was located 7 km S of the RR colony in sec. 6, T. 6 S., R. 6 E. The elevation is approximately 1300 m. The soil is a deep dark silt loam. The colony was located on a 3.6-ha floodplain of an ephemeral watercourse in Wind Cave Canyon. This site was a horse pasture until 1973, and then was burned as part of a research project in the spring of 1976. Prairie dogs were first discovered at the site in the autumn of 1976 and were shot by a park ranger (Dean Shilts, pers. comm.). Survivors or immigrants repopulated the site. When research began in May 1979, the colony covered a 0.47-ha section of the floodplain. By October 1980, the colony expanded 234% to include 1.57 ha, and 206 new burrow entrances were excavated (133% increase). In other words, during the period of study the WCC colony grew rapidly into available habitat that surrounded the colony on all sides. The RR colony

may also have shown similar expansion when first established, but because all suitable habitat was occupied at the time of its discovery, this is uncertain.

The RR population grew from 138 individuals in April 1979 to 160 individuals in October 1980 (16% increase). The autumn population was 4% larger in 1980 than in 1979. However, the early spring population (before the emergence of young) probably is a more accurate measurement of the carrying capacity because these individuals have survived the rigors of winter and the competition of the breeding season (Hoogland, 1979; King, 1955; Smith *et al.*, 1973). The RR spring population decreased 13% from 1979 to 1980, a trend that began in the spring of 1977 (Fig. 1). The WCC population increased from 32 individuals to 85 individuals during the 1.5-year period of study (165% increase). Both the autumn and spring populations increased (77% and 31%, respectively) (Fig. 1).

RESULTS

Differences in the availability of resources. — The standing crop of vegetation at the RR colony was significantly greater than that of the WCC colony ($N = 40$ plots per colony, $t = 4.28$, $p < .001$). Most of this unexpected difference was in the graminoid component of the total biomass, but the RR colony may not have had a larger usable food base (*see below*). The grass community at the RR colony was dominated by tumble grass (*Schedonnardus paniculatus*), tickle grass (*Agrostis hyemalis*) and prairie threeawn (*Aristida oligantha*). Dominant graminoids at the WCC colony were western wheat grass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*).

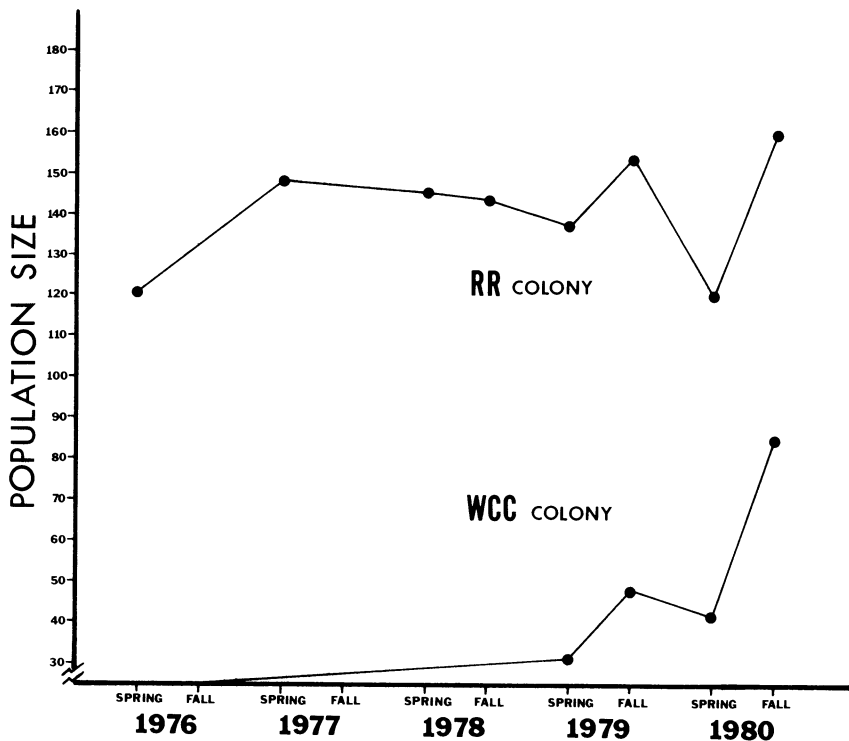


Fig. 1. — A 5-year comparison of total population size between the two study colonies. Trapping occurred during spring and autumn

Vegetation zones were not evident on the RR colony but were particularly visible on the WCC colony, where there were three major zones: (1) an *interior zone*, a highly modified area consisting almost entirely of forb species; (2) an *edge zone*, a slightly modified area dominated by shortgrass species (*e.g.*, blue grama and buffalo grass) and (3) an *outside zone*, undisturbed prairie consisting of mixed grasses (*e.g.*, western wheat grass, *Bouteloua* spp. and *Stipa* spp.) around the outside of the colony. The outside zone was not an area of modified vegetation but an area in which feeding was frequently observed. Prairie dogs were rarely observed feeding farther than 5 m beyond the edge zone. Throughout the study period, prairie dogs at the WCC colony showed a marked feeding preference for the edge and outside zones (Fig. 2). This probably was due to a preference for grasses on the periphery (edge and outside zones) rather than for forbs that dominated the interior. The well-developed burrow systems in the interior were used almost exclusively as sleeping nests and nurseries, but most feeding occurred at the periphery.

Differences in reproduction. — As breeding ceased in late March 1980, 65 of 74 (88%) females of the RR colony and 19 of 21 (90%) females of the WCC colony were pregnant ($X^2 = 0.09$, $df = 1$, $P > .95$). Even though there was no difference in the likelihood of pregnancy, a female on the WCC colony was significantly more likely to wean a litter: 81% and 41% of the females at the WCC and RR colonies, respectively, weaned litters (RR: 30 of 74; WCC: 17 of 21; $X^2 = 10.65$, $df = 1$, $P < .005$). In other words, of the females that became pregnant, pregnancy defection was significantly more likely at the RR colony (RR: 35 of 65; WCC: 2 of 19; $X^2 = 11.30$, $df = 1$, $P < .005$). Further, the litters were significantly larger at the WCC colony (WCC litter size: $\bar{X} \pm SD = 3.3 \pm 1.0$, $N = 17$; RR litter size: $\bar{X} \pm SD = 2.7 \pm 1.2$, $N = 28$; $t = 1.74$, $P < .05$).

Differences in growth and sexual maturity. — When the young of the two colonies emerged from their natal burrows in May-June 1980, there was no difference in their weights (RR young: $\bar{X} \pm SD = 143.6 \pm 43.7$ g, $N = 81$; WCC young: $\bar{X} \pm SD$

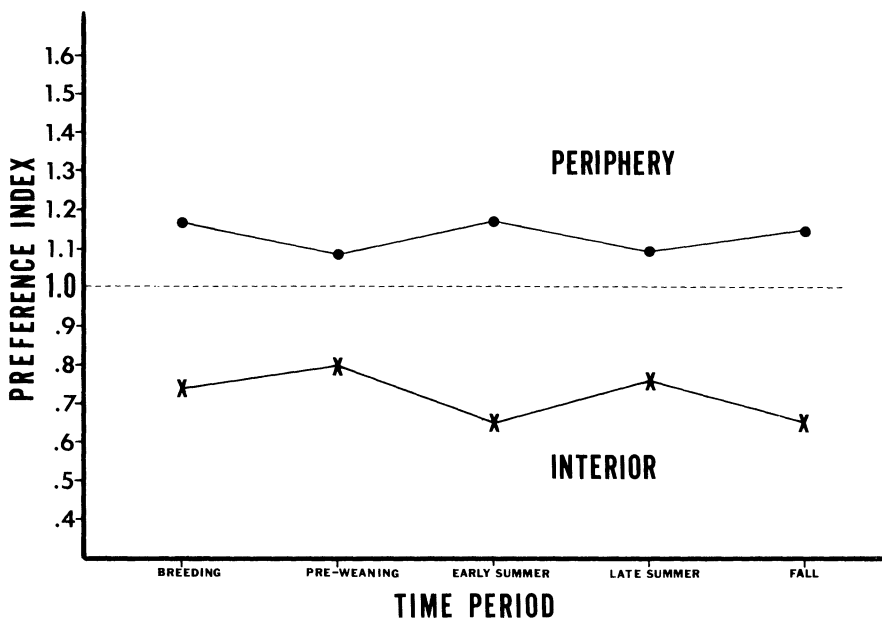


Fig. 2. — Feeding preference of the WCC prairie dogs through five time periods during 1980. The periphery includes both the edge and outside zones. Preference index was calculated following Petrides (1975)

= 138.7 ± 27.7 g, $N = 56$; $t = 0.74$, $P > .50$). However, when recaptured in late October, the juveniles of the WCC colony were significantly larger than those of the RR colony (RR juveniles: $\bar{X} \pm SD = 595.0 \pm 93.0$ g, $N = 58$; WCC juveniles: $\bar{X} \pm SD = 852.6 \pm 96.1$ g, $n = 24$; $t = 11.16$, $P < .001$). A similar trend seemed to occur the previous year, but weight gains in 1979 could not be rigorously compared because trapping of the two colonies occurred at different times.

A yearling male has never been observed to disperse and breed at the RR colony, but four of eight (50%) yearling males in the WCC colony dispersed and bred in 1980. Perhaps due to more rapid maturation, yearling males at the WCC colony were significantly more likely to reproduce compared with those at the RR colony ($X^2 = 9.0$, $df = 1$, $P < .005$).

A substantial number of yearling females at both study colonies became pregnant in 1980 (RR: 7 of 13; WCC: 7 of 9; $X^2 = 1.31$, $df = 1$, $P = .25$). However, yearling females at the WCC colony were (insignificantly) more likely to wean a litter (RR: 2 of 7; WCC: 5 of 7; $P = .14$, Fisher's Exact Test). What may be more important was the relative contribution by these individuals to the total reproductive effort. Compared with the RR colony, yearling females of the WCC colony contributed a significantly greater proportion of both the pregnancies (RR: 7 of 65; WCC: 7 of 19; $X^2 = 7.03$, $df = 1$, $P < .01$) and the weaned litters (RR: 2 of 30; WCC: 5 of 17; $X^2 = 4.57$, $df = 1$, $P < .05$).

Differences in survivorship.—Survivorship of juveniles from June 1979 to February 1980 at the WCC colony was 90% (17 of 19) compared with 49% (27 of 55) at RR ($X^2 = 9.54$, $df = 1$, $P < .005$). In October 1980, 84% (47 of 56) of the juveniles born that year were still alive at WCC compared with 74% (61 of 82) at RR ($X^2 = 1.78$, $df = 1$, $.25 < P < .50$).

Survivorship of adults and yearlings from May 1979 to May 1980 was 69% (22 of 32) at WCC and 67% (90 of 135) at RR ($X^2 = .04$, $df = 1$, $P > .99$). However, survivorship of this cohort was significantly lower at RR (80%) compared with WCC (97%) from June to October 1980 (RR: 94 of 117; WCC: 38 of 39; $X^2 = 6.57$, $df = 1$, $P < .025$). For these same periods, total loss of all residents was 18% and 11% at WCC compared with 39% and 24% at RR.

Differences in density.—Population density between the two study colonies differed markedly throughout the study. The WCC colony maintained a density more than 2X that of the RR colony (April 1980: RR = 18.2/ha, WCC = 40.0/ha; June 1980: RR = 30.6/ha, WCC = 82.6/ha; October 1980: RR = 24.2/ha, WCC = 47.2/ha). Inasmuch as there was little room for expansion at RR, fluctuation in density was due to dispersal, mortality and natality. In contrast, the WCC colony was bordered by surplus habitat into which the prairie dogs were expanding. Density fluctuation in this case was due not only to the factors above, but also to colony expansion (41% increase in surface area) during the study.

DISCUSSION

Clear-cut zonation of vegetation may have been originally present at RR, but has since been obliterated by continued use. The dominant grass species present at the RR colony are rarely represented on undisturbed prairie in Wind Cave National Park (King, 1955), and their presence suggests a long history of plant community modification. The preferred edge zone at WCC was vegetation recently modified from undisturbed prairie that surrounded the young colony. The crucial point is that the feeding area preferred by the prairie dogs at WCC was lacking at RR. The availability of unused habitat may be a requisite for continued population growth. In addition, dominant grass species present at WCC (western wheat grass, blue grama, and buffalo grass) are highly preferred by prairie dogs; those dominant at RR (tumblegrass and threeawn) are not preferred (Hansen and Gold, 1977; Koford, 1958, Summers and Linder, 1978; Wydeven, 1979). Koford (1958, 1961) emphasized that prairie dogs are very selective grazers. Continued grazing pressure on the most preferred grasses may

limit species diversity and result in a predominance of unpalatable species, high in quantity but of limited value as forage (Chew, 1974). It is questionable whether the greater standing crop of vegetation at RR represented a larger food base. What may have been more important was that the prairie dogs at RR had little space in which to seek additional forage, and the available forage was dominated by unpalatable species.

Lack (1954) found an inverse relationship between density and fecundity. Reproductive decline may be caused by a delay in sexual maturity (Kalela, 1957), physiological stress (Christian, 1955, 1961) or nutrient depletion (Batzli and Pitelka, 1971; Cole and Batzli, 1978, 1979). Even though the density at WCC seemed very high during the study period, it may not have been excessive for the resources available. The high productivity of the individuals at WCC compared with those at RR suggested that density-dependent regulation was minimal. Because the ratio of edge (*i.e.*, preferred food) to total area is greater on a small colony compared with a large colony, high animal densities may be typical of small, newly founded colonies. The high density of the WCC colony may be a temporary phenomenon. During population growth, Lidicker (1965) showed an "overshoot effect," with peak densities being slightly above equilibrium densities. The low animal density at RR also may explain the greater graminoid biomass on that colony; a lower grazing intensity would result in less reduction of the vegetation.

There was little difference in survivorship of juveniles between the two colonies from June to October 1980. But Koford (1958) pointed out that late autumn and early winter is a very critical feeding period for prairie dogs. Because they do not hibernate (King, 1955; Hoogland, 1981b), fat storage during this time may ultimately determine survival. Lack (1954) suggested that whenever food is scarce, mortality probably is greatest among small individuals. The lower mean weight of the RR juveniles at the onset of winter may have contributed to their poorer survivorship in 1979.

Alternative explanations.—In addition to habitat availability, other possible explanations for the disparate demographic properties of the two colonies include: (1) differences in ectoparasites and disease; (2) differences in the frequency of dispersal, and (3) differences in the rate of predation.

(1) Because of close contact among individuals, densely colonial species are particularly susceptible to diseases and ectoparasites. The most devastating prairie dog disease is probably sylvatic plague (Pollitzer and Meyer, 1961; Lechleitner *et al.*, 1968), which usually destroys entire colonies shortly after introduction; sylvatic plague is transmitted by fleas (*see* Hoogland, 1979). We were unable to compare the incidence of disease at the two colonies, but plague clearly was not present. Prairie dog ectoparasites include fleas (most common), lice, ticks and mites which may reduce reproduction and survivorship (Hoogland, 1979). In a comparison of flea counts taken from burrow entrances, we found no significant differences (RR: $\bar{X} \pm SD = .40 \pm .81$ fleas per burrow entrance; WCC: $\bar{X} \pm SD = .45 \pm .59$; $N = 80$ burrow entrances per colony, $t = .45$, $P > .50$).

(2) If the frequency of dispersal of prairie dogs away from RR was greater than that of WCC, then this may appear as poorer survivorship. We have no data on this primarily because it was very difficult to distinguish between dispersal and *in situ* mortality. But if dispersal increases in high-density or increasing-density situations (*see* Gaines and McClenaghan, 1980, p. 169-170), this would lead to greater dispersal and thus poorer survivorship at WCC. However, the advantage of leaving the colony was probably greater for individuals at RR. Intercolony dispersal mainly occurs during the time when young are emerging from natal burrows and colony density is greatest (Garrett, 1982). Lack of surplus habitat for colony expansion may have provided greater impetus for dispersal at RR.

(3) Wind Cave National Park is habitat for a number of natural predators of the prairie dog, including hawks (*Buteo* spp.), prairie falcons (*Falco mexicanus*), badgers, (*Taxidea taxus*), bobcats (*Lynx rufus*) and coyotes (*Canis latrans*). If for some reason predation pressure was greater at RR than at WCC, then poorer survivorship would

result. Frequent disturbance by predatory attacks may disrupt daily activities as well (e.g., feeding, reproduction). But predation has rarely been observed at either study colony (RR: three predations in 8 years; WCC: one predation in 3 years). Further, individuals of large colonies detect predators more quickly and should suffer less predation than those of small colonies (Hoogland, 1981b). It seems doubtful that differences in predation accounted for the observed demographic differences.

Conclusion. — The old colony at Rankin Ridge had little available habitat for expansion. The population was not growing, probably fluctuating near its environmental carrying capacity. The WCC colony was young and rapidly expanding into available preferred habitat. The surplus habitat represented essential resources, both food and space for burrows. During the study period, individuals of the new colony enjoyed greater reproductive success and survival, matured more rapidly, and reproduced earlier compared with those at RR. The WCC population probably was on the lower ascending portion of the growth curve (Fig. 1). In 1981, we obtained similar results on maturation of juveniles and survivorship; these data are not included because of possible effects of the estrogen treatment at WCC in 1981. The information from this investigation suggests that the disparity between the two populations is consistent with current explanations of population growth. Inasmuch as density-independent factors affecting the two study colonies were very similar, we suggest the observed demographic differences were primarily due to the availability of habitat for continued population growth.

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